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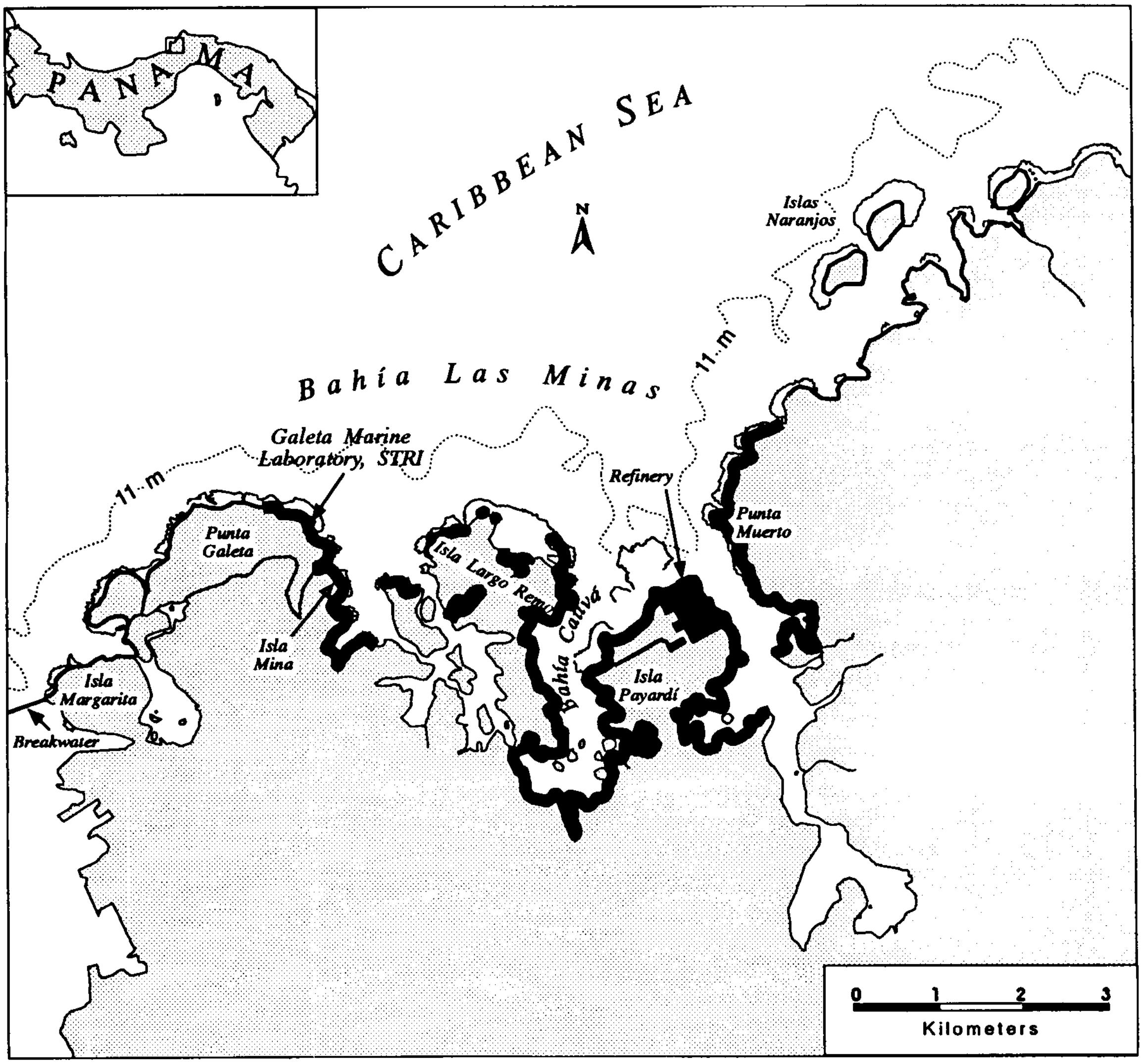
Volume II: Technical Report, Part 2



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Long-term Assessment of the Oil Spill at Bahía Las Minas, Panama Synthesis Report

Volume II: Technical Report, Part 2

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Abbreviations and Acronyms

Refer to Keller et al. (Chap. 1) for a listing of site acronyms (Table 1.4; Fig. 1.5).

ANCOVA	analysis of covariance
ANOVA	analysis of variance
API	American Petroleum Institute
BBSR	Bermuda Biological Station for Research, Inc.
BCI	Barro Colorado Island, Panama
BLM	Bahía Las Minas
BMDP	BMDP Statistical Software, Inc.
CID	collection identification
CONSURV	name of a database (Cubit and Connor, Chap. 4)
CPI	carbon preference index
EC_{50}	effective concentration for 50% of the test population
EOM	extractable organic matter
ESP	Environmental Sciences Program, Smithsonian Institution
ex/em	excitation/emission
FID	flame-ionization detector
GC	gas chromatography
HPLC	high-performance liquid chromatography
HWL	high-water line
HWM	high-water mark
IAEA	International Atomic Energy Agency
IOC	Intergovernmental Oceanographic Commission
IRHE	Instituto de Recursos Hidraúlicos y Electrificación
IS	internal standard
IUCN	International Union for Conservation of Nature and Natural Resources
LAI	leaf area index
LMW	low molecular weight
LSD	least-significant difference
MANOVA	multivariate analysis of variance
MHW	mean high water
MLW	mean low water
MMS	Minerals Management Service
MS	mass spectrometry
m/z	mass/charge
NRC	National Research Council
NSL	non-saponifiable lipid
OCS	outer continental shelf
PAH	polynuclear aromatic hydrocarbon
PCC	Panama Canal Commission
ppm	parts per million

ppt	parts per thousand (o/oo)
PVC	polyvinyl chloride
REDGE	name of a database (Cubit and Connor, Chap. 4)
RF	response factor
RRI	relative retention index
SAS	SAS Institute, Inc.
SCUBA	self-contained underwater breathing apparatus
SD	standard deviation
SE	standard error
SI	Smithsonian Institution
SIM	selected-ion monitoring
SL	saponifiable lipid
SPM	suspended particulate matter
SPSS	SPSS, Inc.
SRB	Scientific Review Board
STRI	Smithsonian Tropical Research Institute
UNEP	United Nations Environmental Program
UNESCO	United Nations Educational, Scientific and Cultural Organization
URE	unresolved
UVF	ultraviolet fluorescence
VMIC	Venezuelan/Mexican Isthmian Crude, the type of oil spilled at Bahía Las Minas

9

Patterns of Damage and Recovery from a Major Oil Spill: the Mangrove Fringe and the Epibiota of Mangrove Roots

Stephen D. Garrity and Sally C. Levings

9.1 Abstract

The submerged prop roots of mangroves on the outer fringe of mangrove forests support diverse assemblages of sessile invertebrates and algae, and act as nursery areas for various mobile animals, including commercially valuable fishes and invertebrates. This study examined effects of a major oil spill on both the physical structure of the mangrove fringe and the assemblages of attached epibiota on submerged prop roots over a 5-yr period. We studied three assemblages of epibiota, each typical of a different fringing habitat: open coasts, channels and lagoons, and drainage streams. Because the presence of an epibiotic assemblage is first dependent upon the presence of biogenic substrata, structural changes to fringing mangroves and the health, size, and abundance of submerged prop roots also were examined.

Initial oiling was heavy in all three habitats. Oil persisted longest and in the largest amounts in drainage streams; there was less oil in channels and on the open coast. The spill reduced the area of mangrove fringe in all habitats: 33% on the open coast, 38% in channels, and 74% in drainage streams. This reduction in habitat lowered the productivity of the mangrove fringe by structural reductions, independent of any toxic effects of persistent hydrocarbons.

Prior to the spill and in unoiled habitats postspill, the most common species or groups of epibiota in each habitat were (1) foliose algae and sessile invertebrates on the open coast, (2) the oyster *Crassostrea virginica* in channels, and (3) the false mussel *Mytilopsis sallei* in drainage streams. On the open coast, foliose algae and sessile invertebrates were coated with oil and died. Both groups gradually repopulated oiled areas, reaching approximate equality with unoiled areas in the fifth year after the spill. However, differences remained in the species and groups present at oiled and unoiled sites. Oyster populations were reduced in oiled channels within Bahía Las Minas for at least 5 yr postspill. Detecting this persistent effect was dependent on analysis of salinity regimes while evaluating the physical similarity of repolicate study sites. The spill virtually eliminated false mussels from oiled drainage streams; false mussels were rare to absent 5 yr after the spill. Adult false mussels transplanted to oiled and unoiled streams were significantly less likely to survive in oiled streams. Settlement occurred at both oiled and unoiled sites in the presence of adults, suggesting that gregarious settlement might play a role in repopulation. Biological interactions affecting repopulation remain to be investigated.

The reduction in the amount of shoreline fringed with mangroves and the slow convergence through time in the composition and abundance of epibiotic assemblages at oiled and unoiled sites demonstrated the extent and persistence of the 1986 oil spill at Bahía Las Minas. These persistent effects on the mangrove fringe and attached epibiota may have had cascading negative effects on species associated with mangrove-fringe nursery grounds.

9.2 Introduction

9.2.1 The Importance of the Mangrove Fringe

The narrow interface between the ocean and the land is among the most productive zones on earth. In temperate regions, saltmarshes line sheltered bays and estuaries, and act as nurseries for fishes and myriad other organisms. In the tropics, mangrove forests dominate such shores. Their outermost fringes function similarly, providing nursery and feeding areas and shelter for many species. In a habitat otherwise dominated by soft or unconsolidated sediments, the submerged trunks and prop roots of fringing mangroves serve as living hard substrata for a diverse and abundant group of plants and sessile animals. Such attached species, or epibiota, not only contribute to the high productivity of mangroves, but also support many mobile, higher-trophic-level organisms, including fish and crustaceans. Thus, the submerged maze of roots and epibiota of the mangrove fringe adds significant structural and trophic complexity and increased diversity to the mangrove forest, and to the nearshore ecosystem as a whole. In this report we document the effects of a major oil spill on the outer fringe of *Rhizophora* forests around Bahía Las Minas, focusing primarily on the epibiota of submerged mangrove prop roots.

9.2.2 Review of Existing Knowledge

Mangrove forests are characteristic of tropical and subtropical coastlines worldwide (Chapman 1976). Mangroves have been exploited and affected by mankind in numerous ways for thousands of years (Macnae 1968; Walsh 1977). On the Atlantic coast of the New World, the red mangrove *Rhizophora mangle* occurs in coastal forests from Bermuda to Argentina (West 1977; Rützler and Feller 1987). It grows along much of the southern peninsula of Florida (Odum et al. 1982; Kangas and Lugo 1990) and is found patchily elsewhere along the southeastern coast of the United States. Red mangroves form mono- or nearly monospecific stands on the seaward fringe of mangrove forests and on the banks of channels, lagoons, and streams within such forests (Lopez 1978; Chapman 1976).

Rhizophora produces multiple, adventitious aerial (hanging) roots (Gill and Tomlinson 1969). The production of lateral roots along with multiple branching and high growth rate of aerial roots (Gill and Tomlinson 1969, 1971; Simberloff et al. 1978) result in the formation of a labyrinthine system of roots around the tree. These roots extend through the intertidal zone and eventually anchor the tree at multiple points, supporting vertical and lateral growth (Gill and Tomlinson 1969; cf., Fig. 5 in Kolehmainen et al. 1974). Roots also exclude salt (Hatcher et al. 1989) and take in oxygen through lenticels (Odum and Johannes 1975). *Rhizophora* prop roots can stabilize sediments (Hatcher et al. 1989) by influencing the flow of water through tidal forests (Wolanski et al. 1980; Wilcox et al. 1975).

Submerged prop roots are host to a wide variety of epibiotic organisms (Rützler and Feller 1987). As aerial and lateral prop roots grow downward through the water, they represent a limited resource in an otherwise primarily soft-substratum environment: hard substratum available for the attachment of marine plants and animals.

Both structurally and functionally, the leading edge of the red mangrove fringe differs from interior sections. Outer, seaward edges of red mangrove stands receive more available light at root level, are in deeper water, and have a greater proportion of hanging, unattached roots vs. attached roots than interior "zones" (cf., Figs. 30*a*, *b* in Rützler and Macintyre 1982; Figs. 1-5 in Kolehmainen and Hildner 1975). Productivity, species number, and biomass of epiphytic algae are highest on roots at the edge of the mangrove fringe and lowest in the interior of mangrove stands (Rodriguez and Stoner 1990; Kolehmainen and Hildner 1975; Round 1981; Wilcox et al. 1975; see also Post 1963; Taylor et al. 1986). Although most productivity studies have concentrated on mangrove trees themselves (Golley et al. 1962; Lugo and Snedaker 1974), epiphytic algae on prop roots contribute substantially to the mangrove habitat's primary productivity (Burkholder et al. 1967; Burkholder and Almodovar 1974; Lugo et al. 1975; Wilcox et al. 1975; Potts 1979; Rodriguez and Stoner 1990).

Fringing prop roots also support a diverse group of sessile marine invertebrates. Studies throughout the range of *Rhizophora* along the Atlantic and Caribbean coasts of the Americas suggest a general root epifauna dominated by sponges, bivalve molluscs, barnacles, or ascidians, with other groups patchily abundant to rare (e.g., Odum et al. 1982 for Florida; Kolehmainen 1972, Robinson 1979 for Puerto Rico; Voss and Voss 1960, Wilcox et al. 1975 for the Bahamas; Rützler and Feller 1987, Ellison and Farnsworth 1990 for Belize; Espinosa 1980 for Mexico; Perez and Victoria 1980 for Colombia; Flores 1980, Sutherland 1980 for Venezuela; Glynn 1972, Batista 1980 for Panama).

Like epiphytic algae, sessile invertebrates on prop roots are distributed unevenly within mangrove stands. Kolehmainen and Hildner (1975) found more species and greater biomass in two outer root zones (on the edge of the forest), compared to the few or no macroinvertebrates on roots in two interior zones. However, even in the outer fringe variability in species number and biomass can be considerable (Kolehmainen et al. 1974; Sutherland 1980; Rützler and Feller 1987). Sutherland (1980) examined recruitment and species composition of epifauna on subtidal roots in Venezuela, and attributed the large, within-site variability among roots to low rates of settlement and stochastic processes.

Little work has been done on functional aspects of prop root epifauna. Perry (1988) experimentally found encrusting barnacles decreased hanging root growth and root production in a Pacific, Costa Rican mangrove forest. In contrast, Ellison and Farnsworth (1990) showed that sponges and ascidians protected hanging roots from attack by boring isopods in Belize. Several species of bivalve mollusc are harvested from prop roots in the Caribbean and Gulf of Mexico (Mattox 1949; Nikolic et al. 1976; Espinosa 1980; Siung 1980) and some have been evaluated for possible aquaculture (Nikolic et al. 1976; Siung 1980). Kolehmainen et al. (1974) lists some other species or groups that have been studied in detail.

Prop roots and their epibiota support a large and varied group of mobile organisms (Odum et al. 1982). Snedaker (1990) recently pointed out that although the legal protection of mangroves in the United States is based wholly on their associated marine fauna, there is a paucity of research on this same fauna. Scattered reports exist for some groups in the Caribbean region (Austin and Austin 1971; Wilcox et al. 1975; Abele 1976; Phillips 1981). Odum et al. (1982) summarized work on mobile organisms for south Florida mangroves in the most complete work to date. Some benthic organisms, especially snails and crabs, were listed; documentation of the use of fringing prop roots by juvenile spiny lobsters was given (see also Marx 1986). Three fringing *Rhizophora* habitats were used by different fishes (riverine, estuarine, and oceanic, 111, 117, and 156 species, respectively). Many species feed on algae and invertebrates associated with prop roots (e.g., App. B in Odum et al. 1982); mangrove roots also serve as physical refugia for juveniles (Hatcher et al. 1989). Eighty-seven of the 90 species of juvenile fishes collected in various habitats in Florida Bay were found in and around red mangroves (Thayer et al. 1987); they concluded that mangroves were a major nursery area for fishes, including commercially valuable species.

The prop roots of fringing *Rhizophora* and their associated biota clearly make important contributions to geomorphology, diversity, structural complexity, and energy flow in tropical and subtropical coastal environments.

9.2.3 Characteristics of Mangrove Fringe and Associated Epibiota in Bahía Las Minas, Panama

9.2.3.1 Fringe Structure

Red mangrove (*Rhizophora mangle* L.) lines most of the shore around Bahía Las Minas. We examined the fringe, or leading edge, of such stands in three habitats along a gradient of decreasing wave exposure from the open ocean. These stands include (1) trees fronting the open ocean, (2) those lining the water's edge in channels and lagoons, and (3) mangroves along the banks of drainage streams and creeks (Fig. 9.1).

Areas on the open coast face the ocean and are fronted by shallow reef flats (Fig. 9.2). There is often deeper water along the edge of the fringe that can be up to 2 m deep. *Rhizophora* is the only species of mangrove present. Damaged sections of fringe are not uncommon. These areas are caused by drift logs, which wash ashore across the reef flat and bash outer trees and prop roots. Overhanging

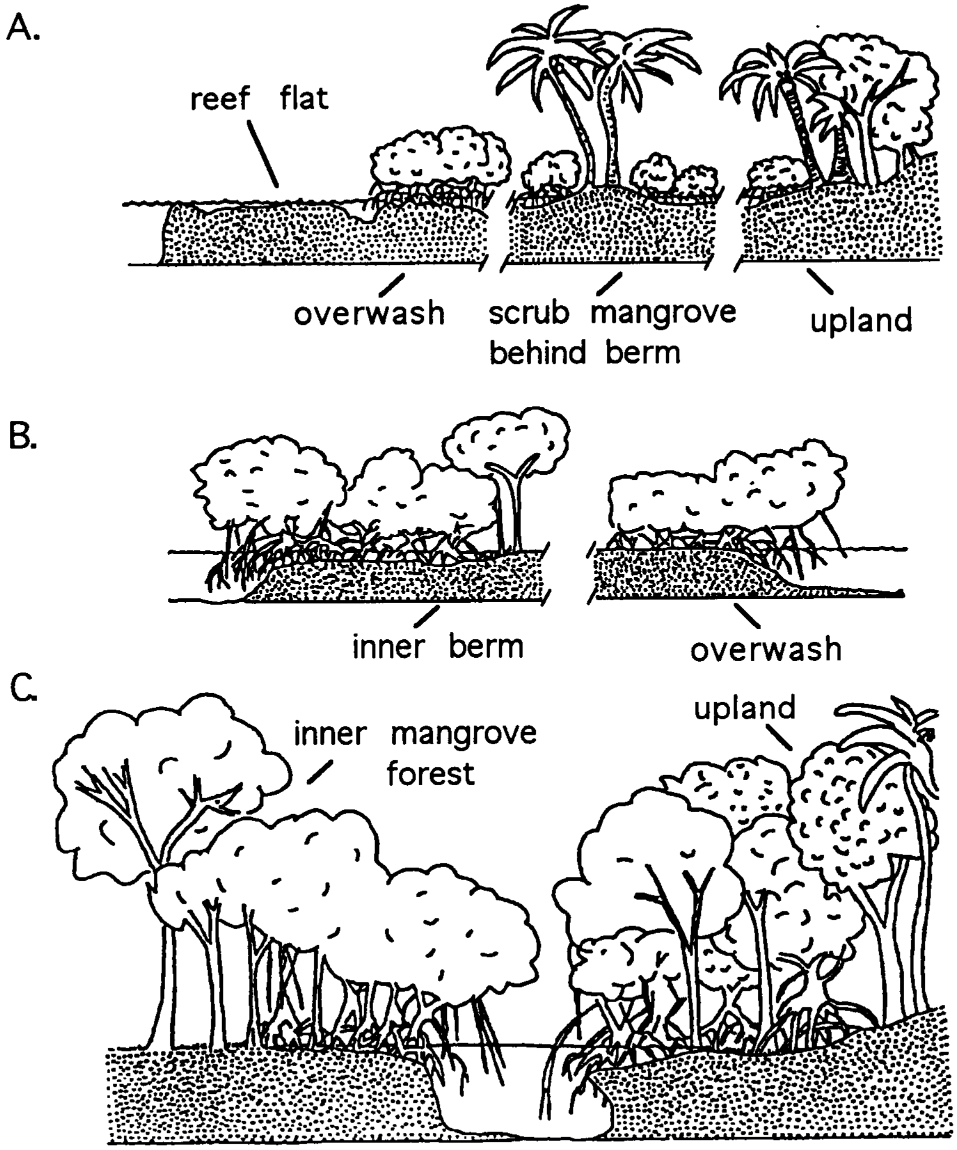

Fig. 9.1 Topography of the outer fringe. *A*. Open coast — the *Rhizophora* fringe behind a broad, shallow reef flat had a depression at its outer edge that ranged from intertidal to >2 m depth, and an intermittently present berm shoreward, behind which was either a scrub mangrove forest or upland. *B*. Channels and lagoons — the outer fringe began over deep (subtidal) water at most sites; an inner berm was generally not present, instead, because of the highly convoluted nature of the habitat. Shallow inner mangroves often led to another outer fringe fronting deep water. *C*. Drainage streams — red mangroves fringing the banks of streams and drainage ditches extended well out over deeper water. There was no raised lip or berm; along larger streams other species became abundant in from the banks.

Fig. 9.2 Open coast: *Rhizophora* fringe. June 1991, site = PADM; *right foreground*, *Thalassia* bed and reef flat; *far right center*, 15-foot boat (scale).

branches lightly shade most prop roots. The outer fringe is either (1) backed by a berm, behind which there is either a scrub mangrove forest or upland or (2) backed by a thicket of short, interior mangroves, which is intermittently overwashed by shallow water, and leads to an inner edge of deeper water fronting a lagoon. Buttonwood (*Conocarpus erectus*) or coconut palm (*Cocos nucifera*) occurs shoreward of the outer fringe at some sites.

Channels lead from the open ocean into lagoons of varying sizes that are often interconnected. The mangrove fringe consists solely of *Rhizophora*, and there is generally no inner berm (Figs. 9.1, 9.3). Physical damage to the fringe (e.g., from logs) is rare. The outer edge generally overhangs deeper water. Behind this, a thicket of shorter trees in very shallow water can either lead to uplands or to another section of outer fringe over deep water. Overhanging branches shade most prop roots along the shoreline.

Natural and man-made drainage streams of various size are found throughout the Bahía Las Minas area. Red mangroves fringe their banks, and extend over

Fig. 9.3 Channels and lagoons: *Rhizophora* fringe. July 1986, western wing of Bahía Las Minas; bank on the *right* was patchily oiled – the few defoliated treetops mark (*center background*) such a patch.

deeper water (Figs. 9.1, 9.4). In larger streams trees are taller than those fringing channels, the open coast, or smaller streams. Other species (e.g., *Avicennia germinans*, *Laguncularia racemosa*, and *Pelliciera rhizophorae*) are found in the fringe, but become more abundant behind the fringe. Occasional gaps result from tree falls, lightning strikes or cutting by local people. Despite this, most prop roots are heavily shaded by overhanging branches; typically, there is a continuous canopy of limbs and foliage over streams.

Fringing habitat types in the Bahía Las Minas area did not fit neatly into existing models of mangrove forest structure (Lugo and Snedaker 1974). Channels had characteristics of both fringe and overwash forest types, as did the open coast. Drainage streams were similar to "riverine forests," with tall *Rhizophora*, but there was no low berm along the banks, pictured as typical of this type of forest, and smaller streams were not lined by tall trees.

Fig. 9.4 Drainage stream: *Rhizophora* fringe. September 1991, site = HIDR; canopy extends over stream from trees on each bank; light area (*center, rear*) is a light gap resulting from a tree fall.

9.2.3.2 Physical Setting

Bahía Las Minas consists of three major wings, separated by causeways built during the last 35 yr (Fig. 9.5; Cubit et al. 1985). One or more rivers, and several smaller streams, feed into each wing. Hydrology and meteorology at Punta Galeta have been extensively studied (Cubit et al. 1986, 1988*a*, 1989). These data provide an integrated view of conditions on reef flats at Bahía Las Minas. Our more limited data from within Bahía Las Minas provide a comparative view of physical conditions in the mangrove fringe.

The daily average range of the tides is ~24.5 cm, with a yearly range of 59.2 cm (Cubit et al. 1986). However, water levels are controlled by a combination of seasonal trade winds, regional variation in sea level, and tidal fluctuations. Prevailing north winds (onshore) tend to hold water in the bay and push water levels up over reef flats. During dry season (approximately December-April), onshore winds are strong and consistent, water levels are high, and wave action is strong.

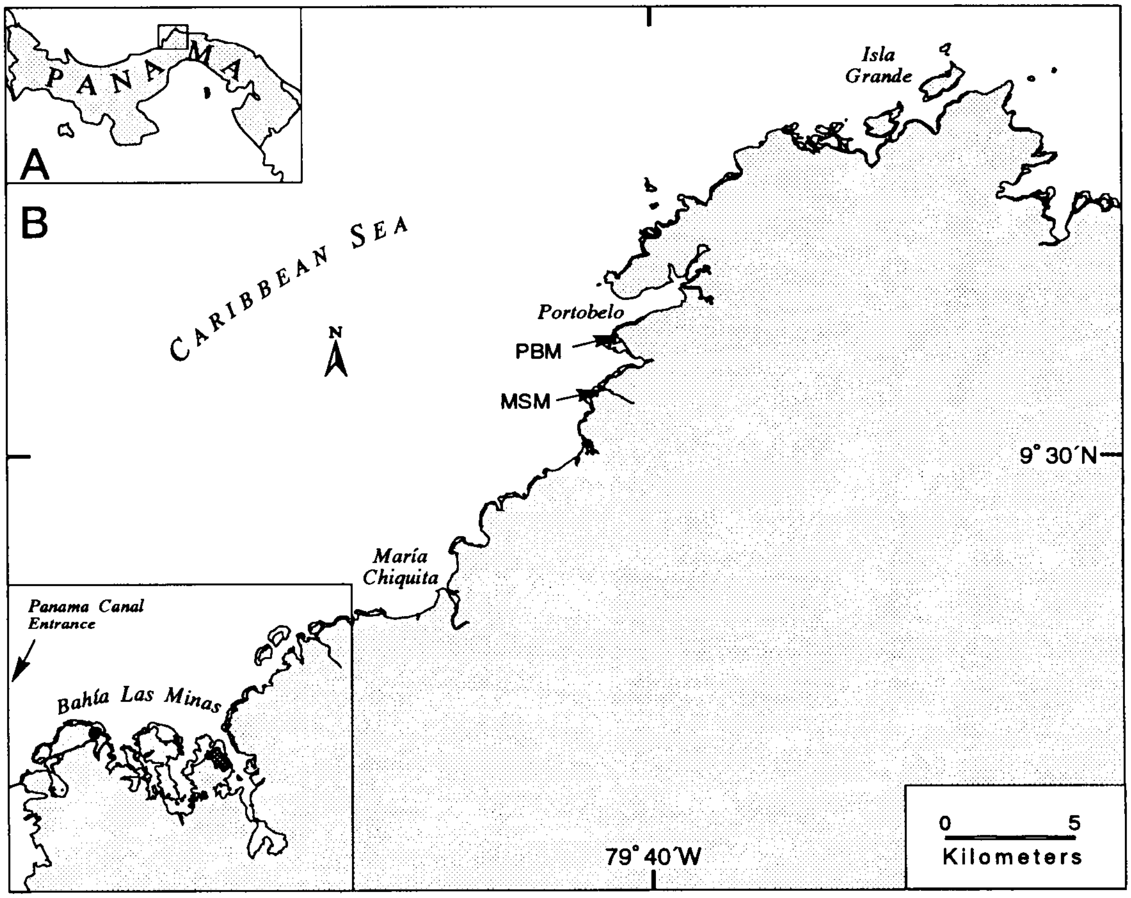

Fig. 9.5 Map of study area and sites. *A*. Caribbean coastline of the Republic of Panama, showing region examined in this study. *B*. Expanded-scale map of the study area, showing unoiled sites for open coast habitat during the first year after the spill (August 1986-May 1987); *lower left*, bounded area shows the approximate limit of heavy oiling from the spill (*dark-shaded area* is the refinery complex, *solid circle* is STRI's Galeta Marine Laboratory). See Table 9.2 for explanations of site abbreviations, habitat types, and monitoring history.

During the early and late wet seasons (May-June and October-November), winds often drop, leading to lower average water levels and little wave action. Onshore winds unpredictably blow between July-October, leading to a "little dry season" when water levels again rise and sea conditions are rough. Water levels within Bahía Las Minas are also dependent on patterns of runoff, but there are no data available from within the bay.

Rainfall is strongly seasonal. Dry season usually begins in December and lasts until April or May. Salinity is oceanic (>30o/oo) at the entrance to the bay, with rare drops during periods of heavy rainfall (Cubit et al. 1989). Salinity in channels and lagoons and in small tidal streams within the bay is nearly oceanic during the dry

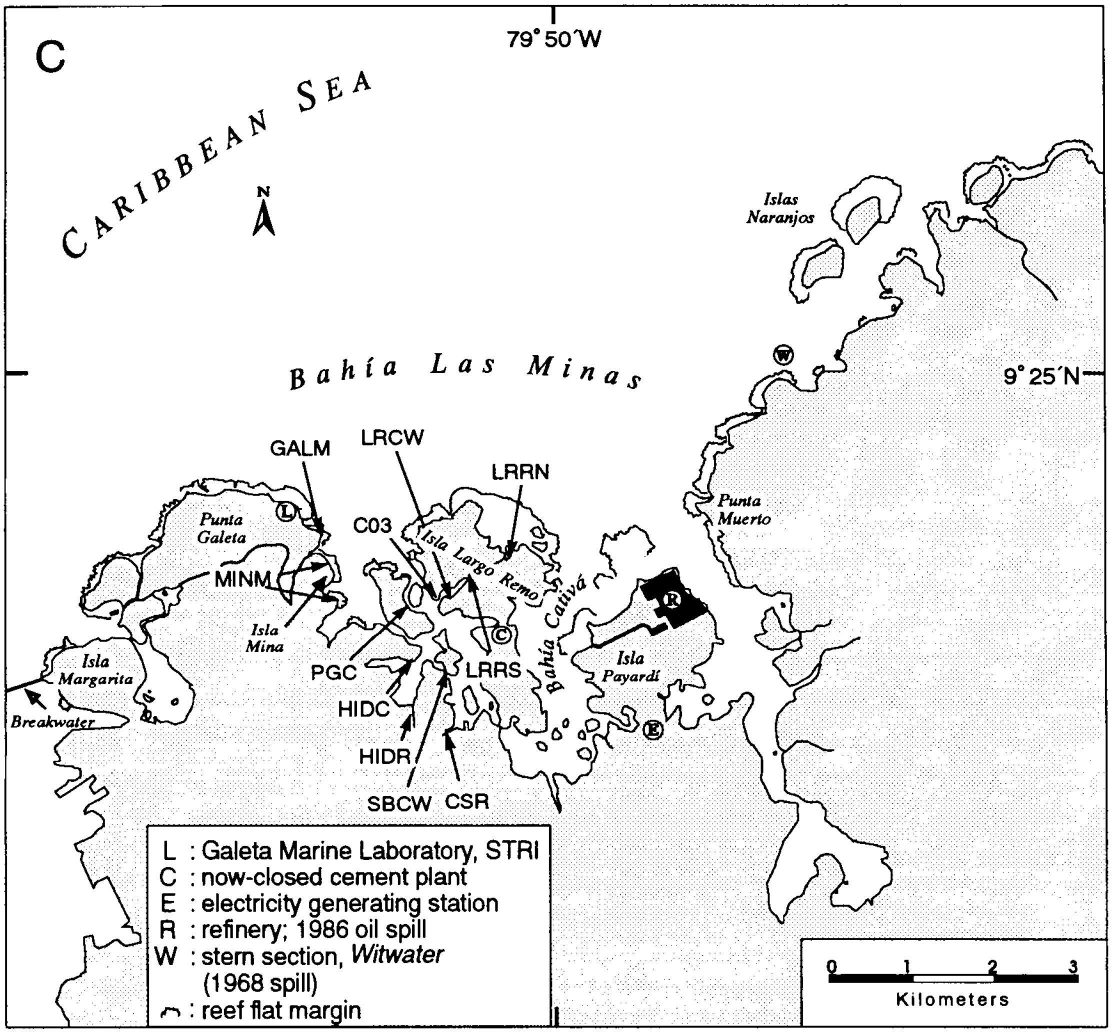

Fig. 9.5 Map of study area and sites (continued). *C.* Expanded-scale map of area affected by oil and locations of the remaining major study sites during the first year after the spill. See Table 9.2 for explanations of site abbreviations, habitat types, and monitoring history.

and early wet seasons. During wet season, a salinity gradient develops as freshwater runoff flows over and mixes with saltier bay waters. During periods of heavy rain, waters deep in the bay may be greatly reduced in salinity. Streams differ in salinity structure based on runoff patterns. Surface waters in larger streams remain fresh or low in salinity throughout most of the year; smaller streams fluctuate in surface salinity in response to local runoff. Flow is greatest during the wet season in streams and channels and during the dry season on the open coast. Waters on the open coast at the entrance of the bay are relatively clear oceanic water, while light transmission is greatly reduced in channels and streams within the bay.

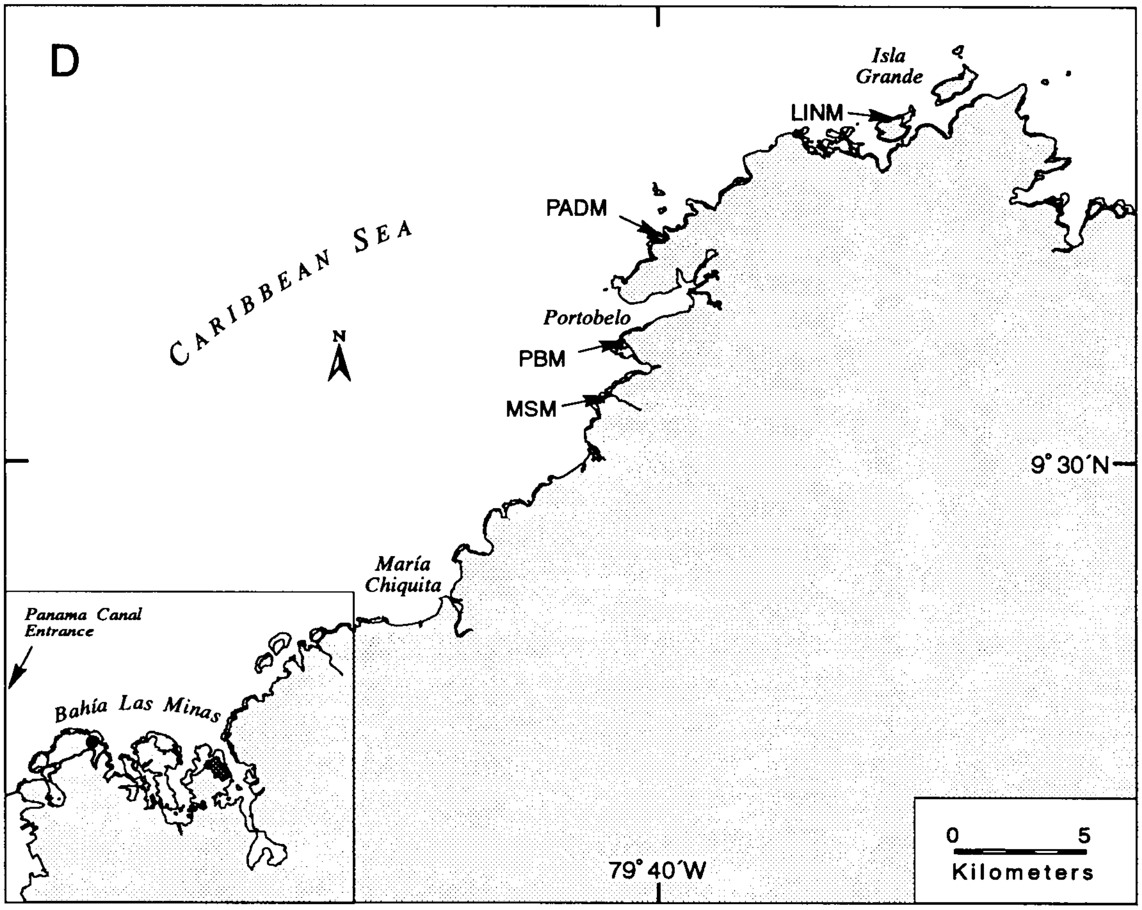

Fig. 9.5 Map of study area and sites (continued). *D.* Expanded-scale map of study area, showing unoiled sites for open coast habitat during the second through fifth year after the spill. See Table 9.2 for explanations of site abbreviations, habitat types, and monitoring history.

9.2.3.3 Epibiotic Assemblages

At Bahía Las Minas each of the three habitat types (open coast, channel, and stream) has a distinct assemblage of organisms living on roots. Table 9.1 shows the rank abundance of various taxa on the open coast, in channels, and in streams based on roots sampled in October 1981 and January 1982. These pre-oiling samples were chosen because all habitats were sampled with approximately the same effort at the same time. Data are the percent of roots on which a given category was found at least once.

Overall, there was a decrease in the number of categories of percent cover (including bare space and mixed-species groups) from open coast (36) to channels (10) and streams (11). This difference appeared although slightly fewer roots

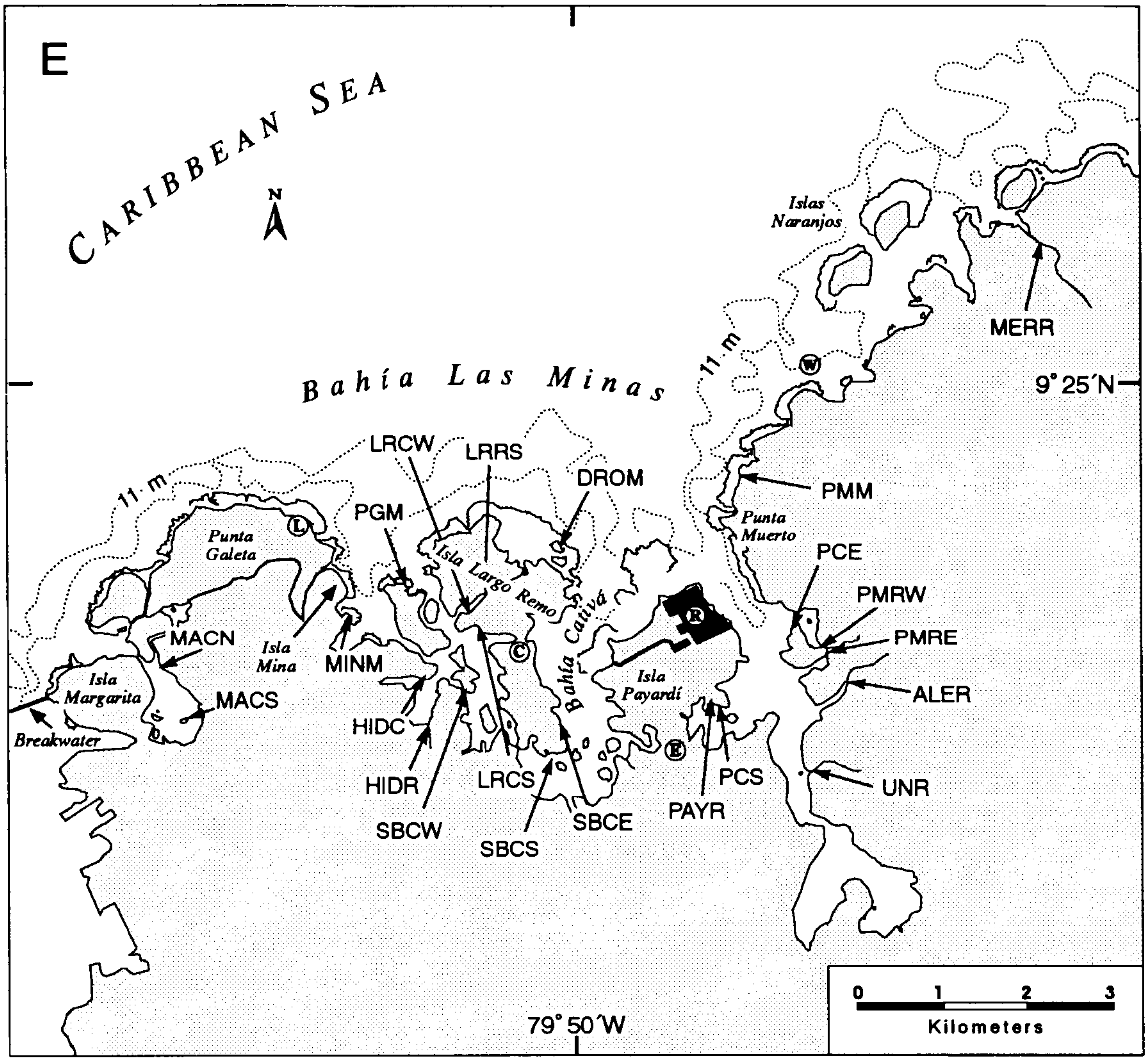

Fig. 9.5 Map of study area and sites (continued). *E.* Expanded-scale map of area affected by oil, showing remaining sites examined during the second through fifth year after the spill. See Table 9.2 for explanations of site abbreviations, habitat types, and monitoring history; refer to Figure 9.5*C* legend.

(N = 70) were sampled on the open coast than in channels or streams (N = 75, each habitat). Individual taxa tended to be rarer in occurrence on the open coast than in channels or streams. The rarest species in channels and streams occurred on almost a third of all roots, while only 25% of the species found on the open coast were that common.

There was limited overlap in species occurrence among habitats, with some exceptions, such as mixed-species groups (e.g., diatoms and mixed-algal turfs) and the alga (*Polysiphonia subtilissima*). Most taxa that occurred in more than one habitat

Table 9.1 Frequency of epibiota on submerged roots of *Rhizophora mangle* in October 1981 and January 1982. Data are the percent of roots on which a category appeared at least once out of the total number of roots sampled.

A. Open Coast
N = 70 roots $\geq$20 cm long

Bare space	85.7
Hydroid sp. 2	77.1
Bostrychia tenella/*B. binderi*	75.7
Caulerpa verticillata	60.0
Crustose coralline algae	57.1
Dictyota bartayresii/*D. pulchella*	45.7
Polysiphonia subtilissima	45.7
Mixed algal turf	44.3
Caloglossa leprieurii/*Catanella repens*	34.3
Tunicate sp. (brown)	32.9
Dynamena sp. (hydroid)	31.4
Coelothrix irregularis	31.4
Ceramium spp./*Centroceras clavulatum*	30.0
Blue-green algae (?*Oscillatoria*)	30.0
Styelid seasquirts	28.6
Anemone spp.	28.0
Herposiphonia tenella	25.7
Diatoms	22.9
Chaetomorpha spp.	21.4
Ectocarpus breviarticulatus	17.1
?*Peyssonnelia* sp. (crust)	15.7
Sigmadocia caerulea (sponge)	15.7
Tedania ignis (sponge)	15.7
Purple sponge	15.7
Caulerpa sertularioides	14.3
Hydroid sp. 1	14.3
Black sponge	14.3
Homotrema (protozoa)	11.4
Amphipod tubes	8.6
Brown sponge	8.6
Tunicate sp. (green)	7.1
Porites furcata	7.1
Pink sponge	5.7
Vermetid spp.	5.7
Red sponge	4.3
Balanus improvisus	2.9

B. Channels and Lagoons
N = 75 roots $\geq$20 cm long

Balanus improvisus	100.0
Crassostrea virginica	100.0
Mytilopsis sallei	100.0
Chthamalus sp.	93.3
Isognomon ?*alatus*	85.3
Bare space	85.3
Brachidontes ?*exustus*	60.0
Encrusting bryozoans	46.7
Vermetid spp.	44.0
Spirorbis spp.	34.7

C. Drainage Streams
N = 75 roots $\geq$20 cm long

Mytilopsis sallei	100.0
Balanus improvisus	89.3
Bare space	88.0
Dead *Mytilopsis*	73.3
Diatoms	60.0
Mixed algal turf	56.0
Polysiphonia subtilissima	45.3
Crassostrea virginica	32.0
Chthamalus sp.	28.0
Spirorbis spp.	28.0
Chaetomorpha spp.	28.0

differed greatly in abundance between habitats. For example, *Chthamalus* sp. was nearly absent from roots in streams and common in channels; *Crassostrea virginica* was rare in streams and common in channels. The alga *Polysiphonia subtilissima*, the barnacle *Balanus improvisus*, and the false mussel *Mytilopsis sallei* were exceptions. *Polysiphonia* was found in approximately equal abundance on the open coast and in drainage streams, and *Balanus* and *Mytilopsis* were similarly or equally frequent in channels and streams. Some entire groups were absent from a given habitat (e.g., bivalve molluscs and encrusting bryozoans from the open coast).

The limited overlap of species was most clearly reflected by differences in the most common species or group found on roots in each habitat. Roots on the open coast were dominated by foliose algae (42-62% cover, among-site mean for each sample date) and sessile filter-feeding invertebrates (13-22%; Figs. 9.6, 9.7). The edible oyster *Crassostrea virginica* was the most common species in channels (50-54%, Fig. 9.8) and the false mussel *Mytilopsis sallei* covered the most space in streams (59-64%; Figs. 9.9, 9.10). Thus, each habitat supported a distinct assemblage of epibiotic organisms.

9.2.4 The Oil Spill

In April 1986 at least 60,000-100,000 bbl of crude oil spilled into the sea from a storage tank at Refinería Panamá, Isla Payardí, Republic of Panama. Oil washed into a large area of mangrove forest near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory.

A study of the mangrove fringe and the epibiota of submerged prop roots was initiated for several reasons. First, the maze of prop roots and associated epibiota along the mangrove fringe form a biologically rich "edge" habitat between the sea and interior mangrove forests. Roots are covered with a great number and high biomass of attached organisms compared to those in interior forests. This rich assemblage is critical to the maintenance of nearshore food webs. Effects of oiling on the epibiota were essentially unknown, but negative effects are likely to have wide-ranging consequences. Also, among the attached organisms life histories vary from ephemeral to long lived, giving a range of possible responses to oiling.

Second, differences in fringing habitat types (*sensu* Lugo and Snedaker 1974) presented the opportunity to examine variation in relative oil effects, and to examine existing models of the effect of oil on fringing mangrove habitats (Getter et al. 1984).

Third, we had sampled the epibiota on hanging roots of fringing *R. mangle* near Galeta before the spill. This sampling, and the single-site study of Batista (1980), provided information on the epibiota of prop roots prior to the Bahía Las Minas spill. Preliminary results have been presented in Cubit et al. (1987), Jackson et al. (1989), and Garrity and Levings (1991, 1992).

We here present data on the 5-yr span of the study, including abundances of epibiota on roots, patterns of recruitment, succession, and aspects of the health, growth, and survival of the mangrove fringe and the roots themselves.

Fig. 9.6 Open coast fringing roots and epibiota. May 1990, site = PADM. Roots in the *center* and *right foreground* are hanging; root to the *left* is embedded in sediments; root in the *center background* is touching the bottom but is not anchored. Note richness of epibiota on roots (hydroids, sponges, foliose and crustose algae, and vermetid tubes) compared to sand bottom (one algal species). Also note several species of fish amidst roots.

9.3 Objectives, Rationale, and Design

9.3.1 Introduction

Each accidental oil spill is a unique event, affected by local hydrographic and meteorological conditions, topography, amount and composition of oil, and cleanup attempts. In essence, the sample size of postspill studies is always one. Designing a sampling program depends upon the spill, the unique characteristics of the site, and the distribution of closely matched habitats nearby. Ideally, oiled and unoiled sites are exactly matched and data are available from all sites both before and after the spill (e.g., *main sequence 1* of Green 1979; Table 1.3). However, these ideal conditions, which approximate those of a planned experiment, are rarely met in practice. This fact has broad implications in the design and interpretation of pollution studies.

Fig. 9.7 Open coast fringing root, submerged tip. June 1991, site = MSM. Segment of root shown is ~15 cm in length. Organisms visible include four species of foliose algae, one algal crust, and calcareous vermetid tubes.

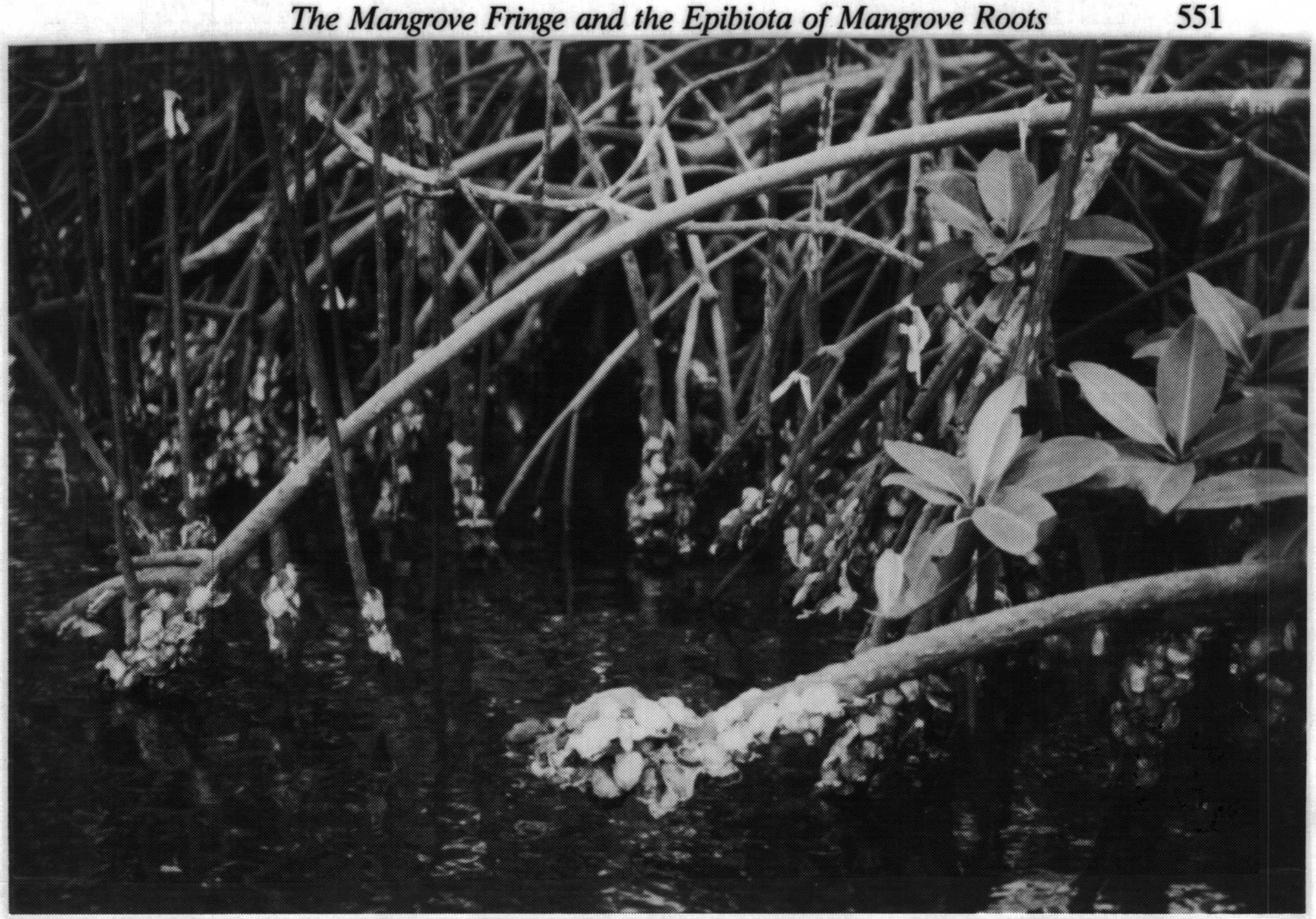

Fig. 9.8 Channels and lagoons: fringe and epibiota. June 1991, site = HIDC. White organisms on roots are *Crassostrea*. Tagged roots in the *background* are from the community development cohort.

The goals of our study were to evaluate the effects of the 1986 Bahía Las Minas oil spill (1) on the epibiota of the mangrove fringe and (2) on the mangrove fringe itself. We attempted to design a rigorous sampling program that could critically examine the effects of oiling on a complex assemblage of organisms whose attachment sites (submerged roots) were themselves alive and potentially affected by oiling.

The comparison of oiled and unoiled sites within habitats was complicated by patterns of oil deposition, water flow, physical stress, and differences between lagoons. In this section, we describe our design, site selection, possible confounding effects, and statistical analyses.

9.3.2 Objectives

There were two major foci of our study. The first was an examination of effects of oiling on the epibiota of mangrove roots. This included:

Fig. 9.9 Unoiled drainage streams: fringing roots and epibiota. May 1990, site = HIDR. Roots hanging off banks were covered with *Mytilopsis sallei*.

1. documentation of the basic ecology of epibiotic assemblages in each habitat, including spatial and temporal variation and major structuring forces (a necessary prelude to assessment of oiling effects),

2. comparison of epibiota at oiled and unoiled sites, and

3. evaluation of possible causes of any differences observed.

The second major focus was an examination of the structure of the fringe itself. Epibiota grow on a living substratum that changes through time. Aerial roots enter the water, grow through the water column, and eventually embed in bottom sediments or die. They thus are a dynamic substratum that could be directly or indirectly affected by oiling or other factors. Differences in the physical structure of the mangrove fringe might be an underlying cause of differences in the epibiota. We examined:

Fig. 9.10 Unoiled drainage streams, submerged view of roots. August 1991, site = HIDR. Root at the *left* is 85 cm long. False mussels covered most space; fuzzy organisms visible in the *center* are a mixture of foliose hydroids and bryozoans.

1. the size, health, and physical condition of roots in the mangrove fringe,
2. density of live and dead roots,
3. growth rates, and
4. structural characteristics of the fringe.

Our observations and field data document the progression of oiling effects in the mangrove fringe. We present these here as a description of the time course and extent of damage from oiling in the mangroves of Bahía Las Minas.

We separate results into two periods: (1) initial effect from the deposition of oil residues during the first year after the spill, and (2) long-term evaluation of damage and recovery during the second through fifth year after the spill.

Finally, we combine results from both the structural and biological components of the study to make an overall evaluation of damage to this productive and important system, 5 yr after the spill.

9.3.3 Selection of Study Sites

9.3.3.1 Goals and Limitations

Our goal in selecting study sites was to sample representatively from the area affected by oiling while making best use of study sites initially sampled in 1981-1982. Two series of sites were used in the short- and long-term sections of the study. The first, sampled in 1986-1987, concentrated on areas sampled in 1981-1982. The second, sampled in 1987-1991, added sites from throughout the area affected by oiling. Sites were selected to be as similar as possible within each habitat type based on the structure of the mangrove fringe and location. We had no prior information on the physical regime at study sites. Beginning in August 1987 at least four sites were sampled in each of the six treatment types (e.g., open, oiled). A history of site changes is shown in Figure 9.5. Site names, abbreviations, and dates of monitoring are listed in Table 9.2, and details are discussed below. Sites will be referred to by coded abbreviations throughout this report.

Site selection was based upon the assumption that we could correctly identify oiled vs. unoiled sites by the visible presence of oil and oil residues. Subsequent sampling and analysis of hydrocarbons from sediments and organisms at our sites (Burns, Chap. 3) represented a test of our method of site selection, as well as of the relevance of data presented in this study for damage assessment (Burns et al. 1993).

Control sites included (1) those sampled in 1981-1982 that had remained visually unoiled (see above methods), (2) other sites within Bahía Las Minas where there was no visible evidence of oiling on roots, and (3) sites at some distance from Bahía Las Minas, physically similar to oiled sites, but where either booms or distance kept oil from reaching mangroves.

Table 9.2 Study sites, site codes, and monitoring dates.

A. Unoiled Open Coast	
María Soto Mangrove (MSM)	August 1986 – May 1991
Portobelo Mangrove (PBM)	August 1986 – May 1991
Isla del Padre Mangrove (PADM)	August 1987 – May 1991
Isla Lintón Mangrove (LINM)	August 1987 – May 1991
B. Oiled Open Coast	
Punta Galeta Mangrove (GALM)	October 1981 – August 1987
Isla Mina Mangrove (MINM)	October 1981 – May 1991
Peña Guapa Mangrove (PGM)	August 1987 – May 1991
Isla Droque Mangrove (DROM)	August 1987 – May 1991
Punta Muerto Mangrove (PMM)	August 1987 – May 1991
C. Unoiled Channels and Lagoons	
Hidden Channel (HIDC)	October 1981 – May 1988
Samba Bonita Channel West (SBCW)	August 1986 – May 1991
Margarita Channel North (MACN)	August 1987 – May 1991
Margarita Channel South (MACS)	August 1987 – May 1991
Largo Remo Channel South (LRCS)	August 1988 – May 1991
D. Oiled Channels and Lagoons	
Peña Guapa Channel (PGC)[1]	August 1986 – May 1987
Largo Remo Channel West (LRCW)[1]	August 1986 – May 1991
Largo Remo Channel Site CO3 (CO3)[1]	August 1986 – May 1987
Payardí Channel East (PCE)	August 1987 – May 1991
Payardí Channel South (PCS)	August 1987 – May 1991
Samba Bonita Channel East (SBCE)	August 1987 – May 1991
Samba Bonita Channel South (SBCS)	August 1987 – May 1991
E. Newly Oiled Channel	
Hidden Channel (HIDC)[2]	August 1988 – May 1991
F. Unoiled Drainage Streams	
Hidden River (HIDR)	October 1981 – May 1991
Río Coco Solo (CSR)	August 1986 – May 1987
Unnamed River (UNR)	August 1987 – May 1991
Río Alejandro (ALER)	August 1987 – May 1991
Quebrada Las Mercedes (MERR)	August 1987 – May 1991
G. Oiled Drainage Streams	
Largo Remo River South (LRRS)	June 1982 – May 1991
Largo Remo River North (LRRN)	August 1986 – May 1987
Payardí River (PAYR)	August 1987 – May 1991
Punta Muerto River East (PMRE)	August 1987 – May 1991
Punta Muerto River West (PMRW)	August 1987 – May 1991

Names are listed for each site; the abbreviation listed is that found in computer data files on deposit.

[1] Sections of Peña Guapa Channel were monitored as Hidden Channel in 1981-1982.

[2] Hidden Channel was oiled between May and August 1988. See text.

There was a distinct geographic component to oiling of the mangrove fringe. The pattern of movement of oil on the open coast was determined by winds and tides (Cubit et al. 1987; Cubit and Levings, Chap. 2; Cubit and Connor, Chap. 4). Within the bay, runoff and tidal currents as well as winds and tides affected the path and extent of oiling. Oil moved into the mouths of the smaller bays within Bahía Las Minas and penetrated them to varying degrees; freshwater outflows often moved oil out of channels and streams. The central bay (closest to the source of oil input) was heavily oiled because winds initially trapped oil within this wing (Cubit et al. 1987). Relatively less oil reached deep into the bay's eastern and western wings. As a result, the mangrove fringe in channels was oiled (1) patchily in the outer sections of the western wing, (2) throughout the central bay, and (3) into middle sections of the eastern wing. Smaller streams were heavily oiled because they experienced a strong tidal influence (two-way flow) and concomitant intrusion of (oily) saltwater. Large streams remained unoiled because of positive downstream flow.

9.3.3.2 Habitat Definition and Site Selection

Three fringing habitats of the red mangrove *Rhizophora mangle* in Bahía Las Minas include (1) shoreward margins of reef flats fronting the open sea, (2) edges of channels leading inward from the sea, and lagoons into which channels lead, and (3) banks of streams and man-made cuts that drain interior mangroves or uplands into lagoons (Figs. 9.2-9.4).

Prior to the spill at Refinería Panamá, the cover of space on *Rhizophora* prop roots in the above three habitats (hereafter called *open coast*, *channel*, and *drainage stream*) was surveyed three times (September-October 1981, January 1982, and June 1982). Roughly 1-km stretches of shore (*sites*) within each habitat were haphazardly chosen in the western wing of Bahía Las Minas (Fig. 9.5).

After the spill, sites were added to include both oiled and unoiled areas and to increase sample sizes. For the first year following the spill (August 1986-May 1987), we concentrated on areas studied during 1981-1982 within the western wing of Bahía Las Minas (Fig. 9.5).

When the long-term study of oiling effects began (August 1987), site changes were made to sample representatively from the coastline affected by the spill and to increase distance between sites. Definition of "oiled" vs. "unoiled" areas was based on examination of aerial photographs of oil slicks, followed by observations by boat. The coast was surveyed for visible oil throughout the area affected by the spill. Oiling at individual sites was verified by measurement of percent cover and vertical extent of fresh oil on prop roots. In each habitat final sites were chosen by randomly selecting among oiled areas that were similar in fringe structure, with the proviso that sites were spread throughout the oiled area, rejecting adjacent locations.

On the open coast three points adjacent to the Galeta Marine Laboratory were sampled as two sites (GALM and MINM) in 1981-1982. These sites were subsequently oiled in April 1986, and resampled during 1986-1987 as oiled sites along with a fourth adjacent point to the south (data included in MINM). In August 1987 three oiled sites around the mouth of Bahía Las Minas were added to MINM, and quarterly sampling was discontinued at adjacent GALM. Because Punta Galeta had been monitored prior to the spill, we remonitored it on the fourth and fifth anniversaries of the spill.

No open, unoiled areas were found near Bahía Las Minas; the closest unoiled sites were located ~25 km east, at María Soto (MSM) and Portobelo (PBM; Table 9.2; Fig. 9.5). In August 1987 two open coast sites were added east of PBM, for a total of four unoiled sites (Fig. 9.5).

In channels and lagoons two large (>1 km) sections of shore within the western wing of the bay were sampled in 1981-1982 (data combined as HIDC). Oiling within this wing was patchy in April 1986; the originally sampled areas ranged from heavily oiled to unoiled. Areas deeper within the western wing had little or no visible oil compared with those nearer the mouth (e.g., LRCW vs. HIDC); they were accordingly split into oiled and unoiled sites. However, we viewed these "control" areas as being lightly oiled rather than unoiled because of their proximity to oiled sites and the continued presence of floating oil nearby. Additional sites within this wing of Bahía Las Minas were added to previously sampled oiled (2) and unoiled (1) sites in July 1986 (Fig. 9.5; Table 9.2).

In August 1987 two oiled sites each were added in the central and eastern wings of Bahía Las Minas, closer to the refinery. We continued to monitor LRCW in the western wing (Fig. 9.5; Table 9.2).

Because of the possible oiling of at least some control sites within Bahía Las Minas (see above), we added two unoiled sites (MACN and MACS; Fig. 9.5) located in a small, shallow lagoon that had been protected by booms during the spill. Margarita Lagoon is much smaller than Bahía Las Minas, with a restricted opening to the sea. A branch of Río Coco Solo drains into its east end. Maximum depth is <1 m throughout, compared to Bahía Las Minas, which is navigable to ocean-going ships (through dredged channels) well into the central and east wings.

In August 1988 a control site within the west wing of Bahía Las Minas (HIDC) was oiled; it was from then on considered newly (lightly) oiled. The source of the oil was a secondary release of the spilled Venezuelan/Mexican Isthmian crude (VMIC) from sediments (Burns, Chap. 3). Only one such release reached this site. A replacement unoiled site within the western wing of Bahía Las Minas (LRCS) was added to the study at this time (Fig. 9.5; Table 9.2).

Two streams were sampled in 1981-1982 (Fig. 9.5; Table 9.2). One, a narrow, man-made cut through the center of Isla Largo Remo, was subsequently heavily oiled throughout its length. We sampled its southwest end as an oiled site (LRRS). The other, a larger stream draining mangroves and uplands into an inner portion of the west wing of Bahía Las Minas, escaped oiling in 1986 (HIDR). In August 1986 we began to monitor an additional unoiled stream (CSR), and sampled the northeast entrance of the oiled drainage stream through Isla Largo Remo as a second oiled site (LRRN).

In August 1987 three oiled and three unoiled streams were added to the study (Fig. 9.5). Río Coco Solo (CSR) was removed because of cutting of its watershed by local fishermen, and LRRN was removed to make sites more spatially distinct and because of difficulties in access.

The four unoiled drainage streams were located in and around Bahía Las Minas (Fig. 9.5). Hidden River (HIDR) was deep in the western wing of the bay while two others (ALER and UNR) were deep in the eastern wing. Quebrada Las Mercedes (MERR) was ~4 km east of Bahía Las Minas. A shallow area of reef flat and seagrass beds fringed its mouth. Of the oiled drainage streams, three were in the eastern wing of Bahía Las Minas; LRRS bisected Isla Largo Remo.

9.3.4 Confounding Effects

In the mangrove fringe each habitat had a different set of confounding factors that might affect comparisons of oiled and unoiled sites. For each habitat we examine the similarity of geographic location and physical factors between oiled and unoiled sites to evaluate possible confounding effects of site selection.

9.3.4.1 Open Coast

The coast of Panama changes between Punta Galeta and Isla Grande. On the open coast, unoiled sites were located ~25 km east of Bahía Las Minas (Fig. 9.5). All sites were similar in that a healthy mangrove fringe was located behind a fringing reef flat. Physical conditions on reef flats are controlled by a combination of meteorological and hydrographical forces that vary with small changes in local topography and aspect (Cubit et al. 1986, 1989). Differences in location of open coast sites could thus affect the physical regime in the mangrove fringe behind the reef flat.

Sites around Bahía Las Minas face directly north. Unoiled sites face northeast. Prevailing winds on this coast are from the north (Glynn 1972; Cubit et al. 1989). Oiled and unoiled sites therefore probably have somewhat different patterns of wind-driven waves. Second, there is a rainfall gradient of ~80 cm/yr between Cristóbal at the Caribbean entrance to the Panama Canal and Portobelo to the east (long-term averages from PanCanal Company, cited in Windsor 1990; Guzmán et al., Chap. 7). Unoiled sites probably receive at least 50 cm more rainfall on average in a year than unoiled ones (Cristóbal mean annual rainfall = 3,257 mm, N = 114; Portobelo mean annual rainfall = 4,069 mm, N = 65; Windsor 1990).

Limited physical data suggest that overall conditions were similar between oiled and unoiled sites. Salinity was generally >30o/oo on the surface and always >30o/oo at 1 m depth at both oiled and unoiled sites (Fig. 9.11). Seasonal variation was slight, with salinities highest at both depths in dry season (February) and lowest during mid- to late rainy season (Augusts and Novembers). Water temperature did not differ between oiled and unoiled open coast sites or between surface and 1 m depth, but showed a somewhat stronger (and opposite) seasonal pattern to salinity

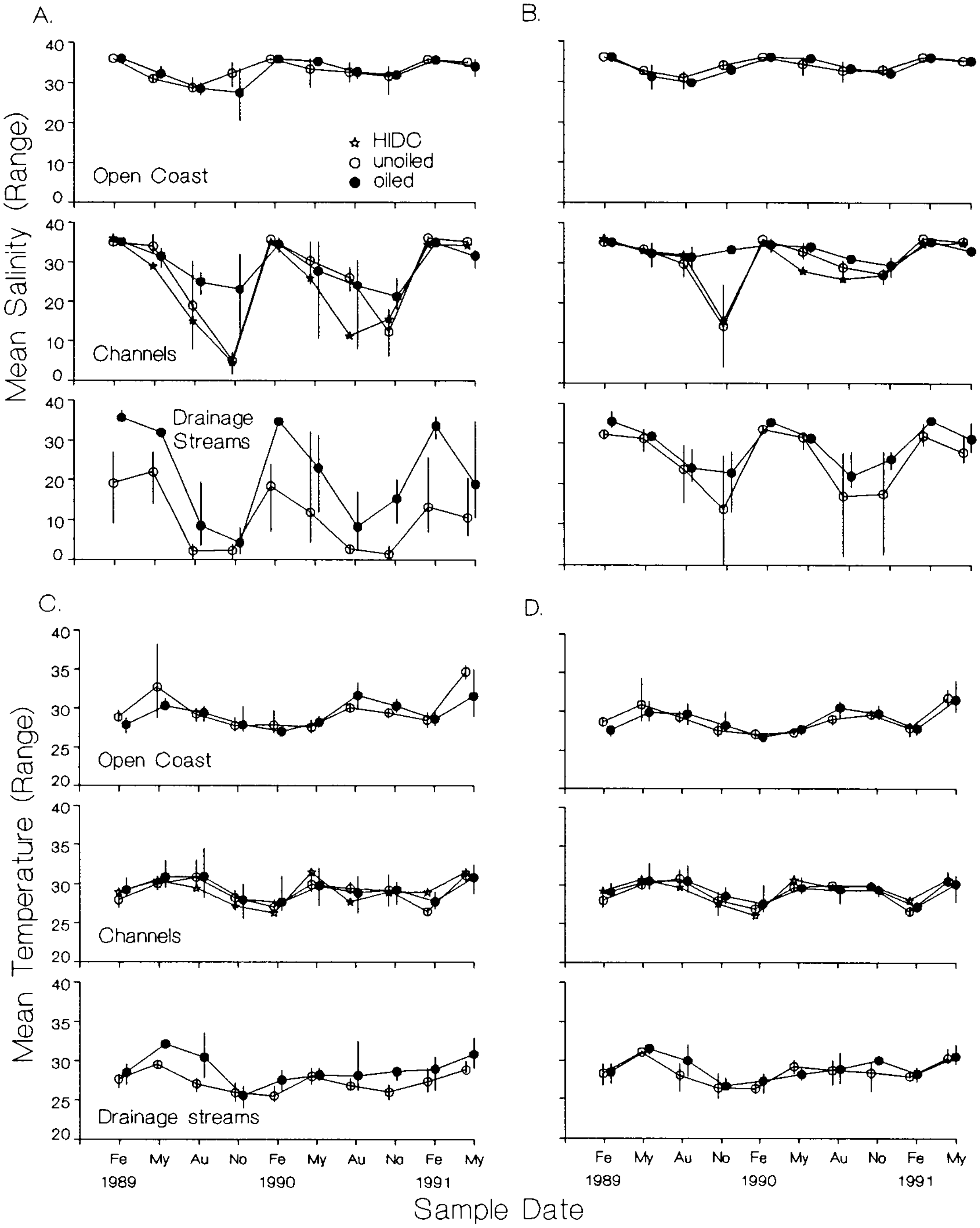

Fig. 9.11 Water temperature and salinity. Symbols are overall means with ranges; *solid circles* = oiled, *open circles* = unoiled, *stars* are values for secondarily oiled HIDC. For each sampling date $N = 2$ readings per site, 4-5 sites combined for each habitat/treatment. *A*. Surface temperature. *B*. Water temperature at 1 m depth. *C*. Surface salinity. *D*. Salinity at 1 m depth.

(Fig. 9.11). Temperatures were lowest during dry season, when wave action and water levels were high, and higher in the wet season (particularly May 1989 and 1991), when low water levels and wave action resulted in heating across the reef flat (see also Cubit et al. 1989).

Open coast sites had high transparency (3-12 m Secchi depth; Fig. 9.12). Water at unoiled sites was clearer than at oiled sites, but differences were unlikely to be relevant at the shallow depth range of mangrove roots. Because unoiled sites were 25 km east of the Bahía Las Minas estuary, the most conservative explanation is that drainage from Bahía Las Minas tended to lower transparency on the nearby open coast. This hypothesis is supported by sediment-size distributions on oiled and unoiled coral reefs in October 1986, before large-scale erosion related to the oil spill began (see Table 3.2).

On the open coast water movement was highest in dry season and dropped during the early wet season (Fig. 9.13). This was similar to patterns of water flow on the fringing reef flat at Punta Galeta (Galeta Environmental Sciences Program, Cubit et al. 1986, 1988*a*, 1989). In late April and May onshore winds stop and seasonal low tides lead to long exposures of reef flats (Cubit et al. 1986, 1989; Cubit and Connor, Chap. 4). There were no differences in water movement between oiled and unoiled open coast sites.

Open coast sites were of necessity spread ~25 km along the coast. Their overall structure was similar. Our measurements of physical conditions were roughly similar, but unoiled sites probably received more rain, and prevailing winds did not blow directly onshore. We cannot determine the effects of these differences among sites, but they appear small compared with the effects of oiling.

9.3.4.2 Channels and Lagoons

The mangrove fringe in channels and lagoons was structurally similar, and sites were located close to one another either in Bahía Las Minas or the nearby Margarita Lagoon. However, Margarita Lagoon is much smaller and shallower than Bahía Las Minas. In addition, there were some differences in the physical regime between oiled and unoiled sites and between lagoons.

There was a sharp seasonal pattern in surface salinity in unoiled channels and lagoons, with surface salinities dropping from nearly oceanic during dry season to ~10o/oo in late wet season (November 1989 and 1990; Fig. 9.11). In oiled channels surface salinities showed the same pattern, but seldom dropped below 25o/oo. During the dry and early wet seasons (February-May) surface salinities were similarly high at oiled and unoiled sites. Seasonal and between-treatment (oiled vs. unoiled) differences were damped at 1 m depth; the only significant drop in salinity occurred in unoiled channels during November 1989. Water temperature in channels showed a weak seasonal cycle. As on the open coast, there were no differences in temperature between oiled and unoiled channels, or between the surface and 1 m depth.

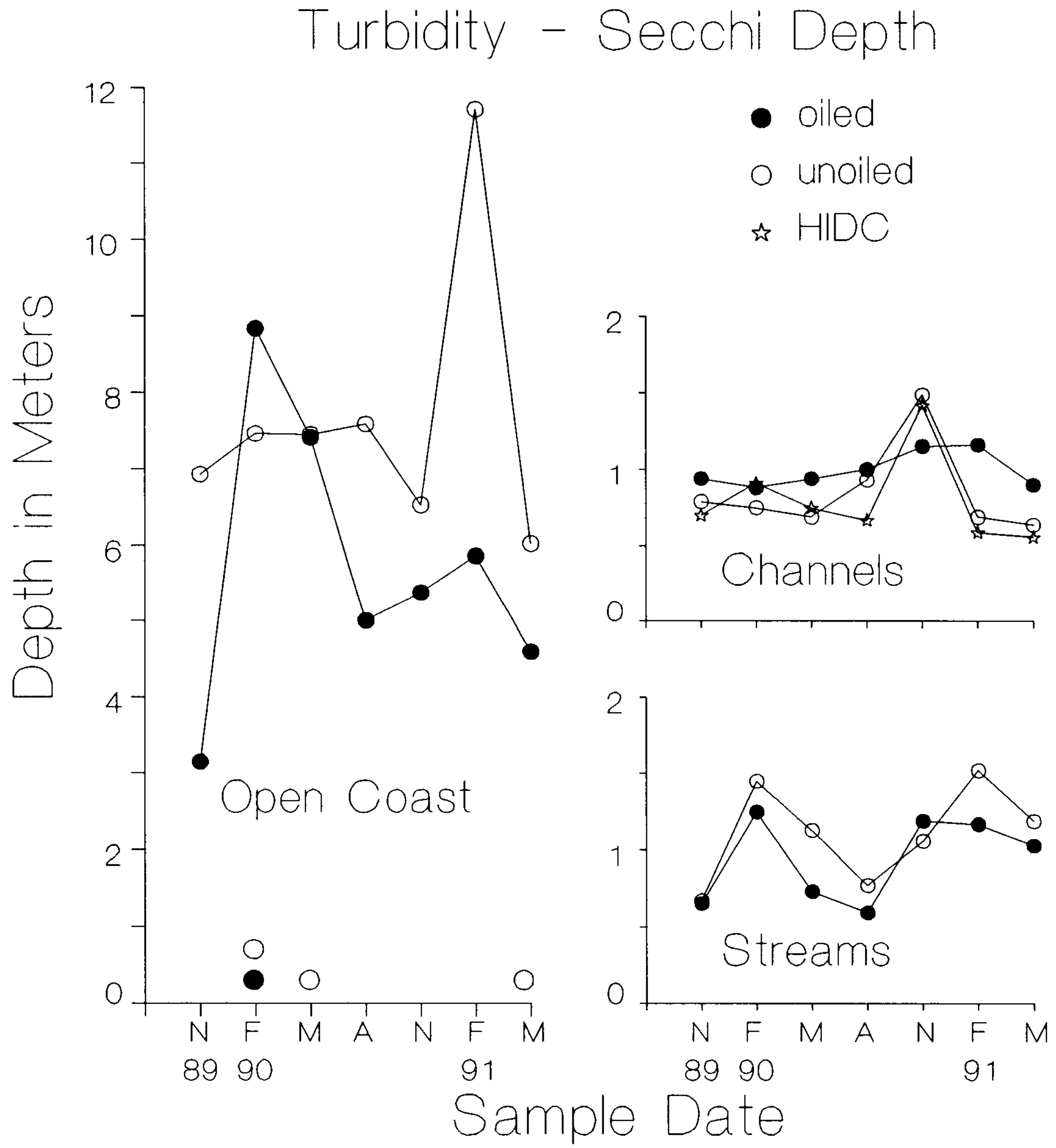

Fig. 9.12 **Water transparency. Data are overall quarterly means (2 readings/site, 4-5 sites/habitat) for oiled and unoiled open coast, channel, and stream turbidity measurements. Circles on the *x*-axis are the number of sites where the Secchi disk reached the bottom. See text for details.**

Surface salinity was correlated with geographic location for oiled and unoiled channels (Fig. 9.5). Surface salinity in unoiled channels in November in the western wing of Bahía Las Minas was significantly lower than at oiled sites (oiled mean = 22.1o/oo, unoiled mean = 11.4o/oo; Mann-Whitney *U*-test, $U = 6.5, P < .02$,

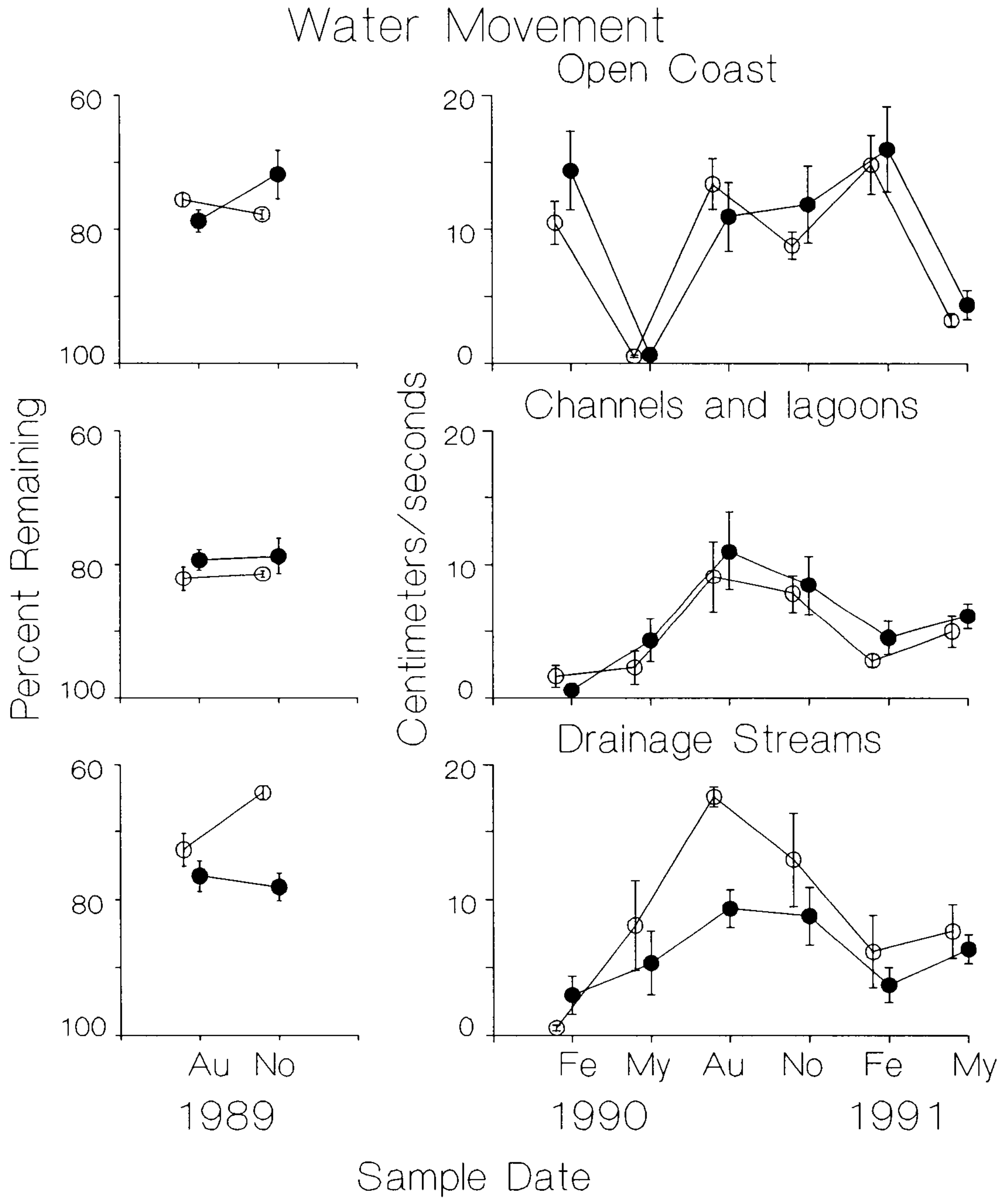

Fig. 9.13 Water movement. Data in the left column are mean and SE of weight loss of plaster clods set subtidally at each site simultaneously for 2 d. Data in the right column are direct measurements of water flow with associated standard errors. *Open circles* = unoiled, *solid circles* = oiled. See text for methods and details.

N = 6, 10). Two unoiled sites in Margarita Lagoon (MACN and MACS) had the lowest surface salinities recorded (<10o/oo in the 3 November samples). Margarita Lagoon and the western wing of Bahía Las Minas have constricted openings to the sea compared with the central and eastern wings of Bahía Las Minas (Fig. 9.5). This characteristic probably concentrates freshwater inflow there, resulting in lower salinities.

Transparency was always low, averaging ~1 m and differing <25 cm at oiled and unoiled sites (Fig. 9.12). Water tended to be clearer at oiled than unoiled sites (6 of 7 dates), perhaps associated with greater saltwater inflow. Water movement in channels was not wave-forced; it appeared most affected by patterns of runoff and tidal flow within the bay. In dry season (February) there was little flow (Fig. 9.13). Onshore winds held water within the bay (based on observed high-water levels), and tidal fluctuations were small (Cubit et al. 1989). Little rain, and thus little runoff, occurred. In April to May the rains began and onshore winds dropped; runoff and tidal fluctuations increased. These factors resulted in increased water movement during rainy season.

Between-treatment differences in surface salinity were an unavoidable result of the pattern of oil movement. All channels close to the mouth of Bahía Las Minas were oiled; no comparable habitat occurs within range of the Galeta Marine Laboratory. We note that areas close to the mouth of Bahía Las Minas and those deep in the western wing had similar epibiotic cover in 1981-1982 (data combined as HIDC below). Statistical analyses were adjusted to examine these differences.

9.3.4.3 Drainage Streams

The mangrove fringe and physical regime differed between oiled and unoiled streams because the processes that controlled oil deposition were related to those that generated the structure of the mangrove fringe itself.

Drainage streams showed strong seasonal changes in salinity, as well as differences in salinity between oiled and unoiled streams (Fig. 9.11). Mean surface salinity was always lower at unoiled than at oiled streams (sign-rank test, *P* = .002 [2-tailed], *N* = 10). Differences were greatest during dry season (February 1989, 1990, and 1991). Unoiled streams were larger, and usually maintained positive outward flow (presumably limiting surface saltwater intrusion). Oiled drainage streams flowed bayward mainly during periods of strong rainy season runoff, and could experience reverse flow and surface salinities >30o/oo during the dry season. Oiled and unoiled streams were most similar in surface salinity following heavy rains during wet season (e.g., November 1989 and August 1990).

Seasonal differences in salinity were damped at 1 m depth (Fig. 9.11). Salinity was >30o/oo during the dry and early wet seasons in both oiled and unoiled streams, then dropped during mid- to late wet seasons. The seasonal decrease in salinities at 1 m depth was greater in unoiled than oiled streams. Absolute differences between salinity at the surface and at 1 m depth were also generally greater in unoiled than oiled streams, but there was considerable variation among sites. For example, in

November 1989 salinity at HIDR was 0o/oo both at the surface and at 1 m depth, while at ALER salinity was 4o/oo on the surface and 25.5o/oo at 1 m depth.

There was little variation in water temperature at either oiled or unoiled streams (Fig. 9.11). However, mean surface temperature was higher in oiled than unoiled streams on 9 of 10 dates (sign-rank test, P = .022 [2-tailed]). Differences were 2°C or higher on 4 of 9 dates. The range of mean surface temperatures in oiled streams was 25.5-32.1°C, while the range of temperatures in unoiled streams was 25.5-29.5°C. There were no differences at 1 m depth.

Water in streams was turbid (0.5-1.5 m Secchi depth) with a strong seasonal pattern (Fig. 9.12). Water was most transparent in dry season and most turbid in early to mid-rainy season. This difference reflected increased incursion of oceanic waters and decreased runoff during periods of reduced rainfall. Oiled streams were more turbid than unoiled ones on 5 of 7 dates, at least in part because of erosion along banks.

Water movement in drainage streams followed the same pattern as that in channels. In dry season (February) there was little flow (Fig. 9.13). Onshore winds held water within the bay and tidal fluctuations were small (Cubit et al. 1989). Little rain, and thus little runoff, occurred. In April to May the rains began, runoff and tidal fluctuations increased, and winds dropped. These factors resulted in increased water movement during rainy season. There were differences between oiled and unoiled streams. Flow was similar in the dry and early wet season (February and May). In mid- or late wet season, or both (August and November), flow was as much as twice as great in unoiled than oiled streams, probably because they drained larger watersheds.

It was not possible to match exactly the size and runoff pattern of streams. Differences between oiled and unoiled streams were an unavoidable complication because they resulted from the pattern of oiling. Smaller streams, with greater surface tidal intrusion, were more likely to be oiled than larger streams with positive freshwater outflow in the early wet season. It should be noted, however, that both Hidden River (HIDR, a large unoiled stream) and Largo Remo River South (LRRS, a small oiled stream) had similar epibiotic communities before the spill.

9.3.4.4 Matching of Sites Sampled Before and After the Spill

Some sites sampled before the spill were oiled and some were not. Comparisons between them were the strongest evidence for an effect of the oil spill on the mangrove fringe and attached epibiota, rather than from natural variation among sites or over time. However, (1) there was a 4-yr gap between before-and-after data and (2) the pattern of oiling with respect to sites sampled before the spill differed among habitats.

On the open coast both sites sampled before the spill were oiled. Thus, we have no direct measure of variation between 1981-1982 and 1986 with respect to oil effects (*main sequence 2* of Green 1979; Table 1.3). In channels, sections of the originally sampled shore were oiled and some escaped oiling (LRCW, PGC, and CO3 vs. HIDC). Thus, differences between these sites meet the criteria for complete before-and-after matching (*main sequence 1* of Green 1979). Two streams were sampled in 1981-1982. One was oiled and one was not (LRRS vs. HIDR). These sites also meet matching criteria.

In addition, although quantitative data were collected only three times prior to the spill, we made multiple trips in the mangroves of Bahía Las Minas between 1981 and 1983. Photographs and notes indicate that the three documented epibiotic assemblages persisted throughout 1981-1983, and were still present at unoiled sites when monitoring began in 1986.

9.3.5 Statistical Analyses

Statistical analyses were chosen based on the structure of individual data sets. We used parametric analyses when data were in the form of continuously distributed variables and met the appropriate assumptions. In general, we chose repeated-measures analysis of variance (ANOVA) because sites were revisited over time and it was possible, though unlikely, that the same root could be resampled. Where data were independent among years or where only one date was sampled, we used 1- or 2-way ANOVA. Nonparametric analyses were chosen when data were categorical variables, or where the assumptions of parametric analyses were not met. Details of particular analyses are given with the results.

Sites were relocated in August 1987 to sample throughout the area affected by oil (Fig. 9.5; Table 9.2). There are thus two sets of postspill data: sites sampled in the first year after oiling (N = 4 quarterly monitorings, August 1986-May 1987) and those sampled 2-5 yr after oiling (N = 16 quarterly monitorings, August 1987-May 1991). The details of changes and the fate of sites sampled in 1981-1982 determined the exact analyses. We restrict repeated-measures analyses to the 4-yr data set (August 1987-May 1991).

Percent cover data were arcsine transformed prior to analysis because most species or groups of interest had percent covers out of the range of 30-70% (Sokal and Rohlf 1981). Because percent cover data were not independent (i.e., data from one root must sum to 100% cover), analysis of variance was restricted to groups of major importance within each habitat: sessile invertebrates and algae on the open coast; oysters, barnacles, sessile invertebrates, and algae in channels and lagoons; and false mussels, sessile invertebrates, barnacles, and foliose algae in drainage streams. These groups totaled <60% cover on roots, and each analysis was treated as independent.

Data were combined into yearly samples/site because these groupings controlled for possible seasonal effects and gave a stronger overall picture of epibiotic cover. These repeated-measures ANOVAs were very conservative. Effectively, if one oiled site had percent cover equaling that of the lowest cover at an unoiled site, the effect of oiling was not significant. We thus have confidence that any differences identified were strong and persistent. We also ran smaller-scale analyses (e.g., sign-rank tests) to examine the scale of differences, if any, between oiled and unoiled sites.

The overall approach suggested by Mead (1988) was followed. Univariate repeated-measures ANOVA was performed for the entire data set and for individual years ($N = 4$). If sphericity assumptions held, unadjusted probability levels were applied; if sphericity tests failed, Huynh-Feldt corrected probability levels were applied. In practice, few data sets failed to pass sphericity tests. The set of analyses was examined to interpret overall patterns of variation. In particular, years that did or did not differ in single-year analyses were useful in interpreting the pattern of recovery at oiled sites over time.

Prespill data were used as indicative of the kind of epibiotic assemblage expected in Bahía Las Minas, but were excluded from statistical analyses because of the 4-yr gap between pre- and postspill sampling and slightly different sampling methodology.

Numbers of roots sampled in a given period varied among sites. Comparisons of algal species richness were made using rarefaction (Simberloff 1978). A sample size of 20 roots was chosen for comparisons using long-term census and community development roots and 10 for comparisons using recruitment dowels.

9.4 Oiling and Reoiling

9.4.1 Introduction, Rationale, and Design

Mangrove roots are a potential substratum for oil deposition as well as for the settlement of epibiota. We measured the amount of oil deposited on roots throughout the study and recorded the presence of visible oil. Oil consisted of progressively weathered tarry residues on roots and attached organisms. For estimates of dissolved hydrocarbons, see Burns (Chap. 3). The deposition, accumulation, and degradation of oil stranded on mangrove roots was complicated by the dynamic, biogenic nature of roots. Root growth, physical condition, and mortality all affected records of oiling over time. Patterns of oiling on roots were also complicated by secondary releases of oil from sediments or other sources.

Floating and stranding of oil was a complex issue in Bahía Las Minas. Oil was present both from the 1986 spill and from other events throughout the study. The Bahía Las Minas area has been and continues to be strongly disturbed by human activities (Cubit et al. 1985). The refinery that was the source of the spill continues to operate, as does an electrical plant at the base of Isla Payardí (Fig. 9.5). Small-boat, freighter, and tanker traffic is constant, with concomitant inputs of hydrocarbon residues. Oil from bilge waters pumped from tankers can form large slicks that subsequently move east with longshore currents (S. Garrity, pers. obs.). Thus, other sources of hydrocarbon contamination are present and might add oil residues to those from the spill.

It was impossible to attempt to fingerprint chemically every oil record. However, there was no chemical evidence that other sources were major contaminants (Burns, Chap. 3). Tissues from bivalves collected at oiled sites showed continuing contamination from VMIC from 1986 through 1991; oil in sediments or on roots was fingerprinted as that spilled in 1986 (oil samples taken in 1986, 1988, 1989, 1990, and 1991; Burns, Chap. 3). We therefore assume that the oil we observed on mangrove roots was predominantly VMIC, but note any possible exceptions from our field observations.

This section documents (1) the amount and persistence over time of oil from the April 1986 spill in fringing mangroves and (2) the amount and sources of reoiling along the mangrove fringe for 5 yr following the spill.

9.4.2 Materials and Methods

Initial measurement of the vertical extent of oil on mangrove roots on open shores, in channels, and in streams immediately after the spill estimated variability in oiling among habitats. In July-August 1986 we measured the vertical distance oil (or oil covered with a film of diatoms) extended on haphazardly chosen prop roots in oiled streams, channels, and on oiled open coast.

We subsequently measured the amount of oil on roots as percent cover of oil. Percent cover was measured using a variation of point-intercept sampling. Strings of varying length with 100 marked points in a stratified-random array were prepared. An appropriately sized string was held against each root and the number of points underlaid by oil was recorded. If oil was present on a root but not found under a point, it was recorded as a "trace" and assigned a cover of 0.01%. For 5 of the 20 roots >75 cm in length, the vertical distribution of oil along the string was recorded, and subsequently transformed to centimeters below mean high water (MHW).

Three types of roots were sampled. First, we randomly chose 20 roots at each site every quarter and recorded percent cover (termed *long-term census* or *random*; see Sect. 9.5.3). This sampling gave us an overall estimate of oil cover at each site, including roots submerged at the time of the spill and those that later grew into the water. The vertical distribution of oil on a subset of these randomly censused roots examined changes in amounts of oil at different depths on roots over time. Second, in November 1987 we began similar subsampling of a marked cohort of roots that entered the water ~18 mo after the spill (termed *community development* or *cohort*). These roots measured cumulative reoiling, but had not been oiled by the initial spill. Third, artificial roots (dowels) placed at each site every quarter measured relative amounts of oil stranding in the fringe over discrete 2-2.5-mo periods (termed *dowels* or *recruitment dowels*).

Data were examined in two ways. First, the proportion of roots (or dowels) with a trace of oil or more on their surfaces measured the fraction of roots (or dowels) in contact with at least some oil. Second, mean percent cover measured the average amount of oil stranded per root.

Field notes were made at each site visit on the extent of oil on fringing roots and its degree of weathering. During May 1990 and May 1991 we estimated the relative freshness of oil on randomly sampled roots. We scored oil "old" if it was highly weathered with a surface texture ranging from dull or flaking to a solid, apparently inert mass. "Fresh" oil included a sheen on roots, sticky black deposits, oil and diatom films, and fresh tar balls. Fresh and old oil could occur on the same root.

The presence or absence of oil slicks and oil in sediments were recorded at each visit to a site. The approximate size and thickness (black film, iridescence, and silvery sheen) of slicks were noted. When possible we recorded the source of slicks (e.g., tanker pumping bilge or leaching from sediments).

9.4.3 Results

9.4.3.1 Qualitative Field Observations

Roots in the water at the time of the spill were coated almost entirely with oil from slicks, often in layers up to 1 cm thick (Fig. 9.14). During the first year after the spill, weathering and degradation of much of this oil occurred (Fig. 9.15). In the second year, many oiled roots died and broke off below MHW (Fig. 9.16); oiled bark also began sloughing off roots (Fig. 9.17). These events removed oil from our sampling regime, but not necessarily from the immediate vicinity. Oil on surviving roots continued to weather and flake off during the third year postspill (Fig. 9.18).

Growth into the water of new roots and growth of oiled roots into the sediment also reduced the amount of oil recorded by our sampling. However, observations suggested this oil spill could not be considered a single event. If so, oil on roots would have disappeared over time as the population of roots changed from those in the water during the spill to roots entering the water afterward. Instead, oil slicks occurred at or near our sites through 1991 (Figs. 9.19, 9.20; Table 9.3), and multiple reoilings of roots occurred (Figs. 9.21*A*, *B*). Oil from the original stranding continued to weather and disappear from roots during the fourth year postspill (Fig. 9.22); we observed blue-green algae and barnacles settling and surviving upon weathered oil (near MHW) on roots. However, heavy bands of obviously fresher oil were found on roots at some sites 5 yr after the spill (Fig. 9.23).

9.4.3.2 Quantitative Measures of Oiling

Initial Oiling

Initial oiling was heavy in all habitats (Fig. 9.14). On the open coast (MINM and GALM) oil coated an average of 55.9 cm (range = 36-70 cm, *N* = 98) of root length in July-August 1986. This exceeded by 146% the average length of roots sampled simultaneously for percent cover (mean = 38.4 cm, range = 20-85 cm, *N* = 80), and probably resulted from wave action distributing oil above mean high water. In oiled channels between Isla Largo Remo and Peña Guapa (Fig. 9.5), oil on roots averaged 37.6 cm (range = 15-94 cm, *N* = 50) compared to an average root length of 40.1 cm (range = 20-111 cm, *N* = 80). Ninety-four percent of available

Fig. 9.14 Oil on roots immediately after the spill. August 1986, site = LRCW. Fresh, sticky oil up to 1 cm thick coated roots and epibiota.

Fig. 9.15 Oil on roots 1 yr after the spill. August 1987, site = PCE. Oil had weathered to an apparently inert mass high on roots, and was being biodegraded lower on roots.

Fig. 9.16 Oil on roots 2 yr after the spill. May 1988, site = DROM. Many heavily oiled roots had broken and lost submerged portions and epibiota.

Fig. 9.17 Oil and root condition 2 yr after the spill. May 1988, site = MINM. Oil on roots continued to weather; disappearance of oil was partly due to oiled bark and tissue loss from heavily oiled roots.

Fig. 9.18 Oil on roots 3 yr after the spill. Original oil continued to weather and flake off roots.

Fig. 9.19 Residual oil slick 3 yr after the spill. February 1989, site = LRRS. Iridescent and black oil covered much of the water's surface.

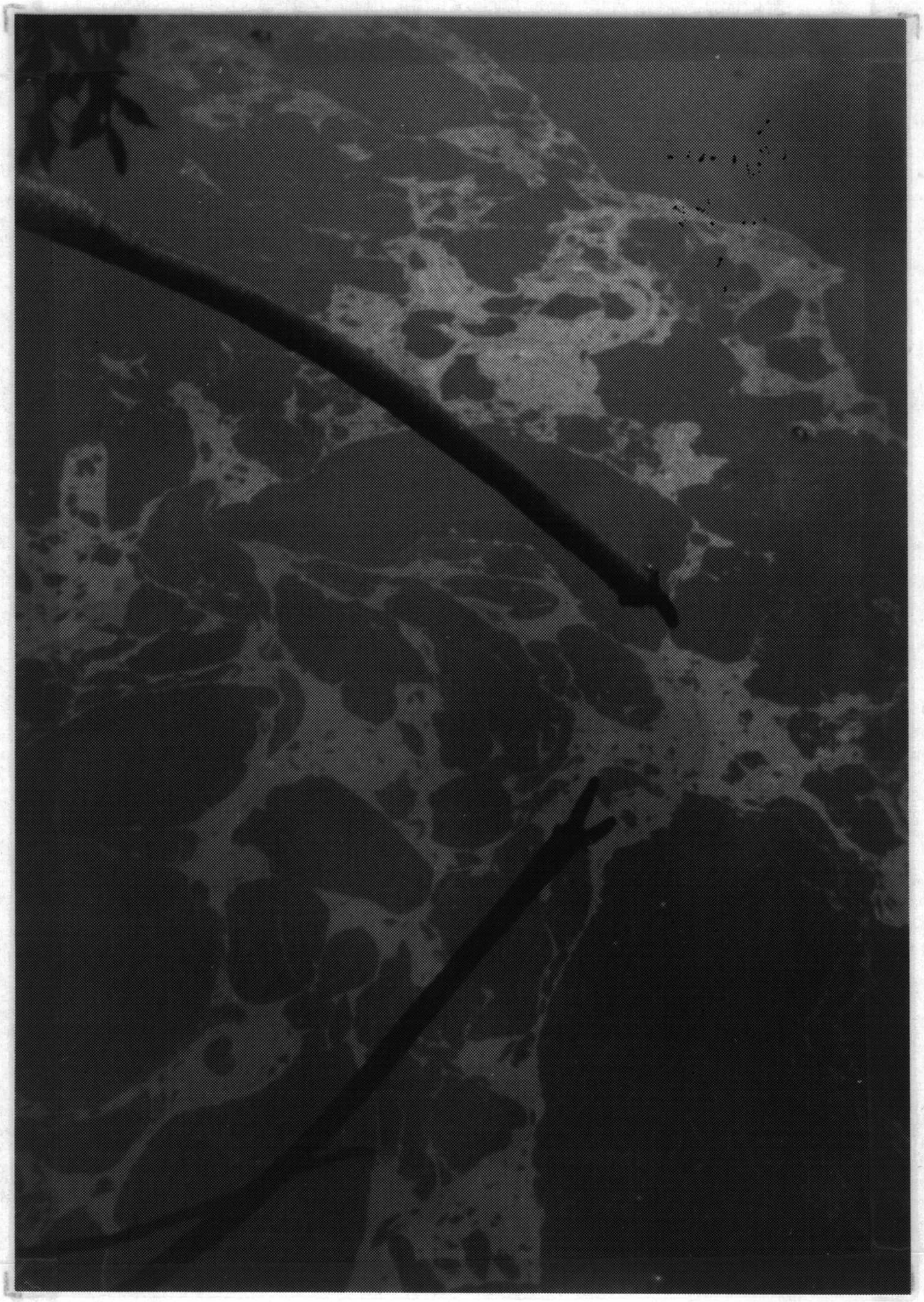

Fig. 9.20 Residual oil slick 5 yr after the spill. September 1991, site = PMRE. Iridescent and silver oil slicks remained common in all oiled streams. Object and reflection are a new lateral root just entering the water (note dark, oiled tip).

Table 9.3 Number of days when oil slicks were visible along the mangrove fringe.

	Open Coast						Channels and Lagoons						Drainage Streams					
	Oiled			Unoiled			Oiled			Unoiled			Oiled			Unoiled		
Date	%	(N)	Type	%	(N)	Type	%	(N)	Type	%	(N)	Type	%	(N)	Type	%	(N)	Type
Aug. 1987	100	(7)	I, S	0	(4)	–	100	(3)	F, S	0	(3)	–	100	(4)	F, I	0	(6)	–
Nov. 1987		ND			ND			ND		0	(2)	–	100	(2)	F, I	0	(2)	–
Feb. 1988		ND			ND		100	(2)	F, I	0	(4)	–	100	(4)	F, I	0	(6)	–
May 1988	100	(4)	I	12.5	(8)	T	80	(5)	F	0	(4)	–	100	(8)	F	0	(6)	–
Aug. 1988	100	(8)	F	0	(9)	–	100	(6)	F, I	27.3	(11)	S, F, B	100	(6)	F	16.7	(6)	S
Nov. 1988	100	(7)	F, I	0	(2)	–	90	(10)	I	14.3	(7)	S	100	(12)	F, I	0	(4)	–
Feb. 1989		ND			ND		100	(1)	I	0	(7)	–	75	(4)	F	0	(4)	–
May 1989	100	(5)	I, S	16.7	(6)	B	83.3	(12)	F, I, S	0	(11)	–	100	(12)	F, I	0	(12)	–
Aug. 1989	100	(8)	I	0	(12)	–	100	(5)	I	20	(5)	B	100	(5)	I	0	(5)	–
Nov. 1989	66.6	(6)	I, S	0	(4)	–	100	(7)	I, S	0	(6)	–	100	(6)	I	0	(4)	–
Feb. 1990		ND		0	(4)	–	87.5	(8)	I, S	0	(8)	–	100	(7)	I	0	(8)	–
May 1990	37.5	(8)	I	0	(14)	–	75	(8)	I	0	(6)	–	100	(7)	F, I	0	(8)	–
Aug. 1990	83.3	(6)	I, S	0	(8)	–	100	(7)	I	0	(9)	–	100	(12)	I	0	(16)	–
Nov. 1990	75	(4)	S	0	(16)	–	100	(7)	F, I	0	(13)	–	100	(12)	F, I	0	(12)	–
Feb. 1991	0	(1)	–	0	(6)	–	91.7	(12)	F, I, S	0	(11)	–	100	(9)	F, I	0	(9)	–
May 1991	55.6	(9)	I	0	(10)	–	95.5	(22)	F, I	0	(14)	–	100	(19)	F, I, S	0	(14)	–
Aug. 1991	75	(4)	S	0	(4)	–	60	(5)	F, I, S	25	(4)	T	100	(4)	I, S	0	(4)	–

% = percent of field logs where oil was present and conditions were suitable to see slicks; *N* = number of logs; *ND* = no data. *Type* = kind of oil present, – (no oil), *F* (black fluid in water), *I* (yellow to brown iridescence), *S* (silvery sheen), *B* (boat bilge from boat traffic), *T* (tar ball).

Fig. 9.21 Bands of residual oil stranded on mangrove roots. *A*. May 1989, site = SBCS. Two bands of fresh oil are visible; the upper one is on *Crassostrea* individual, the lower one is on bark. Live and dead oysters and traces of weathered oil also are visible.

Fig. 9.21 Bands of residual oil stranded on mangrove roots (continued). *B.* May 1989, site = SBCE. Multiple bands of oil are visible on this root, which entered the water in 1988.

Fig. 9.22 Oil on roots 4 yr after the spill. May 1990, site = PMRE. Oil from the original stranding was extremely weathered.

Fig. 9.23 Oil on roots 5 yr after the spill. June 1991, site = PAYR. The root shown here has both weathered oil (*top*) from the original spill and newer oil covered with a diatom film (*center*) from residual oiling. The shiny central portion is fresh oil under a diatom layer.

root surface (MHW to root tip) was covered by oil. Along the banks of streams (LRRS and LRRN), oil averaged 29.0 cm (range = 11-48 cm, $N = 49$) on roots; mean root length was 38.5 cm (range = 20-92 cm, $N = 76$). Seventy-five percent of root surfaces below MHW were oiled. Thus, 4 mo after the spill most of the wetted surface of prop roots of fringing *Rhizophora mangle* around Bahía Las Minas had been oiled.

Changes in Oiling Over Time – Open Coast

On the wave-washed open coast, cover of oil on roots remained high for the first year after the spill (Fig. 9.24). By August 1987, when sampling was expanded throughout the oiled area, oil covered <17% of root surfaces (range = 12-20%, $N = 4$ sites) around the mouth of Bahía Las Minas. Percent cover of oil at these sites dropped to <6% during and after the 1989 dry season, when wave action removed much weathered oil. Total cover was always <7% after August 1989 and was <3% by May 1991.

Although the cover of oil on roots decreased rapidly, the proportion of oiled to total roots sampled remained high over 5 yr. Overall, >40% of roots sampled still had some oil on them until November 1990; this proportion dropped to 35% in May 1991. Most of this oil was from earlier strandings; at oiled sites in May 1990, only 6 of 100 roots sampled ($N = 5$ sites) had "new" oil on them. In May 1991 all oil found was highly weathered ($N = 5$ sites, 100 roots total). The progressive disappearance of weathered oil from roots showed a vertical pattern, with oil first disappearing deeper on roots (Fig. 9.25). By 1991 oil occurred no deeper than 30 cm below MHW, in marked contrast to the complete coating of roots in 1986.

The frequency of episodic reoiling as measured by recruitment dowels on the open coast was affected by site location (Figs. 9.5, 9.24). DROM and PMM, on the central and eastern wings of the bay, had some dowels oiled in 12 of 14 and 8 of 14 quarterly periods between 1987 and 1991. MINM and PGM, both on the west wing of the bay, had some dowels oiled in only 4 of 15 and 4 of 14 quarters, respectively. DROM and PMM were close to two potential sources of reoiling: the refinery and the heavily oiled central bay (see below). MINM and PGM were more distant, and were upstream of the major reoiling sources (the prevailing along-shore current runs from west to east). Reoiling was variable among sites and over time, but the proportion of oiled dowels was generally low during dry season (February 1988, 1989, and 1990) and higher during wet-season months (Fig. 9.24).

In contrast to the relatively high frequency of reoiling events, secondary reoiling did not involve large amounts of oil. Percent cover of oil on dowels was >15% only in August 1988 at DROM, MINM, and PGM, and in May 1989 at MINM and PMM. All seven episodic oilings where mean percent cover was >10% occurred during rainy season, and probably resulted from washouts of oil from intertidal sediments. For example, beginning in February 1989, the seagrass bed at the stomatopod study site LRN began to blow out (Steger and Caldwell, Chap. 6) and may have been one source of oil deposited in May 1989.

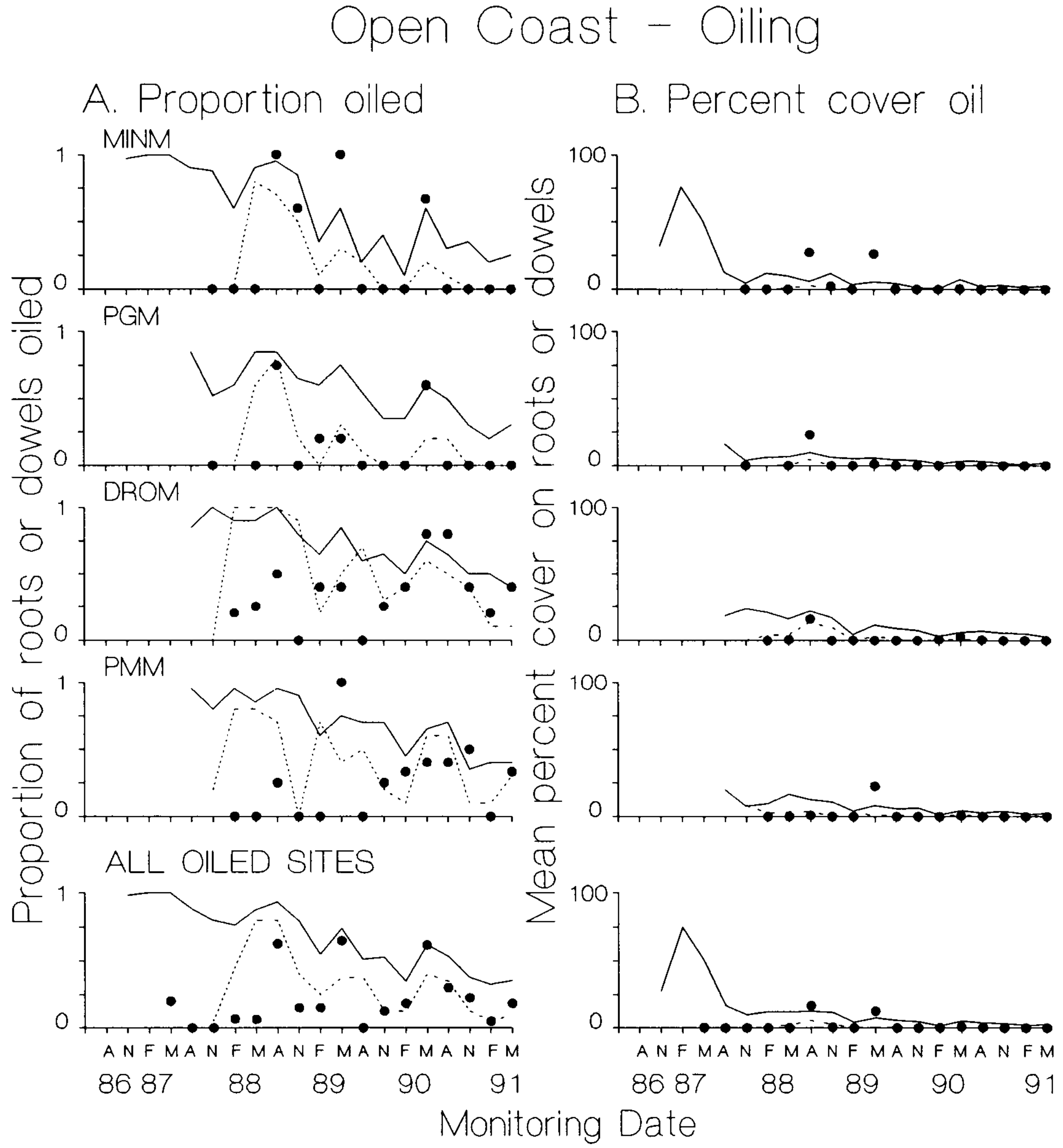

Fig. 9.24 Temporal patterns of oiling on open coast roots and dowels. *A.* Proportion of sampled roots or dowels with oil visible for each oiled site and all sites combined. Numbers of sites and sample sizes varied, see text for details. *B.* Percent cover of oil on root or dowel surfaces for each oiled site and all sites combined. *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

Community development roots all entered the water between September and early November 1987; more than 80% of these roots were oiled by May 1988 (Fig. 9.24). For the remainder of the study the proportion of oiled roots sampled from this

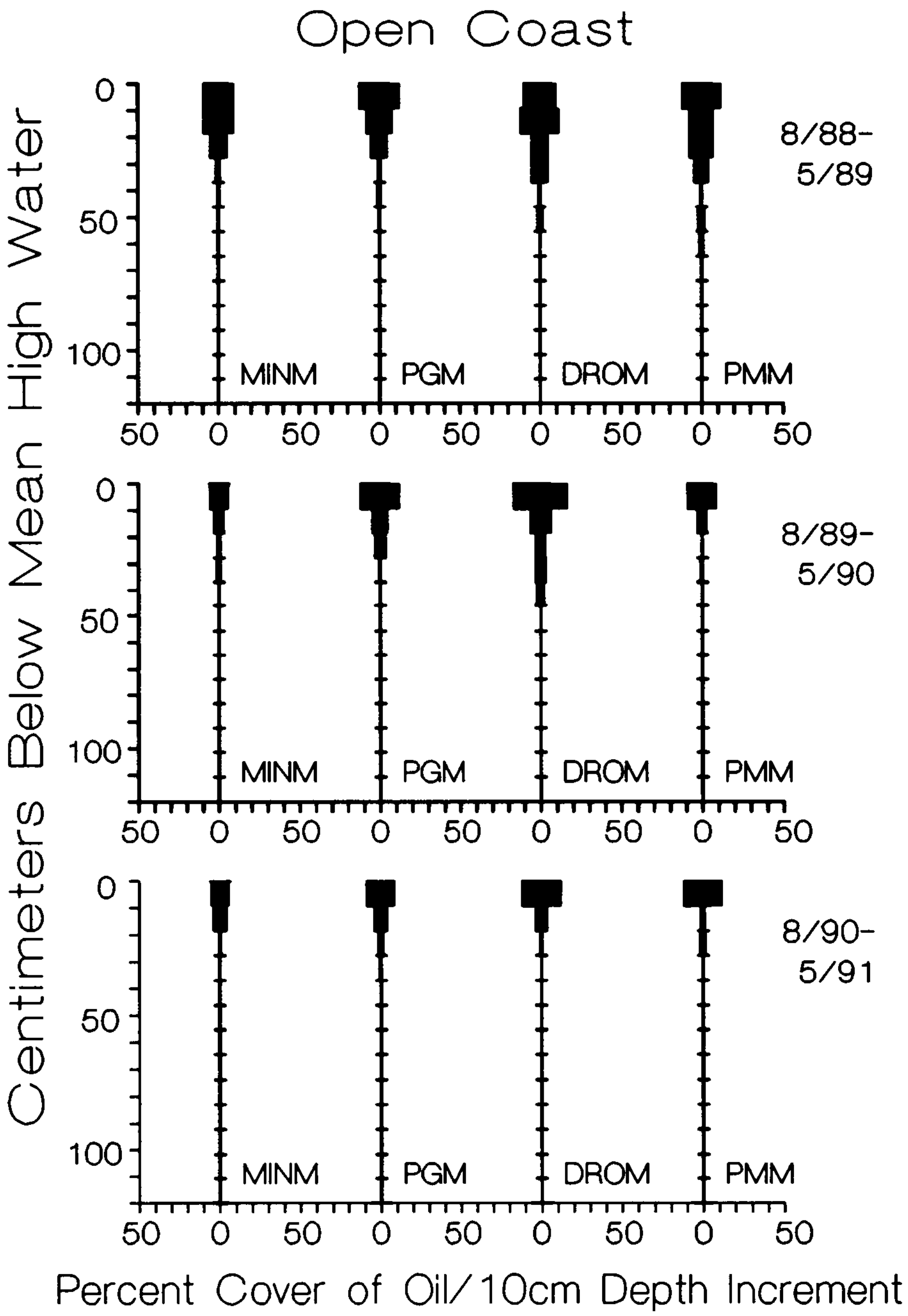

Fig. 9.25 Patterns of oiling with depth in yr 3, 4, and 5 on open coast, random-census roots. Data are mean percent cover of oil (x-axes) for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site. See text for further details.

cohort generally declined (similarly to long-term census roots) to ~10% by May 1991. Variation within sites was considerable, and ephemeral fluctuations upward were often correlated with increases in the proportion of oiled dowels. This association indicates that secondary releases probably washed off roots quickly (Fig. 9.24). Oil cover generally remained low on community development roots. The highest values recorded were in August 1988, at 3 of 4 sites, and were also correlated with relatively high cover of oil on dowels.

Changes in Oiling Over Time - Channels and Lagoons

The initial distribution of oil in channels and lagoons was uneven among the three wings of Bahía Las Minas. Oil was held in the central wing for 6 d by onshore winds (Cubit et al. 1987). Slicks then moved out to sea, spread along the coast, and were blown ashore over the next several weeks. All three wings of the bay were oiled during this time, but oiling was lighter and patchier in the western wing relative to the rest of the bay. For the first year after the spill we only examined oiled channels in the previously studied western wing (see Sect. 9.3). At these sites the average percent cover of oil reached 39% in November 1986 (Fig. 9.26); >95% of roots had at least some oil on their surfaces.

In August 1987 we added sites in the eastern and central wings of the bay. Overall percent cover of oil averaged 33% (range = 28-41%) and >95% of sampled roots were oiled. By dry season 1988 (February) mean oil cover dropped to <20% (range of 6-30%), but oil still occurred on 84% of all roots. Oil cover was higher (17-30%) in the central bay than in either wing (6-15%). Between May and August 1989 mean percent cover of oil dropped again by almost 50% (to ~10%) and 63% of sampled roots were oiled. Cover of oil on roots remained about twice as high in the central bay (11-17%) than in the eastern or western wings (6-9%). Oil cover averaged around 10% (all sites combined) until November 1990, when it dropped again by ~50%, and averaged <5% overall through May 1991.

In contrast, most roots had been in contact with at least some oil for 5 yr following the spill (Fig. 9.26). Overall, nearly 100% of long-term censused roots were oiled to some extent through November 1988. From February 1989 to May 1991 there was an overall decrease in oil occurrence from ~100% to ~60% of roots sampled. Fresh oil was more evident on roots in channels than on the open coast in May 1990 (4 of 5 sites) and 1991 (3 of 5 sites).

Vertical distribution data show oil occurred deeper on roots in channels than on the open coast (Figs. 9.25, 9.27). As on the open coast, oil disappeared first from deeper portions of roots. However, there was some reoiling at depth; we found fresh oil deeper than it had occurred the previous year at two sites (SBCE and LRCW).

Pulses of residual oil, monitored by the oiling of dowels, were frequent in oiled channels and lagoons (Fig. 9.26). One or more sites were oiled in 16 of 17 quarters (all but the one ending in November 1990). As on the open coast, site position affected the probability of reoiling. One or more dowels were oiled on 70%-

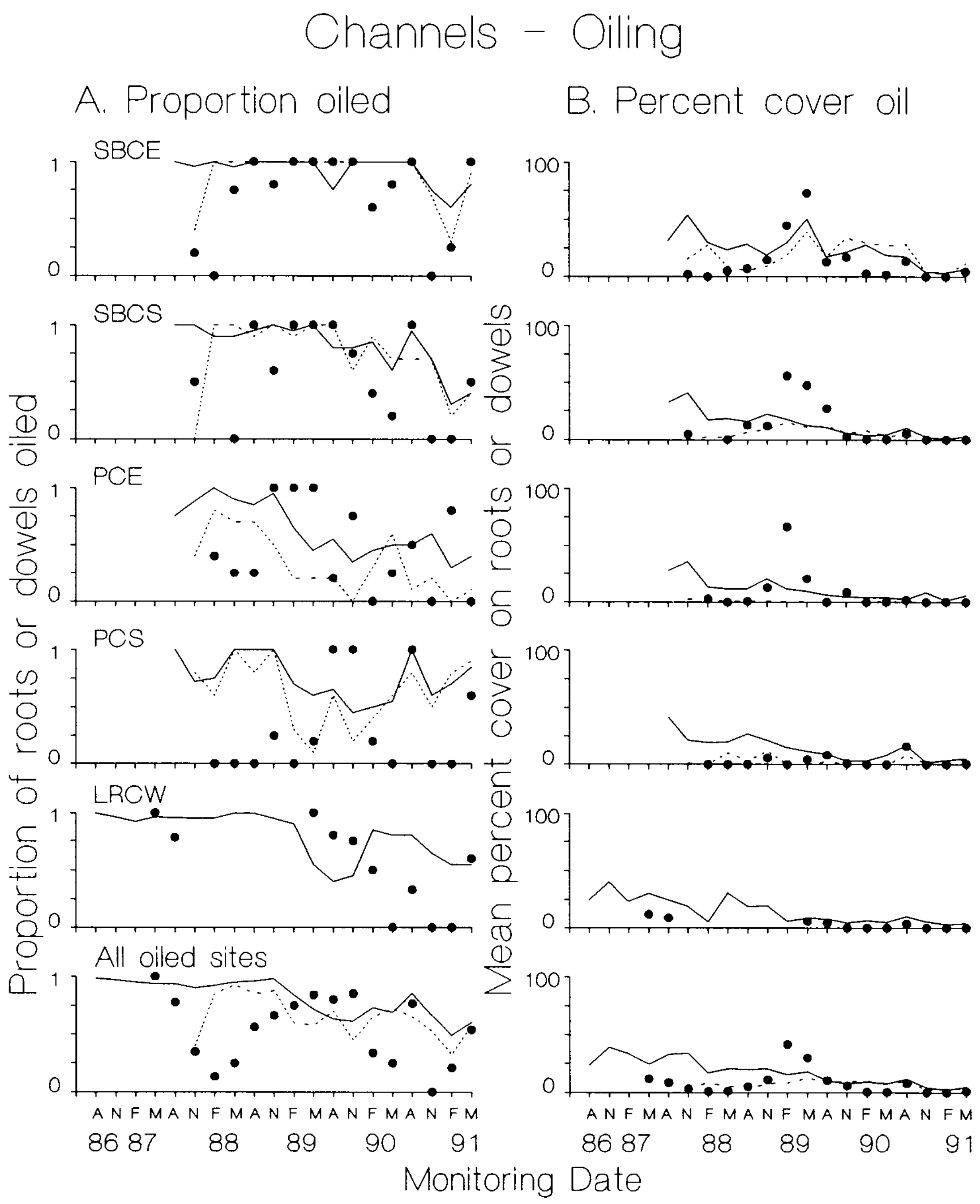

Fig. 9.26 Temporal patterns of oiling on channel roots and dowels. *A*. Proportion of sampled roots or dowels with oil visible for each oiled site and all sites combined. Numbers of sites and sample sizes varied, see text for details. *B*. Percent cover of oil on root or dowel surfaces for each oiled site and all sites combined. *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

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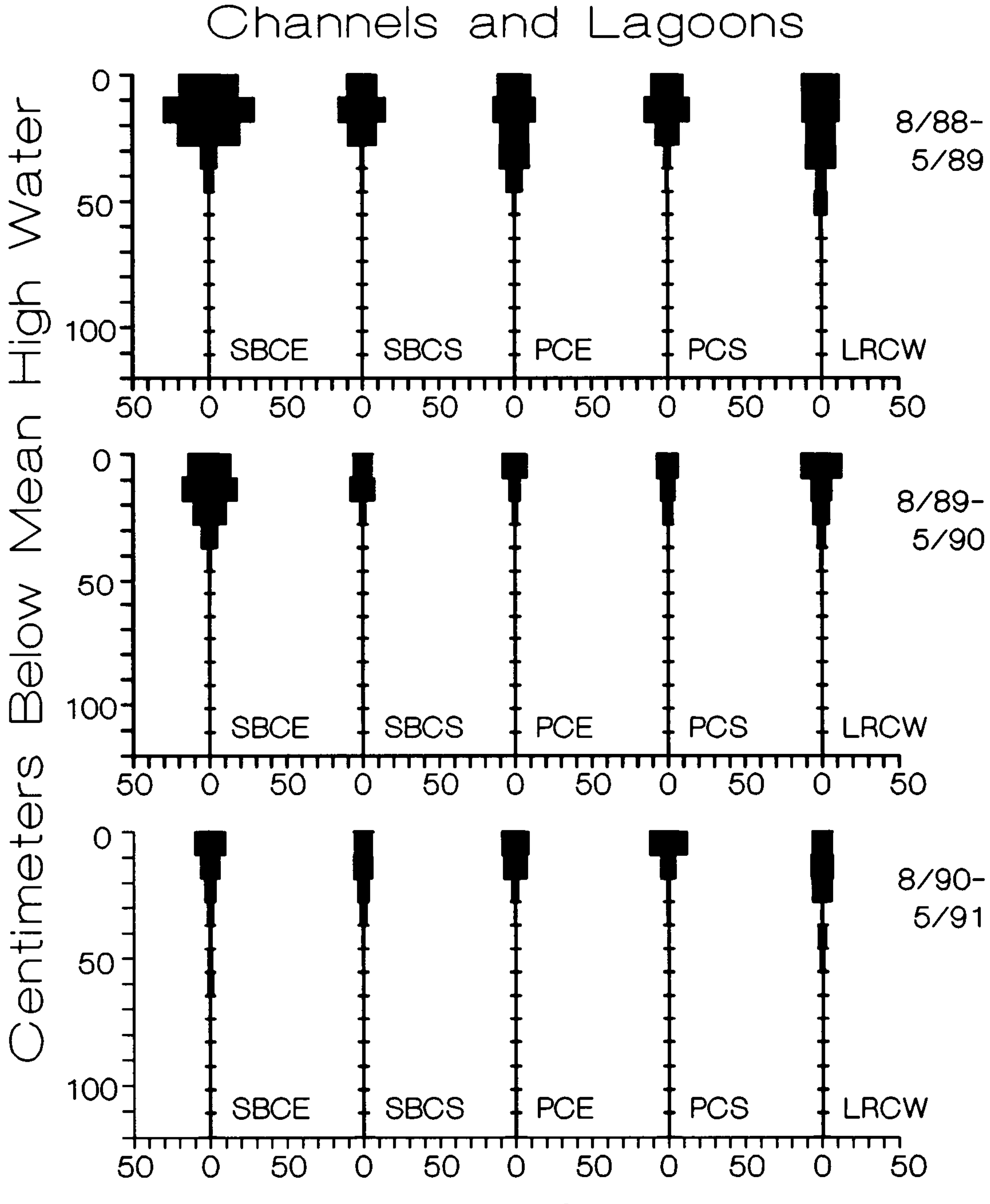

Fig. 9.27 Patterns of oiling with depth in yr 3, 4, and 5 postspill on random-census roots in channels and lagoons. Data are percent cover of oil (*x*-axes) for 10-cm increments on roots downward from MHW (*y*-axes) for 20 roots ≥75 cm long per site. See text for further details.

86% of dates at 4 of 5 sites, but oil was found only 50% of the time at PCS, deep within the eastern wing of the bay (Fig. 9.5).

The greatest amount of oil stranding on dowels occurred from February-August 1989 at 3 of 5 sites (SBCE, SBCS, and PCE). This oiling appeared related to the collapse and cutting of dead mangroves in the central bay, and subsequent washouts of oil. Between November 1990 and May 1991 oil on dowels averaged <5% cover, but >50% of all dowels set out in February had at least some oil on their surfaces in May 1991.

The community development cohort in channels and lagoons was quickly oiled after entering the water (Fig. 9.26); 93% of roots were oiled within 9 mo. Percent cover of oil increased through May 1989 at two sites in the central bay, with highest percent cover at SBCE (maximum of 34% in May 1989). In contrast, little oil accumulated in the eastern wing (maximum cover 2% at PCE, 12% at PCS). Increases in oil cover on these roots were associated with reoiling pulses, as measured by oiling on dowels (Fig. 9.26). Overall cover on cohort roots was <5% between November 1990 and May 1991.

A large release of oil (identified as VMIC; Burns, Chap. 3) came ashore along the fringe of a previously unoiled channel site between May and August 1988 (Fig. 9.28). HIDC, deep within the west wing of Bahía Las Minas, was not visibly oiled during the 1986 spill, although sediments contained traces of VMIC (Burns, Chap. 3). In August 1988 we observed sticky black bands of oil near MHW on roots (Fig. 9.28*C*). Some oil was found on 100% of random-census roots, community development roots, and recruitment dowels in August 1988. The mean cover of oil was 14% on randomly censused roots, 30% on community development cohort roots, and 6% cover on dowels. The cover of oil at HIDC dropped rapidly on randomly censused roots, never reaching 3% in subsequent monitoring (Fig. 9.28*B*). Declines in oil were also rapid on the community development cohort; cover dropped to <1% within a year. No oil was recorded on dowels before or after August 1988 at this site. Only weathered oil was found on randomly censused roots in May 1990 and May 1991 surveys. No oil was recorded deeper than 20 cm below MHW after August 1989.

We examined the entire mangrove fringe of the west arm of Bahía Las Minas to trace the path of this oil. Fresh oil was found only along the western shore of the pass between Peña Guapa and the mainland, from HIDC out to MINM (where we also found evidence of fresh oiling in August 1988; Fig. 9.24). It appears likely that this pulse of oil originated in heavily oiled sediments shoreward of the fringe at MINM. Heavy rains during low tide followed by an incoming tide or northerly winds would have moved oily runoff toward HIDC along the path where we found evidence of fresh oiling (Fig. 9.5). Oiling also occurred during the period of extreme exposures (low tides) in 1988 (Cubit and Connor, Chap. 4), which may have exacerbated the process. All evidence suggests that oiling at HIDC was a one-time event (see also bivalve data in Burns, Chap. 3), unlike the more chronic hydrocarbon contamination in oiled channels.

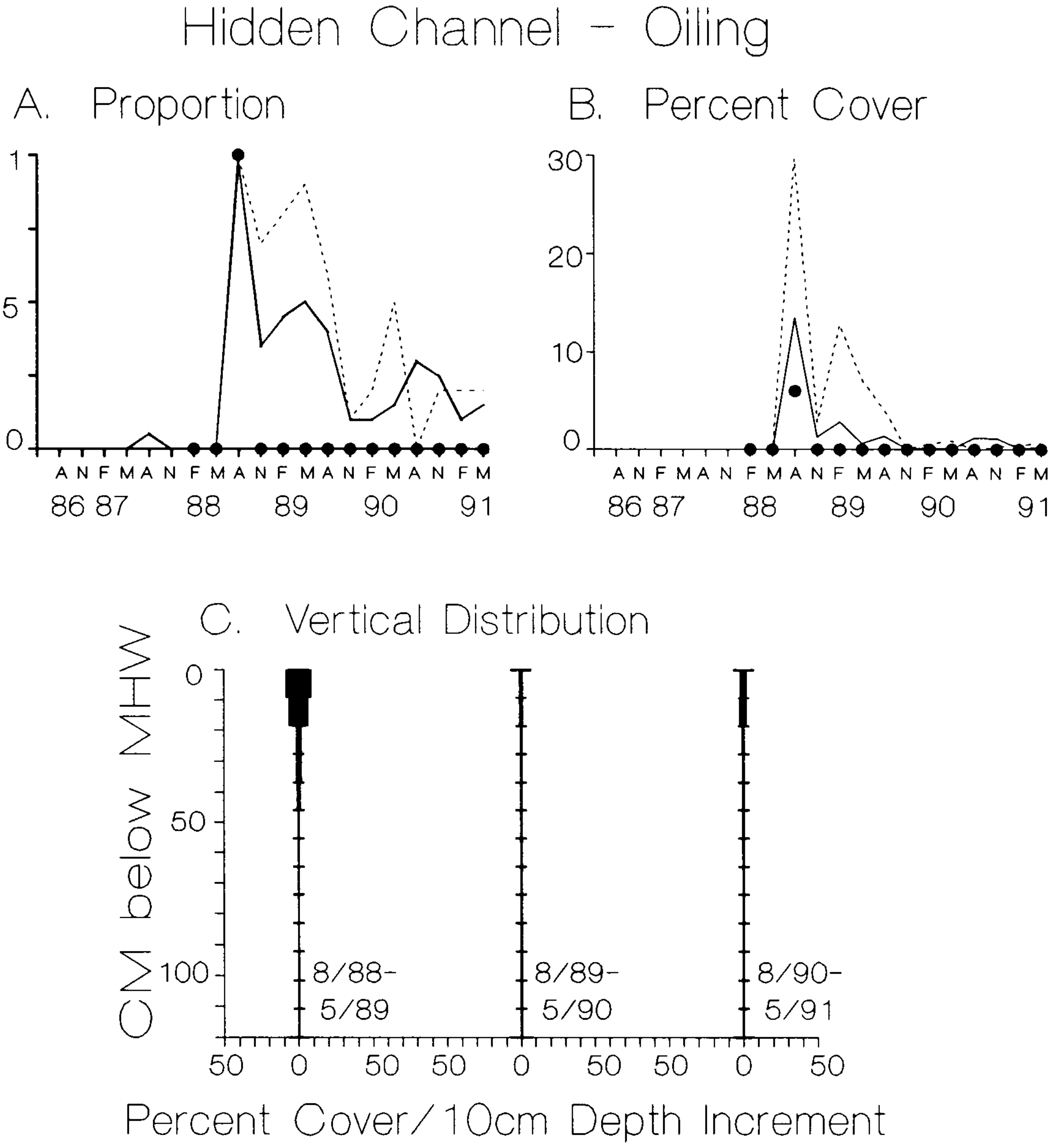

Fig. 9.28 Oil abundance, occurrence, and vertical distribution in a secondarily oiled channel. Hidden Channel (HIDC) was a control site until it was oiled with VMIC between May and August 1988. *A*. Proportion of sampled roots or dowels with oil visible; at each date, *N* = 20 random census, 10 community development cohort, and ~5 recruitment dowels (recovery of the five that were set out varied). *Solid lines* are long-term census roots, *dashed lines* are community development roots, and *solid circles* are recruitment dowels. *B*. Percent cover of oil on roots and dowels, as in *A*. *C*. Vertical distribution of oil on random-census roots in yr 3, 4, and 5 postspill. *N* = 20 roots ≥75 cm long each year. See text for details.

Changes in Oiling Over Time - Drainage Streams

Drainage streams were heavily oiled during the spill, and repetitively reoiled through May 1991 (Fig. 9.29). Ninety percent or more of roots monitored in random censuses were oiled, except in November 1990 and February 1991. Overall, percent cover of oil on roots decreased slowly; it averaged >50% until February 1989 (2.75 yr after the spill). Mean oil cover remained above 20% until November 1990. By May 1991, 98% of roots still had some oil on their surfaces; its overall mean cover was 20%. In both May 1990 and May 1991 fresh oil, or a combination of fresh and weathered oil, was found on all but a few roots (N = 80 roots/date, 4 sites). As on the open coast and in channels, oil cover first decreased deep on roots (Fig. 9.30).

The community development cohort (three sites, none marked at LRRS) entered the water between August and November 1987; cover and occurrence of oil on these roots reached levels similar to random-census roots within 6-12 mo, then closely followed changes on randomly censused roots (Fig. 9.29).

Reoiling pulses, recorded quarterly on dowels, were constant at oiled sites until November 1990 (Fig. 9.29). The proportion of dowels oiled was higher and less variable over time than in the other two habitats, except for LRRS, where a few dowels were unoiled as early as May 1988. For all sites combined, percent cover on dowels was >50% through May 1989. Starting in August 1987, oil cover was relatively low on dowels at LRRS and PMRE, but remained high and variable through August 1990 at PAYR and PMRW. Both percent cover and occurrence of oil were low at all sites in 1991, especially in the last 6 mo of the study.

9.4.3.3 Presence of Oil Slicks

The presence or absence of oil slicks off each study site was recorded at least once during each quarterly monitoring, weather and waves permitting (Table 9.3; Fig. 9.31). Slicks at oiled sites were observed on 92.7% of visits where conditions were suitable for observation (N = 316, all habitats combined) through May 1991. Over time, slicks were found less frequently on the oiled open coast, and were characterized as iridescent or silver sheen rather than black oil after August 1989. Slicks were seen at only 5 of 9 visits in May 1991. In channels and lagoons the frequency of slicks did not decline (96% of 22 visits in May 1991), and some black oil was still found in May 1991. In drainage streams oil slicks were seen on 128 of 129 visits between August 1987 and May 1991, and ranged from black oil to iridescent patches.

9.4.3.4 Sources of Oil Recorded as Secondary Oiling

Likely sources of most new oil seen during the study include (1) oil leached from heavily oiled, intertidal mangrove sediments around Bahía Las Minas (Fig. 9.32; App. Table E.1) and (2) oil gradually released from pools of oil in fill under and

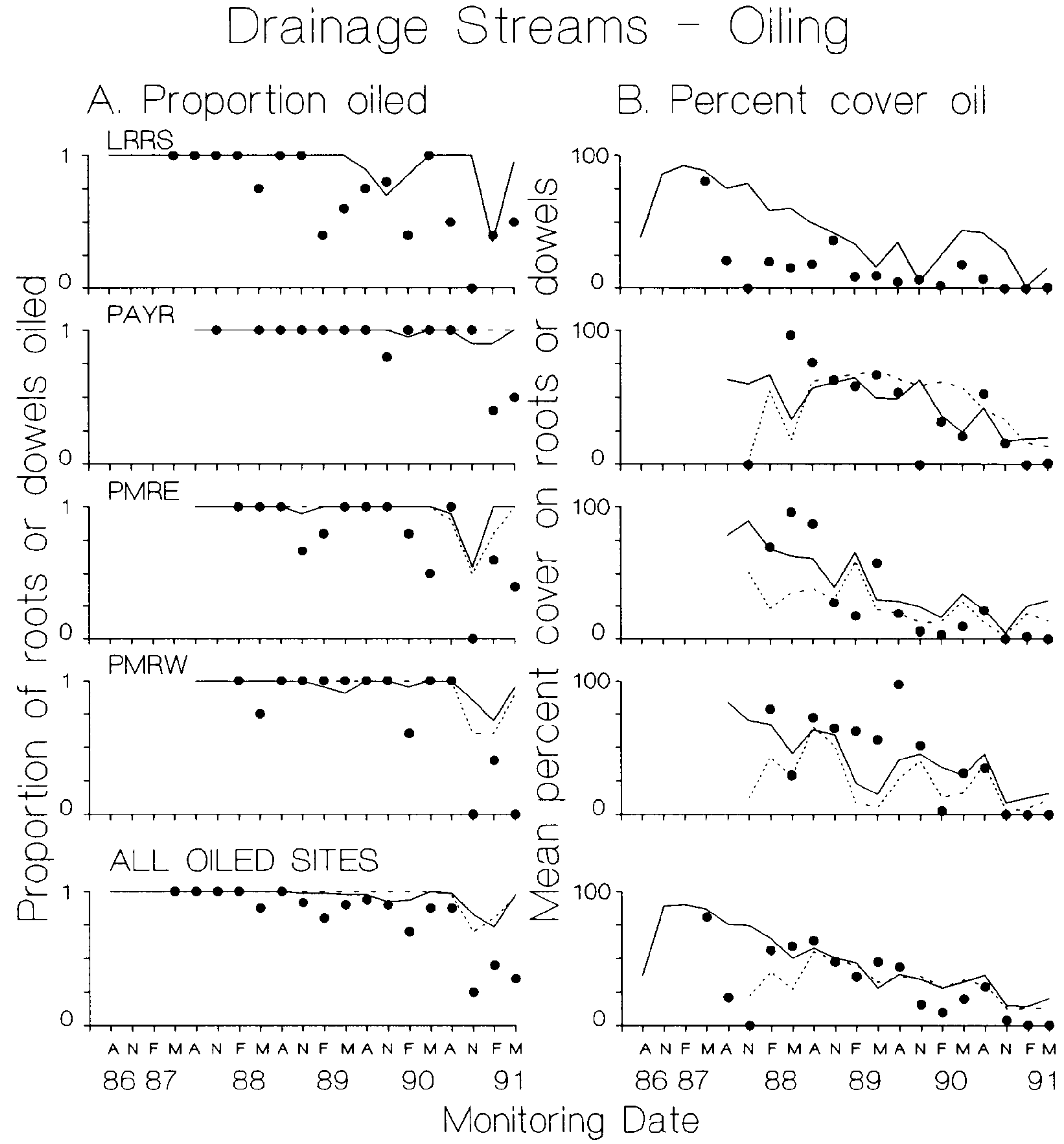

Fig. 9.29 Temporal patterns of oiling on roots and dowels in drainage streams. *A.* Proportion of sampled roots or dowels with oil visible for each oiled site and all sites combined. Numbers of sites and sample sizes varied, see text for details. *B.* Mean percent cover of oil on root or dowel surfaces for each oiled site and all sites combined. *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

around the collapsed storage tank on Isla Payardí. These are secondary releases of the oil originally spilled in 1986.

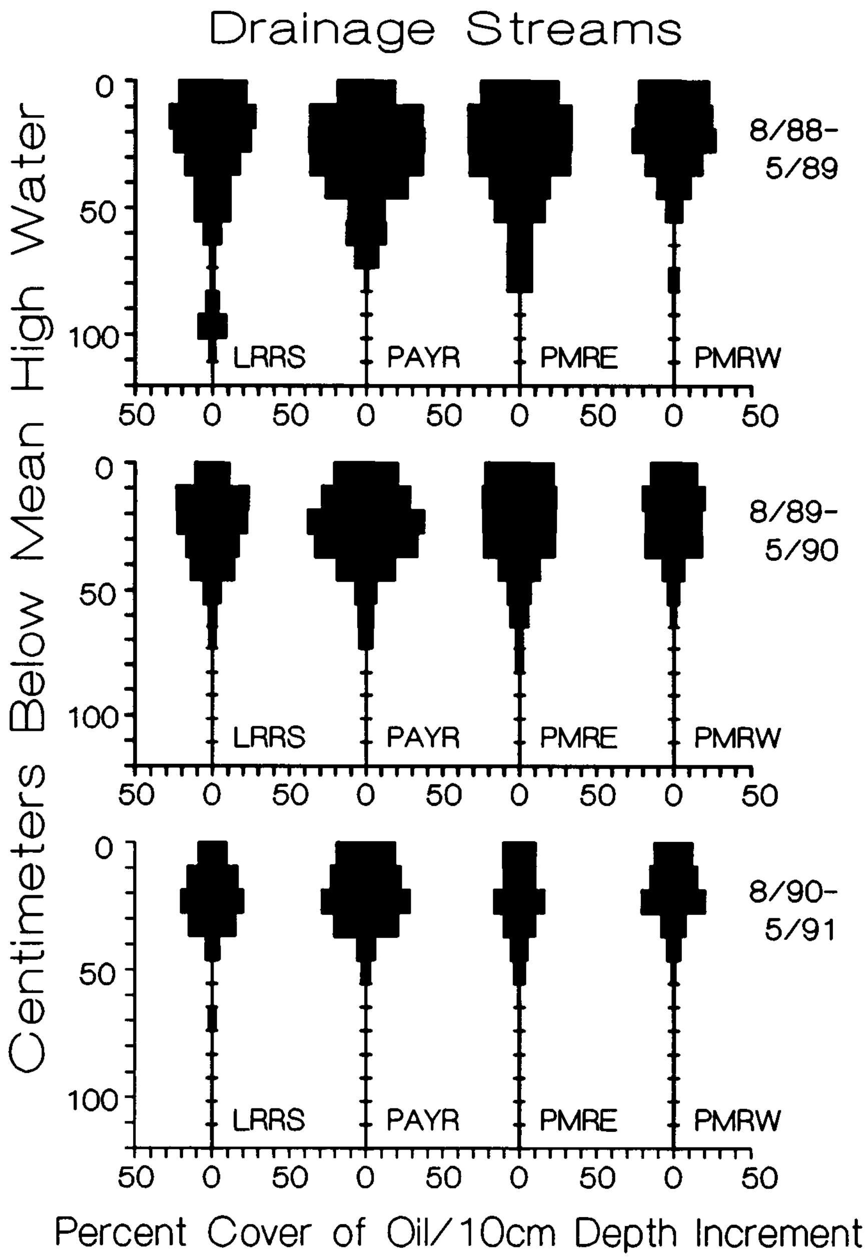

Fig. 9.30 Patterns of oiling with depth in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are percent cover of oil (x-axes) for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long at each site. See text for further details.

Fig. 9.31 Large iridescent oil slick. November 1988, Bahía Las Minas, central wing, between Isla Largo Remo and Isla Payardí. This slick covered the entire width of the bay.

Fig. 9.32 Oil in sediment cores 3-5 yr after the spill. *A.* May 1989, site = PMRW. Large quantities of black oil seeped into the core hole after the core was removed.

Oil seepage from Isla Payardí, especially after periods of heavy rains, resulted in large slicks in the bay in front of the refinery (Fig. 9.31). Oil in sediments was released in at least four ways (see also Duke and Pinzón, Chap. 8). First, water movement suspended surface oil residues and moved them throughout the estuary. Second, death and decay of mangroves after oiling led to increased erosion. As the root mat decayed, sediments eroded and oil trapped in them was released into the water (Fig. 9.33). Third, the felling of dead mangroves, trampling, and, especially, digging associated with replanting activities (Teas et al. 1989) disturbed sediments saturated with oil. Based on the number of propagules or young trees planted and the reported size of the holes, at least 340 m^3 of oiled sediment was dug and left lying on the surface. Fourth, embedded, dead roots acted as oil conduits from deep sediments to the surface (Fig. 9.34).

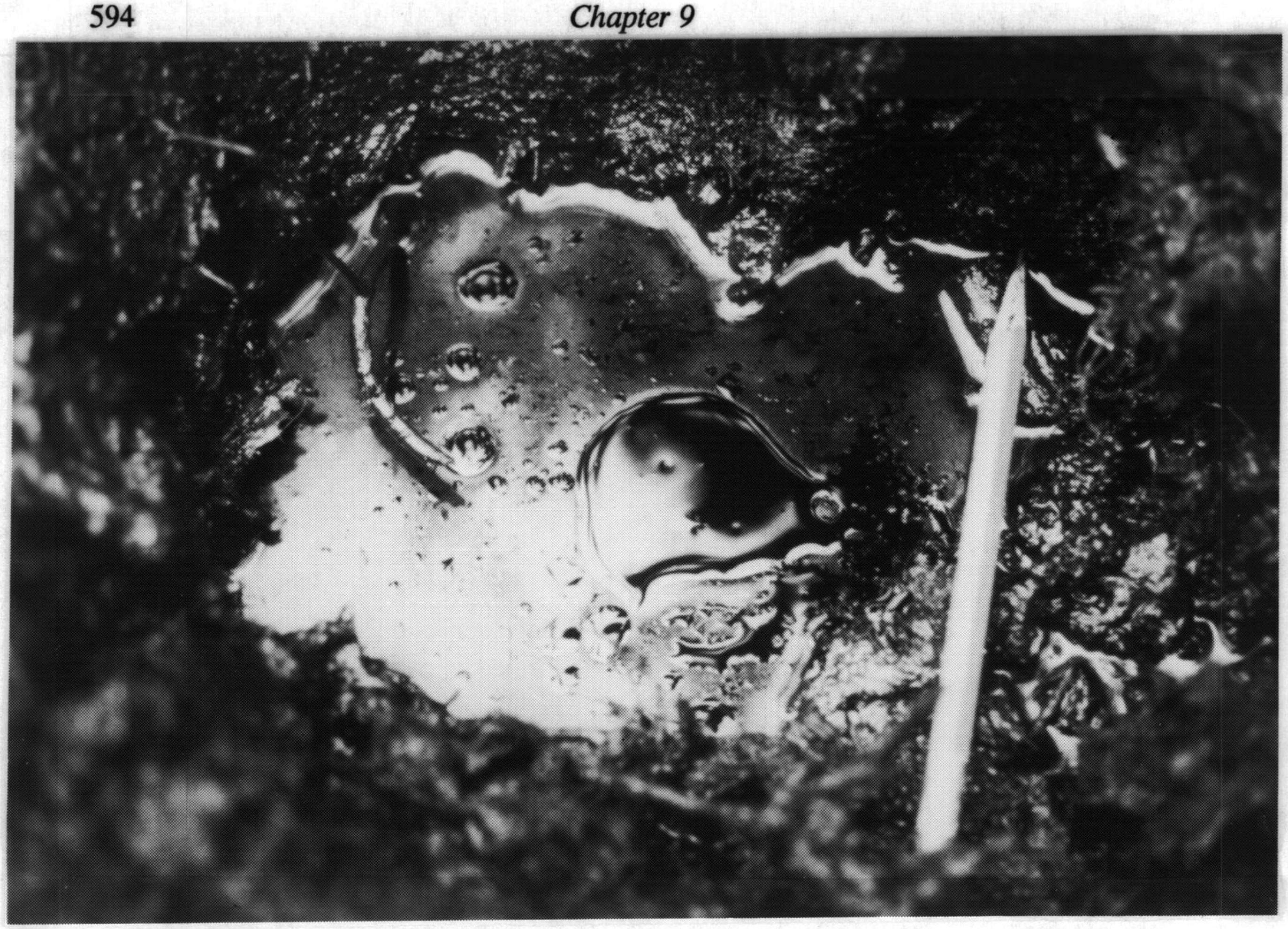

Fig. 9.32 Oil in sediment cores 3-5 yr after the spill (continued). *B.* June 1991, site = PMRE. Black oil seeped into the hole from its edges after the core tube was removed.

9.4.4 Summary

Oil persisted in mangroves, and on the waters surrounding them, through May 1991. Initial oiling was heavy – nearly all roots sampled in each habitat were oiled in the first year after the spill. Oil coated roots for essentially their entire length in August 1986, often in layers up to 1 cm thick. The persistence of oil on roots, measured as the proportion of sampled roots coated by oil each quarter, was greatest in streams, intermediate in channels, and least on the open coast. The abundance of oil, measured as percent cover of oil on sampled roots each quarter, showed a similar pattern over time, dropping off particularly rapidly on the wave-exposed, open coast. Decreases in oil cover resulted from weathering, microbial degradation, loss of bark (and thus of oil on bark), loss of organisms coated with oil, and overgrowth of oil by epibiota. Oil disappeared first from deep parts of roots, but still occurred near MHW (or deeper, especially in streams) in 1991.

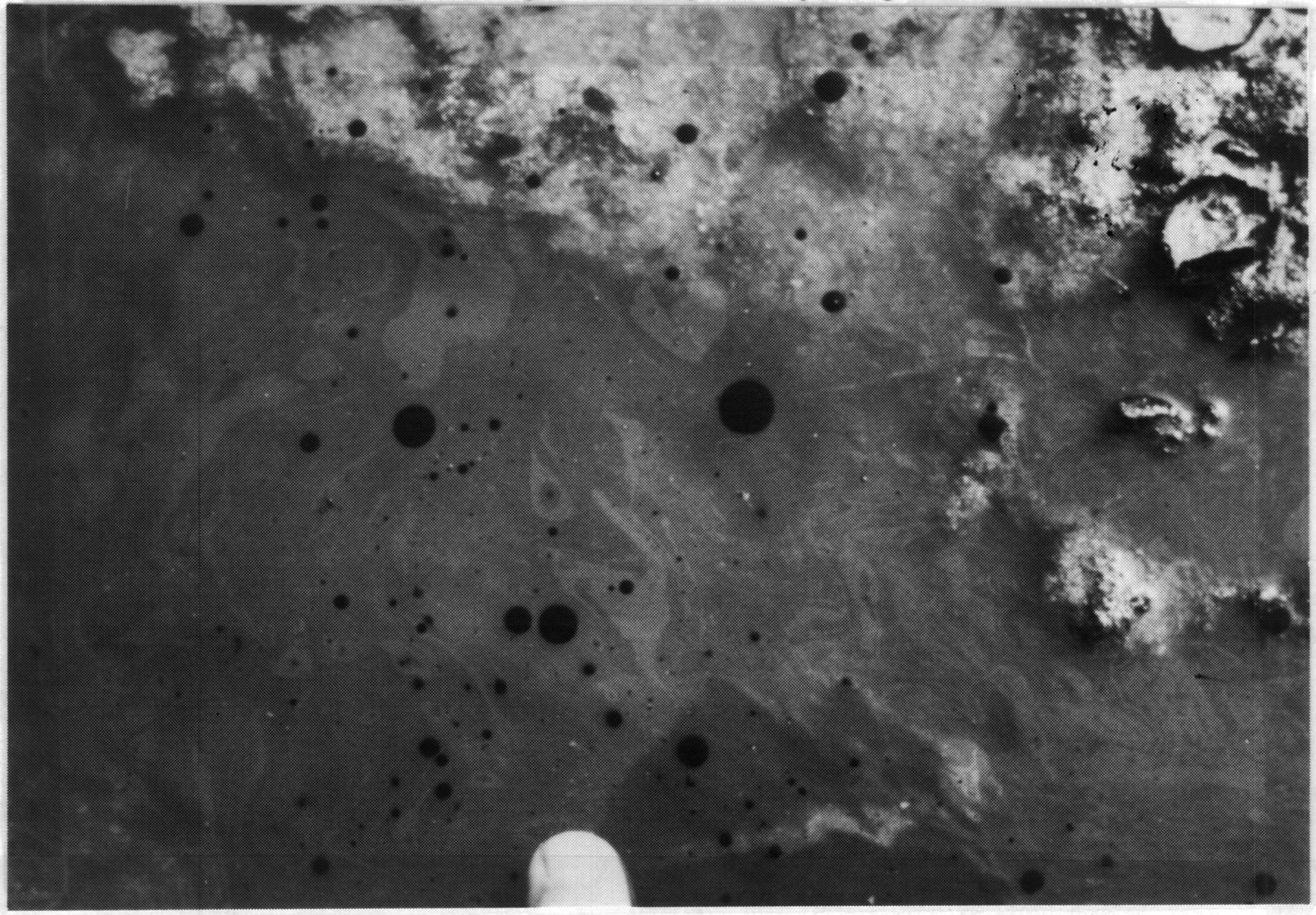

Fig. 9.33 Oil in open coast sediments 5 yr after oiling. June 1991, site = DROM. Black globules and iridescence floated to the surface if sediments were disturbed. *Right*, fingertip = 2 cm wide; circular objects in the *upper right* are remains of rotted, embedded prop roots.

There was considerable reoiling of mangrove roots. Data from both community development roots (which entered the water 15-18 mo after the original spill) and recruitment dowels (which were set out fresh quarterly and collected after ~2.5 mo) suggested that roots in oiled streams were nearly constantly reoiled, while those in channels and on the open coast experienced episodic reoiling, particularly during rainy season. In streams, all community development roots were oiled within 3 mo. About 75% of such roots in channels were oiled within 6 mo, and on the open coast within 9 mo. The proportion oiled rose and fell similarly for randomly censused and community development roots within each habitat. This observation suggested the oil on long-term roots was a mixture of original, increasingly weathered oil, and newer oil from reoiling events. In addition, roots in the water at the time of the spill were gradually replaced by new roots, exposed only to secondary releases. Observations in May 1990 and 1991 support this hypothesis. The cover of oil on

Fig. 9.34 Oil in decaying, embedded mangrove roots. June 1991, site = PCS. The photograph shows a section of a peat plug from a core hole; the shiny black fluid is oil inside a dead remnant of an embedded prop root.

community development roots did not exceed 10% in channels and on the open coast, but reached as high as 55% in streams.

Oiling of dowels measured the relative frequency and amount of oil stranding in the mangrove fringe during successive quarterly intervals from February 1987 to May 1991. From 70 to 100% of all dowels at oiled streams were oiled through August 1990; the proportion dropped sharply over the last three quarters. Percent cover of oil varied, but generally decreased over time, from 80% in May 1987 to <1% in May 1991.

The proportion of oiled dowels in channels remained high through August 1990, except for February and May 1988 and 1990. After August 1990 oiling was highly variable through May 1991. Percent cover of oil on dowels averaged <15% except in February and May 1989, when it exceeded 30%. This increased reoiling in February and May 1989 (especially in the central wing of Bahía Las Minas) was coincident with cutting of oiled channels by refinery workers, as well as the increasing collapse and uprooting of dead trees in oiled channels and subsequent erosion of the substratum.

On the open coast ≤25% of dowels were oiled each quarter, except in August 1988, May 1989, May 1990, and August 1990, suggesting increased oil strandings during early and mid-rainy season. Oil cover always averaged <20% of the surface of dowels on the open coast.

The above evidence points to the episodic emergence of oil from sediments, either following heavy rains (in channels and streams) or following periods of high water and wave action (on the open coast) as a major, continuing source of reoiling. Hydrocarbon collections and chemical analyses support this and, more importantly, identify the oil (see Burns, Chap. 3). A sample of oil from the secondary oiling of a channel control site (between May and August 1988, HIDC) was identified as VMIC. Observations and later analysis of sediment cores (Burns, Chap. 3; App. Table E.1) and of quarterly collections of sentinel organisms show that organisms and sediments remained heavily oiled, primarily by VMIC, through May 1991 (see Burns, Chap. 3). Most oil in these samples was degraded considerably, but oil from a core collected in an oiled stream in May 1991 still had low-molecular-weight fractions typical of freshly spilled oil. This finding shows oil trapped in mangrove sediments degrades more slowly than previously believed and is potentially toxic 5 yr after the spill (Burns, Chap. 3; Burns et al. 1993).

9.5 Components of Research

9.5.1 Introduction and Rationale

Detailed results of our study are presented in the following sections. The four major subsections include: (1) the mangrove fringe and substratum for the epibiota, (2) the epibiota of mangrove roots, (3) the biology of *Mytilopsis sallei*, and (4) experiments on salinity tolerance of bivalves and barnacles. Each section is followed by a discussion of the results.

First, we consider the mangrove fringe and how it physically changed after oiling (Sect. 9.5.2). We focused primarily upon the characteristics of importance to the epibiota. These include (1) the time course of death and collapse in the fringe, and amounts of defoliation (including changes in canopy interception of light), (2) habitat loss, that is, reduction in the extent of the fringe, and (3) changes in the substratum (roots), including density, size, and condition of mangrove roots within surviving fringe.

The second major section presents patterns of change in epibiotic assemblages on surviving mangrove roots in oiled areas compared to unoiled areas (Sect. 9.5.3). This section factors out effects of habitat loss and examines the direct and indirect long-term effects of oiling where partial survival of trees left substratum for epibiotic attachment.

In the third and fourth sections we consider some mechanisms that might have caused the patterns we observed. Section 9.5.4 presents a series of investigations into the biology of *Mytilopsis sallei*, a species that had not returned to oiled areas 5 yr after the spill. In Section 9.5.5 we present preliminary salinity-tolerance experiments on barnacles and bivalves from Bahía Las Minas.

9.5.2 The Mangrove Fringe as Substratum

Submerged prop roots of *Rhizophora mangle* are a living and, thus, variable substratum for attached organisms. The condition of the mangrove fringe itself, including extent, canopy condition, and root density, all have potential effects on the epibiota. Roots enter the water and grow at variable rates. Damage may slow elongation or result in the production of multiple tips. Roots eventually penetrate bottom sediments or break off. Each site's "population" of roots has an age structure and history of damage, which may change through time. There may also be among-habitat differences that relate to the distribution and abundance of the epibiota.

Oiling could alter the density, size, growth rate, or condition of roots, with correlated effects on the epibiota. For example, plants and animals growing on roots are a mixture of intertidal and subtidal species. If roots were shorter at oiled than unoiled sites, less substratum would be submerged at subtidal levels at oiled sites, with less area for attachment of species requiring constant submergence. Reductions in cover could then be due to habitat alteration, not to direct effects of oiling on individual species. It thus was important (1) to ask whether the mangrove fringe itself was in an equivalent state at oiled and unoiled sites throughout the 5 yr of our study and (2) to consider different levels of damage assessment based upon the results.

9.5.2.1 Materials and Methods

Site Sizes and Physical Condition of Fringe

Effects of oiling at the forest and tree level were investigated elsewhere (Jackson et al. 1989; Duke and Pinzón, Chap. 8). We monitored aspects of the trees and their prop roots along the outer mangrove fringe that were of relevance to the epibiota.

Quarterly photographs and field notes qualitatively documented deterioration (defoliation, tree fall, etc.) at oiled sites. We used these data to estimate the relative amount of fringe in different conditions (healthy, defoliated, etc.) over time. Defoliation was estimated as the percent of trees totally leafless on a five-point scale: (1) <10% (background), (2) 11-25% (light), (3) 26-50% (moderate), (4) 51-76% (heavy), and (5) >75% (very heavy-total). We use this information to describe the progression of oiling effects on the mangrove fringe.

Study sites were initially measured in May-August 1987. The ends of each site were marked; subsequent sampling took place within these lengths of shore. A transect tape was run the length of the fringe at each site and total fringe consisting of red mangrove recorded. Non-*Rhizophora* fringe (other plants, sand beaches, etc.) was not counted.

Depths were measured at all sites. Fifty positions (anchored roots) along the shore were flagged at the high water line (HWL), and the vertical distance from each tag to the sediment was measured with a meter stick or weighted meter tape. These measurements (1) gave a depth profile for each site and (2) acted as an easily visible set of reference points of the HWL for field monitoring of hanging roots. Depths were monitored in 1989; results are summarized in Appendix Table E.2.

The extent and physical condition of the mangrove fringe were measured at all sites in May 1991. A transect tape was laid out as before along the edge of each site; the type and condition of the fringe were recorded for each meter. We also recorded the presence or absence of *Rhizophora* forest behind the fringe to the berm or shoreline. Categories of *Rhizophora* fringe were: *mature* (≥2.5 m high); *new* (embedded propagules and saplings); *dead* (fully defoliated, collapsed, or gone but with the substratum pocked with root holes and remnants, presence verified by site photographs taken prior to the destruction of the fringe); and *damaged* (live trees with partial defoliation or some defoliated or dead limbs). We also measured the length of shore represented by non-*Rhizophora* fringe.

Density of Roots

The present abundance and potential future provisioning of roots were compared for oiled and unoiled sites in June 1991. Root density was estimated at 10 randomly chosen points on the shore along each site. At each point a three-sided 0.25-m^2 quadrat, open side in, was thrust into the fringe until a root was touched by the back of the quadrat. Roots within the quadrat that were submerged at least 20 cm, but not yet attached to bottom sediments, were counted. Live and dead roots were recorded separately. To sample future abundance of roots, we recorded the number and status of roots within the quadrat but not yet submerged (i.e., above the quadrat).

The Physical Condition and Size of Roots

The length and diameter at HWL of each mangrove root monitored for percent cover were recorded quarterly. As defoliation of trees and deterioration of prop roots became evident in oiled areas, root condition was monitored. In February 1987 random samples of roots in each habitat were selected independent of other monitoring. In May and August 1987, data were collected for roots sampled for percent cover, but recorded separately. After November 1987 root condition was recorded along with percent cover for each root. A three-letter code separated roots into two approximate age categories: *old* (entered the water >1 yr previously) and *new* (entered the water within the last year). Estimates of age were based on the color and surface structure of the root. New roots were reddish-green, flexible, and thin; old roots were thickened, rigid, and had a grayish-brown, textured surface. The physical condition of roots was also recorded. This included the presence of breaks, the number of actively growing tips, and whether the root appeared live (firm, covered with bark) or dead (rotted or spongy, with partial bark loss, and visible cover of fungus, bacteria, teredo tubes, or a combination of these). Examples are shown in Figure 35*A-D*.

Root Growth

Root growth was examined quarterly for 1 yr. In either February or May 1990 25 randomly selected roots that had not entered the water were individually marked (with numbered plastic tags attached with cable ties) at all sites except PAYR (Fig. 9.36). We recorded each root's type (aerial or lateral), length from point of initiation, and physical condition. We searched for numbered roots quarterly for a year, and recorded root length on each one found. We also noted when the root entered the water or became attached to the bottom, any development of epibiota, and any evidence of herbivory or disturbance. We defer analyses of these data.

Light Interception

We assessed light interception indirectly by measuring the amount of light reaching through the canopy to the high water line (HWL), and then comparing oiled to unoiled sites. This was also a quantitative measure of defoliation in the fringe. Light intensity may have direct and indirect effects on the epibiota of mangrove roots (i.e., algal abundance, heat, and desiccation stress). At each site, on nonovercast days from 1000 to 1400, 20 pairs of light-meter readings (in lux) were taken. Each pair consisted of one reading out in the open and the other next to a hanging root along the fringe. The ratio between the two indicated relative shading. Light intensity was monitored in December 1988, December 1989, and February 1991.

9.5.2.2 Results

Structure of the Outer Mangrove Fringe

Unoiled Sites

For all three habitats mature *Rhizophora* was the major component (88-99%) of the outer fringe at unoiled sites (Tables 9.4-9.6). On the unoiled open coast *Rhizophora* was the only species along the outer fringe of our study sites, but more (5-15%) of the fringe was damaged (Fig. 9.37). Buttonwood (*Conocarpus erectus*) or coconut palm (*Cocos nucifera*) occurred shoreward of the outer fringe at some sites. The mangrove fringe in unoiled channels averaged >99% mature *Rhizophora*, with small patches of new (MACS) and damaged (MACS and MACN) red mangrove. White mangrove (*Laguncularia racemosa*) occurred along ~6% of the bank at HIDR

Fig. 9.35 Variation in root condition. Photographs are examples of root conditions. *A*. June 1991, site = SBCE. This root entered the water between February and June 1991. Its condition code is *NB* (new root, broken/bored tip). The round holes in root are from isopods; the bivalve attached to a root is *Crassostrea*.

Fig. 9.35 Variation in root condition (continued). ***B.*** **May 1990, site = PMRE. An aerial root, barely below MHW level. Root condition code is** ***NB5*** **(new root with broken tip with five actively growing new tips).**

and 12% (along with *Pelliciera rhizophorae*) of the fringe at MERR. Patches of dead or damaged red mangrove (~3-8% of the fringe) were found at 3 of 4 unoiled streams.

Overall lengths of sites did not vary more than several meters between 1987 and 1991 measurements, except as noted in Tables 9.4-9.6. We measured the relative amount of damaged or dead fringe among sites for unoiled open coast and drainage streams in May 1991 (damaged fringe in channels was too rare to test). There were significant among-site differences in structure both in drainage streams and on the open coast (*G*-tests, $P < .001$, 3 df, all tests; Tables 9.4-9.6; App. Table E.3). On the open coast some fringe was damaged at all sites, with greater damage (~15%) at PADM and PBM than at MSM or LINM (5-7%). Logs and entire trees came ashore during the study and damaged prop roots (Fig. 9.37; see also Birkeland et al. 1976). Damaged fringe in unoiled drainage streams ranged from none (UNR) to 8.7% of trees along the bank (ALER). Damage resulted from lightning strikes, treefalls, or cutting (S. D. Garrity, pers. obs.; Fig. 9.38).

Fig. 9.35 Variation in root condition (continued). *C.* May 1990, site = PCE. An oiled, lateral root that had broken and appeared dead, but grew a new tip between February and May 1990. Root condition code is *BR1* (note lesion high on root and the remains of an earlier "new" tip).

Fig. 9.35 Variation in root condition (continued). *D.* June 1991, site = LRCW. Root was oiled during the spill, subsequently broke, rotted, lost bark and tissue, and was invaded by teredo. Condition code = *BR* (broken, rotted). White center of root is a calcareous tube of teredo.

Fig. 9.36 Root growth. May 1990, site = LRCW. A newly emerged lateral root, marked (Dymo tag attached with plastic cable tie) to follow root growth over time. Growth was examined for roots both in and out of the water.

Table 9.4 Characteristics of the outer mangrove fringe on the oiled and unoiled open coast.

	Oiled					Unoiled				
	MINM	PGM	DROM	PMM	Mean	MSM	PBM	PADM	LINM	Mean
Length (m) 1987	330[1]	351	245	357	322	207	399[1]	280	289	294
Length (m) 1991	259	327	244	361	298	198	306	283	308	274
Percent of total in 1991:										
Mature *Rhizophora*	81.5	22.3	21.3	19.7	36.2	91.4	83.7	84.1	92.5	87.9
New *Rhizophora*	0.0	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Dead *Rhizophora*	1.9	19.6	23.4	14.4	14.8	0.0	0.0	0.0	0.0	0.0
Damaged *Rhizophora*	16.6	57.8	55.3	65.9	48.9	5.1	15.0	15.2	6.5	10.4
Non-*Rhizophora* fringe	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inner fringe remaining	43.0	N/A	67.0	15.0	41.7	100.0	100.0	100.0	100.0	100.0

[1] 1987 site measurements were taken in May when sites included adjacent points. *N/A* = not applicable.

Table 9.5 Characteristics of the outer mangrove fringe in oiled and unoiled channels and lagoons.

	Oiled						Newly Oiled	Unoiled				
	SBCE	SBCS	PCE	PCS	LRCW	Mean	HIDC	MACS	MACN	SBCW	LRCS	Mean
Length (m) 1987	213[1]	188	190	116	275	196	162[1]	177	184	179	ND	136
Length (m) 1991	300	189	191	110	271	212	131	179	180	176	183	180
Percent of total in 1991:												
Mature *Rhizophora*	6.7	65.6	77.5	60.9	50.9	52.3	94.7	98.3	98.9	100	100	99.3
New *Rhizophora*	0.0	0.0	0.0	1.8	0.0	0.4	0.0	1.1	0.0	0.0	0.0	0.3
Dead *Rhizophora*	77.7	9.5	6.3	16.4	7.7	23.5	0.0	0.0	0.0	0.0	0.0	0.0
Damaged *Rhizophora*	15.7	24.9	16.2	20.9	41.3	23.8	5.3	0.6	1.1	0.0	0.0	0.4
Non-*Rhizophora* fringe	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inner Fringe remaining	83.0	73.0	0.0	0.0	43.0	39.8	100	100	100	100	100	100

[1] Shoreline monitored at SBCE increased due to root loss. HIDC was unoiled in 1987. There are no 1987 data (*ND)* for LRCS because it was added after HIDC was oiled in August 1988.

Table 9.6 Characteristics of the outer mangrove fringe in oiled and unoiled drainage streams.

	Oiled					Unoiled				
	LRRS	PAYR	PMRE	PMRW	Mean	HIDR	UNR	ALER	MERR	Mean
Length (m) 1987	301	193	167	262	233	309	252	448[1]	355	341
Length (m) 1991	300	174	174	270	230	312	256	500	345	353
Percent of total in 1991:										
Mature *Rhizophora*	0.3	55.2	10.3	21.1	21.7	88.8	96.9	88.0	83.8	89.4
New *Rhizophora*	10.3	2.3	4.0	2.2	4.7	0.0	0.0	0.0	0.9	0.2
Dead *Rhizophora*	86.7	16.7	83.3	53.3	60.0	1.9	0.0	7.6	2.0	2.9
Damaged *Rhizophora*	2.7	25.9	2.3	23.3	13.5	1.3	0.0	0.8	0.9	0.7
Non-*Rhizophora* fringe	0.0	0.0	0.0	0.0	0.0	6.4	0.0	0.0	12.5	4.7
Inner fringe remaining	0.0	N/A	0.0	0.0	0.0	100	100	100	100	100

[1]Area was increased after cutting during 1988 dry season. *N/A* = not applicable.

Overall Differences Between Oiled and Unoiled Sites Within Habitats

The overall structure of oiled sites was initially similar to that of unoiled sites within each habitat type. On the open coast *Rhizophora* fringed the shores of MINM, DROM, and PMM, and coconut palms occurred intermittently shoreward. Several buttonwood trees occurred with red mangroves at PGM. Channels were all fringed with *Rhizophora*. Oiled streams differed from unoiled streams. Three of four may have been abandoned, mosquito-control drainage ditches (LRRS, PMRE, and PMRW), but were kept open as *cayuco* waterways. The fourth (PAYR) was a sluggish, shallow creek. Each was fringed solely by *Rhizophora*.

As at unoiled sites, lengths of sites did not vary appreciably (except as noted in Tables 9.4-9.6) between 1987 and 1991. However, at all oiled sites at least portions of the original fringe could only be recognized by the presence of embedded, rotted roots or *Rhizophora* stumps. In each of the three habitat types, significantly more *Rhizophora* fringe was dead or damaged at oiled than unoiled sites 5 yr after the spill (Tables 9.4-9.6; *G*-tests for each habitat damaged vs. healthy fringe, $P < .001$, all tests, 1 df). Variation in survival of fringe among oiled sites appeared due to patchiness of oil deposition, site location, and topography.

Fig. 9.37 Damage by drift logs to fringing *Rhizophora* roots. May 1987, site = PADM. *Center left*, flagged roots were part of the community development cohort. Light area in the center is a patch of *Thalassia* gouged out by a log; hanging roots around the log's base were broken or lifted out of the water or both.

Open Coast: Sequence and Amounts of Damage

Field notes and site photographs documented the condition of the fringe at oiled sites immediately after the spill and over the next 5 yr. Defoliation (monitored as amount of fringe totally without leaves) was rapid. Background levels of defoliation (<10% of fringe) were found at all open sites in August 1986 (Fig. 9.39). Defoliation was minor (~11-25%) at oiled sites by November 1986, and remained at approximately this level through May 1987 (Fig. 9.40). In August 1987 (when site locations were fixed for the remainder of the study) defoliation was minor at MINM and PGM, but moderate (~26-50%) at DROM and PMM. Prop roots were first observed breaking and rotting in February 1987 (see *Root Condition*, below), and limbs began breaking off defoliated trees by February 1988.

Fig. 9.38 Machete damage to fringing *Rhizophora*. May 1988, site = PADM. Such cutting occurred at all open coast sites during the study; damage ranged from a single cut root to disappearance of entire clumps of mangrove.

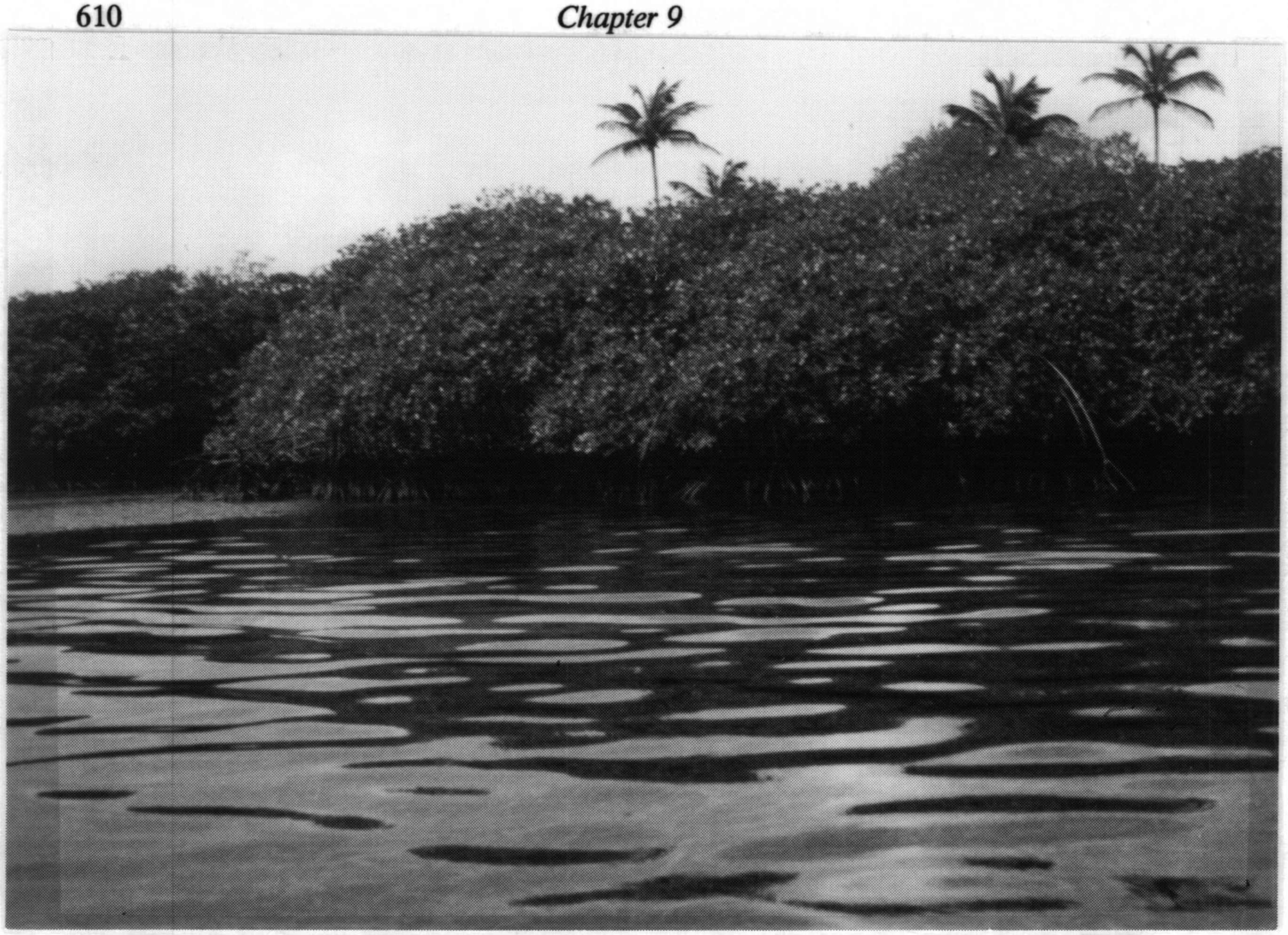

Fig. 9.39 Oiled, open coast fringe immediately after the spill. July 1986, site = MINM. Dark upper band on roots is oil, light lower band is a film of diatoms on oil. There was little or no defoliation. Coconut palms in the *background* are along the berm of the inner fringe.

Two years after the spill (May 1988) levels of defoliation had not changed, but many defoliated trees were dead and had collapsed or disappeared (Fig. 9.41). Dead trees were also cut down at DROM by refinery personnel in March 1988. By February 1989 defoliation decreased to near-background levels at MINM and PGM, and was minor at the other two sites (Fig. 9.42). Two factors were responsible for this. Surviving trees appeared not to undergo further leaf loss, and some dead, defoliated trees had disappeared during the dry season, probably because of collapse caused by wave action, bashing by logs, or both. Over the remainder of the study, defoliated trees continued to collapse and disappear. Defoliation dropped to near-background levels by February 1990 (Fig. 9.43) at all sites; this continued through May 1991 (Fig. 9.44).

In May 1991 ~80% of the outer fringe was damaged, dead, or missing (see *Materials and Methods*, Sect. 9.5.2) at DROM, PMM, and PGM, compared to <20% of the fringe at MINM (*G*-test, $P < .001$, 3 df; Table 9.4). The percent of mature

Fig. 9.40 Oiled, open coast fringe 1 yr after the spill. May 1987, site = DROM. Some trees were partially defoliated; a band of oil on roots just rear of the boat is still visible. The low water level is typical of early rainy season.

outer fringe remaining ranged from 19.7 to 81.5% (Table 9.4). Between 15 and 67% of the forest between the fringe and the berm remained. Little new fringe (mean of 0.1% of total area) had developed along the original fringe 5 yr after oiling. MINM was farthest from the spill site, upcurrent, and partially in Isla Galeta's wind shadow when northerly winds blew oil ashore during the spill (Cubit et al. 1987; Cubit 1991; Cubit and Levings, Chap. 2; Fig. 9.5*C*). It may thus have received less total oil than the other three sites.

Channels and Lagoons: Sequence and Amounts of Damage

The sequence of events in damage and recovery to the structure of fringing mangroves in oiled channels differed from events on open shores. Background damage (e.g., from logs) was rare. In August 1986 oiled channels in the western wing of Bahía Las Minas appeared slightly defoliated (some branches within trees or

Fig. 9.41 Oiled, open coast fringe 2 yr after the spill. May 1988, site = DROM. There was increased defoliation; *center*, some trees appeared dead.

clumps, but no entire trees or clumps, as on open shores; Fig. 9.45). However, by November 1986 all heavily oiled sections of the shore were heavily (~51-75% bare) or nearly totally (~76-100%) defoliated (Fig. 9.46). By May 1987 little further defoliation had occurred, and many prop roots on partially defoliated trees had begun growing multiple tips.

In August 1987 defoliation was nearly total at SBCE, light (~11-25%) at SBCS, moderate (26-50%) at PCE, moderate at PCS, and heavy at LRCW. Where trees were totally defoliated, hanging prop roots had lifted from the water, causing extensive secondary mortality to epibiotic organisms.

Little further defoliation occurred, except at SBCS, which was ranked moderate beginning in February 1988. Also, in February 1988 defoliated trees began to fall, especially at SBCE and LRCW (Fig. 9.47) and personnel from the refinery cut the dead forest behind the fringe at PCS. In May and August 1988 defoliation at SBCS increased to heavy; trees and limbs fell at all other oiled sites.

Fig. 9.42 Oiled, open coast fringe 3 yr after the spill. February 1989, site = DROM. No further defoliation was evident; many dead trees had collapsed or been cut down. The high water level and wave action are typical of dry season.

During November 1988 and February 1989 personnel from the oil refinery were observed cutting dead trees along, and especially in from, the fringe at SBCE, PCE, and PCS. In May 1989 more than 75% of dead, defoliated trees at these sites were either lying on the intertidal mud or had been washed into deeper water along the fringe (Fig. 9.48).

Defoliation decreased to moderate at SBCE in May. This reflected the condition of surviving trees only. By November 1989 most leafless trees had collapsed at LRCW (this site was not cut), and surviving trees were moderately defoliated. Defoliation at SBCS remained heavy until February 1990, when most defoliated trees there had fallen and thus were removed from estimates.

By May 1990 more than 90% of defoliated trees at all sites had fallen, and there was rapid growth of planted and naturally recruited saplings behind the fringe (Fig. 9.49; see also Duke and Pinzón, Chap. 8). By the end of the fifth year after the spill, most of the dead, fallen *Rhizophora* were gone; surviving portions of the original

Fig. 9.43 Oiled, open coast fringe 4 yr after the spill. February 1990, site = MINM. No further defoliation was evident; *center*, the dead area was caused by log bashing. Scale = 17-foot kayak.

fringe appeared relatively healthy, and saplings, although located toward the berm from the original fringe, continued to grow (Fig. 9.50).

Quantitatively, damage to the outer fringe ranged from light to heavy in oiled channels and lagoons (Table 9.5). Mature *Rhizophora* lined the entire network of channels and lagoons in 1986 (Figs. 9.3 and 9.45) and were found on 6.7-77.5% of the shore in May 1991 (a more than ten-fold difference in damage among sites). New fringe had developed along a small proportion ($<.02$) of the original fringe at one site (PCS).

Damage to *Rhizophora* between the fringe and the berm also was highly variable, with between 0 and 83% of the original forest surviving after 5 yr. Survival of this inner intertidal forest was highest where damage to the outer fringe was also highest (Spearman r_s between the amount of berm forest remaining and the amount of dead and damaged fringe = .70, NS). This suggests that topographic differences among sites may have affected relative oil accumulation within a given site.

Fig. 9.44 Oiled, open coast fringe 5 yr after the spill. June 1991, site = PMM. No further defoliation or other evidence of damage from the spill is visible at this scale.

One control site, HIDC, was oiled by a secondary release of VMIC between May and August 1988. In May 1991 its outer fringe appeared more similar to unoiled than oiled sites. Ninety-five percent of its shoreline was mature *Rhizophora* fringe; a tree fall had caused the small amount of damage seen.

Mortality and damage to the outer fringe differed significantly among oiled channels (*G*-test, $P < .001$, 4 df; Table 9.5; App. Table E.3). Two sites in the central wing of Bahía Las Minas had 34% (SBCS) vs. 93% damage (SBCE). Oil was trapped within this wing for 6 d immediately after the spill (Cubit et al. 1987). SBCE was located seaward (toward the refinery) of SBCS, directly in the path of the oil; oil trapped in the fringe at SBCE was so thick that it formed banks of tar and asphalt residues as it weathered. This site thus was probably more heavily oiled than SBCS, which was around a corner in the inner bay (it was also an island, and much oil may have flowed through or around it rather than stranding). LRCW was located at the mouth of LRRS; oil draining through the stream went directly onto this site. The two sites in the east wing of the bay (PCE and PCS) showed moderate damage to the

Fig. 9.45 Oiled channel fringe immediately after the spill. July 1986, site = western wing of Bahía Las Minas. No damage is visible at this scale.

outer fringe. The less-affected PCE (23% damaged) fronted the open bay, and was exposed to some wave action.

Drainage Streams: Sequence and Amounts of Damage

Field notes and site photographs show that *Rhizophora* fringed the entire margins of oiled streams in 1986 (Fig. 9.4). Defoliation at two oiled sites was moderate (~26-50%) by August 1986 (Fig. 9.51), and nearly total (~76-100%) by November. Many small limbs were broken off defoliated trees in May 1987, probably from high winds during dry season (Fig. 9.52). From August 1987 on, additional oiled streams were monitored (Sect. 9.3). LRRS, PMRE, and PMRW were nearly totally defoliated, and PAYR was moderately defoliated in August. At all sites overhanging limbs were brittle and easily broken.

In May 1988 no canopy of overhanging branches remained (compare Fig. 9.53 to 9.51) at LRRS and PMRE. More than 75% of trees along the banks were dead,

Fig. 9.46 Oiled channel fringe 1.5 yr after the spill. November 1987, site = SBCS. Many fringing *Rhizophora* were fully defoliated. Defoliation and loss of lower portions of hanging roots lifted roots above the HWL, killing additional attached plants and animals.

and streams were crossed by fallen limbs and trees. At PMRW about 50% of trees appeared dead, compared to about 25% at PAYR. Refinery personnel cut dead trees along and in from the banks of PMRE and PMRW, sometime between August and November 1988, and planted seedlings behind the fringe at these sites (S. D. Garrity, pers. obs.). LRRS and PAYR were not cut. By May 1989 more than half of the fringe of LRRS had fallen (Fig. 9.54), and more than 75% had collapsed or been cut at PMRE and PMRW. Sapling growth in from the banks was high at all three sites. *Rhizophora* at PAYR appeared relatively healthy; about 25% had collapsed, and surviving fringe was lightly defoliated.

Little additional collapse occurred at any site through May 1990, and growth of planted seedlings and recruits increased noticeably in 1990-1991 (Fig. 9.55). At several sites (e.g., LRRS and PMRW) new seedlings along stream banks grew aerial roots into the water for the first time. At the end of the fifth year postspill, more

Fig. 9.47 Oiled channel fringe 2 yr after the spill. May 1988, site = SBCE. Much of the heavily oiled fringe had died and fallen. *Upper right*, note the oil-coated root now ~2 m above the water. White objects on roots are valves of dead *Crassostrea*.

than 90% of original fringe at LRRS had fallen and disappeared, but new growth covered about 10% of the former fringe (Fig. 9.56).

In a quantitative survey in May 1991, mature *Rhizophora* averaged 22% of total shoreline in four oiled streams, and dead or damaged *Rhizophora* averaged ~75%. New trees occupied <5% of the original fringe. Behind the outer fringe no live adult trees remained, but planted and naturally recruited saplings were abundant from behind the outer fringe to the berm (Fig. 9.56; Table 9.6).

There were significant differences in structure among oiled streams, with relatively high survival of the fringe at PAYR (*G*-test, $P < .001$, df = 3; Table 9.6; App. Table E.3). This site was located in the east wing of Bahía Las Minas behind Isla Payardí, which may have acted as a partial barrier to oil (Fig. 9.5*E*). Damage to the *Rhizophora* fringe was highest at LRRS (11% healthy fringe in May 1991). This stream bisected Isla Largo Remo, and drained interior mangroves into both the

Fig. 9.48 Oiled channel fringe 3 yr after the spill. May 1989, site = SBCE. Fallen fringe was collapsing onto the substratum. Submerged portions of fallen limbs were available for settlement of marine organisms until they rotted; exposed portions were attacked by termites (*Nasutitermes* spp.).

NE and SW sides of the island. Located just west of the refinery, it was a major conduit for oil between the west and central wings of the bay during the spill.

Root Density

At unoiled sites the mean abundance of available roots (live and dead roots/0.25 m^2 of fringe) ranged from 3.5 to 5.0, while significantly fewer (2.3-3.7) occurred per unit area at oiled sites (nested ANOVA, sites nested within oiling condition, $P < .05$ or smaller, each test; Table 9.7). There were no differences between oiled and unoiled sites in the number of live roots about to enter the water 5 yr after the spill (nested ANOVA, $P > .06$ or larger, NS; Table 9.7); dead roots that would have grown into the water were too rare to test.

Fig. 9.49 Oiled channel fringe 4 yr after the spill. May 1990, site = SBCE. The fringe had collapsed along much of the shore; planted and naturally recruited saplings were growing behind the fringe to the berm. Surviving mangroves in the *background* are behind the berm.

Hidden Channel (HIDC), oiled by a secondary release in 1988, showed no effects of oiling on root density or condition. Root density was indistinguishable from that in unoiled channels.

The relative proportion of live and dead roots was analyzed with analysis of covariance on ln(density live roots + 1) compared with ln(density dead roots + 1) (Table 9.7). The full model with interaction was tested using habitat (open coast, channel, and stream) and oiling (oiled and unoiled) as class variables. When the 3-way interaction was not significant, the model was sequentially run testing for the significance of the 2-way interactions. When the 2-way interactions were not significant, the main-effects model was run.

Results were clear (Table 9.7). There were significant effects of oiling and habitat on the proportion of dead roots and root density. More roots were dead at oiled sites regardless of habitat. There were more roots in channels than on the

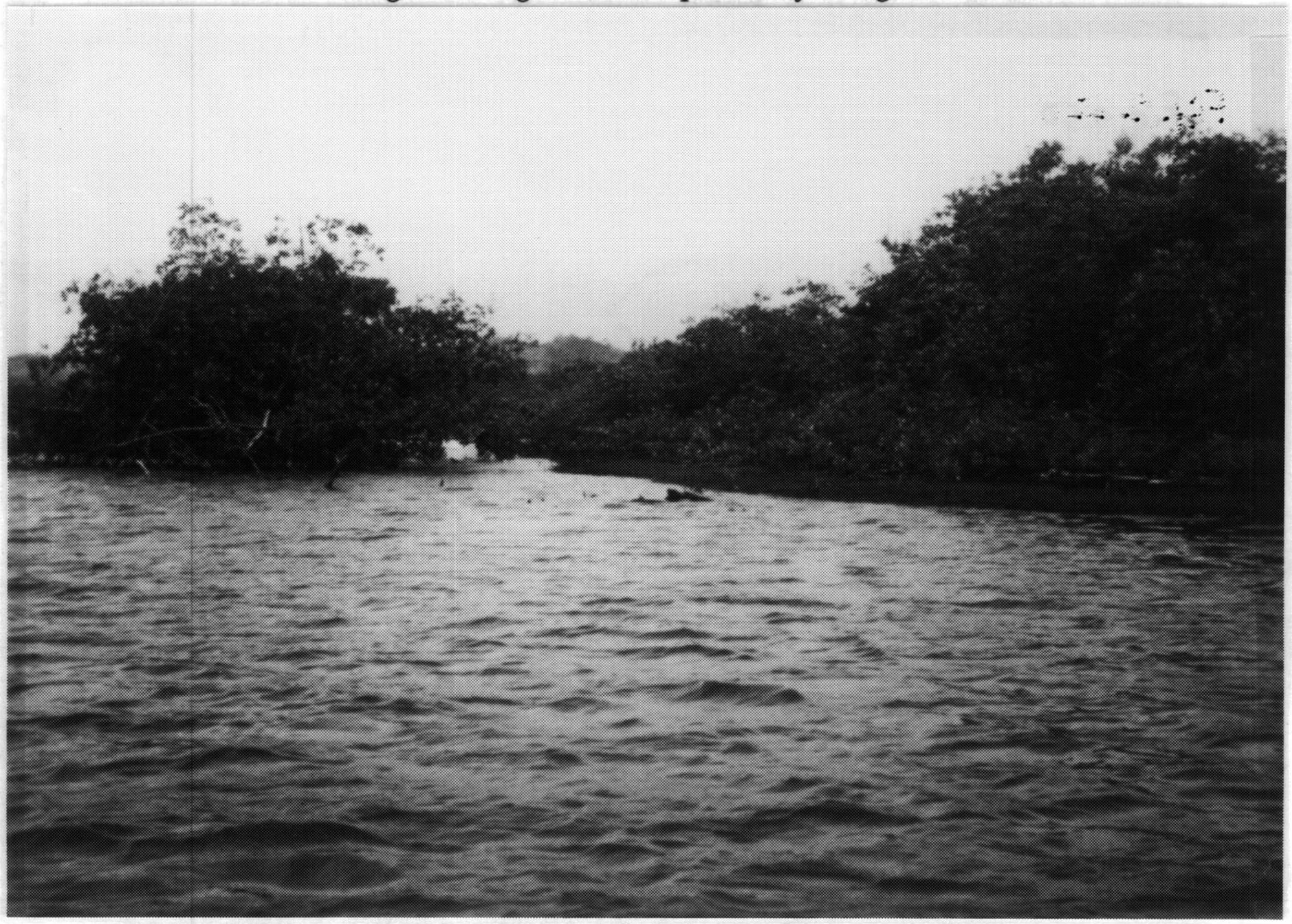

Fig. 9.50 Oiled channel fringe 5 yr after the spill. June 1991, site = SBCE. *Center to right center*, the collapsed fringe was mostly gone, and there was a bare area along the fringe, behind which were healthy planted and recruited red mangrove saplings, then the berm forest. *Rhizophora* at the *left* were surviving trees from the original fringe.

open coast or in streams; the proportion of dead roots at unoiled sites was highest on the open coast.

Root Length and Physical Condition

Root length and diameter were recorded for each root when percent cover data were taken. Site location changed in August 1987; August 1986-May 1987 data are shown in the figures but were not included in the following statistical analyses. Length data were analyzed with repeated-measures ANOVA using data aggregated into annual and seasonal groupings ($N = 4$ yr with 4 quarterly monitoring dates, e.g., yr 1 = August 1987-May 1988, mean for yr 1 = mean of 4 quarterly means of length at each site).

Two series of analyses were run within each habitat using random-census data: (1) effects of year and oiling (oiled and unoiled; yr 1-4) and (2) effects of month and

Fig. 9.51 Oiled stream immediately after the spill. August 1986, site = LRRS. Dark portion of roots was covered with oil. Note partial defoliation of canopy branches crossing the stream.

oiling (oiled and unoiled; February, May, August, and November). We also analyzed root length of the community development cohort (marked roots that entered the water in September-October 1987) and compared it with that for randomly censused roots. Three years of data were available for this comparison, beginning 9 mo after the cohort roots entered the water (e.g., yr 1 = August 1988-May 1989). Both analyses asked if there were effects of root group, season, and oiling on root length.

Randomly Censused Roots – Effects of Habitat, Year, and Oiling

Root length of randomly censused roots varied significantly among habitats, oiling conditions, and years (Figs. 9.57-9.59; Table 9.8). On the open coast, roots were significantly shorter at oiled than unoiled sites, but the mean difference in root length declined over time (Table 9.9). In yr 1 (August 1987-May 1988) roots at oiled sites were ~11% shorter than at unoiled sites (overall mean length of 63.7 cm vs. 71.4 cm). By yr 3 (August 1990-May 1991) the difference was only 5% (59.7 cm vs.

Fig. 9.52 Oiled stream fringe 1 yr after the spill. May 1987, site = LRRS. Defoliation was nearly total and trees appeared dead. *Cayuco* (scale) is ~3 m long.

62.9 cm). Thus, one effect of oiling was a change in the average depth to which roots were submerged on the open coast, i.e., there was a smaller area of root surface available for epibiotic settlement, and it was shallower in the water column at oiled than unoiled sites.

In channels and lagoons there was no effect of oiling on root length, but root length varied significantly among years (Fig. 9.58; Table 9.9). This effect was small, with annual grand means varying between 57.2 and 61.5 cm. Oiling in channels did not change the overall depth distribution of roots.

Differences in root length between oiled and unoiled drainage streams were strong and did not vary among years (Fig. 9.59; Table 9.9). Roots in oiled streams were 22-37% shorter than in unoiled streams throughout the study; they were 32% shorter in August 1990-May 1991. This meant there were fewer deeply submerged roots in oiled drainage streams than in unoiled streams.

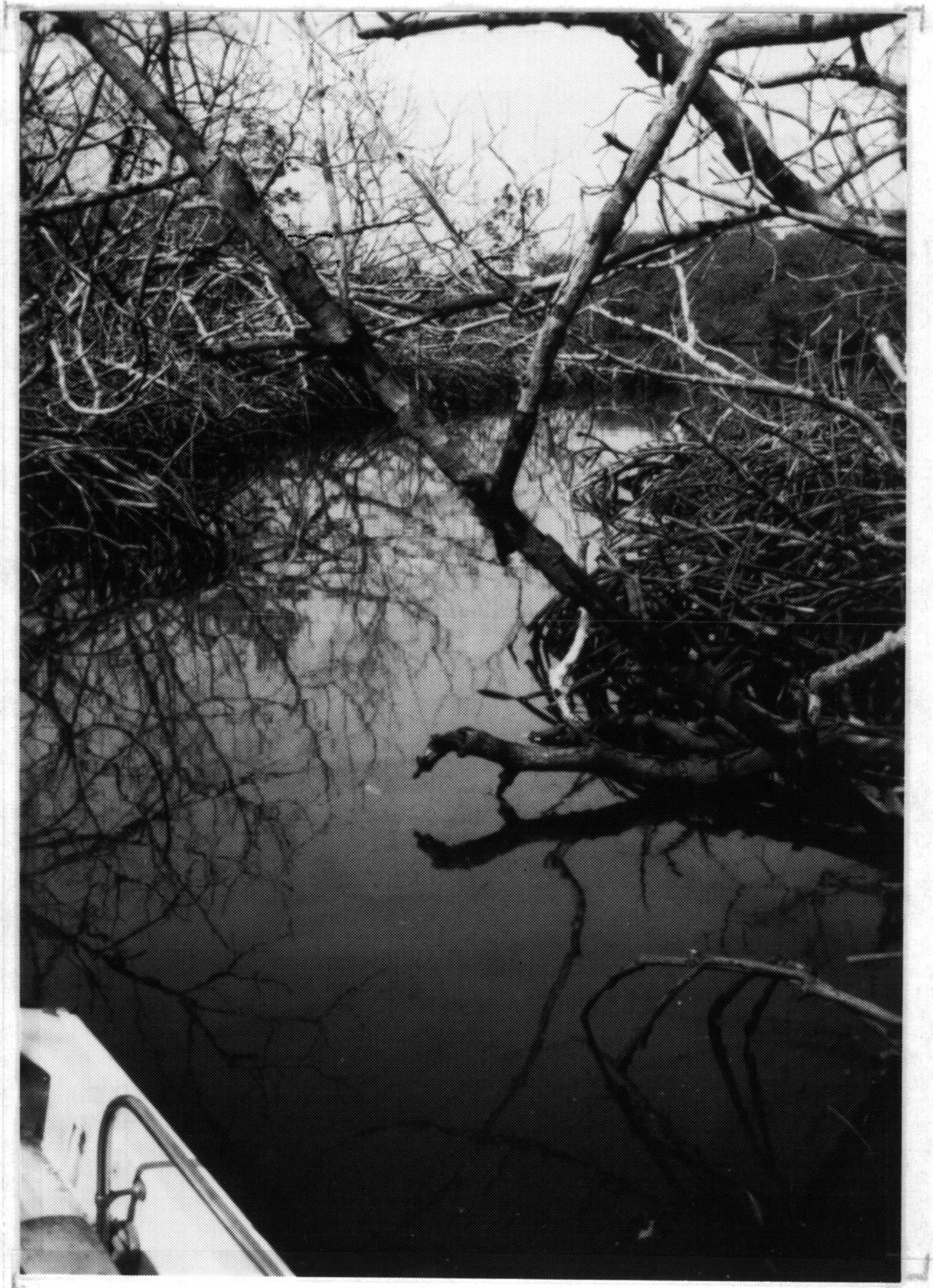

Fig. 9.53 Oiled stream fringe 2 yr after the spill. May 1988, site = LRRS. Defoliated trees appeared dead and some had fallen. Canopy branches crossing the stream had fallen.

Fig. 9.54 Oiled stream fringe 3 yr after the spill. May 1989, site = LRRS. Trees continued to collapse and few live trees and roots occurred along banks. New recruits (no replanting at this site) were visible in from the banks.

Fig. 9.55 Oiled stream fringe 4 yr after the spill. May 1990, site = LRRS. There was continued collapse of the fringe and growth of new saplings in from the banks. Prop roots of some saplings had entered the water. *Center background*, site CO5.

Randomly Censused Roots – Effects of Habitat, Season, and Oiling

To test for seasonal patterns in root length, we tested the effects of month and oiling on root length, comparing samples for each quarter in each year (i.e., May 1988, May 1989, May 1990, and May 1991 at each site). In an overall ANOVA the seasonal pattern of root length was affected by oil and was different for the three habitats (Table 9.10). In general, roots were shorter in the dry and early wet seasons (February and May) than in the mid- and late wet seasons (August and November). On the open coast there was a significant seasonal pattern, which was affected by oiling and was different at oiled and unoiled sites (Fig. 9.57; Table 9.9). In channels oiling did not affect root length, but root length varied seasonally at both oiled and unoiled sites (Fig. 9.58; Table 9.9). In drainage streams oiling strongly affected root length, but the seasonal pattern of change was the same in oiled and unoiled streams (Fig. 9.59; Table 9.9).

Fig. 9.56 Oiled stream fringe 5.5 yr after the spill. September 1991, site = LRRS. Original fringe was >95% collapsed. New saplings continued to grow and spread along the banks.

Community Development Cohort – Effects of Habitat, Year, and Oiling

Nine months after entering the water, there were significant effects of habitat, year, and oiling on root length in the community development cohort (Table 9.11; Figs. 9.57-9.59). On the open coast roots were significantly shorter at oiled than unoiled sites; this difference persisted among years (Table 9.9). In channels neither oil nor year significantly affected root length (Table 9.9). Roots were longer in unoiled than oiled drainage streams; root length increased between the first and second year at unoiled sites, but remained approximately the same in all 3 yr at oiled sites (Table 9.9).

Community Development Cohort – Effects of Habitat, Season, and Oiling

Root length in the community development cohort varied significantly with habitat and oiling but not with season (Table 9.12). On the open coast there was a

Table 9.7 Density of live and dead roots per 0.25 m^2 on the mangrove fringe.

	Open Coast		Channels and Lagoons	Drainage Streams
A. Mean ± SE (*N*)[1]				
Live Roots:				
Oiled	2.6 ± 0.4 (4)		3.0 ± 0.1 (5)	2.9 ± 0.2 (4)
Unoiled	3.6 ± 0.1 (4)		4.5 ± 0.2 (4)	4.0 ± 0.2 (4)
		HIDC	4.4 (1)	
Dead Roots:				
Oiled	0.4 ± 0.3 (4)		0.7 ± 0.2 (5)	0.5 ± 0.2 (4)
Unoiled	0.3 ± 0.1 (4)		0.1 ± 0.1 (4)	0.1 ± 0.1 (4)
		HIDC	0 (1)	
Live Roots Out:				
Oiled	1.0 ± 0.3 (4)		0.9 ± 0.2 (5)	1.4 ± 0.2 (4)
Unoiled	1.1 ± 0.1 (4)		1.6 ± 0.2 (5)	1.4 ± 0.3 (4)
		HIDC	1.0 (1)	
Dead Roots Out:				
Oiled	0.1 ± 0.1 (4)		0 (5)	0 (4)
Unoiled	0 (4)		0 (5)	0 (4)
		HIDC	0 (1)	
B. Analysis of variance *F*-values: density of submerged live and dead roots[2]				
Source:				
Oiling	8.1 *		11.92 *	7.78 *
Sites	0.44 NS		0.40 NS	0.43 NS
C. Analysis of variance *F*-values: density of live roots out of the water[2]				
Source:				
Oiling	0.16 NS		4.64 NS	0.00 NS
Sites	3.54 **		1.87 NS	1.26 NS
D. Analysis of covariance *F*-values and associated probability levels: ln(live roots) vs. ln(dead roots)				
Full Model:				
ln(dead)	1	9.99	.002	
Habitat	2	4.20	.016	
ln(dead) x Habitat	2	0.80	.449	
Oiling	1	21.96	.0001	
ln(dead) x Oiling	1	0.58	.446	
Habitat x Oiling	2	0.34	.713	
ln(dead) x Habitat x Oiling	2	0.89	.413	
Reduced Model (2-way):				
ln(dead)	1	10.00	.002	
Habitat	2	4.20	.016	
Oiling	1	22.61	.0001	
ln(dead) x Habitat	2	0.49	.614	
Habitat x Oiling	2	0.25	.775	
ln(dead) x Oiling	1	0.75	.387	
Reduced Model (main effects):				
ln(dead)	1	10.12	.002	
Habitat	2	4.25	.015	
Oiling	1	22.87	.0001	

[1] Among-site mean and associated SE, *N* = number of sites. HIDC = Hidden Channel.

[2] Level of significance: *NS*: $P > .05$, *: $P < .05$, **: $P < .01$, ***: $P < .001$. See text for further explanation.

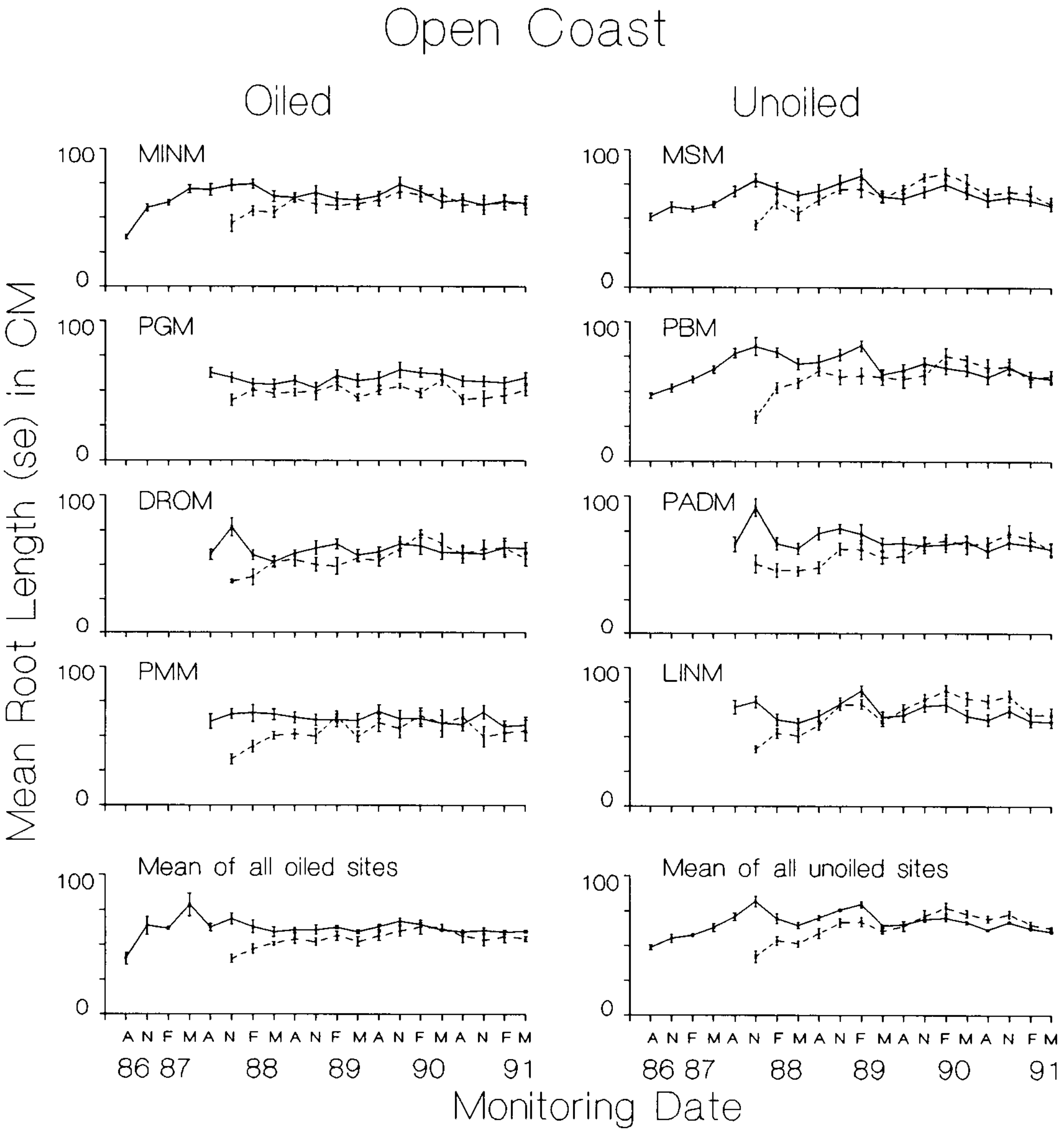

Fig. 9.57 Root length of sampled roots, open coast. Mean (± SE) root lengths of randomly sampled long-term census (*solid lines*) and community development (*dashed lines*) roots for each site and all sites combined (among-site SE). Data from oiled sites are in the left column, from unoiled sites in the right column. Site codes follow Table 9.2. See text for details.

strong reduction in root length associated with oiling; seasonal variation was also significant, but different between oiled and unoiled sites (Table 9.9). In contrast, there were no effects of oil or season on root length in channels (Table 9.9). In streams root length was significantly affected by oiling, but there was no seasonal effect (Table 9.9).

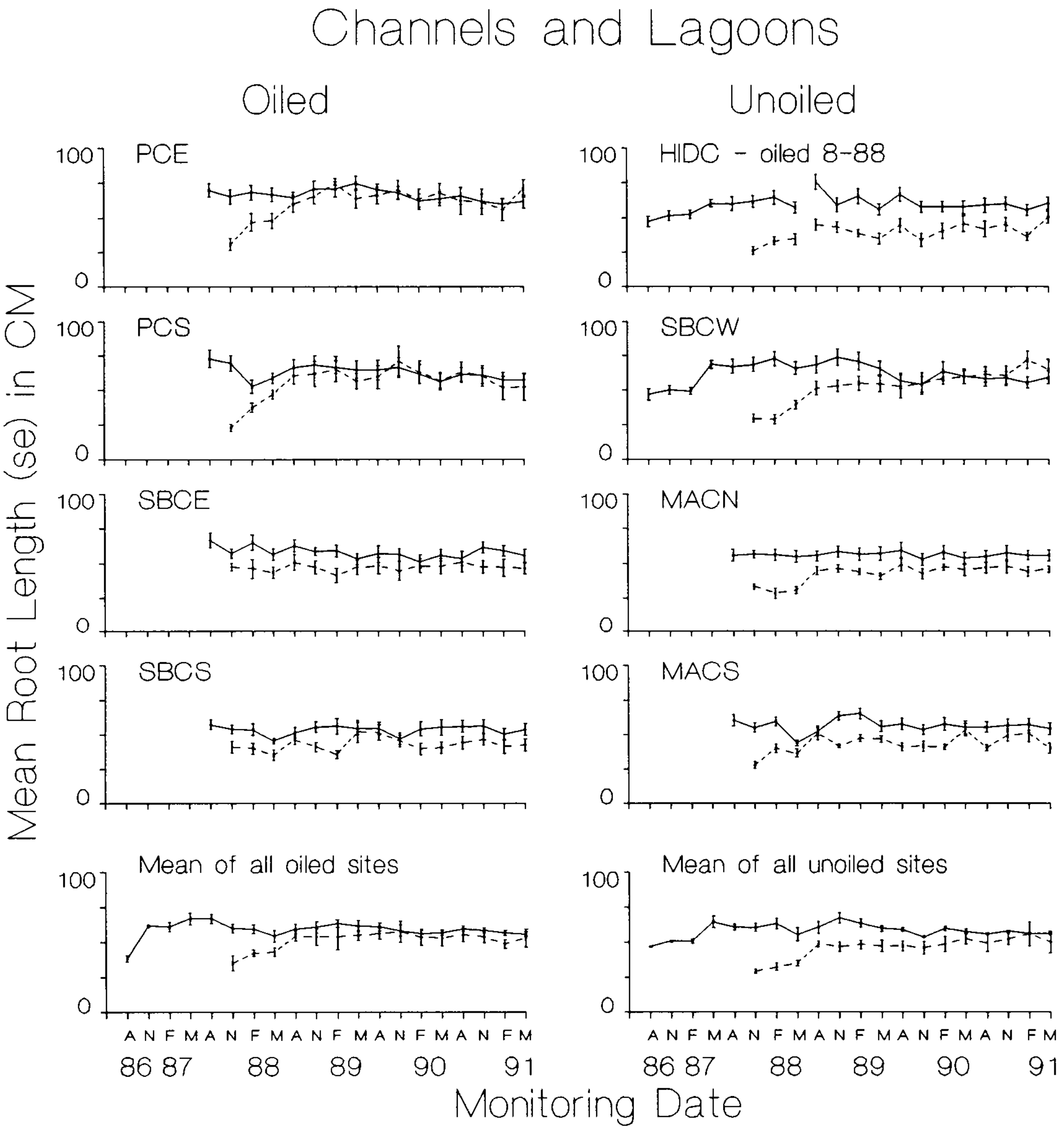

Fig. 9.58 Root length of sampled roots, channels and lagoons. Mean (± SE) root lengths of randomly sampled long-term census (*solid lines*) and community development (*dashed lines*) roots for each site and all sites combined (among-site SE). Data from oiled sites are in the left column, from unoiled sites in the right column. Site codes follow Table 9.2. See text for details.

Community Development Cohort vs. Random-census Roots — Effects of Year and Oiling

The community development cohort entered the water in a known period, so roots were all of "equal age"; this contrasted with variously aged roots from quarterly random censuses. This difference allowed comparisons of root group with oiling and

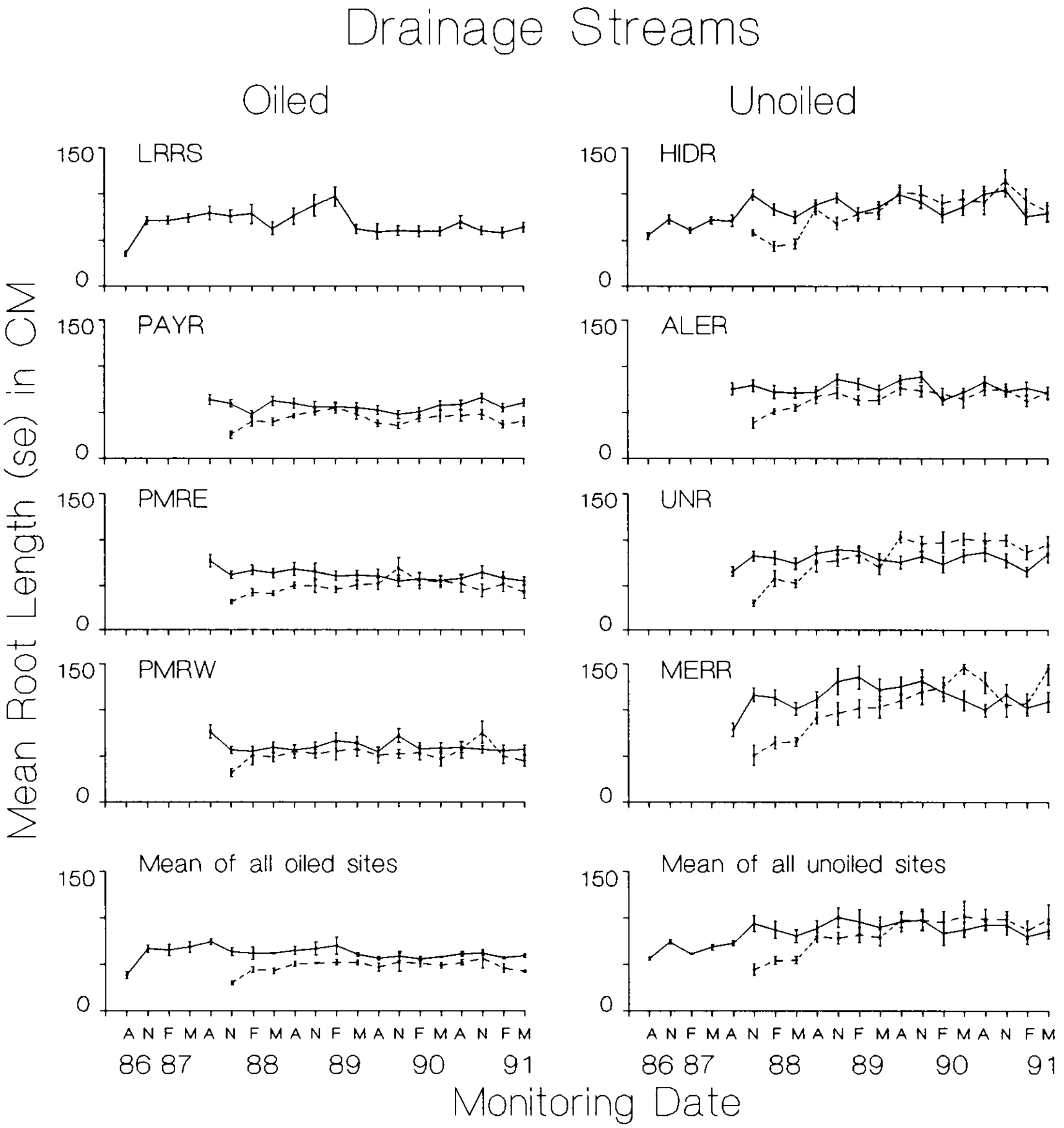

Fig. 9.59 Root length of sampled roots, drainage streams. Mean (± SE) root lengths of randomly sampled long-term census (*solid lines*) and community development (*dashed lines*) roots for each site and all sites combined (among-site SE). Data from oiled sites are in the left column, from unoiled sites in the right column. Site codes follow Table 9.2. See text for details.

year. On the open coast and in drainage streams, the relationship between group and oil varied among the 3 yr of study (Table 9.13*A*-*C*). In the third year after cohort roots in these two habitats entered the water, they were longer than random-census roots at unoiled sites; the opposite was true at oiled sites. In channels the effects of year varied with group, but there were no effects of oiling. Cohort roots

Table 9.8 Three-way repeated-measures analysis of variance on habitat, oiling, and year: root length, random censuses.

Source	df	SS	*F*	*P*
Model				
Between:				
Habitat	2	4,604.5	8.56	.002
Oiling	1	2,917.2	10.85	.004
Habitat x Oiling	2	3,236.9	6.02	.010
error[1]	18	4,841.4		
Within Years:				
Year	3	349.8	10.42	<.0001
Year x Oiling	3	83.2	2.48	.071
Year x Habitat	6	107.1	1.60	.166
Y x H x O	6	243.1	3.62	.004
error[2]	54	604.1		

[1] Sites within groups.
[2] Time x sites within groups.

were on average shorter than those randomly sampled, but the extent of the difference varied over time.

Community Development Cohort vs. Random-census Roots – Effects of Season and Oiling

The seasonal pattern of root length varied with habitat, oiling, and root group. At oiled sites on the open coast (root groups combined) root length was greatest in February, compared with November at unoiled sites. A similar reversal was observed when randomly censused roots (oiling conditions combined) were compared with cohort roots; longest root lengths occurred in November, compared with February. There was an overall seasonal pattern at both oiled and unoiled sites: root lengths tended to be lower in May or August, compared with February or November (Table 9.9). In channels there were no effects of root group, but seasonal patterns shifted with oiling. At unoiled sites (root groups combined) roots were longest in February, and approximately the same length from May to November. At oiled sites root length increased each quarter from February to May. In drainage streams there were no effects of root group or season; as in previous analyses, roots at oiled sites were significantly shorter than those at unoiled sites.

Estimated Surface Area of Roots

The average surface area of roots was calculated from the mean length and diameter of roots in the fifth year after oiling, assuming that roots were

Table 9.9 Probability levels for repeated-measures analysis of variance on root length: annual and seasonal tests.

A. Effects of oiling and year, by habitat: random censuses

Habitat	Oiling	Year	Y x O	Sphericity Test	H.-F. Adj. applied?[1]
Open Coast	.006	.0006	.011	.029	yes
Channels	.899	.019	.906	.184	no
Drainage Streams	.025	.076	.031	.328	no

B. Effects of oiling and season, by habitat: random censuses

Habitat	Oiling	Season	S x O	Sphericity Test	H.-F. Adj. applied?
Open Coast	.006	<.0001	.026	.663	no
Channels	.977	.018	.285	.222	no
Drainage Streams	.025	.023	.099	.826	no

C. Effects of oiling and year, by habitat: community development cohort

Habitat	Oiling	Year	Y x O	Sphericity Test	H.-F. Adj. applied?
Open Coast	.018	.001	.580	.451	no
Channels	.545	.649	.105	.134	no
Drainage Streams	.016	.031	.010	.320	no

D. Effects of oiling and season, by habitat: community development cohort

Habitat	Oiling	Season	S x O	Sphericity Test	H.-F. Adj. applied?
Open Coast	.018	.007	.041	.760	no
Channels	.545	.995	.203	.604	no
Drainage Streams	.016	.603	.528	.0007	yes

E. Seasonal comparisons of random census vs. community development cohort roots

Comparison	Open Coast	Channels	Drainage Streams
Between:			
Group	.100	.087	.634
Oil	.0005	.459	.001
G x O	.275	.729	.480
Within:			
Season	<.0001	.409	.073
S x G	.005	.329	.721
S x O	.001	.016	.713
S x G x O	.583	.952	.121
Sphericity Test	.488	.340	.081
H.-F. Adj. applied?	no	no	no

---

[1] *H.-F.* = Huynh-Feldt adjusted probability levels. If *no*, then probability levels were not adjusted; if *yes*, levels were adjusted.

Table 9.10 Three-way repeated-measures analysis of variance on habitat, oiling, and season: root length, random censuses.

Source	df	SS	*F*	*P*
Model				
Between:				
Habitat	2	4,795.3	9.41	.001
Oiling	1	3,161.5	12.41	.002
Habitat x Oiling	2	3,342.4	6.56	.007
error[1]	19	4,840.3		
Within Seasons:				
Season	3	359.3	14.92	<.0001
Season x Oiling	3	97.3	4.04	.011
Season x Habitat	6	138.6	2.88	.016
S x H x O	6	86.4	1.79	.117
error[2]	57			

[1] Sites within groups.

[2] Season x sites within groups.

Table 9.11 Three-way repeated-measures analysis of variance on habitat, oiling, and year: root length, community development cohort.

Source	df	SS	*F*	*P*
Model				
Between:				
Habitat	2	3,754.2	5.91	.003
Oiling	1	4,077.5	12.84	.012
Habitat x Oiling	2	5,537.6	8.72	.003
error[1]	16	5,081.4		
Within Sites:				
Year	2	343.9	12.35	.0001
Year x Habitat	4	146.7	2.69	.049
Year x Oiling	2	246.7	8.86	<.001
Y x H x O	4	238.2	4.28	.007
error[2]	32			

[1] Sites within groups.

[2] Time x sites within groups.

approximately cylindrical in shape. Estimates were not adjusted for the presence of multiple tips on some roots. Estimated surface area/root was 429 cm^2 on the unoiled open coast and 407 cm^2 on the oiled open coast. In channels mean diameter at MHW was the same at oiled and unoiled sites (2.1 cm) and estimated surface area/root was also similar (372 cm^2 oiled vs. 368 cm^2 unoiled). In drainage streams the difference in root length was almost 30 cm between oiled and unoiled sites; roots

Table 9.12 Three-way repeated-measures analysis of variance on habitat, oiling, and season: root length, community development cohort.

Source	df	SS	*F*	*P*
Model				
Between:				
Habitat	2	5,006.0	5.91	.012
Oiling	1	5,436.7	12.84	.003
Habitat x Oiling	2	7,382.3	8.72	.003
error[1]	16	6,775.6		
Within Sites:				
Season	3	25.1	0.61	.615
Season x Habitat	6	101.0	1.22	.313
Season x Oiling	3	16.2	0.39	.760
S x H x O	6	129.1	1.56	.180
error[2]	48			

[1] Sites within groups.
[2] Time x sites within groups.

Table 9.13 Probability levels for 3-way repeated-measures analysis of variance on root length: effects of root group (community development vs. long-term census roots) and oiling (oiled and unoiled), by habitat type.

Comparison	Open Coast	Channels	Drainage Streams
Between:			
Group	.174	.093	.613
Oil	.0005	.464	.001
G x O	.225	.707	.597
Within:			
Year	<.0001	.169	.376
Y x G	<.0001	.014	.008
Y x O	.162	.284	.026
Y x G x O	.003	.224	.015
Sphericity Test	.380	.064	.876
H.-F. Adj. applied?	no	no	no

H.-F. = Huynh-Feldt adjusted probability levels. If *no*, then probability levels were not adjusted; if *yes*, levels were adjusted.

in oiled streams were also 5% thinner than those from unoiled streams. Estimated surface areas differed correspondingly: 379 cm^2/root in oiled streams and 596 cm^2/root in unoiled streams.

Root Condition

One striking effect of oiling was the significantly higher proportion of dead roots at oiled sites (Figs. 9.35*D*, 9.60-9.62; $P < .001$, repeated-measures ANOVA; Table 9.14; see App. Table E.4 for results of earlier monitoring using slightly different techniques). Dead roots formed a larger fraction of the population at oiled than unoiled sites in all three habitat types. Details of the statistical analyses varied among habitats, but results showed the same general pattern (Table 9.14).

The fraction of dead roots in random censuses declined over time as new roots entered the population and older roots left, either by breaking off or by penetrating the mud. At LRRS 94% of roots were dead in November 1987-May 1988, but only 41% were dead in August 1990-May 1991. Initial levels of damage were lower elsewhere, but the number of dead roots also declined over time.

Gradual replacement of the original population of roots with new roots occurred at all oiled and unoiled sites. However, roots that entered the water ~1.5 yr after the spill (community development cohort) were more likely to die over time at oiled than at unoiled sites (Figs. 9.60-9.62). This difference was significant ($P < .01$) in channels and streams for all 4 yr, and on the open coast in 1990-1991 only (Table 9.14). Results were consistent with the hypothesis that oiling had a continued, negative effect on root health for at least 5 yr after the spill.

We examined variation among sites within habitats in the fraction of dead roots. On the open coast, for all 4 yr at oiled sites and for 3 of 4 yr at unoiled sites, there were no significant differences among sites ($P > .05$, *G*-tests; App. Table E.5). The exception was in 1990-1991, when there were more dead roots at PADM and PBM than at LINM or MSM. Results were correlated with variation in bashing by logs that washed across the reef flat into sections of the fringe (e.g., Fig. 9.37). During six 1990-1991 quarters, roots ($N = 180$ at each site, community development and random-census results combined) were examined for log damage. PADM and PBM averaged 26% and 27% in damage of all roots sampled, respectively. In comparison, only 16% and 8%, respectively, were damaged at LINM and MSM.

For channels and lagoons there were no significant differences among oiled channels in all 4 yr ($P > .05$; App. Table E.5). So few roots were dead at unoiled sites that *G*-tests were unreliable. However, the same low frequency of dead roots occurred consistently among sites and years.

In drainage streams there were significant differences among oiled sites in all 4 yr ($P < .001$, *G*-tests; App. Table E.5). The proportion of dead roots was always highest at LRRS and lower in the other three oiled streams. In contrast, there were no differences among unoiled sites; few roots at any site were dead in all 4 yr.

Relative Defoliation and Light Penetration

The amount of light reaching root level through the canopy was measured three times during the study. Data were analyzed for each habitat using 2-way

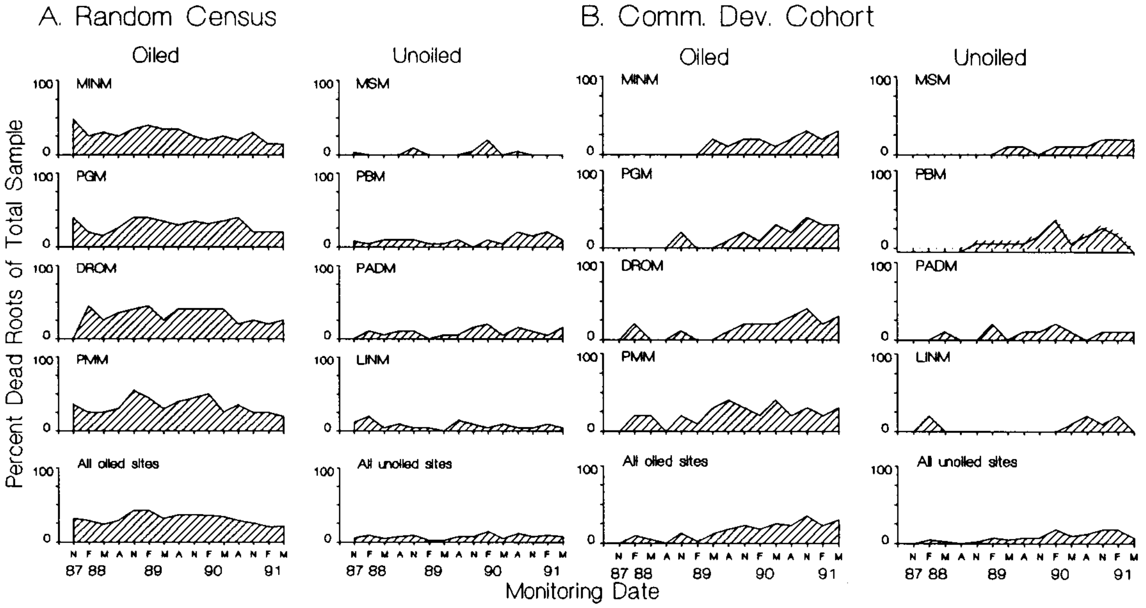

Fig. 9.60 Relative abundance of dead roots on the open coast. Site codes follow Table 9.2. See text for methods and sample sizes. *A.* Percent of roots judged dead in quarterly, random censuses at oiled (left column) and unoiled (right column) sites and overall. *B.* Proportion of roots judged dead in quarterly, random subsampling of marked, community development roots at oiled (left column) and unoiled (right column) sites and overall.

ANOVA with interaction, testing for an effect of year and oiling condition. Results were consistent (Fig. 9.63; Table 9.15). In each case, terms for both the interaction and the effect of date were not significant. There was a significant main effect of oiling in each habitat ($P < .001$, all tests; Table 9.15). This result indicates that (1) significantly more light passed through the canopy to root level at oiled than unoiled sites and (2) differences among oiled and unoiled sites persisted at least through February 1991.

Differences were strongest in drainage streams, where most of the fringe was destroyed (see Sect. 9.5.1). Data from unoiled sites show that this habitat normally had the lowest light transmission of the three examined (overall means of light transmission through the canopy = 39% for open, 29% for channel, and 17% for streams).

The secondarily oiled channel control site (HIDC) showed values intermediate to those from oiled and unoiled sites for each of the three years examined (Fig. 9.63). Given the variability among unoiled channels, light levels at this site cannot be attributed to defoliation from secondary oiling.

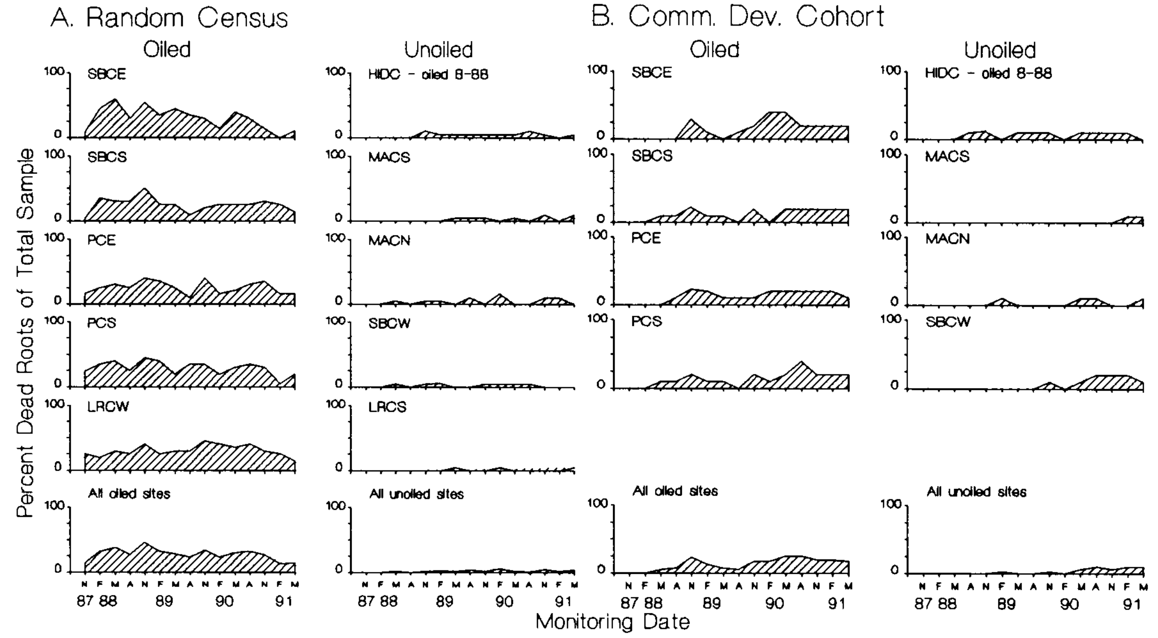

Fig. 9.61 Relative abundance of dead roots in channels and lagoons. Site codes follow Table 9.2. See text for methods and sample sizes. *A*. Percent of roots judged dead in quarterly, random censuses at oiled (left column) and unoiled (right column) sites and overall. *B*. Proportion of roots judged dead in quarterly, random subsampling of marked, community development roots at oiled (left column) and unoiled (right column) sites and overall.

Estimation of Habitat Reduction

Evaluation of damage to epibiotic communities has several levels. Presence of an epibiotic community is first dependent upon the presence of mangrove roots as substratum. Reduction in the density or areal extent of roots on the fringe will reduce the total amount of habitat for the epibiota *independent* of any toxic effects of oiling on attached organisms. Oil spills could thus affect the abundance and productivity of epibiota solely through effects on the structure of the habitat.

As a measure of the overall effect of oiling on the structure of the mangrove fringe 5 yr after the spill, we calculated the difference between the average amount of mature, new, and damaged fringe for oiled and unoiled sites (Tables 9.4-9.6; App. Table E.6). We assumed that the mean for unoiled sites represented the density of fringe expected at oiled sites. This measure was selected because it was conservative (including damaged, but not destroyed areas) and represented a measure of the area where we actually sampled roots. We repeated this procedure with the average number of roots at oiled vs. unoiled sites (roots defined as roots that fell into our sampling universe: submerged at least 20 cm, but not attached to bottom sediments; App. Table E.6). Combining these two measures generated a percent of the total

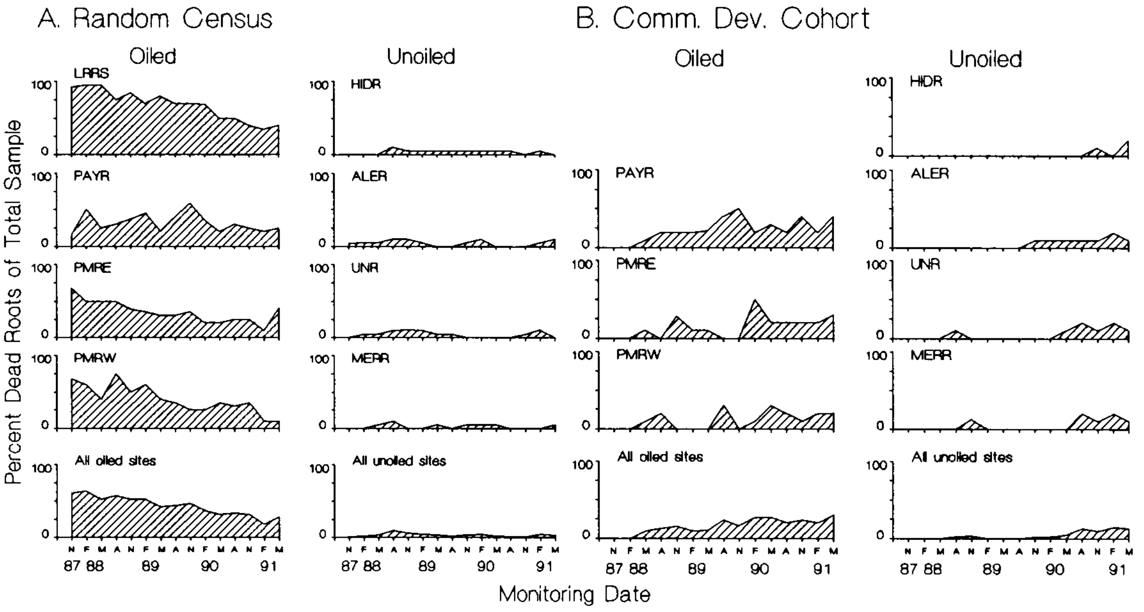

Fig. 9.62 Relative abundance of dead roots in drainage streams. Site codes follow Table 9.2. See text for methods and sample sizes. *A*. Percent of roots judged dead in quarterly, random censuses at oiled (left column) and unoiled (right column) sites and overall. *B*. Proportion of roots judged dead in quarterly, random subsampling of marked, community development roots at oiled (left column) and unoiled (right column) sites and overall.

habitat remaining at oiled sites relative to unoiled sites having two components: linear meters of living *Rhizophora* fringe multiplied by the number of prop roots/0.25 m^2 fringe. This estimate was then multiplied by the mean surface area/root to yield an estimate of the total surface area available for epibiotic settlement.

There was a mean reduction in the amount of shoreline fringed with *Rhizophora* and in the density of live and dead roots in surviving fringe at oiled vs. unoiled sites in all three habitat types (Fig. 9.64). Overall reduction of fringe area averaged 13.3% on the open coast (range of 0.2% at MINM to 22.1% at DROM). The number of roots/0.25 m^2 decreased by an average of 21.8% compared with unoiled sites. When the percent of the remaining fringe at oiled sites (86.7% of that at unoiled sites) was multiplied by the percent of roots found at oiled sites (75.7% of that at unoiled sites), we calculated, on average, that only 66.7% of the habitat remained available for the epibiota on the oiled open coast, with individual sites ranging from 38 to 90% of the habitat remaining. Put another way, on the unoiled open coast every 100-m section of fringe supported ~1,534 roots within our sampling universe, while ~1,075 would have been present at oiled sites.

Roots on the open coast had an estimated 22 cm^2 less surface area/root at oiled than unoiled sites. When this estimate of area is multiplied by the total

Table 9.14 Analysis of variance summary for percent dead roots by habitat type. Values are probability levels associated with ANOVAs on arcsine-transformed data. For *A* and *B*, *Y1*, *Y2*, *Y3*, and *Y4* are univariate ANOVAs for yr 1-4, August 1987-May 1991. The *oil*, *year*, and *Y x O* columns are repeated-measures ANOVAs for all 4 yr. There were three monitorings in 1987 for both types of data and four in 1988-1991. For *C*, data are probability levels for repeated-measures ANOVAs comparing random census and community development roots.

A. Random census, 1987-1991

Habitat	Y1	Y2	Y3	Y4	Oil	Year	Y x O	Spher.	H.F.?
Open coast	.002	.0001	.0002	.016	.0001	.126	.041	.133	no
Channels	.0001	.0001	.0005	.001	.0001	.140	.030	.178	no
Streams	.003	.002	.002	.0003	.001	.008	.006	.393	no

B. Community development cohort

Habitat	Y1	Y2	Y3	Y4	Oil	Year	Y x O	Spher.	H.F.?
Open Coast	.726	.310	.107	.005	.062	.0001	.584	.075	no
Channels	.203	.002	.019	.036	.001	.0001	.146	.300	no
Streams	<.0001	.023	.010	.033	.003	.0001	.038	.053	yes

C. Random census vs. community development cohort

Comparison	Open Coast	Channels	Drainage Streams
Between:			
Group	.001	.0001	.0002
Oil	.0001	.0001	.0001
G x O	.004	.001	.003
Within:			
Year	.0001	.0001	.019
Y x G	.0001	.0001	.0001
Y x O	.495	.046	.028
Y x G x O	.137	.039	.022
Sphericity Test	.014	.631	.161
H.-F. Adj. applied?	yes	no	no

Spher. = sphericity test. *H.F.?* = whether Huynh-Feldt-adjusted probabilities are given because of sphericity-test results.

number of roots/100 m of shore, there was ~65.8 m^2 of root area submerged at unoiled sites, while only ~43.8 m^2 was present at oiled sites. This is approximately 66.6% of the surface area at unoiled sites. Further, more of that area was deep in the water at unoiled sites, with relatively more surface area subject to periodic emersion at oiled sites. Thirteen percent of roots (~5.7 m^2 of submerged area) were dead at oiled sites, while 8% of roots were dead at unoiled sites (~5.3 m^2 of submerged area, calculated as percent dead in June 1991 density estimates multiplied by total estimated surface area).

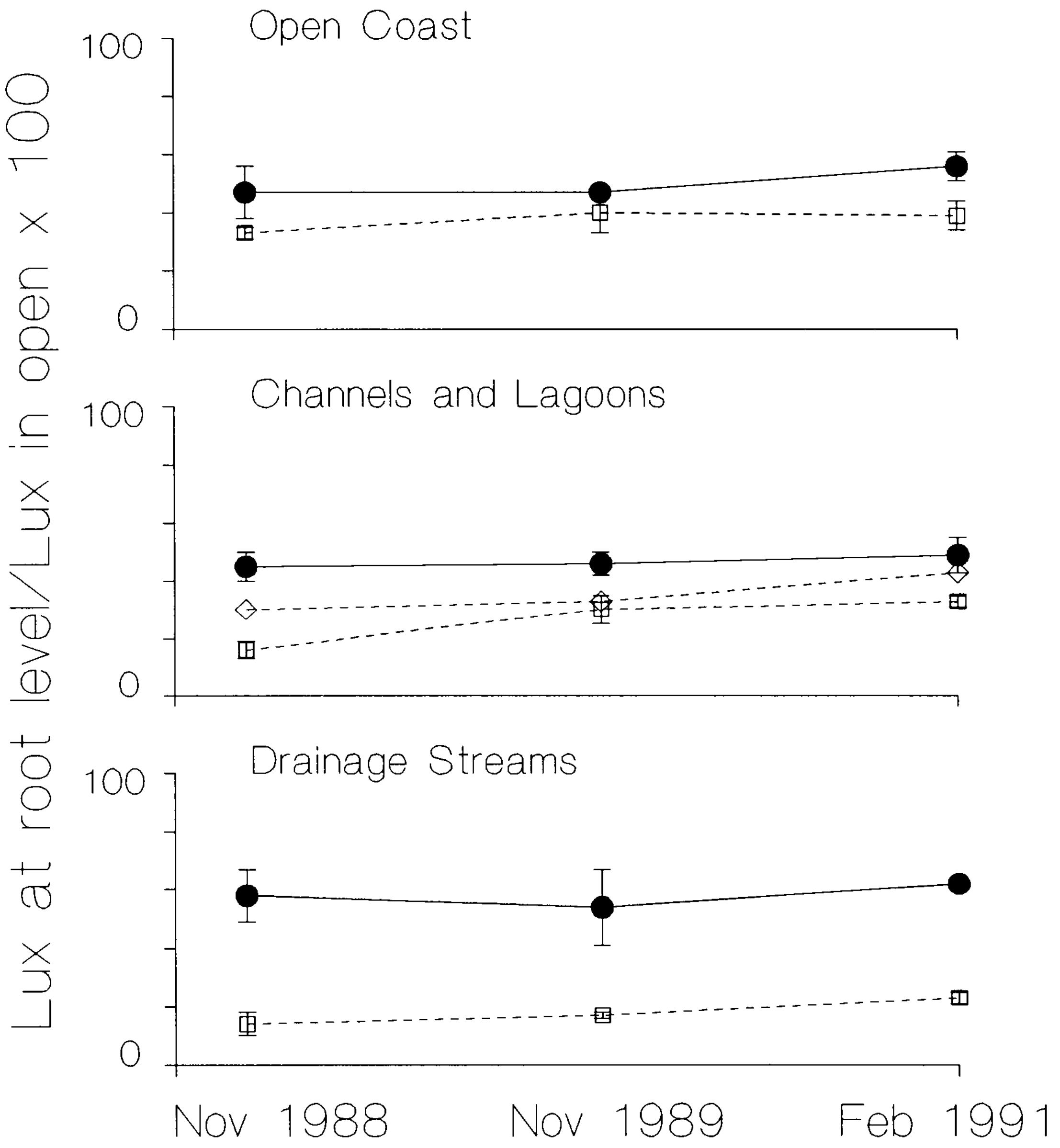

Fig. 9.63 **Transmission of light to root level. Data are paired readings of midday light intensity under and outside the canopy (N = 20 in, 20 out at each site). Each point is the among-site mean ratio of light at root level to that outside the fringe, with associated standard errors. *Solid circles* are values for oiled sites, *open squares* are those for unoiled sites, and *open diamonds* are for HIDC, the secondarily oiled channel site.**

In channels and lagoons, overall damage to the amount of fringe averaged 23.5% with individual sites ranging from 6.3 to 77.6% reductions in area (Fig. 9.64; Tables 9.4-9.6; App. Table E.6). Density of roots/0.25 m^2 at oiled sites was an

Table 9.15 Analysis of variance of light transmission to the water's surface by habitat: probability levels for 2-way ANOVAs by habitat type.

Source	Open Coast	Channels	Drainage Streams
Oil	.006	.0001	.0001
Year	.406	.068	.548
O x Y	.605	.274	.850

average of 20% lower (range = 6.5-23.9%). When the percent of the remaining fringe at oiled sites (76.5% of that at unoiled sites) was multiplied by the percent of roots remaining at oiled sites (80.4% of that at unoiled sites), we calculated, on average, that only 62.1% of the habitat remained available for the epibiota in oiled channels, with individual sites ranging from 17 to 86% of the habitat remaining. We then estimated that a 100-m length of unoiled shore should have ~1,840 roots, while only 1,132 would be present at oiled sites. The fringe at Hidden Channel (HIDC) appeared unaffected by a single episode of oiling in August 1988.

Roots in channels did not differ in depth distribution and had similar estimates of submerged surface area. Total surface area/100 m shore was estimated at 42.1 m^2 in oiled channels, compared with 67.7 m^2 in unoiled channels. In both oiled and unoiled channels most of that area was intertidal. Because root size and diameter did not differ between oiled and unoiled sites, root shape and depth of submergence did not affect estimates of overall damage. Nineteen percent of roots (~8 m^2 of submerged area) were dead in oiled channels, while 2% of roots were dead in unoiled channels (~1.4 m^2 of submerged area).

In drainage streams damage to the fringe was highest, with a 55.7% reduction in the area of the fringe in oiled streams (range = 14.7-92.4%; Fig. 9.64; App. Table E.6). Roots/0.25 m^2 of fringe were 16.2% less abundant at oiled than unoiled sites. When the percent of the remaining fringe at oiled sites (44.3% of that at unoiled sites) was multiplied by the percent of roots remaining at oiled sites (83.8% of that at unoiled sites), we calculated, on average, that only 37.2% of the habitat remained available for the epibiota in oiled streams, with individual sites ranging from 12 to 79% of the habitat remaining. Additionally, we calculated that a 100-m section of unoiled shore in drainage streams should have ~1,445 roots, while only 602 would be present at oiled sites.

When estimated surface area/root was multiplied by the number of roots/100 m shore, only 22.8 m^2 of surface area was submerged at oiled streams, and at least 2/3 of that area was intermittently emersed by tidal fluctuations. At unoiled sites, 86.2 m^2 of root surface was submerged, less than half of which was subject to periodic emersion. Oiled streams had approximately 27% of the submerged surface area found at unoiled streams. In addition, 15% of roots were dead at oiled sites

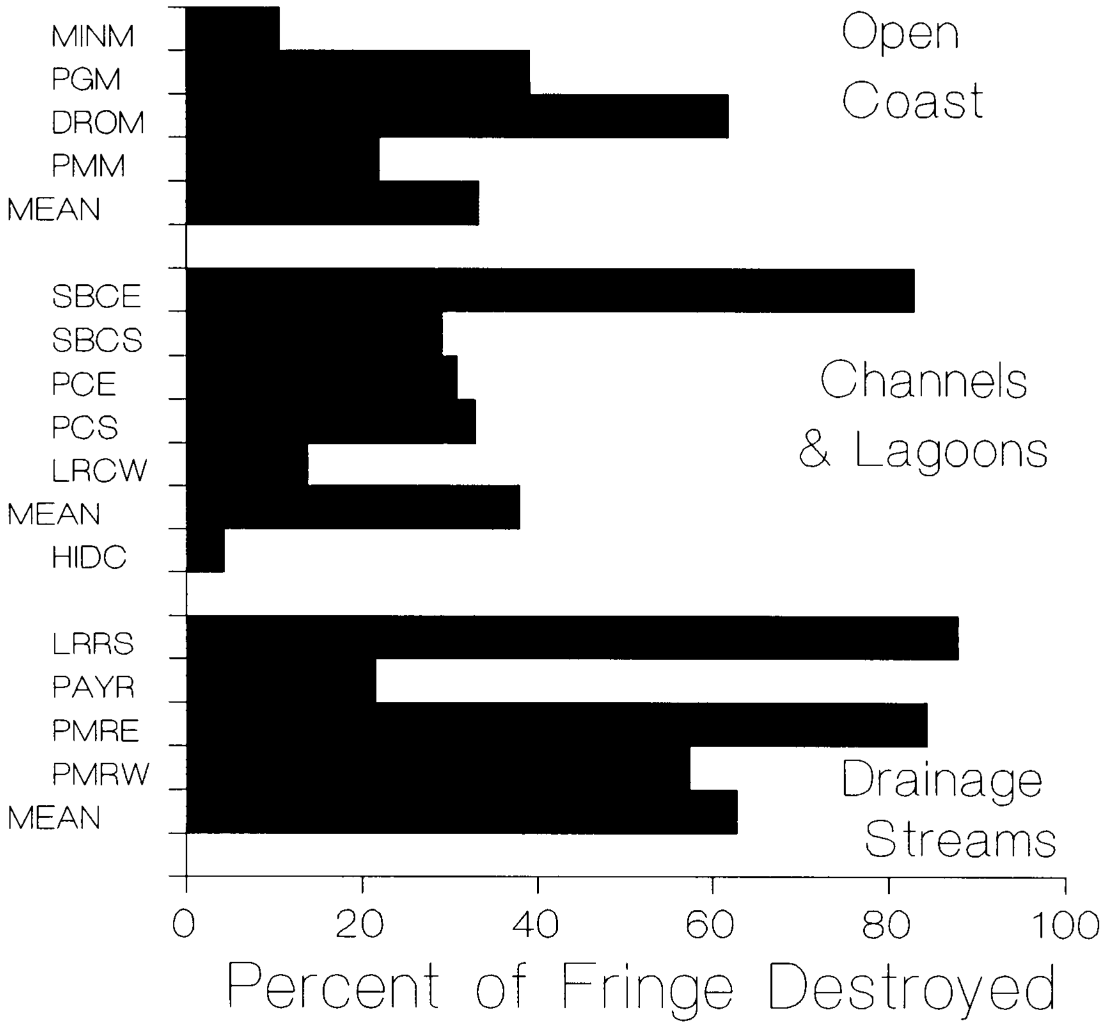

Fig. 9.64 Reduction of oiled fringing habitat after 5 yr. Data are from a transect run along the outer edge of the mangrove fringe at each site in May 1991. The occurrence and condition of mangroves were recorded each meter and effects of root density added. See text and Appendix Table E.6 for details.

(~3.4 m^2 of submerged area) compared with 2% of roots at unoiled sites (~1.7 m^2 of submerged area).

Amounts of Oil and Variation in Damage

Two types of data are available to examine how oiling might have affected red mangroves in the fringe: (1) sediment hydrocarbon concentrations and (2) cover of oil on root surfaces. Figure 9.65 plots the relationship between percent dead fringe, sediment hydrocarbon concentrations, and percent cover of oil on roots. Percent

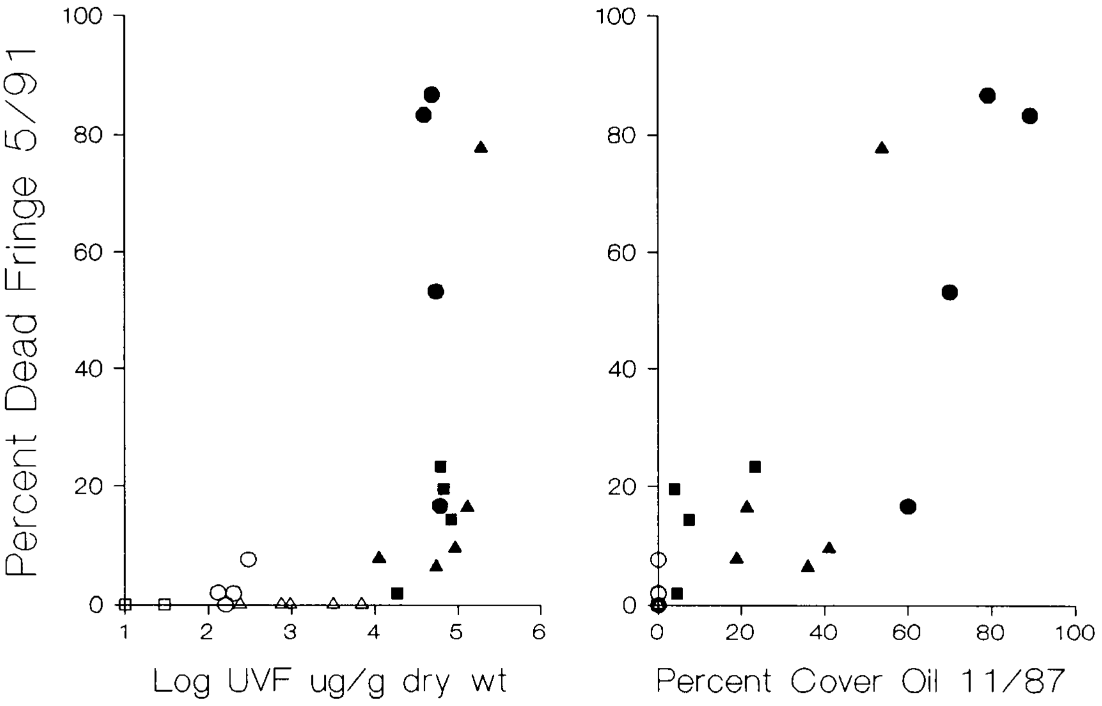

Fig. 9.65 Percent dead fringe in May 1991 versus two measures of oiling. *Left*, mean concentration of hydrocarbons in mangrove sediments collected in 1989 and 1990 (see text for details); *right*, mean percent cover of oil coating mangrove roots in November 1987 (see text). *Solid symbols* = oiled sites, *open symbols* = unoiled sites, *circles* = drainage streams, *triangles* = channels, *squares* = open coast.

dead fringe is the percent of total fringe killed at each site (Tables 9.4-9.6). Sediment hydrocarbon concentrations were calculated as the average of the 0-2 cm and 8-10 cm cores collected in 1989 and 1990 (cited with permission, K. Burns; see also Fig. 3.19). The data for percent cover of oil was arbitrarily chosen as the first date when all sites were sampled simultaneously (November 1987, 18 mo postspill).

Sediment hydrocarbon concentrations at all oiled sites were on the order of 10^4-10^5 μg/g dry weight in UVF units. Even with order-of-magnitude differences in hydrocarbon concentrations and expected order-of-magnitude dose responses (Krebs and Burns 1977), no evidence of dose response existed in the data. However, data on percent cover of oil indicate a different possible interpretation. We suggest that once 50% or more of prop root surfaces were covered by oil for at least 18 mo, 50% or more of the fringe was likely to die. Where oil cover was <50%, some fringe died, but the amount was variable among sites.

Differences in initial amounts of oiling vary in the opposite direction and do not account for this relationship (Sect. 9.4). In August 1986 oil coated more of root surfaces on the open coast (146%), with successively less of the total surface coated in channels (94%) and streams (75%). However, oil disappeared first from the open coast, coating <10% of root surfaces in November 1987 (18 mo postspill). Less surface area in channels was oiled and oil disappeared more slowly, with >20% of root surfaces oiled until February 1989 (33^+ mo). In streams cover was high and persistent. Fifty percent or more of root surfaces were oil coated until May 1988 (24^+ mo) and oil cover was 20% in May 1991 (60^+ mo).

Two partially independent tests of this hypothesis were provided by sediment hydrocarbons from channels. Control sites located in the western wing of Bahía Las Minas were visibly unoiled and had intact mangrove fringes throughout the study (sites SBCW, LRCS, and HIDC; Table 9.5). HIDC received no visible oil in 1986 and had only traces of oil in sediments. This site was oiled by a secondary release of VMIC between May and August 1988, with approximately 14% of root surfaces covered with oil. This was a single event, with no evidence of further deposition of oil residues (see Sect. 9.4).

Sediments from these sites were cored in May 1989 and July 1990. Hydrocarbon concentrations, calculated as above, consisted of weathered VMIC and averaged 10^3 μg/g dry weight in UVF units. These oil residues probably came from resuspended hydrocarbons that were dissolved and then circulated through Bahía Las Minas. Despite these sediment hydrocarbon loads, and the partial coating of roots at HIDC, the mangrove fringe at these three sites was intact. This suggests that without thick and long-lasting coatings of oil, mangroves in the fringe might not have been killed. It does not, however, rule out the possibility of sublethal effects (e.g., Fig. 3.19; Krebs and Burns 1977).

This interpretation is tentative, because we cannot establish the direct toxicity of oil arriving at any one site. Slicks arrived in different stages of weathering over a prolonged period. It is possible that variability in the mortality of trees along the fringe was related to both the amount of oil on roots and the initial toxicity of oil that soaked into sediments.

9.5.2.3 Summary and Discussion

Long-term Effects on the Mangrove Fringe

The Bahía Las Minas spill significantly reduced the area of mangrove fringe and therefore decreased the amount of habitat available for associated plants and animals. This effect was evident at the simplest level: measurement of the number of meters of mangrove-fringed shoreline remaining 5 yr after oiling. All three habitats were affected. Within the surviving fringe, fewer submerged roots were recorded per unit area, further decreasing the amount of potential settlement surface.

Physical characteristics of submerged roots in the mangrove fringe changed after oiling. Roots were shorter in 2 of 3 habitats, so less area was submerged deep in the water column. The reduction of area at subtidal levels may have had especially important effects on epibiota intolerant of emersion or changes in salinity after heavy rainfall.

More roots were dead at oiled than unoiled sites. Dead roots may lack settlement cues for larvae and spores in the plankton, may be an unsuitable substratum for settlement, or may otherwise affect settlement patterns. Thus, the epibiota of fringing prop roots may be affected over the long term by changes far more subtle than the simple reduction of area in the fringe. Further analysis of our data, as well as experimental manipulations, are needed to delineate possible effects.

If estimated surface area on roots is related to the productivity of epibiota on mangrove fringe, there may be substantial among-habitat differences unrelated to oiling. We roughly estimate that, per 100 m of shore, ~66 m^2 of surface area is submerged in channels and on the open coast, while in streams the submerged surface area is ~86 $m^2/100$ m. The presence of ~30% more surface area in streams may set the stage for among-habitat differences in overall productivity. This awaits further investigation.

One secondary effect of the partial defoliation of surviving mangrove fringe was an increase in average light reaching root level. Differences were strongest in drainage streams, which normally had the lowest light transmission of the three habitats examined. The effects on attached epibiota could be either positive or negative, depending upon the group and specific conditions. Assuming that toxic effects of oiling disappeared, light-limited species might grow better at oiled than unoiled sites. However partial defoliation probably also increases heat and desiccation stress on roots, perhaps impeding settlement or growth of small organisms. Experiments are needed to examine these possibilities.

The initial effects of oiling on the mangrove fringe appear to have been caused by direct contact with oil, i.e., smothering, toxicity, or both of hydrocarbon residues (Cubit et al. 1987; Jackson et al. 1989; Garrity and Levings 1992). Beginning less than 3 mo after oiling, red mangroves started to defoliate and die. Five years after the spill, there were long-term effects on structural characteristics of the mangrove fringe.

Patterns and Timing of Damage

The time course of defoliation and collapse differed among habitats. In general, where leaf loss began first, damage to the fringe was most severe 5 yr later. Overall damage was highest in drainage streams, where trees were bare within 6-9 mo after the spill and collapse began within 2 yr. Defoliation was lower and took longer to appear in channels and on the open coast. Most collapse occurred 2.5-4 yr after oiling. The rapidity with which trees defoliate after oiling may partially predict the extent of long-term damage. Given our observations, it would not have been possible to estimate the extent of damage fully until at least 3 yr after oiling.

We tentatively attribute differences in the amount of damage among habitats and sites to characteristics of both the sites themselves and of how oil was deposited. Empirically, if oil covered more than 50% of root surfaces 18 mo after oiling, more than 50% of the fringe was likely to die. This was most likely to occur in sheltered tidal streams. On the open coast, wave action removed most oil within a year and less of the fringe died. In channels less oil was deposited on roots and it did not remain as long as in streams. Thus, damage was heaviest in the most sheltered sections of the bay, where thick coatings of oil persisted over time.

Survival of mangrove fringe also appeared related both to depth and type of substratum (App. Table E.7). Depth was the most important factor in oiled streams and channels. Most trees in the intertidal zone defoliated totally and subsequently died; the entire intertidal surface of prop roots was coated with oil. Those trees with most prop roots anchored in subtidal sediments survived, probably because some oxygen exchange was possible over the root surface. Depth was important on the open coast as well, but substratum type (sediment grain size) also appeared to affect survival. Trees anchored in shallow sand or calcium carbonate rubble survived better than those in shallow mud or peat.

Both of these observations suggest that where oxygen exchange was severely limited by oiling, trees were more likely to die. However, possible toxic effects of dissolved hydrocarbons or of oil trapped in sediments cannot be discounted; levels remained high for at least 5 yr (Burns, Chap. 3).

Fringe Structure: Characteristics Relative to Damage

Despite the reductions in physical space for epibiota to inhabit (e.g., roots) along the oiled fringe of mangrove forests around Bahía Las Minas, the effect of oil was less severe along the fringe than on mangroves from the shallows behind the fringe to the shore, where virtually all trees died (Tables 9.4-9.6; Fig. 9.66; see also Duke and Pinzón, Chap. 8). Even in drainage streams, where mortality of fringing *Rhizophora* was greatest overall, some trees along the banks survived, while those in the shallows back from the bank died. Several studies have noted survival of the outer edge of the mangrove fringe in spills that defoliated and killed interior mangroves (Cintrón et al. 1981) or increased oiling from the fringe landward (Nadeau and Bergquist 1977). Getter et al. (1984) present a model of oil effect on fringe mangroves based upon topography and forest type, suggesting that maximum damage occurs in shallow waters near the berm (except in the case of high water carrying oil over the berm into "inner basin" forests). Had the spill occurred in dry season (as in the *Witwater* spill of 1968), higher water levels and wave action might have concentrated oil, and subsequent damage, inshore of the fringe on (or even behind) the berm. In the Bahía Las Minas event, and other spills, we suggest partial survival of the outer fringe may be extremely important in recovery processes of the epibiota of prop roots and of the mobile organisms dependent upon the epibiotic assemblage for food and shelter.

9.5.3 Abundance and Vertical Distribution of Epibiota

In this section we present detailed results on the epibiota of mangrove roots. To describe unoiled community composition over time, we track percent cover of sessile organisms on randomly chosen roots over a 5-yr period. We also document

Fig. 9.66 Survival of outer *Rhizophora* fringe following oiling. *A*. Aerial photograph, February 1987, of Isla Largo Remo mangroves. Many fringing mangroves on open shores and in channels and lagoons survived oiling (dark margins of forest) while those behind the fringe defoliated and died (light areas). In contrast, most mangroves fringing banks of drainage streams died (LRRS is seen as the light band running through the center of the mangrove forest). (Photograph by C. Hansen; reproduced with permission from Jackson et al. 1989, p. 39, copyright 1989 by the AAAS)

the vertical distribution of epibiota on roots, since the physical regime changes with depth of submergence. Such changes could affect the distribution and abundance of species on roots. We investigated settlement variation using groups of artificial roots, set out for ~2.5 mo and then monitored for percent cover. Finally, we examine successional processes on a cohort of marked roots that entered the water during a single 2-mo interval, by quarterly sampling of a subset of marked roots. The same series of data were taken at oiled sites. We then examine these results, statistically comparing oiled and unoiled sites within habitats, with the goal of differentiating natural variation from changes in the epibiotic community caused by the oil spill.

Fig. 9.66 Survival of outer *Rhizophora* fringe following oiling (continued). *B.* Ground photograph, May 1990, site = PCE. Seaward view of area of devastated *Rhizophora* from the landward fringe (*foreground*) and of surviving trees along the outer fringe (*background*). Small saplings in the foreground were planted by refinery personnel.

9.5.3.1 Materials and Methods

In 1981-1982 a starting point (tree) along the fringe within each site was picked at random. From this point, 25 roots to the left and 25 roots to the right were chosen using a random numbers table. Roots that had not grown at least 5 cm into the water and those firmly embedded in bottom sediments were rejected, and the nearest appropriate root was used instead. Each selected root was lifted from the water and its length from the HWL to the longest tip and its diameter at the waterline were measured. Percent cover of encrusting organisms was estimated visually. A posteriori we rejected roots <20 cm in length to make these samples comparable to those taken from 1986 through 1991 (see below). Sampling was repeated in January and June 1982. For the latter survey, data are available for only 25 roots each in channels and drainage streams.

Mangrove roots and their epibiota were sampled again beginning in July-August 1986, roughly 3 mo after oil began coming ashore. Monitoring continued quarterly at the sites described in the preceding section through May 1991. This sampling was designated *long-term census*. Method of selection of roots was random, as in 1981-1982. Roots attached to the bottom or not extending 20 cm below the high-tide line were rejected and the closest root sampled instead.

Several more quantitative methods of determining percent cover other than visual estimates were examined. Strings of lengths varying in 5-cm increments from 20 to 250 cm, with 100 marked points in a stratified random array, proved to be the most simple and accurate method and were used from August 1987-May 1991. An appropriately sized string was held against the root and what lay under each point was recorded. Organisms present but not found under a point were recorded as traces and assigned a percent cover of 0.01%. Blind-coded trials in which visual estimates were compared with estimates using strings showed that these methods gave virtually identical results (± ~3%).

Beginning in August 1987 the focus of the study was widened and two additional types of data were collected quarterly. First, we investigated the development of assemblages of sessile organisms on mangrove roots from the time roots enter the water. A cohort of actively growing roots just above MHW was marked with flagging tape. Roots were marked at all sites except LRRS, where there were no living roots about to enter the water. Tags were removed from roots that had not entered the water by November 1987. All cohort roots thus entered the water during a 2-mo period, a year-and-a-half after the oil spill. Five randomly chosen roots from the cohort were measured and sampled for percent cover and root condition at each site in November 1987 and February 1988. From May 1988 through May 1991 sample size was increased to 10 roots per site.

Second, patterns of recruitment were followed using artificial roots. Five half-inch diameter hardwood dowels, 91 cm long, were hung vertically in the water at each site and collected 3 mo later (Fig. 9.67). (In May, August, and November 1987, sections of aerial roots rather than dowels were used in pilot experiments). After collection each was floated in seawater in the laboratory and examined under a magnifying light. Percent cover of organisms that had settled was estimated using 91-cm long nylon lines with 100 inked dots in a stratified-random array. The number of sites used was variable until May 1988, after which all 26 sites were included each quarter.

Third, beginning in August 1988 we examined the vertical distribution of organisms on a subsample of long-term census roots. For 5 of the 20 randomly selected roots ≥75 cm in length, data were recorded individually, rather than cumulatively, for each of the 100 points. This allowed us to assign locations (depths) to organisms.

Data were taken in 20 quarterly monitorings, from August 1986 through May 1991, at oiled and unoiled sites on the open coast, in channels, and in drainage streams. Data from each site within a given habitat (open coast, channel, and drainage stream) and treatment (oiled and unoiled) are shown both individually and

Fig. 9.67 Recruitment dowel in position. May 1990, site = LRCS. The dowel was attached, as vertically as possible and below MHW line, to a bare, aerial root using two plastic cable ties. Epibiota on roots to the *right* include *Crassostrea* and *Isognomon*.

combined as among-site means (mean of all site means). Standard-error bars were included only when they would not obscure the mean. In the first year after the spill, 2-3 sites per habitat type were sampled. Beginning in August 1987 means were calculated from quarterly samples of 4-5 sites (20-25 roots/site, 80-100 roots/habitat) in *long-term random censuses*, from 3-4 sites (5-10 roots/site, 20-40 roots/habitat) in the *community development* study, and 4-5 sites (from ~20 dowels, roughly, due to variable losses, set in groups of five at each site) in the *recruitment* study. Site abbreviations on figures and in the text follow Table 9.2.

There were several stages in identification of species during this study. First, when percent-cover estimates of plants and animals began, unidentified taxa were assigned code names until they were identified. Over time, the number of unidentified organisms decreased, mainly through the efforts of taxonomic experts (below). Where individual identifications were not possible, major groupings were used in analyses (e.g., all tunicates). Second, considerable space was occupied by categories or species that could not be differentiated in the field (e.g., diatoms, blue-green algae, mixed-algal turfs, mixed arborescent bryozoans and hydroids, and crustose coralline algae). The composition of such groups was examined in the laboratory, however, because time constraints did not permit laboratory analysis of every sample, such groups were conservatively analyzed as categories. Where two species could not be separated in the field, species names are separated by a slash (e.g., *Bostrychia tenella/B. binderi*).

Foliose algae were identified by Drs. P. M. Peckol, J. D. Cubit and, J. L. Connor, who also attempted to identify the small filamentous forms that could not be differentiated in the field. Algal nomenclature follows Taylor (1960), and Schneider and Searles (1991). Sponges were identified by Dr. J. Wulff. Dr. H. W. Harry confirmed that *Crassostrea virginica* was the only oyster present, although two morphological forms occurred at our sites.

9.5.3.2 Results

Open Coast – Unoiled Sites

Long-term Census

Fringing mangrove roots on the unoiled, open coast supported a diverse epibiotic assemblage, best characterized by foliose and crustose algae (Figs. 9.6, 9.7; see also Batista 1980). Overall mean abundance of foliose algae ranged from 16 to 33% cover from August 1986 through May 1991 (Fig. 9.68). Crustose algae were initially rare, but increased by a factor of ~10 between August 1986 and May 1991; average percent cover among sites was ~12% from November 1988 to May 1991 (Fig. 9.69). Blue-green algae were highly variable in percent cover over time (range = 1-20%; Fig. 9.70). Barnacles, sponges, cnidarians, arborescent hydroids, bryozoans, and other sessile invertebrates together covered 8-18% of root surfaces (Fig. 9.71), but no taxon averaged more than 11% cover at any monitoring (mean of

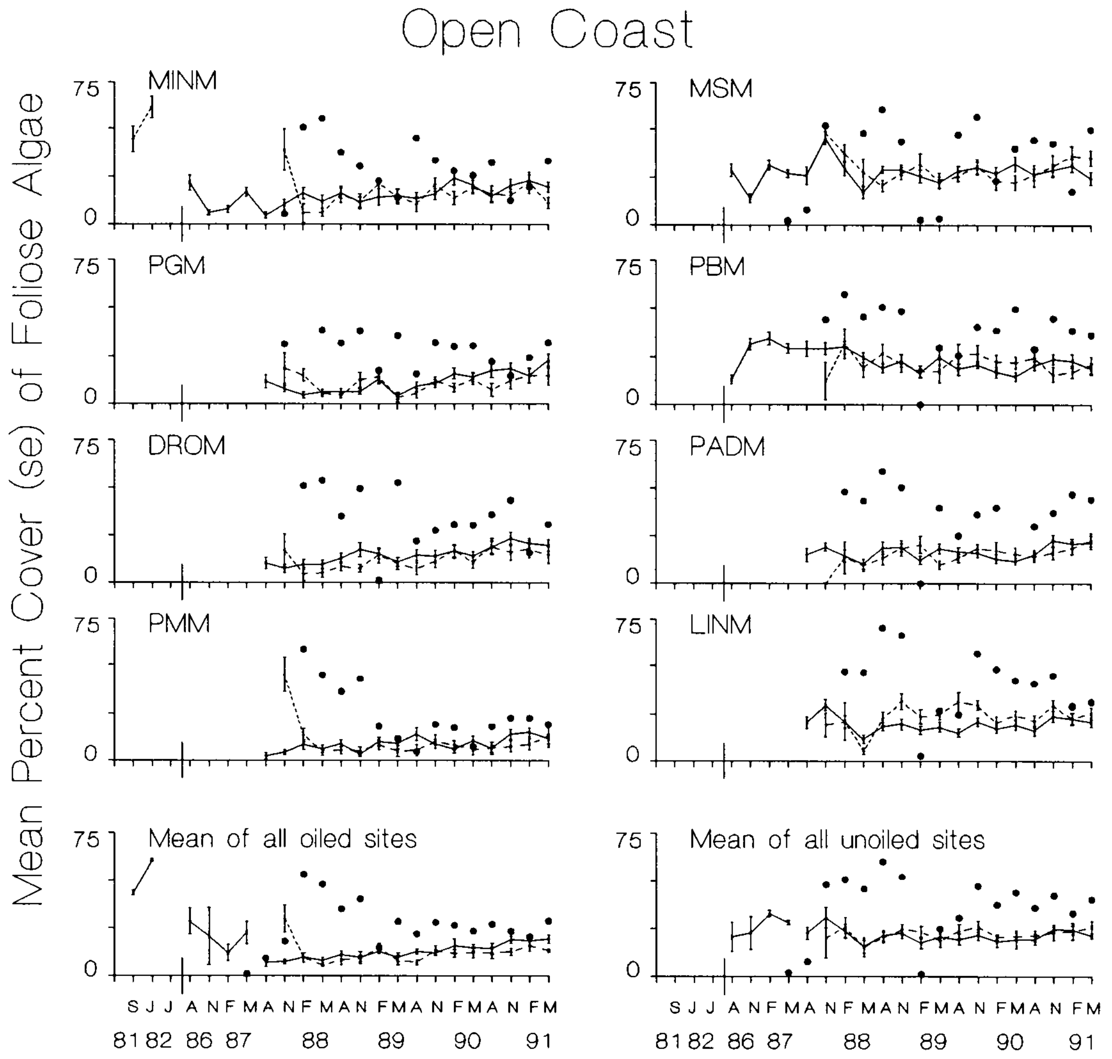

Fig. 9.68 Patterns of foliose algal abundance on roots on the open coast. Data are mean (± SE) percent cover of foliose algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

all unoiled sites; Figs. 9.72-9.75). Diatoms were similar to foliose algae in their pattern of abundance, averaging 12 to 34% cover (Fig. 9.76). The remaining space was either occupied by rare and intermittently present organisms (bivalves, amphipod and polychaete tubes, and vermetids), or was unoccupied. Between 16 and 34% of space on roots was bare (Fig. 9.77).

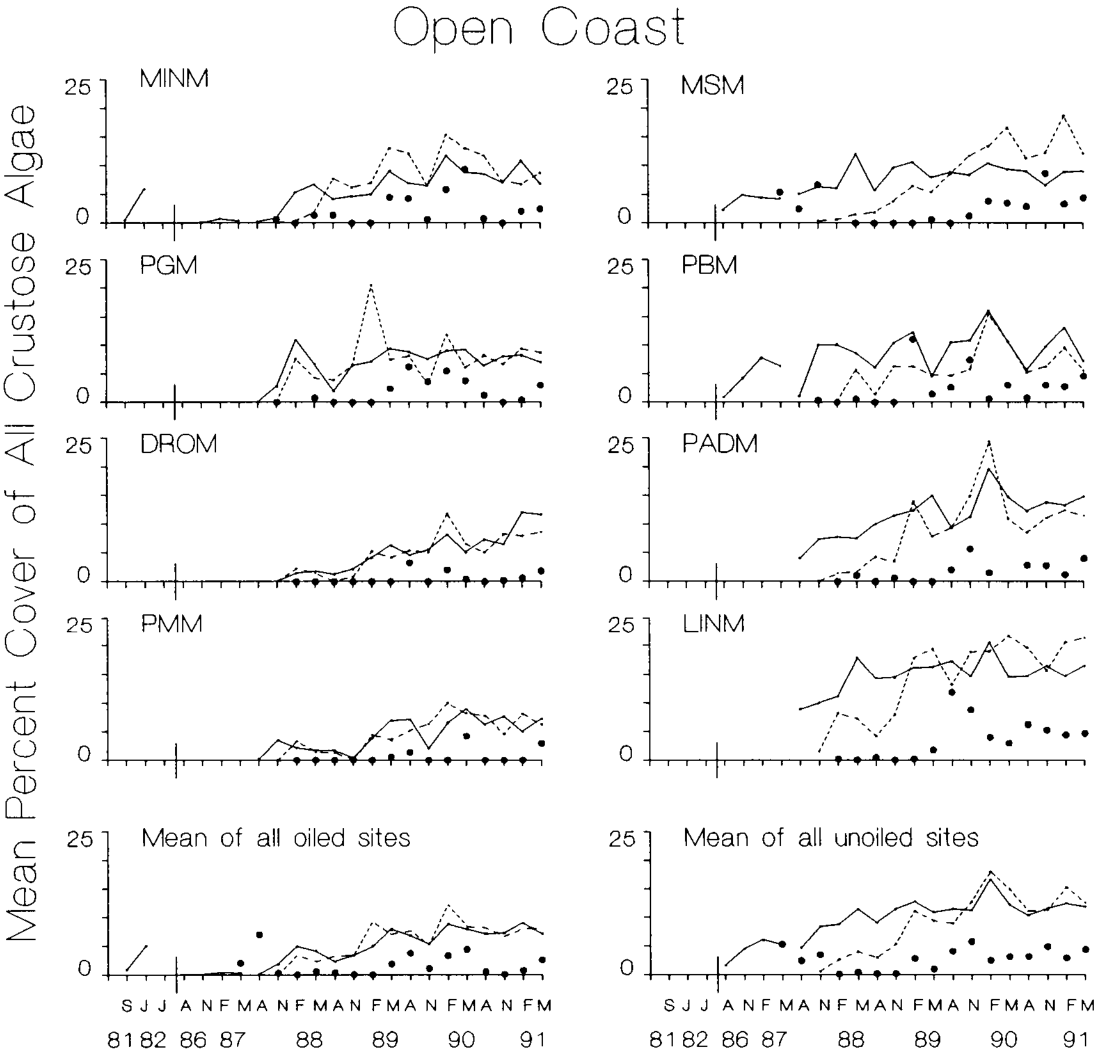

Fig. 9.69 Patterns of crustose algal abundance on roots on the open coast. Data are mean percent cover of crustose algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

Foliose Algae. Differences in species composition among sites were examined for foliose algae, the most abundant and diverse group on roots. Species composition among all unoiled sites from 1986 to 1991 was broadly similar. Rarefaction estimates of the expected number of species in a sample of 20 roots found 8.2-17.0 species of foliose algae expected per site (Fig. 9.78) during the 5-yr sampling period (see App. Table E.8 for a list of foliose algae identified during the study). Rarefaction estimates varied among years. At PBM and PADM, estimated number of species

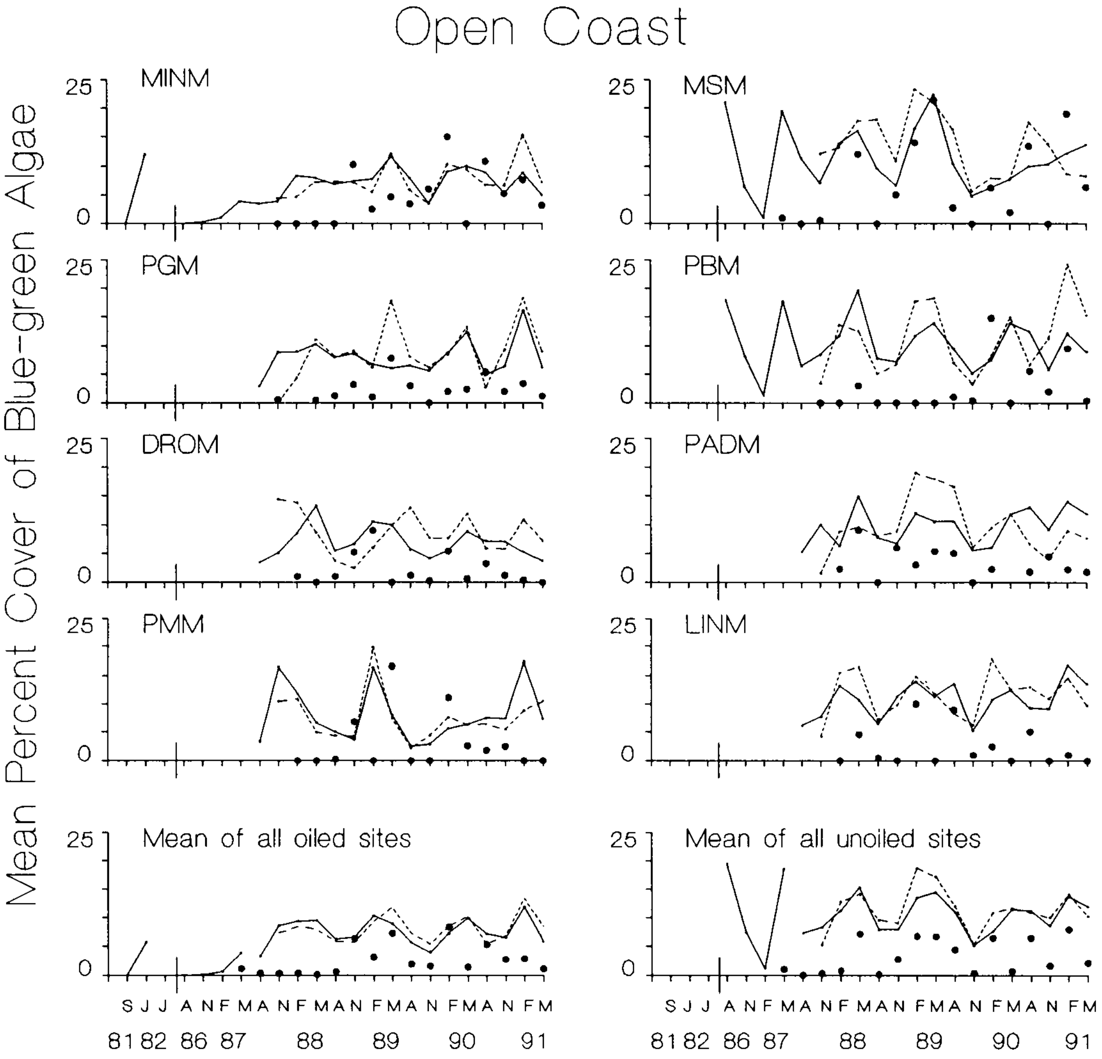

Fig. 9.70 Patterns of blue-green algal abundance on roots on the open coast. Data are mean percent cover of blue-green algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

fluctuated around 10/20 roots. There was a steady increase in estimated number of species/20 roots at MSM and LINM.

An average of ~2 species of algae was found on each sampled root (Fig. 9.79). Mixed-algal turfs were most abundant, occurring on more than 64% of roots at all sites in all years. They consisted of <3-mm high turfs of fine filaments of red, brown, green, and blue-green algae, but were treated as a single species because they could not be differentiated in the field (J. Connor, pers. comm.). There was a weak

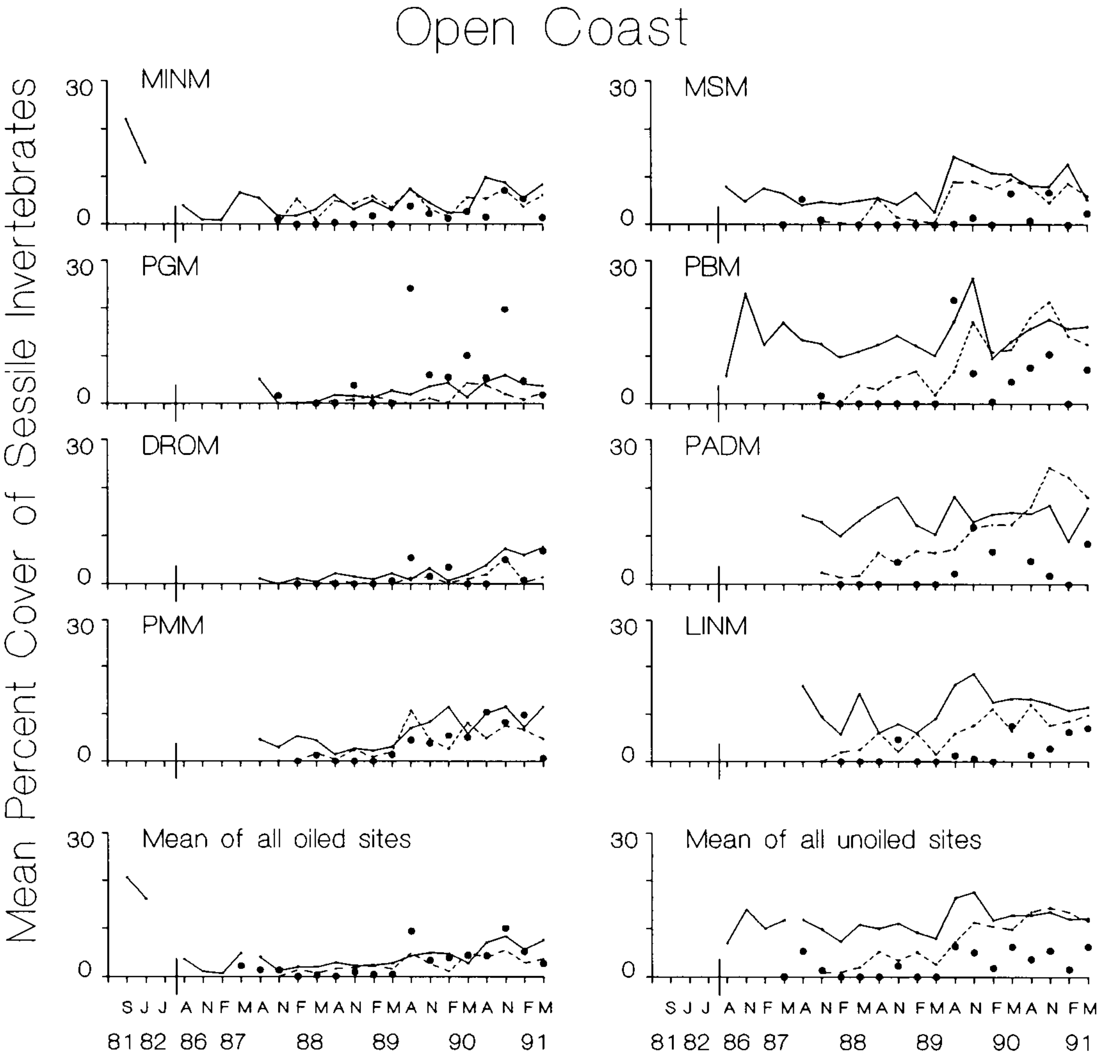

Fig. 9.71 Patterns of abundance of sessile invertebrates on roots on the open coast. Data are mean percent cover of sessile invertebrates for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). "Sessile invertebrates" were defined as all groups except barnacles and bivalves.

positive relationship between percent cover of algae and the mean number of species/root (Fig. 9.80); more species were recorded as the amount of algae increased.

In 4 yr of balanced sampling (August 1987-May 1991) between 30 and 40 species or species groups were recorded each year. Twenty-five to 36.4% of foliose algal species were recorded at all sites, while 30.0-43.3% of species were found at

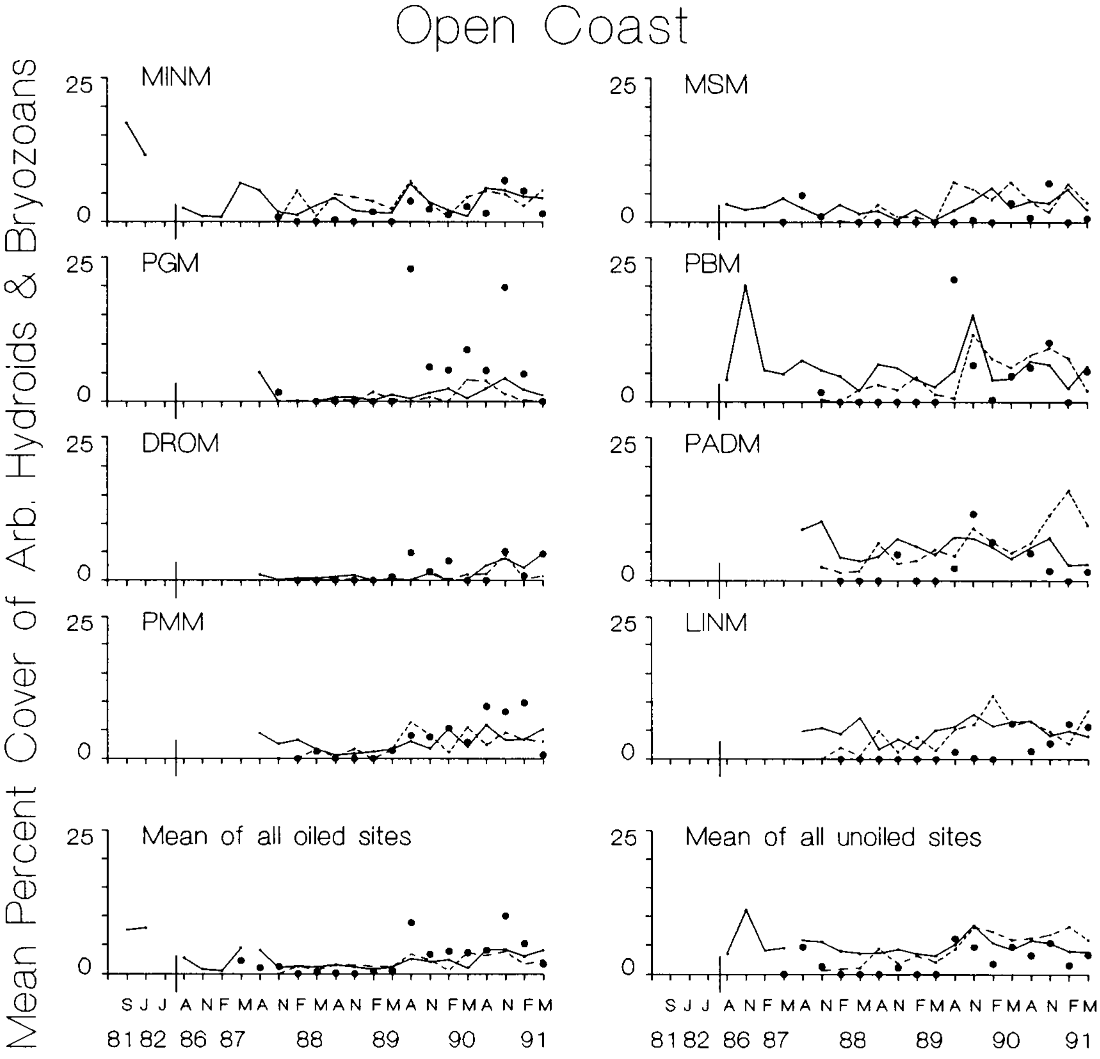

Fig. 9.72 **Patterns of abundance of arborescent hydroids and bryozoans on roots on the open coast. Data are mean percent cover for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census roots (*N* = 20-25/site),** ***dashed lines*** **are community development roots (*N* = 5-10/site), and** ***solid circles*** **are recruitment dowels (*N* ~5/site). See text for details.**

only one site in each year. Ubiquitous species, found at all sites in all 4 yr included: *Acanthophora spicifera*, *Cladophora* spp., *Dictyota bartayresii*, *Amphiroa rigida* var. *antillana*, *Struvea anastomosans*/*Struvea ramosa*, and mixed-algal turfs. Genera of foliose algae that also occurred regularly included: *Galaxaura*, *Caulerpa*, *Ceramium*, *Derbesia*, *Chaetomorpha*, *Laurencia*, *Padina*, *Hypnea*, and *Gelidium*. The identity of rare species shifted among years. For example, *Wrangelia argus* was collected in only

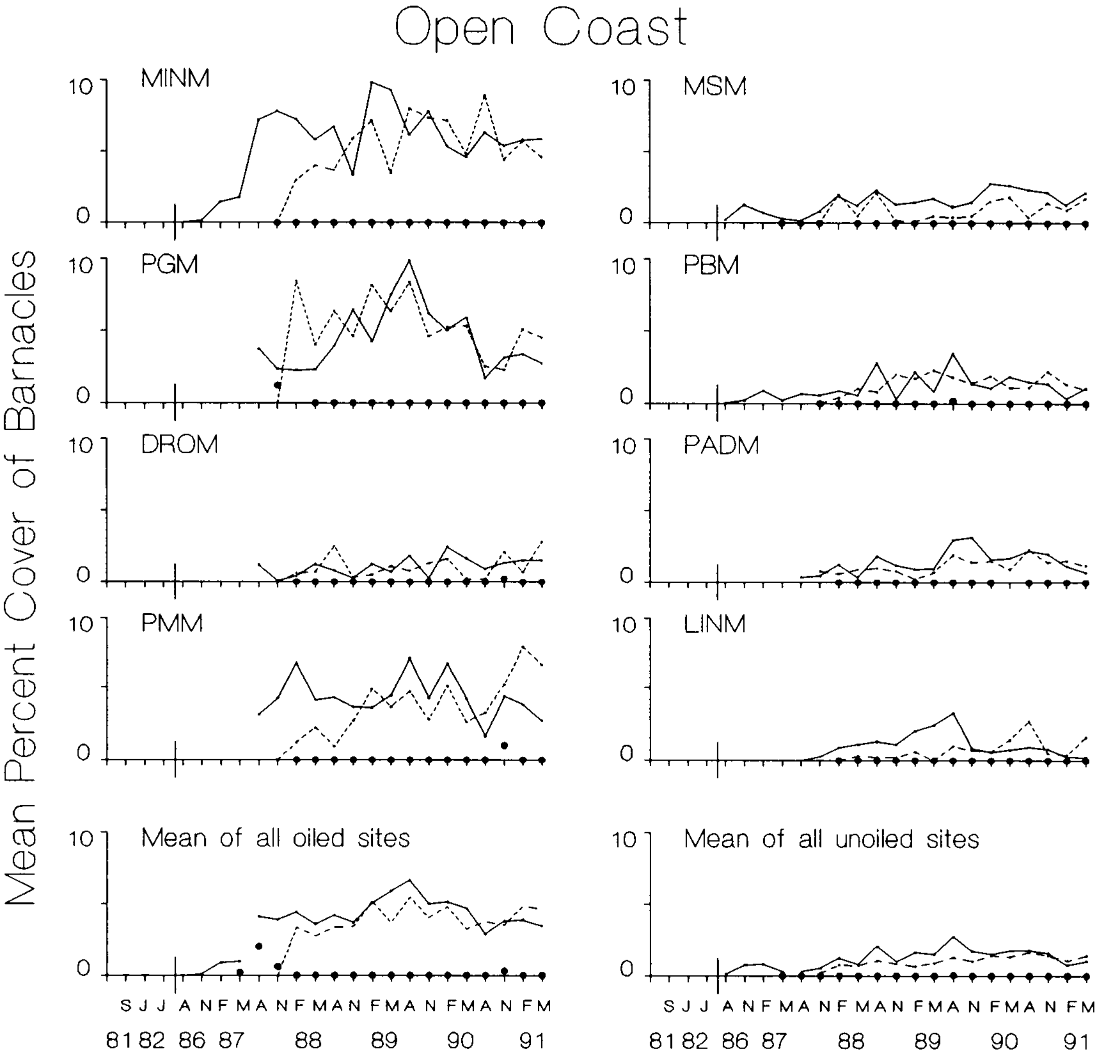

Fig. 9.73 Patterns of barnacle abundance on roots on the open coast. Data are mean percent cover of barnacles for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

one year at one site (MSM), while *Caulerpa racemosa* was found at one site in August 1988-May 1990 and three sites in August 1990-May 1991.

These species of foliose algae are a subset of those found on the hard substratum of reef flats, rocky shores, and coral reefs throughout the Caribbean (e.g., Connor 1984; Norris and Bucher 1982; Taylor et al. 1986; Littler et al. 1989; Cubit 1991). Also present, but patchy on the open coast, were members of the "Bostrychietum" group of species, characteristically associated with mangrove roots

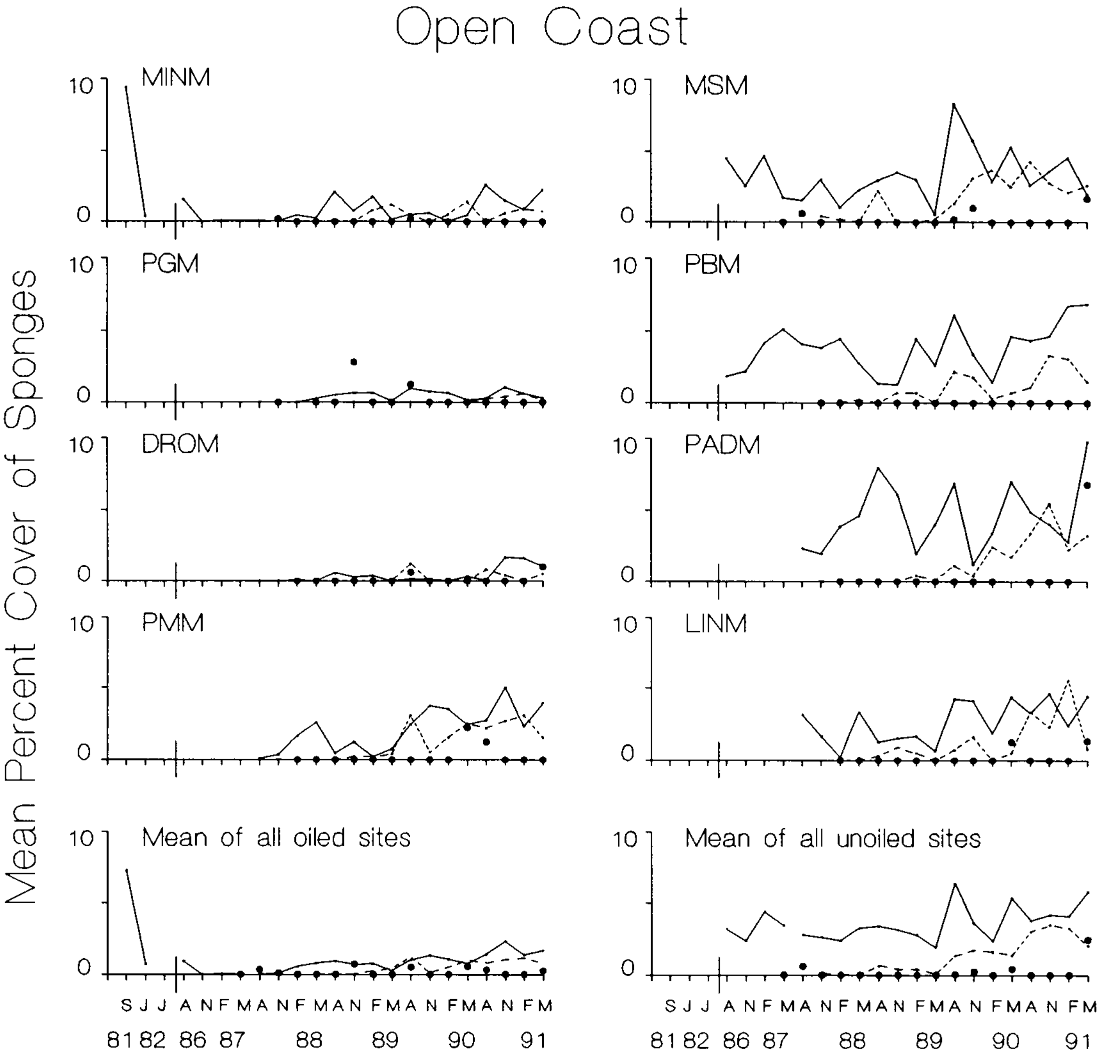

Fig. 9.74 Patterns of sponge abundance on roots on the open coast. Data are mean percent cover of sponges for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

worldwide (Post 1963). This group included: *Bostrychia tenella/B. binderi*, *Caloglossa leprieurii*, *Catenella repens*, *Herposiphonia tenella*, *Murrayella periclados*, and *Polysiphonia subtilissima*.

Foliose algae were distributed from the HWL to the deepest segments of roots (Fig. 9.81). *Bostrychia tenella* and *B. binderi* occurred highest on roots. Beginning ~30 cm below MHW, other foliose algae were found throughout the depth range of roots. The pattern of algal depth distribution did not vary among years.

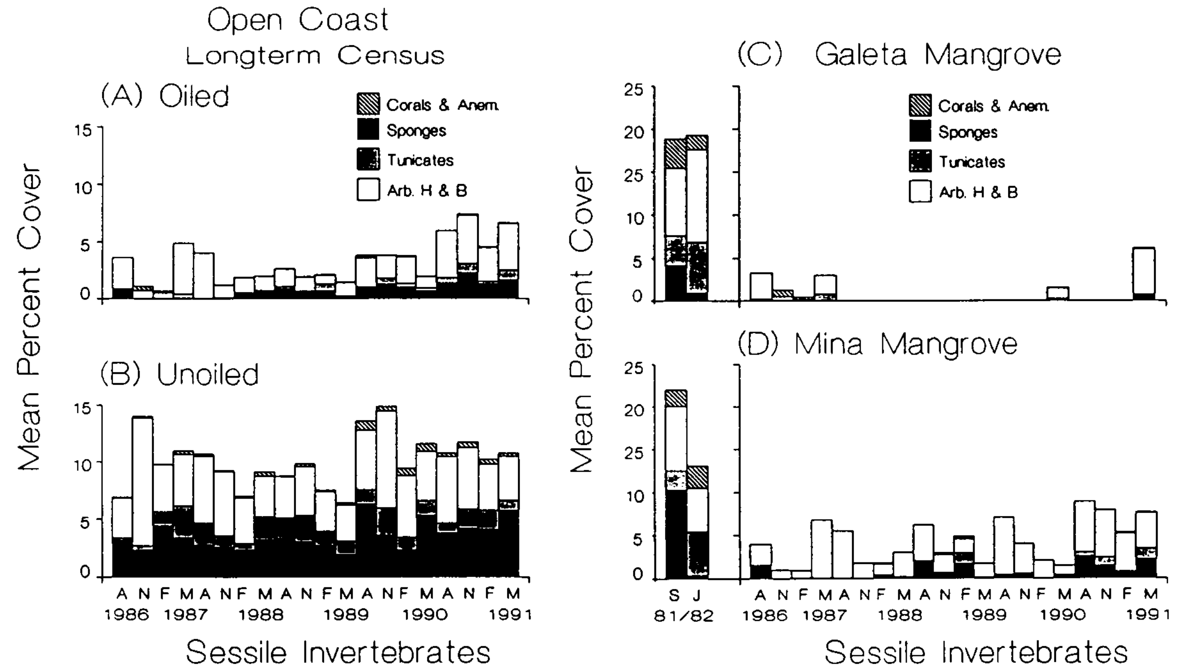

Fig. 9.75 Changes in abundance of sessile invertebrate groups over time on the open coast. *A*. Oiled site means. *B*. Unoiled site means. *C*. Galeta Mangrove (GALM), an oiled site with prespill data. *D*. Mina Mangrove (MINM), another oiled site with prespill data.

Crustose Algae. Crustose algae could not be differentiated to species in the field. We divided them into three groups: fleshy, noncoralline crusts; pink (= healthy) crustose coralline algae; and bleached (= desiccated or dead) crustose coralline algae. Fleshy and coralline crusts increased in abundance between 1986 and 1991 (Figs. 9.82, 9.83). Bleached crustose coralline algae showed a strong seasonal pattern (Fig. 9.84). They were most common in early wet season, which is typified by extended, daytime low tides (Cubit et al. 1986, 1988*a*, 1989).

Fleshy crusts were most abundant at depth, but could occur up to MHW (Fig. 9.85). Bleached coralline crusts were most common in the top 50 cm on roots (approximately the intertidal zone, Cubit et al. 1986), but also occurred deeper. Pink crustose coralline algae occurred from 20 cm below MHW, but were relatively rare above 30 cm below MHW.

Blue-green Algae. Morphologically confusing, blue-green algae formed crusts, turfs, filaments, and stromatolites on roots. Abundance of combined forms was highly variable over time (Fig. 9.70), with peaks in the dry season. Blue-green algae

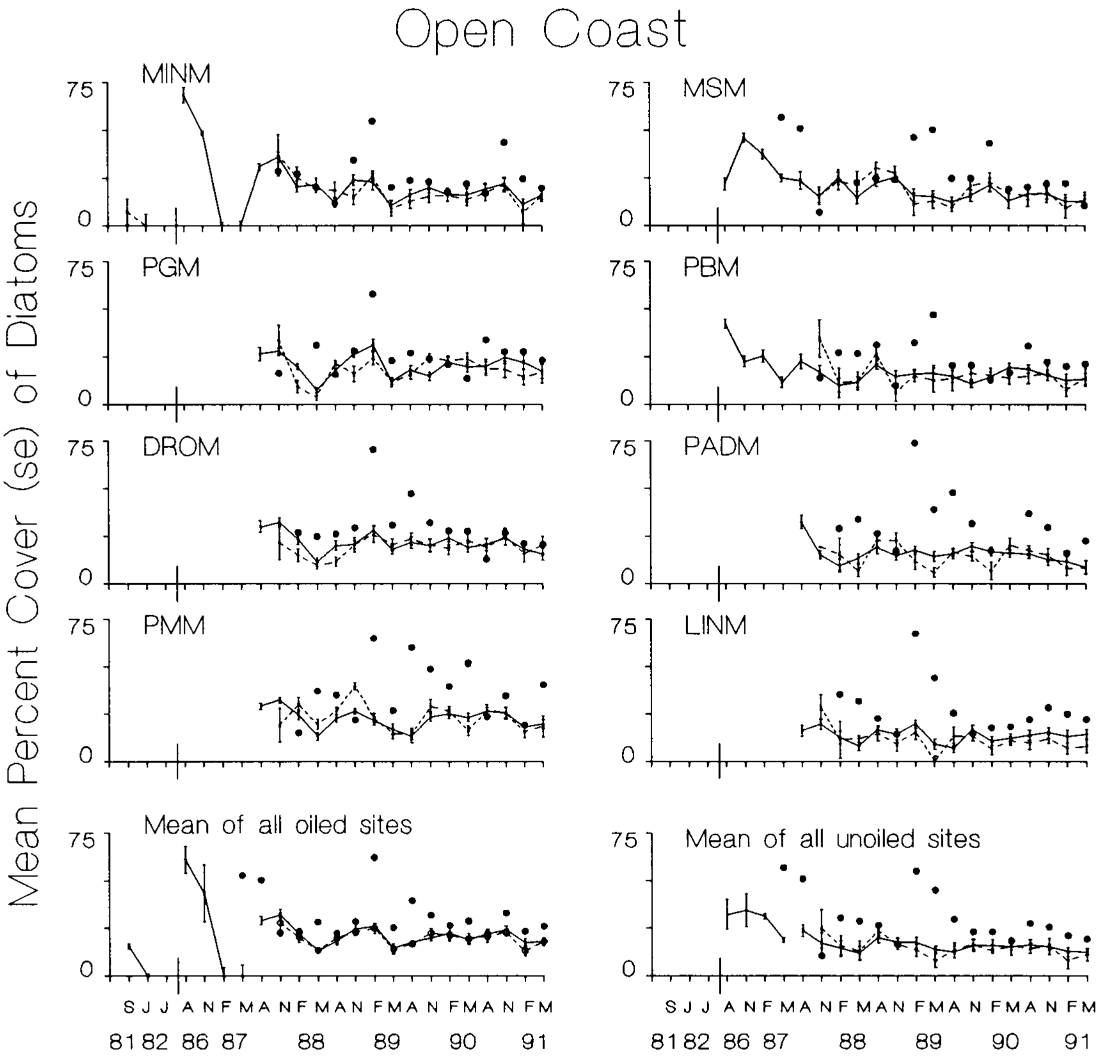

Fig. 9.76 Patterns of diatom abundance on roots on the open coast. Data are mean (± SE) percent cover of diatoms for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

occurred primarily intertidally on roots, and were rare subtidally (Fig. 9.86). They were also a component of mixed-algal turfs.

Sessile Invertebrates. Sessile invertebrates varied in abundance among sites, but when all groups and sites were combined a weak pattern of increased cover in late rainy season (August-November) appeared (Fig. 9.71). Sessile invertebrates were

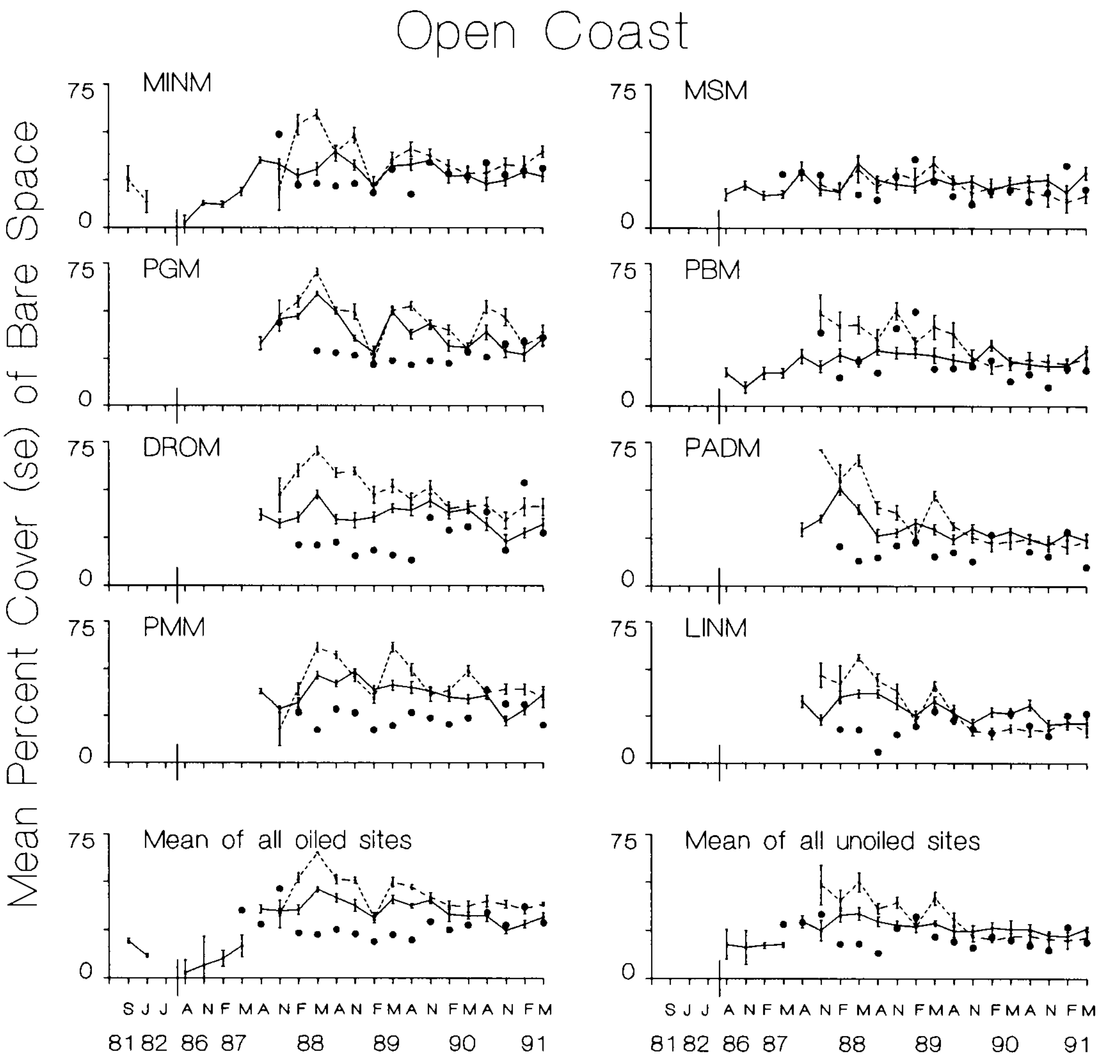

Fig. 9.77 Patterns of abundance of bare space on roots on the open coast. Data are mean (± SE) percent cover of bare space for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

rare above 30 cm depth (especially in 1988, which had severe, wet-season aerial exposures (Fig. 9.87; see also Cubit and Connor, Chap. 4).

Within the group, individual taxa varied considerably among sites and years (e.g., Figs. 9.75, 9.87). For example, tunicates were always abundant at PBM and always rare at MSM and LINM. At PADM tunicates were abundant during only one year (Fig. 9.87*B*).

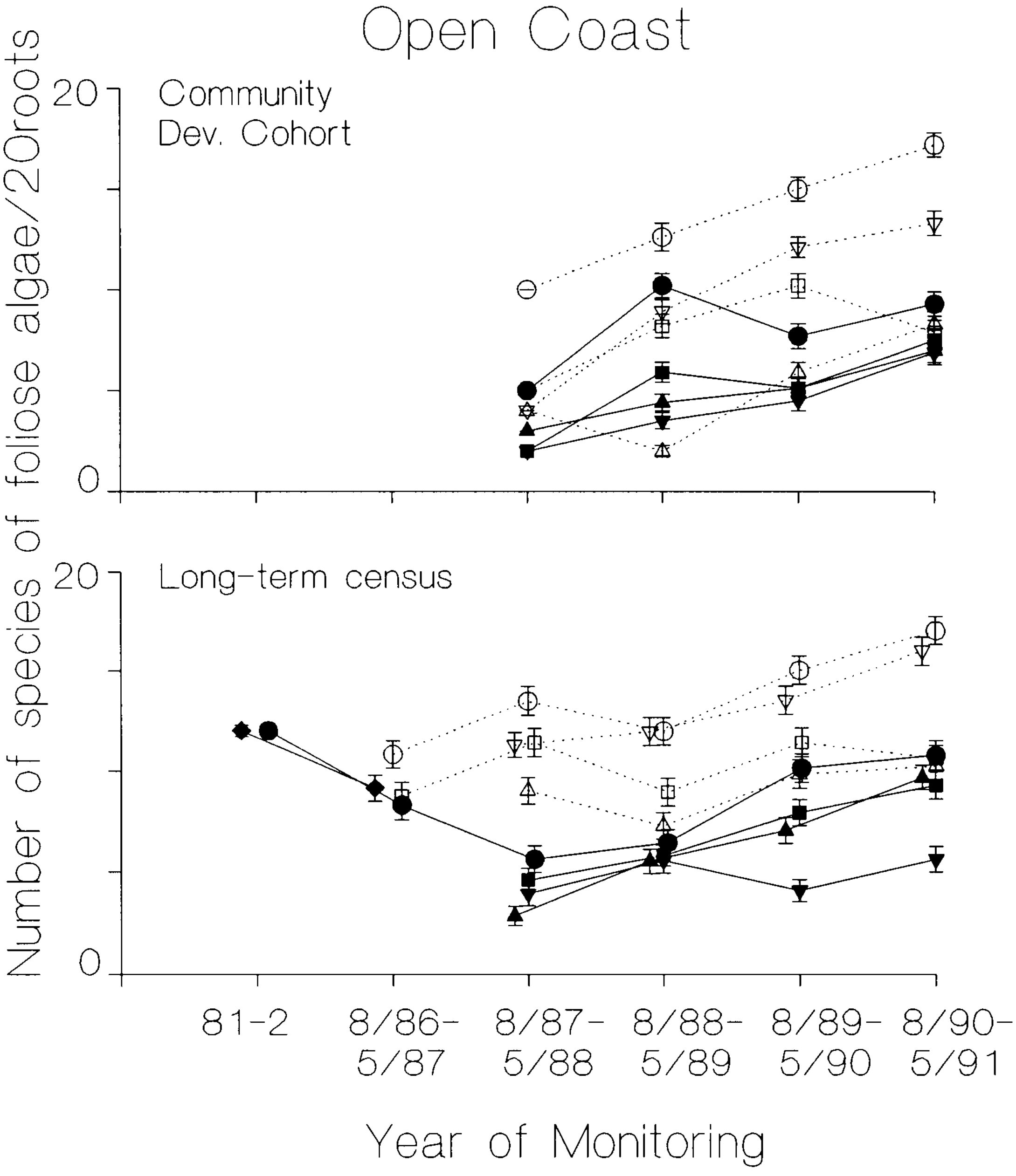

Fig. 9.78 Species richness of foliose algae on the open coast. Mean ± 95% confidence interval for rarefaction estimates of the number of species of foliose algae expected in a sample of 20 roots. *Solid symbols* = oiled sites, *open symbols* = unoiled sites. See text for details.

Barnacles. Barnacles were considered separately from other sessile invertebrates; two species (*Chthamalus* sp. and *Euraphia* sp.) ranged from 0 to <6% cover overall (Fig. 9.73). *Euraphia* occurred at MHW; *Chthamalus* was intertidal in distribution.

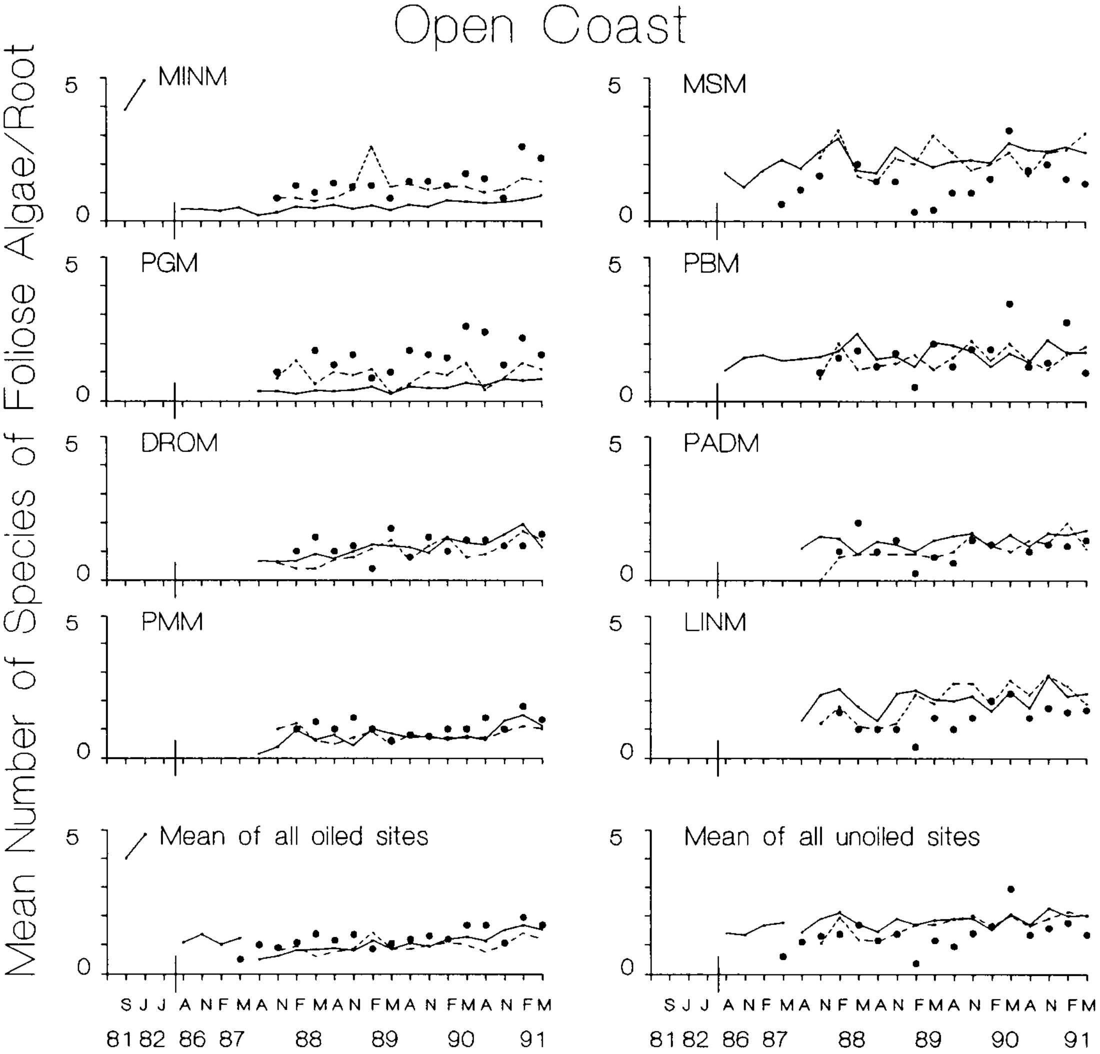

Fig. 9.79 **Mean number of species of foliose algae on roots on the open coast. Data are mean number of species of foliose algae/root for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.**

Diatoms and Bare Space. Diatom abundance varied little over time or among sites, except for a relatively high cover in 1986 at MSM and PBM (Fig. 9.76). During the last 4 yr of the study, mean values ranged from 12 to 24% cover overall. Diatoms were found at all levels on roots, but tended to be more abundant intertidally than subtidally (Fig. 9.86).

Bare space on roots averaged ~20% of root surfaces (range = 16-33% overall; Fig. 9.77). Average values for bare space were highest during 1988

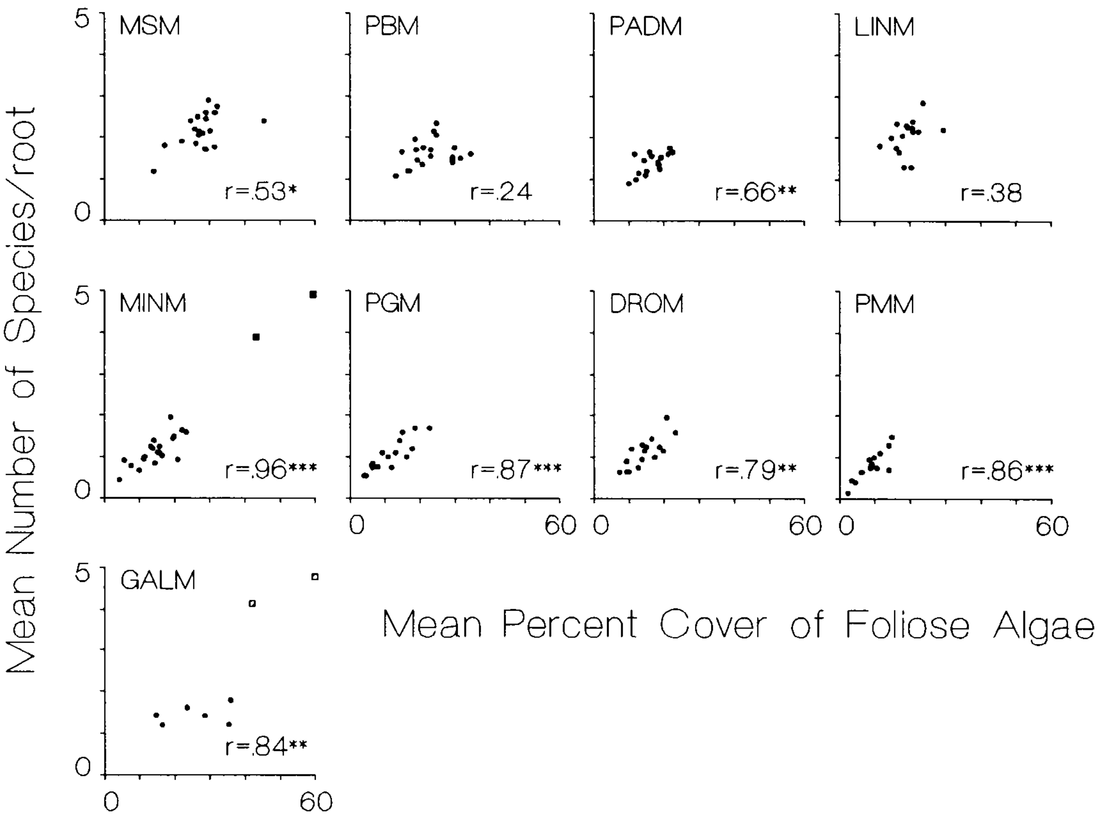

Fig. 9.80 Algal species richness vs. percent cover of algae on randomly censused roots on the open coast. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. r = correlation coefficient, *: P = .05, **: P = .01, ***: P = .001 (significance level of observed correlation). If there is no asterisk the correlation was not significant (P >.05). Points at MINM and GALM shown as *stars* are 1981-1982 data.

exposures, especially at PADM and LINM. Most bare space occurred either high on roots (≤40 cm below MHW), or deep on actively growing root tips (Fig. 9.86).

Recruitment

Percent cover on dowels measured settlement and subsequent survival of marine organisms over the preceding ~2.5-mo immersion. Some combination of epibiota covered all but about 25% of dowel surfaces each monitoring period. Foliose algae and diatoms were most common (Figs. 9.68, 9.76), together usually covering almost 75% of the surface. Recruitment was low, episodic, or both for most other groups.

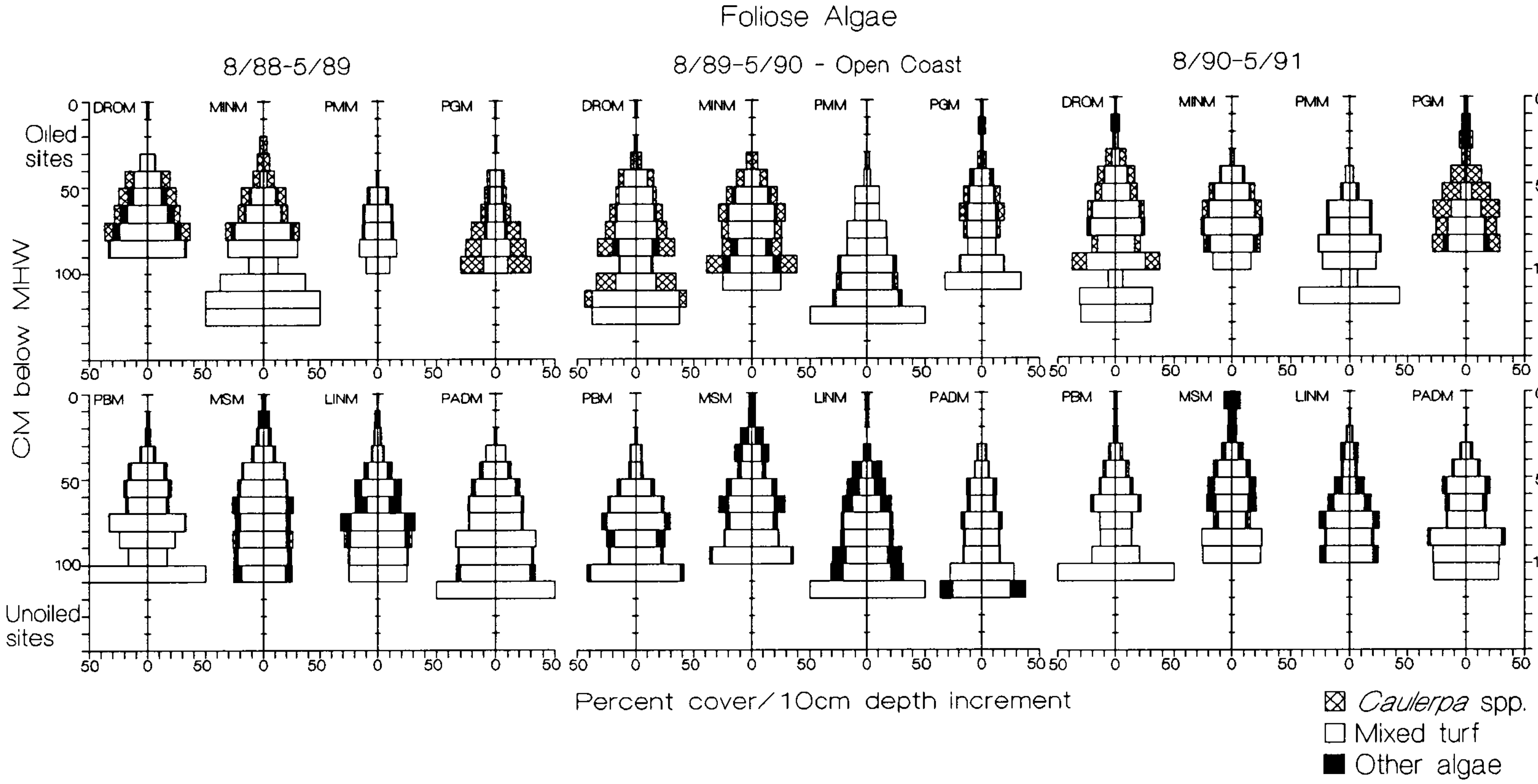

Fig. 9.81 Vertical distribution of foliose algae in yr 3, 4, and 5 postspill on open coast, random-census roots. Data are mean percent cover of foliose algae (*x*-axes) for 10-cm increments on roots downward from MHW (*y*-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

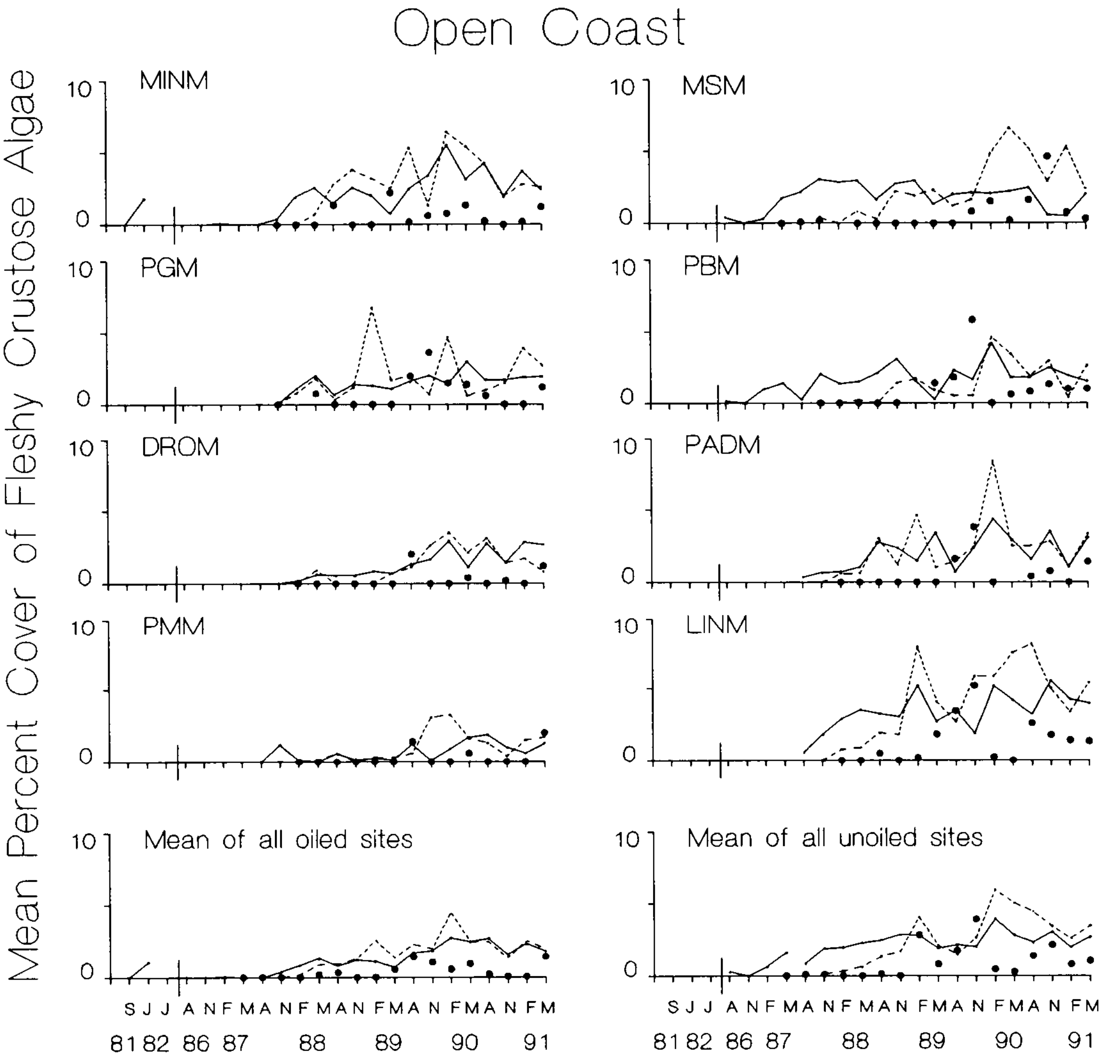

Fig. 9.82 **Patterns of abundance of fleshy crustose algae on roots on the open coast. Data are mean percent cover of fleshy crusts for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census roots (N = 20-25/site),** ***dashed lines*** **are community development roots (N = 5-10/site), and** ***solid circles*** **are recruitment dowels (N ~5/site). See text for details.**

Foliose Algae. Foliose algae averaged >25% cover on dowels in all but three periods (Fig. 9.68). Mixed-algal turfs were abundant; other species of foliose algae were rare. An average of ~3-4 species of foliose algae were estimated to occur on 10 dowels (rarefaction estimates, range = 1.9-6.5 species/10 dowels, N = 4 yr). Higher estimated species numbers were found in the last 2 yr (2.8-6.5/10 dowels), compared with the first 2 yr (1.9-5/10 dowels); this may have been related to prolonged aerial exposures in 1988 (Cubit and Connor, Chap. 4).

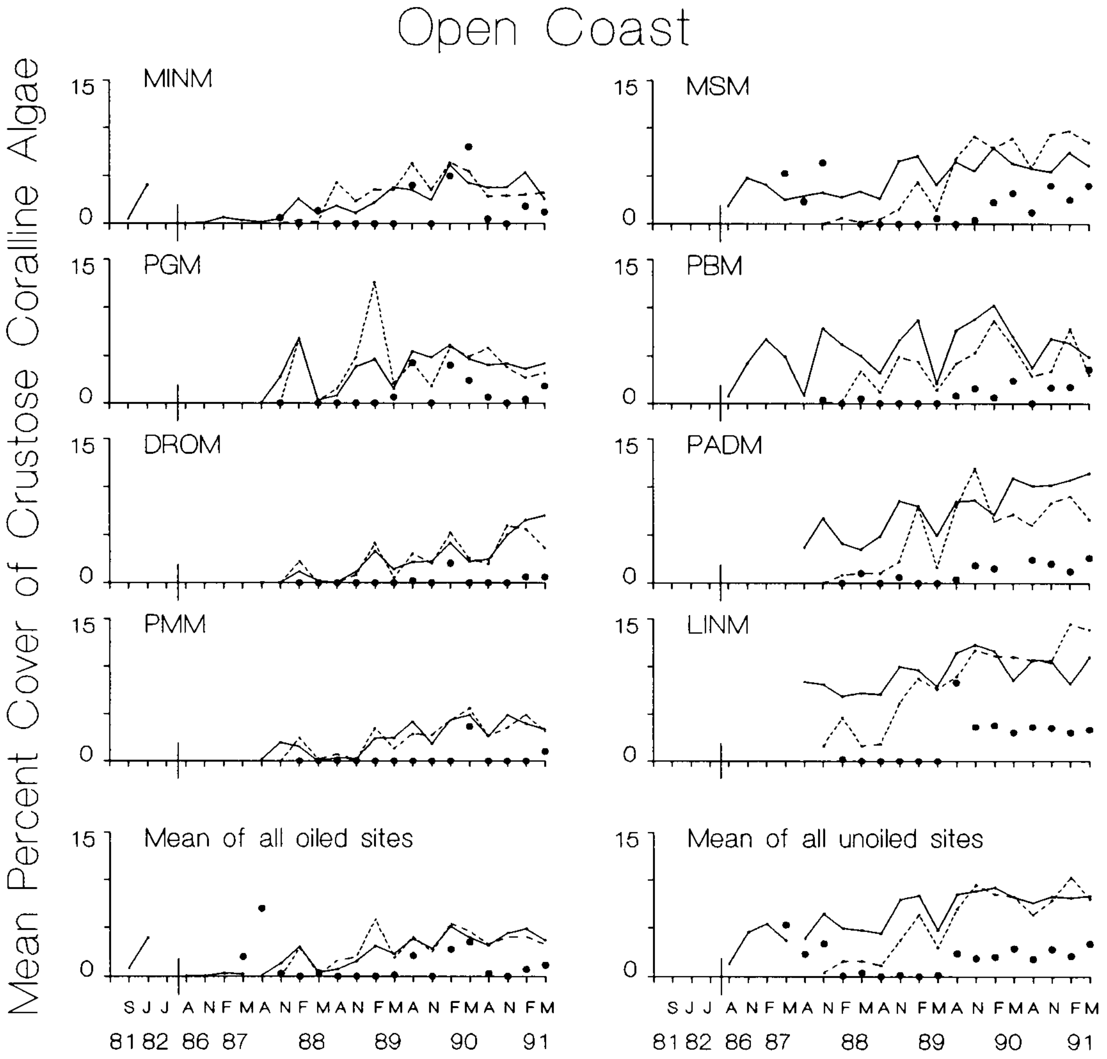

Fig. 9.83 Patterns of abundance of crustose coralline algae on roots on the open coast. Data are mean percent cover of coralline crusts for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

Crustose Algae. Crustose algae never averaged more than 7% cover, with crustose coralline algae most common (Figs. 9.69, 9.83). In 1988 little crustose algae recruited. This was correlated with prolonged periods of emersion (see Cubit and Connor, Chap. 4).

Blue-green Algae. Blue-green algae never averaged more than 25% cover and were highly variable among sites and over time (Fig. 9.70).

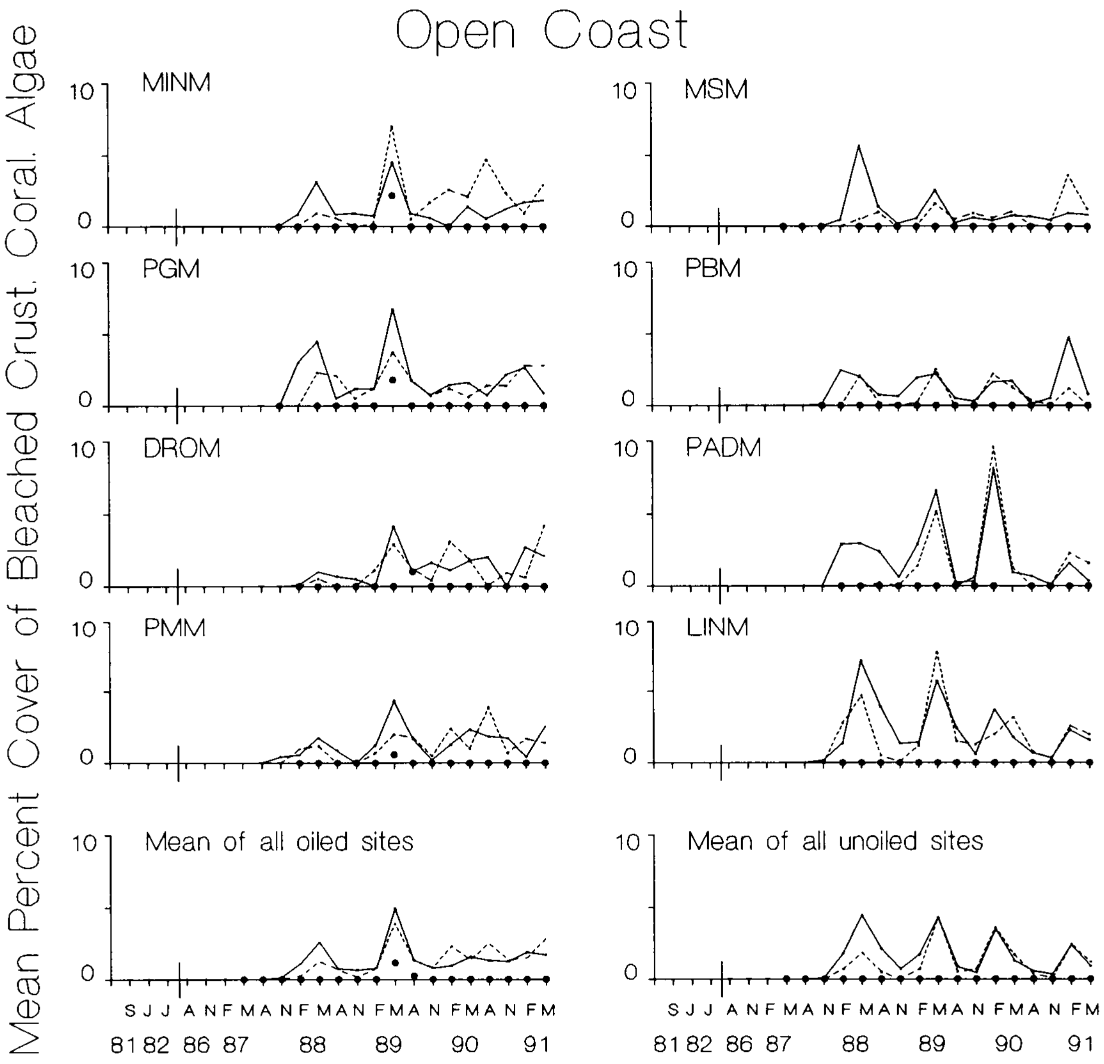

Fig. 9.84 **Patterns of abundance of bleached crustose coralline algae on roots on the open coast. Data are mean percent cover of bleached coralline crusts for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census roots (N = 20-25/site),** ***dashed lines*** **are community development roots (N = 5-10/site), and** ***solid circles*** **are recruitment dowels (N ~5/site). See text for details.**

Sessile Invertebrates. Sessile invertebrates in general failed to recruit in 1988 and early 1989, and covered < 10% of dowels in all replicates (Fig. 9.71). Cover was lowest in February for all years. Arborescent hydroids and bryozoans were the major component of sessile invertebrate recruitment (Fig. 9.72), and mirrored the pattern shown by combined sessile invertebrates. There was one large peak of recruitment at PBM (21% cover in August 1989). Sponge recruitment was very low, failing completely at PBM (Fig. 9.74). One large episode of sponge recruitment occurred

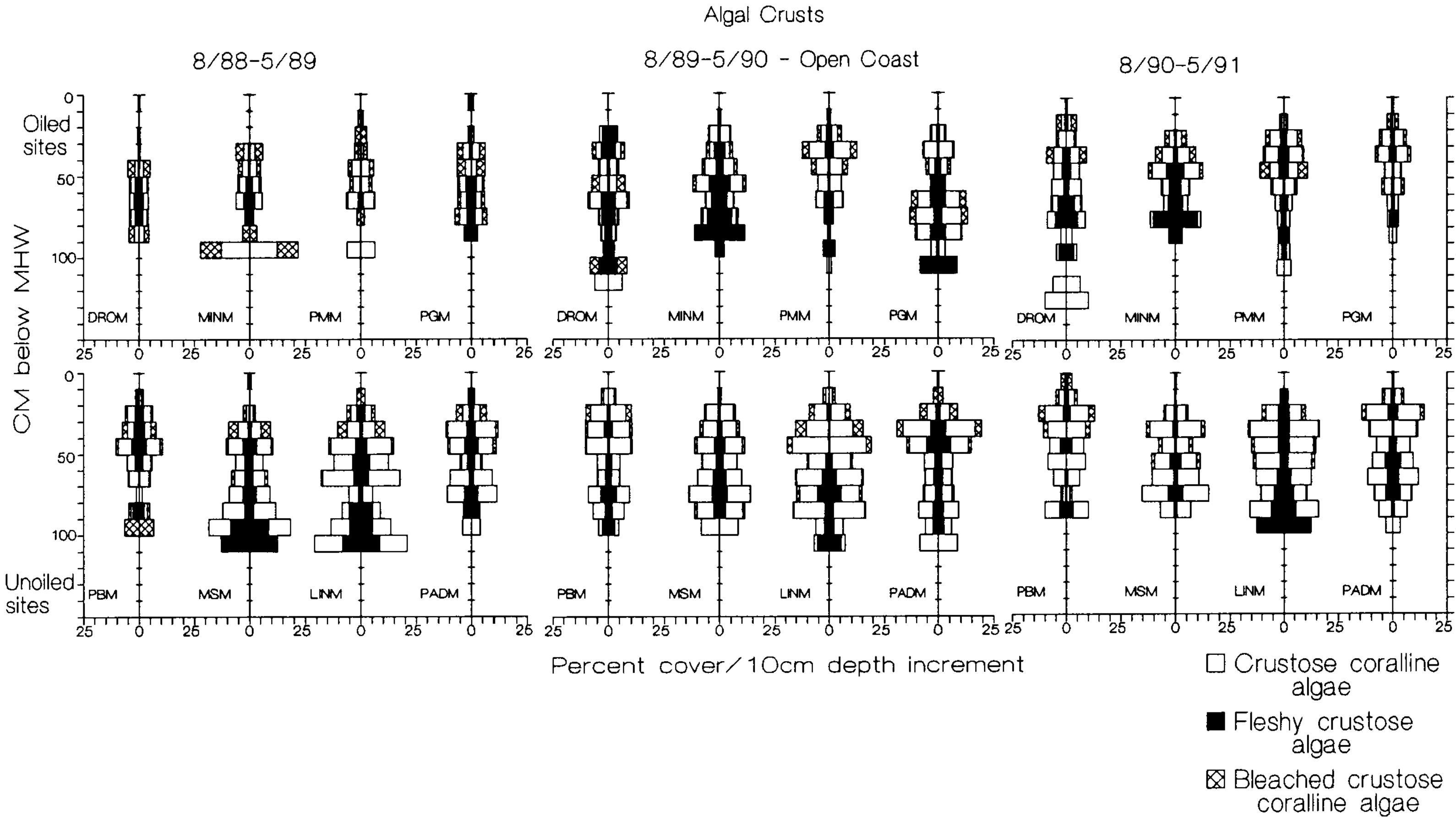

Fig. 9.85 Vertical distribution of crustose algae in yr 3, 4, and 5 postspill on open coast, random-census roots. Data are mean percent cover of crustose algae (x-axes) for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

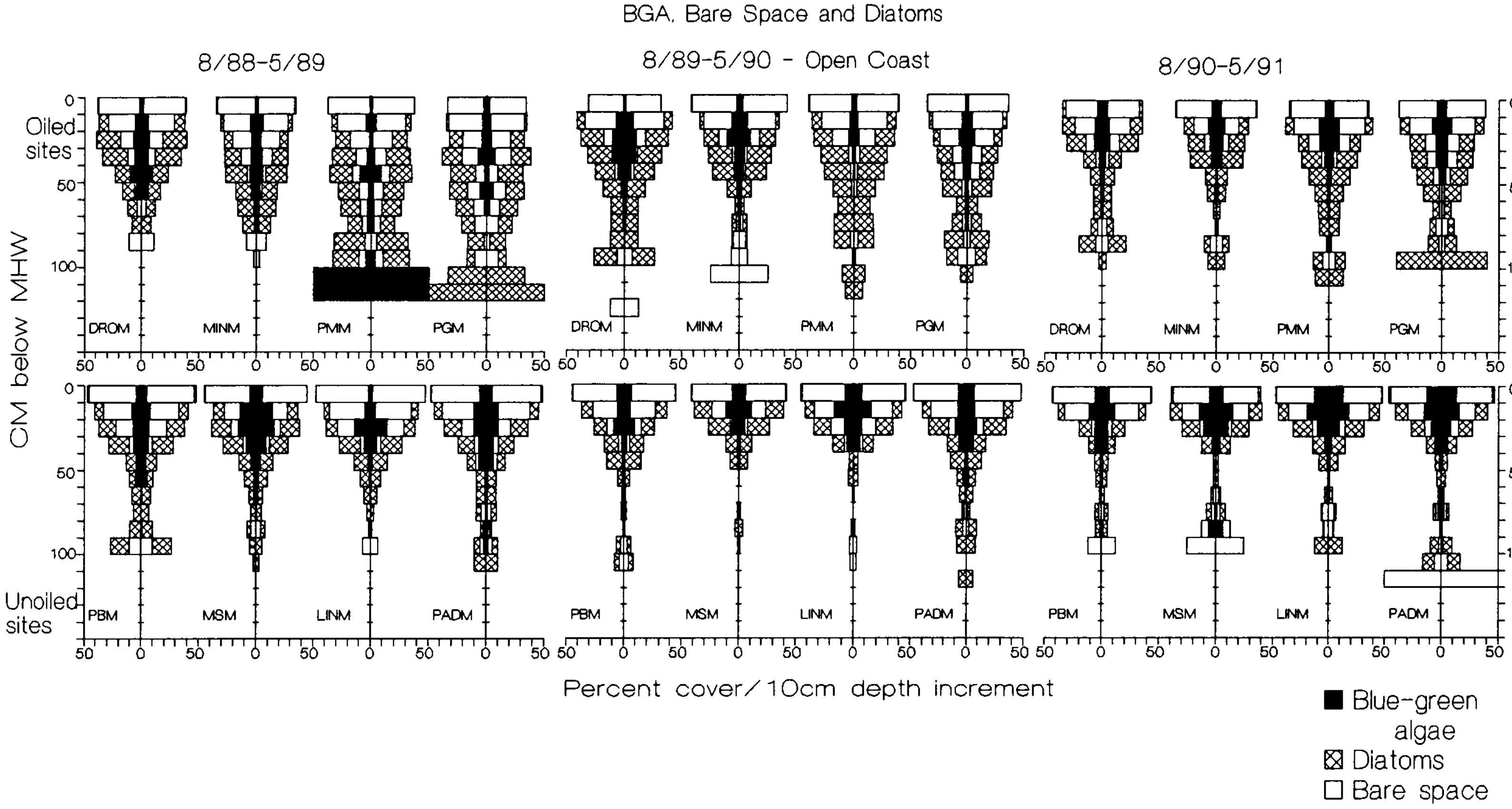

Fig. 9.86 Vertical distribution of blue-green algae (*BGA*), diatoms, and bare space in yr 3, 4, and 5 postspill on open coast, random-census roots. Data are mean percent cover (*x*-axes) of blue-green algae, diatoms, and bare space for 10-cm increments on roots downward from MHW (*y*-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

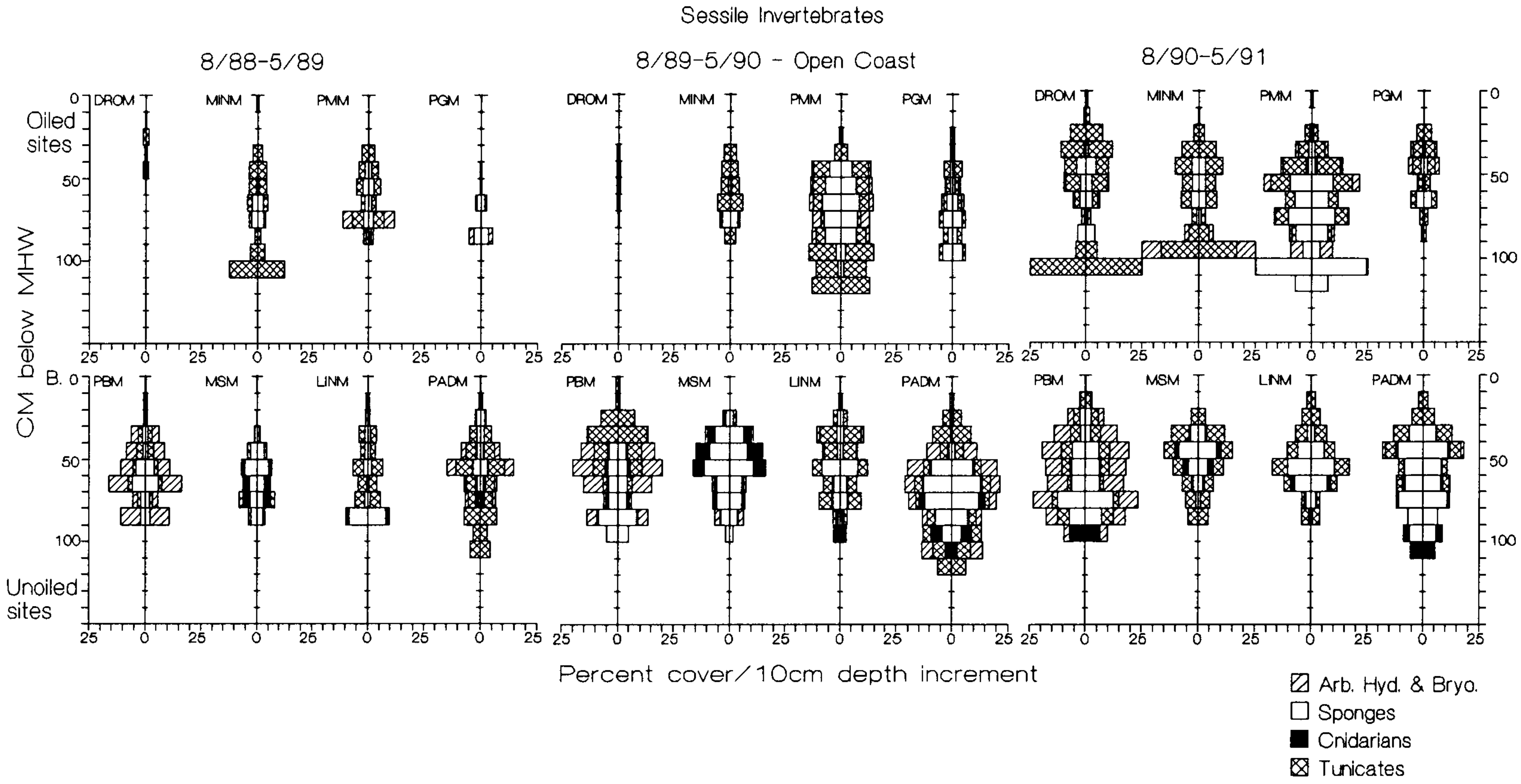

Fig. 9.87 Vertical distribution of sessile invertebrates in yr 3, 4, and 5 postspill on open coast, random-census roots. Data are mean percent cover of various sessile invertebrates (x-axes) for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

at the other three sites in May 1991. Tunicates were always rare, recruiting once at MSM and LINM, and three times at PBM. Encrusting bryozoans recruited only once (LINM, November 1988, 4.6% cover).

Barnacles. Barnacles failed to settle in more than trace amounts at any site in any interval (Fig. 9.73).

Diatoms and Bare Space. Diatoms recruited at all sites in each quarter, with greatest cover in early 1987 and 1989 (Fig. 9.76). Diatoms covered an average of 50% of dowel surfaces, unless foliose algae were abundant. Then cover dropped as low as 10%. Less than 20% of dowel surfaces were usually bare (Fig. 9.77).

Community Development

Rates of development in the assemblage of species found on the open coast differed among groups. Bare space, initially 100% of root surfaces, decreased as various organisms settled.

Foliose Algae. Foliose algae reached levels of abundance similar to those on long-term census (abbreviated *LT*) roots within 3 to 6 mo after roots entered the water, and overall abundances were indistinguishable from LT roots through May 1991 (Fig. 9.68). The mean number of species of foliose algae per root quickly became similar in both long-term census and community development (abbreviated *CD*) cohorts; average values were almost identical in 1989-1991 (Fig. 9.79). As on randomly censused roots, there was a weak positive relationship between algal cover and mean number of species of foliose algae/root (Fig. 9.88).

We examined algal species composition on CD roots from 1987 to 1991. Species recorded were a subset of those found on LT roots. The expected number of species in a sample of 20 roots ranged from 2.0 to 17.2 species of foliose algae during the 3.75 yr CD roots were submerged (Fig. 9.78). For 3 of 4 sites the expected number of species converged on that found on LT roots in the second year CD roots were submerged. At PADM, where fewer species were recorded, mixed-algal turfs were present in high percent cover and other species appeared more slowly.

Crustose Algae. Crustose algae appeared slowly on roots after they entered the water (Figs. 9.82-9.84). By 1989 abundances of fleshy and coralline crusts (both pink and bleached) converged with those on LT roots; fluctuations were similar thereafter in both groups of roots.

Blue-green Algae. Blue-green algae quickly appeared on CD roots. Within 6 mo they were as abundant as on LT roots (Fig. 9.70).

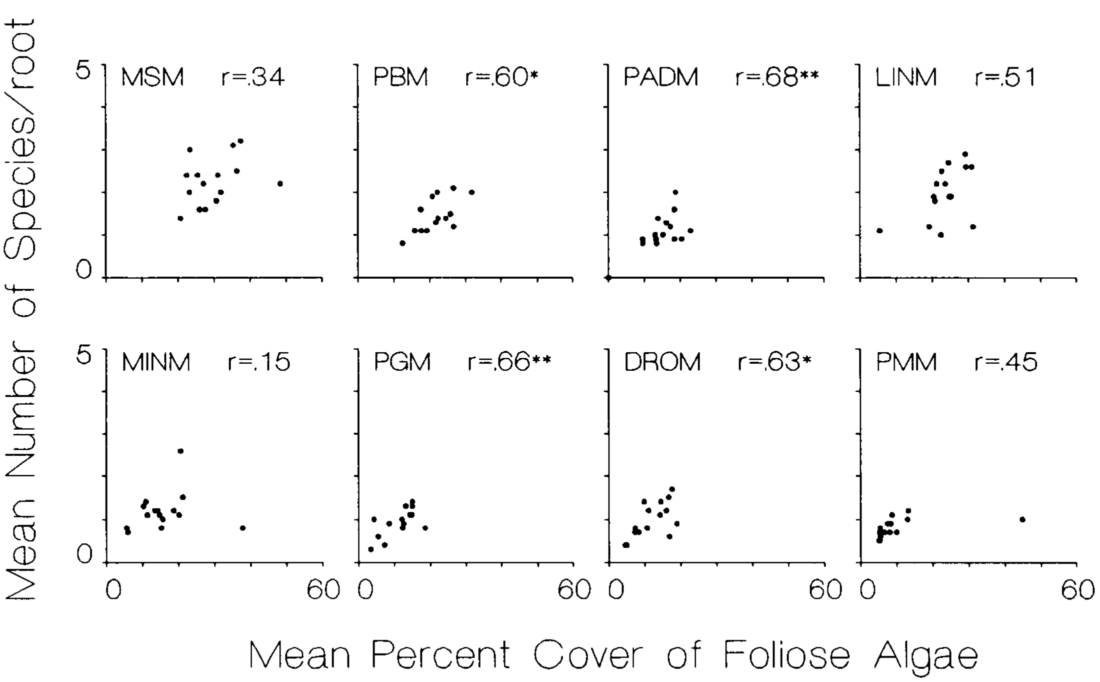

Fig. 9.88 Algal species richness vs. percent cover of foliose algae on community development roots on the open coast. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. r = correlation coefficient, *: P = .05, **: P = .01 (significance level of observed correlation). If there is no asterisk the correlation was not significant (P >.05).

Sessile Invertebrates. As a group, sessile invertebrates were rare for 6 mo after CD roots entered the water, increased slowly through February 1989, then rapidly over the next three quarters (Fig. 9.71). From February 1990 through the end of the study, their overall abundance was similar to that on LT roots. However, different groups appeared on roots at different rates.

Sponges (Fig. 9.73) and tunicates were absent to rare through May 1989, then increased in abundance over time. Sponges covered as much or more space on the CD cohort as on LT roots at 3 of 4 sites from February 1990 on; cover of sponges remained low at PBM. Arborescent hydroids and bryozoans reached abundances similar to those on LT roots in a year, and remained similar through May 1991 (Fig. 9.72). Encrusting bryozoans (always rare on LT roots) never appeared on CD roots. Cnidarians first appeared after a year's immersion, then were rare to absent through May 1991.

Barnacles. Barnacles settled in low abundance at 3 of 4 sites within 6 mo after roots entered the water. At LINM settlement failed for more than 2 yr (Fig. 9.73).

Diatoms and Bare Space. Diatom cover was as high or higher on CD roots as on LT roots within 3 mo of immersion (Fig. 9.76). Overall diatom abundance remained similar (8-16% cover) to that on LT roots through May 1991. Less than 50% of root surfaces were bare within 3 mo, and decreased to ~20% by November 1989 (Fig. 9.77). Reduction in bare space occurred most rapidly at MSM (mean cover of 23% in November 1987, compared to long-term census average of 20%). At other sites convergence took 15-30 mo.

Oiled Open Coast: Results and Comparisons with Unoiled Sites

Long-term Census

Within 4 mo of the spill a bloom of diatoms covered much of the surface of oiled prop roots (Figs. 9.76, 9.89). Crustose algae, blue-green algae, sponges, arborescent hydroids and bryozoans, tunicates, corals, and anemones had been coated with oil and then died; they were rare or absent (Figs. 9.69-9.72, 9.74, 9.75). The amount of bare space on roots was high (Fig. 9.77). By February 1987 the diatom bloom had ended and most other groups had disappeared from roots. Oil covered ~80% of root surfaces.

Foliose Algae. The overall abundance of foliose algae at oiled sites was similar to that at unoiled sites for the first two monitorings after the spill (Fig. 9.68). There was considerable variation between the two oiled sites; GALM had about twice as much cover of foliose algae as the adjacent MINM. At both sites algal turfs were matted with oil; these subsequently died and detached from roots. In August 1987, when the number of sites was increased to four and oiled sites were located throughout the area of oiling, foliose algal cover averaged ~7%, roughly one-third of that at the four unoiled sites (Figs. 9.68, 9.90).

There were continued, significant differences in percent cover of foliose algae between oiled and unoiled sites (Table 9.16). Overall cover of foliose algae varied between 16 and 33% (range of among-site means) at unoiled sites throughout the 5 yr of study; there was no overall trend in abundance over time (Fig. 9.68). In contrast, cover of foliose algae at oiled sites decreased for the first year after oiling, then increased slowly through 1991 (range of mean cover during yr 2-5 = 7-19%, Figs. 9.66, 9.90-9.92). By May 1991 percent cover of foliose algae was similar at oiled and unoiled sites (19% vs. 22%, respectively, Figs. 9.68, 9.91).

Vertical distribution of most foliose algae at oiled sites was similar to that at unoiled sites (Fig. 9.81). Mixed-algal turfs were found from 30 cm below MHW downward, and increased with depth. *Bostrychia* spp. were rare, but occupied space from the upper intertidal to MHW (as at unoiled sites). *Caulerpa* spp. ranged from 20 to 120 cm below MHW and were variable over time and among oiled sites; vertical distribution could not be compared with any confidence because of the scarcity of *Caulerpa* spp. at unoiled sites. *Other algae*, representing a diverse group of foliose species, were rare at oiled sites (especially PMM), and appeared relatively

Fig. 9.89 Open coast fringing roots 3 mo after oiling. August 1986, site = MINM. Oil (black portion) covered roots from above MHW to mid-tide level; oil partially hidden by a bloom of diatoms (white portion) covered lower sections.

restricted in distribution. They occurred between 50 and 80 cm below MHW in 1988-89, 40-120 cm in 1989-90, and 40-90 cm in 1990-1991; depth ranges at unoiled sites for the same years were 10-110 cm, 20-120 cm, and 20-100 cm below MHW.

The number of species of foliose algae/root followed the same pattern as percent cover of foliose algae (Fig. 9.79); significantly fewer species were recorded after oiling (Table 9.16). Number of species of foliose algae/root increased slowly, equalling that at unoiled sites in the fifth year after oiling. This pattern was due to the correlation between percent cover of foliose algae and the number of species/root (Fig. 9.80); as algal cover increased, more species of foliose algae were found per root.

Algal diversity was compared using rarefaction analyses (Fig. 9.78; Simberloff 1978). The number of species of foliose algae expected in a sample of 20 roots fell between the first and second year after oiling. Fewer than 6 species/20 roots were expected at oiled sites in August 1987-May 1988, compared with 9 or more

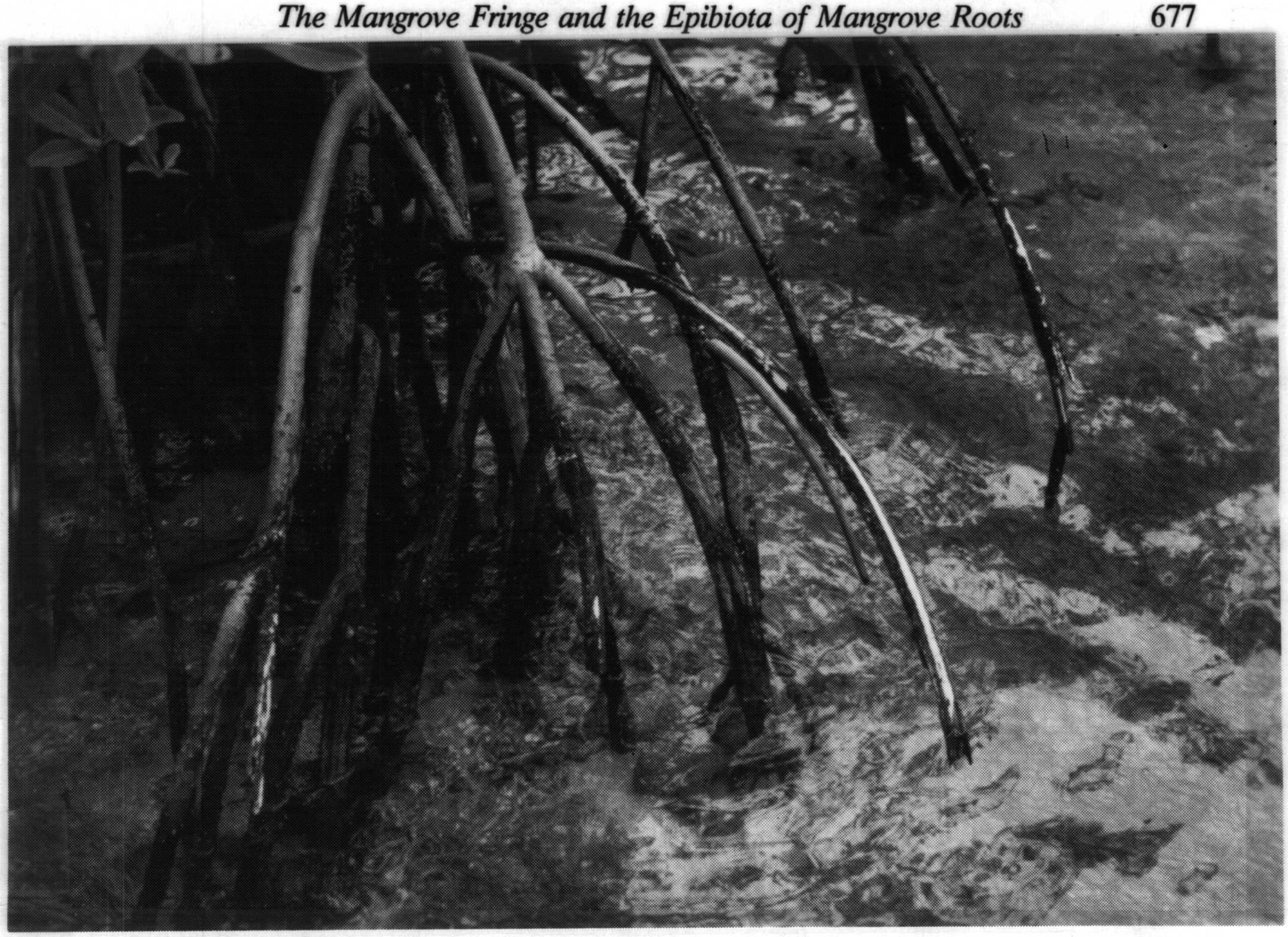

Fig. 9.90 Open coast fringing roots 1 yr after oiling. May 1987, site = MINM. Little evidence of the diatom bloom remained. Oil on roots has decreased by ~50%; little epibiota occurred on them, and the physical condition of many roots had deteriorated.

species/20 roots at unoiled sites. Number of species/20 roots then increased at 3 of four oiled sites through the fifth year after oiling. Fewer species of algae occurred at PMM, where algal abundance also lagged behind the other three sites. In August 1990-May 1991 the three other oiled sites (PGM, MINM, and DROM) had about the same number of species/20 roots as the two least-diverse unoiled sites (PADM and PBM). MINM was within one species of its prespill estimate of 12 species/20 roots (as was the intermittently monitored GALM).

Species of foliose algae occurred at fewer sites on the oiled open coast than on the unoiled open coast. In 3 of the 4 yr of balanced sampling, fewer than 25% of all species found in a given year occurred at all oiled sites; in August 1989-May 1990, 33% of species recorded this year were present (6/18 species) at all oiled sites. Only mixed-algal turfs and *Acanthophora spicifera* occurred at all oiled sites in all 4 yr. In contrast, at least 25% of species found in a given year occurred at all four unoiled sites in each year; six species were recorded at all unoiled sites each year

Table 9.16 Open coast repeated-measures ANOVAs: summary table.

A. Long-term census. Probability levels for annual comparisons of arcsine-transformed percent covers on roots. *Y1*, *Y2*, *Y3*, and *Y4* are univariate ANOVAs for yr 1-4, August 1987-May 1991. The *oil*, *year*, and *Y x O* columns are repeated- measures ANOVAs including all 4 yr.

Group	Y1	Y2	Y3	Y4	Oil	Year	Y x O	Spher.	H.-F.?
Foliose algae	.004	.009	.085	.066	.013	.0003	.0004	.827	no
Species/root	.003	.009	.016	.063	.010	.0001	.0001	.394	no
Crustose algae	.007	.011	.016	.081	.011	.0001	.044	.092	no
Sessile inverts.	.008	.022	.003	.096	.011	.0001	.014	.782	no
Barnacles	.074	.130	.057	.115	.073	.017	.558	.507	no

B. Long-term census vs. community development cohort. Probability levels for repeated-measures ANOVAs on arcsine-transformed percent covers on roots for yr 1-4, August 1987-May 1991. *Group* is the comparison between long-term census and community development roots.

Comparison	Barnacles	Foliose Algae	Species/ root	Crustose Algae	Sessile Inverts.
Between:					
Group	.586	.989	.411	.437	.134
Oil	.006	.0005	.001	.004	.0004
G x O	.974	.916	.782	.379	.527
Within:					
Year	.0001	.044	.0001	.0001	.0001
Y x G	.030	.549	.372	.0003	.0001
Y x O	.769	.557	.257	.610	.009
Y x G x O	.143	.020	.012	.009	.0001
Sphericity Test	.255	.0001	.072	.519	.494
H.-F. Adj. applied?	no	yes	no	no	no

Species/root = mean number of species of foliose algae per root. *H.-F.?* = Huynh-Feldt adjusted probability levels. If *no*, then probability levels were unadjusted because of sphericity-test results. If *yes*, then levels were adjusted.

(see above). More species were unique to the unoiled open coast in each year of the study (range of 9-14 species unique to the unoiled open coast in a given year, 1-3 species unique to the oiled open coast). Species occurred at the same number of sites in oiled vs. unoiled comparisons (2.1 vs. 2.3 sites/species, *t*-test, NS), but there were fewer species overall on oiled open coast.

Aside from a general reduction in species numbers, there were shifts in species composition over time when oiled and unoiled sites were compared. A few species, most commonly *Caulerpa verticillata* and *Acanthophora spicifera*, were found

Fig. 9.91 Open coast fringing root 4 yr after oiling. May 1990, site = MINM. Many roots that entered the water 2^+ yr after the spill quickly developed epibiota at this site. The root pictured is covered with foliose algae (*Padina gymnospora*), diatoms, and hydroids.

Fig. 9.92 Open coast fringing root 5 yr after oiling. June 1991, site = DROM. An oiled, twice-broken root (new growth began approximately at the center; the second break was at the water line with two tips just visible submerged). Only traces of weathered oil remained; epibiota included live and dead barnacles, hydroids, and mixed turf.

more often at oiled than unoiled sites. Overall, algal turfs were found on ~20% fewer roots at oiled than unoiled sites for 5 yr after the spill (present on 63.6% of roots vs. 88.1% of roots at oiled and unoiled sites, respectively, in yr 5 postspill).

Articulated coralline algae (a subset of foliose algae) were rare at oiled sites through May 1991. In each year fewer species were found at oiled than unoiled sites, and abundances were lower. Articulated coralline algae were recorded at least once at all oiled sites in 1987-1988, but were recorded only at MINM in the next 2 yr. In the fifth year after oiling this group occurred at only two sites (MINM and DROM), where two species were found (*Amphiroa fragilissima* and *Jania capillacea*). Both of these species occurred at all unoiled sites, and *Amphiroa rigida* var. *antillana* and *Amphiroa ?beauvoisii* were each found at two unoiled sites.

GALM and MINM are of particular interest because both sites were monitored before the spill; when pre- and postspill patterns at these sites were compared, differences were strong. *Ceramium* spp., *Chaetomorpha* spp., *Bostrychia tenella/B. binderi*, *Dictyota bartayresii*, *Catenella repens/Caloglossa leprieurii*, *Polysiphonia subtilissima*, and mixed-algal turfs were common in 1981-1982 (Table 9.1); all were rare or absent after the spill. For MINM mixed-algal turfs were present on 46% of roots in 1981-1982, but only 24% in 1986-1987. This increased to 52% in 1987-1988, and more slowly to ^19% in 1990-1991. In 1990-1991 a total of 22 species was recorded on 80 roots at MINM; 11 were found on only one root. The second most abundant species next to mixed-algal turfs was *Murrayella periclados* (present on 26% of roots, absent in 1981-1982), followed by *Dictyota bartayresii* (16% of roots in 1990-1991, 41% in 1981-1982) and *Caulerpa verticillata* (11% and 62%, respectively). This may represent a return of different species of algae than those present before the spill.

In particular, "Bostrychietum" species were abundant at MINM and GALM in 1981-1982 (*Caloglossa leprieurii*, found on 38% of roots; *Polysiphonia subtilissima*, 49%; *Herposiphonia tenella*, 22%; and *Bostrychia tenella/B. binderi*, 81%). In 1990-1991 *Bostrychia tenella/B. binderi* were present on only 4% of roots and *Murrayella periclados* was found on 26%. This difference could be related to physical changes in the mangrove fringe (increased light and associated heat and desiccation stress) or to shifts in local species assemblages independent of oiling. The patchy occurrence and year-to-year changes in species composition on the unoiled coast strongly suggest that such changes occur. Although algal cover at MINM converged with that of unoiled sites in 1991, it remained lower than in 1981-1982. Given the differences among years at unoiled sites, we cannot attribute this to oiling effects as opposed to possible long-term changes in epibiotic assemblages on the open coast.

Crustose Algae. Crustose algae were absent or rare at oiled sites for 1.5 yr following the spill (Fig. 9.69). From 1988 on crusts at oiled sites fluctuated like those at unoiled sites, but covered significantly less space than at unoiled sites through May 1990 (Table 9.16). Differences between oiled and unoiled sites were underlaid by a significant, general increase over time in the abundance of both fleshy (Fig. 9.82) and pink coralline (Fig. 9.83) crusts. Bleached coralline crusts followed the same seasonal pattern at both oiled and unoiled sites (Fig. 9.84).

There was little difference in the vertical distribution of crustose algae between oiled and unoiled sites (Fig. 9.85). At oiled sites fleshy crusts could occur from MHW to the deepest levels of roots, and tended to increase with depth. In 1988-89 fleshy crusts at oiled sites occurred at a maximum depth of 90 cm, compared to 110 cm at unoiled sites, but there were no differences in the next 2 yr. Coralline crusts were found at about the same depths on roots in oiled and unoiled sites. In 1988-89 they did not occur shallower than 30 cm below MHW, compared to 10 cm at unoiled sites. In both 1989-90 and 1990-91 upper limits were the same (10 cm depth), and they occurred deeper on roots at oiled sites than unoiled sites. Bleached crustose coralline algae were distributed similarly at oiled and unoiled sites, with a tendency to be more abundant deeper at oiled than unoiled sites each year.

Blue-green Algae. Blue-green algae were almost absent at oiled sites in the first year after the spill (Fig. 9.70). Percent cover increased in late 1987, and abundances then fluctuated seasonally, as at unoiled sites. However, blue-green algae covered less average space at oiled than unoiled sites in 15 of 16 monitorings from 1987 to 1991 (sign-rank test, $P < .001$). Average differences were usually <5%, but this represented an ~20-50% reduction of average cover (independent of filamentous blue-green algae in algal turfs). Blue-green algae (important in nitrogen fixation; Potts 1979, 1980) were thus negatively affected by oiling for at least 5 yr. The vertical distribution of blue-green algae was similar at oiled and unoiled sites (Fig. 9.86).

Sessile Invertebrates. Sessile invertebrates (excluding barnacles and bivalves) dropped to <5% cover (Fig. 9.71) in the first year after oiling. Differences between oiled and unoiled sites were strong and persistent (Table 9.16). Overall sessile invertebrate cover increased slowly at oiled sites, but was still lower than at unoiled sites 5 yr after oiling (~7% vs. 12%, August 1990-May 1991).

Most individual taxa were affected negatively by oiling. Only a few arborescent hydroids and bryozoans were found at oiled sites in the first year after the spill; few or no sponges, anemones, corals, or tunicates occurred (Figs. 9.72, 9.74, 9.75). In 1987-1988 cover of arborescent hydroids and bryozoans was low and variable. Arborescent hydroids and bryozoans became relatively abundant at MINM first, returning patchily to other oiled sites (Fig. 9.72). Sponges slowly appeared at PMM and MINM beginning in 1989, but remained rare through 1991 at DROM and PGM (Fig. 9.74).

When pre- and postspill data from MINM were compared, differences in cover of sessile invertebrates persisted through 5 yr after oiling (Fig. 9.75). Overall cover was still lower than the lower prespill value (8.5 vs. 13.1%, January 1982 total). All groups were present, but cnidarians and tunicates were still rarer than in 1981-1982 (cnidarians: 0.1% cover May 1991, ~2% cover 1981-1982; tunicates: 1.2% cover May 1991, 2-5% cover 1981-1982). Only arborescent hydroids and bryozoans approached prespill levels (4.2% cover May 1991, ~6% cover 1981-1982). Thus, a sessile assemblage like that found before the spill was developing, but rare taxa were still in reduced abundance.

Two years after oiling, the vertical distributions of most groups were difficult to compare between oiled and unoiled areas because most groups were still rare on oiled roots (Fig. 9.87*A*). By May 1990 abundances of sponges and arborescent bryozoans and hydroids were high enough to compare (Fig. 9.87*B*); distributions were similar to those at unoiled sites for both groups. Tunicates and cnidarians remained too rare to assess through May 1991, and patterns for sponges and arborescent bryozoans and hydroids did not change from the preceding year (Figs. 9.87*B*, *C*).

Barnacles. One group increased in abundance after mangrove roots on the open coast were oiled. Beginning in August 1987 oiled sites had a higher percent cover of barnacles, especially *Chthamalus* sp. (Table 9.16; Fig. 9.73). Differences between oiled and unoiled sites were not significant overall because barnacle abundance was variable among oiled sites (low cover at DROM). At unoiled sites a few barnacles were usually present, but mean cover was rarely >1.0%. A possible explanation was the reduced density of the gastropod *Littorina angulifera* we observed on roots in oiled areas immediately after the spill. Grazers can affect recruitment of barnacles by scraping cyprids off surfaces as they settle (e.g., Levings and Garrity 1984). Indirect evidence supports this hypothesis as an explanation of increased barnacle cover. Snail density recovered within a year, and the size structure of barnacles on roots indicated that settlement(s) occurred only during the period when they were absent. There have been no further large recruitments; subsequent increases in percent cover were due primarily to growth of individual barnacles (large individuals persisted through 1991). Experimental evidence is needed to separate the direct effects of oiling from possible secondary effects, like those of grazers affected by oiling.

Diatoms and Bare Space. Bare space and diatoms were always present on roots at oiled as well as unoiled sites (Figs. 9.76, 9.77). Abundances were similar at oiled sites for both categories over time (~25% cover diatoms, ~35% bare space). However, there was a consistent difference between oiled and unoiled sites, with more space on oiled roots, bare or covered by diatoms, than on unoiled roots through the fifth year after oiling (sign-rank tests, $P < .001$, both tests).

As at unoiled sites, diatoms occurred from MHW to the deepest root tip (Fig. 9.86). In the third, fourth, and fifth years after the spill, they were more abundant deep on roots at oiled sites relative to unoiled sites. Bare space on roots at oiled sites occurred primarily at high intertidal levels, or deep on the growing tips of roots, as at unoiled sites. However, bare space was common at intermediate (mid-intertidal to shallow subtidal) depths during 1988-1989 at oiled sites. This may reflect the effects of prolonged aerial exposures in 1988 (Cubit and Connor, Chap. 4).

Recruitment

The pattern of percent cover on dowels at oiled and unoiled sites was generally similar. This suggested that oiling effects were caused by postsettlement processes rather than presettlement processes.

Foliose Algae. Foliose algae were more abundant on dowels at unoiled sites when mean cover for matched intervals was compared (i.e., if mean cover was greater at unoiled sites than oiled sites in a given quarter), but differences were not significant (sign-rank test, NS; Fig. 9.68). Recruitment dowels at oiled sites recorded similar numbers of species of foliose algae as at unoiled sites (range of mean number/10 dowels, rarefaction analyses, 2.0-7.2, oiled vs. 1.9-6.5, unoiled).

Crustose Algae. Crustose algae were more abundant on dowels at unoiled sites when mean cover for matched intervals was compared, but differences were not significant (sign-rank test, NS). Recruitment of crustose coralline algae failed during 1988 at both oiled and unoiled sites (Fig. 9.83). Dead crustose coralline algae were present on dowels at oiled sites during seasonal exposures, but were absent at unoiled sites (Fig. 9.84).

Blue-green Algae. Blue-green algae recruited at both oiled and unoiled sites with a strong seasonal pattern (Fig. 9.70); cover was highest in the dry or early wet season (up to ~8%). There were no significant differences between oiled and unoiled sites (sign-rank test, NS).

Sessile Invertebrates. Sessile invertebrates occurred patchily on dowels, with low settlement in 1988 through the period of seasonal exposures (Cubit and Connor, Chap. 4). Settlement was broadly similar at oiled and unoiled sites (sign-rank test, NS; Fig. 9.71).

When individual groups were examined, some arborescent hydroids and bryozoans recruited each quarter, with high and variable recruitment at PGM compared with other sites (Fig. 9.72). Sponge recruitment at oiled sites was episodic and appeared unrelated among sites; there was no recruitment at oiled sites in May 1991, when sponges were abundant on dowels at 3 of 4 unoiled sites (Fig. 9.74).

Barnacles. Barnacle recruitment was low at both oiled and unoiled sites (Fig. 9.73). In August 1987 barnacles covered 2% of dowels at GALM; barnacles covered trace amounts of space in only two other intervals.

Diatoms and Bare Space. Diatoms covered approximately the same amount of space on dowels at oiled and unoiled sites (sign-rank test, NS; Fig. 9.76). However, significantly more space was bare at oiled than unoiled sites (sign-rank test, $P = .012$; Fig. 9.77). This suggests that settlement was lower overall at oiled than unoiled sites.

Community Development

We used repeated-measures ANOVA to test for the effects of oiling (oiled and unoiled) and root group (long-term census, abbreviated *LT*, vs. community development cohort, abbreviated *CD*).

All CD roots were bare when they entered the water between September and November 1987. As at unoiled sites, epibiota quickly settled, reducing the amount of bare space to ~33% after 3 mo (Fig. 9.77).

Foliose Algae. Foliose algae appeared immediately on CD roots at oiled as well as unoiled sites, and bloomed at two oiled sites (MINM and PMM; Fig. 9.68). Over time there was a significant effect of oiling on percent cover of algae, but not of group (Table 9.16). The significant interaction between year, oiling, and group relates the pattern of increase in cover at oiled sites over time to the relative stability of cover at unoiled sites.

Results were similar for analyses of the mean number of species of foliose algae/root; there was a significant effect of oiling, but no main effect of group. Percent cover of foliose algae was weakly correlated with the number of species of foliose algae/root (Figs. 9.80, 9.88), as in other sampling. Extreme points in Figure 9.88 with high percent covers and low numbers of species/root mark the blooms at MINM and PMM when roots entered the water in November 1987.

In the first 9 mo after CD roots entered the water (yr 1 in Fig. 9.78), foliose algae rapidly colonized roots, equalling the amount of algae on LT roots (Fig. 9.68). However, fewer species were initially recorded on CD than LT roots at all sites, both oiled and unoiled (rarefaction estimates, Fig. 9.78). Over time species "accumulated" on roots that remained submerged but did not enter the sediments. At unoiled sites species appeared most rapidly at MSM, with the same number of species recorded from 9 mo after roots entered the water (yr 2-4). At LINM and PBM 1-3 fewer species were estimated to occur on a sample of 20 CD roots than LT roots through the end of the study. At PADM the process was especially slow, with only two species estimated to occur on 20 roots in the second year after roots entered the water. By the fourth year two fewer species were expected on CD vs. LT roots at this site (8.3 vs. 10.3 species/20 roots). PADM had equally high percent cover, but mixed-algal turfs were very abundant compared to other sites.

At oiled sites algae also increased in abundance immediately after roots entered the water, but fewer species were found (Fig. 9.78). Species number increased most rapidly at MINM. In August 1988-May 1989 the number of species of algae expected in a sample of 20 roots was 10.8 ± 0.6 at MINM. This value was as high as that for the unoiled sites, and suggested a more rapid recovery in species composition than the other three oiled sites. Species counts at MINM then dropped somewhat, but rebounded in the last year of the study.

Crustose Algae. Algal crusts increased in cover at about the same rate at both oiled and unoiled sites for approximately the first year after roots entered the water (Fig. 9.69). Thereafter, crust cover increased more rapidly at unoiled than oiled sites, paralleling results for LT roots (Table 9.16). There were persistent, significant effects of oiling through May 1991; the amount of time roots had been submerged was significantly related to crust cover in the first year after roots entered the water. Results were similar for pink crustose coralline algae, the largest component of crust cover; bleached crustose coralline algae showed seasonal patterns related to exposure on both CD and LT roots (Figs. 9.83, 9.84).

Blue-green Algae. As at unoiled sites, blue-green algae immediately colonized CD roots. Their abundances paralleled those on LT roots within 6 mo and fluctuated seasonally (Fig. 9.70).

Sessile Invertebrates. Sessile invertebrates (excluding barnacles and bivalves) appeared slowly on the CD cohort at both oiled and unoiled sites (Fig. 9.71). At least some arborescent hydroids and bryozoans appeared within 6 mo (Fig. 9.72); sponges were especially slow to colonize (Fig. 9.74). Arborescent hydroids and bryozoans were the first group to converge on average values for LT roots; other groups increased in percent cover more slowly. The second-order interaction between oiling, root group, and year was significant, as were interactions involving time (year x group, year x oiling; Table 9.16). Thus, there was a complex pattern of response to time and oiling. On average it took more than 2 yr for sessile invertebrates to become as abundant on CD as LT roots at unoiled sites. The process was artificially more rapid at oiled sites because so few sessile invertebrates were present on LT roots.

Barnacles. Barnacle cover on CD roots was similar to LT roots within ~1 yr after roots entered the water (Fig. 9.73). As with other groups, barnacles on CD roots at oiled sites covered as much space as on LT roots at oiled sites, rather than resembling cover on roots at unoiled sites. There was an overall main effect of oiling with a significant interaction between root group and year (Table 9.16). The latter reflects the period when barnacles were settling and had not reached cover typical of LT roots.

Diatoms and Bare Space. Diatoms at oiled sites were as abundant within 3 mo as at unoiled sites. Diatom cover on CD roots was indistinguishable from diatom cover on LT roots from November 1987 on (Fig. 9.76). The amount of bare space on roots declined over time (Fig. 9.77). More of the root surfaces were bare during early wet season exposures in May 1988 (Cubit and Connor, Chap. 4). There were no differences in patterns between oiled and unoiled sites.

Unoiled Channels and Lagoons

Long-term Census

We sampled unoiled channels (1) in the western wing of Bahía Las Minas and (2) in Margarita Lagoon (Fig. 9.5). Because these two areas differed structurally and physically (Sects. 9.3, 9.5.2), we tested for differences in epibiotic assemblages between sites in the two lagoons (i.e., MACS and MACN vs. HIDC and SBCW). This was complicated by the secondary oiling of HIDC between May and August 1988. However, because the little oil that came ashore at HIDC stranded high on the roots and disappeared quickly, with minor effects on epibiota (Fig. 9.28), we continued to monitor this site, but also added an alternative unoiled site (LRCS) located within the same wing of Bahía Las Minas.

Randomly sampled mangrove roots fringing unoiled channels and lagoons were best characterized by bivalve molluscs (Fig. 9.93). Bivalve abundance in Bahía Las Minas in 1981-1982 averaged 73-75% cover. At two sites monitored from August 1986-May 1987 (both in Bahía Las Minas, HIDC and SBCW), mean bivalve abundance was 43% cover. From August 1987 to May 1991 four unoiled sites were censused, and mean abundances ranged from 35% (in August 1987-May 1988) to 21% cover (in each of the last 3 yr of the study, Bahía Las Minas and Margarita Lagoon sites combined).

Crassostrea virginica. The edible oyster *Crassostrea virginica* was the most abundant bivalve mollusc in 20 quarterly censuses from 1986 to 1991 (Fig. 9.93). Two sites in Margarita Lagoon (Table 9.2; Fig. 9.5) were added in August 1987, because they were known to have not been oiled during the spill. *Crassostrea* abundance averaged 18-24% cover in Margarita Lagoon (MACS and MACN) in August 1987, compared to 26-33% cover in Bahía Las Minas (HIDC and SBCW). This depression of *Crassostrea* abundance in Margarita Lagoon was significant, and continued through the study (Table 9.17), depressing overall oyster abundance.

However, the abundance of *Crassostrea* clearly but gradually declined at all unoiled sites through November 1989 (Fig. 9.93). It then continued to decrease only at MACS and MACN, and increased slightly from February 1990 through May 1991 in Bahía Las Minas. A sharp, ephemeral dip in *Crassostrea* abundance occurred in November 1989 at SBCW (mean of 20% cover in August 1989, 7% in November, and 18% cover in February 1990). This site, near the mouth of Río Coco Solo, was monitored immediately after 5 d of cumulative rainfall >40 cm (Fig. 9.94). We observed many gaping, rotting *Crassostrea* on roots. Dead *Crassostrea* averaged 17% cover on roots; the average cover of dead oysters over the previous 12 quarterly monitorings was 3.3% (Fig. 9.95). Dead oysters still covered ~9% on roots in February 1990, then decreased to <4% cover through May 1991. This die off appeared related to sustained low salinity (see Sect. 9.5.7, below). At the same time, *Crassostrea* essentially disappeared at MACS, also near the mouth of a branch of Río Coco Solo, never returning to substantial cover. Margarita Lagoon apparently also

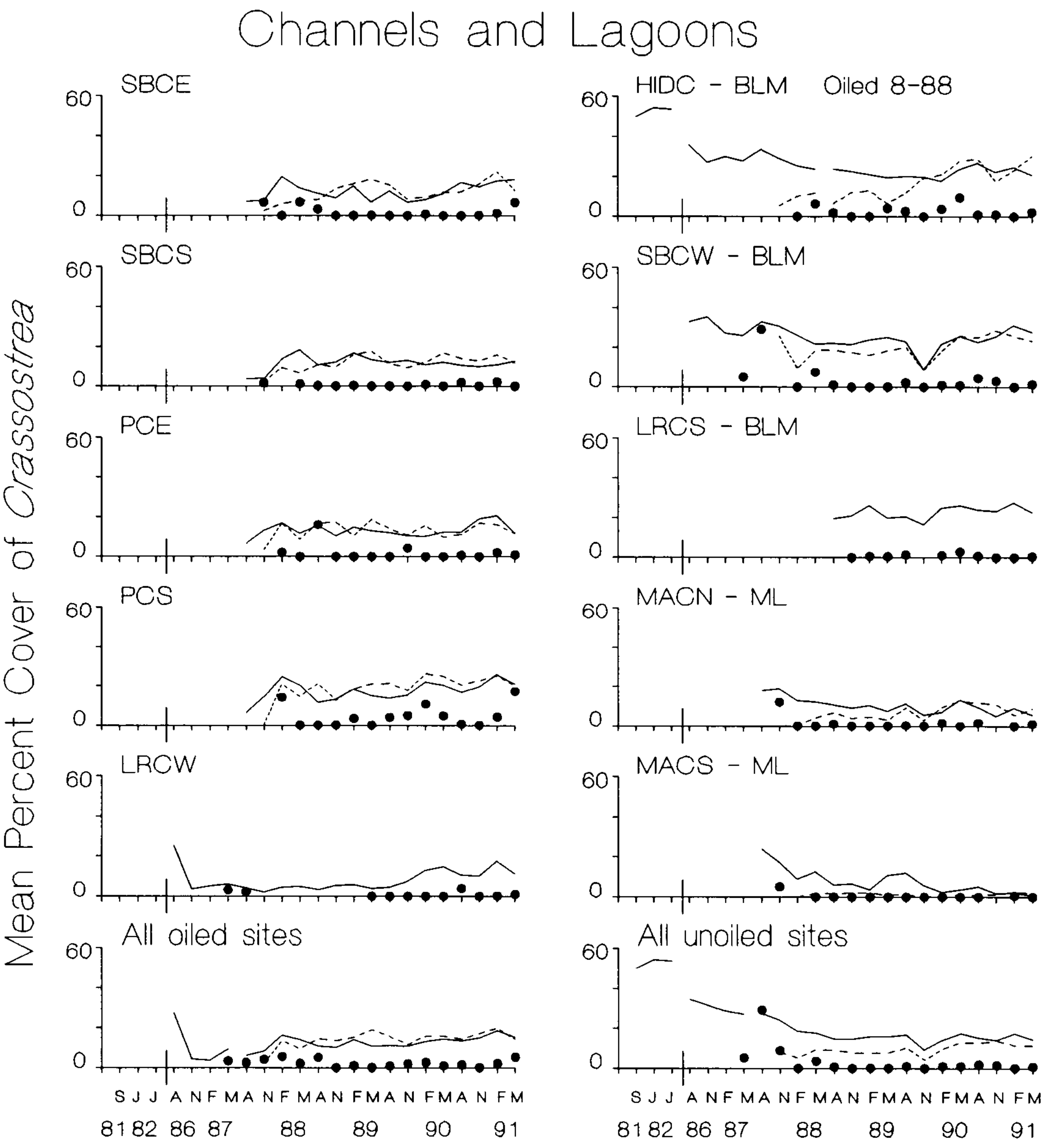

Fig. 9.93 Patterns of abundance of *Crassostrea virginica* on roots in channels and lagoons. Data are mean percent cover of *Crassostrea* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

filled with freshwater during these rains, and reduced salinity persisted at its southern end long enough to kill oysters. Dead *Crassostrea* generally covered < 10% of root surfaces (Fig. 9.95) with occasional peaks (e.g., like that at SBCW described above).

Table 9.17 Channel and lagoon repeated-measures ANOVAs: summary table.

A. Comparisons between unoiled lagoons. These ANOVAs test for differences between sites located in Bahía Las Minas (HIDC and SBCW) and Margarita Lagoon (MACN and MACS) for yr 2-5 postspill, August 1987-May 1991. Probabilities are given for arcsine-transformed percent cover for long-term census and community development roots. *Group* is the comparison between long-term census and community development roots.

Comparison	*Crassostrea virginica*	*Balanus*	Foliose Algae	Sessile Inverts.
Between:				
Lagoons	.003	.201	.266	.218
Group	.052	.123	.357	.198
L x G	.644	.972	.927	.974
Within:				
Year	.261	.006	.175	.162
Y x L	.070	.218	.734	.952
Y x G	.0005	.002	.067	.399
Y x L x G	.407	.541	.405	.762
Sphericity Test	.190	.292	.276	.063
H.-F. Adj. applied?	no	no	no	no

B. Test for oiling effects, adjusted for lagoons. These ANOVAs test for differences between oiled and unoiled sites for yr 2-5 postspill, August 1987-May 1991. Probabilities are given for arcsine-transformed percent cover for long-term census and community development roots. Comparisons chosen were based on results of between lagoon tests. For *Crassostrea virginica*, an unoiled site in Bahía Las Minas (SBCW only) was compared with all oiled sites (PCE, PCS, SBCE, and SBCS) and HIDC was used as an unoiled site. For the other analyses, unoiled sites were MACN, MACS, asnd SBCW. *Group* is the comparison between long-term census and community development roots.

Comparison	*Crassostrea virginica*	*Balanus*	Foliose Algae	Sessile Inverts.
Between:				
Oil	.005	.061	.754	.405
Group	.161	.288	.500	.307
O x G	.202	.613	.882	.814
Within:				
Year	.0001	.098	.225	.0001
Y x O	.010	.004	.710	.152
Y x G	.0001	.001	.125	.042
Y x O x G	.056	.005	.567	.951
Sphericity Test	.411	.177	.291	.255
H.-F. Adj. applied?	no	no	no	no

Species/root = mean number of species of foliose algae per root. *H.-F.?* = Huynh-Feldt adjusted probability levels. If *no*, then probability levels were unadjusted because of sphericity-test results. If *yes*, then levels were adjusted.

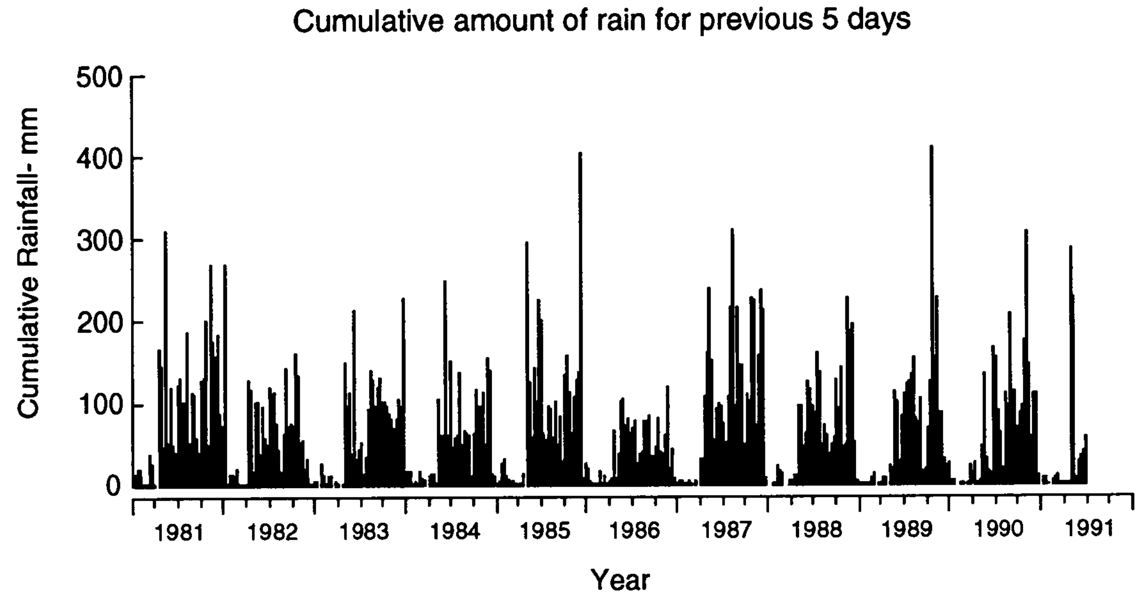

Fig. 9.94 January 1981-June 1991 rainfall records. Cumulative amount of rainfall at Punta Galeta in previous 5-d periods. Courtesy of K. W. Kaufmann and the Galeta Environmental Sciences Program.

There was no comparable reduction in *Crassostrea* on LT roots following the secondary oiling of another site in the western wing of Bahía Las Minas (HIDC) between May and August 1988 (Figs. 9.28, 9.93; see Sect. 9.5.3). This single event deposited oil high on roots (e.g., Fig. 9.21), above most epibiota.

The vertical distribution of *Crassostrea* ran from MHW to the subtidal, although oysters were most abundant intertidally (≤50 cm below MHW; Fig. 9.96). Distribution patterns were similar over time and among sites; dead oysters were found at the same depths as live ones, except they were rare at depths greater than 100 cm.

Other Bivalves. Other bivalve molluscs found on LT roots included *Mytilopsis sallei*, *Brachidontes ?exustus*, and *Isognomon ?alatus*. *Mytilopsis* averaged 12% cover in 1981-1982 sampling; its overall abundance from August 1986 to May 1991 only reached >10% cover once (August 1987; Fig. 9.97). Abundances at HIDC and SBCW were moderate and variable for the first 2 yr, and then they decreased. *Mytilopsis* was always rare or absent at the two Margarita sites (MACS and MACN), and never covered more than 6% on roots at LRCS. It had a wide vertical distribution overall (Fig. 9.98), from MHW to 120 cm below MHW, with most occurring ≥40 cm below MHW.

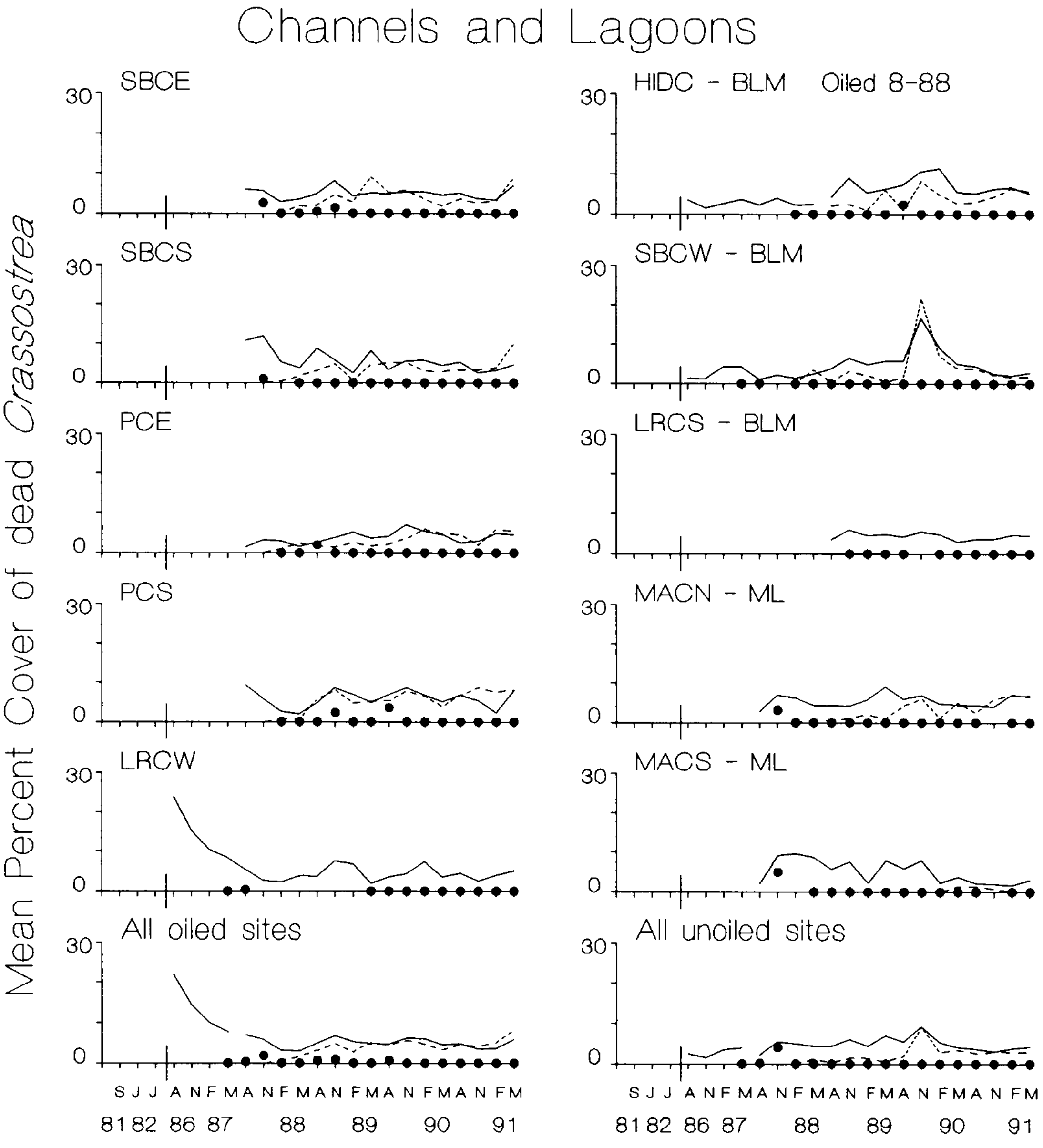

Fig. 9.95 Patterns of abundance of dead *Crassostrea virginica* on roots in channels and lagoons. Data are mean percent cover of dead *Crassostrea* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

The abundance of *Brachidontes* in 1981-1982 surveys averaged 3% cover (Fig. 9.99). During the first year after the spill its abundance averaged 5% cover. From August 1987 to May 1991 it varied between 1 and 3% cover overall, with few found

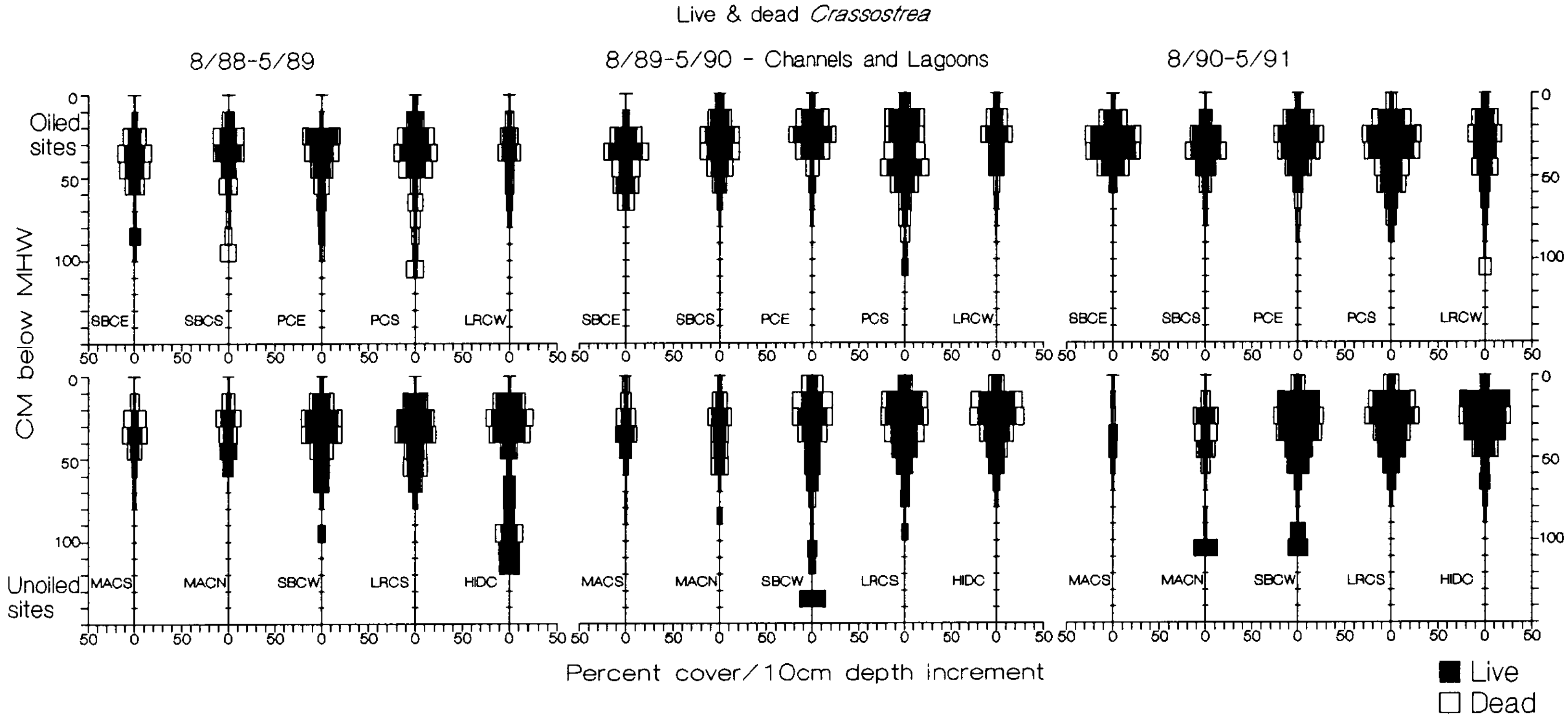

Fig. 9.96 Vertical distribution of live and dead *Crassostrea* in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (x-axes) of live and dead *Crassostrea virginica* for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

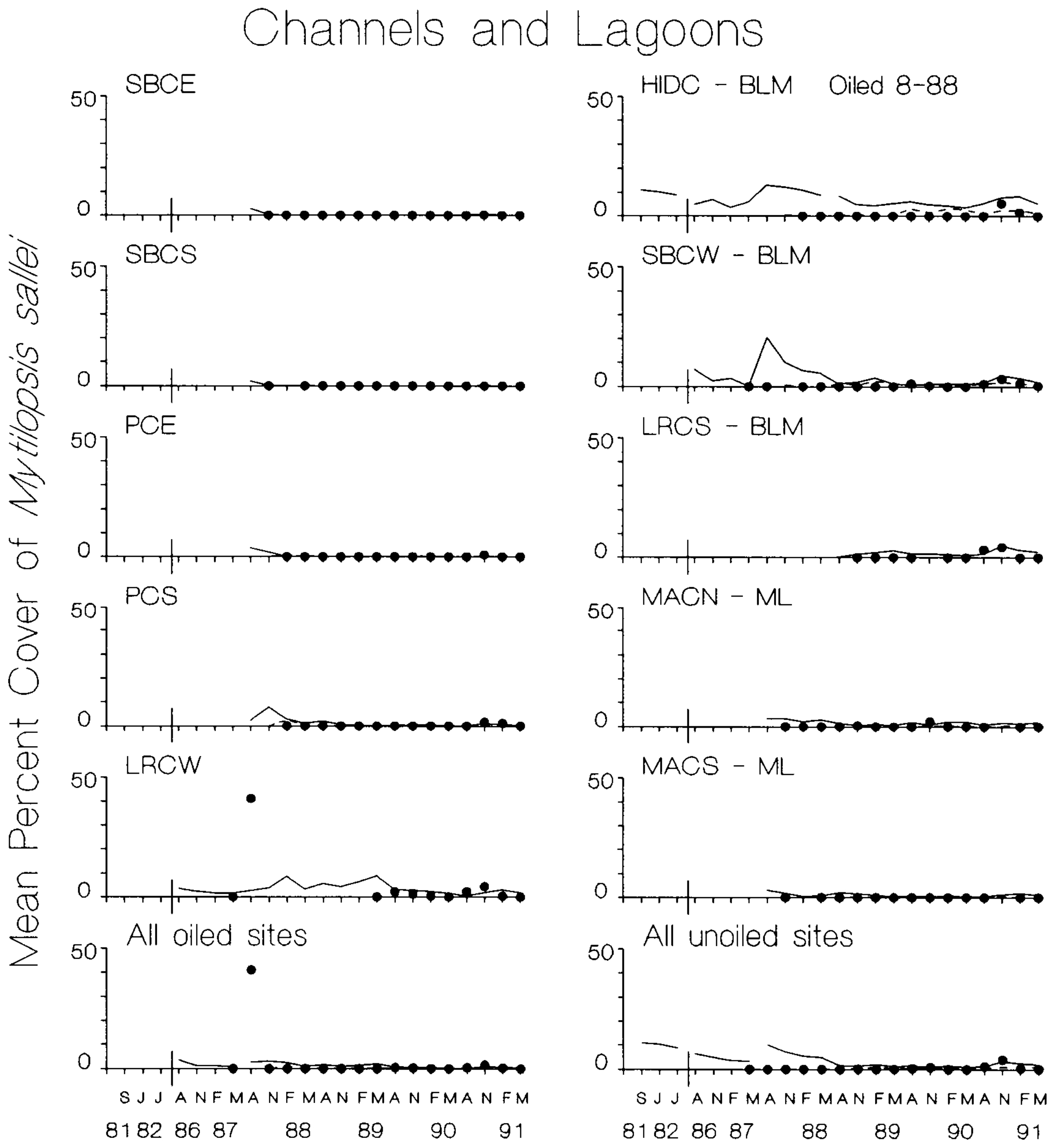

Fig. 9.97 **Patterns of abundance of *Mytilopsis* on roots in channels and lagoons. Data are mean percent cover of *Mytilopsis sallei* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.**

in Margarita Lagoon (MACS and MACN) and variable abundances in Bahía Las Minas (SBCW and LRCS). At HIDC mean abundance was initially 9% cover, but dropped to <1% by February 1988. Abundances thereafter were not greater than

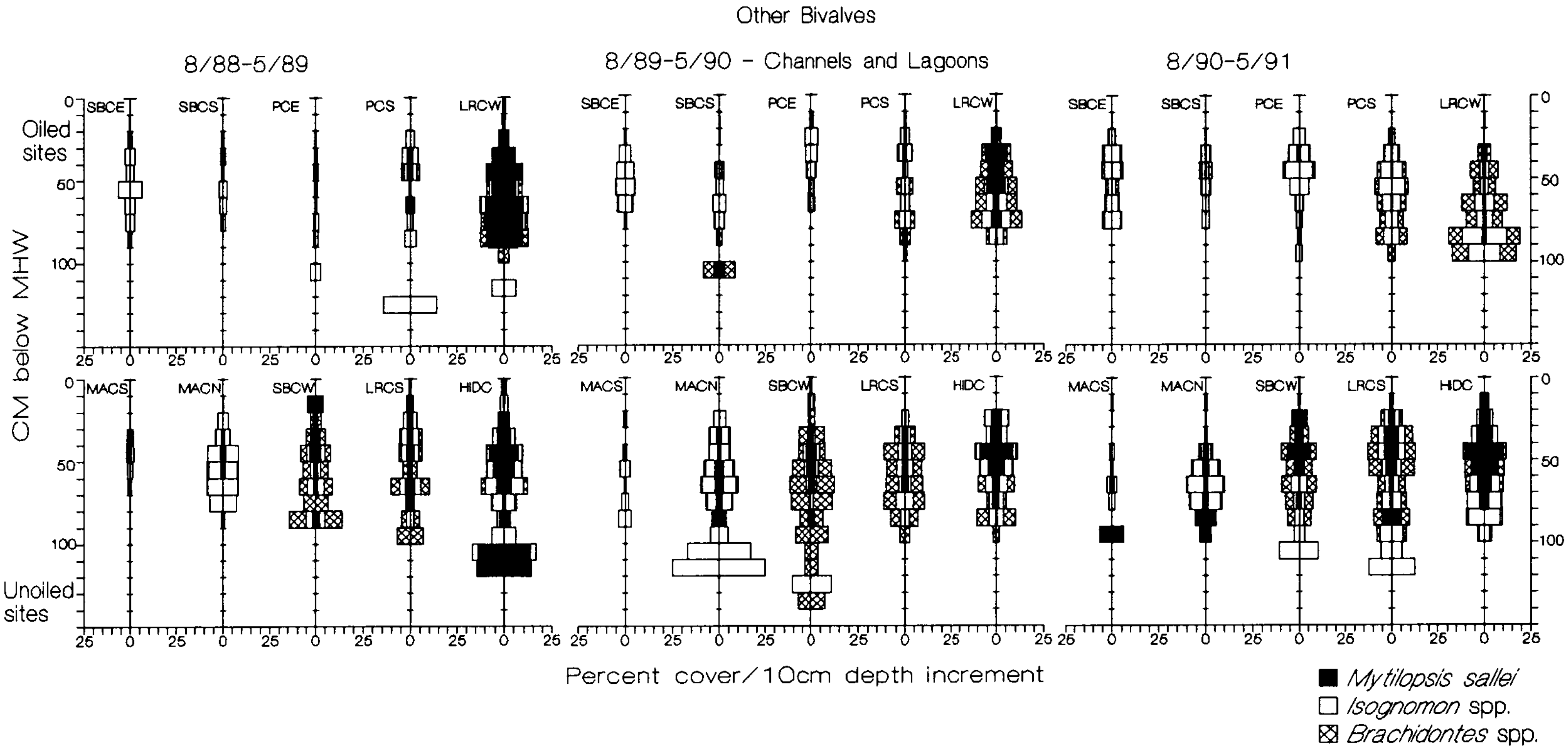

Fig. 9.98 Vertical distribution of other bivalve molluscs in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (*x*-axes) of three species of bivalves for 10-cm increments on roots downward from MHW (*y*-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

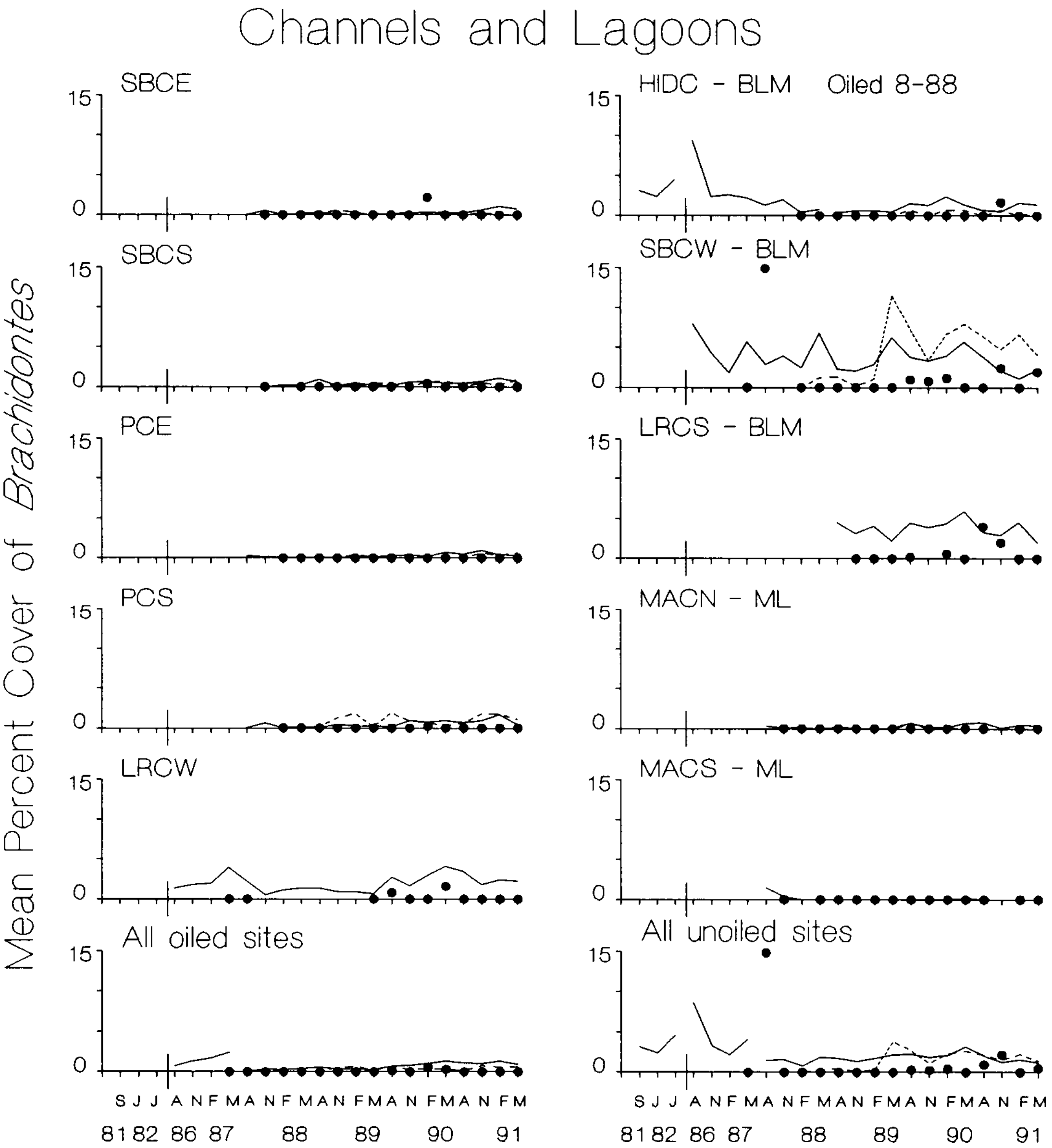

Fig. 9.99 Patterns of abundance of *Brachidontes* on roots in channels and lagoons. Data are mean percent cover of *Brachidontes* spp. for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

~2% cover. *Brachidontes* was usually found at depths ≥20 cm below MHW, and was most abundant on subtidal portions of roots (Fig. 9.98).

Isognomon covered an average of 4-7% of space on roots in 1981-1982 (Fig. 9.100). It was found on LT roots at all sites in each of the 20 quarterly monitorings from August 1986 on, and varied between 1 and 6% cover from August 1986 to May 1991. Abundance patterns varied among sites, but fluctuated widely only at MACN. There was a general trend of decreasing abundance over time, except at SBCW, where *Isognomon* covered >2% of root surfaces. *Isognomon* was rare or absent from MHW to 20 cm depth, was most abundant deeper than 50 cm below MHW, and appeared to have no lower depth limit (Fig. 9.98).

Barnacles. The barnacle *Balanus improvisus* averaged 13% cover on LT roots in 1981-1982 (Fig. 9.101). Its overall abundance remained relatively stable (range of 4-11% cover) from August 1986 to May 1991, despite changes in site locations (Fig. 9.5). There was little variation seasonally, among years, or among sites. Its vertical distribution extended from 10 cm below MHW to 140 cm depth, with increased abundance below 40 cm deep (Fig. 9.102). On randomly sampled roots, there were no significant differences in percent cover of *Balanus* between Margarita Lagoon and Bahía Las Minas ($P > .05$, NS).

Foliose Algae. Foliose algae were not recorded in 1981-1982. From August 1986 on, foliose algae occurred on roots at one or more sites in each of 20 quarterly monitorings (Fig. 9.103), ranging from 4 to 12% cover. There was little variation among sites, and no apparent seasonal pattern. Margarita Lagoon and Bahía Las Minas did not differ ($P > .05$, NS). An average of <1 species was recorded on each root (Fig. 9.104); mean number of species/root tended to increase with percent cover of foliose algae (Fig. 9.105).

An average of ~5 species was calculated to occur in a sample of 20 roots (rarefaction estimates, Fig. 9.106). Species considered typical of the "Bostrychietum" were most abundant. They included *Polysiphonia subtilissima*, *Bostrychia* spp., *Catenella repens*, and *Caloglossa leprieurii*. Mixed-algal turfs, *Caulerpa* spp., and several other species occurred as well. *Polysiphonia* was found on roots from MHW down, but was most abundant either <50 cm below MHW or on deepest portions of roots (Fig. 9.107). *Catenella repens*/*Caloglossa leprieurii* ranged from MHW to 80 cm depth, and was mostly intertidal. *Bostrychia* spp. were rare and occurred between 20 and 80 cm depth. *Caulerpa*, mixed-algal turfs, and "other" algae were all rare, and none occurred above 40 cm below MHW.

Rare Sessile Invertebrates. Sessile invertebrates found in channels and lagoons were rare, and included arborescent hydroids and bryozoans, sponges, encrusting bryozoans, and tunicates. Their combined mean abundance varied from 2 to 4% cover in 1981-1982 (Fig. 9.108). Abundances during August 1986-May 1987 at two sites within Bahía Las Minas ranged from 9 to 18% cover; from August 1987 to May 1991, they ranged from 5 to 15% cover overall at four sites. Variation within sites among times was considerable, but Margarita Lagoon and Bahía Las Minas did not differ significantly ($P > .05$, NS).

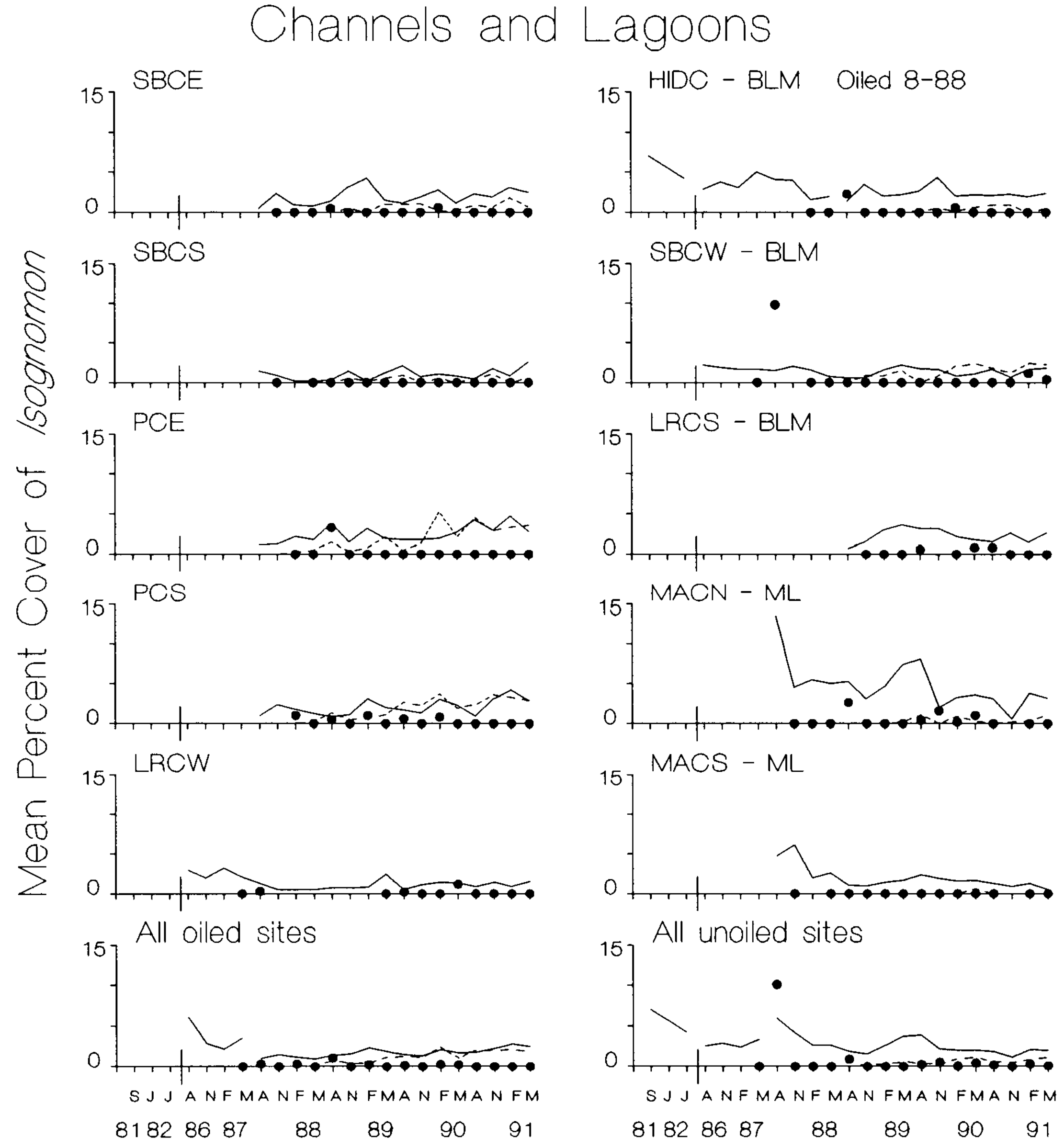

Fig. 9.100 Patterns of abundance of *Isognomon* on roots in channels and lagoons. Data are mean percent cover of *Isognomon* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

Abundances of individual taxa varied among sites and over time. Cnidarians (anemones) were not found at the two Margarita Lagoon sites (MACS and MACN), and were intermittently present and rare (≤1% cover) at LRCS (4 of 12 quarters)

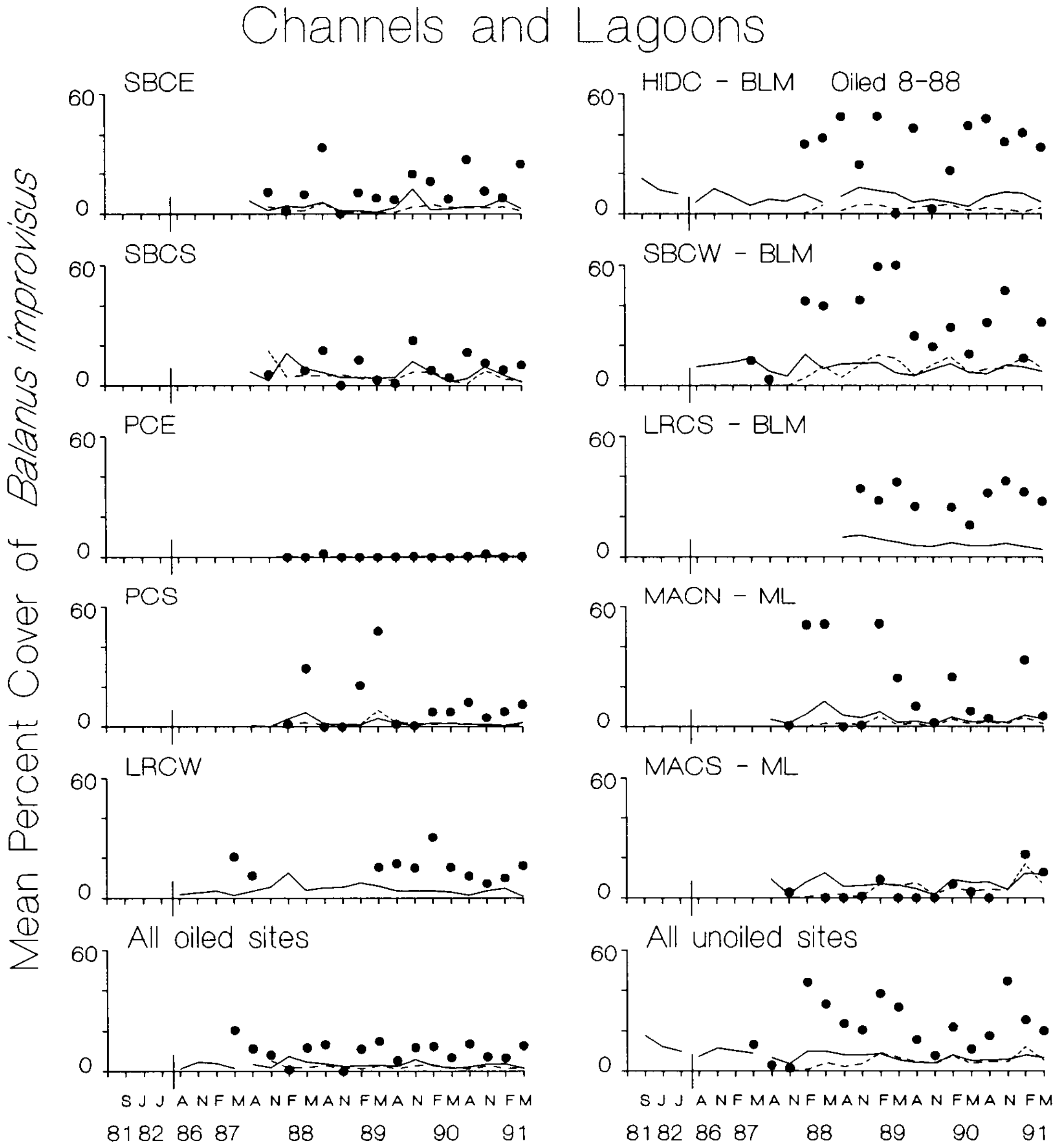

Fig. 9.101 Patterns of abundance of *Balanus* on roots in channels and lagoons. Data are mean percent cover of *Balanus* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

and at HIDC (4 of 11 monitorings before, 4 of 12 monitorings after secondary oiling). Anemones occurred more often at SBCW (14 of 20 monitorings), but covered <1% of root surfaces.

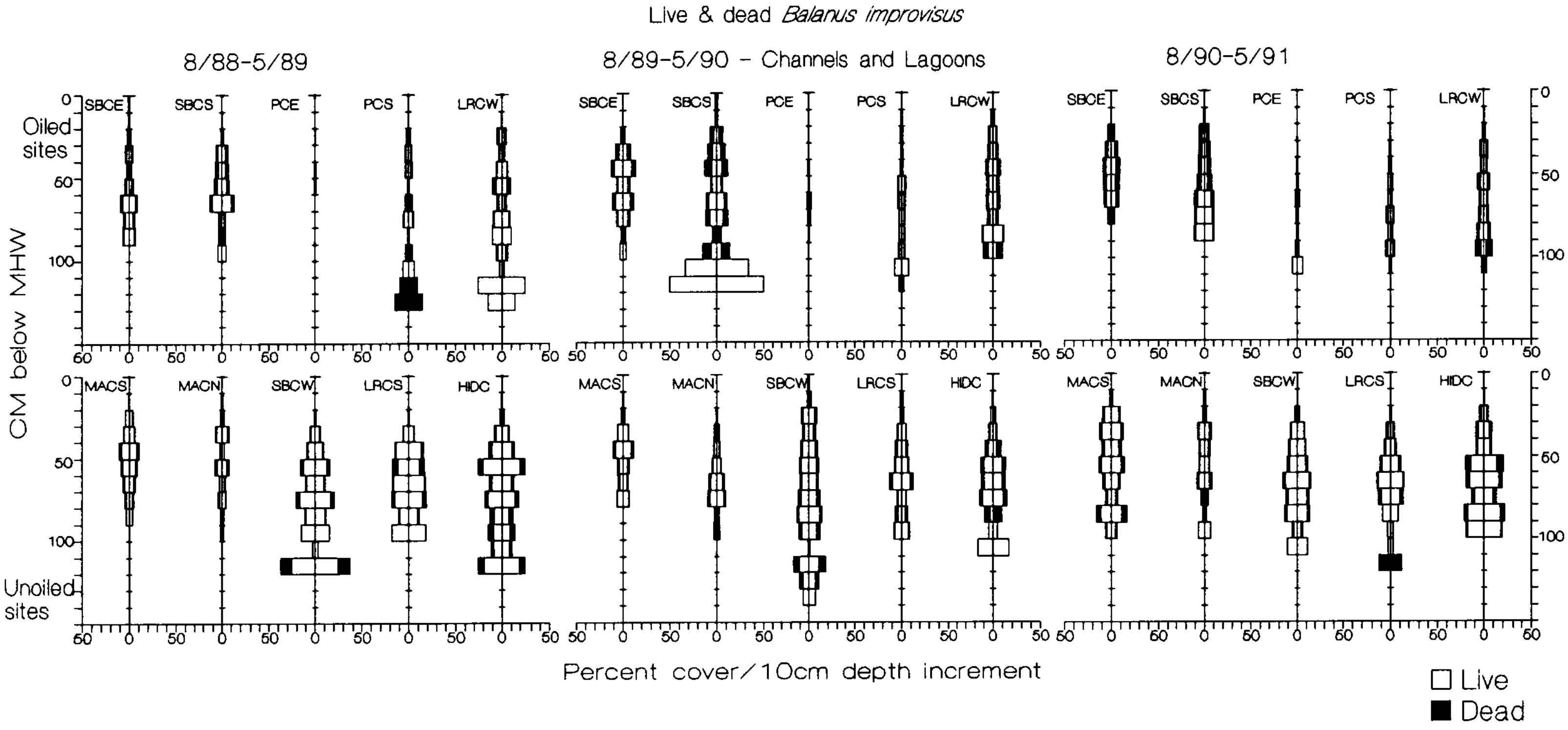

Fig. 9.102 Vertical distribution of *Balanus improvisus* in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (x-axes) of live and dead *Balanus* for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

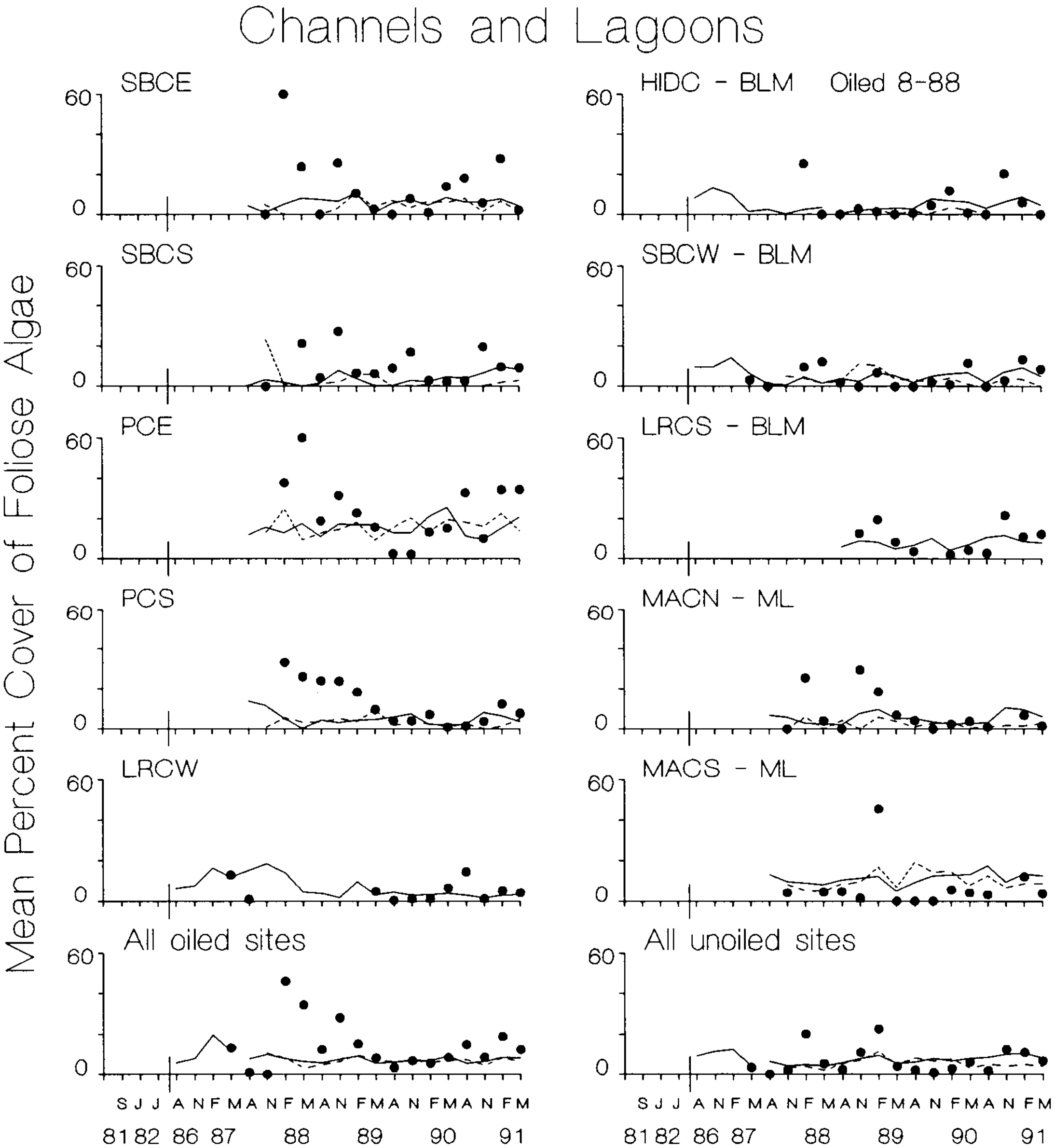

Fig. 9.103 Patterns of abundance of foliose algae on roots in channels and lagoons. Data are mean percent cover of foliose algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

Two species of solitary tunicates were present in 50-100% of all monitorings at all sites but MACS (2 of 16 quarters). Abundances were strongly seasonal, with ephemeral peaks in early rainy season (May; Fig. 9.109). Many tunicates appeared

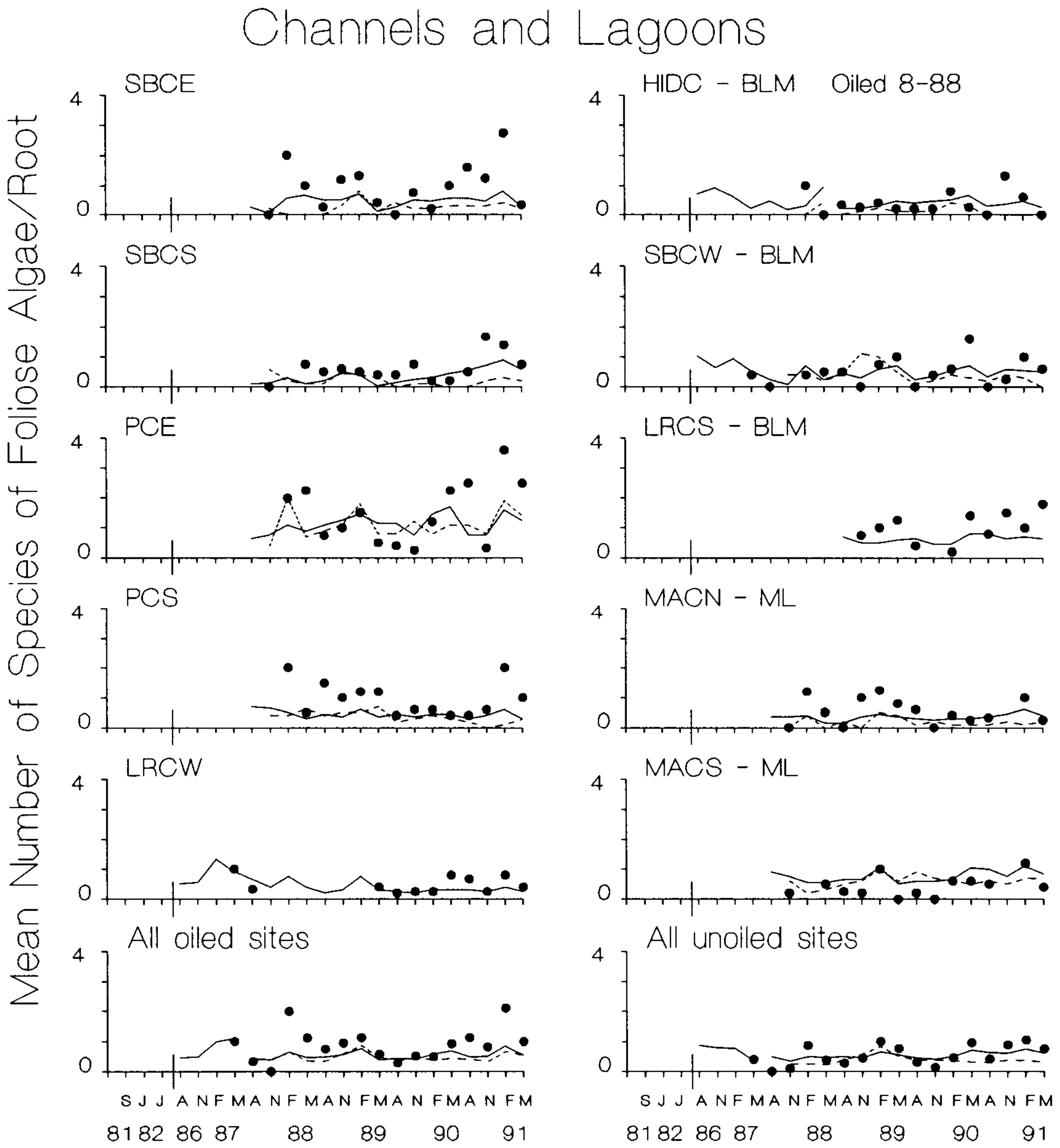

Fig. 9.104 Patterns of algal species richness on roots in channels and lagoons. Data are mean number of species of foliose algae/root for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

senescent in May (pers. obs.), suggesting dry season conditions were optimal for this group. Tunicates never occurred shallower than 40 cm below MHW, and most were found deeper than 50 cm (Fig. 9.110).

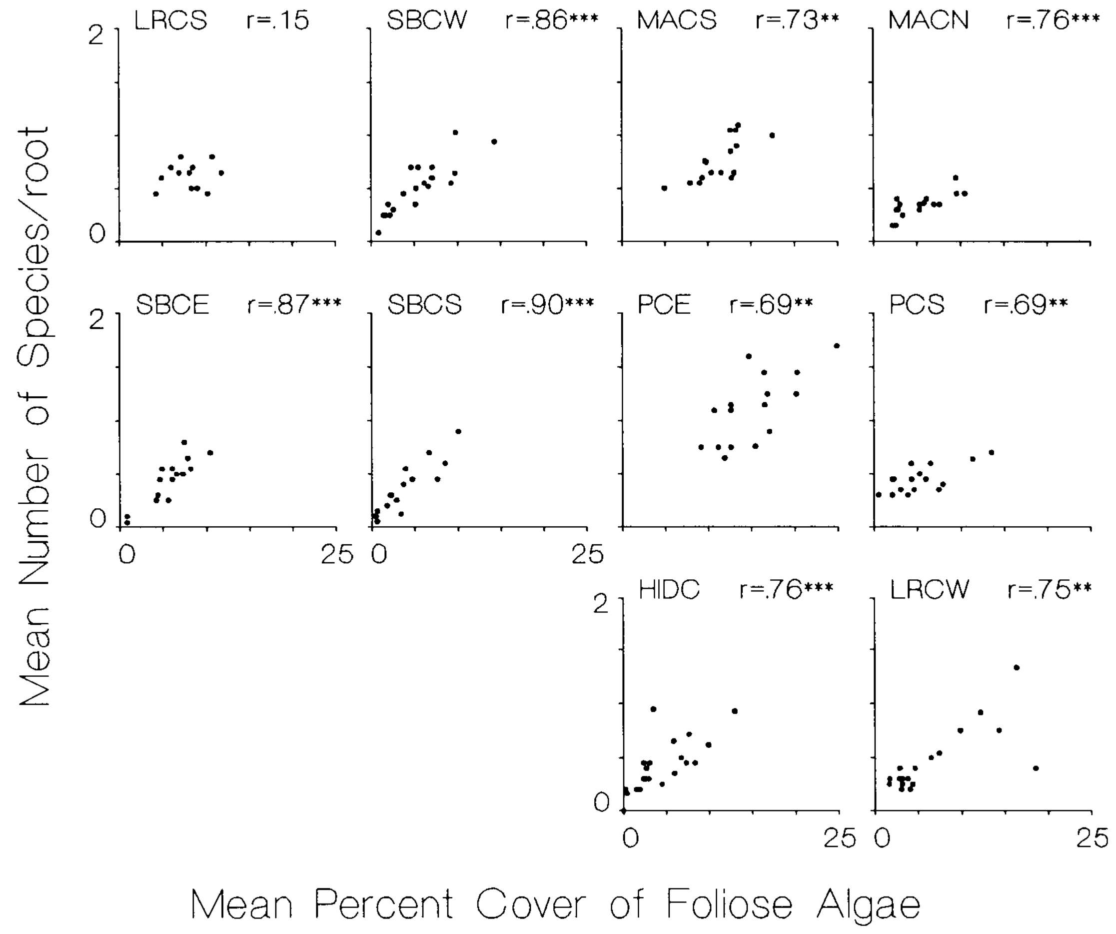

Fig. 9.105 Algal species richness vs. percent cover of foliose algae on randomly censused roots in channels. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. *r* = correlation coefficient, **: *P* = 0.01, ***: *P* = .001 (significance level of observed correlation). If there is no asterisk the correlation was not significant (*P* >.05).

Sponges never averaged more than 5% cover on roots, and were highly variable among sites and over time within sites (Fig. 9.111). They were either absent (8 of 16 monitorings) or rare (≤1% cover) at MACS. In contrast, sponges occurred in 18 of 20 quarters, and averaged ≥1% cover in 12 of 20 quarters at SBCW. With rare exceptions, the vertical distribution of sponges ranged from 40 cm below MHW through subtidal portions of roots (Fig. 9.110).

Arborescent hydroids and bryozoans were absent from randomly sampled roots in the three 1981-1982 surveys; they were rare (≤5% average cover) from August 1986 to May 1991 (Fig. 9.112). Of all rare sessile invertebrates, only hydroids and arborescent bryozoans occurred in any abundance at MACS, peaking in late rainy season 1988 and 1990. However, they were absent in late rainy season 1987

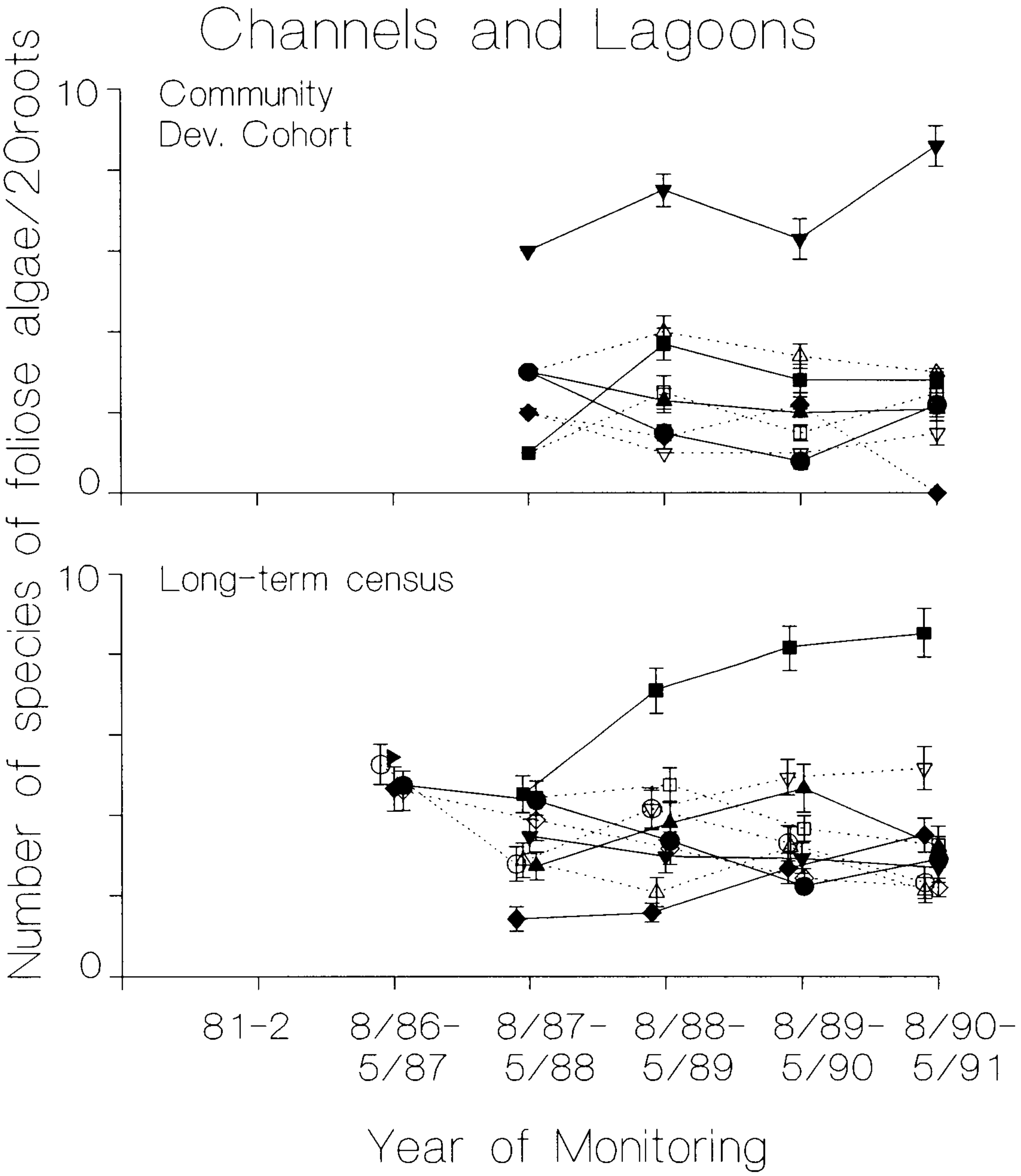

Fig. 9.106 Species richness of foliose algae in channels. Mean ± 95% confidence interval for rarefaction estimates of the number of species of foliose algae expected in a sample of 20 roots. *Solid symbols* = oiled sites, *open symbols* = unoiled sites. See text for details.

and 1989 at this site, and abundances were low and variable at other sites, with no seasonal pattern. This group could occur as shallow as 10 cm below MHW, but was rare shallower than 40 cm, and mostly appeared on the deepest portions of roots

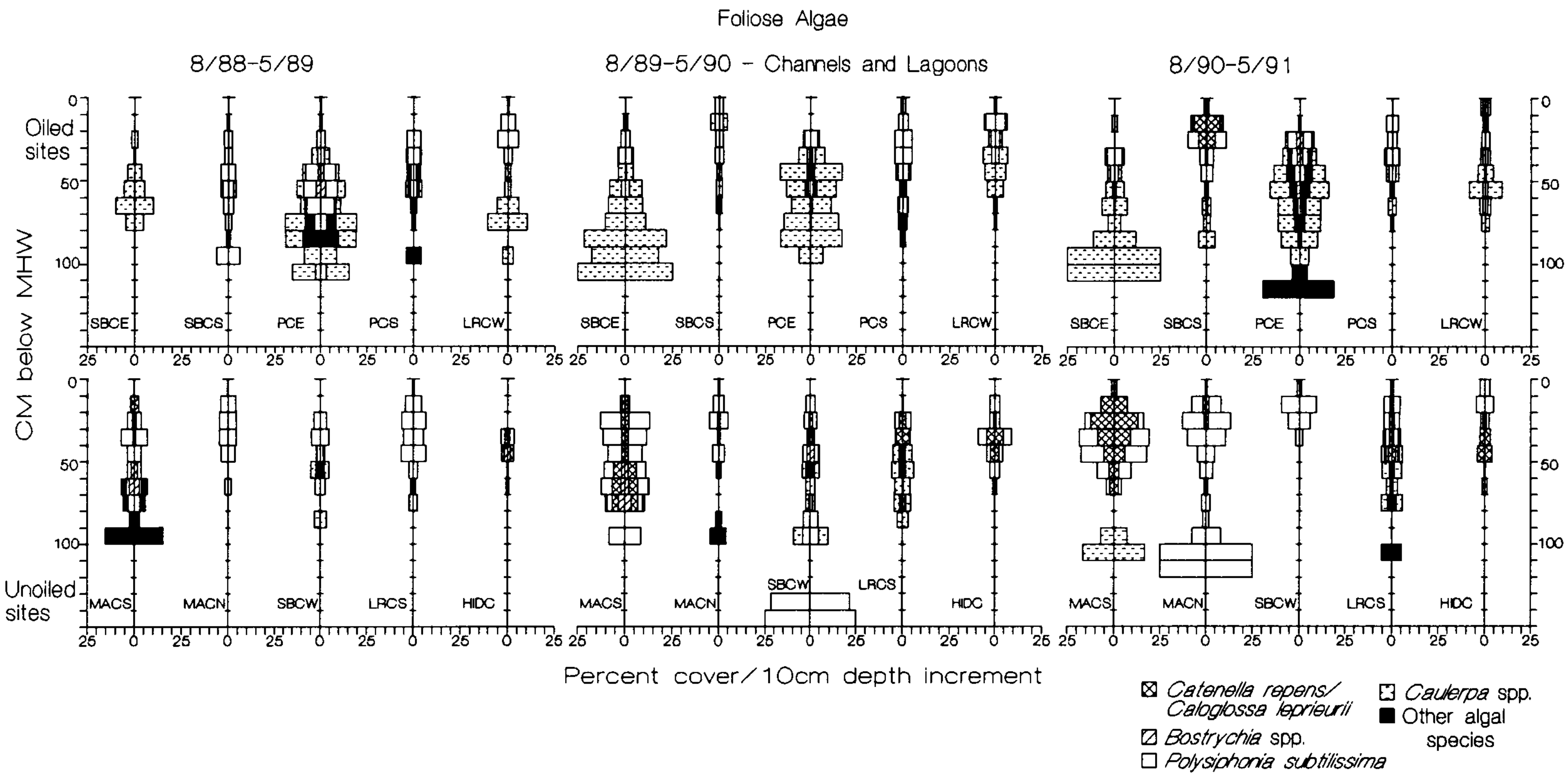

Fig. 9.107 Vertical distribution of foliose algae in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (x-axes) of algae for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

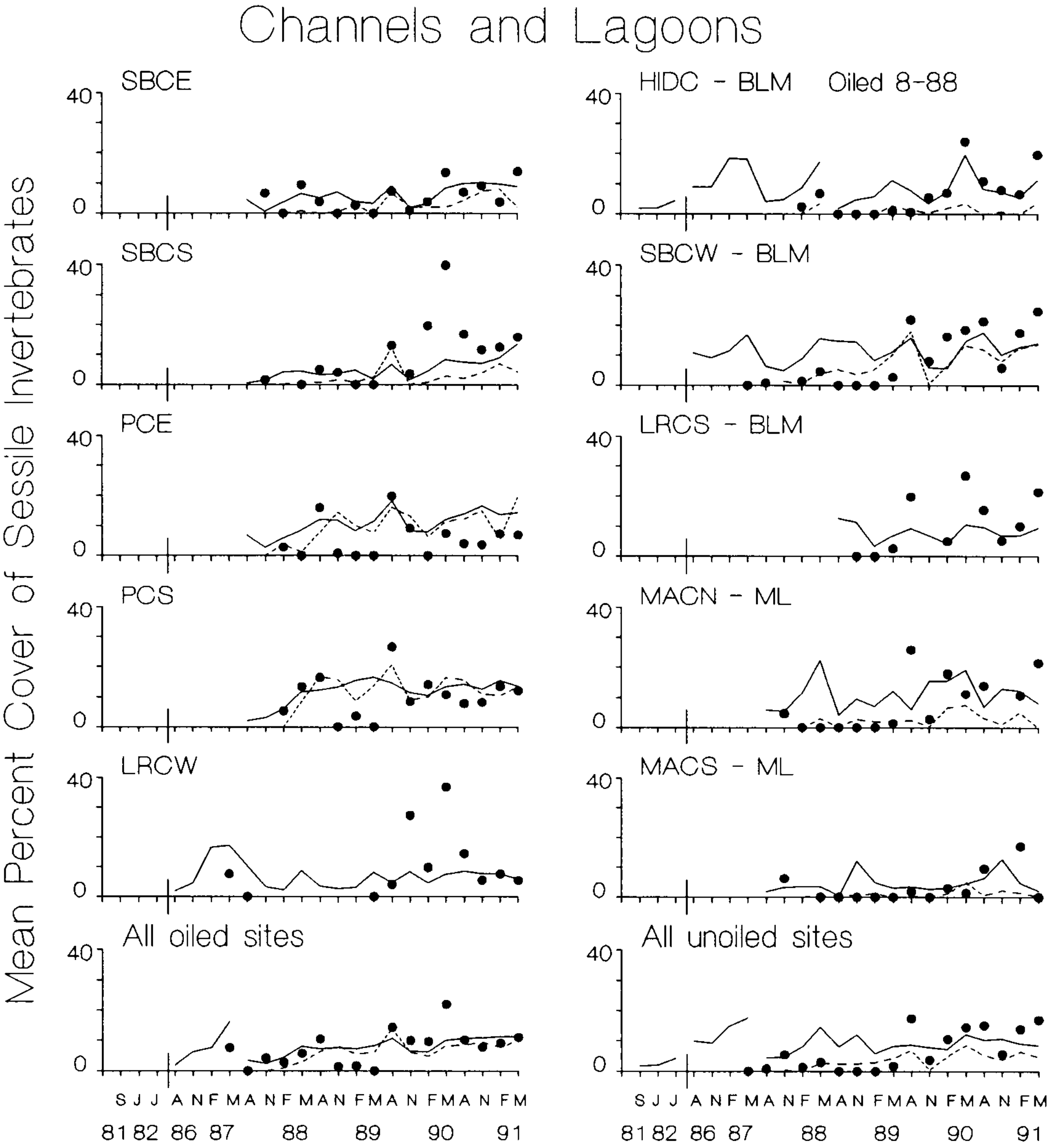

Fig. 9.108 Patterns of abundance of sessile invertebrates on roots in channels and lagoons. Data are mean percent cover of sessile invertebrates for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. "Sessile invertebrates" were defined as all groups except barnacles and bivalves.

(Fig. 9.110). Encrusting bryozoans occurred regularly on roots, but covered <3% of root surfaces. They covered more space in Bahía Las Minas (cover usually >2%) than Margarita Lagoon (cover usually <1%).

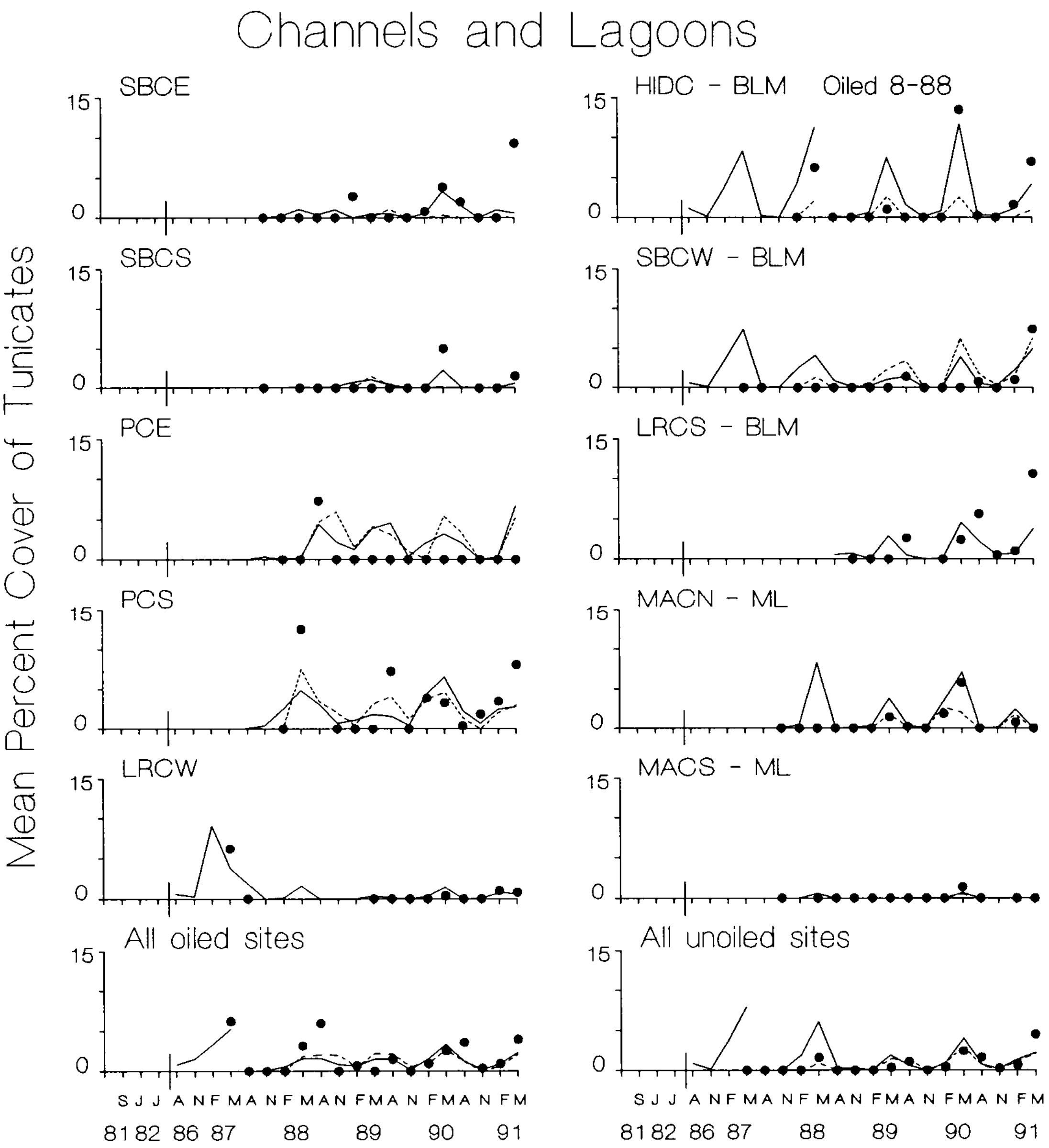

Fig. 9.109 Patterns of abundance of tunicates on roots in channels and lagoons. Data are mean percent cover of tunicates for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

Diatoms and Bare Space. Diatoms ranged between 3 and 16% cover from August 1986 to May 1991 (Fig. 9.113). They were always less abundant in Bahía Las Minas than in Margarita Lagoon. Diatoms were too rare to examine possible

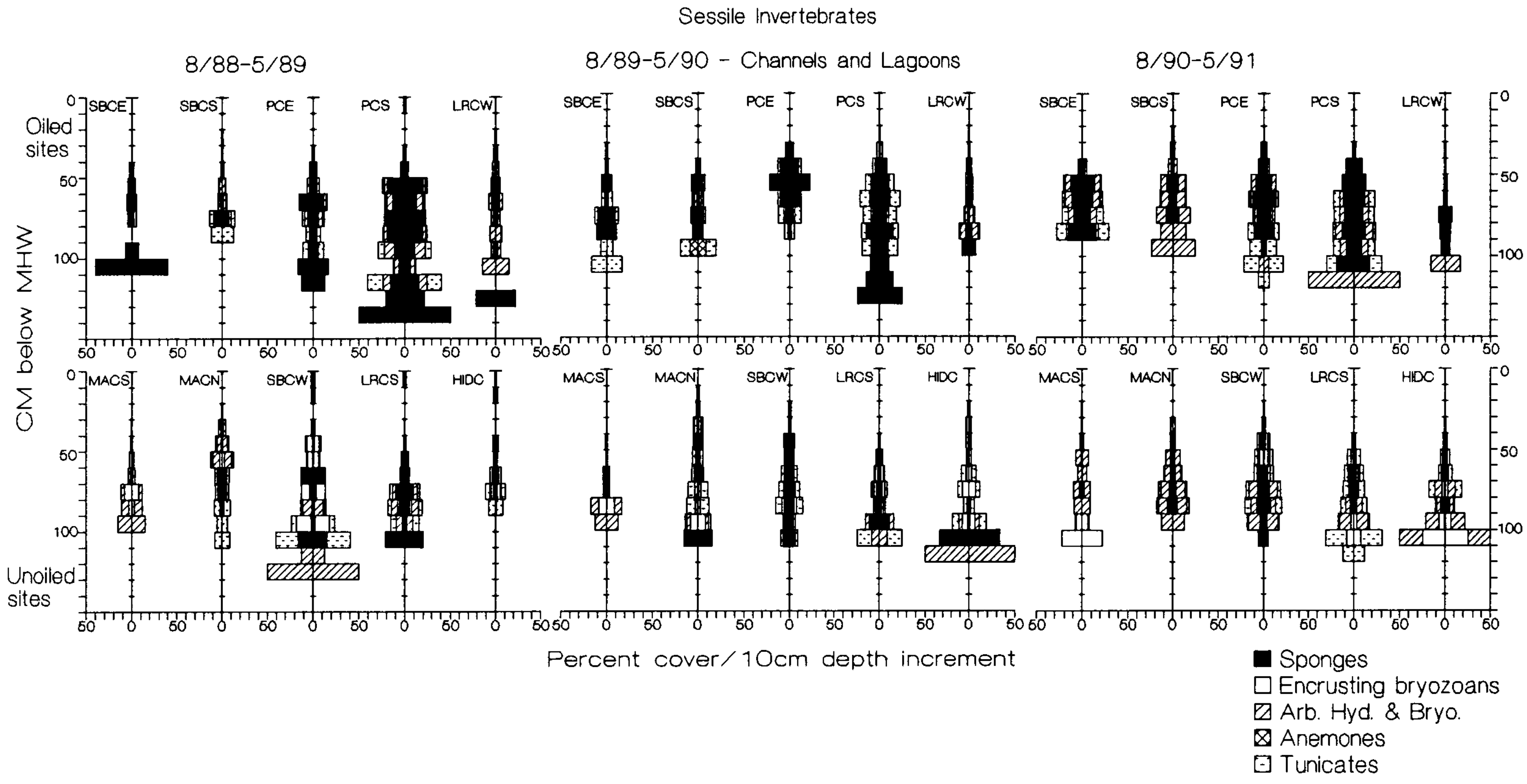

Fig. 9.110 Vertical distribution of sessile invertebrates in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (x-axes) of various sessile invertebrates for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

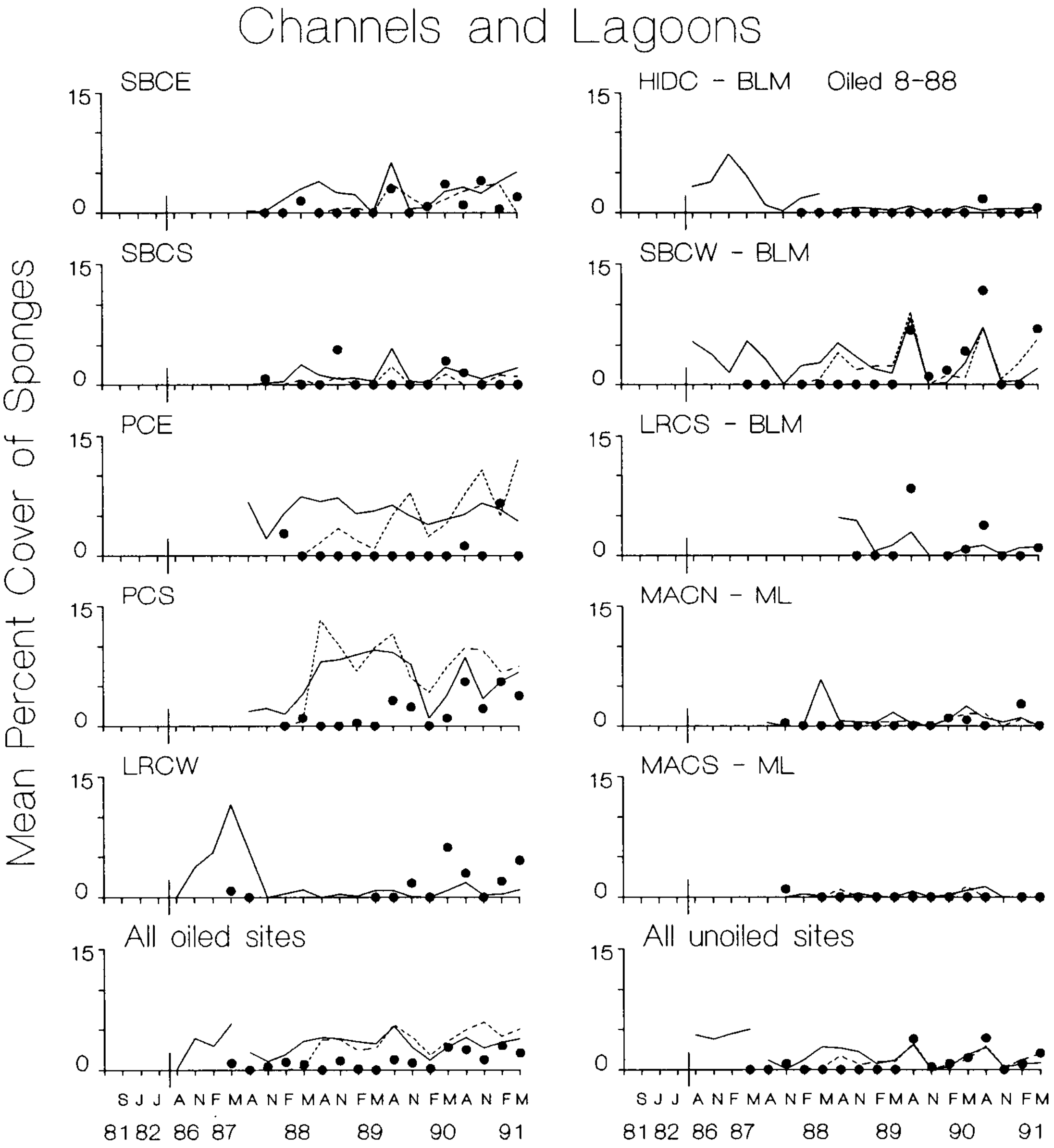

Fig. 9.111 Patterns of abundance of sponges on roots in channels and lagoons. Data are mean percent cover of sponges for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

seasonality at HIDC, SBCW, and LRCS. At MACN and MACS they were rarest during early wet season (May) from 1988 to 1991. This, and their increased abundance over the remainder of rainy season, suggested dry season conditions at

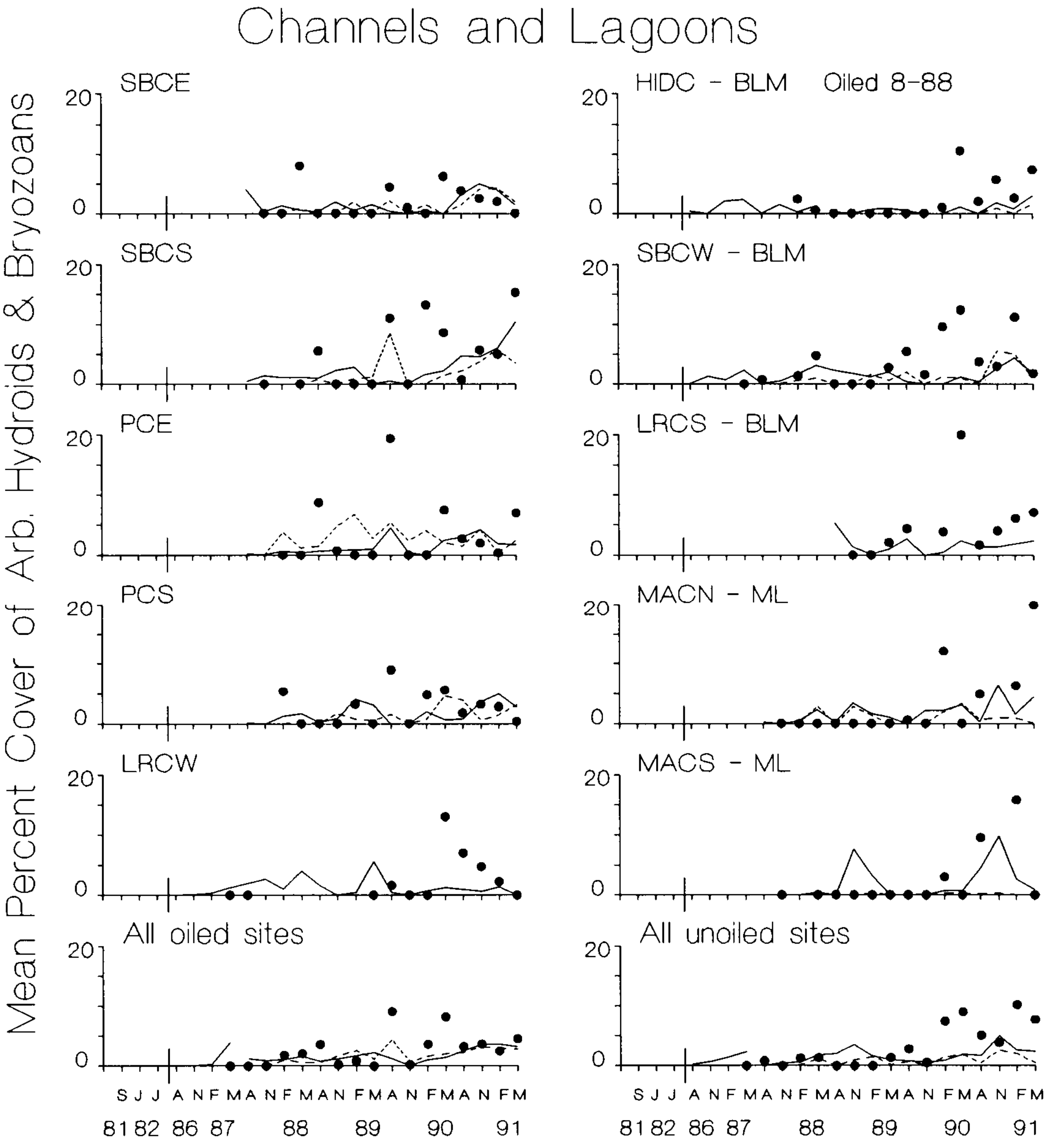

Fig. 9.112 Patterns of abundance of arborescent hydroids and bryozoans on roots in channels and lagoons. Data are mean percent cover of arborescent hydroids and bryozoans for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas, *Arb.* = arborescent. See text for details.

these two sites were least suitable for diatoms. Diatoms extended from MHW to the subtidal zone, although they were least abundant above 20 cm and tended to be most abundant on deepest portions (Fig. 9.114).

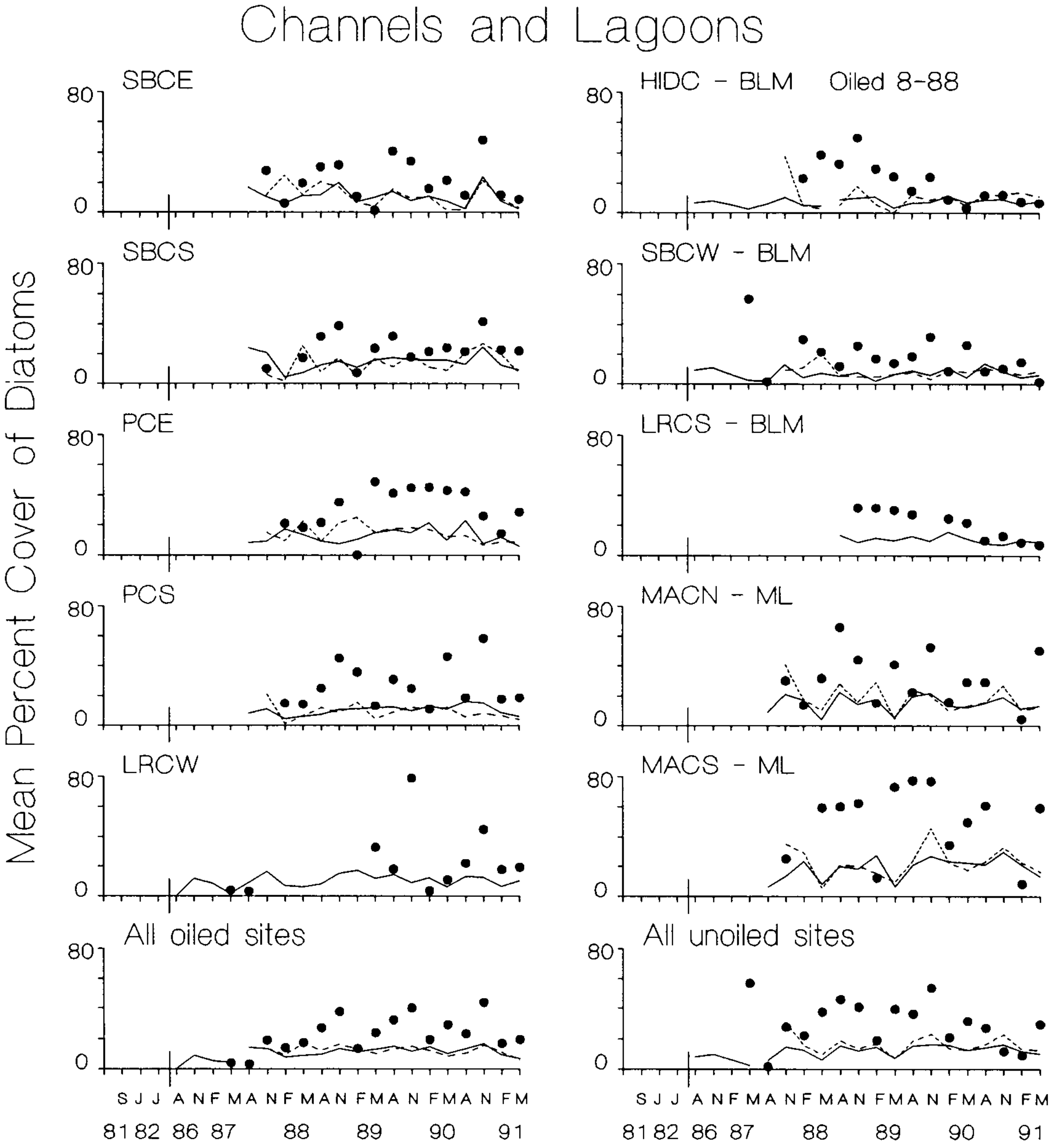

Fig. 9.113 **Patterns of abundance of diatoms on roots in channels and lagoons. Data are mean percent cover of diatoms for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census roots (*N* = 20-25/site),** ***dashed lines*** **are community development roots (*N* = 5-10/site), and** ***solid circles*** **are recruitment dowels (*N* ~5/site).** ***ML*** **= Margarita Lagoon,** ***BLM*** **= Bahía Las Minas. See text for details.**

Approximately 13% of root surfaces were bare from August 1986 to May 1987, when two sites within Bahía Las Minas were sampled (Fig. 9.115). Between 25 and 36% of space on roots was bare during the remaining 4 yr, with no trend of increase

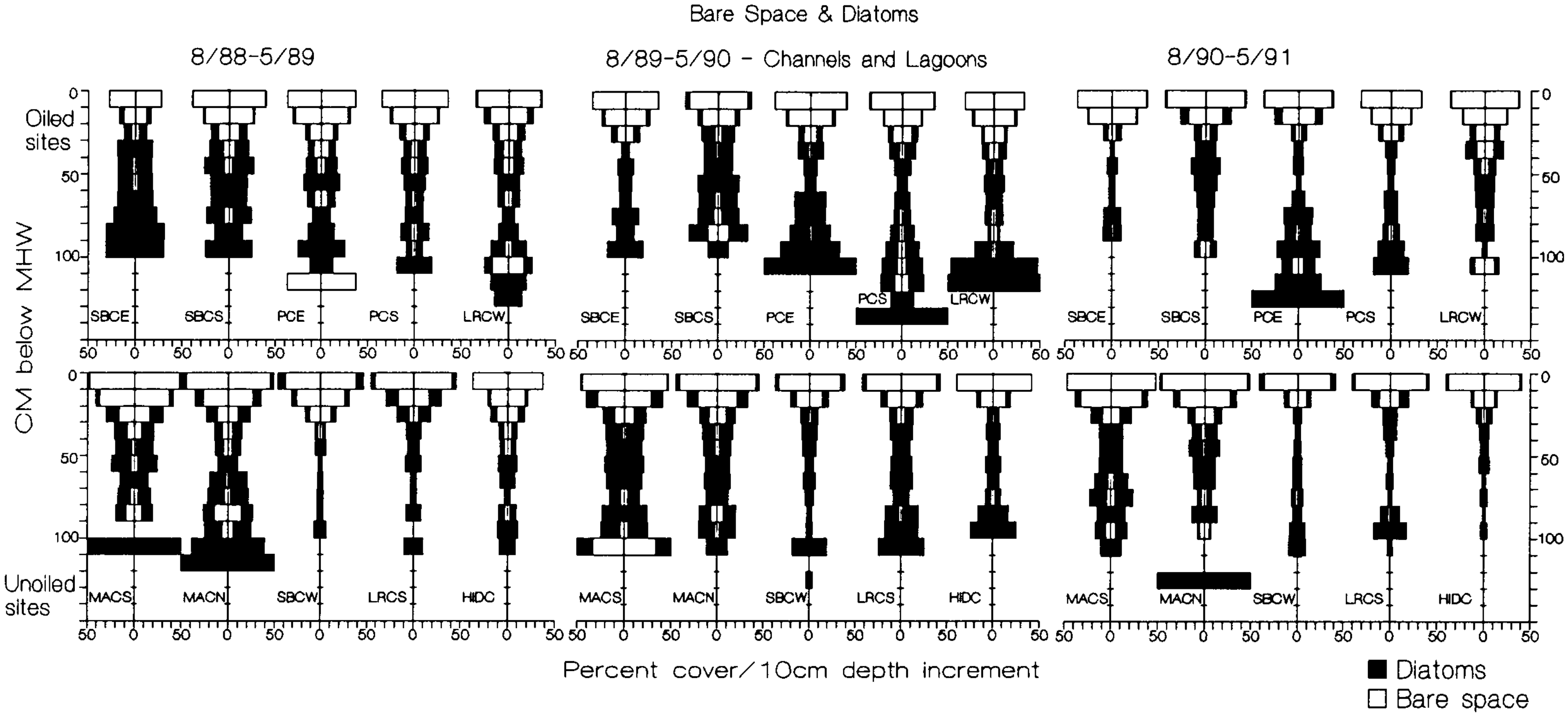

Fig. 9.114 Vertical distribution of diatoms and bare space in yr 3, 4, and 5 postspill on random-census roots in channels. Data are mean percent cover (x-axes) of diatoms and bare space for 10-cm increments on roots downward from MHW (y-axes) for 20 roots ≥75 cm long per site per year. Site codes as in Table 9.2. See text for further details.

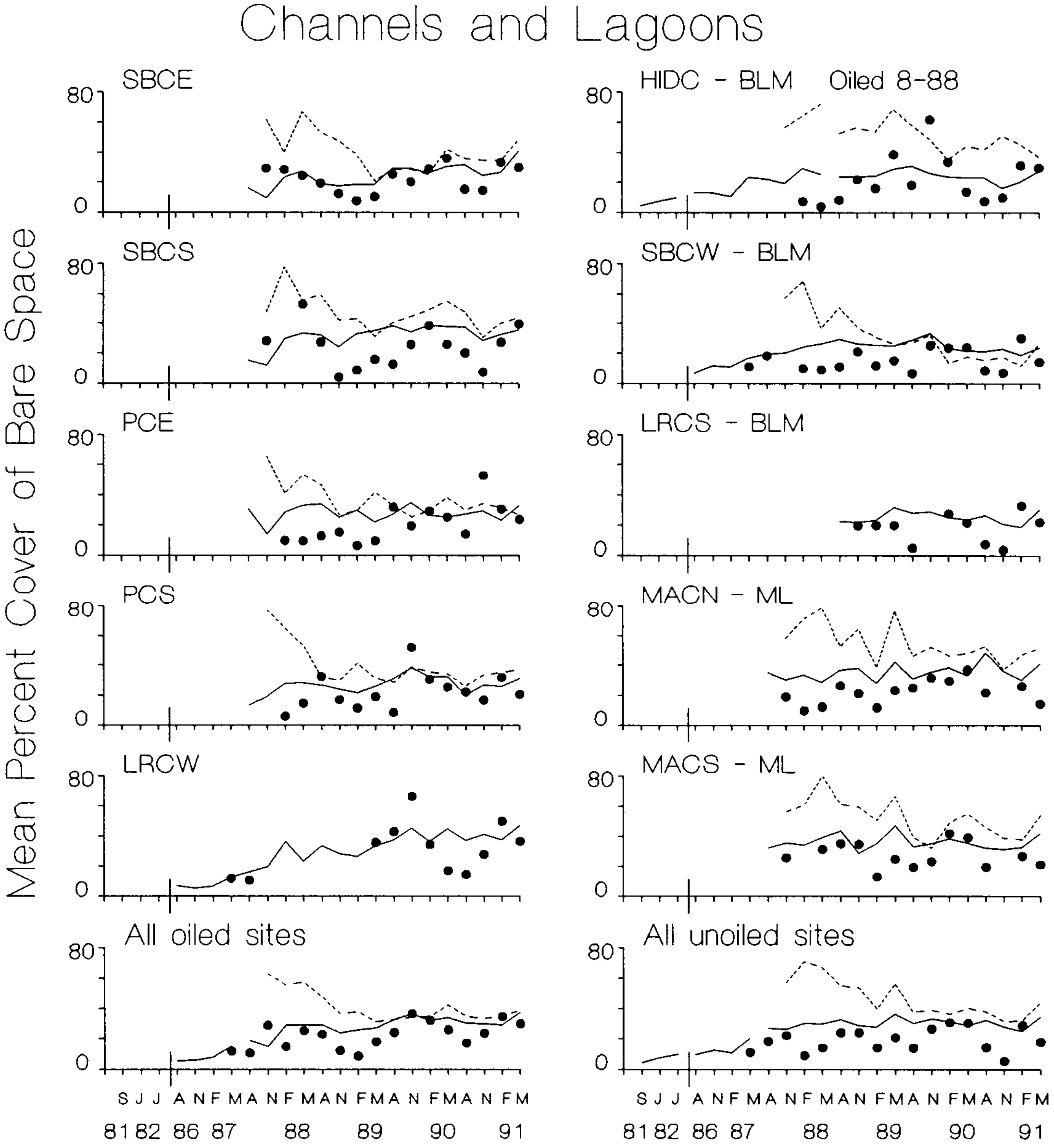

Fig. 9.115 Patterns of abundance of bare space on roots in channels and lagoons. Data are mean percent cover of bare space for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). *ML* = Margarita Lagoon, *BLM* = Bahía Las Minas. See text for details.

or decrease. Most unoccupied space occurred high on roots, from MHW to 30 cm depth (Fig. 9.114). Unlike roots on the open coast, there was little or no bare space deep on root surfaces (Figs. 9.86, 9.114). More space was bare in Margarita Lagoon (MACS and MACN) than in Bahía Las Minas (SBCW, LRCS, and HIDC).

Recruitment

Crassostrea virginica. *Crassostrea* had only one major recruitment event in 17 quarters (May-August 1987, dowels placed only at SBCW, mean of 29% cover; Fig. 9.93). No oysters occurred on dowels in February 1988, November 1988, and November 1989; mean cover in the remaining 13 quarters ranged from <1 to 9%. The single, major recruitment at SBCW, August 1987, was not followed by a corresponding increase in oyster abundance on randomly sampled roots. This suggested that postsettlement mortality or competition might have affected recruits.

Other Bivalves. Of the remaining bivalve molluscs, *Mytilopsis* did not recruit onto dowels from May 1987 to August 1988 and then occurred patchily (<5% cover; Fig. 9.97). No false mussels were found on dowels at MACS; they occurred twice at MACN and HIDC, and in 8 of 16 quarters at SBCW. Recruitment frequency appeared to have little effect on abundances on randomly sampled roots.

Brachidontes recruited little in the 17 quarters examined (Fig. 9.99). The one moderate event (SBCW, May-August 1987 dowels, mean cover of 15%), was not followed by increases in abundance on roots. The greatest increase in *Brachidontes* on roots (May 1989, SBCW) was preceded by over a year of recruitment failure on dowels. Similarly, *Isognomon* recruited in abundance >10% once (at SBCW, August 1987), but there were no subsequent increases in *Isognomon* abundance on roots (Fig. 9.100).

Barnacles. *Balanus improvisus* recruited variably over time with a tendency for reduced cover in late wet season (November; Fig. 9.101). Its abundance on dowels was highest in dry season (February) in 3 of 4 yr, reaching 60% in some replicates. Cover of *Balanus* was always lowest at MACS, deep in Margarita Lagoon. Abundances of barnacles on recruitment dowels were not related to changes in barnacle abundance on roots (Fig. 9.101).

Foliose Algae. Recruitment of foliose algae was variable, but occurred overall mostly in late rainy season (November), dry season (February), and early rainy season (May; Fig. 9.103). Rarefaction estimated that between 1.0 and 4.3 species of foliose algae/10 dowels were expected in channels. In Bahía Las Minas estimates were higher in August 1989-May 1990 (1.5-4.3) than in other years (1-3.3 species/10 dowels). More species of algae were estimated to occur at MACS (mean of 2.6 species/10 dowels) than at MACN (2.0 species/10 dowels).

Sessile Invertebrates. Rare sessile invertebrates showed little recruitment until the fourth year after the oil spill (mean combined cover of <1% from May 1987 to May 1989). Abundances on dowels from then through May 1991 averaged 6% cover (Fig. 9.108). Both sponges and tunicates appeared ephemeral, with recruitment maxima usually corresponding to peaks in abundance on randomly censused roots

(Figs. 9.109, 9.111). Recruitment of arborescent hydroids and bryozoans failed through May 1989, then was variable (Fig. 9.112).

Diatoms and Bare Space. Diatoms recruited in all 17 quarters (Fig. 9.113). There was no overall seasonal variation or long-term trend. Abundances were variable, ranging from 2 to 56% cover. Among sites, MACN and MACS had both higher cover and greater variability of diatoms than sites in Bahía Las Minas. LRCS varied least among dates, showing a steady reduction in diatom cover over time. Approximately 10-25% of space on dowels was bare (Fig. 9.115).

Community Development

The progressive cover of space on initially bare roots was examined at four sites from November 1987 to May 1988 (no roots were marked at LRCS); after the secondary oiling of HIDC, that site was considered separately (see Sect. 9.5.3). The various taxa occupying space on LT roots developed at different rates at different sites on roots that entered the water in September-November 1987 (e.g., Fig. 9.116).

Crassostrea virginica. Crassostrea appeared within 3 mo, with an overall mean abundance on CD roots of 8% cover in November 1987 (Fig. 9.93). However, its overall abundance did not continue to increase, and generally remained below 10% cover until February 1990. In the last year of the study, oyster abundances varied between 11 and 14% cover, roughly the same as on LT roots (Fig. 9.93).

Among-site variation was high. *Crassostrea* essentially failed to settle at MACS and the population of oysters on randomly censused roots declined to almost 0% cover. Abundance of oysters increased most rapidly at SBCW and more slowly at HIDC and MACN. Cover on the CD cohort equalled that on randomly censused roots in between 9 and 36 mo (Fig. 9.93).

HIDC showed a small drop in oyster cover on CD roots 3 mo after it was oiled, one of several decreases along a general trend of increased abundance over time (Fig. 9.93). There was no increase in cover of dead *Crassostrea* on CD roots following oiling of HIDC. At this and other sites, dead oysters gradually became as abundant as on randomly censused roots (Fig. 9.95).

Other Bivalves. Mytilopsis sallei, never abundant on LT roots, was absent to rare on CD roots overall through May 1991 (Fig. 9.97). At the two Bahía Las Minas sites false mussels occurred on CD roots about twice as often as at MACS and MACN (13 of 15 vs. 7 and 8 of 15 quarterly monitorings).

Brachidontes first appeared on CD roots after a year (August 1987). This mussel remained rare overall until May 1989, then matched its abundance on LT roots through May 1991 (Fig. 9.99). Like *Mytilopsis, Brachidontes* was least common in Margarita Lagoon (MACN and MACS).

Isognomon first appeared on CD roots in November 1988, more than a year after they had entered the water. Overall, it increased slowly in abundance over

Fig. 9.116 Community development root with epibiota. November 1989, site = SBCW. Two years after entering the water this root had a full complement of species typical of channel roots.

time, but did not average more than 1% cover through May 1991 (Fig. 9.100). This overall increase was due chiefly to its abundance at a single site, SBCW, where it was similar to *Isognomon* cover on LT roots from November 1988 on. Recruitment failed at MACN.

Barnacles. *Balanus* appeared on CD roots in February 1988. Within four quarters its overall abundance matched that on LT roots (Fig. 9.101). Patterns of barnacle abundance on CD and LT roots were linked closely at MACS and MACN from then on, but not until August 1989 at SBCW. *Balanus* remained rare (1-5% cover) at HIDC through May 1991.

Foliose Algae. Foliose algae immediately appeared on CD roots (November 1987). For the remainder of the study overall algal abundance did not differ between LT and CD samples (Fig. 9.103). Mean number of species/root was < 1 (Fig. 9.104); the mean number of species/root increased with percent cover of algae as on LT roots (Figs. 9.105, 9.117). Species accumulated on CD roots over time, with slightly fewer on CD than LT roots after 4 yr (rarefaction estimates; Fig. 9.106).

Sessile Invertebrates. Sessile invertebrates appeared on CD roots as soon as they entered the water (November 1987; Fig. 9.108). Sponges on CD roots followed the pattern of abundance on LT roots beginning in May 1989 at SBCW and MACN (the two sites where they were common enough to track), and did not differ from their respective long-term census abundances in subsequent monitorings (Fig. 9.111). Tunicates occurred at one or more sites on CD roots from February 1988 through May 1991 (Fig. 9.109). Tunicates only occurred once at MACS (May 1990, < 1% mean cover); at other sites, cover of tunicates fluctuated seasonally like that on LT roots (Fig. 9.109).

Arborescent hydroids and bryozoans also first occurred in February 1988 with low and variable abundance over time (Fig. 9.112). At individual sites abundances sometimes closely tracked those on LT roots (e.g., HIDC and SBCW, November 1990-May 1991; MACN, February 1988-August 1990), but appeared independent at other times (e.g., November 1988 at MACS; November 1991 at MACN and MACS).

Diatoms and Bare Space. Diatoms bloomed immediately on CD roots, reaching an overall mean abundance of 31% cover in November 1987. By February 1988 diatom cover had dropped by 50% and did not subsequently differ from that on LT roots (Fig. 9.113). Diatoms covered more space on CD roots at Margarita Lagoon (MACS and MACN) than in Bahía Las Minas (SBCW and LRCS).

Community development roots were bare when they entered the water after being marked in September 1987. Bare space declined over time to levels similar to LT roots in the last 2 yr of the study (Fig. 9.115). Variability in this decreasing trend was primarily due to increases in early rainy season (May), particularly at MACS.

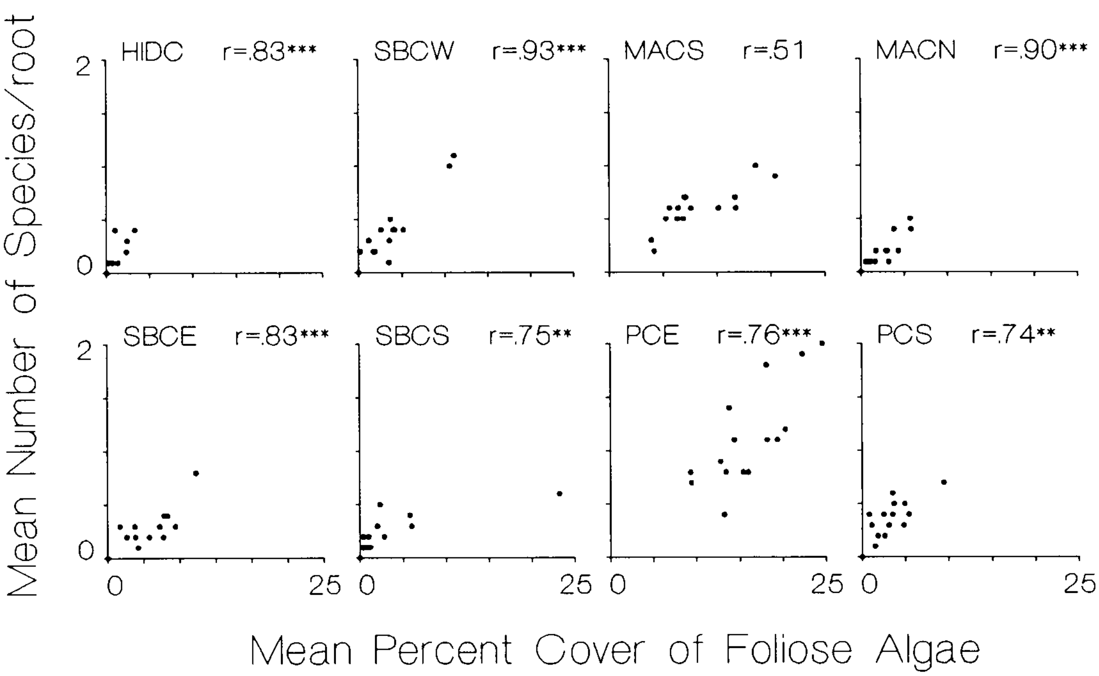

Fig. 9.117 Algal species richness vs. percent cover of foliose algae on community development roots in channels. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. r = correlation coefficient, **: P = .01, ***: P = .001 (significance level of observed correlation). If there is no asterisk the correlation was not significant (P >.05).

Oiled Channels – Results and Comparisons with Unoiled Sites

Long-term Census Roots

Statistical tests of oiling effects in channels were complicated by (1) differences between unoiled sites in Margarita Lagoon and those in Bahía Las Minas and (2) site changes necessitated by the secondary oiling of HIDC in August 1988. Eight of the 10 channel sites had balanced observations, including a marked CD cohort. These included PCE, PCS, SBCE, and SBCS (oiled); MACN, MACS, and SBCW (unoiled); and HIDC (unoiled/secondarily oiled). The remaining two sites, LRCW (oiled) and LRCS (unoiled), lacked a CD cohort, so monitoring included long-term random censuses and recruitment dowels only. Finally, LRCS was monitored for the last 3 yr of the study only, since it was added as a replacement control site when HIDC was oiled.

To avoid underestimating oiling effects and to use all available data, we first tested for significant differences in percent cover between unoiled sites in Bahía Las Minas (HIDC and SBCW) and unoiled sites in Margarita Lagoon (MACS and MACN) for yr 2-5 after the spill, and for yr 3-5 after the spill (HIDC, SBCW, and LRCS vs. MACS and MACN). These two analyses, which used partially overlapping data sets, were done because the Margarita Lagoon sites were in an entirely different bay and watershed from all other sites, whether oiled or unoiled.

If differences between the two sets of unoiled sites were not significant, repeated-measures ANOVAs were run on CD and LT data for the following sites: PCE, PCS, SBCE, and SBCS (oiled) vs. SBCW, MACN, and MACS (unoiled, error df = 10, 30). To be conservative, we did not use data from HIDC, which was lightly oiled in a secondary event in 1988. Analyses were repeated for yr 3-5 postspill for LT data only for the second series of sites (oiled: LRCW, PCE, PCS, SBCE, and SBCS; unoiled: LRCS, SBCW, MACN, MACS, and HIDC; error df = 8, 16).

If differences between lagoons were significant, we rejected sites within Margarita Lagoon as not being representative of those in Bahía Las Minas, and used data only from oiled and unoiled sites within Bahía Las Minas. Such sites for which LT and CD data were available included PCE, PCS, SBCE, and SBCS (oiled), and HIDC and SBCW (unoiled, error df = 8, 24). Despite the secondary oiling at HIDC, we treated it as one of the control sites within Bahía Las Minas, because (1) oil had stranded during high water, and covered portions of roots above most epibiota, causing little apparent damage and (2) any bias introduced because of negative effects of this oiling would tend to reduce, rather than increase differences between oiled and unoiled sites (and thus make our tests more conservative). Analyses were repeated for yr 3-5 postspill for LT data only for the larger number of sites for which these data were available (oiled: LRCW, PCE, PCS, SBCE, and SBCS; unoiled: LRCS, SBCW, and HIDC; error df = 6, 12).

Crassostrea virginica. In August 1986 intertidal portions of prop roots along oiled channels were heavily coated with oil (Figs. 9.14, 9.23). *Crassostrea*, the most common intertidal species (Figs. 9.93, 9.118, 9.119), was severely affected. Its abundance in three prespill samples (1981-1982) ranged from 50 to 54% cover. In August 1986 at three stations along an oiled channel in the western wing of Bahía Las Minas (LRCW, PGC, and CO3; Fig. 9.5), its mean abundance was 27% cover, and dead *Crassostrea* averaged 22% cover on roots (Fig. 9.95). Oysters were only considered dead if their valves were gaping (Fig. 9.119). This probably underestimated immediate mortality. Many oysters considered "live" were covered with oil, with valves glued together by tarry residues, and were probably dead.

In the remaining 9 mo of the first year after the spill, *Crassostrea* abundance plummeted to a mean of 6% cover. The abundance of dead individuals also decreased (overall mean of 11% cover) as valves detached from roots or were covered by oil or other organisms (Fig. 9.120, see below). At two unoiled sites monitored in the first year, overall mean abundance of *Crassostrea* averaged 43% cover, and dead oysters averaged 2.8% cover (Figs. 9.93, 9.95).

From the second through fifth year after the spill, five oiled sites were examined: LRCW, plus two in the central wing of Bahía Las Minas (SBCE and SBCS) and two in the eastern wing (PCE and PCS; Fig. 9.5). Oyster abundance was low overall in August and November 1987 (means of 6 and 8% cover), but increased

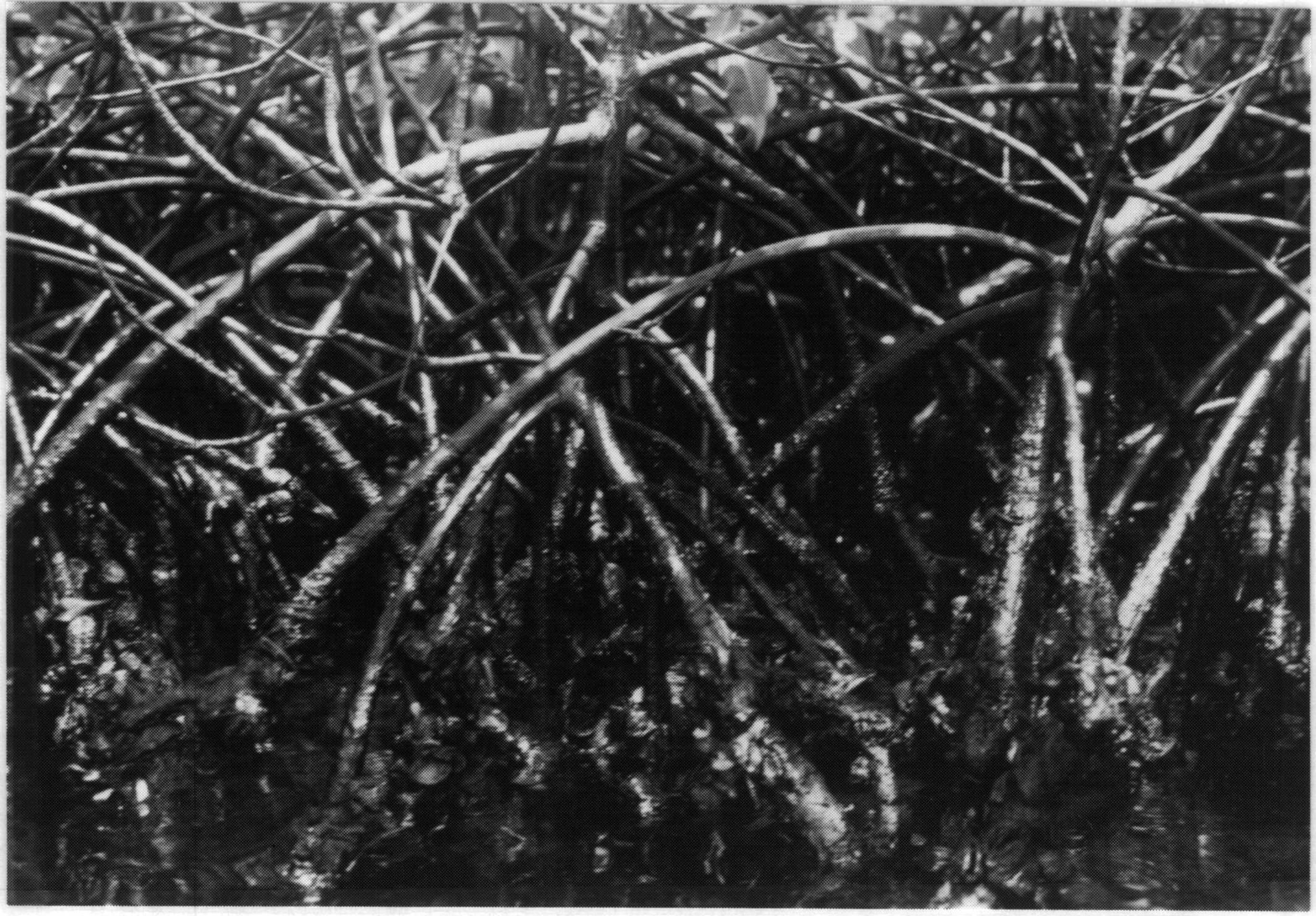

Fig. 9.118 Channel and lagoon fringing roots 3 mo after oiling. August 1986, site = near LRCW. Black oil covered intertidal portions of roots and their epibiota.

to 15% cover in February 1988, and continued to increase slowly over the next 3 yr (Figs. 9.93, 9.121).

There were significant differences in oyster cover between unoiled sites in Margarita Lagoon and Bahía Las Minas when both data sets were analyzed (Table 9.17); we therefore tested for oiling effects using LT and CD data comparing unoiled (HIDC and SBCW) and oiled sites (PCE, PCS, SBCE, and SBCS) within Bahía Las Minas only, as described above. Analyses were repeated using LT data only for yr 3-5 (HIDC, SBCW, and LRCS vs. LRCW, PCE, PCS, SBCE, and SBCS). *Crassostrea* was significantly less abundant at oiled than unoiled sites through 4 yr after oiling for sites where both CD and LT analyses were run, and through May 1991 (5 yr after oiling) for the set of sites where additional LT data only were available (Fig. 9.93; Table 9.17). Thus, until August 1990-May 1991 oysters covered significantly less space at oiled than unoiled sites, although such differences were relatively small by the fifth year after the spill.

Fig. 9.119 Channel and lagoon fringing root 1 yr after oiling. February 1987, site = LRCW. Oiling resulted in three kinds of mortality. Dead bivalves (*Crassostrea* and *Brachidontes*) in the *top half* of the photograph were coated with oil during the spill (note oil cover and gaping valves). Barnacles (*Chthamalus*) and *Crassostrea* (bleached organisms in the *center to lower area*) were subtidal during oiling, but desiccated after the root lifted following defoliation. Other epibiota deeper on the root were lost when root bark and tissue sloughed off (*bottom* of photograph).

Fig. 9.120 Channel and lagoon fringe 3 yr after oiling. May 1989, site = LRCW. Valves from dead *Crassostrea* littered the bottom.

There was little variation among 4 of the 5 oiled channels, but *Crassostrea* remained rare (<5% cover) at LRCW through August 1989. Oyster cover then increased at LRCW over the last 2 yr of the study (Figs. 9.93, 9.121). Vertical distribution of *Crassostrea* on roots in oiled channels was similar to that at unoiled sites in the last 3 yr of the study; oysters were primarily intertidal (MHW − 50 cm; Fig. 9.96).

Other Bivalves. For two less-common species of bivalves, abundances in oiled channels the first year after the spill were lower than in unoiled channels. *Mytilopsis* and *Brachidontes* each covered ~2% of roots at oiled sites and ~5% of roots at unoiled sites.

For a third rare bivalve results were equivocal. *Isognomon* overall abundance was initially higher at oiled (6%) than unoiled (2.5%) channels, but fell over the year at oiled sites to approximate equality (~3.5% in both). This reduction may have

Fig. 9.121 Channel and lagoon fringing roots 5 yr after oiling. June 1991, site = SBCS. Most old, oiled roots had been "interior", anchored roots; new growth of surviving mangroves had moved the fringe outward. *Crassostrea* was the most abundant species on roots.

been induced by oiling because unoiled sites showed a slight increase over the same period.

Patterns differed over the remaining 4 yr for these three species. *Mytilopsis* remained rare or absent at oiled sites, and despite a decrease in cover at unoiled sites from April 1988 on (Fig. 9.97), more false mussels were found at unoiled than oiled sites in 15 of 16 quarters (sign-rank tests, $P < .001$, $N = 16$). *Brachidontes* increased slightly in overall abundance at oiled sites through May 1991, but was never as abundant as at unoiled sites (Fig. 9.99; sign-rank test, $P < .001$, $N = 16$). *Isognomon* cover rose from August 1987 onward, but exceeded that at unoiled sites only once until November 1990 (Fig. 9.100; sign-rank test, $P = .022$, $N = 13$). From November 1990 through May 1991 *Isognomon* covered more space at oiled than unoiled sites. Depth distributions were not affected by oiling for any species (Fig. 9.98).

Barnacles. Balanus was present but rare during the first year after the spill. More barnacles were found in unoiled than oiled channels in 15 of 16 quarters (Fig. 9.101; sign-rank test, $P < .001$, $N = 16$). There were more dead barnacles at oiled sites as well; the proportion of dead to total *Balanus* was ~.31 at oiled sites and ~.16 at unoiled sites. Among oiled sites barnacles were rarest at PCE (always <1% cover) and PCS (>5% cover in 1 of 16 quarters; Fig. 9.101). Depth distributions of *Balanus* were similar at oiled and unoiled sites in the 3 yr examined (Fig. 9.102).

There were no significant differences in barnacle cover between unoiled sites in Bahía Las Minas and Margarita Lagoon for yr 2-5 postspill using CD and LT data (ANOVA, $P > .05$, NS), so four oiled (PCE, PCS, SBCE, and SBCS) and three unoiled (SBCW, MACN, and MACS) sites were compared using repeated-measures ANOVA. The resulting full model (including CD comparisons) was complex (Table 9.17), with a significant 3-way interaction. A model testing only randomly censused roots was not significant overall, indicating that effects of oiling were weak when tested at this level (Table 9.17).

However, when the lagoons were compared in yr 3-5, there were significantly fewer *Balanus* in Margarita Lagoon, compared with Bahía Las Minas (MACS and MACN vs. SBCW, HIDC, and LRCS). We thus tested differences between unoiled SBCW, HIDC, and LRCS and oiled LRCW, PCE, PCS, SBCE, and SBCS. There was a significant effect of oiling within Bahía Las Minas 3-5 yr postspill (Table 9.17). These two analyses combined suggest a small, but significant, effect of oil 5 yr after the spill.

Foliose Algae. Foliose algae averaged 7% cover over the first two monitorings, 16% cover over the next two quarters, and then varied between 5 and 10% cover overall for the remaining 16 quarters (Fig. 9.103). The ephemeral increase (bloom?) from February to May 1988 did not appear to be related to the oil spill because unoiled sites also had algal abundances of ~12% cover in 2 of the 4 earliest postspill monitorings.

There were no significant differences in foliose algal cover between unoiled sites in Bahía Las Minas and Margarita Lagoon using either set of sites (ANOVA, $P > .05$, NS). Four oiled (PCE, PCS, SBCE, and SBCS) and three unoiled (SBCW, MACN, and MACS) sites were compared using data for LT and CD roots. Years 3-5 postspill were analyzed for LT data using five oiled and five unoiled sites (all sites). Both sets of analyses were not significant in all comparisons (Table 9.17). An average of fewer than one species/root was recorded (Fig. 9.104), however, as at unoiled sites, the number of species of algae/root increased with algal cover (Fig. 9.105). About as many species were estimated to occur on 20 roots at both oiled and unoiled sites (Fig. 9.106).

There were strong differences in species composition of foliose algae between oiled and unoiled sites, despite the similarity in species numbers. *Caulerpa* spp. were far more abundant at oiled than unoiled sites (especially *Caulerpa verticillata*) and members of the "Bostrychietum" group were rarer (Fig. 9.107). This difference persisted through 1991.

One oiled site, PCE, stood out from both oiled and unoiled sites. Algal cover was approximately twice as high, and approximately twice as many species were recorded. The strength of this difference increased over time (Figs. 9.103-9.107). PCE was located close to the entrance of the eastern wing of Bahía Las Minas (Fig. 9.5) and was the only channel site that experienced wave action in dry season (pers. obs.). The trajectory of its recovery, including increases in algal cover relative to all other channel sites, suggests that it was actually a site with characteristics intermediate between those on the open coast and those in channels and lagoons. Unfortunately, we have no prespill data for this site.

Sessile Invertebrates. The abundance of rare sessile invertebrates was depressed immediately after the spill at oiled sites (Fig. 9.108). However, between August 1987 and May 1991, sessile cover increased slowly, and was similar to that at unoiled sites. There were no significant differences in cover of sessile invertebrates between unoiled sites in Bahía Las Minas and Margarita Lagoon for either analysis (ANOVA, $P > .05$, NS). Comparisons were made for CD and LT data using four oiled (PCE, PCS, SBCE, and SBCS) and three unoiled (SBCW, MACN, and MACS). Years 3-5 postspill were analyzed for LT data using five oiled and five unoiled sites (all sites). These analyses were not significant in all comparisons (Table 9.17).

Sponges were abundant at LRCW from February 1987 until August 1988, then rare through May 1991 (Fig. 9.111). They varied between <1 and ~5% cover at both SBCE and SBCS. Sponges reached highest levels of abundance at oiled sites in the eastern wing of the bay, averaging ≥5% cover in 12 of 16 quarters at PCE and in 11 of 16 at PCS. This correlated with water movement – PCE faced the open ocean and PCS was near the water intake for the electricity plant (Fig. 9.5). Overall, sponges were more abundant at oiled than unoiled sites in 16 of 16 monitorings (sign-rank test, $P < .001$, $N = 16$). As in unoiled channels, sponges tended to occur ≥30 cm deep, and were most common subtidally (Fig. 9.110).

Tunicate abundance appeared unrelated to oiling. As in unoiled channels, abundances were seasonal, with maxima usually in May monitorings (Fig. 9.109). There were no overall differences in tunicate abundance between oiled and unoiled sites through yr 2-5 (sign-rank test, $P > .05$, NS, $N = 16$). Tunicates were primarily subtidal and rare above 50 cm below MHW, as at unoiled sites (Fig. 9.110).

Arborescent hydroids and bryozoans were rare at oiled sites 3 mo after the spill, but their overall mean abundance in yr 1 (1% cover) did not differ from that at unoiled sites (Fig. 9.112). This group showed a slow increase in abundance through May 1991, and did not differ from unoiled sites (sign-rank test, $P > .05$, NS, $N = 16$).

Encrusting bryozoans, though rare at all sites, were less abundant at all dates in oiled than unoiled sites (sign-rank test, $P < .001$, $N = 20$). Reductions in the abundance of encrusting bryozoans persisted for 5 yr after oiling.

Diatoms and Bare Space. Diatoms varied from absent to 8% cover on LT roots at oiled sites the first year after the spill (Fig. 9.113). From August 1987 to May 1991, abundances ranged from 7 to 17% cover, with no differences between oiled and unoiled sites (sign-rank test, NS). There was little among-site variation in space occupancy, and little evidence of a seasonal pattern, except at MACS and MACN (Fig. 9.113). Diatoms were distributed on LT roots similarly in oiled and unoiled areas – rare above 30 cm depth, common elsewhere (Fig. 9.114).

For the first 3 yr after the spill, more space was bare on roots at unoiled than oiled sites (sign-rank test, 2-tailed, $P = .006$, $N = 12$; Fig. 9.115). From May 1989 to May 1991 more space was bare on roots at oiled than unoiled sites (sign-rank test, 2-tailed, $P = .07$, $N = 8$). This coincided with the drop in oil cover that occurred during the 1989 dry season.

Recruitment

Crassostrea virginica. Some *Crassostrea* recruited in 16 of 17 quarters at oiled sites (Fig. 9.93). Among sites, oysters appeared on dowels in 9 of 15 instances at SBCE, in 7 of 14 at SBCS, 10 of 14 at PCS, and in 6 of 14 at PCE. *Crassostrea* abundance exceeded 10% in only four instances, three times at PCS, and once at PCE. Overall, there was no difference between average cover of oysters at oiled and unoiled sites (sign-rank test, $P > .05$, NS, $N = 17$).

Other Bivalves. Recruitment of other bivalve molluscs was generally low. For *Mytilopsis*, some were found in 7 of 17 quarters. All averaged less than 2% cover except in August 1987, when a major (mean of 49% cover) recruitment occurred at LRCW (Fig. 9.97). Overall, there were no differences between oiled and unoiled sites (sign-rank test, $P > .05$, NS, $N = 9$ intervals when recruitment did not fail). *Brachidontes* recruited in only 3 of 17 quarters overall, and never averaged more than 0.6% cover on dowels (Fig. 9.99). Recruitment events occurred at PCS, SBCE, and SBCE in February 1990, and at LRCW in August 1989 and May 1990. As at unoiled sites, recruitment was not immediately followed by increases in abundance on roots. Overall, recruitment did not differ between oiled and unoiled channels for this species (sign-rank test, $P = .11$, $N = 7$ intervals when recruitment did not fail). Recruitment of *Isognomon* was patchy in time and space. Overall, some occurred on dowels in 7 of 17 quarters, with maximum cover of 1% (Fig. 9.100). For individual sites, *Isognomon* never recruited at SBCS, and in 2 of 15, 5 of 14, 1 of 14, and 3 of 11 quarterly trials at SBCE, PCS, PCE, and LRCS, respectively. Among sites, the greatest recruitment was at PCE, which had a mean of 3% cover in August 1988. Overall, recruitment did not differ between oiled and unoiled treatments (sign-rank test, $P > .05$, NS, $N = 11$ intervals when recruitment did not fail).

Barnacles. Balanus recruited in at least one oiled channel in 16 of 17 quarters (Fig. 9.101). Recruitment was consistently low at PCE and variable at all other sites. There was no consistent pattern of seasonal change by quarter; population minima occurred in every quarter. More *Balanus* recruited at unoiled than oiled sites in 13 of 17 quarters (sign-rank tests, 2-tailed, $P = .05$, $N = 17$).

Foliose Algae. Foliose algae recruited in one or more oiled sites in 16 of 17 quarters from May 1987 through May 1991 (Fig. 9.103). There was no seasonal pattern. Among sites, algae failed to recruit three times at SBCE and once at SBCW. LRCW had the least amount of recruitment (some in 11 of 11 quarters, none >20% cover); PCE had the most (in 15 of 15 quarters, 8 with >20% cover). Overall percent cover of algae was higher at oiled than unoiled sites in 18 of 21 quarters (sign-rank test, $P < .001$, $N = 17$), largely because so much algae recruited at PCE. Between 1.0 and 10.9 species of algae were estimated to occur in a sample of 10 dowels (rarefaction estimates); PCE had the highest numbers of species of algae, as on randomly sampled roots (see Fig. 9.106).

Sessile Invertebrates. Some rare sessile invertebrates occurred on dowels at oiled sites each quarter except August 1987 and May 1989. Overall recruitment was low to moderate except in May 1990, when combined abundances averaged 22% (Fig. 9.108). Pulses of recruitment (≥10% cover) at a given site were always associated with simultaneous pulses at one or more other sites, not always in the same region of the bay (Fig. 9.108).

Recruitment was generally similar between oiled and unoiled sites (sign-rank test, $P > .05$, NS, $N = 17$). Abundances of rare sessile invertebrates were lower in yr 2 and 3 (August 1987-May 1989) than in yr 4 and 5 (August 1989-May 1991); pulses of recruitment corresponded closely at both oiled and unoiled sites (e.g., August 1989 and May 1990).

Sponges appeared on dowels at one or more oiled sites in all but 2 of 17 quarters examined. Overall abundance did not exceed 3% cover (Fig. 9.111). Frequency of recruitment varied among sites, and appeared unrelated to location (e.g., some sponges recruited at SBCE in 8 of 14 quarters vs. 4 of 14 at SBCS, and in 3 of 14 at PCE vs. 9 of 14 at PCS). Pulses of recruitment at unoiled sites were accompanied by ephemeral increases in sponge cover on roots; at oiled sites this relationship appeared weak (Fig. 9.111).

Arborescent hydroids and bryozoans did not recruit onto artificial substrata in the first three trials (May-November 1987); they then appeared at one or more oiled site in 13 of 14 quarters (Fig. 9.112). Recruitment pulses occurred simultaneously at one or more sites in 5 of the 8 quarterly intervals where one or more site had mean cover of >5%. Overall, recruitment of this group was similar to that at unoiled sites; both reflected the general pattern of increased cover on dowels in the last 2 yr after the spill (sign-rank test, $P > .05$, NS, $N = 15$ intervals when recruitment did not fail).

Tunicates recruited at oiled sites in 11 of 17 quarters examined. Recruitment was highest in May or August, and lowest in November or February (Fig. 9.109). Overall, relatively high recruitment was associated with simultaneous increases in tunicate cover on roots. There was little evidence of any pattern of recruitment among sites; only in May 1991 did a pulse occur simultaneously at two sites. However, overall abundances on dowels appeared to vary over time similarly at oiled and unoiled sites.

Encrusting bryozoans recruited in 11 of 17 quarters at oiled sites, with general recruitment failure at all sites in the second and third year after oiling. Results were similar at unoiled sites, with no pattern of differences in recruitment with oiling (sign-rank test, $P > .05$, $N = 11$ intervals when recruitment did not fail).

Diatoms and Bare Space. Diatoms occupied space on dowels in all 17 quarters examined, covering ~15-30% of dowel surfaces (Fig. 9.113). As at unoiled sites, there was no overall seasonal pattern or long-term trend in abundance. Approximately 10-30% of dowel surfaces were bare (Fig. 9.115), with a tendency for more bare space in late wet season. There were no consistent differences in the amount of bare space between oiled and unoiled sites (sign-rank test, NS).

Community Development Roots

Crassostrea virginica. Marked, initially bare roots were followed at all oiled sites except LRCW. *Crassostrea* abundance on CD roots was equivalent to oyster abundance on LT roots within 3 to 12 mo after roots entered the water (Fig. 9.93). Thereafter, abundances fluctuated similarly over time. In the overall repeated-measures ANOVA, comparing oiling (oiled vs. unoiled), group (CD vs. LT), and year (1-4), there was a significant effect of oiling on the abundance of *Crassostrea* through the fifth year after oiling (Table 9.17, sites within Bahía Las Minas only). Cohort of roots (CD vs. LT) differed significantly only in the first year (9 mo of submersion) after they entered the water; thereafter, oiling effects predominated. Percent cover of dead *Crassostrea* was not affected by oiling in yr 2-5, but was affected by type of root (CD vs. LT); there were significant differences until enough oysters had settled that there were dead individuals to count (Table 9.17).

Differences between oiled and unoiled sites thus did not result from the pattern of recruitment or settlement of oysters onto new roots, but because oysters came to cover less space on CD roots at oiled sites. Percent cover on CD roots tracked that of randomly censused roots at the same sites, whether oiled or unoiled. Over time, average percent cover increased slowly at oiled sites to approximately that of unoiled sites.

Other Bivalves. Mytilopsis sallei first appeared on roots in February 1988, at its highest mean overall abundance of the 16 quarters monitored – 1% cover (Fig. 9.97). Its overall abundance was ≤0.3% cover for the subsequent 15 monitorings. It never occurred at either central bay site (SBCE and SBCS), but was found at PCE and PCS in eight and nine quarters, respectively. On average, more false mussels were found on roots at unoiled than oiled sites (sign-rank test, $P = .008$, $N = 15$).

Brachidontes occurred on CD roots in oiled channels from August 1987 on; overall abundances averaged <1% cover through May 1991 (Fig. 9.99). It was found intermittently at each site (6 of 15 quarters at PCE, 12 of 15 at PCS, and 8 of 15 at both SBCE and SBCS). Abundances were also low at unoiled sites through February 1989, but increased in density from May 1989 to May 1991. Overall, *Brachidontes* was more abundant at unoiled than oiled sites (sign-rank test, $P = .022$, $N = 13$ intervals where at least some mussels were present on roots).

Isognomon was not found on oiled CD roots until February 1988 and increased slowly in abundance (Fig. 9.100). As with *Mytilopsis* there were differences between sites at different locations within the bay. SBCE and SBCS (central bay) had lower combined mean cover than PCE and PCS (eastern wing) in 13 of 15 quarters. Overall abundance of *Isognomon* on CD roots in oiled channels was higher than in unoiled channels in 13 of 14 quarters from May 1988 through May 1991 (sign-rank tests, $P = .002$, $N = 14$ intervals where at least some oysters were present on roots).

Foliose Algae. Foliose algae appeared on CD roots in the first monitoring after roots entered the water (overall cover of 11%), then varied between 3 and 9% cover in the remaining 14 quarters (Fig. 9.103). Overall abundances matched those on LT roots immediately and equaled them every quarter through May 1991. There were no significant effects of oiling (Table 9.17). Mean number of species/root increased with percent cover of algae (Fig. 9.117). There was no difference in the average number of species expected in a sample of 20 roots from oiled and unoiled channels (Fig. 9.106). However, there were slightly fewer species of algae estimated to occur on a sample of 20 CD than LT roots (rarefaction results; Fig. 9.106). PCE consistently had higher algal abundances and species numbers on CD roots than the other oiled sites; this paralleled results for randomly censused roots (Figs. 9.103, 9.106).

Sessile Invertebrates. Sessile invertebrates first appeared on oiled CD roots in February 1988; abundances then and through May 1991 were similar to those on LT roots (Fig. 9.108; Table 9.17). At individual sites variability in cover was generally greater on CD than on LT roots (most clearly seen in the relative amplitudes of LT vs. CD fluctuations at PCS). Overall, abundances of sessile invertebrates did not vary between oiled and unoiled sites, but did differ among years (repeated-measures ANOVA; Table 9.17).

For individual groups of rare sessile invertebrates, sponges and arborescent hydroids and bryozoans were more abundant at oiled than unoiled sites (Figs. 9.111, 9.112; sign-rank tests, $P < .002$ or smaller, both tests, $N = 13$ [each test] intervals where at least some of the group were present on roots). Tunicates were approximately equally abundant at oiled and unoiled sites (sign-rank test, $P > .05$, NS, $N = 13$ intervals where at least some tunicates were present on roots). Encrusting bryozoans were more abundant at unoiled than oiled sites (sign-rank test, $P = .008$, $N = 15$).

Diatoms and Bare Space. As at unoiled sites, diatoms appeared immediately at abundances similar to those on LT roots, then tracked the latter closely throughout the study (Fig. 9.113). The amount of bare space dropped rapidly, as at unoiled sites (Fig. 9.115).

LRCS vs. LRCW

Differences in surface salinity between oiled and unoiled sites in channels potentially confounded analyses of oiling effects (Sect. 9.3). However, one comparison existed that was not affected by salinity differences. Two sites were located on either side of a small peninsula that marked the boundary of oil penetration into the west wing of Bahía Las Minas (Fig. 9.5). These sites had almost identical surface salinities (mean [range] at oiled LRCW = 26.7o/oo [8-36.3o/oo], unoiled LRCS = 29.1o/oo [6.5-36o/oo], *N* = 10 at each site). LRCW was monitored from August 1986 to May 1991; LRCS was monitored from August 1988 to May 1991. We compared changes in percent cover of major groups at these sites as a qualitative comparison of closely matched oiled and unoiled sites (Fig. 9.122).

Crassostrea virginica differed in abundance at LRCW and LRCS throughout the 3 yr that both sites were monitored. At LRCS cover averaged 22.7% for the 3 yr sampled, fluctuating between 16.6 and 27.5%. Oyster cover at LRCW was <10% until February 1990, after the initial decrease caused by oiling between April and November 1986 (see also Garrity and Levings 1992). Beginning in 1990 percent cover increased to 13.1% at LRCW, fluctuating between 10.5 and 17.7% until monitoring stopped in May 1991. Patterns of change in percent cover from 1990 on were similar at LRCW and LRCS, but oysters covered an average of 47% less space at LRCW.

We interpret this as evidence that *Crassostrea* was negatively affected by oiling for at least 5 yr at LRCW. Mechanisms that might have caused this difference include reduced settlement, changes in the density or effectiveness of predators related to oiling, or reduced growth or survival caused by sublethal toxic effects of dissolved hydrocarbons. Oysters at LRCW averaged 4.8 μg oil/mg EOM (*N* = 8, UVF units) between December 1988 and May 1991, while oysters at LRCS averaged only 1.1 μg oil/mg EOM (*N* = 7, UVF units, data averaged from Table 3.18). These data show that the two oyster populations differed significantly in their exposure to dissolved hydrocarbons (Mann-Whitney *U*-test, $P < .001$, $N = 7, 8$).

Two of three rare bivalves were significantly more abundant at unoiled LRCS than oiled LRCW (sign-rank tests, 2-tailed, *Brachidontes*: $P = .038$, $N = 12$; *Isognomon*, $P < .01$, $N = 11$). There were no significant overall differences in the rank abundance of *Mytilopsis* (sign-rank test, $P > .4$, $N = 12$). However, there were more *Mytilopsis* at oiled LRCW than unoiled LRCS for 2 of 3 yr (1988-1990, eight quarters in a row).

Balanus improvisus was always more abundant at unoiled LRCS than oiled LRCW (sign-rank test, $P < .01$, $N = 12$). Over the 3 yr both sites were monitored, barnacles covered an average of 41% less space at LRCW than LRCS (range 9-72%,

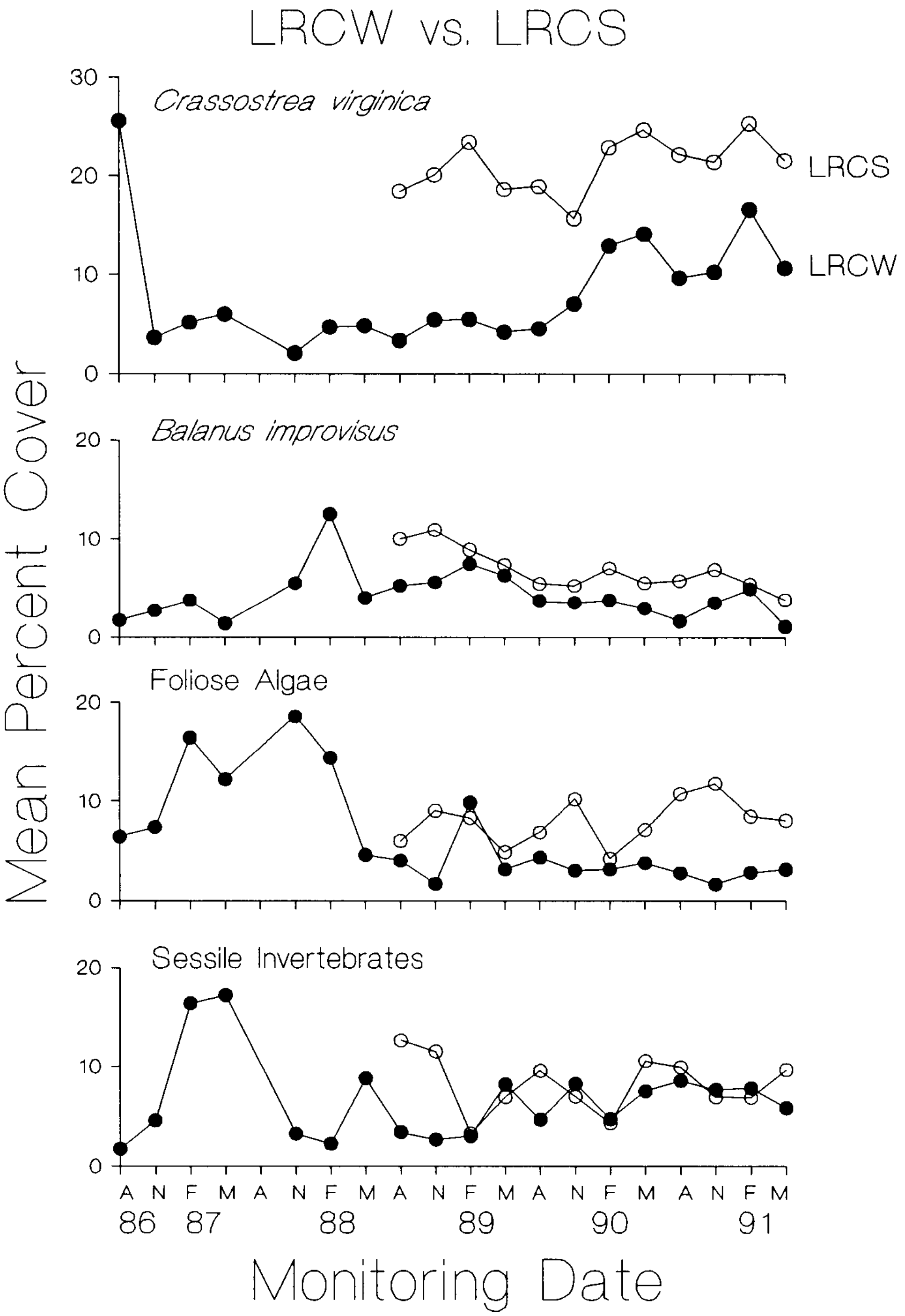

Fig. 9.122 Patterns of abundance of major groups on fringing *Rhizophora* roots at an oiled (LRCW) and unoiled (LRCS) channel site. Data are for long-term census roots (*N* = 20-25/site).

N = 12). As with *Crassostrea*, we interpret this as evidence that *Balanus* was negatively affected by oiling for 5 yr after oiling.

Foliose algae were more abundant at unoiled LRCS than oiled LRCW on 11 of 12 dates (sign-rank test, *P* = .006). However, algal cover had decreased from 1986-1988 levels, when algae were more abundant at LRCW. Rarefaction estimates were ~4.5 species/20 roots at LRCW the first 2 yr after oiling; in 1988-1991 estimates dropped to 2.3-3.4 species/20 roots (Fig. 9.106). At LRCS estimates ranged from 4.2 to 5.2 species/20 roots over the same period. This change in the pattern of algal abundance at LRCW suggests that another factor, perhaps a secondary effect of oiling, was also affecting foliose algae at LRCW. We thus cannot confidently attribute this difference to oiling.

Sessile invertebrates (other than bivalves and barnacles) covered almost identical amounts of space at LRCW and LRCS, indicating no significant effects of oiling 3-5 yr after the spill. Encrusting bryozoans, which were more abundant overall at unoiled than oiled sites, did not differ in abundance when LRCS and LRCW were compared (sign-rank test, *P* = .73, *N* = 12).

Drainage Streams – Unoiled Sites

Long-term Census

Mangrove roots fringing the banks of rivers, small streams, and man-made ditches supported an epibiota that included bivalve molluscs, barnacles, foliose algae, blue-green algae, diatoms, sponges, hydroids, vermetids, and arborescent bryozoans.

Mytilopsis sallei. The false mussel *Mytilopsis sallei* covered the most space on roots (Figs. 9.9, 9.10); in 1981-1982 in two streams in the western wing of Bahía Las Minas it covered 59-65% of root surfaces (HIDR and LRRS; Figs. 9.5, 9.123). During the initial phase of the postspill study (August 1986-May 1987), mean cover of false mussels in two unoiled streams in the same wing of the bay ranged from 36 to 48% (HIDR and CSR; Fig. 9.5). From August 1987 to May 1991 abundances were monitored at four unoiled streams (including HIDR, one of the original sites in the western wing; Fig. 9.5). Average cover of *Mytilopsis* at these sites ranged from 21 to 48% in 16 quarters (Fig. 9.123). The abundance of false mussels after August 1987 was relatively stable, varying from 21 to 31% cover through May 1991. Population trends were distinct at MERR. False mussel cover declined over time, especially in late 1987, but increased slightly in May 1991. Dead false mussels, identified by their gaping valves, averaged 1-2% cover during the same period. Three other bivalve molluscs (*Brachidontes ?exustus*, *Isognomon ?alatus*, and *Crassostrea virginica*) were found in most quarters, but combined abundance never exceeded 2%.

Vertical distribution of *Mytilopsis* was examined during the last 3 yr of the study. Submerged portions of roots along the banks of streams could be longer than those in channels or on the open coast, because the water was deeper. This allowed

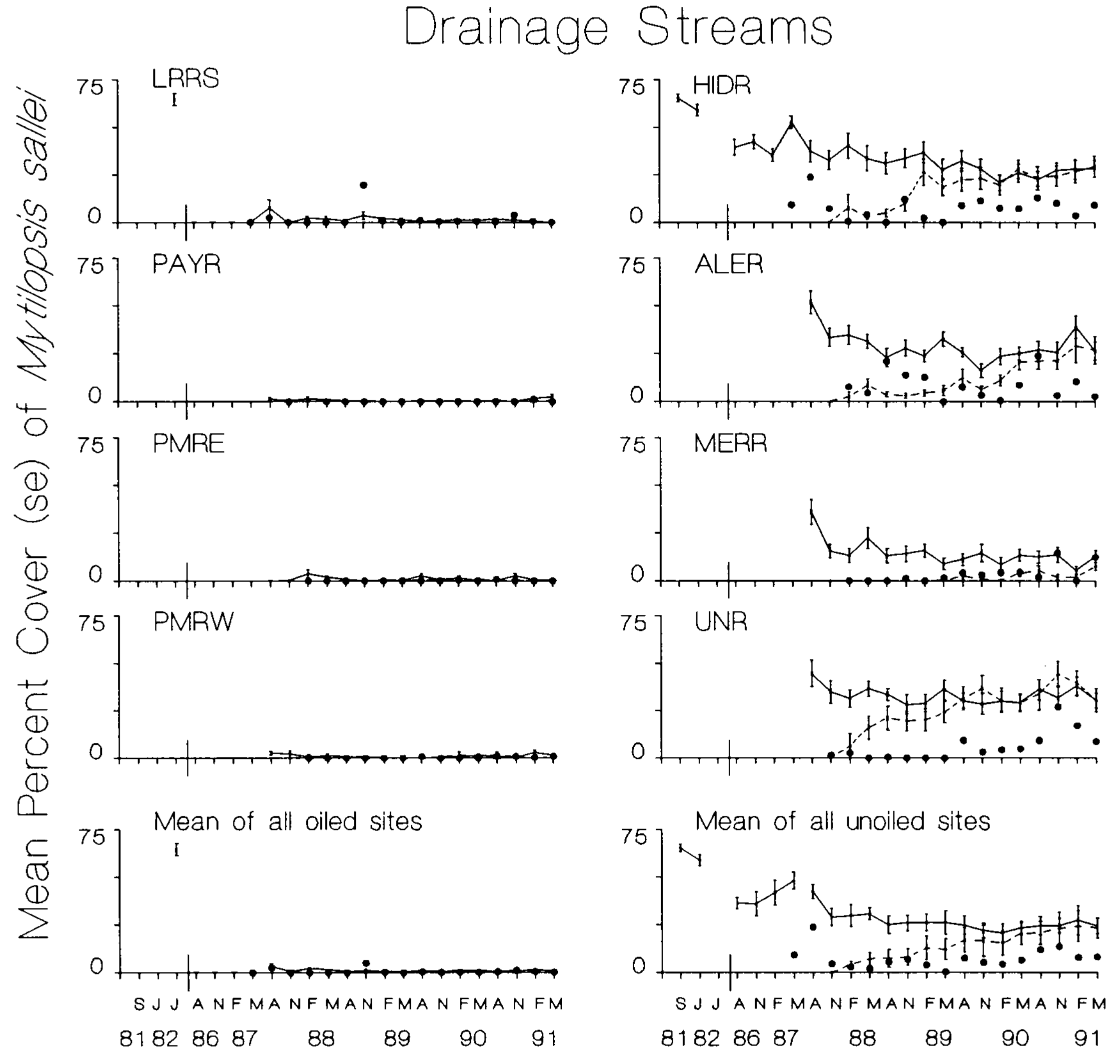

Fig. 9.123 Patterns of abundance of *Mytilopsis sallei* on roots of fringing *Rhizophora* in drainage streams. Data are mean (± SE) percent cover of false mussels for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

us to separate roots into size classes and examine the vertical distribution of epibiota on differently sized roots (Fig. 9.124*A*-*C*; see also Fig. 9.10). Results were similar for all 3 yr. False mussels were rare or absent at MHW to 10 cm depth, increased in abundance with depth to approximately the midpoint of roots, then decreased with depth to the deepest regions of roots. The decrease in abundance deep occurred in all three size classes of roots, strongly suggesting such a reduction resulted from

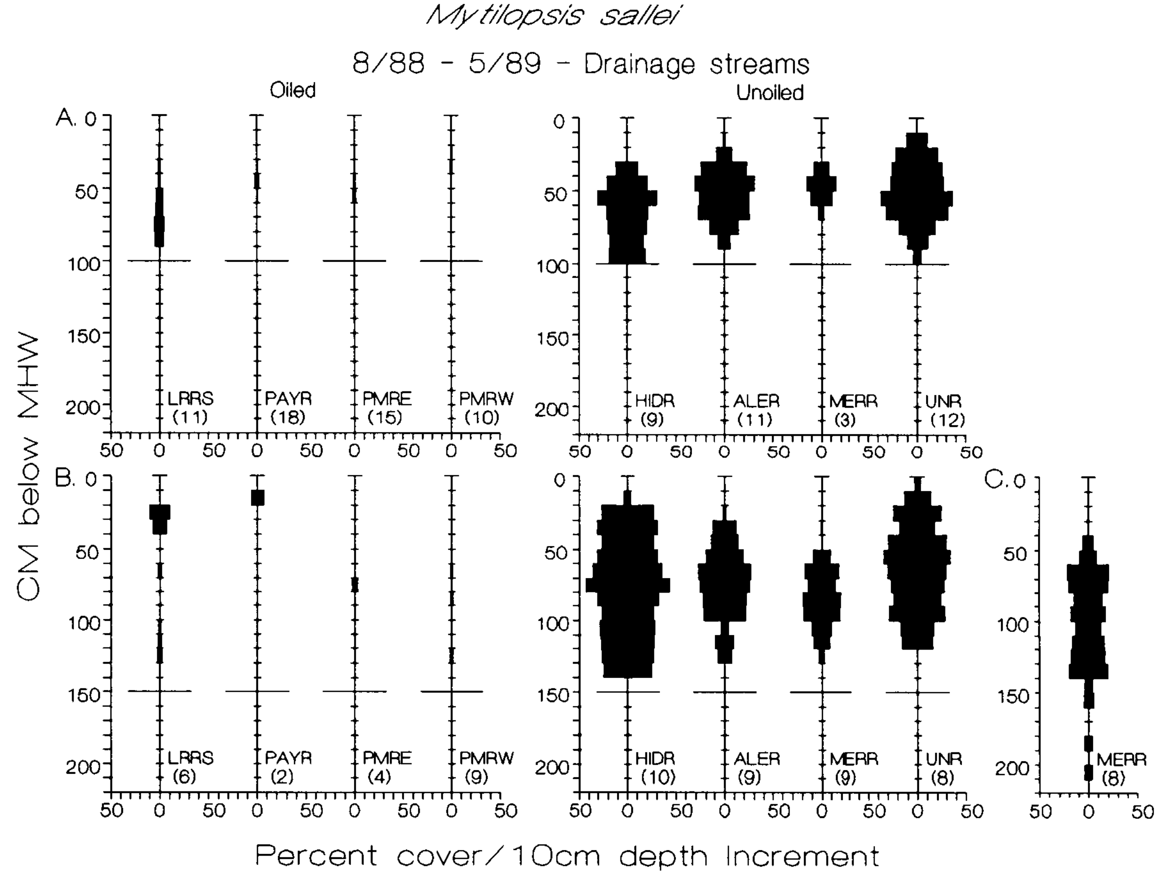

Fig. 9.124 Vertical distribution of *Mytilopsis sallei* in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are mean percent cover (x-axes) of false mussels for 10-cm increments on roots downward from MHW (y-axes) for roots ≥75 cm long. Numbers in parentheses are sample sizes. See text for further details. *A.* Roots 75-100 cm long below MHW. *B.* roots 101-150 cm long. *C.* roots >150 cm long.

fewer mussels occurring on actively growing portions of roots (e.g., tips; Gill and Tomlinson 1971) rather than any physiological factor related to absolute depth.

Barnacles. *Balanus improvisus* occurred on LT roots in all 20 quarterly samples, and ranged in abundance from 1 to 11% cover (Fig. 9.125). *Balanus* cover varied between 5 and 11% in the first year after the spill in two unoiled streams (HIDR and CSR). During the next 4 yr it covered <2% of root surfaces at four unoiled streams in or near Bahía Las Minas. There was a distinct seasonal component to fluctuations. Live *Balanus* were very rare in November (late wet season) in all years at all sites.

The apparent interannual difference was largely due to changes in site locations. At HIDR, a site in the western wing that was monitored in 1981-1982,

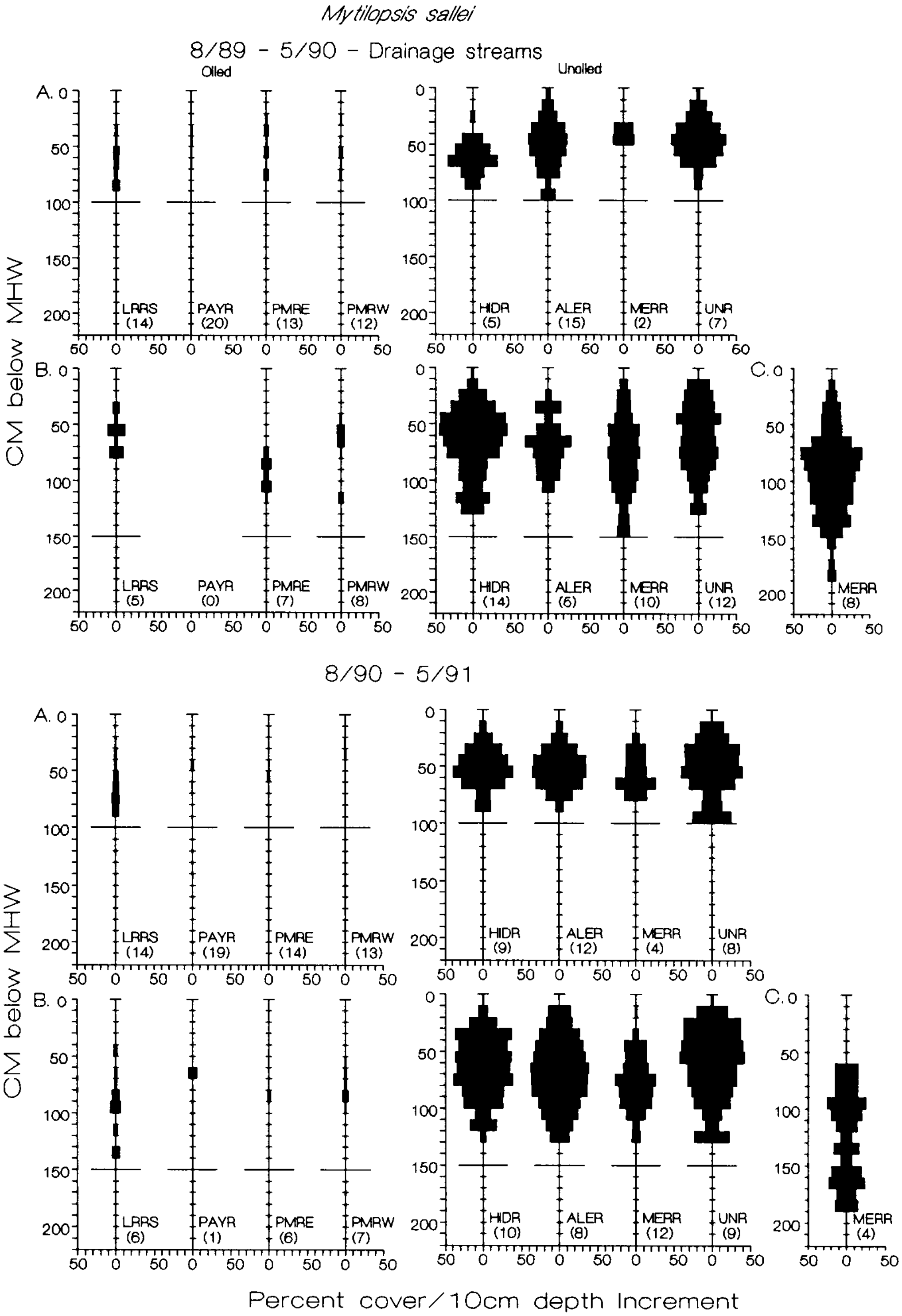

Fig. 9.124 Vertical distribution of *Mytilopsis sallei* in yr 3, 4, and 5 postspill on random-census roots in drainage streams (continued).

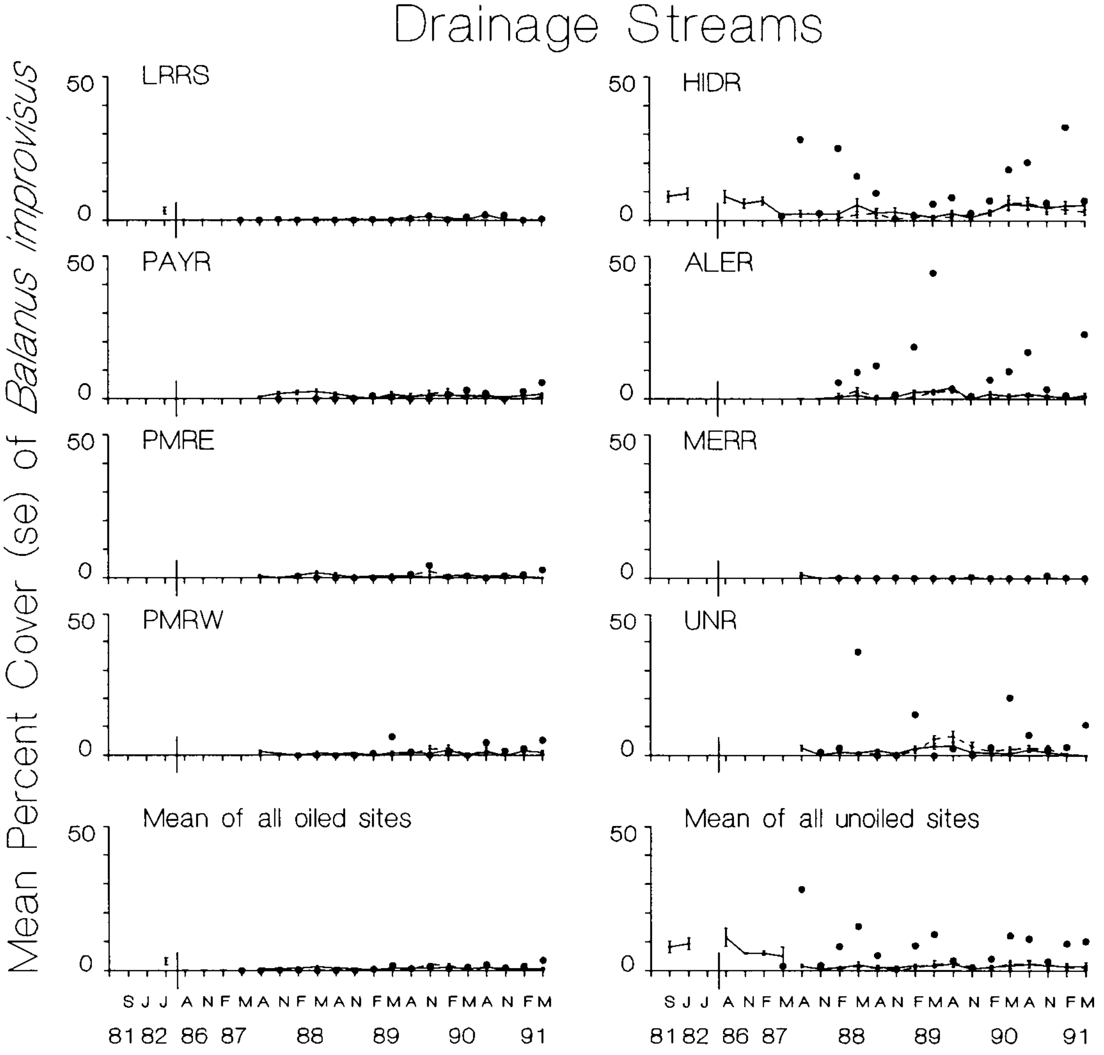

Fig. 9.125 Patterns of abundance of barnacles on roots on fringing *Rhizophora* in drainage streams. Data are mean (± SE) percent cover of *Balanus* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

Balanus cover continued to fluctuate seasonally in a pattern like that seen in the first year after the spill (August 1986-May 1987). This suggested that geographic variation, rather than a real decline in *Balanus* populations, caused the overall difference between August 1986-May 1987 and August 1987-May 1991 (e.g., compare abundances at MERR to those at HIDR; Fig. 9.125).

Vertical distribution of *Balanus* on roots up to 100 cm long was similar over the 3 yr examined. Barnacles did not occur shallower than 20 cm below MHW, were rare to 50 cm depth, and most common from 70-100 cm deep (Fig. 9.126). For longer roots (up to 150 cm), in 2 yr (1989-1990 and 1990-1991) there were no *Balanus* shallower than 50 cm depth, few above 100 cm, and most were 100 cm or deeper on roots. However, in August 1988-May 1989 barnacles occurred from MHW to 130 cm depth on roots. This may have represented an ephemeral recruitment event at HIDR and UNR; a few *Balanus* were found higher on shorter roots at these sites that year (Fig. 9.126).

Sessile Invertebrates. Sponges, arborescent bryozoans and hydroids, encrusting bryozoans, cnidarians, and tunicates were rare individually. Their combined abundance fluctuated widely among sites and over time (Fig. 9.127). Unlike *Balanus* and *Mytilopsis*, they were most abundant at MERR and least common at HIDR. These sessile invertebrates were rare or absent from unoiled sites during the first year after the spill (when HIDR was 1 of 2 sites sampled). This apparent inter-annual pattern appears to be due to variation among streams, not to overall changes in abundance over years (as with *Balanus*, see above). Mean overall abundance over the last 4 yr of study ranged from < 1 to 17% cover, with highest occupancy of space in early wet season (May).

Vertical distributions of sponges and arborescent bryozoans and hydroids are shown in Figure 9.128 (other sessile invertebrates were too rare to display). Both groups were absent to rare at high levels on roots and usually rare at deepest levels, but showed no coherent pattern otherwise. Examination of distributions over time at each site suggests both groups were ephemeral and opportunistic, occurring wherever bare space was available within their limits of physiological tolerance (Figs. 9.127, 9.128).

Foliose Algae. Foliose algae varied in overall abundance from 3 to 12% cover from August 1986 to May 1991 (Fig. 9.129); prespill abundances were 6-9% cover. Among sites, algae were more abundant at HIDR and ALER than MERR and UNR, except for an apparent bloom at MERR in February 1989. An average of fewer than one species of algae was recorded per root (Fig. 9.130). Number of species of algae/root was positively correlated with mean percent cover of foliose algae at all sites (Fig. 9.131). An average of ~3-5 species was expected in a sample of 20 roots (rarefaction estimates; Fig. 9.132). Most species recorded were members of the "Bostrychietum," including *Bostrychia binderi/B. tenella*, *B. montagnei*, *Catanella repens/Caloglossa leprieurii*, *Polysiphonia subtilissima*, and *Herposiphonia tenella*.

Vertical distribution of foliose algae was clearest for the "Bostrychietum" (Fig. 9.133). *Bostrychia* spp. were found only from MHW to 30 cm depth, regardless of root size, site, or year. *Catenella* and *Caloglossa* occurred from MHW to 90 cm depth, but were most abundant above 50 cm. *Polysiphonia subtilissima* occurred to 90 cm depth, but was most common from MHW to 50 cm depth. A mixed group of algae, including ?*Griffithsia*, *Champia*, and *Cladophora*, was found almost entirely at one site in 1 yr (MERR, 1988-1989), and occurred at all but the shallowest levels. Mixed algal turf, common on the open coast, appeared at HIDR at mid-intertidal

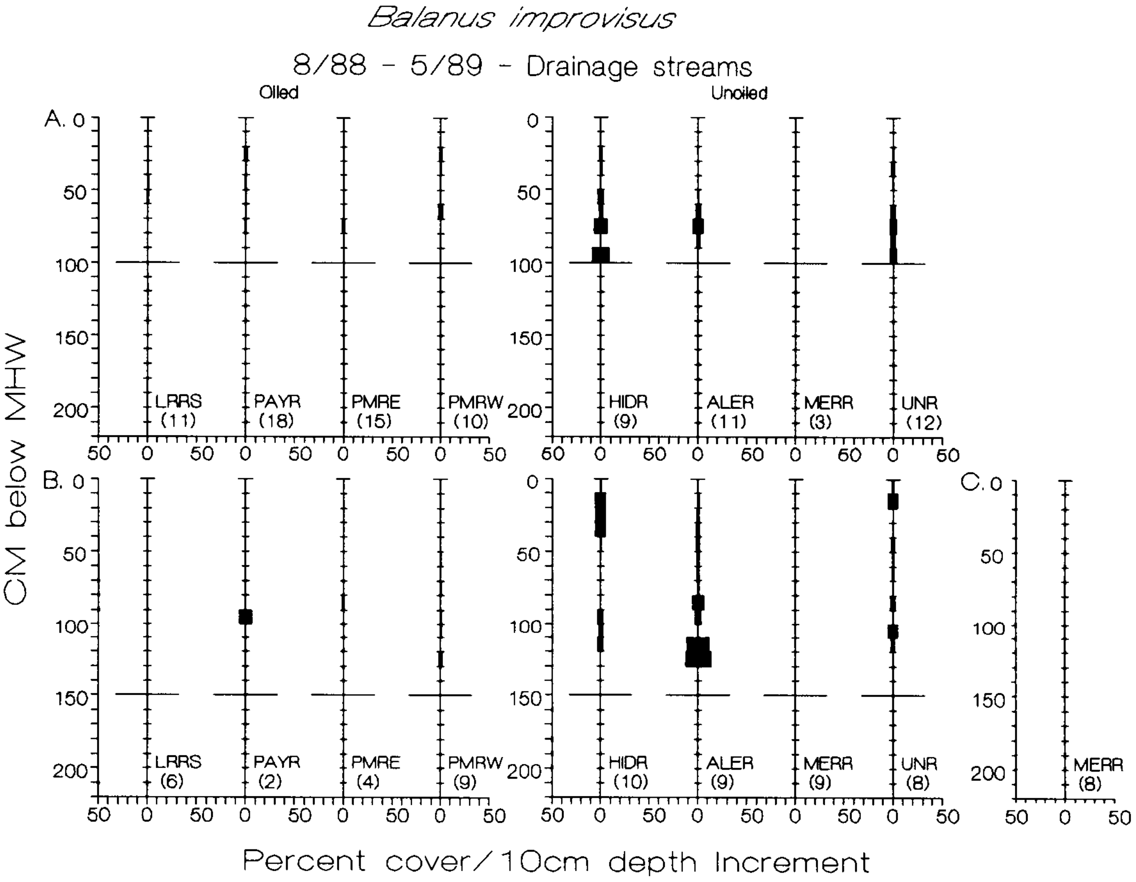

Fig. 9.126 Vertical distribution of *Balanus improvisus* in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are mean percent cover (x-axes) of barnacles for 10-cm increments on roots downward from MHW (y-axes) for roots ≥75 cm long. Numbers in parentheses are sample sizes. See text for further details. *A.* Roots 75-100 cm long below MHW. *B.* roots 101-150 cm long. *C.* roots >150 cm long.

depths during 1988-1989, but did not recur or appear at other sites.

Blue-green Algae. Blue-green algae were absent to rare on LT roots in unoiled streams (0-2% cover; Fig. 9.134). Ephemeral increases in abundance occurred at 3 of 4 sites (not at UNR); vertical distribution was restricted to <10 cm below MHW.

Diatoms and Bare Space. Diatoms were moderately abundant overall, varying from 10 to 30% cover from 1986 until 1991 (Fig. 9.135) with no obvious trend or seasonal pattern. They occurred from MHW to >200 cm depth, but were relatively rare on the shallowest and deepest sections of roots (Fig. 9.136).

On LT roots 17 to 40% of space was bare from August 1986 to June 1991 (Fig. 9.137). There was little variation among sites, and no trend over time or

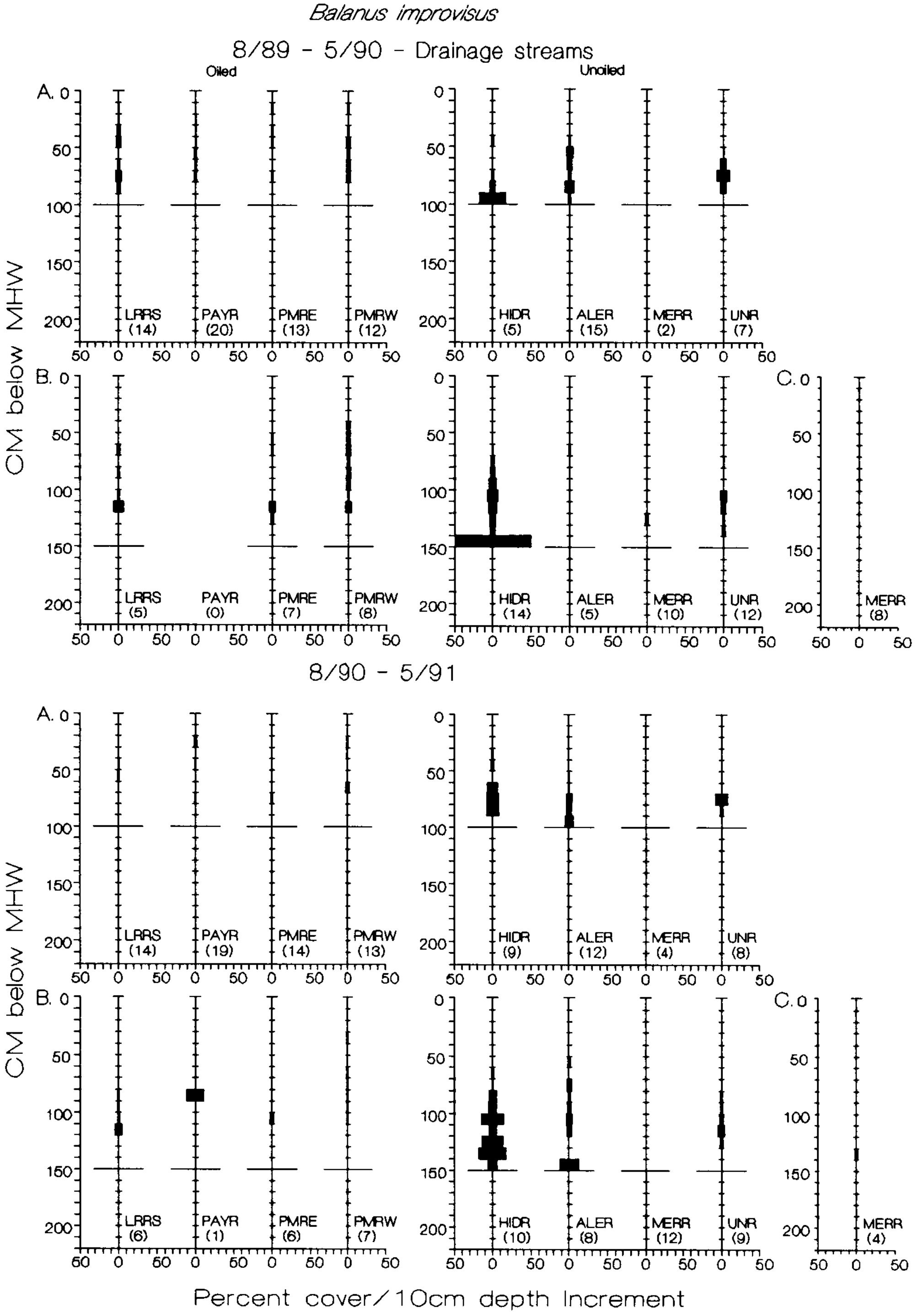

Fig. 9.126 Vertical distribution of *Balanus improvisus* in yr 3, 4, and 5 postspill on random-census roots in drainage streams (continued).

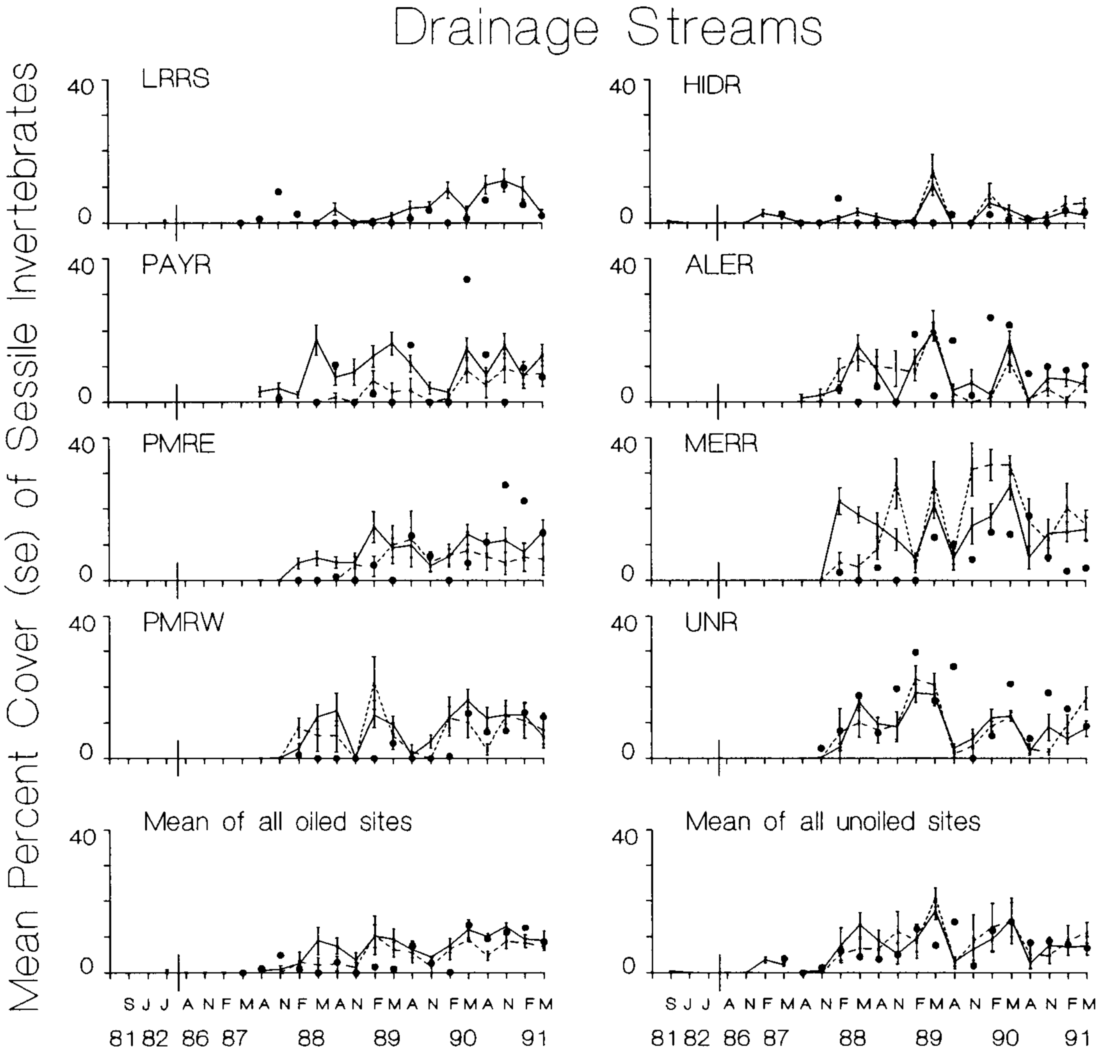

Fig. 9.127 Patterns of abundance of sessile invertebrates on fringing *Rhizophora* roots in drainage streams. Data are mean percent cover (± SE) of sessile invertebrates for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). "Sessile invertebrates" were defined as all groups except bivalves and barnacles. See text for details.

seasonal pattern. Bare space was most common from MHW through 40 cm depth, becoming rare or absent on middle portions of roots, and relatively abundant at deepest levels (Fig. 9.136).

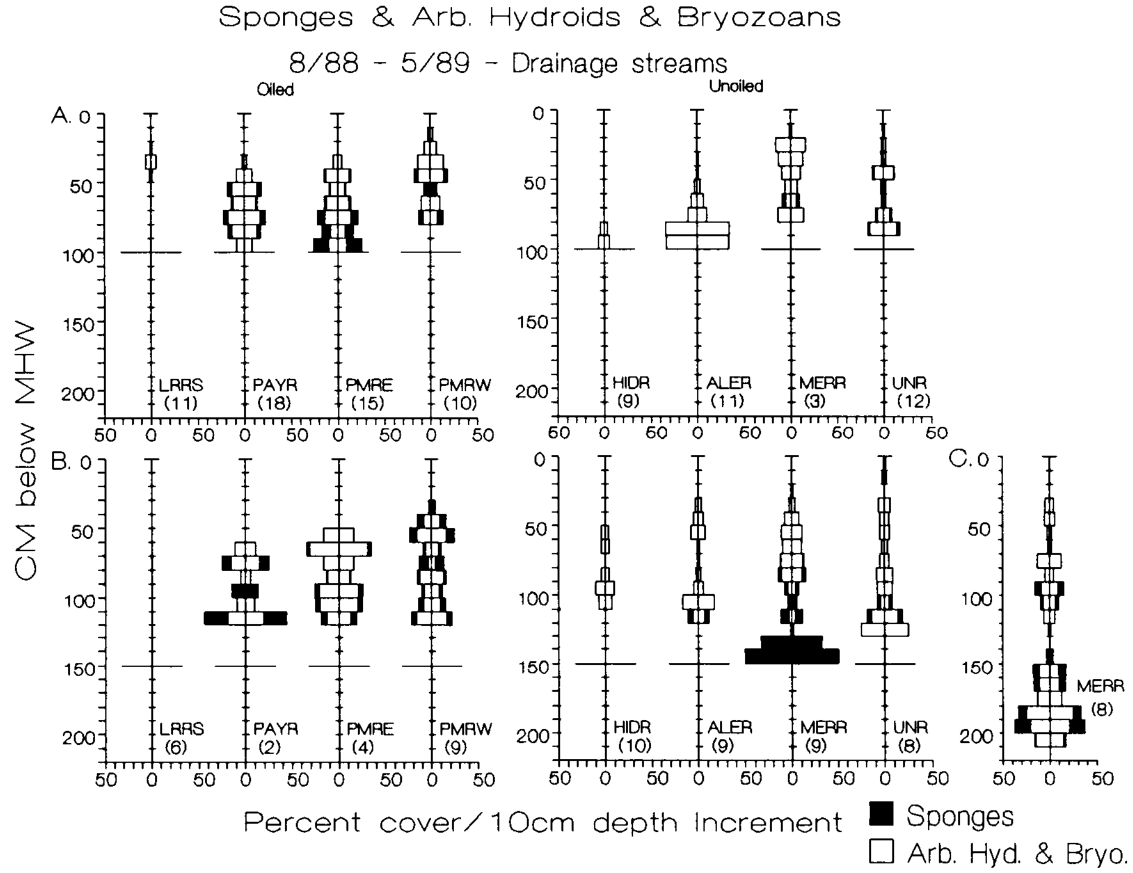

Fig. 9.128 Vertical distribution of sessile invertebrates in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are mean percent cover (x-axes) of sponges and arborescent hydroids and bryozoans for 10-cm increments on roots downward from MHW (y-axes) for roots ≥75 cm long. Numbers in parentheses are sample sizes. See text for further details. *A*. Roots 75-100 cm long below MHW. *B*. roots 101-150 cm long. *C*. roots >150 cm long.

Recruitment

Recruitment substrata were set out quarterly from February 1987 until 1991 (Fig. 9.138). Some recruitment occurred during each of 17 quarters. Combined abundance of recruiting organisms averaged from 19 to 87% cover, and exceeded 65% of available space in all but three intervals (August-November 1987, November 1989-February 1990, and November 1990-February 1991).

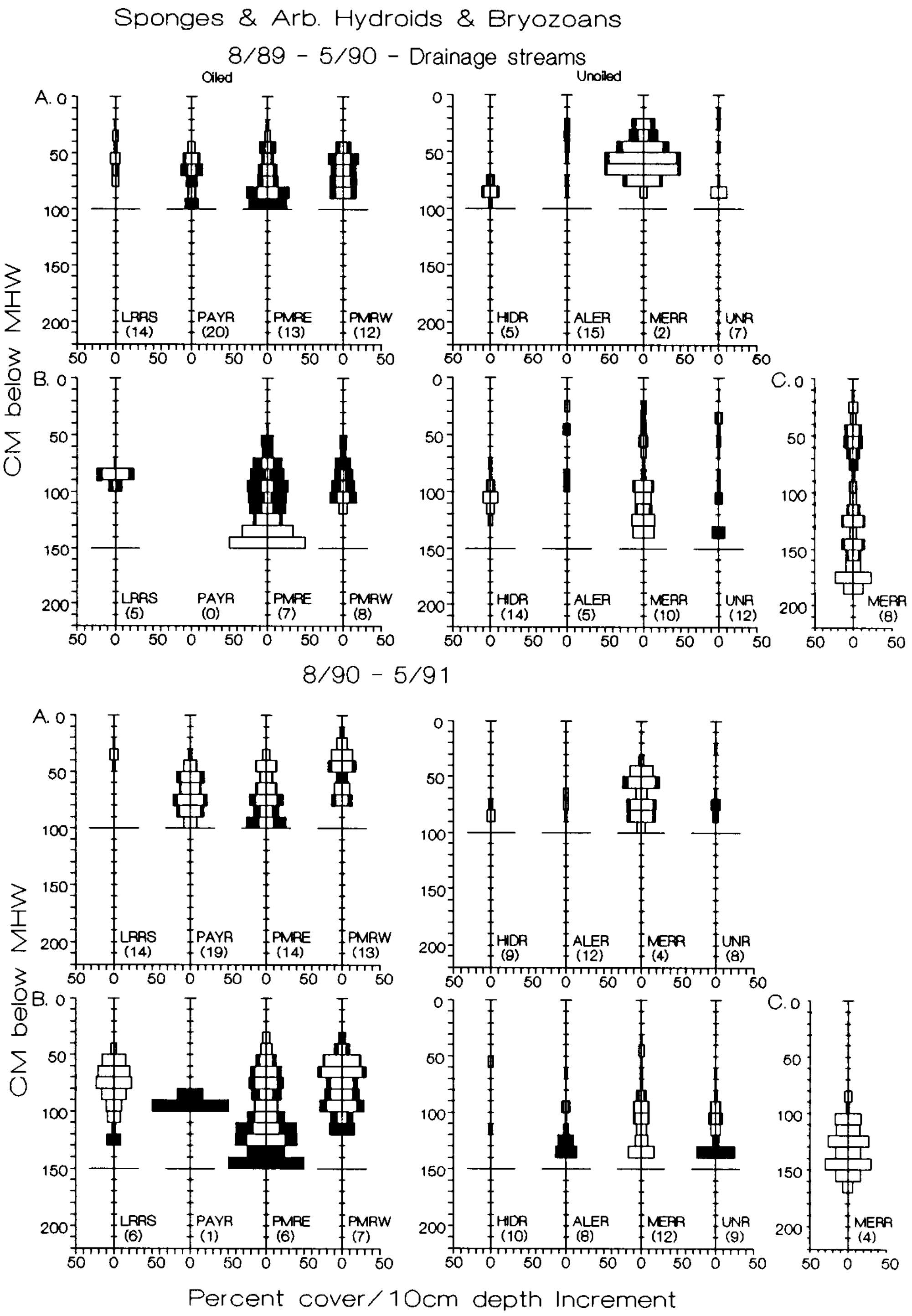

Fig. 9.128 Vertical distribution of sessile invertebrates in yr 3, 4, and 5 postspill on random-census roots in drainage streams (continued).

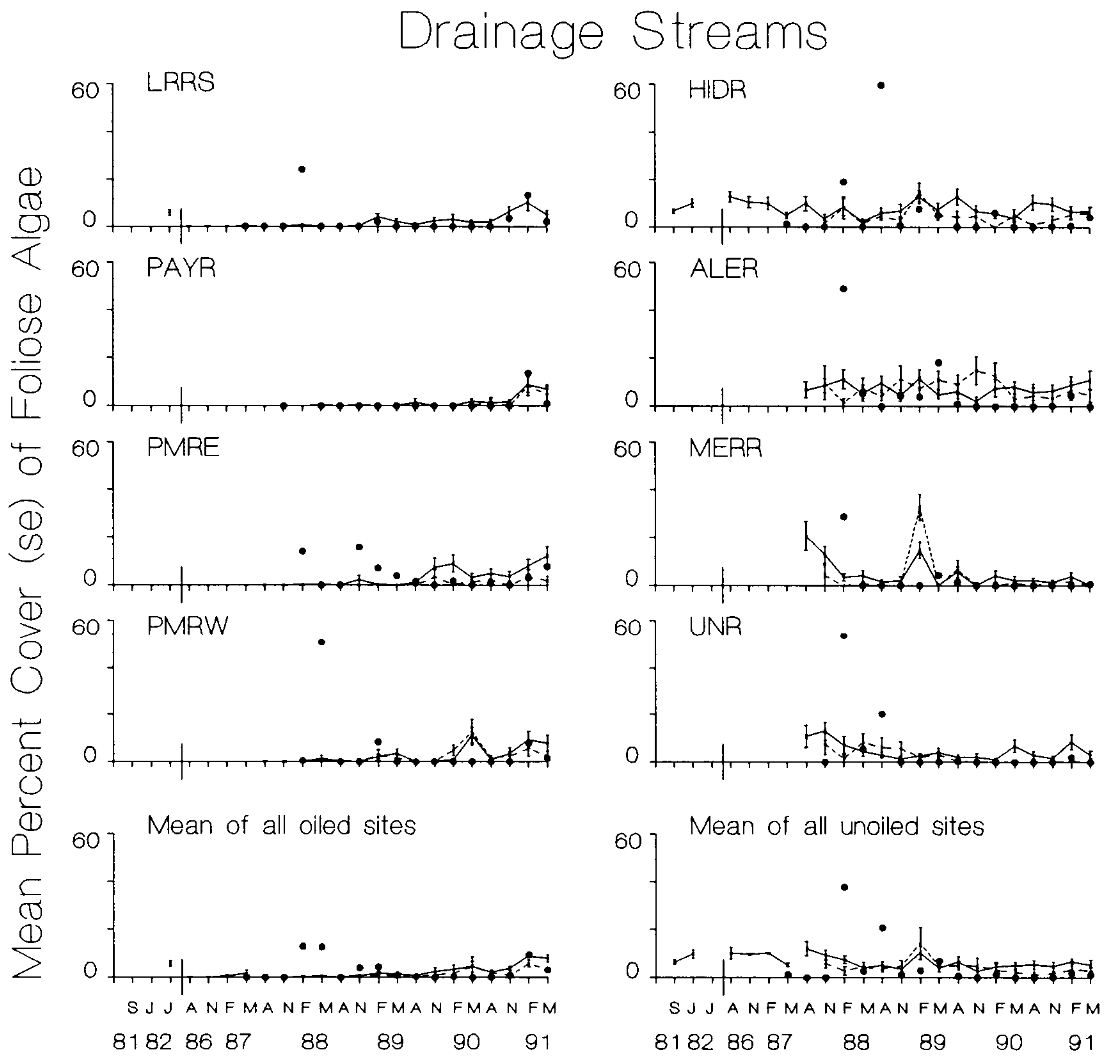

Fig. 9.129 Patterns of abundance of foliose algae on fringing *Rhizophora* roots in drainage streams. Data are mean percent cover (± SE) of foliose algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

Abundances of individual species or groups varied over time and among sites. *Balanus* and *Mytilopsis* recruited at one or more site every quarter, and diatoms recruited at all sites each quarter (Figs. 9.123, 9.125, 9.135).

Mytilopsis sallei. Recruitment of *Mytilopsis* ranged from 0 to 27% cover at individual sites, with least recruitment at MERR (Fig. 9.123). No false mussels recruited there in 5 of 14 quarterly intervals, and abundance on dowels averaged

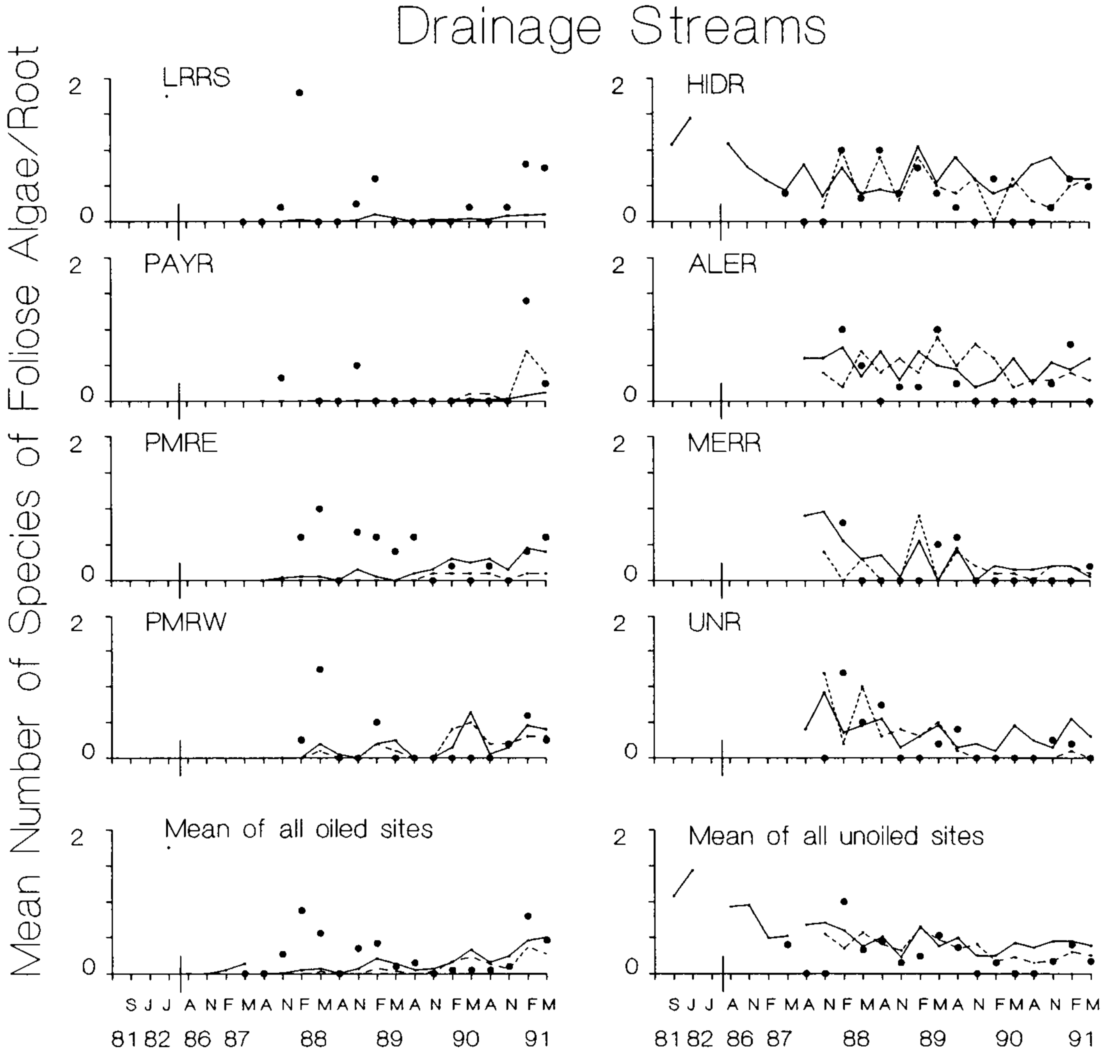

Fig. 9.130 Patterns of algal species richness on roots on fringing *Rhizophora* in drainage streams. Data are mean number of species of foliose algae/root for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (N = 20-25/site), *dashed lines* are community development roots (N = 5-10/site), and *solid circles* are recruitment dowels (N ~5/site). See text for details.

<5% cover in 7 of 9 quarters when some recruitment occurred (14% in November 1990; 12% in May 1991). UNR also had little (4 quarters, mean cover <3% each) or no (3 quarters) recruitment through May 1989; but then recruited in each of the eight quarters through May 1991 (range of mean cover = 3-27%). Recruitment failed twice at HIDR (August 1988 and May 1989) and once at ALER (May 1989). In the 14 quarters when recruitment occurred at HIDR, mussel abundance ranged from 1 to 24% cover, and was >5% cover overall in 10 quarters. ALER had 13

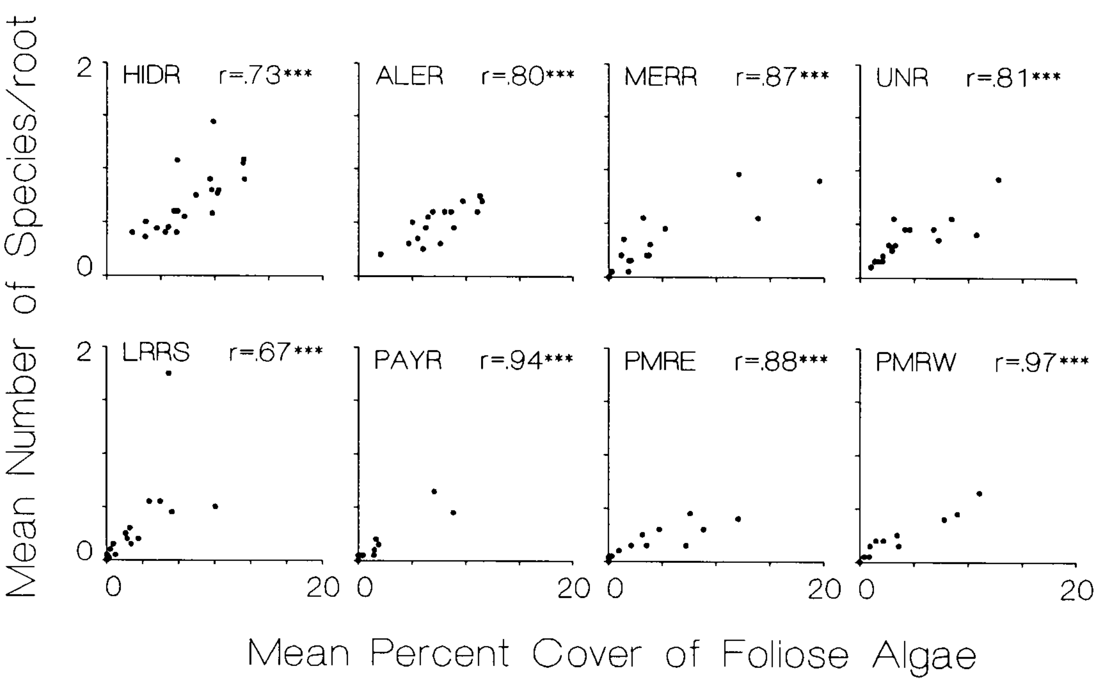

Fig. 9.131 Algal species richness vs. percent cover of foliose algae on randomly sampled roots in drainage streams. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. *r* = correlation coefficient, ***: *P* = .001 (significance level of observed correlation).

instances of recruitment; overall abundances ranged from 1 to 24% cover, and exceeded 5% cover in eight quarters.

Barnacles. Balanus recruited variably in time and among sites (Fig. 9.125). Overall, its abundance ranged from <1 to 28% cover over 17 quarters. There was a strong seasonal component to barnacle recruitment. In each of the 4 yr recruitment failed or nearly failed (overall range = 0-6% cover) in late wet season (November; Fig. 9.139). Among sites, barnacles appeared on dowels at MERR in only 4 of 14 quarters, and never averaged more than 1% cover. Other sites rarely or never had total failure of recruitment (2 of 15 quarters at UNR and 0 of 15 at both HIDR and ALER). Within a site variability could be considerable as well. For example, the most successful barnacle recruitment during the study (ALER, February-May 1989, mean cover = 44%) was followed by near failure (mean cover = 4%).

Sessile Invertebrates. Rare sessile invertebrates (arborescent hydroids and bryozoans, encrusting bryozoans, sponges, vermetids, anemones, and tunicates) recruited at one or more sites in each sampling period (Fig. 9.127). The only abundant group on dowels was arborescent hydroids and bryozoans. Tunicates

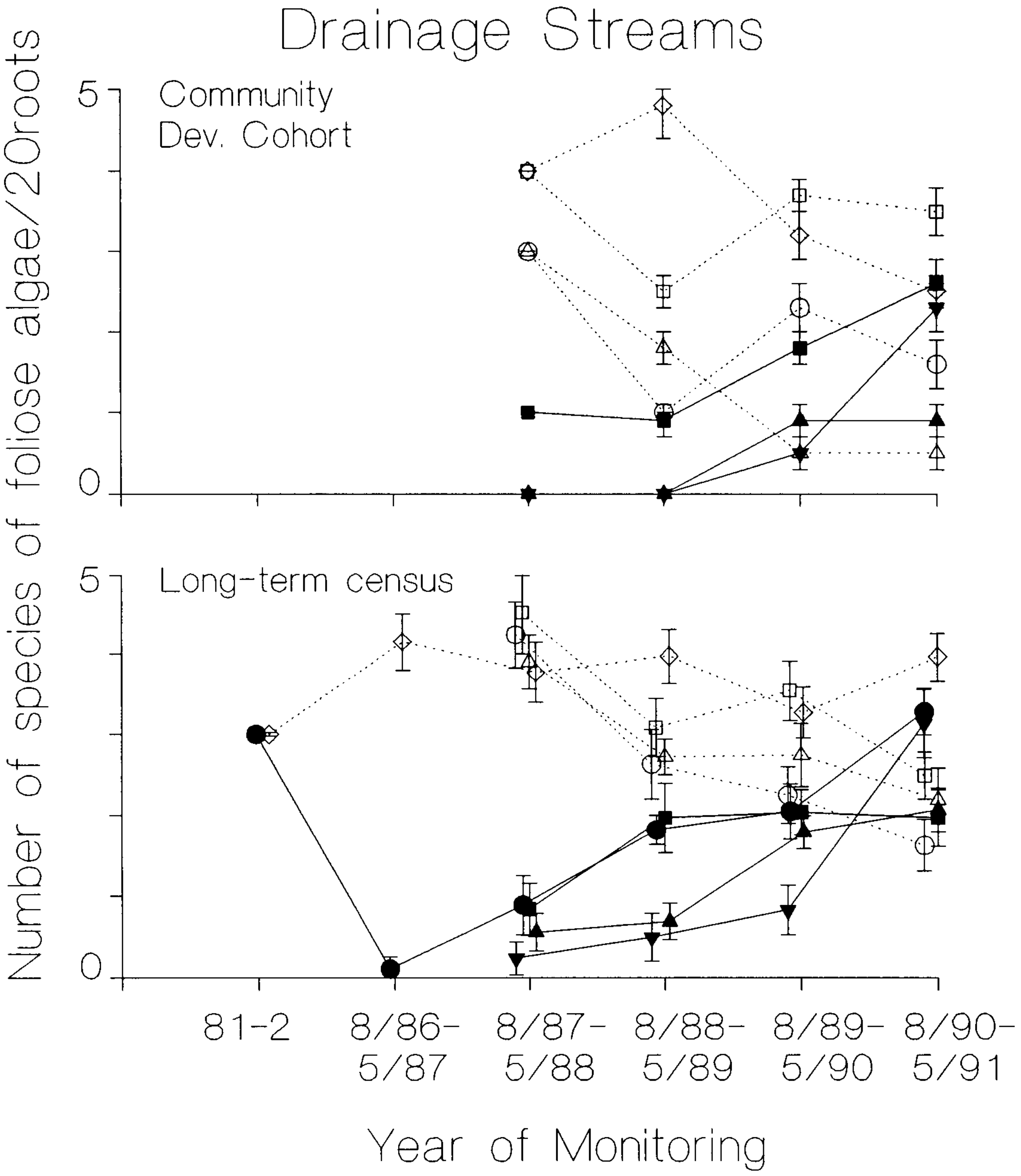

Fig. 9.132 Species richness of foliose algae in drainage streams. Mean ± 95% confidence intervals for rarefaction estimates of the number of species of foliose algae expected in a sample of 20 roots. *Solid symbols* = oiled sites, *open symbols* = unoiled sites. See text for details.

appeared once at ALER and three times at UNR. Sponges recruited at least once at all sites, but regularly and in measurable abundance only at UNR. Anemones were the least abundant and most restricted species found on dowels, occurring only at ALER (N = 3 intervals, cover <1%).

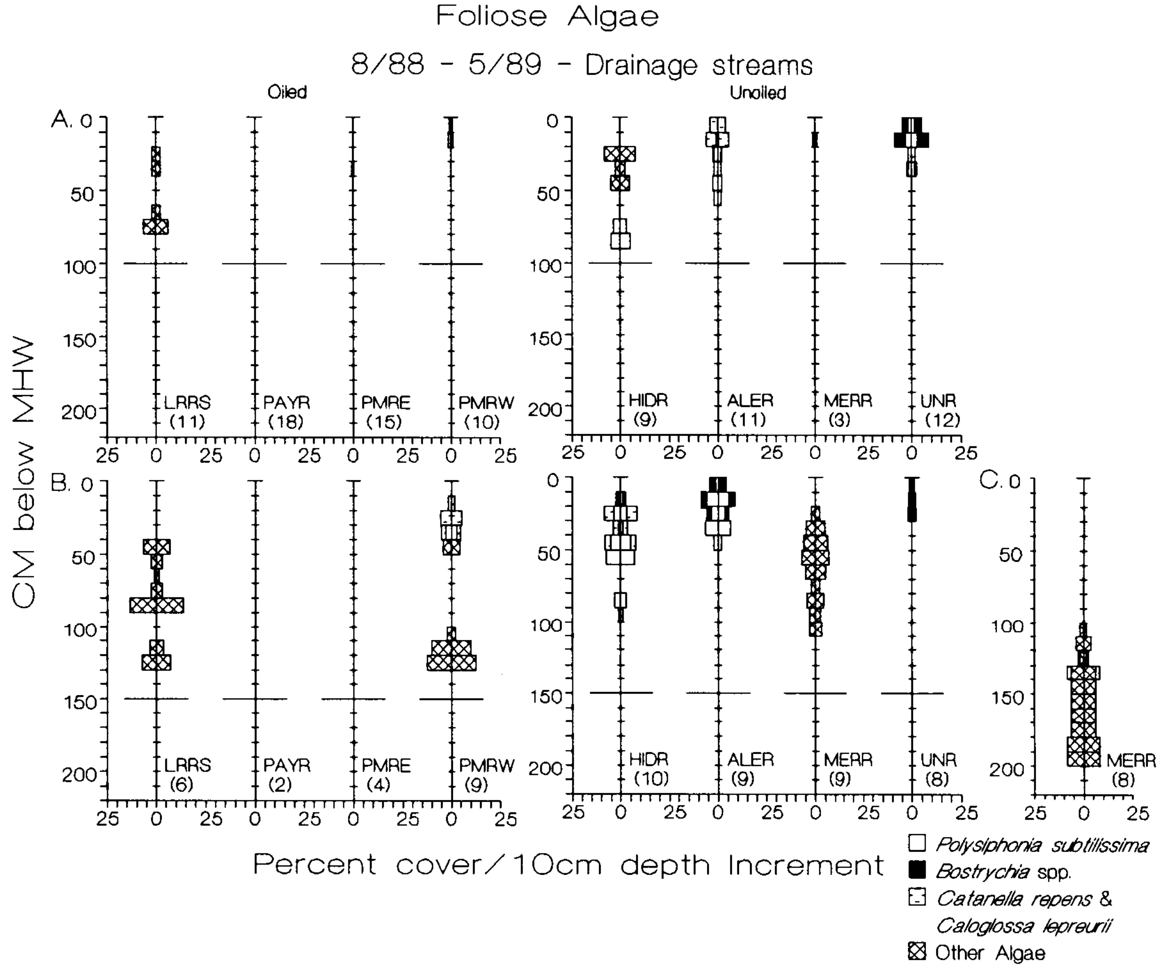

Fig. 9.133 Vertical distribution of foliose algae in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are mean percent cover (*x*-axes) of various foliose algae for 10-cm increments on roots downward from MHW (*y*-axes) for roots ≥75 cm long. Numbers in parentheses are sample sizes. See text for further details. *A*. Roots 75-100 cm long below MHW. *B*. roots 101-150 cm long. *C*. roots >150 cm long.

Recruitment of rare sessile invertebrates varied widely among sites and among dates within sites (Fig. 9.127). HIDR had the least recruitment overall, with failure of all groups in 7 of 17 quarters. Anemones and tunicates never appeared on dowels, sponges and encrusting bryozoans recruited twice, and arborescent hydroids and bryozoans occurred in 8 of 14 quarters (range of mean cover <1-11%). UNR had the most recruitment, with only one total failure in 15 quarters. As at HIDR, the most abundant group was arborescent hydroids and bryozoans. However, sponges also appeared in 7 of 15 intervals, ranging from 2 to 7% cover; tunicates and encrusting bryozoans recruited at least once.

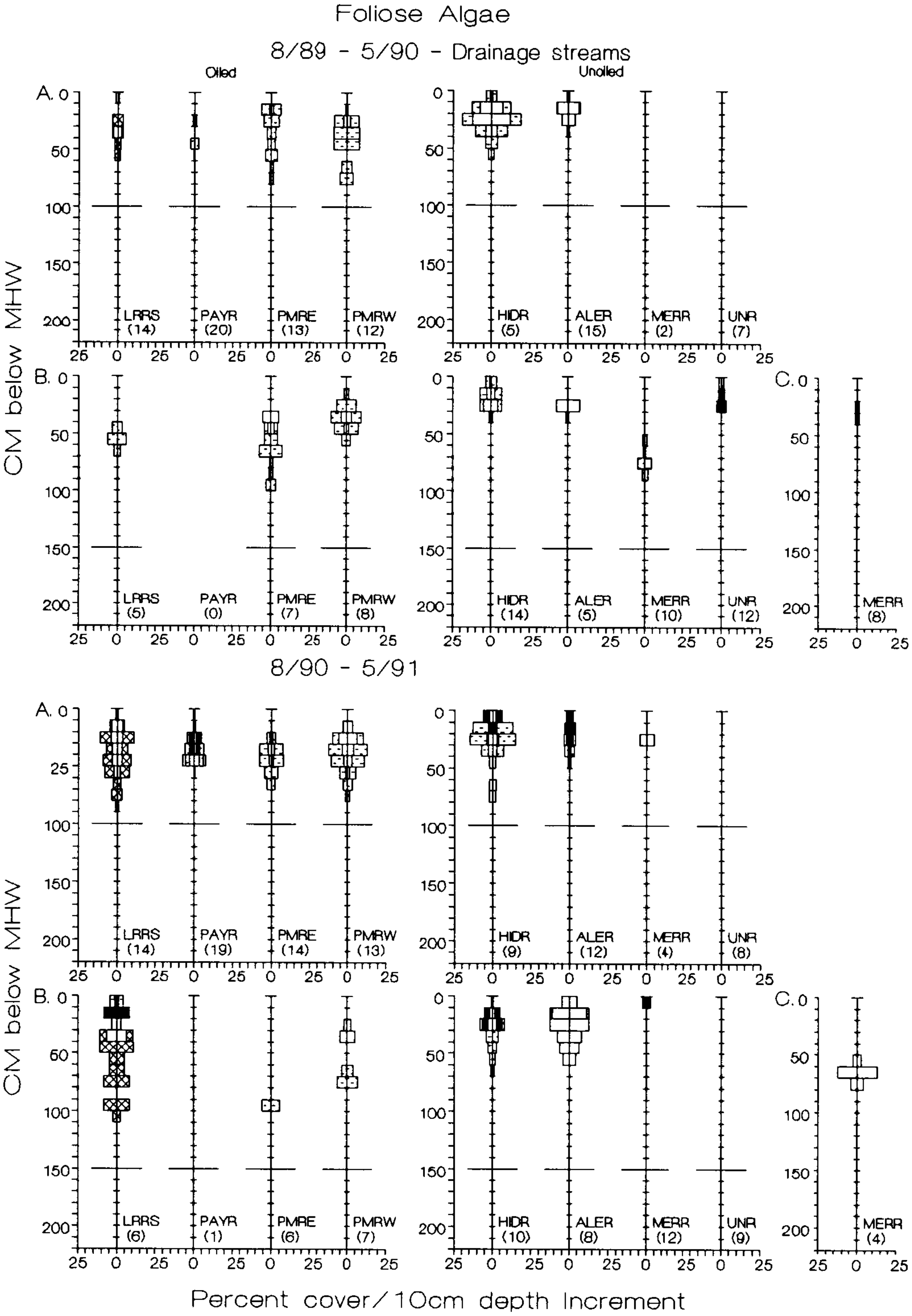

Fig. 9.133 Vertical distribution of foliose algae in yr 3, 4, and 5 postspill on random-census roots in drainage streams (continued).

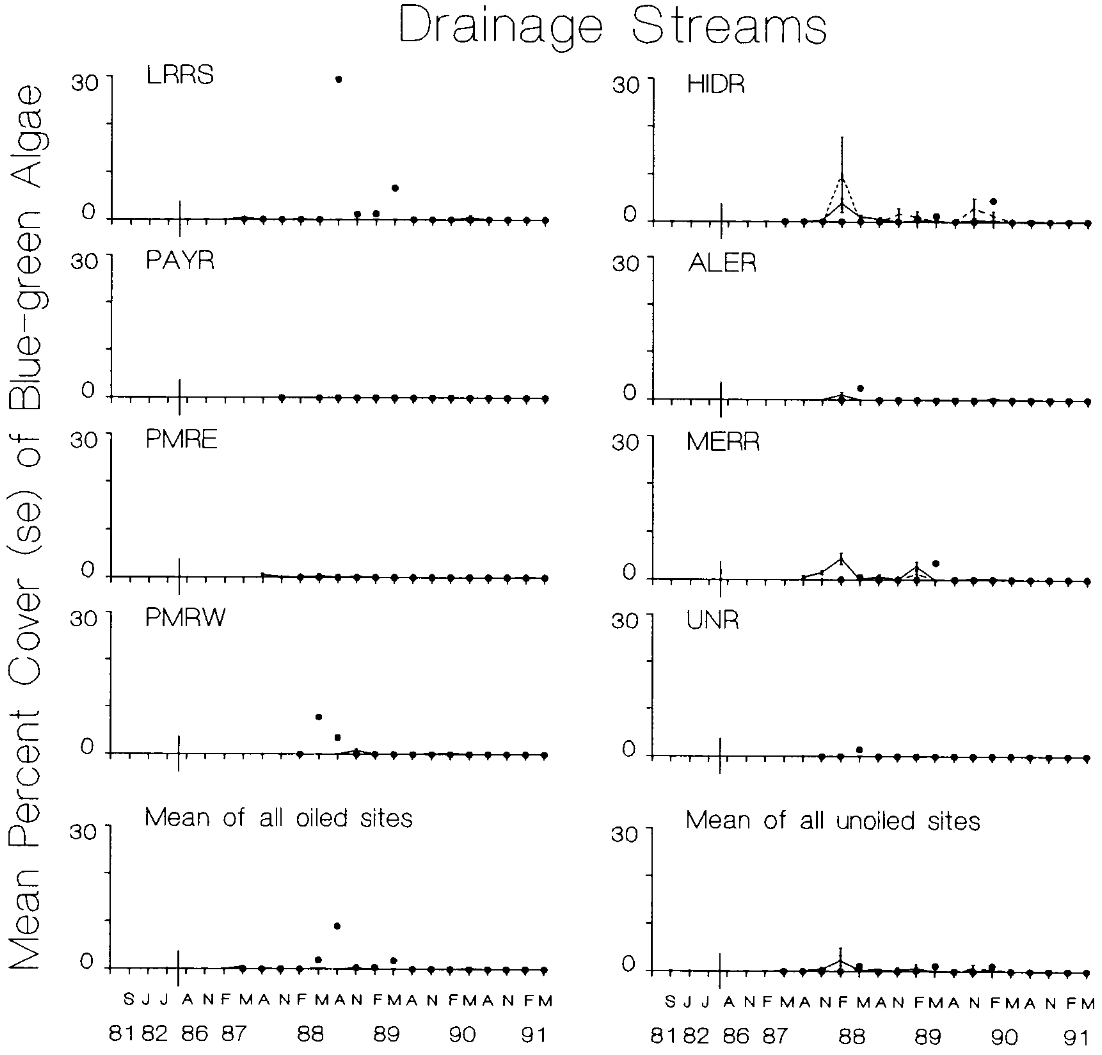

Fig. 9.134 Patterns of abundance of blue-green algae on fringing *Rhizophora* roots in drainage streams. Data are mean percent cover (± SE) of blue-green algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

Foliose Algae. Foliose algae recruited at one or more streams in 12 of 17 quarters (Fig. 9.129). Overall mean abundances were usually ≤5% cover with two exceptions. In February 1988 percent cover of foliose algae averaged >20% at each of four sites, and the overall mean was 38%. In August 1988 algal recruitment failed at two sites (ALER and MERR), but averaged 20% cover at UNR and 63% cover at HIDR. Fewer than one species was recorded per dowel (Fig. 9.130). Rarefaction estimates were broadly similar among streams, with an average of ~1-1.5 species

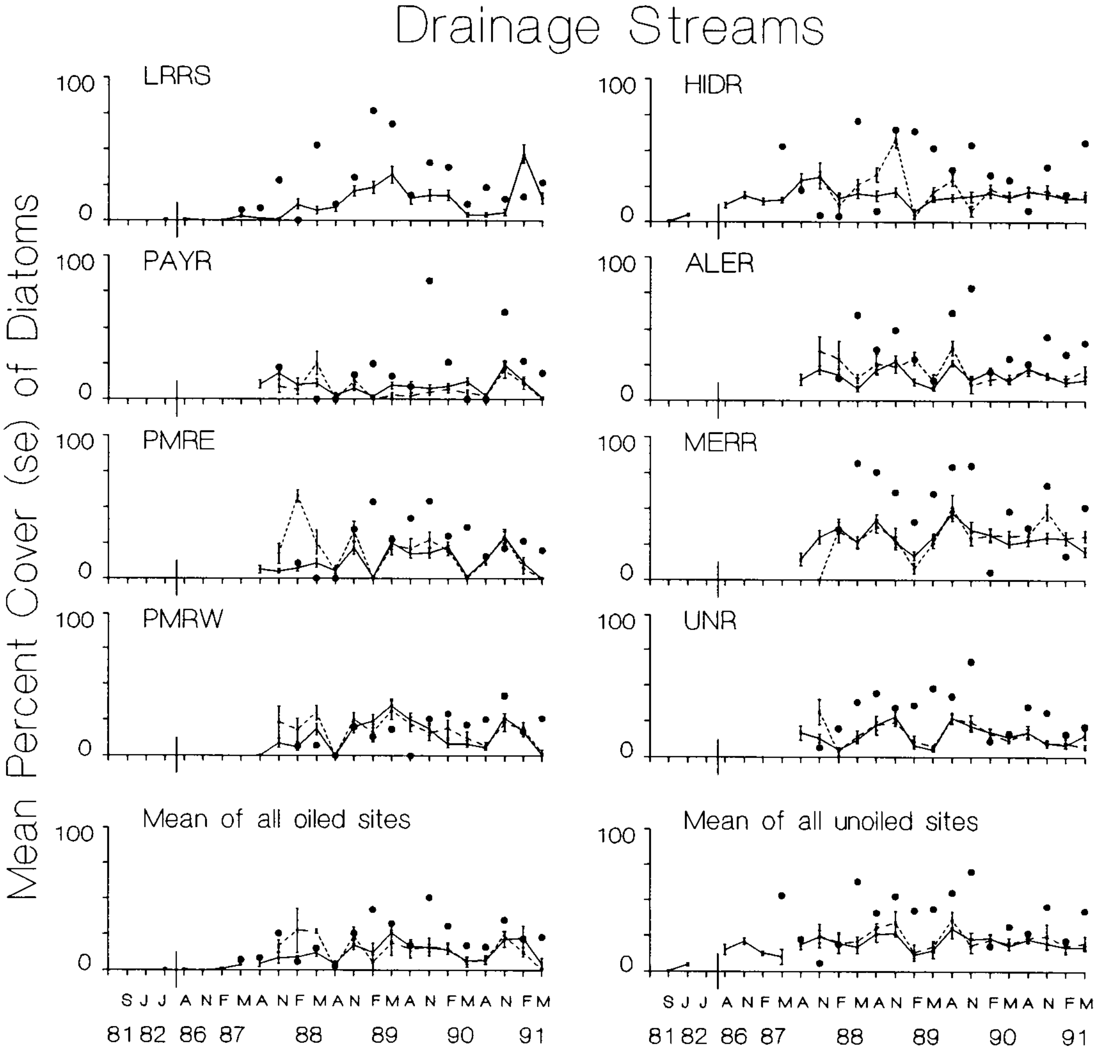

Fig. 9.135 Patterns of abundance of diatoms on fringing *Rhizophora* roots in drainage streams. Data are mean percent cover (± SE) of diatoms for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

expected to be recorded in a sample of 10 dowels. Estimates for HIDR were the highest (1.4-2.5 species/10 dowels), while MERR was the lowest (0.5-1.0 species/10 dowels).

Blue-green Algae. Blue-green algae recruited occasionally in low abundance at all streams, with no seasonal pattern (Fig. 9.134).

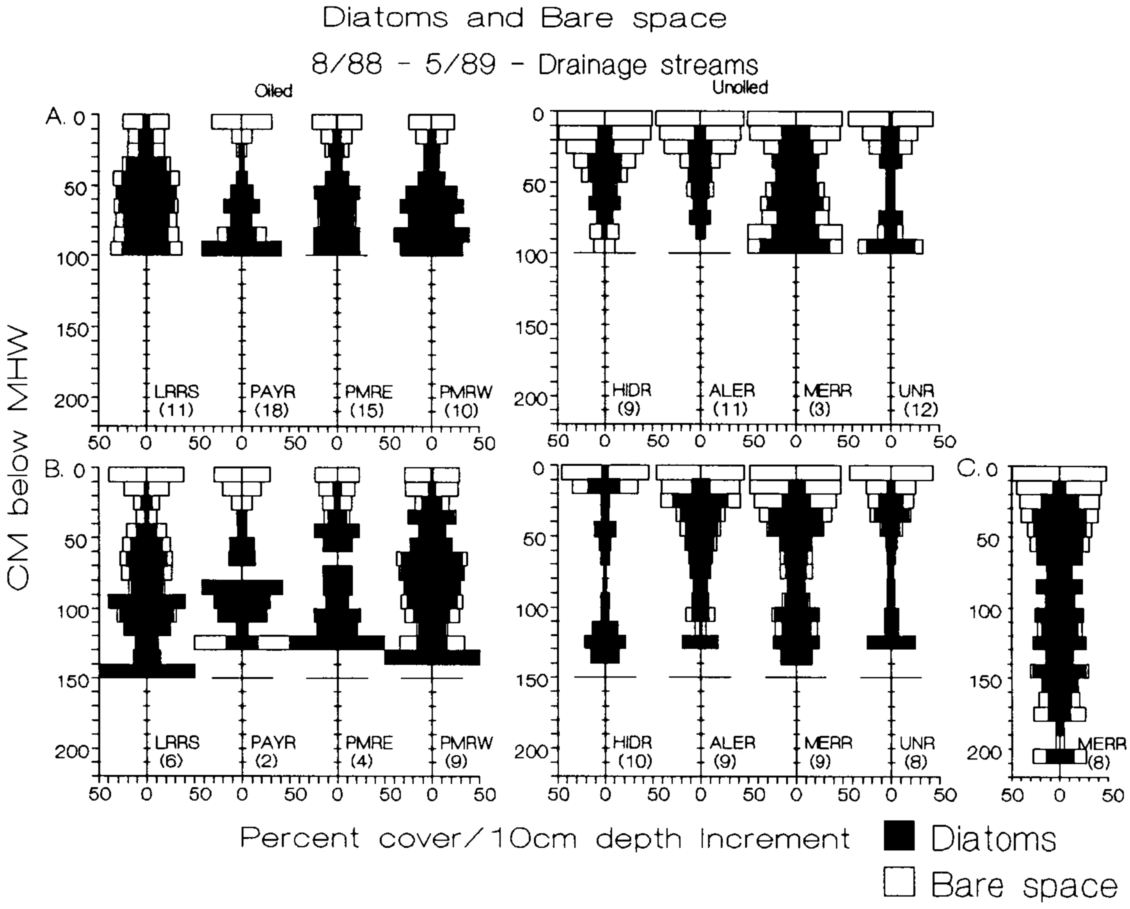

Fig. 9.136 Vertical distribution of diatoms and bare space in yr 3, 4, and 5 postspill on random-census roots in drainage streams. Data are mean percent cover (*x*-axes) for 10-cm increments on roots downward from MHW (*y*-axes) for roots ≥75 cm long. Numbers in parentheses are sample sizes. See text for further details. *A.* Roots 75-100 cm long below MHW. *B.* roots 101-150 cm long. *C.* roots >150 cm long.

Diatoms and Bare Space. Diatom abundance ranged from ~20 to 70% cover overall, except for the August-November 1987 interval (6% cover; Fig. 9.135). Recruitment of diatoms was variable in time for individual sites. However, when data were combined, recruitment appeared seasonal, with lowest abundance on dowels in dry season (February). Approximately 10-30% of root surfaces were bare (Fig. 9.137), with a seasonal pattern of increased bare space during dry or early wet season.

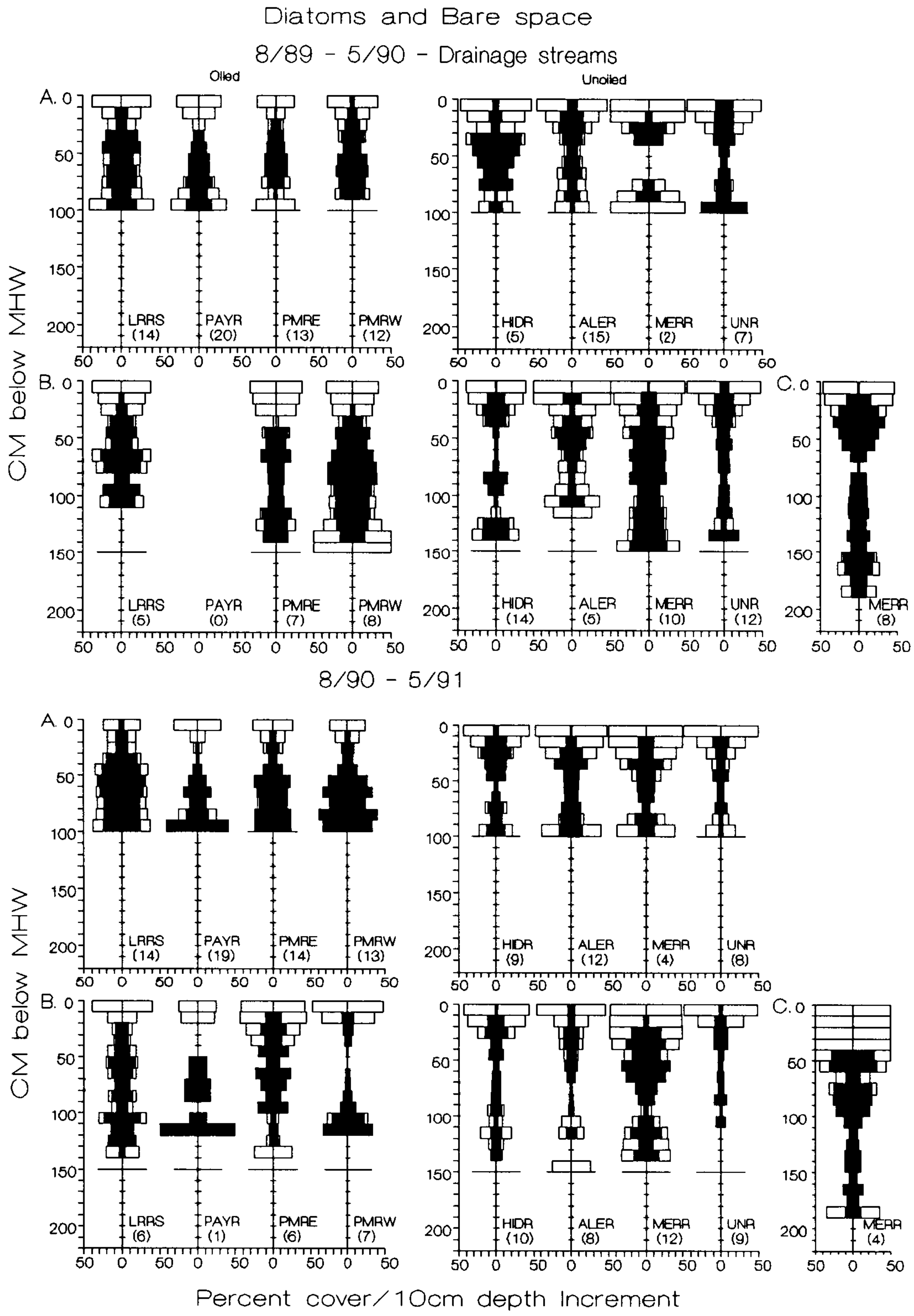

Fig. 9.136 Vertical distribution of diatoms and bare space in yr 3, 4, and 5 postspill on random-census roots in drainage streams (continued).

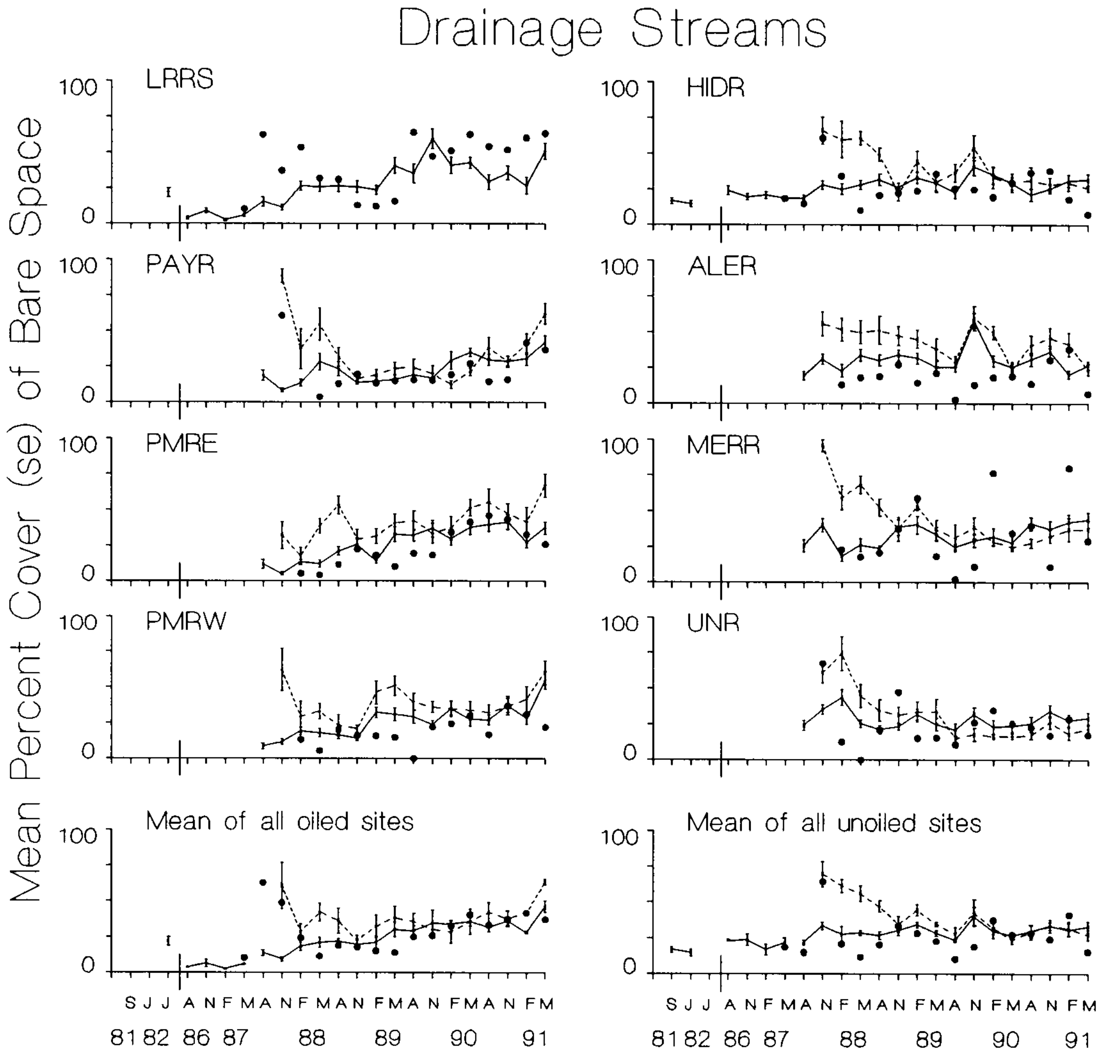

Fig. 9.137 Patterns of abundance of bare space on fringing *Rhizophora* roots in drainage streams. Data are mean percent cover (± SE) of bare space for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*N* = 20-25/site), *dashed lines* are community development roots (*N* = 5-10/site), and *solid circles* are recruitment dowels (*N* ~5/site). See text for details.

Community Development

Mytilopsis sallei. After a 6-mo immersion (February 1988), *Mytilopsis* began settling on roots at all sites except MERR, but covered <4% overall (Fig. 9.123). *Mytilopsis* increased steadily in abundance over time at all sites except MERR. Abundance of false mussels on CD and LT roots converged at variable rates among

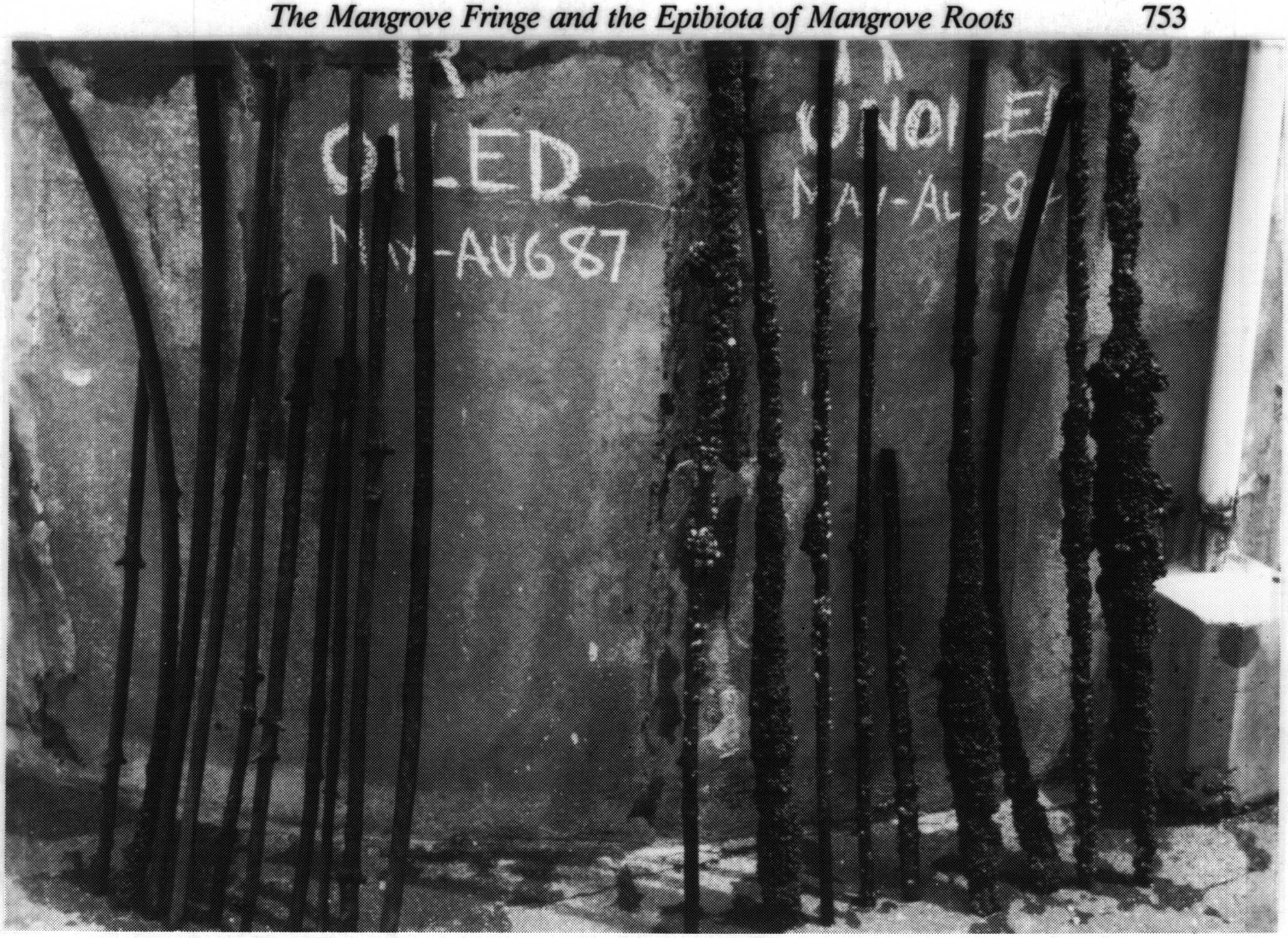

Fig. 9.138 Pilot recruitment experiment results. In pilot experiments, sections of aerial roots were cut and placed in the water for 3 mo at oiled and unoiled sites. The photograph shows recruitment from May until August 1987; the group of 10 roots at the *left* were from an oiled stream (LRRS), the group of nine at the *right* were from an unoiled stream (UNR).

sites – fastest at UNR (12 mo, by November 1988), and slowest at MERR (51 mo, February 1991; Fig. 9.123).

Barnacles. Balanus first occurred on CD roots in May 1988 (overall mean density of 1% cover vs. 1% on LT roots; Fig. 9.125). It remained rare, but equal in overall abundance to cover on LT roots through May 1991. Seasonal fluctuations, including low cover in late wet season, were also similar to those on randomly censused roots. Among sites, *Balanus* was always rare to absent at MERR, and most abundant at HIDR.

Sessile Invertebrates. Sessile invertebrates appeared in February 1988 (Fig. 9.127); the major component was arborescent hydroids and bryozoans (overall mean cover = 5%). Abundance of sessile invertebrates on CD roots did not differ from LT roots for the next 4 yr.

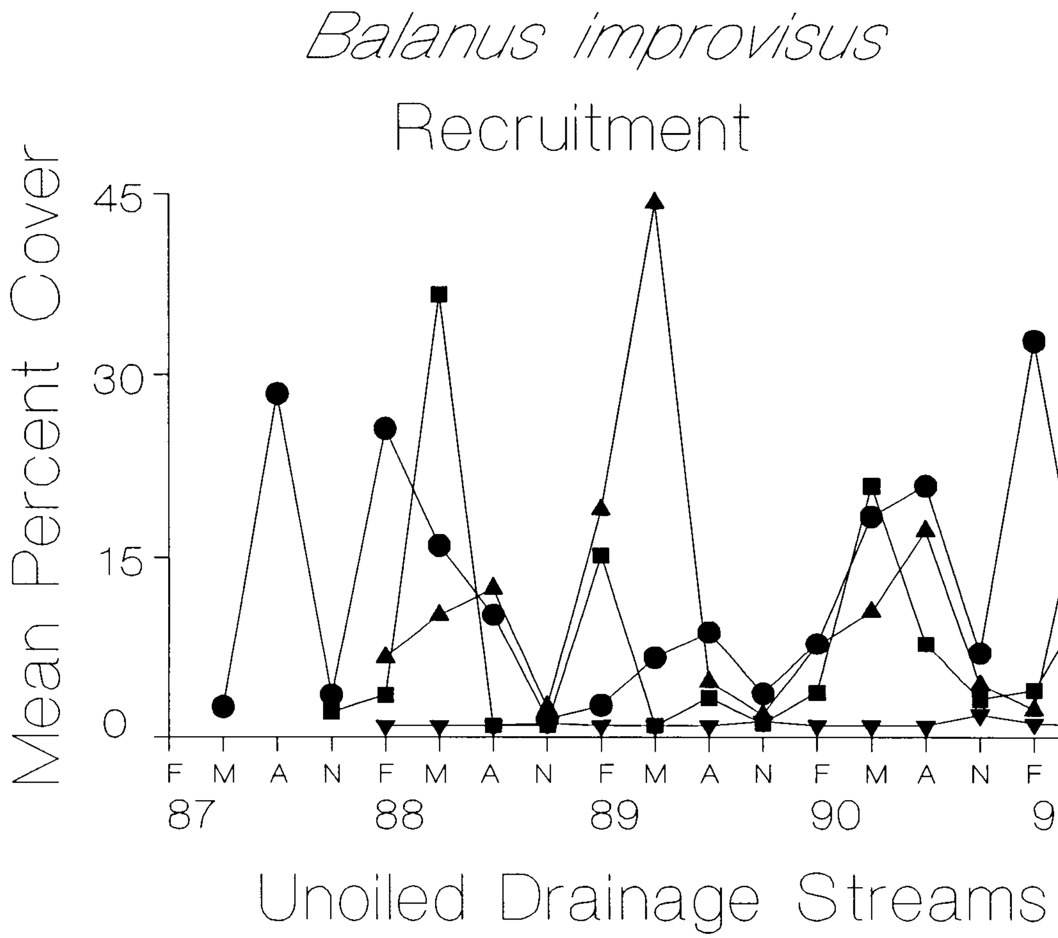

Fig. 9.139 Recruitment patterns of *Balanus* in unoiled streams. Data are means of quarterly abundances of barnacles on dowels for each site examined. See text for details.

Foliose Algae. Foliose algae also appeared by November 1987 at levels similar to those on LT roots (Fig. 9.129). Percent cover of foliose algae then closely followed patterns on LT roots through May 1991. Mean number of species/root was also similar to results from randomly censused roots (Fig. 9.130); percent cover of algae on roots was correlated with the number of species of foliose algae/root (Fig. 9.140). Roots quickly accumulated species, with rarefaction estimates of diversity converging in the first year (Fig. 9.132). At UNR foliose algae became rare on CD roots in late 1989-1991; the cause was unknown.

Blue-green Algae. Blue-green algae formed ephemeral populations on both CD and LT roots. In general, blue-green algae were so rare that cover was <5% (Fig. 9.134).

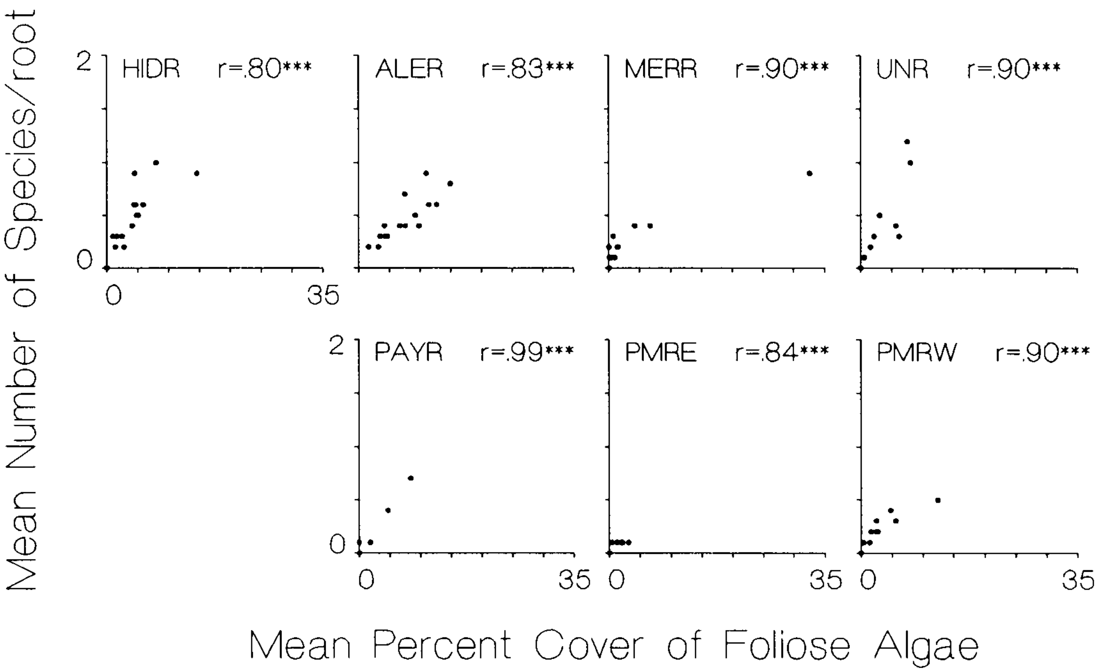

Fig. 9.140 Algal species richness vs. percent cover of foliose algae on community development roots in drainage streams. Mean percent cover of algae/monitoring date plotted against the mean number of species of foliose algae/root. r = correlation coefficient, *: P = .05, **: P = .01, ***: P = .001 (significance level of observed correlation). If there is no asterisk the correlation was not significant.

Diatoms and Bare Space. Diatoms appeared immediately; by November 1987 their abundance on CD roots matched that on LT roots (Fig. 9.135). Abundances were indistinguishable from those on LT roots through May 1991, ranging between 13 and 30% cover.

The amount of bare space on roots declined quickly after roots entered the water (Fig. 9.137) and was equal to that on LT roots within a year after roots entered the water.

Oiled Drainage Streams

Long-term Census Results

Effects of oil were immediate, severe, and persistent in streams. When LRRS, a small drainage stream running through the center of Isla Largo Remo, was monitored before the spill (June 1982), most space on roots was occupied by *Mytilopsis sallei* (>60% cover). For four quarterly samples beginning in August 1986, we remonitored this site, and monitored roots along the banks of its northern mouth as a second site (LRRN). No living *Mytilopsis* occurred on any roots (Figs. 9.123, 9.141). Dead false mussels, most covered with oil, fungus or a bacterial slime,

Fig. 9.141 Oiled stream roots 3 mo after oiling. August 1986, site = LRRS. *Upper left*, fresh oil is visible on a root segment; submerged *Mytilopsis* were dead and covered with a bacterial/fungal film.

occupied an average of 15% cover in August 1986. By May 1987 most of these had detached, and mean abundance of dead *Mytilopsis* was 1% cover. Bacterial and fungal slime, and especially oil (Fig. 9.141) covered most root surfaces. Diatoms, blue-green algae, foliose algae, and dead barnacles were present but rare (Figs. 9.125, 9.129, 9.134, 9.135, 9.142). Bare space on unoiled roots averaged between 15 and 22% cover before the spill; in the first year after the spill it ranged from 4 to 6% cover (Figs. 9.137, 9.143). Oil was the most abundant category of cover on roots (Figs. 9.29, 9.30).

Mytilopsis sallei. In the second through fifth year after the spill, three sites in the eastern wing of Bahía Las Minas were monitored in addition to LRRS. *Mytilopsis* did not return to oiled streams through May 1991 (Fig. 9.123); mean cover at oiled streams was <3%. Among sites, false mussels were present but rare in 16 of 16 quarters at PAYR, PMRE, and PMRW, and absent only once at LRRS. Vertical distribution appeared similar to that at unoiled streams, although false

Fig. 9.142 Oiled stream root 1 yr after oiling. August 1987, site = PMRE. The root appeared healthy despite the heavy coating of oil. Epibiota consisted of oiled diatoms and a single dead barnacle.

Fig. 9.143 Oiled stream roots 2 yr after oiling. May 1988, site = LRRS. Underwater view shows roots with no obvious epibiota. The fuzzy appearance is due to diatoms, fungus, and bacteria.

mussels did not occur on either the shallowest or the deepest portions of oiled roots (Fig. 9.124). This may have resulted from overall scarcity.

False mussel abundance on LT roots was significantly affected by oiling and variable among years ($P < .001$; Table 9.18). *Mytilopsis* was less abundant at oiled than unoiled streams through May 1991, but the strength of this difference varied among years. This was not due to an increase in false mussels at oiled sites over time; rather, *Mytilopsis* abundance in unoiled streams showed a gradual decrease through the period of the study.

There were slight increases in mussel abundance in two oiled streams in 1991 (mean cover of 2 and 3% at PAYR; 3 and 2% at PMRW in February and May 1991, respectively). False mussels (and other organisms) recruited onto some roots that had entered the water that year (Fig. 9.144). This was the first indication of recovery in 5 yr of study; however, persistence of false mussels at these sites has yet to be demonstrated.

Barnacles. Balanus improvisus was present but rare (≤1% cover) overall at oiled sites through May 1991 (Fig. 9.125). Barnacles were also rare overall at unoiled sites. Repeated-measures ANOVA found no effect of oiling (yr 2-5), but a significant effect of year (Table 9.18). Lack of a significant overall ANOVA was due to persistent, low percent cover of barnacles at a single unoiled site, MERR (Fig. 9.125). However, barnacles were more abundant at unoiled than oiled sites in 19 of 20 quarters from 1986 to 1991 (sign-rank test, $P < .001$, $N = 20$); the one time they were more abundant at oiled sites, percent cover was <1% for both oiled and unoiled streams.

Although vertical distributions were difficult to assess because of its scarcity, *Balanus* did not differ in depth distribution between oiled and unoiled streams (Fig. 9.126). Live and dead barnacles were easily differentiated in the field because scutal valves are lost after death, leaving an open test (Fig. 9.142). We compared the proportion of dead to live barnacles over time at oiled and unoiled sites and found there were almost as many dead as live barnacles in oiled streams, while fewer than 30% of barnacles were dead at unoiled sites during any census.

Foliose Algae. Foliose algae remained rare on oiled, LT roots during the second and third year after the spill, then increased slowly from August 1989 to May 1991 (Fig. 9.129). There was a significant effect of oiling on foliose algal abundance for yr 2 and 3 (August 1987-May 1989), but not for yr 4 and 5 (August 1989-May 1991; Table 9.18). The mean number of species of foliose algae/root increased with percent cover (Fig. 9.131), but was always <2. Species numbers were approximately equal at oiled and unoiled sites 5 yr after oiling (Fig. 9.132).

Despite the increase in foliose algae 4 yr after the spill, there were strong differences in species composition between oiled and unoiled streams. Foliose algae in unoiled streams were almost all members of the "Bostrychietum" group (Post 1963), with rare occurrences of other species (Fig. 9.133). These species almost vanished from oiled streams, and slowly returned. Instead, *Cladophora* spp. and

Table 9.18 Drainage stream repeated-measures ANOVAs: summary table.

A. Long-term census. Probability levels for annual comparisons of arcsine-transformed percent covers on roots. *Y1*, *Y2*, *Y3*, and *Y4* are univariate ANOVAs for yr 1-4, August 1987-May 1991. The *oil*, *year*, and *Y x O* columns are repeated- measures ANOVAs including all 4 yr.

Group	Y1	Y2	Y3	Y4	Oil	Year	Y x O	Spher.	H.-F.?
Mytilopsis	.0001	.001	.001	.001	.0005	.0001	.001	.811	no
Balanus	.519	.188	.343	.460	.337	.727	.697	.157	no
Sessile inverts.	.264	.326	.649	.426	.595	.0003	.011	.077	no
Foliose algae	.0001	.009	.136	.893	.006	.034	.0003	.222	no
Species/root	.0001	.016	.143	.524	.015	.212	.011	.208	no

B. Long-term census vs. community development cohort. Probability levels for annual comparisons of arcsine-transformed percent covers on roots for yr 1-4, August 1987-May 1991. *Group* is the comparison between long-term census and community development roots.

Comparison	*Mytilopsis*	*Balanus*	Sessile inverts.	Foliose Algae	Species/ root
Between:					
Group	.068	.566	.898	.121	.289
Oil	.0001	.121	.200	.001	.001
G x O	.151	.852	.548	.893	.848
Within:					
Year	.002	.008	.001	.200	.512
Y x G	.0001	.116	.707	.140	.508
Y x O	.011	.635	.053	.0001	.002
Y x G x O	.0001	.965	.747	.312	.834
Sphericity Test	.0003	.009	.016	.082	.005
H.-F. Adj. applied?	yes	yes	yes	no	yes

Species/root = mean number of species of foliose algae per root. *H.-F.?* = Huynh-Feldt adjusted probability levels. If *no*, then probability levels were unadjusted because of sphericity-test results. If *yes*, then levels were adjusted.

Caulerpa verticillata were found. Five years after oiling, *Bostrychia* spp. were found in only 2 of 4 oiled streams, the *Catanella/Caloglossa* association occurred in three, and no stream had the complete "Bostrychietum." Vertical distribution of algae appeared similar between oiled and unoiled streams from 1988-91, but pointed up differences in species composition between oiled and unoiled sites (Fig. 9.133).

Blue-green Algae. Blue-green algae did not occur in oiled streams in 9 of 16 quarters from August 1987 to May 1991, and never averaged >0.1% cover when found (Fig. 9.134). At unoiled sites blue-green algae occurred in 13 of 16 quarters,

Fig. 9.144 Oiled stream root 5 yr after oiling. June 1991, site = PAYR. This root had been in the water less than 2 yr, and was one of the few that had any development of epibiota. Attached organisms included *Crassostrea*, *Bostrychia*, *Mytilopsis*, and *Isognomon*.

and reached 2% cover. This rare (but highly productive) component of the prop-root epibiota was strongly negatively affected by oiling.

Sessile Invertebrates. Rare sessile invertebrates as a group disappeared in 1986-1987, reappearing in oiled streams the second year after the spill (Fig. 9.127). Arborescent hydroids and bryozoans appeared first, and were always the most abundant component. Encrusting bryozoans, tunicates, anemones, and sponges all were recorded on roots at some oiled site during the second year, but all remained rare. Only sponges occurred at oiled streams as often as at unoiled streams (15 of 16 monitorings at oiled sites vs. 13 of 16 at unoiled sites).

ANOVA comparisons of rare sessile invertebrates showed that they were significantly variable among years (Table 9.18). There was no effect of oiling between August 1987 and May 1991, largely because rare sessile invertebrates covered little space at HIDR throughout the 5 yr of study. There was little difference in depth distributions between oiled and unoiled streams, except for a tendency for the upper limit of sessile invertebrates to occur slightly deeper at oiled sites (and the absence of sessiles below 150 cm depth, a result of the shorter roots in oiled streams; Fig. 9.128).

Diatoms and Bare Space. Diatoms were rare in oiled streams the first year after the spill, averaging 1% cover (Fig. 9.135). They increased in abundance on oiled, LT roots during August 1987-May 1988. Diatom abundance was indistinguishable from that at unoiled sites from November 1988 through May 1991 (e.g., Fig. 9.143). Depth distributions at oiled and unoiled sites were the same in the last 3 yr of the study (Fig. 9.136).

Bare space at all oiled sites increased slowly over time; this was correlated with the gradual disappearance of oil from roots (Figs. 9.29, 9.137). Bare space occurred primarily at the shallowest and deepest levels on roots, similar to the pattern at unoiled sites (Fig. 9.136).

Recruitment

As at unoiled sites, there was at least some recruitment in all 17 quarters examined (Fig. 9.138). Combined abundances of all epibiota on dowels ranged from 9 to 63% cover, in contrast to unoiled sites, where combined cover of recruiting organisms exceeded 65% cover in 14 of 17 quarters. During the first 2 yr that recruitment was followed (February 1987-February 1989), maximum combined abundance was 39% cover at oiled sites; during the last 2 yr it reached 63% cover.

Mytilopsis sallei. *Mytilopsis* recruited in 11 of 17 quarters in at least one oiled stream, compared to 17 of 17 at unoiled streams (Fig. 9.123). More *Mytilopsis* were found at unoiled than oiled sites in all quarters (sign-rank test, $P < .001$, $N = 17$). At oiled streams *Mytilopsis* recruited in abundance once (20% cover, LRRS, November 1988). No recruitment occurred at other oiled sites monitored, and recruitment at unoiled sites was low. At all other times recruitment of false mussels averaged under 4% cover at LRRS and 1% cover or less in other oiled streams.

Other Bivalves. Rare species of bivalves were less likely to be found in oiled than unoiled streams. *Isognomon* appeared in some unoiled stream in eight quarters, but was absent at oiled streams. Settlement of *Crassostrea* failed 16 times in oiled streams vs. five times at unoiled streams. *Brachidontes* settled only once in both oiled and unoiled streams.

Barnacles. *Balanus* occurred in 12 of 17 quarters in at least one oiled stream, but recruited in all 17 quarters in at least one unoiled stream (Fig. 9.125). Barnacle settlement was higher at unoiled than oiled streams in 16 of 17 quarters (sign-rank test, $P < .001$, $N = 17$). *Balanus* never recruited at individual oiled sites in abundances greater than 4-6% cover (1 instance each at PAYR and PMRE, 3 instances at PMRW).

Foliose Algae. Frequency of recruitment was similar at oiled and unoiled streams for most other groups, but cover was higher at unoiled streams in most cases. Foliose algae recruited in 11 quarters, compared to 12 in unoiled streams, and covered more space at oiled streams only in the last year (Fig. 9.129). Number of species of foliose algae expected/10 dowels was similar to that at unoiled sites (rarefaction estimates, range 1990-1991 = 1.5-2.5 species/10 dowels). The most successful recruitment of algae at oiled sites was in PMRW (May 1988, mean of 50% cover), but recruitment failed at the other three sites monitored (and was low at unoiled sites as well). Recruitment failed in all oiled streams in August 1988, when 2 of 4 unoiled sites had considerable (20-63% cover) algal cover on dowels.

Blue-green Algae. Blue-green algae recruited in five quarters at oiled sites and four at unoiled sites, with ephemeral increases at LRRS and PMRW only (Fig. 9.134).

Sessile Invertebrates. Rare sessile invertebrates occurred in 14 quarters vs. 15 at unoiled streams (Fig. 9.127). However, between May 1986 and May 1990 cover was greater at unoiled than oiled sites (sign-rank test, $P = .046$, $N = 13$). In the last year rare sessile invertebrates were more abundant at oiled sites (4 of 4 quarters). Apart from cnidarians, which never recruited, and tunicates, which only appeared once in 17 quarterly intervals (vs. 3 at unoiled sites), patterns of recruitment for individual taxa of rare sessile invertebrates were similar between oiled and unoiled streams. Arborescent hydroids and bryozoans were usually present on dowels, and ranged from rare to abundant. Sponges and encrusting bryozoans were intermittently present and never abundant at either oiled or unoiled sites.

Diatoms and Bare Space. Diatoms recruited in all 17 quarters at both oiled and unoiled streams, but covered more space at unoiled streams on 14 of 17 dates (sign-rank test, $P = .012$, $N = 17$; Fig. 9.135).

There was more bare space on dowels at unoiled than oiled sites from May 1987 to May 1989 (7 of 9 intervals; Fig. 9.137). After May 1989 there was more bare space on dowels at oiled than unoiled sites (7 of 8 intervals). The amount of oil on dowels declined during 1989 (Fig. 9.29), but settlement was reduced at oiled sites and this resulted in increased bare space on dowels.

Community Development

Mytilopsis sallei. Roots that entered the water between September and November 1987 at three oiled streams (LRRS was excluded because there were initially too few healthy roots to tag) differed from those in unoiled streams. *Mytilopsis* cover on CD roots did not increase over time as in unoiled streams (Fig. 9.123). There were significant effects of oiling and of time (Table 9.18); differences were weaker than for comparisons on LT roots, because of the weak increase of *Mytilopsis* on CD roots at 1 of 4 unoiled streams (MERR). By May 1991 the abundance of false mussels was equal on CD roots and LT roots at sites within oiling categories (e.g., all unoiled), but *Mytilopsis* covered significantly more space on both types of roots in unoiled streams than oiled ones.

Barnacles. *Balanus* was absent from CD roots in the first two monitoring periods; its mean abundance remained <1% cover until November 1989, never exceeded ~2% cover, and dropped below 1% cover from November 1990 through May 1991. There was no significant effect of oiling, but significant differences between years (Table 9.18). Overall abundances were similar between oiled and unoiled sites because of the virtual absence of barnacles from MERR, and because *Balanus* was always rare at the other three unoiled sites. As in long-term census results, there was a strong seasonal pattern, with virtual disappearance of *Balanus* in the late wet season (November).

Foliose Algae. Foliose algae were absent to rare on CD roots at oiled sites for 2 yr after they entered the water (November 1987-August 1989; Fig. 9.129). Algal cover then gradually increased through May 1991 (mean overall abundance of 3% cover in May 1991). Algae on CD roots generally tracked abundances of algae on LT roots at oiled sites. There were significant effects of oiling for yr 1 and 2, but not the last 2 yr (Table 9.18). The increase in cover in oiled streams was indicated by the significant interaction between oiling and year. The mean number of species of foliose algae/root increased with percent cover at all sites, but <1 species/root was recorded on average (Fig. 9.140). Species accumulated slowly on roots, with fewer present on average until the fifth year after oiling (Fig. 9.132).

Blue-green Algae. Blue-green algae were ephemeral at both oiled and unoiled sites (Fig. 9.134). Cover was so low, except for occasional periods of recruitment, that no pattern related to oiling was found.

Sessile Invertebrates. Rare sessile invertebrates first occurred on CD roots in February 1988, and remained rare through November 1988 (Fig. 9.127). From that date they did not differ from abundances on LT roots, except in August 1990. ANOVA comparisons showed no differences in abundances between oiled and unoiled sites (Table 9.18).

Diatoms and Bare Space. Diatoms immediately appeared on CD roots in abundance approximately equal to that on LT roots, as at unoiled sites. Bare space declined rapidly, because roots were quickly coated with oil and diatoms (Figs. 9.29, 9.135).

9.5.3.3 Summary and Discussion

This study documented the existence and long-term persistence of a distinct biological community on submerged *Rhizophora* roots in each of the three habitats examined. Differences appeared at least partly due to varying physical conditions among habitats. Biological interactions were probably also important, but examination of the dynamics of different assemblages was beyond the scope of this project.

In each of the biological communities, effects of oiling were severe and persistent. For each habitat, recovery was incomplete 5 yr after the spill but patterns differed among habitats.

Open Coast – Unoiled Sites

Trees fringing the open Caribbean coastline were exposed to considerable wave action and associated drift logs during dry season, and to long periods of daytime emersion in early rainy season. Prop roots supported a diverse epibiota. Productivity and turnover appeared high. The occurrence of any individual species on a given root was variable and unpredictable, but overall patterns of distribution and abundance for major taxa persisted for 5 yr.

Foliose algae were opportunistic, with most species shifting in distribution and abundance from year to year and site to site. Number of species of foliose algae per root increased with time of submergence, and was correlated with cover of algae on roots. Crustose algae increased in abundance on roots during the study, but fluctuated seasonally, with bleached (damaged or dead) coralline crusts abundant during the aerial exposures typical of early wet season. Both crustose and foliose algae were distributed from the low intertidal to deep on roots. Blue-green algae occurred high on roots and were most abundant in dry season, when water levels and wave action were high.

Sessile invertebrates covered considerable space on roots. Arborescent hydroids and bryozoans were always abundant overall, but var^Ied among dates within sites. Sponge abundance increased over time, but varied among sites. Barnacles and tunicates (mostly colonial styelids) were rare overall, and tunicates differed in abundance among sites. All sessile invertebrates except barnacles were limited to relatively deep (low intertidal and subtidal) portions of roots, probably because of stress associated with intermittent emersion.

Recruitment of different groups reflected their abundances on roots. Of the foliose algae, only mixed algal turf recruited regularly; it also was always abundant on roots. Of the invertebrates, only arborescent hydroids and bryozoans and sponges had major pulses of recruitment.

Diatoms were most abundant at high levels on roots and on the region of active growth, near the tip. They colonized bare surfaces, then were replaced by other taxa over time. Bare space, except near the HWL, was ephemeral; any available surface was rapidly colonized.

The dynamics of root growth affected observed patterns of abundance. Most roots either (1) grew rapidly through the water into the substratum (and out of our sampling universe) or (2) grew slowly once submerged, at least partly because of recurring log damage. Such roots remained suspended in the water column for up to 5 yr. Populations of roots in random samples included both types. Rapidly growing roots were typified by ephemeral or opportunistic species; relatively inactive roots, exposed to larvae and sporelings for years, accumulated an increasing number of species of foliose algae, crustose algae, and large-bodied invertebrates like sponges and colonial tunicates.

Open Coast – Effects of Oiling

Foliose algae on randomly censused roots at oiled sites died after oiling and then gradually increased in abundance to levels equivalent to unoiled sites by May 1991, while percent cover at unoiled sites remained relatively stable. Species richness overall was reduced at oiled sites for 4 yr, but not from August 1990 until May 1991; species number was still reduced at one oiled site in May 1991.

Species composition differed between oiled and unoiled sites throughout the study. Individual species were rarer at oiled than unoiled sites for 4 yr after the spill. There were more "unique" species at unoiled than oiled sites. Algal turfs, the most abundant component of the foliose algal group, remained less abundant at oiled than unoiled sites through May 1991, as did articulated coralline algae. Two sites monitored prior to the spill showed a different assemblage of algae 5 yr after the spill. No prespill data exist for unoiled sites monitored from 1986 to 1991 and sites were located 25 km east of Bahía Las Minas. Therefore, we cannot unequivocally assign these changes in species composition to oiling effects because of possible biogeographic influences (*main sequence 4* of Green 1979; Table 1.3). However, the gradual increase in cover at oiled sites and a slow convergence with values at unoiled sites support the hypotheses that (1) algal assemblages were heavily damaged by oil,

(2) recovery was a prolonged process, and (3) shifts in species composition may have occurred after oiling.

Crustose algae were less abundant at oiled sites through May 1991, but showed a long-term pattern of increase at both oiled and unoiled sites. Sessile invertebrates were significantly less abundant at oiled sites through May 1991, despite a trend of increasing cover. The only exception, an increase in barnacle cover at oiled sites, was correlated with the disappearance of a grazing snail.

Diatoms bloomed on top of layers of oil immediately after the spill. This bloom disappeared within 9 mo, followed by a return to lower average diatom cover.

Recruitment onto dowels placed on the open coast was highly variable over time, but similar between oiled and unoiled areas. Recruitment data showed that competent sporelings of foliose algae existed in both oiled and unoiled areas, and that they could settle and grow rapidly. No other organisms (except diatoms) commonly recruited on either oiled or unoiled open coasts. Sessile invertebrates and crustose algae failed to settle during the 1988 period of reef flat exposures.

Foliose algal abundance on CD roots quickly reached levels similar to those in long-term censuses within treatments (oiled and unoiled). However, percent cover of foliose algae at oiled sites on CD roots did not reach levels found on similarly aged roots at unoiled sites. This suggests reduced persistence or growth (or both) of algae at oiled sites.

Of the species common on the open coast, only *Bostrychia* spp. and blue-green algae were regularly found high on roots. Algae and sessile invertebrates were more abundant on low-intertidal to subtidal levels on roots. Both *Bostrychia* spp. and blue-green algae were reduced in abundance 5 yr after oiling; this was correlated with the continued presence of oil residues high on roots.

Overall, we conclude that damage initially was clear and severe, and that recovery, although well on its way, was incomplete after 5 yr. The extreme aerial exposures of 1988 may have slowed recovery by reducing settlement of some groups or species. In addition, roots at oiled sites probably have been submerged less time than at unoiled sites, because so many roots died after oiling. Because some species accumulate on roots over time, this change in the "age" structure of roots may be part of the explanation for the persistent effects of oiling.

Channels and Lagoons – Unoiled Sites

Trees fringing channels and lagoons were not exposed to wave action from the open sea, and damage by drift logs was rare. Water levels were seasonally highest during dry season, when offshore winds pushed water into the estuary, and lowest in early rainy season, when tides were low and extensive runoff had not begun. Even then, environmental conditions were not as harsh as on open coasts, where light levels were higher and pulses of superheated water from fringing reef flats occasionally reached the mangrove fringe (Cubit et al. 1989). The major environmental stress in channels and lagoons appeared to be salinity fluctuations. Heavy rainfall, especially in late rainy season, resulted in increased runoff and decreased surface salinities, especially around the mouths of streams and near bay heads. Margarita Lagoon, a small area with shallow waters, limited water exchange with the ocean, and a stream at its head, probably was particularly susceptible to extended periods of low salinity. There were consistent biological differences between sites in Bahía Las Minas and in Margarita Lagoon.

Mangrove roots in channels and lagoons were chiefly covered with bivalve molluscs, especially *Crassostrea virginica*, and the barnacle *Balanus improvisus*. An overall decrease in *Crassostrea*'s abundance during the study was largely due to the addition of two sites (from August 1987 on) in Margarita Lagoon, although there were real declines at other sites during August 1987-May 1988. Oyster recruitment was generally low and patchy in time and space. Oysters failed to settle on initially bare roots deep in Margarita Lagoon, and the time it took abundances to equal those on LT roots varied at other sites. The bulk of the *Crassostrea* population was intertidal. Three other bivalves (*Mytilopsis*, *Brachidontes*, and *Isognomon*) were rare or occurred episodically; all occurred deeper on roots than *Crassostrea*.

Balanus cover averaged ~10% throughout the study, despite frequent, major periods of recruitment at most sites. Most occurred in the low intertidal-subtidal sections of roots. Results from salinity-tolerance experiments suggest that extended pulses of freshwater in rainy season kept populations low; we also saw evidence of predation on barnacles (crushed or bitten tests).

Foliose algae averaged ~10% cover overall, and were most abundant at depth in Margarita Lagoon. Algae appeared opportunistic, with frequent pulses of recruitment and quick cover of space on roots; depth distribution varied with species group. A group of rare sessile invertebrates generally covered less than 10% of space on roots and were found predominantly subtidally. Recruitment was low initially, but increased over the last 2 yr of the study. Abundances on roots fluctuated in correlation with recruitment patterns at 3 of 5 sites (HIDC, SBCW, and MACS), suggesting that many species were ephemeral. Diatoms always were found at all sites, with an overall abundance of ~20% cover through the study. They appeared to be seasonal, with decreased cover in May monitorings.

As on open coasts, the epibiotic assemblage in channels was affected by physical conditions and root dynamics. Changing salinities probably accounted for the ephemeral or opportunistic nature of many species or groups. Patterns of root growth also affected results. Most roots entering the water were immediately bored by isopods, causing root growth to stop or decrease. As roots grew new tips, most of these were also bored; only occasionally did a root grow uninterruptedly through the water column. This meant that our random samples contained a disproportionate number of roots that extended only into the intertidal zone, where salinity fluctuations were greatest, and where *Crassostrea* dominated space.

Channels and Lagoons – Effects of Oiling

Any discussion of results from channels and lagoons is complicated by several factors, including variation in the amount of original oiling among sites, differences in physical characteristics among sites (particularly between sites in Margarita Lagoon and Bahía Las Minas), the secondary oiling of one control site (Hidden Channel), and reoiling of oiled sites. Unoiled sites within Bahía Las Minas were located relatively deeply in the western wing of the bay. These sites had lower surface salinity in the late wet season than oiled sites, which were located closer to oceanic waters. Margarita Lagoon was shallow and had even more limited oceanic flushing. Salinity fluctuations were large and the entire lagoon was filled with freshwater during periods of heavy rains. Thus, the geographic position of channels strongly influenced their physical regime.

Crassostrea virginica, the dominant species in 1981-1982, remained more abundant at unoiled than oiled sites within Bahía Las Minas through 1991. However, a decrease in *Crassostrea*'s abundance at unoiled sites throughout the same period also contributed to the convergence between oiled and unoiled sites. It is impossible to say whether the decline of this oyster at unoiled sites in Bahía Las Minas was part of a longer-term, natural cycle or was related to possible effects of dissolved hydrocarbons on settlement or on larvae circulating within Bahía Las Minas. Negative effects of oil coatings on oyster settlement have been documented (e.g., Smith and Hackney 1989).

The addition of two control sites in Margarita Lagoon (in August 1987) greatly influenced an overall decrease in oyster abundance at unoiled areas. These sites showed the sharpest declines in *Crassostrea* cover of all unoiled sites and had little or no oyster cover on recruitment dowels or CD roots through May 1991. The percent cover of oysters in unoiled sections of Bahía Las Minas was significantly higher than that in Margarita Lagoon over the 4 yr both were studied. Examination of two closely matched sites, one oiled and one unoiled, suggested that oil, not salinity differences, had affected oyster cover for at least 5 yr. More physical and biological data, especially growth and mortality rates of marked individuals, are needed before conclusions can be reached regarding recovery of this species from oiling.

In contrast, the barnacle *Balanus improvisus* remained marginally more abundant in unoiled channels than in oiled ones through 1991; recruitment was greater at unoiled sites throughout. This pattern also held at two closely matched sites, oiled LRCW and unoiled LRCS. Populations of rare bivalves (*Mytilopsis*, *Brachidontes*, and *Isognomon*) were all reduced at oiled sites through 1990 (*Isognomon*) or 1991 (*Mytilopsis* and *Brachidontes*).

Other less abundant taxa, including diatoms, foliose algae, and rare sessile invertebrates showed little or no differences in percent cover between oiled and unoiled channels over the 4 yr of study. However, foliose algae shifted in species composition, with "Bostrychietum" species remaining rare after 5 yr. Encrusting bryozoans were still reduced in abundance in May 1991 overall, but not when matched LRCW and LRCS were compared.

In summary, there were clear and persistent reductions related to oiling in channels and lagoons. Differences between unoiled sites (Margarita Lagoon vs. Bahía Las Minas) demonstrated the variability in estuarine populations over time and among sites. Oyster populations were relatively high in Margarita Lagoon in 1987, when it became a study site. It is possible that this was related to low rainfall (and probable reduced salinity stress) in the preceding year. Variation in epibiota among estuaries or among years within estuaries will affect the nature and persistence of the effects of oiling, depending on which species are most abundant when oil comes ashore.

Drainage Streams – Unoiled Sites

Submerged prop roots of mangroves lining the banks of streams were characterized by an assemblage of bivalve molluscs, sponges, hydroids, bryozoans, foliose algae, and diatoms. Space was dominated by a single species, the false mussel Mytilopsis *sallei*. Mussel abundance decreased over time, but much of this decrease was associated with changes in site location, especially the addition of Quebrada Las Mercedes in August 1987. Patterns thus reflected spatial as well as temporal variability.

Recruitment of *Mytilopsis* was variable among sites, and occurred primarily during rainy season. Mussel populations developed slowly on initially bare roots, reaching abundances found on LT roots in 24 to 33 mo at 3 of 4 streams. At Quebrada Las Mercedes recruitment essentially failed, taking 51 mo for cover to become equal on the two groups of roots. False mussels were distributed from ~20 cm below MHW to >1.5 m, but were rare on actively growing root tips.

Balanus was common in 1981-1982 and 1986-1987; cover declined during the 4-yr study. This was partially a result of spatial variation among streams and partially due to reductions in average cover at Hidden River, which was monitored intermittently from 1981 until 1991. Recruitment pulses were frequent, except at Quebrada Las Mercedes, but had a strong seasonal component. Recruitment failed or almost failed in late wet season in all years. Salinity fluctuations appeared to control abundance of barnacles overall.

Two groups of algae occurred in streams. One, the "Bostrychietum," was moderately abundant and found primarily at shallow depths; the other, several fleshy red algae, occurred rarely, and grew deeper on roots. Algae generally recruited at low levels, lowest in late rainy season. Despite this, cover of algae, primarily "Bostrychietum" species, on initially bare roots matched abundances on LT roots within 3 mo. Species ranged from MHW to deep on roots; *Bostrychia* spp. occurred shallowest, forming perennial turfs.

Sponges, arborescent hydroids and bryozoans, anemones, and tunicates were rare in streams, varying widely in time and among sites. These taxa occurred deep on roots. Recruitment was rare for all groups except arborescent hydroids and bryozoans. Initially bare roots were colonized within 6 mo of entering the water, and their abundances matched levels on LT roots from then on. Diatoms were always present and recruited rapidly, with no apparent seasonal pattern.

Physical factors appear to be critically important to the dynamics of the epibiotic assemblage in drainage streams. We suggest that the species covering space on roots in streams consist of the following components:

1. marine to brackish-water species (bivalves other than *Mytilopsis*, barnacles, sponges, tunicates, bryozoans, and hydroids), which fluctuate widely at shallow depths with changes in salinity and emersion, but persist longer deep on roots;
2. algae, which occur ephemerally and are primarily dependent on available light, were most abundant either on roots in light gaps or on roots out from the shaded banks (especially fleshy red algae; S. D. Garrity, pers. obs.);
3. perennial algae, specific to shaded mangrove habitats, especially *Bostrychia* spp.;
4. diatoms, which are ubiquitous, rapidly settle onto bare surfaces, and are probably a mix of marine and freshwater species; and
5. *Mytilopsis*, which recruits variably but tolerates a broad range of salinity and eventually covers most of the space on roots.

Drainage Streams – Effects of Oiling

Oiled drainage streams had more saline surface waters than unoiled streams, and lower flow rates in the wet season. These physical differences affected the probability that a stream was oiled. The Bahía Las Minas oil spill occurred in early wet season during a year of low rainfall. Freshwater runoff, which flows over saltwater intrusion, was low. Small streams, creeks, and drainage cuts with low runoff, coupled with strong tidal influence, were more likely to be oiled because low downstream flow (or even positive upstream tidal currents at the surface) allowed oil in. Large streams, even near the refinery, had downstream flow strong enough to flush oil from around their mouths and escaped damage (Fig. 9.5; e.g., PMRE and PMRW vs. UNR). Had the spill occurred during dry season or full wet season, patterns of damage probably would have been different (Cubit and Levings, Chap. 2).

Oiled drainage streams remained severely affected through May 1991. The normally dominant species, *Mytilopsis*, remained rare on LT roots and did not increase in abundance on oiled CD roots despite several minor periods of recruitment. This contrasted sharply with unoiled sites, where *Mytilopsis* remained the most abundant organism, recruited in most intervals, and increased slowly and steadily on CD roots. Even at Quebrada Las Mercedes, where recruitment was highly episodic, false mussel cover increased over time on CD roots.

Settlement dynamics appeared to have strong effects on populations of *Mytilopsis*. Transplant experiments showed that young false mussels could settle and survive in oiled streams in cages in the presence of living adults, but cover of mussels did not increase at oiled streams (see Sect. 9.5.4 below). We are unsure of what ecological processes are involved. Attraction of larvae to conspecific adults is one possibility for which we have some suggestive experimental support. However, it is also possible that predators were sufficiently effective that small *Mytilopsis* were quickly eaten when they settled in oiled streams by May 1990. Bags of transplanted mussels were sometimes opened by crabs at oiled, but not unoiled, streams. At Quebrada Las Mercedes, where settlement was always low, small crabs settled into most cages (determined by the presence of crabs too large to enter or leave cages), raising the possibility of variation in predation pressure among unoiled streams as well. Population dynamics of this species in terms of recovery from perturbation clearly require more investigation.

The abundance of *Balanus* on LT roots in oiled areas converged with those at unoiled areas by mid-1987 because of decreases in abundance at unoiled sites. Recruitment continued to differ between oiled and unoiled streams through May 1991, with little at oiled sites and high variability at unoiled sites. Recruitment was strongly seasonal, with recruitment failure and population reductions generally in late wet season (November). Thus, abundance of this species appears to be closely related to salinity fluctuations. Because oiled and unoiled streams differed in salinity, abundance of barnacles might also be naturally variable. However, barnacle cover was high at Largo Remo River South in 1982, as it was at Hidden River; these streams differed in salinity over 1988-1991. The relationship between salinity and abundance also raises the intriguing possibility that inter-annual variation in rainfall could shift population structure by changing patterns of runoff into the estuary. *Balanus* cover was high in 1981 and 1986 in Hidden River and lower in 1987-1991; both 1981 and 1986 were El Niño years of reduced rainfall. These issues clearly require further investigation.

Foliose algae differed in abundance at oiled and unoiled sites for 3 yr after the spill. There were strong shifts in species recorded, with persistent damage to the "Bostrychietum" group. Initial damage was probably due to trapping of oil in algal mats (as in *Laurencia* beds on reef flats; Cubit and Connor, Chap. 4). The long-term absence of these species may be due to toxic effects of residual oiling, but another, more conservative, possibility exists. "Bostrychietum" species are adapted to the low light and fluctuating salinity of mangrove forests. Destruction of the mangrove fringe along drainage streams increased average light reaching root level. Thus, as the fringe regrows and the canopy becomes re-established, the "Bostrychietum" group may return when the physical conditions are appropriate (perhaps only to exclude less shade-tolerant species). These possibilities should be separated experimentally.

Diatoms in oiled streams increased in abundance to roughly the same levels as those at unoiled sites starting in 1987. Rare sessile invertebrates were similar in abundance in oiled and unoiled streams a year after oiling, largely because all populations were ephemeral. In drainage streams it was only these taxa that appeared unaffected by oiling 5 yr after the spill.

9.5.4 Studies on *Mytilopsis sallei*

The major species on roots in unoiled drainage streams around Bahía Las Minas was *Mytilopsis sallei.* This species is widespread in the New World tropics and subtropics in streams, and tolerates salinities from freshwater to oceanic (Ramachandra et al. 1975; Morton 1981). *Mytilopsis* had not reappeared in oiled streams 4 yr after the spill. Nearly continuous observations of residual oil leaching into the water from the banks of oiled streams suggested an experiment to determine if *Mytilopsis* could survive in oiled streams. The null hypothesis was that the presence of oil did not affect survival of adult *Mytilopsis.* In that case, settlement failure or other stochastic events caused the observed failure to return to oiled streams. When initial results (see below) showed some settlement in streams, a further series of experiments was added to examine settlement variation in the presence of adults.

9.5.4.1 Materials and Methods

Mytilopsis were collected at HIDR (unoiled) and held in running seawater at the Galeta Marine Laboratory for <2 d before the experiments were begun. Twenty-five *Mytilopsis* ≥15 mm in length were placed in each cage (cages made of 1/8-inch vexar mesh, 20 cm long x 4 cm wide). Fifty *Mytilopsis* of the same size range were shucked and checked for presence or absence of ripe gonad. In May 1990 five cages were placed at each of the four oiled and four unoiled streams. All were attached to submerged portions of prop roots with cable ties at approximately the middle of the range of *Mytilopsis* on roots (Fig. 9.145). Cages were retrieved in August. *Mytilopsis* were removed and sorted into groups of live or dead individuals, and measured to the nearest millimeter. A subset (*N* ~5/cage) of the survivors was checked for gonad condition. Any new (<15 mm) *Mytilopsis* that had settled into cages were separated and measured, as were any other bivalves that had settled onto or into the bags. The experimental procedure was repeated during September-November 1990.

Some settlement of *Mytilopsis* into bags occurred in both oiled and unoiled streams during both periods. We examined the possibility that adult *Mytilopsis* were acting as a settlement attractant by adding treatments to the next replicate of this experiment. At each site, along with the previous treatments, we placed (1) five empty cages and (2) five cages containing 25 empty, cleaned *Mytilopsis* shells (≥15 mm in length). Cages were attached to the bottom ends of wooden dowels; dowels were attached with cable ties to hanging roots in each stream (*N* = 4 oiled, 4 unoiled streams) in groups of four: (1) plain dowel (standard recruitment dowel;

Fig. 9.145 *Mytilopsis* settlement and survival experiments. May 1990, site = PMRE. After ~3 mo of exposure, bags of false mussels were collected for examination in the laboratory. Vexar bags were attached to roots below MLW. See text for details of various experiments.

see Sect. 9.5.3, above), (2) dowel plus empty cage, (3) dowel plus cage with dead *Mytilopsis*, and (4) dowel plus cage with live *Mytilopsis*. Dowels and cages were collected after 3 mo, and the live treatment monitored as before. Empty cages and those containing dead *Mytilopsis* were examined for settlers; those found were measured to the nearest millimeter. The percent cover of epibiota was determined for all dowels as described above. We defer consideration of dowel results.

This experiment tested the null hypothesis that the presence of empty shells or live adults did not affect the settlement of *Mytilopsis* relative to an empty cage. The monitoring of the dowels tested for the effects of presence or absence of *Mytilopsis*, plus the physical effect of having the cage attached to the dowel. Any differences between the empty-cage treatment and the empty-shell treatment could have been due to several processes: (1) attraction of recruits by chemical signals released from shells, (2) increased settlement due to the changes in the physical regime (i.e., changed water flow) caused by the presence of the empty shells, or (3) increased area for settlement provided by empty shells.

In February 1991 we once again replicated the basic survival experiment in all eight streams, but added two treatments in two unoiled streams. To test the null hypothesis that the physical changes caused by the presence of shells did not affect settlement, we placed five replicates of the following treatments at ALER and UNR: (1) 25 empty shells/cage and (2) 10 bowls cut from plastic spoons. Spoons were cut at the base of the handle, scrubbed in detergent, and soaked in running seawater for 24 h before being placed in the field. They took up approximately the same volume of the cage as empty shells. Live *Mytilopsis* were not measured individually in the February-May 1991 replicate. We collected the cages in May 1991 and monitored them as before.

9.5.4.2 Results

Survival of Adult False Mussels in Oiled and Unoiled Streams

To test the null hypothesis that there was no effect of oil on survival, caged groups of *Mytilopsis sallei* were transplanted into oiled and unoiled streams (Fig. 9.145). Experimental transplants were placed in the field for ~3 mo. The experiment was replicated four times between May 1990 and May 1991. We analyzed results using a 2-way ANOVA on percent mortality (arcsine transformed) of *Mytilopsis* in the bags that were recovered.

Mortality was highly variable among dates and streams (Fig. 9.146), exceeding 50% in some unoiled streams in some intervals. However, there was a significant main effect of oiling ($P < .05$; Table 9.19). Neither replicate interval or the interaction between date and oiling was significant. We conclude that (1) at least some *Mytilopsis* could survive 3 mo in oiled streams 5 yr after the spill, (2) mortality was higher in oiled than in unoiled streams, and (3) longer-term survival should be investigated.

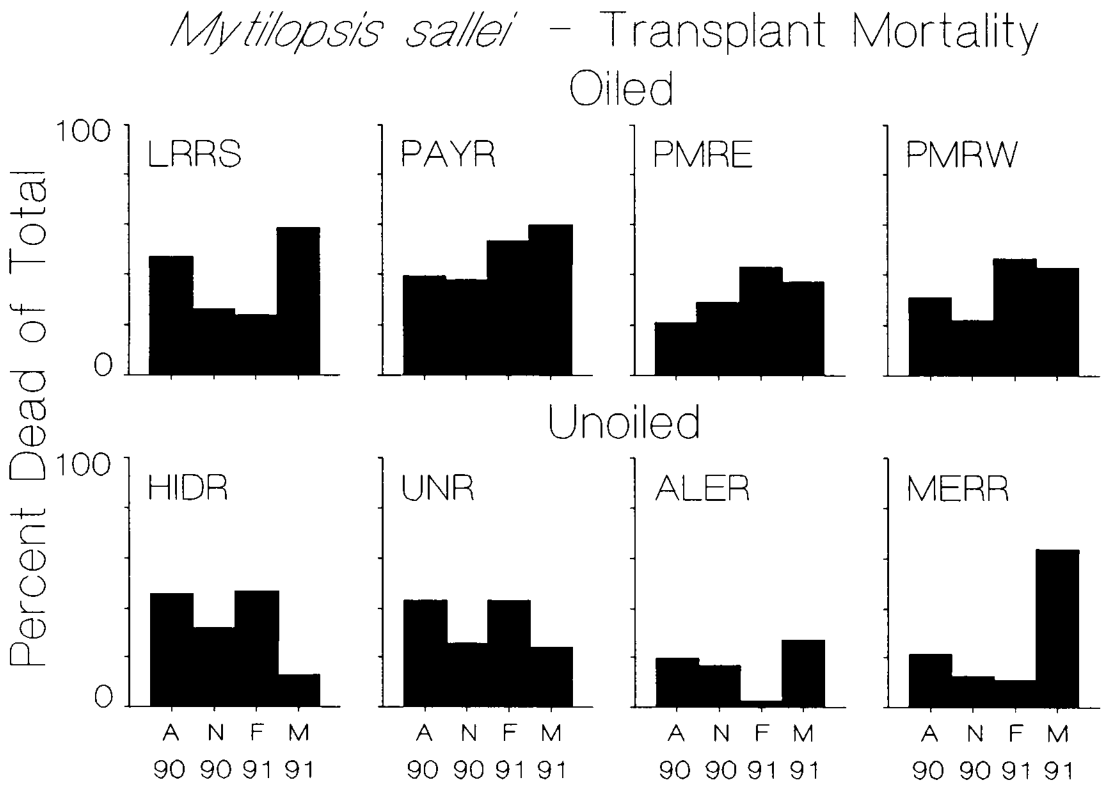

Fig. 9.146 *Mytilopsis* transplant experiments: mortality. Percent dead of total recovered. *A 90* = August 1990, *N 90* = November 1990, *F 91* = February 1991, *M 91* = May 1991. See text for details.

Table 9.19 Analysis of variance table for the *Mytilopsis* transplant experiment. Data were arcsine-transformed percent survival for each replicate; 2-way ANOVA on oiling and date of replicate.

Source	df	SS	*F*	*P*
Oiling	1	0.1283	4.54	.044
Date	3	0.1088	1.28	.302
O x D	3	0.0444	0.52	.670
error	24	0.6778		

Gonad Development

At least some gonad tissue was present in all *Mytilopsis* recovered from transplants to both oiled and unoiled streams. At this crude level, reproduction was possible in both oiled and unoiled streams. The bodies and gonads of animals from oiled streams appeared smaller relative to shell size than those from unoiled streams. This suggests that examination of size-specific body weight or scope-for-growth might be a fruitful way to examine sublethal effects of oiling.

Mytilopsis Settlement in Oiled and Unoiled Streams

The transplant experiment fortuitously provided evidence for settlement variation in oiled and unoiled streams. All *Mytilopsis* transplanted were ≥15 mm long. Surviving individuals attached to the walls of vexar bags and to each other, forming aggregations. After ~3 mo in the field, we sometimes found additional, newly settled mussels among the aggregations or on the walls of bags. In both oiled and unoiled streams, settlement was sometimes so heavy that bags were packed with masses of *Mytilopsis*, and even hidden under aggregations of new *Mytilopsis*. New settlers were separated from the original transplants based on size, counted and measured.

Mytilopsis settled and grew in both oiled and unoiled streams (Fig. 9.147). There was substantial variation in number and size of settlers among streams on any one date. MERR stood out from the other three unoiled streams: recruitment failed or almost failed in 3 of 4 quarters sampled, but was substantial between February and May 1991. There was little correlation in times of heavy recruitment in oiled vs. unoiled streams or within oiling condition. Overall, recruitment (measured as numbers of new individuals in cages) was higher at unoiled than oiled sites (Fig. 9.147).

The number and size structure of new settlers were patchy within, as well as among, streams. Fig. 9.148 shows size-frequency distributions for *Mytilopsis* that settled on two dowels located ~5 m apart in UNR in February 1991. On both dowels a group of settlers <7 mm shell length occurred at the top of the dowel. On dowel 5 there was a second group of settlers, most between 5 and 15 mm in shell length, about half-way down the dowel. Either growth rates of *Mytilopsis* differed between different levels on dowel 5, or an earlier pulse of recruitment missed dowel 4, but reached dowel 5. Such variation among dowels was common.

Results from the transplant experiment suggested two additional hypotheses for lack of repopulation in streams. First, bags contained living *Mytilopsis,* so attraction of settlers to adult conspecifics (gregarious settlement) could have played a role. *Mytilopsis* larvae may be less likely to settle unless conspecifics are present. Second, several bags in oiled streams were ripped open, probably by crabs. These bags were empty or contained a few broken valves when recovered; apparently their contents had been crushed and eaten.

To test the hypothesis of settlement attraction, we performed a multiple transplant experiment at all streams between November 1990 and February 1991. In both oiled and unoiled streams, more settlers were found in bags containing living or dead *Mytilopsis* than in empty bags (Fig. 9.149; Friedman's nonparametric 2-way analysis, $P < .001$ for oiled streams, $P < .001$ for unoiled streams, $N = 17$ complete replicates, each group). These results support the settlement attraction hypothesis.

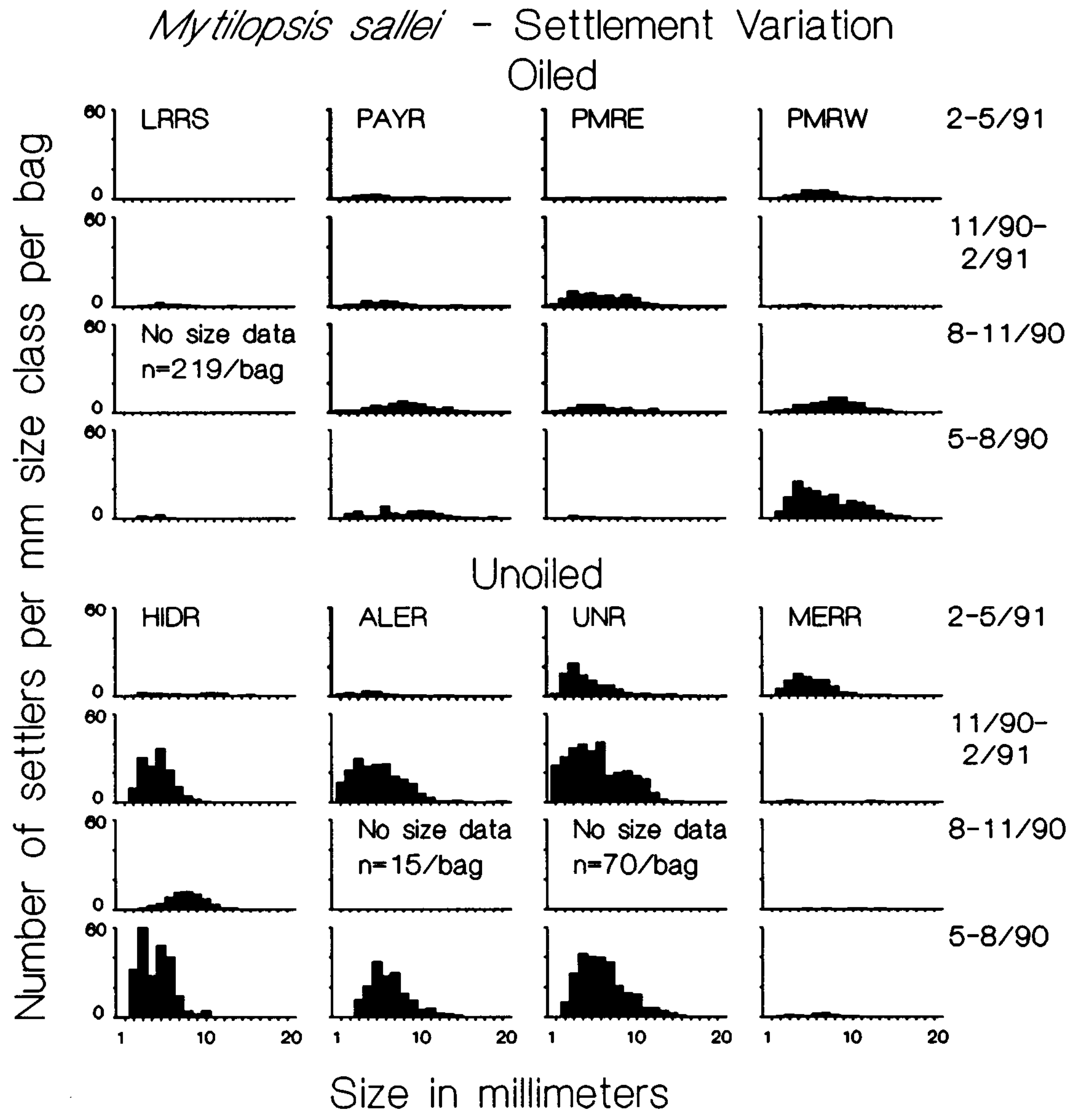

Fig. 9.147 *Mytilopsis* transplant experiments: settlement variation. Size-density distribution of new *Mytilopsis* that entered bags. Dates are intervals that bags were transplanted. For a few dates, false mussels were counted, but not measured. Density/bag is given for these cases. See text for details.

Both live *Mytilopsis* and empty valves might have released cues that attracted metamorphosing larvae. However, they also might have changed flow patterns within bags. Such changes could have increased settlement without invoking any mechanism of attraction. We performed an additional experiment between February and May

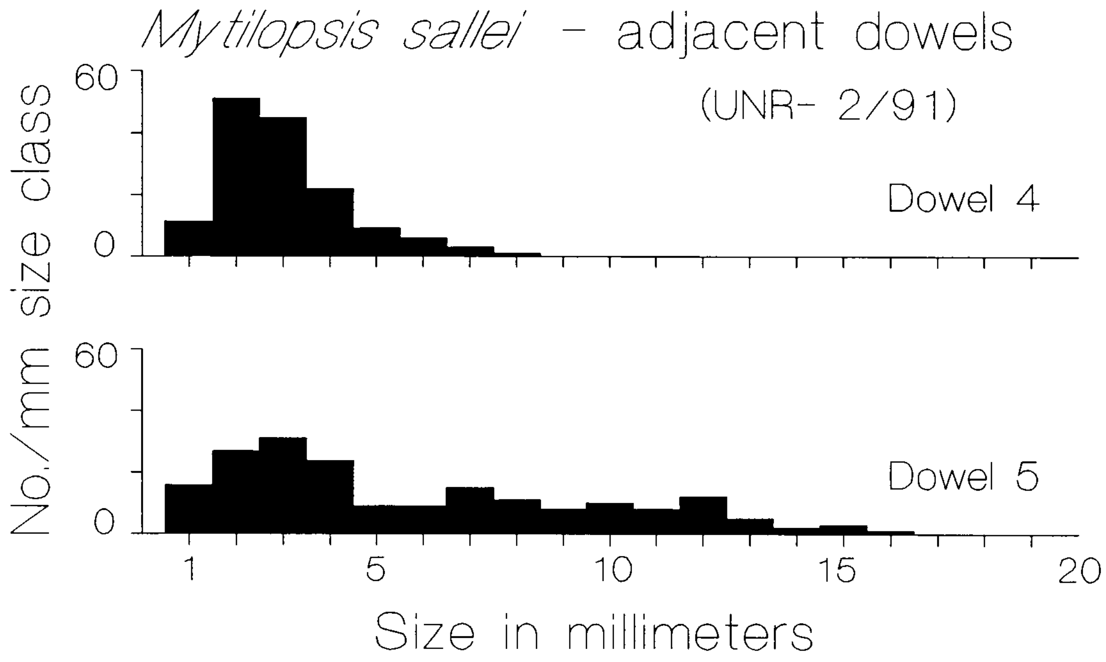

Fig. 9.148 Settlement variation: size structure. Size-frequency distribution from two dowels located ~5 m apart in Unnamed River (UNR), collected in February 1991. See text for details.

1991, using the bowls of plastic spoons as a control for water flow in an additional treatment. Unfortunately, too few complete replicates were recovered to analyze. Settlement attraction remains to be established in *Mytilopsis*.

9.5.4.3 Summary

Mytilopsis sallei did not return to oiled streams for at least 5 yr after the Bahía Las Minas oil spill. Transplant experiments showed that fewer transplanted adults survived in oiled than unoiled streams between May 1990 and May 1991. Since no physical contact with floating oil occurred on roots, these results suggest that acutely toxic effects of dissolved hydrocarbons persisted through at least May 1991 in drainage streams. Gonad tissue was present in *Mytilopsis* recovered from both oiled and unoiled streams, but differences, if any, cannot be quantified with current data.

New settlers entered transplant cages in both oiled and unoiled streams. This suggested that settlement attraction plays a part in population dynamics. This could account for lowered settlement in oiled streams, where adults were absent. We cannot accept or reject the hypothesis of gregarious settlement with current experimental results.

Some bags containing transplanted *Mytilopsis* were ripped open at oiled, but not unoiled, streams and a few broken valves were recovered. Crabs may have

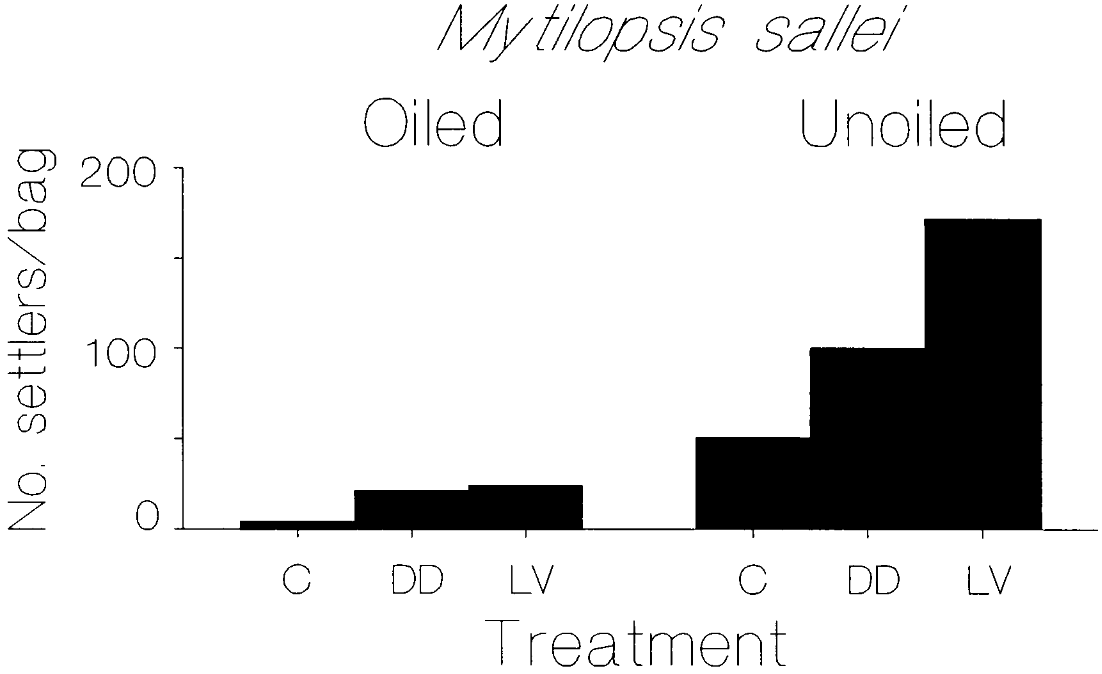

Fig. 9.149 *Mytilopsis* transplant experiments: settlement attraction. Number of settlers/bag for treatments. *C* = empty bag, *DD* = bag containing empty valves from false mussels, *LV* = bags containing live transplants. See text for details.

returned to oiled streams where prey abyndance was low in sufficient numbers to control abundances of recruiting *Mytilopsis.* Crabs were observed at oiled sites in the last 3 yr of the study, and small crabs were found in some mesh bags during these experiments. *Mytilopsis* were so abundant at unoiled sites that crabs probably did not enter or open bags in search of prey.

These observations on settlement dynamics and predation suggest that biological interactions, as well as the toxicity of dissolved hydrocarbons, probably played a strong role in determining the course of repopulation in streams. Further experiments are needed to resolve these issues.

9.5.5 Salinity Tolerances in Estuarine Molluscs and Barnacles

Estuarine animals may be exposed to seasonal or shorter-term changes in salinity that affect their distribution or abundance. Variations in salinity occurred between Margarita Lagoon and Bahía Las Minas, and between sections of Bahía Las Minas located deep in the estuary and closer to the mouth of the bay (see Sect. 9.3). We thus evaluated the potential effects of salinity variation in a series of preliminary experiments on the most abundant bivalves and barnacles in our study sites.

9.5.5.1 Materials and Methods

In February and May 1991 we performed preliminary salinity-tolerance experiments on some bivalve molluscs and a barnacle found in channels and lagoons (*Crassostrea virginica*, *Brachidontes exustus*, *Isognomon alatus*, and *Balanus improvisus*).

Animals were collected in the field and held in running seawater for no more than 2 d before experiments were begun. Individuals of each species were placed in seawater of known salinity; at least two replicates were run at each salinity in each experiment. Control individuals were held at oceanic salinity (~33-35o/oo). All containers were surrounded by running seawater, keeping water temperature the same in all treatments. Animals and salinities were checked daily; water was changed every other day. Experiments continued until all the animals had died or until field work in Panama ended. In February the salinities used were 0, 16, and 33o/oo for *Balanus* and 0, 8, 16, and 33o/oo for *Brachidontes* and *Isognomon*. In May we used salinities of 0, 4, 8.5, 17.5, and 35.5o/oo for *Brachidontes*, *Isognomon*, and *Balanus*. Additionally, *Crassostrea* and *Balanus* were tested at 0, 4, and 17.5o/oo.

9.5.5.2 Results

The four species tested differed in salinity tolerance (Fig. 9.150). *Balanus improvisus* was least tolerant of lowered salinity. All barnacles died within 24-48 h of exposure to salinity of 4o/oo or less, regardless of size (size range = 5-32 mm basal diameter). Survival was >80% in 16o/oo or higher salinity.

Crassostrea virginica was the next most sensitive species to experimentally reduced salinity. After 5 d exposure to 0 or 4o/oo salinity, oysters began to die. Fewer than 7% survived 9 d (when experiments terminated). In contrast, 90% survived 10 d at 17.5o/oo.

Brachidontes was more tolerant of reduced salinity, but expressed a strong behavioral change at salinities <16o/oo. Individuals kept at 8.5o/oo or lower ceased secreting byssal threads, and did not attach to container walls. All those kept at 16o/oo or higher attached within 3 d. Few animals died until after 7 d at reduced salinity (<8.5o/oo), but overall survival was low after 10 d. There was no mortality at salinity >16o/oo.

Isognomon showed no mortality related to lowered salinity over the treatments and length of exposure used in these experiments (10-d maximum, salinity range 0-35.5o/oo). A few animals died after 9 d of exposure to salinity of 0 or 4o/oo, but differences were not significant, and handling effects may have been responsible. Like *Brachidontes*, only animals held at salinity >16o/oo secreted byssal threads and re-attached to containers.

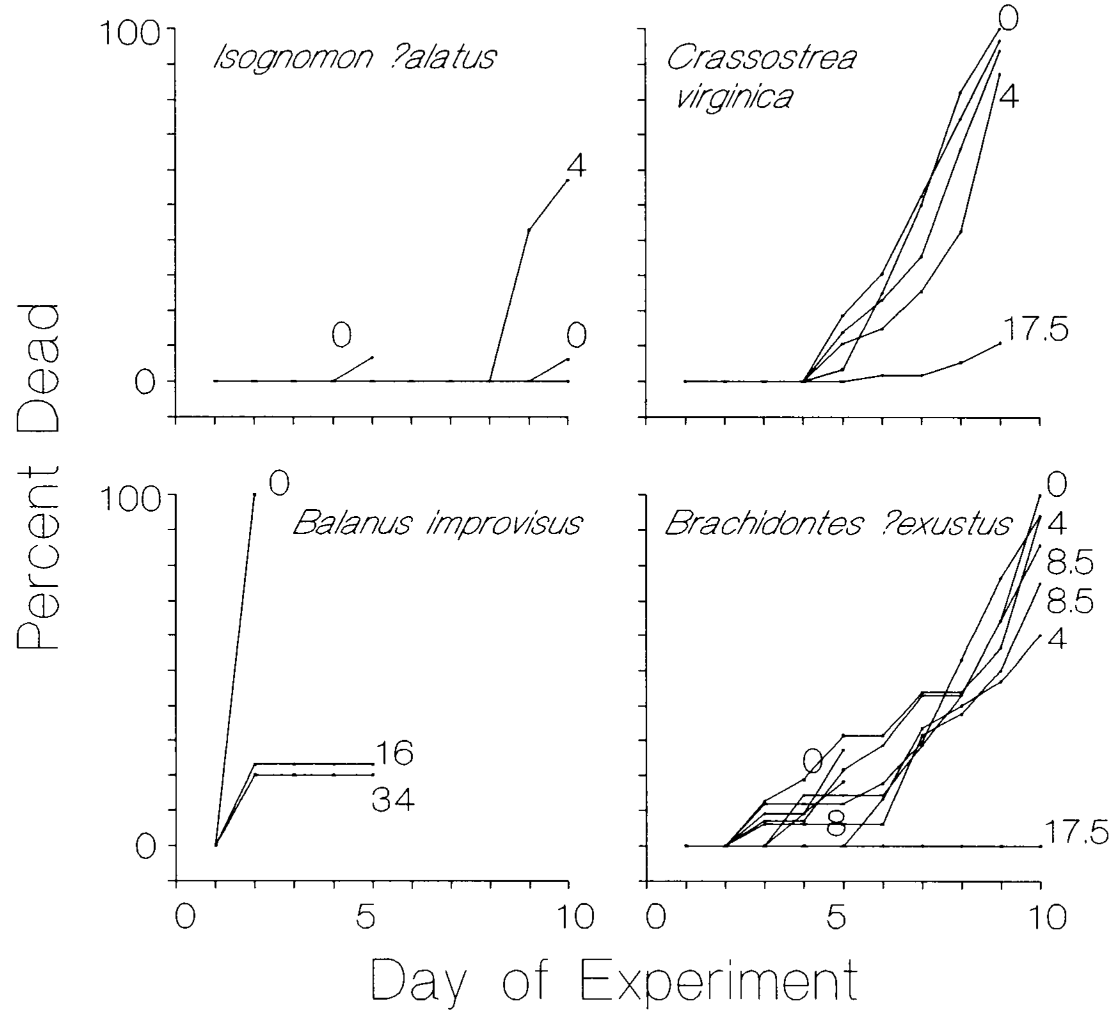

Fig. 9.150 Salinity-tolerance experiments. Percent dead per day for individual salinity- tolerance experiments. Lines are labeled with the salinity (o/oo) for that replicate. For all other experiments survival was 100%. See text for details.

9.5.5.3 Summary

Results for *Balanus* suggest that short-term pulses of low salinity can severely reduce populations. Results are consistent with Poirrier and Partridge (1979), who report replacement of *Balanus improvisus* by a more freshwater-tolerant species in waters of <3o/oo in Louisiana. However, they contrast with other reports that *Balanus improvisus* is able to survive in a wide range of salinities (Foster 1970; Fyhn 1976; Davenport 1976; Cawthorne 1979). They found that ability to adapt to changes in salinity depends on the previous salinity regime and the rate of change of salinity

(Foster 1970; Davenport 1976); further, activity ceases after several days at salinity <3o/oo. Rapid and persistent changes in salinity, like those in our experiments, were not tested. Thus, the control of *Balanus* density by salinity stress appears likely (Foster 1987), but remains an open question pending further experiments and observations.

Our experimental results on *Crassostrea* were consistent with published information, including reports of oyster die offs after periods of heavy rain and reduced salinity in tropical areas (Nikolic et al. 1976; Mattox 1949; Wiedemann 1973; Von Cosel 1973). We conclude that periods of reduced salinity (<4o/oo) lasting more than a week would be expected to have a severe negative effect on oyster populations. Results and conclusions were consistent with field observations and data from several unoield sites where heavy oyster mortality followed major freshwater influxes (e.g., Margarita Lagoon sites and SBCW).

Brachidontes can survive reduced salinity longer than either *Crassostrea* or *Balanus*, but periods of low salinity lasting a week or more could reduce populations. *Isognomon* can withstand relatively long periods of low salinity (at least 10 d), but requires higher salinities for normal behavior (see also Siung 1980).

No experiments were performed on *Mytilopsis sallei* because this species (and a congener) have been extensively tested (Castagna and Chanley 1973; Ramachandra et al. 1975; Deaton et al. 1989). False mussels can survive and reproduce in salinity ranging from 0 to 50o/oo. The major limit to their occurrence appears to be a requirement for fluctuating salinity to initiate spawning (Morton 1981; see also Morton 1983). Throughout our study, *Mytilopsis* was found in streams and channels at salinities ranging from oceanic to freshwater (see Sect. 9.5.3).

Each species, except *Mytilopsis*, was potentially negatively affected by rapid changes in salinity. Prolonged (>10 d) drops to salinity <4o/oo would probably reduce populations of all species. Changes in salinity gradients within Bahía Las Minas and variation in salinity among years (e.g., years with El Niño decreases in rainfall) may cause shifts in populations. This possibility remains to be explored, but should be considered in further studies of these species.

9.6 Discussion

9.6.1 Value of Bahía Las Minas Study Relative to Other Work

Despite the past frequency and high probability of future spills in nearshore, tropical waters (Keller et al., Chap. 1), very little work has been done on the effects of oiling on shoreline communities at low latitudes (NRC 1985). There is general agreement on the biological and economic value of mangrove forests, and on the vulnerability of mangroves and their biota to oiling (Odum and Johannes 1975; Gundlach and Hayes 1978; Cairns and Buikema 1984; Linden and Jernelov 1980; Cintrón et al. 1981; Saenger et al. 1983; Teas 1983; Getter et al. 1984; Vandermeulen and Gilfillan 1984; Hatcher et al. 1989; NRC 1985; Jacobi and Schaffer-Novelli 1990). However, the actual effects of oil on mangroves and associated species are little understood at present (Gundlach and Hayes 1978; Lewis 1983; NRC 1985). Current theories of oil effect and recovery in nearshore environments are primarily based on relatively few, postspill investigations. Of necessity, most such studies have been one-time surveys (Baker et al. 1980), following "spills of opportunity" (NRC 1985). They thus lack baseline, prespill data, and seldom have long-term, postspill monitoring (Baker et al. 1980).

A handful of field studies concerning accidental oiling of mangroves and associated flora and fauna are cited repeatedly in the literature, often with little regard to the limitations of the original data (e.g., Lopez 1978; Table 1 in Baker et al. 1980; Table 1 in Getter et al. 1981; Table 1 in Lewis 1983; Table 3.1 in Getter et al. 1984; Table S-12 in NRC 1985; Table 15.1 in Marshall et al. 1990). For example, there are two primary sources regarding the *Witwater* spill of December 1968 off Punta Galeta, Panama. In the first, Rützler and Sterrer (1970) present no data in their commentary of observed, immediate effects (oiling of roots and sediment and near elimination of the prop-root epibiota). They conclude that "this fragmentary survey taught us the importance of immediate research on the effects of oil pollution in the sea" (p. 224, Rützler and Sterrer 1970). In the second (Birkeland et al. 1976), A. Reimer sampled species abundances in "the mangrove community" (aerial roots, coral rubble, and algal mat from the bottom) in ten 0.25-m^2 random quadrats over a 9-mo period. These scant data were then compared with anecdotal references to oiled and unoiled mangrove root communities from Rützler and Sterrer (1970). Major conclusions were (1) the fauna of *Crassostrea*, *Brachidontes*, sponges, tunicates, and bryozoans had not returned to the area after 33 mo, but (2) "unfortunately, this conclusion is invalidated by the lack of quantitative data before the spill and other possible causal factors" (p. 45, Birkeland et al. 1976). The longer-term effect of "loss visible 66 mo after the spill," cited in NRC (1985), Getter et al. (1981), Lewis (1983), and Marshall et al. (1990), was based on a note added in press (June 1974) ("66 mo after the *Witwater* spill, the state of the epibiotic communities on the mangrove roots still appears to remain in the same condition," p. 45, Birkeland et al. 1976). In short, (1) sampling methods in the two studies of the *Witwater* spill were inadequate, and (2) the authors recognized that inherent flaws invalidated any conclusions. Yet, of the secondary papers listed above, only Baker et al. (1980) offered any caution concerning the effects of this spill ("long term effects not detailed," Table 1 in Baker et al. 1980).

Most field work on other, often-cited spills and their effects on mangroves is equally anecdotal, unquantified, or based upon inadequate sampling methods. Nevertheless, theories of damage, recovery, or restoration of mangroves have been based upon these studies (e.g., Getter et al. 1984; Lewis 1983; Lopez 1978; Getter 1981) or on data of even more questionable value (e.g., Getter et al. 1984). Even the best studies using experimental (controlled) spills have been unreplicated (Ballou et al. 1989) or have used unrealistically low amounts of oil (McGuinness 1990).

The Bahía Las Minas oil spill study was similar to others in that it followed an unplanned event. However, several critical differences enabled us to make the present study more quantitative and thorough than previous work. Although not without faults, the study should be of considerable value to those concerned with fate and effects of tropical, nearshore oil spills, and to workers involved in contingency planning, recovery processes, and mitigation theory.

First, due to the proximity of STRI's Galeta Marine Laboratory, prespill data on the epibiota of mangrove roots existed. Although not extensive, these data documented the basic patterns of abundance of major space occupants on roots in several different, fringing mangrove habitats, and thus served as a baseline for postspill work. Second, studies of the effects of the spill on fringing mangrove roots and their inhabitants were initiated quickly, while oil was still coming ashore. Third, during the short-term segment of the overall study (August 1986-May 1987), sites monitored prior to the spill, or sites adjacent to them, were used when possible, in order to maximize the comparative value of prespill survey data. Fourth, a long-term examination of the effects of this spill was possible. Basic methods remained similar to prespill and short-term work, but the study was expanded in scope and designed for quantitative statistical analyses. This segment eventually consisted of an unbroken set of 16 quarterly monitorings, from August 1987 through May 1991; to our knowledge, the most quantitative data set taken on a tropical oil spill to date.

An important part of the study was our examination of potentially confounding effects, and how they might affect the strength of our conclusions. Sites were selected to be as similar in fringe structure as possible, but no information was available in advance on variation in physical factors, or how such variation might affect the epibiota. Accurate evaluation of the effects of oiling would have been impossible without the data we collected on the physical regime of each site.

On the open coast there were relatively small physical differences between oiled and unoiled sites, despite their considerable separation in space. Rainfall was higher at unoiled than oiled sites, but did not result in salinity differences. This allowed us to statistically compare all oiled to all unoiled sites. The strong effects of oiling identified were unlikely to have been influenced by physical differences.

In channels the surface waters of unoiled sites were less saline than oiled sites during periods of heavy rainfall (August and November). This reflected the more limited opening to the sea of Margarita Lagoon and the west wing of Bahía Las Minas relative to the central and eastern wings (where all but one oiled sites were located). In particular, sites in Margarita Lagoon were less salty than those in Bahía Las Minas. However, oiled and unoiled sites were comparable in that (1) sites that were oiled and those that escaped oiling had similar epibiotic cover before the spill, (2) observations of dead bivalves and barnacles at oiled sites immediately after the spill showed that these animals had been present before the spill, (3) the most physically similar oiled and unoiled sites (LRCS vs. LRCW) showed differences like those between all oiled and all unoiled sites, and (4) epibiotic cover in oiled channels was returning or had returned to abundance levels similar to those at unoiled sites by the end of the study. Thus, although laboratory tests, observations, and, particularly, the reduced abundances of oysters in Margarita Lagoon suggested the importance of occasional, rapid salinity changes, most of the differences we identified between oiled and unoiled sites were caused by oiling, rather than physical factors.

It is also important to note that if Margarita Lagoon rather than Bahía Las Minas had been oiled, we could have mistakenly attributed persistent differences between lagoons to oiling effects, when salinity stress was actually the main cause of these differences. This demonstrates the importance of testing alternative hypotheses before attributing effects to one of a set of possible hypotheses, in this case oiling.

In drainage streams oiled sites were more influenced by surface tidal flow of higher salinity than unoiled streams, which were typified by a stronger, downstream flow of freshwater. These differences affected oil deposition during the spill and thus controlled our subsequent choice of sites. Smaller, tidal streams were heavily oiled along much or all of their lengths, while oil did not penetrate past the mouths of larger streams. Differences in salinity regimes appeared less important to recovery processes than in channels, perhaps because of the wide salinity tolerance of the dominant organism, *Mytilopsis sallei*. Additionally, in prespill sampling a large stream (HIDR) and a small, tidal creek (LRRS, subsequently oiled) had similar epibiota before the spill. This, and the presence of live and dead bivalves and barnacles at oiled sites immediately after the spill, suggest strong similarity between epibiota of large and small streams, despite considerable environmental differences. Perhaps episodic low-salinity events in the smaller streams prevent more oceanic species from out-competing *Mytilopsis*.

Unlike the recovery observed in oiled channels over time, little repopulation, especially of *Mytilopsis*, occurred in oiled streams for 5 yr after the spill. The most conservative comparison of data and observations is from LRRS, a small creek that was monitored in 1981-1982 and subsequently as an oiled site. At this site (and all other oiled sites, not monitored before the spill) strong and persistent effects of oiling were still reducing populations 5 yr postspill. The dynamics of recovery in this habitat appeared strongly affected both by continued oiling and by biological interactions. Despite occasional recruitment at oiled sites, populations of false mussels did not increase or converge over time with those in unoiled streams.

Hydrocarbon data and observations of oil in slicks and sediments in oiled streams suggest a direct, continued effect of dissolved hydrocarbons. Transplant experiments demonstrated overall reduced survival of *Mytilopsis* in oiled streams through May 1991. Indirect effects of oiling may also have played a role. Experiments run during the last year of the study showed that *Mytilopsis* could settle and survive, in the presence of adult *Mytilopsis*, in oiled as well as unoiled streams (Sect. 9.5.5). Larvae could apparently survive existing levels of hydrocarbons, but may have needed adult mussels present, perhaps for settlement cues. Predation by crabs on newly settled mussels appeared greater in oiled than unoiled streams. Whether this represented increased predator density or decreased resource availability, it may have accounted for at least some of the lack of false mussel recovery. Alternatively, newly settled *Mytilopsis* may not survive over time due to dissolved and suspended hydrocarbon concentrations in oiled streams. Depression of growth rates or eventual toxicity from pulses of oil released from sediments appear likely.

In summary, environmental differences existed between oiled and unoiled sites in two of the three fringing mangrove habitats examined. If such differences had not been identified, they would have been unknown, confounding factors affecting our assessment of damage to the epibiota by oiling. However, (1) the existence of prespill data and observations from channels and streams, (2) the convergence of oiled and unoiled sites over time in channels, (3) comparison of closely matched sites in channels, and (4) experimental results strongly suggest that the effects of oiling that we identified were real and persisted at least 5 yr after the spill.

9.6.2 Applicability of Results

The long-term value of this study rests in its usefulness to those dealing with actual and potential damages from oil spills in nearshore waters, for example, in contingency planning, impact analysis, and design of possible mitigation strategies. It is therefore important to ask if the fringing mangrove habitat studied in Panama is representative of those throughout the Caribbean and along Florida's southern tip. Can results of the present study be generalized, and the lessons learned be extended to the fringes of mangrove forests throughout the region, or worldwide?

There are few comprehensive descriptions or long-term data sets concerning epibiota of mangrove roots. There is, however, a large, scattered literature for individual species or groups. Evidence ranges from comprehensive reviews (e.g., Florida: Odum et al. 1982), experimental manipulations (e.g., Belize: Ellison and Farnsworth 1990; Florida: Bingham and Young 1991*a*, *b*), algal collections (e.g., Belize: Norris and Bucher 1982), and studies of individual species (e.g., Cuba: Nikolic et al. 1976).

The epibiotic bivalves and barnacles that we describe from Panama have also been reported from throughout the Caribbean (e.g., Mattox 1949; Bacon 1971; Kolehmainen 1972; Von Cosel 1973; Wilcox et al. 1975; Martinez and Almeida 1976; Nikolic et al. 1976; Perez and Victoria 1980; Siung 1980; Sutherland 1980; Odum et al. 1982). Scattered reports from Africa, Asia, and the eastern Pacific (e.g., Stephenson et al. 1958; Sandison and Hill 1966; Hunter 1969; Sasekumar 1974; Berry 1975; Frith et al. 1976; Por et al. 1977; Pinto and Wignarajah 1980; Perry 1988; Budiman 1988; Rainbow et al. 1989; partial reviews in Lawson 1966; Morton 1983) indicate that bivalves and barnacles are often abundant components of the epibiota of mangrove roots in protected waters over a wide geographic range. Recent synonymy of *Crassostrea rhizophorae* with *Crassostrea virginica* (Harry 1985) extends our results to intertidal oyster beds in temperate regions, because this economically important species is distributed from Brazil to eastern Canada (Harry 1985).

Foliose algae have been collected from mangrove roots around the world, especially because of interest in the "Bostrychietum" group of species (Post 1963). Algae have been reported on roots throughout the Caribbean (e.g., Norris and Bucher 1982; Almodovar 1964; Burkholder and Almodovar 1974; Kolehmainen and Hildner 1975; Taylor et al. 1986; Rodriguez and Stoner 1990; Littler et al. 1989). Algae growing on mangrove roots have been studied throughout the Old World tropics (e.g., Davey and Woelkerling 1980; King and Wheeler 1985; Lambert et al. 1987; Chihara and Tanaka 1988; Basson et al. 1989). Many species have wide geographic distributions, and similar algae occur worldwide on mangrove roots, notably species of the "Bostrychietum" group.

Any nearshore oil spill off the tip of Florida is likely to strand upon fringing *Rhizophora* and associated epibiota. There is no comprehensive survey of the epibiotic assemblage from south Florida, but the little information available indicates that there are some strong similarities to Bahía Las Minas (e.g., Odum and Heald 1972; Odum et al. 1982; Courtney 1975; Mook 1976, 1980, 1981, 1983; Bingham 1990; Bingham and Young 1991*a*, *b*; S. D. Garrity and S. C. Levings, unpublished).

In summary, the assemblages of epibiotic organisms studied in Panama appear to be typical of the Caribbean, and extend into the mangroves of South Florida. Similar assemblages of plants and animals appear to occur worldwide. Oil spills into tropical estuaries thus will probably affect communities similar to those examined in this study, but the details of the effects will differ depending upon the dynamics of the local community.

9.6.3 Immediate Effects of Oiling – August 1986-May 1987

In patches where oil came ashore heavily, successive deposition of oil coated roots with layers of tar up to 1 cm thick. Oil had immediate effects on many organisms in all three habitats. Within 3 to 9 mo after the spill, the most common species or taxa were less abundant in oiled than unoiled areas (*Crassostrea* in channels, foliose algae on the open coast) or had virtually disappeared (*Mytilopsis* in oiled streams). Foliose algae, which rotted quickly, left little evidence of direct mortality 3 mo after the spill. However, we found dead *Mytilopsis* (still byssally attached to roots) and dead *Crassostrea* (ventral valves still cemented to roots) in August 1986. This is direct evidence of mortality caused by oiling.

Within 6 mo the direct evidence of mortality caused by oiling was gone (Garrity and Levings 1992). At this time the epibiota had been killed, but the mangrove fringe was still intact. Mangrove trees and prop roots died beginning approximately 3-6 mo after oiling. By March 1987, when root condition was first monitored, more roots were dead at oiled than unoiled sites (App. Table E.4). Nine mo after the spill, structural changes to the fringe had begun.

After the initial stage of the spill and for species that did not leave traces after death, comparisons between oiled and unoiled sites were required to document the effects of oiling. Many less-common species also showed relative decreases in abundances correlated with oiling soon after the event. On the open coast these included crustose algae, sponges, arborescent hydroids and bryozoans, and other sessile invertebrates. In channels they included *Balanus*, *Mytilopsis*, and other sessile invertebrates. In oiled streams they included diatoms, foliose algae, and *Balanus*.

A few species or taxa showed no early, postoiling differences in abundance between oiled and unoiled areas. These included barnacles on the open coast, diatoms in channels, and sessile invertebrates (other than barnacles and bivalves) in streams. Of these, barnacles and sessile invertebrates were rare (<5% cover), while diatoms averaged ≤20% cover. One taxon, diatoms, bloomed ephemerally on the oiled open coast from 3 to 6 mo after the spill.

The die-offs we observed cannot be confidently related solely to either the chemical or mechanical effects of oiling. Virtually the entire root surface in all habitats was coated with oil in August 1986; few plants and animals escaped direct contact with oil in the initial stages of the spill. For this large spill, oil and its associated effects were not restricted to small portions of root surfaces or a limited vertical distribution. This virtually complete coating of roots was a result of oil coming ashore during early wet season exposures (Cubit et al. 1986, 1988*a*, 1989; Cubit and Levings, Chap. 2). Direct contact of oil and epibiota would have been less during dry season because water levels are higher and tidal amplitude less.

The mechanical (smothering) effects of thick coats of oil may have been sufficient to account for observed effects on the epibiota (and appears to account best for patterns of mangrove die off). This type of damage has been observed for a nontoxic spill on Fanning Island (Russell and Carlson 1978). However, the continued presence of potentially toxic hydrocarbons in organisms and sediments for at least 5 yr suggests that toxic effects of oiling were possible and that sublethal effects were likely over the long term (Burns, Chap. 3).

9.6.4 Long-term Oil Effects and Recovery, August 1987-May 1991

Effects of the 1986 Bahía Las Minas oil spill were clear and severe at the level of populations of epibiota on roots (see Sect. 9.5.3, *Summary and Discussion*). Most species or groups were reduced in abundance after oiling, whether on sampled roots or dowels, and (1) rates of recovery varied among groups and habitats and (2) recovery of the fringing mangrove root epibiota was not complete in any habitat after 5 yr.

Processes that affected recovery differed among habitats. On the open coast settlement patterns were similar between oiled and unoiled sites. Persistent differences were thus caused by postsettlement processes. In channels settlement was (1) not significantly different (*Crassostrea*, rare bivalves, and diatoms), (2) was greater at oiled than unoiled sites (foliose algae), or (3) was less at oiled than unoiled sites (barnacles). This suggests that both pre- and postsettlement processes caused persistent long-term effects of oiling. In general, postsettlement effects appeared more important for bivalves, which covered the most space on roots at unoiled sites. In drainage streams differences in settlement (1) did not occur (foliose algae), (2) disappeared by 5 yr after oiling (sessile invertebrates), or, most commonly, (3) persisted through the end of the study (*Mytilopsis*, rare bivalves, barnacles, and diatoms). Lowered adult survival was demonstrated for *Mytilopsis*, suggesting that postsettlement mortality was probably also important in drainage streams.

In all habitats percent cover on roots in the CD cohort converged on the pattern of percent cover shown by randomly censused roots in the same habitat. Thus, percent cover on CD roots in oiled channels came to resemble that of LT roots in oiled channels, *not* that of cover on LT roots in unoiled channels. Negative effects of the spill were thus found on roots that entered the water 15-18 mo after the spill. These prolonged effects could have been due to the toxicity of dissolved hydrocarbons or to complex indirect effects of oiling on tree health, larval settlement, activity of predators, or other unidentified factors.

Aside from effects on the epibiota, estimation of total effect is dependent upon information on the mangrove fringe itself (see Sect. 9.5.2, *Summary and Discussion*). The presence of a mangrove root epibiota depends upon the presence of prop roots growing through the water column; this in turn depends upon the continued presence of *Rhizophora* along the outer fringe. We factored out these variables in the main body of the study (since the same number of roots was randomly sampled at oiled and unoiled sites) in order to focus on direct effects on epibiotic species. However, data on (1) root length, abundance, and provisioning and (2) fringe survival showed severe and continued effects upon the structure of the system itself, which exacerbated negative effects of oiling on the epibiota.

Fringe survival 5 yr after the spill was poor at oiled sites. Much of the oiled stream, channel, and open coast mangrove fringe defoliated within 9 mo, died, and eventually collapsed. The abundance of submerged, unattached prop roots was less at oiled than unoiled sites for all three habitats in 1991, indicating a further reduction in the area available for settlement of epibiota. There was no difference in the abundance of roots about to enter the water along surviving fringe in 1991 between oiled and unoiled sites, suggesting either that surviving *Rhizophora* at oiled sites are now as healthy as those at unoiled sites or that damage to roots at oiled sites occurs after they enter the water.

Reductions in root length have two main effects. First, there is less total submerged area available for epibiotic settlement and production. Second, there is less space deep on roots. The depth distribution of substrata is of particular importance because physical tolerances limit many species found on roots. Many of the taxa recorded on roots are primarily subtidal species; reduction of area deep on roots would disproportionately reduce the average potential habitat for these species. Examples include many foliose algae, sponges, tunicates, cnidarians, and some barnacles.

It is important to note that this was not a "worst case" scenario for damage from a major oil spill. There was not a catastrophic loss of all epibiota from the region. Oiling was patchy within Bahía Las Minas, leaving some areas virtually untouched (e.g., deep in the west wing). Even where oiling was heavy, some sections of the fringe survived to provide settlement surfaces. This combination of factors left some surviving organisms in all habitats to serve as sources for larvae and spores. Despite the fact that damage was not as severe as it might have been, effects were clearly measurable 5 yr after the spill.

Reduction in the amount of shoreline fringed by mangroves, in combination with slow recovery of epibiotic cover on remaining roots and possible reduced productivity from toxic effects of residual oil, reinforces the extent and persistence of the 1986 Bahía Las Minas oil spill. The large, long-term effect of this spill on the mangrove fringe has probably had cascading negative effects on other species dependent upon it for food and habitat (Cubit and Vâsquez, unpublished). Our results put added emphasis on the need to prevent oiling of highly productive, shallow-water habitats in tropical oceans.

9.6.5 Some Suggestions for Prevention of Damage to the Mangrove Fringe from Oil Spills

- The outer fringe of mangrove forests should be of particular concern in any scenario involving oil spill protection and recovery for several reasons. First, the prop roots of the mangrove fringe support a more diverse and productive epibiota than mangroves in inner forests. This epibiota provides shelter, food, and nursery areas for myriad mobile marine organisms, many of commercial value. Second, the outer mangrove fringe acts as a physical barrier to drift logs in wave-exposed habitats. Such logs were a significant cause of mortality for propagules and young trees that were planted or naturally recruited into oil-devastated mangroves behind the fringe in Panama. Third, the intertwined matrix of prop roots and associated epibiota has been shown to significantly reduce current flow through mangrove clumps. The reduction of water movement associated with their survival following an oil spill should thus reduce erosion from inner, intertidal areas, reducing stress on this and other nearshore environments (e.g., seagrass beds and coral reefs).

- Fringing mangroves may occur in many different physical environments. In Panama, fringing mangroves along wave-exposed open coasts, channels and lagoons, and streams and tidal creeks each had unique structural, physical, and biological characteristics. These affected both vulnerability to and ability to recover form the oil spill. A clear, prior understanding of the characteristics of fringing mangroves appears vital for decisions on how best to react to any spill.

- Sheltered shores were slowest to recover and had highest levels of residual oiling. Routine protection of inner bays and estuaries where mangroves grow is strongly suggested following an oil spill. First, if resources are limited, protection of tidal creeks will probably prevent the greatest amount of long-term damage. It will also probably lessen the amount of oil deposited in sediments that could later serve as reservoirs for secondary releases of oil. Larger streams appear less vulnerable because of their stronger outward flow, and may require less protection. Second, for channels and lagoons, focused, full protection of discrete, closely spaced sections of fringing mangroves (rather than an atempt to protect the entire shoreline that is unlikely to succeed) is recommended in a worst-case spill. In Panama, clumps of fringing mangroves survived in all sites. These survivors preserved at least some hard-substratum environment (roots) and associated epibiota, and may have served as reservoirs of larvae for settlement as recovery proceeded and new roots entered the water.

- Complete evaluation of damage to the epibiota required ~6 mo, while the fringe continued to deteriorate for ~3 yr. Short-term evaluation of damage from oiling will probably not be sufficient for other major spills. Where trees defoliated first, more of the fringe later died. This may be of possible use in predicting the eventual amount of damage without complete long-term studies.

- The amount of damage to the mangrove fringe was dependent on water levels and flow rates when oil came ashore. The direct contact of oil with epibiota or prop roots would be expected to vary between rainy and dry seasons in Panama. Seasonal or annual variation in water level, stream flow, wave action, or other factors must be part of contingency plans for spill response; different habitats will be oiled depending upon exact hydrological and meteorological conditions.

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10

Effects of the 1986 Bahía Las Minas, Panama, Oil Spill on Plants and Animals in Seagrass Communities

Michael J. Marshall, Victoria Batista, and Digna Matías

10.1 Abstract

Subtidal seagrass beds on the Caribbean coast of Panama were oiled by the 1986 Bahía Las Minas spill. The concentration of oil was as high as 4,020 ppm in surface sediments 5 mo after the spill, and was still as much as 665 ppm after 2 yr in both surface and subsurface sediments.

Thalassia testudinum, the most abundant plant, initially showed signs of blade damage (browning) in some oiled areas, but recovered from this sublethal effect. In contrast to the recovery of *Thalassia* within beds, shoreward margins died off in a band 20-90 cm wide 2-3 yr after the spill; an even wider strip of shallow *Thalassia* died earlier in some areas. The biomass of *Syringodium filiforme*, the second-most-abundant seagrass, was lower at oiled sites than at unoiled sites during the second and third years postspill. This seagrass was more sensitive to the spill than *Thalassia*, which did not have a prolonged reduction in standing crop. Biomass of fleshy algae did not differ significantly between oiled and unoiled sites. Calcareous algal biomass was an order of magnitude less at oiled sites than at unoiled sites during the first survey 7 mo after the spill, but this difference did not persist.

Densities of fauna from sediment cores (in this report *infauna* = infauna + small, sedentary epifauna) were reduced by a factor of approximately three at oiled sites compared to unoiled sites; densities of epifauna from push-net samples were reduced by a factor of one-and-a-half.

The design of this element of the study was to compare faunal abundances at oiled and unoiled sites that had no comparable presill data. In such a design, the best evidence of a detrimental effect of the spill is an initial lower density at oiled sites, followed by increasing numbers at oiled sites and, eventually, similar densities at oiled and unoiled sites. This pattern held for total infauna (except polychaetes, which were not counted) and several infaunal taxa (amphipods, tanaids, sipunculids, and ophiuroids), but not for total epifauna, which increased at unoiled sites 18-24 mo postspill to densities not matched at oiled sites. Among epifauna, only fish densities increased through time at oiled sites and eventually matched those at unoiled sites. Several abundant epifaunal taxa (shrimp, tanaids, amphipods, gastropods, and ophiuroids) were more numerous at unoiled than at oiled sites because of peaks or increases in density. Two epifaunal taxa (isopods and brachyurans) were similar in abundance at oiled and unoiled sites; mysids and hermit crabs were more numerous at oiled sites. One of the easiest groups to monitor, epifaunal echinoderms, appeared

strongly affected by the spill; a total of 2,407 individuals was collected at unoiled sites, compared to only 97 at oiled sites during 3 yr of postspill monitoring. Large sea urchins and holothurians were still more abundant at unoiled sites 6 yr after the spill.

Because subtidal seagrasses died only along shoreward margins of oiled beds, vegetative cover remained intact, although reduced in area, and oiled beds contained most of the characteristic plants and animals. In addition to reduced numbers of animals at oiled sites, relative abundance of taxa was altered by the spill. The two most abundant infaunal taxa (excluding polychaetes) at unoiled sites were amphipods and tanaids; gastropods and hermit crabs dominated at oiled sites. Caridean and penaeid shrimp dominated the epifauna at both oiled and unoiled sites, with tanaids the second-most-abundant taxon at unoiled sites and hermit crabs at oiled sites. The rank abundance of less abundant taxa also differed. Taxa that repopulated slowly did so either because they were sensitive to weathered oil and petroleum compounds that remained in sediments, or certain modes of reproduction prevented rapid re-establishment of populations.

10.2 Introduction

10.2.1 Physical Structure

Seagrass beds along the central Caribbean coast of Panama are usually found in shallow lagoons between small patch or fringing reefs and mangrove forests. The largest seagrass beds (1-2 ha) are located on the seaward edges of coastal bays. Numerous such beds in this size range and those located behind fringing reefs occur between the Atlantic entrance to the Panama Canal and Bahía Las Minas (Fig. 10.1). A large oil spill, which oiled all the lagoonal seagrass beds in this area to varying degrees, occurred at Bahía Las Minas during April 1986 (Jackson et al. 1989; Keller et al., Chap. 1).

Seagrass beds on the Caribbean side of central Panama are located along a geographically complex coastline that is broken up by bays at river mouths and by numerous small islands within bays. This geographical complexity, which protected some seagrass beds from heavy oiling, has resulted in the development of seagrass beds under varied combinations of exposure to wind-driven waves, tidal currents, freshwater from rivers and land runoff, and numerous other physical factors.

10.2.2 Ecological Role and Biota

The general ecological role of seagrass beds has been documented by numerous authors (e.g., Kikuchi and Peres 1977; Zieman 1982). Seagrass beds stabilize sediments and act as sediment traps, provide substrata for many species of epiphytes and epifauna, provide food as both green blades and detritus for many invertebrate and fish species, and are important nursery grounds for many species of

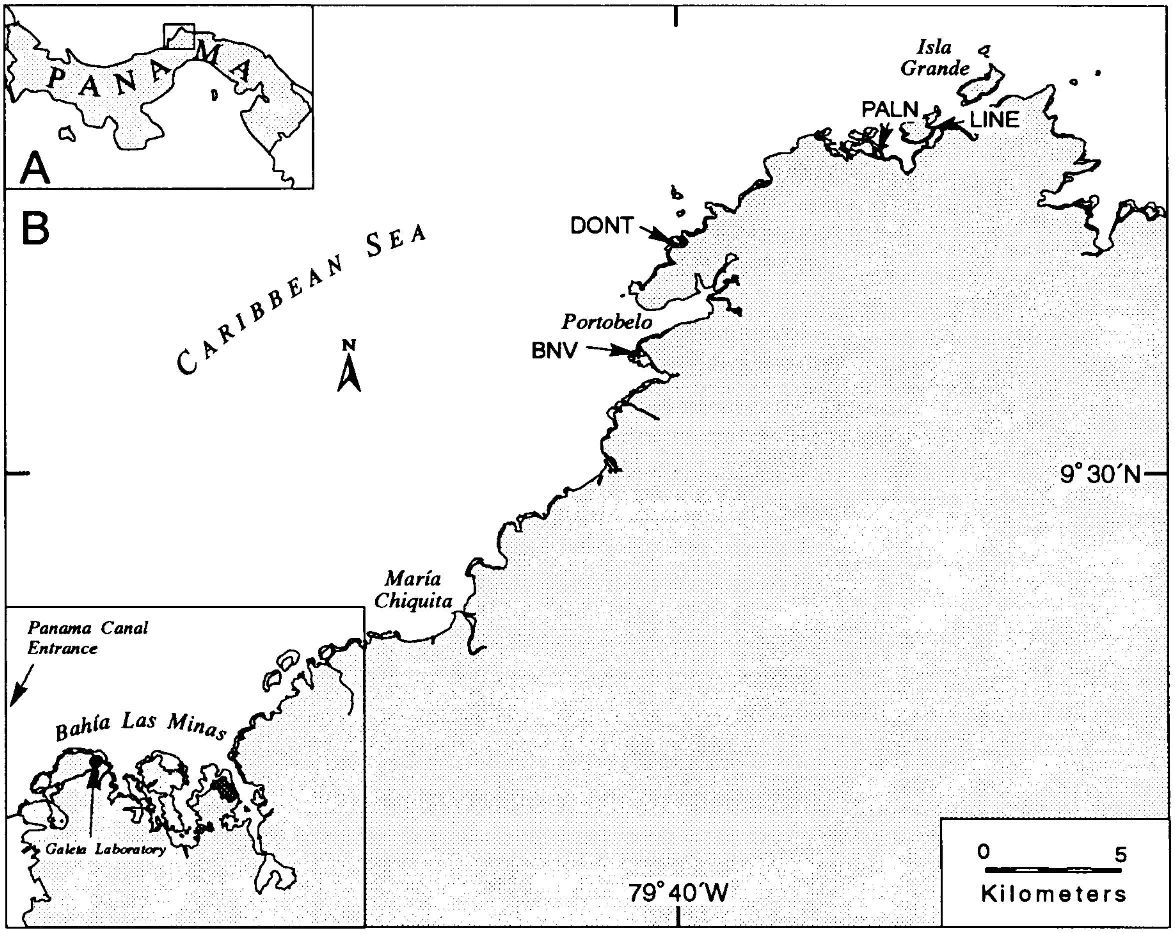

Fig. 10.1 Map of the study area and research sites. *A*. Location of the area on the Caribbean coast of Panama. *B*. Location of unoiled sites near Portobelo (*BNV* and *DONT*) and Isla Grande (*PALN* and *LINE*). The boxed area (*lower left*) includes the site of the 1986 oil spill.

fish and crustaceans. Thus damage or loss of seagrass beds may have ecological effects that extend well beyond their immediate area.

In this study the primary habitat-structuring seagrass was *Thalassia testudinum*; *Syringodium filiforme* was common but contributed one to two orders of magnitude less biomass than *Thalassia*. Associated macroalgae included calcified greens (*Halimeda* spp., including *H. opuntia*, *H. monile*, and *H. incrassata*; *Udotea* spp.; and *Penicillus* spp., including *P. capitatus* and *P. pyriformis*) and reds (*Amphiroa* spp., including *A. fragilissima*, and *Jania* spp.). Fleshy macroalgae included browns (*Sargassum* spp. and *Dictyota* spp., including *D. bartayresii*), greens (*Caulerpa sertularioides*), and reds (*Ceramium* spp.; *Hypnea* spp., including *H. cervicornis* and *H. musciformis*; *Gracilaria* spp., including *G. mammillaris*; and *Laurencia papillosa*).

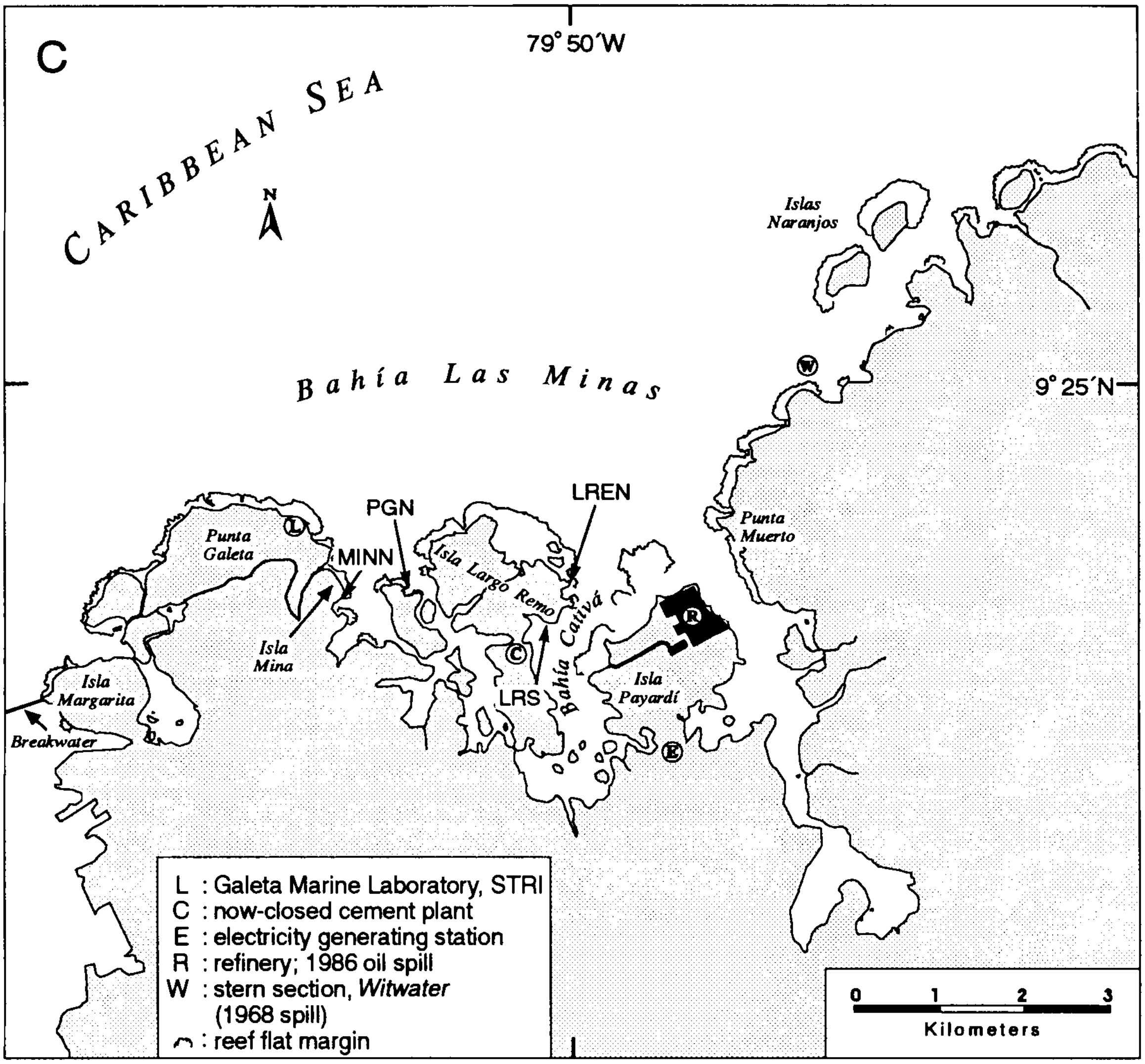

Fig. 10.1 Map of the study area and research sites (continued). *C.* Location of the refinery (*R*) and oiled sites in Bahía Las Minas (*MINN*, *PGN*, *LREN*, and *LRS*).

Polychaetes were the numerically dominant "infaunal" (infauna and sedentary epifauna collected in sediment cores) taxon, and were represented by at least 27 families, such as orbiniids, spionids, cirratulids, nereids, eunicids, arabellids, terebellids, and sabellids (Marshall 1991). Also abundant in sediment-core samples were various crustaceans (amphipods, tanaids, isopods, shrimp, brachyurans, anomurans, and ostracods), gastropod and bivalve molluscs, sipunculids, ophiuroids, and cumaceans. Numerically dominant taxa in epifaunal (push net) samples included crustaceans (shrimp, tanaids, amphipods, brachyurans, anomurans, isopods, and ostracods), gastropods, ophiuroids, and fish (see also Marshall 1991; Heck 1977; Weinstein and Heck 1979). Holothurians and echinoids were common or present, and undoubtedly contributed much of the epifaunal biomass because of their large size. Holothurians may play an important role in reworking sediments (e.g., Hammond 1982) and echinoids can be important grazers of *Thalassia* (e.g., Keller 1983).

10.2.3 Literature Review

Beds of seagrasses and associated animal communities in Panama (described in Heck 1977; Weinstein and Heck 1979; Marshall et al. 1990; Marshall 1991) and other areas are susceptible to many types of human perturbations (Thayer et al. 1975; Jacobs 1980; Phillips 1980; Zieman et al. 1986; Williams 1988). The response of seagrass communities to oiling depends on the elevation of beds in the littoral zone (Zieman et al. 1986; Marshall et al. 1990). Local climatic and oceanographic conditions at the time of exposure to oil, oil type, and other factors may also be important. Sediment texture, degree of exposure to waves and currents, tidal flushing, timing of recruitment of affected species, suspended sediment loads, initial seagrass density, and other factors may all have a further role in determining the severity of initial effects on oiled seagrass beds and rates of recovery processes after exposure to oil.

Many seagrass beds throughout the world have been contaminated with oil from tanker wrecks and intentional discharges from tankers (Table 10.1). Despite an omnipresent threat of oil spills to seagrass beds and concern about consequences of their destruction (e.g., Thayer et al. 1975; Shepherd et al. 1989), little is known about the potential for recovery of seagrass communities from oiling (Zieman et al. 1986; Thorhaug and Marcus 1987).

Following a spill of heavy crude oil in Puerto Rico, *Thalassia* beds reportedly "degenerated" quickly after heavy surf caused much oil to mix with sand and sink (Diaz-Piferrer 1962). A later spill of Venezuelan crude near Cabo Rojas, Puerto Rico, killed many invertebrates (Table 10.1) and caused *Thalassia* blades to brown and be shed. The root and rhizome mat of seagrasses in this area were exposed due to postspill erosion, but the plants were not killed; they produced new blades from exposed rhizomes (Nadeau and Bergquist 1977). In the earlier Puerto Rican spill effects on fauna were not monitored; effects on infauna after the later spill were not detectable.

The most completely studied spill affecting seagrasses, the *Amoco Cadiz* spill on the coast of France, oiled *Zostera* beds (den Hartog and Jacobs 1980; Jacobs 1980). Panamanian seagrass beds and French *Zostera marina* beds contain many groups in common at higher taxonomic levels, and initial effects of the spills on common groups, such as amphipods, tanaids, and ophiuroids were similar in the two regions (see den Hartog and Jacobs 1980; Jacobs 1980; Marshall 1991). The studies in France continued for 1 yr after the spill and were based on prespill studies at the oiled seagrass beds approximately 1 yr before the *Amoco Cadiz* spill. Several major

Table 10.1 Oil spills affecting seagrass beds.

Spill	Amount Spilled	Reported Effects	References
1968, *Witwater*, Bahía Las Minas, Panama	3.18 million L diesel oil and Bunker C	None	Rützler and Sterrer (1970), Birkeland et al. (1976)
1972, *Argea Prima*, Puerto Rico	10.68 million L crude oil	*Thalassia* beds degenerated	Diaz-Piferrer (1962)
1973, *Zoe Colocotronis*, Cabo Rojo, Puerto	5.34 million L Venezuelan crude	Some *Thalassia* died; some later regrowth; some epifauna killed; infauna not affected	Nadeau and Bergquist (1977)
1975, *Garbis*, Florida Keys	0.24-0.48 million L crude clingage and water emulsion	*Thalassia* not damaged; many pearl oysters (*Pinctada radiata*) killed	Chan (1976)
1978, *Amoco Cadiz*, France	236 million L light Middle East crude	*Zostera marina* damaged but not killed; amphipod diversity and numbers reduced; number of tanaids, cumaceans, and echinoderms reduced	den Hartog and Jacobs (1980), Jacobs (1980)
1986, Refinería Panamá, Bahía Las Minas, Panama	>9.6-16.0 million L medium-weight crude	Intertidal *Thalassia* killed and eroded; shoreward margins killed subtidally; effects on infauna and epifauna	Cubit et al. (1987), Jackson et al. (1989), Marshall (1991), this report

groups virtually disappeared after the spill, but quickly recovered. However, 26 species of amphipods disappeared from oiled *Zostera* beds, and after 1 yr only one species had returned.

10.3 Objectives, Rationale, and Design

10.3.1 Overview

The Bahía Las Minas refinery spill in Panama presented an opportunity to observe the amount of damage done by oiling to two seagrass species, numerous algal species, and fauna associated with tropical seagrass beds. Long-term monitoring also allowed us to observe taxon-specific resilience to oiling under various environmental conditions. Comparisons between effects of the *Amoco Cadiz* spill and the Panama spill are instructive for the shared faunal groups, but there are many plant and animal taxa in tropical seagrass beds that are not present in temperate *Zostera* beds.

Few prespill data were available (see Heck 1977; Heck and Wetstone 1977; Weinstein and Heck 1979; Vasquez Montoya 1983). Therefore, it was necessary to employ a sampling design corresponding to *main sequence 4* of Green (1979; Table 1.3), in which effects of the spill must be inferred from spatial patterns, i.e., differences between oiled and unoiled sites (Keller et al., Chap. 1).

Starting in September 1986, 5 mo after the spill, 12-16 seagrass beds were surveyed. Of these, four oiled and four unoiled sites were selected for long-term monitoring. Sampling included measurements of seagrass biomass, biomass of associated macroalgae, counts of infauna and epifauna from sediment cores, and counts of epifaunal groups that were caught with a manually operated push net.

A hypothesis of no difference between temporal variation in the density (or biomass) of taxon X in oiled and unoiled seagrass beds was tested by repeated-measures ANOVA (BMDP Program 5V) on $\ln(x + 1)$-transformed data. Data were transformed because of correlations between means and variances (Cochran's procedure; Winer 1962). The values tested were means of nested-replicate samples collected at the four oiled and four unoiled sites at each sampling. ANOVAs on infaunal collections included only January 1987, 1988, and 1989 data to satisfy the requirement of equal-time intervals in repeated-measures analyses.

10.3.2 Confounding Effects

Unoiled sites had to be located approximately 20 to 40 km from the spill site because the coast between Bahía Las Minas and Portobelo (Fig. 10.1) lacked suitable seagrass beds. All oiled sites were within 6 km of the refinery. Such spatial separation can result in confounding of naturally occurring spatial differences between oiled and unoiled areas with differences caused by the spill. Two lines of evidence indicate that such spatial differences were not great in this study. First, convergence through time in abundance at oiled and unoiled sites is consistent with a model of initial similarity, decline at oiled sites through death or emigration, and then repopulation by juvenile recruitment, immigration, or both. This pattern was observed for seagrass biomass and some infaunal and epifaunal taxa. Second, the available prespill data on epifaunal invertebrates (Heck 1977) show that the five most abundant taxa were the same in 1974-1975, 11-12 yr before the spill, at an area that became oiled and at unoiled sites after the spill. Therefore, confounding of differences in abundance due to area and oiling appears not to have been great for the most abundant epifaunal invertebrate taxa.

The use of major taxa instead of species as taxonomic units for most organisms possibly strengthened the design of this study. Warwick (1988) demonstrated that enumeration of collections to major taxa in pollution studies provided the same level of information as did species counts. The faunal groups to which most collections were sorted in this study are characteristic of tropical seagrass beds. However, species composition of major taxa may be highly variable at adjacent sites (Virnstein and Howard 1987*a*, *b*).

10.3.3 Study Sites

Seagrass beds from Isla Margarita, near the Atlantic entrance of the Panama Canal, to Isla Lintón (near Isla Grande) were chosen as study sites (Fig. 10.1). Criteria used in selecting sites were that each seagrass bed was adjacent to mangroves and was subtidal. All sites were located behind small fringing reefs. Bottom profiles were produced for each site at 1-m intervals along three transects extending from the shore to the seaward edge of each seagrass bed. Bottom type and living cover were noted in each interval of the transects. Depths were adjusted to high-tide marks (tar and oil stains in the oiled area) on mangrove trees at each site. Physical parameters, including depth, salinity, and water temperature, were measured at each site.

Depth profiles show bottom features, including bed widths, at each site (Fig. 10.2). Most of the seagrass beds were separated from the shoreline by a narrow band of sand or muddy sand. The beds studied terminated in deeper-water zones of coral rubble, rock, or sand/mud flats. The seagrass beds varied in width; the narrowest bed was at Largo Remo South (LRS) and the widest was at Palina Norte (PALN). Differences in width were due to variable bottom slopes and lagoon dimensions.

Samples of surface sediments were collected at each site for granulometric analysis. Each sample consisted of five surface scrapes. Sediments were processed by wet-sieving through a Wentworth series of brass-mesh sieves. Organic content was determined by combustion. Data from the most completely analyzed set of sediment samples are summarized in Table 10.2. Sediments were more coarse (lower ϕ) at unoiled than at oiled sites. Silt-clay fractions differed between oiling categories, but sediment organics were similar.

10.4 Oiling and Reoiling

Sediments collected from seagrass beds were analyzed as described in Burns (Chap. 3; Table 10.3).

Ultraviolet fluorescence (UVF) and gas chromatography/ mass spectrometry (GC/MS) analyses of a set of samples collected 18-20 cm below the sediment surface

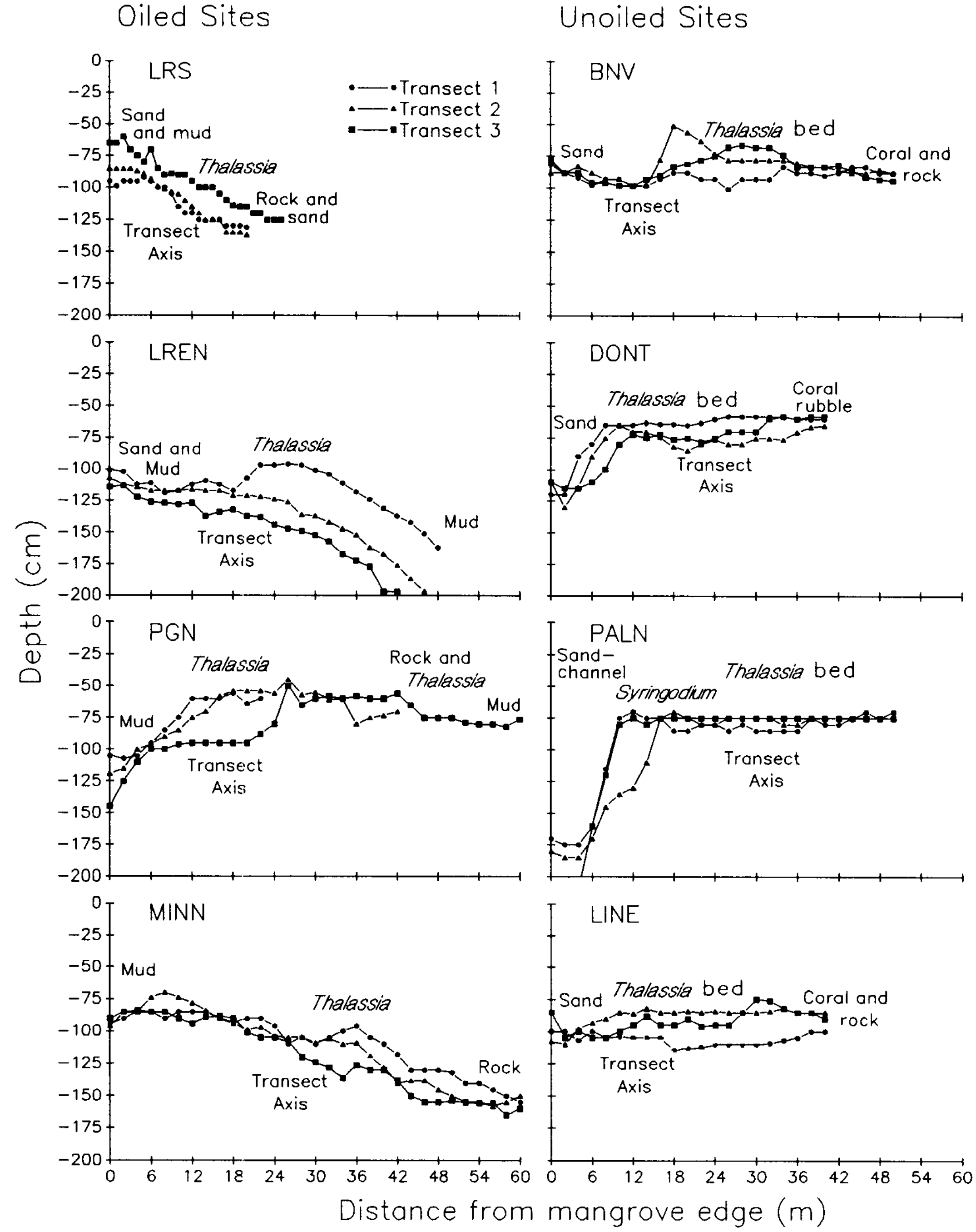

Fig. 10.2 Depth profiles of all oiled and unoiled study sites. Depths were standardized to the high water mark on adjacent mangrove trees.

Table 10.2 Site descriptions of the seagrass beds studied. All beds were <1 m deep.

Site Name/ Coordinates	Site Acronym	Oiling Status	Distance to Refinery (km)	Coastal Orientation	Sediment Characteristics				
					Mean(ϕ)	%silt-clay	%org.	°C	o/oo
Buenaventura/ 9°32’58"N, 79°40’85"W	BNV	unoiled	22.5	N	0.59	11.25	5.58	28.1	33.7
Doncella Thalassia/ 9°34’80"N, 79°40’20"W	DONT	unoiled	27.0	N	0.78	11.23	5.25	28.1	33.7
Palina North/ 9°36’78"N, 79°35’83"W	PALN	unoiled	37.1	NE	0.15	6.60	3.94	28.1	34.1
Lintón East/ 9°37’20"N, 79°34’83"W	LINE	unoiled	39.0	E	0.08	4.87	4.17	28.1	34.1
Largo Remo South/ 9°23’59"N, 79°50’28"W	LRS	heavily oiled	1.5	S	1.23	3.84	5.37	28.7	32.6
Largo Remo Entrance/ 9°23’72"N, 79°50’05"W	LREN	heavily oiled	1.5	NE	1.61	8.11	5.24	28.7	32.6
Peña Guapa North/ 9°23’73"N, 79°50’95"W	PGN	heavily oiled	3.8	N	1.24	5.86	5.20	28.7	32.6
Mina North/ 9°23’72"N, 79°50’05"W	MINN	heavily oiled	5.3	NE	1.85	8.86	5.96	28.7	32.6

Table 10.3 Hydrocarbons in seagrass sediments determined by ultraviolet flourescence (UVF) and by gas chromatography (GC-URE). Units are µg/g dry weight (see Burns, Chap. 3). Site categories (heavily oiled, moderately oiled and unoiled) are based on oiling levels based on knowledge of the spill path and on oil observed at each site.

	1986		1987		1988	
Station	UVF	GC-URE	UVF	GC-URE	UVF	GC-URE
A. Surface sediments						
Unoiled beds						
DONT	0	0	6	0	0	0
PALN	0	0	1	0	0	0
LINE			102	14	4	0
BNV					6	0
Moderately oiled bed						
NARC	596	82			98	7
Heavily oiled beds						
LREN	4,020	2,021	6,683	203	658	60
LRS	792	111	1,198	137	501	51
MINS/N	1,499	151	957	75	607	52
PGN			211	19	188	11
B. Surface and subsurface (1988 only) sediments						
Heavily oiled bed						
LREN						
0-2cm	4,020	2,021	6,683	203	391	19
8-10cm					665	64
18-20cm					553	39

demonstrated that, unlike *Zostera marina* beds in France, root and rhizome mats of seagrasses in Panama did not prevent oil penetration into deep sediment layers. Oil concentrations were higher 8-10 and 18-20 cm below the sediment surface than at the sediment-water interface (0-2 cm). UVF analysis of surface sediments showed that oil concentrations in some areas (especially LREN) were very high in 1987. In 1988 surface-sediment oil concentrations had decreased by an order of magnitude, but were still 188-658 µg/g.

Chronic reoiling probably occurred through releases of oil from crushed-rock landfill beneath the refinery and from mangrove sediments. All of the oiled seagrass beds in this study were either immediately adjacent or very close to heavily oiled mangrove forests. The potential for continued reoiling is discussed in Duke and Pinzón (Chap. 8) and Garrity and Levings (Chap. 9).

10.5 Components of Research

10.5.1 Plant Biomass

10.5.1.1 Methods and Materials

Samples of seagrasses, algae, and benthic fauna were collected at wadeable depths, initially with a PVC coring tube (10.16 cm inside diameter) and later with a slightly larger, thin-walled aluminum pipe (11.0 cm inside diameter). Biomass measurements and counts were standardized to the area of the larger aluminum pipe. Each sample consisted of three pooled cores. All cores in pooled samples were taken within a 0.5 m radius of randomly selected points. Eight such pooled samples, each covering an area of 285 cm^2, were collected quarterly at eight seagrass beds (four oiled and four unoiled). Samples were collected at 12 sites in September 1986 and at 16 sites in November 1986; only data from the eight sites monitored long-term (September 1986-January 1989 [July 1989 for plant measurements]) are presented here.

Sample locations within each seagrass bed were haphazardly selected during the first two collections. After November 1986 a grid system was used to locate cores. Permanent corner markers were placed at each site and a set of grid positions based on measurements from the corner posts was randomly selected at each sampling.

Algae were divided into calcareous and fleshy categories; seagrasses were separated by species beginning with the January 1987 collection. Seagrass materials were then fractioned. Blades were cut at sheath edges (if still attached to shoots) to separate above- and below-ground plant tissues. Before seagrass tissues were dried, attached macroalgae were removed and combined with the algal fractions. All plant materials were weighed after drying at 90°C for 5 d.

10.5.1.2 Results

Total, subsurface, and blade biomass of seagrasses (*Thalassia* and *Syringodium* combined) initially were lower at oiled and than at unoiled sites (Fig. 10.3). This difference disappeared by November 1986 as biomass increased at oiled sites and decreased (except blades) at unoiled sites. After November 1986 seagrass biomass at both oiled and unoiled sites decreased steadily through July 1989, 3 yr after the spill. Repeated-measures ANOVAs (App. Table F.1) had significant oiling x time interactions for total seagrass, subsurface, and blade biomass, and for *Syringodium* subsurface biomass (Fig. 10.4), showing that differences between oiled and unoiled sites depended on collection date.

Fluctuations in *Syringodium*- and *Thalassia*-blade biomass were different at oiled and unoiled sites. *Syringodium*-blade biomass slowly decreased at oiled sites, and fluctuated around a higher mean value at unoiled sites. In contrast, *Thalassia*-blade biomass followed similar patterns at oiled and unoiled sites; blade biomass

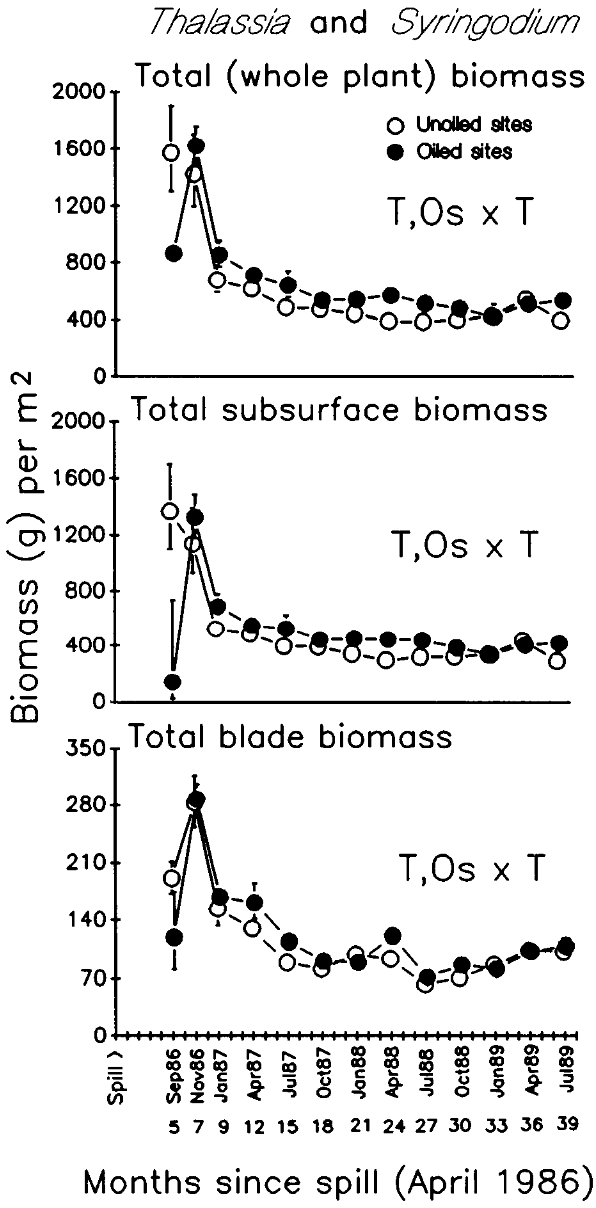

Fig. 10.3 Total, total subsurface, and total blade biomass of *Thalassia testudinum* and *Syringodium filiforme* combined. Data are from core samples; standard-error bars were back-transformed from $\ln(x+1)$. Results of repeated-measures ANOVAs are: *Os* = significant difference ($P < .05$) between oiled and unoiled sites, *T* = significant difference through time, *Os x T* = significant interaction between oiling and time, and *all NS* = no significant differences. Refer to Appendix Table G.1.

decreased 9-18 mo postspill, fluctuated for approximately 9 mo, and then increased 27-39 mo postspill.

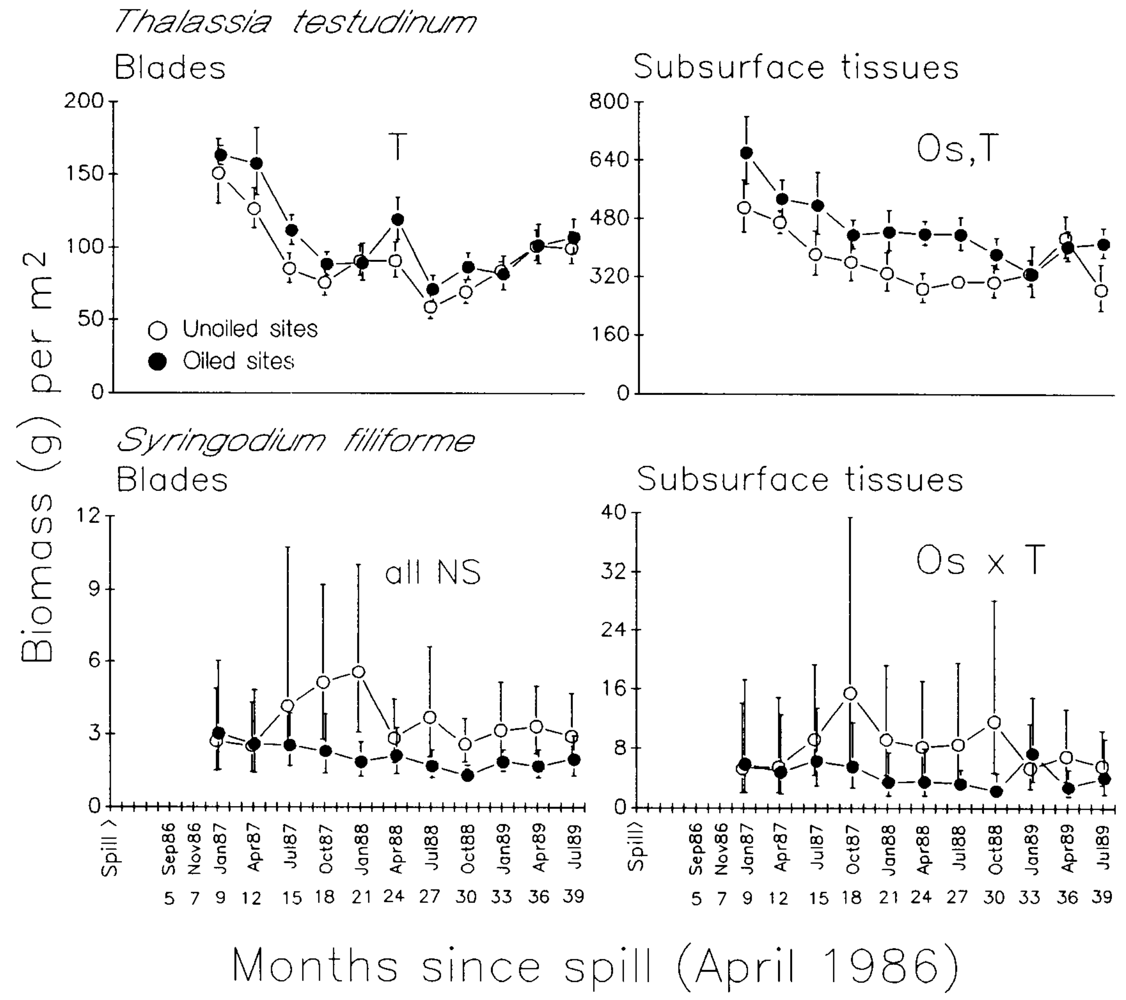

Fig. 10.4 Biomass of *Thalassia testudinum* and *Syringodium filiforme* blades and subsurface tissues. Data are from core samples; error bars and ANOVA results are explained in the caption to Figure 10.3. Refer to Appendix Table F.1.

Increased algal biomass, as was measured on oiled coral reefs (Guzmán et al., Chap. 7), was not observed at oiled seagrass beds (Fig. 10.5). Fleshy algal dry weights followed similar patterns in both oiled and unoiled beds. Living calcareous algae initially were virtually absent from oiled sites; biomass increased, starting 9 mo postspill, until it exceeded that at unoiled sites during two censuses nearly 3 yr postspill. Biomass at unoiled sites declined by an order of magnitude during the first year of monitoring, and did not return to the high levels measured initially. Variation in fleshy algal biomass at oiled and unoiled sites was not significantly different; there was a general decrease in biomass through time (App. Table F.1).

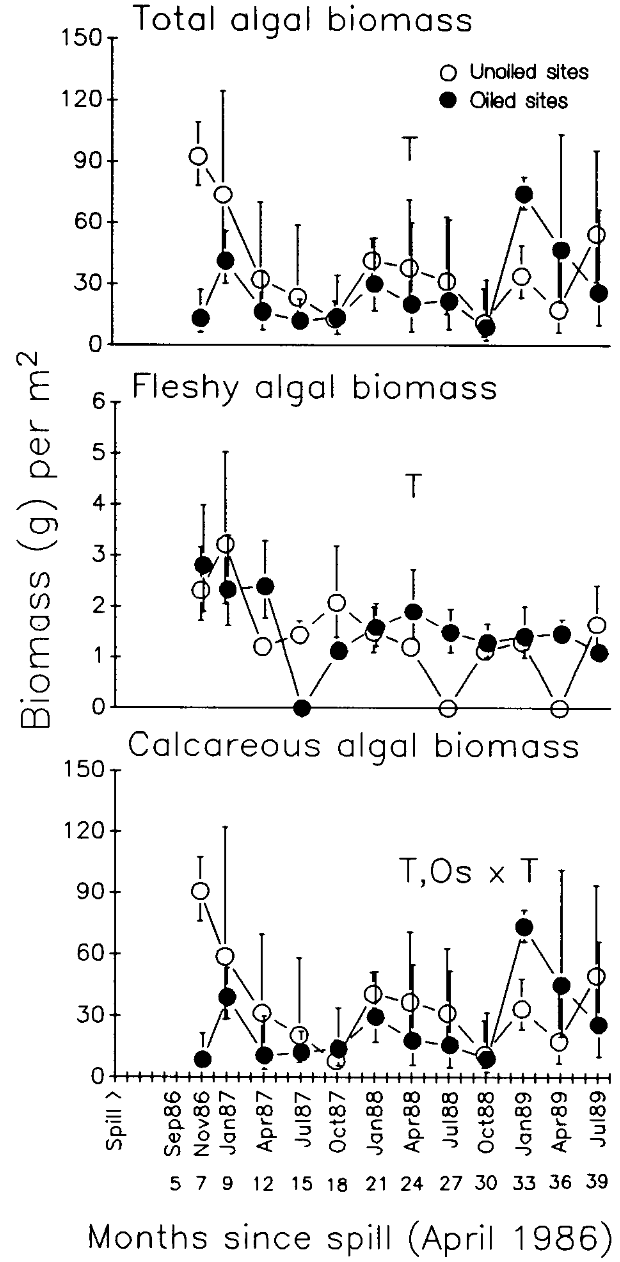

Fig. 10.5 Biomass of all algae combined, fleshy algae, and calcareous algae. Data are from core samples; error bars and ANOVA results are explained in the caption to Figure 10.3. Refer to Appendix Table F.1.

Calcareous algal biomass fluctuated differently through time at oiled and unoiled sites; biomass was greater at unoiled sites at nine of the 12 surveys, but was greater at oiled sites three times.

10.5.1.3 Discussion

Subtidal seagrass beds in various regions have been exposed to crude oil (Marshall et al. 1990). Effects of oil spills on *Thalassia* have varied from spill to spill. Die-offs of intertidal *Thalassia* beds occurred after the 1986 Bahía Las Minas spill (Jackson et al. 1989; Steger and Caldwell, Chap. 6). Shallow subtidal *Thalassia* beds exposed to crude oil and, possibly, oil dispersants in some areas (Jackson et al. 1989; Keller et al., Chap. 1) were killed along shoreward margins at some sites. Seagrass samples collected 5 mo after the spill had lower biomass at oiled than at unoiled sites (Fig. 10.3). Because *Thalassia* biomass was one or two orders of magnitude greater than that of *Syringodium* (Fig. 10.4), most of this reduction was due to a sublethal effect on *Thalassia*. Two months after this initial survey, seagrass biomass was similar at oiled and unoiled sites, and starting in January 1987 subsurface *Thalassia* biomass was generally greater at oiled sites until nearly 3 yr after the spill (Fig. 10.4).

Laboratory results suggest a higher level of tolerance of oil and dispersant for *Thalassia* than *Syringodium* (Thorhaug and Marcus 1987). *Syringodium* biomass generally was lower in oiled areas than in unoiled seagrass beds 15-30 mo after the spill. This finding, and toxicity tests (Thorhaug and Marcus 1985, 1987), suggest that *Syringodium* is more sensitive to oiling than *Thalassia*. Chronic oiling after a spill, the situation in Panama (Burns, Chap. 3), has not been applied in laboratory or field experiments (Ballou et al. 1987) with seagrasses and associated fauna. Oil seeping from the landfill beneath the refinery and washing out from oil-saturated sediments of mangroves years after the spill (Burns, Chap. 3; Guzmán et al., Chap. 7; Garrity and Levings, Chap. 9) did not kill *Thalassia* away from the shoreline, but may have damaged *Syringodium* populations (Fig. 10.4). The pronounced thinning of subtidal *Thalassia* was not due to the spill because it occurred at both oiled and unoiled sites.

Fleshy algae did not bloom postspill in seagrass beds (Fig. 10.5), although algal blooms occurred on nearby coral reefs (Guzmán et al., Chap. 7). Fleshy algae are much less abundant and less diverse in Panamanian seagrass beds than in other areas (Heck 1977; Lapointe 1989). For example, the biomass of drift algae often rivals seagrass biomass in southern Florida Bay. We did not observe an effect of the spill on fleshy algae, which are ecologically important in many seagrass beds (reviewed by Virnstein 1987). However, measurements did not begin until 7 mo after the spill and we cannot determine whether there was an initial, ephemeral negative or positive effect of the spill on algal biomass.

Effects of oil spills on calcareous algae in tropical seagrass beds have not been studied previously. Heck and Wetstone (1977) qualitatively described the calcareous algae of several of the beds oiled by the 1986 spill; there were numerous species of calcareous algae 12 yr before the spill. Their virtual absence soon after the spill and the subsequent similarity in biomass at oiled and unoiled sites (Fig. 10.5) support the possibility of a detrimental effect of the spill on this algal type.

10.5.2 Shoreward Margins of Seagrass Beds

10.5.2.1 Methods and Materials

Evidence of an effect of the oil spill on the shoreward margins of seagrass beds was first noticed in July 1988, 2.5 yr after the spill. A marker that had been placed well inside the bed at LRS (approximately 2-3 m within the margin) was found in muddy sand devoid of seagrass cover approximately 4-5 m shoreward of the margin of the bed. Measurements from markers on mangrove trees showed that the site marker was in its original position. We found decaying seagrass shoots and rhizomes buried near the marker post, suggesting that the seagrass around the marker had died. The seagrass bed at this site was bordered by a heavily oiled mangrove shoreline and a mud flat that smelled strongly of oil at the beginning of the study.

After this finding at LRS we marked the landward edge of each seagrass bed. Stakes were placed at 1- to 2-m intervals along the inner edge of each bed in July 1988. During subsequent collections the distance between each stake and the nearest edge of the seagrass bed was determined. If the bed had advanced beyond or receded away from the line of stakes, stakes were placed at the new edge. At BNV, an unoiled seagrass bed, stakes usually disappeared between collection dates, probably because of theft.

10.5.2.2 Results

Shoreward edges of seagrass beds generally receded from mangrove shorelines at oiled sites, particularly PGN, 2-3 yr after the spill (Fig. 10.6). The margin at LREN initially receded, then grew shoreward. At one of three unoiled sites (DONT) the edge of the bed receded slightly. The other two unoiled sites (PALN and LINE) showed little or no change in shoreward-edge position during the year-long monitoring. The shoreward edge at PGN receded still farther between August 1989 and November 1992, when additional measurements were made at oiled sites. A 20-20-cm lowering of the sediment surface was evident at this site just beyond the edge of the living seagrass plants. The edge at LRS had moved 1-2 m shoreward, but the margins at LREN and MINN had not shifted over the 3-yr interval.

10.5.2.3 Discussion and Summary

Progressive change in the position of the shoreward edge of seagrass beds clearly began earlier than July 1988, at least at one site, as evidenced by the position of the marker stake at LRS. Based on the 4-5 m exposure of the stake at this site, seagrass die-off during the first 2 yr postspill may have been extensive in Bahía Las Minas. The oil spill affected subtidal seagrass beds primarily through this decrease in area along shoreward margins, rather than through a long-term, sublethal reduction in biomass within beds.

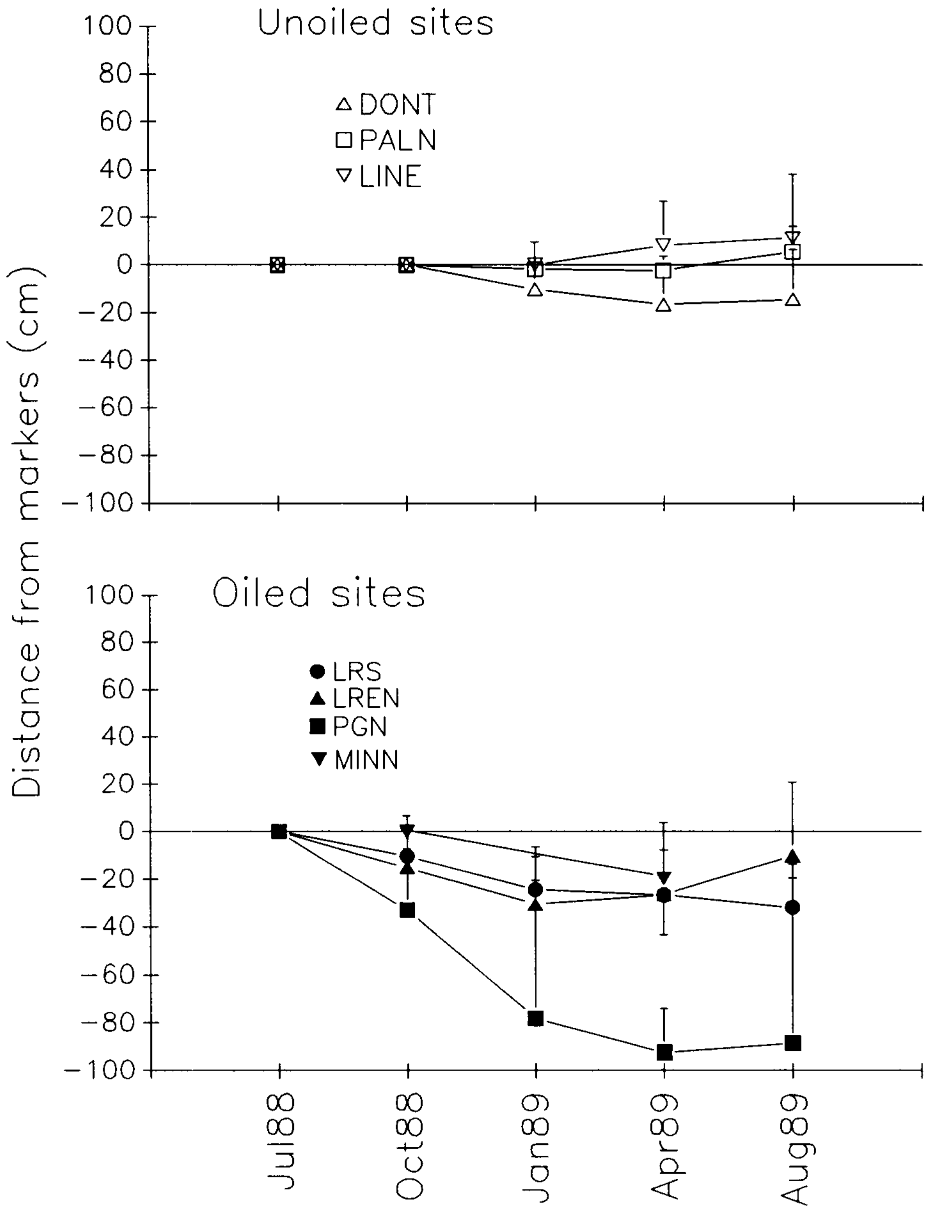

Fig. 10.6 Position of the shoreward margin of seagrass beds relative to permanent marker posts, the *zero line*, put in place during July 1988. There were further changes in the extent of some oiled seagrass beds between 1989 and 1992, including a 1-2 m shift at LRS, after the regular field work was completed. See text for details.

Oil released from mangrove sediments may have reached toxic concentrations along bed margins during reoiling events. "Bleed waters" contaminated with petroleum hydrocarbons and their breakdown products have been suggested as a chronic problem following oil spills in mangrove areas (Marshall et al. 1990). This effect has been largely ignored in other studies.

10.5.3 Infaunal (Core) Sampling

10.5.3.1 Methods and Materials

Core samples were collected as described in Section 10.5.1. Core samples were sieved through 500-μm mesh screen. All organisms and sediments retained were fixed in buffered 10% formalin with rose bengal. Animals were picked from the large amounts of plant material and sediments that were retained and preserved in 70% ethanol. Animals were sorted to major taxa during initial processing. Polychaetes from the first two collections were separated into families.

After completion of the September 1986, November 1986, and January 1987 collections, samples were split to accelerate processing. Sample splitting was combined with a reduction in the number of samples processed per bed, from eight to five. The sample-splitting device, a commercially available riffle splitter, was tested for bias prior to use. The splitting procedure involved several steps. Entire core samples were initially sieved through 1/2 in. (1.27 cm) mesh to separate seagrasses, algae, and large animals prior to splitting. Then samples were split to 1/4 or 1/8 fractions. Counts were adjusted to full sample counts by multiplying split counts by the appropriate factor (4 or 8) and adding the numbers of large animals retained on the 1/2-in. mesh sieve. Seagrasses and algae were also split to 1/4 or 1/8 fractions. Animals hidden between seagrass blades or among the root and rhizome mass were picked and combined with the animals from the sediment fraction. Seagrass and algal fractions were then recombined with the 3/4 or 7/8 portions for biomass determinations (Sect. 10.5.1).

Although animals collected in this manner are called *infauna* in this report, they included sedentary epifauna associated with seagrass blades or the sediment surface as well as true infauna.

10.5.3.2 Results

Total counts for seven censuses of all infaunal taxa except polychaetes differed greatly at oiled and unoiled sites (Table 10.4). The same was true for all major taxa, except gastropods and hermit crabs. Several taxa (amphipods, sipunculids, ophiuroids, and echinoids) were present in unoiled seagrass beds at abundances an order of magnitude higher than in oiled seagrass beds (two orders of magnitude for tanaid crustaceans). The polychaete counts shown in Table 10.4 are from the first two samplings only (September and November 1986), which is why they are presented separately. If all collections of polychaetes had been counted, their total would have exceeded that of all other taxa combined.

As the abundance of infauna other than polychaetes increased at oiled sites, numbers declined at unoiled sites between 1987 and 1989 and converged with those at oiled sites 2-3 yr after the spill (Fig. 10.7). This pattern resulted in a significant oiling x time interaction (App. Table F.2). Densities of some of the most abundant infaunal taxa, amphipods, tanaids, isopods, cumaceans, sipunculids, and ophiuroids,

Table 10.4 Infaunal counts and percentages for cores collected at oiled and unoiled sites for all censuses combined. Taxa are ordered by abundance at unoiled sites. Counts of polychaetes are for the September and November 1986 samplings only.

	Unoiled Sites		Oiled Sites	
Taxon	Count	Percent	Count	Percent
Amphipoda	6,114	42.8	454	9.3
Tanaidacea	2,753	19.3	74	1.5
Gastropoda	1,152	8.1	1,236	25.3
Bivalvia	1,009	7.1	681	13.9
Isopoda	549	3.8	298	6.1
Sipunculida	542	3.8	79	1.6
Shrimp	534	3.7	398	8.1
Ophiuroidea	507	3.5	12	0.2
Brachyura	506	3.5	259	5.3
Hermit crabs	343	2.4	832	17.0
Cumacea	318	2.2	254	5.2
Ostracoda	142	1.0	67	1.4
Mysidacea	99	0.7	27	0.6
Pycnogonida	98	0.7	62	1.3
Copepoda	51	0.4	109	2.2
Burrowing shrimp	28	0.2	16	0.3
Echinoidea	18	0.1	1	<0.1
Stomatopoda	14	0.1	12	0.2
Polyplacophora	10	0.1	7	0.1
Coelenterata	4	<0.1	3	0.1
Fish	1	<0.1	3	0.1
Holothuroidea	1	<0.1	0	0.0
Platyhelminthes	0	0.0	1	<0.1
Total count	14,287		4,885	
Polychaeta	5,960		3,556	

varied through time in a similar manner (Fig. 10.8); some were more abundant at oiled than at unoiled sites 3 yr after the spill. Other common taxa did not have a significant oiling x time interaction and a pattern of convergence, although bivalves and brachyurans showed such a trend (Fig. 10.9), as did total echinoderms (Fig. 10.7). Gastropod numbers fluctuated considerably and hermit crabs tended to be more abundant at oiled than at unoiled sites.

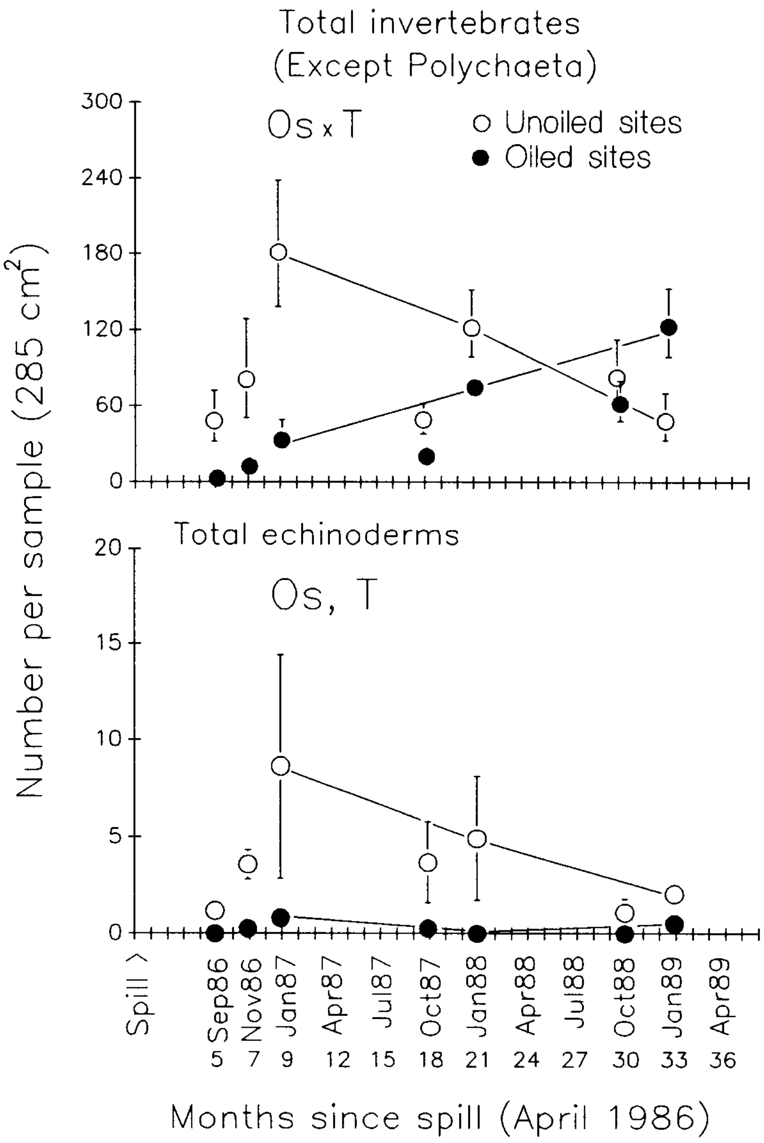

Fig. 10.7 Total count of invertebrates except polychaetes and of echinoderms in core samples, September 1986 through January 1989. Error bars and ANOVA results are explained in the caption to Figure 10.3. Repeated-measures analysis was conducted for the January collections only (connected points); refer to Appendix Table F.2.

10.5.3.3 Discussion and Summary

The general pattern of increase through time in numbers of infauna at oiled sites after the spill is indicative of repopulation following a nearly complete die-off (Figs. 10.7, 10.8). It is not known why numbers generally declined at unoiled sites.

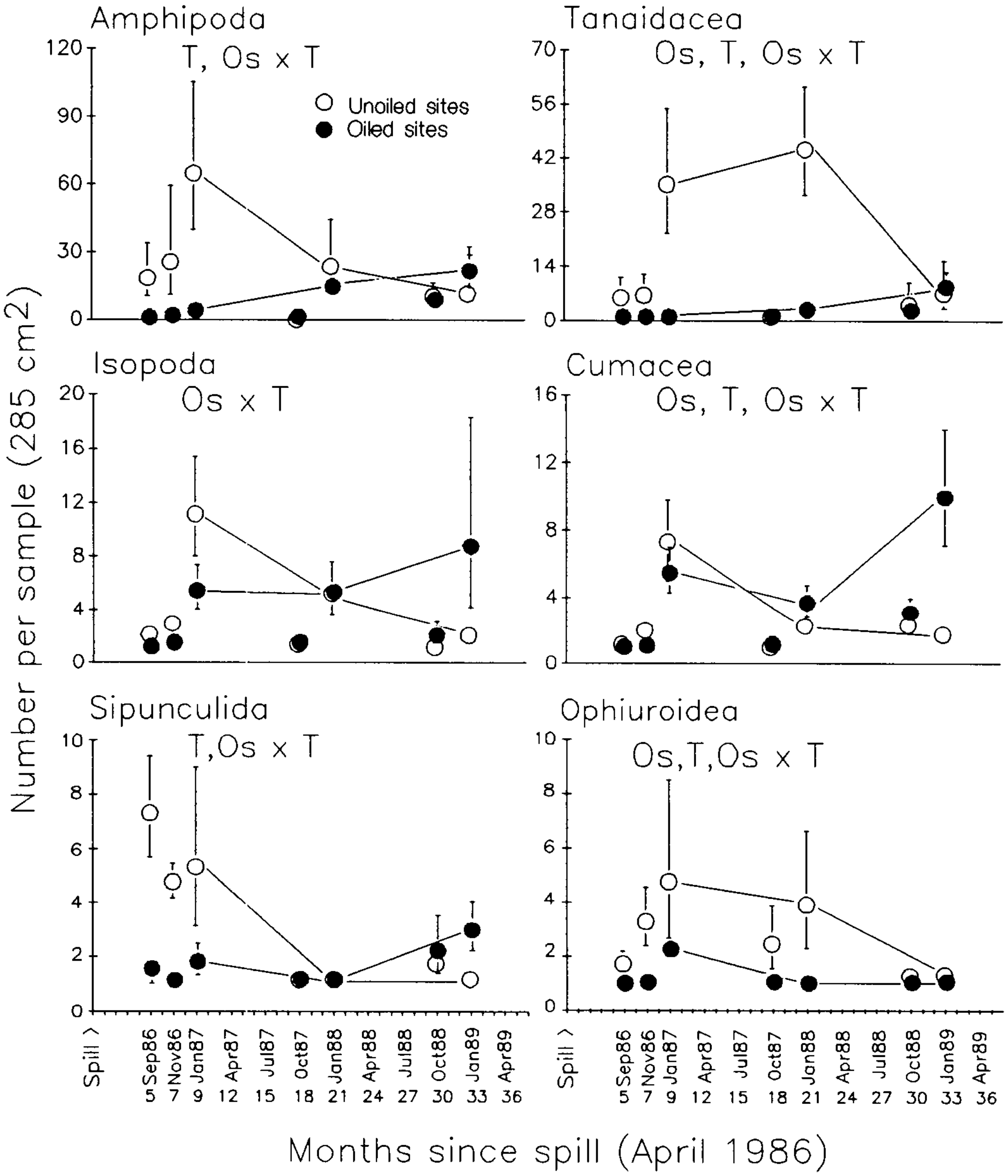

Fig. 10.8 Density of amphipods, tanaids, isopods, cumaceans, sipunculids, and ophiuroids in core samples, September 1986 through January 1989. Error bars and ANOVA results are explained in the caption to Figure 10.3. Repeated-measures analysis was conducted for the January collections only (connected points); refer to Appendix Table F.2.

Interestingly, this trend coincided with a steady decline in seagrass biomass to approximately 25% of the level measured at the start of the study (Fig. 10.3).

Abundances of gastropods, bivalves, and brachyurans were not strongly affected by the spill, either because these groups were not killed by exposure to oil

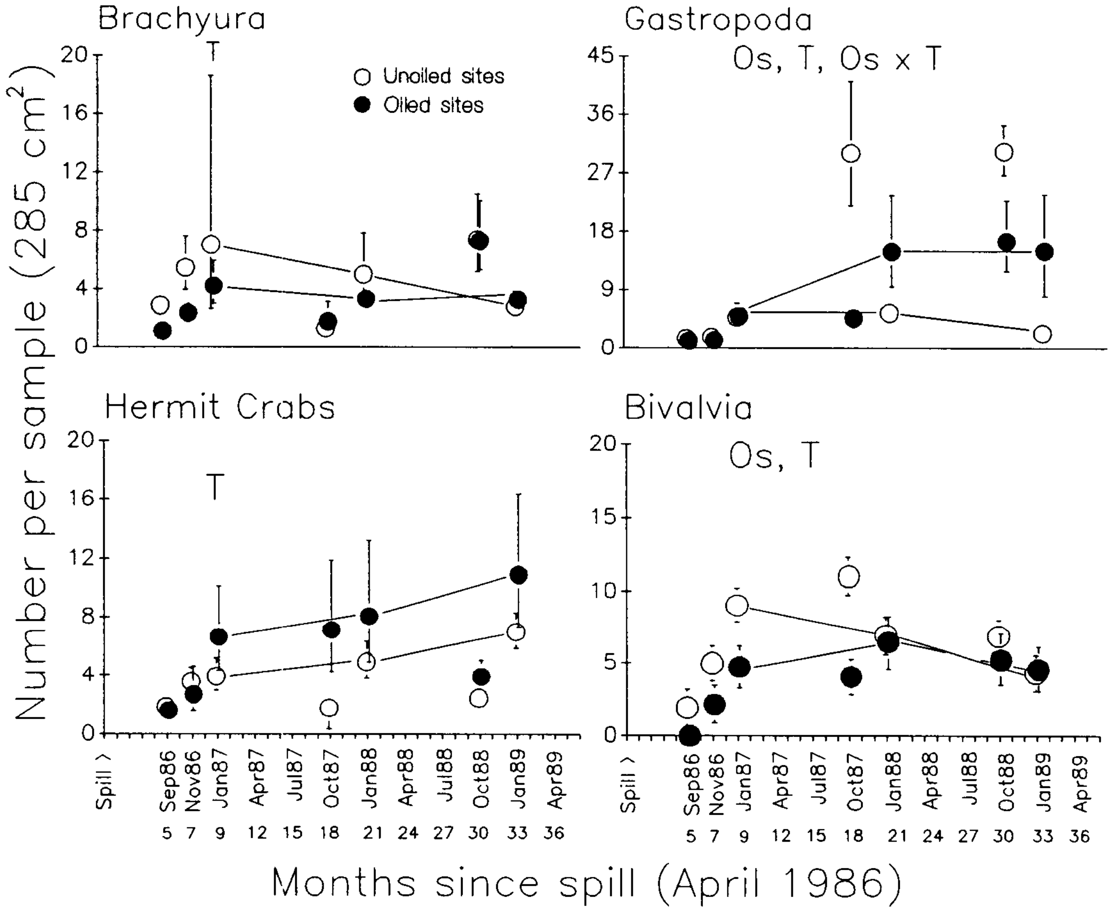

Fig. 10.9 Density of gastropods, bivalves, brachyurans, and hermit crabs in core samples, September 1986 through January 1989. Error bars and ANOVA results are explained in the caption to Figure 10.3. Repeated-measures analysis was conducted for the January collections only (connected points); refer to Appendix Table F.2.

or they had repopulated by the time the study started 5 mo postspill (Fig. 10.9). By this time, oil in seagrass sediments was highly weathered (Burns, Chap. 3).

Temporal trends in the abundance of amphipods in oiled seagrass beds (Fig. 10.8) followed the pattern displayed by amphipods in *Zostera* beds following the *Amoco Cadiz* oil spill (den Hartog and Jacobs 1980). In both regions amphipods were highly sensitive to oiling and slow to recover in abundance. It is not possible to determine whether this pattern was due to residual-oil toxicity or some other factor.

Ophiuroids were lower in abundance at oiled than at unoiled sites until 2.5 yr postspill, when numbers fell at unoiled sites (Fig. 10.8). After the *Amoco Cadiz* oil spill they were reduced in numbers but were not totally eradicated. Ophiuroids may have been killed by toxic, water-soluble oil fractions drawn into their watervascular systems or by oily sediments in the case of deposit-feeding species. Surface-dwelling species of *Ophiothrix* and *Ophiocoma*, the most common genera in push-net samples (Sect. 10.5.4), may have been killed by direct contact with oil.

Tanaid populations also were more sensitive to oiling after the spill at Bahía Las Minas (Fig. 10.9) than after the *Amoco Cadiz* spill. These small crustaceans typically live at the sediment-water interface, have direct development, and presumably are not mobile over long distances as adults or juveniles. All three factors could explain their slow repopulation of oiled seagrass beds.

10.5.4 Epifaunal (Push Net) Sampling

10.5.4.1 Methods and Materials

Mobile and sedentary epifauna were collected, starting in November 1986, by push net. The push net was attached by a 10-m-long rope to a pole, which initially (November 1986) was located haphazardly. Later samples were collected from random starting points within a grid system. The push-net frame, made of 1/2 in. iron rod, measured 0.75 m wide by 0.35 m high. The bag was made of Nytex screen with 1 mm openings. Initially, five (later six) push-net samples were collected at each site. The area of each sample was 7.5 m^2. Animals were preserved in 10% formalin and were later transferred to 70% ethanol. Epifauna were sorted to major taxa and shrimp were identified to species.

Carapace lengths of two caridean shrimp species (*Hippolyte zostericola* and *Latreutes fucorum*) were measured using an ocular micrometer for up to 160 individuals per site per sampling. The reproductive status of each adult female was assessed by methods described in Bauer (1987). Ovarian fullness and brooded-egg stages were scored by separate indices (Table 10.5). Juveniles were classified as recent recruits if they were in the smallest quartile of the size range of each species.

Carapace lengths and reproductive data for caridean shrimp were analyzed graphically to examine possible differences in population structure, recruitment intensity, and reproductive response between unoiled and oiled sites.

10.5.4.2 Results

Total counts of epifauna collected by push net followed similar patterns at oiled and unoiled sites (Fig. 10.10). Trends in the counts were significantly different (App. Table F.3), and totals generally were greater at unoiled than at oiled sites. Epifaunal collections were sorted to the major taxa listed in Table 10.6. Like infaunal taxa, epifauna responded variously to the spill.

Some of the most abundant epifaunal taxa, shrimp, tanaids, amphipods, gastropods, ophiuroids, and fish, were more abundant at unoiled than at oiled sites (Table 10.6; Fig. 10.11). As was the case for infauna, tanaids were two orders of magnitude more abundant at unoiled than at oiled sites; they had two pulses in abundance in unoiled seagrass beds that were not matched at oiled sites.

Table 10.5 Index used to evaluate levels of ovarian fullness and brooded-egg developmental stages for the caridean shrimp *Hippolyte zostericola* and *Latreutes fucorum*.

Code	Status
Brooded-egg developmental stages	
1	no eggs on pleopods
2	brooded eggs without eyes
3	brooded eggs with eyes
Ovarian fullness indices	
4	empty ovaries
5	ovaries less than 1/2 full
6	ovaries greater than 1/2 full

Echinoderms also differed markedly, with numbers one to two orders of magnitude greater at unoiled sites. This difference occurred due to a pulse in numbers between April 1987 and April 1988 at unoiled but not at oiled sites (Figs. 10.10, 10.11).

Two abundant taxa, brachyurans and isopods, did not have significantly different densities at oiled and unoiled sites (Fig. 10.12). Two other taxa, hermit crabs and mysids, were more abundant at oiled than at unoiled sites (Fig. 10.13).

Shrimp were numerical dominants in oiled and unoiled seagrass beds (Table 10.6); 17 species of shrimp were collected and identified (Marshall 1991). The hippolytids *Latreutes fucorum* and *Thor manningi* and the palaemonid *Periclimenes americanus* generally were more abundant at unoiled than at oiled sites (Fig. 10.14). *L. fucorum* showed signs of repopulation at oiled sites 1.5-2 yr postspill; the other two species remained very low in abundance 2 yr after the spill.

Four other shrimp families or species, penaeids, alpheids, *Sicyonia laevigata*, and *Palaemon northropi*, had significant oiling x time interactions, but fluctuated without apparent pattern at oiled and unoiled sites (Fig. 10.15). Nocturnally active penaeids, alpheids, and sicyonids probably were not adequately sampled because they lie buried during the day. Two hippolytids, *Hippolyte zostericola* and *Latreutes parvulus*, generally were more numerous at oiled than at unoiled sites (Fig. 10.16).

Although juvenile penaeids were common, they were not identified to species because of taxonomic difficulties (Stoner 1980). Common adults included *Penaeus duorarum* and *Metapenaeopsis martinelli.*

Combining crustacean taxa into groups based on egg-care strategies suggested that species with direct development were most strongly affected by the spill (Fig. 10.17). Peracarid reproduction and development in oiled seagrass beds may have been negatively affected by oil, and recruitment from distant seagrass beds would not have replaced adults or juveniles killed by oil. Mysids were an exception to this pattern (Fig. 10.13). Adult mysid mobility or an insensitivity to oiling may explain abundance patterns of this group. Partial brooders, mostly decapod crustaceans, initially were less abundant in oiled seagrass beds, but densities in oiled beds reached

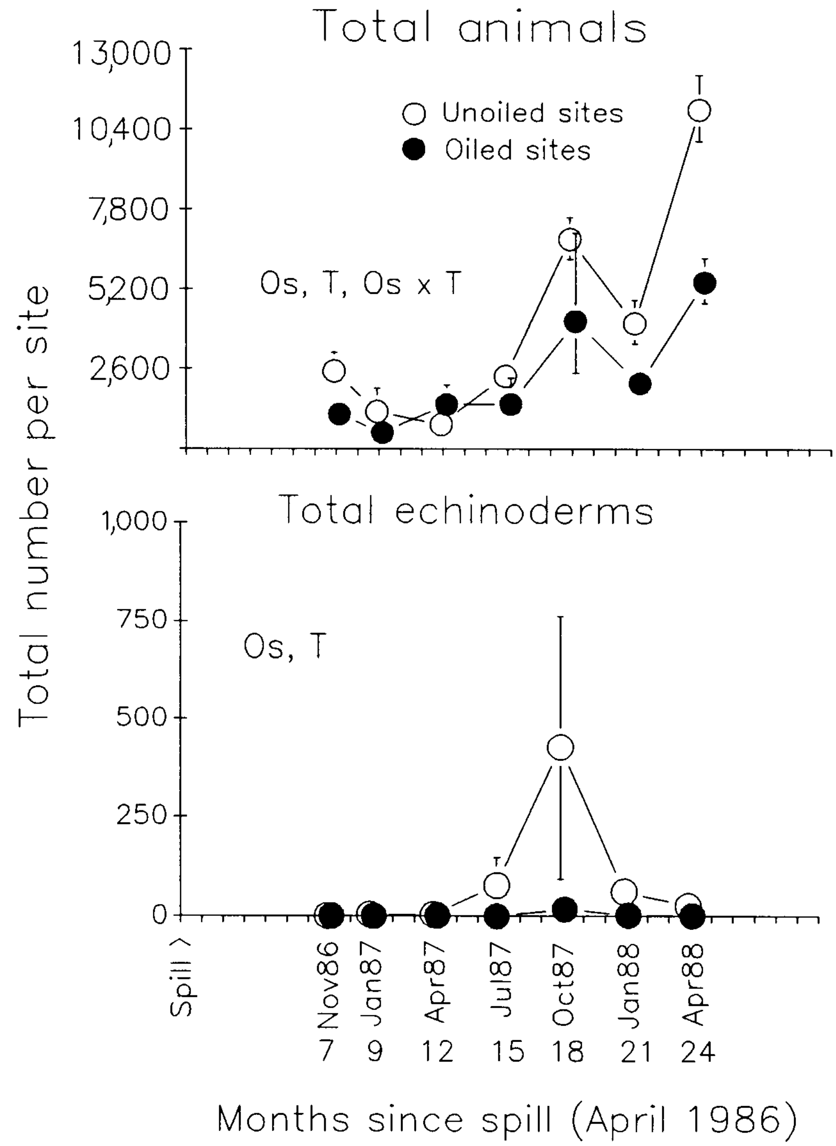

Fig. 10.10 Total number of animals and echinoderms in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.3. Most of the echinoderms were ophiuroids (Table 10.6).

those in unoiled beds 1 yr postspill. In this case recruitment from unoiled seagrass beds, especially by *Hippolyte zostericola*, may have replaced individuals killed by the spill soon after it occurred. If reproduction had been adversely affected, the consequences would not be apparent in population counts because of continuing recruitment from distant seagrass beds. Species with completely pelagic larvae, such

Table 10.6 Total counts of epifaunal taxa from November 1986 through April 1988. Taxa are ordered by abundance at unoiled sites.

	Unoiled Sites		Oiled Sites	
Taxon	Count	Percent	Count	Percent
Shrimp[1]	53,819	47.0	41,507	55.8
Tanaidacea	26,860	23.4	658	0.9
Amphipoda	10,612	9.3	7,678	10.3
Gastropoda	4,441	3.9	2,657	3.6
Brachyura	4,333	3.8	3,656	4.9
Hermit Crabs	4,217	3.7	9,865	13.3
Isopoda	2,334	2.0	1,405	1.9
Ophiuroidea	2,134	1.9	88	0.1
Fish[2]	2,080	1.8	970	1.3
Ostracoda	1,102	0.9	551	0.7
Cumacea	886	0.8	394	0.5
Mysidacea	617	0.5	3,330	4.5
Pycnogonida	549	0.5	797	1.1
Stomatopoda	354	0.3	855	1.1
Holothuroidea	225	0.2	7	<0.1
Echinoidea	48	<0.1	2	<0.1
Total count	114,611		74,420	

[1] Caridea and Penaeidea
[2] Gobiidae and Scaridae

as penaeids and sicyonid shrimp, showed less of an effect of the spill on juvenile stages because all recruitment was presumably from distant seagrass beds.

Reproduction, recruitment, and population structure of two hippolytid shrimp were observed to determine how partial brooders were affected by the spill. The two most abundant hippolytids, *Hippolyte zostericola* and *Latreutes fucorum*, were chosen for this comparison. Temporal trends in densities suggested that these two shrimp were variably sensitive to oiling (Figs. 10.14, 10.16). In both cases, however, ovarian maturation and brooded-egg development appeared insensitive to oiling (Fig. 10.18). Percentages of egg-brooding (ovigerous) females as a fraction of reproductively mature females (defined as all females above or equal to the carapace length of the smallest ovigerous female observed for each species) showed no trends in either species that suggested an effect of the spill. Percentages of clutches of undifferentiated eggs (eggs without eyes) among ovigerous females of both species suggested that exposure to oil did not halt egg development. A toxic effect on embryos might have stopped development at an early stage, and a larger percentage of undifferentiated eggs would then have been expected at oiled sites. The incidence of concomitant incubation and ovarian maturation was also similar in oiled and

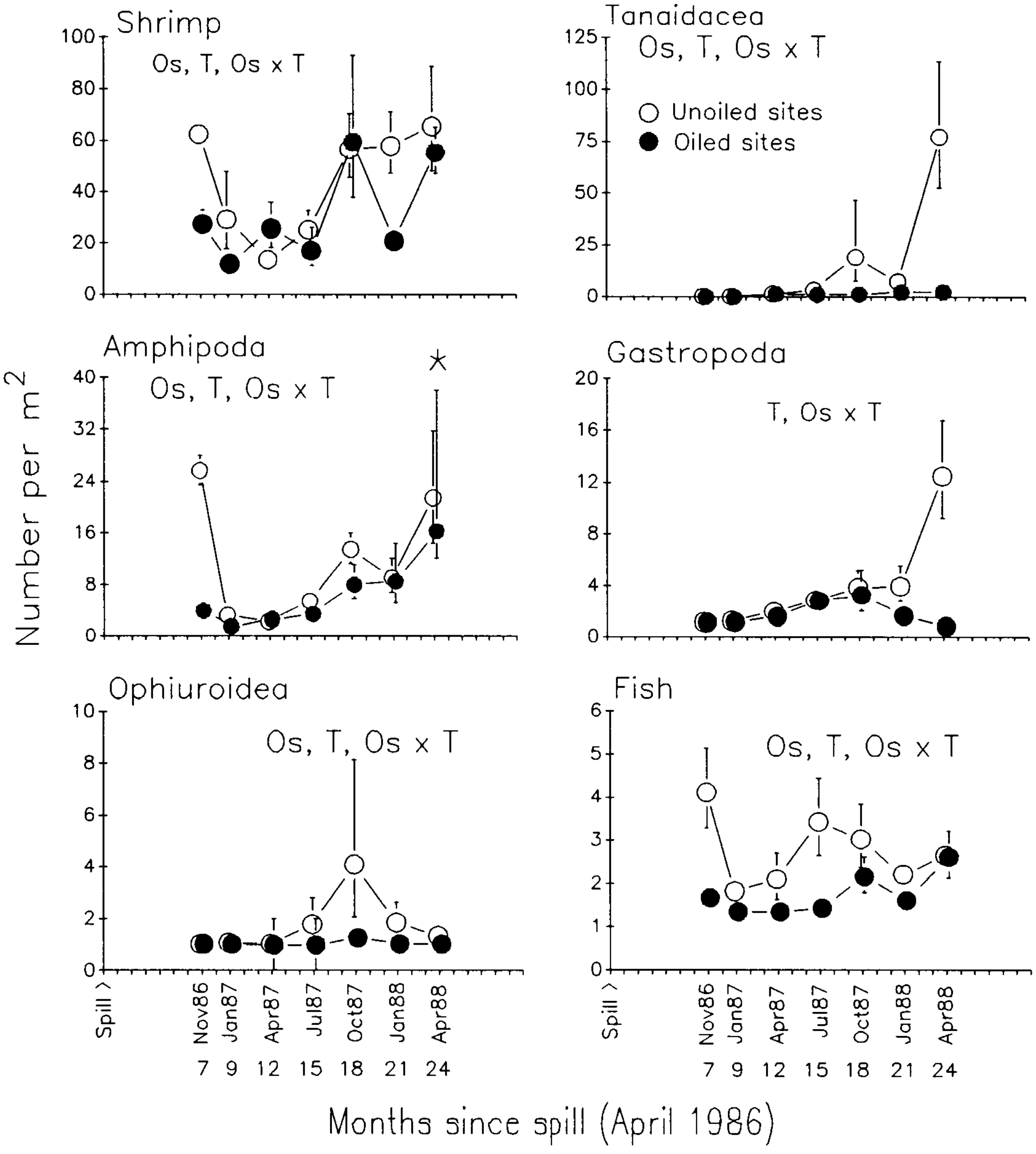

Fig. 10.11 Density of shrimp, tanaids, amphipods, gastropods, ophiuroids, and fish in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.3.

unoiled seagrass beds. These results indicate that reproductive processes were not affected by oiling in either of these two abundant caridean species. Recruitment intensities (Fig. 10.19) and population structures (Fig. 10.20) of these species also followed similar overall patterns in oiled and unoiled seagrass beds.

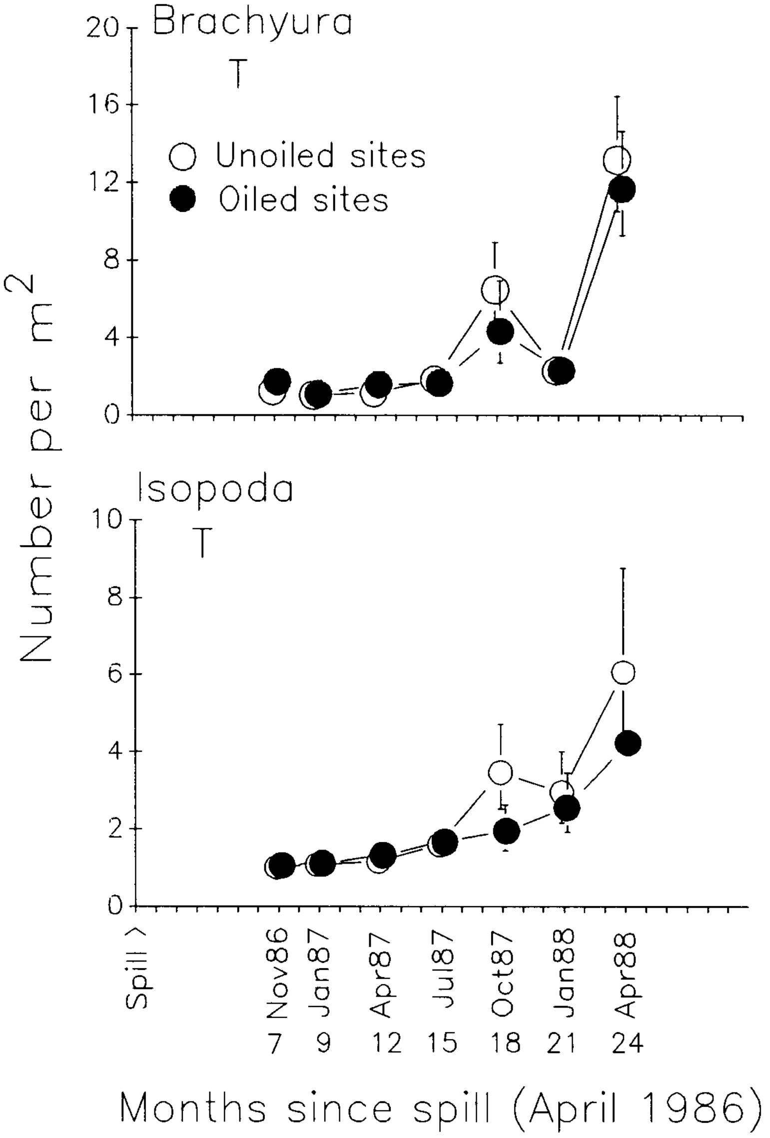

Fig. 10.12 Density of brachyurans and isopods in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.3.

10.5.4.3 Discussion and Summary

As was the case for total infauna other than polychaetes (Fig. 10.7), total epifauna increased in abundance at oiled sites after the spill (Fig. 10.10). This five-fold increase, again, was consistent with a pattern of postspill repopulation of oiled

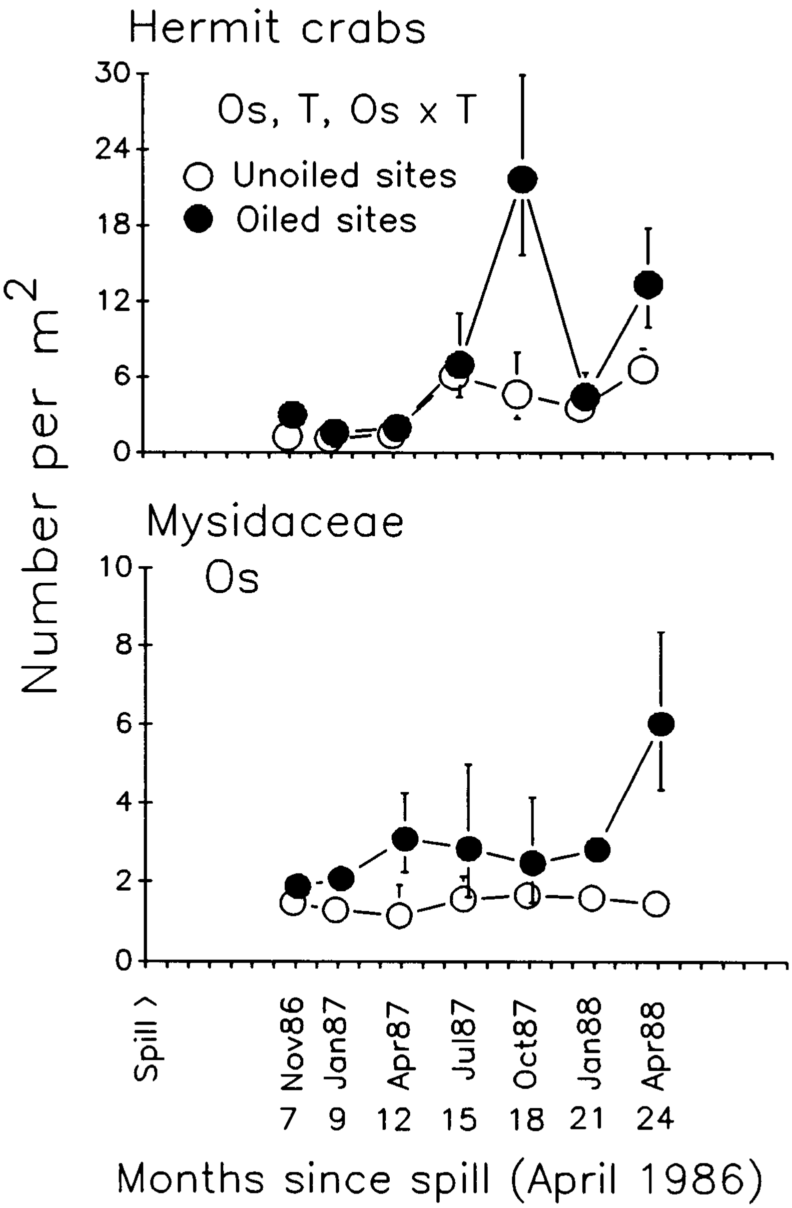

Fig. 10.13 Density of hermit crabs and mysids in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.3.

sites. However, unlike infauna, epifaunal abundance did not converge at oiled and unoiled sites by 2 yr postspill. Instead, numbers of epifauna increased markedly at unoiled as well as oiled sites. This increase countered both the decreasing biomass of seagrass (Fig. 10.3) and decreasing number of infauna (Fig. 10.7). The decline in

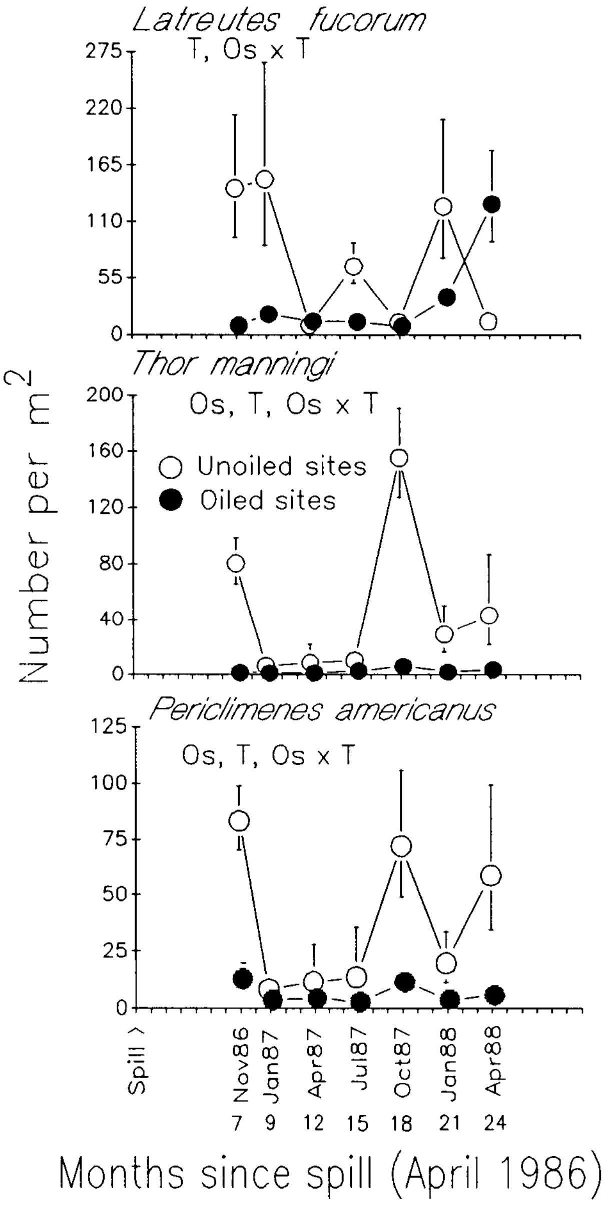

Fig. 10.14 Density of *Latreutes fucorum*, *Thor manningi*, and *Periclimenes americanus* in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.4.

seagrass biomass could not have been caused by the increase in epifauna, which included some seagrass grazers, because the changes were well out of phase. An effect of certain epifauna on infauna (and other epifauna), however, cannot be discounted (e.g., Young et al. 1976; see reviews by Klumpp et al. 1989; Howard et

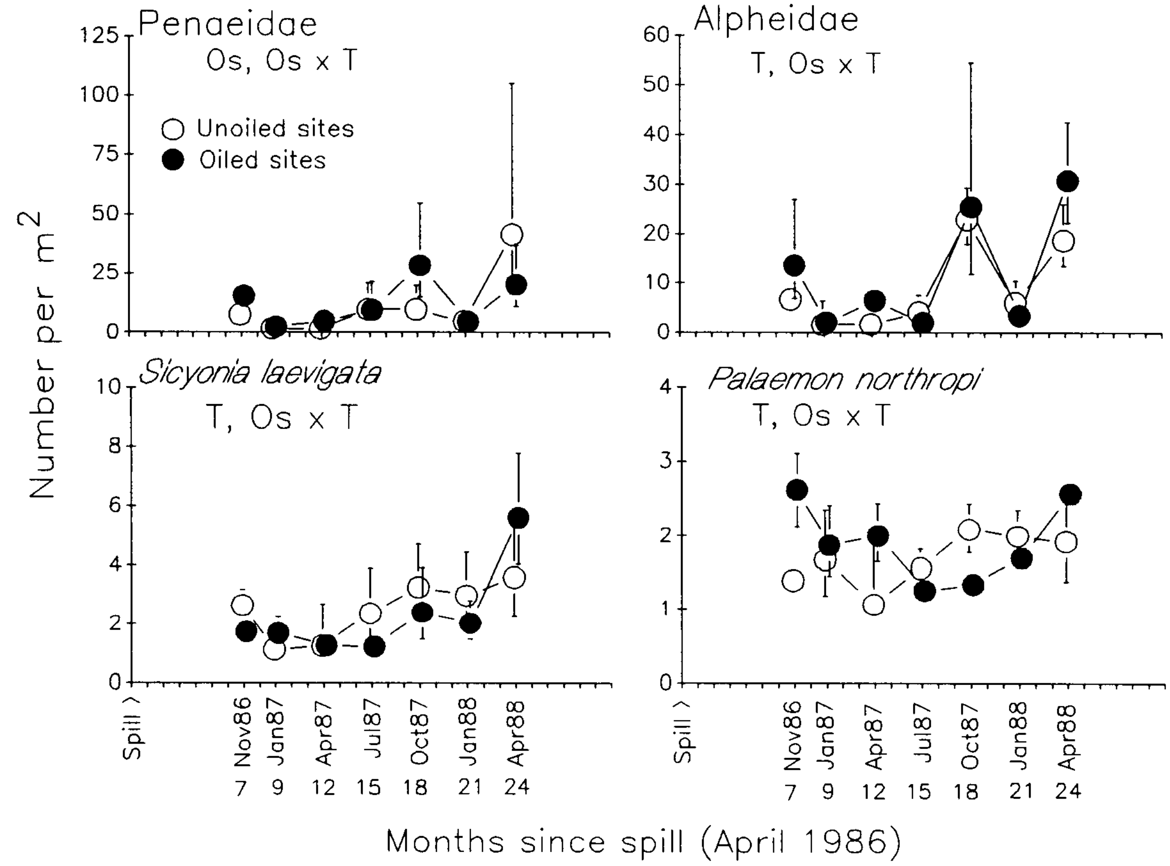

Fig. 10.15 Density of penaeids, alpheids, *Sicyonia laevigata*, and *Palaemon northropi* in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.4.

al. 1989; Bell and Pollard 1989). For example, a tanaid predator adversely affects survival of newly metamorphosed echinoids in temperate waters (Highsmith 1982*a*).

In 1974-1975 epifauna were collected by otter trawl with 19-mm mesh wings and a 6.3-mm mesh liner, and at greater depth than the present study (Heck 1977). The otter trawl apparently did not retain tanaids and amphipods, which probably were too small. On the other hand, fish were far more abundant and diverse in the 1974-1975 collection (Heck and Wetstone 1979) than the unoiled sites of the present study, again, probably because of the different sampling apparatus. Discounting these three taxa, the three most common taxa in the two collections had the same rank abundance: shrimp, gastropods, and brachyurans; echinoderms and anomurans were the fourth and fifth most common taxa, but echinoderms were relatively more abundant in Heck's collection (Heck's sites 1-3, near Isla Mina, were used; his site 4, near Islas Naranjos, was not included; only unoiled sites of the present study were

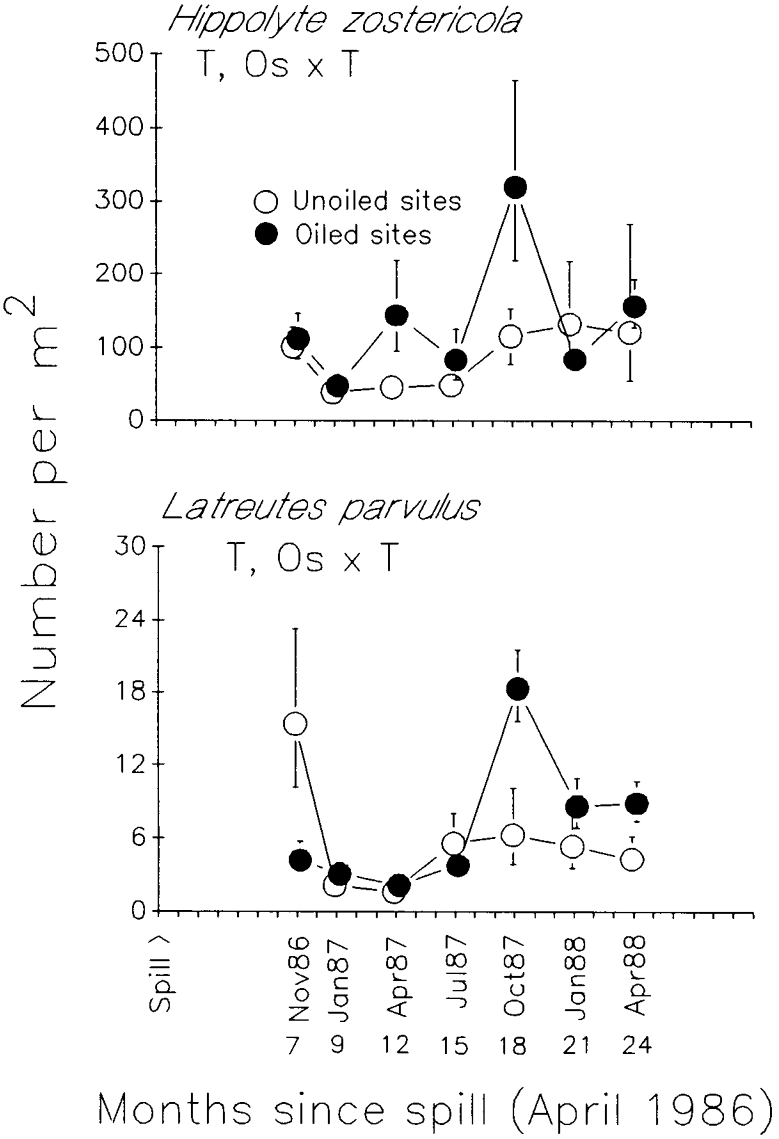

Fig. 10.16 Density of *Hippolyte zostericola* and *Latreutes parvulus* in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.4.

used in this comparison). This similarity in rank abundance 11-12 yr before the spill between an area that became oiled and postspill sites that were not oiled strengthens the interpretation that postspill patterns at oiled sites were caused by the oil spill, and were not simply pre-existing geographic differences in abundance between the oiled and unoiled study areas.

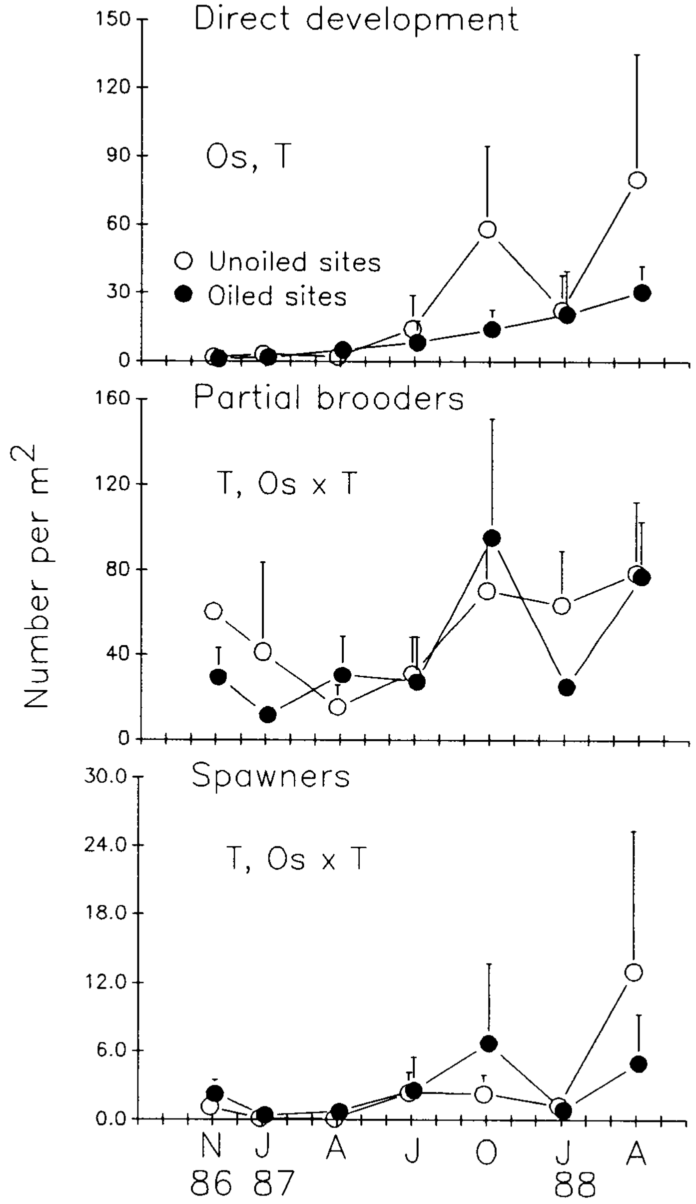

Fig. 10.17 Density (from push-net counts) of crustaceans with three major reproductive patterns: (1) direct development, (2) partial brooders, and (3) spawners (nonbrooders). Error bars and ANOVA results are explained in the caption to Figure 10.3; refer to Appendix Table F.5.

Judging by total counts at oiled and unoiled sites, which differed by a factor of 2.9 for infauna other than polychaetes and by 1.5 for epifauna, infauna were more strongly affected by the spill than epifauna. This pattern would be expected if oil in

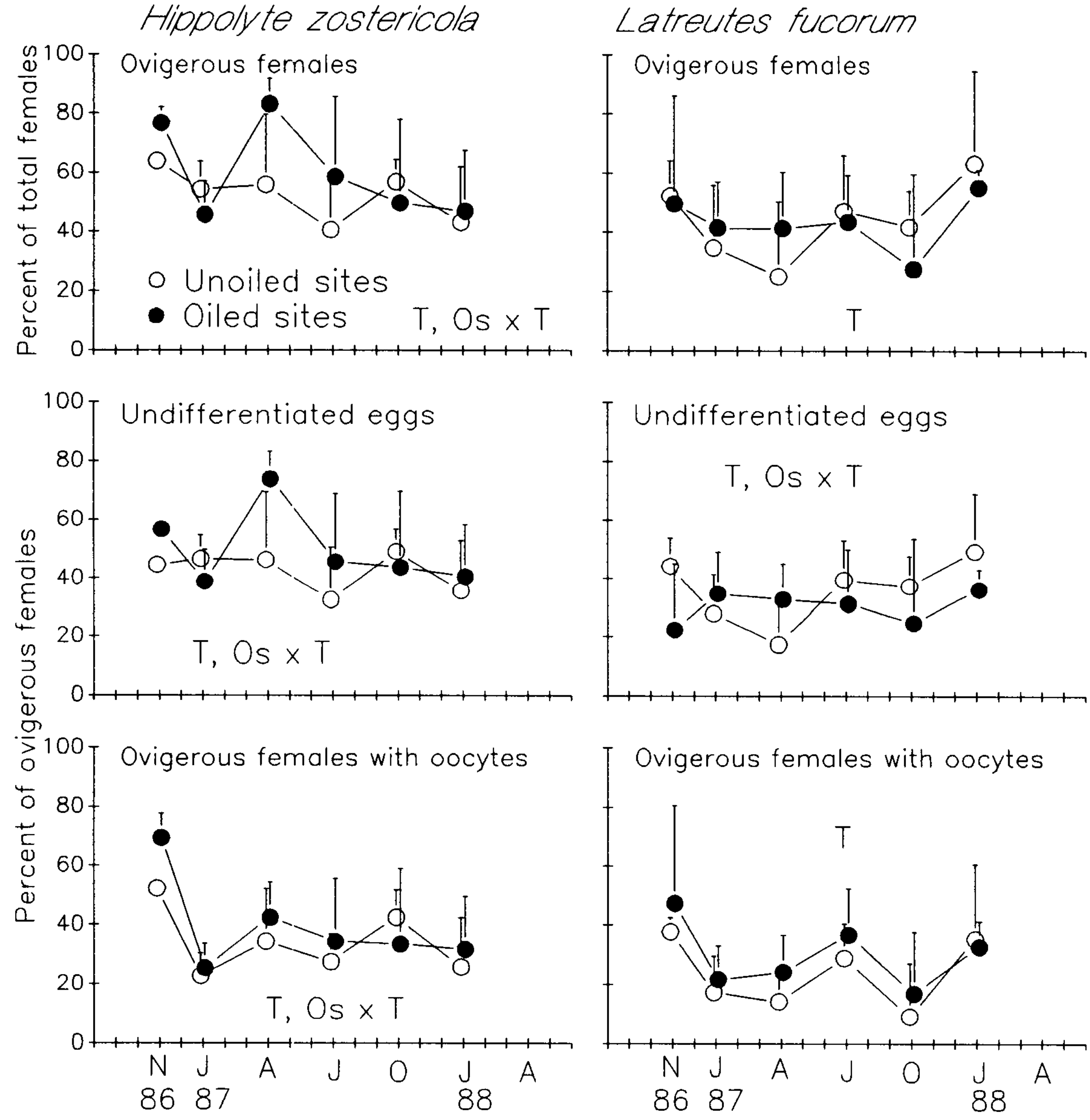

Fig. 10.18 **Reproductive patterns for two hippolytid shrimp (*Hippolyte zostericola* and *Latreutes fucorum*) based on egg and ovarian developmental stages described in Table 10.5. Refer to Appendix Table F.6.**

seagrass sediments (Table 10.3; Burns, Chap. 3) affected infaunal life cycles more than epifaunal recruitment and survival.

Echinoderm numbers differed by an order of magnitude between unoiled and oiled sites (2,407 vs. 97, respectively; Table 10.6; Fig. 10.10). Although holothurians and echinoids were not abundant, their numbers differed greatly and they can be

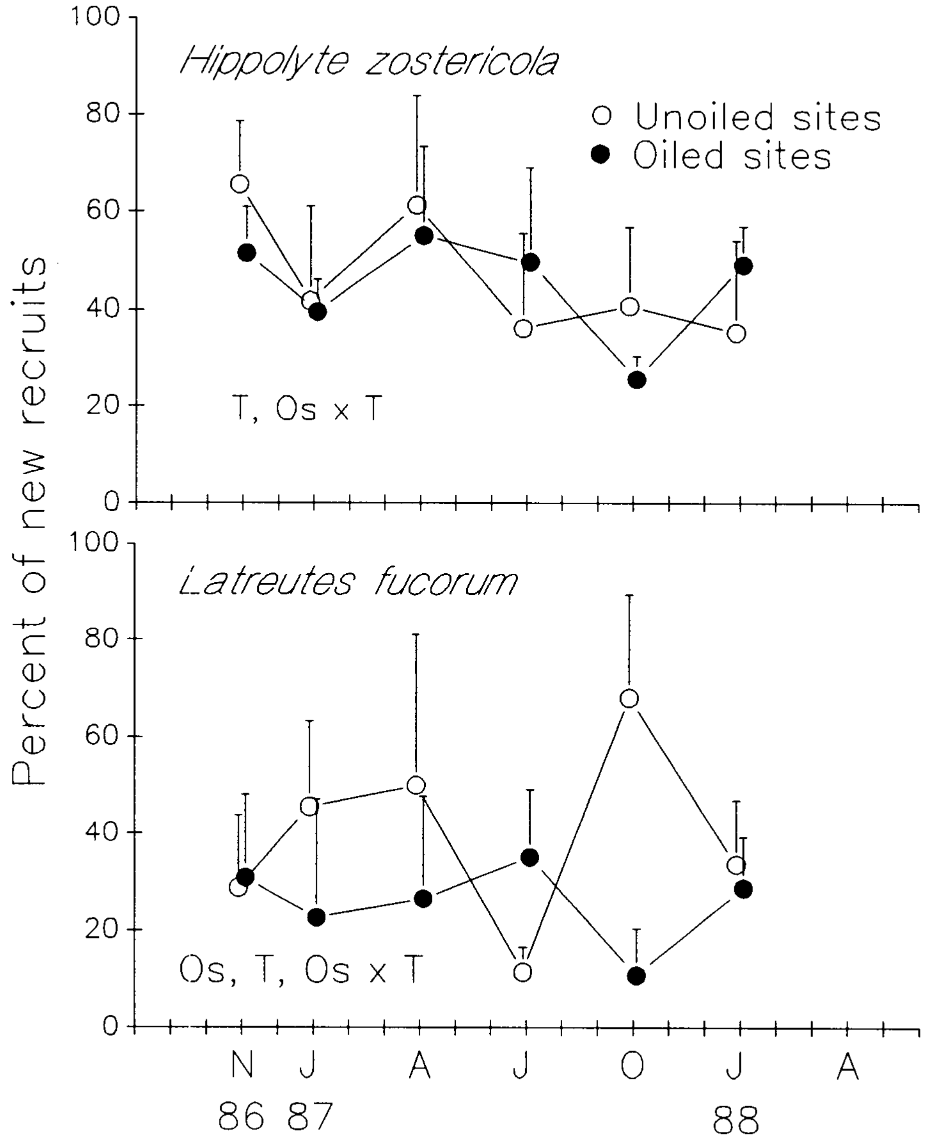

Fig. 10.19 Recruitment intensities for two hippolytid shrimp (*Hippolyte zostericola* and *Latreutes fucorum*). Individuals were considered "new recruits" if they were in the smallest 25% of the size range. Refer to Appendix Table F.6.

counted readily in the field. These groups may be useful as "indicator" taxa of oil pollution (see also Cubit and Connor, Chap. 4; Nelson-Smith 1973). In August 1992, more than 6 yr postspill, large epifaunal echinoderms were counted in 20-m^2 transects at each of the eight previously sampled beds; ophiuroids were not counted.

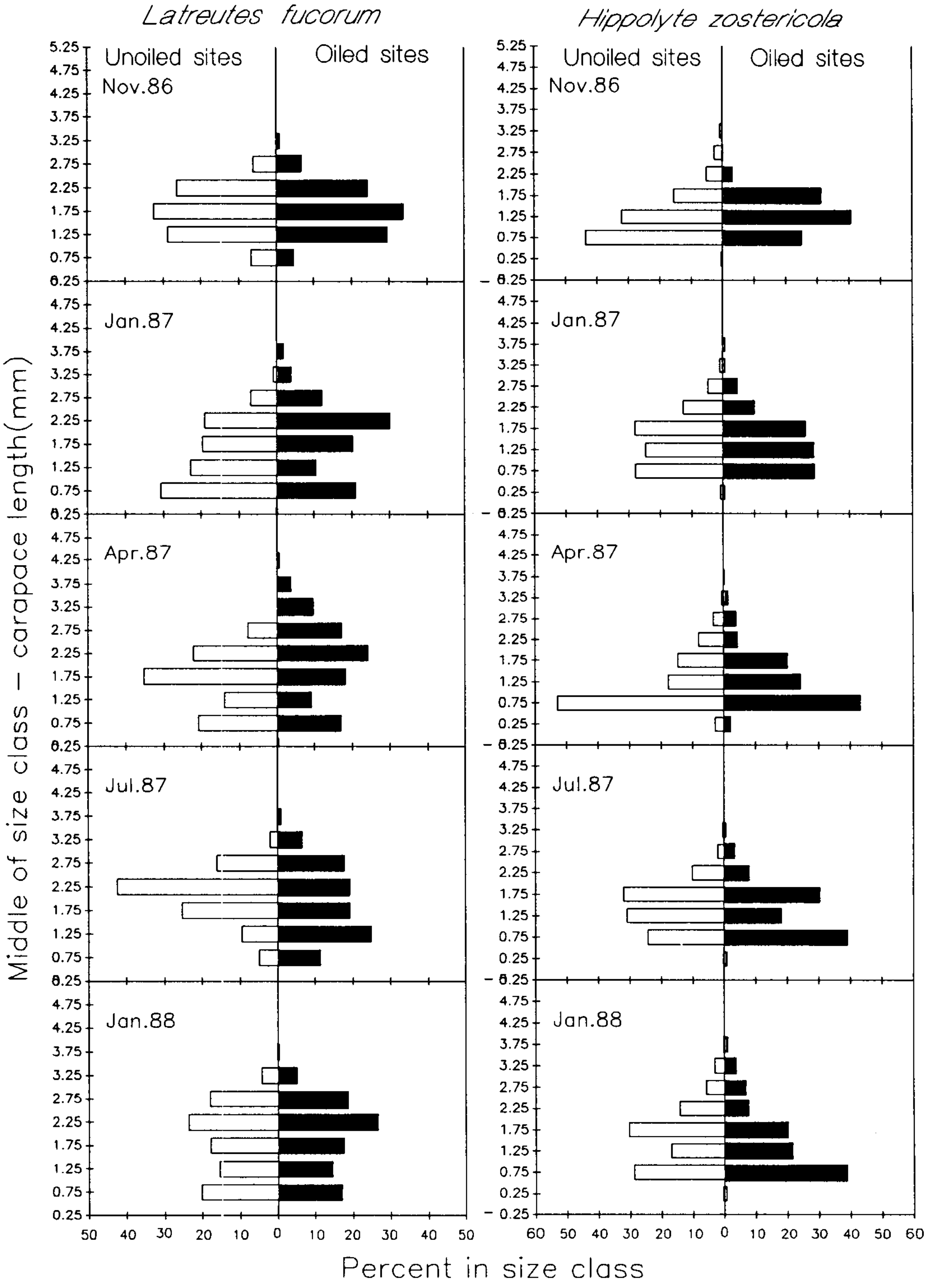

Fig. 10.20 Size distributions of two hippolytid shrimp (*Hippolyte zostericola* and *Latreutes fucorum*), November 1986-January 1988, at oiled and unoiled sites.

No large echinoderms were seen in the oiled seagrass beds, in contrast to 16 echinoids and six holothurians counted at unoiled sites (22/80 m^2). A few echinoids and one *Oreaster reticulatus* (asteroid) were observed outside the transects at oiled sites; numerous echinoderms were seen outside the transects at unoiled sites, including an additional transect of 20 m^2 at PALN containing 34 echinoids, seven holothurians, and one *O. reticulatus*.

Hippolyte zostericola appeared unaffected by the oil spill (Fig. 10.16), while a second caridean, *Latreutes fucorum*, appeared highly sensitive (Fig. 10.14). Oil sensitivities of these and other carideans in seagrass beds have not been reported previously. Most of these species are abundant in seagrass beds throughout the Caribbean and Gulf of Mexico (Bauer 1985; Virnstein 1987). Caribbean caridean species typically have continuous reproduction coupled with high temporal and spatial variation in recruitment patterns (Bauer 1987). The apparent lack of an effect of the spill on the development, reproductive output, and recruitment of *Hippolyte zostericola* and *Latreutes fucorum* from the first postspill collection suggest that (1) the biological activity of the weathered oil was low, (2) the reproductive potential of these two species is widely different, and (3) the density differences were mostly due to initial toxic effects in oiled seagrass beds.

10.6 Discussion, Conclusions, and Recommendations

Analysis of a set of sediment-core samples collected in 1988 showed that oil penetrated thick mats of seagrass roots and rhizomes (Table 10.3), which did not protect infauna from oil to a depth of at least 20 cm below the sediment surface. Oil persisted within sediments, in a weathered state, at concentrations well above levels at the sediment surface.

The Bahía Las Minas oil spill apparently had a transitory effect on subtidal seagrasses and a lasting effect (2-3 yr or more) on some animal taxa. The fauna of oiled seagrass beds remained highly altered compared to unoiled beds 5-7 mo to 2-3 yr postspill. Population declines caused by the spill apparently were quickly overcome only by species with high reproductive potential, planktonic stages, or both. Animals with low dispersal abilities and low reproductive potentials either took longer to recover or did not show signs of a recovery during 2-3 yr of postspill monitoring.

Although seagrass plants did not die-off in the subtidal areas sampled for infauna and epifauna, the loss of a large fraction of the fauna of seagrass beds probably disrupted food webs. Predators specializing on amphipods or tanaids probably switched to alternate prey or emigrated. Also, the loss of recruits from decimated populations in oiled seagrass beds may have resulted in population declines in distant, unoiled areas. Such indirect effects may occur well beyond the spatial confines and temporal limits of acute oil spill events, and should be considered in assessments of oil spill damage.

The fauna of seagrass beds can be highly variable from site to site. Amphipod abundance tends to decrease with latitude (Nelson 1980) and caridean species composition varies greatly between seagrass beds in the tropics and subtropics (Thorhaug and Roessler 1977; Bauer 1985; Marshall 1985; Holmquist et al. 1989*a*); these studies and this report identify different numerically dominant species of caridean shrimp in *Thalassia* beds. *Latreutes fucorum*, an oil-sensitive species in this study, accounted for 57% of the total number of carideans in Puerto Rican *Thalassia* beds. The overall effect of an oil spill on seagrass communities should be determined largely by the mixture of oil-sensitive and -tolerant species.

Despite faunal and floral affinities between Panama and shallow seagrass beds elsewhere in the Caribbean and Gulf of Mexico, differences between these areas may affect the outcome of a major oil spill. For example, large areas of shallow seagrass beds occur on bank tops in Florida Bay. These areas are nearly exposed, with seagrass blades protruding through the surface of the water during extreme low tides. Flushing rate, a factor that can alter removal rates of oil (Burns et al. 1991), is much lower in Florida Bay than Bahía Las Minas because tidal flow is restricted by numerous mud banks (Holmquist et al. 1989*b*). These banks support over one-half of the standing crop of seagrasses in Florida Bay (Powell et al. 1989). Fleshy algae are also much more important in Florida Bay (Lapointe 1989) than in Panama. The seagrass beds included in this study were all in lagoons bordered by subtidal coral reefs and adjacent to mangrove-lined shores. They are very small compared to seagrass beds of South Florida, are rarely exposed during low tides, and are flushed by relatively strong currents. Any prediction of effects of a major oil spill on seagrass habitats must take into account these and other differences in hydrodynamics, topography, and ecology.

The approach employed in this study of monitoring community composition of a wide size range of infauna retained on 0.5-mm mesh and epifauna retained by 1-mm mesh required many thousands of hours of laboratory work. Nevertheless, it was not possible to process most of the sediment-core and much of the push-net material. Based on the data presented here, planning of future investigations should consider focusing on certain groups. Large, epifaunal echinoderms (holothurians, echinoids, and asteroids) appeared particularly well suited for oil-spill studies because they are easy to identify and count in the field, and they appeared to have a strong, persistent numerical response to the spill in the shallow depths sampled.

Loss of area of oiled subtidal seagrass beds may have been considerable, particularly if the die-off of a 5-m wide band along the shoreward margin of LRS was widespread. Such loss of habitat could have extensive, long-lasting effects on the fauna of seagrass beds. Future studies should map beds (see Duke and Pinzón, Chap. 8) and possibly measure seagrass productivity, as well as standing crop.

10.7 Acknowledgments

Many persons helped us with the seagrass community study of the oil spill project. Those who deserve special thanks are Juan del Rosario, Carlos Gonzalez, Jose Gil, Itzel Angulo, Katie Goetz Moss, Alex Moss, Karl Kaufmann, and Helena Fortunato. Professor Luis D'Croz (Universidad de Panamá) graciously allowed us to work in his laboratory and helped us locate many of our assistants. Drs. Jeff Brawn (Illinois Natural History Survey), and Roger Green (University of Western Ontario) assisted with various aspects of the analyses presented herein. Digna Matías and Xenia Guerra collected the 1992 echinoderm data. Mote Marine Laboratory provided time for Dr. Marshall to complete this final report. We thank the editors for their efforts on this chapter.

11
Conclusions

Jeremy B. C. Jackson and Brian D. Keller

11.1 The Bahía Las Minas Ecosystem

Mangrove forests, seagrass beds, and coral reefs characterize Caribbean shores, such as Bahía Las Minas, and many other regions of the tropics worldwide. The physical structure of these habitats almost always is built, stabilized, and maintained by a few species of large, long-lived, photosynthetic organisms. Collectively, biogenic habitats buffer tropical coasts from freshwater runoff and erosion from the land, and wave energy from the open sea.

The red mangrove *Rhizophora mangle* protects shores from impacts of debris and waves, reduce water circulation, increase sedimentation, and provide shade and shelter. Seagrasses, especially turtlegrass (*Thalassia testudinum*), may cover hectares seaward of the mangrove fringe, and are supported by dense root and rhizome mats that stabilize sediments against erosion. Coral reefs are built primarily by a few species of corals and crustose coralline algae that produce the limestone framework and cement that is filled by skeletal debris of associated organisms. Reefs are the outer defense of the land against the sea, with calm-water, sediment-trapping lagoons and reef flats behind.

Mangroves, seagrass beds, and coral reefs are habitats for a great diversity of species. Many of the associated animals consume and thereby strongly influence the species composition and abundance of the habitat-structuring organisms on which they depend. The best-known cases are grapsid crabs feeding on mangrove seeds, and sea urchins, schooling fishes, territorial damselfish, and snails feeding on seagrasses, reef corals, and fleshy macroalgae (see Sect. 1.4).

11.2 Fate of the Spilled Oil and Environmental Damage

11.2.1 Pattern of Oiling and Methods of Assessment

The fate of the spilled oil fell conveniently into three phases: (1) spillage and entrapment in Bahía Cativá, (2) escape and dispersal into the larger Bahía Las Minas ecosystem and beyond, and (3) residual storage, chemical degradation, release, and redispersal thereafter. Details of the spill are described in Keller et al. (Chap. 1), Cubit and Levings (Chap. 2), Cubit and Connor (Chap. 4), and elsewhere (Cubit et al. 1987; Jackson et al. 1989). Most of Bahía Cativá was bathed in oil for 6 d, where biological effects were the most severe. The pattern of oiling afterward was more complex, and depended on many factors including distance from the refinery, directions of oil and water movement, adjacent topography, and sea level. Eventual deposition and storage of oil were greatest in low-energy environments, especially mangrove channels and streams, and seagrass sediments. Chemical dispersant was applied in some areas and may have contributed to localized toxic effects nearby. The restricted use of dispersant could not, however, have caused the widespread, subtidal reduction in living corals observed (Burns, Chap. 3; Guzmán et al., Chap. 7) and other widespread biological damage. In particular, the extensive mortality of subtidal corals on the Galeta reef was far removed from areas where dispersants were used.

The initial assessment of where the oil went, and in what quantities, was based on visual assessment from land, sea, and air. Sites along the coast in each habitat type were qualitatively ranked into three or four categories ranging from heavily oiled to unoiled. Subsequent chemical analyses of amounts and types of hydrocarbons present in samples of sediments, water, and organisms were generally in excellent agreement with ranks based only on visual assessment (Burns, Chap. 3). Moreover, there was also unprecedented agreement between results of different chemical analytical methods (UVF and GC) shown by highly significant correlations for very large numbers of samples.

These results further justify the "experimental treatment" approach for assessment of biological effects by analysis of variance, which was the cornerstone of most of the biological studies (Green 1979). Nevertheless, levels of oiling sometimes varied greatly within treatments in the same habitat type, so that a "dose-response" approach (e.g., Sheehan 1984*a*, *b*) relating amount of oiling to degree of biological effects on a site-by-site basis provided superior resolution when adequate hydrocarbon data were available. Good examples are the correlation of amounts of hydrocarbons to coral injury and growth rate, mangrove-leaf longevity and biomass, and proportions of dead mangrove roots.

11.2.2 Characterization, Persistence, Degradation, and Release of Oil from the 1986 Spill

Precise characterization of an unspilled sample of the original oil from the refinery allowed detailed study of subsequent chemical alteration in different environments and uptake by organisms (Burns, Chap. 3). Moreover, comparisons of the oil spilled at Bahía Las Minas with other common crude oils of the Caribbean region suggest that the fate and effects of the oil we observed could be expected in similar circumstances elsewhere.

Oil persisted in greatest quantities after the spill within sediments, and both the amount and length of persistence were inversely correlated with prevailing energy conditions and sediment grain size in the environment, a pattern that has been documented many times before (Vandermeulen 1982; Corredor et al. 1990). Sediments from reefs classified visually as heavily oiled showed initially high concentrations of hydrocarbons comparable to those near large oil fields or depots, but amounts decreased by an order of magnitude within 2.5 yr, and to trace amounts thereafter. Heavily oiled seagrass sediments had 10 to 100 times more oil than reef sediments, but this level also decreased by an order of magnitude within 2.5 yr.

Mangrove sediments contained the most oil (to 37% dry weight of sediments 5 mo after the spill), and oil was still present in large quantities 5 yr after the spill.

Oil in reef and seagrass sediments was greatly weathered and degraded in the first samples collected only 5 mo after the spill, but could still be clearly identified as coming from the refinery. In striking contrast, mangrove sediments from a heavily oiled stream contained a fairly fresh oil residue with a full suite of *n*-alkanes preserved 5 yr postspill. Moreover, significant levels of low-molecular-weight aromatics were still leaching from disturbed sediments 5 yr after the spill. Similar chemical stability has been demonstrated for oil trapped in saltmarsh sediments 20 yr after the oil spill at West Falmouth, Massachusetts (Teal et al. 1992) and in mangrove sediments in Puerto Rico (Corredor et al. 1990). Oil is still being flushed out of mangrove sediments at Bahía Las Minas in large quantities, as demonstrated by its abundance on recently submerged mangrove roots and experimental substrata, and by the almost chronic occurrence of oil slicks in mangroves and over reefs during the rainy season.

11.2.3 Sentinel Organisms

Bivalves preferentially accumulate more soluble, lower-molecular-weight hydrocarbons in oil-contaminated ecosystems (e.g., Widdows et al. 1982). Quarterly samples of the false mussel *Mytilopsis sallei* from streams and the oyster *Crassostrea virginica* from channels and lagoons were analyzed to monitor amounts of lower-molecular-weight hydrocarbons being released in mangrove environments (Burns, Chap. 3). Mussels had two times greater concentrations of these substances in their tissues than oysters. However, the significance of this result for estimating environmental levels is complicated by different uptake kinetics and possible tissue-saturation levels of the two species for animals exposed to the same environment.

Sentinel organisms used to monitor hydrocarbons must be, by definition, highly tolerant of hydrocarbons in the environment. Alternatively, one can also monitor the distribution and abundance of highly *intolerant* species as bioindicators of hydrocarbon pollution (Gray et al. 1980; Clark 1982), especially if they can be easily and quickly counted in the field. Echinoderms may fulfill these requirements well. Sea urchins were greatly reduced or eliminated after the spill in the seaward edge of two heavily oiled reef flats, and were still absent from one of the flats 5 yr afterward. Likewise, ophiuroids, holothurians, and echinoids were rare on heavily oiled seagrass beds throughout 2.5 yr of sampling, and holothurians and echinoids were still rare 6 yr after the spill in the shallow areas sampled. In contrast, four species of sea urchins tended to be more abundant at oiled subtidal reefs than at unoiled reefs 4 yr after the spill. Identifying pollution-sensitive species that also play key roles in communities may be very helpful (Kelly 1989) and requires further study.

11.3 Major Biological Effects and Their Persistence

The 1986 Bahía Las Minas oil spill had major biological effects in all environments examined including the principle habitat-structuring organisms of coral reefs, reef flats, mangroves, and seagrass beds. Moreover, initial effects of the spill displayed less taxonomic selectivity than observed after many natural disasters like hurricanes (Woodley et al. 1981). There were widespread lethal and sublethal effects on both infaunal and epifaunal populations. All trophic levels were affected, including primary producers, herbivores, carnivores, and detritivores. Highly mobile animals, such as large fishes, may have escaped direct effects of the spill, but were not studied.

11.3.1 A Model of the Chain Reaction of Habitat Loss and Biological Effects

Initial effects of the oil spill in Bahía Las Minas have set off a chain reaction of events that continue to severely affect organisms in all habitats, even though they may no longer be exposed to oil from the spill (Fig. 11.1). Analysis of aerial photographs showed that 64 ha, or roughly 7% of the entire area of mangroves in Bahía Las Minas in 1986, were killed by the oil spill, and smaller but extensive areas of seagrass beds were also killed. Death and injury of these habitat-structuring organisms resulted in physical destruction of habitats. Dead trees rotted and fell, logs and storms battered the shore, seagrass rhizome mats entirely disappeared, and sediments in all these environments eroded at rates up to several centimeters per yr. In some cases, like the seagrass bed at Isla Largo Remo North, 14 cm of sediment were removed.

The eroded sediments, and unknown amounts of varyingly degraded oil, were deposited in large amounts in neighboring environments, as measured by a more than doubling of resuspended sediments settling onto heavily oiled coral reefs between 1988 and 1991, while no increase occurred at unoiled reefs. There was also extensive deposition of sediments eroded from the seagrass bed at Isla Largo Remo North onto the adjacent bed at Isla Largo Remo West. Moreover, surviving mangroves and seagrasses, as well as associated organisms, are still repeatedly exposed to relatively fresh and toxic hydrocarbons, which further retards possibilities of recovery and decreases the productivity of these communities.

The secondary biological consequences of erosion and redeposition of oily sediments include greatly increased levels of injuries and decreased growth and sexual reproduction for surviving subtidal reef corals in Bahía Las Minas compared to reefs outside the bay. Other more speculative, but very plausible, effects are seen in the shift toward somewhat greater dominance of oiled reefs by fleshy macroalgae, which act as sediment traps. Also, changes occurred in food webs on reefs now dominated by damselfishes instead of larger and more voracious schooling fishes that were present in considerable abundance at the Punta Galeta reef before the spill (Hay et al. 1983).

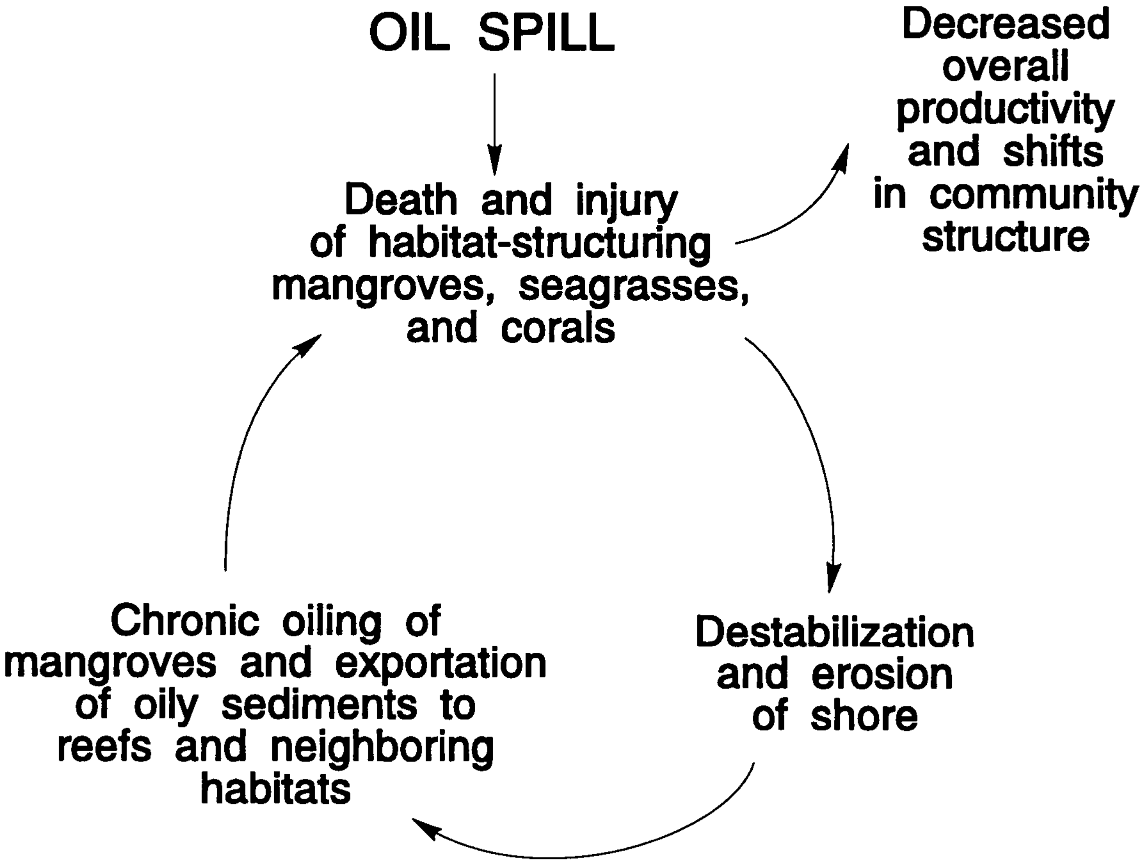

Fig. 11.1 A model of the chain reaction of habitat and biological damage due to the 1986 oil spill at Bahía Las Minas.

The inevitable consequence is that the entire Bahía Las Minas ecosystem is more vulnerable to subsequent natural or anthropogenic disturbances. Hints of this appear in the patterns of macroalgal mortality on reef flats due to extremely low tides in 1988. Macroalgae died back much more on previously oiled reefs, suggesting that re-establishing populations were more vulnerable to natural disturbances than those unaffected by the oil spill. Another example is the comparative failure of recruitment in Bahía Las Minas of corals that broadcast gametes into the sea, as compared with much higher recruitment on other reefs where the same species suffered apparently natural catastrophic mortality less than 2 yr after the oil spill.

11.3.2 Reef Flats

The biology of the Punta Galeta reef flat has been studied for 20 yr. Natural variations in abundance are well documented for sessile organisms and sea urchins for most of that time, and extensive data exist for stomatopods covering nearly a decade. In addition, communities were intensively watched just before and during the time the oil came ashore, and for months afterward. Thus, in this case, observations of biological effects are not just based on statistical comparisons of conditions before and after the oil spill, because in many cases scientists watched organisms die as they were immersed in oil.

Macroalgae, crustose coralline algae, and sessile invertebrates at and near the seaward edge of the reef flat were directly exposed to oil and suffered heavy mortality, resulting in the lowest cover of these organisms measured in 20 yr (Cubit and Connor, Chap. 4). Elevation of the reef flat varies by only a few centimeters over wide areas, so the spatial pattern of damage was highly dependent on sea level and weather at the time of the spill. Apparent recovery (ignoring issues of resilience to future damage and a few particular species) was complete within a year, except for sessile invertebrates at the seaward edge, which declined everywhere after the lowest sea levels ever recorded at Punta Galeta in 1988.

Effects on mobile animals were more variable, depending on their physiology and behavior. Sea urchins suffered an immediate, precipitous decline that could be distinguished statistically from normal variation despite the typically highly episodic fluctuations of sea urchin populations characteristic of this environment (Cubit and Connor, Chap. 4). Recovery was rapid at all but a single reef flat adjacent to the refinery.

Stomatopods were virtually eliminated from one site where the seagrass bed disappeared; these had not recovered after 5 yr (Steger and Caldwell, Chap. 6). Seagrass beds disappeared from at least three additional sites; in all cases, reef flat topography caused oil to be trapped in the beds. Abundance and size decreased at the other oiled site as well, compared to two unoiled or slightly oiled sites. The consequence was more rapid growth, and decrease in aggression and competition for living cavities among survivors which actually enjoyed greater habitat quality and less injury than those on unoiled reef flats.

The small infauna of the foliaceous macroalga *Laurencia* suffered considerable mortality immediately after the spill, but populations were very similar among oiled and unoiled reef flats within 1 yr when detailed comparative investigations began (Cubit and Connor, Chap. 4).

Snails also died at heavily oiled sites on a reef flat near Punta Galeta, but not at one control site until the latter was affected by a small diesel fuel spill (Garrity et al., Chap. 5).

The Bahía Las Minas spill resulted in a band of community die-off and rapid recovery of most taxa, but this may not always be the case. A spill of a more toxic oil than weathered crude or a more prolonged and extensive exposure to oil could result in greater mortality and slower recovery on reef flats.

11.3.3 Reef Corals

The cover, size, and diversity of live corals decreased greatly on two oiled reefs compared to their values before the oil spill, while values initially increased on unoiled reefs (Guzmán et al., Chap. 7). These differences persisted, although diminished, even after the occurrence of precipitous, unexplained coral mortality at unoiled reefs between 1986 and 1988. In contrast, numbers of corals increased on oiled reefs as formerly large colonies were reduced to larger numbers of small, surviving fragments of live tissue. Likewise, the frequency of injuries to corals was much higher on heavily oiled reefs. These patterns were significantly correlated with both the amount of oil in reef sediments and subsequently increased amounts of resuspended sediments at heavily oiled reefs. The apparent sublethal consequences for corals included decreased growth, reproduction, and recruitment, which resulted in little prospect for rapid recovery.

11.3.4 Mangrove Forests

The area, condition, and maturity (successional state) of mangrove forests in Bahía Las Minas were determined using a combination of multiple aerial photographic surveys of the region taken over the past 25 yr, and ground surveys of present conditions to calibrate the images in the photographs and make additional observations (Duke and Pinzón, Chap. 8). Deforestation after the 1986 oil spill amounted to 64 ha, mostly in an approximately 50-m wide coastal strip, and as wedges penetrating entrances of smaller streams. This is about 7% of the total area of mangroves in the bay. By comparison, the 1968 oil spill following the wreck of the tanker *Witwater* resulted in the death of 46 ha, or roughly 72% of the 1986 value.

Measurements were made of the status of the canopy of surviving trees as an assay of forest condition. Factoring out salinity as a confounding variable, the numbers of leaves per shoot, leaf longevity, and leaf biomass per hectare all decreased significantly with the amount of oil in mangrove sediments. Thus, the oil spill affected far more than the area of forest that actually died.

11.3.5 Mangrove Fringe and the Epibiota of Mangrove Roots

The oil spill had immediate biological effects on the epibionts of mangrove prop roots on the open coast, in channels and lagoons, and in streams (Garrity and Levings, Chap. 9). Within 3 to 9 mo most of the common taxa were greatly reduced or eliminated. This was clearly evident in all but coastal mangroves by piles of recently dead mollusc shells at oiled sites, as well as by statistical comparisons of community composition at a smaller number of sites before and after the spill. Community composition on roots had not recovered completely in any of the three environments after 5 yr.

Open-coast roots in Bahía Las Minas were dominated by foliose macroalgae before the spill, and the same was true at unoiled sites afterward. These populations had nearly recovered at the end of the study. Channel and lagoonal root community composition varied considerably with local differences in salinity, other environmental factors, and patterns of reoiling and new oiling. Nevertheless, there was a catastrophic decrease in abundance of oysters and other bivalves at oiled sites after the spill compared to unoiled mangroves, with little or no recovery evident after 5 yr. The same was true in streams where roots had been dominated by false mussels, along with lesser populations of barnacles and foliose algae. None of these has recovered.

In addition to these effects on epibiota, there was substantial loss of mangrove roots as substrata. The area of mangrove fringe lost 5 yr after the spill totaled 33%, 38%, and 74% on the open coast, in channels, and in drainage streams, respectively. This habitat loss probably affected associated mobile fauna, as well as the sessile epibiota.

11.3.6 Seagrass Beds

The reef flat seagrass bed at Largo Remo North died and disappeared completely (Steger and Caldwell, Chap. 6), and the area of shallow subtidal beds decreased (Marshall et al., Chap. 10), after the oil spill. Biomass of surviving parts of beds declined considerably, but such thinning occurred at unoiled beds as well. Numbers of infauna were much lower in oiled beds after the spill, and these differences persisted for more than 2 yr. Amphipods, ophiuroids, sipunculids, and tanaids were the groups affected most, whereas hermit crabs increased, perhaps due to increased availability of shells. Epifauna showed generally similar patterns. The most lasting difference was in the total number of echinoderms (ophiuroids, echinoids, and holothurians) that were moderately abundant at unoiled sites but still virtually absent from oiled seagrass beds after 2.5 yr. This pattern still held after 6 yr for large echinoids and holothurians (ophiuroids were not counted).

11.4 Processes of Repopulation (Recovery)

The re-establishment of populations to levels similar to those before an oil spill depends on at least six factors.

1. **Severity of initial damage**: The amount of biological damage after the spill, relative to fluctuations due to natural processes characteristic of the species or region in question, provides a measure of severity independent of the typically large differences that exist between habitats and regions. By this criterion, effects of the 1986 oil spill were severe for all habitats, with the exception of many of the inhabitants of reef flats exposed to the open sea (Sect. 11.3.2).

2. **Extent of habitat destruction**: The extent of mortality of habitat-structuring species and the persistence of oil in the local environment together determine the magnitude of habitat loss (Sect. 11.2.4).

3. **Frequency and severity of previous damage**: The known biological history of the ecosystem may be of great importance in assessing re-establishment of populations.

4. **Life-history characteristics**: Maximum potential recruitment and growth rates, and modes of reproduction and dispersal, limit the speed at which repopulation can occur.

5. **Multiple stable states**: Interactions with other pre-existing or newly invading species, and the potential for nonlinear dynamics, threshold effects, and the development of alternative communities may prevent return to pre-existing conditions for indefinite periods.

6. **Restoration**: Success of human intervention to restore damaged habitats depends fundamentally on the amount and quality of basic biological knowledge of the species involved.

The model of habitat and biological damage after the oil spill (Fig. 11.1) was based on observations during this study. We expect that habitat-structuring organisms will recruit and repopulate areas damaged by the spill, and that this will eventually lead to stabilization of the shore and decreased releases of oil (Fig. 11.2). Mangrove trees have started the long process of recruitment and growth in many areas, but require at least 50 yr to reach full adult size. However, reef-building corals are not recruiting on oiled reefs in sufficient numbers to replace the lost cover, and seagrass plants have not spread or recruited into the shoreward, subtidal margins and intertidal beds that were killed. We cannot accurately estimate the time required for coral reef and seagrass habitats to recover, but note that massive corals such as the dominant forms in Panama may require a century or more to reach the size of many of the colonies killed by the spill.

11.4.1 Recruitment and Growth Potential

How fast a species repopulates a devastated area depends on its generation time, which is in turn a function of rates of reproduction, recruitment, and growth to sexual maturity (e.g., Hutchinson 1978; Connell and Keough 1985; Pimm 1991). Generation times are long for all the important habitat-structuring species in this study, including red mangroves, turtlegrass, and the formerly dominant corals, which produce relatively few offspring and may take 10 to 50 yr to mature. In contrast, individuals of associated mobile and epibiotic species, like sea urchins and oysters, produce millions of gametes and tens of thousands of larvae, and mature in one or a few years.

Evidence suggests that remnant oil in Bahía Las Minas reduced considerably the recruitment of sea urchins, stomatopods, reef corals, and mangrove epibionts. In the last two cases, recruitment is still extremely low throughout the bay, and the

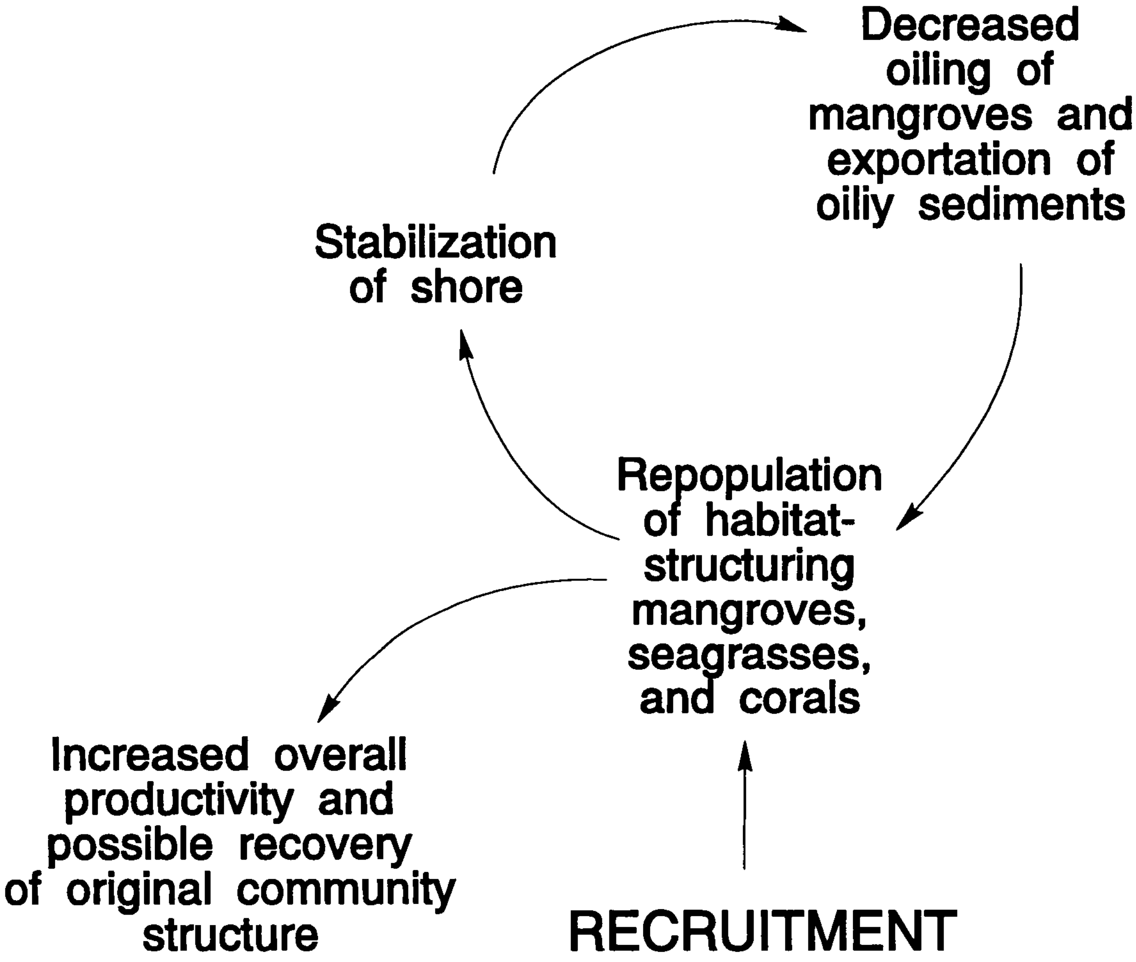

Fig. 11.2 A model of the presumed cycle of repopulation of habitat-structuring organisms and diminishing release of oil.

others have recovered except at sites closest to the refinery. Likewise, growth rates of corals and, most strikingly, of mangrove seedlings and trees, were reduced at oiled sites. Recovery of trees in heavily oiled forests is so slow that it was possible to pick out damage due to the 1968 *Witwater* oil spill in photographs taken more than 20 yr afterward.

11.4.2 Modes of Reproduction and Dispersal

Two striking patterns have emerged in relation to the oil spill. The first involves the relative importance of clonal (asexual) versus sexual reproduction (Jackson et al. 1985). Most mobile species in Bahía Las Minas, including sea urchins, stomatopods, and gastropods only reproduce sexually, usually by the spawning of gametes into the water which, if fertilized, develop through one or more larval stages before settlement on the bottom. Larval dispersal typically ranges from hundreds of meters to hundreds of kilometers (Jackson 1986). In contrast, most algae, seagrasses, red mangroves, corals, and other modular sessile animals (e.g., sponges and soft corals) reproduce clonally (asexually) as well as sexually, usually by some form of fragmentation, partial mortality, or budding of independent propagules (Jackson et al. 1985; Jackson 1991). Clonal dispersal typically occurs over distances of only a few meters (Jackson 1986).

Recruitment of the latter groups since the oil spill has been almost entirely by clonal propagation, with virtually no larval recruitment of any formerly dominant species at heavily oiled sites. Thus, foliaceous macroalgae at the seaward edge of the reef flat recruited exclusively from small surviving remnants, and sessile animals, including zoanthids and corals, were washed in by waves from more seaward, subtidal populations. Similarly, the numbers of subtidal coral colonies *increased* after the oil spill as formerly large colonies were reduced to several small remnants. Survival of coral populations on oiled reefs has depended almost entirely on these bits and pieces rather than new larval recruits.

The second pattern involves the relative proportions of brooding versus broadcasting species, and is most obvious for corals (Guzmán et al., Chap. 7; Jackson 1986, 1991; Richmond and Hunter 1990). Brooders produce larger larvae that settle immediately or in a few days, and may never rise to the surface. In contrast, broadcasters spawn gametes that require usually two or more weeks of development in the water column after fertilization before they are competent to settle. Thus, larvae of broadcasting species should be more vulnerable to chronic oil slicks in Bahía Las Minas than brooding species, and this seems to be the case.

Recruitment rates of brooding corals are normally much higher than broadcasting species, but both occur commonly on unoiled reefs in Panama and elsewhere (Szmant 1986; Bak 1987; Guzmán et al. 1991; Jackson 1991; Soong 1991). In contrast, recruits of broadcasting species were almost absent from heavily oiled reefs after 5 yr. In general, colonies of brooding corals are smaller than those of broadcasting species, which include the most important framework builders of Caribbean reefs, in particular *Acropora palmata*, *A. cervicornis*, *Montastrea "annularis,"* the brain corals (*Diploria* spp.), and *Siderastrea siderea*. Thus, we expect a shift in community composition on heavily oiled reefs toward dominance by small brooding species, as observed by Bak (1987) in his survey of chronically oiled and unoiled reefs at Aruba.

Other abundant taxa whose recruitment was affected by the oil spill are all broadcasters, including sea urchins, stomatopods, barnacles, and bivalves. Experiments using transplanted false mussels into mangrove root environments showed some decrease in adult survival, but greatly reduced recruitment at oiled sites (Garrity and Levings, Chap. 9). In addition, mussel larvae appear to be attracted to shells of other mussels. Thus, lack of recruitment in oiled streams may also be due to lack of suitable settlement cues, a factor that could contribute to threshold effects in repopulation.

11.4.3 Alternative Communities

Population collapse due to any catastrophe can result in major shifts in the relative abundance of predators and prey, or of different competitors. Such shifts can lead to the establishment of alternative stable communities at the same site. This happens when a devastated species is unable to become re-established in the face of the overwhelming presence of its enemies, and other species may take its place (Sutherland 1974; May 1977). Good examples for coral reefs include the collapse of the staghorn coral *Acropora cervicornis* after a major hurricane in Jamaica, and the development of apparently stable non-coral communities on the Great Barrier Reef following devastations by the crown-of-thorns starfish (Knowlton 1992).

There is as yet no evidence for threshold effects due to the oil spill in Bahía Las Minas, but there are several possibilities. Sea urchins may have a profound effect on seagrass beds (Camp et al. 1973; Greenway 1976; Vadas et al. 1982; Keller 1983), yet sea urchins have been all but eliminated from oiled seagrass beds for years. Another possibility involves the probable build up of brooding corals on heavily oiled reefs. If these species become well established once levels of secondary oiling decline, then it may be very difficult for broadcasting species to find space to settle and displace them.

11.4.4 Cleanups and Restoration

Human assistance of repopulation may be a valuable option, especially when threshold effects seem to prevent the re-establishment of desired populations of either habitat-structuring organisms or their associates (Cairns and Buikema 1984; Jordan et al. 1987; Guzmán 1991). However, it is crucial that any such efforts be guided by a clear understanding of the critical biological characteristics of the species involved. Otherwise, intervention can do more harm than good.

This appears to have been the case in the clearing and planting of seedlings in heavily oiled mangroves (Duke et al. *in press*; Duke and Pinzón, Chap. 8). Clearing and planting reduced the numbers of older seedlings that survived the spill and postspill recruits, even though their abundance would have been adequate for recovery without additional transplanted seedlings. Moreover, the clearing of dead mangroves for the massive planting effort destroyed natural shelter provided by the dead timber, roots, and soil, causing greatly increased erosion. Thus, both seedling height and abundance are now much greater at *unplanted* sites. Careful cleaning of individual trees with minimal disturbance of the habitat would have been much more successful.

Another possible problem involves cleanup of spills. Repopulation of sessile organisms on reef flats, and the very survival of populations of reef corals, have depended upon growth and localized dispersal of surviving remnants of once much larger plants and animals. These remnants could easily be eliminated by aggressive cleaning of oily substrata, which would greatly retard repopulation of these communities because clonal propagation is generally effective only over very short distances compared to dispersal of spores or larvae (Connell and Keough 1985; Jackson 1985, 1986).

11.5 Recommendations for Future Studies

11.5.1 Importance of Scale of Observations

A regional perspective is essential for understanding biological consequences of any large, catastrophic event. For example, coral reefs throughout the Caribbean have suffered extensive damage in the last decades from disease, bleaching, indirect effects of the mass mortality of the sea urchin *Diadema antillarum*, deforestation, and pollution (D'Elia and Taylor 1988; Lessios 1988; D'Elia et al. 1991), independent of any effects of oil spills. Knowledge of the dynamics of populations in areas adjacent to Bahía Las Minas was essential to factor out such effects from those potentially due to the oil spill. Examples of regional changes included the decline of corals outside Bahía Las Minas between 1986 and 1988, and decreased recruitment of stomatopods on reef flats all along the coast between 1987 and 1989.

Lack of a regional perspective was a shortcoming in the STRI Marine Environmental Sciences Program before the oil spill, as evidenced by the entirely fortuitous nature of the data on coral community composition at oiled and unoiled sites before the spill. No amount of long-term data from a single site can factor out regional from local effects, despite the contribution to scientific understanding of detailed observations of biotic interactions and physical effects. Long-term monitoring should always involve a network of sites such as that used to follow outbreaks of crown-of-thorns starfish on the Great Barrier Reef (Done 1985, 1992).

Time-series aerial photographs coupled with ground-truth observations were highly successful in documenting damage to mangrove forests from two major oil spills. This technique should also be applicable for measuring changes in aereal extent of seagrass beds, and thus provide most of the necessary information on habitat loss. In the case of seagrasses, measurements of plant growth and standing crop along with densities of grazing sea urchins and fishes should lead to an understanding of the dynamics of the habitat.

By many standards this study was long-term. However, considering the life cycles of habitat-structuring organisms such as corals and mangrove trees, it was not. For mangrove forests, aerial photography at 5-yr intervals coupled with observations and experiments on population dynamics and forest productivity should be adequate for a core monitoring program. Reef corals require annual censuses of fixed quadrats to follow individual survival and growth. These should be combined with observations and experiments on recruitment and survivorship of small individuals, which are highly susceptible to mortality (Hughes and Jackson 1985).

11.5.2 Importance of Initial Damage Assessment

No statistical design can make up for lack of basic observations immediately before, during, and after a catastrophic event like an oil spill. If there is advance warning, photographs of habitats and the most cursory surveys may be invaluable for subsequent assessment of biological effects. Aerial photographic surveys should be made immediately throughout the region of the spill, both to document the spread of oil and to provide a record of vegetational distributions that may serve as baseline data for biological effects. In general, the guiding principle should be to emphasize simple, easily repeatable observations to determine the scale and pattern of the spill and its immediate biological consequences. More detailed and difficult observations should come afterward when the general scope of the problem is better understood and greater resources may be available.

Our results demonstrate that careful visual surveys can provide an excellent indication of patterns of oiling in both intertidal and subtidal environments. Moreover, the value of these surveys would have been increased greatly by collection of more sediment and seawater samples for simple volumetric calculations of amounts of oil. None of this requires detailed analytical hydrocarbon analyses, which can therefore be reserved to address important questions of weathering and toxicity rather than mere dispersal. Analyses need not exceed the accuracy and precision required to answer ecological questions. Strong support for this approach is evident in this final report, which has turned up few contradictions to initial impressions of the oil spill based on preliminary surveys (Jackson et al. 1989).

Initial biological surveys should emphasize abundant species or those known to play an important ecological role in their community (habitat structure, predators). These should include observations of the condition as well as numbers or cover of species. For example, the incidence of recent injuries to corals was one of the best early indicators of the effects of the spill on reefs, especially those for which cover data before the spill were unavailable. Simple mapping of the dimensions of seagrass beds, measurements of growth rates of leaves, and counts of large, obvious organisms like sea urchins, holothurians, and starfish would have provided a much more rapid and inclusive picture of possible effects of the oil spill on seagrass beds than the collection of infaunal samples that are time consuming to process.

11.5.3 Exploitation of Basic Biological Knowledge Versus the "Black-box Syndrome"

Understanding the consequences of an oil spill requires basic biological knowledge of the taxa involved. Prediction is impossible without data on vital statistics, natural enemies, behavior and reproductive characteristics. Whenever possible, therefore, studies should emphasize groups that are well understood biologically, even if they are not always the most abundant or ecologically important in the community. Otherwise, one is reduced to simply cataloging differences in abundance between oiled and unoiled sites, and treating the entire problem of biological effects and recovery as a "black box."

Thus, for stomatopods, growth rates increased and injuries decreased on oiled reefs because empty living cavities were available without animals having to fight for them, rather than any direct effect of the oil. Similarly, mangrove canopy production decreased as trees adjusted to loss of roots in oiled sediments, coral recruitment patterns changed according to simple, species-specific differences in patterns of larval development and dispersal, and failure of bivalves to recruit to mangrove roots may be due to larval settlement preferences as well as physiological effects of residual oil in the environment. In all these cases, however, more emphasis on ecological processes rather than simply monitoring would have substantially increased our ability to predict patterns of future repopulation.

11.5.4 Retrospective Analysis

The reconstruction of effects of the 1968 *Witwater* oil spill on mangrove forest structure is the most dramatic example of the power of retrospective analyses. Aerial photographs combined with the dissection of four trees growing on new land of known age was the key to identifying damage that was missed in earlier studies (Rützler and Sterrer 1970; Birkeland et al. 1976). Patterns of leaf nodes on mangrove seedlings to measure past growth, and sclerochronological studies of coral growth, injury, and regeneration are other powerful tools for identifying biological effects long after an event has passed (Dodge and Lang 1983; Knowlton et al. 1992; Duke and Pinzón 1992).

11.5.5 Modeling Different Scenarios

Every oil spill is different in the kinds and amounts of oil spilled, the weather and sea conditions at the time of the spill, and the special characteristics of the areas affected. Nevertheless, it is important to identify which of these differences are fundamental to the consequences of an oil spill, and which are simply interesting details. Thus, small differences in sea level and weather conditions, as occurred during the *Witwater* and 1986 oil spills, may make an enormous difference in patterns of damage after a spill (Cubit and Levings, Chap. 2). However, reef flat communities tend to repopulate very rapidly, so that such differences in damage may be of little practical importance, within limits (Sect. 11.4). On the other hand, quite similar areas of mangroves died after both spills, despite the difference in prevailing conditions and amounts and type of oil spilled. So for mangroves, the single most important factor is whether oil is trapped in the forest, almost regardless of how it got there.

In general terms, the chain reaction of habitat and biological damage triggered by tropical oil spills should eventually be countered by cycles of habitat recovery and shoreline stabilization (Fig. 11.3). There is still habitat loss and coastal erosion in Bahía Las Minas from the 1968 *Witwater* spill, and much of this seems "permanent." As should be expected, slow-growing, long-lived organisms require considerable time to recover fully from extensive die-offs, almost regardless of their causes.

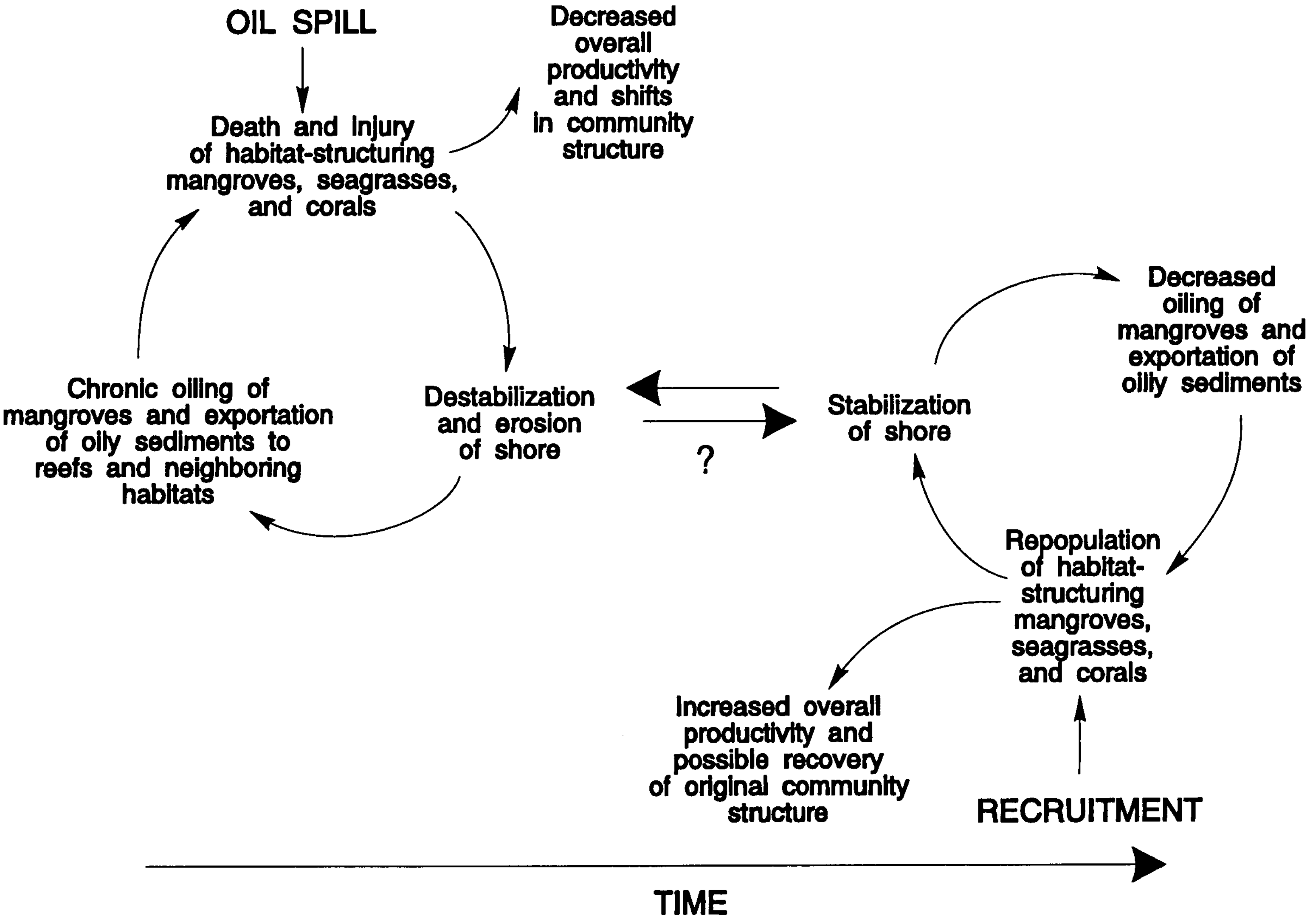

Fig. 11.3 Models of habitat damage and recovery, showing the likely link at the process of shoreline stabilization.

11.5.6 Coupling Laboratory Experiments with Field Studies

Carefully designed laboratory experiments simulating field pollution levels and testing various aspects of the life histories of key organisms could advance our knowledge of effects of hydrocarbons on biota. For example, life-history parameters of adult reef-building corals (growth, survivorship, reproduction, etc.) and coral planulae (settlement, survivorship, development, etc.) should be investigated further in controlled laboratory experiments. Table 1.1 provides at least a partial list of tropical organisms to consider for such research.

11.5.7 Comparisons and Interpretations

No two sites in a particular habitat are exactly the same at some level of detail, so that a basic problem in site replication is the degree of difference acceptable for the scientific questions being asked. Field biologists characteristically use their judgement to determine the suitability of replicate sites. Although statistical procedures exist to identify "outliers," decisions by experienced biologists should be sufficient for choosing replicate sites in most environmental assessments. The main point is to decide how similar sites are and then limit questions appropriately.

This problem extends to statistical comparisons of oiled and unoiled sites, particularly if no prespill data exist. If sites were similar before a spill and significantly different afterward, there is an "optimal" demonstration of an effect of the spill (Green 1979). However, if sites were not studied before a spill, any postspill differences may or may not have been caused by the spill, or may be a combination of natural and spill-related factors. This is the reason for the extensive discussion of site differences as confounding effects in Chapters 4 and 9.

A final consideration involves applying findings from a study such as this one to other regions. This study was undertaken with the implicit assumption that Panamanian coastal habitats were similar enough to South Florida for the results to have some applicability there. For example, the model of habitat and biological damage (Fig. 11.1), should be generally applicable to any tropical coastal environment as long as confounding factors are understood.

11.6 Responses to Oil Spills

It cannot be overemphasized that all reasonable efforts must be taken to keep oil out of mangroves, seagrass beds, and equivalent habitats elsewhere, such as saltmarshes. Oil trapped in these environments can persist and remain toxic for decades, and is virtually certain to set off the kinds of chain reactions illustrated in Figure 11.1. No oil processing or shipment facility near such habitats should be without adequate booms and other equipment ready for *immediate* deployment. The average time for repopulation to original levels after inadequate protection is probably on the order of 50 yr. For all these reasons, realistic and well-maintained programs to keep oil out of mangroves should be an absolute policy requirement regardless of cost (which is almost certainly less than the real cost in lost resources if a mangrove forest is oiled).

Although less visible, almost the same can be said for coral reefs. Large acroporids that provide most of the vertical structure and habitat complexity in shallow reefs worldwide are the most sensitive corals to effects of oil (Brown and Howard 1985; Bak 1987; Guzmán et al. 1991). Moreover, because these species rely to a large extent on clonal propagation (Highsmith 1982*b*; Jackson 1991), repopulation may take decades despite the very rapid growth rates of these species (Bak 1987; Knowlton 1992).

Data for seagrasses are much less complete, especially for survival and dynamics of the beds themselves. However, the death and destruction of the entire bed at Isla Largo Remo North serves as a warning for what could happen after a major spill in areas of large intertidal seagrass beds, as in Florida Bay and the Bahamas.

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Appendix A
Oil Spills in Tropical Seas

App. Table A.1 Tanker spills occurring in tropical waters, 1974-15 June 1990. Amount spilled = bbl. Summarized from MMS Worldwide Tanker Spill Database.

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
9	2	74	H Endurance	7,330	Nigerian Crude	09:00N	013:00W	2	Freetown, Sierra Leone, W Af.
13	2	74	Sea Spray	44,000	Crude	Unsp	Unsp	0	Northern Southeast Asia
17	3	74	Aegis Leader	14,660	Bunker Fuel	Unsp	Unsp	103	Abu Dhabi, Persian Gulf
10	4	74	Visahakit I	5,637	Bunker/Fuel Oil	13:45N	100:30E	62	Gulf of Thailand
22	4	74	Korea Hope	3,665	Fuel Oil	Unsp	Unsp	26	Str. of Malacca, Singapore
27	6	74	Najd	21,990	Residue Oil/Oilcakes	22:00N	039:00E	105	Jeddah, Red Sea, Saudi Arabia
15	7	74	Great Loyalty	3,665	Bunker Fuel	Unsp	Unsp	324	Str. of Malacca, Singapore
16	7	74	Monmouth	3,665	Fuel Oil	Unsp	Unsp	29	N Indian Oc., Asia-India
23	7	74	Theodoros V	146,000	Crude	21:08N	018:41W	74	Mid-Atl., 400 m N of Dakar, Senegal
25	9	74	Eleftheria	73,300	Lubricants	06:00N	016:00W	2	Atlantic Oc.-Sierra Leone, W Af.
26	9	74	Transhuron	32,441	Crude (Naphtha?)	11:30N	073:01E	65	Kiltan Island-SW Coast of India
10	10	74	Trojan	73,300	Fuel Oil	Unsp	Unsp	60	Pac. Oc.?/China Sea?-Phillipines
16	10	74	Nikko Maru	3,665	Bunker Fuel	Unsp	Unsp	26	Str., S China Sea, Singapore
13	11	74	Savfuel	4,398	Fuel Oil	17:20N	087:30W	45	Lighthouse Reef-Belize, Bri. Hond.
0	1	75	Heiwa Maru	28,000	Crude	Unsp	Unsp	0	Singapore
6	1	75	Showa Maru	51,310	Crude	01:09N	103:49E	26	Str. of Malacca
21	1	75	Lucky Era	3,665	Bunker Fuel	22:27N	072:38W	80	Eastern Reef, Mayaguana I., Bahamas
22	1	75	Michael C. Lemos	8,952	Iranian Crude	17:42N	064:45W	43	St. Croix, U.S. Virgin Islands
11	2	75	Panglobal Friendship	14,660	Fuel Oil	11:04N	061:34W	43	Carribean Zone, 20 mi off Trinidad
13	2	75	Capulonix	5,864	Crude	Unsp	Unsp	29	N Indian Oc., India
3	3	75	Tramontana	7,330	Bunker Fuel	Unsp	Unsp	402	Mauritius I., African Indian Oc.
14	3	75	Asiatic	7,330	Asphalt	02:28N	101:40E	26	Str. Malacca, Port Dickerson, Sumatra
26	3	75	Tarik Ibn Ziyad	109,950	Crude	23:00S	043:00W	376	Rio de Janeiro, Brazil
1	4	75	Shell 2 (Barge)	14,660	Asphalt	Unsp	Unsp	58	Mid-Northern Pac. Oc., Guam
17	4	75	Tosa Maru	12,594	Bunker	01:20N	103:50E	26	Str. of Malacca, Singapore
13	5	75	Epic Colocotronis	42,000	Venezuelan Crude	19:16N	067:55W	43	Carribean, 60 mi NW of PR
13	7	75	Princess Anne-Marie	99,416	Basrah Crude	23:30S	105:30E	397	Barrow Island, Australia
15	8	75	Aries	7,330	Fuel Oil	Unsp	Unsp	47	Pac. Oc., W Coast Mex., B. Bamba
30	8	75	Dimitrios D M	3,665	Fuel Oil	Unsp	Unsp	9	Pac. Oc.?, Panama
26	10	75	San Rocco	7,330	Bunker Fuel	19:20N	069:24W	43	Carrib., 1 mi W Cayo Limon, Dom. Rep.

App. Table A.1 Tanker spills occurring in tropical waters, 1974-June 15, 1990 (continued).

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
28	10	75	Kriti Sun	21,990	Bunker Fuel	01:14N	103:41E	26	Str. of Malacca, 3 mi Singapore I.
9	12	75	Z-102 (Barge)	11,905	No. 6 Fuel	18:29N	066:08W	43	Puerto Rico
26	12	75	William Wheelwright	5,131	Fuel Oil	Unsp	Unsp	2	Atlantic Oc., W Africa, Liberia
15	1	76	Esso Regulus	21,990	Gasoline	Unsp	Unsp	25	Celebes Sea?, Borneo
4	2	76	Saint Peter	249,220	Colombian? Crude	01:30N	079:30W	8	30 mi W of Punta Manglares, Col.
16	2	76	Nanyang	129,766	Crude	22:25N	115:41E	97	S China Sea, 90 mi E of Hong Kong
18	2	76	Scorpio	220,000	Crude	18:00N	091:00W	46	Gulf of Campeche?, 11 mi from port, Mex.
5	4	76	Mysella	22,000	Crude	Unsp	Unsp	26	Str. of Malacca, Singapore
16	5	76	Euroasia Monarch	3,600	Crude	Unsp	Unsp	0	Port, Gabon, Southern W Af.
28	6	76	Mesurado	3,665	Fuel Oil/Gasoil	05:48N	010:01W	2	2 mi off Lower Buchanan, Liberia
0	7	76	Braz.ian Faith	38,929	Unspecified	03:30N	102:00E	26	Str. of Malacca
5	7	76	Capetan Mathios	3,665	Bunker Fuel	24:16N	079:10W	80	W of Andros I., Caribbean, Bahamas
24	7	76	Diego Silang	38,929	Crude	01:47N	102:53E	26	Str. of Malacca, Malaysia
28	7	76	Cretan Star	219,900	Chinese/Arab. Crude	20:20N	070:05E	29	450 mi off Bombay, India
12	9	76	Olympic Rider	3,244	Crude	04:04S	039:40E	32	Near Kenya
26	9	76	Al Bilad	3,600	Crude	Unsp	Unsp	0	Port, SW Africa, Nigeria
9	10	76	Corona Energy	7,330	Bunker Fuel	Unsp	Unsp	46	Pac. Oc., Mexico
27	10	76	Citta Di Savona	6,488	Crude	01:20N	103:50E	26	Str. of Malacca, Singapore
3	12	76	N 30 (Barge)	10,000	Crude	Unsp	Unsp	0	American Atlantic, Trinidad, Cuba
20	12	76	Janill	3,665	Bunker Fuel	16:00N	087:30W	46	Caribbean, Puerto Cortez, Hond.
23	2	77	Hawaiian Patriot	623,364	Indonesian Crude	22:01N	165:29W	89	320 mi W of Hawaii (Kauai I.)
0	3	77	Celeste	3,892	Unspecified	Unsp	Unsp	7	Orinoco River, Venez.
20	3	77	Anson	14,660	Crude	08:21N	062:43W	7	Orinoco River, Venez.
0	4	77	Golden Crane	212,570	Naphtha	Unsp	Unsp	30	Mid-Northern Ind. Oc.
15	4	77	Universe Defiance	21,990	Bunker Fuel	11:55N	017:39W	38	S Atl. Oc., Guinea
27	5	77	Caribbean Sea	181,672	Venezuelann Crude	11:34N	089:51W	45	S of El Salvador, Cen. Amer.
29	7	77	Oswego Tarmac	73,300	Asphalt	Unsp	Unsp	43	Caribbean, Neth. Antilles
4	12	77	Texaco Brisbane	7,330	Bunker Fuel	Unsp	Unsp	25	Near Borneo
22	2	78	Cassiopeia	7,330	Bunker Fuel	12:49N	073:05W	44	Caribbean Sea, Colombia
23	2	78	San Marco	6,000	Crude	05:30N	100:28E	27	Str. of Malacca, Penang
22	3	78	Aegis Leader	3,690	Fuel Oil/Bunker	06:03N	095:06E	27	Off Sumatra

App. Table A.1 Tanker spills occurring in tropical waters, 1974-June 15, 1990 (continued).

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
2	4	78	Sealift Mediterranea	23,195	Special Naval Fuel	03:30N	102:00E	26	Rondo I., Str. of Malacca
7	4	78	Astron	7,330	Bunker Fuel	18:44N	068:27W	43	20 mi NW C. Engano Light-Dom Rep
17	5	78	Athenian Victory	3,665	Bunker Fuel	Unsp	Unsp	68	Gulf of Aden, Djibouti
26	5	78	World Horizon	5,200	Crude	Unsp	Unsp	0	African/Indian Oc.
26	5	78	Aminona	146,600	Gasoline	02:18S	044:13W	304	Atl. Oc., Banco do Meio, Braz.
0	8	78	Overseas Joyce	1,816	Crude	08:57N	079:33W	8	Balboa Channel, Panama
11	8	78	Kountouriotis	36,650	Bunker Fuel	04:52N	098:03E	27	Str. of Malacca, Sumatra
21	8	78	Theopaes	1,297	Crude	16:48N	069:00W	43	290 km SW of San Juan, PR
21	10	78	Lima	51,000	Crude	Unsp	Unsp	0	Port, SW Africa, Nigeria
7	11	78	Feoso Sun	7,330	Bunker Fuel	14:31N	120:37E	60	Manila Bay, Phillipines
12	11	78	Mara	73,300	Fuel Oil	12:00N	068:00W	43	Carib., 8 mi Curaçao, Neth. Ant.
19	12	78	Peck Slip (Barge)	11,000	Bunker C/Fuel	18:03N	065:50W	43	Cape San Juan, PR
2	1	79	Master Michael	41,857	Diesel Fuel	15:10N	072:10W	44	Caribbean Sea btw. Haiti-Venez.
5	4	79	Fortune	65,019	Kuwait Crude	01:30N	104:36E	26	88 km NE of Singapore
0	5	79	Barge 8	7,300	Crude	Unsp	Unsp	0	Hong Kong, anchored near coastline
12	6	79	Mariheron	3,665	Bunker Fuel	02:54S	104:54E	325	Musi R., Palembang, Sumatra
21	6	79	Petro Rouscat	4,398	Fuel Oil	Unsp	Unsp	1	River in Cameroon, W Af.
28	6	79	Aviles	74,089	Kerosene Jet Fuel	13:00N	068:36E	66	280 mi NW Cochin, Arab. Sea, India
19	7	79	Aegean Captain	102,620	Venezuelann Crude	11:19N	060:31W	42	30 km NE Trinidad-Tobago
19	7	79	Atlantic Empress	1,016,761	Arabian Crude	11:19N	060:31W	42	30 km NE Trinidad-Tobago
2	8	79	Atlantic Empress	987,714	Arabian Crude	13:05N	055:28W	42	450 km E of Barbados
11	8	79	Fortuna	7,330	Fuel Oil	Unsp	Unsp	25	Reef, S China Sea?, Borneo
16	8	79	Ioannis Angelicoussi	220,000	Crude	06:01S	011:42E	334	Cabinda Gulf Oil, Malongo, Angola
18	8	79	World Protector	4,690	Furnace Oil	18:56N	072:51E	65	Bombay Harbor, India
16	9	79	Devali I	7,300	Crude	Unsp	Unsp	0	American Atlantic Sto. Domingo
18	9	79	Golden Sun	5,864	Fuel Oil	Unsp	Unsp	25	S China Sea?, Borneo
0	10	79	Titipor	158,004	Diesel Fuel	03:06S	060:00W	305	Tomanaus Roads, Brazil
2	10	79	Delsan 1	7,330	Gasoline	Unsp	Unsp	60	Pac. Oc.?, Phillipines
5	10	79	Cys Dignity	43,571	Crude	11:02N	064:29W	43	Off Isla de Margarita, Venez.
27	10	79	Gunvor Maersk	109,950	Fuel Oil	03:00S	060:00W	306	Amazon R., Manaus Roads, Braz.
10	11	79	Mobil Service 2	10,995	Fuel Oil	Unsp	Unsp	27	Str. of Malacca

App. Table A.1 Tanker spills occurring in tropical waters, 1974-June 15, 1990 (continued).

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
21	12	79	Choyo Maru	7,330	Bunker Fuel	07:45S	115:09E	324	17 mi N of Bali I., Flores Sea
16	1	80	Salem (Deliberately)	117,000	Kuwaiti Crude	12:38N	018:34W	38	Atl. Oc., S of Gambia, W Af.
28	1	80	Princess Anne-Marie	28,571	Crude & Fuel	21:50N	084:40W	81	Cabo San Antonio, Cuba
30	1	80	Delsan 2	3,665	Gasoline	Unsp	Unsp	0	Pac. Oc.?, reef off Phillipines
11	3	80	Maria Alejandra	29,320	Bunker Fuel	20:32N	018:13W	74	Atl. Oc., off Mauritania, W Af.
3	4	80	Albahaa B	29,320	Bunker Fuel	07:00S	045:00E	331	200 mi off Dar-es-Salaam, Tanzania
4	4	80	Mycene	29,320	Bunker Fuel	07:42N	015:10W	2	Off Sierra Leone, W Af.
27	4	80	Han Cheong	9,523	Range Oil	07:14N	134:28E	23	Palau I., Guam, Pac. Oc.
7	6	80	Texaco Connecticut	4,047	Alaskan Crude	09:08N	079:42W	8	Gamboa, Panama Canal
6	7	80	Zavyety.Ilyicha	146,000	Crude	Unsp	Unsp	0	Indian Oc.
27	9	80	(Barge)	1,000	Fuel Oil	12:58S	038:29W	339	Salvador, Brazil
11	11	80	Pnoc Transmar	10,995	Bunker Oil	15:00N	122:00E	60	Pac. Oc., Luzon, Phillipines
20	11	80	Nakata Eleven	2,452	Kerosene	06:10N	001:21E	36	Lome, Togo
21	2	81	Erodena (Erodona)	3,571	Fuel Oil	17:51N	077:37W	44	Port Kaiser, Jamaica
11	5	81	Qasqha	18,325	Gasoline	Unsp	Unsp	25	S China Sea?, Borneo
11	6	81	Sascha	14,660	Bunker Fuel	03:43S	116:32E	324	Makassar Str., off Borneo
15	7	81	Irenes Sincerity	3,665	Bunker Fuel	23:30N	065:00E	102	Arabian Sea, 180 mi SW of Karachi
30	10	81	Golden Ace	40,315	Solid Residue & Coke	07:49N	116:00E	25	S China Sea near Borneo
5	11	81	Gogo Rider	3,665	Naphtha/Fuel Oil?	13:09N	054:13E	67	Gulf of Aden/Ind. Oc., Socotra I.
30	11	81	Stuyvesant	3,600	Crude	15:40N	095:00W	40	Gulf of Tehuantepec, Mexico
19	12	81	G. Ace	5,131	Fuel Oil	15:00N	120:00E	61	Entrance to Poro, Phillipines
10	7	82	Algol	7,330	Bunker Fuel	Unsp	Unsp	8	Caribbean Sea, off Panama
15	12	82	Oriental Navigator	3,665	Petroleum Coke	Unsp	Unsp	60	Pac. Oc.?, Phillipines
27	12	82	Charalambos	7,300	Peruvian Crude	22:00N	087:00W	81	Gulf of Mexico, Yucatan, Mexico
7	1	83	Assimi	379,007	Iranian Crude	24:25N	058:08E	103	Ras Al Hadd, 58 mi from Muscat
19	1	83	Nikos M	3,600	Crude	Unsp	Unsp	0	Gulf of Aden, Djibouti Waters
16	7	83	Manhattan Duke	3,665	Bunker Fuel	09:50S	147:30E	321	Basilisk Reef, Port Moresby, New Guinea
17	9	83	Eptanissos	2,405	Venezuelan Crude	10:24N	075:33W	43	Near Cartagena, Colombia
6	10	83	Theodegmon	3,000	Venezuelan Crude	08:17N	062:44W	6	Orinoco River, near Puerto Ordaz, Venez.
18	10	83	Monemvasia	30,024	Indonesian Crude	01:16N	104:48E	26	South China Sea, near Singapore
26	11	83	Pnoc Basilan	125,000	Kerosene & Gasoline	16:21N	120:19E	60	S China Sea off Agoo, Phillipines

App. Table A.1 Tanker spills occurring in tropical waters, 1974-June 15, 1990 (continued).

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
20	1	84	Sitiawan	3,665	Fuel Oil	Unsp	Unsp	0	S China Sea?, port off Malaysia
7	3	84	Tanker	3,548	Kerosene	Unsp	Unsp	325	Southern Sumatra, Indonesia
16	10	84	Rover Star	7,330	Bunker Fuel	24:06N	058:45E	103	Gulf of Oman, 30 mi off Muscat
24	10	84	Lajpat Rai	73,300	Crude	19:00N	073:00E	65	Butcher I. Oil Term., Bombay, India
29	10	84	USS Roanoke	8,917	JP-5 Naval/Kerosene	21:22N	158:00W	88	Entrance to Pearl Harbor, HI
2	11	84	Catherine Y	3,665	Bunker Fuel	12:30N	087:00W	45	Pacifico 3 mi off Corinto, Nicaragua
26	11	84	Almak	25,000	Crude	12:10N	069:00W	43	Curaçao, West Indies
26	1	85	Barge (Fonton)	4,810	Crude	Unsp	Unsp	25	East Kalimantan, Indonesia
30	1	85	(Barge)	4,548	Crude	Unsp	Unsp	25	East Kalimantan, Indonesia
11	4	85	Napo	3,665	Fuel Oil	Unsp	Unsp	44	Caribbean, Cuba
5	7	85	Cowreh (Barge)	3,665	Fuel Oil	Unsp	Unsp	2	Atlantic Oc., Sierra Leone
13	12	85	American Legion	1,905	No. 6 Fuel/Bunker C	13:27N	144:39W	51	Entrance to Apra Harbor, Guam
7	2	86	St. Thomas (Barge)	1,500	#5 Medium Fuel	18:20N	065:00W	43	Crown Bay, St. Thomas, Virgin I.
22	6	86	Lukhovitsy	8,500	Cargo Fuel Oil	22:OON	082:00W	81	Cunfuegos (Cienfuegos) Harbour, Cuba
9	7	86	Pantas	14,660	Gasoline	01:45N	102:40E	26	Str. of Malacca off Batu Pahat
2	8	86	Golden Peace 101 (Ba)	2,520	Fuel Oil	Unsp	Unsp	25	Off Sarawak, E. Malaysia Lutong Miri
16	8	86	Maysun	14,000	Bunker C/Fuel Oil	Unsp	Unsp	60	55 mi off Nogas Island, Phillipines
20	1	87	Hana (Barge)	1,000	No. 6 Fuel Oil	21:07N	157:27W	88	Honolulu btw. Oahu & Molokai, Hawaii
2	7	87	Eleni S.	13,194	Diesel & Fuel Oil	06:23N	003:40E	36	12 mi E of Lagos, Nigeria
7	7	87	Stolt Avance	1,405	Fuel	01:11N	103:53E	26	Str. of Malacca, Singapore
22	7	87	Elhani	16,095	Crude	01:06N	103:46E	26	Outside Singapore, Indonesian water
20	12	87	Vector/Coll. W/ Dona	8,810	Crude Oil	12:30N	120:00E	60	Phillipines btw. Mindoro-Marinduque
25	2	88	Happy Kari	7,500	Crude	22:00N	038:00E	105	Jeddah, Saudi Arabia, Red Sea
1	7	88	Golar Liz	3,500	Crude	01:06N	103:43E	26	Singapore, near Str. of Malacca
10	10	88	Century Dawn	74,905	Crude	01:15N	103:59E	26	Port, Singapore waters
22	1	89	Shanta Shibani 2	7,330	Fuel Oil	Unsp	Unsp	62	S China Sea, Vietnam
22	1	89	Caribbean Navigator	3,665	Gasoline	Unsp	Unsp	8	Pac. Oc., Panama
15	2	89	Grantot (Barge)	16,126	Fuel Oil	Unsp	Unsp	43	Caribbean Sea, Sto. Domingo
26	4	89	Kanchenjunga	92,857	Iraqi Light Crude	21:25N	039:02E	105	Jeddah, Saudi Arabi 6 mi from port
27	6	89	Twe 23 de Agosto	14,660	Gasoline	Unsp	Unsp	45	Caribbean Sea, port in Cuba
28	6	89	Puppy P	40,314	Fuel Oil	Unsp	Unsp	328	Mid-N Indian Oc., India

App. Table A.1 Tanker spills occurring in tropical waters, 1974-June 15, 1990 (continued).

D	Mo	Yr	Vessel Name	Amount Spilled	Type of Oil	Lat.	Long.	Marsden Square	Location of Spill
6	8	89	Vishu	37,000	Crude	Unsp	Unsp	0	Phillipine waters, North SE Asia
29	1	90	Fernando	1,190	Crude Oil	14:00N	121:00E	60	Manila Bay, Bataan Pen., Phillipines
21	5	90	Capahuari	10,952	Kerosene	12:00S	078:00W	343	1 mi from port of Supe, Peru

Notes: spills were defined as tropical if they occurred between the Tropic of Cancer and the Tropic of Capricorn; *Unsp* = Unspecified. Where exact locations were missing, but tropical location could be safely assigned (e.g., the *Fernando*), spills were included. Database is available from the Branch of Environmental Modeling, Minerals Management Service, 381 Elden St., Mail Stop 4340, Herndon VA 22070.

Appendix B
Hydrocarbon Chemistry

App. Table B.1 Analyses of mangrove root sentinel organisms. Key to analysis numbers for each sampling date, given as *MO-#* in the following pages of this table.

Site	Dec 88	Feb 89	May 89	Aug 89	Nov/Dec 89	Mar 90	May 90	Aug 90	Nov/Dec 90	May 91
LRRS	1	34	46		80	90	108	130	148	192
PAYR	2, 3 (o)		45	58	79	89	107	129	147	195
PMRE	4, 5 (o)				70	88	106	128	146	194
PMRW	6, 7 (o)	33B		57	69	87	105	127	145	193
HIDR	8				72	94	112	134	152	188
UNR	9	36			82	93	111	133	151	189
ALER	10			60	71	92	110	132	150	191
MERR	11	35	47	59	81	91	109	131	149	190
SBCE	12, 13	38			75	99	117	139	157	203
SBCS	14, 15			62	74	98	116	138	156	202
PCE	16, 17			61	84	97	115	137	155	201
PCS	18, 19	37	50		73	96	114	136	154	204
LRCN	20		49		83	95	113	135	153	205
MCS	21					104	122	144		197
MCN	22	40	52		78, 86	103	121	143	161	196
HIDC	23			64	77	102	120	142	160	200
SBCW	24	39	51	63	76	101	119	141	159	198
LRCS	25				85	100	118	140	158	199
MINM	26	42			124				345, 346	
PGNM	27		54	66	123				347, 348	
DROM	28		53						349, 350	
PMM	29	41		65					351, 352	
MSM	30	44	56		126					
PBM	31	43		68						
PADM	32		55	67						
LINM	33				125					

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites SBCS, LRRS, and LRCS.

	SBCS				LRRS				LRCS			
Compound	MO-14	MO-15	MO-62	MO-98	MO-01	MO-34	MO-46	MO-80	MO-90	MO-25	MO-85	MO-100
Naphthalene*		1.0			0.2			0.3		0.1	0.1	
C_1-Naph	0.1	0.5			0.2			1.3		0.1	0.4	1.5
C_2-Naph	0.8	1.3	0.2		0.2			1.2		0.1	0.1	2.7
C_3-Naph	3.0	3.8	1.7		0.4	0.1	0.3	4.0	0.2	0.1	0.1	1.2
C_4-Naph	6.3	9.1	2.5	0.0	0.7	0.3	0.5	7.1	0.3	0.1		0.3
Fluorene*			0.0		0.0			0.1		0.0	0.0	0.1
C_1-Fluor	1.0	1.4	0.4		0.0			1.1		0.0	0.0	
C_2-Fluor	2.7	3.4	1.2		0.0	0.8		2.7				
C_3-Fluor			2.5		0.1			6.9				
Dibenzothiophene*	0.2	0.3	0.2		0.0	0.1	0.1	0.4	0.0	0.0	0.0	
C_1-DBT	2.1	2.4	1.8	0.1	0.1	0.4	0.4	2.2	0.2	0.1	0.1	0.0
C_2-DBT	7.4	8.0	5.7	0.3	0.3	4.0	3.3	7.5	1.0	0.5	0.2	
C_3-DBT	6.9	8.2	4.3	0.4	0.6	10.4	8.4	10.4	3.1	0.5	0.1	
C_4-DBT	1.2	2.3	1.9	0.0	0.7	13.3	10.9	11.5	3.3	0.1		
Phenanthr/anthrac*	0.6	0.3	0.2					0.6	0.1	0.1	0.1	0.1
C_1-Phen	3.2	8.0	1.3	1.1	0.0	0.8	0.6	4.2	1.0	0.3	0.2	0.3
C_2-Phen	4.1	5.0	2.4	0.2	0.2	1.8	1.5	9.6	1.4	0.4	0.1	0.3
C_3-Phen	2.0	2.4	1.8	0.2	0.3	4.5	3.3	8.1	0.6	0.3		
C_4-Phen	0.6	2.9	0.9	0.2	0.3	4.6	3.2	5.1	1.5	0.1		
Fluoranthene*	0.4	0.4	0.1		0.0	0.3	0.2	0.4	0.2	0.1	0.1	0.2
Pyrene*	0.4	0.5	0.1	0.0	0.0	0.4	0.3	0.8	0.3	0.1	0.1	0.1
C_1-Pyr	1.7	4.7	0.3	0.1	0.2	2.7	2.2	4.1	1.7	0.2	0.3	
C_2-Pyr					0.7	9.6	6.9	12.8	3.9	0.2	0.1	
Benzanthracene*			0.1		0.1		0.1	0.2		0.0	0.0	
Chrysene*	4.6	10.2	1.1		1.4	2.1	1.2	1.4	0.9	0.2	0.3	0.1
C_1-Chrys	6.4	4.9	2.2	0.3	3.8	5.5	3.7	4.4	1.5	0.3	0.1	0.1
C_2-Chrys	7.0	5.0	3.4	0.3	10.7	17.7	13.0	16.8	8.0	0.8		
C_3-Chrys			0.4		10.4	16.4	10.8	13.5	4.0	0.2		
C_4-Chrys			0.1		6.1	7.8	5.6	6.0	1.6			
Benzfluoranth(b,k)												
Benzo(a)pyrene*	3.8		0.4	0.5	1.3	2.1	1.3	1.8	1.1	0.1	0.0	0.1

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites SBCS, LRRS, and LRCS.

	SBCS				LRRS				LRCS			
Compound	MO-14	MO-15	MO-62	MO-98	MO-01	MO-34	MO-46	MO-80	MO-90	MO-25	MO-85	MO-100
Perylene*					0.1	0.1	0.1	0.1	0.1	0.0	0.8	3.0
Indenopyrene												
Dibenzanthracene*								0.1				
Benzoperylene*					0.1	0.3	0.2	0.4				
Total ng/mg EOM	66.7	86.0	37.0	3.8	39.3	105.9	78.2	147.0	36.0	5.1	3.3	10.1

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites MINM, SBCE, and PMRE.

	MINM			SBCE					PMRE		
Compound	MO-26	MO-42	MO-124	MO-12	MO-13	MO-38	MO-75	MO-99	MO-04	MO-70	MO-88
Naphthalene*	3.0	0.4	11.5	0.3	0.4	0.1	0.0				0.4
C_1-Naph	2.4	1.0	19.4	0.0	0.1	0.0	0.4		0.1		1.0
C_2-Naph	8.4	1.9	15.3	0.2	0.3	0.8	2.8	0.1	0.4		0.8
C_3-Naph	2.3	2.0	15.2	0.6	0.9	3.2	8.0	0.3	1.0	0.3	0.7
C_4-Naph	6.0	2.1		1.7	2.1	5.0	8.8	0.6	1.1	0.9	0.7
Fluorene*	0.2	0.1		0.0	0.0	0.1	0.5		0.1	0.1	
C_1-Fluor				0.2	0.4	1.2	3.9		0.4	0.8	
C_2-Fluor	3.1			0.6	0.9	2.5	8.1	0.6	1.4	2.7	3.3
C_3-Fluor	13.1			1.3	2.7	5.9	23.6		3.1	3.9	7.4
Dibenzothiophene*	0.7	0.1		0.1	0.2	0.3	0.6		0.3	0.1	0.2
C_1-DBT	2.9	0.4	0.5	0.4	0.6	2.8	5.6	0.6	3.1	0.6	1.2
C_2-DBT	32.6	2.8	1.5	3.2	4.3	10.0	24.0	2.2	8.6	5.8	3.6
C_3-DBT	75.9	3.7	2.9	4.1	7.1	16.7	30.9	4.9	12.4	14.5	8.0
C_4-DBT	53.8	2.3	2.7	3.6	5.7	21.4	19.8	3.7	10.3	18.9	13.6

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites MINM, SBCE, and PMRE.

	MINM			SBCE					PMRE		
Compound	MO-26	MO-42	MO-124	MO-12	MO-13	MO-38	MO-75	MO-99	MO-04	MO-70	MO-88
Phenanthr/anthrac*	0.9	0.3	0.2	0.0	0.1	0.2	0.8	0.0	0.3		0.2
C_1-Phen	4.0	0.8	2.6	0.9	0.6	3.0	5.8	0.6	3.5	0.8	
C_2-Phen	15.2	2.1	3.9	1.9	2.9	6.7	16.0	1.6	9.2	3.2	
C_3-Phen	26.6	1.9	2.2	2.1	3.5	7.8	14.7	2.0	9.6	8.7	3.2
C_4-Phen	17.5	0.8	1.5	1.6	2.5	5.9	8.7	1.7	4.9	8.2	4.9
Fluoranthene*	2.6	0.3	0.7	0.2	0.4	0.8	0.6	0.3	0.4	0.2	0.5
Pyrene*	1.7	0.1		0.4	0.6	0.9	0.9	0.3	0.6	0.5	1.0
C_1-Pyr	7.1	0.3	3.6	2.2	2.9	5.7	2.7	1.6	1.9	2.7	6.2
C_2-Pyr	21.0	0.6	2.0	4.8	6.6	14.8	5.6	3.8	4.8	8.8	21.9
Benzanthracene*	0.5		0.1	0.1	0.2	2.5	0.2	0.1		0.2	0.4
Chrysene*	8.2	0.4	0.9	1.4	1.4	0.4	1.8	1.0	1.1	1.7	2.9
C_1-Chrys	22.8	0.9	0.9	3.1	3.9	11.1	4.0	2.7	3.8	3.8	10.8
C_2-Chrys	65.7	2.8		5.3	7.4	26.0	7.3	6.0	9.8	10.2	39.9
C_3-Chrys	58.9	1.7		2.5	3.6	14.7	3.1	2.4	6.3	7.2	33.7
C_4-Chrys	30.9	1.1		0.6	1.1	4.3	1.5	0.5	1.3	3.6	12.1
Benzfluoranth(b,k)											
Benzo(a)pyrene*	5.5	0.3		0.6	1.0	2.7	2.2	1.0	0.9	2.0	4.8
Perylene*	23.9	0.0		0.0	0.0	0.1	0.2	0.0	0.0	0.3	0.6
Indenopyrene											
Dibenzanthracene*							0.4	0.1		0.4	0.2
Benzoperylene*	1.5	0.0				0.2	0.7	0.1		0.9	1.0
Total ng/mg EOM	518.8	31.3	87.5	44.0	64.4	177.8	214.3	38.9	100.6	112.1	185.1

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites PAYR and PMRW.

	PAYR						PMRW					
Compound	MO-02	MO-03	MO-45	MO-58	MO-79	MO-89	MO-06	MO-07	MO-33B	MO-57	MO-69	MO-87
Naphthalene*			0.1		0.4							0.2
C_1-Naph		0.0	0.3		1.5							0.6
C_2-Naph	0.7	0.9	0.2		0.6	0.0						0.9
C_3-Naph	5.9	5.7	0.2		0.4	0.3	0.1	0.1	0.1	0.3	0.2	0.7
C_4-Naph	12.9	6.9	0.3		0.2	0.1	0.4	0.5	0.6	0.4	0.5	0.7
Fluorene*	0.2	0.1			0.1	0.0					0.1	0.1
C_1-Fluor	2.7	2.1					0.2				0.7	0.2
C_2-Fluor	10.9	7.4					0.7	0.7	1.2	0.8		1.2
C_3-Fluor	18.6	11.3					2.1	2.0	3.1	1.6		3.5
Dibenzothiophene*	2.2	1.6	0.1	0.0	0.1	0.0	0.2	0.1	0.1	0.1	0.1	0.2
C_1-DBT	19.6	13.2	0.5		0.2	0.4	1.3	1.0	0.7	0.5	0.5	0.4
C_2-DBT	60.9	39.6	2.2	0.6	1.3	0.7	5.0	4.2	5.0	2.7	2.8	3.3
C_3-DBT	51.3	35.9	4.4	1.8	2.5	1.1	8.0	6.7	11.0	5.0	6.0	3.5
C_4-DBT	27.1	20.3	6.1	1.8	2.3	1.4	6.7	5.5	15.6	5.4	7.6	6.0
Phenanthr/anthrac*	2.0	1.7	0.1		0.3	0.1	0.3		0.1			0.1
C_1-Phen	21.1	13.7	0.9	0.4	0.5	0.5	1.3	0.6	1.0	1.0	1.1	1.3
C_2-Phen	48.6	32.3	1.6	0.4	0.7	0.7	3.9	2.1	2.5	1.7	1.7	1.0
C_3-Phen	38.9	29.9	2.5	0.5	0.7	0.5	5.0	3.2	4.5	2.1	3.8	1.3
C_4-Phen	16.1	12.8	2.3	0.3	0.3	0.2	3.0	2.3	4.5	1.9	3.7	2.0
Fluoranthene*	1.2	0.8	0.5		0.7	0.2	0.4	0.3	0.8	0.5	0.2	0.7
Pyrene*	1.4	1.1	0.4	0.3	0.3	0.3	0.4	0.4	0.9	0.5	0.4	0.5
C_1-Pyr	8.2	7.6	1.9	0.1	0.7	0.6	1.4	1.8	4.5	1.5	1.7	2.8
C_2-Pyr	11.8	10.8	5.7	2.7	4.5	2.0	4.0	3.8	13.4	6.1	6.2	11.6
Benzanthracene*	0.2	0.2	0.1	0.0			0.1	0.1	0.1	0.1	0.2	0.2
Chrysene*	3.1	2.3	0.7	0.1	0.7	0.3	1.5	1.5	2.0	0.9	1.7	1.0
C_1-Chrys	7.4	5.4	3.4	0.3	1.5	0.8	3.7	3.4	6.2	2.3	1.9	3.2
C_2-Chrys	14.1	9.2	12.2	1.1	4.1	3.7	8.8	7.2	19.9	46.5	4.7	12.3
C_3-Chrys	4.8	6.5	9.4		2.7	2.0	5.4	2.5	15.5	5.3	2.7	9.6
C_4-Chrys		0.6	1.5			0.1			5.8	2.6	0.7	2.8
Benzfluoranth(b,k)												
Benzo(a)pyrene*	0.5	0.5	1.6	0.1	0.5	0.5	0.8	0.6	1.8	0.7	1.2	1.1

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites PAYR and PMRW.

	PAYR						PMRW					
Compound	MO-02	MO-03	MO-45	MO-58	MO-79	MO-89	MO-06	MO-07	MO-33B	MO-57	MO-69	MO-87
Perylene*		0.0	0.1		3.4	0.1	0.0	0.1	6.1	3.1	0.1	6.2
Indenopyrene												
Dibenzanthracene*								0.2				
Benzoperylene*			0.2		0.1				0.3		0.3	0.2
Total ng/mg EOM	392.5	280.5	59.7	10.6	31.1	16.7	64.8	50.7	127.1	93.7	50.9	79.2

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites PCE and PCS.

	PCE					PCS					
Compound	MO-16	MO-17	MO-61	MO-84	MO-97	MO-18	MO-19	MO-37	MO-50	MO-73	MO-96
Naphthalene*	0.4	0.3		0.4		0.2				0.1	0.0
C_1-Naph	0.0			1.5	0.0	0.1	0.1			0.3	0.0
C_2-Naph	0.1			0.8	0.7	1.3	3.5	0.0		1.2	0.4
C_3-Naph	0.2	0.1		0.7	1.9	4.1	10.7	0.6	0.4	2.2	1.0
C_4-Naph	0.3	0.1		0.7	1.3	0.4	13.9	1.0	0.5	1.7	0.9
Fluorene*	0.0	0.0		0.0	0.0	0.1	0.3	0.3	0.0	0.3	0.0
C_1-Fluor				0.2	0.4	0.9	2.9	4.2	0.4	1.0	0.3
C_2-Fluor		0.2	0.1	0.6	1.0	2.8	10.3	5.4	0.5	1.1	0.6
C_3-Fluor		0.5	0.5			6.9	25.0	16.5	1.5	2.0	
Dibenzothiophene*	0.0	0.0		0.1	0.1	0.6	2.0	0.7	0.1	0.4	0.1
C_1-DBT	0.1	0.1	0.1	0.3	0.5	4.7	17.0	5.0	0.6	1.1	0.4
C_2-DBT	1.4	1.2	0.7	1.4	1.8	15.3	51.4	30.2	1.8	1.7	2.3
C_3-DBT	2.8	2.7	1.5	2.5	2.0	17.6	57.1	54.3	2.9	1.6	2.4
C_4-DBT	2.8	2.8	1.5	3.0	1.6	10.5	35.4	69.3	2.9	1.1	2.3

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites PCE and PCS.

	PCE					PCS					
Compound	MO-16	MO-17	MO-61	MO-84	MO-97	MO-18	MO-19	MO-37	MO-50	MO-73	MO-96
Phenanthr/anthrac*		0.0		0.2	0.1	0.4	1.6	1.6	0.0	1.7	
C_1-Phen	0.3	0.3	0.2	1.0	2.2	2.2	11.4	11.8	0.6	2.2	0.7
C_2-Phen	0.8	0.5	0.4	1.0	1.4	7.7	27.3	31.6	1.2	2.0	1.1
C_3-Phen	1.2	1.0	0.5	1.0	0.9	7.7	25.9	43.0	1.1	1.4	0.9
C_4-Phen	1.0	1.0	0.4	1.4		3.2	11.2	24.9	0.8	0.6	0.3
Fluoranthene*	0.3	0.3	0.1	0.2	0.3	0.1	0.3	3.1	0.3	0.1	0.1
Pyrene*	0.2	0.1	0.1	0.2	0.3	0.3	0.9	5.1	0.1	0.2	0.1
C_1-Pyr	0.8	0.6	0.3	1.5	3.5	1.1	4.0	21.2	0.5	0.4	0.8
C_2-Pyr	1.9	1.5	0.5	3.6	3.2	1.4	5.8	34.7	0.7	0.3	1.2
Benzanthracene*	0.0	0.0		0.1	0.4	0.1	0.3	0.1	0.0	0.0	0.1
Chrysene*	0.5	0.3	0.1	1.0	2.3	0.5	2.0	0.6	0.2	0.2	0.3
C_1-Chrys	1.3	0.9	0.2	2.4	2.0	1.2	5.0	1.1	0.4	0.3	0.6
C_2-Chrys	3.2	2.0	0.5	5.2	5.1	1.8	7.7	2.1	0.6	0.4	1.5
C_3-Chrys	1.8	0.9		2.6	2.6	0.5	3.0	1.1	0.5	0.1	0.8
C_4-Chrys	0.5			0.9			0.6			0.1	
Benzfluoranth(b,k)						9.0		0.7			
Benzo(a)pyrene*	0.2	0.1		0.6	0.8	0.3	1.3		0.4	0.2	0.7
Perylene*	0.8			3.2	5.9		0.1	0.0	0.1	0.0	0.1
Indenopyrene											
Dibenzanthracene*											
Benzoperylene*		0.4		0.0							0.1
Total ng/mg EOM	22.7	17.9	7.9	38.1	42.3	102.9	338.2	370.2	19.0	26.4	20.1

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites LRCN, HIDC, and PGNM.

	LRCN			HIDC				PGNM			
Compound	MO-20	MO-49	MO-83	MO-23	MO-64	MO-77	MO-102	MO-27	MO-54	MO-66	MO-123
Naphthalene*			0.0	0.1			0.0				
C_1-Naph				0.0			0.1	0.1			
C_2-Naph				0.1			0.2	0.1			
C_3-Naph	0.0	0.2		0.1	0.0	1.0	0.0	0.7	0.0		0.3
C_4-Naph	0.1	0.3		0.2	0.1	3.6		2.9			
Fluorene*	0.0	0.0		0.0	0.0	0.0	0.0	0.0			0.0
C_1-Fluor	0.0	0.2		0.1	0.1	1.3	0.1				
C_2-Fluor	0.1	0.3		0.2	0.2	2.8	0.3	4.5		0.5	0.4
C_3-Fluor	0.5	1.2		0.9	0.4	14.5		18.2		0.7	0.9
Dibenzothiophene*	0.0	0.1		0.0	0.0	0.3	0.0	0.2	0.0	0.0	0.0
C_1-DBT	0.1	0.3		0.3	0.2	1.1	0.1	2.8	0.1	0.4	0.2
C_2-DBT	0.6	1.6		1.9	1.2	11.0	0.4	40.4	0.9	3.5	2.4
C_3-DBT	1.1	4.3	0.1	2.5	1.5	29.0	0.8	69.8	2.8	7.6	5.1
C_4-DBT	1.0	4.9	0.0	1.5	0.9	3.9	0.9	48.7	2.7	6.8	5.0
Phenanthr/anthrac*		0.2		0.0				0.1			
C_1-Phen	0.1	0.4	0.0	0.3	0.3	2.7	0.2	2.4	0.1	0.7	0.4
C_2-Phen	0.3	0.5		1.2	0.8	4.7	0.4	14.9	0.9	2.9	2.6
C_3-Phen	0.4	1.1		1.4	0.8	10.8	0.4	23.4	1.4	4.0	2.2
C_4-Phen	0.2	1.0		0.6	0.5	8.9	0.3	11.3	0.8	2.1	1.5
Fluoranthene*	0.0	0.1	0.0	0.1	0.1	0.7	0.1	0.3	0.1	0.1	0.2
Pyrene*	0.0	0.1	0.0	0.1	0.1	1.2	0.3	0.8	0.0	0.2	0.1
C_1-Pyr	0.2	0.6	0.1	0.6	0.4	7.0	0.4	4.3	0.3	1.0	1.4
C_2-Pyr	0.2	1.0	0.1	0.7	0.5	16.0	0.5	5.9	0.4	1.4	1.1
Benzanthracene*	0.0	0.0		0.1	0.0	0.2	0.1	0.2	0.0	0.1	0.1
Chrysene*	0.1	0.2	0.1	0.3	0.2	4.6	0.1	2.3	0.2	0.8	0.6
C_1-Chrys	0.2	0.4		0.5	0.2	8.5	0.2	4.5	0.3	1.2	0.8
C_2-Chrys	0.4	0.9		0.6	0.2	21.0	0.3	9.3	0.6	2.1	1.2
C_3-Chrys	0.2			0.2	0.1	23.3	0.1	7.0	0.5	1.8	0.7
C_4-Chrys				0.0	0.1	16.1	0.1	4.3	0.1	0.8	0.2
Benzfluoranth(b,k)						8.4					
Benzo(a)pyrene*	0.2	0.3	0.1	0.2	0.1		0.1	1.9	0.2	1.0	0.6

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites LRCN, HIDC, and PGNM.

	LRCN			HIDC				PGNM			
Compound	MO-20	MO-49	MO-83	MO-23	MO-64	MO-77	MO-102	MO-27	MO-54	MO-66	MO-123
Perylene*	0.0		0.0	0.0	0.0	1.1	0.1	0.2			
Indenopyrene						0.6					
Dibenzanthracene*						0.4					
Benzoperylene*				0.0		2.2	0.0	0.3	0.0	0.3	
Total ng/mg EOM	6.0	20.2	0.6	14.7	9.2	207.2	6.5	281.6	12.3	39.9	28.2

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites DROM, PMM, and MACN.

	DROM		PMM			MACN
Compound	MO-28	MO-53	MO-29	MO-41	MO-65	MO-78
Naphthalene*				0.1		0.1
C_1-Naph		0.2		0.1		0.3
C_2-Naph				0.3		0.6
C_3-Naph	0.2	0.1		0.3	0.3	1.8
C_4-Naph						2.2
Fluorene*				0.0	0.0	0.2
C_1-Fluor						0.8
C_2-Fluor						1.8
C_3-Fluor						3.1
Dibenzothiophene*	0.1	1.1	0.0		0.0	0.2
C_1-DBT	0.3	0.3	0.2	0.2	0.2	0.6
C_2-DBT	1.4	1.9	0.3	0.7	0.6	2.5
C_3-DBT	4.5	4.2	0.8	4.0	1.2	2.2
C_4-DBT	9.5	3.5	2.3	12.2	2.0	1.4

App. Table B.1 Analyses of mangrove root sentinel organisms (continued). Summary concentrations (ng/mg EOM) of individual PAHs determined by SIM GC/MS; sites DROM, PMM, and MACN.

	DROM		PMM			MACN
Compound	MO-28	MO-53	MO-29	MO-41	MO-65	MO-78
Phenanthr/anthrac*	0.2					0.4
C_1-Phen	1.3	0.5	0.5	0.7	0.5	1.4
C_2-Phen	4.6	1.9	0.5	2.6	1.2	2.3
C_3-Phen	4.7	3.3	1.0	2.6	1.1	2.0
C_4-Phen	4.6	1.5	1.2	4.1	0.8	0.9
Fluoranthene*	0.3	0.4	0.1	0.1	0.1	0.7
Pyrene*	0.6	0.4	0.1	0.2	0.1	0.7
C_1-Pyr	7.0	0.6	0.4	2.3	0.6	0.7
C_2-Pyr	16.8	1.6	1.2	5.3	1.1	1.1
Benzanthracene*	0.1		0.0		0.0	0.6
Chrysene*	1.9	0.3	0.4	1.1	0.3	0.9
C_1-Chrys	4.6	0.4	1.1	1.8	0.5	0.5
C_2-Chrys	12.8		1.9	4.2	1.0	0.5
C_3-Chrys	15.0		0.9	3.1	0.4	0.5
C_4-Chrys	7.0			1.6	0.1	0.3
Benzfluoranth(b,k)	5.3	0.2	0.5	1.3	0.3	
Benzo(a)pyrene*						0.4
Perylene*	0.4			0.1		0.1
Indenopyrene	0.2					
Dibenzanthracene*	0.1					
Benzoperylene*	1.0		0.1	0.2	0.0	0.3
Total ng/mg EOM	104.6	22.2	13.5	49.5	12.5	31.9

App. Table B.2 Analyses of mangrove sediments. Key to analysis numbers for each sampling date, given as *MS-#* in the following pages of this table.

Site	9/86 0-2 cm	9/86 18-20 cm	5/89 0-2 cm	5/89 8-10 cm	5/89 18-20 cm	7/90 0-2 cm	7/90 8-10 cm	7/90 18-20 cm	1991 Ooze Oil
LRRS			S-11	S-13	S-15	S-12	S-14	S-16	RO1
PAYR			S-38	S-40	S-42	S-39	S-41	S-43	RO2
PMRE			S-31	S-33	S-35	S-32	S-34	S-36	RO3
PMRW			S-44	S-46	S-48	S-45	S-47	S-49	RO4
HIDR			S-106			S-105			RU1
UNR			S-102			S-101			RU2
ALER			S-112			S-111			RU3
MERR			S-104			S-103			RU4
SBCE			S-25	S-27	S-29	S-26	S-28	S-30	CO1
SBCS	S-1	S-6	S-2	S-4	S-7	S-3	S-5	S-8	CO2
PCE			S-50	S-52	S-54	S-51	S-53	S-55	CO3
PCS			S-56	S-58	S-60	S-57	S-59	S-61	CO4
LRCW			S-62	S-64	S-66	S-63	S-65	S-67	CO5
MACS	P2-89	P2-74	S-120			S-119			CU1
MACN	P2-35	P2-81	S-95	S-96	S-97	S-98	S-99	S-100	CU2
HIDC	P2-47	P2-43	S-71	S-72	S-73	S-74	S-75	S-76	CU3
SBCW			S-108	S-129	S-130	S-107	S-127	S-128	CU4
LRCS			S-116	S-125	S-126	S-115	S-123	S-124	CU5
MINM			S-19	S-21	S-23	S-20	S-22	S-24	OO1
PGNM			S-77	S-78	S-79	S-80	S-81	S-82	OO2
DROM	S-17	S-18	S-83	S-84	S-85	S-86	S-87	S-88	OO3
PMM			S-89	S-90	S-91	S-92	S-93	S-94	OO4
MSM			S-114			S-113			OU1
PBM			S-118			S-117			OU2
PADM			S-122			S-121			OU3
LINM			S-110			S-109			OU4

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-1	MS-2	MS-2	MS-3	MS-4	MS-5	MS-6	MS-6	MS-7	MS-8	MS-9	MS-10
Naphthalene*	2,394	107	104	69	20	27	173	166			36	44
C_1-Naph	42,596	256	204	58	27	37	2,092	2,416		3	217	116
C_2-Naph	293,627	485	530				7,960	10,615	13		1,814	346
C_3-Naph	483,891	1,568	1,447		241		9,014	13,436	228	33	7,193	425
C_4-Naph	299,149	5,265	3,558		2,813		5,506	8,437	237	37	12,173	259
Fluorene*	13,067						267	485		1	117	16
C_1-Fluor	45,797		813		280		970	1,713	25	13	1,543	56
C_2-Fluor	65,022	3,110	2,211	1,206	2,000		1,616	2,610	61	13	5,770	70
C_3-Fluor	51,870	15,113	7,644	4,068	3,882	2,283	2,727	3,495	100	42	12,877	74
Dibenzothiophene*	40,229	263	388		41	84	957	1,556	6	7	976	82
C_1-DBT	110,110	2,015	1,010	659	1,674	170	3,032	4,765	120	33	8,920	194
C_2-DBT	115,770	13,711	10,515	4,165	7,551	534	5,533	7,007	249	85	29,442	324
C_3-DBT	59,588	27,487	20,197	10,554	6,250	2,967	3,924	3,880	217	67	26,738	179
C_4-DBT	2,454	16,053	16,257	17,100	2,895	3,344	1,686	1,563	110	39	12,511	42
Phenanthr/anthrac*	29,365						749	1,243	3	3	687	62
C_1-Phen	61,899	1,027	1,474	324		205	1,724	3,094	25	28	5,084	131
C_2-Phen	51,397	3,398	2,725	895	761	646	3,124	3,533	98	28	13,578	135
C_3-Phen	28,346	6,338	5,692	3,600	1,581	767	1,859	1,706	72	16	10,023	52
C_4-Phen	7,928	4,008	5,489	4,571	758	556	569	556	28	10	3,235	
Fluoranthene*	544	326	662	117	68	97	43	48	3	40	235	16
Pyrene*	736	663	944	455	169	339	71	89	5	84	450	32
C_1-Pyr	3,087	6,078	5,040	1,828	405	618	184	251	16	50	1,124	7
C_2-Pyr			10,571					392	21	57		31
Benzanthracene*	347	123	172		13	52	7	21	1	27	35	
Chrysene*	5,805	1,772	2,906	689	157	307	100	206	8	37	794	13
C_1-Chrys	14,482	4,494	7,087	704	430	1,083	193	494	15	17	1,794	
C_2-Chrys	32,814	12,791	19,286	930	1,903	4,815	388	1,130	47	40	4,605	
C_3-Chrys	26,312	11,163	16,116		2,156	4,240	180	881	34		3,021	
C_4-Chrys	13,092	7,920	12,654		1,037	2,057		439	21		870	
Benzfluoranth(b,k)												
Benzo(a)pyrene*	15,652	8,924	1,439	1,720	1,516	3,020	157	133	22	58	1,729	

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-1	MS-2	MS-2	MS-3	MS-4	MS-5	MS-6	MS-6	MS-7	MS-8	MS-9	MS-10
Perylene*	852	438	183		65	128		8	1	4	86	
Indenopyrene												
Dibenzanthracene*	201				57	72		12				
Benzoperylene*	2,339	1,490	195		275	416		28	4	44	134	
Total ng/mg EOM	1,920,761	156,387	157,513	53,711	39,024	28,865	54,802	76,405	1,791	916	167,810	2,708

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-10	MS-11	MS-12	MS-13	MS-14	MS-15	MS-16	MS-17	MS-18	MS-19	MS-20
Naphthalene*	25	7	46		22		3	10			17
C_1-Naph	107	6			12		0	716		0	17
C_2-Naph	478			1			8	3,077		5	18
C_3-Naph	824			8				3,166			
C_4-Naph	713			16				1,901			
Fluorene*	25			2		0		126			
C_1-Fluor	133			3		1		382			
C_2-Fluor	288		664	4	218	5		499			
C_3-Fluor	482		2,966	51	1,736	6	272	545			881
Dibenzothiophene*	124	9	54	6	30	0		350			
C_1-DBT	561	121	520	12	193	1		910	1		
C_2-DBT	1,045	117	2,612	53	652	8		1,115	5		331
C_3-DBT	789	258	6,218	168	3,291	8	322	660	6	208	1,266
C_4-DBT	363	312	10,042	239	5,519	3	811	287	3	621	1,535
Phenanthr/anthrac*	107	3		4		3		229			
C_1-Phen	357	35	254	21	243	3		526	2		
C_2-Phen	608	77	805	39	728	8	143	543	8	17	173
C_3-Phen	379	148	2,410	63	1,264	4	200	321	8	66	203
C_4-Phen	132	103	3,742	91	1,140	1	188	100		195	415

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-10	MS-11	MS-12	MS-13	MS-14	MS-15	MS-16	MS-17	MS-18	MS-19	MS-20
Fluoranthene*	15	6	159	7	106	12	12	9	17	12	37
Pyrene*	26	30	477	28	745	27	83	16	20	17	34
C_1-Pyr	54	127	2,255	73	1,884	12	278	57	17	128	201
C_2-Pyr	72	441	4,125	221	2,189	12	602	120	13	412	613
Benzanthracene*	4			7	28	1	21	10	11		
Chrysene*	32	106	1,784	47	75	6	42	53	17	106	328
C_1-Chrys	50	99	1,688	58	1,266	3	380	120	16	162	536
C_2-Chrys	108	112	3,031	132	7,271	7	1,017	326	17	406	1,112
C_3-Chrys			3,035	3	6,451		730	264	7	441	1,040
C_4-Chrys			627		5,093		470	220		516	1,168
Benzfluoranth(b,k)											
Benzo(a)pyrene*	14	179	2,604	72	4,152	25	350	5	165	267	988
Perylene*			191		167	1	16	8	6	21	68
Indenopyrene											
Dibenzanthracene*					66		8		1	5	9
Benzoperylene*	4				367	9	53	2	32	45	139
Total ng/mg EOM	7,915	2,294	50,306	1,431	44,910	168	6,008	16,674	374	3,651	11,129

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-21	MS-22	MS-23	MS-24	MS-25	MS-26	MS-27	MS-28	MS-29	MS-30	MS-31	MS-32
Naphthalene*					193	2	108	65		59	10	3
C_1-Naph					713	3	565	131	46	103	23	8
C_2-Naph				0	4,026	21	9,012	1,169	302	772	62	12
C_3-Naph				33	14,408		26,064	4,096	421	2,337	306	18
C_4-Naph		20		104	20,088		28,423	5,924	235	3,846	1,585	62
Fluorene*					135		164	100	30	264		
C_1-Fluor					2,366		3,145	510	83	2,503	116	

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry wt.) of individual PAHs determined by SIM GC/MS.

Compound	MS-21	MS-22	MS-23	MS-24	MS-25	MS-26	MS-27	MS-28	MS-29	MS-30	MS-31	MS-32
C_2-Fluor				50	7,916		5,998	1,481	100	8,163	1,485	71
C_3-Fluor	6	118		145	14,226	741	906	4,356	153	22,989	3,099	545
Dibenzothiophene*		2		3	1,977		393	129	75	721	54	13
C_1-DBT		4		10	11,157		8,056	1,040	218	2,315	548	33
C_2-DBT		40		111	25,698	398	14,388	3,303	300	12,469	3,356	328
C_3-DBT	9	326		145	21,752	727	11,420	5,573	149	21,762	4,549	730
C_4-DBT	18	479		195	14,238	976	7,254	5,023	38	19,320	2,791	709
Phenanthr/anthrac*			1		2,068				41			5
C_1-Phen		18	0		7,422		926	491	87		159	107
C_2-Phen		47		61	11,749	120	5,074	1,017	140	2,025	1,375	149
C_3-Phen	3	187		106	8,090	234	3,504	1,089	45	2,409	1,897	331
C_4-Phen	7	159		89	4,150	290	1,672	853		3,488	1,082	286
Fluoranthene*	1	8	0	3	191	16	165	113	5	402	46	14
Pyrene*	4	19	1	18	396	45	291	178	13	1,178	114	37
C_1-Pyr	8	80		76	1,860	179	1,250	702	26	4,637	450	148
C_2-Pyr	12	105		144	3,758	394	2,582	1,666	69	8,525	1,113	424
Benzanthracene*		3		3			84	53	3	647	25	
Chrysene*	1	40		22	1,569	127	725	600	22	2,063	425	171
C_1-Chrys	1	80		68	3,022	193	2,467	1,906	59	8,091	1,034	414
C_2-Chrys	18	198		208	7,860	608	8,190	6,631	231	25,413	3,050	1,396
C_3-Chrys	26	107		168	7,888	710	5,987	5,388	263	15,985	2,571	1,323
C_4-Chrys	21	17		117	4,776	686	4,119	3,749	164	9,038	1,804	1,185
Benzfluoranth(b,k)												
Benzo(a)pyrene*	19	69	1	86	3,873	371	3,377	3,869	168	5,026	765	585
Perylene*	1	5		6	241	25	199	177	9	244	49	35
Indenopyrene												
Dibenzanthracene*				2		5	71	65	8	406		27
Benzoperylene*	1		2	18	481	64	301	508	148	1,424	417	266
Total ng/mg EOM	156	2,130	4	1,992	208,288	6,934	156,883	61,956	3,650	188,622	34,359	9,434

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-33	MS-34	MS-35	MS-35	MS-36	MS-36	MS-38	MS-39	MS-40	MS-40	MS-41	MS-42
Naphthalene*	19		0	5		2	23	25	45	63	27	2
C_1-Naph	52		4	16		4	42	83	83	151	84	3
C_2-Naph	1,879	5	134	262	78	90	47	456	119	110	84	6
C_3-Naph	6,623	22	328	696	219	254	88	3,428	472	1,187	312	7
C_4-Naph	6,179	45	499	1,243	156	201	168	7,079	4,401	7,387	1,789	9
Fluorene*	22	3	6	7	1	1		20		52	11	1
C_1-Fluor	2,092	26	371	424	20	30		520	481	167	274	2
C_2-Fluor	4,072	58	631	878	41	65	102	1,807	2,469	4,980	1,534	4
C_3-Fluor	6,857	251	511	1,133	5	110	613	2,903	7,670	17,692	3,033	18
Dibenzothiophene*	432	7	14	15	2	2	20	180	163	139	77	2
C_1-DBT	4,611	19	723	1,145	75	104	72	1,897	1,172	398	1,074	4
C_2-DBT	10,274	123	1,193	2,320	124	234	578	6,394	10,013	18,650	5,453	22
C_3-DBT	9,862	360	731	1,285	80	184	1,660	5,148	15,739	27,045	5,173	15
C_4-DBT	6,560	340	343	482	30	95	1,574	3,014	9,191	15,316	2,972	10
Phenanthr/anthrac*					15	19	22	57				2
C_1-Phen	1,764	49	49	103	46	68	261	551	474	813	288	10
C_2-Phen	5,934	106	384	704	73	136	456	2,018	1,874	3,546	1,015	6
C_3-Phen	5,936	135	346	525	40	93	663	2,465	4,244	6,451	1,507	3
C_4-Phen	2,868	126	118	171	17	36	564	1,477	3,354	4,336	1,111	1
Fluoranthene*	148	12	10	18	7	7	61	101	280	320	79	4
Pyrene*	240	28	14	26	9	12	164	204	600	648	237	14
C_1-Pyr	1,079	90	61	66	11	17	565	776	2,592	2,529	891	13
C_2-Pyr	2,393	181	152	123	22	34	2,250	1,948	5,046	4,209	1,965	72
Benzanthracene*	66	6	6	8	1	1	16	25	92	207	38	3
Chrysene*	817	44	43	55	8	8	349	399	1,339	2,078	374	9
C_1-Chrys	2,251	137	127	156	14	13	906	1,099	3,252	4,864	1,080	10
C_2-Chrys	5,887	454	317	370	34	34	2,940	3,155	7,812	11,187	3,066	37
C_3-Chrys	4,450	388	248	293	29	25	3,100	3,053	6,419	8,457	2,839	75
C_4-Chrys	3,109	234	167	198	21	16	2,409	2,205	4,143	547	1,798	74
Benzfluoranth(b,k)												
Benzo(a)pyrene*	1,181	118	63	42	11	7	559	488	866	1,235	416	31

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-33	MS-34	MS-35	MS-35	MS-36	MS-36	MS-38	MS-39	MS-40	MS-40	MS-41	MS-42
Perylene*	89	9	6	3	2	1	113	91	193	79	87	5
Indenopyrene												
Dibenzanthracene*		8	4	3	1		25	37	36	115	16	3
Benzoperylene*	563	56	38	11	4	3	113	90	165	299	75	13
Total ng/mg EOM	98,308	3,442	7,641	12,786	1,197	1,906	20,525	53,195	94,800	145,257	39,080	491

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-43	MS-44	MS-45	MS-45	MS-46	MS-47	MS-48	MS-49	MS-50	MS-51	MS-52	MS-53
Naphthalene*	2	34	64	80	5	14	1	8	46	29	5	14
C_1-Naph	7	94	130	188	16	50	1	28	100	80	13	36
C_2-Naph	44	323	225	257	42	327	20	343	65		14	69
C_3-Naph	267	1,816	1,554	2,618	101	2,490	29	2,948		142	4	122
C_4-Naph	450	7,217	8,024	9,899	261	5,991	21	2,840		1,017	2	883
Fluorene*	8				1		4	7		40	1	
C_1-Fluor	87		697	961	60	731	12	506		261		
C_2-Fluor	132	281	2,654	4,469	115	1,869	10	1,368	1,679	740		642
C_3-Fluor	19	3,649	4,224	8,381	226	2,010	14	1,548	5,444	2,433		2,171
Dibenzothiophene*	8	161	163	118	9	84	6	167			2	56
C_1-DBT	252	1,879	2,324	2,148	34	2,606	22	2,145			3	94
C_2-DBT	384	9,090	9,849	12,252	329	6,285	29	4,500	6,439	1,450	23	2,647
C_3-DBT	245	9,561	14,201	10,172	437	4,205	23	3,008	15,293	4,730	30	4,783
C_4-DBT	101	5,603	4,797	5,210	211	2,116	10	1,460	11,776	4,034	11	3,573
Phenanthr/anthrac*	4				4		2					
C_1-Phen	36	378	624	471	30	273	11	381	581	409		239
C_2-Phen	173	3,129	3,491	3,819	247	2,048	18	1,473	2,806	842		814

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-43	MS-44	MS-45	MS-45	MS-46	MS-47	MS-48	MS-49	MS-50	MS-51	MS-52	MS-53
C_3-Phen	118	3,997	3,496	3,894	218	1,946	12	1,398	4,321	1,092		1,371
C_4-Phen	41	2,308	1,497	1,889	78	938	3	630	3,540	1,229		1,178
Fluoranthene*	9	138	188	136	12	77	6	55	245	123	5	70
Pyrene*	26	375	297	230	25	131	11	106	732	156	11	150
C_1-Pyr	57	1,468	1,506	866	69	652	23	427	3,019	427	12	663
C_2-Pyr	136	3,497	3,568	1,642	171	1,483	50	971	6,317	666	29	1,037
Benzanthracene*	4	58	41	80	4	39	2	23	125			4
Chrysene*	23	1,190	1,328	935	53	561	5	319	1,458			27
C_1-Chrys	57	3,154	3,248	2,476	129	1,472	3	860	4,283			80
C_2-Chrys	215	8,949	9,024	5,992	342	3,965	4	2,202	12,750			73
C_3-Chrys	258	8,115	9,488	5,537	273	3,011		1,805	10,105			84
C_4-Chrys	238	4,526	6,772	4,875	213	1,945		1,216	5,781		5	320
Benzfluoranth(b,k)												
Benzo(a)pyrene*	53	1,013	1,654	82	27	297	4	52	851	98	4	43
Perylene*	8	107	168	73	4	52	1	27	117	44		
Indenopyrene												
Dibenzanthracene*	5			50				9				
Benzoperylene*	7	42	119	28	3	32		40	18			
Total ng/mg EOM	3,474	82,152	95,414	89,831	3,746	47,700	357	32,871	97,888	20,041	175	21,242

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-54	MS-55	MS-56	MS-57	MS-58	MS-59	MS-60	MS-61	MS-62	MS-63	MS-64	MS-65
Naphthalene*	1	3	135	261	184	88	20	2	10	20	3	2
C_1-Naph	0	5	272	522	358	474	36	6	18	53	5	8
C_2-Naph	2	11	155	519		8,559	31	18	20	54	3	9
C_3-Naph	1	31	289	726	1,474	34,819	71	90	20	417	2	11
C_4-Naph		105	1,096	4,554	4,934	41,995	141	108		1,780		6

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-54	MS-55	MS-56	MS-57	MS-58	MS-59	MS-60	MS-61	MS-62	MS-63	MS-64	MS-65
Fluorene*	0	0			73	822	5	4			1	3
C_1-Fluor		9		396	774	8,011		24		171	5	10
C_2-Fluor		46	1,399	2,717	4,172	13,907		35		546		17
C_3-Fluor		91	4,501	2,315	12,268	16,670	409	71	45	1,370		21
Dibenzothiophene*	1	4	141		296	2,912	26	7		65	3	9
C_1-DBT	2	28	725	649	2,037	28,618	25	57		489	5	19
C_2-DBT	9	192	6,876	8,752	20,746	79,234	266	153		3,099	26	55
C_3-DBT	11	161	9,320	19,135	27,664	36,289	1,609	153	131	3,514	34	46
C_4-DBT	4	64	7,524	21,283	22,047	20,761	2,656	154	150	2,539	35	15
Phenanthr/anthrac*	1	3				701		4	61		7	12
C_1-Phen	10	23			1,840	7,833	178	43	44	206		23
C_2-Phen	15	67	1,309	2,887	4,470	21,640	587	74		888	13	32
C_3-Phen	3	57	2,157	5,505	8,142	18,195	839	56	66	1,451	12	9
C_4-Phen	2	22	1,833	6,721	7,303	8,846	739	42	62	1,092	12	
Fluoranthene*	4	17	293	271		827	49	12		93	10	11
Pyrene*	8	25	800	1,803	3,722	1,369	431	24		200	21	113
C_1-Pyr	15	31	3,461	9,257	11,647	6,330	1,275	59	29	827	55	118
C_2-Pyr	36	68	8,335	21,318	23,561	13,960	3,082	187	204	2,215	209	125
Benzanthracene*		5	107	309	983	282	149	8		31	5	9
Chrysene*		13	1,546	4,943	404	3,655	304	40	27	541	23	21
C_1-Chrys		23	4,239	13,046	17,815	10,000	2,410	91	80	1,421	47	32
C_2-Chrys	5	52	15,615	36,502	65,551	26,501	9,112	386	311	4,279	228	41
C_3-Chrys		49	18,286	37,309	52,383	20,036	7,379	415	395	4,046	212	
C_4-Chrys		21	14,378	25,393	35,119	13,336	4,637	391	340	3,662	352	
Benzfluoranth(b,k)												
Benzo(a)pyrene*		6	5,685	7,658	4,313	1,384	513	27	64	331	105	9
Perylene*			594	1,240	531	221	62	4	3	50	8	2
Indenopyrene												
Dibenzanthracene*			141	278	409	89	72	3		20	6	
Benzoperylene*			1,018	1,371	894	313	132	14	24	142	84	

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-54	MS-55	MS-56	MS-57	MS-58	MS-59	MS-60	MS-61	MS-62	MS-63	MS-64	MS-65
Total ng/mg EOM	131	1,232	112,229	237,640	336,113	448,677	37,246	2,763	2,104	35,610	1,530	786

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-66	MS-67	MS-68	MS-69	MS-70	MS-71	MS-72	MS-73	MS-74	MS-75	MS-76	MS-77
Naphthalene*	10	35	253	109	130				0		0	47
C_1-Naph	17	77	528	184	235				10	0	1	77
C_2-Naph	10	47	628	299	278	3	8		14	2	6	92
C_3-Naph	2	66	1,041	296	288		3		6	5	6	102
C_4-Naph		290	437	449	572				2	4	4	503
Fluorene*	1	10	113			0	1	0	2	1	1	
C_1-Fluor	10	127	508				4	1	7	9	7	
C_2-Fluor	9	480	4,107		5,515		2	1	4	9	8	
C_3-Fluor	18	1,422	20,186	2,227	38,385		2		12	11	13	1,570
Dibenzothiophene*	3	42	5,312	135	1,709	1	1	0	4	2	2	55
C_1-DBT	6	238	1,063			1	2	0	5	5	3	118
C_2-DBT	39	1,857	17,098			2	6	1	16	15	21	962
C_3-DBT	68	4,662	36,057	3,527	56,472				17	28	23	3,452
C_4-DBT	99	5,635	31,718	7,780	123,447				17	33	14	4,676
Phenanthr/anthrac*	9					3	7		13	3	3	
C_1-Phen		272	3,037	1,010	11,147						20	383
C_2-Phen	22	1,179	8,204	686	21,215	2	9		24		20	594
C_3-Phen	15	1,354	10,563	2,045	29,133				17	11	11	1,290
C_4-Phen	21	1,233	10,869	2,603	36,042				10	12	9	1,756
Fluoranthene*	19	145	1,328	175	3,069	1	4	1	5	8	8	133
Pyrene*	49	886	7,454	2,725	38,629	2	11	1	8	8	37	368
C_1-Pyr	77	2,859	26,349	7,965	109,727		12		20	60	58	1,994
C_2-Pyr	260	6,008	50,642	16,488	217,396	11	22		258	57	106	6,026
Benzanthracene*	7	256	1,772	555	848	1	1		2	5	3	33

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-66	MS-67	MS-68	MS-69	MS-70	MS-71	MS-72	MS-73	MS-74	MS-75	MS-76	MS-77
Chrysene*	30	433	6,476	805	1,026	2	3		24	8	6	1,039
C_1-Chrys	48	4,193	27,451	7,804	10,763				28	24	10	2,462
C_2-Chrys	322	16,800	67,815	28,461	43,627				12	97	35	6,039
C_3-Chrys	296	13,418	68,759	23,283	35,684				126	116	22	6,128
C_4-Chrys	297	8,599	45,105	16,114	25,033				177	169	29	6,144
Benzfluoranth(b,k)												
Benzo(a)pyrene*	50	1,254	5,689	2,205	3,070	2	3	0	19	20	11	816
Perylene*	3	142	513	190	275				1	1	1	81
Indenopyrene												
Dibenzanthracene*		146	521	241	464		1		5			36
Benzoperylene*	1	409	1,002	469	520	1	1	0	10	13	10	201
Total ng/mg EOM	1,818	74,571	462,598	128,831	814,699	32	102	6	875	736	509	47,176

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-78	MS-79	MS-80	MS-81	MS-82	MS-83	MS-84	MS-85	MS-86	MS-87	MS-88
Naphthalene*	7	7	75	29	7	42	54	2	42	26	
C_1-Naph	17	46	135	62	13	97	134	6	89	63	
C_2-Naph	29	2,015	104	673	17	93	6,183	159	50	151	5
C_3-Naph	193	4,696	174	2,789	243	822	14,874	409	74	521	77
C_4-Naph	985	3,340	847	3,525	464	2,965	12,132	319	227	773	187
Fluorene*		101	26	13		9	347	15			0
C_1-Fluor		585	212		52	94	2,694	68	70		10
C_2-Fluor	328	844	470	332	165	1,452	4,371	99	176		92
C_3-Fluor	797	941	2,563	855	263	4,972	5,668	145	1,169	3,933	254
Dibenzothiophene*	19	499	78	102	9	42	934	15		164	4

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-78	MS-79	MS-80	MS-81	MS-82	MS-83	MS-84	MS-85	MS-86	MS-87	MS-88
C_1-DBT	49	1,895	204	369	35	339	6,099	132	43	287	18
C_2-DBT	1,547	2,998	1,448	1,505	713	6,170	12,079	244	158	1,661	352
C_3-DBT	1,881	1,899	5,717	1,869	710	9,231	8,346	150	1,152	1,991	481
C_4-DBT	1,036	910	9,067	1,206	481	6,216	3,657	67	2,322	1,779	266
Phenanthr/anthrac*	16	113		90	3		68	7			
C_1-Phen	74	963		221	49	223	2,377	70	46		13
C_2-Phen	425	1,752		189	215	1,798	6,011	13	347	1,421	169
C_3-Phen	712	1,086	1,724		207	2,728	3,422	63	509	929	209
C_4-Phen	416	259	3,248		116	1,771	1,152	21	569	461	86
Fluoranthene*	41	53	288		40	77	97	6	74	118	6
Pyrene*	107	83	552	84	93	257	167	7	192	114	12
C_1-Pyr	405	429	3,195		221	848	612	17	550	570	32
C_2-Pyr	1,070	876	7,416		405	1,258	1,078	46	1,023	1,891	56
Benzanthracene*	17	20			11	27	29	3	17	23	3
Chrysene*	177	225	535		45	623	339	11	466	128	21
C_1-Chrys	456	453	1,049		125	1,300	1,178	40	909	434	44
C_2-Chrys	1,361	1,354	1,623		476	3,016	3,558	131	2,226	1,614	98
C_3-Chrys	1,539	1,509	1,067		418	2,776	3,397	181	1,960	2,835	121
C_4-Chrys	1,427	974	1,104		234	2,119	2,547	180	2,200	2,242	82
Benzfluoranth(b,k)											
Benzo(a)pyrene*	166	109		44	33	604	605	35	826	345	17
Perylene*	15	12				34	34	2	39	31	1
Indenopyrene											
Dibenzanthracene*	20	10				37	80	7		72	2
Benzoperylene*	62	51				143	190	35	261	205	6
Total ng/mg EOM	15,397	31,108	42,921	13,956	5,863	52,183	104,513	2,706	17,786	24,784	2,723

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-89	MS-89	MS-90	MS-91	MS-91	MS-92	MS-93	MS-94	MS-95	MS-98	MS-100	MS-101
Naphthalene*	1	0	1			147	61	11	5	1	2	
C_1-Naph	2	0	2	0		298	145	25	7	3	4	3
C_2-Naph	1		1			258	141	34	5	3	4	3
C_3-Naph	0					785	452	104	4	7	4	1
C_4-Naph						3,644	698	202	1	31	17	
Fluorene*	0		0		0	27	30	10	1	2		1
C_1-Fluor	0				1	530	720	65	7	14		3
C_2-Fluor	1		3		1	2,000	531	127	8	18		3
C_3-Fluor	3	2	12	1	2	8,324	3,979	799	38	66		3
Dibenzothiophene*	0	0	0	0	0	102			3	7	4	3
C_1-DBT	0	0	1	0	0	578	133	45	8	16	20	3
C_2-DBT	3	3	8	2	2	9,005	1,184	237	31	74	87	6
C_3-DBT	6	10	18	3	3	17,330	4,994	629	51	149	223	4
C_4-DBT	10	17	40	3	4	20,129	8,268	1,539	59	198	291	1
Phenanthr/anthrac*	2	0	1	2	0				9		33	3
C_1-Phen	1	2	2	1	2	615	631	174	20	27		19
C_2-Phen	3	4	11	2	3	2,707	1,712	428	41	61	59	20
C_3-Phen	5	6	15	2	3	6,674	2,597	510	34	65	37	3
C_4-Phen	4	8	19	2	2	6,146	17,155	479	27	50	28	
Fluoranthene*	1	1	3	3	1	157	108	72	28	62	62	3
Pyrene*	1	1	9	5	3	508	628	482	33	67	96	4
C_1-Pyr	3	4	21	5	4	2,487	1,830	1,013	29	57	63	5
C_2-Pyr	10	17	64	14	12	3,603	2,605	1,637	149	234	133	137
Benzanthracene*	0	0	0	0	0	3	7	3	2	14	7	1
Chrysene*	4	2	4	4	2	1,221	118	37	27	41	12	8
C_1-Chrys	8	7	13	3	1	2,479	858	202	21	18	20	5
C_2-Chrys	18	21	75	9	12	6,581	5,291	1,563	44	36	91	3
C_3-Chrys	18	31	150	12	16	6,369	5,095	750	22	17	11	
C_4-Chrys	22	37	121	9	14	5,731	2,979	314	28	15	36	
Benzfluoranth(b,k)	1	3	11	4	4	247	231	119	46	97		1
Benzo(a)pyrene*	8	13	54	9	9	2,117	1,561	603	66	86	49	2

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-89	MS-89	MS-90	MS-91	MS-91	MS-92	MS-93	MS-94	MS-95	MS-98	MS-100	MS-101
Perylene*	2	2	9	2	2	476	272	131	11	17	9	1
Indenopyrene	2	6	11	6	11	151	264	184	53	36		
Dibenzanthracene*	5	4	22	2	3	379	312	69	18	14		
Benzoperylene*	10	19	50	21	33	1,503	1,323	527	73	33	108	
Total ng/mg EOM	158	220	753	126	149	113,312	66,914	13,123	1,008	1,636	1,511	246

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-102	MS-103	MS-104	MS-105	MS-106	MS-107	MS-107	MS-108	MS-108	MS-109	MS-110	MS-111
Naphthalene*		1		0	5	21	10	1		13		
C_1-Naph	2			0	4	32	20	1		20		
C_2-Naph	3			1	2	16	7	4		12		3
C_3-Naph	2					6	11	2		10		36
C_4-Naph	0			1		36	37			14	0	47
Fluorene*	1	0		1		4	3	1	1	0	0	1
C_1-Fluor	2	0		2		25	41	2	2	1	1	8
C_2-Fluor	3	1		2		39	44	7	3	1	1	20
C_3-Fluor	4	0		4		135	163	8	2	2	1	35
Dibenzothiophene*	2	1	1	2	2	7	8	4	2	0	0	4
C_1-DBT	2	0	0	3	3	13	14	6	3	0	0	35
C_2-DBT	6	1		14	22	47	62	16	9	4	1	81
C_3-DBT	4	2		20	15	120	171	16	9	6	1	77
C_4-DBT	2	1		15	36	259	211	14	12	7	1	84
Phenanthr/anthrac*	6	0		1	2			4	2	1	1	2
C_1-Phen	13	3	1	7	12	82	113	12	8	2	2	9
C_2-Phen	15	2	1	15	97	123	194	19	15	6	2	44
C_3-Phen	7	1		18	4	157	145	12	6	8	2	50
C_4-Phen	2	0		10	11	147	119	10	6	6	1	28

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-102	MS-103	MS-104	MS-105	MS-106	MS-107	MS-107	MS-108	MS-108	MS-109	MS-110	MS-111
Fluoranthene*	16	1	0	3	2	13	18	4	3	2	2	38
Pyrene*	16	1	0	5	14	16	16	9	6	3	2	59
C_1-Pyr	14	1		9	75	181	151	16	12	5	3	47
C_2-Pyr	238	137	58	231	211	651	491	117	47	16	11	52
Benzanthracene*	5	2	1	1	1		1	4	2	1	2	20
Chrysene*	10	4	3	10	9	141	127	8	5	1	2	21
C_1-Chrys	3	3	3	8	31	217	245	12	7	2	1	12
C_2-Chrys	2			8		547	564	32	20	6	2	28
C_3-Chrys				5		724	800	40	22	4	2	25
C_4-Chrys				21		582	618	41	30	3	1	18
Benzfluoranth(b,k)	9	1		2	2	18	16	10	7	2	4	70
Benzo(a)pyrene*	11	1		3	2	341	330	24	16	3	4	73
Perylene*	3	1		2		56	53	3	2	1	1	13
Indenopyrene	3			1		16	15	5	3	1	1	32
Dibenzanthracene*	1			1		41	55	5	2	0	0	7
Benzoperylene*	2			1		49	63	10	7	1	1	29
Total ng/mg EOM	407	163	67	429	561	4,865	4,936	479	270	164	53	1,107

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-112	MS-113	MS-115	MS-115	MS-116	MS-116	MS-117	MS-118	MS-119	MS-120	MS-121	MS-122
Naphthalene*	1	0	2	3	3	1			1	1	3	
C_1-Naph	0	0	6	8	6	2			0	0	1	
C_2-Naph	0	0	9	13	1	4			1		2	
C_3-Naph	1		6	13	6	2			1		3	
C_4-Naph	1		3	12	5	2					3	
Fluorene*	1	0	2	4	2	2	0		1	0	1	0
C_1-Fluor	2	0	7	9	8	22		0	1	1	5	

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-112	MS-113	MS-115	MS-115	MS-116	MS-116	MS-117	MS-118	MS-119	MS-120	MS-121	MS-122
C_2-Fluor	3	1	10	16	12	12		0	1	1	7	
C_3-Fluor	4	1	29	45	39	33	0		2	3	9	
Dibenzothiophene*	3	0	5	14	5	6	0	0	2	1	0	
C_1-DBT	4	0	10	32	9	9	0	0	2	1	0	0
C_2-DBT	10	1	28	59	30	30	1	1	4	3	3	0
C_3-DBT	6	1	52	65	59	43	4	0	4	3	7	
C_4-DBT	2	0	97	93	169	127	4		2	3	1	
Phenanthr/anthrac*	19	1	4	11	5	4			5	5	1	0
C_1-Phen	30	1	27	45	24	26	1	0	5	5	2	1
C_2-Phen	43	2	40	63	34	33	1		7	7	10	0
C_3-Phen	24	0	60	47	44	39	3		6	4	3	
C_4-Phen	5		27	29	56	43	2			2	1	
Fluoranthene*	103	3	4	10	5	4	0	0	15	16	5	0
Pyrene*	106	2	8	17	11	10	1	0	17	19	9	0
C_1-Pyr	58	2	29	55	33	37	3	0	8	8	1	
C_2-Pyr	230	10	112	109	122	96	9	1	75	39	1	3
Benzanthracene*	30	1	7	14	4	4	1	0	6	8	0	0
Chrysene*	36	1	10	21	12	10	1	0	8	1	0	0
C_1-Chrys	26	0	24	42	28	24	3		2	3		0
C_2-Chrys	12		85	135	103	82	7			3		
C_3-Chrys			111	161	137	108	39					
C_4-Chrys			74	145	103	95	0					
Benzfluoranth(b,k)	110	2	13	21	15	13	1		18	26	1	
Benzo(a)pyrene*	106	2	52	99	51	45	2		22	30	1	0
Perylene*	14	0	5	7	7	5	0		2	2	1	
Indenopyrene	36	1	6	9	4	5	1		14	20		
Dibenzanthracene*	7		8	8	8	7			1	1		
Benzoperylene*	21	0	19	46	17	15	1		12	15		0
Total ng/mg EOM	1,055	37	991	1,482	1,177	999	85	4	244	234	80	6

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-123	MS-123	MS-124	MS-124	MS-125	MS-125	MS-126	MS-127	MS-128	MS-129	MS-130	MS-131
Naphthalene*	0				0					19		
C_1-Naph	1				2	1				28		
C_2-Naph	2	2	1		8	7		8		12		
C_3-Naph	4	9	4	5	48	149	0	67				
C_4-Naph	7	15	4	6	156	524	0	73	0			13
Fluorene*	1	2	1	1	3	4	0	3	0			
C_1-Fluor	6	14	4	6	45	135	2	24	1			3
C_2-Fluor	9	21	6	9	141	440	3	46	2			
C_3-Fluor	16	44	5	8	227	709	4	58	2			47
Dibenzothiophene*	1	3	0	1	4	10	0	4	0	10	0	1
C_1-DBT	3	7	2	3	52	155	1	33	1	13	0	3
C_2-DBT	14	38	6	7	270	826	4	117	2	28	1	23
C_3-DBT	23	71	4	4	164	548	5	94	2	47		427
C_4-DBT	41	119	3	2	145	453	8	66	2			345
Phenanthr/anthrac*			1				1	0	0	19	0	
C_1-Phen	6	13	3	6	26	73	3	23	1	35	1	10
C_2-Phen	20	52	4	8	105	298	4	66	2	14	1	107
C_3-Phen	10	24	2		82	239	3	68	2			315
C_4-Phen	11	28	2		30	92	3	36	1			124
Fluoranthene*	3	7	2	2	6	26	13	9	5	15	1	10
Pyrene*	11	26	5	4	12	39	10	17	5	45	2	22
C_1-Pyr	24	54	6	6	28	84	7	20	3	43	2	92
C_2-Pyr	39	94	15	11	44	101	21	49	5	162	6	95
Benzanthracene*	1	2	1	1	2	9	2	3	3		0	35
Chrysene*	2	5	2	1	3	13	2	10	3	10	1	26
C_1-Chrys	3	10	9	1	13	41	2	20	1		0	61
C_2-Chrys	15	38			57	170	7	55	2			150
C_3-Chrys	17	46			56	157	9	58	1			105
C_4-Chrys	18	27			29	86	6	41	1			46
Benzfluoranth(b,k)	3	7	3	1	8	27	6	8	5			12
Benzo(a)pyrene*	10	33	3	3	19	56	8	31	7	17		39

App. Table B.2 Analyses of mangrove sediments (continued). Summary concentrations (ng PAH/g dry weight) of individual PAHs determined by SIM GC/MS.

Compound	MS-123	MS-123	MS-124	MS-124	MS-125	MS-125	MS-126	MS-127	MS-128	MS-129	MS-130	MS-131
Perylene*	2	8	1		2	11	1	4	1			4
Indenopyrene	1	6	1		1	5	2	4	4			
Dibenzanthracene*	1	2	0		2	5	0	3	0			1
Benzoperylene*	5	18	1	1	4	12	1	10	2			7
Total ng/mg EOM	329	845	102	95	1,792	5,505	140	1,129	65	515	16	2,131

App. Table B.3 Sites and dates of samples analyzed for hydrocarbons. *f*: front; *m*: middle; *b*: back; *ss*: surface sediments; *sc*: sediment core; *bc*: bivalve tissue composite (except open coast sites, where barnacles were collected); *tc*: coral tissue composite; *oo*: oil oozing into mangrove sediment core holes; *wc*: water column.

Site	Jun86	Jul86	Sep86	Nov86	Apr87	Dec88	Feb89	May89	Aug89	N/D89	Mar90	May90	J/A90	N/D90	M/J91
Mangrove															
LRMf			3ss, 1sc												
LRMm			3ss, 1sc												
LRMb			3ss												
SBSf			3ss, 1sc												
SBSm			3ss, 1sc												
SBSb			3ss, 1sc												
MARM			3ss, 1sc												
NARM			1sc												
MARS		2ss	3ss, 1sc												
HRBf			3ss, 1sc												
HRBm			3ss, 1sc												
HRBb			3ss, 1sc												
MSM						1bc	1bc	1ss, 1bc		1bc			1ss		
PBM						1bc	1bc	1ss	1bc				1ss		
PADM						1bc		1ss, 1bc	1bc				1ss		
LINM						1bc		1ss		1bc			1ss		
GALM															
MINM						1bc	1bc	1sc		1bc			1sc	2bc	1oo
PGM						1bc		1sc, 1bc	1bc	1bc			1sc	2bc	1oo
DROM						1bc		1sc, 1bc					1sc	2bc	1oo
PMM						2bc	1bc	1sc	1bc				1sc	2bc	1oo
HIDC						1bc		1sc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1bc
SBCW						1bc	1bc	1sc, 1bc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1bc
MACN						1bc	1bc	1sc, 1bc		2bc	1bc		1sc		1bc
MACS						1bc		1ss			1bc		1ss		1bc
LRCS						1bc		1sc		1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
PGC															
LRCW						1bc		1sc, 1bc		1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
CO3															
PCE						2bc		1sc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
PCS						2bc	1bc	1sc, 1bc			1bc	1bc	1sc, 1bc	1bc	1oo, 1bc

App. Table B.3 Sites and dates of samples analyzed for hydrocarbons (continued).

Site	Jun86	Jul86	Sep86	Nov86	Apr87	Dec88	Feb89	May89	Aug89	N/D89	Mar90	May90	J/A90	N/D90	M/J91
SBCE						2bc	1bc	1sc		1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
SBCS						2bc		1sc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
HIDR						1bc		1sc, 1bc		1bc	1bc		1sc		1bc
CSR															
UNR						1bc	1bc	1sc		1bc			1sc		1bc
ALER						1bc		1sc	1bc	1bc	1bc		1sc		
MERR						1bc	1bc	1sc, 1bc	1bc	1bc	1bc		1sc		1bc
LRRS						1bc	1bc	1sc, 1bc		1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
LRRN															
PAYR						2bc		1sc, 1bc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
PMRE						2bc		1sc		1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
PMRW						2bc	1bc	1sc	1bc	1bc	1bc	1bc	1sc, 1bc	1bc	1oo, 1bc
LRM			2wc												
GALS			1wc												
Coral Reef															
GALC			3tc, 4ss			3tc, 3ss							3tc, 3ss		
LRE1			(4ss)[1]			3tc, 3ss							3ss		
LRE2						3tc, 3ss							3tc, 3ss		
PAYW						3tc, 3ss							3ss		
PAYN			3tc, 4ss			3tc, 3ss							3tc, 3ss		
PM						3tc, 3ss							3tc, 3ss		
NARS			3tc, 4ss			3tc, 3ss							3tc, 3ss		
MAR3						3tc, 3ss							3tc, 3ss		
DONR			4ss			3tc, 3ss							3tc, 3ss		
DMA						3tc, 3ss							3ss		
PALW			3tc, 4ss			3tc, 3ss							3tc, 3ss		
JUG						3tc, 3ss							3ss		
Seagrass Bed															
DONT			4ss	1ss	1ss	1ss									
PALN			4ss	1ss	1ss	1ss									
LINE					1ss	1ss									
BNV						1ss									
NARC			3ss	1ss		1ss									
PGN					1ss	1ss									

App. Table B.3 Sites and dates of samples analyzed for hydrocarbons (continued).

Site	Jun86	Jul86	Sep86	Nov86	Apr87	Dec88	Feb89	May89	Aug89	N/D89	Mar90	May90	J/A90	N/D90	M/J91
LREN			4ss	1ss	1ss	1ss, 1sc									
LRS			3ss	1ss	1ss	1ss									
MINN				1ss	1ss	1ss									
LRN2			11ss												
MARG	7ss														
LRLC			4ss												
LRN3			3ss												
Reef Flat															
GALT			6ss												

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[1] LRE1 and LRE2 were not differentiated at this sampling.

App. Table B.4 Triterpane peaks identified in Burns (Chap. 3) based on pattern provided by Battelle Laboratories and confirmation at BBSR based on relative retention times as measured from pure standards and further confirmation based on molecular ion retention times.

Peak No.	Abbreviated Notation	Empirical Formula	Molecular Weight	Compound
A	Tricyclic A	Unknown	-	Tricyclic triterpanes (unidentified)
B	Tricyclic A	Unknown	-	Tricyclic triterpanes (unidentified)
C	$C_{28}\alpha,\alpha,\beta$	$C_{28}H_{48}$	384	17α(H),18α(H),21β(H)-28,30-bisnorhopane
1	$C_{27}\alpha(T_s)$	$C_{27}H_{46}$	370	18α(H),-22,29,30-trisnorneohopane
2	$C_{27}\alpha(T_m)$	$C_{27}H_{46}$	370	17α(H),-22,29,30-trisnorhopane
3	$C_{29}\alpha,\beta$	$C_{29}H_{50}$	398	17α(H),21β(H)-30-norhopane
4	$C_{29}\beta,\alpha$	$C_{29}H_{50}$	398	17α(H),21α(H)-30-normoretane
5	$C_{30}\alpha,\beta$	$C_{30}H_{52}$	412	17α(H),21β(H)-hopane
6	$C_{30}\beta,\alpha$	$C_{30}H_{52}$	412	17β(H),21α(H)-moretane
7	$C_{31}\alpha,\beta$	$C_{31}H_{54}$	426	17α(H),21β(H)-30-homohopanes (22S & 22R)
8	$C_{32}\alpha,\beta$	$C_{32}H_{56}$	440	17α(H),21β(H)-30,31-bishomohopanes (22S & 22R)
9	$C_{33}\alpha,\beta$	$C_{33}H_{58}$	454	17β(H),21β(H)-30,31,32-trishomohopanes (22S & 22R)

Appendix C
Subtidal Reef Corals

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census. Data are means (SE in parentheses) except for number of species. Common species were defined arbitrarily as those with >2% cover in at least 2 of the 72 possible occurrences (12 reefs x two depths x first three censuses).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
Acropora cervicornis	0.5-3	85	0.00 (0.00)	0.00 (0.00)							0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.29 (0.57)
		86	0.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.86 (0.63)
		88	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.28 (0.18)
		89	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.45 (0.31)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.18 (0.12)
		91	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	1.22 (0.34)
	>3-6	85	0.00 (0.00)	0.00 (0.00)							0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	3.26 (1.07)
		86	0.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	3.19 (1.04)
		88	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)	0.00 (0.00)	0.67 (0.25)
		89	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.61 (0.28)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.90 (0.43)
		91	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.15 (0.40)
Acropora palmata	0.5-3	85	0.59 (0.39)	6.56 (1.88)							4.86 (1.44)	4.75 (4.08)	7.18 (2.23)	10.46 (2.97)
		86	0.01 (0.01)	0.26 (0.26)		0.00 (0.00)	0.00 (0.00)			2.02 (0.99)	8.04 (2.43)	8.38 (4.91)	4.54 (1.64)	15.18 (4.05)
		88	0.03 (0.03)	0.00 (0.00)	0.03 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.99 (0.58)	3.72 (1.79)	0.16 (0.08)	0.18 (0.11)	5.00 (1.42)
		89	0.00 (0.00)	0.54 (0.26)	0.71 (0.36)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.34 (0.32)	1.82 (0.87)	9.80 (2.45)	0.15 (0.15)	1.53 (0.93)	6.72 (2.36)
		90	0.05 (0.05)	0.03 (0.03)	0.39 (0.39)	0.00 (0.00)	0.00 (0.00)	0.05 (0.04)	0.00 (0.00)	0.08 (0.08)	4.99 (1.48)	0.66 (0.44)	3.45 (1.51)	0.72 (0.31)
		91	0.00 (0.00)	0.14 (0.09)	0.77 (0.48)	0.00 (0.00)	0.12 (0.12)	0.00 (0.00)	0.00 (0.00)	0.09 (0.09)	4.07 (1.22)	0.71 (0.58)	0.00 (0.00)	0.44 (0.18)
	>3-6	85	0.00 (0.00)	0.00 (0.00)							2.02 (0.99)	0.00 (0.00)	1.87 (0.98)	0.00 (0.00)
		86	0.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	1.89 (1.06)	5.33 (3.47)	1.72 (1.07)	2.22 (1.60)
		88	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.57 (0.57)	0.51 (0.51)	0.00 (0.00)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.34 (1.24)	0.39 (0.38)	0.00 (0.00)	0.00 (0.00)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	5.29 (2.48)	0.34 (0.34)	0.09 (0.09)	0.00 (0.00)
		91	0.00 (0.00)	0.00 (0.00)	0.34 (0.28)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.43 (1.43)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Agaricia agaricites	0.5-3	85	2.50 (0.31)	1.28 (0.29)							5.41 (1.79)	2.64 (0.56)	1.91 (0.62)	2.32 (0.54)
		86	1.44 (0.22)	0.29 (0.12)		0.30 (0.09)	0.06 (0.04)			2.99 (0.50)	1.68 (0.49)	1.55 (0.64)	3.96 (0.90)	4.80 (0.98)
		88	1.37 (0.17)	0.58 (0.07)	0.02 (0.02)	0.74 (0.13)	0.91 (0.18)	0.17 (0.05)	0.87 (0.15)	1.12 (0.19)	0.21 (0.09)	1.04 (0.26)	1.61 (0.30)	0.45 (0.12)
		89	1.75 (0.19)	0.61 (0.11)	0.39 (0.10)	1.13 (0.19)	0.89 (0.20)	0.30 (0.10)	1.87 (0.22)	0.89 (0.14)	0.55 (0.16)	0.41 (0.21)	0.60 (0.45)	1.56 (0.30)
		90	0.16 (0.04)	0.19 (0.07)	0.13 (0.08)	0.56 (0.18)	0.03 (0.03)	0.43 (0.15)	0.34 (0.18)	0.72 (0.18)	0.06 (0.03)	0.04 (0.04)	0.15 (0.07)	0.20 (0.09)
		91	0.03 (0.03)	0.08 (0.08)	0.07 (0.04)	0.05 (0.04)	0.00 (0.00)	0.04 (0.04)	0.05 (0.03)	0.76 (0.29)	0.67 (0.32)	0.00 (0.00)	0.08 (0.08)	0.78 (0.28)

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
	>3-6	85	7.56 (1.23)	5.52 (0.69)							6.92 (1.27)	9.17 (2.18)	5.69 (0.97)	1.39 (0.24)
		86	2.40 (0.44)	1.73 (0.41)		0.76 (0.23)	2.85 (1.32)			2.78 (0.56)	3.31 (0.61)	7.33 (1.12)	4.77 (0.99)	1.00 (0.28)
		88	2.18 (0.92)	1.77 (0.37)	0.02 (0.02)	1.22 (0.27)	3.58 (0.73)	0.13 (0.10)	1.53 (0.99)	0.99 (0.21)	0.90 (0.23)	2.54 (0.78)	5.74 (1.38)	0.56 (0.24)
		89	3.00 (0.48)	2.67 (0.46)	2.21 (0.51)	1.77 (0.36)	5.71 (1.76)	1.05 (0.45)	8.06 (2.20)	2.05 (0.37)	1.60 (0.47)	2.18 (0.52)	2.66 (0.59)	1.30 (0.49)
		90	0.23 (0.13)	0.57 (0.22)	0.41 (0.17)	0.40 (0.16)	0.03 (0.03)	0.43 (0.18)	0.29 (0.19)	1.89 (0.38)	0.26 (0.14)	0.05 (0.05)	0.42 (0.20)	0.19 (0.09)
		91	1.03 (0.27)	0.64 (0.25)	0.18 (0.08)	0.13 (0.06)	0.07 (0.07)	0.17 (0.14)	0.50 (0.31)	0.94 (0.34)	0.73 (0.24)	0.17 (0.09)	0.19 (0.09)	0.45 (0.18)
Agaricia tenuifolia	0.5-3	85	0.00 (0.00)	0.00 (0.00)							0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.43 (0.17)
		86	0.04 (0.03)	0.20 (0.10)		0.39 (0.14)	0.05 (0.03)			0.38 (0.17)	1.79 (0.89)	0.28 (0.28)	0.00 (0.00)	0.12 (0.07)
		88	0.49 (0.13)	0.00 (0.00)	0.06 (0.04)	0.11 (0.04)	0.17 (0.07)	0.19 (0.07)	1.09 (0.25)	0.14 (0.07)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.19 (0.11)
		89	0.00 (0.00)	0.00 (0.00)	0.24 (0.11)	0.34 (0.15)	0.77 (0.17)	0.16 (0.07)	0.65 (0.15)	0.26 (0.13)	0.92 (0.35)	0.00 (0.00)	0.47 (0.27)	0.46 (0.24)
		90	1.14 (0.25)	0.59 (0.15)	0.19 (0.08)	0.52 (0.12)	0.30 (0.14)	0.58 (0.16)	1.25 (0.29)	1.00 (0.30)	0.66 (0.22)	1.34 (0.32)	1.04 (0.31)	0.37 (0.13)
		91	1.17 (0.15)	0.29 (0.12)	0.10 (0.06)	0.47 (0.14)	0.81 (0.39)	0.31 (0.15)	0.79 (0.19)	1.32 (0.29)	0.13 (0.10)	2.25 (0.49)	1.78 (0.34)	0.42 (0.17)
	>3-6	85	0.00 (0.00)	0.02 (0.02)							0.13 (0.11)	0.00 (0.00)	0.02 (0.02)	3.46 (0.81)
		86	1.49 (0.43)	0.56 (0.24)		3.88 (0.88)	3.56 (1.44)			1.02 (0.40)	1.15 (0.25)	0.23 (0.18)	0.43 (0.17)	6.66 (1.19)
		88	1.81 (0.71)	0.10 (0.08)	0.36 (0.26)	0.00 (0.00)	0.25 (0.25)	1.68 (0.69)	3.22 (0.97)	0.26 (0.10)	0.03 (0.03)	0.34 (0.29)	0.00 (0.00)	7.56 (1.31)
		89	0.00 (0.00)	0.00 (0.00)	0.21 (0.09)	0.91 (0.44)	0.86 (0.44)	1.80 (0.74)	0.89 (0.38)	1.03 (0.65)	0.62 (0.25)	1.41 (0.48)	0.90 (0.46)	3.90 (0.83)
		90	4.77 (1.30)	2.09 (0.55)	0.90 (0.25)	0.83 (0.17)	2.92 (0.49)	0.97 (0.20)	2.82 (0.43)	0.64 (0.19)	1.81 (0.47)	2.84 (0.39)	5.43 (0.84)	1.19 (0.44)
		91	1.13 (0.26)	1.04 (0.30)	0.71 (0.18)	0.94 (0.31)	4.65 (1.51)	0.76 (0.22)	2.14 (0.36)	4.45 (0.75)	0.41 (0.23)	3.20 (0.55)	2.63 (0.42)	1.90 (0.56)
Colpophylia natans	0.5-3	85	0.00 (0.00)	0.04 (0.04)							0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.19 (0.12)
		86	0.00 (0.00)	0.00 (0.00)		0.07 (0.07)	0.00 (0.00)			2.27 (1.25)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.43 (0.23)
		88	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.32 (0.32)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	1.30 (1.13)	0.00 (0.00)	0.23 (0.21)	0.00 (0.00)	0.10 (0.10)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.08 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		91	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.17 (0.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)
	>3-6	85	0.00 (0.00)	0.65 (0.43)							0.14 (0.14)	1.14 (1.14)	0.03 (0.03)	0.75 (0.34)
		86	4.36 (3.50)	0.12 (0.12)		0.22 (0.22)	0.55 (0.55)			0.26 (0.20)	2.40 (1.22)	0.61 (0.45)	0.71 (0.45)	0.32 (0.25)
		88	0.24 (0.24)	0.00 (0.00)	0.17 (0.17)	0.97 (0.97)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	0.29 (0.22)	1.32 (1.32)	0.14 (0.14)
		89	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.30 (0.30)	0.61 (0.61)	4.59 (2.44)	0.05 (0.05)	0.17 (0.14)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.52 (1.25)	0.00 (0.00)	0.36 (0.30)	1.22 (1.22)	0.05 (0.05)	0.97 (0.97)	1.38 (0.90)	0.31 (0.20)	0.00 (0.00)
		91	0.00 (0.00)	0.00 (0.00)	1.57 (1.10)	0.15 (0.15)	0.00 (0.00)	0.32 (0.32)	0.89 (0.57)	0.00 (0.00)	0.35 (0.25)	0.00 (0.00)	0.16 (0.16)	0.00 (0.00)

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
Diploria clivosa	0.5-3	85	0.72 (0.38)	4.96 (1.72)							3.50 (0.88)	0.44 (0.44)	1.90 (1.13)	0.50 (0.38)
		86	1.55 (0.73)	0.95 (0.53)		1.06 (0.28)	1.08 (0.35)			2.68 (0.71)	2.54 (0.66)	1.75 (0.99)	4.34 (1.95)	0.57 (0.30)
		88	0.02 (0.02)	1.48 (0.44)	0.95 (0.21)	0.00 (0.00)	0.39 (0.13)	0.58 (0.14)	0.96 (0.37)	2.01 (1.14)	0.15 (0.07)	0.89 (0.28)	2.81 (0.89)	0.04 (0.04)
		89	0.28 (0.17)	1.76 (0.46)	2.03 (0.77)	0.06 (0.04)	0.39 (0.13)	1.52 (0.34)	0.15 (0.15)	0.30 (0.19)	1.10 (0.41)	1.21 (0.47)	0.67 (0.67)	0.00 (0.00)
		90	0.11 (0.08)	1.03 (0.32)	2.16 (0.98)	0.18 (0.08)	0.27 (0.13)	0.11 (0.08)	0.22 (0.15)	0.60 (0.22)	1.43 (0.39)	0.00 (0.00)	1.78 (0.45)	0.00 (0.00)
		91	0.00 (0.00)	0.42 (0.24)	0.15 (0.10)	0.03 (0.02)	0.16 (0.11)	0.00 (0.00)	0.29 (0.17)	0.33 (0.14)	1.90 (0.40)	0.02 (0.02)	0.16 (0.10)	0.01 (0.01)
	>3-6	85	0.00 (0.00)	0.00 (0.00)							0.00 (0.00)	0.00 (0.00)	0.10 (0.10)	0.13 (0.13)
		86	0.00 (0.00)	0.67 (0.67)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	0.16 (0.11)	0.15 (0.15)	0.24 (0.24)	0.05 (0.05)
		88	0.00 (0.00)	0.00 (0.00)	0.09 (0.09)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.11 (0.11)	0.03 (0.03)	0.46 (0.32)	0.00 (0.00)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	0.18 (0.18)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.03)	0.15 (0.13)	0.00 (0.00)
		90	0.00 (0.00)	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.03)	0.07 (0.04)	0.00 (0.00)	0.12 (0.08)	0.00 (0.00)
		91	0.00 (0.00)	0.08 (0.05)	0.00 (0.00)	0.00 (0.00)	0.08 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Diploria strigosa	0.5-3	85	0.04 (0.03)	3.39 (1.35)							3.63 (0.91)	1.69 (1.31)	0.79 (0.32)	1.04 (0.43)
		86	0.04 (0.04)	0.46 (0.25)		0.15 (0.07)	0.20 (0.14)			1.02 (0.47)	2.21 (0.56)	0.99 (0.36)	0.71 (0.38)	0.39 (0.16)
		88	0.00 (0.00)	0.38 (0.28)	0.16 (0.08)	0.37 (0.31)	0.07 (0.03)	0.02 (0.02)	0.45 (0.31)	1.38 (0.51)	1.85 (0.57)	2.08 (0.77)	1.51 (0.40)	0.54 (0.22)
		89	0.00 (0.00)	0.52 (0.32)	0.95 (0.46)	0.10 (0.06)	0.16 (0.09)	0.00 (0.00)	0.61 (0.54)	2.40 (0.82)	0.90 (0.29)	3.22 (1.26)	1.60 (0.98)	0.22 (0.13)
		90	0.00 (0.00)	0.19 (0.12)	0.76 (0.30)	0.02 (0.01)	0.36 (0.36)	0.41 (0.27)	0.05 (0.05)	2.27 (0.74)	1.13 (0.53)	1.49 (0.66)	1.82 (0.89)	0.64 (0.26)
		91	0.00 (0.00)	0.20 (0.13)	0.33 (0.21)	0.02 (0.01)	0.14 (0.07)	0.25 (0.15)	0.50 (0.33)	0.45 (0.33)	0.89 (0.27)	0.58 (0.27)	0.40 (0.18)	0.02 (0.02)
	>3-6	85	0.00 (0.00)	0.50 (0.24)							2.81 (1.36)	0.20 (0.20)	0.47 (0.33)	0.20 (0.10)
		86	0.35 (0.35)	0.00 (0.00)		0.38 (0.38)	0.19 (0.15)			2.23 (2.12)	0.40 (0.16)	0.47 (0.28)	1.51 (0.62)	0.15 (0.11)
		88	0.00 (0.00)	0.12 (0.09)	1.72 (1.72)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.70 (0.70)	2.07 (0.61)	0.98 (0.67)	1.27 (0.57)	0.04 (0.04)
		89	0.00 (0.00)	0.00 (0.00)	1.59 (0.91)	0.40 (0.39)	0.05 (0.05)	0.00 (0.00)	0.00 (0.00)	1.32 (0.60)	0.15 (0.09)	0.41 (0.18)	0.67 (0.67)	0.31 (0.27)
		90	0.00 (0.00)	0.05 (0.04)	0.43 (0.28)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.11 (0.08)	0.19 (0.18)	0.47 (0.24)	0.31 (0.22)	0.00 (0.00)
		91	0.00 (0.00)	0.61 (0.38)	0.36 (0.21)	0.09 (0.09)	0.04 (0.04)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.44 (0.34)	0.27 (0.13)	0.05 (0.05)	0.00 (0.00)
Montastrea annularis	0.5-3	85	0.00 (0.00)	0.00 (0.00)							2.24 (1.52)	0.00 (0.00)	0.00 (0.00)	7.52 (3.28)
		86	0.00 (0.00)	0.00 (0.00)		0.03 (0.03)	0.00 (0.00)			0.82 (0.44)	1.58 (0.92)	0.66 (0.66)	0.50 (0.50)	10.59 (3.37)
		88	0.00 (0.00)	0.00 (0.00)	0.07 (0.05)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.32 (0.25)	0.37 (0.31)	0.04 (0.04)	0.00 (0.00)	3.31 (1.43)
		89	0.00 (0.00)	0.00 (0.00)	0.42 (0.29)	1.85 (1.26)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.25 (0.25)	0.43 (0.43)	0.28 (0.28)	0.00 (0.00)	3.76 (2.04)
		90	0.00 (0.00)	0.00 (0.00)	1.48 (0.97)	0.00 (0.00)	0.10 (0.07)	0.52 (0.38)	0.03 (0.03)	0.00 (0.00)	0.00 (0.00)	0.47 (0.37)	0.00 (0.00)	5.29 (2.20)
		91	0.00 (0.00)	0.00 (0.00)	1.17 (0.62)	0.00 (0.00)	0.30 (0.22)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.60 (0.41)	0.00 (0.00)	1.03 (0.73)

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
	>3-6	85	0.00 (0.00)	0.01 (0.01)							12.66 (3.77)	0.07 (0.07)	0.33 (0.33)	3.91 (1.99)
		86	0.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.00 (0.00)			2.73 (1.58)	8.12 (2.37)	3.44 (1.77)	1.81 (1.81)	0.77 (0.53)
		88	0.00 (0.00)	0.00 (0.00)	7.55 (5.05)	1.59 (1.59)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.25 (0.25)	1.65 (1.26)	0.04 (0.04)	1.16 (0.80)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	1.42 (1.11)	1.05 (0.93)	0.24 (0.24)	0.00 (0.00)	0.00 (0.00)	0.38 (0.24)	9.25 (3.26)	0.49 (0.49)	0.09 (0.09)	0.02 (0.02)
		90	0.00 (0.00)	0.00 (0.00)	1.92 (0.70)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.14 (0.13)	5.19 (2.31)	0.51 (0.29)	0.00 (0.00)	0.28 (0.24)
		91	0.00 (0.00)	0.92 (0.85)	2.47 (1.46)	0.23 (0.23)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	4.22 (1.42)	6.51 (2.61)	0.00 (0.00)	0.00 (0.00)
Porites astreoides	0.5-3	85	3.45 (0.41)	3.96 (0.41)							3.13 (0.54)	4.19 (1.61)	1.09 (0.35)	0.78 (0.18)
		86	2.71 (0.27)	1.39 (0.18)		1.90 (0.21)	0.87 (0.25)			1.33 (0.18)	2.12 (0.30)	2.87 (0.94)	3.32 (0.74)	1.66 (0.35)
		88	1.79 (0.21)	2.07 (0.15)	1.52 (0.17)	1.10 (0.12)	0.91 (0.16)	1.41 (0.18)	1.35 (0.14)	1.01 (0.16)	2.41 (0.39)	1.70 (0.20)	1.27 (0.19)	1.34 (0.29)
		89	1.53 (0.21)	2.13 (0.18)	1.69 (0.23)	1.30 (0.18)	1.55 (0.26)	1.53 (0.21)	1.91 (0.30)	1.75 (0.25)	1.53 (0.36)	1.57 (0.28)	1.96 (0.47)	1.37 (0.27)
		90	1.78 (0.21)	0.94 (0.13)	1.15 (0.15)	1.40 (0.22)	1.05 (0.17)	1.51 (0.26)	1.55 (0.26)	1.19 (0.18)	1.10 (0.16)	1.13 (0.22)	0.40 (0.12)	1.36 (0.33)
		91	2.15 (0.19)	1.73 (0.19)	0.49 (0.12)	1.23 (0.18)	1.34 (0.31)	0.82 (0.21)	1.03 (0.17)	1.43 (0.27)	1.38 (0.21)	1.49 (0.29)	1.09 (0.25)	0.82 (0.20)
	>3-6	85	1.35 (0.41)	3.09 (0.48)							2.13 (0.35)	2.00 (0.82)	1.03 (0.24)	0.78 (0.15)
		86	0.77 (0.33)	0.90 (0.26)		0.60 (0.19)	3.75 (1.13)			0.81 (0.28)	1.34 (0.25)	1.90 (0.41)	1.53 (0.34)	1.09 (0.20)
		88	0.04 (0.02)	0.42 (0.14)	0.41 (0.20)	0.25 (0.15)	0.58 (0.25)	0.43 (0.32)	1.00 (0.33)	0.42 (0.12)	2.67 (0.32)	1.79 (0.34)	0.41 (0.16)	0.14 (0.06)
		89	0.27 (0.14)	0.71 (0.30)	0.67 (0.20)	0.68 (0.19)	1.13 (0.48)	1.30 (0.49)	0.21 (0.11)	1.01 (0.37)	1.33 (0.37)	2.04 (0.43)	0.84 (0.18)	0.66 (0.17)
		90	0.34 (0.20)	0.76 (0.18)	0.16 (0.08)	0.73 (0.42)	1.49 (0.34)	0.38 (0.12)	0.97 (0.22)	1.14 (0.22)	1.08 (0.31)	1.63 (0.24)	0.66 (0.19)	0.56 (0.14)
		91	1.11 (0.31)	1.44 (0.21)	0.22 (0.07)	0.35 (0.11)	1.13 (0.32)	0.28 (0.15)	0.63 (0.21)	0.97 (0.28)	0.83 (0.28)	1.00 (0.21)	0.82 (0.30)	0.30 (0.11)
Porites furcata	0.5-3	85	2.27 (0.51)	0.11 (0.08)							0.00 (0.00)	0.24 (0.17)	0.19 (0.17)	0.01 (0.01)
		86	1.59 (0.50)	0.24 (0.19)		2.11 (0.93)	0.05 (0.04)			1.04 (0.27)	0.09 (0.08)	0.00 (0.00)	0.36 (0.26)	0.27 (0.19)
		88	0.66 (0.11)	0.46 (0.17)	0.39 (0.08)	0.38 (0.08)	0.12 (0.04)	0.23 (0.05)	0.67 (0.11)	0.92 (0.17)	0.21 (0.06)	0.08 (0.06)	0.06 (0.03)	0.04 (0.02)
		89	0.97 (0.16)	0.44 (0.18)	0.08 (0.04)	0.30 (0.08)	0.08 (0.03)	0.18 (0.05)	0.11 (0.03)	0.11 (0.04)	0.01 (0.01)	0.00 (0.00)	0.05 (0.04)	0.13 (0.06)
		90	1.78 (0.25)	0.14 (0.05)	0.07 (0.03)	0.18 (0.09)	0.04 (0.02)	0.29 (0.09)	0.14 (0.05)	0.34 (0.16)	0.01 (0.01)	0.10 (0.10)	0.00 (0.00)	0.03 (0.02)
		91	0.83 (0.13)	0.04 (0.02)	0.04 (0.03)	0.22 (0.06)	0.00 (0.00)	0.13 (0.09)	0.17 (0.08)	0.06 (0.03)	0.03 (0.03)	0.03 (0.03)	0.17 (0.06)	0.05 (0.04)
	>3-6	85	7.28 (2.26)	4.30 (1.11)							0.00 (0.00)	0.19 (0.16)	0.11 (0.05)	0.22 (0.13)
		86	2.36 (0.93)	2.13 (0.79)		1.26 (0.54)	0.43 (0.19)			0.72 (0.28)	0.14 (0.14)	0.00 (0.00)	0.64 (0.19)	0.16 (0.10)
		88	2.35 (1.29)	1.17 (0.53)	0.19 (0.15)	0.01 (0.01)	0.25 (0.17)	0.05 (0.05)	0.30 (0.13)	0.20 (0.06)	0.32 (0.10)	0.21 (0.11)	0.08 (0.07)	0.30 (0.13)
		89	1.21 (0.36)	0.61 (0.26)	0.16 (0.05)	0.40 (0.11)	0.82 (0.41)	0.07 (0.03)	0.30 (0.08)	0.18 (0.07)	0.05 (0.02)	0.00 (0.00)	0.17 (0.06)	0.11 (0.06)
		90	1.22 (0.74)	0.45 (0.13)	0.04 (0.02)	0.18 (0.05)	0.11 (0.05)	0.13 (0.05)	0.24 (0.09)	0.32 (0.10)	0.01 (0.01)	0.00 (0.00)	0.02 (0.02)	0.13 (0.05)
		91	0.67 (0.19)	0.58 (0.18)	0.07 (0.03)	0.20 (0.06)	0.13 (0.06)	0.19 (0.07)	0.21 (0.08)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.19 (0.10)	0.20 (0.15)

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
Porites porites	0.5-3	85	2.67 (0.48)	0.27 (0.13)							0.55 (0.21)	0.25 (0.19)	0.10 (0.07)	0.07 (0.05)
		86	0.93 (0.28)	0.15 (0.05)		0.51 (0.17)	0.00 (0.00)			1.16 (0.38)	0.97 (0.36)	1.61 (1.20)	0.56 (0.31)	0.04 (0.04)
		88	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06 (0.05)	0.00 (0.00)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	0.06 (0.03)	0.11 (0.05)	0.02 (0.01)	0.00 (0.00)	0.05 (0.02)	0.04 (0.02)	0.07 (0.07)	0.10 (0.07)	0.00 (0.00)	0.03 (0.02)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		91	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	>3-6	85	0.10 (0.10)	0.13 (0.09)							2.47 (0.79)	0.00 (0.00)	0.13 (0.09)	0.03 (0.03)
		86	0.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.21 (0.21)			0.00 (0.00)	1.28 (0.62)	0.38 (0.16)	0.00 (0.00)	0.00 (0.00)
		88	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.05)	0.00 (0.00)	0.00 (0.00)
		89	0.00 (0.00)	0.00 (0.00)	0.04 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.22 (0.13)	0.28 (0.13)	0.00 (0.00)	0.00 (0.00)
		90	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
		91	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Siderastrea siderea	0.5-3	85	4.68 (0.84)	1.62 (0.36)							3.12 (0.61)	2.50 (1.70)	1.08 (0.54)	1.14 (0.54)
		86	4.62 (0.93)	0.25 (0.19)		3.94 (0.77)	8.15 (1.23)			6.67 (1.37)	2.69 (0.72)	5.30 (1.73)	0.80 (0.35)	3.03 (0.97)
		88	1.58 (0.37)	0.94 (0.22)	7.20 (1.12)	1.72 (0.56)	7.02 (0.71)	1.61 (0.29)	4.98 (0.83)	8.44 (1.02)	2.04 (0.57)	3.19 (0.69)	4.02 (0.89)	3.08 (0.92)
		89	3.40 (0.69)	1.79 (0.38)	7.63 (1.07)	4.48 (1.37)	5.04 (0.76)	2.19 (0.41)	6.79 (1.25)	12.21 (1.40)	1.52 (0.46)	0.09 (0.05)	0.74 (0.44)	2.34 (1.02)
		90	0.43 (0.21)	0.74 (0.21)	6.40 (1.00)	2.83 (0.68)	3.14 (0.61)	2.90 (0.55)	4.32 (0.95)	9.11 (1.33)	2.46 (0.49)	3.06 (0.78)	0.48 (0.22)	4.70 (1.23)
		91	2.26 (0.68)	1.05 (0.27)	4.28 (0.78)	1.83 (0.65)	2.89 (0.81)	3.11 (0.73)	5.25 (1.04)	7.33 (1.30)	1.51 (0.48)	4.45 (0.94)	1.71 (0.67)	0.34 (0.29)
	>3-6	85	6.81 (1.68)	7.04 (1.24)							5.10 (1.26)	6.55 (2.76)	5.75 (1.31)	1.14 (0.44)
		86	10.40 (2.51)	4.22 (1.48)		2.34 (1.30)	8.44 (2.56)			8.73 (1.78)	2.78 (0.66)	5.21 (1.31)	6.46 (1.31)	1.78 (0.54)
		88	4.03 (1.83)	5.81 (2.87)	2.64 (1.28)	1.24 (0.94)	0.58 (0.27)	0.43 (0.18)	2.95 (1.07)	4.56 (0.84)	3.71 (0.76)	6.54 (1.34)	6.89 (2.51)	0.13 (0.13)
		89	2.69 (1.02)	3.77 (1.45)	3.94 (1.08)	0.87 (0.51)	2.42 (1.26)	4.45 (3.60)	2.17 (1.70)	4.83 (1.19)	2.04 (0.85)	3.02 (0.70)	3.81 (0.92)	1.09 (0.53)
		90	4.38 (2.25)	4.10 (1.32)	4.35 (0.90)	1.10 (0.62)	1.36 (0.43)	2.00 (0.50)	3.77 (1.32)	6.35 (1.16)	1.53 (0.57)	4.53 (1.10)	1.49 (0.56)	0.34 (0.16)
		91	3.18 (0.83)	3.17 (0.90)	4.06 (0.76)	0.89 (0.30)	1.20 (0.52)	1.10 (0.37)	2.17 (0.67)	4.19 (1.00)	1.85 (0.58)	2.26 (0.65)	0.57 (0.26)	0.01 (0.01)
Total Coral Cover	0.5-3	85	18.46 (1.57)	22.78 (2.43)							27.74 (2.52)	17.69 (4.01)	15.16 (2.54)	27.25 (3.87)
		86	14.54 (1.48)	4.85 (0.92)		10.92 (1.26)	10.72 (1.40)			23.28 (2.00)	24.59 (2.48)	25.04 (5.46)	20.07 (3.09)	41.47 (4.12)
		88	7.20 (0.59)	6.27 (0.56)	10.54 (1.11)	5.26 (0.72)	9.70 (0.80)	5.05 (0.37)	10.79 (0.91)	16.51 (1.63)	11.46 (1.80)	10.59 (1.20)	11.82 (1.20)	14.84 (2.12)
		89	8.13 (0.76)	7.91 (0.70)	15.91 (1.77)	9.96 (1.80)	9.49 (0.86)	6.10 (0.53)	12.76 (1.42)	20.42 (1.64)	17.53 (2.44)	7.40 (1.43)	7.94 (1.43)	18.41 (2.93)
		90	5.65 (0.46)	4.13 (0.50)	12.90 (1.61)	5.81 (0.81)	5.47 (0.88)	6.90 (0.94)	9.40 (1.42)	15.38 (1.56)	12.11 (1.52)	10.29 (1.46)	9.25 (1.63)	14.04 (2.33)
		91	6.75 (0.71)	4.15 (0.51)	7.79 (1.16)	4.11 (0.69)	5.64 (1.00)	4.79 (0.87)	8.13 (1.09)	11.99 (1.46)	10.78 (1.19)	11.16 (1.10)	5.61 (0.77)	5.27 (0.87)

App. Table C.1 Percent cover of common coral species, total coral cover, and number of coral species, by depth, reef, and date of census (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
	>3-6	85	26.26 (2.82)	28.00 (1.94)							37.77 (3.53)	19.90 (2.97)	16.88 (1.93)	17.94 (2.27)
		86	24.91 (3.54)	10.88 (2.31)		9.98 (2.27)	20.17 (3.75)			22.12 (2.85)	26.68 (2.54)	27.50 (3.39)	21.35 (2.63)	20.27 (2.26)
		88	14.40 (2.34)	9.85 (3.13)	17.69 (5.96)	5.76 (1.91)	5.63 (0.87)	2.73 (0.94)	9.58 (1.44)	8.11 (1.07)	13.40 (1.80)	18.12 (2.76)	19.76 (2.99)	9.82 (1.27)
		89	9.03 (1.06)	7.94 (1.48)	12.06 (1.72)	6.92 (1.37)	11.33 (2.67)	8.68 (3.85)	13.06 (3.28)	14.02 (2.04)	18.93 (3.42)	17.67 (2.69)	10.39 (1.23)	9.48 (1.10)
		90	11.28 (2.27)	8.50 (1.45)	10.72 (1.85)	5.13 (1.40)	6.01 (0.80)	4.38 (0.67)	9.39 (1.67)	12.05 (1.39)	17.41 (3.12)	12.64 (1.28)	9.63 (0.95)	3.85 (0.66)
		91	7.63 (1.04)	8.76 (1.23)	10.96 (1.97)	3.08 (0.45)	7.31 (1.69)	2.90 (0.57)	6.86 (0.94)	10.99 (1.08)	11.19 (1.83)	14.28 (2.45)	5.29 (0.64)	4.59 (0.75)
Number of Species	0.5-3	85	15	14							16	12	15	23
		86	17	15		17	10			24	19	14	17	27
		88	12	12	13	13	13	9	12	13	16	18	14	15
		89	11	14	18	16	19	15	16	19	19	15	14	23
		90	10	11	14	11	12	13	12	14	13	18	11	14
		91	8	11	14	10	7	8	9	12	18	16	12	15
	>3-6	85	12	21							25	11	25	31
		86	17	16		12	11			19	30	22	28	23
		88	16	15	14	10	7	7	7	14	22	18	17	13
		89	9	11	20	14	11	9	13	20	27	22	19	24
		90	9	14	15	13	8	10	8	21	18	19	17	14
		91	10	13	14	10	11	8	13	10	18	15	13	16

App. Table C.2 Percent cover of common sessile organisms (except scleractinians) by depth, reef, and date of census. Data are means (SE in parentheses).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
Macroalgae	0.5-3	85	61.97 (1.85)	55.22 (2.47)							43.35 (2.58)	76.49 (3.97)	57.74 (3.51)	46.91 (3.69)
		86	59.26 (2.49)	48.78 (6.34)		59.00 (3.02)	68.81 (3.49)			52.16 (2.65)	54.17 (2.80)	38.94 (5.38)	43.00 (5.41)	30.79 (3.47)
		88	36.00 (3.32)	40.38 (3.10)	59.81 (3.03)	29.92 (3.12)	34.84 (3.22)	7.13 (1.00)	47.78 (3.61)	56.57 (3.98)	17.16 (3.58)	13.96 (2.87)	22.91 (3.29)	31.54 (4.00)
		89	38.58 (3.32)	45.70 (2.93)	55.88 (2.82)	40.73 (3.00)	52.36 (2.45)	41.29 (2.47)	56.35 (2.34)	55.01 (2.31)	28.41 (3.12)	61.68 (4.46)	41.79 (4.85)	48.61 (3.79)
		90	26.31 (2.26)	42.83 (3.45)	70.24 (2.71)	69.93 (2.78)	72.65 (2.62)	72.46 (3.43)	51.21 (4.15)	62.16 (3.36)	60.25 (4.23)	59.77 (6.00)	36.53 (5.26)	54.58 (4.06)
		91	69.09 (3.35)	81.61 (1.72)	82.91 (1.71)	92.16 (0.97)	88.77 (1.51)	84.89 (2.88)	81.55 (2.16)	69.68 (3.47)	72.81 (2.55)	58.90 (5.06)	71.86 (3.93)	80.86 (1.94)
	>3-6	85	55.71 (3.96)	53.65 (2.31)							46.18 (3.01)	78.40 (2.78)	67.14 (2.17)	53.94 (3.57)
		86	54.57 (4.25)	56.67 (6.67)		29.50 (4.59)	44.41 (5.81)			63.17 (3.78)	60.61 (2.99)	41.12 (4.17)	61.24 (3.40)	46.91 (3.58)
		88	35.56 (9.46)	53.39 (5.63)	57.08 (9.03)	23.09 (9.18)	0.00 (0.00)	10.40 (3.98)	59.47 (10.32)	71.34 (4.01)	16.73 (3.61)	17.14 (4.46)	51.36 (6.70)	53.20 (6.36)
		89	32.34 (6.20)	40.97 (5.06)	59.52 (2.66)	22.72 (4.01)	29.41 (5.33)	55.86 (8.62)	52.64 (5.86)	61.70 (3.63)	41.69 (4.42)	42.02 (4.39)	69.10 (2.46)	49.65 (3.36)
		90	25.22 (7.57)	63.92 (5.21)	64.53 (3.68)	67.50 (4.66)	72.27 (3.48)	80.95 (2.80)	52.24 (4.77)	69.25 (2.92)	55.52 (5.15)	31.29 (4.35)	74.46 (5.00)	69.30 (4.31)
		91	69.17 (4.56)	72.23 (3.92)	83.98 (2.53)	91.18 (1.75)	84.05 (2.45)	81.33 (3.98)	88.73 (1.31)	84.92 (1.32)	81.44 (1.90)	69.20 (3.87)	83.35 (3.27)	89.19 (1.28)
Crustose Coralline Algae	0.5-3	85	3.19 (0.62)	1.98 (0.47)							4.78 (1.03)	3.38 (1.72)	5.85 (1.00)	9.86 (1.67)
		86	8.77 (1.35)	36.67 (6.44)		3.88 (0.65)	1.94 (0.33)			6.88 (1.37)	13.48 (2.06)	15.67 (3.47)	14.77 (2.95)	8.86 (1.27)
		88	35.01 (3.61)	37.55 (3.25)	14.04 (2.46)	22.15 (3.24)	1.08 (0.37)	61.49 (3.30)	13.60 (2.76)	10.75 (2.68)	13.32 (2.87)	12.60 (2.12)	56.89 (3.31)	20.38 (3.37)
		89	33.06 (3.28)	33.63 (2.95)	9.05 (1.59)	11.60 (2.12)	2.15 (0.43)	36.62 (2.96)	14.90 (1.70)	8.85 (1.61)	41.40 (3.48)	19.58 (4.14)	28.96 (4.92)	18.10 (2.54)
		90	62.78 (2.43)	46.98 (3.42)	8.67 (2.39)	5.81 (1.33)	2.44 (0.70)	11.45 (3.02)	25.84 (4.11)	15.22 (3.67)	25.02 (4.22)	23.87 (5.31)	49.96 (5.49)	8.29 (2.30)
		91	15.81 (2.91)	2.65 (0.61)	3.58 (0.96)	0.31 (0.18)	1.05 (0.71)	7.56 (2.59)	1.36 (0.55)	13.46 (3.61)	12.24 (2.26)	23.64 (5.15)	6.77 (2.02)	8.89 (1.57)
	>3-6	85	0.83 (0.39)	2.48 (0.87)							1.69 (0.65)	1.31 (0.85)	2.56 (0.48)	1.93 (0.40)
		86	1.79 (0.51)	28.19 (7.05)		0.69 (0.32)	1.55 (0.53)			0.97 (0.20)	4.04 (0.63)	14.32 (3.96)	6.90 (0.94)	2.91 (0.62)
		88	32.79 (9.29)	8.06 (2.91)	1.88 (1.06)	4.76 (3.36)	0.00 (0.00)	8.60 (8.17)	4.06 (1.90)	3.52 (1.88)	10.49 (2.36)	19.33 (4.63)	25.72 (7.03)	7.76 (2.14)
		89	7.92 (2.70)	27.48 (4.97)	3.03 (0.58)	1.98 (0.58)	10.48 (4.60)	2.13 (0.94)	26.54 (4.60)	11.14 (3.08)	23.31 (3.57)	29.02 (3.87)	12.54 (2.01)	10.32 (1.40)
		90	50.52 (8.47)	25.93 (5.17)	0.84 (0.27)	4.35 (1.67)	0.79 (0.44)	4.97 (2.29)	33.66 (4.85)	4.99 (1.10)	25.40 (4.35)	53.16 (4.72)	14.86 (4.96)	5.31 (1.33)
		91	11.64 (3.36)	15.13 (3.63)	0.21 (0.16)	1.28 (0.62)	0.78 (0.38)	9.49 (2.84)	2.26 (0.70)	2.87 (0.64)	6.12 (1.25)	14.97 (3.62)	1.02 (0.48)	3.66 (1.22)
Gorgonians	0.5-3	85	0.00 (0.00)	0.06 (0.02)							0.03 (0.02)	0.13 (0.08)	0.05 (0.02)	0.00 (0.00)
		86	0.00 (0.00)	0.10 (0.06)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	0.00 (0.00)	0.03 (0.02)	0.01 (0.01)	0.00 (0.00)
		88	2.81 (0.51)	1.05 (0.15)	0.57 (0.15)	0.71 (0.22)	0.21 (0.11)	0.38 (0.15)	1.02 (0.17)	0.55 (0.22)	0.15 (0.11)	0.36 (0.08)	0.60 (0.23)	0.30 (0.10)
		89	1.68 (0.20)	0.61 (0.14)	0.78 (0.23)	0.38 (0.12)	0.21 (0.13)	0.01 (0.01)	1.27 (0.21)	0.65 (0.19)	0.46 (0.27)	0.18 (0.04)	0.77 (0.42)	0.39 (0.16)
		90	1.53 (0.27)	0.32 (0.10)	0.34 (0.14)	0.41 (0.18)	0.00 (0.00)	0.17 (0.08)	0.63 (0.17)	0.22 (0.13)	0.11 (0.11)	0.01 (0.01)	0.66 (0.25)	0.66 (0.38)
		91	2.34 (0.36)	0.45 (0.12)	0.86 (0.23)	0.02 (0.02)	0.30 (0.24)	0.46 (0.19)	0.63 (0.29)	0.32 (0.18)	0.17 (0.13)	0.01 (0.01)	1.20 (0.36)	0.95 (0.33)

App. Table C.2 Percent cover of common sessile organisms (except scleractinians) by depth, reef, and date of census. Data are means (SE in parentheses) (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
	>3-6	85	0.04 (0.04)	0.02 (0.02)							0.00 (0.00)	0.05 (0.05)	0.02 (0.01)	0.00 (0.00)
		86	0.00 (0.00)	0.04 (0.04)		0.00 (0.00)	0.00 (0.00)			0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)
		88	5.68 (1.85)	0.02 (0.02)	0.45 (0.30)	0.00 (0.00)	0.00 (0.00)	0.90 (0.90)	1.78 (1.00)	0.46 (0.19)	0.14 (0.09)	0.09 (0.06)	0.95 (0.63)	0.00 (0.00)
		89	1.14 (0.30)	0.78 (0.20)	0.19 (0.07)	0.00 (0.00)	0.04 (0.04)	0.78 (0.61)	1.35 (0.50)	0.19 (0.12)	0.39 (0.19)	0.01 (0.01)	0.54 (0.23)	0.00 (0.00)
		90	2.88 (0.97)	0.13 (0.10)	0.11 (0.07)	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	0.80 (0.34)	0.80 (0.31)	0.01 (0.01)	0.00 (0.00)	0.15 (0.15)	0.00 (0.00)
		91	2.19 (0.54)	0.37 (0.16)	0.13 (0.13)	0.00 (0.00)	0.33 (0.20)	0.82 (0.42)	0.37 (0.25)	0.00 (0.00)	0.29 (0.21)	0.08 (0.06)	2.14 (0.63)	0.00 (0.00)
Millepora spp.	0.5-3	85	3.85 (0.44)	3.91 (0.50)							0.26 (0.09)	1.58 (0.63)	2.43 (1.16)	1.29 (0.42)
		86	2.93 (0.43)	6.75 (2.21)		2.36 (0.36)	0.59 (0.24)			5.40 (0.86)	0.81 (0.30)	4.07 (1.16)	8.61 (3.59)	2.58 (0.65)
		88	2.17 (0.22)	2.10 (0.16)	0.55 (0.17)	1.13 (0.19)	0.38 (0.11)	1.21 (0.15)	0.60 (0.15)	0.73 (0.15)	0.16 (0.06)	1.01 (0.23)	0.38 (0.10)	0.48 (0.12)
		89	1.01 (0.20)	2.04 (0.41)	0.57 (0.17)	1.18 (0.18)	0.95 (0.24)	1.07 (0.19)	0.64 (0.17)	0.45 (0.13)	0.20 (0.08)	6.36 (2.07)	0.95 (0.47)	1.63 (0.38)
		90	1.27 (0.17)	1.09 (0.24)	0.27 (0.10)	0.78 (0.19)	0.72 (0.23)	0.54 (0.25)	0.30 (0.10)	0.62 (0.30)	0.08 (0.05)	0.22 (0.20)	0.23 (0.11)	0.61 (0.16)
		91	1.03 (0.17)	1.17 (0.25)	0.09 (0.09)	0.86 (0.18)	0.67 (0.21)	0.14 (0.07)	0.06 (0.04)	0.36 (0.10)	0.04 (0.03)	0.00 (0.00)	0.32 (0.11)	1.33 (0.29)
	>3-6	85	1.67 (0.40)	2.57 (0.68)							0.20 (0.07)	0.35 (0.18)	0.15 (0.07)	1.61 (0.32)
		86	1.50 (0.54)	0.77 (0.24)		0.69 (0.29)	1.72 (0.61)			2.43 (1.66)	0.14 (0.07)	0.24 (0.19)	1.61 (0.58)	2.98 (0.62)
		88	1.01 (0.30)	0.31 (0.15)	0.00 (0.00)	0.87 (0.26)	0.96 (0.74)	0.05 (0.05)	0.00 (0.00)	0.33 (0.15)	0.11 (0.05)	0.54 (0.28)	0.07 (0.07)	0.99 (0.48)
		89	0.92 (0.32)	0.56 (0.24)	0.38 (0.16)	0.79 (0.28)	1.19 (0.65)	0.03 (0.03)	0.06 (0.04)	0.38 (0.12)	0.04 (0.03)	0.28 (0.13)	0.19 (0.07)	1.10 (0.25)
		90	0.14 (0.11)	0.39 (0.22)	0.16 (0.08)	0.55 (0.17)	0.10 (0.10)	0.16 (0.10)	0.14 (0.08)	0.47 (0.18)	0.07 (0.07)	0.44 (0.22)	0.40 (0.23)	0.93 (0.21)
		91	0.23 (0.10)	2.07 (0.44)	0.07 (0.07)	0.66 (0.17)	0.78 (0.32)	0.12 (0.09)	0.16 (0.08)	0.00 (0.00)	0.02 (0.02)	0.02 (0.02)	0.48 (0.19)	1.51 (0.37)
Sponges	0.5-3	85	2.00 (0.48)	7.72 (1.04)							3.41 (1.21)	0.00 (0.00)	11.00 (2.59)	5.93 (1.17)
		86	3.04 (0.48)	2.14 (0.76)		1.86 (0.32)	1.20 (0.29)			3.79 (0.75)	3.83 (1.07)	3.02 (0.99)	8.77 (3.72)	3.54 (0.81)
		88	2.54 (0.94)	9.00 (1.48)	1.01 (0.45)	0.87 (0.24)	1.28 (0.24)	1.44 (0.32)	2.47 (0.87)	2.11 (0.78)	1.11 (0.26)	1.15 (0.63)	5.98 (1.97)	2.25 (0.94)
		89	0.87 (0.14)	5.72 (1.18)	2.52 (1.25)	2.03 (0.50)	1.80 (0.30)	1.10 (0.17)	1.70 (0.39)	3.78 (0.77)	4.90 (1.32)	0.59 (0.27)	16.83 (4.47)	5.50 (1.84)
		90	0.26 (0.08)	4.38 (1.62)	1.95 (0.91)	1.71 (0.59)	1.97 (0.53)	1.55 (0.41)	1.32 (0.40)	1.73 (0.63)	2.31 (0.74)	3.51 (1.70)	3.07 (1.49)	1.60 (0.45)
		91	1.24 (0.28)	9.39 (1.77)	4.00 (1.25)	1.55 (0.39)	2.90 (0.84)	1.93 (0.73)	2.89 (0.86)	4.12 (1.46)	3.97 (1.00)	1.92 (0.97)	14.18 (3.66)	2.63 (0.70)
	>3-6	85	3.84 (0.93)	4.22 (1.00)							1.42 (0.39)	0.00 (0.00)	6.52 (0.89)	2.33 (0.56)
		86	3.62 (0.58)	1.66 (0.47)		2.74 (0.52)	7.21 (2.31)			5.25 (1.34)	3.41 (0.89)	3.94 (1.01)	5.75 (1.19)	2.42 (0.82)
		88	1.78 (0.41)	2.31 (0.49)	0.86 (0.37)	1.71 (0.55)	3.25 (0.81)	0.35 (0.24)	0.84 (0.48)	2.61 (0.97)	2.70 (0.64)	0.59 (0.33)	2.08 (1.21)	0.22 (0.11)
		89	0.68 (0.17)	0.61 (0.12)	4.90 (1.01)	3.39 (0.48)	6.63 (1.96)	1.88 (0.51)	1.02 (0.29)	2.39 (0.83)	2.78 (0.77)	2.89 (1.07)	2.75 (0.75)	1.33 (0.30)
		90	1.64 (0.60)	0.70 (0.26)	5.81 (2.05)	2.72 (0.36)	3.56 (0.57)	1.22 (0.31)	0.47 (0.24)	4.14 (1.82)	0.72 (0.35)	0.72 (0.23)	0.51 (0.27)	0.81 (0.21)
		91	0.48 (0.16)	2.06 (0.47)	0.82 (0.28)	2.58 (0.75)	4.16 (0.67)	1.20 (0.30)	1.09 (0.49)	1.07 (0.73)	0.95 (0.41)	1.45 (0.51)	7.73 (3.40)	1.03 (0.28)

App. Table C.2 Percent cover of common sessile organisms (except scleractinians) by depth, reef, and date of census. Data are means (SE in parentheses) (continued).

			Moderately Oiled	Heavily Oiled						Moderately Oiled	Unoiled			
Species	Depth (m)	Yr	MAR3	GALC	LRE1	LRE2	PAYW	PAYN	PM	NARS	DONR	DMA	PALW	JUG
Rubble	0.5-3	85	5.76 (1.00)	7.06 (0.93)							20.39 (2.24)	0.00 (0.00)	6.46 (2.75)	5.99 (3.09)
		86	7.78 (2.23)	0.10 (0.10)		20.32 (2.86)	16.34 (3.20)			1.97 (0.79)	1.93 (0.77)	10.89 (4.25)	3.81 (1.91)	11.99 (2.94)
		88	14.04 (2.73)	3.15 (1.20)	12.26 (2.38)	39.86 (3.75)	52.24 (3.22)	22.84 (3.40)	23.64 (3.33)	12.64 (3.53)	56.44 (4.57)	60.18 (3.74)	1.18 (0.62)	30.22 (4.33)
		89	16.41 (2.51)	4.06 (0.56)	13.97 (1.98)	32.82 (3.06)	32.63 (2.62)	13.30 (1.95)	12.32 (1.35)	10.63 (1.41)	7.00 (1.61)	3.07 (1.22)	2.62 (0.62)	7.34 (1.99)
		90	2.10 (0.50)	0.00 (0.00)	5.19 (1.34)	14.55 (2.06)	16.58 (2.51)	6.53 (1.73)	10.94 (2.89)	4.63 (1.22)	0.10 (0.10)	2.32 (1.44)	0.00 (0.00)	20.15 (4.09)
		91	3.49 (1.41)	0.00 (0.00)	0.31 (1.79)	0.00 (0.00)	0.42 (0.42)	0.09 (0.09)	5.23 (1.87)	0.14 (0.10)	0.00 (0.00)	4.18 (2.69)	0.00 (0.00)	0.00 (0.00)
	>3-6	85	8.29 (2.35)	6.78 (1.16)							12.10 (1.57)	0.00 (0.00)	6.03 (0.88)	21.97 (3.67)
		86	11.87 (4.32)	1.26 (0.56)		55.62 (5.36)	24.62 (6.04)			5.32 (1.88)	4.82 (1.73)	12.66 (3.63)	2.30 (0.84)	24.20 (3.68)
		88	8.60 (5.91)	26.04 (5.92)	21.75 (7.67)	63.81 (9.73)	90.17 (1.64)	76.78 (9.06)	24.27 (9.35)	13.64 (3.94)	56.35 (4.41)	44.18 (6.79)	0.00 (0.00)	28.01 (6.28)
		89	47.77 (6.63)	21.34 (4.92)	19.81 (2.75)	64.12 (4.67)	40.92 (7.35)	30.63 (8.89)	5.29 (3.33)	10.13 (1.65)	12.71 (3.31)	7.92 (1.07)	4.39 (0.75)	28.09 (3.81)
		90	8.32 (4.92)	0.24 (0.24)	17.66 (3.86)	19.75 (4.43)	17.22 (3.64)	7.98 (1.90)	3.22 (1.76)	8.19 (2.27)	0.82 (0.66)	1.75 (1.06)	0.00 (0.00)	19.60 (4.56)
		91	8.64 (3.47)	0.00 (0.00)	3.08 (1.79)	1.22 (1.22)	2.60 (1.86)	2.42 (1.77)	0.53 (0.33)	0.16 (0.16)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Zoanthids	0.5-3	85	4.77 (0.52)	1.26 (0.37)							0.03 (0.03)	0.74 (0.74)	1.31 (0.60)	1.96 (0.57)
		86	3.68 (0.51)	0.62 (0.29)		1.67 (0.44)	0.40 (0.18)			6.52 (1.89)	1.18 (0.42)	2.34 (0.80)	0.95 (0.34)	0.78 (0.31)
		88	0.24 (0.09)	0.49 (0.14)	1.26 (0.77)	0.10 (0.04)	0.27 (0.13)	0.49 (0.10)	0.10 (0.05)	0.13 (0.06)	0.19 (0.14)	0.15 (0.05)	0.25 (0.19)	0.00 (0.00)
		89	0.28 (0.08)	0.33 (0.06)	1.31 (0.41)	1.31 (0.70)	0.41 (0.26)	0.51 (0.11)	0.10 (0.05)	0.20 (0.08)	0.11 (0.05)	1.14 (0.42)	0.13 (0.05)	0.02 (0.02)
		90	0.10 (0.06)	0.26 (0.20)	0.44 (0.17)	1.01 (0.72)	0.19 (0.13)	0.40 (0.23)	0.36 (0.18)	0.03 (0.03)	0.01 (0.01)	0.00 (0.00)	0.30 (0.17)	0.08 (0.05)
		91	0.26 (0.19)	0.59 (0.24)	0.47 (0.15)	1.00 (0.61)	0.25 (0.25)	0.15 (0.12)	0.17 (0.12)	0.03 (0.03)	0.00 (0.00)	0.19 (0.19)	0.07 (0.05)	0.07 (0.05)
	>3-6	85	3.36 (0.57)	2.28 (0.65)							0.64 (0.30)	0.00 (0.00)	0.70 (0.37)	0.14 (0.07)
		86	1.74 (0.44)	0.52 (0.21)		0.77 (0.20)	0.32 (0.18)			0.74 (0.29)	0.30 (0.12)	0.22 (0.15)	0.85 (0.37)	0.30 (0.17)
		88	0.18 (0.12)	0.01 (0.01)	0.30 (0.20)	0.00 (0.00)	0.00 (0.00)	0.20 (0.20)	0.00 (0.00)	0.01 (0.01)	0.07 (0.06)	0.01 (0.01)	0.06 (0.06)	0.00 (0.00)
		89	0.21 (0.17)	0.32 (0.11)	0.12 (0.08)	0.09 (0.06)	0.00 (0.00)	0.03 (0.03)	0.05 (0.05)	0.05 (0.03)	0.14 (0.08)	0.22 (0.11)	0.09 (0.05)	0.03 (0.02)
		90	0.00 (0.00)	0.18 (0.09)	0.16 (0.10)	0.00 (0.00)	0.05 (0.05)	0.30 (0.17)	0.07 (0.07)	0.10 (0.08)	0.05 (0.03)	0.00 (0.00)	0.04 (0.04)	0.21 (0.09)
		91	0.02 (0.02)	0.43 (0.22)	0.76 (0.34)	0.00 (0.00)	0.00 (0.00)	1.72 (0.90)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)

App. Table C.3 Yearly mean growth rates (mm) from 1977 to 1986 for *Siderastrea siderea* on 11 reefs grouped by level of oiling in 1986 (unoiled, moderately oiled, and heavily oiled). SE in parentheses. Where not specified, *N* for all means = 5.

	Unoiled				Moderately Oiled		Heavily Oiled				
Yr	DONR	DMA	PALW	JUG	MAR3	NARS	GALC	LRE2	PAYW	PAYN	PM
86	4.50	4.30	3.20	4.50	5.30	3.90	4.40	3.20	4.00	3.40	3.90
	(0.35)	(0.56)	(0.41)	(0.96)	(0.41)	(0.46)	(0.48)	(0.34)	(0.35)	(0.46)	(0.78)
85	5.60	4.70	4.50	4.70	6.60	5.00	6.00	3.40	4.84	3.50	5.20
	(0.29)	(0.64)	(0.69)	(0.94)	(0.48)	(0.69)	(0.45)	(0.90)	(1.39)	(0.55)	(0.51)
84	5.80	4.40	4.10	5.30	5.70	5.10	5.30	3.70	5.50	3.60	5.60
	(0.20)	(0.66)	(0.37)	(1.20)	(0.54)	(0.87)	(1.01)	(0.89)	(1.24)	(0.46)	(0.95)
83	6.10	4.60	4.90	5.94	4.40	4.40	5.10	4.30	4.20	3.90	5.80
	(0.29)	(1.04)	(0.64)	(1.24)	(0.48)	(0.29)	(1.01)	(0.37)	(0.75)	(0.64)	(0.64)
82	6.10	4.00	4.50	5.40	5.90	4.20	5.50	3.40	4.00	3.70	5.50
	(0.19)	(0.81)	(0.50)	(0.48)	(0.83)	(0.46)	(0.84)	(0.60)	(0.69)	(0.25)	(0.45)
81	5.10	4.20	4.90	4.30	5.10	5.10	4.80	3.50	4.60	4.70	5.50
	(0.37)	(0.80)	(0.40)	(0.44)	(0.62)	(0.33)	(0.66)	(0.67)	(0.70)	(1.36)	(1.00)
80	4.70	4.70	4.70	3.50	5.40	4.80	6.30	3.70	3.70	4.20	5.40
	(0.30)	(0.98)	(0.62)	(0.35)	(0.62)	(0.56)	(1.24)	(0.62)	(0.51)	(0.82)	(1.03)
79	4.60	5.30	4.30	3.80	5.20	4.70	4.20	2.80	4.70	5.70	5.80
	(0.37)	(1.01)	(0.46)	(0.58)	(0.60)	(0.49)	(0.75)	(0.20)	(0.82)	(1.11)	(0.66)
78	4.90	4.50	4.10	4.70	5.30	5.20	4.70	2.80	3.50	3.60	5.50
	(0.58)	(0.79)	(0.58)	(0.78)	(0.37)	(0.60)	(0.93)	(0.46)	(1.04)	(0.29)	(0.92)
77	4.20	4.60	4.90	4.90	5.20	5.00	5.70	3.40	4.00	4.90	5.10
	(0.20)	(0.76)	(0.24)	(0.43)	(0.60)	(0.65)	(0.78)	(0.43)	(0.32)	(0.62)	(0.97)

App. Table C.4 Yearly mean growth rates (mm) from 1977 to 1986 for *Montastrea annularis* on eight reefs grouped by level of oiling in 1986 (unoiled, moderately oiled, and heavily oiled). SE in parentheses. Where not specified, *N* for all means = 5.

	Unoiled				Moderately Oiled		Heavily Oiled				
Yr	DONR	DMA	PALW	JUG	MAR3	NARS	GALC	LRE2	PAYW	PAYN	PM
86	8.80	6.70	9.00	12.13		7.60		5.38		6.67	8.25
	(2.13)	(1.27)	(2.08)	(1.31)		(0.40)		(0.56)		(0.88)	(1.25)
				N = 4				*N* = 4		*N* = 3	*N* = 2
85	7.50	6.60	8.70	10.38		8.40		6.88		9.50	7.75
	(1.55)	(1.35)	(2.35)	(1.28)		(0.70)		(0.56)		(1.15)	(0.25)
				N = 4				*N* = 4		*N* = 3	*N* = 2
84	9.40	7.10	10.30	12.25		9.50		9.13		6.67	6.00
	(1.48)	(1.41)	(2.01)	(1.90)		(1.04)		(1.00)		(1.74)	(1.00)
				N = 4				*N* = 4		*N* = 3	*N* = 2
83	11.00	6.20	9.00	10.38		10.20		9.38		8.17	8.50
	(2.08)	(1.11)	(1.79)	(1.41)		(0.72)		(1.52)		(0.93)	(4.00)
				N = 4				*N* = 4		*N* = 3	*N* = 2
82	7.90	6.40	7.40	12.38		8.30		8.13		8.17	8.50
	(1.62)	(0.83)	(1.43)	(1.77)		(1.49)		(1.47)		(0.93)	(1.50)
				N = 4				*N* = 4		*N* = 3	*N* = 2
81	7.90	4.90	7.30	10.88		8.10		8.38		8.33	8.50
	(1.70)	(0.76)	(1.33)	(1.70)		(1.09)		(1.58)		(2.32)	(2.00)
				N = 4				*N* = 4		*N* = 3	*N* = 2
80	8.20	6.80	9.00	11.75		8.70		9.38		9.00	5.75
	(1.14)	(1.25)	(1.46)	(1.61)		(1.14)		(1.25)		(2.00)	(0.75)
				N = 4				*N* = 4		*N* = 3	*N* = 2
79	6.30	7.00	10.10	12.50		7.70		9.63		8.67	6.25
	(1.66)	(1.14)	(1.94)	(2.52)		(1.22)		(2.26)		(0.73)	(0.25)
				N = 4				*N* = 4		*N* = 3	*N* = 2
78	8.20	6.60	9.70	12.75		10.00		8.00		7.50	7.00
	(1.10)	(0.89)	(1.01)	(1.88)		(1.39)		(1.46)		(0.29)	(1.00)
				N = 4				*N* = 4		*N* = 3	*N* = 2
77	8.90	6.80	10.40	14.25		10.30		11.63		7.67	5.50
	(1.01)	(0.88)	(1.56)	(1.45)		(0.93)		(2.53)		(0.33)	(0.00)
				N = 4				*N* = 4		*N* = 3	*N* = 2

App. Table C.5 Yearly mean growth rates (mm) from 1977 to 1986 for *Porites astreoides* on 10 reefs grouped by level of oiling in 1986 (unoiled, moderately oiled, and heavily oiled). SE in parentheses. Where not specified, N for all means = 5.

	Unoiled				Moderately Oiled		Heavily Oiled				
Yr	DONR	DMA	PALW	JUG	MAR3	NARS	GALC	LRE2	PAYW	PAYN	PM
86	5.70 (0.51)	5.00 (0.74) $N = 4$	5.38 (0.24) $N = 4$	4.90 (0.48)	4.80 (0.66)	5.00 (1.06) $N = 4$	3.80 (0.34)	3.40 (0.37)		4.90 (0.83)	3.90 (0.33)
85	5.80 (0.73)	3.63 (0.43) $N = 4$	4.63 (0.66) $N = 4$	5.30 (0.75)	4.30 (0.41)	4.13 (0.24) $N = 4$	4.10 (0.37)	3.40 (0.37)		5.20 (0.64)	5.40 (0.58)
84	6.30 (1.50)	4.00 (0.50) $N = 4$	3.75 (0.25) $N = 4$	5.90 (0.40)	3.90 (0.43)	5.25 (0.32) $N = 4$	5.40 (0.93)	3.60 (0.48)		5.50 (0.96)	3.80 (0.41)
83	5.10 (0.33)	4.75 (0.52) $N = 4$	5.38 (0.55) $N = 4$	6.90 (0.60)	4.60 (0.81)	4.63 (0.66) $N = 4$	4.50 (0.87) $N = 4$	4.00 (0.76)		6.30 (1.59)	4.30 (0.70)
82	4.40 (0.62)	4.88 (0.24) $N = 4$	5.88 (1.48) $N = 4$	7.00 (0.79)	4.70 (0.72)	4.50 (0.87) $N = 4$	4.25 (1.11) $N = 4$	4.30 (0.49)		5.75 (0.43) $N = 4$	3.90 (0.29)
81	5.00 (0.42)	5.00 (0.20) $N = 4$	6.00 (0.74) $N = 4$	6.30 (0.20)	5.40 (0.90)	5.63 (0.69) $N = 4$	5.13 (1.33) $N = 4$	3.13 (0.31) $N = 4$		4.25 (0.32) $N = 4$	3.80 (0.54)
80	6.70 (0.56)	5.13 (1.25) $N = 4$	6.88 (1.25) $N = 4$	6.00 (0.35)	4.60 (0.70)	4.75 (0.97) $N = 4$	5.75 (0.66) $N = 4$	3.25 (0.60) $N = 4$		5.75 (1.75) $N = 2$	3.60 (0.24)
79	5.70 (0.54)	3.88 (0.24) $N = 4$	5.63 (1.64) $N = 4$	5.20 (0.58)	5.10 (0.29)	5.25 (1.27) $N = 4$	5.25 (0.66) $N = 4$	3.38 (0.43) $N = 4$		6.00 (2.00) $N = 2$	4.80 (0.64)
78	5.20 (0.58)	4.63 (0.38) $N = 4$	6.38 (1.16) $N = 4$	6.13 (0.94) $N = 4$	4.20 (0.46)	4.17 (0.93) $N = 3$	5.38 (0.77) $N = 4$	3.17 (0.17) $N = 3$		5.00 (0.00) $N = 1$	3.60 (0.24)
77	5.90 (0.46)	6.38 (0.90) $N = 4$	5.38 (0.63) $N = 4$	5.38 (0.97) $N = 4$	4.13 (0.80) $N = 4$	4.25 (0.25) $N = 2$	4.38 (1.36) $N = 3$	2.50 (0.00) $N = 1$			3.67 (0.60) $N = 3$

App. Table C.6 Yearly mean growth rates (mm) from 1977 to 1986 for *Diploria strigosa* on eight reefs grouped by level of oiling in 1986 (unoiled, moderately oiled, and heavily oiled). SE in parentheses. Where not specified, N for all means = 5.

	Unoiled				Moderately Oiled		Heavily Oiled				
Yr	DONR	DMA	PALW	JUG	MAR3	NARS	GALC	LRE2	PAYW	PAYN	PM
86	5.70	4.70	6.80	4.60		4.40		4.50		4.80	3.60
	(0.20)	(0.56)	(0.58)	(0.53)		(0.87)		(0.82)		(0.82)	(0.58)
85	5.20	4.40	8.10	4.90		4.80		6.00		5.60	3.70
	(0.82)	(0.75)	(1.09)	(0.62)		(0.87)		(1.30)		(1.37)	(0.46)
84	5.40	4.50	8.60	5.00		4.30		5.90		6.50	3.50
	(0.73)	(0.42)	(0.86)	(0.57)		(0.64)		(1.25)		(2.02)	(0.45)
83	5.20	4.70	7.90	5.20		4.80		5.40		5.80	3.70
	(0.64)	(0.34)	(0.94)	(0.56)		(1.27)		(1.02)		(1.25)	(0.30)
82	4.30	4.60	7.40	5.40		5.70		5.30		5.90	4.80
	(0.75)	(0.40)	(0.91)	(1.18)		(0.93)		(0.34)		(1.81)	(0.98)
81	4.70	4.90	8.60	5.40		5.60		5.60		6.20	3.90
	(0.49)	(0.46)	(0.93)	(0.89)		(1.02)		(0.43)		(1.75)	(0.43)
80	5.40	5.50	7.60	4.60		5.00		4.80		5.60	4.20
	(0.91)	(0.65)	(0.81)	(0.43)		(0.89)		(0.60)		(1.04)	(0.75)
79	4.80	5.20	6.90	5.20		4.20		6.10		7.40	3.90
	(0.54)	(0.56)	(0.62)	(0.73)		(0.34)		(0.89)		(1.98)	(0.70)
78	4.80	4.50	6.60	4.80		5.20		5.70		6.40	4.20
	(0.86)	(0.42)	(0.71)	(0.34)		(0.41)		(0.80)		(1.43)	(0.80)
77	4.10	4.00	6.88	4.20		4.60		5.40		6.70	4.50
	(0.78)	(0.42)	(1.26) $N = 4$	(0.46)		(0.78)		(0.73)		(1.49)	(0.71)

Appendix D
Mangrove Forests

App. Table D.1 Mean length (*L*; cm), width (*W*; cm), weight (*Wt*; g), and wet area (cm^2) of fresh green leaves (*Wet*) and oven-dried leaves (*Dry*) collected from the 26 sites of the study area. SE is in parentheses. See Table 8.9.

	Site	Wet L	Wet W	Wet Wt	Dry L	Dry W	Dry Wt	Area
1	WOMI	106.6 (4.1)	51 6 (1.9)	2.07 (0.1)	98.45 (4.0)	46.50 (1.8)	0.80 (0.1)	40.55
2	WOPG	100.7 (4.8)	51.9 (2.5)	2.43 (0.3)	93.00 (4.9)	46.35 (2.5)	0.85 (0.1)	39.23
3	CODR	104.7 (3.8)	47.4 (1.7)	2.68 (0.2)	94.89 (3.2)	40.11 (1.5)	0.83 (0.1)	36.56
4	EOPM	99.8 (3.5)	49.9 (1.6)	2.10 (0.1)	91.45 (3.4)	43.65 (1.5)	0.78 (0.05)	36.66
5	GOMS	104.2 (3.8)	46.6 (1.6)	1.94 (0.1)	96.70 (3.6)	42.20 (1.5)	0.78 (0.1)	35.80
6	GOPB	102.6 (5.3)	47.4 (2.5)	2.07 (0.2)	97.45 (5.1)	42.70 (2.4)	0.85 (0.1)	36.87
7	GOPA	100.9 (3.7)	43.4 (1.9)	1.76 (0.2)	92.25 (2.8)	38.63 (1.8)	0.74 (0.1)	32.44
8	GOLI	91.4 (4.5)	45.0 (3.5)	1.56 (0.1)	85.88 (3.1)	36.76 (1.5)	0.63 (0.04)	29.39
9	GOMG	100.8 (5.7)	47.9 (2.7)	1.88 (0.2)	93.75 (5.8)	43.56 (2.7)	0.80 (0.1)	36.52
10	CCSB	116.1 (4.6)	59.1 (2.2)	2.45 (0.2)	107.35 (4.3)	52.65 (2.1)	0.90 (0.1)	50.41
11	CCPQ	123.3 (4.9)	63.0 (2.7)	3.23 (0.2)	111.55 (4.7)	55.35 (2.5)	1.22 (0.1)	57.15
12	ECPY	122.5 (3.1)	57.5 (1.6)	2.60 (0.1)	112.00 (3.1)	51.00 (1.6)	1.01 (0.1)	51.03
13	WCLR	113.7 (2.7)	53.2 (1.6)	2.18 (0.1)	104.20 (2.3)	47.55 (1.4)	0.77 (0.04)	43.90
14	MCSU	119.7 (3.7)	55.7 (2.0)	2.84 (0.2)	108.50 (3.3)	48.65 (1.7)	1.09 (0.1)	48.66
15	MCNO	112.5 (2.6)	49.9 (1.3)	2.15 (0.1)	105.50 (2.7)	44.15 (1.1)	0.81 (0.03)	40.72
16	WCNO	96.0 (2.3)	46.1 (1.2)	1.74 (0.1)	89.05 (2.0)	42.10 (1.2)	0.68 (0.04)	32.44
17	WCSU	104.6 (2.3)	52.0 (1.3)	2.11 (0.1)	97.40 (2.1)	47.20 (1.1)	0.81 (0.04)	39.47
18	WCLS	115.0 (3.8)	57.0 (2.5)	2.55 (0.2)	104.55 (3.7)	50.60 (2.2)	1.00 (0.1)	48.16
19	ERPS	127.7 (4.9)	61.6 (2.5)	2.81 (0.2)	114.80 (4.4)	53.65 (2.3)	1.04 (0.1)	57.69
20	ERPN	129.1 (2.4)	65.2 (1.5)	3.19 (0.1)	118.35 (2.5)	58.25 (1.5)	1.25 (0.1)	60.39
21	WRRB	111.8 (3.9)	50.3 (1.6)	2.11 (0.1)	104.05 (3.8)	46.20 (1.6)	0.77 (0.1)	41.24
22	CRKU	122.4 (2.1)	59.8 (1.2)	2.67 (0.1)	113.41 (2.4)	53.41 (1.3)	1.04 (0.04)	52.62
23	WRHD	114.4 (4.1)	57.1 (2.1)	2.43 (0.2)	107.15 (4.0)	52.65 (2.0)	0.89 (0.1)	47.92
24	ERUN	122.8 (2.4)	60.4 (1.2)	2.56 (0.1)	111.05 (2.2)	51.75 (1.0)	0.92 (0.04)	53.29
25	ERJA	126.2 (3.0)	56.6 (1.3)	2.45 (0.1)	116.50 (3.0)	49.60 (1.2)	0.89 (0.04)	51.49
26	NRME	118.1 (4.1)	62.4 (2.7)	2.62 (0.2)	111.05 (4.4)	56.55 (2.7)	1.03 (0.1)	54.08

App. Table D.2 Height frequency of leafy shoots (N = 21) measured from the top of the canopy in 26 sites.

		Height Class (m, ≤)						
Site	Replicate	-0.5	-1.0	-1.5	-2.0	-2.5	-3.0	-3.5
1 WOMI	A	10	8	3				
2 WOPG	A	7	12	2				
3 CODR	A	15	6					
	B	5	7	5	4			
	C	15	1	5				
4 EOPM	A	12	6	3				
5 GOMS	A	13	6	2				
6 GOPB	A	4	11	2	4			
7 GOPA	A	10	4	7				
	B	6	5	7	3			
	C	6	5	8	2			
8 GOLI	A	5	9	5	2			
9 GOMG	A	11	9	1				
10 CCSB	A		2	12	7			
11 CCPQ	A	6	6	3	6			
12 ECPY	A	4	13	3	1			
	B	12	3	4	2			
	C	8	9	4				
13 WCLR	A		6	6	9			
14 MCSU	A		5	8	8			
15 MCNO	A	1	8	8	3	-	-	1
16 WCNO	A	12	6	3				
17 WCSU	A		9	11	1			
18 WCLS	A			1	12	8		
	B	10	7	4				
	C	8	6	2	5			
19 ERPS	A	8	4	4	4	1		
	B	8	11	2				
	C	4	6	8	3			
20 ERPN	A		1	9	11			
21 WRRB	A			1	12	8		
22 CRKU	A		2	11	8			
23 WRHD	A			8	10	2	1	
	B	8	9	4				
	C	3	9	6	3			
24 ERUN	A		6	7	8			
25 ERJA	A	4	12	3	2			
26 NRME	A		6	8	5	2		

App. Table D.3 Mean annual salinity (o/oo) and temperature (°C) for the litter/shoots sites, for the periods June 1989 to June 1990 and June 1990 to June 1991. SE is in parentheses. See Table 8.4.

		1989 - 1990		1990 - 1991	
	Site	Salinity	Temperature	Salinity	Temperature
1	WOMI	32.56 (1.08)	28.78 (0.32)	32.99 (0.72)	29.16 (0.35)
2	WOPG	32.11 (1.58)	29.45 (0.29)	32.65 (0.80)	29.64 (0.43)
3	CODR	33.59 (0.44)	29.39 (0.36)	33.79 (0.30)	29.39 (0.65)
4	EOPM	33.62 (0.48)	29.58 (0.61)	32.76 (0.67)	29.82 (0.67)
5	GOMS	33.98 (0.49)	29.64 (0.28)	32.98 (0.65)	29.87 (0.54)
6	GOPB	33.43 (0.65)	29.81 (0.35)	32.11 (0.98)	29.98 (0.44)
7	GOPA	34.51 (0.26)	29.22 (0.36)	34.17 (0.40)	29.68 (0.38)
8	GOLI	34.41 (0.41)	28.75 (0.27)	34.63 (0.55)	29.01 (0.25)
9	GOMG	33.65 (0.55)	29.80 (0.32)	32.47 (1.06)	29.59 (0.39)
10	CCSB	30.77 (1.13)	29.44 (0.32)	29.17 (1.35)	29.62 (0.54)
11	CCPQ	28.72 (1.66)	29.02 (0.44)	27.60 (2.45)	30.09 (0.54)
12	ECPY	29.68 (1.32)	28.48 (0.36)	28.30 (2.24)	29.45 (0.47)
13	WCLR	28.03 (3.33)	30.10 (0.60)	26.94 (2.82)	30.37 (0.60)
14	MCSU	25.80 (3.61)	27.37 (0.62)	22.41 (4.06)	28.68 (0.60)
15	MCNO	24.83 (3.56)	27.64 (0.31)	21.77 (4.28)	28.66 (0.37)
16	WCNO	26.89 (2.98)	29.63 (0.46)	27.47 (2.57)	29.96 (0.38)
17	WCSU	28.86 (2.52)	29.53 (0.45)	27.16 (2.78)	30.00 (0.38)
18	WCLS	29.24 (2.74)	29.43 (0.45)	28.44 (2.46)	30.09 (0.46)
19	ERPS	24.19 (3.58)	29.03 (0.49)	25.05 (2.86)	29.56 (0.48)
20	ERPN	28.28 (2.31)	30.26 (0.51)	26.31 (2.52)	30.16 (0.48)
21	WRRB	27.73 (2.96)	28.83 (0.59)	31.26 (1.28)	30.16 (0.52)
22	CRKU	29.33 (1.68)	29.80 (0.48)	28.00 (1.90)	30.76 (0.49)
23	WRHD	18.08 (3.60)	28.39 (0.41)	18.80 (4.06)	28.72 (0.38)
24	ERUN	8.48 (2.94)	26.93 (0.31)	12.33 (3.76)	28.03 (0.40)
25	ERJA	10.57 (3.13)	27.11 (0.36)	13.51 (3.93)	27.97 (0.44)
26	NRME	13.84 (3.67)	27.49 (0.36)	16.95 (3.96)	27.91 (0.53)

App. Table D.4 Oil concentration in mangrove sediments (mg/g) determined by the UVF method for the litter/shoots sites. See Table 8.5.

	Site	Sep 86	May 89	Jul 90	Average 89/90
1	WOMI	-	5.67	20.40	13.03
2	WOPG	-	30.67	72.08	51.38
3	CODR	5.97	54.77	31.48	43.12
4	EOPM	-	2.67	113.11	57.89
5	GOMS	-	0.00	0.00	0.00
6	GOPB	-	0.00	0.04	0.02
7	GOPA	-	0.02	0.01	0.02
8	GOLI	-	0.01	0.02	0.02
9	GOMG	-	-	-	-
10	CCSB	-	164.76	187.87	176.32
11	CCPQ	202.30	80.94	45.11	63.03
12	ECPY	-	110.88	76.62	93.75
13	WCLR	-	6.35	30.69	18.52
14	MCSU	0.14	0.14	0.35	0.25
15	MCNO	1.12	0.60	0.89	0.74
16	WCNO	0.06	0.04	1.38	0.71
17	WCSU	-	0.47	8.83	4.65
18	WCLS	-	2.03	2.37	2.20
19	ERPS	-	41.61	12.18	26.89
20	ERPN	-	22.13	54.64	38.39
21	WRRB	-	-	-	-
22	CRKU	-	-	-	-
23	WRHD	0.80	0.15	0.24	0.20
24	ERUN	-	0.12	0.21	0.17
25	ERJA	-	0.12	0.48	0.30
26	NRME	-	0.06	0.20	0.13

App. Table D.5 Structural characteristics of the forests for the litter/shoots sites. *BA* = basal area; *SA* = angle of stem with ground; *R/S* = ratio of *Rhizophora* species to total stems; *RD* = number of *Rhizophora* seedlings per m^2; *LB* = leaf biomass; *TB* = total biomass; *ND* = no data. SE is in parentheses. See Table 8.7.

	Site	Height (m)	Diam. (cm)	BA (m^2/ha)	Density (stem/ha)	SA (deg.)	RS	Tree Dens. (tree/ha)	RD (no./m^2)	LB (g)	TB (g)
1	WOMI	3.27 (0.34)	5.8 (0.7)	10.97	5,187	29.17	1.00	1,153	0.07	198	3,989
2	WOPG	4.73 (0.49)	9.3 (1.5)	10.97	3,041	57.22	1.00	1,689	0.00	272	8,547
3	CODR	3.11 (0.16)	4.6 (0.4)	15.85	12,548	54.81	1.00	2,896	0.11	354	6,083
4	EOPM	3.46 (0.41)	6.0 (0.7)	20.72	12,683	43.09	0.88	2,238	0.07	580	13,643
5	GOMS	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
6	GOPB	4.12 (0.21)	6.8 (0.6)	19.50	6,814	48.59	1.00	3,833	0.00	370	8,647
7	GOPA	2.94 (0.14)	5.0 (0.4)	23.16	15,773	43.42	1.00	4,151	0.00	487	8,827
8	GOLI	3.65 (0.14)	4.5 (0.3)	23.16	17,740	41.97	1.00	ND	0.14	544	9,572
9	GOMG	3.19 (0.24)	6.8 (0.6)	14.63	5,178	27.92	1.00	2,157	0.00	238	5,146
10	CCSB	6.03 (0.93)	11.1 (2.1)	17.07	12,051	70.89	0.57	11,190	0.18	1,789	79,840
11	CCPQ	4.26 (0.41)	7.0 (0.6)	24.38	13,202	26.38	1.00	2,640	0.60	777	19,557
12	ECPY	5.5 (0.55)	10.7 (0.8)	14.63	2,304	57.29	1.00	960	10.61	255	8,108
13	WCLR	7.83 (0.85)	14.7 (2.1)	9.75	931	64.38	1.00	815	1.17	190	8,313
14	MCSU	7.11 (0.45)	11.8 (0.6)	19.50	2,036	57.03	1.00	254	1.91	288	10,009
15	MCNO	5.73 (0.46)	10.1 (1.2)	21.94	5,606	58.61	0.78	3,114	5.30	608	20,646
16	WCNO	4.35 (0.30)	8.5 (0.8)	13.41	3,372	50.91	1.00	2,146	3.75	247	6,506
17	WCSU	4.51 (0.71)	7.2 (1.6)	13.41	22,134	43.64	1.00	10,061	2.62	1,625	53,141
18	WCLS	5.93 (0.56)	9.9 (0.8)	12.19	2,060	48.00	1.00	1,236	1.59	216	6,694
19	ERPS	8.14 (0.45)	6.3 (0.5)	13.41	4,969	86.82	1.00	4,969	1.77	364	9,531
20	ERPN	5.21 (0.55)	11.3 (1.7)	15.85	6,256	54.25	1.00	5,775	ND	358	8,585
21	WRRB	8.04 (1.06)	11.3 (1.7)	12.19	2,279	54.25	0.90	1,367	0.92	359	14,813
22	CRKU	4.12 (0.21)	13.7 (1.3)	19.50	2,750	54.69	1.00	1,719	2.12	333	11,103
23	WRHD	12.55 (0.75)	23.1 (1.8)	14.63	458	72.29	0.83	382	1.13	203	11,944
24	ERUN	4.55 (0.49)	8.0 (1.1)	13.41	5,976	49.32	1.00	4,346	0.21	442	12,589
25	ERJA	13.36 (0.70)	17.3 (1.6)	15.85	890	82.60	0.62	890	0.42	290	15,108
26	NRME	26.74 (0.87)	30.3 (1.7)	25.60	433	88.33	0.43	433	0.57	406	33,273

App. Table D.6 Mean annual standing crop (leaves per shoot) and annual production rates for new leaves and leaves lost (numbers of leaves/100 shoots/d) in *Rhizophora mangle* canopies in the 26 litter/shoots sites. SE is in parentheses. See Table 8.10.

		1990			1991		
	Site	Standing Crop	New Leaves	Leaves Lost	Standing Crop	New Leaves	Leaves Lost
1	WOMI	7.41 (0.29)	3.15	3.27	6.33 (0.18)	2.80	2.98
2	WOPG	7.89 (0.30)	3.29	3.38	6.28 (0.32)	3.26	3.52
3	CODR	7.38 (0.19)	3.09	2.92	7.70 (0.18)	2.83	2.96
4	EOPM	7.29 (0.24)	3.39	3.29	7.52 (0.24)	2.98	3.46
5	GOMS	8.44 (0.18)	3.03	2.70	9.06 (0.21)	3.25	2.88
6	GOPB	9.79 (0.12)	3.34	3.27	9.51 (0.12)	3.00	3.54
7	GOPA	9.61 (0.07)	3.26	3.07	9.62 (0.25)	3.04	3.97
8	GOLI	7.52 (0.26)	2.42	2.82	7.20 (0.11)	2.37	2.35
9	GOMG	8.96 (0.23)	3.17	3.29	9.33 (0.22)	3.54	4.02
10	CCSB	6.48 (0.38)	2.71	3.15	5.07 (0.34)	2.77	2.91
11	CCPQ	5.89 (0.28)	2.48	2.92	4.87 (0.23)	3.00	3.04
12	ECPY	6.10 (0.24)	3.12	3.07	6.53 (0.29)	3.20	3.31
13	WCLR	6.96 (0.36)	3.17	3.13	6.24 (0.51)	2.83	3.24
14	MCSU	6.93 (0.29)	3.20	3.16	7.63 (0.23)	3.21	3.22
15	MCNO	8.20 (0.23)	2.55	2.81	7.71 (0.13)	2.48	2.69
16	WCNO	7.90 (0.22)	3.66	3.50	7.70 (0.32)	2.92	4.02
17	WCSU	6.07 (0.16)	2.77	2.98	7.02 (0.15)	3.00	2.99
18	WCLS	8.28 (0.24)	2.85	3.02	7.87 (0.26)	3.10	3.18
19	ERPS	6.79 (0.27)	3.05	3.29	6.92 (0.15)	2.95	3.03
20	ERPN	6.11 (0.26)	3.40	3.76	6.07 (0.30)	3.03	3.31
21	WRRB	7.13 (0.26)	3.00	3.02	6.20 (0.36)	2.40	2.75
22	CRKU	5.58 (0.15)	2.94	2.94	5.47 (0.25)	2.97	3.12
23	WRHD	5.32 (0.33)	2.83	3.16	5.89 (0.28)	3.08	3.11
24	ERUN	7.26 (0.24)	2.61	3.08	6.89 (0.19)	2.77	3.02
25	ERJA	8.73 (0.30)	2.95	3.28	7.74 (0.24)	2.19	2.69
26	NRME	5.11 (0.32)	2.05	2.67	4.77 (0.13)	2.22	2.91

App. Table D.7 Annual litter-fall rate (number/m^2/day) for five components of *Rhizophora mangle* canopies: leaves, stipules, total reproductive parts (*TR*), flowers, and mature hypocotyls (*MH*). SE of between-trap variation is in parentheses for sites where replicate traps were maintained for 1 yr. See Table 8.11.

	Site	Leaves	Stipules	TR	Flowers	MH
1	WOMI	3.40	3.06	1.33	1.15	0.031
2	WOPG	3.38	3.67	1.56	0.88	0
3	CODR	2.24	2.12	0.82	0.72	0.002
4	EOPM	3.09	3.34	1.46	1.30	0
6	GOPB	3.05	3.11	1.30	0.49	0
7	GOPA	3.16	3.28	1.75	0.61	0
8	GOLI	2.56 (0.12)	2.47 (0.13)	0.88 (0.13)	0.63 (0.07)	0.003 (0.002)
9	GOMG	3.10 (0.38)	3.22 (0.37)	2.06 (0.35)	0.22 (0.08)	0
10	CCSB	1.31	1.39	0.10	0.10	0.002
11	CCPQ	2.96	3.02	1.37	1.17	0.004
12	ECPY	2.59 (0.29)	2.49 (0.24)	0.60 (0.02)	0.56 (0.03)	0.027 (0.026)
13	WCLR	3.06	3.33	1.41	1.29	0.003
14	MCSU	3.97 (0.16)	4.03 (0.06)	1.45 (0.16)	1.30 (0.17)	0.062 (0.027)
15	MCNO	5.02 (1.04)	4.69 (0.87)	3.16 (0.96)	2.93 (0.87)	0.001 (0.001)
16	WCNO	2.04	2.21	1.37	1.28	0.002
17	WCLS	3.27 (0.58)	3.89 (0.69)	3.03 (1.74)	2.86 (1.68)	0.005 (0.002)
18	WCSU	4.81	4.68	3.33	2.96	0.005
19	ERPN	1.66	1.55	0.44	0.41	0.012
20	ERPS	2.98 (0.08)	2.93 (0.19)	0.70 (0.06)	0.67 (0.05)	0.029 (0.024)
21	WRRB	3.08	3.86	1.93	1.82	0.014
22	CRKU	4.69	4.76	3.56	3.41	0.023
23	WRHD	3.55	4.21	3.13	3.00	0.006
24	ERUN	3.28	2.81	1.47	1.41	0.010
25	ERJA	3.13	3.38	2.37	2.30	0
26	NRME	4.02	4.48	4.91	4.73	0.010

App. Table D.8 Annual litter-fall rate (g dry weight/m^2) for five components of *Rhizophora mangle* in the 26 litter/shoots sites: stipules, leaves, reproductive parts, wood, and total components; *ND* = no data. SE of between-trap variation for some sites is in parentheses. See Table 8.12.

	Site	Stipules	Leaves	Reprod. Parts	Wood	Total
1	WOMI	0.19	1.35	0.34	0.12	2.00
2	WOPG	0.32	1.65	0.20	0.26	2.42
3	CODR	0.14	1.06	0.13	0.02	1.36
4	EOPM	0.22	1.55	0.15	0.16	2.08
5	GOMS	ND	ND	ND	ND	ND
6	GOPB	0.27	1.64	0.12	0.12	2.14
7	GOPA	0.26	1.46	0.12	0.04	1.88
8	GOLI	0.17 (0.01)	1.43 (0.07)	0.12 (0.02)	0.16 (0.05)	1.88 (0.14)
9	GOMG	0.24 (0.04)	1.47 (0.13)	0.14 (0.02)	0.05 (0.002)	1.90 (0.16)
10	CCSB	0.14	1.10	0.06	0.08	1.37
11	CCPQ	0.31	2.36	0.38	0.22	3.27
12	ECPY	0.17 (0.02)	1.42 (0.24)	0.35 (0.22)	0.81 (0.44)	2.75 (0.26)
13	WCLR	0.22	1.82	0.18	0.19	2.42
14	MCSU	0.24 (0.04)	1.91 (0.20)	0.87 (0.27)	0.07 (0.01)	3.08 (0.17)
15	MCNO	0.24 (0.04)	2.00 (0.24)	0.35 (0.07)	0.18 (0.03)	2.80 (0.32)
16	WCNO	0.18	1.40	0.28	0.08	1.97
17	WCSU	0.34	2.49	0.53	0.11	3.49
18	WCLS	0.31 (0.05)	1.89 (0.29)	0.44 (0.21)	0.09 (0.02)	2.73 (0.54)
19	ERPS	0.20 (0.01)	1.68 (0.09)	0.36 (0.22)	0.24 (0.08)	2.47 (0.37)
20	ERPN	0.11	1.01	0.15	0.09	1.36
21	WRRB	0.26	1.89	0.42	0.19	2.76
22	CRKU	0.27	1.84	0.53	0.31	2.95
23	WRHD	0.25	2.00	0.55	0.43	3.23
24	ERUN	0.20	1.68	0.20	0.20	2.30
25	ERJA	0.20	1.80	0.28	0.31	2.60
26	NRME	0.36	2.09	0.71	0.29	3.43

App. Table D.9 Derived parameters of canopy condition, based on shoot observations, litter-fall studies, and allometric relationships for the 26 litter/shoots sites, during 1989 - 1990. Shoot density (shoots/m^2); leaf density (leaves/m^2); leaf area (for green leaves, cm^2); canopy leaf area (or leaf area index, LAI, m^2/m^2); canopy leaf biomass (g dry weight/m^2); *ND* = no data. See Table 8.13.

	Site	Shoot Density	Leaf Density	Leaf Area	Canopy Leaf Area	Canopy Leaf Biomass
1	GOPB	94.4	924.6	22.90	2.118	496.5
2	GOPA	96.7	911.9	22.52	2.054	422.2
3	GOLI	97.7	790	26.31	2.078	442.4
4	GOMG	98.1	910.7	23.52	2.142	430.8
5	GOMS	ND	ND	ND	ND	ND
6	WOMI	103.1	734.2	22.92	1.683	290.7
7	WOPG	108.1	901.3	23.90	2.154	440.7
8	CODR	76.0	527.4	23.57	1.243	251.6
9	EOPM	94.9	700.1	24.18	1.693	351.4
10	MCSU	126.6	879.4	22.56	1.984	423.0
11	MCNO	179.0	1,481.5	18.18	2.693	591.1
12	WCNO	57.1	452.0	32.64	1.475	311.5
13	WCSU	173.0	1,091.3	26.83	2.928	565.3
14	WCLS	123.0	1,133.1	30.00	3.400	653.8
15	WCLR	98.8	707.1	35.29	2.496	420.7
16	CCSB	45.4	335.3	46.86	1.571	280.0
17	CCPQ	109.1	666.3	39.40	2.625	531.0
18	ECPY	83.2	505.2	32.25	1.629	276.9
19	WRHD	128.4	773.9	32.00	2.477	435.7
20	ERJA	104.1	998.4	35.54	3.548	575.1
21	ERUN	111.3	817.3	36.86	3.012	420.1
22	NRME	189.2	1,150.8	32.54	3.745	597.3
23	ERPS	93.1	653.4	34.08	2.227	369.2
24	ERPN	44.7	278.3	37.27	1.037	170.6
25	WRRB	115.6	904.3	34.70	3.138	555.2
26	CRKU	160.7	906.6	26.21	2.376	354.5

App. Table D.10 Canopy leaf biomass (t/ha) estimated from shoot observations and litter fall of *Rhizophora mangle*, and annual leaf production (t/ha) determined from monthly litter fall; *ND* = no data. See Table 8.14.

	Site	Canopy Leaf Biomass	Annual Leaf Production	Turnover Ratio
1	WOMI	2.91	4.92	0.59
2	WOPG	4.41	6.03	0.73
3	CODR	2.52	3.89	0.65
4	EOPM	3.51	5.65	0.62
5	GOMS	ND	ND	ND
6	GOPB	4.97	5.98	0.83
7	GOPA	4.22	5.34	0.79
8	GOLI	4.42	5.23	0.85
9	GOMG	4.31	5.35	0.80
10	CCSB	2.80	4.00	0.70
11	CCPQ	5.31	8.62	0.62
12	ECPY	2.77	5.19	0.53
13	WCLR	4.21	6.64	0.63
14	MCSU	4.23	6.96	0.61
15	MCNO	5.91	7.30	0.81
16	WCNO	3.11	5.13	0.61
17	WCSU	5.65	9.10	0.62
18	WCLS	6.54	6.88	0.95
19	ERPS	3.69	6.15	0.60
20	ERPN	1.71	3.70	0.46
21	WRRB	5.55	6.90	0.80
22	CRKU	3.54	6.70	0.53
23	WRHD	4.36	7.30	0.60
24	ERUN	4.20	6.15	0.68
25	ERJA	5.75	6.58	0.87
26	NRME	5.97	7.62	0.78

App. Table D.11 Mean growth parameters of *Rhizophora mangle* seedlings in refinery oil gaps and natural gaps of similar age in two fringe habitats scored between late 1989 and late 1990. SE is in parentheses. See Table 8.15.

Site	Node Production (nodes/yr)		Height Production (cm/yr)		Height/Node (cm/node)	
Exposed Oiled						
2 WOPG	8.0	(0.3)	27.2	(4.2)	3.2	(0.42)
3 CODR	9.8	(0.5)	72.5	(11.1)	7.0	(0.96)
4 EOPM	9.0	(0.1)	31.8	(3.0)	3.5	(0.32)
Exposed Unoiled						
6 GOPB	7.3	(0.4)	25.2	(5.8)	3.1	(0.69)
7 GOPA	7.5	(0.2)	27.6	(3.2)	3.6	(0.38)
8 GOLI	7.4	(0.3)	36.2	(6.9)	4.5	(0.78)
Sheltered Oiled						
19 ERPS	8.8	(0.4)	41.2	(5.3)	4.5	(0.56)
20 ERPN	8.1	(0.4)	45.4	(7.1)	5.1	(0.75)
21 WRRB	8.3	(0.2)	22.7	(2.1)	2.8	(0.25)
Sheltered Unoiled						
24 ERUN	5.2	(0.4)	6.4	(1.2)	1.2	(0.17)
25 ERJA	9.3	(0.2)	69.2	(10.0)	7.3	(1.00)
26 NRME	8.7	(0.2)	85.7	(11.4)	9.5	(1.17)

App. Table D.12 Five parameters of forest structure for *Witwater* spill sites, measured in October 1991, in two fringe habitats. See Table 8.20. Site codes are in Appendix Table D.15.

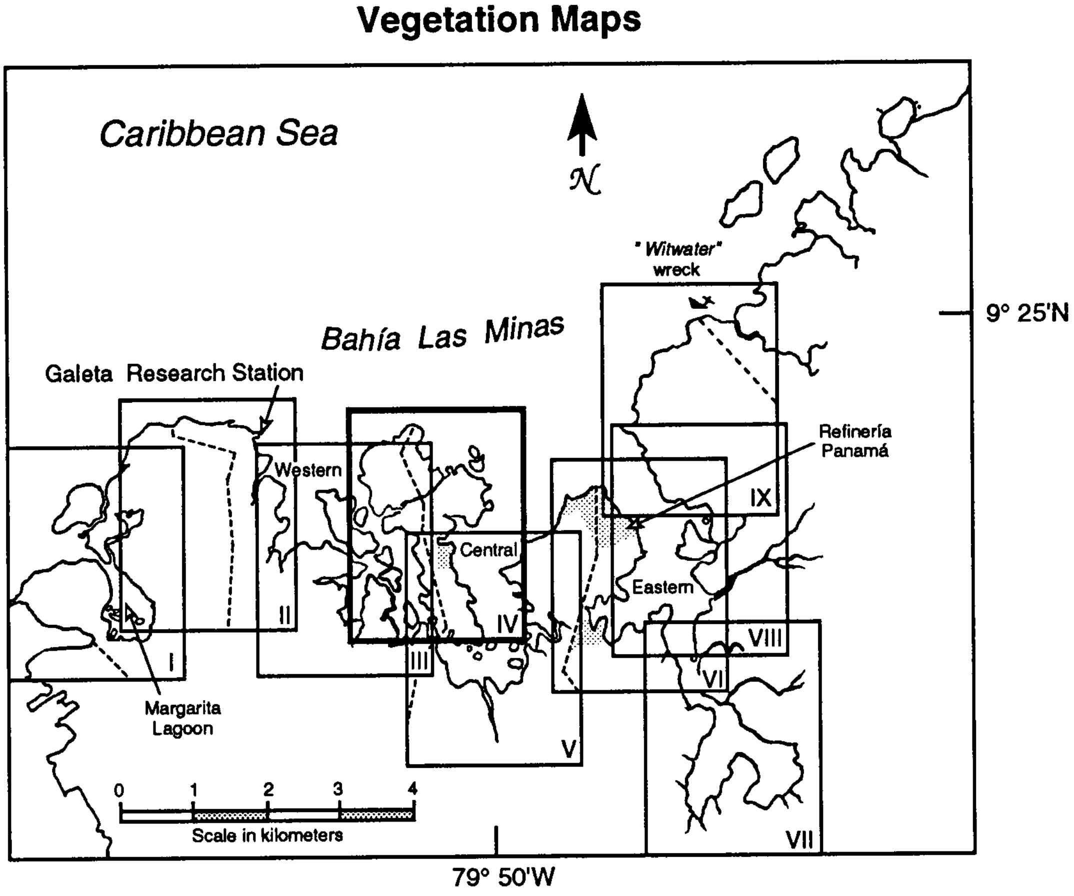
	Open Sites			Channel Sites		
	WWGL	WWMI	WWPG	WWCE	WWLS	WWMR
Density (number/m^2)						
Seedlings	2.04	1.39	0.57	3.00	4.61	1.32
Trees	1.09	0.52	1.47	3.42	4.69	0.70
Total	3.13	1.91	2.06	6.42	9.31	2.02
Diameter (cm)						
Seedlings	0.38	0.36	0.37	0.36	0.37	0.34
Trees	3.96	5.35	3.60	2.21	2.17	5.74
Total	1.60	1.69	2.68	1.34	1.26	2.18
Height (m)						
Seedlings	0.31	0.29	0.25	0.32	0.29	0.27
Trees	4.55	6.21	4.35	2.03	2.57	7.90
Total	1.76	1.86	3.18	1.23	1.42	2.87
Leaf Biomass (t/ha)						
Seedlings	0.07	0.03	0.02	0.10	0.14	0.03
Trees	3.36	2.79	4.24	3.29	5.27	4.61
Total	3.43	2.83	4.26	3.39	5.42	4.64
Total Biomass (t/ha)						
Seedlings	0.15	0.07	0.04	0.24	0.32	0.06
Trees	62.29	67.20	83.95	35.36	65.18	117.50
Total	62.44	67.27	84.01	35.60	65.53	117.56

App. Table D.13 Five structural parameters for four trees of *Rhizophora mangle* growing in a site approximately 10 yr old, sampled in May 1990. See Table 8.21.

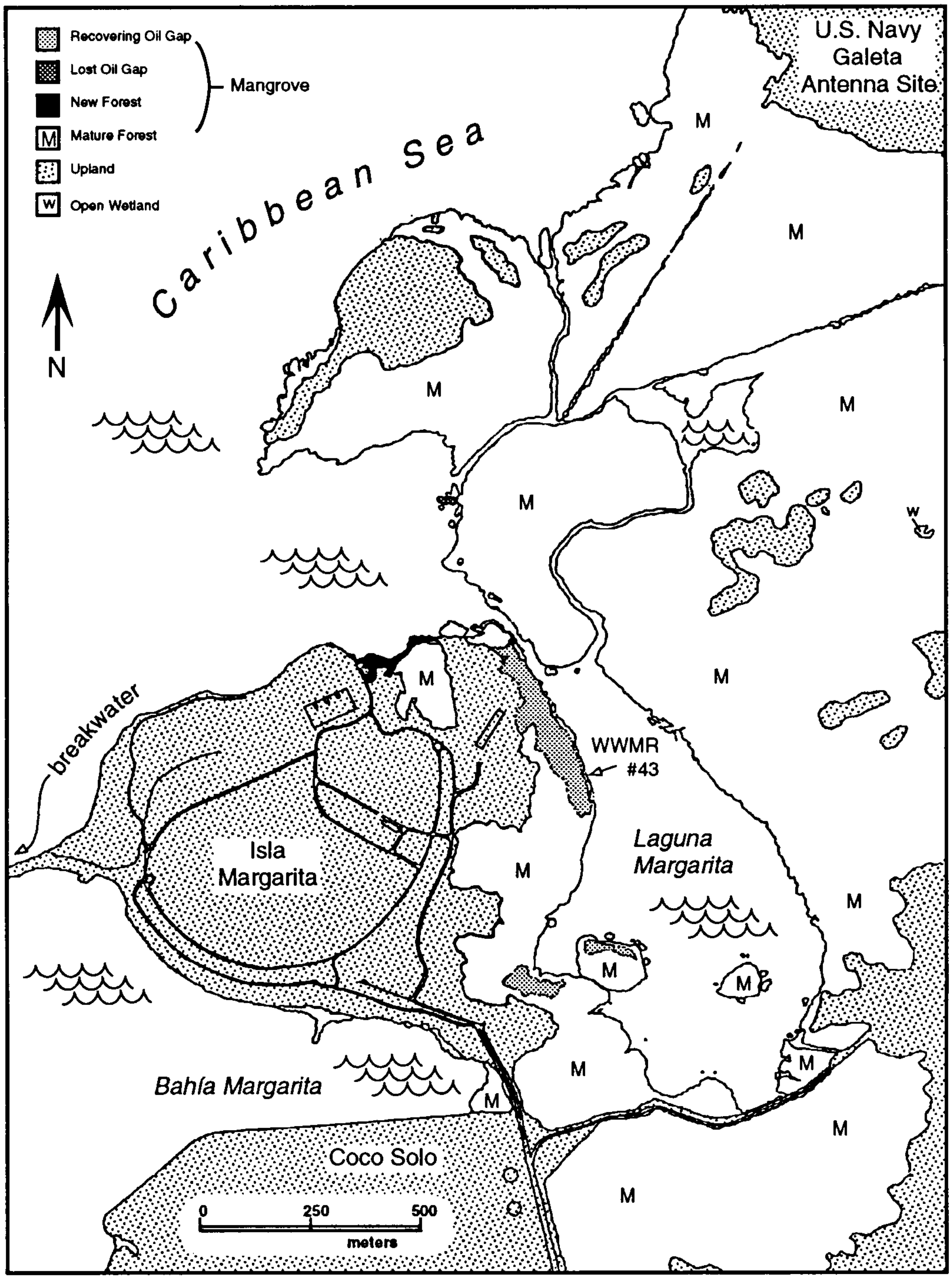
Parameter	Tree 1	Tree 2	Tree 3	Tree 4
Height (m)	11.16	12.11	12.55	12.95
Girth Diameter (cm)	6.01	8.45	8.01	9.20
Nodes (no.)	104	95	109	102
Leaf Biomass (kg/tree)	0.82	1.28	1.23	1.47
Total Biomass (kg/tree)	21.37	41.06	38.62	50.3

App. Table D.14 Listing of 12 studies and the specific sites used in the mangrove forest project. Locations are marked in Appendix Figures D.1 to D.19. Studies include: litter fall (*LF*), shoot observations (*S*), mature forest demography (*FD*), *Witwater* oil-gap demography (*WD*), refinery oil-gap demography (*SD*), refinery oil- gap seedling growth (*SG*), light gap study (*LG*), study of unoiled tree growth (*4T*), study of node production (*NP*), allometry of leaf size and weight (*A*), monitoring of water salinity and temperature (*ST*), and the test study of wire markers on shoot growth (*WT*).

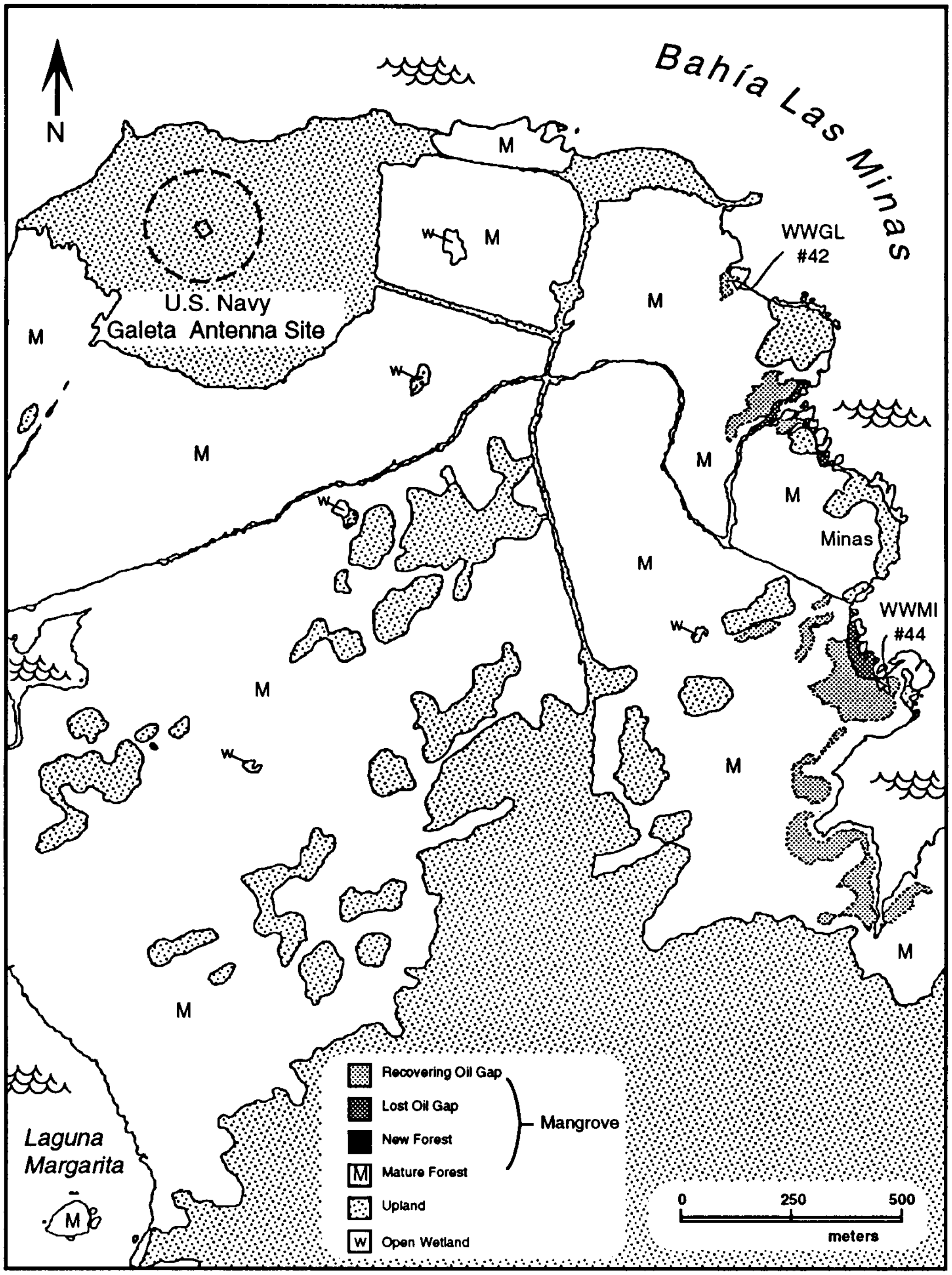
Site	#	LF	S	FD	WD	SD	SG	LG	4T	NP	A	ST	WT
WOMI	1	X	X	X	-	X	-	-	-	-	X	X	-
WOPG	2	X	X	X	-	X	X	-	-	-	X	X	-
CODR	3	X	X	X	-	X	X	-	-	-	X	X	-
EOPM	4	X	X	X	-	X	X	-	-	-	X	X	-
GOMS	5	-	X	-	-	-	-	-	-	-	-	-	-
GOPB	6	X	X	X	-	-	X	-	-	-	X	X	-
GOPA	7	X	X	X	-	-	X	-	-	-	X	X	-
GOLI	8	X	X	X	-	-	X	-	-	-	X	X	-
GOMG	9	X	X	X	-	-	-	-	-	-	X	X	-
CCSB	10	X	X	X	-	X	-	-	-	-	X	X	-
CCPQ	11	X	X	X	-	X	-	-	-	-	X	X	-
ECPY	12	X	X	X	-	X	-	-	-	-	X	X	-
WCLR	13	X	X	X	-	X	-	-	-	-	X	X	-
MCSU	14	X	X	X	-	-	-	-	-	-	X	X	-
MCNO	15	X	X	X	-	-	-	-	-	-	X	X	-
WCNO	16	X	X	X	-	-	-	-	-	-	X	X	-
WCSU	17	X	X	X	-	-	-	-	-	-	X	X	-
WCLS	18	X	X	X	-	-	-	-	-	-	X	X	-
ERPS	19	X	X	X	-	-	X	-	-	-	X	X	-
ERPN	20	X	X	X	-	-	X	-	-	-	X	X	-
WRRB	21	X	X	X	-	X	X	-	-	-	X	X	-
CRKU	22	X	X	X	-	X	-	-	-	-	X	X	-
WRHD	23	X	X	X	-	-	-	-	-	-	X	X	-
ERUN	24	X	X	X	-	X	X	-	-	-	X	X	-
ERJA	25	X	X	X	-	-	X	-	-	-	X	X	-
NRME	26	X	X	X	-	X	X	-	-	-	X	X	-
WOLN	28	-	-	-	-	X	-	-	-	-	-	-	-
ECNS	29	-	-	-	-	X	-	-	-	-	-	-	-
CCRE	30	-	-	-	-	X	-	-	-	-	-	-	-
WOGL	31	-	-	-	-	X	-	-	-	-	-	-	X
G1	32	-	-	-	-	-	-	X	-	-	-	-	-
G2	33	-	-	-	-	-	-	X	-	-	-	-	-
G3	34	-	-	-	-	-	-	X	-	-	-	-	-
G4	35	-	-	-	-	-	-	X	-	-	-	-	-
G5	36	-	-	-	-	-	-	X	-	-	-	-	-
G6	37	-	-	-	-	-	-	X	-	-	-	-	-
G7	38	-	-	-	-	-	-	X	-	-	-	-	-
G8	39	-	-	-	-	-	-	X	-	-	-	-	-
WCFT	40	-	-	-	-	-	-	-	X	-	-	-	-
WWPG	41	-	-	-	X	-	-	-	-	-	-	-	-
WWGL	42	-	-	-	X	-	-	-	-	-	-	-	-
WWMR	43	-	-	-	X	-	-	-	-	-	-	-	-
WWMI	44	-	-	-	X	-	-	-	-	-	-	-	-
WWLS	45	-	-	-	X	-	-	-	-	-	-	-	-
WWCE	46	-	-	-	X	-	-	-	-	-	-	-	-
N1	113	-	-	-	-	-	-	-	-	X	-	-	-
N2	121	-	-	-	-	-	-	-	-	X	-	-	-
N3	122	-	-	-	-	-	-	-	-	X	-	-	-
N4	123	-	-	-	-	-	-	-	-	X	-	-	-
N5	212	-	-	-	-	-	-	-	-	X	-	-	-
N6	213	-	-	-	-	-	-	-	-	X	-	-	-
N7	222	-	-	-	-	-	-	-	-	X	-	-	-



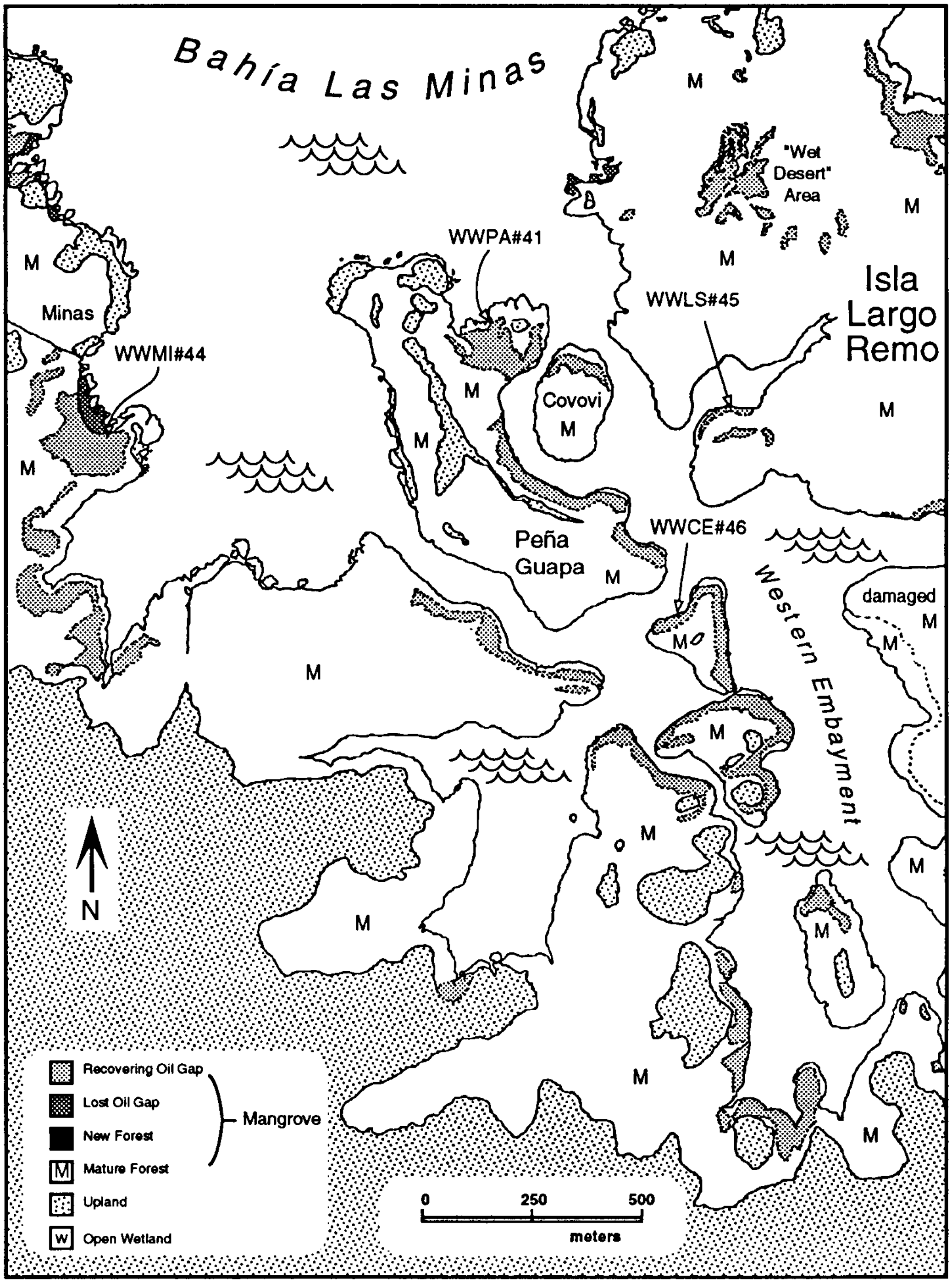
App. Fig. D.1 Map of Bahía Las Minas and vicinity, showing the series of nine inset map outlines used in this treatment in two series, for 1973 (App. Figs. D.2-D.10) and 1990 (App. Figs. D.11-D.19).



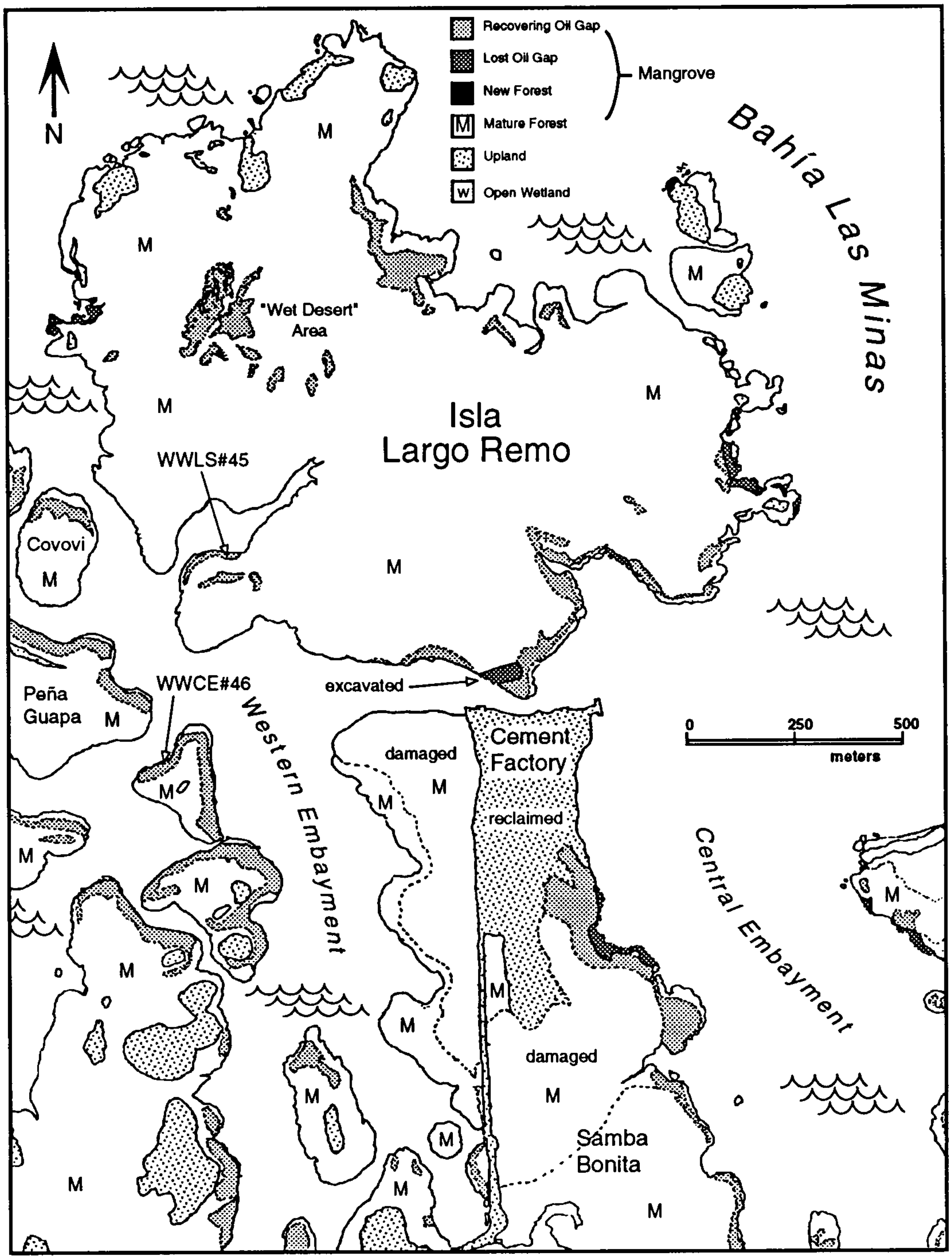
App. Fig. D.2 Map I from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



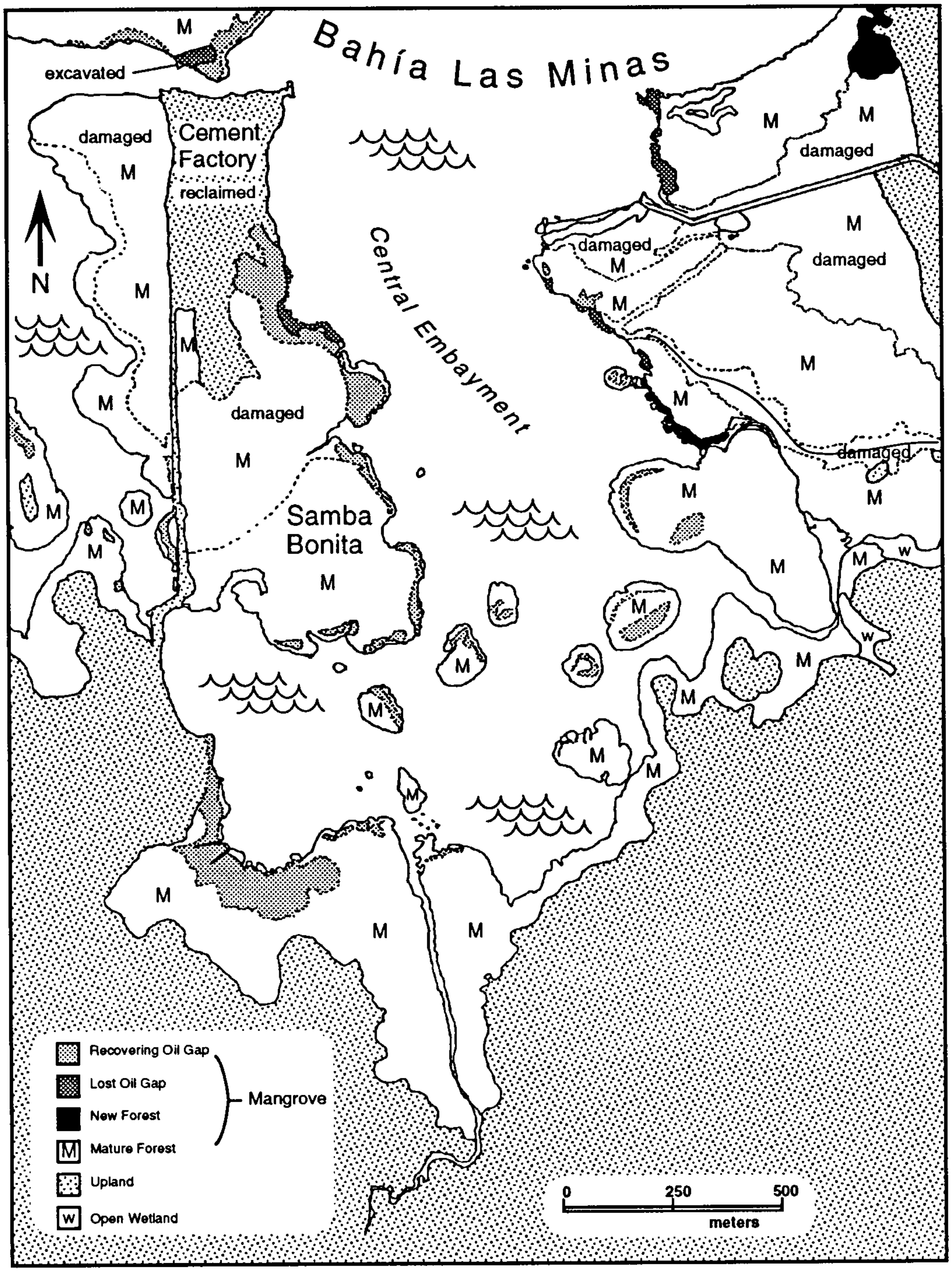
App. Fig. D.3 Map II from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



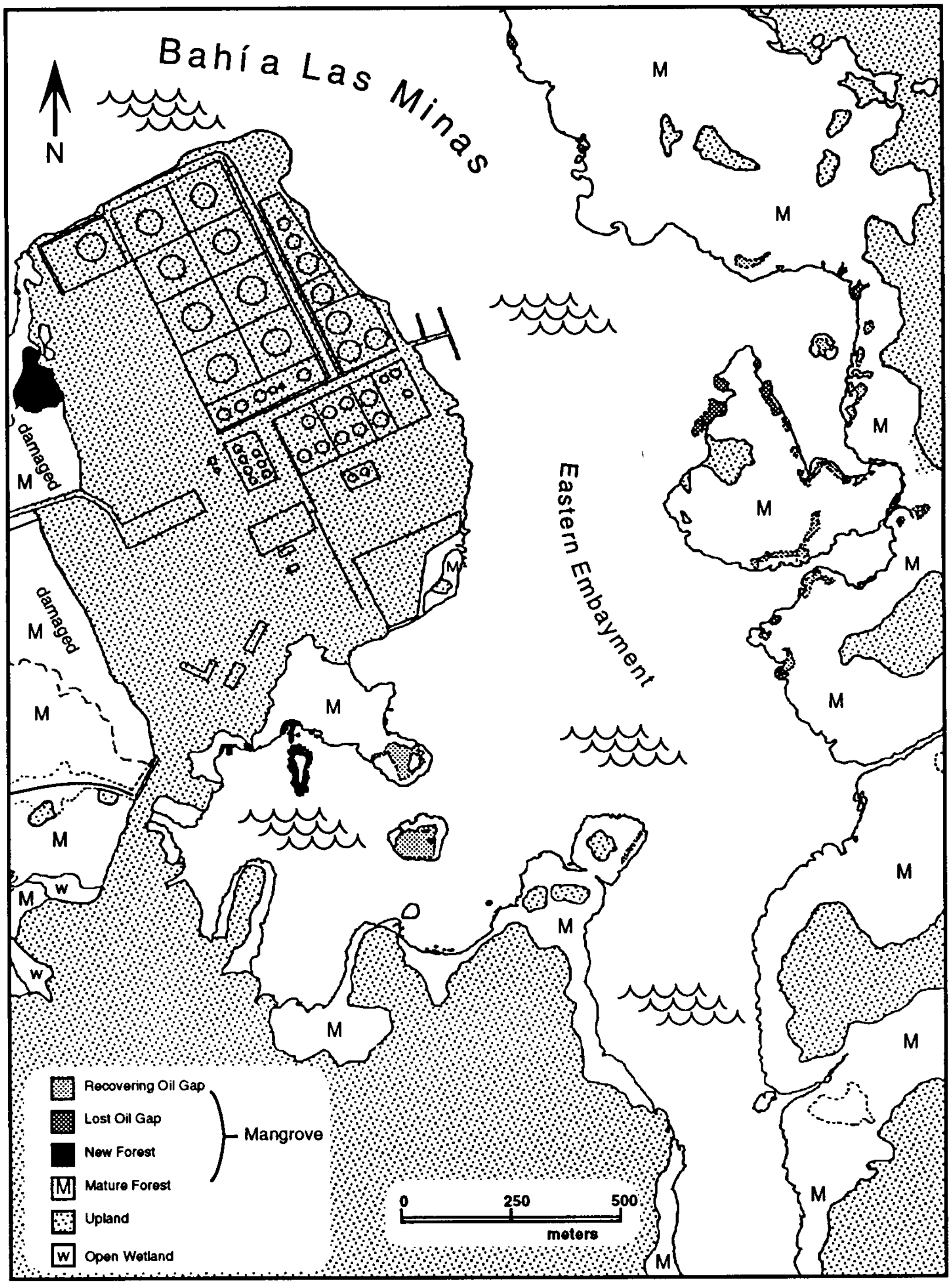
App. Fig. D.4 Map III from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



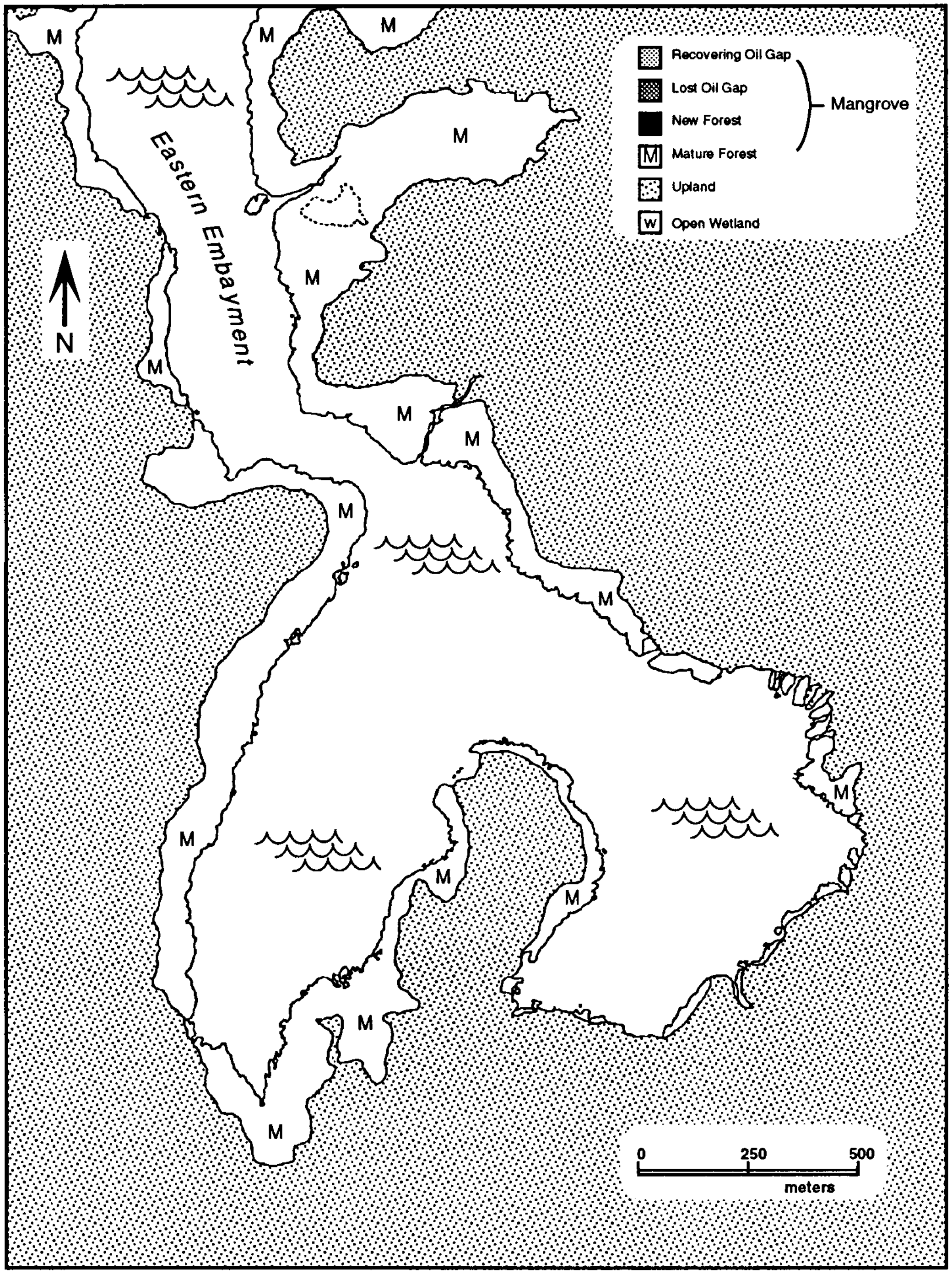
App. Fig. D.5 Map IV from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



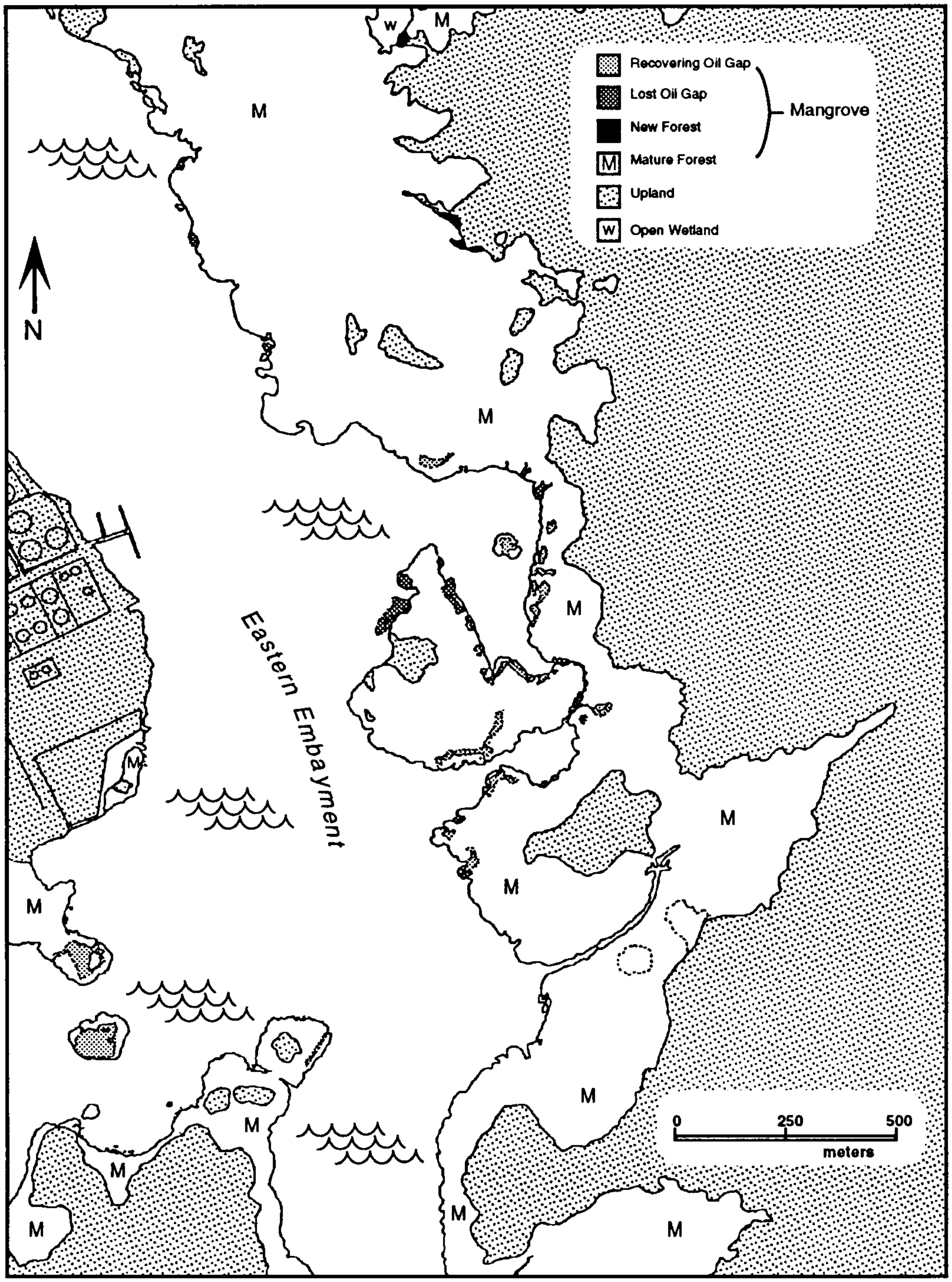
App. Fig. D.6 Map V from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



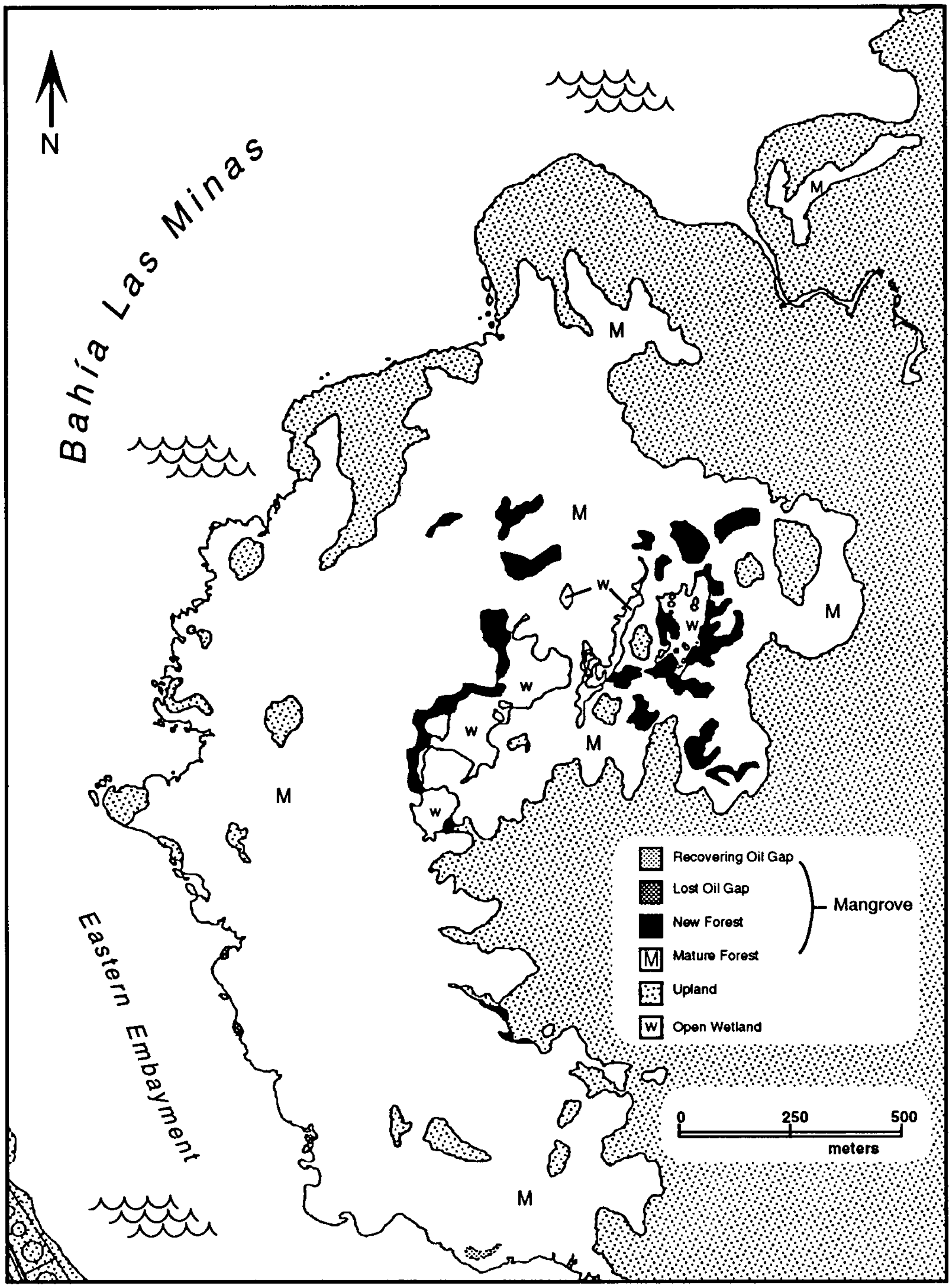
App. Fig. D.7 Map VI from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



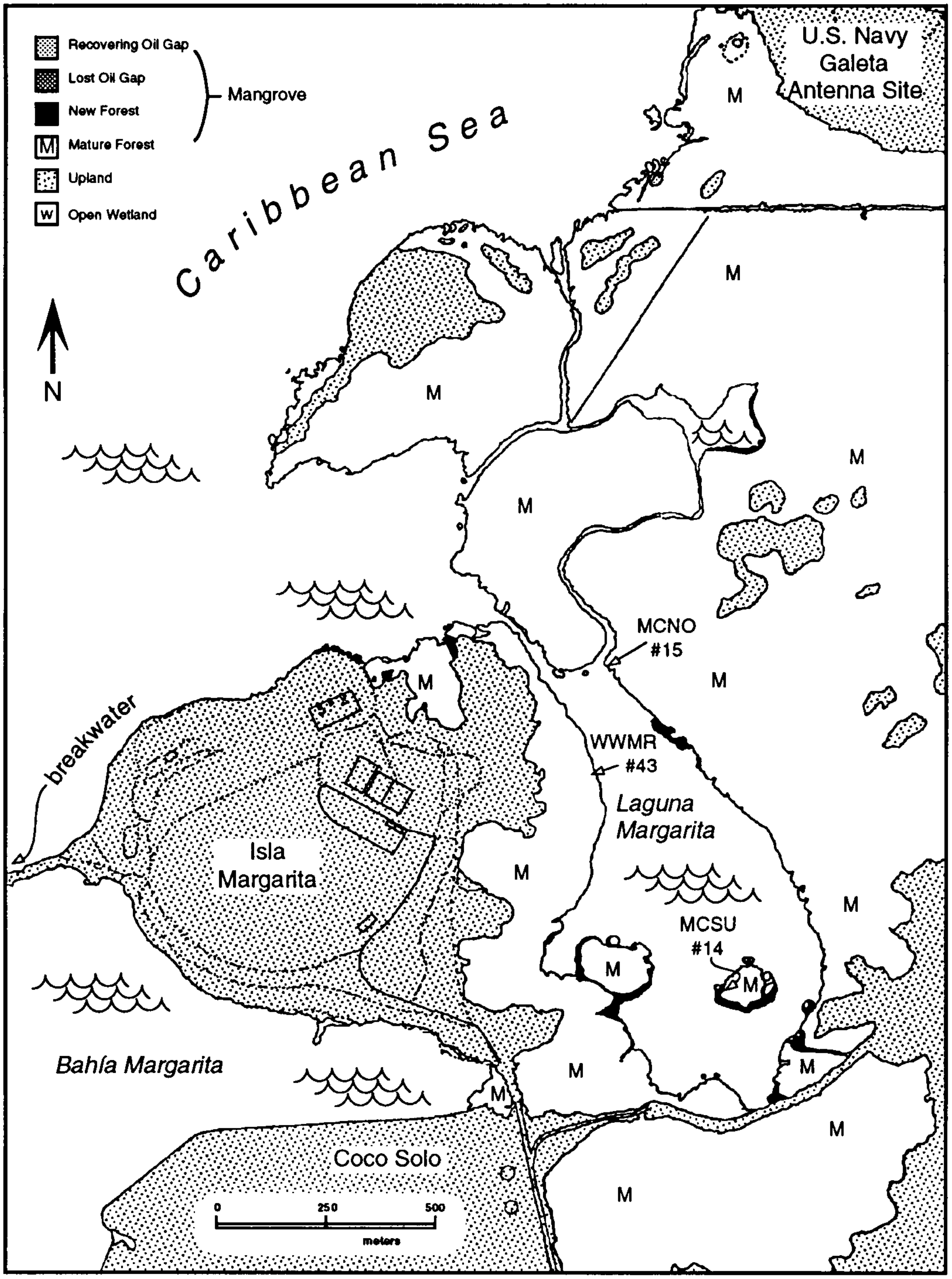
App. Fig. D.8 Map VII from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



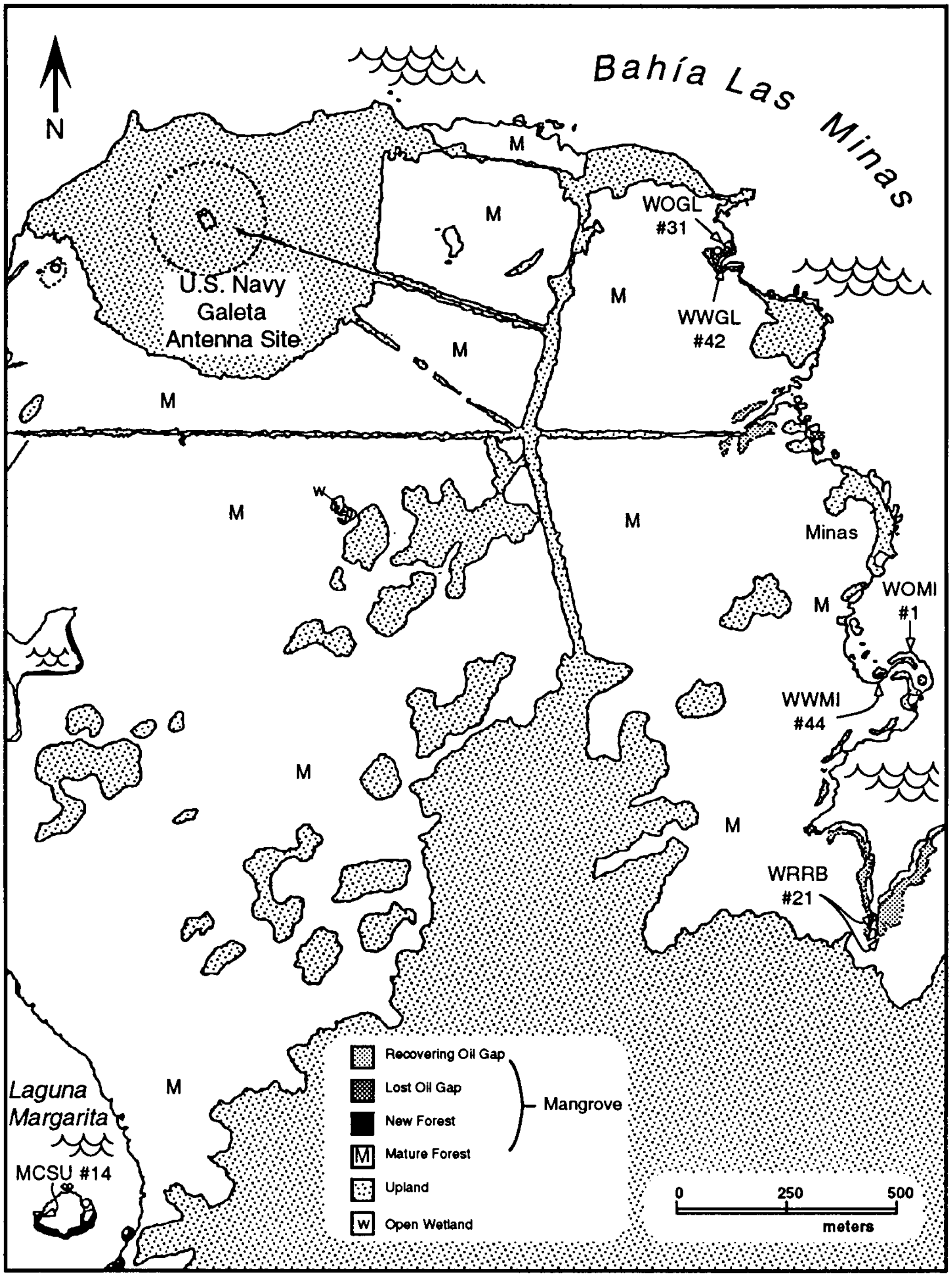
App. Fig. D.9 Map VIII from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



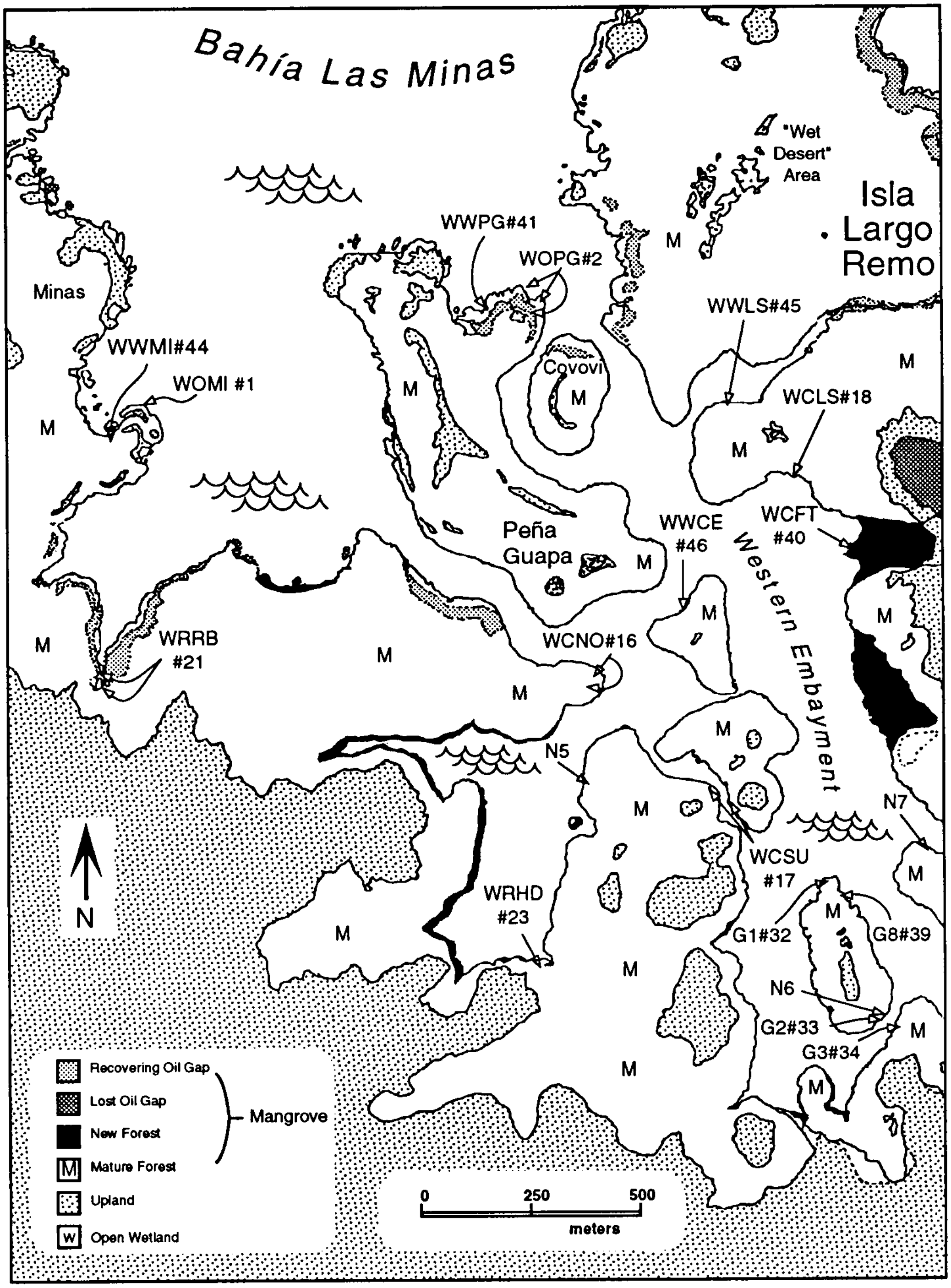
App. Fig. D.10 Map IX from 1973 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of study sites in the present study, specifically referring to the 1968 *Witwater* oil gaps.



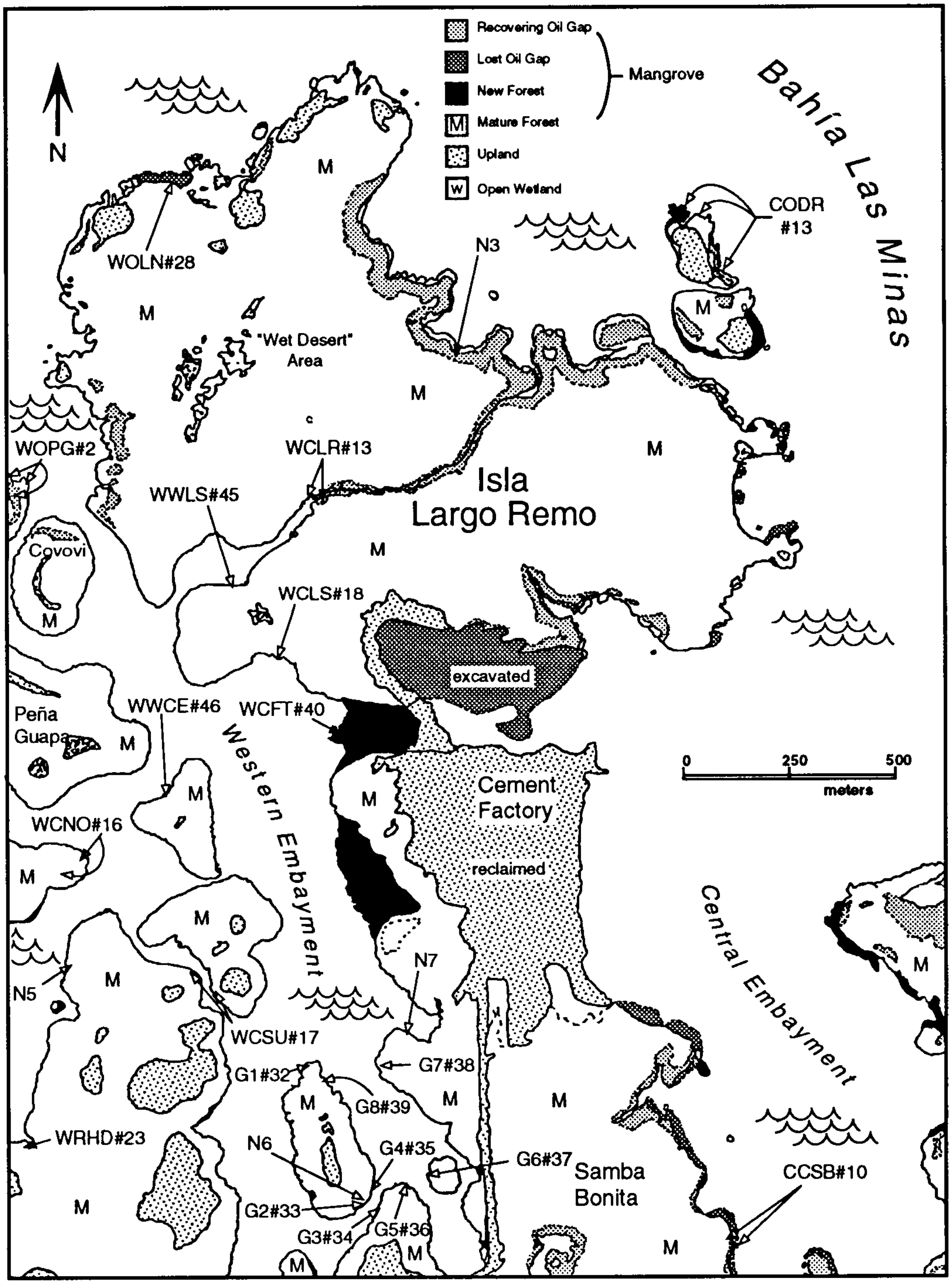
App. Fig. D.11 Map I from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



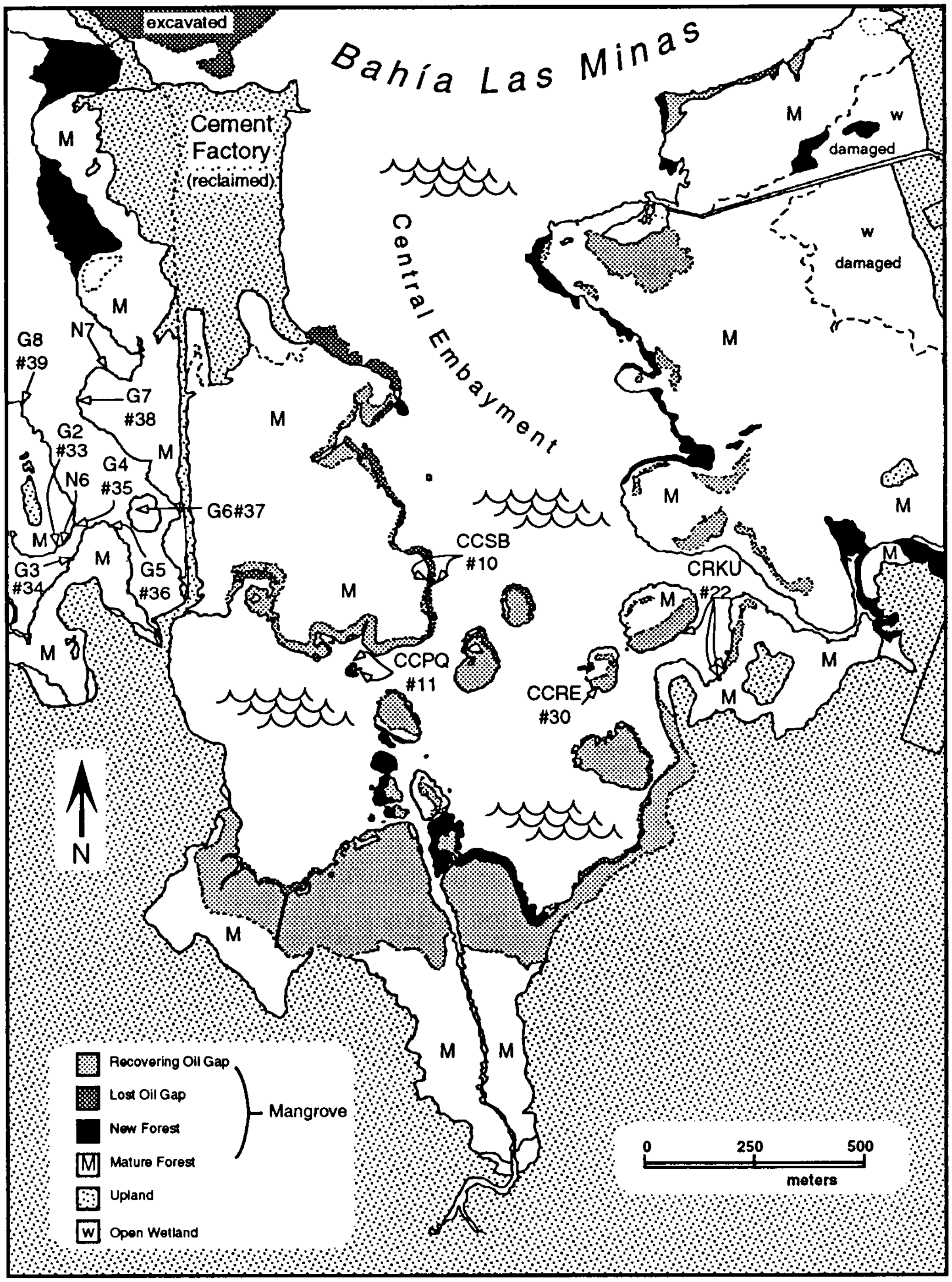
App. Fig. D.12 Map II from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



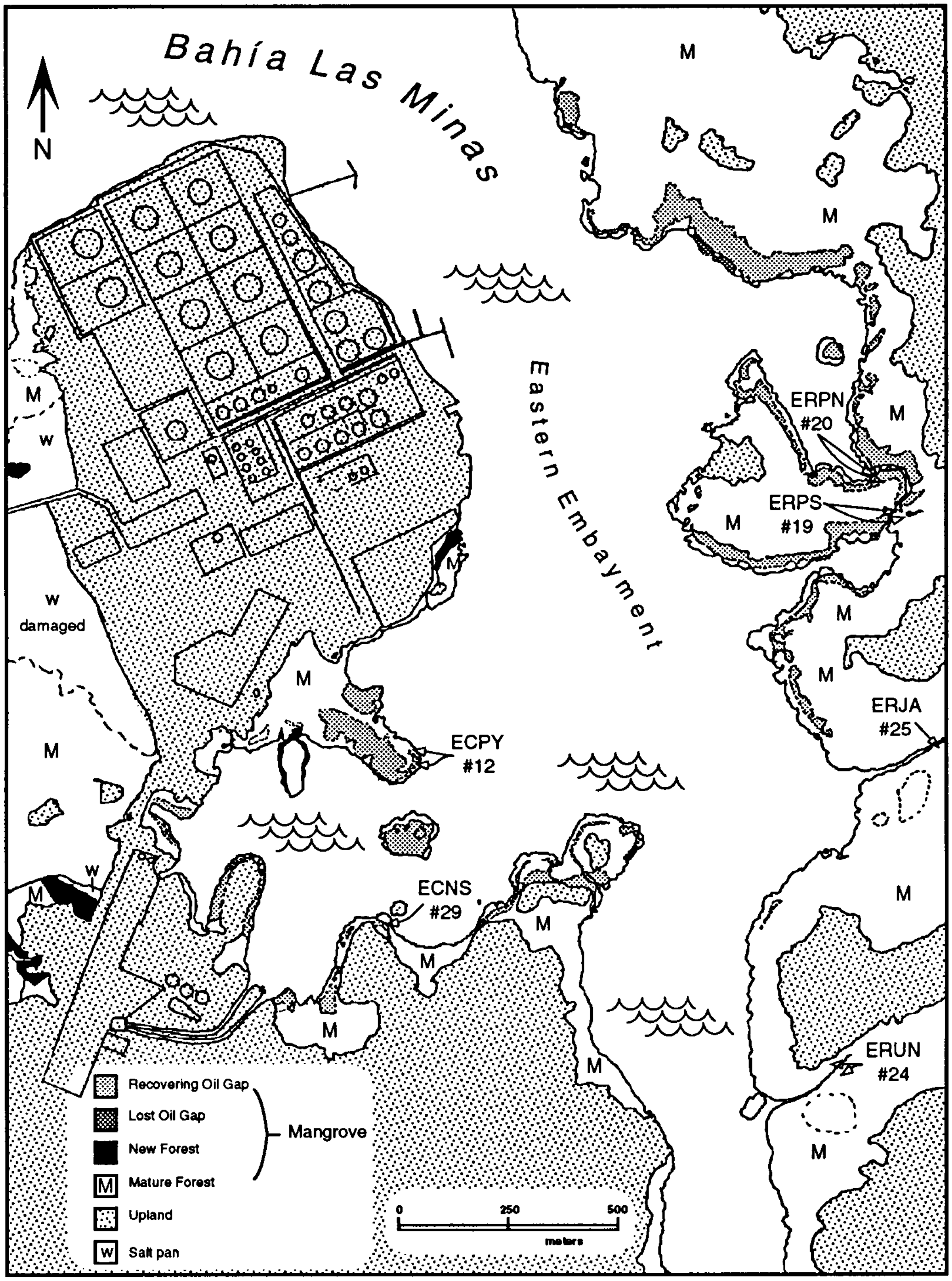
App. Fig. D.13 Map III from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



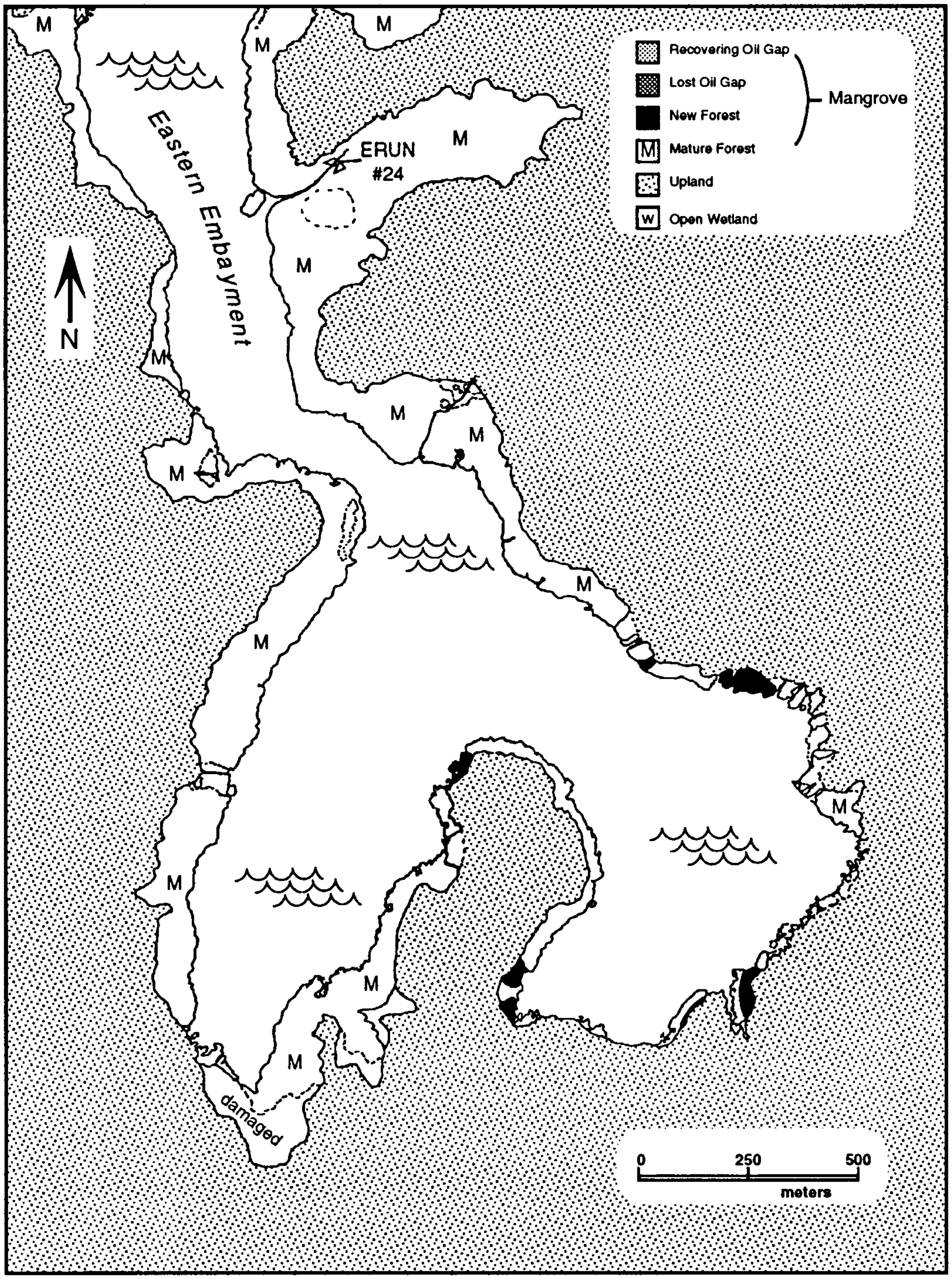
App. Fig. D.14 Map IV from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



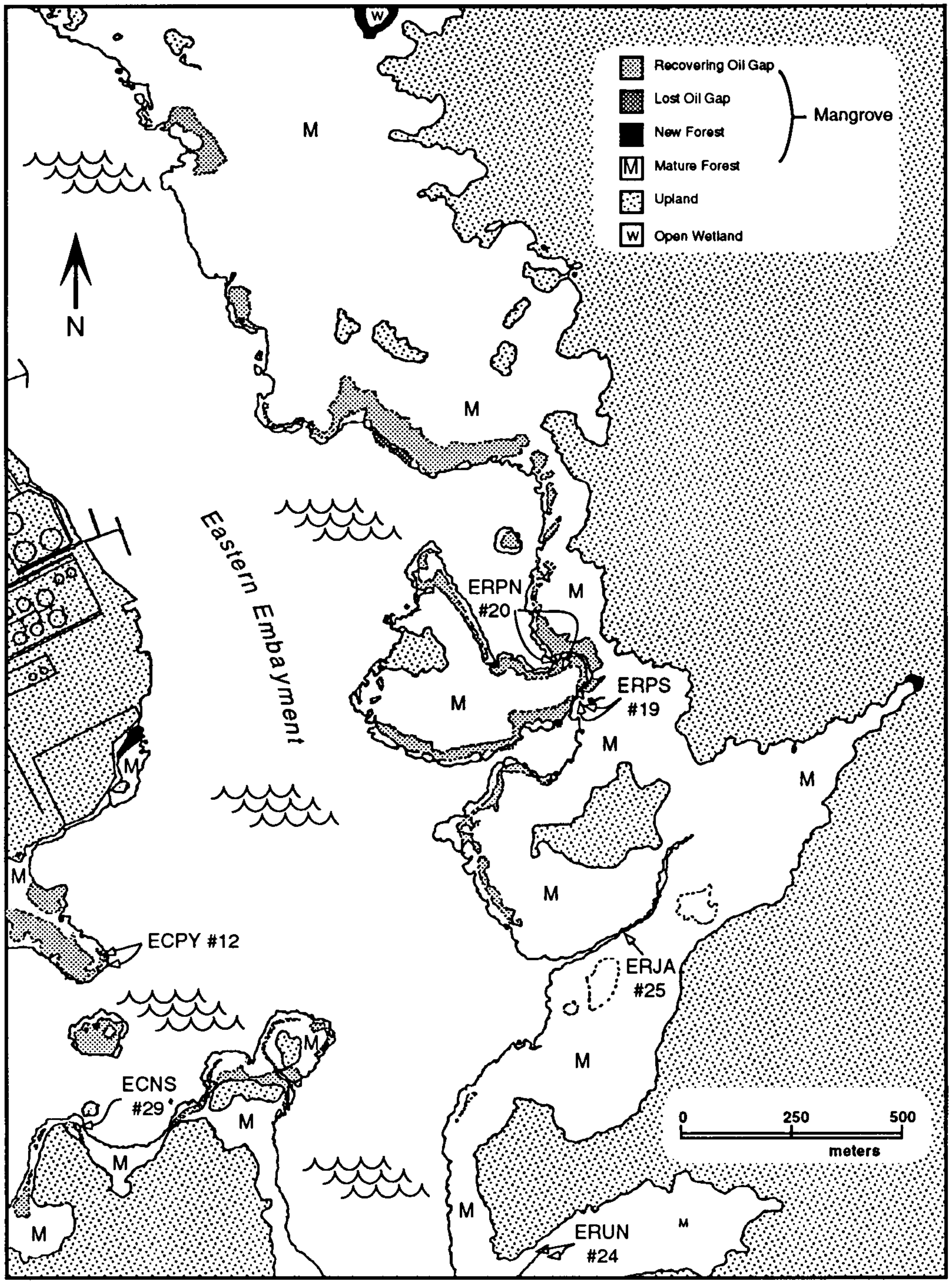
App. Fig. D.15 Map V from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



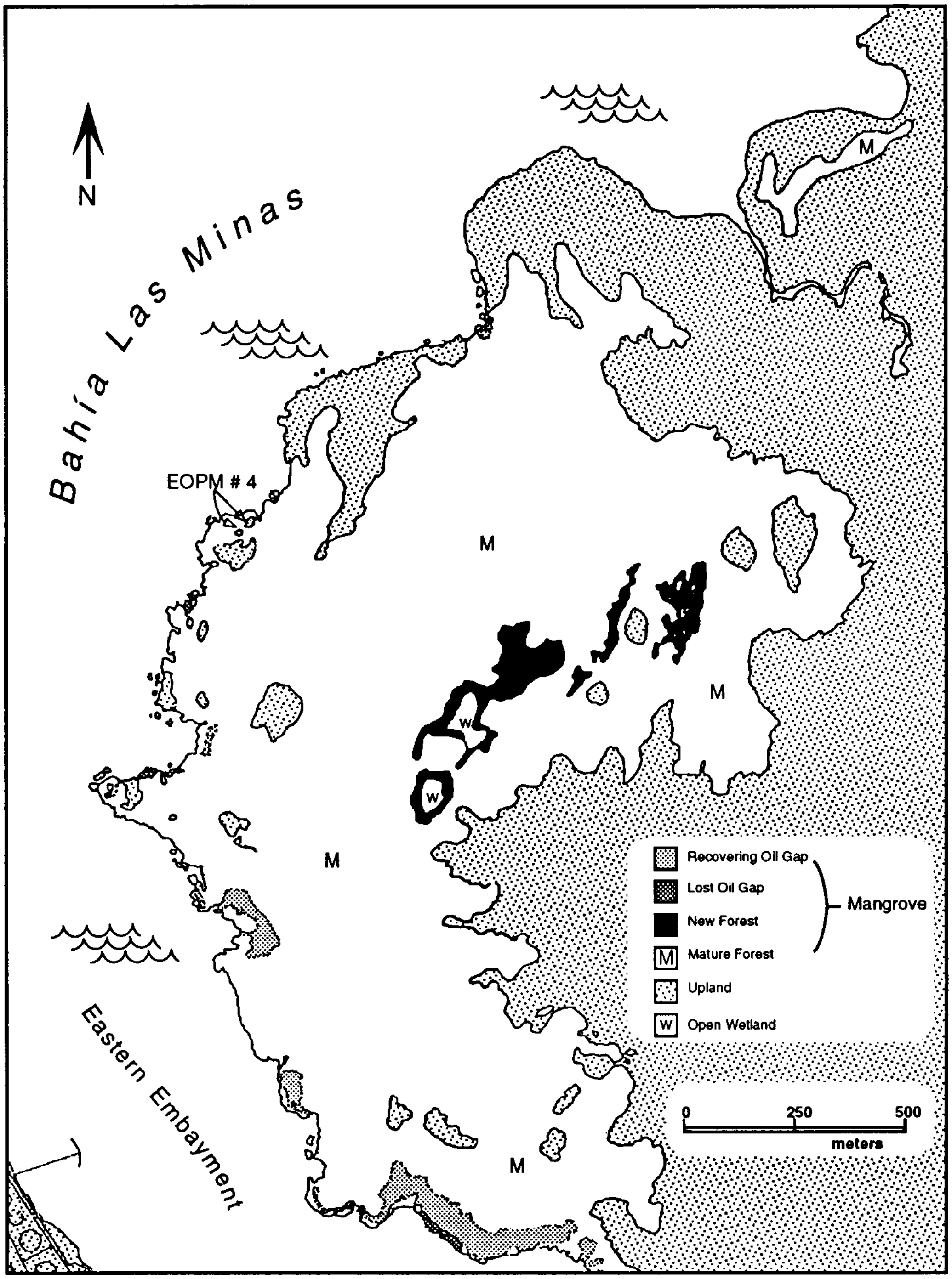
App. Fig. D.16 Map VI from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



App. Fig. D.17 Map VII from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



App. Fig. D.18 Map VIII from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.



App. Fig. D.19 Map IX from 1990 aerial photographs of Bahía Las Minas (App. Fig. D.1), showing areas of deforestation and change in local mangrove forests. Note the position of all relevant study sites in the present study.

Appendix Abstract and Description D.1 The aging technique for *Rhizophora mangle* seedlings used in this study, as described in Duke and Pinzón (1992). The abstract and description of the technique are presented here for reference.

Biotropica 24(2) 1992.

Aging *Rhizophora* seedlings from leaf scar nodes: a technique for studying recruitment and growth in mangrove forests.

Norman C. Duke and Zuleika S. Pinzón M.

ABSTRACT

This paper proposes a rapid and non-destructive technique to age *Rhizophora* seedlings in the field, using the sequence of leaf nodes along main stems. Based on three to four year-old *R. mangle* seedlings planted in a bay on the Caribbean coast of Panama, it was found that rates of annual node production (= half of leaf production) in the terminal leafy shoot was relatively constant between individuals in the same and similar sites, and for each individual when re-measured three or four times over 19 months. Marked differences, however, were scored between sites under obviously different light conditions, notably in shade (closed canopy) or sun (open canopy); estimates range from 3.8 (SE ± 0.3) to 7.0 (SE ± 0.6) nodes.shoot^{-1}.year^{-1}, respectively (note, these were comparable with branch shoots on mature trees nearby). Therefore, neighbouring seedlings in sites with the same light condition could be aged by dividing total counts of main stem nodes by the respective rate. But, of greater interest, seedlings in open sites were found to have annual peaks of internodal extension along their main stems. It followed that seedlings like these could be aged by counting the number of peaks. This provided a more robust means to age seedlings having unknown growth histories, since it did not assume constant annual node production. These characteristics of seedling growth offer a relatively simple means to age individuals, and to quickly characterize demographic patterns in seedling communities. The technique is limited by bark development obscuring nodes on lower stems, occurring after approximately six or more years in *R. mangle*. Furthermore, because node production was not apparently influenced by age, then the technique may also apply to distal branches of larger trees in appropriate light conditions.

Description of The Aging Technique

This technique offers a way to age younger individuals of one member of the family Rhizophoraceae. It relies on the sequence of nodes formed in conjunction with pairs of leaf scars along continuous stems. The following points summarize and describe the technique in five sections, since stem growth may be characterized by either seasonally variable internodal distances, or long series of near zero distances, or all these may be obscured by bark development on lower sections of the stem.

A. Seedlings and saplings, notably of *R. mangle* with internodal distances periodically $>>0.5$ cm, can be aged in two steps provided they meet two criteria.

First, the uppermost apical shoot is the primary shoot (i.e. the one emanating from the hypocotyl), and the main stem is reasonably straight (note: a branch point creates a response in axillary stem internode extension similar to the first flush observed immediately above the hypocotyl; see Fig. 6). This type of seedling is considered decurrent. Second, there is a complete sequence of nodes still visible from the uppermost shoot, down the main stem to the hypocotyl. In addition, note that based on present data for *R. mangle* in open canopy sites, the rate of node production is 7 nodes.year^{-1} (range, 4 - 9). Also, initial height extension, which is characteristically large immediately above the hypocotyl, occurs during at least the first five or six nodes, i.e. the first year. Therefore, seasonal periodicity of internodal extension will not be clearly visible in seedlings having <23 nodes, i.e. $<$three years growth.

The steps for determining age are as follows. **Step 1.** As a general rule, internodal distances are measured between encircling stipular scars where they are separate from the leaf scars (Note the position of the node number arrows in the inset of Fig. 1 [= 8.5]). Starting from the substratum, measure the height of the hypocotyl or zero node, followed by successively higher nodes along the main stem until reaching the base of the enclosing uppermost pair of interpetiolar stipules. This is scored as the last node in the present sequence. **Step 2.** Internodal extension is estimated as the difference between the height of the node above, minus the one below (see Fig. 1 [= 8.5]). Plot the data in a graph with node number (x-axis) versus internodal extension (y-axis), similar to that shown in Fig. 5. For the x-axis, it is assumed that node production rate is constant, allowing even increments of node number. If the seedling is of known age, there are at least two dates which can be applied immediately to the x-axis. These are the recruitment date for the zero node, and the date of observation for the uppermost node. The number of regular peaks of height extension (as seen in Fig. 5) will provide an estimate of age in years.

B. For younger seedlings, i.e. those with <23 nodes, node counts may be compared with either the estimate provided in this study, or one based on nearby seedlings of either estimated or known age. In addition, seedlings with damaged main stems can be included in this set, since node production was comparable in those axillary, cum-uppermost apical shoots. These latter seedlings are considered excurrent.

C. For seedlings with minimal internodal distances, notably < = 0.5 cm in *R. mangle* (shaded seedlings or dwarf plants), the estimation of age is more problematic. In this case, node counts are all that are available, and knowing annual node production rate is pre-requisite.

D. For older seedlings with minimal internodal distances (like those in Section C), and where rough bark obscures lower nodes, extrapolation of estimates can be based on node production and height increase per year. In this method, allowances must be made for the burst of extension immediately above the hypocotyl, which could be derived from younger seedlings in the immediate vicinity, having their lower nodes visible.

E. Branch shoots on mature trees may be studied in similar ways to those outlined above, where appropriate. In some cases, rates of growth could be estimated for branches which meet the first criteria, and having internodal distances > >0.5 cm for *R. mangle* (as noted in Section A). In such stems, up to 50 or 60 nodes were found in preliminary field investigations. This suggests that some branch stem growth can be assessed retrospectively in mature trees growing over the last seven or eight years.

Appendix E
The Mangrove Fringe and the Epibiota of Mangrove Roots

App. Table E.1 Observations of oil in mangrove-sediment cores at oiled sites.

Site	Observations on each of 3 cores/site
	A. May 1989 (observations by J. MacPherson, BBSR).
Oiled Open Coast	
MINM	1. oily smell
	2. oily smell
	3. no oily smell
PGM	1. no oily smell
	2. oily smell, oil visible
	3. oily smell, oil draining from core
DROM	1. oily smell
	2. oily smell
	3. oily smell
PMM	1. no oily smell
	2. no oily smell
	3. no oily smell
Oiled Channels and Lagoons	
SBCE	1. oil saturating dead roots
	2. oily smell at all levels
	3. oil saturation to 12 cm, oil draining from core
SBCS	1. oily smell, oil draining from core
	2. oily smell, oil draining from core
	3. oily smell
PCE	1. oily smell, oil draining from core
	2. oily smell
	3. oily smell, oil draining from core
PCS	1. oily smell, oil draining from core
	2. oily smell, oil saturated roots to 30 cm
	3. oily smell, visible oil to 13 cm
LRCW	1. oily smell
	2. faint smell deep in core
	3. faint smell deep in core
Oiled Drainage Streams	
LRRS	1. oily smell throughout core
	2. faint oily smell
	3. no oily smell
PAYR	1. oily smell all depths
	2. oil saturated throughout
	3. visible oil and oily smell throughout
PMRE	1. oily smell, iridescent sheen all depths
	2. oily smell, iridescent sheen all depths
	3. oily smell all depths
PMRW	1. oily smell, surface globules of oil
	2. oily smell, surface globules of oil
	3. no oily smell or visible oil

App. Table E.1 Observations of oil in mangrove-sediment cores at oiled sites (continued).

Site	Observations on each of 3 cores/site
	B. July 1990 (observations by M. Stoelting, BBSR, and S. D. Garrity).
Oiled Open Coast	
MINM	Iridescent slick in water and on sediments
	1. iridescent oil and black oil
	2. iridescent oil and black oil
	3. iridescent oil and black oil
PGM	Iridescent slick in water and on sediments
	1. iridescent oil and black oil
	2. iridescent oil and black oil
	3. iridescent oil and black oil
DROM	Iridescent/silver slick in water and on sediments.
	1. iridescent oil and much black oil
	2. iridescent oil and little black oil
	3. iridescent oil and little black oil
PMM	Small iridescent slicks in water and on sediments
	1. iridescent oil and black oil
	2. iridescent oil
	3. no visible oil
Oiled Channels and Lagoons	
SBCE	Small iridescent slick in water and on sediments
	1. much black oil and iridescent oil
	2. much black oil and iridescent oil
	3. less black oil, much iridescent oil
SBCS	Small iridescent slicks in water and on sediments
	1. much black oil and iridescent oil
	2. moderate black oil and iridescent oil
	3. little black oil, much iridescent oil
PCE	Iridescent slick at water's edge and on sediments
	1. much black oil and iridescent oil
	2. much black oil and iridescent oil
	3. much black oil and iridescent oil
PCS	Silver sheen slick entire area, iridescent patches at water's edge
	1. black oil and iridescent oil
	2. black oil and iridescent oil
	3. black oil and iridescent oil
LRCW	Scattered silver and iridescent slicks in water, iridescent oil on sediments
	1. iridescent oil
	2. black oil and iridescent oil
	3. no visible oil

App. Table E.1 Observations of oil in mangrove-sediment cores at oiled sites (continued).

Site	Observations on each of 3 cores/site
Oiled Drainage Streams	
LRRS	Silver and iridescent slick on 100% of water, some irridescence on sediments
	1. black oil and iridescent oil
	2. black oil and iridescent oil
	3. iridescent oil
PAYR	Scattered silver and iridescent oil in water, iridescent oil on sediments
	1. little black oil and iridescent oil
	2. little black oil and iridescent oil
	3. much black oil and iridescent oil
PMRE	Silver sheen and scattered iridescent patches on water
	1. little black oil and iridescent oil
	2. much black oil
	3. black oil and iridescent oil
PMRW	Silver and iridescent slick on 100% of water, iridescent oil on sediments
	1. moderate black oil, much iridescent oil
	2. much black oil and iridescent oil
	3. moderate black oil, much iridescent oil
	C. June 1991 (observations by S. D. Garrity).
Oiled Open Coast	
MINM	1. iridescent sheen, little black oil
	2. much black oil
	3. little black oil
PGM	1. iridescent sheen
	2. much black oil
	3. much black oil
DROM	1. moderate black oil
	2. little black oil
	3. moderate black oil
PMM	1. no oil, no oily smell
	2. black oil, amount unspecified
	3. black oil, amount unspecified
Oiled Channels and Lagoons	
SBCE	1. much black oil
	2. much black oil
	3. much black oil
SBCS	1. no oil, oily smell
	2. moderate black oil
	3. moderate black oil
PCE	1. black oil/tar, amount unspecified
	2. black oil, amount unspecified
	3. black oil, amount unspecified
LRCW	1. little black oil
	2. iridescent sheen
	3. much black oil

App. Table E.1 Observations of oil in mangrove-sediment cores at oiled sites (continued).

Site	Observations on each of 3 cores/site
Oiled Drainage Streams	
LRRS	1. moderate black oil 2. moderate black oil 3. little black oil
PAYR	1. little black oil 2. little black oil 3. little black oil
PMRE	1. much black oil 2. much black oil 3. much black oil
PMRW	1. much black oil 2. oily smell 3. oily smell

App. Table E.2 Mean depth in centimeters.

	Date	Coll.	Depth (cm)	SE	*N*
A. Oiled Open Coast					
Isla Droque Mangrove	02Mar1989	sg	55.64	2.16	55
Isla Mina Mangrove	02Mar1989	sg	64.69	1.51	51
Peña Guapa Mangrove	02Mar1989	sg	55.18	2.41	51
Punta Muerto Mangrove	02Mar1989	sg	55.09	3.22	54
B. Unoiled Open Coast					
Isla Lintón Mangrove	09Sep1989	sg	55.39	1.91	51
María Soto Mangrove	05Mar1989	sg	61.40	1.82	57
Isla del Padre Mangrove	01Mar1989	sg	65.88	3.83	51
Portobelo Mangrove	01Mar1989	sg	62.30	2.19	50
C. Oiled Channels and Lagoons					
Largo Remo Channel West	31May1989	cg	23.36	2.47	50
Payardí Channel East	30May1989	cg	34.16	1.58	50
Payardí Channel South	30May1989	cg	52.40	2.02	50
Samba Bonita Channel East	30May1989	cg	22.50	2.15	50
Samba Bonita Channel South	30May1989	cg	38.07	1.16	28
D. Newly Oiled Channels and Lagoons					
Hidden Channel	24May1989	cg	37.06	1.45	50
E. Unoiled Channels and Lagoons					
Largo Remo Channel South	31May1989	cg	45.36	2.17	50
Margarita Channel North	01Jun1989	cg	31.76	1.51	50
Margarita Channel South	02Jun1989	cg	18.00	0.85	48
Samba Bonita Channel West	24May1989	cg	63.54	2.88	50
F. Unoiled Drainage Streams					
Río Alejandro	26May1989	cg	172.54	10.72	50
Hidden River	03Mar1989	sg	130.04	13.20	50
Quebrada Las Mercedes	02Mar1989	sg	93.88	6.84	50
Unnamed River	26May1989	cg	127.96	4.97	50

Coll. = data collector; *cg* = C. Gonzalez, *sg* = S. D. Garrity. Data collected by cg need to be checked.

App. Table E.3 *G*-tests for heterogeneity among sites: fringe structure, May 1991. Meters of shoreline with healthy vs. damaged fringe.

Unoiled Open Coast

	LINM	MSM	PADM	PBM	Total
Damaged/dead	20	10	43	46	119
Not damaged/dead	285	181	238	256	960
Total	305	191	281	302	1,079

G-test: df = 3, $G = 24.75$, $P < .0001$

Oiled Open Coast

	DROM	MINM	PGM	PMM	Total
Damaged/dead	192	48	253	290	783
Not damaged/dead	52	211	74	71	408
Total	244	259	327	361	1,191

G-test: df = 3, $G = 322.17$, $P < .0001$

Unoiled Channels and Lagoons

	LRCS	MACN	MACS	SBCW	Total
Damaged/dead	0	2	1	0	3
Not damaged/dead	183	178	178	176	718
Total	183	180	179	176	718

G-test: df = 3, $G = 4.51$, $P = .212$ (50% of the cells have expected counts <5, test may not be valid)

Oiled Channels and Lagoons

	LRCW	PCE	PCS	SBCE	SBCS	Total
Damaged/dead	133	43	41	280	65	562
Not damaged/dead	138	148	69	20	124	499
Total	271	191	110	300	189	1,061

G-test: df = 4, $G = 352.27$, $P < .0001$

App. Table E.3 *G*-tests for heterogeneity among sites: fringe structure, May 1991 (continued).

Unoiled Drainage Streams

	ALER	HIDR	MERR	UNR	Total
Damaged/dead	42	10	10	0	62
Not damaged/dead	440	297	335	248	1,320
Total	482	307	345	248	1,382

G-test: df = 3, $G = 42.20$, $P < .0001$

Oiled Drainage Streams

	LRRS	PAYR	PMRE	PMRW	Total
Damaged/dead	268	74	149	207	698
Not damaged/dead	32	100	25	63	220
Total	300	174	174	270	918

G-test: df = 3, $G = 133.44$, $P < .0001$

App. Table E.4 Root condition, March-August 1987.

Site	Date (1987)	% Damaged /dead	% Live	*N*
A. Unoiled Open Sites				
María Soto Mangrove (MSM)	May	2	98	50
	August	0	100	20
Portobelo Mangrove (PBM)	May	0	100	50
	August	0	100	20
Isla del Padre Mangrove (PADM)	August	0	100	20
Isla Lintón Mangrove (LINM)	August	5	95	20
B. Oiled Open Sites				
Punta Galeta Mangrove (GALM)	March	35	65	88
	May	32	68	25
	August	65	35	20
Isla Mina Mangrove (MINM)	March	26	74	415
	May	44	68	75
	August	55	45	20
Peña Guapa Mangrove (PGM)	August	45	55	20
Isla Droque Mangrove (DROM)	August	55	45	20
Punta Muerto Mangrove (PMM)	August	60	40	20

App. Table E.4 Root condition, March-August 1987 (continued).

Site	Date (1987)	% Damaged /dead	% Live	*N*
C. Unoiled Channel Sites				
Hidden Channel (HIDC)	March	11	89	191
	May	4	96	50
	August	5	95	20
Samba Bonita Channel West (SBCW)	March	3	97	225
	May	2	98	50
	August	0	100	20
Margarita Channel North (MACN)	August	0	100	20
Margarita Channel South (MACS)	August	0	100	20
D. Oiled Channel Sites				
Peña Guapa Channel (PGC)	March	41	59	249
	May	28	72	50
Largo Remo Channel West (LRCW)	March	34	66	162
	May	32	68	25
Largo Remo Channel CO3 (CO3)	March	36	64	110
Payardí Channel East (PCE)	August	50	50	20
Payardí Channel South (PCS)	August	55	45	20
Samba Bonita Channel East (SBCE)	August	60	40	20
Samba Bonita Channel South (SBCS)	August	60	40	20
E. Unoiled River Sites				
Hidden River (HIDR)	May	0	100	50
	August	10	90	20
Río Coco Solo (CSR)	May	0	100	50
Unnamed River (UNR)	August	0	100	20
Río Alejandro (ALER)	August	0	100	20
Quebrada Las Mercedes (MERR)	August	0	100	20
F. Oiled River Sites				
Largo Remo River South (LRRS)	March	97	3	238
	May	54	46	50
	August	90	10	20
Largo Remo River North (LRRN)	March	98	2	176
	May	58	42	50
Payardí River (PAYR)	August	35	65	20
Punta Muerto River East (PMRE)	August	65	35	20
Punta Muerto River West (PMRW)	August	75	25	20

Data were collected before standardization of methods; March: random sample of roots at study site; May and August: roots sampled in long-term censuses, recorded separately from percent-cover data.

App. Table E.5 *G*-tests for heterogeneity among sites in root condition. Number of live and dead roots in random samples by year and habitat, November 1987-May 1991. Site codes as in Table 9.2.

A. Oiled Open Coast

November 1987-May 1988

	DROM	MINM	PGM	PMM	Total
Dead	14	23	17	19	73
Live	51	42	48	46	187
Total	65	65	65	65	260

G-test: df = 3, *G* = 3.26, *P* = .354

August 1988-May 1989

	DROM	MINM	PGM	PMM	Total
Dead	29	27	28	32	116
Live	51	53	52	48	204
Total	80	80	80	80	320

G-test: df = 3, *G* = 0.75, *P* = .861

August 1989-May 1990

	DROM	GALM	MINM	PGM	PMM	Total
Dead	32	9	21	26	32	120
Live	48	11	59	53	48	219
Total	80	20	80	79	80	339

G-test: df = 4, *G* = 5.52, *P* = .238

August 1990-May 1991

	DROM	GALM	MINM	PGM	PMM	Total
Dead	18	5	16	20	21	80
Live	62	14	64	60	59	259
Total	80	19	80	80	80	339

G-test: df = 4, *G* = 1.12, *P* = .892

App. Table E.5 *G*-tests for heterogeneity among sites in root condition (continued).

B. Unoiled Open Coast

November 1987-May 1988

	LINM	MSM	PADM	PBM	Total
Dead	8	1	3	5	17
Live	57	64	62	60	243
Total	65	65	65	65	260

G-test: df = 3, $G = 7.20$, $P = .066$

August 1988-May 1989

	LINM	MSM	PADM	PBM	Total
Dead	4	2	5	6	17
Live	76	78	75	74	303
Total	80	80	80	80	320

G-test: df = 3, $G = 2.38$, $P = .498$ (50% of the cells have expected counts <5, test may not be valid)

August 1989-May 1990

	LINM	MSM	PADM	PBM	Total
Dead	8	5	9	5	27
Live	72	75	71	75	293
Total	80	80	80	80	320

G-test: df = 3, $G = 2.07$, $P = .558$

August 1990-May 1991

	LINM	MSM	PADM	PBM	Total
Dead	5	1	9	13	28
Live	75	79	71	67	292
Total	80	80	80	80	320

G-test: df = 3, $G = 14.46$, $P = .002$

App. Table E.5 *G*-tests for heterogeneity among sites in root condition (continued).

C. Oiled Channels and Lagoons

November 1987-May 1988

	LRCW	PCE	PCS	SBCE	SBCS	Total
Dead	15	15	21	23	14	88
Live	45	50	44	42	51	232
Total	60	65	65	65	65	320

G-test: df = 4, G = 4.73, P = .317

August 1988-May 1989

	LRCW	PCE	PCS	SBCE	SBCS	Total
Dead	24	25	26	33	26	134
Live	56	55	54	47	54	266
Total	80	80	80	80	80	400

G-test: df = 4, G = 2.79, P = .593

August 1989-May 1990

	LRCW	PCE	PCS	SBCE	SBCS	Total
Dead	30	17	24	24	16	111
Live	50	63	56	56	64	289
Total	80	80	80	80	80	400

G-test: df = 4, G = 8.31, P = .081

August 1990-May 1991

	LRCW	PCE	PCS	SBCE	SBCS	Total
Dead	22	19	18	11	19	89
Live	58	61	62	69	61	311
Total	80	80	80	80	80	400

G-test: df = 4, G = 5.15, P = .272

App. Table E.5 *G*-tests for heterogeneity among sites in root condition (continued).

D. Unoiled Channels and Lagoons

November 1987-May 1988

	HIDC	MACN	MACS	SBCW	Total
Dead	0	1	0	1	2
Live	65	64	65	64	258
Total	65	65	65	65	260

G-test: df = 3, *G* = 2.79, *P* = .425 (50% of the cells have expected counts <5, test may not be valid)

August 1988-May 1989

	LRCS	MACN	MACS	SBCW	Total
Dead	1	2	1	2	6
Live	79	78	79	75	311
Total	80	80	80	77	317

G-test: df = 3, *G* = 0.73, *P* = .865 (50% of the cells have expected counts <5, test may not be valid)

August 1989-May 1990

	LRCS	MACN	MACS	SBCW	Total
Dead	1	5	3	3	12
Live	79	75	77	77	308
Total	80	80	80	80	320

G-test: df = 3, *G* = 3.02, *P* = .389 (50% of the cells have expected counts <5, test may not be valid)

August 1990-May 1991

	LRCS	MACN	MACS	SBCW	Total
Dead	1	4	4	1	10
Live	79	76	76	79	310
Total	80	80	80	80	320

G-test: df = 3, *G* = 3.97, *P* = .265 (50% of the cells have expected counts <5, test may not be valid)

App. Table E.5 *G*-tests for heterogeneity among sites in root condition (continued).

E. Oiled Drainage Streams

November 1987-May 1988

	LRRS	PAYR	PMRE	PMRW	Total
Dead	61	19	37	37	154
Live	4	46	28	28	106
Total	65	65	65	65	260

G-test: df = 3, *G* = 65.21, *P* <.0001

August 1988-May 1989

	LRRS	PAYR	PMRE	PMRW	Total
Dead	61	26	30	45	162
Live	18	53	48	35	154
Total	79	79	78	80	316

G-test: df = 3, *G* = 39.38, *P* <.0001

August 1989-May 1990

	LRRS	PAYR	PMRE	PMRW	Total
Dead	51	30	21	24	126
Live	28	49	59	56	192
Total	79	79	80	80	318

G-test: df = 3, *G* = 29.58, *P* <.0001

August 1990-May 1991

	LRRS	PAYR	PMRE	PMRW	Total
Dead	33	20	20	17	90
Live	47	60	60	63	230
Total	80	80	80	80	320

G-test: df = 3, *G* = 9.10, *P* = .028

App. Table E.5 *G*-tests for heterogeneity among sites in root condition (continued).

F. Unoiled Drainage Streams

November 1987-May 1988

	ALER	HIDR	MERR	UNR	Total
Dead	3	0	1	2	6
Live	62	65	64	63	254
Total	65	65	65	65	260

G-test: df = 3, *G* = 4.58, *P* = .205 (50% of the cells have expected counts <5, test may not be valid)

August 1988-May 1989

	ALER	HIDR	MERR	UNR	Total
Dead	5	5	3	7	20
Live	74	74	75	71	294
Total	79	79	78	78	314

G-test: df = 3, *G* = 1.76, *P* = .625 (25% of the cells have expected counts <5, test may not be valid)

August 1989-May 1990

	ALER	HIDR	MERR	UNR	Total
Dead	3	4	3	1	11
Live	77	76	77	79	309
Total	80	80	80	80	320

G-test: df = 3, *G* = 2.08, *P* = .556 (50% of the cells have expected counts <5, test may not be valid)

August 1990-May 1991

	ALER	HIDR	MERR	UNR	Total
Dead	3	2	1	3	9
Live	77	78	79	74	308
Total	80	80	80	77	317

G-test: df = 3, *G* = 1.46, *P* = .692 (50% of the cells have expected counts <5, test may not be valid)

App. Table E.6 Calculation of the percent of the mangrove fringe remaining. Site codes as in Table 9.2.

A. Open Coast

	MINM	PGM	DROM	PMM	Mean
Expected percent fringe at unoiled sites	98.3	98.3	98.3	98.3	98.3
Observed percent fringe at oiled sites	97.1	80.4	76.6	85.6	85.2
Percent fringe remaining (observed/expected)	99.8	81.8	77.9	87.1	86.7
Expected number of roots/0.25m^2 fringe	3.9	3.9	3.9	3.9	3.9
Observed number of roots/0.25m^2 fringe	3.5	2.9	2.3	3.5	3.1
Percent roots remaining (observed/expected)	89.7	74.4	49.0	89.7	75.7
Percent habitat remaining[1]	89.5	60.9	38.2	78.1	66.7

B. Channels and Lagoons

	SBCE	SBCS	PCE	PCS	LRCW	HIDC	Mean[2]
Expected percent fringe at unoiled sites	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Observed percent fringe at oiled sites	22.4	90.5	93.7	83.6	92.2	100.0	76.5
Percent fringe remaining (observed/exp.)	22.4	90.5	93.7	83.6	92.2	100.0	76.5
Expected number of roots/0.25m^2 fringe	4.6	4.6	4.6	4.6	4.6	4.6	4.6
Observed number of roots/0.25m^2 fringe	3.5	3.6	3.5	3.7	4.3	4.4	3.7
Percent roots remaining (observed/expected)	76.1	78.3	73.9	80.4	93.5	95.7	80.4
Percent habitat remaining[1]	17.1	70.9	69.2	67.2	86.2	95.7	62.1

C. Drainage Streams

	LRRS	PAYR	PMRE	PMRW	Mean
Expected percent fringe at unoiled sites	90.3	90.3	90.3	90.3	90.3
Observed percent fringe at oiled sites	13.3	83.4	16.6	46.6	40.0
Percent fringe remaining (observed/expected)	14.7	92.4	18.4	51.6	44.3
Expected number of roots/0.25m^2 fringe	4.0	4.0	4.0	4.0	4.0
Observed number of roots/0.25m^2 fringe	3.3	3.4	3.4	3.3	3.4
Percent roots remaining (observed/expected)	82.5	85.0	85.0	82.5	83.8
Percent habitat remaining[1]	12.1	78.5	15.6	42.6	37.2

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[1] Calculated as the number of meters of fringe remaining along a 100-m section of shore multiplied by the percent of roots found at an oiled site, e.g., MINM: 99.8 x .897 = 89.5.

[2] Calculated as the mean of SBCE, SBCS, LRCW, PCE, and PCS.

App. Table E.7 Substratum characteristics at each site; qualitative description.

Habitat	Site	Description
Open, oiled	Isla Mina Mangrove	sand, shell fragments, coral rubble, calcareous algal fragments
	Peña Guapa Mangrove	sand, shell fragments, peat, coral rubble, inorganic mud
	Isla Droque Mangrove	sand, shell fragments, coral rubble, peat, calcareous algal fragments
	Punta Muerto Mangrove	sand, rock, organic mud, coral rubble, shell fragments
Open, unoiled	María Soto Mangrove	sand, coral rubble
	Portobelo Mangrove	sand, coral rubble, inorganic mud, rock, peat, shell fragments
	Isla Padre Mangrove	sand, peat, shell fragments, rock
	Isla Lintón Mangrove	sand, shell fragments, coral rubble, peat, calcareous algal fragments, inorganic mud
Channel, oiled	Samba Bonita East	peat, inorganic mud
	Samba Bonita South	organic and inorganic mud, peat
	Payardí Channel East	peat, calcareous algal fragments, inorganic mud
	Payardí Channel South	inorganic mud
	Largo Remo West	peat, organic mud
Channel, unoiled	Margarita Channel South	peat, coral fragments, inorganic mud
	Margarita Channel North	inorganic mud, peat
	Hidden Channel[1]	inorganic mud, peat
	Samba Bonita West	peat, organic mud
	Largo Remo South	peat, organic mud
Streams, oiled	Largo Remo River South	inorganic mud, peat
	Payardí River	thick inorganic mud
	Punta Muerto River East	peat, inorganic mud
	Punta Muerto River West	inorganic mud
Streams, unoiled	Hidden River	fine sediment
	Unnamed River	fine sediment
	Río Alejandro	fine sediments, inorganic mud, peat
	Quebrada Las Mercedes	peat, inorganic mud

Note: these descriptions are from three cores sampled at each site for sediment- hydrocarbon analyses in May 1989. *Inorganic mud* = grey soil, low in dark organic matter; *organic mud* = dark brown soil, highly organic.

[1] Hidden Channel secondarily oiled between May and August 1988.

App. Table E.8 List of foliose algae collected from mangrove roots on the Caribbean coast of Panama.

Chlorophyta

- *Acetabularia calyculus*
- *Acetabularia crenulata*
- *Bryopsis pennata*
- *Caulerpa mexicana*
- *Caulerpa racemosa*
- *Caulerpa racemosa* var. *laetevirens*
- *Caulerpa sertularioides*
- *Caulerpa verticillata*
- *Chaetomorpha brachygona*
- *Chaetomorpha crassa*
- *Chaetomorpha minima*
- *Cladophora* sp.
- *Codium repens*
- *Derbesia* sp.
- *Dictyosphaeria cavernosa*
- *Enteromorpha flexuosa*
- *Halimeda monile*
- *Halimeda opuntia*
- *Microdictyon boergesenii*
- *Neomeris annulata*
- *Penicillus capitatus*
- *Rhizoclonium ?hookeri*
- *Struvea anastomosans*
- *Struvea ramosa*
- *Ventricaria ventricosa*

Phaeophyta

- *Dictyota bartayresii*
- *Dictyota menstrualis*
- *Dictyota pulchella*
- *Ectocarpus breviarticulatus*
- *Padina gymnospora*
- *Sargassum ?hystrix* var. *buxifolium*

Rhodophyta

- *Acanthophora spicifera*
- *Amphiroa beauvoisii*
- *Amphiroa fragilissima*
- *Amphiroa rigida* var. *antillana*
- *Amphiroa ?tribulus*
- *Bostrychia binderi*
- *Bostrychia montagnei*
- *Bostrychia tenella*
- *Caloglossa leprieurii*
- *Catenella repens*
- *Centroceras clavulatum*
- *Ceramium fastigatum*
- *Ceramium rubrum*
- *?Champia parvula*
- *Coelothrix irregularis*
- *Eucheuma* sp.
- *Galaxaura comans*
- *Galaxaura oblongata*
- *Gelidiella acerosa*
- *Gelidium americanum*
- *Gracilaria mammillaris*
- *?Griffithsia* sp.
- *Herposiphonia tenella*
- *Heterosiphonia* sp.
- *Hypnea cervicornis*
- *Jania capillacea*
- *Laurencia obtusa*
- *Laurencia papillosa*
- *Murrayella periclados*
- *Polysiphonia subtilissima*
- *Spyridia hypnoides*
- *Wrangelia argus*

Note: does not include crustose algae.

Appendix F
Seagrass Communities

App. Table F.1 Maximum-likelihood (Wald) tests of significance of fixed effects for biomass of plants from core samples collected at oiled and unoiled sites.

Test	df	Chi-square	*P*
Total seagrass biomass			
Oiling	1	1.53	.2
Time	12	579.23	.000
O x T	12	373.89	.000
Total *Thalassia* biomass			
Oiling	1	6.05	.014
Time	10	50.00	.000
O x T	10	13.88	.2
Total *Syringodium* biomass			
Oiling	1	0.52	.5
Time	10	10.42	.4
O x T	10	24.59	.006
Total subsurface biomass			
Oiling	1	0.00	.9
Time	12	32.37	.001
O x T	12	33.73	.001
***Thalassia* subsurface biomass**			
Oiling	1	5.94	.015
Time	10	41.71	.000
O x T	10	14.93	.1
***Syringodium* subsurface biomass**			
Oiling	1	0.51	.5
Time	10	10.57	.4
O x T	10	28.51	.001
Total blade biomass			
Oiling	1	0.32	.6
Time	12	410.68	.000
O x T	12	26.92	.008
***Thalassia* blade biomass**			
Oiling	1	2.13	.1
Time	10	181.59	.000
O x T	10	8.82	.6
***Syringodium* blade biomass**			
Oiling	1	1.23	.3
Time	10	9.40	.5
O x T	10	11.47	.3
Total algal biomass			
Oiling	1	0.27	.6
Time	11	29.72	.002
O x T	11	16.46	.1
Fleshy algal biomass			
Oiling	1	0.25	.6
Time	11	34.24	.000
O x T	11	17.38	.09

App. Table F.1 Maximum-likelihood (Wald) tests of significance of fixed effects for biomass of plants from core samples collected at oiled and unoiled sites (continued).

Test	df	Chi-square	*P*
Calcareous algal biomass			
Oiling	1	0.26	.6
Time	11	28.07	.003
O x T	11	20.02	.045

App. Table F.2 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of major taxonomic groups sorted from core samples collected at oiled and unoiled sites. Analyses were for January data only (1987, 1988, and 1989); see text for details.

Test	df	Chi-square	*P*
Total count except polychaetes			
Oiling	1	2.01	.2
Time	2	2.23	.3
O x T	2	51.62	.000
Brachyura			
Oiling	1	0.65	.4
Time	2	6.85	.033
O x T	2	2.76	.3
Cumacea			
Oiling	1	7.01	.008
Time	2	38.73	.000
O x T	2	76.42	.000
Echinoidea			
Oiling	1	0.73	.4
Time	2	5.08	.08
O x T	2	1.36	.5
Gastropoda			
Oiling	1	7.63	.006
Time	2	10.01	.007
O x T	2	11.55	.003
Amphipoda			
Oiling	1	5.85	.016
Time	2	2.96	.2
O x T	2	48.91	.000
Bivalvia			
Oiling	1	12.93	.000
Time	2	11.21	.004
O x T	2	1.85	.4

App. Table F.2 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of major taxonomic groups sorted from core samples collected at oiled and unoiled sites (continued).

Test	df	Chi-square	*P*
Hermit crabs			
Oiling	1	1.05	.3
Time	2	8.88	.012
O x T	2	0.17	.9
Isopoda			
Oiling	1	0.75	.4
Time	2	5.09	.09
O x T	2	6.56	.038
Mysids			
Oiling	1	0.11	.7
Time	2	12.37	.002
O x T	2	8.48	.014
Ophiuroidea			
Oiling	1	16.83	.000
Time	2	15.98	.000
O x T	2	11.06	.004
Burrowing shrimp			
Oiling	1	0.85	.4
Time	2	17.58	.000
O x T	2	7.90	.019
Sipunculida			
Oiling	1	0.07	.8
Time	2	12.79	.002
O x T	2	12.95	.002
Tanaidacea			
Oiling	1	32.14	.000
Time	2	46.53	.000
O x T	2	100.02	.000

App. Table F.3 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of major taxonomic groups sorted from push-net samples collected at oiled and unoiled sites.

Test	df	Chi-square	*P*
Total Pushnet Counts			
Oiling	1	10.32	.001
Time	6	55,956.61	.000
O x T	6	4,225.40	.000

App. Table F.3 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of major taxonomic groups sorted from push-net samples collected at oiled and unoiled sites (continued).

Test	df	Chi-square	*P*
Amphipoda			
Oiling	1	21.11	.000
Time	6	1,228.25	.000
O x T	6	111.74	.000
Brachyura			
Oiling	1	0.01	.9
Time	6	269.32	.000
O x T	6	5.34	.5
Fish			
Oiling	1	23.97	.000
Time	6	172.73	.000
O x T	6	63.35	.000
Gastropoda			
Oiling	1	3.38	.066
Time	6	663.23	.000
O x T	6	26.86	.000
Hermit crabs			
Oiling	1	4.60	.032
Time	6	4,279.19	.000
O x T	6	1,348.96	.000
Isopoda			
Oiling	1	2.52	.1
Time	6	107.76	.000
O x T	6	5.73	.5
Mysids			
Oiling	1	11.76	.001
Time	6	8.79	.2
O x T	6	8.75	.2
Ophiuroidea			
Oiling	1	4.13	.042
Time	6	32.34	.000
O x T	6	14.60	.024
Shrimp			
Oiling	1	6.76	.009
Time	6	5,068.28	.000
O x T	6	124.00	.000
Tanaidacea			
Oiling	1	23.71	.000
Time	6	87.17	.000
O x T	6	55.68	.000

App. Table F.4 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of shrimp species sorted from push-net samples collected at oiled and unoiled sites.

Test	df	Chi-square	*P*
Hippolyte zostericola			
Oiling	1	3.14	.08
Time	6	1,931.94	.000
O x T	6	15.91	.014
Latreutes fucorum			
Oiling	1	4.88	.027
Time	6	57.67	.000
O x T	6	240.79	.000
Latreutes parvulus			
Oiling	1	1.02	.3
Time	6	2,594.10	.000
O x T	6	69.98	.000
Leander tenuicornis			
Oiling	1	1.31	.3
Time	6	10,808.78	.000
O x T	6	249.19	.000
Metapenaeopsis martinelli			
Oiling	1	1.99	.2
Time	6	33.92	.000
O x T	6	37.93	.000
Palaemonetes northropi			
Oiling	1	1.55	.2
Time	6	7,343.84	.000
O x T	6	723.34	.000
Penaeus duorarum			
Oiling	1	0.52	.5
Time	6	138.07	.000
O x T	6	83.06	.000
Periclimenes americanus			
Oiling	1	19.23	.000
Time	6	25,377.76	.000
O x T	6	941.50	.000
Periclimenes longicaudatus			
Oiling	1	1.64	.2
Time	6	36.04	.000
O x T	6	20.90	.002
Processa fimbriata			
Oiling	1	3.69	.055
Time	6	33,705.32	.000
O x T	6	62,933.25	.000
Sicyonia laevigata			
Oiling	1	0.24	.6
Time	6	278.86	.000
O x T	6	76.22	.000

App. Table F.4 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of shrimp species sorted from push-net samples collected at oiled and unoiled sites (continued).

Test	df	Chi-square	P
Thor manningi			
Oiling	1	46.85	.000
Time	6	853.14	.000
O x T	6	550.24	.000
Trachycaris restrictus			
Oiling	1	1.27	.3
Time	6	26.00	.000
O x T	6	27.63	.000

App. Table F.5 Maximum-likelihood (Wald) tests of significance of fixed effects for counts of three brooding types sorted from push-net samples collected at oiled and unoiled sites.

Test	df	Chi-square	*P*
A. Total brooders			
Oiling	1	5.47	.019
Time	6	136.76	.000
O x T	6	12.49	.052
B. Brood to zoea			
Oiling	1	3.50	.061
Time	6	6,457.56	.000
O x T	6	52.82	.000
C. Pelagic larvae (= spawners)			
Oiling	1	0.16	.7
Time	6	807.69	.000
O x T	6	176.18	.000

App. Table F.6 Maximum-likelihood (Wald) tests of significance of fixed effects for frequencies of recruits and reproductive stages of two shrimp species.

Test	df	Chi-square	*P*
Hippolyte zostericola			
A. Recruits			
Oiling	1	0.04	.8
Time	5	359.16	.000
O x T	5	597.76	.000
B. Ovigerous females			
Oiling	1	3.21	.07
Time	5	785.44	.000
O x T	5	131.86	.000
C. Ovigerous females with full ovaries			
Oiling	1	0.46	.5
Time	5	1,270.42	.000
O x T	5	65.56	.000
D. Percent brooding females with undifferentiated eggs attached to pleopods			
Oiling	1	2.93	.09
Time	5	64.21	.000
O x T	5	22.14	.000
Latreutes fucorum			
A. Recruits			
Oiling	1	7.23	.007
Time	5	693.80	.000
O x T	5	2,081.49	.000
B. Ovigerous females			
Oiling	1	0.13	.7
Time	5	13.94	.016
O x T	5	6.85	.3
C. Ovigerous females with full ovaries			
Oiling	1	0.72	.4
Time	5	140.28	.000
O x T	5	2.22	.8
D. Percent brooding females with undifferentiated eggs attached to pleopods			
Oiling	1	1.48	.2
Time	5	11.60	.041
O x T	5	46.31	.000

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