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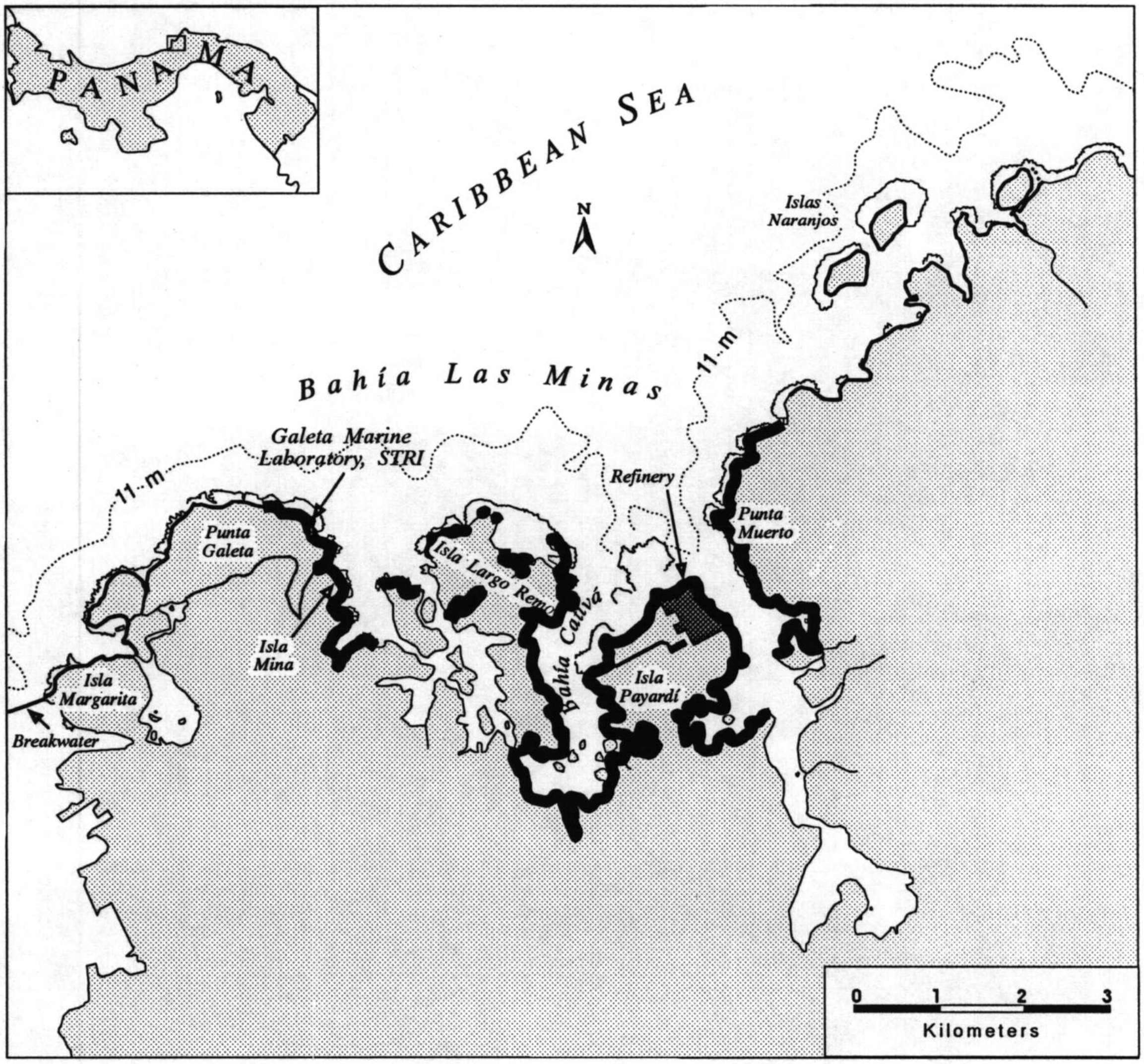
Long-term Assessment of the Oil Spill at Bahía Las Minas, Panama Synthesis Report

Volume I: Executive Summary



U.S. Department of the Interior
Minerals Management Service
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Long-term Assessment of the Oil Spill at Bahía Las Minas, Panama Synthesis Report

Volume I: Executive Summary

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Introduction

Unplanned Environmental Assessments

Environmental assessments ideally consist of monitoring natural variation or of studying *planned* environmental modifications, such as the release of heated effluents from a power plant, and their effects. In both cases the kinds of ecological data to collect, degree of replication, frequency of sampling, and so on can be carefully designed. In contrast, unplanned environmental modifications, such as those caused by major oil spills, generally cannot be studied using optimal designs because pre-existing monitoring data are not available as balanced sampling at both affected and unaffected areas. In such cases all that can be done in designing an assessment is to make the best use of available data.

Even optimally designed environmental assessments lack the rigor of controlled experiments, and conclusions about cause and effect must consider factors other than the presumed one. For example, in comparing areas affected and unaffected by an oil spill, there may be additional area-specific differences not related to the spill that explain some of the observations. Because effects of major oil spills on benthic communities can be severe, studies employing suboptimal designs may detect postspill changes, as was the case after a major oil spill at Bahía Las Minas, Panama.

Objectives of the Study and Organization of the Report

The study has two main objectives:

1. to monitor the long-term changes that may occur in the distribution and abundance of marine organisms as a result of the 1986 oil spill at Bahía Las Minas, and

2. to understand the ecological processes causing any observed changes.

This summary is organized into sections about the spread and stranding of oil under different sets of environmental conditions, the concentration and characterization of the spilled oil in environmental and organismal samples, and effects of the spill on particular populations and communities.

Here, following a brief review of oil spills in tropical seas, we describe the Bahía Las Minas ecosystem and the 1986 oil spill, and relate its size to that of other major oil spills. The region of the spill has a history of development and industrialization, and was polluted by a major tanker spill of diesel oil and Bunker C in 1968. After reviewing this background, we briefly describe relevant biological studies that were conducted prior to the 1986 spill, and review how existing information was incorporated into the design of each element of the study. A listing and map of all study sites is provided in Volume II.

Oil Spills in Tropical Seas

At least 157 major oil spills, defined as more than 1,000 bbl, originated from ships and barges in the tropics between 1974 and 15 June 1990. Of these, 99 occurred in coastal or restricted waters, mostly near such potentially vulnerable ecosystems as coral reefs, seagrass beds, reef flats, sand beaches, and mangrove forests. There were 24 tanker or barge spills near Caribbean coastlines, as well as spills from other sources. At least 19 refineries ring the Caribbean. A pipeline for transshipment of crude oil crosses Panama, and there are facilities in Bonaire, Curaçao (closed in 1985), the Bahamas, and Grand Cayman for transfer of crude oil from supertankers to smaller tankers. Spills occurred recently at the Caribbean end of the pipeline across Panama and at two of the refineries, including the 1986 spill in Panama.

Despite the frequency of spills, there has been very little study of effects of oiling on nearshore tropical communities. There is general agreement on the biological and economic value of mangroves forests and on the vulnerability of mangroves and their biota to oiling. Similarly, reef flats are known to be highly productive, to serve as nursery and foraging areas for spiny lobsters, and to be vulnerable to oiling. However, knowledge of effects of oil on mangroves and associated species is limited, and reef flats have been neglected. Most studies of mangroves have been one-time efforts following spills of opportunity, and thus lack baseline, prespill data and seldom include long-term postspill monitoring.

In contrast to intertidal habitats, the vulnerability of subtidal coral reefs and seagrass beds to oil spills has been much more controversial, despite a general paucity of data.

The Bahía Las Minas Ecosystem

The pattern, magnitude, and persistence of effects of the 1986 Bahía Las Minas oil spill can only be understood in the context of the special characteristics of tropical embayments. Bahía Las Minas (Fig. 1) is a topographically complex, shallow-water, embayment whose margins were dominated at the time of the spill by extensive mangrove forests, seagrass beds, and coral reefs. These habitats characterize Caribbean shores and many other regions of the tropics worldwide. In almost every case, the physical structure of these environments is built, stabilized, and maintained by a few species of relatively large, long-lived, photosynthetic organisms. Together they buffer the coastal zone from freshwater runoff and erosion from the land, and wave energy from the open sea.

Mangroves, seagrasses, corals, and coralline algae produce enormous quantities of biogenic structural materials (wood, rhizomes, and limestone) whose very presence baffles water movements and promotes the deposition of sediments. The red mangrove *Rhizophora mangle* forms dense, anastomosing thickets of prop roots and trunks that extend outward from land. Mangroves protect the shore from the impacts of debris such as floating logs and waves, reduce water circulation,

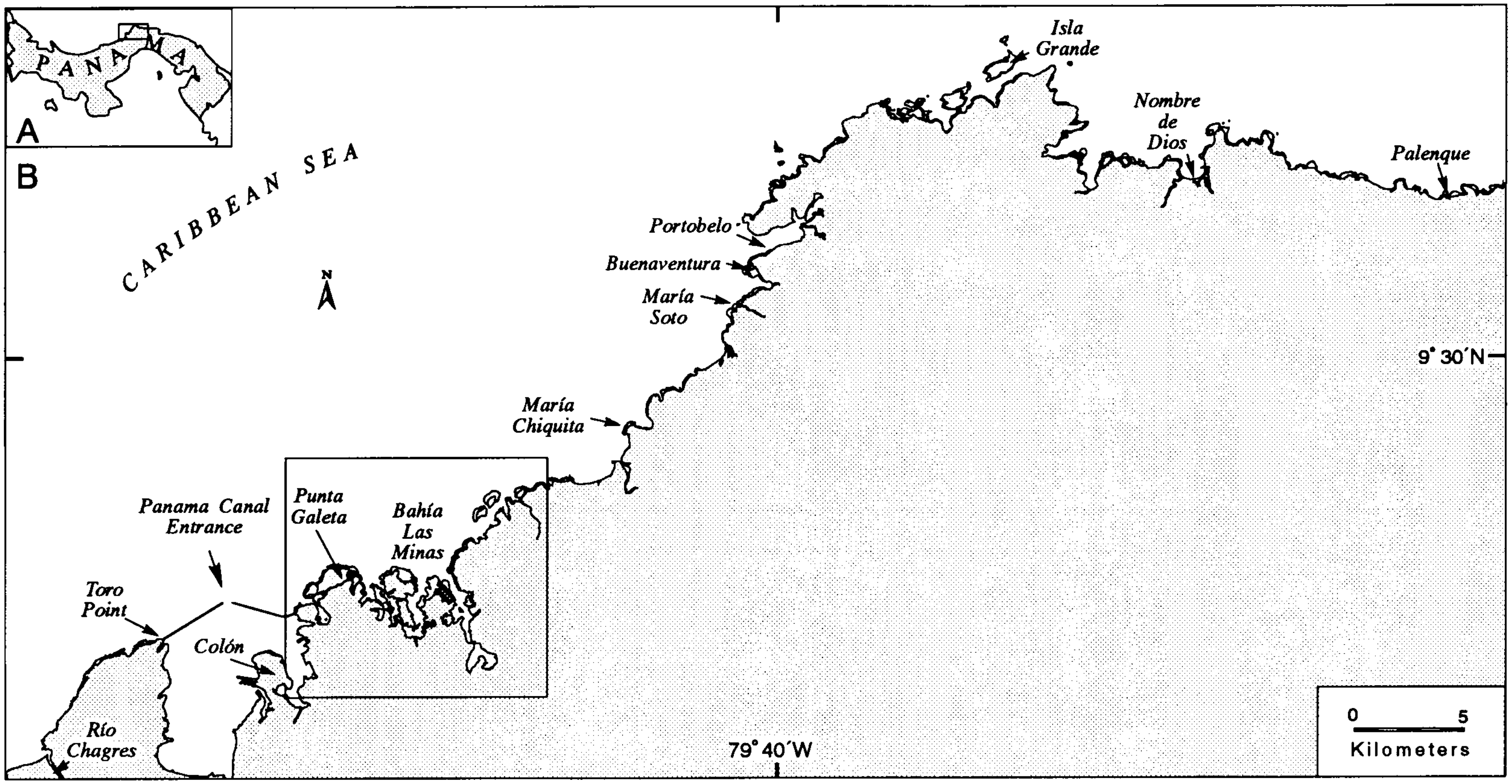

Fig. 1 Region of Panama affected by the 1986 oil spill. *A*. Republic of Panama, showing the study region (*boxed area*, see *B*) on the Caribbean coast. *B*. Study region, showing the area of the most heavily oiled coastal habitats in and near Bahía Las Minas (*Boxed area*, see *C*).

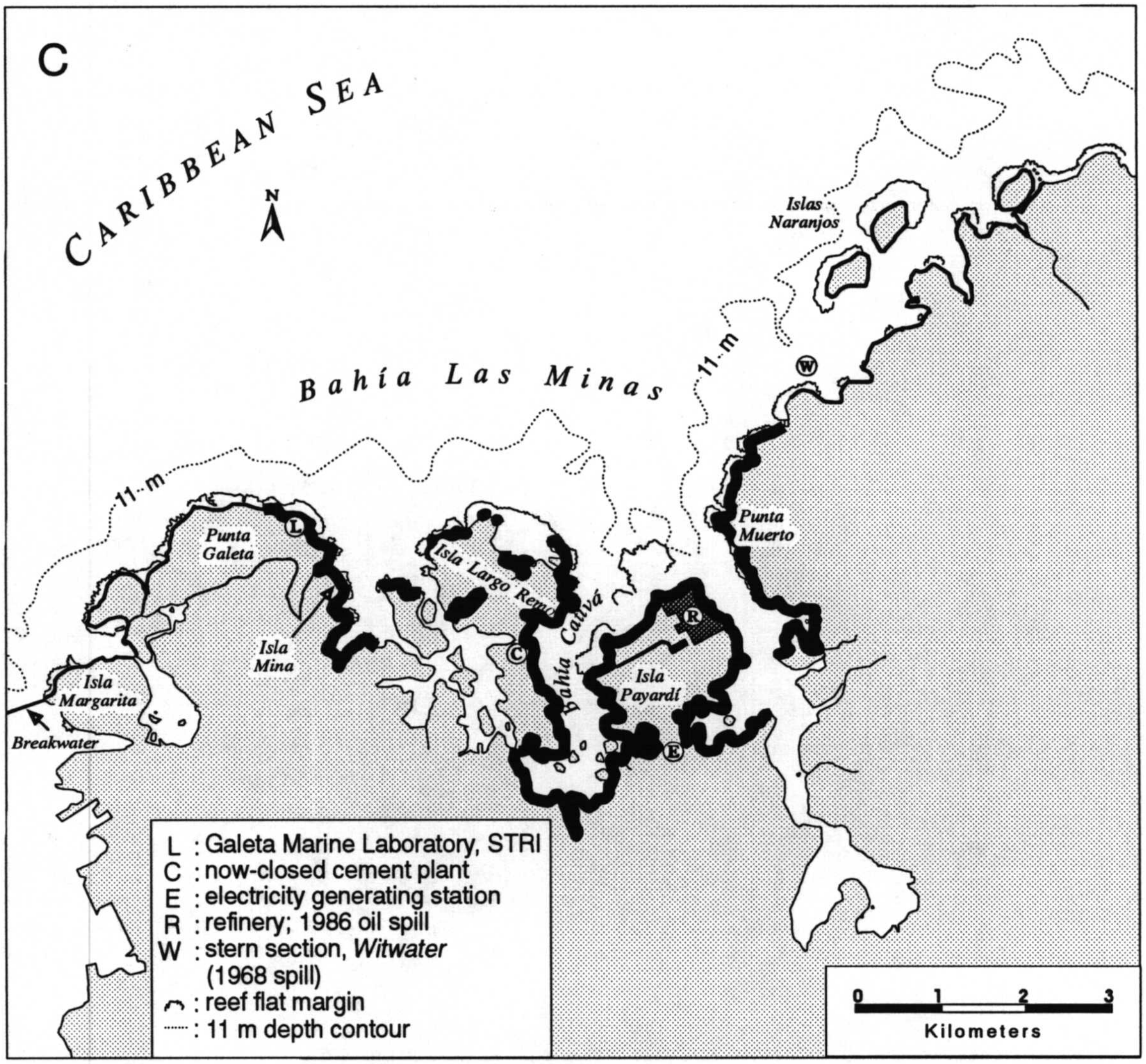

Fig. 1 **Region of Panama affected by the 1986 oil spill (continued).** ***C.*** **Map of Bahía Las Minas depicting the approximate distribution of heaviest oiling (*heavy line*) and moderate oiling (*medium line*). Oiling was not observed in the embayments east of Isla Margarita, southwest of Isla Largo Remo, and southeast of Isla Payardí.**

increase sedimentation, and provide deep shade and shelter at all but the most open coastal margins. Seagrasses, especially turtlegrass (*Thalassia testudinum*), form dense beds that may extend for hectares seaward of the mangrove fringe, depending on the local bottom profile, size of the embayment, and degree of protection by coral reefs. Seagrass beds are supported by dense root and rhizome mats up to half-a-meter thick that stabilize sediments against erosion. In addition, long seagrass leaves slow water movements and increase sedimentation. 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. The physical complexity of reefs depends on the growth form of dominant coral species; branching corals form dense thickets whereas massive species form a more open framework. Regardless, 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 provide habitat for a great diversity of species that depend largely or entirely on biogenic characteristics of the habitat, much like the animals and herbaceous vegetation of a deep forest. Moreover, many of these organisms 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. The principal groups of associated consumers and other organisms studied in this report are listed in Table 1.

Nearly all the oiled study sites and many of the unoiled mangrove sites were in Bahía Las Minas. However, many unoiled sites were northeast of this embayment in a region referred to here as the *Costa Arriba*, from María Chiquita to Isla Grande (Fig. 1). These included unoiled open-coast mangroves, reef flats (plus one site west of the bay), seagrass beds, and coral reefs. Environmental conditions and other factors differ between the two areas. Implications of these differences to findings of the study are discussed in later sections.

The 1986 Oil Spill at Bahía Las Minas, Panama

In 1986 a major oil spill polluted Caribbean coastal environments of Panama, including a biological preserve at a marine laboratory of the Smithsonian Tropical Research Institute (STRI). For the reef flat at this site, baseline biological and environmental data for some parameters had been collected for more than 15 yr. There had also been surveys and short-term studies of reef flat gastropods, reef flat stomatopod crustaceans, coral reefs, mangroves, the epibiota of fringing mangrove roots, and seagrass communities. These prespill studies provided a relatively comprehensive background for assessing biological effects of the spill. Furthermore, observations of effects of the spill began as oil was washing ashore. Such promptness is important because many ecological changes start immediately after such acute pollution, and direct observations of immediate postspill die offs may be important.

The oil spill occurred on 27 April 1986 at a petroleum refinery at Bahía Las Minas, Panama (Fig. 1). Approximately 38.3 million L (240,000 bbl) of medium-weight crude oil drained from a ruptured storage tank. The oil was 70% Venezuelan and 30% Mexican Isthmian, with a specific gravity of 27° at 15.6°C (American Petroleum Institute) or about 0.89 g/cc. Approximately 22.3 million L (140,000 bbl) flooded through the containment dike around the storage tank and overwhelmed separators and a retaining lagoon. In May 1986 a refinery official reported recovery of 9.6 million L (60,000 bbl) of oil from the sea. We do not know, however, how

Table 1 Principal habitat-structuring organisms and associated consumers and other organisms studied, in order of their presentation in the report.

Habitat-structuring Organisms	Associated Consumers and Other Organisms
Crustose coralline and fleshy macroalgae on reef flats	Sea urchins, stomatopods, snails, and infauna of *Laurencia* turf
Reef corals and associated sessile biota	Fishes and sea urchins
Red mangroves	Epibionts on prop roots, grapsid crabs
Seagrasses	Infaunal and epifaunal invertebrates, fish, and algae

much oil was *not* recovered and can only surmise that the volume of oil that spilled into the sea from the grounds of the refinery was at least 9.6-16.0 million L (60,000-100,000 bbl).

The volume of this spill was greater than that of any other oil spill reported near coral reefs and mangroves in the tropical Americas, such as the 1975 *Epic Colocotronis* and 1978 *Peck Slip* spills at Puerto Rico. Compared with recent major spills from oil tankers in other tropical areas, however, the Bahía Las Minas spill was moderate in size (among the top 20% by volume). Considering some other well-studied oil spills, the Bahía Las Minas spill was much larger than the 1969 spill from the barge *Florida* near Woods Hole, Massachusetts, similar in size to the 1969 Santa Barbara spill, and much smaller than the spills from the tankers *Torrey Canyon* (1967), *Amoco Cadiz* (1978), and *Exxon Valdez* (1989).

During the first six days after the spill onshore winds held the spilled oil in Bahía Cativá, adjacent to the refinery (Fig. 1). Shifting winds and runoff from rains then pushed a large quantity of oil out to sea past a boom placed across the mouth of this embayment. Starting 6 May 1986, aircraft sprayed approximately 21,000 L of the dispersant Corexit 9527 (Exxon Chemicals) over oil slicks. A C-130 aircraft was observed spraying dispersant from a very low altitude (at or under tree level) at the mouth of Bahía Cativá, including areas near the coastlines of western Isla Largo Remo, northwestern Isla Payardí, and Punta Muerto. It was reported that more than 11,000 L of dispersant were used in this spraying alone. In addition, a small crop-duster aircraft was observed spraying dispersant on slicks between Islas Naranjos and the mainland. Other such applications of dispersant were observed off the breakwater of the Panama Canal, offshore of Bahía Las Minas, and offshore of Portobelo (Fig. 1). Additional back-pack spraying of dispersant was used in some areas of mangroves.

No dispersant was sprayed near Punta Galeta. Application of the dispersant nine days after the spill instead of within the first 24 hours, as well as calm sea conditions, probably rendered chemical dispersion ineffective. Although some coastal areas were exposed to dispersant, particularly Bahía Cativá and areas near Islas Naranjos, many oiled areas, including Punta Galeta, were not directly exposed to this compound. The overall dosage of dispersant was low based on a 1:20 dispersant:oil ratio from laboratory studies. Such a ratio would have required a total of 480,000-800,000 L of dispersant, an order of magnitude greater than the estimated total used. Localized effects of the dispersant may have occurred, particularly at sites between Isla Largo Remo and Punta Muerto, and in Bahía Cativá. However, the limited use of dispersant cannot explain the widespread subtidal biological effects reported later in this report.

By 15 May oil had spread along the coast and washed across fringing reefs into mangroves, small estuaries, and sand beaches within 10 km of the refinery. During the first two months after the spill, the distribution of oil was surveyed from low-flying aircraft between Río Chagres, 27 km west of the refinery (Fig. 1), and Punta San Blas, 98 km to the east. Surveys by helicopter, airplane, foot, and boat were conducted from Río Chagres to Nombre de Dios. During these surveys visual assessments were made of the degree of oiling (heavy, moderate, light, or absent) and of the habitats and types of organisms obviously oiled or affected by oiling.

The shoreline deposition of extensive, black oil slicks was limited to the coast between Isla Margarita and María Chiquita with the exception of two partially isolated lagoons in Bahía Las Minas (Fig. 1; the lagoons east of Isla Margarita and southwest of Isla Largo Remo). The length of heavily oiled coastline was approximately 82 km (straight-line distance = 11 km) and included more than 1,000 ha of mangroves and extensive intertidal reef flats and subtidal reefs. Only a few patches of oil were observed to strand east of María Chiquita and west of the entrance to the Panama Canal. However, oily sheens were observed offshore from Isla Margarita to Nombre de Dios. Approximately one month after the spill, oily sheen was observed offshore of Punta San Blas. The offshore slicks appeared to be transported by the easterly coastal current, aided by an unusual period of southerly winds. Instances of strandings of black slicks occurred northeast of Portobelo where generally prevailing northeasterly winds were likely to deposit slicks coming from far offshore.

In similar habitats within the heavily polluted area apparent degrees of oiling were highly variable. Probable causes of this heterogeneity included distance from the refinery, directions of movement of the spilled oil, and water depth. The greatest amounts of oil in mangroves, reef flats, and seagrass beds occurred within a few kilometers of the refinery. There was obviously less oil in these habitats at Islas Naranjos and Isla Margarita (Fig. 1). Large differences in visible oiling also occurred on a much smaller scale of a few hundred meters, depending on coastal orientation. Much of the oil escaping from Bahía Cativá spread to the west. Accordingly, coasts that faced north to northeast were much more heavily oiled than coasts that faced west or south. Furthermore, seasonal low tides occurred between 10 and 19 May 1986, causing oil to accumulate along the seaward margins of reef flats. As a result, visible oiling was heaviest in intertidal habitats just above mean low water, such as mangrove roots and associated sediments, reef flat seagrass beds, coral rock, and beaches.

Chemical analyses of petroleum hydrocarbons in surface sediments generally verified these visual assessments of variability in degrees of oiling (Burns, Chap. 3). Samples collected five months after the spill contained concentrations of oil as high as 372,856 μg oil/g sediment and as low as 1,830 μg/g in heavily oiled mangrove surface sediments. Subtidally, surface sediments from heavily oiled seagrass beds ranged from 97 to 24,555 μg/g, and 19 to 715 μg/g at heavily oiled coral reefs. There was considerable variability in concentrations of oil among samples at a given site, confirming observations of small-scale patchiness as well.

Several different procedures were used to clean up the spilled oil. Some oil was removed from the sea using "skimmers" and shore-based pump trucks. As noted above, approximately 9.6 million L (60,000 bbl) of oil were recovered. Channels were dug through mangroves, apparently to drain oil from these areas. However, these channels appeared to increase the movement of oil beyond the seaward mangrove fringe to inner areas, as well. Disturbance from workers crushed windrows and may have increased subsequent erosion. In other areas oiled rocks, rubble, and debris were physically removed and seawater was sprayed onto sandy areas. Skimming and pumping floating oil appeared to be effective ways to recover oil from this kind of shallow-water spill. Shallow water and mangroves impeded many of the kinds of cleanup operations deployed after major oil spills, perhaps for the better, because some of these procedures can be environmentally or biologically destructive.

During the five years since the spill oil slicks have been regularly observed above coral reefs at Bahía Las Minas and along the mangrove fringe. The appearance of these slicks ranged from metallic sheens to brown patches. Slicks appeared to originate mainly from fringing mangroves, where much of the spilled oil washed ashore. As dead mangrove trees (*Rhizophora mangle*) decayed, the wooden physical structure disappeared, followed by erosion of oiled sediments. *Rhizophora* seedlings (survivors, recruits, and planted individuals) apparently have not prevented this erosion. Some slicks also appeared to come from oiled landfill beneath the refinery.

Other Human Disturbances in the Study Area

Coastal Development

Much of the study area has a long history of exposure to various kinds and degrees of human disturbance and pollution. More than a century ago construction of the Panama Canal and the city of Colón started, followed by decades of excavation, dredging, land filling, and erosion. Swamps were drained and sprayed for control of mosquitoes starting early this century.

On the mainland there has been extensive deforestation for more than 30 years, resulting in increased erosion, increasing siltation stress over the last 15 years, and heavy deposition of sediments on coral reefs.

Petroleum Refinery and Other Industrialization

During construction of a petroleum refinery at Bahía Las Minas (started in 1956), more than 4 million m^3 of fossil and living coral reef were excavated for landfill from areas totaling more than 15 ha. The refinery started operating in 1961. Other industrialization at Bahía Las Minas includes an electricity generating station and a now-closed cement plant (Fig. 1). The cement plant operated from 1967 until 1975, and its small port facility is still in use.

1968 Tanker Witwater *Spill*

In 1968 the breakup of the tanker *Witwater* (Fig. 1) caused a spill of approximately 3.2 million L (20,000 bbl) of diesel oil and Bunker C at Bahía Las Minas. Observations of ecological effects of the spill were mostly qualitative or *ex post facto* because the Galeta Marine Laboratory was just being established.

Oil Spills Since the 1986 Refinery Spill

Since the 1986 refinery spill a few small oil spills have occurred in the study area. These included a small diesel spill near the Toro Point control site of the reef flat gastropod study in May 1988, and fuel-oil spills in December 1988 and June 1990 from the electricity generating station at the mainland connection of Isla Payardí (Fig. 1). The June 1990 spill was followed by the death of some mangrove seedlings and an increased frequency of coral injuries.

Also, occasional small spills occur at the port facility of the refinery, and some oil slicks and tar balls have washed ashore from offshore shipping. Chemical analyses enable most of these sources of oil contamination to be differentiated. We have no information about the frequency or volume of such small spills before this study began.

Biological Studies Prior to the 1986 Oil Spill

Punta Galeta Reef Flat

Measurements of percent cover of plants and sessile invertebrates and counts of sea urchins constituted the longest-term biological baseline data available in the region. Monitoring of some parameters started as early as 1970, 16 yr prior to the spill. These data documented natural variability of populations in this habitat and allowed analyses of postspill changes through time and across space at Punta Galeta. No other sites were monitored prior to the spill.

1985 Coral Reef Survey

During 1985, the year before the spill, coral reefs were surveyed along the central Caribbean coast of Panama. Two of these reefs were in the region of the oil spill and provided the basis for a prespill-postspill comparison of percent cover for one reef that was heavily oiled and one reef that was moderately oiled. In addition, four of the surveyed reefs east of Bahía Las Minas were unoiled, thereby providing a form of control in evaluating effects of the spill. These data and those used for retrospective analyses approximated an "optimal sampling design" for assessing effects of the spill, with data soon before and after the spill and at oiled and unoiled areas.

1979-1983 Reef Flat Stomatopod Studies

The population biology, ecology, and behavior of stomatopod crustaceans had been investigated for 5 yr at a number of reef flat sites near Punta Galeta. These studies provided background data for examining populations after the oil spill, using two previously studied sites that were heavily oiled by the spill and two previously studied sites that were unoiled or lightly oiled. For some parameters and sites, prespill-postspill comparisons could be made.

Surveys of Epibiota of Mangrove Roots and Reef Flat Gastropods

In 1981 and 1982 surveys of epibiota attached to mangrove prop roots were conducted in three habitats: open coast, channel and lagoon, and drainage stream. Also, the gastropods at a reef flat near Punta Galeta were surveyed during 1982-1983. These surveys provided data about community composition and population density prior to the spill that could be used in prespill-postspill comparisons.

Other Studies

Since 1968, ecological and biological investigations in the region of the 1986 oil spill have resulted in more than 130 publications. Detailed long-term data on hydrographic and meteorological conditions at Punta Galeta were also collected. Such extensive prespill information is rarely available in studies of the effects of oil spills.

Retrospective Analyses

Two additional approaches were employed to obtain prespill data: analyses of growth bands in coral skeletons and of aerial photographs of mangrove forests. Both approaches add to our understanding of the history of the region and any biotic changes prior to the spill, and allow an examination of effects of the 1968 *Witwater* spill, which was never studied extensively.

Incorporation of Available Studies in Sampling Designs

Subtidal Reef Corals

A survey of six reefs the year prior to the spill enabled an analysis of coral cover before and after the spill at oiled and unoiled reefs. Because only one reef was heavily oiled and only one moderately oiled, five additional heavily oiled reefs and one additional moderately oiled reef were included in postspill surveys. Because of this imbalance, some statistical analyses and the design of some postspill coral studies employed a balanced subset of sites, i.e., four oiled and four unoiled. As a result of this "hybrid" design certain statistical analyses employed the six reefs surveyed both before and after the spill, others employed the 12 reefs surveyed postspill (which included the six reefs in the prespill survey), and a final type of analyses used a balanced subset of the 12 reefs. A "before and after, oiled and unoiled" design also applied to analyses of coral growth using sclerochronology.

Reef Flat Sessile Biota, Algal-turf Infauna, and Sea Urchins

Monitoring of reef flat sessile biota and sea urchins started as long ago as 1970 at Punta Galeta. After the 1986 spill three additional sites were established, one oiled and two unoiled, and monitoring of sessile biota and sea urchins focused on the reef-edge zone, where oiling was heaviest. Monitoring of infauna of algal turf was initiated postspill at all four sites. This study also was a "hybrid" design, with long-term, prespill-postspill analyses of sessile biota and sea urchins conducted for Punta Galeta and postspill analyses of all three data sets for all four sites. Because of the long-term, detailed biological and physical data across zones of the Punta Galeta reef flat and the spatial pattern of oiling of this habitat, the primary kind of data analysis for effects of the spill compared zones at this site at particular surveys.

Mangrove Forests

Monitoring of mangrove forests did not start until 3 yr after the oil spill, and the design of this study followed the design of the ongoing study of the mangrove fringe and epibiota of mangrove roots. Despite the lack of prespill monitoring, aerial photography of the region enabled an analysis of general patterns of vegetation before and after both the 1968 *Witwater* spill and the 1986 refinery spill, a "before and after, oiled and unoiled" design.

Reef Flat Stomatopods

Four of the reef flats studied from 1979-1983 were used in postspill monitoring; two were heavily oiled and two were lightly oiled to unoiled. Because of a recruitment failure not previously observed, two unoiled sites outside of Bahía Las Minas were added to the study a few years after the spill to document the spatial scale of the stomatopod recruitment failure. Data analyses also were "hybrid" because not all types of data had been collected at all sites prior to the spill and two sites were added postspill.

Mangrove Fringe and Epibiota of Mangrove Roots

Five sites surveyed in 1981 and 1982 were initially retained in postspill sampling; one of these sites was unoiled soon after the spill but became oiled 2 yr afterward, and monitoring of another site ended a year after the spill. To achieve adequate replication of oiled and unoiled conditions in the three habitats, additional sites were incorporated in the design of postspill monitoring. A year after the spill some new sites were selected to increase distance between them, sample the oiled area more representatively, and avoid pseudoreplication within areas. Data on long-term community composition were not compared statistically prespill and postspill due to a 4-yr gap in sampling and slightly different sampling methods. Collection of additional kinds of data was initiated postspill, and statistical analyses of all data sets compared oiled and unoiled sites postspill.

Reef Flat Gastropods

Reef flat gastropods were surveyed at one site during 1982-1983 that was oiled in 1986. Postspill monitoring was conducted at this site and two unoiled sites (certain intertidal zones at each one) that were selected after the spill. Statistical analyses were not conducted because of the 4-yr gap in pre- and postspill sampling at the oiled site (which invalidated the assumption of approximately equal sampling intervals in repeated-measures ANOVA) and oiling of one of the unoiled sites 2 yr after the spill.

Subtidal Seagrass Communities

All monitoring of seagrass beds was initiated after the spill and statistical analyses were comparisons of oiled and unoiled sites through time.

Hydrocarbon Chemistry

The first postspill collection of samples for chemical analysis was made at some of the sites that had been established for biological studies. Additional sites were sampled to obtain a broader coverage. Subsequent collections were all made at biological study sites.

Weather, Sea Conditions, and Topography Affecting Oil Deposition During the 1986 Bahía Las Minas Oil Spill

Introduction

When oil first washed into the long-term ecological research site of the Smithsonian's Galeta Marine Laboratory, it became the most scrutinized oil spill in the tropics. From daily observations at this site it was apparent that spatial patterns of oil deposition were largely governed by weather and sea conditions, which in turn may determine spatial patterns of biological damage in nearby mangrove forests, reef flats, and other intertidal and subtidal habitats.

Case studies are regularly used to estimate effects of future oil spills. As a measure of such potential effects, results of the study of the Bahía Las Minas spill must be qualified by the range of weather and sea conditions that could be expected over the whole year. To put the spill into a broader context, physical processes that determined the pattern of oiling should be taken into account (see Cubit and Levings, Chap. 2, Vol. II).

Biological Communities and Physical Structure of the Coastline

The oil spill occurred on a coastline of coral reefs, seagrass meadows, sand beaches, sand forests, small estuaries, and mangrove forests. This is the largest complex of mangroves and reefs on the central Caribbean coast of Panama. The outer coast in the region of the oil spill consists primarily of fringing reefs with extensive drying, intertidal reef flats (Fig. 2). Seaward, reefs begin with a forereef slope of hard substrata covered predominantly by algae, and secondarily by corals and other sessile invertebrates. Where the forereef slope rises into the intertidal zone, it becomes part of the reef flat. Most reef flats on this coast have a raised outer crest of hard carbonate pavement deposited by crustose coralline algae, shown by the dark shaded structure in Figure 2. In the study areas this reef crest is at approximately the level of mean low tide and is covered with a mixture of calcareous and fleshy algae. Landward of the reef crest there is a mixture of coral bench, loose coral rubble, and loose sediments. Seagrasses and rhizophytic green algae grow in loose sediments of this interior portion of the reef flat, and various other algae grow epiphytically on seagrasses and attached to hard substrata of the exposed coral bench and coral rubble. Sediments are accumulated and held together by seagrasses, rhizophytic algae, and mats of attached algae.

Berms or beaches of sand often form on back-reef flats. Mangroves, mostly the red mangrove *Rhizophora mangle*, colonize intertidal levels of these sand deposits forming the seaward fringe of mangrove forests. On these elevated areas of sand, forests of other woody and herbaceous plants grow just above the level of mean high tide. In intertidal areas behind beaches, mangroves continue landward and cover intertidal substrata (Fig. 2). Mangroves line the margins of freshwater streams where these streams enter the range of the tides.

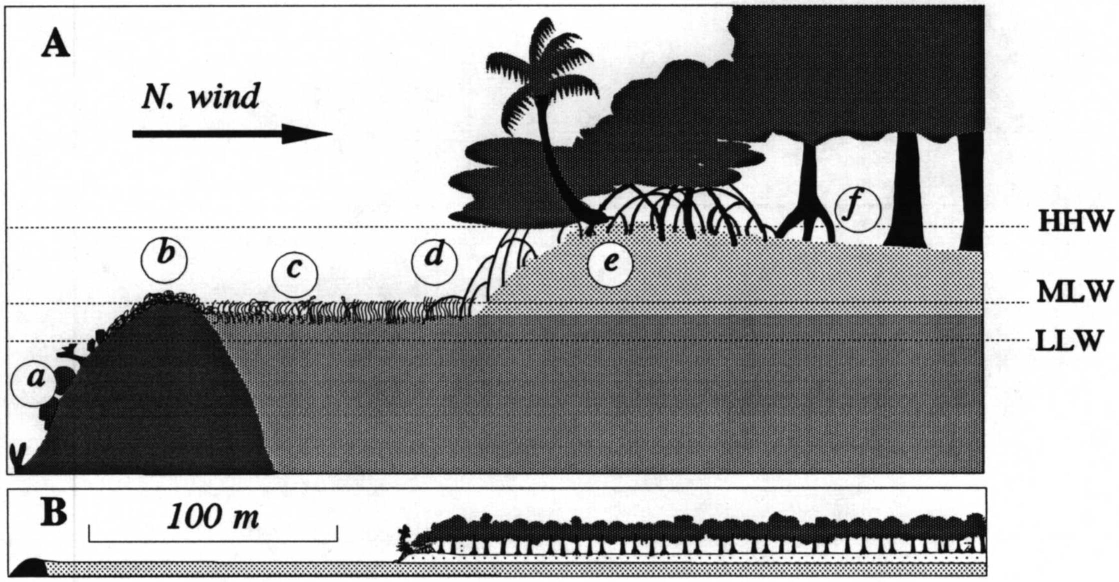

Fig. 2 Schematic cross sections of the wave-exposed outer coast of the central Caribbean coast of Panama. The prevailing wind is northerly. The shoreline consists of extensive, nearly flat habitats on a coral reef foundation. *A.* Cross section compressed horizontally to show the principal habitats and benthic communities: *a.* forereef slope of hard substrata covered by algae, corals, and other sessile invertebrates; *b.* elevated reef crest of hard substrata covered by algal turfs, crustose coralline algae, and sessile invertebrates; *c.* interior reef flat of coral bench, loose coral rubble, and sand covered by seagrasses, rhizophytic (root-forming) algae, and attached algae; *d.* back-reef flat of fine sediments covered by seagrasses and rhizophytic algae; *e.* beaches and berms of loose sediments supporting the seaward fringe of red mangroves and sand forests covered by coconut palms, sea-grape, and other woody and herbaceous plants; and *f.* interior mangrove forests with coarse to fine substrata supporting primarily red, black, and white mangroves. In this diagram the reef flat habitat corresponds to the area between the lowest low water level on the seaward side of the reef and the beach or mangroves on the landward side. The *dotted lines* show approximate water levels: the highest high-water level (*HHW*) produced by combinations of such factors as storm surges, waves, and seasonally high water levels; mean low-water level (*MLW*); the lowest low-water level (*LLW*) produced by combinations of factors, including extreme low tides and seasonally low water levels. *B.* Cross section shown to the approximately correct horizontal scale. The broad reef flat is backed by beach, sand forest, and mangroves. The hard substrata are constructed in place, mostly by crustose coralline algae and corals; the soft substrata consist of fragments of calcareous green algae, coralline (red) algae, corals, and other calcareous organisms.

Patterns of Weather and Sea Conditions in the Region of the 1986 Oil Spill

Weather and sea conditions on this coast vary according to dry- and wet-season alternations, which are common in low-latitude tropics. The dry season (roughly December to April) is characterized by low rainfall, strong onshore (northerly) trade winds, and high mean water levels over reef flats. During the wet season (roughly May to November) winds are variable but predominantly onshore, mean water levels are lower, and rainfall ranges from 2,000 to 4,000 mm. In most years, a "little dry season," with strong onshore winds and little rain interrupts the wet season between July and October.

This coast has a microtidal regime; the mean diurnal range of the tides is approximately 30 cm. Actual water levels are determined by a combination of factors in addition to tidal fluctuations, including seasonal variations in mean sea level, wind stress, and wave build-up over reef flats. Strong onshore trade winds of the dry season increase the amplitude of breaking waves, which raises water levels over reef flats and drives strong currents across them. This water flow exits through channels in reef flats or through mangrove forests behind them.

The watershed for the area affected by the oil spill extends less than 10 km inland. Numerous small streams, but no large rivers, drain into the region of Bahía Las Minas.

Observations of Oil Movement and Deposition

Observations of oil movement onto the outer coast in Bahía Las Minas were made beginning 9 May 1986, 12 d after the spill, when the first large oil slicks arrived at Punta Galeta. Onshore winds drove accumulations of oil onto beaches and reef flats, concentrating oil in small embayments, inlets, and lagoons. In subsequent surveys the most heavily oiled shoreline was between Isla Margarita and Punta Muerto (Fig. 1). Between Isla Margarita and María Chiquita, the only areas that did not appear oiled were in upper reaches of sheltered embayments lined by mangroves.

During the spill, oil accumulated in the following zones of the outer coast: (1) seaward edges of reef flats (between *a* and *b* in Fig. 2), (2) seaward sides of berms on back-reef flats (near *d*), and (3) mid-to-low portions of sand beaches and outer-coast fringing mangroves (between *d* and *e*). In mangrove channels and streams, oil accumulated along berms at the outer edges of mangroves and in thickets of red mangrove roots lining these habitats.

The time of the spill is also a period of low tides and low mean water levels that produced the patterns of oil deposition described above. During low tides seaward borders of reef flats were exposed above water level and onshore winds concentrated oil slicks there. During high tides back-reef berms, beaches, and mangrove berms acted as barriers that also accumulated oil. Relatively little oil was able to move over these raised barriers and enter sand forests and interior mangrove forests. Because of the lack of rain, water flow was slow and oil penetrated into streams. Increased flow in May, June, and July flushed out some of the oil that had accumulated in mangroves growing along streams.

Objectives, Rationale, and Design

Patterns of oil accumulation are examined that would have been produced by different combinations of weather and sea conditions. The goals were to determine: (1) the extent to which winds, stream discharge, and water levels during the 1986 spill represented conditions in other seasons and years and (2) the frequencies of combinations of water levels, onshore winds, and stream discharge rates that would have produced this or other patterns of oil deposition and, therefore, different spatial distributions and severity of biological damage.

Using the environmental database from Punta Galeta, it was possible to: (1) calculate seasonal frequencies of various combinations of winds and water levels along the outer coast of Bahía Las Minas and (2) combine rainfall data from Punta Galeta with the relationships between rainfall, soil moisture, and runoff developed for Barro Colorado Island, Panama, to estimate seasonal patterns of freshwater discharge from coastal streams.

Results and Implications

Reef flats could be directly exposed to oil slicks at any time of year, but most often between February and August. The seasonal peak in exposure times is in April and May; thus, the 1986 oil spill occurred when the lowest levels of reef flats were most vulnerable to direct contact with oil slicks. May 1986 was "average"; exposure was close to the median for May in all years. In contrast, the 1968 *Witwater* oil spill occurred in late December, when the probability of exposure of reef flats is low.

The 1986 oil spill occurred at the beginning of the April-through-October period when combinations of high water levels and strong onshore winds are rare. In May 1986 these conditions were near zero, so that oil did not penetrate deep into sand forests and mangroves. Instead, low water levels caused oil to be deposited mostly in a narrow band along the seaward fringe of beaches and mangroves. If the oil spill had occurred between November and March, like the December 1968 *Witwater* spill, strong onshore winds, high waves, and high water levels probably would have carried more oil into sand forests and interiors of mangrove forests at Bahía Las Minas.

Streams are most vulnerable to oiling late in the dry season and early in the wet season when flow is reduced under all variations of the flow regime examined. The 1986 oil spill occurred during this transition from the dry season to the wet season, when stream discharge probably did not provide much force to oppose the entry of oil into streams while fresh oil slicks were coming ashore.

Discussion

Weather and sea conditions during the spill determined the movement and deposition of oil into intertidal habitats, and, therefore, spatial patterns and biota affected by oiling. For any particular spill, the pattern and severity of damage would depend on when oil stranded in the cycles between the dry and wet seasons.

The April 1986 Refinery Oil Spill

Conditions of winds and water levels during the 1986 oil spill were well within the normal range. This is a season of weak onshore winds and low mean water levels, and oil slicks accumulated along seaward edges of reef flats, beaches, and mangrove forests (habitats *b*, *c*, and *d* in Fig. 2). Biological damage was high in these zones of oil deposition. Seas were also relatively calm, with little turbulence to mix oil into the water column. Nevertheless, oil was visible within live polyps of subtidal corals, and mortality of subtidal corals was high to a depth of 6 m.

If the oil spill had occurred during the dry season, stronger onshore winds, higher water levels, and increased wave action would have driven more oil over natural barriers and into higher-elevation habitats of the outer coast, including high beaches, sand forests, and interior mangrove forests (habitats *e* and *f* in Fig. 2). Greater wave action would also have mixed more oil into the water column, whereas high water levels would have reduced exposure of reef flats and other habitats to direct contact with oil slicks. Biota at the seaward edge of reef flats would have escaped the prolonged direct immersion in oil that occurred in 1986.

Stream habitats in mangroves are at greatest risk of oil contamination during the dry season, when onshore winds are stronger, water levels higher, and stream discharge rates lower. They are at least risk in the mid and late wet season, when onshore winds are weaker, water levels lower, and stream discharge rates higher.

The December 1968 Witwater *Spill*

The tanker *Witwater* (Fig. 1) ruptured about 4 km offshore of Punta Galeta, spilling approximately 20,000 bbl of diesel oil and Bunker C oil into the ocean. December is a month of high mean water levels, few hours of reef flat exposures, strong onshore winds, and strong wave action that probably churned oil into the water column. Lower levels of reef flats were probably under water and only exposed to suspended and soluble portions of the oil. The highest elevations of reef flats were probably not exposed directly to accumulations of oil for more than a few hours. Freshwater streams were probably discharging during the *Witwater* spill. Onshore winds may have pushed oil into some streams with small drainages, but it is unlikely that larger streams were oiled.

There are few data to test hindcasts of biological damage caused by the *Witwater* spill, but the existing data agree with our predictions. Patterns of abundance of sessile biota on the reef flat at Punta Galeta in 1970 are consistent with the hypothesis that some species on high substrata, but not low substrata, were recovering from this oil spill. In addition, patches of barren areas and young mangrove trees in 1973 aerial photographs of the Bahía Las Minas region indicate probable mortality of mangroves during the 1968 *Witwater* spill. Compared with patterns of mortality caused by the 1986 spill, the 1973 photographs showed areas of mortality that extended farther into mangrove forests. This mortality also extended deeper into embayments, but not into freshwater streams.

Summary and Generalization to Other Oil Spills

An oil spill in the dry season should cause greater immediate biological damage along freshwater streams in mangroves and higher tidal habitats, such as sand forests and interior mangrove forests. In addition, wave action would mix more oil into the water column. A spill in the wet season should cause greater immediate damage in lower intertidal habitats, such as reef flats and fringing mangroves. Intermediate patterns of damage are expected in the transitions between seasons. Dry season conditions should also drive more oil back into sand forests and interior mangrove forests, causing more extensive destruction in these habitats than was observed in 1986. Moreover, residual deposits of oil in these habitats would constitute a larger reservoir of oil for long-term, chronic oiling of all coastal habitats, as occurred on a probably smaller scale after the 1986 spill.

Results of the study of the 1986 Bahía Las Minas oil spill may be used extensively in formulating oil-spill policies for tropical environments. Variations in effects of weather and sea conditions on oil deposition should be taken into account when applying our results to other areas.

Hydrocarbon Chemistry

Introduction

The hydrocarbon chemistry program interfaced directly with studies of biological effects and recovery in coral reef, seagrass, and mangrove ecosystems (see Burns, Chap. 3, Vol. II). Our goals were to provide dose-response information and study biogeochemical processes modifying spilled oil over time in tropical coastal environments.

Methods

To answer dose-response questions, sampling was designed to measure hydrocarbon concentrations at replicate sites in each habitat under study. Only some long-term biological study sites had been established in 1986 when the first collection was made. This collection covered a large area, but for some habitats, such as mangroves, none of the long-term sites was sampled; for other habitats only some of the long-term sites were sampled. More complete sediment and organism collections were made 2.5-3 yr and 4 yr postspill, with quarterly collections of bivalve molluscs starting 2.5 yr after the spill. These collections were made at coral reef and mangrove study sites.

Reef surface sediments were collected using cleaned glass jars as scoops. Mangrove sediments were collected using coring devices. Coral tissues were removed from the skeleton by air-blasting or scraping into glass jars; soft tissues of bivalve molluscs were scraped into jars. Samples were extracted and analyzed for hydrocarbons using ultraviolet fluorescence (UVF), flame-ionization gas chromatography (GC), and selected-ion-monitoring gas chromatography/mass spectroscopy (SIM GC/MS), following published guidelines. Lipid weights (total extractable organic matter [EOM]) were determined by evaporating aliquots of $MeCl_2$-extracts on the pan of a microbalance. Total protein content of coral tissues was measured using the standard Folin-phenol procedure.

Regressions of GC and UVF estimates of oil content in sediments and organisms generally were significant (Fig. 3). This correlation between methods provides a new perspective on the concept of "legally defensible methods," which has included only GC/MS measurements of the content of aromatic hydrocarbons. They are, however, only one of the toxic fractions of crude oils. There is no single method that yields quantitative data on all petroleum components in environmental samples. The use of a range of complementary methods tailored to provide answers to specific environmental questions allows for the most efficient use of resources, a significant lowering of analytical detection limits, and a more accurate understanding of the biogeochemical processes affecting changes in oil residues over time.

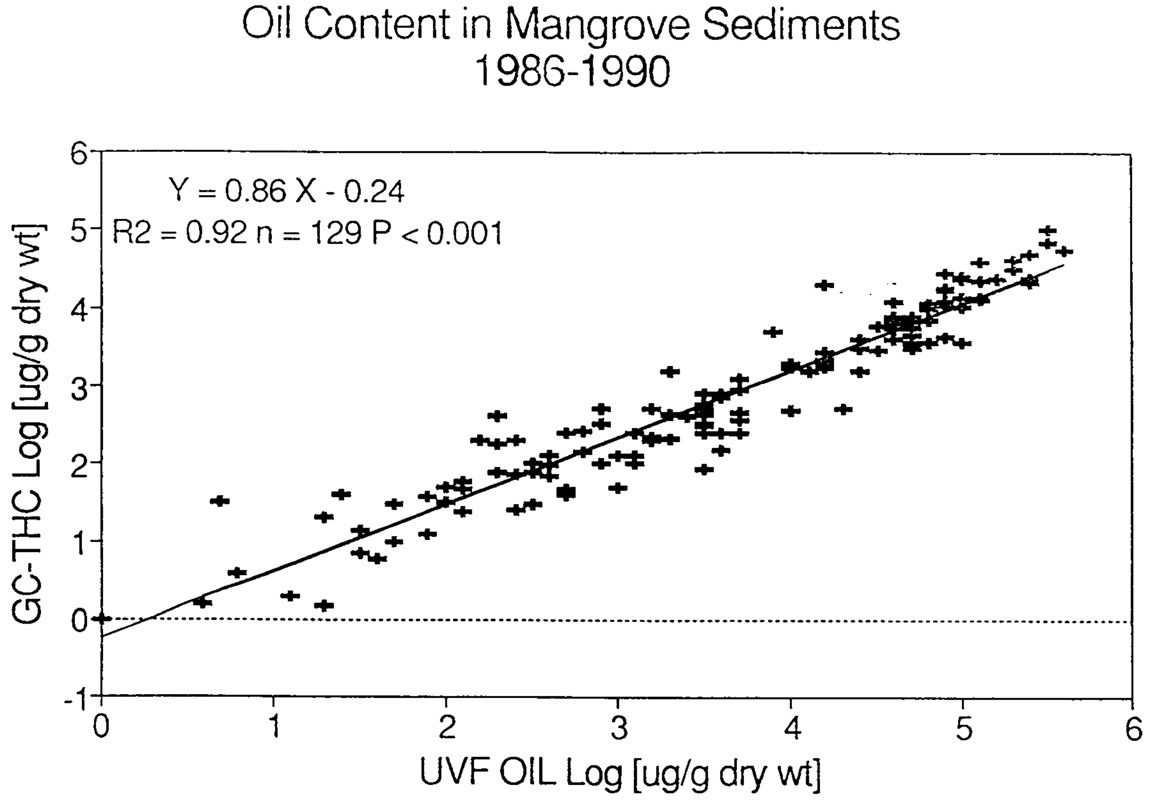

Fig. 3 Regression of the log of the concentration of oil in mangrove sediments (μg oil/g sediment dry weight) determined by UVF and GC methods. The data are from all cores and depths for samples collected in 1986, 1989, and 1990. *THC* = total hydrocarbons.

Initial Sediment Survey, 1986

Analysis of sediment samples collected over a wide area 6 mo after the spill generally confirmed visual rankings of severity of oiling (Table 2) and the large- and small-scale patchiness of the distribution of oil. Concentrations of oil were highest in organic-rich mangrove sediments, reaching levels of more than 30% of sediment dry weight. Analysis by GC showed that the initial rate of degradation of alkane hydrocarbons in mangrove sediments was rapid compared to that in temperate saltmarshes. The size distribution of coral reef sediments showed deposition of fine particles onto reefs in heavily oiled areas of Bahía Las Minas within 6 mo of the spill.

Table 2 Visual degree of oiling related to UVF oil equivalents in surface sediments collected 6 mo after the Bahía Las Minas oil spill. Values are μg/g dry weight. *ND* = no data.

	Visual Degree of Oiling			
Habitat	Heavy	Moderate	Light	Unoiled
Mangrove	>1,800	ND	<700	<200
Seagrass Bed	>300	<200[1]	<150	nondetectable
Coral Reef	>40[2]	<30	ND	nondetectable

[1] Except two samples at LRN2.
[2] Except one sample at LRE.

Long-term Studies of Coral Reefs

Six months after the spill there were clear associations between concentrations of oil in reef sediments and coral tissues and effects on coral populations, including abundance, injuries, and growth. Within 2.5-3 yr postspill, oil levels in sediments and coral tissues dropped almost to background levels, and after 4 yr levels of oil were barely detectable. This pattern of oil concentrations through time suggests that long-term damage to reefs resulted from initial strong effects of the spill on coral and other populations associated with reefs, aggravated later by inputs of contaminated fine sediments washing out of mangroves.

The extensive die-off of subtidal reef corals summarized in a later section stands in sharp contrast to conclusions based on laboratory dosing experiments and small-scale field experiments. These indicated that corals suffer only transient physiological effects and should not be killed unless oil is dispersed into subsurface waters. Small amounts of dispersant were sprayed from aircraft over offshore areas and channels. The amount of dispersant relative to oil, the limited areas over which it was sprayed, and weathering of the oil before dispersant was applied would not significantly disperse the large amount of spilled oil. Thus, chemical dispersion alone would not account for the mortality of subtidal corals over the extended area documented in this study.

Oil in Seagrass Beds

Six months after the spill high levels of oil were at least 20 cm deep in sediments of seagrass beds. Organic-rich sediments accumulated enough oil to cause acutely toxic effects on sensitive fauna for at least 2.5 yr postspill. During this time erosion along shoreward margins of subtidal, oiled beds, where seagrasses died, would be expected to redistribute oil in shallow subtidal and intertidal ecosystems.

Persistence of Oil in Mangroves

Sediment Oil Loads and Weathering Patterns of the Spilled Oil

Sediment cores in oiled mangroves 6 mo after the spill showed that concentrations of oil at the surface were more than 30% of sediment dry weight in some areas and that oil had penetrated at least 20 cm into sediments. Oil concentrations remained high in mangrove surface sediments for at least 4 yr, and more oil was transported to depth in later years.

Weathering processes of evaporation, dissolution, microbial degradation, and photochemical decomposition dramatically altered the composition of oil residues in surface sediments just 6 mo after the spill. In contrast, comparable degradation in temperate saltmarshes requires approximately 2 yr. Using GC/MS selected-ion-monitoring and other techniques, the identity of even highly weathered residues was verified years after the spill.

Oil slicks were observed repeatedly during the 5 yr after the spill to leach out of oiled mangroves and move along the coast, sometimes redistributing oil into previously unoiled sites. Oil buried at at least one site was preserved relatively intact since 1986 in anoxic sediments. Evidence that oil oozing from deep sediments was from the 1986 spill was based on individual PAH and triterpane biomarker patterns obtained by SIM GC/MS. Preliminary evidence of the toxicity of mangrove sediments years after the spill came from adapting the Microtox bioluminescent bacterial assay to solid-phase testing.

Bivalve Bioindicators of Water Quality

Bivalves preferentially accumulate the more soluble, lower-molecular-weight hydrocarbons in an oil-contaminated ecosystem. Because these compounds are also the most acutely toxic fractions of oil, the tissue content of bivalves provides evidence of continued release of toxic, bioavailable petroleum residues into coastal waters. Doses estimated from bivalves may not correspond exactly with those estimated from sediments, but provide instead a time-integrated estimate of the degree of contamination in the water column. Uptake is related to the lipid content of the organisms in addition to the amount of oil in surrounding waters. The maximum limit of accumulation in bivalves is generally up to approximately 30 μg oil/mg lipid.

Water-soluble fractions of crude oil were accumulated by bivalves during the entire study (Fig. 4); false mussels contained on average about twice the levels of oysters. Seasonality in levels of oil is suggested because the highest levels of oil in bivalve tissue occurred in the samples collected in February-March of 1989 and 1990; this peak corresponds with increased oil mobilization during this season of strong winds and heavy wave action.

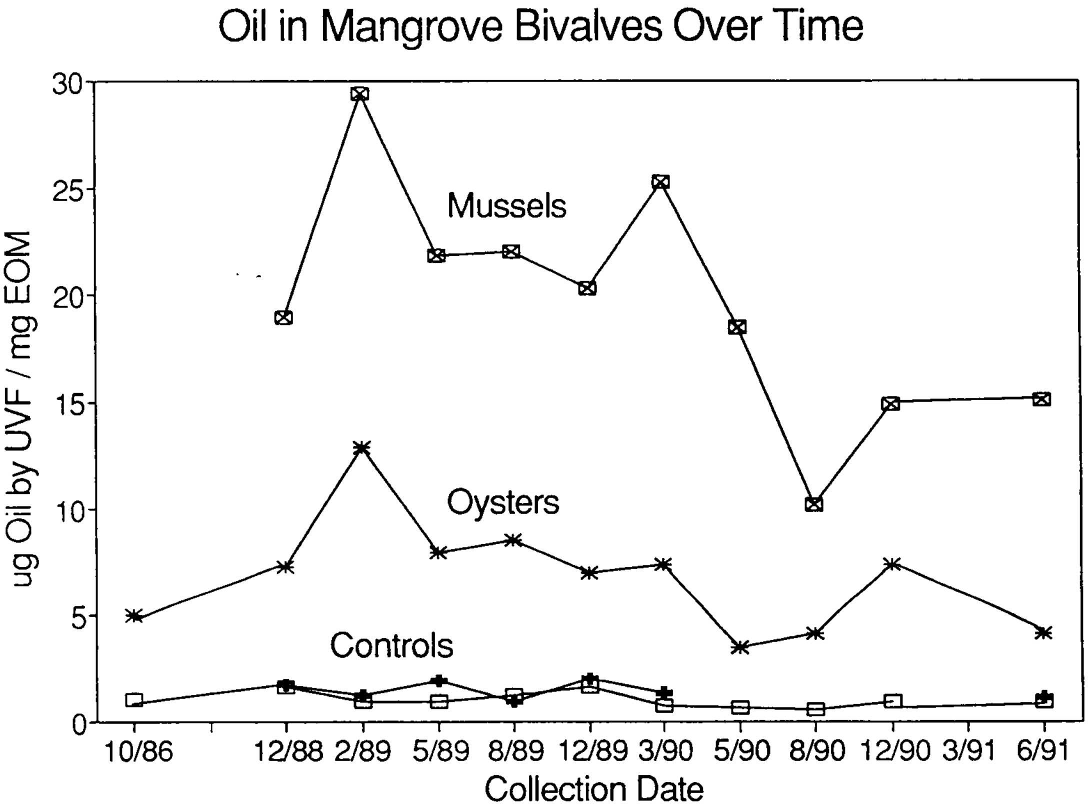

Fig. 4 Concentration of oil in false mussels and oysters as averages of replicate sites. Units are µg oil/mg EOM by UVF analysis. The data are from Table 3.18, Volume II, which shows the range of values. *Controls* = values at unoiled sites.

Further Discussion of Changes in Oil Composition Over time

Analysis by GC showed that the initial rate of degradation of alkane hydrocarbons in mangrove sediments was rapid compared to that in temperate saltmarshes. Pools of oil trapped in mangrove sediments were then surprisingly consistent in composition for more than 5 yr; the relatively fast rate of degradationof alkanes was not maintained for aromatic hydrocarbons. Continued high concentrations of these relatively toxic hydrocarbons, even in samples that appeared by GC to be highly weathered, indicates that the life span of these compounds in mangrove sediments is much longer than 5 yr.

Alternative Sources of Contamination

The source of contamination was unquestionable in areas heavily contaminated by the 1986 spill. GC and UVF patterns in environmental samples differed from the spilled oil in ways explained by weathering processes. Particular scrutiny was given to samples taken near the site of the 1968 *Witwater* wreck. Nearby mangroves, seagrass sediments, and coral reef sediments were contaminated primarily with degraded oil from the refinery spill, although traces of degraded fuel oil were seen in mangrove and coral reef sediments. Only one unoiled mangrove site had significant contamination by another oil in 1986; this appeared to be a light fuel oil.

At unoiled reef and seagrass sites, residual contamination by tar balls and fuel residues likely originating from ships was visible by the highly sensitive UVF method. One unoiled reef was contaminated by a relatively fresh oiling with heavy fuel oil. During the 1990 collection, reefs in Bahía Las Minas were exposed to a spill of fuel oil, but fuel oil was not detected in reef sediments or coral tissues. However, similar events were evident in the UVF spectrum of oil residues in bivalves at a mangrove site beginning in August 1989.

Effects of the 1986 Bahía Las Minas Oil Spill on Reef Flat Sessile Biota, Algal-turf Infauna, and Sea Urchins

Introduction

Reef flats are broad, shallow platforms of coralline rock and calcareous sediments formed by coral-algal reefs when they reach sea level. These highly productive habitats are extensive throughout the tropics and subtropics. Reef flats are also the primary protective structures for developed property and coastal ecosystems such as mangrove forests and coastal wetlands.

The seaward or windward sides of most reef flats are protected by concrete-like pavements built by coralline algae and corals. These coralline revetments are usually the highest parts of reef flats and are the principal structures determining the dissipation of wave energy, rates of water flow, and other hydrographic factors on reef flats. Behind the revetments coralline rubble and sediments accumulate. Much of this material is generated *in situ* by coralline red algae, calcareous green algae (especially *Halimeda* species), and invertebrates with calcareous shells and skeletons.

Although hundreds of species are found on reef flats, a few species tend to predominate. Algae, seagrasses, and sessile invertebrates with photosynthetic symbionts cover most of the surface of reef flats. This highly productive photosynthetic lawn provides both food and cover for abundant and diverse mobile invertebrates (echinoderms, small crustaceans, polychaetes, and gastropods) that provide the trophic link between primary producers and carnivores such as larger invertebrates, fishes, and shore birds.

The shallowness of reef flats and other tidal flat ecosystems makes them highly vulnerable to oil spills. Reef flats are built and protected from erosion by the plants and animals that grow on them. Thus, an oil spill may damage the actual physical structure of reef flats, not just the veneer of biota on the surface.

The reef flat at Punta Galeta has been studied since 1970. The prespill database consists of extensive monitoring of abundances and spatial distributions of plants and animals on the reef flat in relation to concurrent changes in weather and sea conditions. These data demonstrate that the abundances of reef flat species are highly dynamic, changing mainly in response to environmental fluctuations. They enabled us to compare abundances of the flora and fauna before and after the oil spill, using physical monitoring data to distinguish effects of oil from effects of variations in sea and weather conditions. In addition, the distinct pattern of oil deposition on the reef flat enabled us to compare changes in the biota in zones that differed in direct exposure to oil. After the oil spill we also began monitoring additional oiled and unoiled sites to measure the extent to which postspill events at Punta Galeta represented general phenomena (see Cubit and Connor, Chap. 4, Vol. II).

Objectives, Design, and Confounding Factors

Objectives

The purpose of this element of the study was to examine the types of ecological changes caused by the 1986 Bahía Las Minas oil spill and to try to elucidate processes of cause-and-effect that can be applied to understanding effects of oil spills in similar shallow-water ecosystems. Important factors determining the amount of damage include sea and weather conditions, shoreline configuration, biotic zonation, substratum types, and topography of tidal flats.

Design and Consideration of Confounding Factors

The 1986 oil spill was not a controlled experiment. Unlike a designed experiment, there was only one, unreplicated oil spill, oil remained in one geographic area, and only a single reef flat had been studied before the spill. The primary information in this study was derived therefore from within-site and within-survey comparisons of zones of the Punta Galeta reef flat with different degrees of oiling, instead of comparisons of oiled and unoiled sites after the spill. Such postspill comparisons were conducted mainly to determine how much results at Punta Galeta could be extrapolated to other locations and to detect any large-scale phenomena not related to the spill. We examined alternative hypotheses that mortalities during the oil spill were caused by differences that existed among zones, including exposure to desiccation, insolation, high temperatures, and other physical stresses, which were at a seasonal peak of severity during the oil spill. Detailed, long-term baseline data for changes in the biota at Punta Galeta in relation to the physical environment allowed these hypotheses to be tested.

Seasonal and year-to-year variations of weather and sea conditions strongly affect the abundances of plants and animals on reef flats in Bahía Las Minas. The most important factor is the duration of exposure above water level during the warmer, sunnier, parts of the day. These daytime exposures are most frequent between March and June. Exposures cause mass mortalities of many reef flat plants and animals, so that their effects must be taken into account in evaluating effects of the 1986 oil spill. Total daytime exposure times for 1986 were moderate compared with other years. In 1988, however, total exposure times were much higher than any year on record.

Postspill comparisons were also made among additional sites to (1) determine the extent to which results from Punta Galeta could be extrapolated to other locations and (2) detect possible regional phenomena occurring after the spill, but not caused by oil. To find such sites, the coastline from the Río Chagres to Palenque was surveyed, a distance of approximately 110 km (Fig. 1).

Components of Research

Observations of Oil Movement, Deposition, and Initial Direct Effects on Reef Flat Biota

During the first month of the oil spill, daily observations were made of oil movement, oil deposition, and apparent response of the flora and fauna of reef flats. Between 10 and 19 May 1986 the reef flat was exposed above water level during low tides, creating a barrier for oil moving ashore. This caused oil to accumulate along the seaward side of reef flats during low tides (Fig. 5), with organisms in this zone directly immersed in oil. By 24 May 1986 enough oil had worn away to reveal a 1-3 m wide band of white carbonate substratum, which included bleached corals and coralline algae. The band paralleled the shore at about the lowest low-water line, marking a zone previously occupied by a mixture of zoanthids, corals, and calcareous and fleshy algae (between *a* and *b* in Fig. 2).

In contrast to the reef flat at Punta Galeta, raised berms and lack of drainage channels on back-reef flats elsewhere in Bahía Las Minas caused oil to accumulate in seagrass beds (*c* and *d* in Fig. 2).

Spatial Cover of the Sessile Biota of the Reef Flat: Surveys of Algae, Seagrasses, and Sessile Invertebrates

A long-term database of the spatial cover of sessile biota on the Punta Galeta reef flat was derived from three sets of surveys, termed *ZONE* (1971-1977), *CONSURV* (1981-1982 and 1986), and *REDGE* (1983-1984 and 1986-1990). The database was restructured to allow detailed comparisons among surveys, particularly to compare prespill and postspill data. The surveys all used a point-intercept method to measure percent cover, but employed different sampling designs. We therefore compare population changes within surveys, but do not compare absolute abundances among surveys because differences in sampling designs could account for some between-survey differences.

The oil spill occurred during the time of year when macroalgae, which predominate, were at a seasonal low point in abundance. By comparing data only within the same time of year, this seasonal component was reduced, allowing more reliable comparison of the spatial component corresponding to the gradient of oiling.

Most mortality during the oil spill occurred in the coralline zone, near the seaward edge of the reef flat, in the area of the REDGE transects (Fig. 6). The higher-resolution data of these transects demonstrated that mortality of sessile biota during the oil spill varied according to the gradient of oil deposition on the reef flat (Fig. 7). In general, algae regenerated faster after the oil spill than sessile invertebrates, although *Halimeda opuntia* was slow to recover.

Stony corals were less abundant at oiled sites than unoiled sites in the first all-site census in 1987, but were approximately equal by June 1990. Monitoring data for the biota and physical environment demonstrate that this convergence in abundance was due to mass mortality of organisms at all sites during extreme low water levels

Fig. 5 Aerial photograph of Punta Galeta during the 1986 Bahía Las Minas oil spill, showing the accumulation of oil along the seaward edge of the reef flat.

during 1988. Convergence neither indicated that corals recovered, nor that such mortality was "normal."

Censuses of Sea Urchin Populations

Sea urchins were counted in three permanent transects in three habitats on the Punta Galeta reef flat: at the seaward section (the *reef edge transect*), in an intertidal *Thalassia* bed (the Thalassia *transect*), and in the back-reef area of coral rubble and loose sediment (the *rubble transect*). Each transect was 1 x 20 m. After the spill matching transects were established at the three additional sites.

Baseline data at Punta Galeta showed that abundances of *Lytechinus variegatus*, *Eucidaris tribuloides*, *Tripneustes ventricosus*, and *Diadema antillarum* were much lower after the oil spill than the overall prespill mean. However, these low postspill abundances could be explained by normal seasonal reductions or by long-

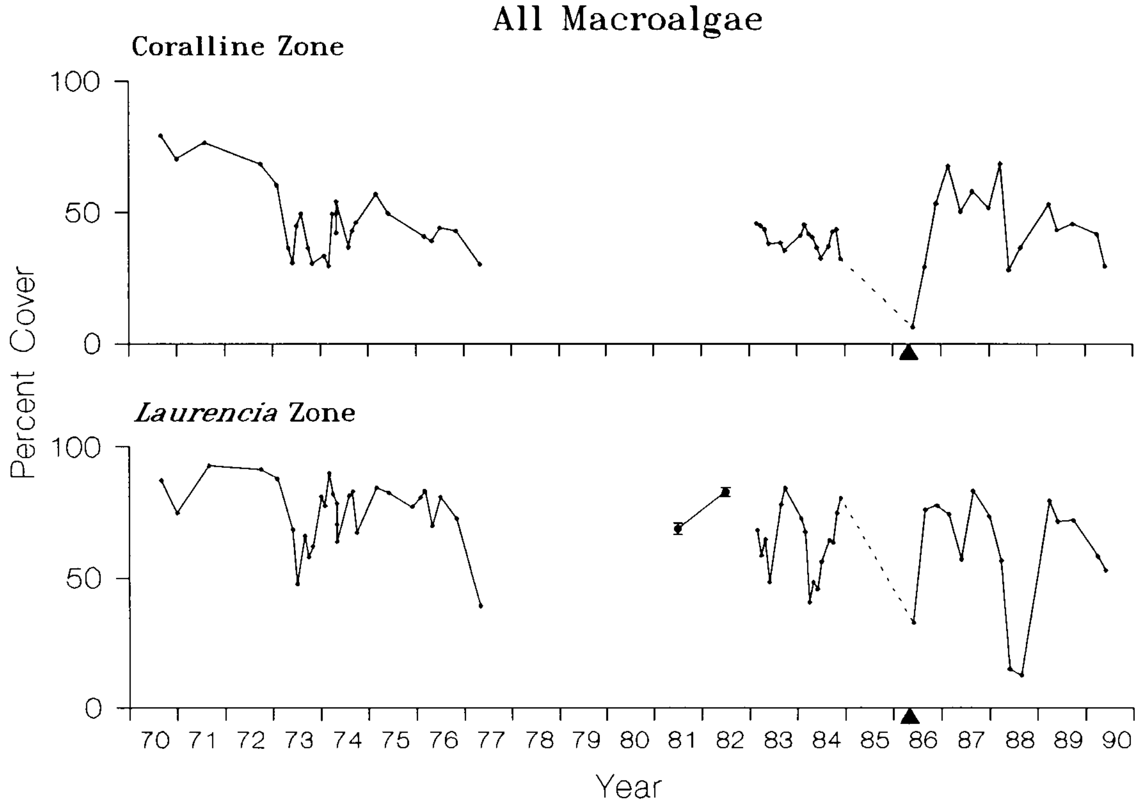

Fig. 6 Percent cover of macroalgae in the coralline and *Laurencia* zones at Punta Galeta, 1970-1990. Data for 1981 and 1982 are yearly means ± 1 SE from the CONSURV surveys. The *solid triangle* marks the time of 1986 Bahía Las Minas oil spill.

term trends. The abundances of *Echinometra lucunter* and *E. viridis* decreased detectably in the reef edge transect (Fig. 8), which was nearest heavy deposition of oil at the seaward edge of the reef flat. Anomalies of postspill recruitment also occurred in this transect, which could be caused by the same factors producing very low abundances of sea urchins in all postspill surveys at Largo Remo (Fig. 9), the site nearest the refinery.

Infaunal Populations of Laurencia papillosa *Turf: Postspill Comparisons Among Sites*

Core samples were taken from mats of the dominant alga, *Laurencia papillosa*, near the seaward edge of the four reef flats. Cores were collected by driving a 5.2 cm diameter stainless-steel pipe through the algal mat into the hard substratum. Samples were positioned in clusters at intervals along transects spaced 0, 2, 4, and 6 m from the seaward edge of the *L. papillosa* zone. After collection, they were

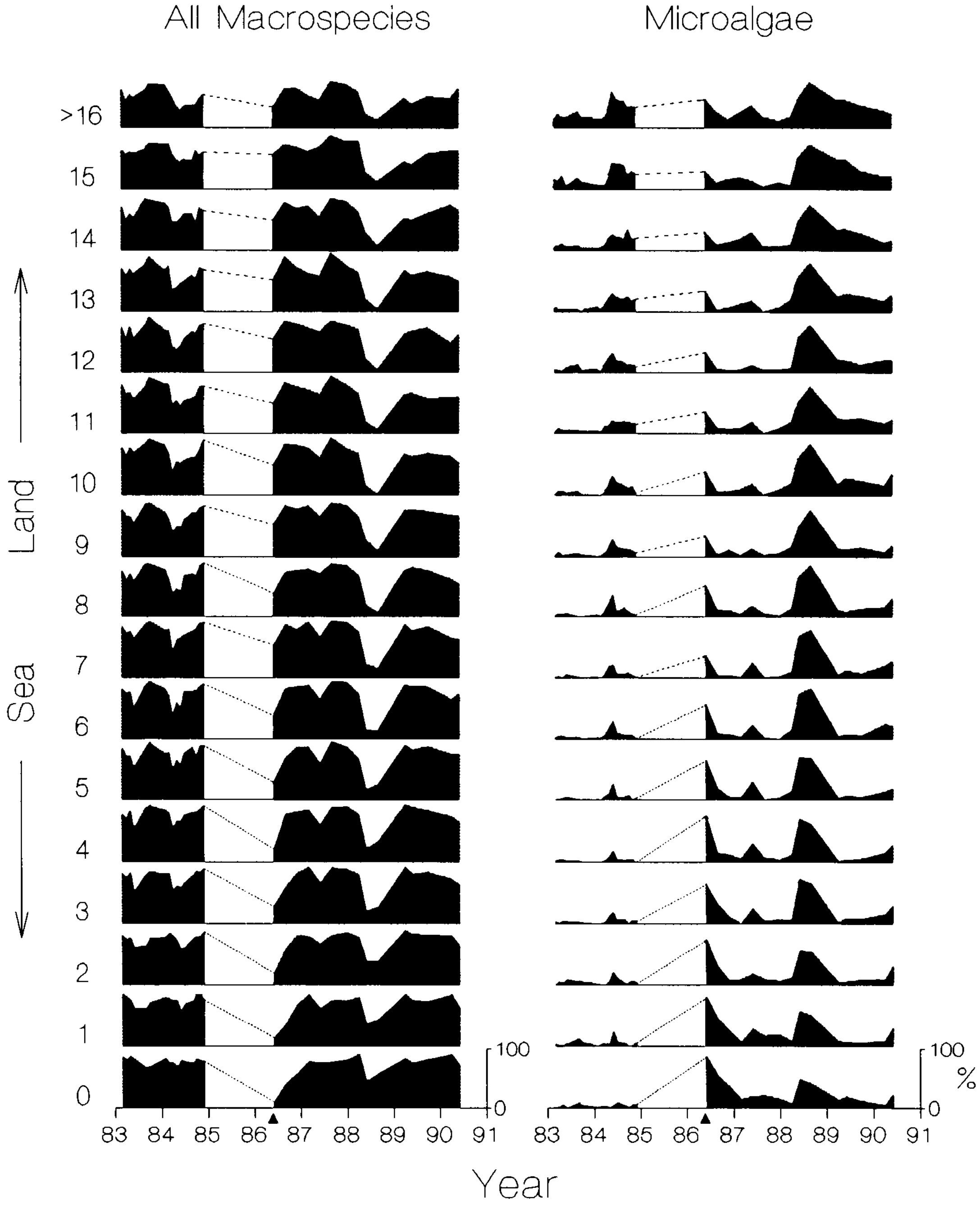

Fig. 7 Prespill-postspill changes in the percent cover and zonation of all macrospecies and microalgae on the reef flat at Punta Galeta, plotted by meter interval from the seaward edge of the reef flat. The numbers 0-16 at the *left* are meter intervals going away from the ocean (0 is closest to the ocean). The *solid triangle* on the baseline marks the time of the oil spill. The *dashed lines* span 1985, when no surveys were made.

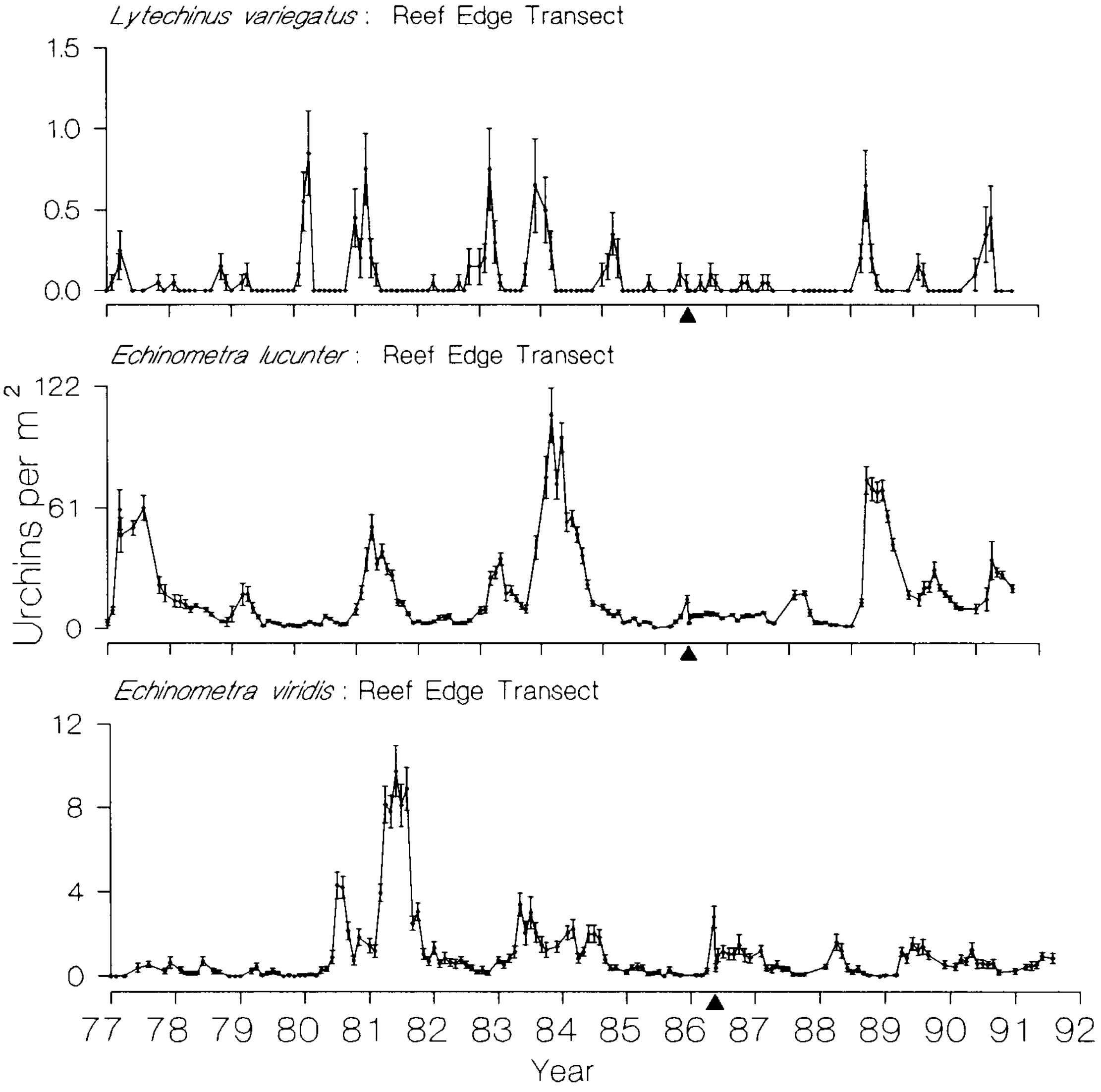

Fig. 8 Monthly population densities of sea urchin populations in the reef edge transect at Punta Galeta, 1977-1991. *A. Lytechinus variegatus*, *Echinometra lucunter*, and *E. viridis*. The data are means ± 1 SE of counts in the 20 square-meter quadrats for each survey date. The *solid triangle* marks the arrival of the first oil slicks at Punta Galeta in May 1986.

preserved for later separation and identification of algae and infauna.

Isopods, amphipods, tanaids, gastropods, and polychaetes comprised most of the infauna. When sampling began approximately 15 mo after the oil spill, tanaids were the only major group to show clearly lower densities at oiled sites (Fig. 10). In April 1990 tanaids were still much less abundant at oiled sites than unoiled sites, even though they had exhibited an extraordinary decline in abundance at unoiled sites between October 1988 and April 1989. This decrease corresponded to the

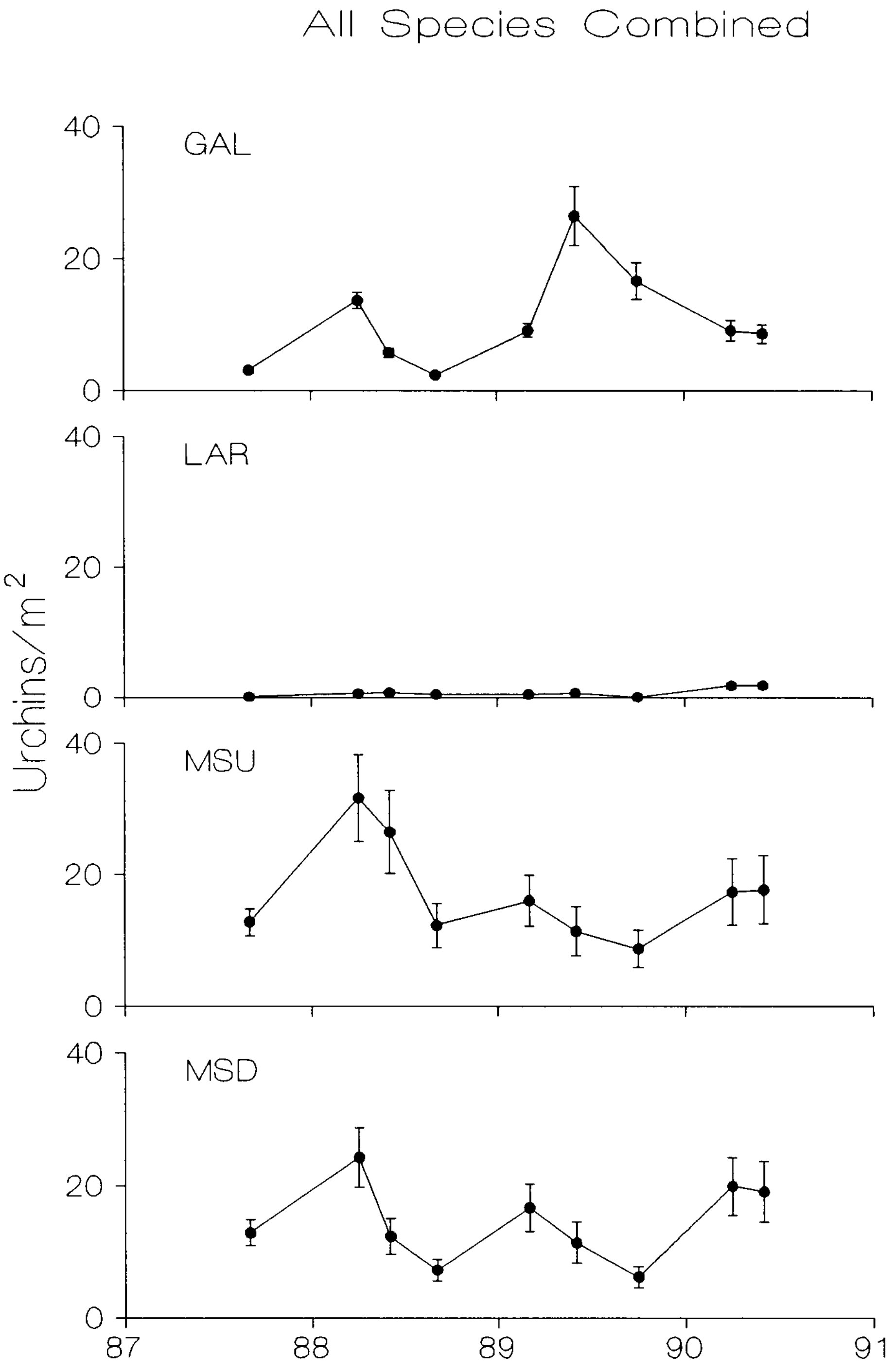

Fig. 9 Intersite comparison of total populations of all species of sea urchins in all transects. The data are means and standard errors. *GAL* = Punta Galeta (oiled), *LAR* = Largo Remo (oiled), *MSU* = María Soto Arriba (unoiled), *MSD* = María Soto Abajo (unoiled).

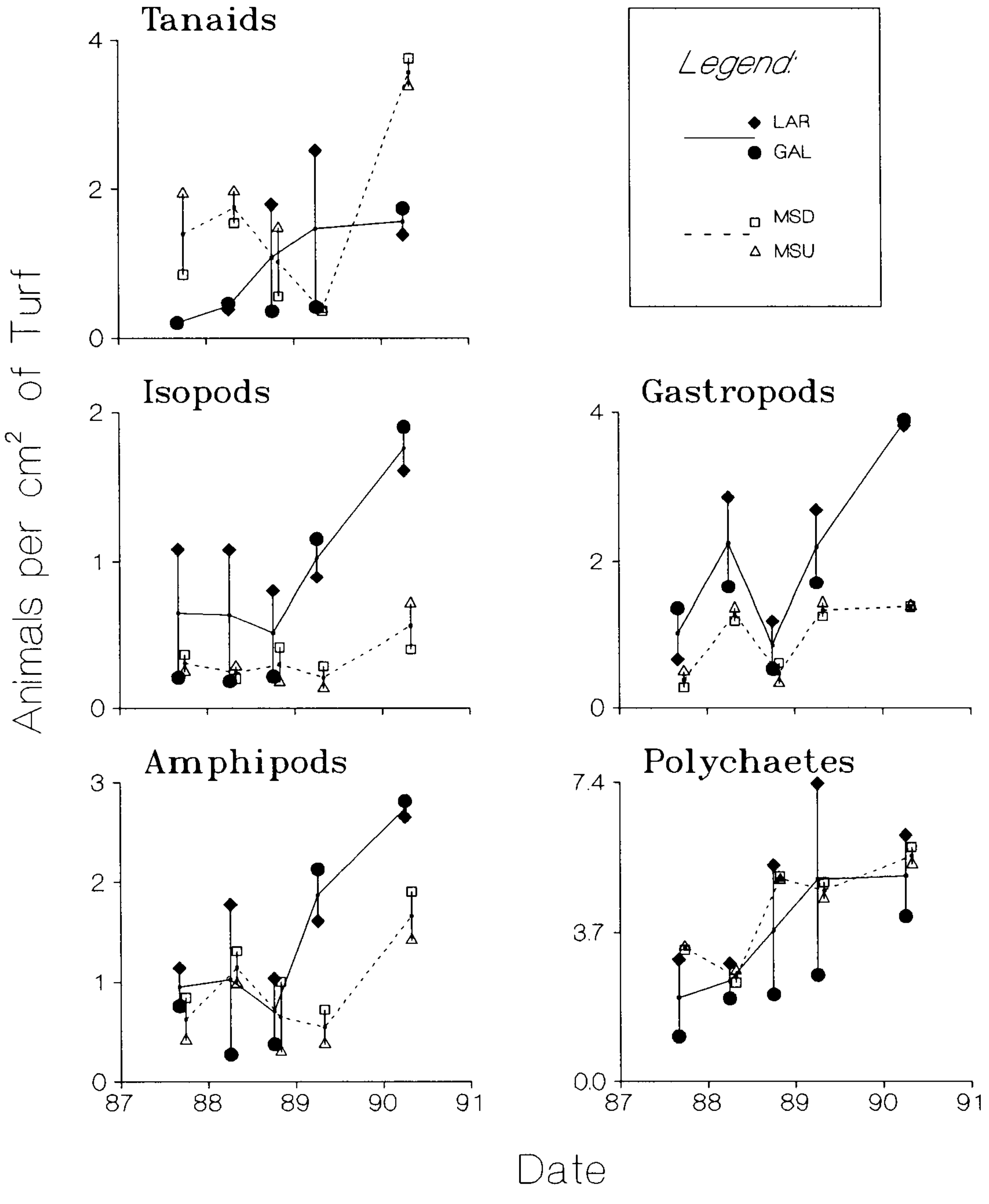

Fig. 10 Summary comparisons of infaunal populations at oiled and unoiled sites. As shown in the legend at the *upper right*, each symbol represents a site; *solid symbols* are oiled sites, *open symbols* are unoiled sites. *Solid lines* connect mean values for the pair of oiled sites, *dashed lines* connect mean values for the pair of unoiled sites.

appearance of fresh heavy fuel oil in sediment samples taken approximately 7 km upwind. In contrast, isopods and amphipods were more abundant at oiled sites than unoiled sites by 1990. Gastropods were consistently more abundant at oiled sites than unoiled sites.

Discussion and Conclusions

General Discussion

The dependence of damage on environmental conditions is particularly important in applying case studies. Results of this study that are appropriate to use more generally are cause-and-effect processes that produced spatial patterns and severity of damage, and factors that determined rates of recovery. Absolute measures from this study, such as total damage or recovery rate, are not adequate by themselves to estimate risks from other oil spills. A much more comprehensive understanding and application of effects can be achieved by considering the full range of potential effects under various possible conditions, rather than only effects of this particular spill.

Patterns of mortality coinciding with deposition of oil indicate that the primary cause of initial mortality was direct contact and not a widespread, toxic effect of oil mixed in water. Such exposure of the biota of reef flats depended on factors such as wind direction, wind speed, water level, wave action, topography of the reef flat, and zonation of the biota. In this case, effects were concentrated on the part of the reef flat that probably had the highest rates of productivity. Ecological information on reef flats is too meager to determine effects of these losses, and assessment of total damage therefore is not possible.

In the formulation of alternative hypotheses, the strongest was that seasonally low water levels, rather than oil, caused postspill reductions in the biota of the reef flat. Baseline environmental and biological data from Punta Galeta combined with among-site comparisons ruled out such stress-based hypotheses in two ways: (1) compared with stresses and mortality recorded in other years, stresses during the 1986 oil spill were not severe enough to account for the observed mortality in the oiled zones and (2) even in the worst of years, these stresses produced spatial patterns of damage that were the reverse of the damage seen during the oil spill. However, results of the biological surveys also demonstrated that some mortality associated with the oil spill and failure to recover afterward were probably *not* caused by oil. In addition, the combination of among-site comparisons and physical monitoring demonstrated that reef flat corals did not continue to recover because of a period of the lowest water levels on record in 1988. Comparisons of oiled and unoiled sites showed that these low water levels killed corals regardless of persistent effects of oil.

Processes Affecting Regeneration and Recovery

After the 1986 oil spill rates of recovery of populations of plants and animals on reef flats depended on the following factors:

1. The severity of damage to the population.
2. Differences in mode of recruitment and recolonization, including recruitment of planktonic larvae and spores, immigration of mobile animals, regeneration from fragments surviving *in situ*, and vegetative spreading from fragments washed in by wave action. Immigration and wave-driven transport of fragments depended on the existence of subtidal populations very near the damaged zones.
3. The inherent growth rate of the species.
4. Long-term destruction of the habitat.
5. The persistence of oil at the site.

Ecological models for colonization and population dynamics of intertidal zones are usually based on the arrival of planktonic spores and larvae, which was not the primary mode of recolonization of reef flats. Except for sea urchins and some infauna, recovery of most reef flat biota depended on perrenation (spreading growth) from fragments that survived *in situ* or arrival of fragments of sessile species and immigrants of mobile animals from immediately adjacent habitats that suffered less damage (Table 3). Thus, postspill recovery of biological communities on warm-water tidal flats is dependent on the survival of a critical minimum population for each species, below which re-establishment of species may not occur for a very long period. Delayed recruitment of the original set of species could allow the establishment and pre-emption of space by another assemblage of benthic organisms, or "alternate stable state," at the damaged site.

Differences in modes of regeneration and lack of damage from cleanup activities may explain why algal populations recolonized faster after the oil spill on reef flats at Bahía Las Minas than reported after spills on intertidal shores in the temperate zone. The dependence of postspill recovery on fragments that survive *in situ* or arrive from nearby sources implies that simple, but immediate, planting of fragments could speed recovery of sessile flora and fauna, thereby reducing the risk of permanent change of tidal flat ecosystems. Cleanup activities may slow recovery by removing remnants of algae that survive spills.

General Applicability of Results of This Study

Results of this study indicate that the severity of damage to tidal flat communities depends on the following factors, in addition to toxicity of the spilled oil:

Table 3 Modes of recruitment and recolonization contributing to the recovery of benthic biota on reef flats after the Bahía Las Minas oil spill.

Mode	Examples
Arrival of planktonic larvae from open ocean	Sea urchins, some infauna
Immigration of mobile animals from adjacent, but less damaged, habitats	Infauna of algal beds, especially those without planktonic larvae, such as amphipods and isopods
Wave transport of fragments of sessile species from adjacent, but less damaged, habitats	Colonial animals (e.g., *Palythoa*, *Millepora*); possibly some algae
Regrowth from remnants surviving *in situ*	Most algae; some colonial animals (e.g., *Zoanthus*)

1. Sea and weather conditions affecting the surface movement and vertical mixing of oil.
2. Range in water levels, tidal flat topography, and other factors determining the amount of habitat at or near water level during a spill.
3. Shoreline configurations that concentrate or block oil slicks.
4. Zonation and along-shore distribution of biota in relation to the vertical and horizontal topography of the tidal flat.
5. The propensity of the substratum to absorb oil.

Such information is often overlooked in risk analyses.

Oil on tidal flats, including reef flats, creates a dilemma for cleanup decisions. On one hand, cleanup activities increase damage, but on the other hand, no cleanup of tidal flats with porous substrata could prolong chronic oiling. Regardless of substratum, cleanup activities should be controlled to maintain surviving populations above the critical minimum level required for regeneration and recovery. Cleanup methods are needed that would remove residual oil, but not residual biota.

The 1986 Bahía Las Minas oil spill was not a worst-case example for reef flats. The weathered crude oil that arrived on most of the reef flats was of relatively low toxicity, and weather and sea conditions restricted oil deposition to narrow strips of reef flats. Thus, biological damage was relatively moderate, and populations of most species remained above the "critical minimum" and regenerated rapidly.

Effects of an Oil Spill on the Gastropods of a Tropical Intertidal Reef Flat

Introduction

Gastropod molluscs are abundant and diverse consumers on reef flats, but little is known about their ecology. The goal of this study was to document effects of the 1986 Bahía Las Minas oil spill on reef flat snail populations, using pre- and postspill comparisons at a site near the Punta Galeta reef flat, and comparisons with unoiled reef flats after the spill (see Garrity et al., Chap. 5, Vol. II).

Six habitats (zones) on the reef flat at Galeta Navy Reef (GNRF) were sampled in November 1982 and January 1983, more than 3 yr prior to the spill, and after the spill from August 1986 through May 1989. Moving from the shore toward the sea, they included high rubble, low rubble, sand, reef rock, beds of seagrasses (primarily *Thalassia testudinum*), and beds of algae (primarily *Laurencia papillosa*). The high rubble habitat was never submerged, although sometimes wet during extremely rough weather. The low rubble habitat occurs partly within the intertidal zone and was regularly to intermittently submerged. The sand habitat occurs just below the low rubble habitat, partly in and partly below the intertidal zone; snails were monitored in the intertidal part of this habitat. The reef rock habitat is relatively flat and well within the intertidal zone. *Thalassia* beds were partly exposed during low tides. *Laurencia* beds occurred near the seaward wave-fringe of the reef flat, and were exposed only when calm seas occurred along with very low water levels.

Tidal fluctuations in this region are small and often overridden by winds and currents. In general, water levels and wave action are high in the dry season (December-March). In the early rainy season (April-May), onshore winds cease and water levels drop, often leading to long exposures of reef flats.

Objectives, Rationale, and Design

Quarterly monitoring was initiated of snail abundance and size structure in August 1986 using methods identical to those in 1982-1983. These data provide an opportunity to examine effects over time of a major oil spill on the gastropods of a tropical reef flat. Time considerations limited monitoring to one replicate of each of the six oiled and unoiled zones. This lack of replication of zones within treatments prevents direct statistical comparison of possible effects of oiling. The section of oiled reef flat (GNRF) sampled in 1982-1983 and postspill is approximately 0.5 km west of the Punta Galeta reef flat. Beginning in August 1986, unoiled reef flats west of Toro Point (TPR) and at María Soto (MSR) were also sampled. Two unoiled sites were used because no one area had all the zones at GNRF; TPR was oiled by a small diesel spill in May 1988.

Oiling and Reoiling

Oil from the 1986 spill was not deposited uniformly across GNRF. The high rubble zone had very little oil in August 1986 (oil cover = 2%), whereas the low rubble and reef rock zones were heavily oiled (85% and 92% oil cover, respectively). Oil was present in the other three zones, but was not quantified. The unoiled sites had no oil attributable to the spill. No oiling was observed at MSR. Tar balls were found in the low rubble and reef rock zones at TPR after 1986. A boat ran aground at this site in May 1988 and released an undetermined amount of diesel fuel, which left an oily sheen across the flat.

Percent cover of oil was monitored again in November 1988. The high rubble zone at GNRF still had little oil. Somewhat more was recorded in this zone at TPR (oil cover = 5%), mainly because of a large tar ball in one quadrat. In the low rubble zone at GNRF, oil cover had dropped from 85% to 4%, and only traces were recorded at TPR. Similarly, oil covered only 14% of the reef rock zone at GNRF compared to 92% soon after the spill. Again, only traces of oil were recorded at TPR. Because of the continuing presence of tar balls and the May 1988 diesel spill, TPR should be classified as lightly oiled compared to GNRF (heavily oiled) and MSR (unoiled).

Components of Research

Gastropod Abundances

Gastropods were identified and counted in 0.25-m^2 quadrats along a transect in each zone. Prior to the spill the high rubble zone at GNRF was characterized by the large herbivorous snail *Tectarius muricatus* and the smaller *Littorina angustior.* Many snails were oiled there in August 1986, a few months after the spill. Oiled snails may have migrated from the low rubble zone. Activities of a cleanup crew at this time appeared to reduce the abundance of several snail species and move two additional species into the high rubble zone, but these changes were ephemeral. Dead snails were still found there in November 1986.

Total snail abundance in the high rubble zone was similar at the unoiled site and GNRF in August and November 1986. From February 1987 through May 1989, however, density was greater at the unoiled site because *Littorina lineolata* increased markedly in abundance there. After the small diesel spill at TPR in May 1988, the abundance of some species declined. Density returned to previous levels by August 1988, then declined during the rest of the study. At GNRF decreased recruitment, particularly of *L. lineolata*, appeared to be the major long-term effect of the spill in this zone.

Nerita tessellata and *N. versicolor* were the most abundant snail species in the low rubble zone at GNRF prior to the spill. In August 1986 many snails had oiled shells and much of this zone was coated with oil. A comparison of shell sizes of live and dead individuals of two common species, *N. versicolor* and *Planaxis nucleus*, indicated that small snails died proportionately more than large ones. After the activities of a cleanup crew in August-September 1986, four of five species decreased in abundance or disappeared, one increased, and two new species were found. However, by November 1986, snail densities had generally returned to levels measured prior to the cleanup, as in the high rubble zone.

Total snail abundance in the low rubble zone was generally greater but more variable at the unoiled site than at GNRF during the study. There was some evidence of mortality due to the small diesel spill at TPR. At GNRF there appeared to be a persistent effect of oiling in this zone through May 1988, 2 yr after the spill. However, by August 1988 snails were as abundant as they had been prior to the spill.

Nerita spp. were the most abundant snails in the reef rock zone at GNRF prior to the oil spill. Effects of the 1986 spill were severe, with snails generally far less abundant at GNRF than at the unoiled site during the 3 yr of postspill monitoring (Fig. 11). Although *Nerita* spp. were common at the unoiled site, *Littorina* spp. were the most abundant species during the study. Only in May 1988, following the localized diesel spill, was snail abundance as low at TPR as at GNRF, but populations quickly recovered. There apparently was a strong, persistent effect of oiling in the reef rock zone at GNRF.

Batillaria minima and *Neritina virginea* occurred in the sand zone at GNRF in 1982; *B. minima* was patchily abundant while *N. virginea* was rare. After the spill, *N. virginea* was absent and *B. minima* was far less abundant than in 1982. Snail populations were further disturbed by the cleanup procedure, which involved high-pressure spraying of seawater. Pulses of recruitment then caused large variations in gastropod density at both the oiled and unoiled site during the rest of the study. Oiling had no detectable effects on snails in this zone, given the variation in populations at both sites over time.

The *Thalassia* zone at GNRF was characterized by *Cerithium eburneum* and *C. literatum* 4 yr prior to the spill. In August 1986 *C. eburneum* was not found and *C. literatum* was rare; in November 1986 neither species was found at GNRF. Both species occurred in low abundance at the unoiled reef at MSR during August and November 1986. No snails were recorded at either site after November 1987, except for a few *Batillaria* at MSR. As in the sand zone, oiling had no detectable effects on snails, given the variation in populations at both sites over time.

The *Laurencia* zone had relatively high gastropod diversity but low abundances in 1982. Both predaceous and herbivorous gastropods occurred; the most common were *Cypraea zebra*, *Smaragdia* sp., and *Thais deltoidea*. No gastropods were found in August and November 1986 at GNRF, but *T. deltoidea* reappeared in low abundance in February through August 1987. No snails were found at GNRF from November 1987 through May 1989. At TPR, one to four species were found in low abundance at each monitoring through August 1987. Since then, as at GNRF, no snails were recorded.

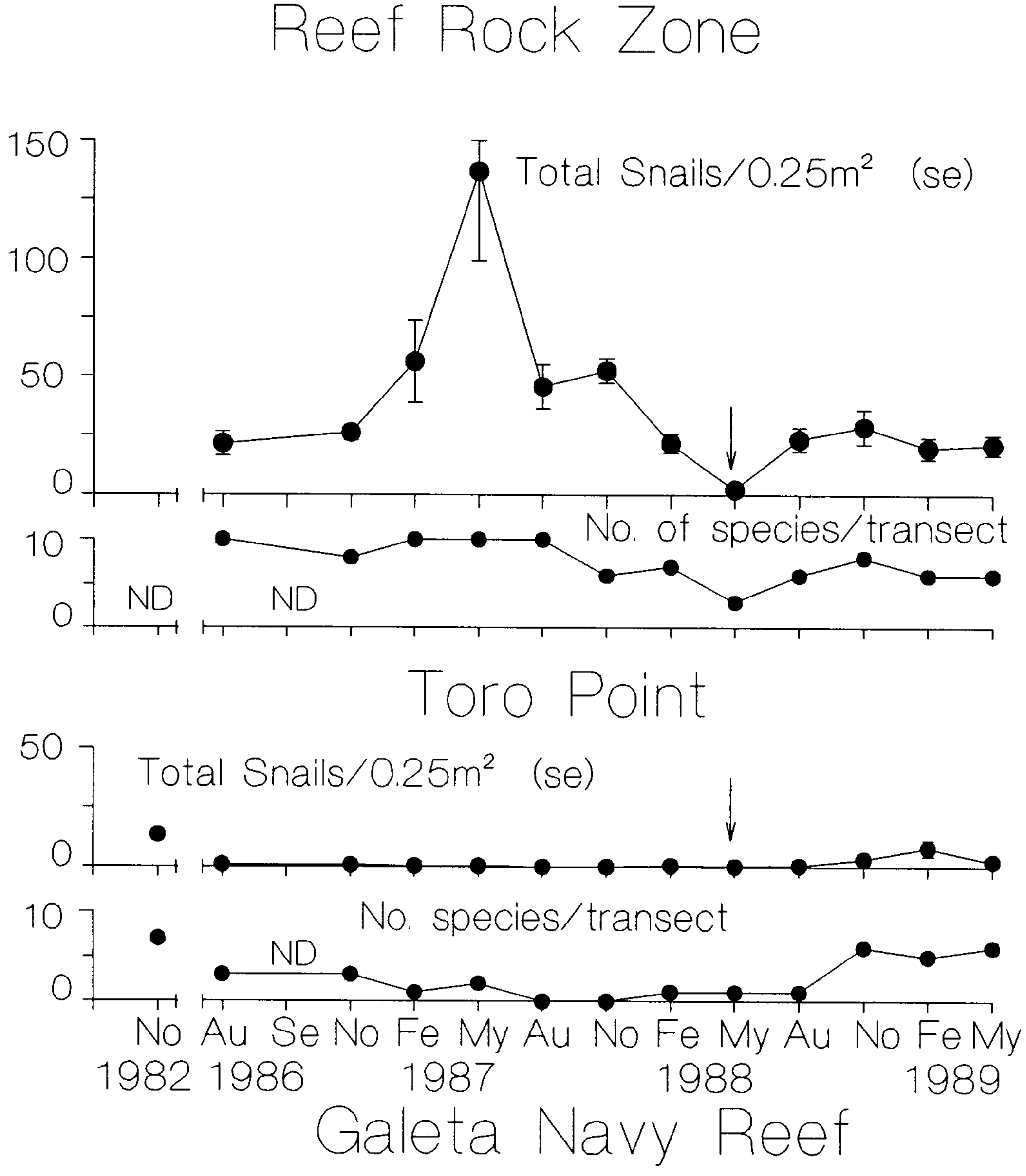

Fig 11 **Total gastropod abundance and number of species in the reef rock zone. Abundance data are mean densities (SE) of all gastropod species combined for each site at each sampling date.** ***Vertical arrow*** **indicates the diesel spill at TPR in May 1988. Number of species is the total recorded in 20 0.25-m^2 quadrats at each sampling date.** ***ND*** **= no data.**

Gastropod Recruitment

Shell lengths were measured for common species counted in the quadrats. Recruitment was defined as a pulse of small individuals, and there were fewer pulses of recruitment at GNRF than the other two sites. Between August 1986 and May

1989, four pulses of recruitment were recorded in the high rubble zone at GNRF, while 13 were observed at TPR. Three species recruited only at TPR. In the low rubble zone 15 episodes of recruitment occurred at GNRF compared to 19 at TPR over nearly 3 yr. One species, *Planaxis nucleus*, recruited only at GNRF, while three species recruited only at TPR. In the reef rock zone there were four recruitment pulses at GNRF compared to 15 at the unoiled site. Four species that recruited at TPR during this period did not recruit at GNRF. On intertidal sand four episodes of recruitment occurred both at GNRF and MSR between August 1986 and May 1989. No species recruited at just one site. It was not possible to follow recruitment in the *Thalassia* and *Laurencia* zones due to the low abundance of gastropods.

Discussion

Effects of the oil spill at Bahía Las Minas on gastropod molluscs inhabiting GNRF must be evaluated cautiously. Conclusions are speculative, given: (1) the four years between pre- and postspill monitoring, (2) the natural scarcity of gastropods in some habitats, (3) the patchy distribution of many species, (4) the unknown extent of natural variation, and (5) lack of prespill data at TPR and MSR. Despite this, there were indications that the spill had adverse effects on gastropod populations in some zones of GNRF. Especially important were (1) observations of dead oiled snails, (2) large numbers of dead snails at GNRF when none were recorded at TPR and MSR, and (3) failure of recruitment in the most heavily oiled zones.

Despite the daytime exposures at the time of the May 1988 diesel spill at TPR, physical stress alone cannot explain the snail mortality observed there. First, hundreds of dead, freshly oiled snails occurred at TPR during the May 1988 monitoring after the diesel spill; no such dead snails were found at the other two sites. Second, snail abundances generally increased at TPR from May to August 1988, despite continued daytime exposures, and some species recruited.

Reef Flat Stomatopods

Introduction

Stomatopod crustaceans (mantis shrimp; Fig. 12) are found in most tropical and subtropical seas. Most species occur in shallow coastal habitats burrowing in soft sediments or occupying cavities in hard substrata. Mantis shrimp are characterized by a pair of powerful raptorial appendages used to capture and process prey, which are also potent weapons in intra- and interspecific combat. Gonodactylid stomatopods occupy and defend cavities in hard substrata as refuges from predators. They are principal components of many intertidal communities as both important predators and prey. As prey, they are an abundant source of food for herons, egrets, fishes, and octopuses. As predators, they are capable of structuring local populations of hermit crabs and gastropods, their primary prey.

The population biology, ecology, and behavior of gonodactylids have been studied more thoroughly than any other organisms in the vicinity of the Galeta Marine Laboratory. In all, over 50,000 gonodactylids were collected and catalogued from 1979 to 1983 with respect to species, sex, size, reproductive condition, injuries, molt status, and growth. In addition, we determined local stomatopod densities, estimated stomatopod-size to cavity-size relationships, locally manipulated stomatopod densities to determine their effect on local prey populations, and conducted numerous field and laboratory observations to document various agonistic and reproductive behaviors. Much of the current information available on the ecology and behavior of gonodactylid stomatopods worldwide comes from this research program. For all these reasons, gonodactylids were used as a model system to study subtle, sublethal effects of the oil spill on population dynamics and processes (see Steger and Caldwell, Chap. 6, Vol. II).

Physical Structure

The primary habitat for gonodactylid stomatopods on the central Caribbean coast of Panama is low intertidal and shallow subtidal *Thalassia testudinum* (seagrass) beds, which may occur on wave-exposed coasts between the crustose coralline algal and coral reef crest and shore. These seagrass beds often form up to a few cm above mean low water, and are frequently exposed during low tides. During most of the year *Thalassia* beds are lush; blades are several cm long and provide a thick canopy covering the substratum. However, during extreme diurnal low tides of May and June, if prevailing winds are light or offshore, beds are exposed for several hours during the heat of the day and blades die back to a short stubble.

Thalassia rhizomes and root systems stabilize organically rich calcareous sediments to form a firm substratum. *Gonodactylus* are most numerous in intertidal seagrass beds, provided that there also exist pieces of coral rubble, crustose coralline algae, or other hard substrata that provide cavities to serve as homes. Gonodactylids

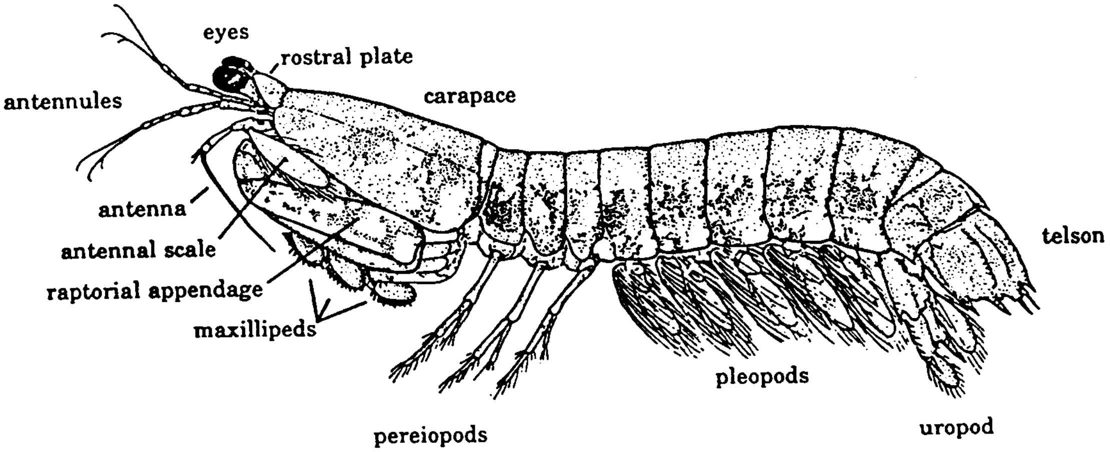

Fig. 12 Typical stomatopod crustacean with major body parts and appendages labeled.

also occur in other intertidal and shallow subtidal habitats, particularly on reef flats containing consolidated carbonate rock, coral rubble, or heavy algal turfs.

Our studies of gonodactylid populations took place at five primary locations within 4 km of the Galeta Marine Laboratory. Each location had extensive seagrass beds interspersed with pieces of coral rubble and coralline algae that served as homes for stomatopods. All selected seagrass beds were exposed at spring low tides.

Gonodactylid Stomatopods

Six species of *Gonodactylus* are found living in cavities in hard substrata on the Punta Galeta coast. Two of these species have only been recorded subtidally. Of the four remaining *Gonodactylus* found on intertidal reef flats and seagrass beds surrounding Punta Galeta, three species are common. *G. bredini* is the most abundant, accounting for approximately 80% of intertidal gonodactylids. *G. oerstedii* comprises about 15% of intertidal gonodactylids and *G. austrinus* about 5%; *G. spinulosis* is exceedingly rare. The abundance of gonodactylids on reef flats around Punta Galeta is quite high. The best estimate of prespill densities comes from data taken at Isla Margarita in August 1979, where there were 9.6 ± 0.59 (mean ± 1 SE) *Gonodactylus* per m^2. Density estimates from other seagrass beds and at other times of the year generally were quite similar.

Individuals settle onto reef flats as postlarvae after spending probably 2-3 mo in the plankton. At this stage they are typically 6-9 mm long and resemble miniature adults except that they lack external reproductive organs and are transparent. One year after settlement these gonodactylids are 25-33 mm long. Female *G. bredini* and *G. austrinus* may begin breeding when they are around 25 mm total length, but *G.*

oerstedii females delay first reproduction until they are approximately 40 mm long. Males of all three species appear to begin breeding at about the same size as females. By the end of the second year these gonodactylids are approximately 40 mm long. At 3 yr they are in the 45-50 mm range. Reproduction is on a lunar cycle, with most females mating and laying eggs near the time of the full moon. They then brood eggs and larvae for 1 mo, and larvae enter the plankton on the next full moon. Small females reproduce every 3-6 mo, but older females typically breed every other month. At least some females breed in the population each lunar cycle; typically 25 to 40% of sexually mature females are reproductive at any given time. Recruitment generally occurs during the new moon, but does not occur every lunar cycle even though a considerable proportion of females in the population reproduce. Recruitment is most likely during the dry and early wet season (February-May), with a second small peak in October or November.

All three common *Gonodactylus* species have similar tolerances to high temperatures, desiccation, and low salinities that may be encountered during tidal exposures. Adults of all three species can survive water temperatures up to 39°C for 30 min., but suffer greater than 50% mortality at 40°C. Temperature and salinity tolerances of eggs and larvae in female cavities are high and match those of adults. Despite this tolerance of extreme heat, we have observed mass mortality of gonodactylids during exposures.

Gonodactylids require cavities in hard substrata, which provide refuge from predators, a place to process prey, and safe shelter in which to mate and brood eggs and larvae. Without a cavity, the life expectancy of a gonodactylid is probably very short. Suitable cavities, particularly for large individuals, are often in short supply. Competition is often intense for existing cavities, and much of the complex aggressive repertoire that has been documented for these species is involved in acquiring and defending homes. Given the potent weapons these animals possess and the value of a cavity, it is not surprising that contests for cavities are fierce and frequently result in injuries. Such competition will tend to force animals to accept cavities smaller than preferred. The more intense the competition, the smaller the cavity-volume to stomatopod-size ratio, which is a good indicator of cavity limitation and competition in a population.

In addition to gonodactylids, the large burrowing stomatopod, *Lysiosquilla glabriuscula*, was common on reef flats prior to the spill. These animals attain a length of 22 cm, form lifelong pair bonds, and live for several years. Between 1979 and 1983, *Lysiosquilla* burrows on low intertidal seagrass beds and reef flats were located and marked. Some burrows were observed for up to 4 yr and very few disappeared. In August 1983, when these sites were last surveyed prior to the 1986 oil spill, there were 22 marked and active *Lysiosquilla* burrows at the sites surveyed after the spill.

Objectives, Rationale, and Design of the Long-term Study

Much of the coast hardest hit by the oil spill included sites where from 1979 to 1983 the behavior and ecology of gonodactylid stomatopods had been studied. In September 1986 the effect of the spill was assessed at four of these study sites. This report covers results of this initial survey and the long-term field study that continued from February 1987 through February 1991.

The initial postspill survey concentrated on population consequences, particularly demographic structure at oiled and unoiled sites. We also examined physiological and behavioral effects associated with oiling that pointed to some of the mechanisms involved in producing population changes.

An assessment of long-term effects of the oil spill on gonodactylids was carried out from February 1987 to February 1991, and was designed to examine the persistence and consequences of the effect of the spill on several parameters that the initial postspill survey had indicated were affected by oiling, including: (1) population structure, (2) recruitment, (3) growth, (4) injuries, (5) stomatopod-size to cavity-volume relationships, (6) habitat change, and (7) changes to populations of *Lysiosquilla*.

Confounding Effects

There were three potentially important confounding effects: natural variation in gonodactylid recruitment, effects of other species, and habitat change. Prespill studies demonstrated that recruitment of juvenile *Gonodactylus* into the population varies from month to month, seasonally, and from year to year. *Gonodactylus* populations have not been studied sufficiently long to understand the extent of fluctuations in recruitment, whether these changes occur long enough to affect demographic structure, and the geographical extent of such changes. It is against this background of natural variation in recruitment that we must then try to interpret possible consequences of the oil spill on recruitment and population structure.

Only stomatopods were surveyed; there are no quantitative data on changes in abundance or behavior of other predators, prey, or competitors with stomatopods. Effects that might be attributed directly to oiling could be secondarily mediated through other species.

One of the most dramatic effects recorded in this study was the destruction of the *Thalassia* bed at a heavily oiled site, the subsequent loss of soft sediment, and its replacement with unconsolidated coral rubble. To further complicate matters, the red mangrove forest directly behind this site was also deteriorating, resulting in the release of some oil and silt onto the site. These confounding factors make it difficult to attribute decreases in stomatopod recruitment and abundance to a particular cause. The decline in stomatopods could be due to a lack of suitable substrata, a lack of prey, reoiling of the site, or some combination of factors. With only one study site having undergone such severe and confounded degradation, it is difficult, if not impossible, to tease apart cause and effect.

Site Selection and Design

The plan was to sample sites that received significant oiling and compare them to other locations that had received little or no oil. It was important to select sites for which there were prespill data on stomatopod populations. In September 1986 seagrass beds were inspected for evidence of oiling. From a number of possible beds, four were selected, two that had been moderately to heavily oiled (Isla Largo Remo North [LRN] and Isla Mina [MINA]; Fig. 1) and two that had been lightly oiled to unoiled (Isla Largo Remo West [LRW] and Isla Margarita [MAR4]). By February 1989 a general decline in gonodactylid recruitment had occurred at all sites. To help determine the scale of this phenomenon two additional control sites that had received no oiling during the spill were established at María Soto (SOTO) and Punta Escucha (ESCU).

None of the seagrass beds was sampled in 1986 for hydrocarbons, so they cannot be classified by petroleum concentrations. In some cases, chemical analyses in adjoining habitats were consistent with visual classification.

We had hoped to analyze data using repeated-measures analysis of variance, however, the two oiled sites physically and biologically diverged through time. This also occurred somewhat at the two reference sites, and the two control sites proved to be more dissimilar than expected. For these reasons, and due to lack of normality and unequal variances in much of the data, the repeated-measures design was abandoned and within-site variance estimates were used, when necessary, to compare sites with one another and through time.

Oiling and Reoiling

At LRN, one of the oiled sites, an oil sheen appeared when we walked through the area from September 1986 until February 1988; oil sheens continued to appear sporadically through February 1991. Oil was also found in coral rubble at LRN each visit. At MINA, the other oiled site, oil was released from sediments until September 1987; oil was found in rubble in September 1986 and February 1987, but not in September 1987 or thereafter. Oil was not released from sediments and was not found in coral rubble at LRW, MAR4, SOTO, or ESCU, the reference and control sites.

Components of Research

General Sampling Methods

Stomatopods were collected from all pieces of hard substratum found in 30 0.5-m^2 quadrats. The substrata were measured and then broken apart to remove stomatopods from cavities. Little effect of repeated sampling on rubble quality or abundance was noted. To increase samples sizes, additional pieces of coral rubble were collected from adjacent areas. These samples were used to calculate densities of *Gonodactylus* per unit volume of rubble and to provide enough individuals for estimating growth, reproduction, recruitment, and the frequency of injuries. Animals were brought to the laboratory and examined under a dissecting microscope to determine species, sex, size, injuries, and the reproductive state of females. Each animal was kept for 3 d to record whether it molted or laid eggs. If animals molted or were collected with their molt skins, growth was measured by the change in carapace length.

Effects of Oiling on Habitat Characteristics

The most dramatic long-term effect of the oil spill was the transformation of the habitat at LRN, an oiled site. Before the oil spill there was an intertidal bed of *Thalassia testudinum* with scattered pieces of small coral rubble, bordered by a stand of *Rhizophora mangle*. The area now is dominated by large pieces of unconsolidated coral rubble resting on a fine, sand-silt substratum, bordered by a 15 m wide mud flat. Considering the loss of sediments, turtlegrass, and mangroves, there is little chance in the near future for the habitat at this site to recover fully. In contrast, except for a few widely dispersed patches of dead mangroves along the shore, the other oiled site (MINA) appears today much as it did before the oil spill. Possible explanations for the recovery of MINA may have to do with patterns of water flow and the lack of a heavy stand of mangroves adjacent to the site.

LRW, a reference site, was not affected directly by oiling. Although erosion at LRN affected this site, there seemed to be no long-term effects of this sedimentation. The habitat at MAR4 was not obviously affected.

Densities of Gonodactylus

The most obvious initial effect of the oil spill was the loss of large *Gonodactylus*, particularly females, from the two oiled sites. This was most likely a direct effect of oiling, which either killed these individuals or caused them to leave the area. Large gonodactylids are seasonally forced to move to deeper water by prolonged exposure of intertidal seagrass beds at the time of year the spill occurred, but such movements usually do not result in mass mortality. By July and August large gonodactylids return to higher intertidal seagrass beds to resume breeding in these areas. The fact that they had not returned after the spill, but that smaller individuals were breeding in these areas, strongly suggests that large stomatopods were killed during the spill.

Postlarval Recruitment

Recruitment appeared to be low in the months immediately following the oil spill, and the decline seemed greatest at those sites receiving the most oil. While these data suggest that oil was interfering with the settlement of new recruits, more reliable indications of the effect of oiling on recruitment come from February data, when recruitment levels are generally more constant and often several times higher than during early to mid-wet season. These data suggest that recruitment was curtailed for as long as 2 yr following the spill, and that the effect was most severe where oiling was heaviest. However, there also was a general suppression of recruitment that seems to have taken place on a large scale. Because data are lacking from sites throughout the western Caribbean, we cannot determine whether this decline was localized and related to the oil spill or was a more widespread phenomenon that affected the entire region.

Cavity Volume

Prespill measurements of the ratio of cavity volume to stomatopod size preferred by *Gonodactylus* in populations around Punta Galeta demonstrated that this ratio typically is not realized. Competition forces gonodactylids to fight, particularly those requiring large cavities, and animals usually must occupy a cavity smaller than preferred. This effect cascades down to smaller stomatopods. The elimination of large gonodactylids from the population at oiled sites immediately following the spill made available many preferred-size cavities for surviving animals. However, as populations at oiled sites recovered and more large animals reappeared, competition was re-established, and animals again had to settle for suboptimal homes. At LRN, however, where habitat deterioration produced an abundance of large cavities, animals can still find a home of the preferred size (Fig. 13).

Wounds and Injuries

Another measure of competition in gonodactylid populations is the proportion of wounding. A decrease in wounding at oiled sites immediately following the spill probably resulted from the reduced numbers of large gonodactylids and less competition for cavities. At MINA, where destruction of the habitat did not occur, injuries had returned to prespill levels less than 1 yr after the spill.

Growth

Growth rates of stomatopods increased at heavily oiled sites immediately following the oil spill, but this did not persist. Competition may have rapidly returned to prespill levels at MINA, as indicated by the data on injuries. Growth may have been temporarily promoted at this site by an increase in prey, particularly hermit crabs.

The Disappearance of Lysiosquilla glabriuscula

During the first sampling after the oil spill in September 1986, searches failed to locate any of the 22 *Lysiosquilla glabriuscula* burrows that had been marked in 1983, although the marking stakes still existed at several locations. We do not know

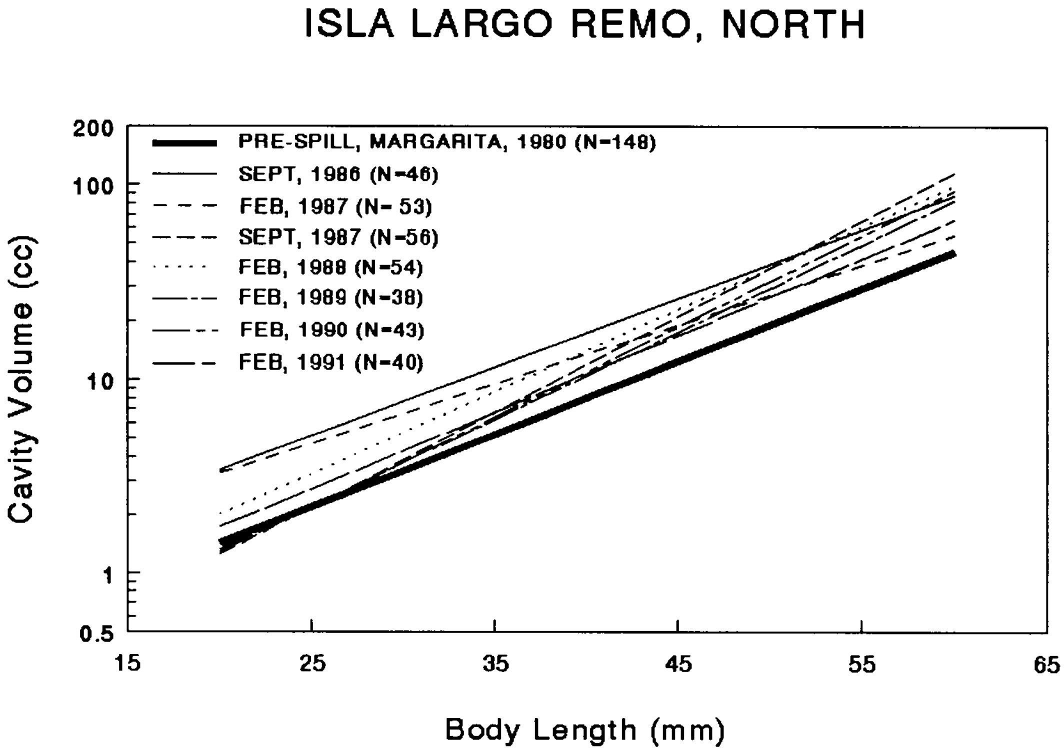

Fig. 13 Relationship at LRN between the size of resident *Gonodactylus* and the volume of the cavity occupied. All data are postspill for rubble taken from LRN except for prespill data taken at Isla Margarita in 1980 (*heavy solid line*). Sample sizes are in parentheses.

why no recruitment occurred over the past 5 yr, although such events may be rare for these exceptionally long-lived animals.

Discussion and Conclusions

Oiling Effect on Gonodactylid Population Structure and Density

In September 1986 a significant loss of large *Gonodactylus*, particularly females, occurred at oiled sites. Large females move into shallow water to brood at the time of year of the spill, apparently causing their disproportionately high postspill mortality at the oiled sites. Such mortality did not occur at reference sites.

Low levels of postlarval recruitment from at least February 1987 through February 1989 and migration of larger gonodactylids were two processes that significantly affected densities. MINA, the oiled site where seagrass habitat was not destroyed, illustrated best the complexity of factors affecting gonodactylid densities. Total density did not change early in the monitoring because a decline in medium-sized individuals due to low recruitment was offset by an increase in larger gonodactylids due to immigration. Total densities were balanced later between a decline in larger individuals due to earlier low levels of recruitment and an increase in smaller gonodactylids due to increased recruitment. The net effect was that the total density of gonodactylids did not vary significantly at MINA even though densities of most size classes did.

It appears that recruitment was low on a large geographic scale from 1987 through 1989 due to an unexplained phenomenon and that oiling reduced the level of recruitment further at heavily oiled sites in 1987 and possibly 1988. The levels of recruitment measured in 1990 indicated that both the effects of oiling and the general depression of recruitment had ended by then. The dynamics of larval dispersal and recruitment are not understood well enough to pinpoint the mechanism behind either the effect of oiling or the large-scale depression.

Effect of Density on Competition

The intensity of competition for cavities is a function of the abundance of gonodactylids relative to cavities. When the availability of cavities limits populations, the intensity of competition for cavities is high and individuals are forced to occupy cavities smaller than they prefer. As densities of gonodactylids decrease or increase, the cavity-volume relationship should change also.

The density of large gonodactylids drives competition, and the cavity-volume relationship can be pictured as a line anchored by the density of large individuals. If the density of large animals changes, the intercept of the line changes but not its slope. If the density of smaller animals changes without a change in the density of larger animals, the slope changes. If all densities are changing, the line moves in complex patterns, with both position and slope changing. The nonlethal, indirect effects of density changes on competition should be viewed as a long-term effect of the oil spill.

Injuries, Densities, and Cavity Competition

Oiling affected the number of injured gonodactylids. The reduced number of injured individuals was an indirect effect brought about by the reduction in densities of large gonodactylids. Except when there was a very large effect of oiling, the association between density and number injured was not clear and factors other than density *per se* were affecting the frequency of injuries.

Changes and Recovery of Subtidal Reef Corals

Introduction

Coral reefs are shallow-water communities formed by growth of corals, crustose algae, and other calcareous organisms whose skeletons form a stable, wave-resistant structure. Reefs are a major habitat of tropical waters, where they may form a continuous band fringing the coast or barriers seaward of mangroves and seagrass beds. Coral reefs support a high diversity of plants and animals, and are ranked among the most biologically productive and diverse of all natural ecosystems.

The extent of effects of oil on reef corals in their natural environment is controversial and poorly understood. Some studies suggest harmful effects and lasting decreases in abundance through increased mortality or decreased reproduction or recruitment. Results of experiments on effects of oil and dispersants in the laboratory or field are contradictory. Some studies suggest little or no mortality or persistent sublethal effects of oil on corals, while others suggest more serious or lasting damage. In either case, extrapolation of such experimental results to the field is hampered by the unnatural spatial scale and duration of the manipulations, and because laboratory and field experiments were not designed to mimic real oil spills.

Coral Reefs of the Study Region

Subtidal reefs along the Caribbean coast of Panama are mostly fringing reefs that give way to sediment plains at depths of 10 to 25 m. The study reefs include eight within or near Bahía Las Minas that were varyingly affected by the oil spill, and four unoiled control reefs between Portobelo and Isla Grande (Fig. 1; see Guzmán et al., Chap. 7, Vol. II). Bahía Las Minas has been subjected to decades of human disturbance, including construction of the Panama Canal and the city of Colón, mosquito-control programs, construction of a refinery and a large cement plant, erosion and sediment discharge due to increased deforestation and housing construction, and a major oil spill from the tanker *Witwater* in 1968. The region of the control reefs has suffered from deforestation and subsequent discharge of sediments.

Physical Environment

During the study sea-surface salinities were generally lower and temperatures somewhat higher at Bahía Las Minas than at unoiled reefs. Sediment loads varied considerably throughout the year, but higher values were always observed at reefs in Bahía Las Minas, where they reached 1,200 mg/cm^2/yr. Deposition of resuspended sediments on oiled reefs rose significantly during the 4 yr of postspill measurements. Consistently higher rainfall at Portobelo suggests that increasing sediment loads at Bahía Las Minas were not due to differences in runoff, and may therefore be related to the oil spill.

Sessile Biota

The sessile biota of subtidal coral reefs along the central Caribbean coast of Panama is composed mainly of scleractinian corals, hydrocorals, gorgonians, crustose algae, macroalgae, zoanthids, anemones, and sponges. The most abundant organisms before the oil spill were macroalgae (45% cover), scleractinian corals (27%), sponges (5%), and crustose algae (3%); the main reef-building scleractinian and hydrocoral species were the major focus of this study. These included the scleractinians *Siderastrea siderea*, *Porites astreoides*, *Diploria clivosa*, *Agaricia agaricites*, and *D. strigosa*, and the hydrocoral *Millepora complanata*.

Crustose algae and macroalgae flourished after coral mortality throughout the region at all depths. *Halimeda* spp., *Sporolithon episporum*, *Hydrolithon boergesenii*, *Caulerpa* spp., and *Dictyota* spp. were the most abundant species from 0.5 to 12 m depth. Other groups, such as sponges, octocorals, zoanthids, and anemones, may compete aggressively for reef space, and often overgrow living corals and colonize large areas of dead reef framework.

Objectives, Rationale, and Design

Here we describe responses of the reef community and some reef coral populations during 6 yr of biological and physical monitoring. The goal of this study was to determine lethal and sublethal effects of the 1986 oil spill on subtidal reef corals and other sessile organisms, and prospects for recovery. Three different statistical designs were used based on the type of data available before the spill and observations made soon afterward. The statistical procedure for all three designs was repeated-measures analysis of variance (ANOVA), with individual reefs as replicates for each treatment (amount of oiling).

The use of control reefs placed the oiled reefs within a wider context, with sampling methods standardized across all study sites. Many ecological studies compare an altered site with a single control site, assuming that they were not different before the alteration. This is not the case for coral reef communities, where reef habitats and populations vary greatly over all spatial and temporal scales. This range of natural variation can only be measured by comparing several control sites. When only a single control site is used, interpretation of the effects of an anthropogenic disturbance is confounded with natural changes.

Oiling and Reoiling

The amount of oil floating above reefs was visually assessed during the 3 mo following the spill (May-July 1986) by air, boat, and underwater observations. Oiling was ranked on the basis of the amount of oil visible at the surface as heavy, moderate, or none. Results of subsequent analyses of petroleum hydrocarbons in tissues of corals and reef sediments generally corroborated the classification of reefs by visual inspection. Reef sediments and coral tissues were collected for hydrocarbon analyses during August-September 1986, December 1988-March 1989, and July 1990 at oiled and unoiled reefs where coral cover, injury, growth, and reproduction were recorded.

We also noted the presence or absence of oil slicks over reefs from August 1987 to December 1991 (Table 4). Heavy oil slicks continued to emerge from mangroves (Fig. 14) and landfill beneath the refinery, most frequently following heavy rains, but also after very high tides. The pattern of this chronic oiling was consistent with that observed immediately after the oil spill. Given the large amounts of oil apparently still trapped in mangrove sediments, this chronic pollution due to the original oil spill is likely to last many more years. The chemical composition and toxicity of the oil has changed considerably, so that chronic effects may be less than those observed soon after the oil spill.

During December 1988 and June 1990 an unestimated amount of diesel fuel spilled into Bahía Las Minas from a storage tank at an electricity generating station (Fig. 1). Three study sites may have been affected by these additional spills.

After the 1986 spill much oil sank and became incorporated in sediments and coral tissues. Initial collections for chemical analyses of hydrocarbons at heavily oiled reefs were made 4 mo after the spill, and still showed average concentrations per reef of up to 406 μg oil/g dry wt. of sediment. The values were higher than reported for sediments near oil depots in the Persian Gulf, although lower than "hot spots" in the Gulf of Paria, Trinidad. By 1990 oil concentrations in reef sediments had decreased, but traces of oil were still visible 4 yr after the spill. Oil concentrations in coral tissues in 1986 averaged 0.1 to 28.8 μg oil/mg EOM by UVF analysis, and subsequently declined to almost nondetectable levels during 1988-1989 and 1990.

The dispersant Corexit 9527 was both observed and reported to have been applied mostly offshore in May 1986, and always >2-3 km away from the heavily oiled reef at Punta Galeta. Thus, its use cannot have been a major factor in the effects of oil at Punta Galeta, but may have contributed to effects observed at other oiled reefs in Bahía Las Minas.

After the spill oil concentrations in reef sediments and coral tissues declined at oiled reefs while sedimentation rates increased. Oiling and sedimentation are confounded as potential factors causing deleterious effects on reef corals; their relative contributions may have paralleled their levels through time in reef environments.

Components of Research

Cover of Sessile Organisms

Coverage of sessile organisms was measured in quadrats placed along transects perpendicular to the shore at each reef. Reefs were visually classified as heavily oiled (six), moderately oiled (two), and unoiled (four); of these reefs, six had been surveyed before the spill (one heavily oiled, one moderately oiled, and four unoiled). Quadrats from all transects on each reef were pooled into two depth intervals:

Table 4 Percent days when oil slicks were observed above the study reefs from August 1987 to December 1992. Numbers of observations are in parentheses. Reefs are listed from east to west within each category of oiling.

	Percent Days With Oil Slicks[1]				
Reef	1987	1988	1989	1990	1991
Unoiled					
JUG	17 (6)	0 (18)	0 (31)	0 (41)	0 (24)
PALW	0 (7)	0 (18)	0 (30)	0 (37)	4 (26)
DMA	0 (6)	0 (16)	0 (26)	0 (28)	0 (27)
DONR	0 (6)	0 (14)	0 (26)	0 (30)	0 (26)
Moderately Oiled					
NARS	8 (12)	36 (28)	24 (38)	52 (42)	29 (31)
MAR3	0 (2)	0 (7)	0 (25)	0 (27)	4 (23)
Heavily Oiled					
PM	30 (10)	68 (19)	59 (39)	65 (63)	35 (40)
PAYN	67 (12)	92 (40)	69 (45)	79 (72)	77 (44)
PAYW	33 (3)	82 (11)	78 (46)	85 (65)	79 (43)
LRE1	25 (4)	100 (7)	65 (34)	71 (55)	80 (35)
LRE2	22 (9)	82 (39)	55 (54)	63 (75)	67 (46)
GALC	80 (10)	81 (21)	23 (47)	21 (78)	11 (46)

[1] Oil is commonly observed every day, the entire year, in different areas of Bahía Las Minas.

0.5-3 m (shallow) and >3-6 m (deep). The typical number of quadrats per reef was 120. Data analysis for coral cover, numbers and sizes of colonies, numbers of species, and Shannon-Wiener diversity H' (based on percent cover of corals and on number of coral colonies) per m^2 was done using single mean values for each depth interval on each reef.

Differences between 1985 and 1986, 4 mo after the oil spill, revealed extensive effects of the spill; total coral cover decreased by 76% at 0.5-3 m and by 56% between >3 and 6 m at the heavily oiled Punta Galeta reef (Fig. 15). The decrease was less at the moderately oiled reef, and coral cover generally increased or stayed the same at the four unoiled reefs. The average size of coral colonies between 1985 and 1986 also decreased significantly in relation to oiling and depth, whereas the number of colonies did not. This suggests that more corals suffered partial mortality, and thus decreased in size and total cover, than died outright. Similarly, diversity based on coral cover decreased on oiled reefs, whereas diversity based on number of colonies was unchanged as a function of oiling. No major reduction in the number of species was observed.

Postspill monitoring of 12 reefs closely matched the pattern observed on the six reefs surveyed both pre- and postspill. The principal change in pattern by the 1988 monitoring was a striking decrease in coral cover, size, and diversity at unoiled

Fig. 14 Aerial photograph of oil slicks moving out of a partially deforested mangrove area, and coastline erosion 3 yr after the oil spill (by C. Hansen).

reefs (Fig. 15). Despite the decrease in coral cover throughout the study region, differences between oiled and unoiled reefs persisted.

Differences between 1985 and 1986 did not reveal extensive effects of oil in other groups of sessile organisms. Macroalgal cover did not change immediately in response to the oil spill, although an increase in crustose coralline algae was nearly significant on the oiled reefs at both depths.

Recent Injury of Corals (Partial Mortality)

Quarterly surveys of recent injuries to four common coral species were made postspill along transects parallel to the reef crest at two shallow depths (0.5-1 and >1-2 m). Sizes of coral colonies were measured and proportions of recent injuries (bare or gouged white skeleton) were estimated.

Both the frequency and size of recent injuries increased substantially during 1986 with the amount of oiling, particularly at the shallower depth. *Siderastrea siderea* was affected more than *Diploria clivosa* and *Porites astreoides*. Variation

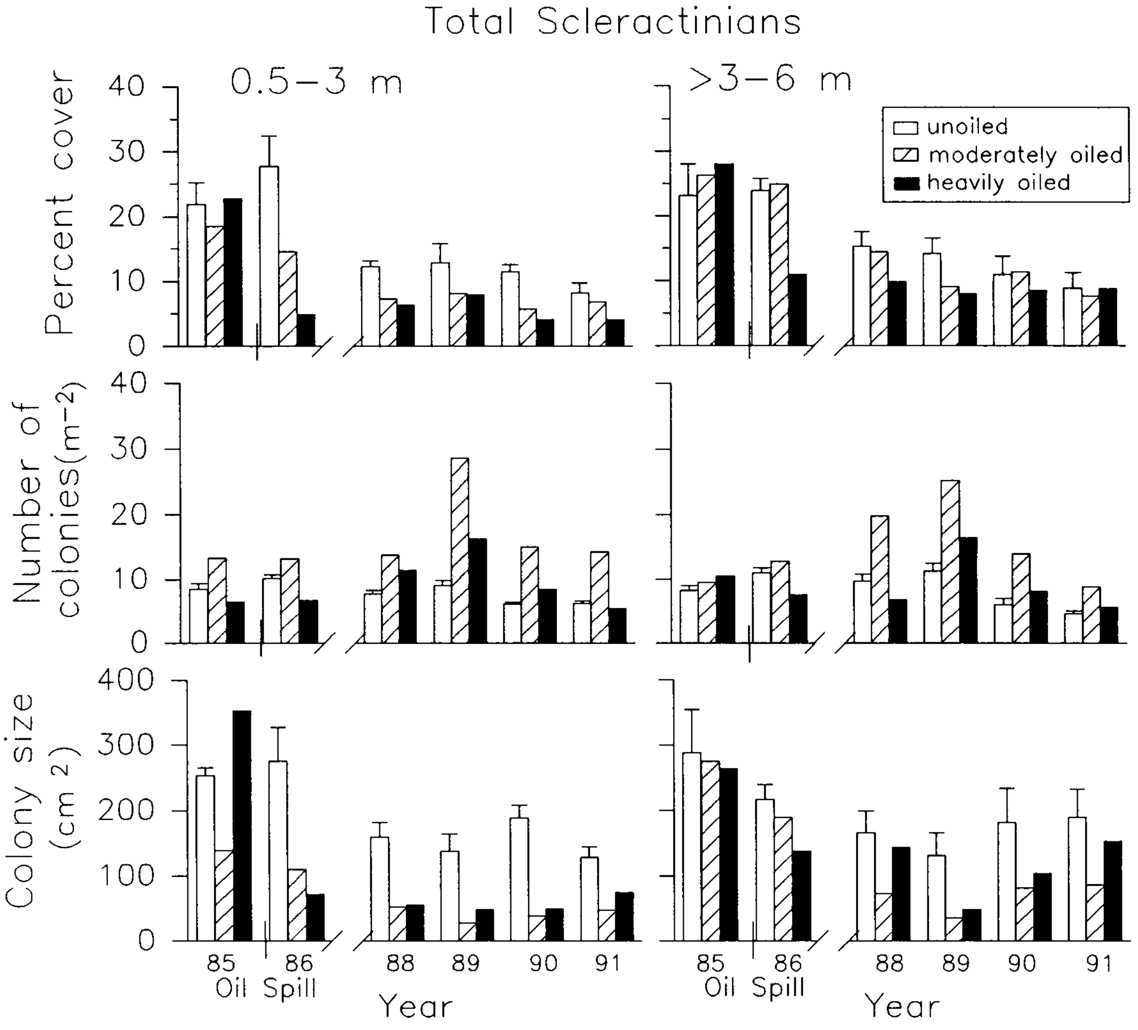

Fig. 15 Changes through time in mean number and size of coral colonies and percent cover of all coral species combined in relation to the degree of oiling from the 1986 spill and depth for four unoiled, one moderately oiled, and one heavily oiled reef for all years. The time of the oil spill is indicated by the *vertical line*. SE is shown for the four unoiled reefs, except when smaller than the symbols used.

through time in total recent injury indicated that colonies were most affected at heavily and moderately oiled sites during the first year after the spill, and then again beginning in June 1989 until the final census in March 1991 (Fig. 16). At times, two coral species showed a significant correlation between the percentage of injured colonies and the concentration of hydrocarbons in reef sediments (Fig. 17).

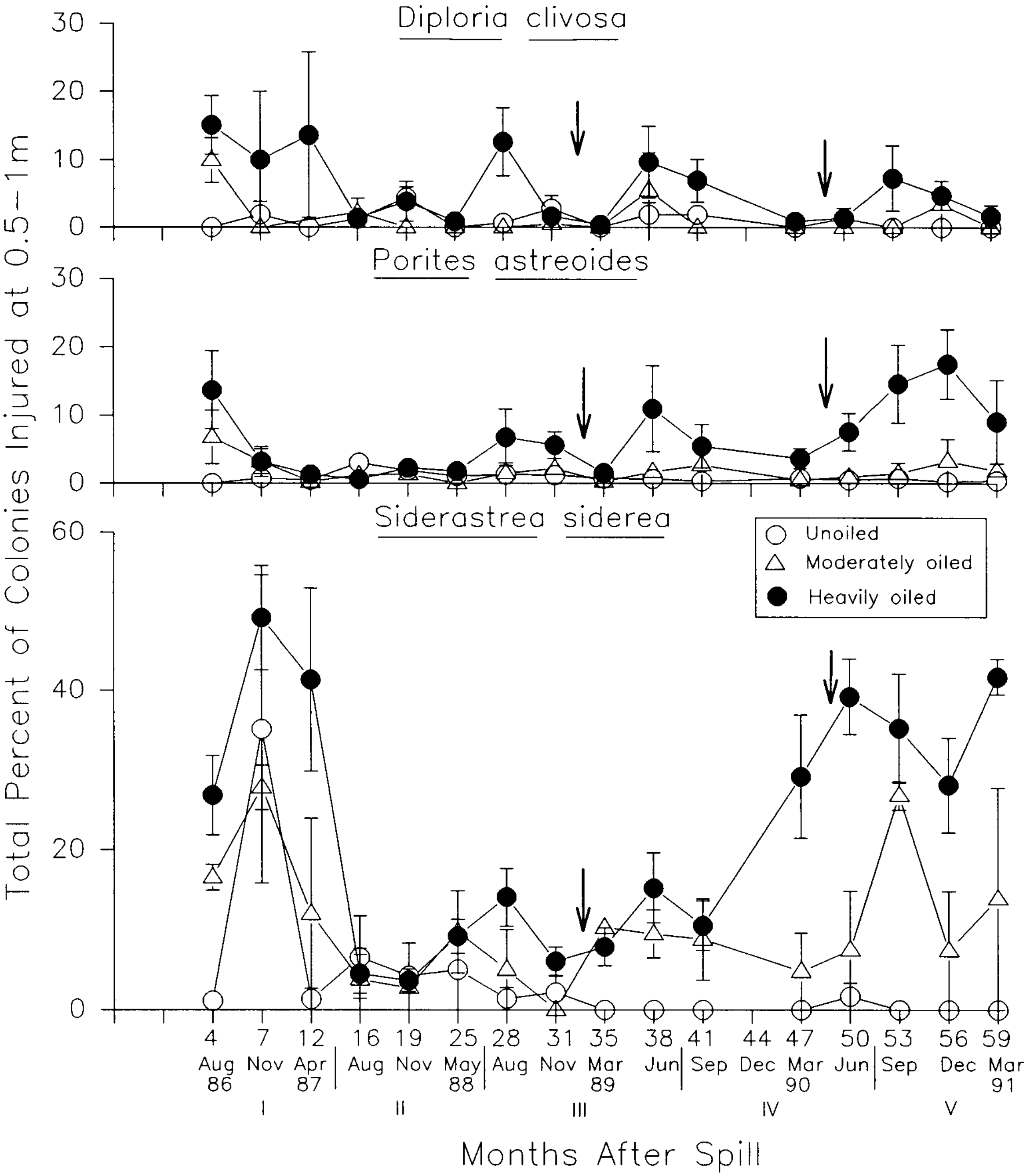

Fig. 16 Changes through time in the percentage of recently injured corals in relation to the degree of oiling and depth (0.5-1 m) from August 1986 to March 1991. Error bars are 1 SE. *Vertical arrows* indicate the 1988 and 1990 diesel spills. The *vertical lines* at the bottom indicate the pooled surveys used for statistical analyses.

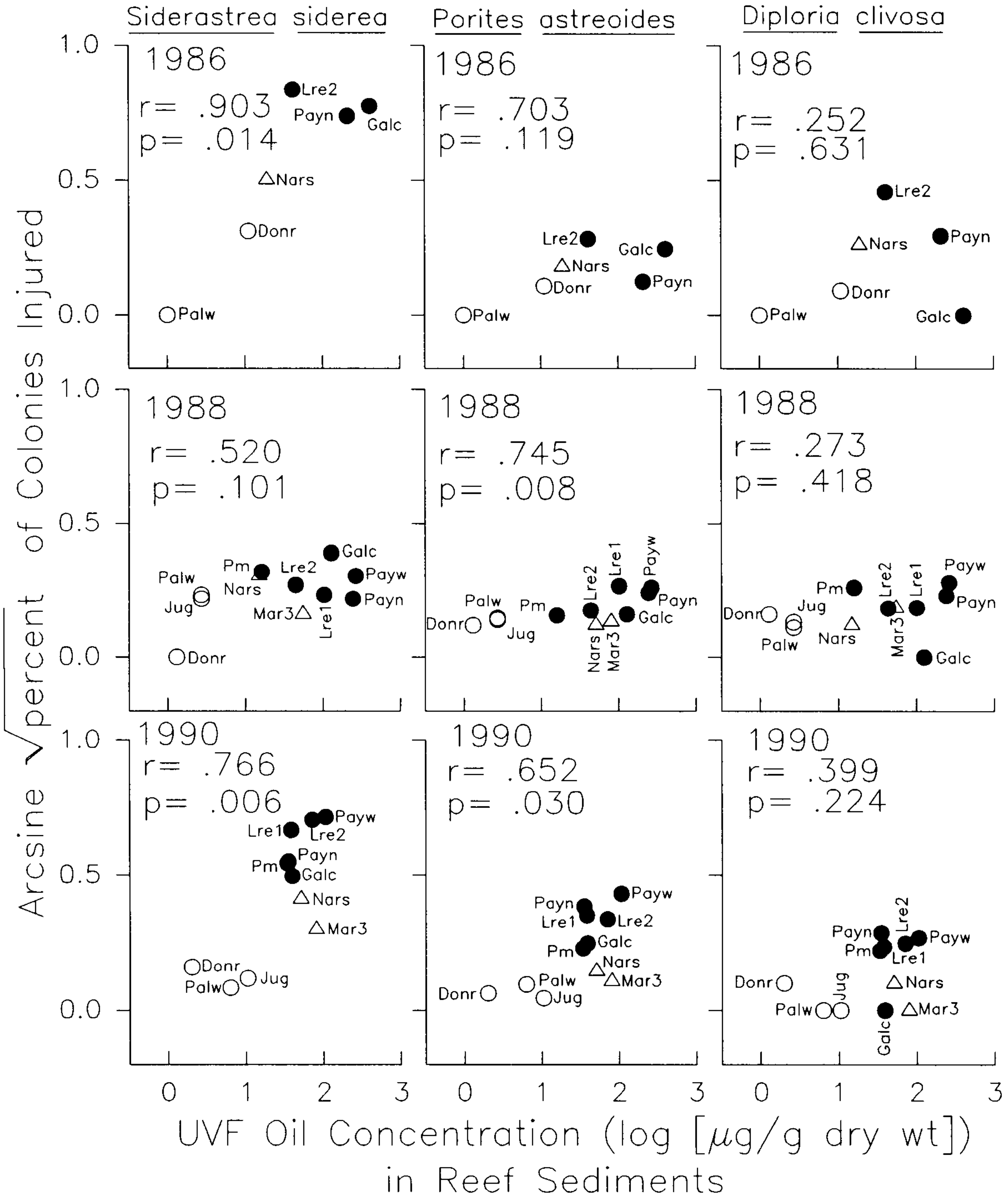

Fig. 17 Relationship between percent of colonies injured and oil concentration in reef sediments during 1986, 1988, and 1990 for *Siderastrea siderea*, *Porites astreoides*, and *Diploria clivosa*. Notice that the correlation for *S. siderea* was not significant during 1988.

Resistance of Corals to Stress

Responses of two common coral species to stress were compared at oiled and unoiled reefs. Rasping and air-blasting injuries approximately 6 cm^2 were inflicted on the same colony, and then monitored photographically. This preliminary experiment indicated that *Porites astreoides* usually regenerated faster than *Siderastrea siderea*, regeneration at oiled reefs was faster than at unoiled reefs, and that rasping injuries regenerated faster than tissue lesions with intact skeletal microstructures.

Coral Growth (Sclerochronology)

Growth rates (skeletal extensions) were determined from the width of annual growth bands for four common coral species. Data were obtained from photographic prints of x-radiographs of sections cut parallel to the growth axis of coral skeletons. Three sets of samples were collected. In 1987, 190 colonies were collected from 11 reefs (four unoiled, two moderately oiled, and five heavily oiled) to compare growth during the year of the spill (1986) with the 9 yr prior to the spill. Specimens of two species were collected at the end of 1988 and during 1989 to examine growth 3 yr before and 3 yr after the spill.

Growth rates during the year of the spill compared with growth over the previous 9 yr were reduced at moderately and heavily oiled reefs relative to unoiled reefs for *Montastrea annularis* and *Diploria strigosa* (Fig. 18); growth of *Porites astreoides* was reduced at heavily oiled reefs relative to moderately oiled and unoiled reefs. *Siderastrea siderea* showed no pattern of variation in growth related to the degree of oiling by the spill. Growth after the spill declined significantly for *S. siderea* but not for *P. astreoides* at heavily oiled reefs. Although *P. astreoides* showed an initial reduction in 1986 but no effect 2 yr later, the reverse was true for *S. siderea*. Both species showed significant negative correlations between growth rate and the concentration of oil in reef sediments in both 1986 and 1988 (Fig. 19); negative trends in 1986 for two other species were not significant.

Coral Reproduction

Siderastrea siderea, the dominant reef-building coral of the region, was chosen to evaluate sublethal effects of oil pollution on coral reproduction. *S. siderea* is gonochoric (separate sexes) and broadcasts gametes into the water column where fertilization and embryogenesis occur. In Panama there is one reproductive cycle per year, and the spawning season is most likely after the September full moon. Two unoiled and two heavily oiled reefs were sampled monthly for more than 1 yr starting more than 3 yr after the spill. Coral tissues were decalcified and prepared for histological sections. Gonads were counted, classified according to developmental stage, and measured in cross section. An additional collection was made about 4.5 yr after the spill at a heavily oiled reef, taking tissue samples from injured and healthy areas of the same colonies.

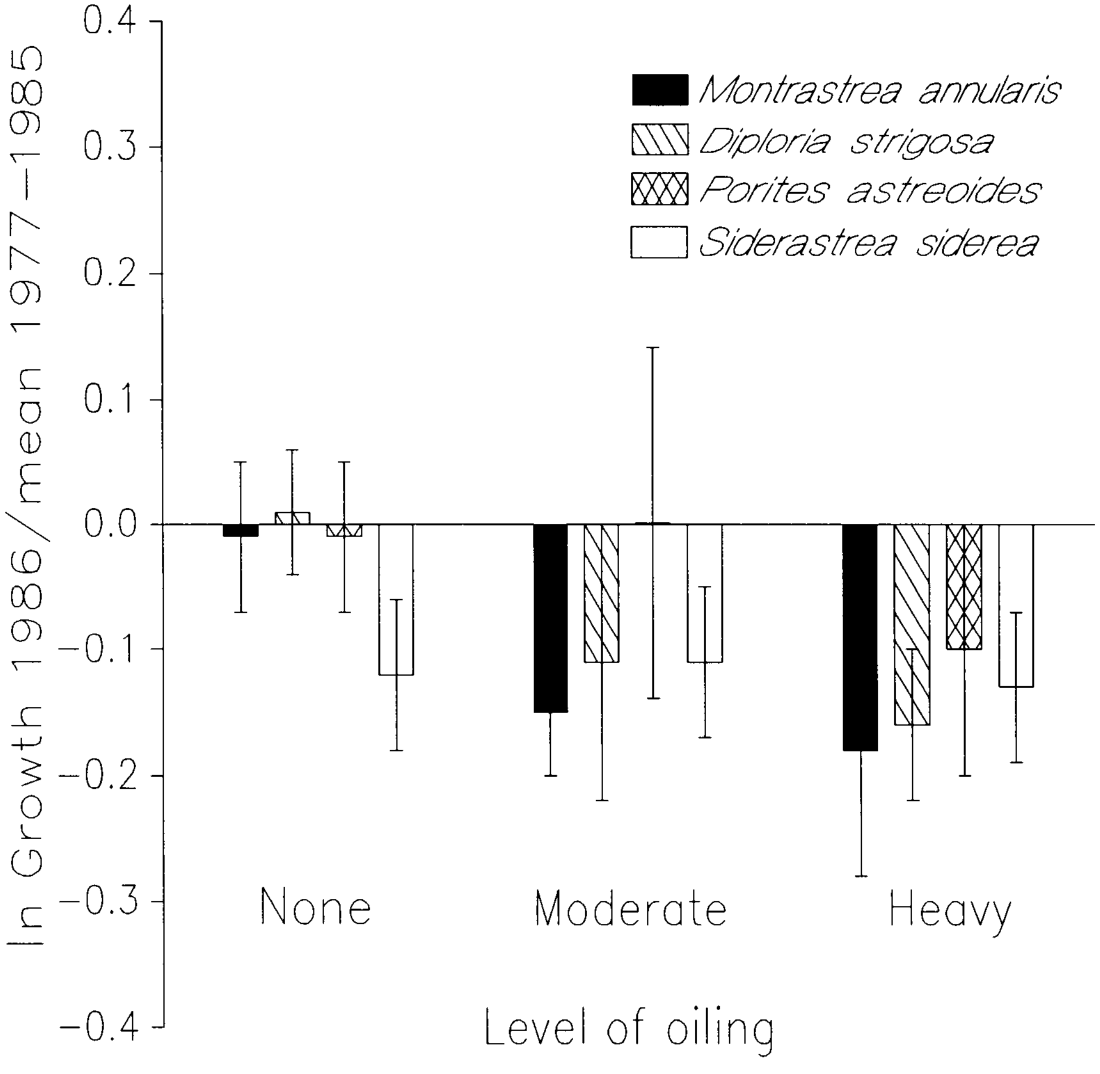

Fig. 18 Mean growth and SE of four species of corals in 1986 relative to their mean annual growth during the nine previous years in relation to exposure to oil during the 1986 spill. Data include only those corals with bands for the most recent 10 yr. Values below the *0.0-line* show that growth in 1986 was less than the average for the previous 9 yr.

Numbers of colonies with gonads and numbers of gonads per colony were not sensitive to level of oiling, but gonads were significantly smaller at oiled reefs than at unoiled reefs (Fig. 20). Injured areas of colonies contained significantly smaller gonads, and significantly smaller and fewer oocytes per gonad.

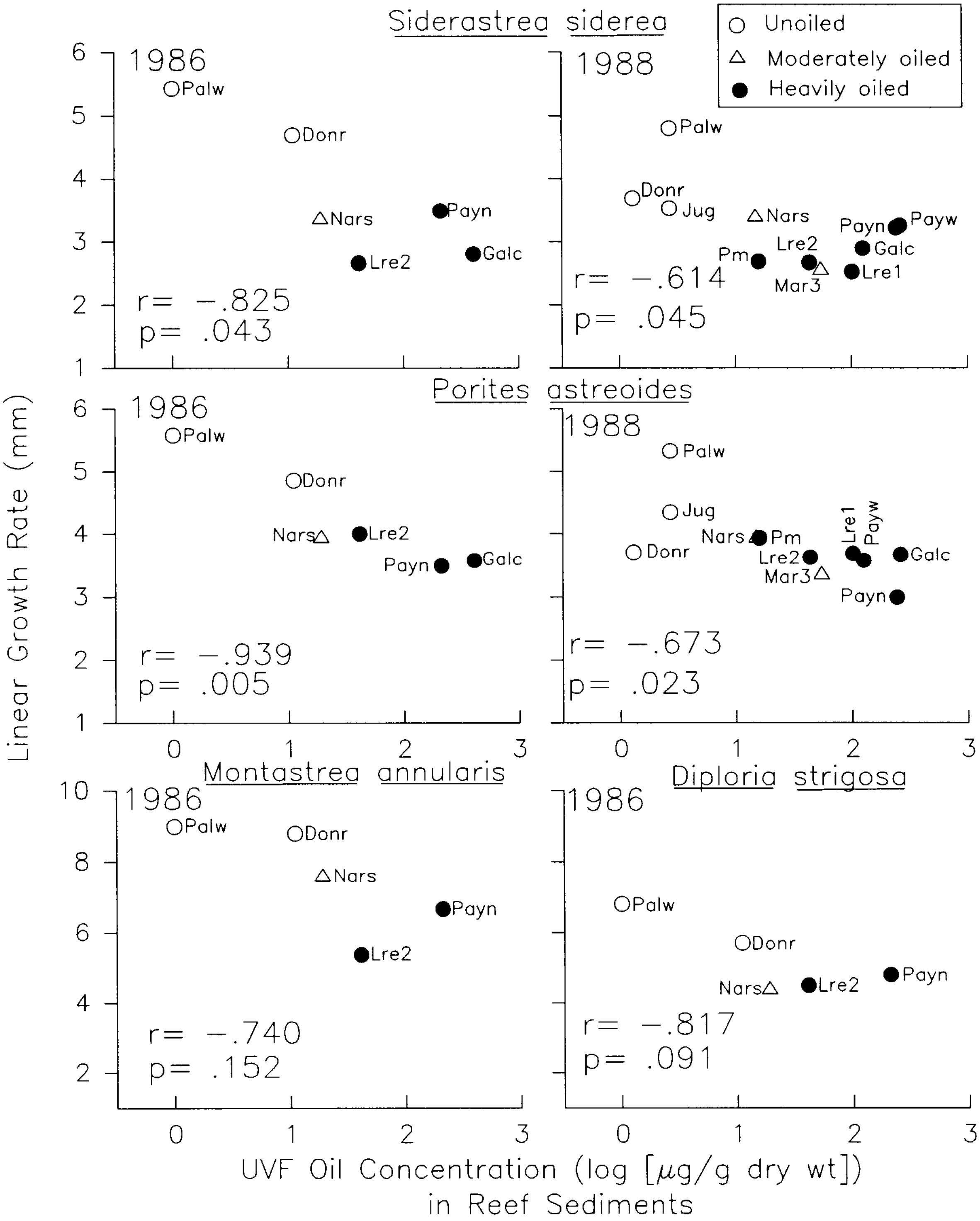

Fig. 19 Linear growth rates of *Siderastrea siderea*, *Porites astreoides*, *Montastrea annularis*, and *Diploria strigosa* vs. oil concentration in reef sediments during the year of the spill, and 1988 (only the two former species). Notice that the concentration of oil in sediments was always higher at the heavily oiled sites PAYN and GALC.

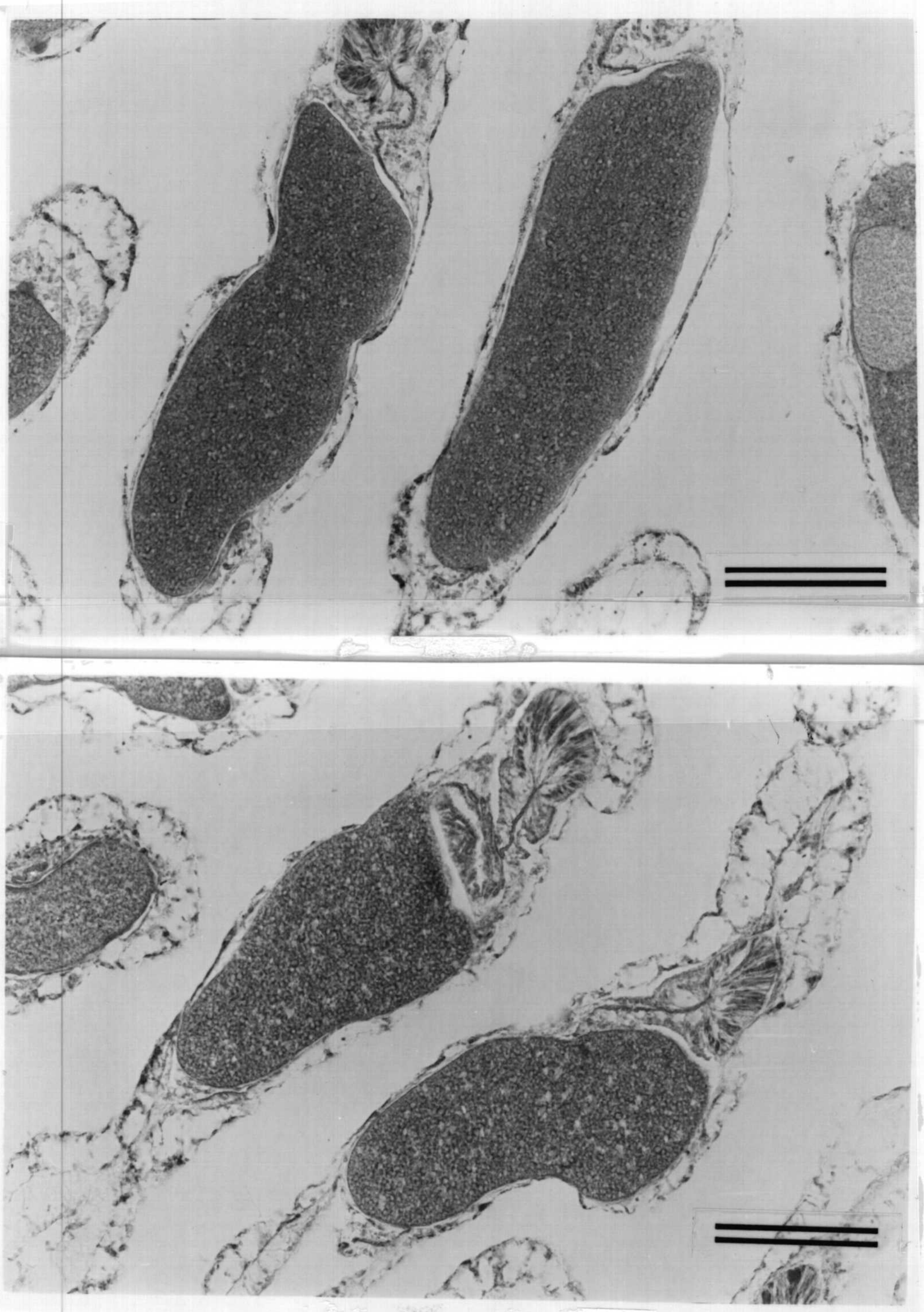

Fig. 20 Photomicrographs of histological preparations of *Siderastrea siderea* tissue showing cross sections of female gonads. Eggs are at stage IV of development at an unoiled reef (*top*) and a heavily oiled reef (*bottom*). Notice that egg area is greater at the unoiled reef. Specimens were collected at the same time. Scale bar = 100 µm.

Coral Recruitment

Four unoiled and six heavily oiled reefs were surveyed for recent recruitment in September 1991, 5.5 yr after the oil spill. The total number of new individuals apparently derived from sexually produced larvae and less than 4 cm in diameter were counted along transects at two depths (1.5-3 and 4.5-6 m). Density of coral recruits was significantly higher at unoiled reefs than at oiled reefs (Fig. 21). Eighteen species of recruits were identified, most of which are brooders; recruits of 7 of the 18 species were not observed at heavily oiled reefs.

Abundances of Herbivores

Sea urchins and three families of herbivorous fishes were counted along transects at four depths at oiled and unoiled reefs in 1990 or 1991 because these groups are known to have a major influence on recruitment, growth, and maintenance of coral populations. Sea urchins were more abundant on oiled reefs, but the differences were not significant. The relative abundance of nonterritorial surgeonfishes and parrotfishes was significantly higher at unoiled reefs than oiled reefs, whereas territorial damselfishes were more abundant at oiled reefs.

Discussion and Conclusions

Does Oil Affect Reef Corals?

Results of this study demonstrate by several methods deleterious effects of oil pollution on Caribbean reef corals. These effects include: (1) reductions of live coral cover, abundance, and diversity to 6 m depth immediately after the spill; (2) a strong, positive correlation between injured corals and oiling and, more directly, with the concentration of hydrocarbons in the environment for some species; (3) a decrease in coral growth rates on oiled reefs during the year of the spill and 3 yr thereafter, as well as a negative correlation between growth of two coral species and the concentration of oil in reef sediments during the year of the spill (1986) and 2 yr afterward; (4) a decline in fecundity of the important reef-building coral *Siderastrea siderea* on oiled reefs, as measured by size of gonads in surviving colonies 5 yr after the oil spill; and (5) little prospect for rapid reef recovery, as indicated by very low coral recruitment rates on heavily oiled reefs.

Effectiveness of Different Assays of Environmental Effects on Coral Reef Communities

Different techniques vary greatly in utility for assessment of environmental effects on coral reefs. The present study confirmed the danger of inference based on laboratory or small-scale field experimental studies of effects of oil on corals. Experiments to test effects of chronic oiling must apply oil with seawater over many months or years.

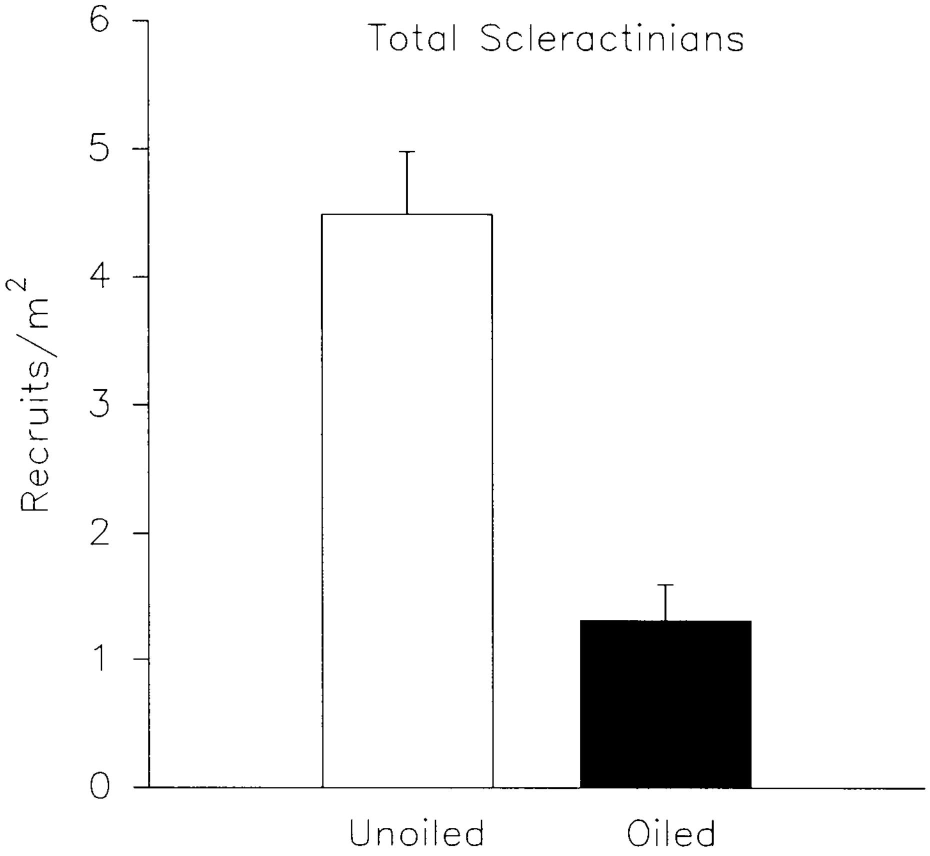

Fig. 21 Mean number of recruits (all scleractinians combined) per m^2 at unoiled and oiled sites. Total reef area surveyed was 480 m^2 and 720 m^2 at unoiled and oiled reefs, respectively.

The approaches used in this study differ in their difficulty and effectiveness for detection of responses of corals to oil, particularly with regard to possible differences among species. Most difficult and least effective are surveys of distribution and abundance to measure changes in populations and communities. Nevertheless, measurement of population and community parameters is essential as the only assay of the consequences of oil pollution for an ecosystem. Monitoring of community composition would have been far more effective and useful if combined with repeated observations of marked corals or fixed quadrats. Such methods are necessary to obtain data on changes in processes affecting coral populations that cannot be obtained from randomized transect methods.

The simplest and most sensitive technique was the survey of recent injuries. Reproductive condition during the spawning season and recruitment onto natural substrata also provided simple, yet highly sensitive measures of effects of the oil spill. These data are of particular importance for projection of possible scenarios of reef community recovery.

Problems of high variance and adequate replication complicate measurement of effects of oil on growth rates of corals in the field using sclerochronology, but the potential for powerful retrospective analysis makes this technique worth the effort. A better approach to measuring growth effects would be the construction of master-index chronologies of growth for populations of large corals using several cores that span at least 50 yr. This procedure can help factor out local variations in growth from coral to coral, due to considerable differences among individuals on the same or nearby reefs, while preserving variance due to pervasive changes in environment (climate change, dredging, oil spills, etc.).

General and Specific Oil Effects

The oil spill affected various coral species differently. Results of this study lend further support to the claim that branching corals are most sensitive to human disturbance. Among massive forms, there were considerable differences among species in the degree of injuries associated with oiling, and variation in growth associated with the spill showed further interspecific differences often unrelated to those seen for injuries. Unraveling these patterns would require far more knowledge of coral physiologies and life histories.

Reef Recovery

Assuming that larvae are available at least some of the time and that sexual reproduction is the primary mode of repopulation by corals in Bahía Las Minas, we would expect a slow shift toward greater relative abundance of brooding species, including agariciids, poritids, and perhaps small species like *Favia fragum* and *Siderastrea radians*. In this case, several decades might be required to develop populations similar to those before the oil spill. Alternatively, repopulation may occur chiefly by growth and asexual proliferation of surviving portions of colonies, which are rare but do occur on oiled reefs. Assuming these remnants continue to survive and grow at normal rates, which is less likely for smaller colonies than larger colonies even in the absence of oil, equivalent populations might become established in 10-20 yr. These estimates are minimal, however, based on the unlikely premise that chronic oil pollution and other events will not further depress coral populations, as occurred at all the unoiled reefs between 1986 and 1988.

General Conclusions

Effects of the oil spill on corals in Bahía Las Minas were severe, and populations have not begun to recover after 5 yr (Fig. 15). Levels of injury are still as high as just after the spill, sexual reproduction (Fig. 20) and larval recruitment (Fig. 21) are reduced, and there has been virtually no recruitment of most formerly dominant coral species. Likewise, reduced populations of grazing fishes imply that macroalgal populations will increase and overgrow the few surviving corals.

Mangrove Forests

Introduction

Mangrove forests comprise a diverse group of specialized rainforest plant species that grow along subtropical and tropical shores between mean sea level and highest spring tides. In the Caribbean, this range is often less than 0.5 m, but mangroves sometimes are many kilometers wide, especially near large estuaries and rivers. Mangroves interact with and serve as a buffer between terrestrial and marine environments and can be viewed as both a sink for runoff from the land and protection against coastal erosion, and a habitat with high primary production and nursery grounds for fisheries.

Mangroves have a unique combination of adaptations, including the ability to grow in seawater, specialized root structures for both physical support and for breathing air, and buoyant propagules for dispersal by sea currents. The red mangrove, *Rhizophora*, is viviparous (live-bearing) and releases large, buoyant propagules that have well-advanced primary root structures and large amounts of food reserves. These attributes promote rapid seedling development as soon as conditions are suitable.

Large oil spills in tropical coastal areas may disrupt these processes (see Duke and Pinzón, Chap. 8, Vol. II). When exposed roots, lower trunks, and surrounding substratum become oiled, many trees die from either suffocation or toxicity, depending on the type and condition of oil. Widespread death of trees creates deforested gaps, here called *oil gaps*, among surrounding areas of surviving trees. Oil gaps are different from other kinds of forest gaps because oil often remains in the environment long after a spill and may retard the establishment and growth of new trees.

The 1986 Spill at Bahía Las Minas

The 1986 oil spill at Bahía Las Minas took place in three main phases. First, after oil overflowed retaining facilities it was held temporarily in the central, mangrove-lined embayment (Fig. 1). The effect of the spill on mangroves was most severe in this embayment, and approximately half the area of mangroves was killed within 2 mo. Trees probably died from a combination of toxic and suffocating effects, and few trees remained alive from the water's edge to half-way up the intertidal zone. The second phase of the spill occurred several days later when rainfall coupled with a temporary wind shift washed floating oil over retaining booms and out to sea. Fianlly, oil was then redeposited on other mangroves, extending from Punta Galeta to Punta Muerto and, to a lesser extent, farther up the coast. In this later phase the effect of the spill was patchy, and many oiled sites faced the open sea. With few exceptions, these sites were characterized by bands of deforestation behind rows of one or two surviving trees bordering the water.

Oil has remained in mangrove areas long after the spill, mostly trapped in anaerobic sediments. There now appear to be myriad pockets of oil in the substratum, comparable to a giant, oil-soaked sponge. Walking on the surface still causes oil to ooze out, and heavy rains disturb and flush out these pockets, causing new slicks. Therefore, biological effects of this spill are expected to persist for some time because areas of deforestation must regenerate in the presence of residual oil (Fig. 22).

The 1986 spill killed approximately 64 ha of mangrove forests dominated by *Rhizophora mangle*. The total area of sublethal effects is expected to extend much further, possibly up to 500 ha. Studies were divided into three major parts: describing the primary effect of deforestation, recovery of deforested areas, and the status of surviving forests surrounding oil gaps. Because of the extent of planting conducted by the refinery in 1986 and 1987, the possible benefit of such intervention was also evaluated.

Another Large Spill in Bahía Las Minas in 1968

In December 1968 the tanker *Witwater* broke in half in the middle of Bahía Las Minas, releasing 15,000-20,000 bbl of diesel and Bunker C fuel oil. The coastline was oiled from Isla Margarita and the Panama Canal breakwater to shores east of Bahía Las Minas (Fig. 1). While the effect of this spill on mangrove trees was not reported at the time, damage was assessed during the present study when examination of aerial photographs taken in 1973 revealed large areas of deforestation similar to those seen in aerial photographs of the 1986 spill taken in 1990. The extent of this effect, similarities with the present spill, its occurrence in the same bay, and the fact that mangrove trees are long lived all meant that it was essential for the present study to include an appraisal of *Witwater* deforestation and forest recovery.

Objectives, Rationale, and Design

From the beginning of studies in 1989, we emphasized processes in the ecosystem to better assess habitat recovery, how long this might take, and whether rehabilitation was beneficial. Two major discoveries, a technique for aging *Rhizophora* seedlings and the *Witwater* deforestation, provided unanticipated assistance with the major objectives: (1) to delineate the extent of mangrove forests and of deforestation in and near the area of the oil spill and (2) to study forest structure, recruitment, and growth in both deforested and surviving oiled forests.

Study Area and Vegetation Maps

The study was conducted chiefly in the vicinity of Bahía Las Minas, but also extended north of Portobelo to Isla Grande (Fig. 1). The bay is densely fringed with mangrove forests growing in a variety of habitats, from exposed coastal sites behind reef flats to those bordering tidal channels and farther upstream along freshwater-

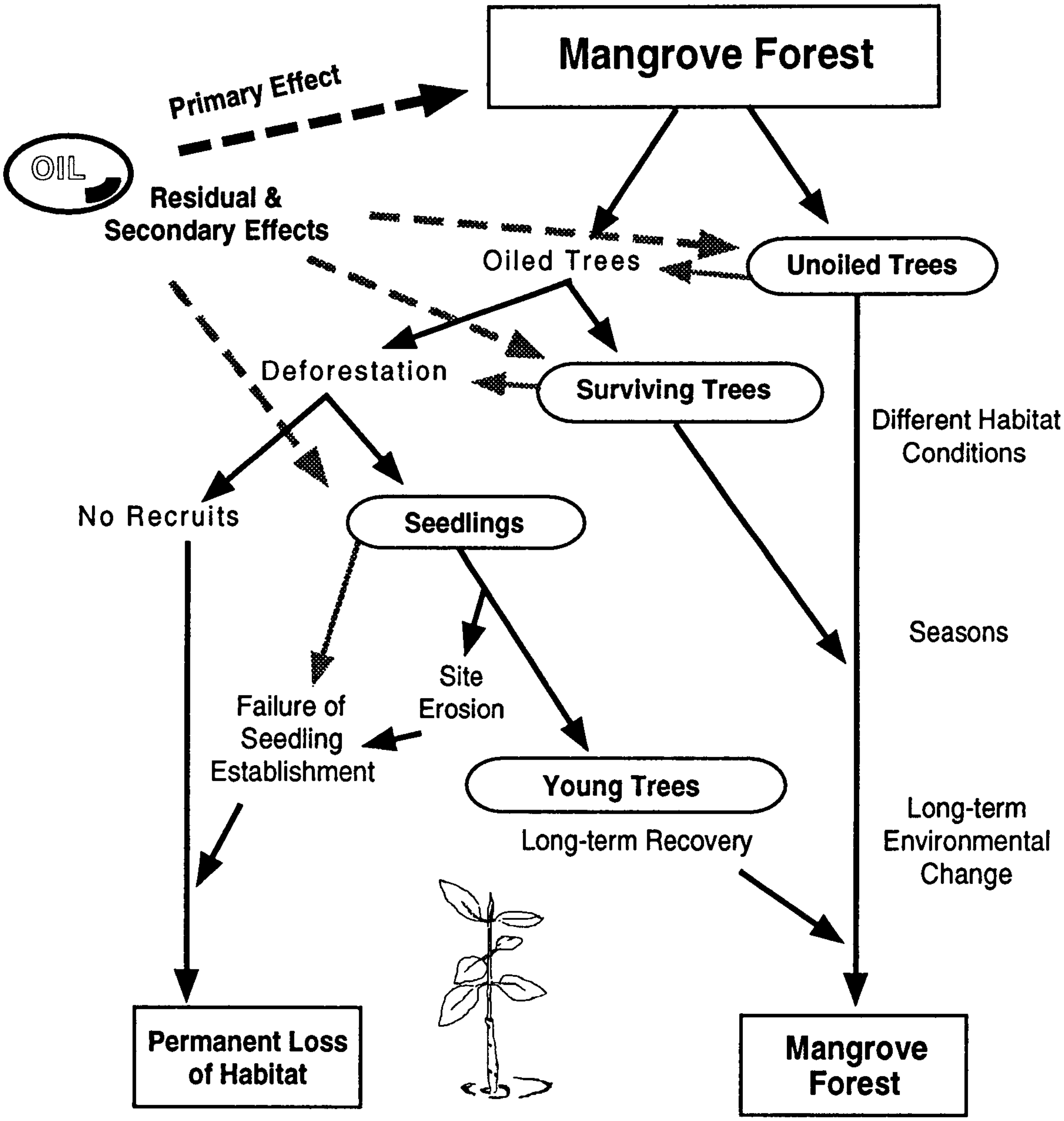

Fig. 22 Schematic diagram depicting the primary and secondary effects of a large oil spill on mangrove forests, and the major paths to either recovery (*solid arrows*) or permanent loss of habitat (*narrow dashed arrows*). This study paid particular attention to both seedlings in oil gaps and mature trees that survived oiling. During the recovery process, which may take several decades, mangrove forests are also subject to natural fluctuations in environmental conditions, further influencing their recovery.

dominated estuarine reaches. Parts of these forests have been altered and removed for port and industrial development but, otherwise, their chief use includes fishing, scavenging, and cutting of mangrove saplings at a subsistence level.

Study sites were chosen mainly in coordination with ongoing studies of mangrove roots (next section) and hydrocarbons in mangrove sediments. Sites included both oiled and unoiled areas of mangroves in two major habitat types in Bahía Las Minas, exposed, open coast fringing forests backing shallow reef flats and sheltered forests fringing channels that bordered deeper embayments. A third habitat, unaffected by oiling, was sheltered forest fringing rivers and bordering streams that were influenced by frequent runoff. Oiled streams (next section) did not have sufficiently low salinity to affect forest characteristics, although root epibiota differed from the community found in channels. Sites were included in river habitats for further comparison, especially because of the influence of salinity on growth of mangrove trees.

Using aerial photographs, outlines of mangrove forests and other features were drawn on transparent acetate film. Areas were categorized as mangrove, oil gaps, other deforestation, intertidal bare areas, natural upland areas, roads, major buildings, and port facilities.

Mangrove Species, Forest Structure, and Allometric Relationships

Most studies were of *Rhizophora mangle*, the red mangrove. This species dominated lower intertidal areas of extensive deforestation, although a small number of four other species were also affected or in close proximity: *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), *Pelliciera rhizophorae*, and *Conocarpus erectus* (buttonwood mangrove).

Forest structure was assessed for both seedlings and trees. Seedlings in fixed plots were tagged and scored for hypocotyl height, total height, diameter just above the hypocotyl, node count, and species. Tree structure was characterized by measurements of tree height, girth, basal area, and stem density. For seedling growth there was a problem in comparing oiled and unoiled sites because controls (unoiled gaps) should have been set up at the time deforestation took place in 1986. The present work relied instead on finding reforested sites resulting from either cutting by local fishermen or natural light gaps.

Estimates of total biomass of *R. mangle* were calculated from existing allometric relationships and additional ones developed during the study. In particular, total leaf area is a measure of the photosynthetic ability of plant communities, and thus represents a measure of forest well-being.

Seedling Growth and Demography

Seedlings were monitored using marked plants to follow individual growth and fixed plots for demography. In late 1989 *Rhizophora mangle* seedlings were tagged in light-gaps in both exposed and sheltered habitats, and oiled and unoiled areas.

Each seedling was scored for various physical parameters. All sites were revisited, starting in late 1990, and the same parameters were scored again. The demographic study of seedlings commenced in April 1990; all seedlings in 12-m^2 plots were tagged, numbered, and scored for species, total height to the topmost leaf node, hypocotyl height, girth just above the hypocotyl or established prop roots, and total number of nodes along the main stem (Fig. 23). Sites were revisited in June-July 1991 and the seedlings were retagged and rescored in the same way.

Growth was also studied using some small trees that had colonized an area of landfill, and in an experimental study of tagged seedlings in artificial light gaps.

Condition and Growth of Tree Canopies

Canopy growth and condition of mature *Rhizophora mangle* were based on studies of litter fall and observations of upper-canopy shoots. These studies were conducted concurrently at approximately monthly intervals at sites from Isla Margarita to Isla Grande (Fig. 1). Litter fall was measured using 1-m^2 traps constructed of mesh attached to a frame; litter was sorted to categories including leaves, interpetiolar stipules, wood, immature buds, mature buds, flowers, immature fruit, mature fruit, immature hypocotyls, mature hypocotyls, expended fruit, and miscellaneous debris. Leafy-shoot replicates of *R. mangle* were tagged in the uppermost canopy of trees at all sites, and scored monthly for shoot status, noting node positions of particular leaves, branch shoots, and reproductive parts in various stages of development. From these data various parameters were calculated, including leaves per shoot, leaf production, and leaf fall.

Trials to Estimate Canopy Herbivory

An exploratory study was set up to test a method that might exclude at least crabs, and thus provide a means to estimate their contribution to overall herbivory. Crab-excluders consisted of plastic dinner plates cut to the center and placed on stems. After a year damage to new leaves on experimental branches was noticeably less than on neighboring unmanipulated branches. This method therefore appears effective and may contribute to future studies.

Environmental Factors and the Amount of Residual Oil in Sediments

Salinity and water temperature fronting each of the sites were measured at approximately 20 cm depth monthly and are presented in Volume II. Monthly values of solar radiation and rainfall were obtained from the Galeta Marine Laboratory. Data on residual oil in sediments used in this study were chiefly those from the UVF method of determining oil concentration.

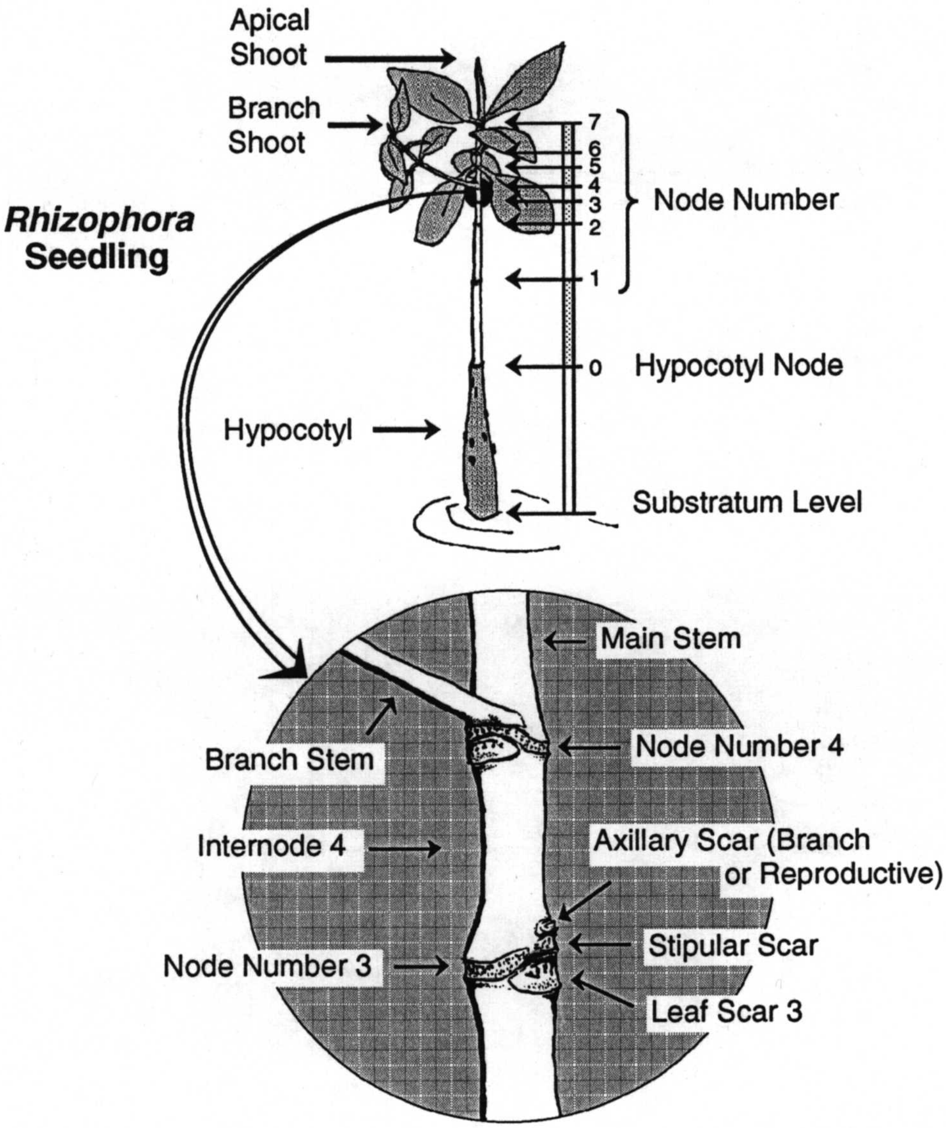

Fig. 23 Diagram of a *Rhizophora* seedling with a portion of the stem magnified to show the nodes and the hypocotyl. Note the node structure, each comprising three parts, of two leaf-petiole scars, two encircling stipular scars, and some axillary structures or their scars. Also included is the convention used for numbering leaf nodes and internodes from above the hypocotyl or "zero" node, up to the one positioned immediately below the apical shoot. In this example there are seven nodes along the main stem. Note also that approximately half the hypocotyl is beneath the substratum.

Deforestation and Mangrove Forests

Extent of Deforestation Caused by the Refinery Spill in 1986

Maps of Bahía Las Minas were drawn from aerial photographs, showing all oil gaps from the 1986 spill, the surrounding area and mangrove forests, and sites of major human development; one is shown as an example of the major patterns observed (Fig. 24). The 1986 spill caused extensive areas of deforestation, particularly in the northeastern-facing, shallow embayment on Isla Largo Remo shown in this map.

Changes Prior to 1986 – the 1968 Witwater *Spill*

Another series of maps, using the same layout, was based on 1973 photographs and shows the deforestation caused by the spill of the tanker *Witwater* in 1968. Differences in patterns of deforestation after the two major spills apparently are related to higher tides and stronger onshore winds at the time of year of the *Witwater* spill. Some areas have still not recovered, possibly because residual oil remains in the soil.

Comparing the Effects of Two Spills

Maps provide the most effective means of describing mangrove deforestation caused by large oil spills, and for comparing effects of different spills. The 1986 oil spill killed 64 ha of mangrove forests, approximately 7% of intertidal forested areas in the bay. Most of this area (69%) was concentrated in the central embayment where oil was first contained, and 23% was killed in the eastern embayment. By comparison, 46 ha, or 5% of total forested areas, were killed after the 1968 *Witwater* spill, and this area was concentrated in the western and central embayments (52% and 30%, respectively). Differences in specific patterns of deforestation were probably influenced by the different seasons and tidal regimes, as much as by the different sources and types of oil. Despite these differences, however, it is interesting to note the similarities, which include coastal fringing strips of deforestation approximately 50 m wide and often fronted by an isolated row of surviving trees along the original fringe, lens-shaped oil gaps on convex coastal margins, and funnel-like gaps at smaller stream entrances.

Condition of Mangroves Surrounding Deforested Areas

Forest Structure

It seemed likely that mangrove trees have a wider response to oiling than dying, and that oiled survivors may eventually recover from sublethal effects. One possibility is that oiled forests surrounding deforested gaps may become less dense.

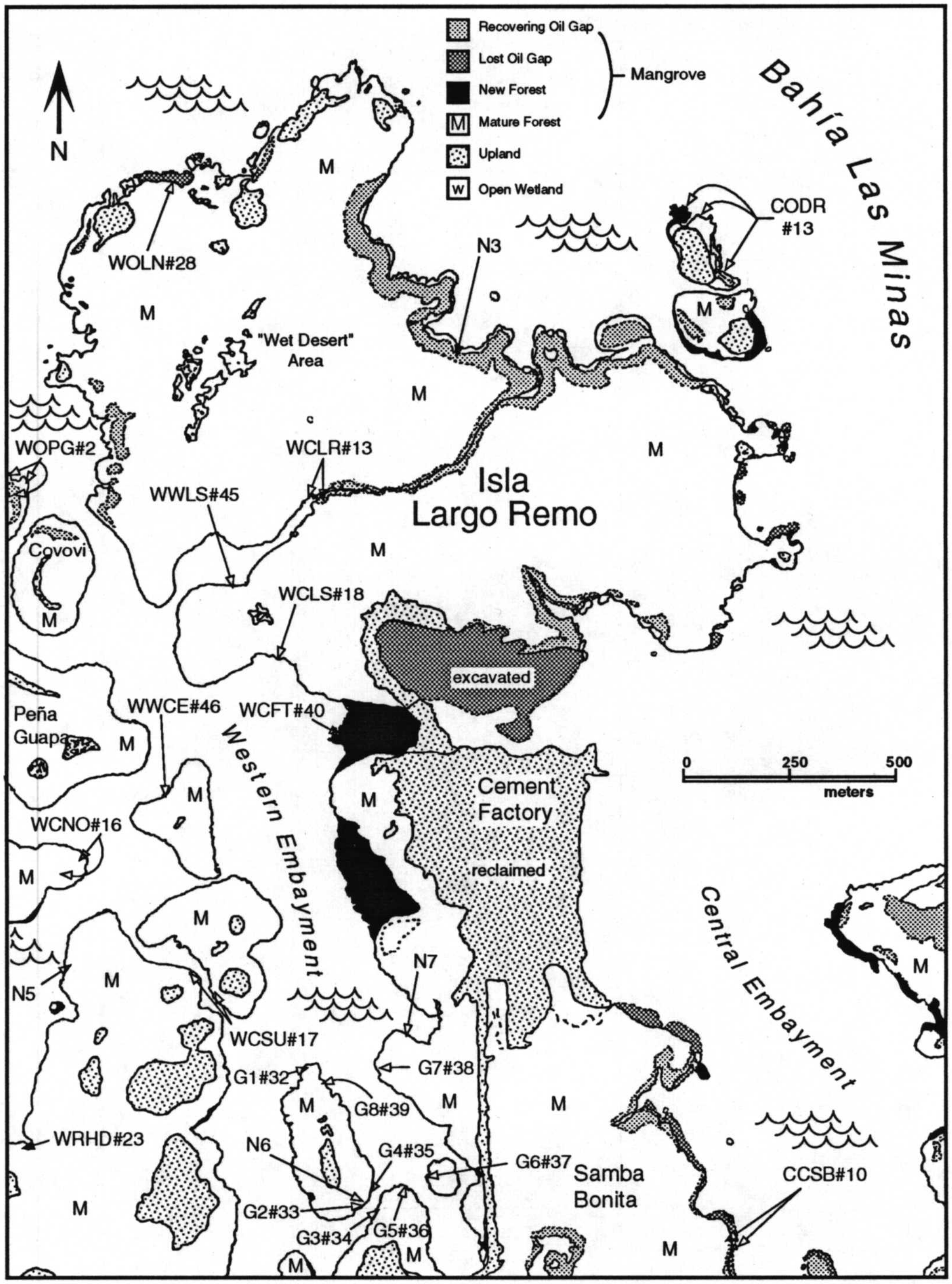
Recovering Oil Gap
Lost Oil Gap
New Forest
M Mature Forest
Upland
W Open Wetland
Mangrove
N
Bahía Las Minas
CODR #13
WOLN#28
N3
M
"Wet Desert" Area
WOPG#2
WCLR#13
WWLS#45
Isla Largo Remo
Covovi
WCLS#18
excavated
Peña Guapa
WWCE#46
WCFT#40
Western Embayment
0 250 500 meters
Cement Factory
reclaimed
WCNO#16
Central Embayment
N5
N7
WCSU#17
G1#32
G7#38
G8#39
WRHD#23
N6
G4#35
G6#37
Samba Bonita
G2#33
G3#34
G5#36
CCSB#10

Fig. 24 Map, (*previous page*) based chiefly on 1990 aerial photographs, showing major oil-deforestation patterns in mangrove forests following the 1986 refinery spill. It centers on the islands of Largo Remo and Samba Bonita, located in the middle of Bahía Las Minas. The legend includes: recovering and lost oil gaps, the latter being those with no recruitment and apparently changed into other habitats; new areas of mangrove forest created since 1973 (most of these are associated with the construction of the cement factory and port); mature, essentially intact forests; and upland areas above highest tidal levels. Notice that oil gaps are mostly narrow bands and patches, fringing seaward margins of forests, or along small inlets and tidal streams. No deforestation was observed in the western embayment, while it was extensive in the central area.

Structural characteristics of such forests were collected for comparisons with similar sites and habitats in places well away from the 1986 oiling.

Species composition changed between habitats, with a greater presence of species other than *Rhizophora*, particularly *Laguncularia racemosa*, at unoiled river sites. In general, major structural parameters, including height and diameter, were inversely correlated with mean annual salinity. However, total above-ground biomass was not. Exposed sites had significantly lower total biomass, approximately 80 t/ha, reflected in smaller trees with an average lean angle of approximately 45° and a relatively low canopy approximately 3.5 m tall. The total biomass of channel and river sites was equivalent, at approximately 190 t/ha, but there were obvious differences, with river sites having taller, more erect trees, (approximately 14 m) compared with channel sites (approximately 5.5 m). Densities, however, were significantly less at river sites.

Seedling Assemblages in Unoiled Forests

Seedlings apparently survive under closed canopies for up to 2 yr while this part of the population, or "seedling bank," is replenished annually.

Canopy Condition and Productivity 3-5 Years Postspill

The canopy may be considered as a "pulse" for gauging the condition of the forest; the main functional components of the canopy are leaves. Larger leaves were found at lower salinities and higher concentrations of oil in sediments; shape was not significantly altered. Generally, leaf production was lowest from December to February, the dry season, and peaked in May to July, during the wet season. Leaf fall tended to follow this trend at channel and river sites but not at open coast sites, where the trend was reversed. Oiled sites showed no consistent differences from the fluctuations at unoiled sites. In contrast, there were consistent differences in the numbers of leaves per shoot, with numbers always lower by 1 or 2 leaves at oiled sites. Furthermore, these numbers declined over the 2 yr of observations. Seasonal production of reproductive parts was influenced more by habitat differences than by oiling.

Leaf biomass was similar in all unoiled habitats, but was substantially lower (23-33%) at oiled sites. The biomass of canopy leaves also was inversely correlated with the concentration of oil in sediments (Fig. 25). Turnover ratios reflect differences in standing crop because there was no appreciable difference in annual leaf production; variation in turnover indicates that leaf longevity was reduced by about 18% at oiled sites.

Status of Deforested Areas

Recruitment and Growth of Seedlings in 1986 Oil Gaps

Recovery processes in oil gaps were restricted almost entirely to seedling recruitment and growth, rather than expansion of fringing survivors. Some seedlings survived the oiling that killed surrounding trees. Peaks of internodal extension in these seedlings may reflect a diminishing influence of residual oil on growth following the spill. Seedlings in oil gaps and unoiled natural gaps grew at comparable rates 4 yr after the spill; oil appeared to suppress growth chiefly in faster-growing individuals.

At sheltered sites, the peak of older seedlings advanced by about 3-4 node classes in the second year (May 1991), while the younger peak stayed fixed at 1-3 nodes (Fig. 26). This younger peak represents the formation of a new seedling bank. Therefore, the canopy has redeveloped in these plots and is comparable to that seen in mature forests, but at a much lower height. The situation at exposed sites was quite different because these areas had no seedling-bank peak, indicating that there was no canopy closure. Canopy closure appears to indicate the end of the first stage of forest recovery.

Densities of recruits in oil gaps 4 yr after the spill ranged from <0.1 to 23.4 seedlings/m^2. Comparable densities were observed in unoiled gaps of similar age, so it appears that the major influences on recruitment and establishment were mainly related to natural factors, although there may have been secondary consequences of oiling. There are no natural phenomena in Panama known to cause destruction of mangrove habitat comparable to that from the two large oil spills documented in this report.

Assisted Recruitment in 1986 Oil Gaps

The recovery of mangrove forests in Bahía Las Minas after the 1986 spill was further influenced by a large-scale project of planting at least 86,000 seedlings. They were often planted with broad-spectrum fertilizer and unoiled upland soil because this improved early growth and survival at oiled sites. The density of planted seedlings ranged from 0.1 to 0.3 seedlings/m^2, in the low range of densities of natural recruits. At planted sites there were 5-11 times more natural recruits than planted ones (Fig. 26); at sites where there had been no planting, natural recruits were 11-39 times more dense. Thus, this restoration project had a negative effect on natural recruitment, which generally was sufficient to repopulate oil gaps. Although planted

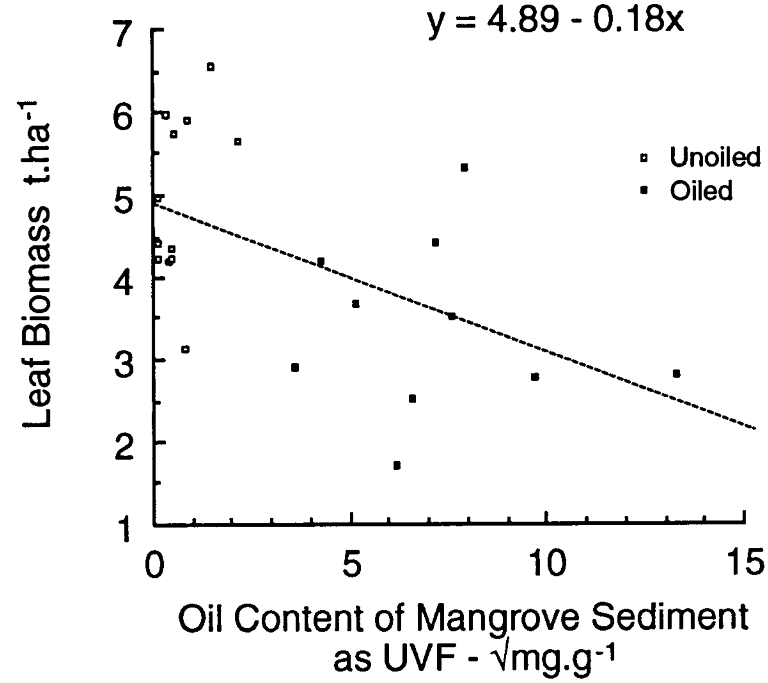

Fig. 25 Mean annual estimate of leaf biomass of *Rhizophora mangle* trees vs. the mean concentration (UVF; square-root transformation) of oil in sediments during 1989-1990. Notice that leaf biomass was highest, around 5 t/ha, at low concentrations of oil ($r = -0.54$; $N = 22$; $P < .01$).

seedlings apparently grew taller than natural counterparts, any benefit of planting was outweighed by the disruption of natural recruitment and growth.

Status of Forest Recovery in 1968 Witwater *Oil Gaps*

Witwater oil gaps ranged over habitats similar to those studied for the assessment of the 1986 refinery spill. Tree densities at sheltered *Witwater* sites were more than double those at exposed sites, but trees were slightly smaller and estimates of total above-ground biomass were equivalent, at approximately 71-73 t/ha. This value is only about 10% less than the above-ground biomass of unoiled exposed forests (80 t/ha), but is less than half the value of unoiled sheltered forests (190 t/ha).

Growth of Trees in an Unoiled 1979 Gap

Growth of *R. mangle* at an unoiled site was assessed by dissecting and weighing different parts of trees from a well-developed forest that had colonized

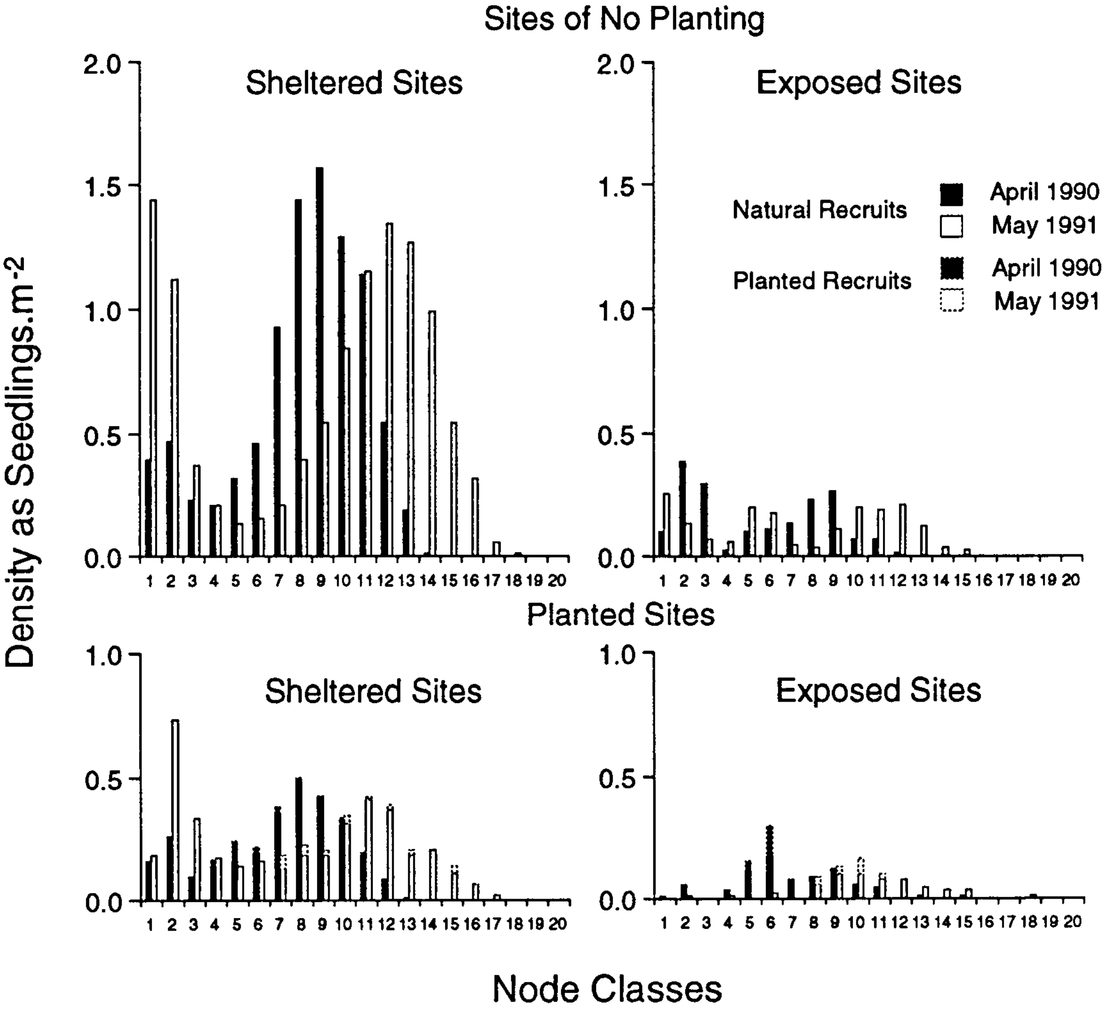

Fig. 26 Node classes and mean densities of *Rhizophora mangle* seedlings (*cum* saplings) at exposed and sheltered sites of no planting and planted sites scored in April 1990 and June 1991. Notice the lower densities, the proportion of planted recruits, the bimodal peaks in sheltered sites, and the lack of a seedling bank at exposed sites. Planted exposed-coast sites were the least populated in the entire survey.

dredge spoil in 1979. Trees had grown to a height of 12 m in approximately 10 yr, comparable to growth of a species of *Rhizophora* in Thailand.

Discussion

Natural Processes of Forest Recovery

Gaps in mangroves differ from those in other tropical forests chiefly because they result from trees that die standing, instead of tree-falls, and because gaps in mangroves are rarely created by the death of only old trees. Gap creation and closure is believed to be the main process by which mangrove forests naturally regenerate; in Panama the most likely cause of natural light gaps is probably lightning strikes. Viviparous development of seedlings has been considered to be an adaptation for longevity and long-distance dispersal in the marine habitat, but it is possibly more important for re-establishment in gaps via a "seedling bank."

Propagules of established seedlings are buried in the substratum by at least one-third of their length. This is unusual because the substratum in mature forests is often a tough mat of fibrous roots, apparently impenetrable to floating seedlings. Seedlings are often positioned away from established prop roots, where they might be established if entrapment among roots was important. In fact, those near roots have severe leaf damage caused by herbivorous crabs. Other crabs make burrows through the root mat approximately 15 mm in diameter, slightly larger than the diameter of *Rhizophora* hypocotyls. Considering these observations and others, it appears that *Rhizophora* propagules are often "planted" in crab burrows.

The Influence of Oil on Forest Recovery

One of the chief questions in this study was whether gaps deforested by oil have different rates of recovery than natural gaps. One qualification needs to be emphasized: oil gaps are usually much larger than natural gaps, at least in Panama. This difference affects two important factors, light and substratum stability. Large deforested areas receive more light than smaller gaps, and thus enhance tree growth but provide less protection for new recruits. Clearly, there is a trade-off in these opposing factors for the recovery of mangrove forests.

Data on leaf biomass for 2 yr of seedling growth after the 1986 spill, *Witwater* plots (23 yr old), and surviving mature forests show that leaf biomass in gaps sharply increases in the first few years, after which it apparently levels off at amounts observed in mature canopies. This leveling off with age is not apparent in total above-ground biomass and there was a significant difference between habitats (Fig. 27). While exposed sites showed almost complete return to normal, sheltered sites appeared to be stunted by more than 50%. If growth were to continue at this rate, recovery might take another 30-40 yr, an estimate far greater than the growth of the four unoiled trees nearby, which were calculated to require 15 yr to achieve normal stand biomass.

Concerns with Assisted Rehabilitation

Human assistance may not improve recovery of oiled mangroves compared with situations where there is no further interference. Until more is known it seems essential both to study natural processes involved and follow the fate of earlier efforts attempting to accelerate recovery. Assessment of the rehabilitation effort in Panama suggests two important factors affecting longer-term recovery of oil gaps. First, although planting provided no apparent benefit toward the general recovery of

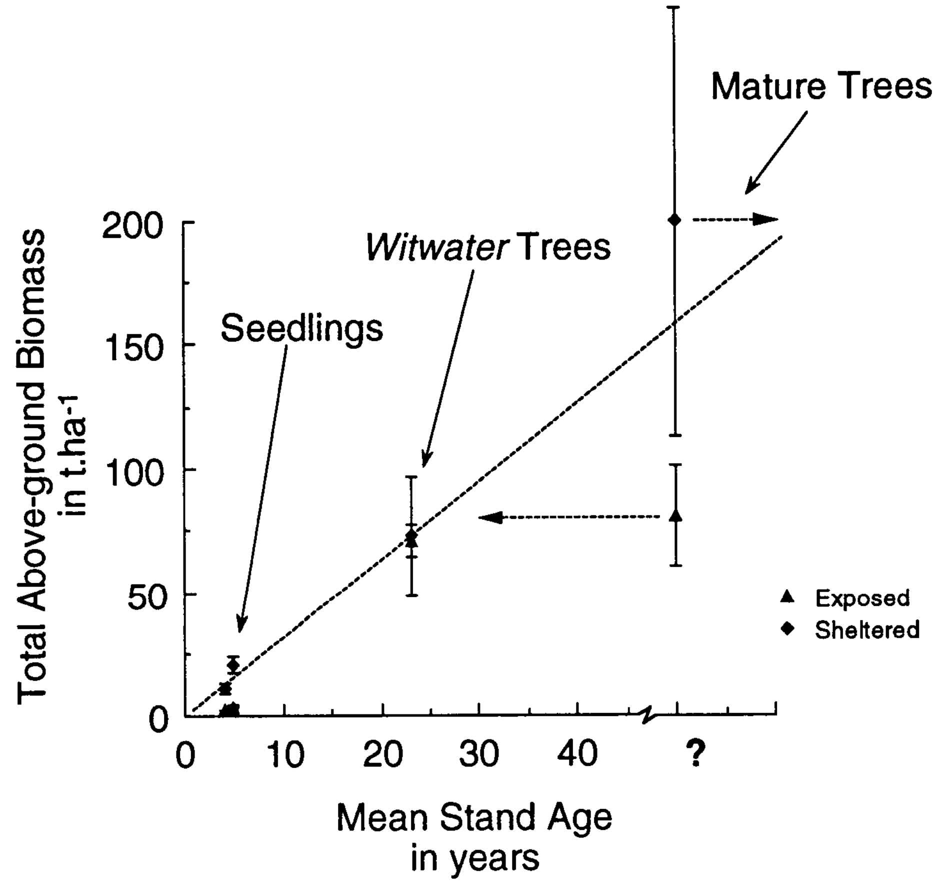

Fig. 27 Mean total above-ground biomass and age of *Rhizophora mangle* plants from refinery and *Witwater* oil gaps showing a linear trend toward higher amounts in progressively older stands. These values may be compared with mature forest estimates for exposed and sheltered habitats, but while exposed *Witwater* oil gaps had apparently returned to normal, the sheltered sites appeared to be severely suppressed compared with growth at the unoiled sheltered site. Estimates showed that this site was close to the normal mature-forest biomass after approximately 10 yr, and this compared well with growth of *R. apiculata* in southeast Asia.

mangroves in Bahía Las Minas, growth of some planted seedlings was improved with fresh soil. Second, standing dead timber and roots appear to provide shelter for new recruits, so these structures should not be cut or removed. In Bahía Las Minas erosion and deterioration of standing dead trees at exposed sites was accelerated by large drift-logs, which caused permanent loss of habitat in some cases. To prevent such scouring, posts could be positioned among recruits to protect them. It may, however, be desirable to plant seedlings in areas where natural recruitment is low.

Loss of Habitat, Particularly Exposed Coastal Fringes

Erosion of oil gaps at exposed sites was evident 3 or 4 yr after the spill. This process involves the mobilization of rotting and broken tree fragments, and was less important at sheltered sites. Colonization and re-establishment of these sites appears retarded, and some oil gaps on exposed coasts may be altered permanently, as appears to have occurred after the 1968 *Witwater* spill.

Conclusions

Listing of Major New Findings

Major results and findings include: (1) vegetation maps delineate areas of mangroves and oil-gap deforestation after the 1986 refinery spill, (2) similar maps delineate deforestation caused by the 1968 *Witwater* spill, providing the first record of this effect, (3) surviving forest canopies were reduced by oil in sediments and showed no signs of recovering 5 yr after the spill, (4) recruitment can be prolific, but growth was retarded by residual oil in sediments, (5) recruitment at exposed oil-gap sites was destroyed by drift-logs and removal of sediment, (6) planting seedlings provided no benefit to recovery, but site protection from drift-logs might help, (7) node counts and sequences provided a method to age *Rhizophora* seedlings, and (8) seedlings under closed canopies (seedling bank) pre-empt gap creation, and possibly promote rapid closure.

Suggestions for Future Studies of Large Oil Spills

Based on observations of this spill and others, a tentative protocol for postspill efforts might include the following steps: (1) protect mangrove forests from major oil spills, (2) carefully remove oil reaching mangrove trees, where practical, (3) cutting and removal of trees, dead or alive, should be discouraged, (4) aerial photographs should be made immediately, with supporting ground-truth data for areas of deforestation, including tree and animal species most affected by the spill, (5) the potential for natural recovery needs to be evaluated once the extent of obvious damage is known, and (6) sites for long-term biological studies need to be established for basic comparative data on forest structure and species composition that could be used to guide future management activities.

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

Introduction

The Importance of the Mangrove Fringe

The interface between the ocean and the land is among the most productive zones on earth; in the tropics mangrove forests often dominate such shores. The submerged maze of roots and epibiota of the mangrove fringe add structural and trophic complexity and increased diversity to mangrove forests, and the nearshore ecosystem as a whole (see Garrity and Levings, Chap. 9, Vol. II).

Mangrove forests are characteristic of tropical and subtropical coastlines

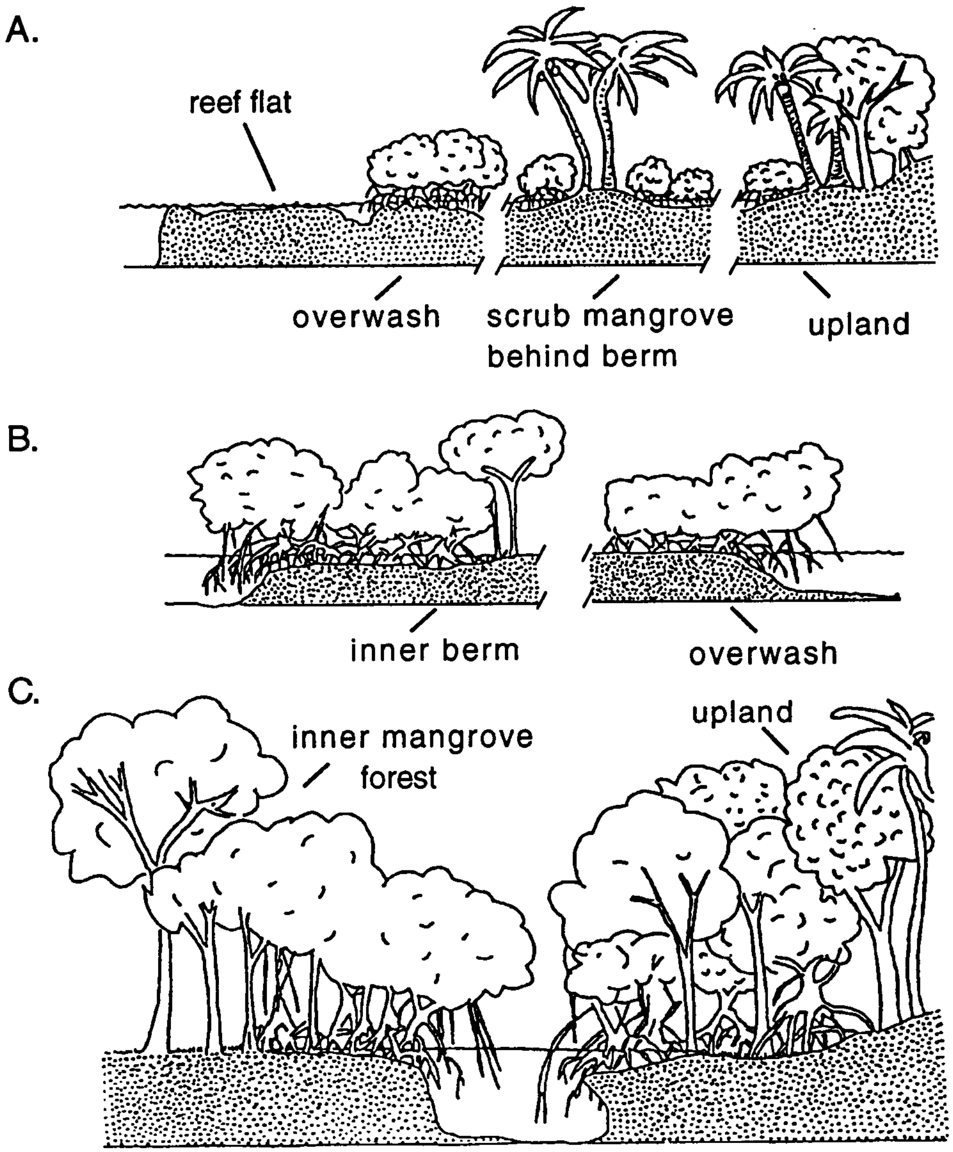

Fig. 28 Topography of the outer fringe. *A*. Open coast – the *Rhizophora* fringe behind a broad, shallow reef flat had a depression at its outer edge that ranged from intertidal to >2 m depth, and an intermittently present berm shoreward, behind which was either a scrub mangrove forest or upland. *B*. 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.

forest structure. 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 banks, pictured as typical of this type of forest, and ditches were not lined by tall trees.

Bahía Las Minas has three major wings separated by causeways built during the last 35 yr (Fig. 1). One or more rivers and several smaller streams feed into each wing. The average daily tidal range is ~24.5 cm, with a yearly range of 59.2 cm; water levels are controlled by a combination of seasonal trade winds, regional variation in sea level, and tidal fluctuations. Rainfall is strongly seasonal; the dry season usually begins in December and lasts until April or May. Salinity is oceanic (>30o/oo) at the entrance to the bay; salinity in channels and lagoons and in small tidal streams within the bay is nearly oceanic during the dry and early wet seasons. During the wet season salinity gradients develop. 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.

At Bahía Las Minas each of these three habitats has a distinct assemblage of organisms living on mangrove prop roots. Overall, there was a decrease in the number of categories of epibiota from the open coast (36) to channels (10) and streams (11), and individual taxa tended to be rarer on the open coast than in channels or streams. There was limited overlap in species occurrence among habitats; roots on the open coast were dominated by foliose algae and sessile filter-feeding invertebrates, the edible oyster *Crassostrea virginica* was the most common species in channels, and the false mussel *Mytilopsis sallei* covered the most space in streams.

Objectives, Rationale, and Design

Objectives

Our two major goals were to determine effects of oiling on the epibiota of mangrove roots, and the structure of the fringe itself, along the gradient from the open coast to channels and lagoons to drainage stream and ditch habitats. Mangrove roots are dynamic substrata that could be directly or indirectly affected by oiling or other factors. Results were separated into two periods: initial effect from the deposition of oil residues during the first year after the spill and long-term damage and recovery during the second through fifth year after the spill. Results of both the structural and biological components of the study were combined to make an overall evaluation of damage 5 yr after the spill.

Selection of Study Sites

Each accidental oil spill is a unique event, affected by local hydrographic and meteorological conditions, topography, amount and composition of oil, and cleanup attempts. Ideally, oiled and unoiled sites are exactly matched and data are available from all sites before and after the spill. 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.

Study sites were chosen 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. Beginning in August 1987 at least four sites were sampled in oiled and unoiled areas in each of the three habitats. Site selection was based upon the assumption that oiled and unoiled sites could be correctly identified by the visible presence of oil and oil residues, tested later by chemical sampling. There was a distinct geographic component to oiling of the mangrove fringe. As a result, the mangrove fringe in channels was oiled (1) patchily in the outer sections of the western wing of Bahía Las Minas, (2) throughout the central bay, and (3) into middle sections of the eastern wing. Small streams and drainage ditches were heavily oiled because of a strong tidal influence; large streams remained unoiled because of positive downstream flow.

Roughly 1-km stretches of shore (*sites*) within each habitat were haphazardly chosen in the western wing of Bahía Las Minas in 1981-1982. After the spill, sites were added to include both oiled and unoiled areas and to increase sample sizes, and some sites were changed to sample more representatively from the coastline affected by the spill and to increase distance between sites. No open coast, unoiled areas were found near Bahía Las Minas; the closest unoiled sites were located ~25 km east. In August 1988 an unoiled site in the west wing of Bahía Las Minas was oiled by secondary release of the spilled oil; it was then reclassified as newly (lightly) oiled, and an additional unoiled site was added.

Confounding Effects

Physical conditions on reef flats are controlled by a combination of meteorological and hydrological forces that vary with small changes in local topography and aspect. Differences in location of open coast sites could thus affect the physical regime in the mangrove fringe behind reef flats so that variation in some parameters was probably confounded with oiling because of the ~25 km distance between oiled and unoiled areas. Unoiled sites probably received more rain, and prevailing winds did not blow directly onshore. We cannot determine effects of these differences among sites, but they appear small compared with effects of oiling.

Oiled and unoiled channels and lagoons were in Bahía Las Minas or Margarita Lagoon (unoiled). Margarita Lagoon is smaller and shallower than Bahía Las Minas, and there were differences in the physical regime between oiled and unoiled sites and between lagoons. Differences in surface salinity between oiled and unoiled sites were a result of the pattern of oil movement; all channels close to the mouth of Bahía Las Minas were oiled and no comparable habitat occurs elsewhere in the region.

The mangrove fringe and physical regime also differed between oiled and unoiled streams because processes that controlled oil deposition were related to those that contribute to the structure of the mangrove fringe itself. Small streams, with greater surface tidal intrusion, were more likely to be oiled than large streams with freshwater outflow in the early wet season. Before the spill a large stream and a small stream had similar epibiotic communities.

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 through time. However, there was a 4-yr gap between data collected before and after the spill and the pattern of oiling with respect to sites sampled before the spill differed among habitats.

Statistical Analyses

In general, repeated-measures analysis of variance (ANOVA) was used because sites were revisited over time. Nonparametric analyses were chosen when data were categorical variables or assumptions of parametric analyses were not met. Prespill data were used as indicative of the kind of epibiotic assemblage expected in unoiled areas of Bahía Las Minas, but were excluded from statistical analyses of the entire data set because of the 4-yr gap 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.

Oiling and Reoiling

Methods

We measured the amount of oil deposited on roots and recorded whether oil was visible. Oil consisted of progressively weathered tarry residues on roots and attached organisms. Oil was present both from the 1986 spill and from other events; there was no chemical evidence of major contamination other than the 1986 refinery spill.

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. Subsequently the amount of oil on roots was measured as percent cover of oil, using a variation of point-intercept sampling. Three types of roots were sampled. First, 20 roots were randomly chosen at each site each quarter and percent cover recorded (termed *long-term census*). Second, similar subsampling was begun of a marked cohort of roots that had entered the water ~18 mo after the spill (termed *community development*). Third, artificial roots (*recruitment dowels*) placed at each site each quarter measured amounts of oil stranding in the fringe during 2-2.5-mo periods.

The presence or absence of oil slicks and oil in sediments were recorded at each visit to a site. When possible the source of slicks was recorded.

Results

Roots in the water at the time of the spill were coated nearly entirely with oil, often in layers up to 1 cm thick. Oil on surviving roots weathered and flaked off throughout the 5-yr study. Oil slicks occurred at or near study sites through 1991, and multiple reoilings occurred of roots that were in the water at the time of the spill and those that entered the water afterward.

Four mo after the spill most of the wetted surface of prop roots fringing Bahía Las Minas had been oiled. On the wave-washed open coast, cover of oil on roots remained high for the first year after the spill (Fig. 29). Although the cover of oil on roots decreased rapidly, the proportion of oiled roots remained high over 5 yr. Reoiling was frequent, but did not involve large amounts of oil. In channels and lagoons the average cover of oil reached 39% in November 1986 and >95% of roots had at least some oil on their surfaces. Five years later cover averaged <5%, but most roots had been in contact with at least some oil. Pulses of residual oil were frequent in oiled channels and lagoons, including a large release that contaminated a previously unoiled site between May and August 1988. Drainage streams were heavily oiled during the spill and were repetitively reoiled for 4.5 yr. Five years after the spill 98% of roots still had some oil on their surfaces and mean cover was 20%.

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. In channels and lagoons the frequency of slicks did not decline, 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. Likely sources of most new oil seen during the study include heavily oiled, intertidal mangrove sediments around Bahía Las Minas and pools in landfill under and around the collapsed storage tank at the refinery.

The Mangrove Fringe as Substratum

Submerged prop roots of *Rhizophora mangle* are a living and, thus, variable substratum for attached organisms. Oiling could alter the density, size, growth rate, or condition of roots, with correlated effects on epibiota. 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 the study and (2) to consider different levels of damage assessment based upon the results.

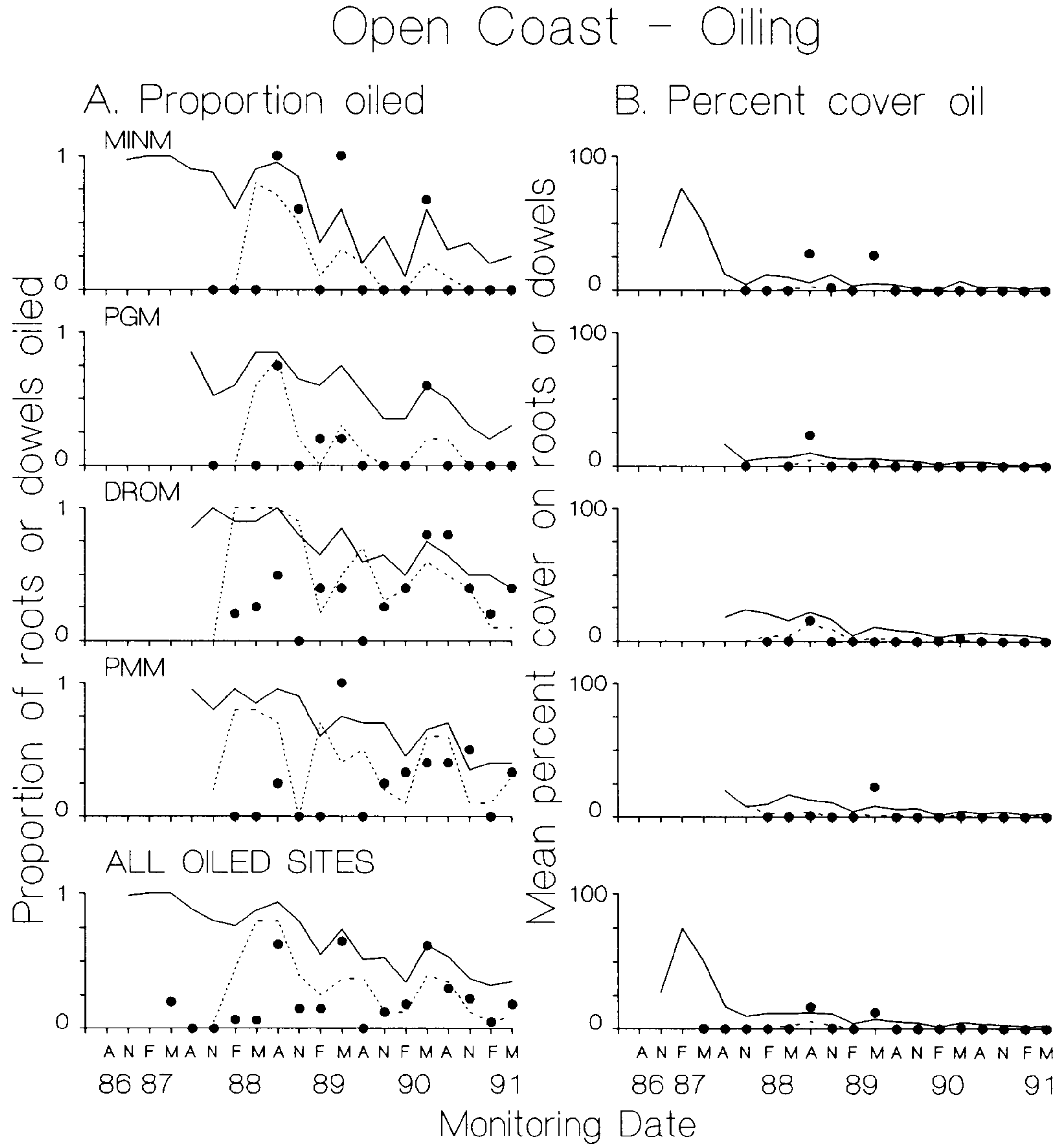

Fig. 29 Temporal patterns of oiling on open coast roots and dowels. *A*. Proportion of sampled roots or dowels with oil visible for each oiled site and all sites combined. Numbers of sites and sample sizes varied, see Volume II for details. *B*. Percent cover of oil on root or dowel surfaces for each 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).

Methods and Results

Quarterly observations were made of the condition of canopy, trees, and roots of the mangrove fringe, and the length, diameter, and provisioning of randomly chosen roots.

For all three habitats mature *Rhizophora* was the major component of the outer fringe at unoiled sites, and the overall structure of oiled sites was initially similar to that of unoiled sites within each habitat type. In each habitat significantly more *Rhizophora* fringe was dead or damaged at oiled than unoiled sites 5 yr after the spill, although the sequence and amounts of damage differed among habitats. There were also significant effects of both oiling and habitat on the proportion of dead roots and root density. More roots were dead at oiled sites regardless of habitat. The density of live and dead roots combined was higher in channels than on the open coast or in streams.

Length of roots varied significantly among habitats, oiling conditions, and years, and the seasonal pattern of root length was affected by oil and differed among habitats. There also were significant effects of habitat, year, and oiling on root length in the community development cohort, but there was not a significant effect of season. Five years after the spill, the average surface area per root ranged from 429 cm^2 and 407 cm^2 on the unoiled and oiled open coast, 368 cm^2 and 372 cm^2 in channels, and 596 cm^2 and 379 cm^2 in drainage streams.

Significantly more light passed through the canopy to root level at oiled than unoiled sites, and these differences persisted at least through February 1991. Differences were greatest in drainage streams, where most of the fringe was destroyed.

There was a clear reduction in the amount of shoreline fringed with *Rhizophora* and in the density of live and dead roots in surviving fringe at oiled and unoiled sites in all three habitat types. When the percent of the remaining fringe at oiled sites compared to unoiled sites was multiplied by the percent of roots, on average only 67% of the habitat was available on the oiled open coast relative to unoiled areas. For channels and drainage streams, values were 62% and 37%, respectively.

Sediment hydrocarbon concentrations at oiled sites were on the order of 10^4-10^5 $\mu g/g$ dry weight in UVF units. There was no evidence of dose response between these concentrations and percent dead fringe, but data on percent cover of oil suggest a different interpretation (Fig. 30). If 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. Variability in mortality of trees along the fringe may have been related to both the amount of oil on roots and the initial toxicity of oil that soaked into sediments.

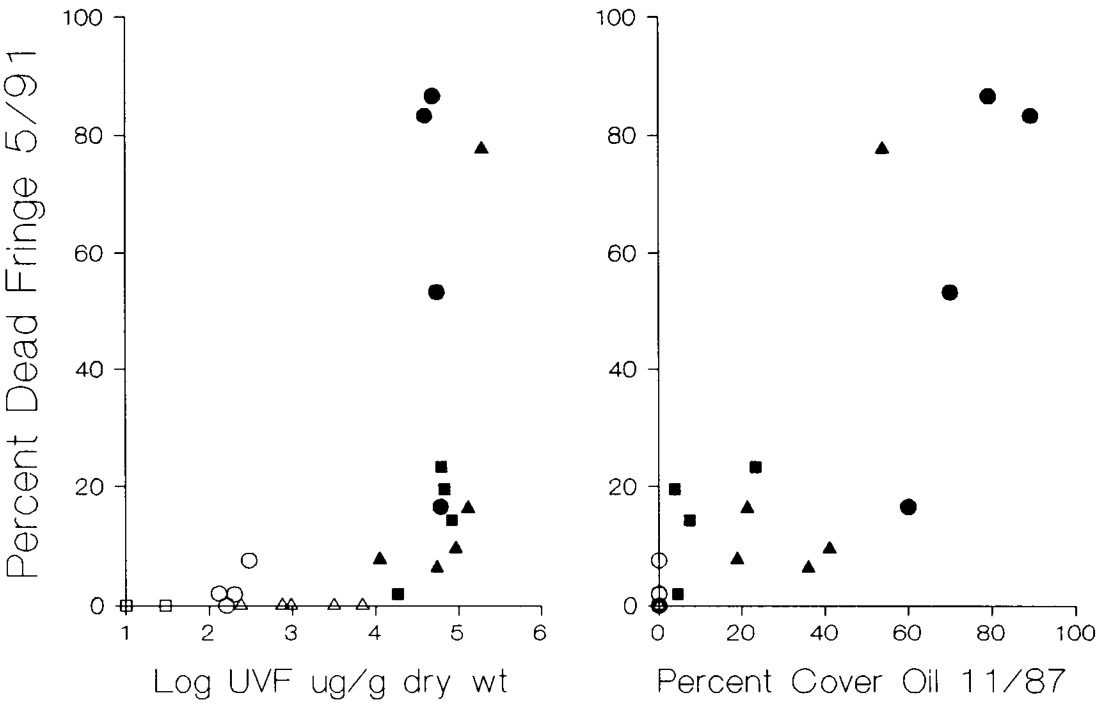

Fig. 30 Percent dead fringe in May 1991 versus two measures of oiling. *Left,* mean concentration of hydrocarbons in mangrove sediments collected in 1989 and 1990 (see Vol. II for details); *right,* mean percent cover of oil coating mangrove roots in November 1987. *Solid symbols* = oiled sites, *open symbols* = unoiled sites, *circles* = drainage streams, *triangles* = channels, *squares* = open coast.

Summary and Discussion

The Bahía Las Minas spill significantly reduced the area of mangrove fringe and therefore reduced the amount of habitat available for associated plants and animals. Roots were shorter in two of three oiled habitats, leaving less submerged area, which may have affected 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. Five years after the spill there were long-term effects on structural characteristics of the mangrove fringe.

The time course of defoliation and collapse also 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. It would not have been possible to estimate the extent of damage fully until at least 3 yr after oiling. Differences in the amount of damage among habitats and sites appeared related to characteristics of both the sites themselves and how oil was deposited. 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.

Abundance and Vertical Distribution of Epibiota

The percent cover of sessile organisms on randomly chosen roots was monitored over a 5-yr period at oiled and unoiled sites. The vertical distribution of epibiota on roots was measured because the physical regime changes with depth, and such changes could affect the distribution and abundance of species on roots. Settlement variation was investigated using groups of artificial roots, set out for ~2.5 mo and then monitored for percent cover. Finally, successional processes were examined for a cohort of marked roots that entered the water during a single 2-mo interval. Oiled and unoiled sites are compared within habitats, with the goal of differentiating natural variation from changes in the epibiotic community caused by the oil spill.

Materials and Methods

Percent cover of sessile organisms on randomly selected roots that were >20 cm long below the high-water line (HWL) and not attached to the bottom was estimated visually in 1981-1982 and by a point-intercept method quarterly from July-August 1986 until May 1991. Beginning in August 1988 the vertical distribution of organisms was examined on a subsample of roots.

In August 1987 a cohort of actively growing roots just above the HWL were marked with flagging tape. 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 1.5 yr after the oil spill. Randomly chosen roots from the cohort were measured and sampled for percent cover and root condition from November 1987 through May 1991 to monitor community development.

Recruitment was followed using artificial roots (dowels or sections of aerial roots) hung vertically in the water and collected 3 mo later. After collection percent cover of organisms that had settled was estimated using a stratified-random point-intercept method.

Results

Fringing mangrove roots on the unoiled, open coast supported a diverse epibiotic assemblage, best characterized by foliose (Fig. 31) and crustose algae. Mixed-species turfs were the most abundant category of foliose algae. Crustose algae were initially rare, but increased greatly during the study. Blue-green algae were highly variable in percent cover over time. Barnacles, sponges, cnidarians,

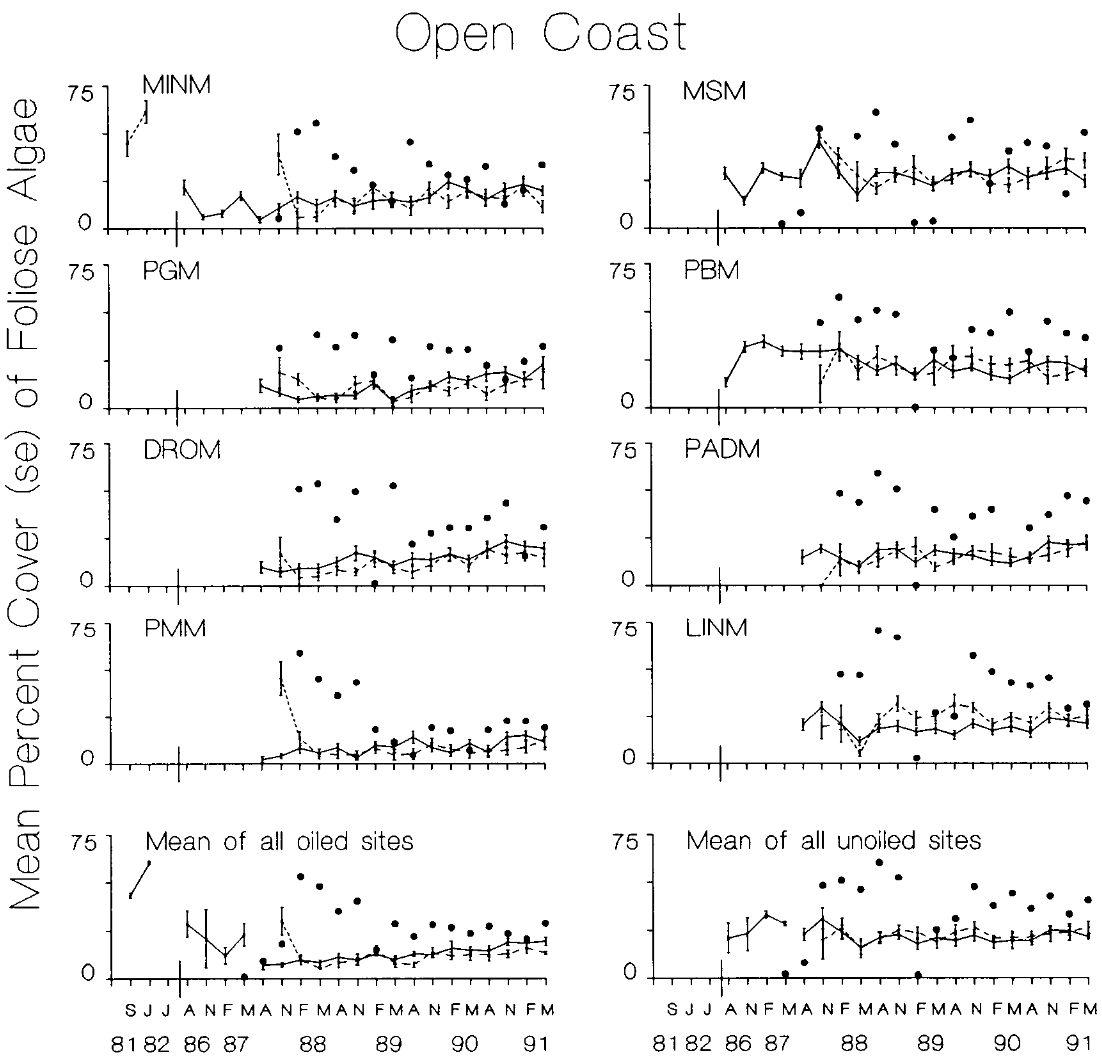

Fig. 31 **Patterns of foliose algal abundance on roots on the open coast. Data are mean (± SE) percent cover of foliose algae for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census roots (*N* = 20-25/site),** ***dashed lines*** **are community development roots (*N* = 5-10/site), and** ***solid circles*** **are recruitment dowels (*N* ~ 5/site).**

arborescent hydroids, bryozoans, and other sessile invertebrates together covered 8-18% of root surfaces (Fig. 32), but no taxon averaged more than 11% cover at any monitoring. Diatoms were similar to foliose algae in their pattern of abundance, averaging from 12 to 34% cover. The remaining space was either occupied by rare and intermittently present organisms or was unoccupied; between 16 and 34% of space on roots was bare. Depth distributions are presented in Volume II. Foliose algae and diatoms were the most common groups recruiting in this habitat, together

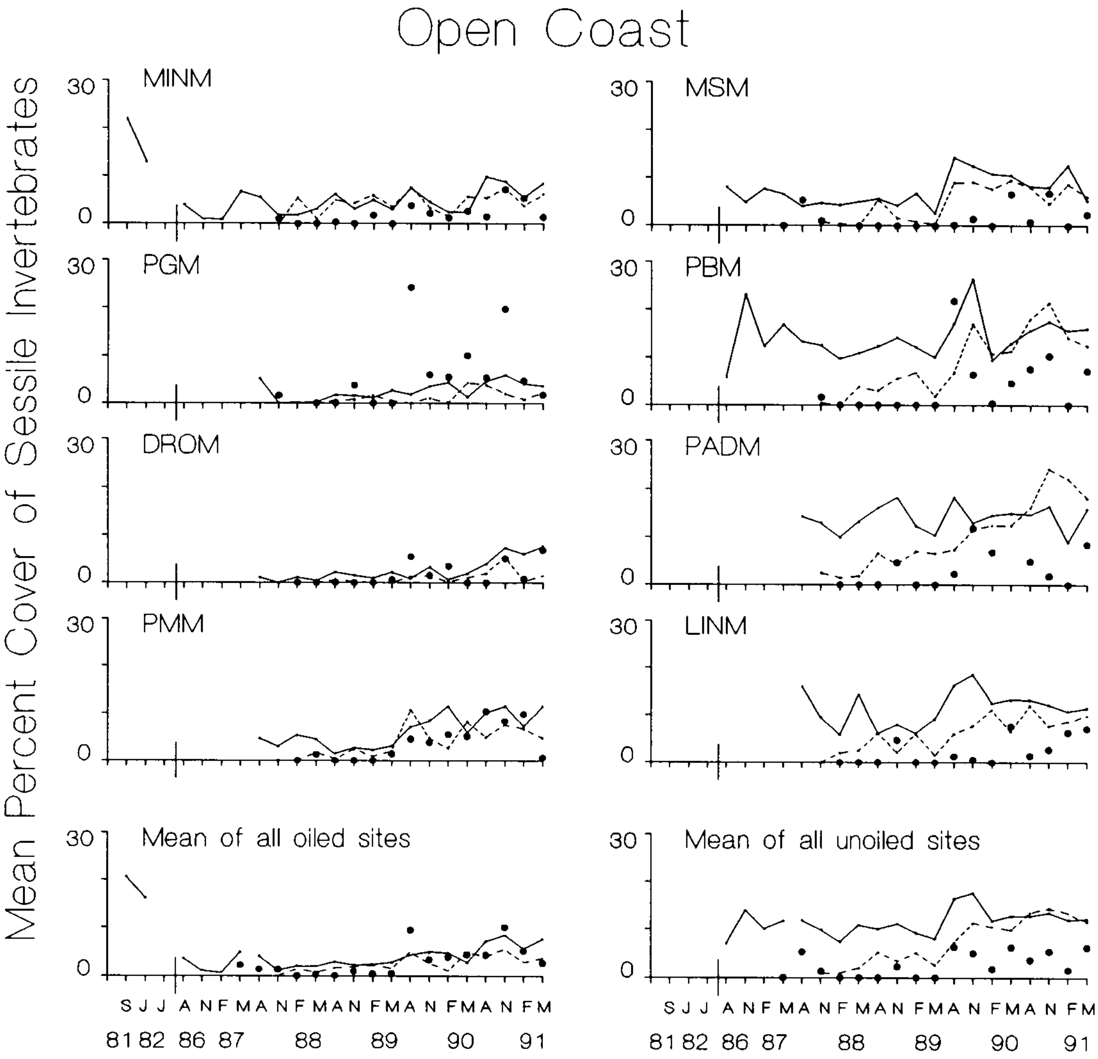

Fig. 32 **Patterns of abundance of sessile invertebrates on roots on the open coast. Data are mean percent cover of sessile invertebrates for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column).** ***Solid lines*** **are long-term census 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.**

usually covering almost 75% of the surface. Recruitment was low, episodic, or both for most other groups. Foliose algae reached levels of abundance on community development roots similar to those on long-term census roots within 3 to 6 mo after roots entered the water. Crustose algae and sessile invertebrates required 2-3 yr for convergence in abundance.

On the oiled open coast, within 4 mo of the spill a bloom of diatoms covered much of the surface of oiled prop roots. Crustose algae, blue-green algae, sponges, arborescent hydroids and bryozoans, tunicates, corals, and anemones had been coated with oil and then died. By February 1987 the diatom bloom had ended and most other groups had disappeared from roots. Oil covered ~80% of root surfaces. Cover of foliose algae decreased for the first year after oiling, then increased slowly through 1991. By May 1991 percent cover of foliose algae was similar at oiled and unoiled sites. The number of species of foliose algae per root followed the same pattern as percent cover, but there were differences in species composition. Crustose algae were absent or rare at oiled sites for 1.5 yr following the spill. From 1988 through May 1990 crusts at oiled sites covered significantly less space than at unoiled sites. Sessile invertebrates dropped to <5% cover in the first year after oiling. Cover increased slowly at oiled sites, but was still lower than at unoiled sites 5 yr after oiling. The pattern of recruitment at oiled and unoiled sites was generally similar, suggesting that oiling effects were caused by postsettlement rather than presettlement processes. As at unoiled sites, epibiota quickly settled on community development roots starting ~1.5 yr after the spill.

The edible oyster *Crassostrea virginica* was the most abundant bivalve mollusc in unoiled channels and lagoons (Fig. 33). It gradually declined at unoiled sites through November 1989, then continued to decrease only in Margarita Lagoon and increased slightly from February 1990 through May 1991 in Bahía Las Minas. Other common space occupiers included three additional species of bivalves, the barnacle *Balanus improvisus*, foliose algae, sessile invertebrates other than bivalves and barnacles, and diatoms. There was only one major recruitment of *Crassostrea* in 17 quarters of monitoring; barnacle recruits sometimes were abundant (up to 60% cover). On community development roots, oyster abundance reached the level of abundance on long-term census roots during the final year of the study.

Crassostrea was severely affected by the spill in oiled channels, then gradually increased in abundance (Fig. 33). Other common groups generally followed this pattern, but with various rates of recovery. Some oysters recruited at oiled sites during most censuses; cover of recruits did not differ between oiled and unoiled sites. *Balanus* recruitment generally was more abundant at oiled than at unoiled sites. *Crassostrea* abundance on community development and long-term census roots converged within 3 to 12 mo after roots entered the water.

The false mussel *Mytilopsis sallei* covered the most space on roots in unoiled drainage streams (Fig. 34). Other common groups included the barnacle *Balanus improvisus*, sessile invertebrates other than bivalves and barnacles, and diatoms. Barnacles, *Mytilopsis*, and diatoms recruited during all quarterly monitorings. After 6 mo *Mytilopsis* began settling on community development roots and increased steadily in abundance over time at most sites. Abundance of false mussels on community development and long-term census roots converged at variable rates among sites (12-51 mo).

Effects of the spill were immediate, severe, and persistent in oiled streams; *Mytilopsis* did not return to oiled streams during the 5-yr study (Fig. 34). Most other

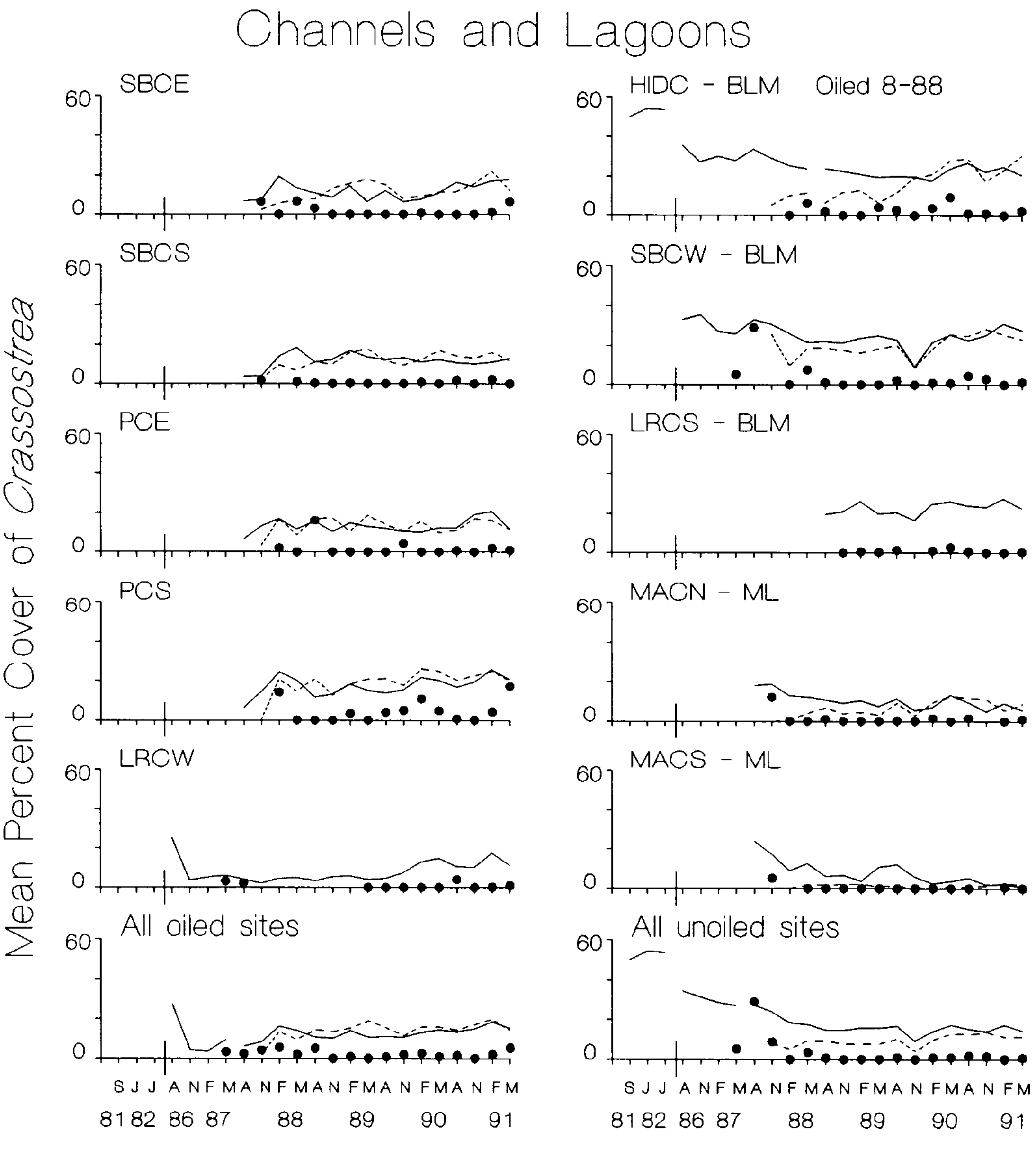

Fig. 33 **Patterns of abundance of *Crassostrea virginica* on roots in channels and lagoons. Data are mean percent cover of *Crassostrea* for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* are long-term census roots (*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.**

groups showed variable signs of at least partial recovery. False mussels recruited in oiled streams, but not as frequently and abundantly as at unoiled sites. *Mytilopsis*

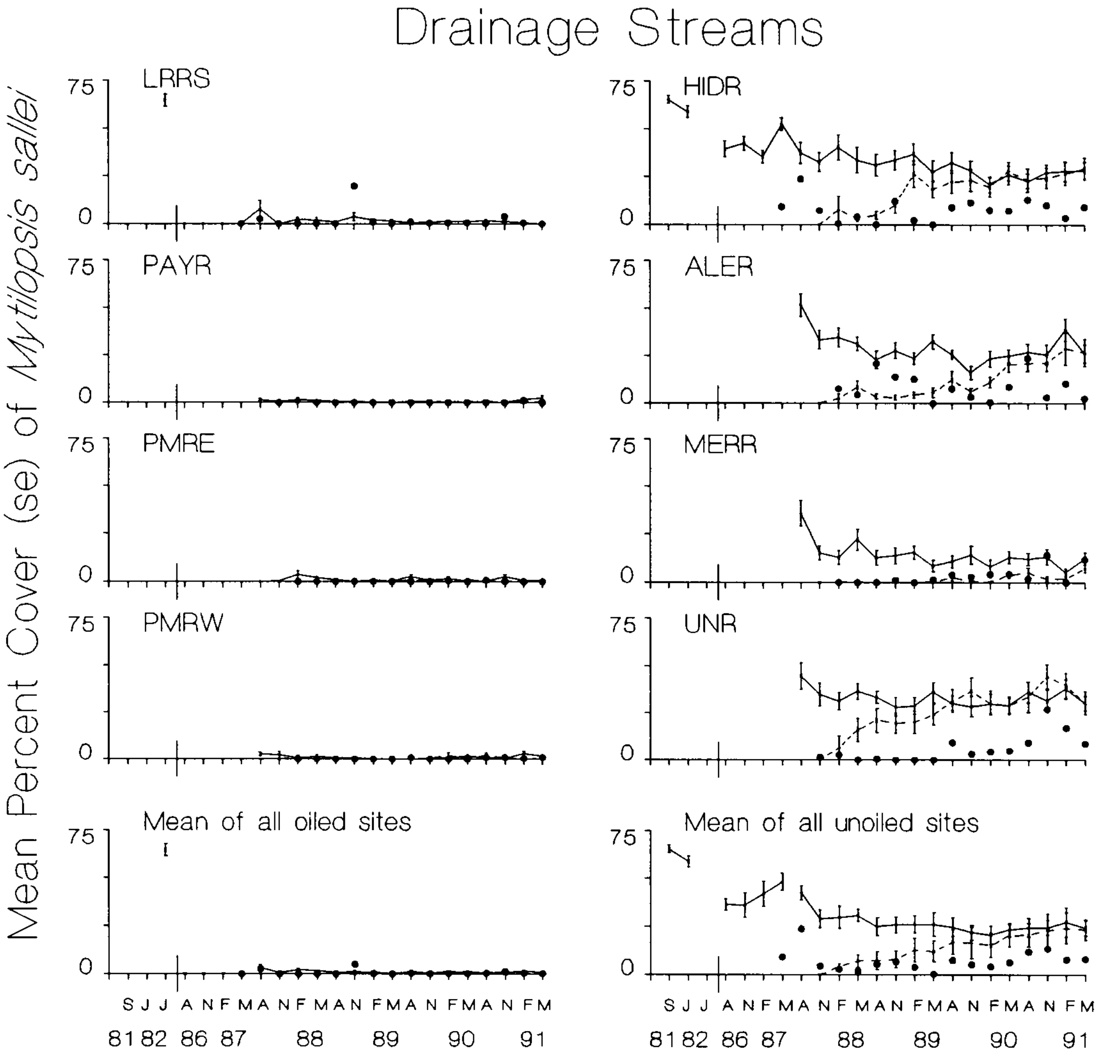

Fig. 34 **Patterns of abundance of *Mytilopsis sallei* on roots of fringing *Rhizophora* in drainage streams. Data are mean (± SE) percent cover of false mussels for each oiled site and of all oiled sites (left column), and for each unoiled site and of all unoiled sites (right column). *Solid lines* 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).**

cover on community development roots did not increase over time as in unoiled streams; other groups displayed variable recovery.

Summary and Discussion

In each of the habitats effects of oiling were severe and persistent; recovery was incomplete 5 yr after the spill, but patterns differed among habitats. Prop roots on the unoiled open coast supported a diverse epibiota; productivity and turnover appeared high. The occurrence of species on roots was variable and unpredictable, but overall patterns of distribution and abundance for major taxa persisted over 5 yr. The number of species of foliose algae per root increased with time of submergence, and was correlated with cover of algae. Sessile invertebrates covered considerable space on roots; groups differed in spatial and temporal variation. Root growth affected patterns of abundance; rapidly growing roots were typified by ephemeral or opportunistic species, while relatively inactive roots accumulated an increasing number of species of foliose algae, crustose algae, and large-bodied invertebrates like sponges and colonial tunicates.

Composition of foliose algal species differed between oiled and unoiled open coast sites throughout the study; individual species were rarer at oiled than unoiled sites for 4 yr after the spill. The gradual increase in cover at oiled sites, and slow convergence with values at unoiled sites, suggests 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. 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. Overall, damage was clear and severe initially; recovery, although proceeding, was incomplete after 5 yr.

Mangrove roots in unoiled channels and lagoons were chiefly covered with bivalve molluscs, especially the oyster *Crassostrea virginica*, and barnacles. Oyster abundance gradually decreased during the study; recruitment was generally low and patchy. 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. *Crassostrea* remained more abundant at unoiled than oiled sites in Bahía Las Minas through 1991; a decrease in abundance at unoiled sites contributed to the convergence between oiled and unoiled sites. 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 normally characteristic "Bostrychietum" species remaining rare after 5 yr.

Space on roots in unoiled drainage streams was dominated by a single species, the false mussel *Mytilopsis sallei*. Recruitment of *Mytilopsis* was variable among sites, and occurred primarily during rainy season. Mussel populations developed slowly on initially bare roots. Physical factors appear to be important to the dynamics of the epibiotic assemblage in this habitat. Oiled drainage streams remained severely affected through May 1991, with *Mytilopsis* still rare and not increasing in abundance on oiled community development roots despite several minor periods of recruitment.

Studies on *Mytilopsis sallei*

Mytilopsis sallei did not return to oiled streams for at least 5 yr after the Bahía Las Minas oil spill. Transplant experiments using mussels in plastic-mesh cages showed that fewer transplanted adults survived in oiled than unoiled streams between May 1990 and May 1991. Because no physical contact with oil occurred, it appears that acutely toxic effects of dissolved hydrocarbons persisted through at least May 1991. Settlement occurred in transplant cages in both oiled and unoiled streams (Fig. 35), suggesting that settlement attraction plays a part in population dynamics. This could account for lowered settlement in oiled streams, where adults were absent.

Some bags containing transplanted *Mytilopsis* were ripped open at oiled streams, but not unoiled ones. Crabs may have returned to oiled streams 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 the 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, may have played an important role in determining the course of repopulation in streams.

Salinity Tolerances in Estuarine Molluscs and Barnacles

The tolerance to exposure to low salinity of the common molluscs and barnacles on estuarine mangrove roots was tested in the laboratory. Results for *Balanus improvisus* suggest that short-term pulses of low salinity can severely reduce populations. Periods of reduced salinity (<4o/oo) lasting more than a week would be expected to have a severe negative effect on *Crassostrea virginica* populations. The less-common bivalves (*Brachidontes* and *Isognomon*) can survive reduced salinity longer than *Crassostrea*. It is known that *Mytilopsis sallei* can survive and reproduce in salinity ranging from 0 to 50o/oo; the major limit to occurrence appears to be a requirement for fluctuating salinity to initiate spawning.

Each species except *Mytilopsis* was potentially negatively affected by rapid changes in salinity. Prolonged (>10 d) drops to <4o/oo would probably reduce populations of all species. Changes in salinity gradients within Bahía Las Minas and variation in salinity among years may cause shifts in populations.

Discussion

Environmental differences existed between oiled and unoiled sites in two of the three habitats examined. If such differences had not been identified, they would have confounded the assessment of damage to epibiota by oiling. However, (1) prespill data and observations of channels and streams, (2) convergence of oiled and unoiled sites over time in channels, (3) comparison of closely matched sites in channels, and (4) experimental results all strongly suggest that oiling in some cases

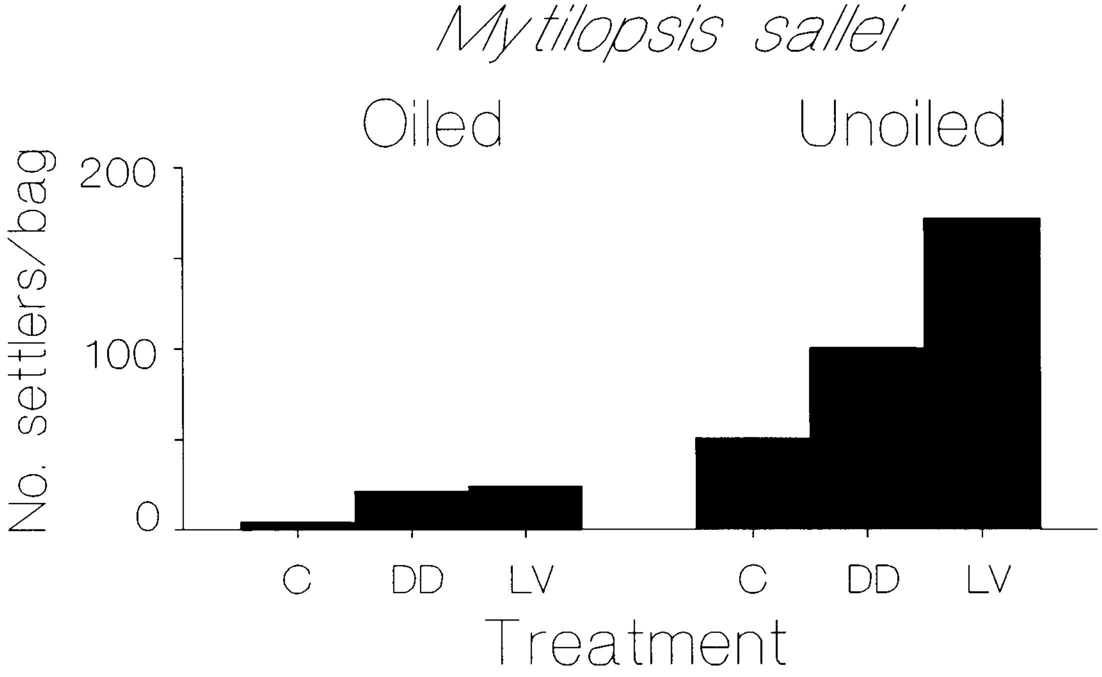

Fig. 35 *Mytilopsis* **transplant experiments: settlement attraction. Number of settlers/bag for treatments.** *C* **= empty bag,** *DD* **= bag containing empty valves from false mussels,** *LV* **= bags containing live transplants.**

had severe effects on populations and communities that persisted at least 5 yr after the spill.

In patches where oil came ashore heavily, successive deposition of oil coated roots with layers of tar up to 1 cm thick. Within 3 to 9 mo after the spill, the most-common species or taxa were less abundant in oiled than unoiled areas or had virtually disappeared. Foliose algae, which rotted quickly, left little direct evidence of mortality 3 mo after the spill. However, attached valves of dead bivalve molluscs provided direct evidence that lasted only 6 mo postspill. Nine months 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 effects of oiling. Mechanical (smothering) effects of thick coats of oil may have been sufficient to account for observed effects on the epibiota. 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.

Recovery of fringing mangrove root epibiota was not complete in any habitat after 5 yr. Pre- and postsettlement processes affecting recovery differed among habitats and within habitats among taxa. Effects of the spill on mangrove root length, abundance, and provisioning and on fringe survival had severe and continued effects on the physical structure of habitats, which exacerbated negative effects of oiling on root epibiota. The large, long-term effect of this spill on the mangrove fringe has probably also had cascading negative effects on other species dependent on it for food and habitat.

Sheltered shores were slowest to recover and had highest levels of residual oiling. Protection of inner bays and estuaries where mangroves grow is strongly suggested following an oil spill. Protection of tidal streams would probably prevent the greatest amount of long-term damage, and may lessen the amount of oil deposited in sediments that could later serve as reservoirs for secondary releases of oil.

Complete evaluation of damage to the epibiota required ~6 mo, while the fringe continued to deteriorate for ~3 yr. Where trees defoliated first, more of the fringe later died. This may be useful in predicting the eventual amount of damage.

The amount of damage to the mangrove fringe depended on water levels when oil came ashore. There would be less direct contact of oil with epibiota or prop roots at other times of year. Seasonal or annual variation in water levels must be part of contingency plans for spill response; different habitats will be oiled depending on hydrological and meteorological conditions.

Effects of the 1986 Bahía Las Minas, Panama, Oil Spill on Plants and Animals in Seagrass Communities

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Introduction

Seagrass beds along the central Caribbean coast of Panama usually occur in shallow lagoons between small patch or fringing reefs and mangrove forests. They are exposed to various combinations of exposure to waves, tidal currents, freshwater runoff, and other physical factors.

Seagrass beds stabilize sediments and act as sediment traps, provide substrata for many species of epiphytes and epifauna, provide food for many invertebrate and fish species, and are nursery grounds for fish and crustaceans. In this study (see Marshall et al., Chap.10, Vol. II) the primary habitat-structuring seagrass was *Thalassia testudinum*; *Syringodium filiforme* was common but contributed 1-2 orders of magnitude less biomass. Associated macroalgae included calcified greens and reds, and fleshy browns and greens. Polychaetes were the numerically dominant "infaunal" (infauna and sedentary epifauna collected in sediment cores) taxon, and were represented by at least 27 families. Also abundant in sediment-core samples were various crustaceans, gastropod and bivalve molluscs, sipunculids, ophiuroids, and cumaceans. Numerically dominant taxa in epifaunal (push net) samples included crustaceans, gastropods, ophiuroids, and fish. Holothurians and echinoids were common or present, and contributed substantially to epifaunal biomass.

The response of seagrass communities to oiling appears to depend on the elevation of beds in the littoral zone. Despite an omnipresent threat of oil spills to seagrass beds and concern about consequences of their destruction, little is known about the potential for recovery of seagrass communities from oiling.

Objectives, Rationale, and Design

Few prespill data were available, and it was necessary to infer effects of the spill from postspill differences between oiled and unoiled sites. Monitoring started 5 mo after the spill, ultimately at four oiled and four unoiled beds. 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.

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. 1). Criteria used in selecting sites were that beds were adjacent to mangroves and were subtidal. All sites were located behind small fringing reefs, and sampling was at depths <1 m. Sediments were more coarse at unoiled than at oiled sites and silt-clay fractions were greater, but sediment organics were similar. Spatial separation between oiled and unoiled areas can confound naturally occurring spatial differences with effects of the spill, but spatial differences appear not to have been great in this study.

Oiling and Reoiling

Surface sediments in heavily oiled seagrass beds contained high concentrations of hydrocarbons in 1986 and 1987, with values ranging from 211 to 6,683 μg/g (UVF). By 1988 values at the surface were 188-658 μg/g, and subsurface values at one site were greater than the surface concentration. Reoiling of seagrass beds was likely because of their proximity to heavily oiled mangroves.

Components of Research

Plant Biomass

Samples consisted of three pooled sediment cores, with a total area of 285 cm^2. Eight samples were collected at each site. Before seagrass tissues were dried, attached macroalgae were removed and combined with the rest of the algal fraction. All plant materials were weighed after drying at 90°C for 5 d.

Total, subsurface, and blade biomass of seagrasses initially were lower at oiled and than at unoiled sites (Fig. 36). This difference disappeared by November 1986 as biomass increased at oiled sites and decreased, except for blades, at unoiled sites. After November 1986 seagrass biomass at both oiled and unoiled sites decreased steadily until collections ended 3 yr after the spill. Calcareous algal biomass decreased at unoiled sites and increased at oiled sites; values generally were similar starting 9 mo postspill. Fleshy algal biomass generally was similar at oiled and unoiled sites, and there was a general decrease through time.

There was an initial sublethal effect of the spill on subsurface biomass of *Thalassia*; biomasses converged at oiled and unoiled sites 7 mo after the spill. *Syringodium* biomass generally was lower in oiled than in unoiled beds 15-30 mo after the spill, and it appears that *Syringodium* is more sensitive to oiling than *Thalassia.*

Shoreward Margins of Seagrass Beds

After observing death of seagrasses around a marker stake approximately 2.5 yr after the spill, stakes were placed along shoreward margins of beds for systematic measurements of variations. Shoreward edges of seagrass beds generally receded from mangrove shorelines at oiled sites 2-3 yr after the spill, in contrast to unoiled sites (Fig. 37). Thus, the oil spill apparently affected subtidal seagrass beds more by a decrease in area along shoreward margins than by a long-term, sublethal reduction in biomass. This suggests that oil released from mangrove sediments may have reached toxic concentrations along bed margins during reoiling events.

Infaunal (Core) Sampling

Core samples were sieved through 500-μm mesh screen. Animals were picked and sorted to major taxa. Although animals collected in this manner are called

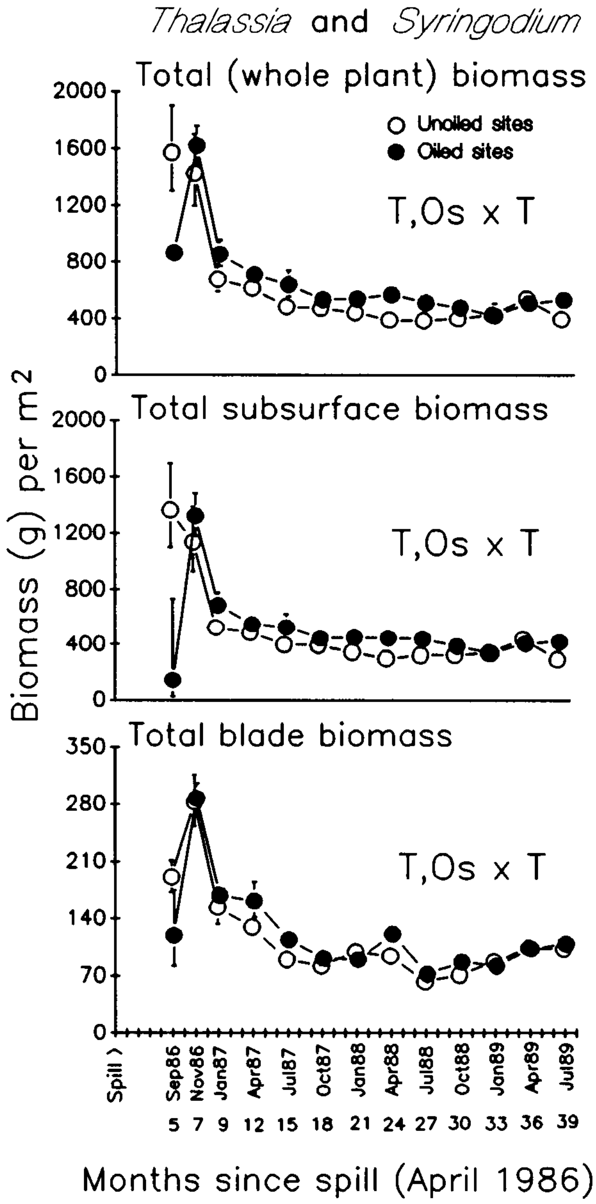

Fig. 36 Total, total subsurface, and total blade biomass of *Thalassia testudinum* and *Syringodium filiforme* combined. Data are from core samples; standard-error bars were back-transformed from $\ln(x+1)$. Results of repeated-measures ANOVAs are: *Os* = significant difference ($P < .05$) between oiled 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, Volume II.

infauna in this report, they included sedentary epifauna associated with seagrass blades or the sediment surface as well as true infauna.

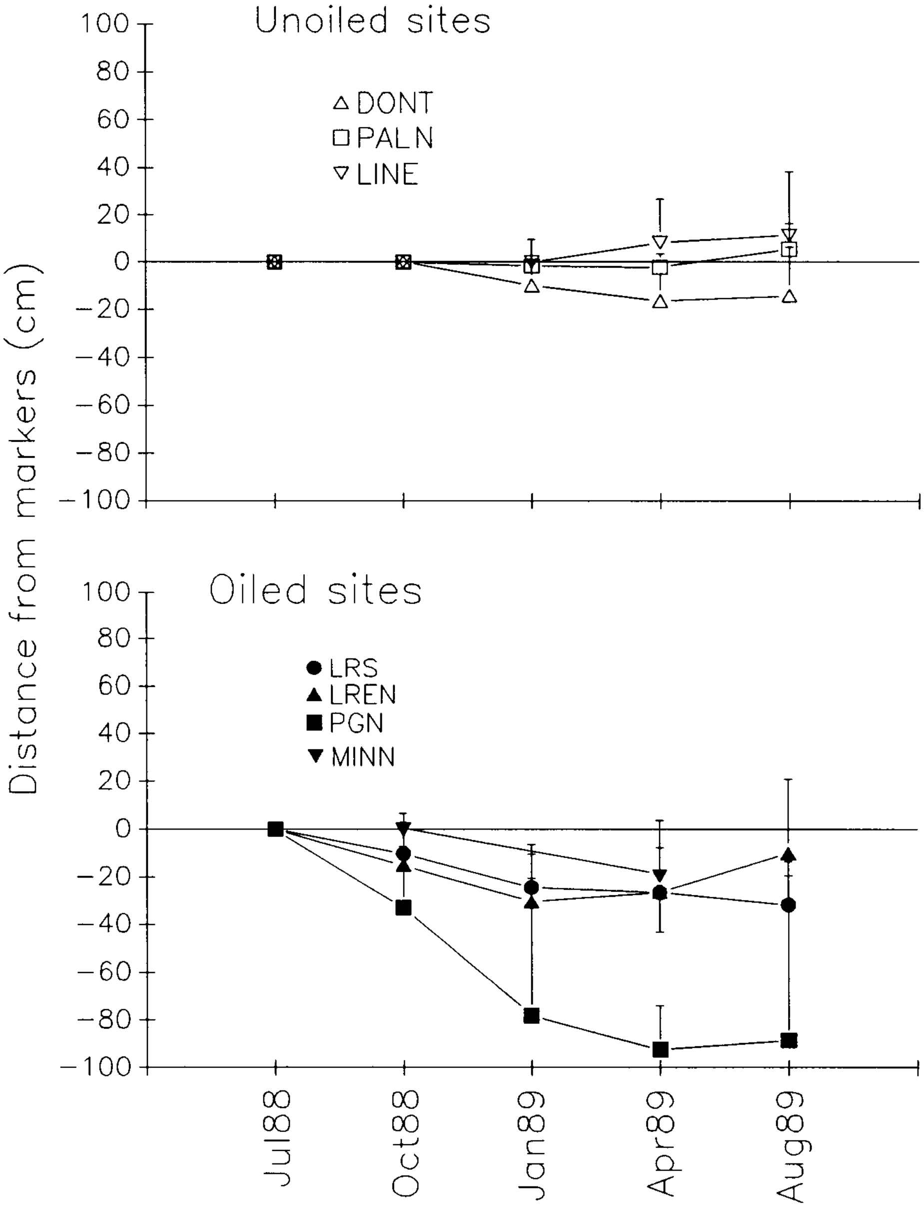

Fig. 37 Position of the shoreward margin of seagrass beds relative to permanent marker posts, the *zero line*, put in place during July 1988.

As the abundance of infauna 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. 38). Densities of some of the most abundant infaunal taxa (amphipods, tanaids, isopods, cumaceans, sipunculids, and ophiuroids) also converged

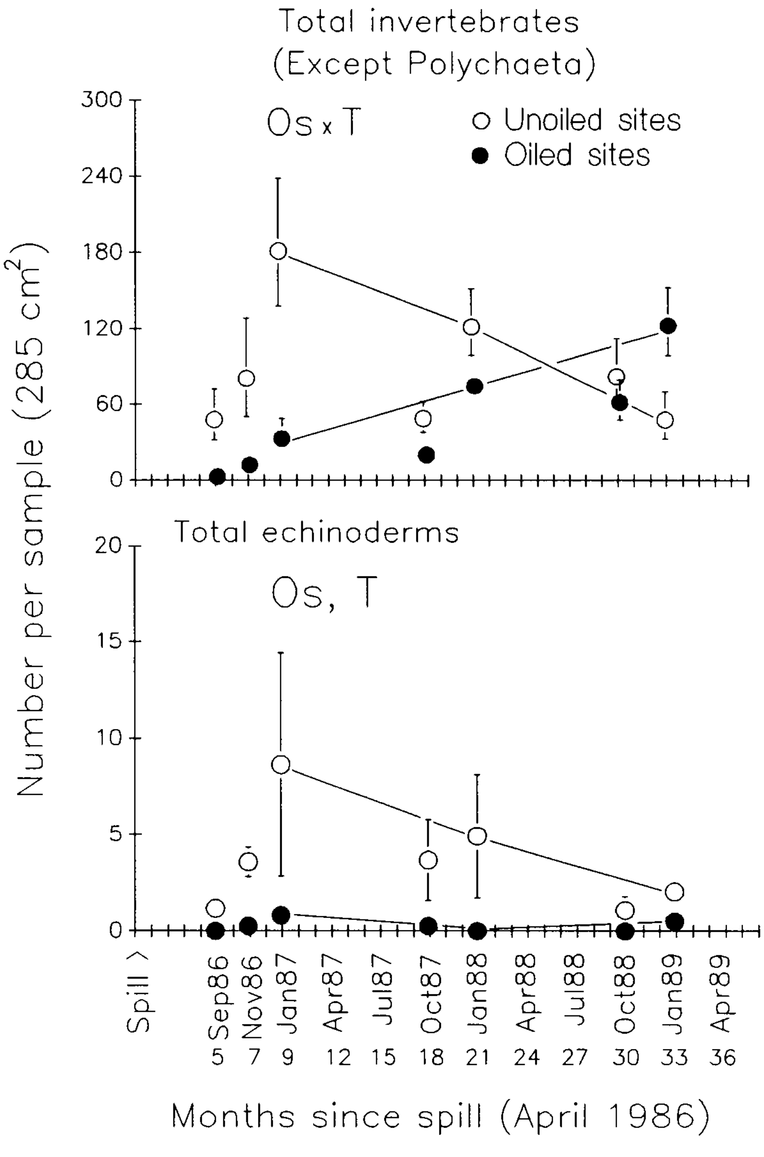

Fig. 38 Total count of invertebrates except polychaetes and of echinoderms in core samples, September 1986 through January 1989. Error bars and ANOVA results are explained in the caption to Figure 37. Repeated-measures analysis was conducted for the January collections only (connected points); refer to Appendix Table F.2, Volume II.

similarly. Other common taxa did not converge in density, and hermit crabs were generally more abundant at oiled than at unoiled sites.

The general pattern of increase through time in numbers of infauna at oiled sites after the spill is indicative of repopulation after what appeared to be a nearly complete die off. It is not known why numbers generally declined at unoiled sites, but this trend coincided with a steady decline in seagrass biomass to approximately 25% of the level measured at the start of the study. Tanaid and amphipod crustaceans and ophiuroids were taxa that appeared to be particularly sensitive to oiling.

Epifaunal (Push Net) Sampling

Mobile and sedentary epifauna were collected by pushing a net with a 0.75 x 0.35 m mouth a set distance (10 m) in the same oiled and unoiled seagrass beds that were sampled for plants and infauna. Epifauna were sorted to major taxa and shrimp were identified to species. The size and reproductive status of two shrimp species were also recorded.

Total numbers of epifauna generally were greater at unoiled than at oiled sites (Fig. 39), as were some of the most abundant epifaunal taxa (shrimp, tanaids, amphipods, gastropods, ophiuroids, and fish). Echinoderms also differed markedly, with total numbers 1-2 orders of magnitude greater at unoiled sites because of a pulse in numbers between April 1987 and April 1988 that occurred at unoiled sites but not at oiled sites. Two abundant taxa (brachyuran and isopod crustaceans) did not have significantly different densities at oiled and unoiled sites, and two other taxa (hermit crabs and mysid shrimp) were more abundant at oiled than at unoiled sites. Combining crustacean taxa into groups based on egg-care strategies suggested that species with direct development were most strongly affected by the spill. Recruitment and size structures of two abundant shrimp species followed similar patterns in oiled and unoiled seagrass beds.

As was the case for infauna, total epifauna increased in abundance at oiled sites after the spill consistent with a pattern of postspill repopulation of oiled 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. Judging by total counts at oiled and unoiled sites, which differed by a factor of 2.9 for infauna and by 1.5 for epifauna, infauna were more strongly affected by the spill than epifauna. This pattern would be expected if oil in seagrass sediments affected infaunal life cycles more than epifaunal recruitment and survival. Echinoderm numbers differed by an order of magnitude between unoiled and oiled sites, suggesting that these groups may be particularly useful as "indicator" taxa of oil pollution. The apparent lack of an effect of the spill on the development, reproductive output, and recruitment of two common shrimp 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.

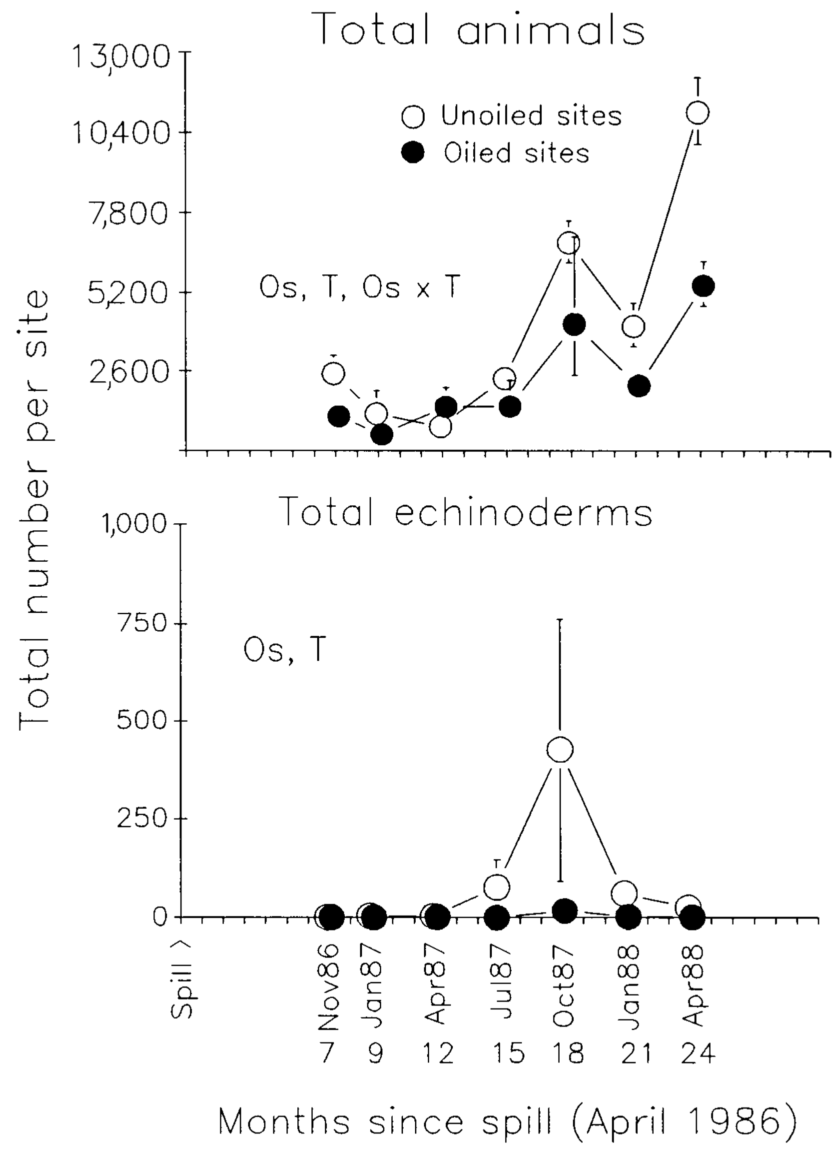

Fig 39 Total number of animals and echinoderms in push-net collections, November 1986 through April 1988. Error bars and ANOVA results are explained in the caption to Figure 37; refer to Appendix Table F.3, Volume II.

Discussion, Conclusions, and Recommendations

The oil spill apparently had a transitory effect on subtidal seagrasses but a more lasting effect (≥2-3 yr) on particular animal taxa. Population declines caused by the spill apparently were quickly overcome 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 recovery during 2-3 yr of postspill monitoring. Large, epifaunal echinoderms (holothurians, echinoids, and asteroids) appeared particularly well suited for monitoring oil spills because they are easy to identify and count in the field and appeared to have a strong, persistent numerical response to the spill. Loss of area of oiled subtidal seagrass beds may have been considerable but was not investigated promptly. Such loss of habitat could have extensive, long-lasting effects on the fauna of this community.

Conclusions

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.

Fate of the Spilled Oil and Environmental Damage

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 (Fig. 1), (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 Volume II and elsewhere. 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 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 (ultraviolet fluorescence and gas chromatography) shown by highly significant correlations for very large numbers of samples of sediments from different habitats and of bivalve molluscs, spanning as much as 4 yr of sampling..

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. 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.

Characterization, Persistence, Degradation, and Release of Oil from the 1986 Spill

Chemical 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. 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. 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 39% dry weight of sediments 5 mo after the spill), and oil was still present in large quantities 4 yr after the spill (as high as 25%).

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 and in mangrove sediments in Puerto Rico. 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.

Sentinel Organisms

In oil-contaminated ecosystems, bivalves preferentially accumulate more soluble, lower-molecular-weight hydrocarbons. 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. 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, 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 and requires further study.

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. 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.

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. 40). 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 such as grunts that were present in considerable abundance at the Punta Galeta reef before the spill.

The inevitable consequence is that the Bahía Las Minas ecosystem is more vulnerable to subsequent natural or anthropogenic disturbances. An example of this was the pattern 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.

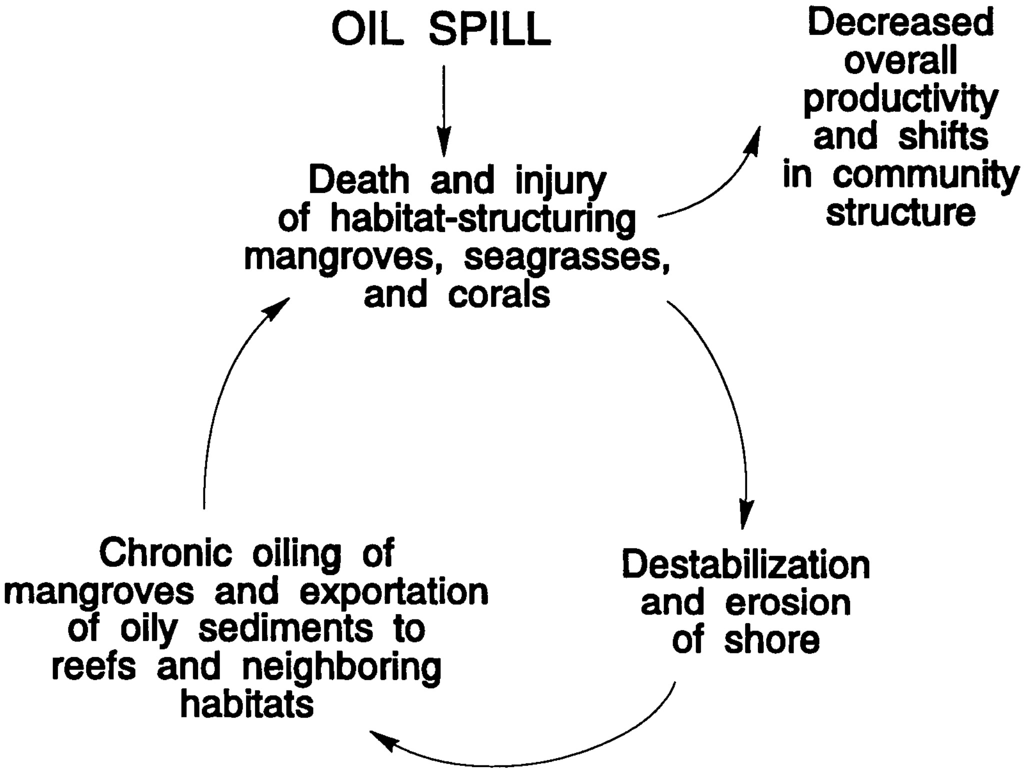

Fig. 40 A model of the chain reaction of habitat and biological damage due to the 1986 oil spill at Bahía Las Minas.

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. 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. 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. 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.

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.

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.

Reef Corals

The cover, size, and diversity of live corals decreased greatly on two oiled reefs compared to their values before the oil spill (Fig. 17), while values initially increased on unoiled reefs. These differences persisted from 1988 through 1991, although diminished, even after the occurrence of precipitous, unexplained coral mortality at unoiled reefs between 1986 and 1988 (cover dropped from 28% to 12%; Fig. 17). 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. For some species, 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.

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. 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.

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 . 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 (Fig. 33). 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.

Seagrass Beds

The reef flat seagrass bed at Largo Remo North died and disappeared completely, and the area of shallow subtidal beds decreased, 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 most affected, 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).

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.

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.

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. 40) 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. 41). 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.

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. 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 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.

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. 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

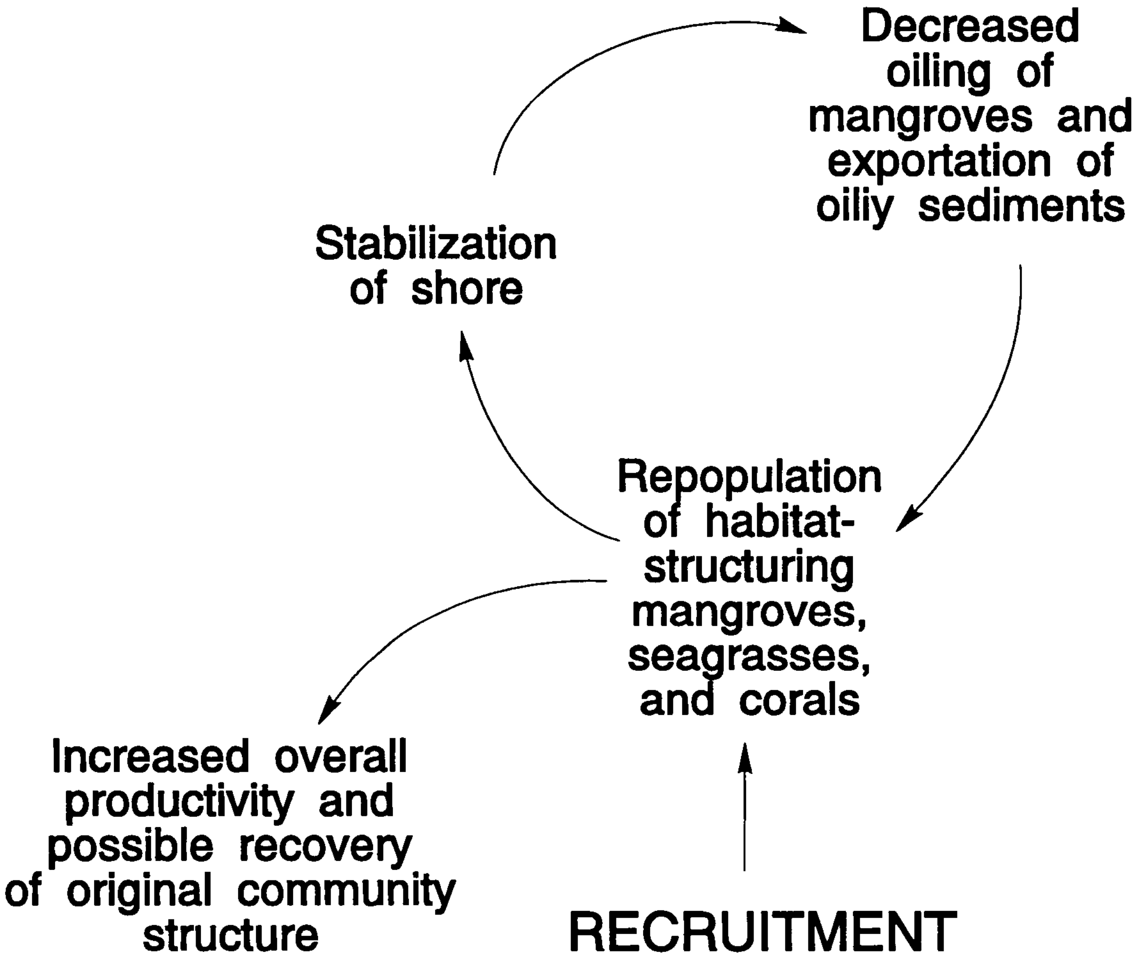

Fig. 41 A model of the presumed cycle of repopulation of habitat-structuring organisms and diminishing release of oil.

of kilometers. 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. Clonal dispersal typically occurs over distances of only a few meters.

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. 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. 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 in a 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. 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.

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. 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.

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, 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.

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. 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. 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.

Recommendations for Future Studies

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, 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.

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.

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.

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.

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.

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. 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.

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. However, reef flat communities tend to repopulate very rapidly, so that such differences in damage may be of little practical importance, within limits. 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. 42). 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.

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.

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. 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

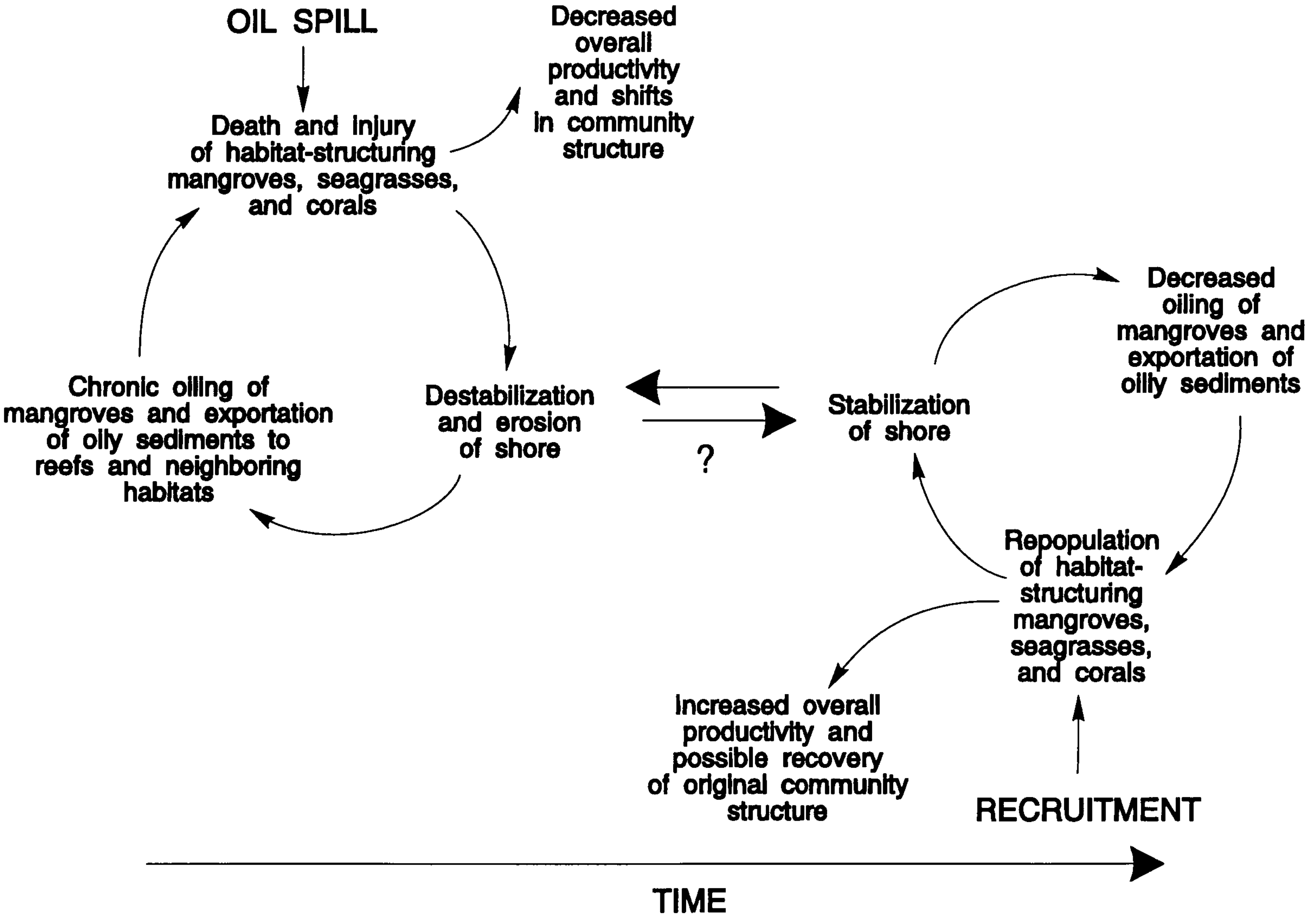

Fig. 42 Models of habitat damage and recovery, showing the likely link at the process of shoreline stabilization.

and spill-related factors. This is the reason for the extensive discussion of site differences as confounding effects in parts of Volume II.

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. 40), should be generally applicable to any tropical coastal environment as long as confounding factors are understood.

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 40. 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. Moreover, because these species rely to a large extent on clonal propagation, repopulation may take decades despite the very rapid growth rates of these species.

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.

*U.S. G.P.O. 1993-301-078:80415

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally-owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

March 3, 1849

MINERALS MANAGEMENT SERVICE