MACROFAUNA COMMUNITIES OF EXPOSED SANDY BEACHES ON THE SOUTHERN CALIFORNIA MAINLAND AND CHANNEL ISLANDS

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ABSTRACT

Exposed sandy beaches are important intertidal habitats and coastal resources in southern California. A high proportion of the mainland coast (74%, 93%, and 66% of Santa Barbara, Ventura, and Los Angeles counties, respectively) is sandy beach, much of which is heavily used by humans. Lower proportions of the California Channel Island coasts are sandy (52%, 33%, and 14% of San Miguel, Santa Rosa, and Santa Cruz islands, respectively). Island beaches receive little direct human disturbance and some are important rookeries for pinnipeds and nesting birds. Recent studies used similar methods to sample macrofauna and other factors on 36 sandy beaches of the southern California mainland and Channel Islands. Monitoring of physical characteristics, macrophyte wrack, and selected macrofauna species occurs only on Santa Rosa Island beaches. The beaches sampled were primarily modally intermediate morphodynamic types. Species richness, abundance, and biomass of macrofauna inhabiting exposed sandy beaches in southern California were high compared to values reported for similar beaches of other regions. Species richness was higher on mainland beaches than on island beaches. Species richness and abundances of selected taxa were positively correlated with macrophyte wrack cover. Beach grooming practices that remove wrack may have significant impacts on macrofauna communities.

Keywords: Species richness, abundance, biomass, macrophyte wrack.

INTRODUCTION

Sandy beaches comprise approximately three-quarters of the world's shorelines (Bascom 1980). On the mainland coast, 74%, 93%, and 66% of Santa Barbara, Ventura, and Los Angeles counties, respectively, are sandy beaches (Smith et al. 1976; Dugan et al. 1998a). The overall proportion of sandy beach is lower for the shores of the California Channel Islands, about 23% (Littler and Littler 1980). However, that proportion varies considerably with island size, geology, and history. Sandy beaches compose 52%, 33%, and 14% of the shorelines of the larger northern Channel Islands of San Miguel, Santa Rosa, and Santa Cruz, respectively (Dugan et al. 1998a).

Exposed sandy beaches in California are inhabited by an abundant invertebrate macrofauna community (Straughan 1982, 1983; Dugan et al. 1995), which is an important food resource for vertebrate predators such as shorebirds, seabirds, marine mammals, and fishes, including federally listed species such as the western snowy plover (*Charadrius alexandrinus nivosus*). Sandy beaches of the region are also nesting sites for two endangered bird species: western snowy plovers and California least terns (*Sterna antillarum browni)*. The California grunion, *Leuresthes tenuis*, deposits eggs for incubation in the high intertidal zone of sandy beaches. A number of species of pinnipeds have large rookeries on the isolated and undisturbed beaches of the northern Channel Islands, particularly San Miguel and San Nicolas islands (Le Boeuf and Bonnell 1980).

Sandy beaches are also considered extremely valuable as recreational and scenic resources for humans, both residents and tourists (Leatherman 1997). Human use varies considerably between the isolated shores of most of the California Channel Islands (except Santa Catalina Island) and the heavily used, disturbed, developed, and managed mainland shores of the majority of the Southern California Bight. Many mainland beaches are also subject to regular grooming, in which trash, debris, and drift macrophytes are removed.

The interpretation of earlier studies of sandy beach macrofauna communities on the California mainland and Channel Islands (e.g., Straughan 1982; 1983) has been limited with respect to recent advances in sandy beach community ecology. Those studies occurred prior to the use of a morphodynamic classification of beaches by Dean's

parameter and other indices to ordinate beaches for comparisons of macrofauna community structure (e.g., McLachlan 1990). Dean's parameter is a dimensionless index of sediment fall velocity and wave height and period that expresses the dynamic interaction between the wave regime and available sediments (Short and Wright 1983; Short 1966). Using this classification, three general categories of exposed sandy beaches are identified: reflective, intermediate, and dissipative. Reflective beaches (Dean's parameter <1) are characterized by small waves (<0.5 m), narrow surf zones, coarse sediments, and steep slopes and are a harsh environment for intertidal fauna. Dissipative beaches (Dean's parameter >6) are characterized by large waves (>2 m), wide surf zones, fine sand, and flat slopes, and are the most physically benign sandy beach habitat for fauna. Intermediate beaches (Dean's parameter 1-6) exhibit characteristics that fall between those extremes (Short and Wright 1983) and are the most temporally variable beach type. Information on the morphodynamics of sandy beaches on the California coast is limited compared to other parts of the world (e.g., Australia; Short 1996).

Along the morphodynamic spectrum, several general patterns have been identified for macrofauna communities of exposed sandy beaches in both regional and global comparisons (McLachlan 1990; McLachlan et al. 1993, 1996). Macrofauna species richness increases and total community abundance and biomass increase logarithmically from reflective to dissipative beach types (McLachlan 1990; McLachlan et al. 1993, 1996).

Despite the high prevalence of exposed sandy beaches along the coast of southern California, macrofauna communities of beaches have received relatively little attention from marine ecologists. Monitoring programs for sandy beaches are limited relative to the effort expended for rocky shores. Our beach surveys were designed to provide new information on beach morphodynamics and other factors affecting macrofauna community structure on exposed sandy beaches on the southern California coast.

MATERIALS AND METHODS

Detailed methods for our surveys of macrofauna communities and of selected macrofauna species appear in Dugan et al. (1995), Engle et al. (1995), and Dugan (1997). Detailed methods for the Channel Islands National Park monitoring program appear in Dugan et al. (1990) and Richards (1995; 1996).

Amounts of accumulated macrophyte wrack were estimated (as percent cover, total cover, and/or volume) using point-contact transects across the intertidal zone from the lowest edge of the terrestrial vegetation or base of the sea bluff to the high swash zone. Physical characteristics measured at each site included: beach zone widths, slope, sediment characteristics, and wave regime.

Surveys were conducted on spring low tides. At least 3.0 m^2 (Jaramillo et al. 1995) of intertidal habitat was sampled at each beach during the one-time macrofauna surveys of both types in all but three of the surveys (Ford Point, Becher's Pier, and Southeast Anchorage, Santa Rosa Island). The macrofauna samples consisted of uniformly spaced cores of 100 to 200 mm diameter and 100 to 200 mm depth collected at uniform intervals across the intertidal zone from the lowest edge of terrestrial vegetation or the base of the sea bluff to the lowest swash zone. Three to ten transects were sampled and cores were pooled at 10 or 15 intertidal levels depending on the survey. The sand from cores collected at each level was processed in sieves with 1.0 to 1.5 mm apertures and the animals retained were either preserved for later analysis or processed live and released. Means of abundance and biomass were calculated and expressed as numbers or grams m^{-1} of beach (a vertical meter-wide strip of intertidal) as suggested by Brown and McLachlan (1990).

RESULTS

Study Sites

The macrofauna of a total of 36 beaches were surveyed using comparable methods between 1988 and 1996 (Table 1, Table 2, Figure 1). Along the mainland coast, macrofauna surveys were conducted at three beaches in Santa Barbara County, 12 beaches in Ventura County, and two beaches in Los Angeles County (Table 1, Figure 1). Several of the mainland beaches we surveyed are subject to regular grooming to remove accumulated trash and macrophyte drift. On the northern Channel Islands, surveys were conducted at three beaches on San Miguel Island, eight beaches on Santa Rosa Island, and six beaches on Santa Cruz Island (Figure 1, Table 2). Two beaches were surveyed on Santa Catalina Island (Figure 1, Table 2).

Macrofauna community surveys were conducted at a total of 23 sites (Table 1, Table 2). Those surveys were conducted in conjunction with measures of macrophyte wrack at 15 of those sites. Surveys targeting 11 macrofauna species, macrophyte wrack, and physical charactertistics were conducted at 15 sites (Table 1, Table 2). Monitoring of selected macrofauna species, macrophyte wrack, and physical characteristics was conducted at 5 to 9 sites on Santa Rosa Island during August or September of 1994, 1995, and 1997 (Figure 1, Table 3). Additional surveys for grunion eggs were conducted on a number of Santa Cruz Island beaches in 1996 and 1997 (see Engle et al. 1998).

Beach Characteristics

The orientations of many of the beaches surveyed on the mainland and Channel Islands ranged from west through south to southeast (Figure 1). On the northern shores of the Channel Islands, a number of the beaches we surveyed had unique north to northwest or northeast orientations including Cuyler's Harbor, Sandy Point, Becher's Pier, Water Canyon, Southeast Anchorage, Fraser Cove, Prisoners Harbor, and Isthmus Cove (Figure 1).

Despite the variety of orientations to prevailing swells among the study sites, the majority of the beaches we

Table 1. Beach names, locations, dates, types, and investigators for macrofauna surveys conducted on the mainland coast of southern California. Sites are listed from north/west to south/east in each county.

Beach Name and Location	Date(s)	Survey Type	Investigators
Santa Barbara County			
Sands Beach	10/13/96	community	Dugan, Hubbard
East Campus Beach	9/27/96	community	Dugan, Hubbard
Santa Claus Lane	9/15/96	community	Dugan, Hubbard
Ventura County			
La Conchita Beach	9/16/96	community	Dugan, Hubbard
Oil Piers	9/13/96	community	Dugan, Hubbard
Solimar	10/22/95	selected species	Lafferty, Ambrose
Solimar	9/12/96	community	Dugan, Hubbard
Marina Park	9/26/96	community	Dugan, Hubbard
Surfers Knoll	10/12/96	community	Dugan, Hubbard
5th Street	10/10/96	community	Dugan, Hubbard
Silver Strand	10/23/95	selected species	Lafferty, Ambrose
Silver Strand	10/11/96	community	Dugan, Hubbard
Ormond 3	9/28/96	community	Dugan, Hubbard
Ormond 2	9/25/96	community	Dugan, Hubbard
Ormond 1	9/25/96	community	Dugan, Hubbard
Deer Creek	9/29/96	community	Dugan, Hubbard
Leo Carrillo N.	9/24/96	community	Dugan, Hubbard
Los Angeles County			
Santa Monica	10/24/95	selected species	Lafferty, Ambrose
Manhattan Beach	10/21/95	selected species	Lafferty, Ambrose

Table 2. Beach names, locations, dates, types, and investigators for macrofauna surveys conducted by the authors on the California Channel Islands.

Beach Name and Location	Date(s)	Survey Type	Investigators
San Miguel Island			
Simonton Cove	9/25/96	selected species	Engle, Martin
Cuyler's Harbor	9/27/96	selected species	Engle, Martin
South East Beach	9/26/96	selected species	Engle, Martin
Santa Rosa Island			
Sandy Point	10/25/88	community	Dugan, Hubbard
Bee Rock West	7/19/89	community	Dugan, Hubbard
China Camp	5/23/89	community	Dugan, Hubbard
Ford Point	5/6/88	community	Dugan, Hubbard
Abalone Rocks	10/26/96	community	Dugan, Hubbard
Southeast Anchorage	5/8/88	community	Dugan, Hubbard
Water Canyon	5/24/89	community	Dugan, Hubbard
Becher's Pier	5/7/88	community	Dugan, Hubbard
Santa Cruz Island			
Prisoners Harbor	9/21/95	selected species	Engle, Martin, Hubbard
Fraser Cove	9/27/95	selected species	Engle, Martin, Hubbard
Forney Cove	9/26/95	selected species	Engle, Martin, Hubbard
Christi Beach	9/25/95	selected species	Engle, Martin, Hubbard
Pozo	9/24/95	selected species	Engle, Martin, Hubbard
Smuggler's	9/6/95	selected species	Engle, Martin, Dugan, Lafferty
Santa Catalina Island			
Little Harbor	11/6/95	selected species	Lafferty, Ambrose
Isthmus Cove	11/7/95	selected species	Lafferty, Ambrose

surveyed on the Channel Islands and the adjacent mainland coast were modally intermediate morphodynamic types with values of Dean's parameter between 1.5 and 6.6 measured during the surveys. Although a value of Dean's parameter >6 was obtained during one survey, no modally dissipative beaches were surveyed in our study. Reflective beaches occurred at Ford Point and Becher's Pier on Santa Rosa Island, the Isthmus on Santa Catalina Island, and at East Campus beach on the Santa Barbara County mainland. Values of Dean's parameter for the reflective beaches surveyed ranged from 0.2 to 0.6.

Mean sediment sizes ranged from 0.15 to 0.85 mm diameter. The coarsest sediments (0.85) occurred at Isthmus Cove on Santa Catalina Island, a reflective beach. Sediment size varied more among island beaches (0.15 to 0.85 mm) than among mainland beaches (0.20 to 0.71 mm).

Active intertidal widths ranged from 27 to 80 m. The intertidal zones of the reflective beaches surveyed were narrower (29 to 38 m) than those of the intermediate-type beaches. Intertidal slopes (measured at the water table outcrop) ranged from 1 to 7 degrees.

Macrophyte Wrack

Macrophyte wrack amounts were measured during the one-time surveys at 28 of the beaches and during the monitoring of Santa Rosa Island beaches. Estimates of the mean cover of marine macrophyte wrack on ungroomed beaches varied from 0.01 to 20.3%. On the five beaches subject to regular grooming, the mean cover of marine wrack was much lower, ranging from 0.0 to 0.3%. The mean intertidal cover of marine wrack on ungroomed mainland beaches varied over two orders of magnitude (0.03 to 5.03 m^2 per running meter of beach). On groomed beaches, the total cover of marine wrack varied from 0.0 to 0.39 m^{-1}. Where estimated (nine sites; Santa Cruz Island and San Miguel Island), mean wrack volumes ranged from 0.003 to 4.69 m^3 per running meter of beach.

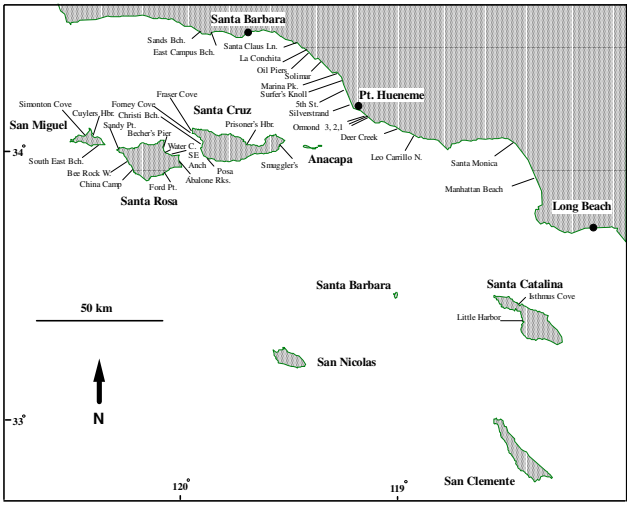

Figure 1. Locations of sandy beach surveys and monitoring studies on the southern California mainland and the Channel Islands.

Table 3. Beach names, locations, dates, and types of monitoring conducted on Santa Rosa Island (Richards, Davis).

Beach Name	Year	Wrack Cover	Upper Intertidal Cores	Lower Intertidal Cores	Subtidal Transects
Soledad West	1994	√	√	√	
	1995	√	√	√	
	1997	√	√	√	
Sandy Point	1994	√	√	√	
	1995	√	√	√	
	1997	√	√	√	
Bee Rock West	1994	√	√	√	
	1995				
	1997	√	√	√	
China Camp	1994	√	√	√	
	1995	√	√	√	
	1997	√	√	√	
Ford Point	1994	√	√	√	
	1995				
	1997	√	√	√	
Abalone Rocks	1994	√	√	√	
	1995	√	√	√	
	1997	√	√	√	
Southeast	1994			√	√
Anchorage	1995			√	√
	1997			√	√
Water Canyon	1994	√	√	√	
	1995	√	√	√	
	1997	√	√	√	
Becher's Pier	1994	√	√	√	
	1995	√	√	√	

The majority of macrophyte wrack reported on mainland beaches consisted of giant kelp, *Macrocystis pyrifera*, and surfgrass, *Phyllospadix* sp., drift. At some beaches on the Channel Islands, red algae and eelgrass, *Zostera*, drift also comprised significant components of the wrack. Carrion was also a component of the wrack on some of the Channel Island beaches.

Macrofauna

Species Richness

Surveys of the macrofaunal communities of eight sandy beaches on Santa Rosa Island documented more than 50 species, including snails, bivalves, crustaceans, polychaetes, insects, spiders, and fertilized eggs of the California grunion (see also Dugan et al., in press; Dugan et al. 1995). Species richness for individual beaches in single surveys ranged from 5 to 23 species of macrofauna on Santa Rosa Island. The lowest number of species (five) occurred on a reflective, embayed, south-facing beach, Ford Point. At least 10 species occurred in samples from the other beaches surveyed on that island.

Sandy beaches on the mainland coasts of Ventura and Santa Barbara counties were generally richer in species than beaches of the Channel Islands. A total of more than 60 species of macrofauna occurred in surveys on 15 beaches. Species richness ranged from 11 to 37 species. More than 20 species of macrofauna occurred in our samples at seven of the 15 sites and samples from three sites contained 30 or more species. The greatest number of species of macrofauna (37) occurred on a low intermediate-type beach, Oil Piers; and the second greatest number of species (33) occurred on a reflective beach, East Campus. Species richness, especially from the upper intertidal sampling levels, was consistently lower on the three mainland beaches subject to regular grooming and wrack removal with $\leq$16 species in those samples (range 11 to 16 species; Surfer's Knoll, 5th Street, Silverstrand). Beaches with naturally low amounts of wrack also had lower species richness (15 to 22 species; e.g., Ormond 1, 2, 3, Leo Carrillo) than those with abundant wrack.

Eggs of the California grunion, *Leuresthes tenuis*, occurred at or above the high tide strand level on several of the beaches surveyed. On the Channel Islands, grunion eggs occurred in the macrofauna surveys at Smuggler's Cove on Santa Cruz Island, and at Becher's Pier on Santa Rosa Island. Grunion eggs occurred in the upper intertidal at Prisoners Harbor, Pozo, and Christi Beach on Santa Cruz Island in subsequent surveys (see also Engle et al. 1998). On the mainland, grunion eggs occurred in surveys at Solimar and Silverstrand beaches.

Abundance

The means of total macrofauna abundance varied more than 25-fold among sites, ranging from 3,360 to 88,500 m^{-1} among the 23 sites sampled. The maximum total macrofauna abundance observed was lower on the the island beaches (56,000 m^{-1}) than on the mainland beaches (88,500 m^{-1}). Macrofauna abundances, particularly in the upper beach sampling levels, were generally lower on groomed mainland beaches than on ungroomed beaches. The lowest abundance occurred on a groomed beach (3,360 m^{-1}; 5th Street).

The most abundant and widespread species was the common sand crab, *Emerita analoga*. This species occurred on every beach sampled and was the most abundant species on 22 of the 36 beaches surveyed. The presence of high densities of *E. analoga* in the swash zone accounted for the majority of the animals on many of the beaches sampled, with sand crabs making up 5 to 98% of the total macrofaunal abundance. Abundances of this species were >10, 000 m^{-1} in samples from eight sites and ranged over two orders of magnitude, from 355 to 79,000 m^{-1}, in samples collected on the mainland in late summer and early fall. On island beaches, abundances of *E. analoga* ranged from 372 to 24,000 m^{-1} in late summer and early fall samples.

Other macrofauna species occurring in abundances >10,000 m^{-1} at some sites and comprising the most abundant species in some surveys included, the isopods, *Excirolana chiltoni* (up to 33,000 m^{-1}) and *Tylos punctata* (up to 14,700 m^{-1}); talitrid amphipods, *Megalorchestia* spp. (up to 25,500 m^{-1}); and a polychaete, *Euzonus mucronata* (up to 23,900 m^{-1}).

Two free-living bivalve species, the Pismo clam, *Tivela stultorum*, and the bean clam, *Donax gouldii* had markedly different occurrences in surveys on the Channel Islands and those on mainland beaches. *Donax gouldii* did not occur in any samples from Channel Island beaches. The distribution of *T. stultorum* was also more limited on island beaches, occurring at only one beach on Santa Rosa Island and one on Santa Cruz Island. The two species co-occurred in nine of the mainland beach surveys. *Donax gouldii* did not occur in surveys on two Ventura County beaches where *T. stultorum* occurred. Where they occurred, estimated abundances ranged from 32 to 770 clams m^{-1} for *T. stultorum* and 51 to 1,940 m^{-1} for *D. gouldii* in mainland surveys. Intertidal abundances of *T. stultorum* at the two sites on the Channel Islands were much lower, ranging from 1 to 23 m^{-1}. A gastropod, the purple olive snail, *Olivella bipiicata,* occurred only in samples from Channel Island beaches (Santa Cruz and Santa Rosa islands).

Biomass

Total macrofaunal biomass was measured directly only for the Ventura County and Santa Barbara County mainland sites. Mean biomass (wet) was more variable than abundance and varied over two orders of magnitude, ranging from 660 to 21,000 gm^{-1}. All but five sites had biomass values of >4,000 gm^{-1}, and the lowest biomass values (<1,000 gm^{-1}) occurred in our surveys of two groomed beaches. *E. analoga* was the dominant component of the biomass at all but two beaches. This species alone accounted for 22 to 99% (580 to 19,200 gm^{-1}) of the biomass in the surveys. The biomass of one site (Ormond 2) was dominated by the Pismo clam, *T. stultorum* (6,590 gm^{-1}), and that of second site (East Campus) by the spiny sand crab, *Blepharipoda occidentalis* (1,820 gm^{-1}).

Associations with Macrophyte Wrack

Species richness, where measured in conjunction with wrack sampling, was positively correlated with the amount of marine macrophyte wrack ($p < 0.05$). This is due primarily to the presence of a number of species of insects and crustaceans associated with stranded drift algae and macrophytes. Beetle species included a carabid, *Dyschirius marinus*, a tenebrionid, *Phalaria rotundata*, a hydrophilid, *Cercyon luniger*, a histeriid, *Neopachylophus sulcifrons*, a curculionid, *Emphyastes fucicola*, and several staphylinids including *Thinopinus pictus.* Kelp fly larvae and pupae of two species, *Coelopa vanduzeei* and *Fucellia costalis*, occurred in association with macrophyte wrack. Two isopod species, *Alloniscus perconvexus* and *Tylos punctata*, and several species of talitrid amphipods, *Megalorchestia* spp., were often abundant on ungroomed beaches with accumulated macrophyte wrack.

Upper beach macrofauna including talitrid amphipods (*Megalorchestia* spp.), kelp flies, and a variety of beetles were widespread and occurred in our surveys on all but two beaches. The only beaches lacking upper beach fauna (including *Megalorchestia* spp.) were the groomed beaches in Los Angeles County (Santa Monica and Manhattan). The abundance of talitrid amphipods, *Megalorchestia* spp., ranged from 0 to 30,000 m^{-1} and was positively correlated with the cover of marine wrack for the mainland and the combined island surveys ($p < 0.01$). Abundances of *Megalorchestia* spp. were generally higher on ungroomed beaches (220 to 30,000 m^{-1}) than on groomed beaches (0 to 560 m^{-1}). The abundance of beetles was also positively correlated with the amount of marine wrack ($p < 0.01$).

DISCUSSION

Exposed sandy beaches of the coasts of southern California and the Channel Islands harbor a high diversity, abundance, and biomass of macroinvertebrate species for modally reflective and intermediate beaches. Modally dissipative beaches were not present in the study region (see Dugan et al. 1998b). The lack of macrofauna data from dissipative beaches in our dataset precludes a definitive evaluation of possible relationships between community structure and morphodynamics in the Southern California Bight. However, our results suggest that other factors, including recruitment dynamics for species such as *E. analoga* (e.g., Dugan and Hubbard 1996; Wenner et al. 1993), *D. gouldii*, and *T. stultorum* (Coe 1955); isolation; disturbance; human activities; and the input of macrophyte wrack, may strongly influence the structure of macrofauna communities inhabiting exposed sandy beaches in southern California.

The results of our surveys and of earlier studies (Straughan 1982; 1983) indicate that the macrofauna communities of exposed sandy beaches of southern California are generally more species rich than reported for beaches of similar morphodynamic type elsewhere in the world. For example, in a recent synthesis of studies of macrofauna community structure of beaches in Australia, South Africa, Chile, and Oregon using survey techniques similar to those we used, the greatest number of macrofauna species reported from a single beach was 30 on a macrotidal ultradissipative beach in Australia (McLachlan et al. 1996). Species richness ranged from 5 to 19 macrofauna species per beach for ten intermediate beaches in New South Wales, Australia (Hacking 1998). In Chile, species richness for ten beaches ranged from 1 to 14 species with the greatest number of species occurring on a dissipative beach and the lowest numbers (1 to 4) on reflective beaches (McLachlan et al. 1993; Jaramillo and McLachlan 1993; Note: the most abundant Chilean macrofauna are congeners of California species). In addition, on three fully dissipative beaches in Oregon, macrofauna species numbers ranged from 17 to 21 species (McLachlan 1990), a value lower than we found on many of the intermediate and even some of the reflective beaches surveyed in our study.

Beaches on the Channel Islands generally had fewer species of macrofauna than mainland beaches. The relatively lower species richness of macrofauna communities and the lack of some common species, such as *D. gouldii*, on Channel Islands beaches suggest that island isolation and

prevailing currents influence recruitment and colonization and species distributions. *Donax gouldii* is a southern species with a range that extends into southern Baja California (McLean 1978). The northern distributional limit of this species varies and it has been observed as far north as Pismo Beach following recent ENSO (El Niño Southern Oscillation) events (Dugan, pers. obs. 1984) and in Santa Cruz County (McLean 1978). Despite the apparent ability of the planktonic larvae of this species to colonize new areas on the mainland, it did not occur on any of the Channel Islands beaches we surveyed or in 52 surveys of beaches on San Miguel, Santa Cruz, San Nicolas, or Santa Catalina islands by Straughan (1982). That result suggests that even in strong west and north-flowing Davidson current regimes, larvae of this species may not be able to reach and colonize the Channel Islands. In addition, the size structures of populations of Pismo clams, *T. stultorum*, on the northern Channel Islands suggest that recruitment may be quite infrequent, occurring at intervals of 10 years or more (Dugan et al., in press; Engle et al. 1998; Richards 1995, 1996).

Our surveys of exposed sandy beaches on the California mainland and Channel Islands found the abundance of macrofauna to be high relative to that reported for reflective and intermediate state beaches in other parts of the world. For macrofauna of exposed sandy beaches, abundances of >10,000 animals m^{-1} are considered high and occur primarily on dissipative beaches (McLachlan et al. 1996). Macrofaunal abundances >10,000 m^{-1} were reported for only 13 of 75 beaches from around the world; those 13 were high intermediate to dissipative types (McLachlan et al. 1996). Total abundances of macrofauna less than 10,000 m^{-1} occurred on only five of the 23 beaches where we conducted complete community surveys, and three of those beaches were subject to grooming. Abundances of an order of magnitude greater (100,000 m^{-1}) have been reported only for dissipative beaches in Oregon (McLachlan 1990). On many of the beaches we surveyed, the majority of individuals were sand crabs, *E. analoga*. High macrofaunal abundances (>10,000 m^{-1}) were also reported for intermediate to dissipative state beaches in Chile where *E. analoga* occurs (Jaramillo and McLachlan 1993; McLachlan et al. 1993).

The biomass of macrofauna on southern California sandy beaches was variable but generally high relative to that reported for intermediate state beaches in other parts of the world. McLachlan et al. (1996; 1993) consider dry biomass of >1,000 gm^{-1} to be high and 5,000 gm^{-1} a ceiling value for macrofauna communities of exposed sandy beaches. Macrofaunal biomass >1,000 gm^{-1} was reported for only 13 of 75 beaches from around the world; those 13 were high intermediate to dissipative types (McLachlan et al. 1996). We estimated (dry biomass = 25% of wet biomass, McLachlan, pers. comm.) mean dry biomass values >1,000 gm^{-1} for surveys at ten of 15 sites and a maximum value of >5,000 gm^{-1} on modally intermediate beaches in southern California. Again, on many of the beaches we surveyed, *E. analoga* composed the majority of the macrofaunal biomass. Relatively high macrofaunal biomass (>1,000 gm^{-1}) was also reported for four intermediate to dissipative state beaches in Chile where *E. analoga* occurs (Jaramillo and McLachlan 1993; McLachlan et al. 1993).

Macrofauna communities inhabiting sandy beaches are supported primarily by allocthonous sources of carbon as little or no primary production occurs on the beach itself (Brown and McLachlan 1990). In southern California, the main sources of primary production are drift macrophytes and phytoplankton. Drift macrophyte input was estimated as 473 kg wet weight $m^{-1}y^{-1}$ for an exposed sandy beach in southern California (Hayes 1974). The metabolism of macrofauna communities of sandy beaches is dependent upon the production of nearshore kelp forests, seagrass and macroalgal beds, and oceanographic processes. Drift macrophyte consumers, including talitrid amphipods and insects, inhabit the upper beach and move down to the mid- and low intertidal to feed. Suspension feeders, which utilize phytoplankton and associated particulate organic material, including hippid crabs and bivalves, inhabit the lower intertidal zone. Scavengers and predators, such as albuneid crabs, isopods, polychaetes, and beetles, prey upon primary consumers of both types and feed on drift carrion. Vertebrate predators utilize all of the trophic levels of this food web as prey. Changes in either wrack input or phytoplankton production may shift community structure and energy flow in the infaunal community and higher trophic levels. Many beaches on the southern California mainland are subject to grooming, the regular removal of trash, macrophyte wrack, and other debris with heavy equipment. The ecological effects of this widespread managment practice have rarely been examined, and no direct studies exist for California beaches. The fact that several of the mainland beaches we surveyed are subject to regular grooming allowed an opportunity to compare these beaches to less disturbed sites. In general, macrofauna species richness, abundance, and biomass were lower in surveys from groomed beaches and those with low amounts of wrack, particularly for upper intertidal species, than in samples from beaches with abundant wrack. In addition, the significant relationships between the abundance of selected taxa (talitrid amphipods; beetles) and the amounts of wrack found in our study suggests that the community structure of sandy beach macrofauna is closely linked with the input and fate of marine macrophyte wrack. Human alteration of wrack dynamics through beach grooming appears to be associated with substantial alteration in macrofauna community structure of exposed sandy beaches in southern California.

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