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Rocky Intertidal Macroinvertebrates of the Southern California Bight: An Overview and Checklist

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Abstract – A total of 349 epibenthic taxa of macroinvertebrates were recorded from 7 mainland and 15 island rocky intertidal sites in the Southern California Bight. The occurrence of these taxa among the 22 sites is presented as a checklist organized by phyla and classes. The majority of these were mollusks (188), followed by sponges (42) and crustaceans (30). Highest numbers of taxa were recorded from: Coal Oil Point (125); Big Fisherman's Cove, Santa Catalina Island (124); Santa Rosa Island (122); Willows Anchorage, Santa Cruz Island (122) and Government Point (120). Sites having the highest numbers of common taxa (*i.e.*, those whose average densities exceeded one individual per m^2) were located on islands, and included: Willows Anchorage, Santa Cruz Island (38 taxa); Catalina Harbor, Santa Catalina Island (36); Prisoners Harbor, Santa Cruz Island (34); Frenchy's Cove, Anacapa Island (33); Cave Canyon, Santa Barbara Island (33) and Big Fisherman's Cove, Santa Catalina Island (33). The most abundant taxa (based on density and averaged over all sites) were *Chthamalus fissus/C. dalli*, followed by *Littorina keenae*, *Phragmatopoma californica* and *Tetraclita rubescens*. Based on percent cover, the most abundant taxa were *C. fissus/C. dalli*, *P. californica*, *Mytilus californianus* and *Anthopleura elegantissima*. With the exception of sponges, the number of northerly and southerly range extensions along the Pacific Coast recorded by this study were few.

Introduction

Rocky intertidal community structure at a series of mainland and island sites in the Southern California Bight was studied intensively between 1975 and 1979 as a part of a broad investigation of the Bight by the Bureau of Land Management (now Minerals Management Services) Outer Continental Shelf Program. Site records for the taxa of epibenthic macroinvertebrates from this 3-yr study are contained in individual chapters of the unpublished annual reports for the project (Littler 1978a, b, 1979). The main objectives of this paper are to: 1) integrate these disparate records and make them available in a concise format and 2) provide the data base for a biogeographic study of the rocky shore macroinvertebrates of the Bight (Seapy & Littler 1980), which was published as a part of the proceedings of the previous symposium on the California Islands (Power 1980).

A review of the existing literature on the invertebrate taxa of the Southern California Bight was completed by Bright (1974) prior to the initiation of the Outer Continental Shelf Program in 1975. Bright compiled species lists, which were arranged by major taxonomic groups. A useful aspect of these lists was the inclusion of habitat type for each species. A more thorough and taxonomically-current listing of invertebrate species from the Bight was compiled by Straughan & Klink (1980). This paper consisted of chapters on the various taxonomic groups written by specialists actively working on the invertebrates of the Southern California Bight. Unfortunately, species habitats were not included. Data on species abundances obtained at island sites before the inception of the BLM's Outer Continental Shelf Program are limited to the studies of Caplan & Boolootian (1967) at San Nicolas Island and Littler & Murray (1975) at San Clemente Island.

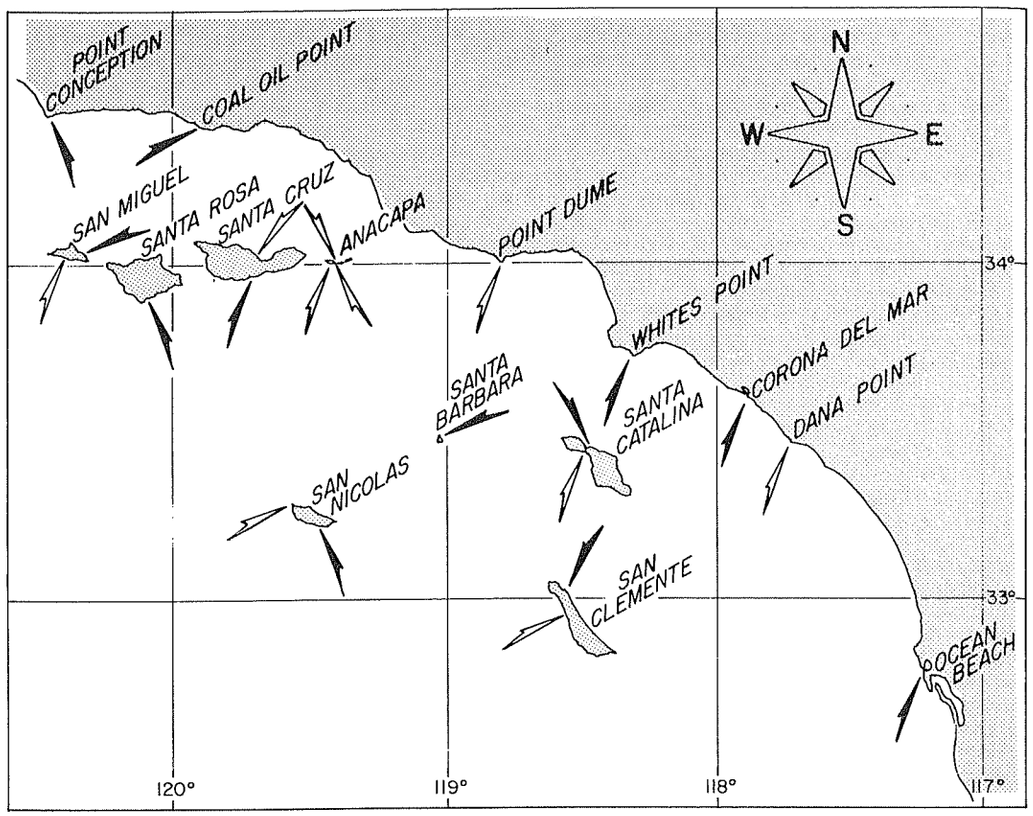

Figure 1. Location of the 22 rocky intertidal sites studied between 1975 and 1979 during the Bureau of Land Management study of the Southern California Bight.

No attempt is made here to review the literature concerned with specific studies on species of intertidal invertebrates from the Southern California Bight since two texts already have performed this task. Morris & co-authors (1980) presented synopses of the major species of rocky shore invertebrates from the California coast. Individual chapters of the book were written by specialists and each included a comprehensive list of literature citations. The classic text on rocky shore invertebrates of the Pacific coast, *Between Pacific Tides*, was revised by D. W. Phillips (Ricketts *et al.* 1985). The annotated systematic index in this book was thoroughly updated and includes the more recent literature from the Bight.

Characterization of the Study Area

The Southern California Bight (Fig. 1) has been defined (Anon. 1973) as the open embayment of the Pacific Ocean bounded on the east by the North American coastline extending from Point Conception, California, to Cabo Colnett, Baja California, Mexico and on the west by the California Current. Eight islands are included within the Bight, four of which are northern (San Miguel, Santa Rosa, Santa Cruz and Anacapa Islands) and four southern (San Nicolas, Santa Barbara, Santa Catalina and San Clemente Islands). In terms of its topography, the Bight is a complex region, made up of basins delineated by submarine ridges, banks and islands.

Cockerell (1939) was perhaps the first author to note that the region of the southern California islands, especially near the 4 northern islands, are remarkable for the impingement and mixing of both cold and warm waters. Santa Cruz and Santa Rosa Islands periodically are exposed to both cold and warm currents, while San Clemente and Santa Catalina Islands are bathed by relatively warm southern waters and San Miguel and San Nicolas Islands are exposed to the cold California Current throughout much of the year (discussed by Neushul *et al.* 1976; Seapy & Littler 1980). Seasonal differences in the strength of the southward-flowing California Current (Wyllie 1966) and, concomitantly, counterclockwise flow of the Southern California Eddy (Fig. 2) contribute to the complex intermingling of physical conditions in the Bight. Zoogeographically, the islands in the Bight are intermediate between the cold-water and warm-water faunas to the north and south of Point Conception, with the offshore and northern islands having greater cold-water species affinities and the southern and nearshore islands having greater warm-water affinities (Seapy & Littler 1980).

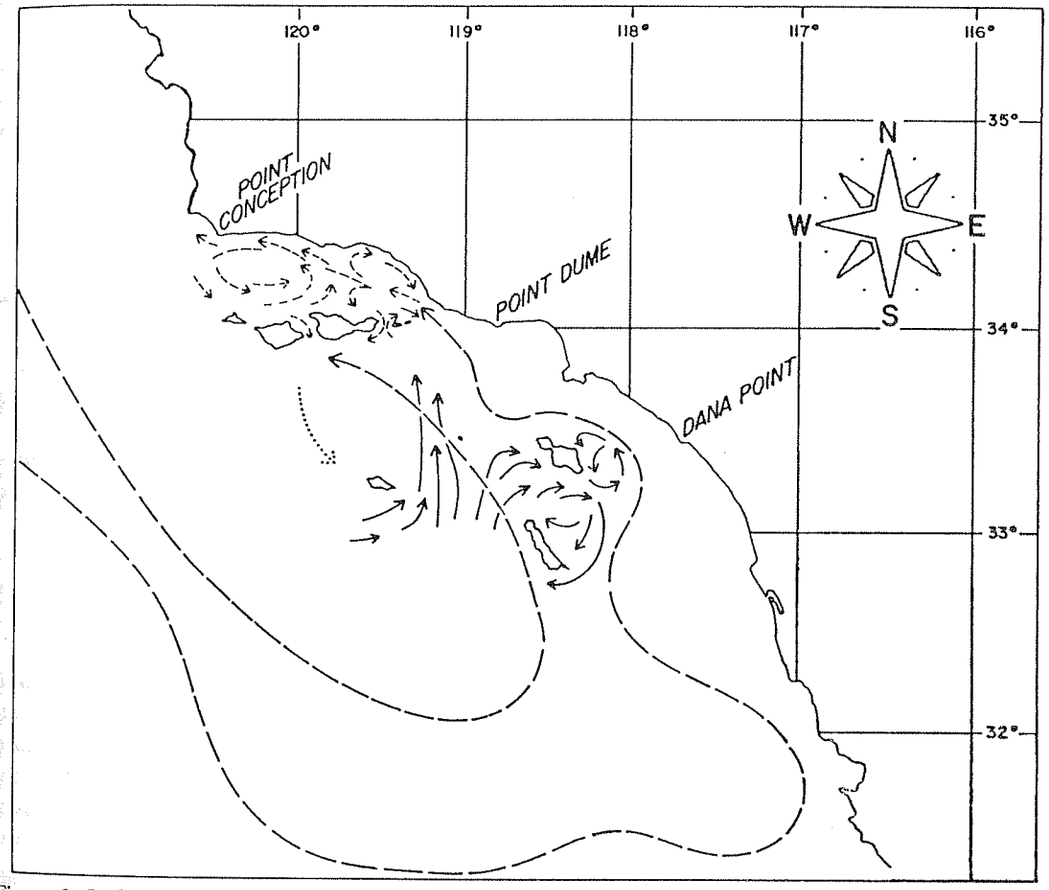

Figure 2. Surface current flow in the Southern California Bight (after Seapy 1974). Long dashed lines represent mean geostrophic flow contours for the month of August, averaged over a 16 yr period Wyllie 1966). Short dashed lines indicate surface current flow during August 1969 (Kolpack 1971). Solid lines are surface currents derived from 10 m drogue releases during October 1958 (Scripps Institution of Oceanography 1962), while the single dotted line between Santa Rosa and San Nicolas Islands is based on Neushul & co-authors (1967).

Table 1. Sampling schedule between 1975 and 1978 at the 22 rocky intertidal sites in the Southern California Bight. Seasons were defined as May to August (Summer; S), September to November (Fall; F), December and January (Winter; W) and February to April (Spring; Sp).

Sites	Abbrev.	1975-1976				1976-1977				1977-1978				
		S	F	W	Sp	S	F	W	Sp	S	F	W	Sp	S
MAINLAND														
Government Point, Santa Barbara County	GP					x	x	x	x		x		x	
Coal Oil Point, Santa Barbara County	COP	x	x	x	x	x	x	x	x	x	x	x	x	
Malibu, Los Angeles County	MAL											x		
Whites Point, Los Angeles County	WP		x	x	x	x	x	x		x	x	x	x	
Corona del Mar, Orange County	CDM	x	x	x	x	x	x	x	x	x		x		
Dana Point, Orange County	DP										x			
Ocean Beach, San Diego County	OB		x		xx		x	x	xx		xx		xx	
ISLANDS														
San Miguel Island (Crook Point)	SMI-CP												x	
San Miguel Island (Cuyler Harbor)	SMI-CH		x	x	xx	x	x	x	x				x	
Santa Rosa Island (South Point)	SRO						x	x	x	x	x		x	
Santa Cruz Island (Willows Anchorage)	SCR-WA		x	x	x	x	x	x	x	x			xx	
Santa Cruz Island (Prisoners Harbor)	SCR-PH												x	
Anacapa Island (Cat Rock)	ANA-CR											x		
Anacapa Island (Frenchy's Cove, south side)	ANA-SF											x		
Anacapa Island (Frenchy's Cove)	ANA-FC											x		
San Nicolas Island (West Point)	SNI-WP											xx		
San Nicolas Island (Dutch Harbor)	SNI-DH		x	x	x	x	x	x	x	x	x	x	x	x
Santa Barbara Island (Cave Canyon)	SBA	x	x	x	x	x	x	x	x				x	
Santa Catalina Island (Catalina Harbor)	SCA-CH										x			
Santa Catalina Island (Big Fisherman's Cove)	SCA-FC	x	x	x	x	xx	x	x	x			x		
San Clemente Island (northwest coast)	SCL-NW												x	
San Clemente Island (Wilson Cove)	SCL-WC		x	x	x	x	x	x	x	x	x		x	

Materials & Methods

Rocky intertidal communities were sampled between July 1975 and April 1979 at 7 mainland and 15 island sites in the Southern California Bight (Fig. 1, Table 1). The latitude and longitude and a series of descriptive physiographic attributes that characterize each site are given in Table 2.

At each of the 22 sites, species abundances (density and percent cover) were determined from a minimum of 30, 0.15 m^2 rectangular quadrats, positioned at 1-m intervals along each of 2-4 transect lines (depending on the slope of the beach) that extended through the intertidal zone (described for each site in Littler, 1978a, b, 1979). Further details of the field methods are given in reviews of the first and second years of the study by Littler (1980a, b). Because density data were available from the quadrat samples, we were able to distinguish between those taxa at each site whose mean densities were either greater or less than 1 m^{-2}, averaged over all tidal intervals sampled and all seasonal site visits.

For the purposes of this study, macroinvertebrates are defined as conspicuous taxa, recognizable by the unaided eye in the field. Thus, small and cryptic animals such as the gammarid and caprellid amphipods were not included. In the field the macroinvertebrates were identified and enumerated in the quadrats. If a species identity was questionable, specimens were preserved in 10% sea water-formalin solution and subsequently identified by the senior author or outside taxonomic experts (see Acknowledgments). Two groups, the hydrozoans and bryozoans, generally were not identified to the species level. We could identify most specimens of hydroids only to the level of genus due to the lack of a taxonomic treatment of the group for the Pacific coast (Rees & Hand, 1975). Bryozoans are difficult to identify, and none of the taxonomic experts on this group were available at the time to assist with the project. As a result most bryozoans, with the exception of those few species which the senior author could identify with reasonable confidence, were lumped together as either "erect" or "encrusting" forms. Finally, the highly mobile supratidal isopod *Ligia occidentalis* was not represented in any of the quadrat samples and was collected only sporadically as voucher specimens. Although this is a common species on rocky shores throughout the Bight, we have not included it here because the site records were so inconsistent.

In an earlier paper (Seapy & Littler 1980), we compared the faunal compositions of the islands in the southern California Bight to elucidate biogeographic patterns. The biogeographical classification for each species could not be included in that paper because of space constraints, but is included here. Taxa at each site were classified as either northern, southern, transitional or widespread. The ranges of northern and southern species frequently overlap in a region of about two and one-half degrees latitude centered at Point Conception, which Newman (1979) termed the Californian Transitional Zone (Fig. 3). Northern species are defined here as ranging northward from northern Baja California (at about Bahia del Rosario) into and often beyond the Oregonian Province. Southern species, on the other hand, range southward from central California (in the Monterey Bay area) into and, less commonly, through the Californian Province. Transitional species are narrowly defined as endemics restricted to the range of overlap, *i.e.*, between northern Baja California and central California (Fig. 3). Species classified as widespread range broadly to the north and south of southern California; at a minimum, through the Californian and Oregonian Provinces between central Baja California and northern California. The interested reader is referred further to the analysis of the biogeographic provinces and their latitudinal boundaries on the Pacific coast of North America by Brusca & Wallerstein (1979).

A voucher collection of the macroinvertebrates from each of the study sites was assembled and deposited with the National Museum of Natural History, Smithsonian Institution, Washington, DC. A secondary voucher collection is archived at the Santa Barbara Museum of Natural History, Santa Barbara, CA.

Results and Discussion

The macroinvertebrate taxa totaled 349 and are listed according to their respective phyla and classes in the Appendix. Most were mollusks (188), of which 149 were gastropods. Sponges were well represented (42 taxa), followed by crustaceans (30) and ascidians (25). The numbers of taxa belonging to the various phyla and classes at each site are summarized in Table 3. The highest numbers were recorded from: Coal Oil Point (125); Big Fisherman's Cove, Santa Catalina Island (124); Santa Rosa Island (122); Willows Anchorage, Santa Cruz Island (122); Government Point (120) and Dutch Harbor, San Nicolas Island (115). Government Point and Coal Oil Point were the only mainland sites with more than 100 total taxa. Considerable variability in the numbers of taxa occurred among the island sites, ranging from 61 at Crook Point, San Miguel Island to 124 at Big Fisherman's Cove, Santa Catalina Island. However, the variable sampling frequency at the study sites (Table 1) diminishes the relevance of these total counts.

For between-site comparisons, a more meaningful measure than total counts is the number of taxa whose densities were greater than 1 m^{-2}. Using this method, the highest numbers of taxa were all recorded at island sites (Table 3) and included: Willows Anchorage, Santa Cruz Island (38 taxa); Catalina Harbor, Santa Catalina Island (36); Prisoners Harbor, Santa Cruz Island (34); Frenchys Cove, Anacapa Island (33); Cave Canyon, Santa Barbara Island (33) and Big Fisherman's Cove,

Table 2. Physiographic attributes for the 22 rock intertidal sites. Water temperature categories are assigned on the basis of long term (10 yr) mean values from CalCOFI stations (Anon. 1963) as cold (<14.0°C), moderately cold (14.0-14.5°C), moderately warm (15.5-16.0°C) and warm (>16.0°C).

Study Area	Latitude and Longitude	Water Temperature	Substrate	Tidal Range (m)	Wave Exposure	Sand Influence	Disturbance Source
MAINLAND							
Government Point	34°26'35"N 120°27'06"W	cold	Monterey shale/siltstone	-0.3 to +2.1	heavy (mid-intertidal)	moderate	oil seeps
Coal Oil Point (Goleta)	34°24'27"N 119°52'40"W	cold (moderate)	Monterey shale/siltstone	-0.6 to +0.9	moderate	heavy	oil seeps
Malibu	34°00'42"N 118°47'30"W	warm (moderate)	Monterey shale/siltstone	-0.3 to +2.4	moderate	moderate (lower intertidal)	none
Whites Point (Los Angeles)	33°43'11"N 118°19'39"W	warm (moderate)	Monterey shale & unstable granitic	-0.3 to +0.9	moderate	none	domestic wastes
Corona del Mar	33°35'14"N 117°51'54"W	warm	unstable granitic boulders on sand-stone/siltstone	-0.3 to +0.9	moderate	moderate (upper intertidal)	human usage (heavy)
Dana Point	33°27'25"N 117°42'44"W	warm (moderate)	granitic boulders	0.0 to +2.1	moderate	moderate (lower intertidal)	none
Ocean Beach (San Diego)	32°44'35"N 117°15'15"W	warm	poorly consolidated friable sandstone	+0.3 to +4.0	heavy	moderate (upper intertidal)	human usage (moderate)
ISLANDS							
San Miguel Island (Crook Point)	34°01'28"N 120°22'43"W	cold	sandstone	+0.3 to +2.7	heavy	none	none
San Miguel Island (Cuyler Harbor)	34°02'55"N 120°20'08"W	cold	irregular volcanic flow breccia	-0.3 to +2.7	moderate	moderate (lower intertidal)	none
Santa Rosa Island (South Point)	33°53'31"N 120°06'31"W	cold (moderate)	smooth sandstone	+0.3 to +3.4	moderate	moderate (lower intertidal)	none
Santa Cruz Island (Willows Anchorage)	33°57'43"N 119°45'16"W	intermediate	irregular volcanic breccia	+0.3 to +4.0	moderate (surge)	none	none
Santa Cruz Island (Prisoners Harbor)	34°01'14"N 119°41'14"W	intermediate	volcanic rock	-0.6 to +2.4	low	none	none
Anacapa Island (Cat Rock)	34°00'19"N 119°25'05"W	intermediate	volcanic rock	0.0 to +2.1	moderate	none	none
Anacapa Island (Frenchy's Cove, south side)	34°00'24"N 119°24'38"W	intermediate	volcanic rock	-0.3 to +2.7	moderate	none	human usage (heavy)
Anacapa Island (Frenchy's Cove)	34°00'31"N 119°24'21"W	intermediate	volcanic boulders	-0.3 to +2.7	low	none	human usage (light)
San Nicolas Island (West Point)	33°16'43"N 119°34'41"W	cold	sandstone	0.0 to +1.5	heavy	none	none
San Nicolas Island (Dutch Harbor)	33°12'54"N 119°28'22"W	cold	sandstone	-0.3 to +1.5	moderate	heavy	none
Santa Barbara Island (Cave Canyon)	33°28'43"N 119°01'36"W	intermediate	vesicular volcanic rock	+0.3 to +3.7	moderate (surge)	none	none
Santa Catalina Island (Catalina Harbor)	33°25'42"N 118°30'42"W	warm	vesicular volcanic rock	-0.3 to +2.1	low	none	none
Santa Catalina Island (Big Fishermen's Cove)	33°26'47"N 118°29'04"W	warm	vesicular volcanic rock	-0.6 to +3.0	low	none	none
San Clemente Island (northwest coast)	33°58'06"N 118°34'18"W	warm	large volcanic boulders and rocks	-0.3 to +1.5	moderate	none	none
San Clemente Island (Wilson Cove)	33°00'06'N 118°33'03"W	warm	stable granitic boulders	-0.3 to +2.1	low	none	none

Table 3. Numbers of taxa recorded at each of the 22 rocky intertidal sites in the Southern California Bight. Values in parenthesis indicate the number of species at each site whose densities exceed 1 m^{-2}. The study site abbreviations are given in Table 1.

Taxonomic Group	GP	COP	MAL	WP	CDM	DP	OB	SMI -CP	SMI -CH	SRO	SCR -WA	SCR -PH	ANA -CR	ANA -SF	ANA -FC	SNI -WP	SNI -DH	SBA	SCA -CH	SCA -FC	SCL -NW	SCL -WC
PORIFERA Combined	13	13	5	7	9	4	5	7	15	10	9	2	10	9	11	8	14	11	7	10	8	17
CNIDARIA Combined	11 (1)	5 (1)	3 (1)	1 (1)	1 (1)	1 (1)	2 (1)	3 (1)	7 (1)	8 (1)	3 (1)	6 (2)	6 (1)	8 (1)	4 (1)	5 (1)	7 (1)	9 (2)	6 (2)	7 (3)	2 (1)	7 (2)
ANNELIDA Polychaeta	4	5 (2)	5 (2)	6 (3)	5 (1)	3 (3)	3 (2)	4 (3)	2	4 (1)	5 (3)	4 (2)	4 (3)	5 (3)	4 (3)	5 (3)	6	4 (3)	3 (2)	5 (2)	5 (2)	6 (2)
ARTHROPODA Crustacea	13 (7)	13 (7)	8 (6)	10 (6)	11 (5)	13 (4)	10 (5)	8 (6)	13 (5)	14 (6)	18 (5)	13 (8)	9 (5)	9 (6)	7 (5)	11 (5)	12 (5)	15 (6)	11 (7)	13 (7)	8 (5)	14 (6)
MOLLUSCA Gastropoda	43 (12)	57 (12)	24 (15)	47 (13)	42 (9)	36 (13)	22 (9)	17 (8)	36 (9)	54 (12)	52 (17)	34 (14)	38 (13)	22 (11)	32 (19)	37 (12)	48 (14)	35 (14)	41 (17)	55 (13)	37 (12)	43 (11)
Bivalvia	10 (3)	6 (2)	3 (3)	8 (2)	8	4 (3)	5 (4)	6 (3)	8 (3)	10 (3)	13 (6)	7 (6)	6 (4)	6 (4)	2 (2)	4 (1)	7 (3)	10 (4)	9 (5)	10 (4)	5 (2)	6 (3)
Polyplacophora	8	6 (2)	4 (2)	4 (3)	9 (3)	5 (3)	3 (2)	6 (2)	6 (2)	8 (2)	9 (3)	5 (2)	3 (3)	4 (3)	4 (3)	6 (2)	6 (4)	6 (3)	4 (3)	10 (3)	5 (3)	7 (3)
Combined	61 (15)	69 (16)	31 (20)	59 (18)	59 (12)	45 (19)	30 (15)	29 (13)	50 (14)	72 (17)	74 (26)	46 (22)	47 (20)	32 (18)	38 (24)	47 (15)	61 (21)	51 (21)	54 (25)	75 (20)	47 (17)	56 (17)
ECHINODERMATA Combined	5	8	2	4 (1)	5 (1)	3	1 (1)	3	5	7 (1)	8 (3)	1	3 (1)	2	2	7 (2)	5	7 (1)	2	6 (1)	1	2
ECTOPROCTA & ENTOPROCTA	5	4	2	1	4	0	0	1	2	0	2	6	2	4	2	1	2	1	7	2	1	1
UROCHORDATA Ascidiacea	8	8	5	0	4	5	2	6	8	7	3	1	1	5	0	6	8	8	4	6	4	1
TOTAL All Species	120 (23)	125 (26)	61 (29)	88 (29)	98 (20)	74 (27)	53 (24)	61 (23)	102 (20)	122 (26)	122 (38)	79 (34)	82 (30)	74 (28)	68 (33)	90 (26)	115 (27)	106 (33)	94 (36)	124 (33)	76 (25)	103 (27)

Santa Catalina Island (33). All other island sites and all of the mainland sites had 30 or fewer common taxa.

The three most abundant taxa from each site, in terms of both mean density and mean percent cover, are listed in Table 4. The barnacles *Chthamalus fissus/C. dalli* contributed the greatest density of all taxa at 16 of the 22 sites and ranked second or third at the remaining six sites. *Littorina keenae* was among the top three taxa in terms of density at 10 sites, followed by *Phragmatopoma californica* (7 sites), *Tetraclita rubescens* (6), *Balanus glandula* (5) and *Macclintockia scabra* (4). On the basis of percent cover, the taxa that were most frequently represented among the top three at each site included: *C. fissus/C. dalli* (16 sites); *P. californica* (14); *Mytilus californianus* (8); *Anthopleura elegantissima* (7); *Tetraclita rubescens* (5) and *B. glandula* (4). It is noteworthy that *T. rubescens* was among the top three taxa in terms of density and percent cover only at island sites.

The geographic ranges of the species recorded from the Bight are included in the Appendix. As we described earlier (Fig. 3 in Seapy & Littler 1980), the proportionate representation by species classified as "northern" increases going from the southern to the northern island sites, whereas an opposite trend is seen for species characterized as "southern". Transitional species were represented more or less evenly at the various sites, although maximal percentages occurred at Anacapa and Santa Barbara Islands. These two islands would appear to be intermediate in terms of the mixing of cold and warm water faunas.

Comparisons of published geographic ranges of species with their occurrences among the sites in the Bight are noteworthy in a number

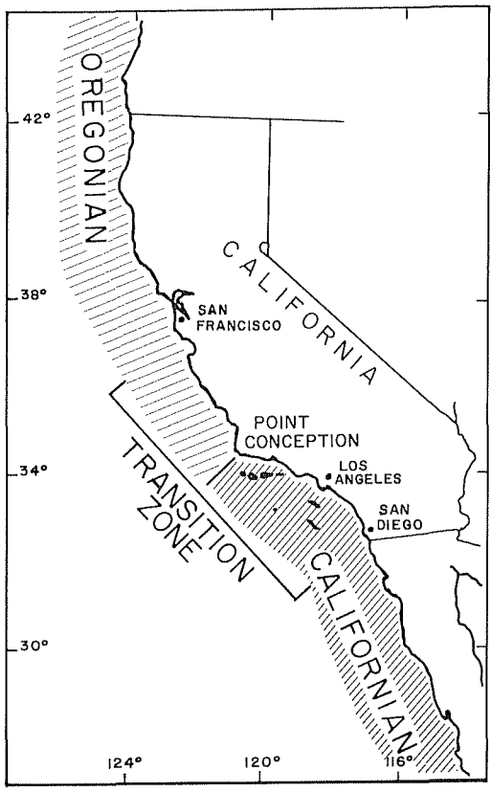

Figure 3. Zoogeographical provinces of the California and northern Baja California coast (after Seapy & Littler 1980).

of cases. Bakus & Green (1987) reported that 22 of 58 species of sponges collected at intertidal and subtidal sites in the Bight during the BLM sampling program represented new range extensions. However, there are few range extensions among the other invertebrate groups. The records of two species of sea cucumbers from this study represented substantial northward range extensions. *Pseudocnus californicus* was recorded here from Santa Barbara Island and West Point, San Nicolas Island, but its northernmost limits were reported previously to be Isla Santa Margarita in southern Baja California (M. Bergen, pers. comm.). We collected *Pachythyone lugubris* from Dutch Harbor, San Nicolas Island, while the northernmost limit of this species was previously considered to be Cedros Island in central Baja California (M. Bergen, pers. comm.).

Several minor range extensions were noted among the molluscs. *Opalia funiculata* was reported by McLean (1978) to range from Santa Monica (south of Los Angeles) to Panama. We found this species to be widespread throughout the Bight, occurring at all of the mainland sites and many of the islands. The southernmost limits of three species included in Morris & co-authors (1980) are extended by the present records. *Tectura scutum* was reported to extend southward to Point Conception; we encountered it from Cuyler Harbor, San Miguel Island, Santa Rosa Island and at both sites on San Nicolas Island. Along the mainland, however, we did not find *T. scutum* at any site south of Government Point. *Nucella canaliculata* was listed as ranging from Alaska to central California (Cayucos). We recorded this species at our northernmost mainland site, Government Point. Finally, the southernmost limit of the chiton, *Tonicella lineata*, on the Pacific coast was given as San Miguel Island, and we recorded this species from Santa Rosa, Santa Cruz and San Nicolas Islands.

Because the sampling effort represented by this study was intensive and most of the taxa were identified to the species level, one would expect that a number of range extensions and possibly a few new species would have been discovered. Except for the sponges, this was not the case. The sponges represented the exception because the BLM baseline survey of the Bight was the first comprehensive survey of intertidal sponges from southern California (Bakus & Green, 1987).

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Table 4. Abundant taxa at the 22 rocky intertidal sites. Mean densities and cover values are averaged over the tidal range intervals sampled at each site and are listed for the three highest ranking taxa.

Study Area	Mean Density (n m^{-2})	Mean Cover (%)
MAINLAND		
Government Point	*C. fissus/dalli* (11,971) *L. keenae* (294) *A. elegantissima* (249)	*C. fissus/dalli* (10.1) *P. californica* (8.4) *A. elegantissima* (6.9)
Coal Oil Point (Goleta)	*C. fissus/dalli* (1,651) *Lacuna spp.* (1,255) *A. elegantissima* (412)	*A. elegantissima* (15.4) *M. californianus* (8.2) *C. fissus/dalli* (2.7)
Malibu	*C. fissus/dalli* (7,618) *M. californianus* (1,183) *L. keenae* (269)	*M. californianus* (29.2) *C. fissus/dalli* (8.1) *P. californica* (4.6)
Whites Point (Los Angeles)	*B. glandula* (582) *Mc. scabra* (336) *C. fissus/dalli* (238)	*B. glandula* (1.6) *A. elegantissima* (1.4) *S. purpuratus* (1.1)
Corona del Mar	*C. fissus/dalli* (408) *Mc. scabra* (59) *Pg. samuelis* (25)	*A. elegantissima* (1.0) *C. fissus/dalli* (1.0) *S. purpuratus* (0.5)
Dana Point	*C. fissus/dalli* (14,777) *L. keenae* (244) *P. californica* (78)	*C. fissus/dalli* (20.0) *P. californica* (1.0) *A. elegantissima* (0.5)
Ocean Beach (San Diego)	*C. fissus/dalli* (997) *Lo. digitalis* (274) *Po. polymerus* (274)	*P. californica* (4.8) *M. californianus* (2.3) *Lo. digitalis* (1.6)
ISLANDS		
San Miguel Island (Crook Point)	*P. californica* (3,171) *C. fissus/dalli* (1,235) *B. glandula* (617)	*P. californica* (23.7) *M. californianus* (10.4) *B. glandula* (1.5)
San Miguel Island (Cuyler Harbor)	*C. fissus/dalli* (1,407) *B. glandula* (378) *L. keenae* (140)	*P. californica* (9.2) *D. fewkesi* (4.4) *C. fissus/dalli* (3.9)
Santa Rosa Island (South Point)	*P. californica* (2,532) *B. glandula* (1,340) *C. fissus/dalli* (1,077)	*M. californianus* (11.6) *P. californica* (10.5) *B. glandula* (3.5)
Santa Cruz Island (Willows Anchorage)	*L. keenae* (532) *C. fissus/dalli* (386) *T. rubescens* (310)	*A. elegantissima* (2.6) *M. californianus* (1.6) *T. rubescens* (1.2)
Santa Cruz Island (Prisoners Harbor)	*C. fissus/dalli* (5,200) *B. glandula* (1,302) *L. keenae* (366)	*C. fissus/dalli* (7.8) *M. californianus* (6.9) *B. glandula* (4.3)
Anacapa Island (Cat Rock)	*C. fissus/dalli* (4,109) *P. californica* (1,153) *T. rubescens* (678)	*P. californica* (14.2) *C. fissus/dalli* (6.3) *M. californianus* (5.8)
Anacapa Island (Frenchy's Cove, south side)	*C. fissus/dalli* (6,480) *P. californica* (2,927) *L. keenae* (963)	*P. californica* (18.7) *C. fissus/dalli* (12.2) *M. californianus* (8.3)
Anacapa Island (Frenchy's Cove)	*P. californica* (1,206) *L. keenae* (471) *C. fissus/dalli* (395)	*P. californica* (12.5) *C. fissus/dalli* (1.1) *L. keenae* (0.5)
San Nicolas Island (West Point)	*T. rubescens* (639) *C. fissus/dalli* (287) *Mc. scabra* (228)	*T. rubescens* (4.4) *A. elegantissima* (3.3) *S. purpuratus* (2.1)
San Nicolas Island (Dutch Harbor)	*C. fissus/dalli* (2,183) *A. elegantissima* (136) *L. scutulata* (91)	*D. fewkesi* (8.2) *A. elegantissima* (5.5) *C. fissus/dalli* (5.4)
Santa Barbara Island (Cave Canyon)	*C. fissus/dalli* (1,475) *T. rubescens* (350) *L. keenae* (240)	*C. fissus/dalli* (3.0) *M. californianus* (3.0) *Ps. exogyra* (2.8)
Santa Catalina Island (Catalina Harbor)	*C. fissus/dalli* (10,279) *L. keenae* (476) *Co. californica* (308)	*C. fissus/dalli* (10.0) *T. rubescens* (2.7) *Sr. squamigerus* (0.7)
Santa Catalina Island (Big Fisherman's Cove)	*C. fissus/dalli* (802) *T. rubescens* (450) *Dn. lituella/rastrum* (341)	*Dn. lituella/rastrum* (3.4) *T. rubescens* (3.2) *C. fissus/dalli* (2.1)
San Clemente Island (northwest coast)	*C. fissus/dalli* (4,526) *P. californica* (907) *Sp. bifurcatus/ Br. adamsianus* (389)	*P. californica* (7.9) *C. fissus/dalli* (4.6) *H. cracherodii* (2.1)
San Clemente Island (Wilson Cove)	*C. fissus/dalli* (1,528) *Mc. scabra* (167) *T. rubescens* (148)	*C. fissus/dalli* (3.6) *T. rubescens* (1.2) *Mc. scabra* (0.7)

A. = Anthopleura
B. = Balanus
Br.= Brachidontes
C. = Chthamalus
Co.= Corynactis
D. = Dodecaceria
Dn.= Dendropoma
H. = Haliotis
L. = Littorina
Lo.= Lottia
Mc.= Macclintockia
M. = Mytilus
P. = Phragmatopoma
Pp.= Pagurus
Po. = Pollicipes
Ps.= Pseudochama
S. = Strongylocentrotus
Sp.= Septifer
Sr.= Serpulorbis
T. = Tetraclita

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Appendix

Individual site records for the 349 macroinvertebrate taxa arranged by phyla and classes. Ranges are indicated as northern (N), southern (S), transitional (T) or widespread (W); as defined in Materials and Methods. The 22 study site abbreviations are given in Table 1. Open circles indicate the presence of a given species or taxon at a given site and closed circles indicate that a species or taxon occurred at a mean density greater than 1 m^{-2} at that site.

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
PORIFERA: Calcarea																							
Clathrina coriacea (Montagu, 1818)	S					O		O		O	O					O			O			O	
Clathrina sp.						O									O								
Leucandra heathi Urban, 1905	N	O	O	O	O	O	O	O			O		O	O	O	O	O		O	O	O	O	O
Leucetta losangelensis (de Laubenfels, 1930)	T	O	O	O		O				O	O		O	O	O	O	O	O	O			O	O
Leucilla nuttingi (Urban, 1902)	N	O	O						O	O					O	O	O						
Leucosolenia eleanor Urban, 1905	N					O						O											
Leocosolenia nautilia de Laubenfels, 1930	T																		O				
Scypha sp.																			O				
Scypha coronata (Ellis & Solander, 1786)	W																			O			
PORIFERA: Demospongiae																							
Acarnus erithacus de Laubelfels, 1927	N	O	O		O					O							O						O
Antho lithophoenix (de Laubenfels, 1927)	T?																						
Aplysilla polyraphis (de Laubenfels, 1930)	N						O										O			O	O		
Axocielita originalis (de Laubenfels, 1930)	N	O	O	O	O		O		O	O	O	O	O	O	O	O	O					O	
Callyspongia spp.														O									
Cliona spp.			O						O	O							O						
Geodia mesotriaena von Lendenfeld, 1910	W									O										O			O
Halichondria panicea (Pallas, 1766)	N				O													O					
Haliclona cf. permollis (Grant, 1827)	W	O			O			O								O	O				O	O	
Haliclona spp.		O	O	O	O	O	O	O	O				O	O	O	O	O	O		O	O	O	O
Haliclonissa sp.										O										O			
Hymeniacidon sinapium de Laubenfels, 1930	N	O		O	O	O				O	O										O	O	O
Hymeniacidon sp.			O										O	O					O				
Leptoclathria asodes (de Laubenfels, 1930)	N																						

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
PORIFERA: Demospongiae (Cont.)																							
Lissodendoryx firma (Lambe, 1895)	N	O									O												O
Lissodendoryx topsenti (de Laubenfels, 1930)	T		O																				
Lissodendoryx sp.															O								
Microciona microjoanna de Laubenfels, 1930	N																						O
Ophlitaspongia pennata var. *californiana* de Laubenfels, 1932	N	O							O	O			O	O			O	O			O		O
Oxeostilon sp.																							O
Pachastrella dilifera de Laubenfels, 1934	S																		O		O		
Penares cortius de Laubenfels, 1930	N																		O				O
Plocamia karykina (de Laubenfels, 1927)	N					O			O	O	O		O	O		O	O	O	O	O	O		O
Plocamilla illgi Bakus, 1966	N	O								O													O
Plocamissa igzo (de Laubenfels, 1932)	N												O	O	O	O		O					
cf. *Pseudosuberites* sp.			O																				
Sigmadocia sp.																							O
Spheciospongia confoederata de Laubenfels, 1930	N		O			O		O		O							O	O					
Spirastrella sp.		O								O	O						O						
Stelletta clarella de Laubenfels, 1930	N		O										O						O	O	O	O	O
Suberites sp.		O	O						O	O	O			O		O	O	O					
Tethya aurantium (Pallas, 1766)	N										O				O	O							
Toxadocia sp.																				O			O
CNIDARIA: Hydrozoa																							
Abietinaria spp.		O							O	O	O									O	O		
Aglaophenia inconspicua Torrey, 1902	N?									O					O								
Aglaophenia spp.		O	O							O	O											O	
Campanularia/Phialidium spp.		O	O									O			O		O		O				

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
CNIDARIA: Hydrozoa (Cont.)																							
Eudendrium californicum Torrey, 1902	N	O																					
Eudendrium spp.		O	O								O				O				O				
Halecium sp.																					O		
Obelia sp.				O																			
Plumularia spp.		O													O		O		O				
Sertularella spp.		O									O	O		O		O			O	O	O		O
Sertularia spp.		O	O	O							O	O			O			O	O	O			
Syncoryne eximia (Allman, 1859)	N?	O							O	O							O		O				
Synthecium cylindricum (Bale, 1888)	N?															O							
CNIDARIA: Anthozoa																							
Anthopleura elegantissima (Brandt, 1835)	W	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Anthopleura xanthogrammica (Brandt, 1835)	W									O	O						O	O					
Astrangia lajollensis Durham, 1947	S?											●						O			O		O
Cactosoma arenaria Carlgren, 1931	T												O										O
Clavularia sp.															O								
Corynactis californica Carlgren, 1936	T							O		O		O		O	O		O		●	●	●		●
Diadumene spp.														O									O
Epiactis prolifera Verrill, 1869	N	O									O		O	O		O	O	O		O	●		O
Zaolutus actius (?) Hand, 1955	T													O									
ANNELIDA: Polychaeta																							
Dodecaceria fewkesi Berkeley & Berkeley, 1954	N	O	O	O					●	O	O		O		O		O	O					O
Hydroides gracilis (Bush, 1904)	T?	O	●	●	●	●	●	●				O	O	O	O	●	O				O	O	O
Phragmatopoma californica (Fewkes, 1889)	T	O	●	O	●	O	●	●	●	O	●	●	●	●	●	●	O	●	●	●	●	●	●

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
ANNELIDA: Polychaeta (Cont.)																							
Phyllochaetopterus prolifica Potts, 1914	N				O																		
Salmacina tribranchiata (Moore, 1923)	N			O	O	O											O			O			
Spirobranchus spinosus Moore, 1923	T?		O		●	O			O		O	●	●	●	●	●	O	●	●	●	●	●	●
Spirorbis spp.		O	O	●	O	O	●	O	●		O	O	●	●	●	O	O	O	●	O	O	O	O
Vermiliopsis infundibulum (Philippi, 1844)	N																		O			O	O
Vermiliopsis spp.																		●					
ARTHROPODA: Crustacea																							
Alpheus clamator Holmes, 1900	S												O										
Balanus glandula Darwin, 1854	N	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	O	●	●	●	O	●
Cancer antennarius Stimpson, 1856	N	O	O		O	O	O			O		O	O				O		O		O		
Cancer anthonyi Rathbun, 1897	S	O																					
Cancer gracilis Dana, 1852	N									O													
Cancer jordani Rathbun, 1900	W	O	O				O	O		O	O		O				O						O
Cancer productus Randall, 1839	N												O										
Cancer sp. (juvenile)		O																					
Chthalamus fissus Darwin, 1854 &	S	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	O
Chthalamus dalli Pilsbry, 1916	N																						
Cycloxanthops novemdentatus (Lockington, 1877)	S																O						
Hapalogaster cavicauda Stimpson, 1859	N																	O					
Herbsti parvifrons Randall, 1839	S																		O				

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
ARTHROPODA: Crustacea (Cont.)																							
Lophopanopeus leucomanus heathii Rathbun, 1900	T				O								O	O	O				O				O
Lophopanopeus l. leucomanus (Lockington, 1877)	T												O								O		
Loxorhynchus crispatus Stimpson, 1857	W						O					O											
Megabalanus californicus (Pilsbry, 1916)	S	●	●	O			O	O	●	●	●	O	O	O	●		O	O	●	●	●	O	●
Pachycheles rudis Stimpson, 1859	W	O						O	O	O	O		O						O				
Pachygrapsus crassipes Randall, 1839	W	●	●	●	●	●	O	●	●	O	●	●	●	●	●	●	O	●	●	●	●	●	●
Pagurus granosimanus (Stimpson, 1859)	N										O	O											
Pagurus hirsutiusculus venturensis Coffin, 1957	T	O	●	●	●	O	O		O	O	O	●	O				●	●	O	O	O		O
Pagurus samuelis (Stimpson, 1859)	W	O			●	●	●	O		O	O	●	O	O	O	●	O	O	O	O	●	●	O
Paraxanthias taylori (Stimpson, 1860)	S						O						O			O			O	●	O		O
Petrolisthes cabrilloi Glassell, 1945	S					O					O							O					
Pollicipes polymerus Sowerby, 1833	W	●	O	●	O	O	O	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●
Pugettia dalli Rathbun, 1893	W		O																				
Pugettia producta (Randall, 1839)	W	●	●	O	O	O	O	O		O	O	●	O	O	O	O	O	O	O	O	O	O	O
Pugettia richii Dana, 1851	N					O					O	O	O						O	O	O		O
Randallia ornata (Randall, 1839)	?		O																				
Tetraclita rubescens Darwin, 1854	S	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda																							
Acanthina punctulata (Sowerby, 1825)	T	●			O		O		O	●	O	●	O				●	O				O	
Acanthina spirata (de Blainville, 1832)	T	O	●	O		O	O	O	O	O	O	●	O	●	O	●	●					O	
Acmaea mitra Rathke, 1833	N										O							O					
Acteocina harpa (Dall, 1871)	N				O						O												
Aeolidia papillosa (Linnaeus, 1761)	W												O	O			O					O	
Alia carinata (Hinds, 1844)	W	●	●	O	O	●	●	O		O	●	O	O	O		●	O	O			O	O	O
Alvinia compacta (Carpenter, 1864)	N		O																				
Alvinia oldroydae (Bartsch, 1911)	S															O							
Amphissa versicolor (Dall, 1871)	N	O	O		O					O	O	O	●	O	O	O	O	O	O	O	O		
Amphithalamus tenuis Bartsch, 1911	T										O									●		O	
Ancula pacifica MacFarland, 1905	N									O													
Anisodoris nobilis (MacFarland, 1905)	N										O						O						
Aplysiopsis smithi (Marcus, 1961)	N							O									O						
Aplysia californica Cooper, 1863	W	O	O	O	O	O	O	O					O		O		O		O				
Astraea undosa (Wood, 1828)	S												O							O			
Barleeia spp.		O	O		O					O	O		O			●	O	O		O		O	
Berthella californica (Dall, 1900)	N													O					O				
Bittium attenuatum (Carpenter, 1864)	N														O					O			
Bittium interfossa (Carpenter, 1864)	T																					O	
Bittium quadrifilatum (Carpenter, 1864)	S		O																				

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Calliostoma annulatum (Lightfoot, 1786)	N		O																				
Calliostoma canaliculatum (Lightfoot, 1786)	N	O								O													
Calliostoma gemmulatum (Carpenter, 1864)	S		O																				
Calliostoma ligatum (Gould, 1849)	N																	O					
Calliostoma tricolor Gabb, 1865	T		O																				
Ceratostoma nuttalli (Conrad, 1837)	S				O							O	O	O	O			O	O	O	O	O	O
Cerithiopsis carpenteri Bartsch, 1911	N	O	O		O					O	O							O					O
Cerithiopsis cosmia Bartsch, 1907	S				O						O						O						O
Conus californicus Reeve, 1844	S	O	O		O	O	O				O	O		O	O	O	O			O	O	O	
Coryphella trilineata O'Donoghue, 1921	N													O									
Crepidula adunca Sowerby, 1825	N		O								O												
Crepidula norrisiarum Williamson, 1905	S		O		O							O	O			O							
Crepidula perforans (Valenciennes, 1846)	W					O	O				O	O	O								O		
Crepipatella lingulata Gould, 1846	W	O	O		O	O			O	O	O	O	●				O		O	●	O		O
Cymakra gracilior (Tryon, 1884)	T	O									O												
Cypraea spadicea Swainson, 1823	S		O				O													O			
Cysticus politulus (Dall, 1919)	S																				O		O
Dendropoma lituella (Morch, 1861)	W												●	●	O	●		●	O	●	●	●	●
Dendropoma rastrum (Morch, 1861)	W												●					●	O		●		●
Diaulula sandiegensis (Cooper, 1862)	W												O				O						

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Dirona albolineata Cockerell & Eliot, 1905	N												O										
Discurria insessa (Hinds, 1842)	W	O	O	O		O	O			O	O	O		O			O	O					
Doriopsilla albopunctata (Cooper, 1863)	W										O		O		O		O		O				O
Epitonium tinctum (Carpenter, 1864)	W	●	●	●	O	O	O	O		O	O	●	●	O	●	●	●	O	O	●	O	O	O
Erato columbella Menke, 1847	S																						
Fissurella volcano Reeve, 1849	W		O	●	●	●	●	●		O	●	O	●	●	●	●	●	●	●	●	O	●	●
Flabellinopsis iodinea (Cooper, 1863)	N		O														O						
Fusinus luteopictus (Dall, 1877)	T																				O		O
Haliotis cracherodii Leach, 1814	W	O	O		O	O	O	O	O	O	O	O	O	O		O	●	●		O	O	●	O
Haliotis sp. (juvenile)					O	O						O	●			O		O	●	O	O		
Haminoea virescens (Sowerby, 1833)	W		O		O	O							O			O				O	O		
Hermissenda crassicornis (Eschscholtz, 1831)	W	O				O			O	O							O				O	O	
Hipponix cranioides Carpenter, 1864	W				O	O		O					O	O		●			O	●	O	O	O
Hipponix tumens Carpenter, 1864	W												O								O		O
Homalopoma baculum (Carpenter, 1864)	T				●	O						●	O			●		O	O	●	O	O	
Homalopoma luridum (Dall, 1885)	N				●	●	O				O	O	O	O		O		O	O	●	O		O
Homalopoma paucicostatum (Dall, 1871)	T																	O					
Hopkinsia rosacea MacFarland, 1905	N										O			O			O	O					
Iselica ovoidea (Gould, 1853)	W																				O		
Lacuna marmorata Dall, 1919	N	●	●	●	O	O				O	O						O						O

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Lacuna unifasciata Carpenter, 1857	S	●	●	●	O	O	O	O	O	O	O		O	O		●	O		O				
Lirularia succincta (Carpenter, 1864)	N												O										
Littorina keenae Rosewater, 1978	W	●	O	●	●	O	●	●	●	●	●	●	●	●	●	●	●	O	●	O	●	●	●
Littorina scutulata Gould, 1849	W	●	O	●	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●	O	●	●	●
Lottia asmi (Middendorff, 1847)	W	O	O			O	O			O	O						O	O			O		
Lottia conus (Test, 1945)	S		●	●	●	●	●	●					O						O	O	●	O	O
Lottia digitalis (Rathke, 1833)	W	●	O	●	●	O	●	●	●	●	●	O	●	●	●		●	●	●	●	●	O	O
Lottia gigantea Sowerby, 1834	W	O	O	●	O	O	O	●	O	●	●	O	O	O	●		●	●	●	O	O	O	O
Lottia limatula (Carpenter, 1864)	W	O	O	●	●	●	●	O	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●
Lottia ochracea (Dall, 1871)	W	O								O	O			O			O	O					
Lottia pelta (Rathke, 1833)	N	●	O	●	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Lottia strigatella (Carpenter, 1864)	W	O	●	●	●	●	●	●		O	●	●	●	●	●	●	●	O	●	●	●	●	●
Macclintockia scabra (Gould, 1846)	W	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Macron lividus (A. Adams, 1855)	S					O	O																O
Maxwellia gemma (Sowerby, 1879)	S																		O		O		
Megathura crenulata (Sowerby, 1825)	S				O	O																	O
Mitra idae Melville, 1893	W						O	O			O	O	O						O		O	O	
Mitrella aurantiaca (Dall, 1871)	W																				O		O
Mitromorpha carpenteri Glibert, 1954	S																		O	O	O		

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Nassarina pencillata (Carpenter, 1864)	S	O	O		O					O							O			O	O		
Navanax inermis (Cooper, 1862)	S																			O			O
Norrisia norrisi (Sowerby, 1838)	S		O		O	O	O				O	O	O			O	O	O	O	O	O	●	O
Nucella canaliculata (Duclos, 1832)	N	O																					
Nucella emarginata (Deshayes, 1839)	N	●	O	●			O	O	O	●	●	●	O	O	O	O	O	●			O		
Ocenebra atropurpurea Carpenter, 1865	N											O	O							O	O		O
Ocenebra circumtexta Stearns, 1871	W	O			O	O	O			O	O	●	●	●	O	●	O	●	●	●	●	O	O
Ocenebra foveolata (Hinds, 1844)	S				O																	O	
Ocenebra gracillima Stearns, 1871	T		O																O	O		O	O
Ocenebra interfossa Carpenter, 1864	N				O						O		O								O		
Ocenebra spp.												O											
Odostomia eucosmia Dall and Bartsch, 1909	S	O																		O			
Odostomia nota Dall and Bartsch, 1909	T	O	O	O				O															
Odostomia sp.			O																				
Olivella biplicata (Sowerby, 1825)	W		O	O							O												
Opalia funiculata (Carpenter, 1864)	S	O	O	O	O	O	O	O		O	O	O	O	O	O		O	O	O	O		O	
Parviturbo acuticostatus (Carpenter, 1864)	S																						O
Petaloconchus montereyensis Dall, 1919	T				O								●	●		●		O	●	●	●	●	●
Pseudomelatoma penicillata (Carpenter, 1864)	S	O	O									O	O				O						
Roperia poulsoni (Carpenter, 1864)	S		O																				

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Rostanga pulchra MacFarland, 1905	W										O		O	O									
Seila montereyensis (Bartsch, 1907)	S		O		O		O				O		O	O			O		O	O	O		
Serpulorbis squamigerus (Carpenter, 1857)	S		●		●	●	●				O	●	●	●	●	●	O	●	O	●	●	●	●
Siphonaria brannani (Stearns, 1873)	T								●										●				
Spurilla oliviae (MacFarland, 1966)	N													O		O							
Tectura fenestrata (Reeve, 1855)	N	O	O								O						O						
Tectura paleacea (Gould, 1853)	N	O	●	O			O				O				O		O						O
Tectura scutum (Rathke, 1833)	N	O								O	O						O	O					
Tegula aureotincta (Forbes, 1852)	S					O															O		
Tegula eiseni Jordan, 1936	S				O	O	O														O		
Tegula funebralis (A. Adams, 1855)	W	●	●	●	●	●	●	O	●	●	●	●	O	O			●	O		O	O		O
Tegula gallina (Forbes, 1852)	S				O	O	●						O							●		O	
Tenaturris janira (Dall, 1919)	T																					O	
Tricolia compta (Gould, 1855)	T		O																				
Tricolia pulloides (Carpenter, 1865)	W	O	●		O		O			O	O		O				O				O	O	●
Tricolia rubrilineata (Strong, 1928)	T										O				●								
Trimusculus reticulatus (Sowerby, 1835)	W		O			O				O				O				O				O	
Trinchesia sp.																	O						
Triphora catalinensis Bartsch, 1907	T	O			O	O					O											O	O
Triphora pedroana Bartsch, 1907	T		O		O	O					O			O		O	O		O	O	O	O	

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Gastropoda (Cont.)																							
Turbonilla kelseyi Dall & Bartsch, 1909	S	O	O	O		O				O	O												
Turbonilla tenuicula (Gould, 1853)	S		O																				
Tylodina fungina (Gabb, 1865)	S																				O		
Volvarina taeniolata Morch, 1860	S																				O		
Williamia peltoides (Carpenter, 1864)	W	O	O							O			O				O					O	
MOLLUSCA: Bivalvia																							
Brachidontes adamsianus (Dunker, 1857)	S	●			O	O	●	●	●	●	●	●	●	●	●	●	●	O	●	●	●	●	●
Chama arcana Bernard, 1976	W		O			O				O	O	●	●	O	O		O		●	●	●		
Clamys hastata hastata (Sowerby, 1842)	N												O										
Cryptomya californica (Conrad, 1837)	W																				O		
Glans subquadrata (Carpenter, 1864)	N	O	O		O	O						O	O						O	●	O	O	
Hiatella arctica (Linnaeus, 1767)	W	O						O	O	O	O		O	O	O		O		O				
Hinnites giganteus (Gray, 1825)	W	O											O						O				
Lasaea subviridis Dall, 1899	N	O								O	O		O				O		O				
Modiolus capax (Conrad, 1837)	S				O	O					O								O		O		
Modiolus carpenteri Soot-Ryen, 1963	T	O							O	O	O		O				O	O		O			O
Modiolus rectus (Conrad, 1837)	W	O																					
Mytilus californianus Conrad, 1837	W	●	●	●	●	O	●	●	●	●	●	●	●	●	●		●	●	●	●	●	O	●
Mytilus edulis Linnaeus, 1758	W	O	O	●	●	O	O	●	O	O	O	●	●	●	●				O	●	O	O	O

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Bivalvaa (Cont.)																							
Ostrea lurida Carpenter, 1864	W																			O			
Philobrya setosa (Carpenter, 1864)	W					O							O							O	O		
Prototbaca staminea (Conrad, 1837)	W				O																		O
Pseudochama exogyra (Conrad, 1837)	W		O		O							●	●							O	O		
Semele rupicola Dall, 1915	S										O												
Septifer bifurcatus (Conrad, 1837)	W	●	●	●	O	O	●	●	●	●	●	●	●	●	●	●	●	O	●		●	●	●
MOLLUSCA: Polyplacophora																			O				
Callistochiton crassicostatus Pilsbry, 1893	S												O						O				
Chaetopleura gemma Dall, 1879	W																						
Cryptochiton stelleri (Middendorff, 1846)	N	O																					
Cyanoplax dentiens (Gould, 1846)	N	O				O			O	O	O		O				O				O	O	O
Cyanoplax hartwegii (Carpenter, 1855)	S	O	O	O	●	●	●	●	O	O	O	●	●	●	●	●	●	O	●	●	●	●	●
Ischnochiton regularis (Carpenter, 1855)	N		O																				
Lepidochitona keepiana Berry, 1948	T		O			O	O														O		
Lepidozona cooperi (Dall, 1879)	N																				O		O
Lepidozona pectinulata Carpenter in Pilsbry, 1893	S					O															O		O
Mopalia acuta (Carpenter, 1855)	T										O										O		
Mopalia ciliata (Sowerby, 1840)	W	O	O		O	O			O		O	O	O				O						
Mopalia hindsii (Reeve, 1847)	N	O																					

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
MOLLUSCA: Polyplacophora (Cont.)																							
Mopalia lignosa (Gould, 1846)	N									O													
Mopalia muscosa (Gould, 1846)	W	O	●	O	●	O	O	O	O	O	O	O	O		O	O	●	O	O	O	O	O	O
Nuttallina californica (Reeve, 1847)	N	O		●		●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Nuttallina fluxa (Carpenter, 1864)	S	O	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Nuttallina sp.																		O					
Stenoplax conspicua (Pilsbry, 1892)	S					O							O										
Stenoplax heathiana Berry, 1946	N																				O		
Tonicella lineata (Wood, 1815)	N										O		O					O					
ECHINODERMATA: Asteroidea																							
Astrometis sertulifera (Xantus, 1860)	S					O													O		O		O
Dermasterias imbricata Grube, 1857	N		O																				
Henricia leviuscula (Stimpson, 1857)	W	O									O		O					O	O		O		
Leptasterias hexactis (Stimpson, 1862)	N								O		O		●					O	O				
Leptasterias pusilla (Fisher, 1930)	T		O							O	O		●										
Linckia columbiae Gray, 1840	S																				O		
Orthasterias koehleri (de Loriol, 1897)	N		O																				
Patiria miniata (Brandt, 1835)	N	O	O		O	O	O			O	O		O	O				O			O	O		
Pisaster giganteus (Stimpson, 1857)	N	O	O		O					O	O		O		O	O	O	O	O				
Pisaster ochraceus (Brandt, 1835)	N	O	O	O	O	O	O		O	O	O		O	O	O		O	O	O				
Pycnopodia helianthoides (Brandt, 1835)	N	O																					

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
ECHINODERMATA: Echinoidea																							
Strongylocentrotus franciscanus (A. Agassiz, 1863)	W					O												O			O		
Strongylocentrotus purpuratus (Stimpson, 1857)	W	O		O	●	●	O	●	O	O	●	O	●	●		O	O	●	●	O	●	O	O
ECHINODERMATA: Holothuroidea																							
Pseudocnus californicus (Semper, 1868)	S																	●	O				
Pachythone lugubris (Deichmann, 1939)	S																O						
Eupentacta quinquesemita (Selenka, 1867)	N												O										
ECTOPROCTA: Bryozoa																							
Bugula neritina (Linnaeus, 1758)	S		O			O						O											
Cellaria sp.												O											
Crisia occidentalis Trask, 1857	W	O																		O			
Crisia serrulata (Gabb & Horn, 1862)	S																			O			
Crisia sp.												O											
Diaperoecia californica (d'Orbigny, 1852)	W																			O			
Filicrisia franciscana (Robertson, 1910)	N									O													
Filicrisia sp.																				O			
Flustrellidra corniculata (Smitt, 1871)	N	O																					
Hippodiplosia insculpta (Hincks, 1882)	W					O																	
Lichenopora sp.																				O			
Membranipora tuberculata (Bosc, 18002)	S		O	O		O						O											
Tricellaria spp.		O	O										O		O	O	O	O		O	O		O

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI –CP	SMI –CH	SRO	SCR –PH	SCR –WA	ANA –CR	ANA –SF	ANA –FC	SNI –DH	SNI –WP	SBA	SCA –CH	SCA FC	SCL –NW	SCL –WC
ENTOPROCTA																							
Barentsia discreta (Busk, 1886)	?														O								
UROCHORDATA: Ascidiacea																							
Aplidium arenatum (Van Name, 1945)	N			O																			
Aplidium californicum (Ritter & Forsyth, 1917)	W	O									O						O		O		O	O	
Aplidium solidum (Ritter & Forsyth, 1917)	N										O												
Archidistoma diaphanes (Ritter & Forsyth, 1917)	N																	O					
Archidistoma psammion (Ritter & Forsyth, 1917)	N	O	O	O			O		O	O	O		O		O		O	O	O	O			
Archidistoma ritteri Van Name, 1945	N	O				O			O	O							O	O	O		O		O
Archidistoma spp.						O			O									O			O		
Didemnum carnulentum (Ritter & Forsyth, 1917)	W		O	O		O	O	O						O			O	O	O	O	O	O	
Didemnum sp.										O													
Diplosoma macdonaldi Herdman, 1886	T								O	O									O				
Distaplia occidentalis Bancroft, 1899	N	O								O	O		O				O					O	
Distaplia spp.										O			O										
Euherdmania claviformis (Ritter, 1903)	T		O	O			O			O	O				O		O			O	O		
Metandrocarpa taylori Huntsman, 1912	N																	O					
Molgula regularis Ritter, 1907	?	O	O								O												
Molgula verrucifera Ritter & Forsyth, 1917	T						O	O	O						O				O	O			
Polyclinum planum (Ritter & Forsyth, 1917)	N	O																					
Polyclinum sp.																							

Phylum: Class	Range	GP	COP	MAL	WP	CDM	DP	OB	SMI -CP	SMI -CH	SRO	SCR -PH	SCR -WA	ANA -CR	ANA -SF	ANA -FC	SNI -DH	SNI -WP	SBA	SCA -CH	SCA FC	SCL -NW	SCL -WC
UROCHORDATA: Ascidiacea (Cont.)																							
Ritterella aequalisiphonis (Ritter & Forsyth, 1917)	N	O	O	O					O	O													
Ritterella pulchra (Ritter, 1901)	N	O																					
Styela montereyensis (Dall, 1872)	N		O								O												
Styela plicata (LeSueur, 1823)	T		O			O																	
Styela truncata Ritter, 1901	N											O											
Styela spp.			O				O								O								
Synoicum parfustis (Ritter & Forsyth, 1917)	N																		O				

Dynamics and Distribution of Black Abalone Populations at San Nicolas Island, California

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Abstract — Dense populations of black abalones (*Haliotis cracherodii* Leach) were monitored in permanent intertidal plots at nine sites on San Nicolas Island from 1981 through 1990. Densities were essentially constant at all four sites along the north shore of the island throughout the study period. Densities at five sites along the south shore were more variable, possibly reflecting asynchronous variation in recruitment, mortality resulting from wave disturbance, and removal by people. Temporal variation of abalone densities apparently was not influenced by sea otters or abalone withering syndrome during this study. Abalones were strongly aggregated in space. Highest densities occurred in areas of irregular substrata, apparently as a result of preference for crevices and vertical faces. The locations of dense patches were persistent in time.

Introduction

The distribution, abundance, and dynamics of abalone populations typically are difficult to determine. Abalone populations most often occur in shallow nearshore waters, distributed in patches across large tracts of rocky substrata. Under such circumstances direct measurements of population size and variation are difficult, requiring costly, labor-intensive diving surveys of large areas (Tegner 1989). Black abalones (*Haliotis cracherodii* Leach) are a notable exception to the pattern because they occur primarily in rocky intertidal habitats (Cox 1962; Morris *et al.* 1980).

Black abalones occur along the western shore of North America from southern Oregon, USA, to Cabo San Lucas, Baja California Sur, Mexico (Morris *et al.* 1980; Tegner 1989). In recent history they have been particularly abundant in the California Islands, especially San Miguel, Santa Rosa, Santa Cruz, San Nicolas, and San Clemente (Littler 1980; Kanter 1980; Douros 1985, 1987; Tissot 1990; United States National Park Service, unpubl. data).

Sea otters (*Enhydra lutris* [L.]) were reintroduced to San Nicolas Island in August 1987 as part of the recovery program for sea otters in California (United States Fish and Wildlife Service 1987; Rathbun *et al.* 1990). Sea otters apparently were abundant at the island prior to the unrestrained fur harvests of the 18th- and 19th-centuries (Ellison 1937; Ogden 1941), but have been locally extinct at San Nicolas during the 20th-century. At the time of this writing (August 1991) the success of the reintroduction program is promising but uncertain. Sea otters are widely known for their abilities as predators of abalones. Off central California, subtidal populations of abalones are confined largely to cryptic microhabitats which afford refuge from foraging sea otters (Lowry and Pearse 1973; Cooper *et al.* 1977; Pollard 1991). Established sea otter populations and commercially harvestable stocks of abalones are generally regarded as mutually exclusive in space (Estes & VanBlaricom 1985; Tegner 1989). Thus, the reintroduction of sea otters to San Nicolas Island likely will alter patterns of abundance and distribution in the four primarily subtidal species which occur at the Island: green abalone (*Haliotis fulgens* Philippi), pink abalone (*H. corrugata* Wood), red abalone (*H. rufescens* Swainson), and white abalone (*H. sorenseni* Bartsch). The possible effects of predation by sea otters on black abalone populations are more difficult to predict. Black abalones have remained relatively abundant in