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Perspectives on the Structure and Dynamics of Nearshore Marine Assemblages of the California Channel Islands

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Abstract. The remarkably diverse and complex marine ecosystems surrounding southern California's offshore Channel Islands have been the subject of considerable scientific investigation during the past decade by governmental agencies and research institutions. Current levels of ecological knowledge of Channel Island nearshore marine environments have resulted from inventory surveys, monitoring surveys, and experimental studies. Since 1980, the Channel Islands Research Program (CIRP) has conducted over 100 subtidal research cruises around the islands and cooperated in numerous intertidal and subtidal surveys with Channel Islands National Park. Here I present perspectives on the spatial composition and temporal dynamics of Channel Island marine assemblages based on data from CIRP, the Channel Islands National Park, and others. Each of the 8 Channel Islands has a distinct marine community character, resulting from a unique combination of geographic, physical, and biological features. Water temperature, associated with oceanic currents, island position within a southeast to northwest gradient, and upwelling off Point Conception, likely accounts for most of the large-scale biogeographic patterns. Wave exposure, substratum type, and bottom relief affect smaller-scale species distributions. Short-term (e.g., storms) and long-term (e.g., El Niño) changes in oceanographic conditions, along with biological interactions (e.g., sea urchin overgrazing of macroalgae) and little-understood catastrophic die-offs (e.g., sea star wasting disease, abalone withering syndrome) may greatly change community composition. Human activities, especially resource harvesting, also affect nearshore species assemblages. The creation of non-harvested natural areas and additional long-term monitoring at the Channel Islands are needed to separate natural population variations from human impacts.

Keywords: Channel Islands; California; intertidal; subtidal; surveys; monitoring; marine ecology; marine biogeography; oceanography; water temperature; geology; sea urchin overgrazing; echinoderm disease; abalone withering syndrome; human impacts.

Introduction

Little was known about shallow-water ecosystems around the 8 California Channel Islands in 1965, when the First California Islands Symposium was held. Island marine environments were relatively remote, and scuba diving was just emerging as a means for extended access to subtidal habitats. Much has happened in the nearly 3 decades since the first symposium. As an indication of the escalating level of biological attention, the number of papers related to nearshore biota increased from 3 at the first symposium (Philbrick 1967) to 12 at the 1978 Meeting (Power 1980) to more than 25 at the third symposium in 1987 (Hochberg 1993). Now, 7 yr after the third symposium, even greater progress has been made. At this time it seems appropriate to provide some perspectives on the state of our understanding of nearshore marine ecosystems around the Channel Islands.

In a simplified view, increased understanding of natural systems typically progresses through 3 levels: descriptive, monitoring, and integrative. Initial descriptive studies are best characterized as one-time reconnaissance or baseline surveys conducted to identify physical features and inventory species. This static view of physical and biological structure provides a "snapshot" of resource distribution and abundance. Monitoring level studies, on the other hand, consider the dynamic nature of a system. These repeated surveys elucidate temporal patterns, including short-term vs long-term, natural vs human-influenced, cyclical vs unpredictable, and minor perturbations vs catastrophic disturbances. The third level or integrative phase covers a variety of studies, usually manipulative field experiments, that are employed to evaluate survey data trends in such a way that causal mechanisms can be understood and predictive models developed.

Most studies of nearshore marine life at the Channel Islands have been descriptive in nature. Early observational reports generally have been replaced by representative qualitative and quantitative surveys conducted since 1970. The past 18 yr have seen a major rise in monitoring surveys, primarily conducted by federal agencies including the Bureau of Land Management, National Park Service, National Marine Fisheries Service, and U.S. Fish and Wildlife Service. Excellent monitoring databases exist for nearshore marine mammals and seabirds (e.g., DeMaster et al. 1988; Lewis et al. 1988). The record for intertidal and subtidal algae, invertebrates, and fishes is less comprehensive. Monitoring data exist for tens of sites for periods ranging from 3 to 13 yr (e.g., Littler 1980;

Harrold and Reed 1981; Davis 1988; Richards and Davis 1988; Ambrose et al. 1993). In addition, specific fisheries-related studies have been conducted by the California Department of Fish and Game. Experimental studies tend to be unrelated individual projects associated with university degree programs; however, some have been outgrowths of the monitoring efforts of agency programs (e.g., Harrold and Reed 1985; Coyer et al. 1993).

Extensive quantitative baseline surveys conducted for the Bureau of Land Management during 1975–1978 vastly increased our knowledge of mammal, bird, giant kelp, and intertidal resources at the Channel Islands (Bureau of Land Management 1980). In addition to various short-term surveys, 6 rocky and 6 sandy intertidal sites at the islands were monitored seasonally for 3 yr, but no shallow subtidal habitats were surveyed (Littler 1980; Straughan and Hadley 1980).

From 1980 to the present, 3 major programs (in addition to the marine mammal and seabird studies) have added significantly to all levels of understanding of Channel Islands intertidal and subtidal systems. First, the U.S. Fish and Wildlife Service conducted descriptive, monitoring, and experimental studies at San Nicolas Island prior to and during the translocation of sea otters from central California (Harrold and Reed 1981). A second program began when Channel Islands National Park, consisting of San Miguel, Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara islands, was created in 1980. Part of its mandate was to inventory nearshore marine biota, monitor population dynamics, and evaluate trends to assist the California Department of Fish and Game in managing these resources. Channel Islands National Park implemented an innovative long-term monitoring program to track target species at representative rocky intertidal (15) and subtidal (16) sites around the 5 park islands (except that no intertidal studies were conducted at Santa Cruz Island because it was privately-owned until 1988) (Davis 1988; Richards and Davis 1988).

A third program, the Channel Islands Research Program (CIRP), was established in 1980 by the Tatman Foundation to study the distribution, abundance, and ecology of marine life around all 8 islands. A network of marine biologists and students associated with the University of Southern California Wrigley Marine Science Center, University of California at Santa Barbara, and other institutions have conducted descriptive natural history surveys, long-term monitoring studies, and field experiments. Reconnaissance survey data have been gathered during 102 cruises for more than 1,000 species of marine algae, invertebrates, and fishes, as well as hundreds of habitat sites representing all regions around the islands. My perspectives on the structure and dynamics of Channel Islands nearshore marine assemblages come primarily from having coordinated CIRP for the past 14 yr.

Physical Influences on Channel Islands Marine Life

The abrupt change in coastline orientation south of Point Conception creates a broad oceanic embayment known as the Southern California Bight. The 8 Channel Islands are clustered within an oval portion of the bight about 225 km long and 85 km wide (Fig. 1). There are remarkable differences in island marine assemblages within this relatively small physical distance. Each of the islands has a distinct nearshore community character, resulting from a combination of geographic, physical, and biological features. Broad-scale species distributional trends appear to be determined largely by the intermixing of several oceanic water masses and currents in the Southern California Bight (Fig. 1; see paper by D. Browne in these proceedings). The complex water movements result in differential temperature, nutrient, and larval recruitment conditions among the islands. In addition, prevailing winds periodically push surface water offshore from the Point Conception area, causing upwelling of cold, nutrient-rich water that bathes the northwestern islands, but rarely reaches the southeastern islands. Smaller-scale distribution patterns are affected by local physical conditions, such as wave exposure, substratum type, and bottom relief.

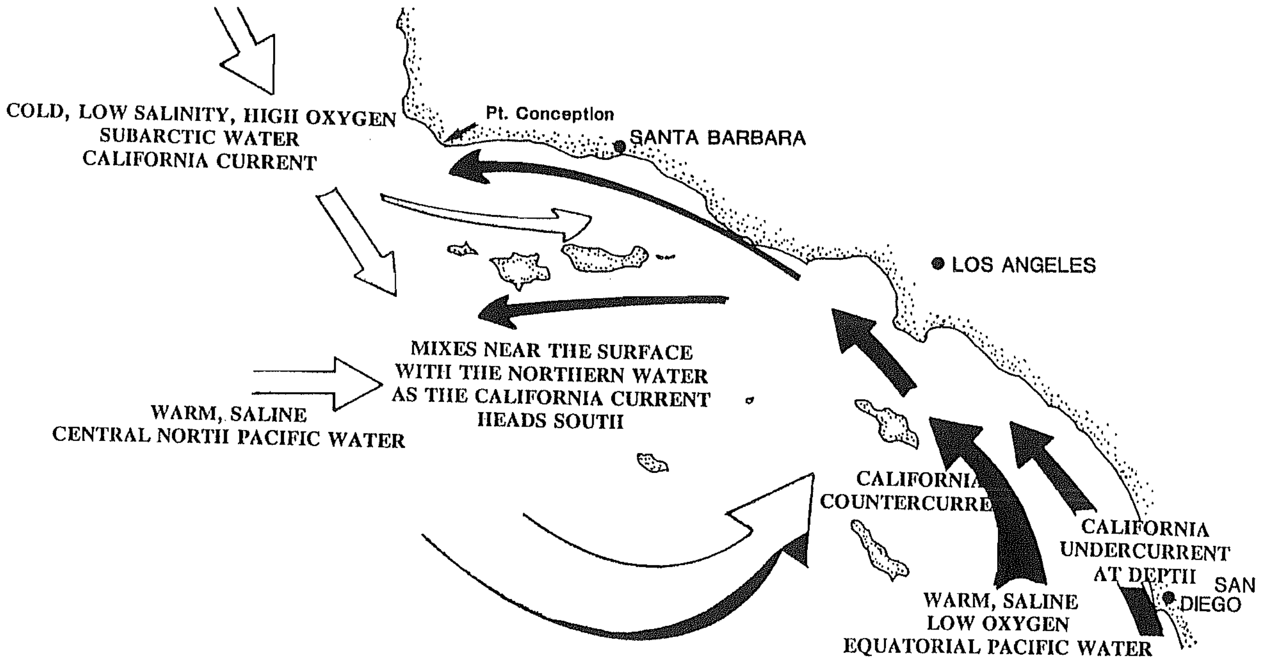

Figure 1. Generalized oceanic circulation around the California Channel Islands (modified after Browne; see paper in these proceedings).

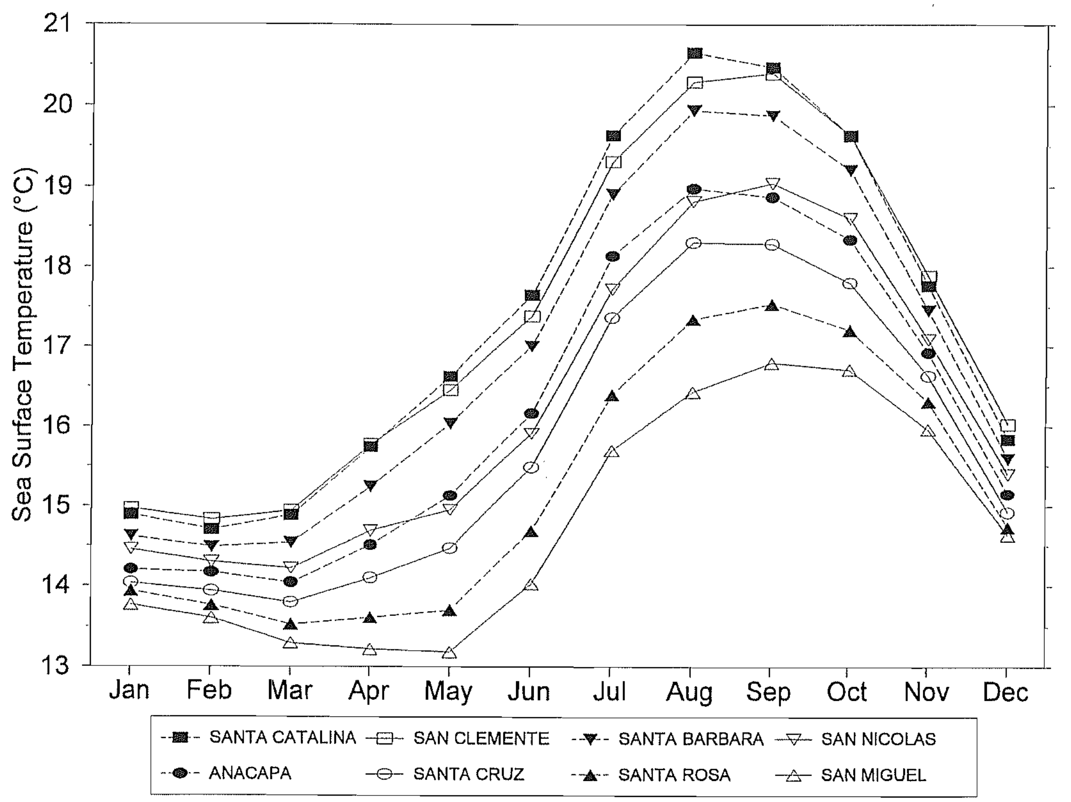

Figure 2. Mean monthly sea surface temperatures at the 8 Channel Islands for the period 1982–1992. Data were taken from National Weather Service (San Francisco) semi-weekly oceanographic analyses.

Large-scale factors

The concept that the marine flora and fauna at the islands reflect the oceanographic conditions to which they have been exposed was proposed by Neushul et al. (1967) at the First Channel Islands Symposium. In the years since, data gathered by the CIRP (Engle 1993 and unpubl.), Bureau of Land Management (Murray et al. 1980; Seapy and Littler 1980), and others have confirmed this proposition. Island-wide distributional trends for shallow-water species assemblages at the 8 islands are especially well correlated with water temperature. Other hydrographic conditions, such as nutrient concentrations and larval drift, typically covary with temperature because all are determined largely by oceanic current movements and wind-driven upwelling. Temperature is the easiest parameter to measure and clearly has major effects on marine species, so it is emphasized in these perspectives, but with the realization that temperature correlation does not necessarily mean temperature causality.

Water temperature regimes for nearshore habitats around the islands are incompletely known. Specific data are available for various locations, depths, and times. Broad-scale sea surface temperatures (SST) obtained from satellite infrared photographs provide the best long-term records of concurrent temperature regimes at all 8 islands. Depending on the depth, season, and particular location, surface temperatures may differ considerably from subsurface values, yet SST do reflect reasonably consistent general temperature relationships (List and Koh 1976; Bernstein et al. 1977).

Mean monthly SST for each island for the 11-yr period 1982–1992 reveal characteristic island trends (Fig. 2). All islands generally show a similar pattern of seasonal fluctuations, with lowest SST in January–March (except

Table 1. Examples of warm-water subtidal species typically common or abundant at Santa Catalina Island and uncommon or absent at San Miguel Island.

- Phylum Chlorophyta (green algae)
  - *Codium cuneatum* (sponge weed)
- Phylum Phaeophyta (brown algae)
  - *Dictyopteris undulata* (net wing algae)
  - *Hydroclathrus clathratus* (perforated bubble kelp)
  - *Sargassum palmeri* (native sargassum weed)
  - *Zonaria farlowii* (banded algae)
- Phylum Rhodophyta (red algae)
  - *Gelidium nudifrons* (agar weed)
  - *Lithothrix aspergillum* (coralline algae)
- Phylum Porifera
  - *Aplysina fistularis* (sulpher sponge)
- Phylum Cnidaria (sea anemones, cup corals, sea fans, etc.)
  - *Muricea californica* (golden gorgonian)
  - *Muricea fruticosa* (brown gorgonian)
- Phylum Arthropoda - Class Crustacea (shrimp, crabs, etc.)
  - *Hemisquilla ensigera* (California mantis shrimp)
  - *Panulirus interruptus* (California spiny lobster)
- Phylum Mollusca (snails, clams, etc.)
  - *Haliotis fulgens* (green abalone)
  - *Tegula eiseni* (banded turban snail)
- Phylum Phoronida
  - *Phoronopsis californica* (orange phoronid worm)
- Phylum Echinodermata
  - *Centrostephanus coronatus* (coronado urchin)
  - *Linckia columbiae* (comet star)
  - *Lovenia cordiformis* (fragile heart urchin)
- Phylum Chordata - Subphylum Urochordata
  - *Metandrocarpa taylori* (orange tunicate)
- Phylum Chordata - Subphylum Vertebrata
  - *Alloclinus holderi* (island kelp fish)
  - *Chaenopsis alepidota* (orangethroat pikeblenny)
  - *Gymnothorax mordax* (moray eel)
  - *Halichoeres semicinctus* (rock wrasse)
  - *Heterodontus francisci* (horn shark)
  - *Hypsypops rubicundus* (garibaldi)
  - *Lythrypnus dalli* (blue-banded goby)
  - *Paralabrax clathratus* (kelp bass)

for Santa Rosa and San Miguel islands, where upwelled water flowing southeast from Point Conception causes low SST also in April and May) and highest SST in July–October. However, most islands consistently have separate temperature regimes, the exceptions being the pairs Santa Catalina/San Clemente and San Nicolas/Anacapa. Inter-island SST differences are greatest in August (maximum difference = 4.3° C) and least in January (maximum difference = 1.2° C). Ranking the islands from warmest to coldest conditions based on mean annual SST results in the following order: Santa Catalina, San Clemente, Santa Barbara, San Nicolas, Anacapa, Santa Cruz, Santa Rosa, and San Miguel islands. Three island SST groupings are evident: (1) Santa Catalina, San Clemente, and Santa Barbara islands have the warmest surrounding waters; (2) San Nicolas, Anacapa, and Santa Cruz islands have intermediate conditions; and (3) Santa Rosa and San Miguel islands have the coldest sea surface temperatures.

Overall, there is a clear southeast to northwest trend of decreasing surface water temperatures for the 8 islands that correlates well with differences in species assemblages documented by CIRP and others. Murray et al. (1980) and Seapy and Littler (1980) reported generally similar island groupings based on detailed quantitative intertidal surveys conducted at one site per island (2 sites at San Nicolas Island) during 1975–1978. The only differences are that both of the Bureau of Land Management studies tended to align San Nicolas Island with the cold-water islands, and Murray et al. (1980) put Anacapa Island with the warm-water group. Long-term CIRP records favor the intermediate status indicated by the SST data for both San Nicolas and Anacapa islands because mixtures of warm- and cold-water species exist at these islands. San Nicolas was the only island at which Seapy and Littler (1980) evaluated 2 intertidal sites. Interestingly, the southeast end had more cold-water affinities while the west end had more intermediate affinities.

Nearshore algae, invertebrate, and fish species whose biogeographic ranges show obvious warm- or cold-water affinities best demonstrate island-wide relationships between water temperatures and species abundances. At one extreme, Table 1 lists examples of warm-water species that typically are common or abundant in subtidal habitats at Santa Catalina Island, but uncommon or absent at San Miguel Island. Species listed in Table 2 provide examples of the reverse extreme, cold-water subtidal species usually common or abundant at San Miguel Island, but uncommon or absent at Santa Catalina Island. Islands with intermediate temperature regimes (San Nicolas, Anacapa, Santa Cruz) tend to have intermediate relative abundances of the "indicator" species in Tables 1 and 2. Many of these species (along with others showing less extreme trends) play a major role in the structure and function of particular ecosystems, and thus account for much of the differential character of each island.

Table 2. Examples of cold-water subtidal species typically common or abundant at San Miguel Island and uncommon or absent at Santa Catalina Island.

- Phylum Phaeophyta (brown algae)
  - *Pterygophora californica* (California sea palm)
  - *Desmarestia ligulata* (acid weed)
  - *Laminaria setchellii* (Setchell's oar weed)
- Phylum Rhodophyta (red algae)
  - *Callophyllis* spp.
  - *Cryptopleura ruprechtiana*
  - *Gigartina corymbifera*
  - *Nienburgia andersoniana*
  - *Opuntiella californica*
  - *Prionitis lanceolata*
- Phylum Porifera
  - *Acarnus erithacus* (red volcano sponge)
  - *Leucetta losangelensis* (white sponge)
  - *Tethya aurantia* (orange puffball sponge)
- Phylum Cnidaria (sea anemones, cup corals, sea fans, etc.)
  - *Aglaophenia* spp. (ostrich-plume hydroid)
  - *Balanophyllia elegans* (orange cup coral)
  - *Epiactis prolifera* (proliferating anemone)
  - *Tealia lofotensis* (white-spotted rose anemone)
- Phylum Annelida - Class Polychaeta
  - *Dodecaceria fewkesi*
  - *Eudystylia polymorpha* (feather duster worm)
  - *Phragmatopoma californica* (colonial sand tube worm)
  - *Salmacina tribranchiata* (fragile tube worm)
- Phylum Arthropoda - Class Crustacea (shrimp, crabs, etc.)
  - *Cancer antennarius* (common rock crab)
  - Mysidacea swarms (opposum shrimp)
  - *Pugettia producta* (northern kelp crab)
- Phylum Mollusca (snails, clams, etc.)
  - *Acmaea mitra* (white cap limpet)
  - *Astraea gibberosa* (red turban snail)
  - *Haliotis rufescens* (red abalone)
- Phylum Echinodermata
  - *Asterina miniata* (bat star)
  - *Eupentacta quinquesemita* (white cucumber)
  - *Orthasterias koehleri* (rainbow star)
  - *Pycnopodia helianthodes* (sunflower star)
- Phylum Chordata - Subphylum Urochordata
  - *Boltenia villosa* (spiny-headed tunicate)
  - *Cystodytes lobatus* (lobed tunicate)
  - *Pycnoclavella stanleyi* (tiny bulb tunicate)
  - *Styela montereyensis* (stalked tunicate)
- Phylum Chordata - Subphylim Vertebrata
  - *Artedius corallinus* (coralline sculpin)
  - *Embiotoca lateralis* (striped surfperch)
  - *Hypsurus careyi* (rainbow surfperch)
  - *Orthanopias triacis* (snubnose sculpin)
  - *Oxylebius pictus* (painted greenling)
  - *Sebastes carnatus* (gopher rockfish)
  - *Sebastes caurinus* (copper rockfish)
  - *Sebastes chrysomelas* (black and yellow rockfish)
  - *Sebastes mystinus* (blue rockfish)
  - *Sebastes serranoides* (olive rockfish)

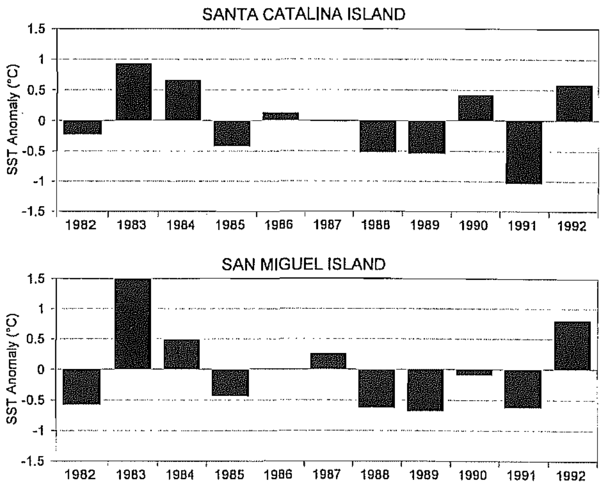

Figure 3. Mean annual sea surface temperature (SST) anomalies from the 1982–1992 average for Santa Catalina and San Miguel islands. Data were taken from National Weather Service (San Francisco) semi-weekly oceanographic analyses.

Temperature-related oceanographic phenomena influencing marine life at the islands vary considerably over time scales ranging from minutes to decades or more. It is likely that most nearshore organisms are able to withstand typical short-term fluctuations, such as those caused by changing tidal currents. However, seasonal or longer trends may kill sensitive species or enhance the survival of tolerant species, resulting in profound community effects (see Tegner and Dayton 1987; Dayton et al. 1992). The dynamic nature of annual sea surface temperatures at the warmest (Santa Catalina) and coldest (San Miguel) islands during the period 1982–1992 is shown in Figure 3. Both islands generally exhibit similar trends in annual SST deviations from the 11-yr mean, but differences in the magnitudes of the anomalies are evident. Most of these differences appear to be related to the presence or absence of upwelling off Point Conception, which can greatly affect seawater conditions at San Miguel Island. For both islands, the major warm-water years (usually associated with El Niño phenomena) were 1983, 1984, and 1992, whereas 1988, 1989, and 1991 were notably colder than the 11-yr average.

During the warm-water years, major die-offs of giant kelp (*Macrocystis pyrifera*) and other cooler-water species were evident, especially at the southeastern islands. Catastrophic wasting "diseases", notably in sea stars and sea cucumbers, clearly were correlated with periods of high temperatures (J. Engle unpubl.). Organisms associated with kelp forests were affected in complex ways when the community dominant *Macrocystis* deteriorated. Those species dependent on the kelp declined, but other species benefited from lessened competition for space and light. In many areas, reduced availability of drift kelp apparently caused sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*) to move out of crevices and overgraze remaining macroalgae, resulting in low diversity, sea urchin/coralline crust dominated communities (see Harrold and Reed 1985).

In order to put temperature patterns of the past decade in perspective, an even longer time scale is necessary. Daily surface water temperature records taken at the Scripps Institution of Oceanography pier (La Jolla) since 1920 reveal remarkable long-term trends that likely occurred in similar fashion at the Channel Islands. Notably, the 32-yr period from 1944–1975 was characterized by cooler than average temperatures, except for the 1957–1959 El Niño years. In contrast, the 18-yr period from 1976 to the present has been warmer than the 73-yr mean, except for 3 cool years (1980, 1988, 1989). This long-term warm-water trend may help to explain important community changes documented at the islands during the 1980s and early 1990s, including increased numbers of southern species at the northwestern islands, "disease" epidemics, other die-offs, and sea urchin overgrazing phenomena. Thus, the species assemblages present today at the 8 Channel Islands likely reflect the cumulative effects of nearly 2 decades of warm-water conditions. Clearly, long-term monitoring of physical and biological parameters is essential to understanding ecosystem dynamics

Small-scale factors

Complex oceanographic phenomena related to island location within the Southern California Bight probably account for most large-scale differences in nearshore marine assemblages at the Channel Islands. However, each island also has a differing mix of local conditions that provide smaller-scale geographic diversity. Key factors include degree of wave exposure, extent of marine habitats, and nature of the substratum. Prevailing wind and swells arrive from the northwest, west, or southwest, so each island has an exposed side (NW–SW) and a protected side (NE–SE). The amount of wave exposure depends on island size, shape, orientation, and position in relation to other islands. For example, San Nicolas Island is relatively small, smoothly oval in shape (with few coves), oriented with its long axis W–E, and located far from the wave shadows of other islands. Therefore, nearly all of its shallow-water habitats are moderately or fully exposed. Species restricted to calm waters are rare or absent at this island. At the other extreme, Santa Catalina Island is large, irregular in shape (with many coves), and located in the inshore portion of the Southern California Bight where it receives varying degrees of wave protection from other islands and the mainland. Habitats around Santa Catalina exhibit a wide range of exposures, with both calm- and rough-water species assemblages well represented.

Occasionally, large swells generated by storms, especially in winter, cause major disturbances to island nearshore environments. Local effects vary greatly, depending on degree of exposure to the storm waves. An unusual number of particularly intense storms impacted kelp forests and other nearshore communities during the 1980s. At least 10 storms produced wave heights exceeding 6 m, six of which occurred during the winter of 1982–1983, at the start of El Niño (Seymour et al. 1989). No storms of this magnitude happened during the 1960s or 1970s. A January 1988 storm may have been the largest in more than a century, and catastrophic effects from swells > 10 m high reached depths of at least 25 m in San Diego (Dayton et al. 1989). Severe impacts were noted by CIRP on the southwest sides of Santa Catalina and San Clemente islands, where most boulders had been tumbled, and the beaches were littered with detached algae as well as dead invertebrates and fishes.

The distribution and abundance of specific resources depends not only on their presence in particular habitats, but also on the areal extent of these habitats at each island. Figure 4 compares the relative extents of intertidal shores, subtidal shelves (< 18.3 m depth), and major kelp beds at the 8 islands. Intertidal length, related to island size and shape, is greatest for Santa Cruz, Santa Catalina, San Clemente, and Santa Rosa islands. The amount of shallow subtidal habitat around each island depends on how rapidly the bottom slopes to deep water. Santa Rosa Island has by far the greatest shallow shelf area of the 8 islands (35%). Santa Cruz, the largest island, and San Nicolas, a relatively small island, have similar amounts of subtidal habitat (15%). Santa Catalina has the second longest shoreline of all the islands, but the third lowest extent of shallow shelf. Only tiny Santa Barbara and Anacapa islands have less shelf.

Beds of giant kelp around the islands have been mapped via aerial photographs of surface canopy (Hodder and Mel 1978). The extent of major kelp beds is not necessarily related to either island size or the amount of subtidal shelf (Fig. 4). Small San Nicolas Island has the greatest area of kelp beds (30%), followed by San Clemente Island (22%). Santa Rosa Island has more than twice the subtidal shelf area as Santa Cruz Island, but both islands have similar amounts of kelp forests (about 15%) because much of Santa Rosa's subtidal shelf is sand bottom. Santa Catalina is a slightly larger island than San Clemente, but has less subtidal shelf area and an order of magnitude less kelp. Surprisingly, Santa Catalina has the least amount of kelp of all the islands—a bit less than Anacapa, and only one-third that of Santa Barbara Island.

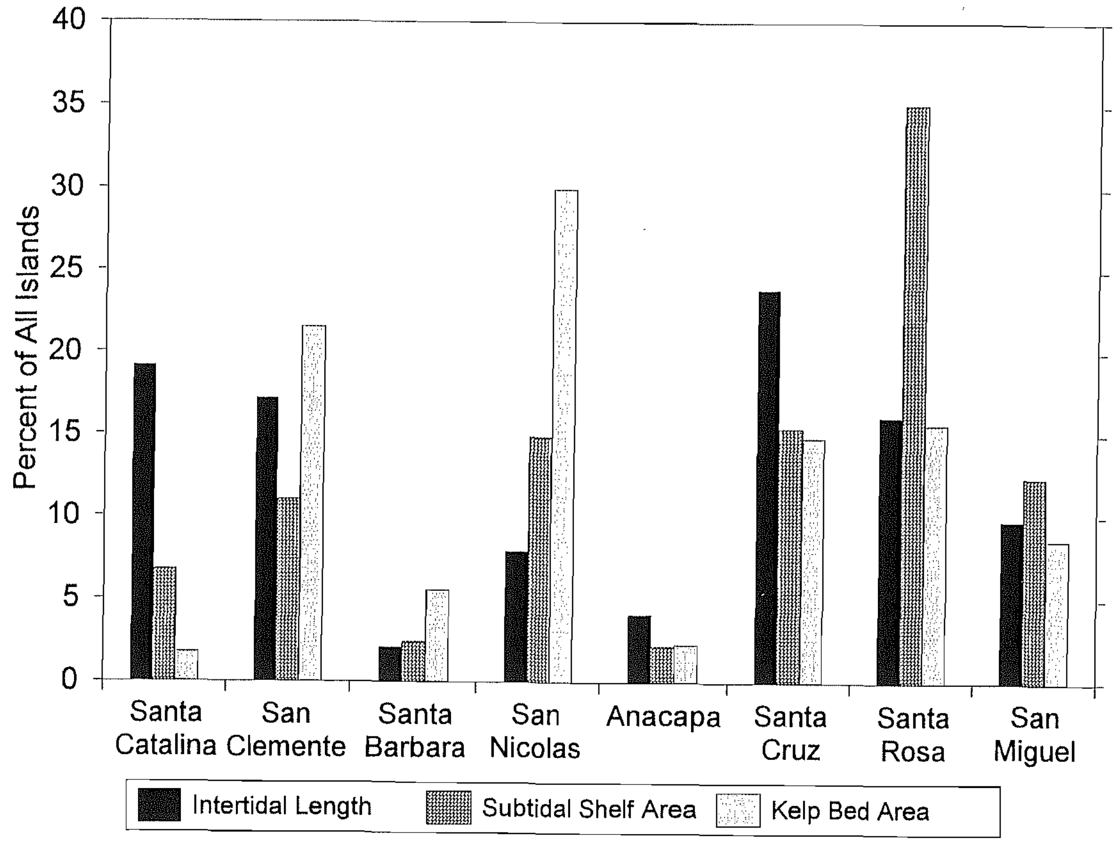

Figure 4. Relative extents of intertidal shores, subtidal shelves (< 18.3 m depth), and giant kelp beds among the 8 Channel Islands. Intertidal data are from Littler and Littler (1979). Kelp data are from Hodder and Mel (1978). Subtidal shelf areas were measured from United States Coast and Geodetic Survey charts.

The distribution of marine resources at each island could be understood more completely by comparing the areal extents of major substratum types (e.g., bedrock, boulder, sand) supporting different species assemblages. Shallow-water substratum types at the Channel Islands have not been mapped. Kelp beds mapped at the islands grow only on bedrock or boulder habitats, but non-kelp areas are not necessarily all sand bottoms. Warm-water (low-nutrient) conditions, high wave exposure, silt overlying rock, sea urchin overgrazing, and other factors prevent kelp from occupying all available shallow subtidal rocky habitats. Bedrock, boulder, and sand substrata have been mapped for intertidal shores at the Channel Islands (Fig. 5; Littler and Littler 1979). Bedrock habitats predominate at all islands (61–74% of shore), except for Santa Catalina (35%). Santa Catalina is unique in having nearly 50% boulder intertidal substrata. In contrast, San Miguel Island has no boulder shores. San Miguel, San Nicolas, and Santa Rosa islands have the most sandy beaches (33–36% of shore). Overall, the 8 islands consist of 63% bedrock, 16% boulder, and 22% sand intertidal habitats.

Characteristic marine assemblages develop on bedrock, boulder, or sand habitats because these substrata provide differing qualities of stability, attachment, and microhabitats. Other geological features important in structuring island communities include the type of rock (e.g., hard metamorphic, soft sedimentary), physical relief (e.g., flat bottom, tall pinnacles), and small-scale topography (e.g., smooth, rugose). For example, most of the reefs at San Nicolas Island are composed of low relief, soft-sedimentary-rock rich in nestling (e.g., sea urchins) and boring (e.g., pholad clams) fauna that create pitted microhabitats. However, this habitat is relatively unstable because strong swells can erode rock surfaces or break off entire shelves, killing the resident biota. Santa Barbara Island, on the other hand, has mostly hard volcanic substrata featuring craggy bedrock reefs, many with high-relief ledges, pinnacles, and walls. Diverse, long-lived communities exist on this type of stable bottom.

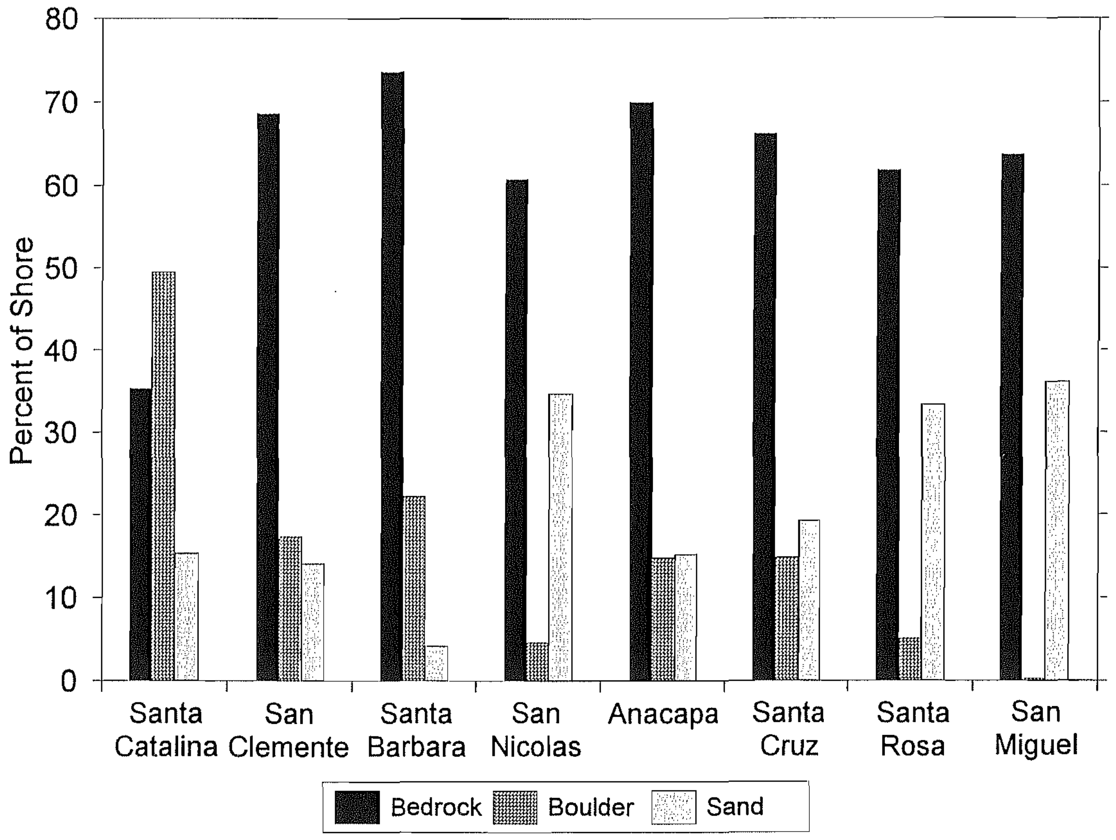

Figure 5. Relative extents of bedrock, boulder, and sand intertidal habitats for each of the 8 Channel Islands. Data are from Littler and Littler (1979).

Biological Influences on Channel Islands Marine Life

Complex physical and biological phenomena operate simultaneously and often synergistically to influence the composition of Channel Islands nearshore communities. Identifying the separate effects of these influences is difficult, at best. In general, physical factors operating at all spatial scales from regional to local establish the environmental limits within which biological interactions occur. Intra- and interspecific biological interactions often affect marine assemblages on a local scale. Competition, mutualism, predation, parasitism, and disease contribute to species patchiness, thereby increasing diversity. Particular effects of competition (for space, light, food, etc.) and predation (herbivory and carnivory) have been documented in California intertidal and subtidal systems (see Foster and Schiel 1985 and Foster et al. 1988 for reviews). On the other hand, surprisingly little is known about the role of disease in structuring marine species assemblages. This perspective will highlight 2 biological influences that have greatly affected Channel Islands marine communities on a regional scale, especially during the past 15 yr. These are (1) extensive overgrazing of giant kelp forests by sea urchins, and (2) catastrophic die-offs of various echinoderms and abalone, probably caused by infectious disease agents.

Sea urchin/giant kelp interactions

Beds of giant kelp occur on rock reefs (5–35 m in depth) at all eight Channel Islands, although 82% of the total kelp area occurs at just four islands (San Nicolas, San Clemente, Santa Rosa, Santa Cruz) (Fig. 4). These structurally-complex marine forests support diverse and productive assemblages of nearshore species. Therefore, any change in the population structure of the competitive dominant *Macrocystis* radically alters community composition. During the past 15 yr, many Channel Island rocky subtidal habitats have undergone dramatic fluctuations between lush kelp-dominated systems and sea urchin/coralline crust "barrens." For example, of 16 subtidal monitoring sites established by Channel Islands National Park in representative kelp forests at 5 islands in the early 1980s, 8–12 sites were overgrazed by sea urchins during 1986–1990 (Richards et al. 1993a, b, in press). Sea urchin abundances have declined since 1990; now kelp again dominates all but 4 of the sites (D. Richards pers. comm. 1993). This temporal pattern also was noted at other sites and islands by the CIRP.

A simplified possible scenario for these cyclical events is that the kelp first deteriorated during extended periods of warm water coupled with low nutrients. Additional kelp was lost during unusually powerful winter storms. Both of these conditions occurred to an extreme degree during the 1980s, especially during the 1982–1984 El Niño event (Tegner and Dayton 1987; Seymour et al. 1989; Tegner and Dayton 1991; Dayton et al. 1992). Lack of drift kelp caused sea urchins to emerge from crevices and overgraze remaining algae, creating sea urchin/coralline crust dominated habitats (Harrold and Reed 1985). These "barrens" communities persisted for years until sea urchin populations declined (e.g., due to storms, starvation, or diseases), or hydrographic conditions became optimal for massive recruitment of kelp and other macroalgae. Abundant algal food overwhelmed the remaining sea urchin's grazing abilities. They retreated to crevices and consumed drift algae once again. Thus kelp-dominated habitat was restored. The extreme oscillations between kelp and barrens communities during the 1980s would likely have been less severe (or perhaps nonexistent) if a major sea urchin predator, the sea otter, had not been eliminated from the Channel Islands in the 1800s (VanBlaircom and Estes 1988). In addition, fisheries at the Channel Islands harvest considerable numbers of 2 other important sea urchin predators, California sheephead (*Semicossyphus pulcher*) and spiny lobster (*Panulirus interruptus*) (Tegner and Dayton 1981; Tegner and Levin 1983; Leet et al. 1992).

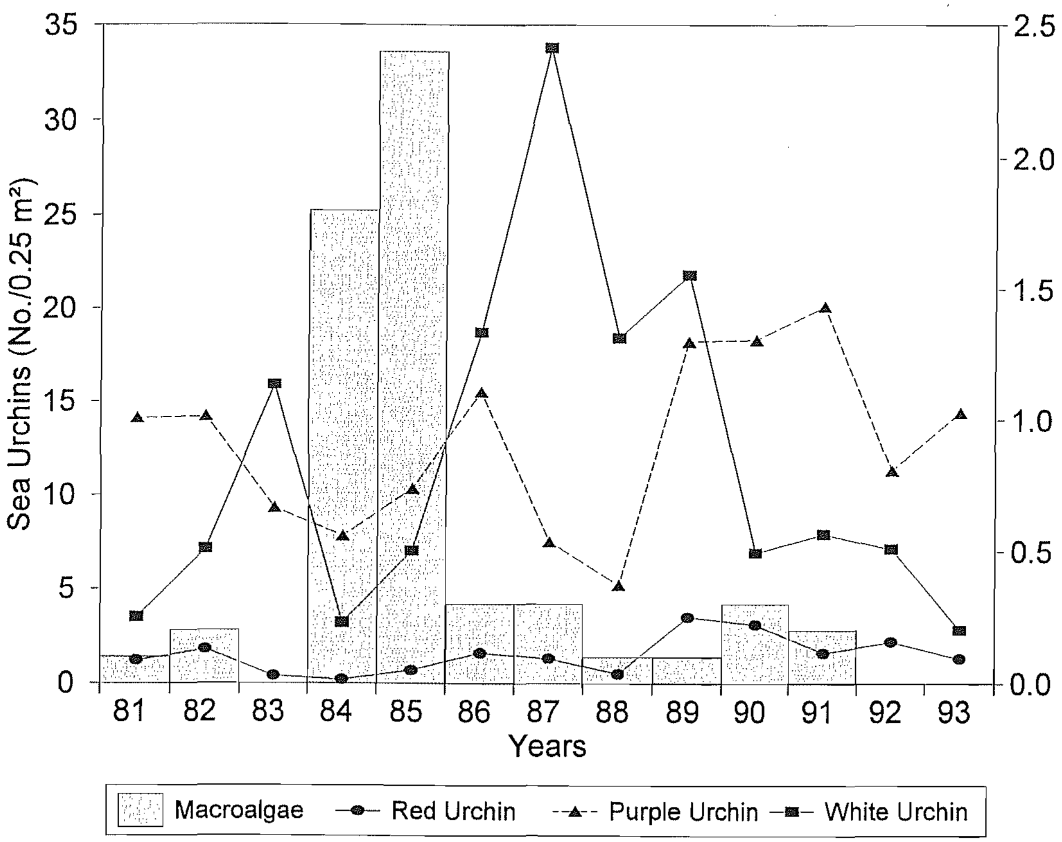

Figure 6. Temporal patterns of abundances for 3 species of sea urchins and macroalgae at Survey Rock, Anacapa Island. Ephemeral filamentous and crustose coralline algae were not included. Each point represents a mean from 30, 0.25 m² quadrats (10 randomly-placed quadrats along each of 3 contiguous 20-m transects) at 12 m depth.

Three species of sea urchins, red (*Strongylocentrotus franciscanus*), purple (*S. purpuratus*), and white (*Lytechinus anamesus*), individually or in combination are responsible for overgrazing kelp habitats. Sea urchin/coralline crust dominated communities have been found around every Channel Island, except for the northeast (lee) sides of Santa Catalina and San Clemente islands, where red, purple, and white sea urchins are least common, and a nonovergrazing species (*Centrostephanus coronatus*) is most common (Engle et al. unpubl.).

The Channel Islands Research Program has been monitoring the community dynamics of a shallow subtidal habitat dominated by red, purple, and white sea urchins at Anacapa Island (Ambrose et al. 1993). Figure 6 shows abundances of the 3 sea urchin species and macroalgae (not including ephemeral filamentous and crustose coralline algae) along a fixed transect (12 m depth) at this site since 1981. Purple and white sea urchins predominate. Macroalgae cover was highest (but still only about 2%) in 1984–1985 (at the end and just after El Niño), when sea urchin abundances generally were lower and a major settlement of many species of macroalgae occurred. White sea urchins, normally found on deep-water sand or mud bottoms, increased dramatically after El Niño to a high of 136/m^2 in 1987, followed by declines back to 1981 levels (12/m^2) by 1993.

Lytechinus similarly invaded kelp habitats at other locations around the Channel Islands (Richards et al. in press). An example of the unusual severity of this invasion was the complete loss of eelgrass beds (*Zostera* sp.) along the north shore of Anacapa Island due to *Lytechinus* overgrazing (Engle et al. unpubl.). Fronts of white sea urchins (up to 200/m^2) eliminated extensive grass meadows that probably took decades to become established. It is possible that widespread movements of *Lytechinus* into shallow water habitats during the mid-1980s were triggered by lack of adequate drift algal food in deep water habitats due to the extreme decline in kelp productivity during the 1982–1984 El Niño event.

Catastrophic die-offs of echinoderms and abalone

It has become increasingly evident in recent years that disease agents can cause catastrophic changes in sea life populations, resulting in long-term modifications in marine ecosystems (e.g., Lessios 1988). In the summer of 1978, mass mortality of many species of sea stars (and the sea cucumber *Parastichopus parvimensus*) was observed at Santa Catalina Island and along the mainland from Los Angeles south (J. Engle, pers. obs.; J. Word 1978, pers. comm.). During the following years this catastrophic die-off expanded to all of the Channel Islands, but islands to the south and east had the heaviest losses. Incidence of this "wasting disease" clearly was associated with the warmest months of those years with above-average water temperatures, especially during the 1982–1984 El Niño event. All species of sea stars in shallow water were affected, but some types suffered greater losses than others. National Park Service monitoring surveys at 5 islands documented 64% and 86% declines in *Pisaster giganteus* and *Asterina miniata* densities from 1982–1985 (Richards et al. in press). Since 1985, sea star populations at the Channel Islands have increased, notably at the colder-water islands where losses had been less severe. However, for most islands, only partial recovery to pre-1978 abundances appears evident. In addition, periodic recurrences of this wasting disease have been observed, especially during the warmer-water years 1990 and 1992 (Richards et al. 1993a; J. Engle, pers. obs.).

The epidemiology of sea star wasting disease is not well known. It appears to be caused by a contagious warm-water bacterium of the genus *Vibrio* (S. Schroeter and J. Dixon 1988, pers. comm.). In addition to sea stars and *Parastichopus*, other sea cucumbers as well as brittle stars may have been affected. Major die-offs of sea urchins (mostly *Lytechinus* and *S. purpuratus*) also have been observed, primarily at the warmer-water islands during the El Niño years 1984 and 1992. At Santa Barbara Island, massive mortality during Summer 1992 at 3 National Park monitoring sites that had been overgrazed by sea urchins since the mid-1980s resulted in all 3 habitats becoming kelp-dominated a year later (D. Richards 1993, pers. comm.).

Despite the fact that sea urchins are related to sea stars and also suffer die-offs during some warm-water periods, no study has determined whether the sea star wasting disease might be a more general echinoderm wasting disease. Regardless of the relationship between sea star and sea urchin mass mortality, there is a definite range of susceptibilities among echinoderm species to the causative agent(s) (Engle et al. unpubl.). Sea stars appear to be more vulnerable than sea urchins. Among sea urchin species, the order from most to least sensitive appears to be *Lytechinus*, *S. purpuratus*, and *S. franciscanus*.

Abalone populations at the Channel Islands suffered huge losses during the 1980s from which they have not recovered. The cause remains unknown. Intertidal black abalone (*Haliotis cracherodii*) monitored by Channel Islands National Park at 4 islands have declined by 90% since 1985 (Richards and Davis in press). In the early years, die-offs were observed primarily at Anacapa, Santa Cruz, and Santa Rosa islands. By 1993, catastrophic mortality had been documented at all the islands, except perhaps Santa Catalina where less information is available. The severe loss of black abalone prompted the California Department of Fish and Game to close the commercial and sport fishery starting in fall of 1993. Black abalone mortalities are associated with "withering syndrome" in which the foot is shrunken or withered, and weakened individuals lose their grip on rock surfaces. Hypotheses concerning the cause of withering syndrome include disease organisms, starvation, elevated water temperatures, pollution, and various combinations of these conditions (Tissot 1991; Davis et al. 1992; Haaker et al. 1992; Lafferty and Kuris 1993). It may be more than a coincidence that withering syndrome began just after the 1982–1984 El Niño, at the same time that major changes occurred in sea urchin and kelp populations.

Subtidal species of abalones, including reds (*Haliotis rufescens*), pinks (*H. corrugata*), greens (*H. fulgens*), and whites (*H. sorensoni*) also have declined during the past decade or more at the Channel Islands, but there are few monitoring data available to quantify these changes. California Department of Fish and Game commercial harvest records for the entire state indicate that landings of reds in 1990 were 17% of the 1931–1967 average, pinks 1% of 1948–1970 average, greens 6% of 1968–1972 average, and whites 0.02% of 1972–1976 average (Leet et al. 1992). Subtidal abalone declines may be due to overharvest; however, all sizes of red and pink abalones at park monitoring sites on Santa Cruz and Santa Rosa islands declined during the years following the 1982–1984 El Niño, coincident with black abalone losses (Davis et al. 1992).

There have been reports of withering syndrome in subtidal abalones, but the evidence to date is incomplete. Competition between abalones and sea urchins for algal food sources also may be a factor in recent declines (Davis et al. 1992). For example, in areas where kelp declined and sea urchins overgrazed remaining macroalgae, there likely was little or no food available for abalones (Fig. 6; Harrold and Reed 1985). In addition, abalones in a sea-urchin-/coralline-crust-dominated habitat are conspicuous and thus more vulnerable to predators, including humans. Even less is known about deep-water (20–65 m) white abalones, except that they were relatively common at certain island locations during the 1970s, but now have virtually disappeared (G. Davis 1993, pers. comm.). So few white abalones are known to exist that there is concern for the survivability of this species.

Human Influences on Channel Islands Marine Life

The Channel Islands are relatively isolated from many of the impacts of human activities that affect the nearshore environment of the southern California mainland. For example, water pollution from mainland outfalls and storm runoff sources is greatly diluted before reaching the islands (although migratory mammals, sea birds, and fishes may ingest and transport certain pollutants from the mainland to the islands). Island intertidal shores also experience less disturbance from direct visitation because they are less accessible. However, increasing numbers of people are visiting all but the 2 islands controlled by the military (San Clemente and San Nicolas), raising important concerns about impacts such as disturbance of sea bird and marine mammal colonies. Also, ship traffic and oil development activities near the islands carry the risk of catastrophic oil and other chemical spills (e.g., see Foster et al. 1971).

One activity that directly influences marine life at the Channel Islands is the sport and commercial harvesting of selected algae, invertebrates, and fishes (mostly for food, but also for biological supply and aquarium trade specimens). Nearshore resources sought by recreational and/or commercial fishermen and scuba divers include giant kelp, lobster, abalones, rock scallops, squid, sea urchins and many fish species. Mostly these are ecologically-important species whose removal faster than their populations can be replenished may greatly change the composition of nearshore ecosystems. Fishing pressures in recent decades have been relatively intense as technological advances increase capture efficiency. Emphasis on particular species changes rapidly over time depending on resource availability, California Department of Fish and Game regulations, and economic incentives (such as growing demand from abroad for California seafood products). It is difficult to gauge the extent and ecological effect of fisheries take at the Channel Islands because location-specific collection data often are not available, and there are essentially no unharvested "control" areas where natural ecosystem dynamics can be compared to that of harvested areas.

A major change in commercial fishing emphasis at the Channel Islands during the past 2 decades came with the development of a lucrative market in Japan for the roe of red sea urchins. Since its inception in 1971, red sea urchin harvest has risen steadily to become the most valuable fishery in California, worth more than $21 million to fishermen in 1989 (Leet et al. 1992). During the 1970s, most of this harvest came from the northern Channel Islands. As the supply of large red urchins diminished, the fishery expanded in the 1980s to the southern islands, the southern California mainland, and then to central and northern California.

It was thought that the removal of a major herbivore from rocky subtidal habitats would reduce destructive grazing of giant kelp, leading to expansion of kelp beds and increases in the abundances of kelp-dependent organisms, especially fishes. However, long-term field experiments to test this hypothesis were not conducted, in part because unharvested control sites did not exist. In retrospect, it is not obvious that kelp beds at the Channel Islands benefited by intensive harvesting of red sea urchins. In fact, as described above, sea urchin overgrazing of kelp habitats greatly intensified during the mid 1980s. Purple and white sea urchins were responsible for most of the overgrazing (e.g., see Fig. 6). Perhaps even more kelp beds would have been overgrazed if red sea urchins had not been harvested; however, it also is possible that removal of red sea urchins eliminated a major competitor of the smaller sea urchin species, resulting in population increases for purple and/or white sea urchins.

Recently, a market test fishery for purple sea urchins has begun. Future large-scale harvesting of purple sea urchins could change profoundly the structure and dynamics of Channel Islands marine communities. Clearly, controlled field experiments to evaluate potential consequences of this new fishery are necessary.

The ecological effects of continual sport and/or commercial harvest of kelp, other invertebrates, and most medium-large fishes from shallow waters at the Channel Islands also are difficult to assess. Sustained-yield fisheries may exist for some resources (e.g., perhaps giant kelp, lobsters, kelp bass); however, many species appear to be overfished (Leet et al. 1992). Long-lived species with slow growth rates and irregular recruitment especially are vulnerable to overharvest. For example, giant sea bass (*Stereolepis gigas*) can live 75 yr or more. Their populations declined so precipitously from the late 1970s to the early 1980s that all sport and commercial take was banned in 1982. In recent years, the CIRP has noted increased numbers of small-medium individuals at several of the islands.

Another long-lived fish, the Pacific angel shark (*Squatina californica*), used to be common on sand habitats at the islands, but now is uncommon, probably because of overfishing. Angel sharks were subject to intensive harvest during the 1980s, using inshore set gill nets. Landings rose rapidly to a peak of approximately 550,000 kg in 1985–1986, but the fishery has since declined by 83% to about 91,000 kg in 1991 (Leet et al. 1992). The people of California voted to ban the use of gill nets from state waters (within 3 mi of shore), starting in 1994. The regulation may allow gradual recovery for the angel shark and other nearshore fishes at the Channel Islands whose populations declined because of widespread gill netting.

Conclusion

Our understanding of the remarkably diverse and complex nearshore marine ecosystems surrounding the Channel Islands has increased markedly during the past 2 decades as a result of expanded programs of reconnaissance surveys, monitoring surveys, and experimental investigations. The combined studies have revealed the distinct marine community character of each island, resulting from unique combinations of geographic, physical, and biological features. Oceanographic and geologic influences apparently are the primary driving forces for determining the distribution and abundance of nearshore island species. Most broad-scale patterns are associated directly or indirectly with water temperature. Overall, there is an obvious southeast to northwest trend of decreasing surface water temperatures for the 8 islands that correlates well with differences in species assemblages. Biological phenomena (e.g., competition, predation, disease) and human impacts (primarily resource harvesting) interact with physical processes on a regional or local scale to further influence island marine community compositions.

The past decade has been an exceptionally dynamic time for shallow subtidal communities at the Channel Islands. The period was characterized by an unusually severe El Niño event in 1982–1984 and many subsequent devastating storms. The major disturbances occurred within the broad context of an 18-yr period (1976–1993) of generally warmer than normal seawater temperatures. Dramatic fluctuations in the composition of nearshore species assemblages were evident in the 1980s. At many locations, kelp-dominated communities switched to sea-urchin-/coralline-crust-dominated communities when up to 3 species of sea urchins overgrazed all macroalgae. Catastrophic die-offs of sea stars, other echinoderms, and abalone, possibly caused by warm-water disease agents, spread rapidly around the islands. Finally, sport and commercial fisheries affected the population dynamics of island marine species. Examples of important fishery changes during the past decade are the intensive harvesting of red sea urchins, which drastically reduced the number of large sea urchins at all islands, and the development of a large gill-net fishery for Pacific angel sharks, which apparently decimated island populations.

Even though considerable progress has been made in recent years toward understanding the structure and dynamics of Channel Islands shallow-water ecosystems, much remains to be done. Reconnaissance surveys have concentrated on subtidal rock habitats, primarily giant kelp forests. Further surveys of representative intertidal rock and sand habitats, as well as subtidal soft-bottom habitats, are needed at most islands. For example, eelgrass (*Zostera* sp.) beds and elk kelp (*Pelagophycus porra*) forests represent important habitats at the 8 islands, but their distributions are incompletely known. Nearshore deep-water habitats (> 30 m) have received little attention due to the practical limitations of scuba diving; however, remote-operated vehicles have become more cost-effective and now may be available for deeper surveys.

One-time surveys and miscellaneous observations are insufficient to characterize the temporal dynamics of island marine communities. Important physical and biological trends at the islands in recent years were identified or confirmed through the use of long-term monitoring surveys, such as those conducted by Channel Islands National Park. In addition to the excellent existing programs, expansion of monitoring studies to include other representative locations and habitats would provide more comprehensive coverage of all the islands. Gaps in rocky habitat monitoring programs include San Clemente Island (no monitoring), Santa Catalina Island (only 1 intertidal and 1 subtidal site), and Santa Cruz Island (no intertidal monitoring). Soft-bottom habitats currently are not monitored at any island. Kelp canopy cover at all islands could be monitored via aerial photographic surveys. Finally, because the composition of Channel Islands species assemblages is associated closely with water temperature, placement of thermisters at several depths at each monitoring site would provide "ground truth" for satellite sea surface temperature records.

Specific research studies, especially field experiments, are necessary to evaluate patterns and trends identified by reconnaissance and monitoring surveys. An important goal is to separate natural phenomena from the effects of human activities, primarily resource harvesting. A major impediment to such studies is the lack of marine habitats that are protected from sport and commercial fisheries. Representative nonharvested natural areas at each of the Channel Islands could serve as dynamic "control" areas for evaluating fishery effects, provide a source of recruits for harvested areas, and preserve pristine communities for the benefit of the public (see Davis 1989). The combined results of inventory, monitoring, and experimental studies can provide valuable information necessary for resource managers to make reasoned decisions that will balance public needs (e.g., seafood, oil products, recreation) with the long-term benefits of sustainable, diverse ecosystems at the California Channel Islands.

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Understanding the Oceanic Circulation in and around the Santa Barbara Channel

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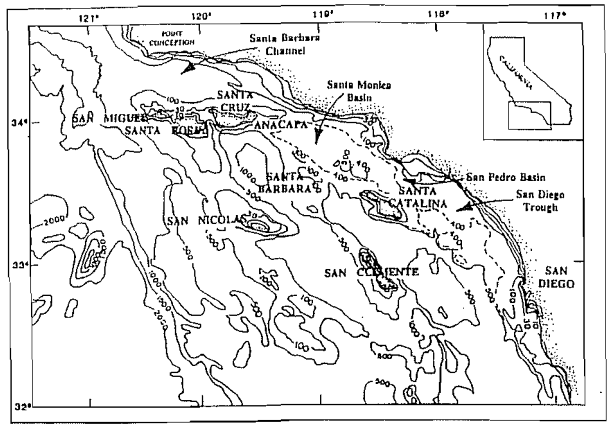
Abstract. The major oceanic circulation patterns characteristic to the Santa Barbara Channel and the greater Southern California Bight are discussed. The bathymetry, sources of water and their physical properties, wind regime (interior and exterior to the bight), geostrophy, and externally driven coastally trapped waves are presented, giving their relative importance in driving the circulation in the region. Characteristics of prominent meso-scale circulation features such as eddies, temperature fronts, and geostrophically induced fluctuations in the coastal currents in the bight and the channel are explained. A new synoptic approach for determining surface currents and surface wind stress in the Santa Barbara Channel is presented as the most plausible way to estimate surface pollutant trajectory. Research supporting this new approach to determining ocean surface trajectories is one of the major objectives of the presently ongoing Minerals Management Service (MMS) study, entitled the Santa Barbara Channel-Santa Maria Basin Circulation Study. Another objective is to use the knowledge gained from the study plus real time data from monitoring stations in the channel for accurate and timely prediction of oil spill trajectory in support of local response to an actual oil spill; a full list of objectives and general field plan are summarized.

Keywords: Oceanic circulation; oceanographic forecaster; California Current; California Undercurrent; California Countercurrent; eddy or eddies; upwelling; thermal front; recirculation; coastally-trapped waves; oil spill trajectory; bi-directional flow; geostrophic currents; upwelling favorable winds.



NOTE: Measurements in fathoms.

Figure 1. Southern California Bight bathymetry (Hickey 1992).

Circulation in the Southern California Bight

One cannot understand the circulation in the Santa Barbara Channel without first having a basic understanding of the circulation in the Southern California Bight, of which the Santa Barbara Channel is a part. The Southern California Bight (Fig. 1) is bounded to the north and east by the California coast, from Point Arguello to the U.S./Mexican international border. It is bounded offshore to the west by the Santa Rosa-Cortes Ridge. Within the bight are submarine valleys and mountains, the peaks of which form the various offshore islands. The ridges and troughs generally run northwest to southeast, with the exception of the Santa Barbara Channel, which runs east to west. The oceanic circulation in the Southern California Bight owes its complexity principally to the bight's composite bottom topography. Any flow entering the 14 basins making up the Southern California Bight at depths below 250 m must do so from the southeast along the San Diego Trough and into the Santa Monica-San Pedro basins. The Santa Monica-San Pedro basins act as a conduit for water flow into the rest of the bight, opening up to the southeast at 737 m, to the northwest into the Santa Barbara Basin at 250 m, and to the west into the Santa Cruz Basin at 650 m. Together, the Santa Monica-San Pedro basins are 100 km long, 40 km wide, and 900 m deep at the deepest point.

The sources of water in the Southern California Bight are (1) the cold, low salinity, highly oxygenated sub-arctic water brought in by the California Current; (2) the warm, saline, central north Pacific water that advects in from the west; and (3) the warm, highly saline, low oxygen content (Equatorial) water entering the bight from the south, principally by way of the California Undercurrent (at 300 m depth), and secondarily by the California Counter-Current closer to the surface (Fig. 2). The distribution of these waters in the bight is such that the top 200 m is typically low in salinity and high in oxygen content, which identi-