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Artificial armored shorelines: sites for open-coast species in a southern California bay

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Abstract Artificial hard substrates have been used to stabilize naturally soft bay shorelines for centuries. Despite the loss of over half of the natural shoreline in many bays, little attention has been paid to the communities inhabiting armored shorelines and to the ecological implications of armoring. The goal of the present study was to examine factors affecting spatial and temporal variation of intertidal, hard-substrate biota (emergent species and fishes), with emphases on the influence of exposure, distance from the open ocean, and similarity to open-coast, hard-substrate communities. We examined community composition at eight San Diego Bay (California, USA) sites (an exposed and a protected site at four bay locations) in June and November 2000 and two open-coast sites in August 2000. At all bay sites, the shore was armored with granite boulders, a form of shoreline stabilization referred to as “riprap.” Community structure was more variable spatially than temporally on the scales we studied, affected more by distance from the bay mouth and exposure to wave energy than by differences between June and November. Exposed sites near the bay mouth were more similar to natural open-coast sites, sharing about 45% of their species, than protected sites and sites farther from the mouth, which shared as few as 8%. Species richness was generally higher in exposed than protected bay sites.

Species tended to occur higher in the intertidal zone at exposed than protected sites, and higher in November, when sea level was higher, than in June. Such results will be useful to shoreline managers who examine the ecological implications of hardening long stretches of coastline and may suggest ways to incorporate artificial structures into ecosystems in a more meaningful way.

Introduction

Bay environments play a vital role in the economic, social, and political development of a region. Such development often involves modification or “armoring” of soft shorelines, defined as the placement of bulkhead, seawalls, and riprap (mounds or walls of stones) in areas previously lacking hard substrate. These structures can extend from the subtidal zone, through the intertidal zone, and into purely terrestrial realms, often replacing more than half of a bay’s natural shoreline. In San Diego Bay, California, for example, 74% (73.1 km) of the total shoreline is now armored with artificial hard substrate (USDON/SWDIV and SDUPD 2000), a process that began in the 1800s when southern California bays began to be developed to support human activities (Chapman 1963).

Armored structures are usually designed with shoreline support as the primary goal. With the exception of riprap installed to restore fish habitat in some freshwater areas (e.g. Waidbacher 1989; Binns and Remmick 1994), little consideration is generally paid to the ecological consequences of armoring. As a result, ecological roles and characteristics of armor biota, especially estuarine and marine, are poorly documented. Most relevant reports focus on subtidal communities only and ignore the intertidal component of these habitats, which may serve as artificial but significant links between terrestrial, estuarine, and coastal communities. Most available intertidal information is restricted to environmental impact assessments (e.g. MEC Analytical Systems 1997).

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The goal of the present study was to identify the factors influencing the dominant types of organisms using intertidal riprap in San Diego Bay.

Certain characteristics of artificial hard substrate in the intertidal zone of a bay suggest that its flora and fauna would differ from natural, open-coast, rocky-intertidal communities. First, armor design does not currently include substantial water-retaining tidepools. Such pools can provide a refuge from desiccation, and they host different suites of species than emergent intertidal rock (Wilson et al. 1992; Metaxas and Scheibling 1993). Second, the hard material used to construct riprap (typically granite) often differs from soft, open-coast rock in southern California (sandstones, Tway 1991). Rock type can influence settlement, abundance, feeding, and boring success of intertidal organisms (Raimondi 1988; James and Underwood 1994; Allouc et al. 1996). Third, bay environments generally have reduced flow speeds relative to the open coast, and abundances of many species on the open coast are linked to exposure level (Leonard et al. 1998). Fourth, colonization history differs between artificial structures and natural rocky habitat. Artificial structures present large areas of open space to populations, many of which are space limited. Although clearing of space on the open coast by disturbance is a natural process, generally new patches of open space are relatively small and sources of colonizers close by. Even after initial colonization, maintenance of intertidal, hard-substrate communities in bays may differ from that on the open coast due to location and composition of the larval pool. Settlers on bay intertidal riprap may have a greater component of bay-derived larvae from bay species. Open-coast, natural intertidal rock may be settled by a greater proportion of coastal larvae.

Several characteristics of intertidal bay riprap, however, lead to the expectation that its flora and fauna might have more in common with natural, open-coast, rocky-intertidal sites than with soft bay substrates. Although bays in San Diego at one time contained small amounts of natural intertidal hard substrate (Orcutt and Dall 1885), the general characteristics of riprap (hard rock) are much more similar to natural open-coast sites than to the average soft-bottom, often vegetated, natural bay substrate. In addition, many invertebrate and fish species inhabiting natural open-coast shores are also found inside southern California bays (Miller and Lea 1972; Pondella 1998), and these species may prefer the hard substrate of riprap to natural soft-bottom bay habitat.

The main goals of the present study were to: (1) characterize the composition and abundance of fishes, emergent invertebrates, and algae at intertidal riprap sites in San Diego Bay; (2) determine whether species abundance and vertical zonation differed as a function of exposure, location within the bay, and distance from the bay mouth; (3) determine whether species abundance and zonation differed between June and November; and (4) compare community composition and intertidal height of San Diego Bay riprap sites to open-coast,

rocky-intertidal communities. We provide the only published report of armored intertidal shoreline biota for southern California. The main hypotheses of this study were that intertidal bay riprap communities contain at least some elements of natural rocky-coast communities, and that the location of riprap within San Diego Bay and the degree of exposure correlate with the extent to which these elements develop and persist. We predicted that sites closest to the mouth (because of their proximity to the open coast) and sites of higher exposure (because physically they more closely resemble natural, open-coast, rocky sites) would be ecologically most similar to open-coast, rocky sites. We also predicted that the intertidal height of individual species would respond to temporal and spatial environmental variation. Higher average intertidal height was expected in energetic areas characterized by more splash and, in the fall, when seasonal sea level is highest (Davis 2000).

Materials and methods

Flora and fauna of eight riprap seawall sites in San Diego Bay and two open-coast sites in San Diego were measured in June (riprap) and August (open coast) 2000 (Fig. 1). In November 2000, the eight bay riprap sites were sampled again to address temporal changes in biota. Riprap sites included paired "exposed" and "protected" sites at four locations in the bay (Fig. 1). "Exposed" sites had direct water access to the mouth of the bay, and "protected" sites had a land mass, in all cases a narrow man-made peninsula, sheltering the site from the open bay. The four bay locations were Shelter Island (SI), Harbor Island (HI), Embarcadero Park (EP), and Chula Vista (CV), which are 4.5, 7, 10, and 20 km from the bay mouth, respectively. All eight sites are constructed of similar gray-granite boulders with a median diameter of about 0.5–1 m, have similar slopes of about 150°, and have been in place for >25 years. Temperature regimes and tidal influence, however, as

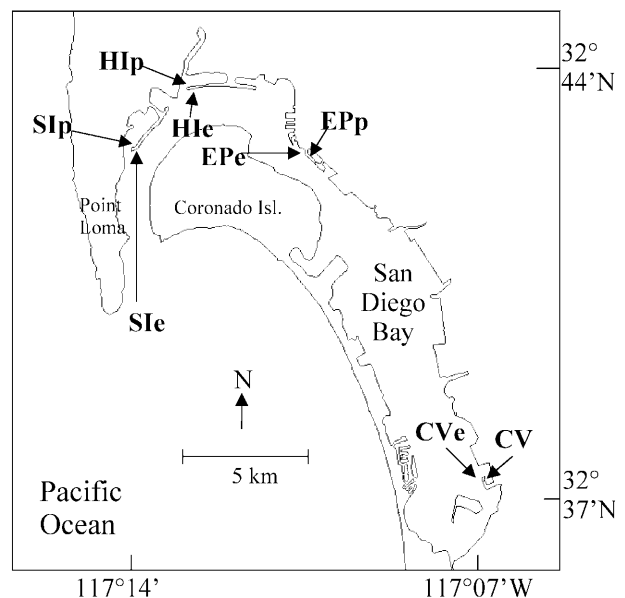


Fig. 1. San Diego Bay. Location of eight riprap study sites (location names: *SI* Shelter Island; *HI* Harbor Island; *EP* Embarcadero Park; *CV* Chula Vista; *e* exposed; *p* protected)

measured using subtidal temperature loggers (Stowaway Tidbits) in October 2000, differed among sites. Waters were colder at stations nearer to the mouth of the bay: temperatures ranged from 16°C to 19°C at SI and from 19°C to 20°C at CV. Sites towards the back of the bay experienced less temperature variation, both diel and semidiurnal, than sites near the mouth. Strong semidiurnal temperature signals measured at exposed mouth sites probably reflect the tidal influence of open-coast water. In summer, salinity is higher in the back of the bay than near the mouth, though in winter this trend reverses (Largier et al. 1997).

The open-coast sites were chosen to include the two predominate types of intertidal rock in San Diego: smooth and conglomerate sandstone. Ocean Beach (OB; 117°W; 32°45'N) is located in the smooth sandstone of Sunset Cliffs, 10 km north of the San Diego Bay mouth. False Point (FP; 117°W; 32°49'N), the conglomerate sandstone site, is located in southern La Jolla, 18 km north of the bay mouth. Both have more gradual slopes (about 5°) and higher wave exposure than the riprap sites, although the two open-coast sites differ in exposure. FP, facing southwest, is relatively protected by the La Jolla headland. OB faces west and is fully exposed.

Emergent-organism surveys

Surveys were designed to quantify abundance and zonation of emergent intertidal invertebrates and algae at the eight riprap sites and to compare them to the two coastal sites. Sampling was conducted during daylight hours when low tides were <0.0 cm mean lower low water (MLLW) (Table 1). At each site, four transect lines were laid perpendicular to the shoreline from the top of the riprap seawall or intertidal bench to the water level at low tide (below MLLW). Transect lines were spaced 2 m apart along the shore.

Invertebrates and algae were measured in 0.25 m², 25-point quadrats (Foster et al. 1991), placed at 0.5 m intervals along the transect lines. The lowest quadrat on each transect line was located at the low tide level of the sampling day (Table 1). Subsequent quadrats were placed on the flattest, most visible surface containing a point measured 0.5 m up from the previous quadrat. For example, if the point fell on the edge of a boulder face, the quadrat would be centered on the boulder face. Crevices were not sampled unless shallow and visible, and rocks were not turned over. Because the two coastal sites had more gradual slopes than the riprap sites, many more quadrats would have fit per transect line using 0.5 m spacing. Due to time constraints imposed by the duration of low tide, quadrat spacing at the coastal sites was 1 m. The number of quadrats per transect ranged from 8 to 11 at the riprap sites and from 13 to 16 at the open-coast sites.

Invertebrates and algae falling under each of 25 regularly spaced grid points within the quadrats were identified to the lowest possible taxonomic level. When a quadrat point fell over a primary space user and an epibiont, for example coralline algae on a mussel, both organisms were listed. Only those species that could be identified

with confidence to species level were analyzed as such. Species for which identification was uncertain were grouped into categories, for example "non-coralline red algae" and "bryozoans".

Intertidal height of each quadrat was measured relative to the low tide of the sampling day, which was identified using Harbor-master software. A graduated pole was placed vertically at the low water mark, a rope was stretched horizontally from the level of each quadrat to the pole, and a height reading was taken from the pole.

Emergent-organism data analysis

To test hypotheses pertaining to organism abundance patterns, percent cover of each species (or higher taxon) was calculated along each of the four transects at a site. To address the question of whether the four locations, two exposure levels, and two time periods had different abundances of a taxon, three-way analysis of variance (ANOVA) was used with location, exposure, and season as factors, and transects as replicates. Regression analysis was used to test for relationships between species abundance and distance from the bay mouth, with transects averaged to obtain site values. One-way ANOVA was used to test the hypothesis that species abundance at the four San Diego Bay locations in June was different than species abundance at the two open-coast sites in August. For this final analysis, percent cover was averaged between the exposed and protected sites at a location to obtain a location average. All percent cover data were arcsine-square root transformed prior to statistical analyses to meet assumptions of normality and homoscedasticity.

To address vertical zonation patterns, we calculated average intertidal height of individuals belonging to each abundant taxon along a transect. *T*-tests were used to test for differences in height of a taxon between exposed and protected sites at a location, with each transect's height value as the replicate. Only those taxa occurring along two or more transects at both exposed and protected sites at a location were compared. Each location was analyzed separately, because different species occurred at different locations within the bay. In order to keep the height range consistent at both the exposed and protected sites (Table 1), the four lowest quadrats at the exposed Harbor Island site in June (at -45 cm MLLW) were excluded from analysis.

Regression analysis was used to test for relationships between intertidal height and distance from the bay mouth only for taxa occurring either at all four exposed bay sites or at all four protected sites. Differences in height of taxa between San Diego Bay ($n=2, 3,$ or 4) and the open coast ($n=2$) were examined using *t*-tests. Only taxa that occurred in two or more transects at both open-coast sites and either two or more exposed sites or two or more protected sites were used. Ideally, a nested-design ANOVA would have been used with bay versus open coast as the main factor, site as the subgroup, and transect as the replicate, but subgroup replication was insufficient.

Table 1. Sampling dates (summer and fall 2000) and intertidal height ranges (*low* and *high*) of quadrats at the two open-coast sites (FP False Point; OB Ocean Beach) and the eight San Diego riprap

sites (SI Shelter Island; HI Harbor Island; EP Embarcadero Park; CV Chula Vista; Exp exposed riprap; Pro protected riprap). The direction each rocky shore or riprap wall faces is also listed

Location	Site	Direction	Summer sampling (cm MLLW)			Fall sampling (cm MLLW)		
			Date	Low	High	Date	Low	High
FP	Coast	SW	2 Aug	-33	182			
OB	Coast	W	1 Aug	-37	168			
SI	Exp	S	4 Jun	-54	183	11 Nov	-22	192
	Pro	NW	5 Jun	-48	171	11 Nov	-22	188
HI	Exp	S	6 Jun	-45	162	13 Nov	-30	201
	Pro	N	9 Jun	-9	165	13 Nov	-30	165
EP	Exp	W	8 Jun	-22	155	12 Nov	-30	204
	Pro	N	8 Jun	-22	171	12 Nov	-30	207
CV	Exp	N	7 Jun	-33	171	10 Nov	-3	185
	Pro	E	7 Jun	-33	149	10 Nov	-3	192

To test the hypothesis that intertidal height of a species was higher in November than June (due to the seasonal increase in sea level, Davis 2000), we used ANOVAs. Each taxon was only analyzed if it occurred in two or more transects at a site in both June and November. For taxa that occurred in sufficient abundance at only one of the eight sites, *t*-tests were used with time of year as the factor and height per transect as the replicate. If a species occurred in sufficient abundance at more than one site, two-way ANOVAs were used with site and time of year as factors. We were interested only in the outcome of the time of year factor and used two-way ANOVAs to account for and remove that variability attributable to site. To create time-of-year uniformity in height ranges (see Table 1), only quadrats higher than 22 cm and 3 cm below MLLW were considered in intra-annual comparisons at SI and CV, respectively.

Fish surveys

Fish abundance and composition were measured at the eight riprap sites, but not at the open-coast sites, by snorkeling at high tide in July 2000. Alongshore, 50-m long transects were established parallel to the riprap wall. Transects extended about 2 m seaward from the intersection of the waterline with the riprap seawall. Surveys were conducted when the tide level was 90–120 cm above MLLW by the same two snorkelers at all eight sites. The two snorkelers started at opposite ends of the 50 m transect, met at the half-way point, then swam back along the transect to the starting point. All fishes were identified to species.

Because transect width was constant, fish abundance was calculated per meter of transect length. Data from the two passes and from the two snorkelers were not used as replicates, as individual fish may have been counted twice, but were combined and standardized to 100 m. *T*-tests were used to test the null hypothesis that

exposed and protected sites within each location had similar species abundance and density. Regression analysis was used to test relationships between species abundance and distance from the mouth.

Community analysis

General comparisons of community composition among the eight riprap and two open-coast sites were made using principal component analysis. Three separate sets of principal components (PCs) were calculated based on: (1) emergent-species data at bay and open-coast sites in June and August, respectively; (2) emergent-species data at bay sites in November; and (3) fish data at bay sites in July. PCs were calculated for each site as linear combinations of the species percent cover data (emergent species) or species abundance (fishes). Only the first two PCs in each analysis, which together explained >40% of the variance in species percent cover data, were used to identify groupings of sites.

Values (according to the Bray–Curtis similarity index) for emergent species and fishes were calculated between sites based on percent cover data (arcsine–square root transformed). Regression analysis was used to test the hypothesis that similarity of a site to the open coast was negatively correlated with distance from the mouth of San Diego Bay. ANOVA was used to test the hypothesis that exposure level was more important in driving similarity between sites than distance from the mouth.

Results

At least 34 invertebrate, 14 algal, and 1 seagrass species were recorded in the intertidal zone of San Diego Bay riprap (Tables 2, 3). Because some taxa could not be

Table 2. Percent cover of emergent intertidal flora at two open-coast sites in San Diego (FP False Point; OB Ocean Beach) and eight riprap sites in San Diego Bay; riprap sites included paired protected (*Pro*) and exposed (*Exp*) sites in four bay locations (SI Shelter Island; HI Harbor Island; EP Embarcadero Park; CV Chula Vista), listed in order of increasing distance from the bay mouth. Flora are classified as red algae (*R*), green algae (*G*), brown

algae (*B*), or seagrass (*S*), and are listed in approximate order of occurrence from open coast to the back of the bay. Lower-case letters correspond to categories of percent cover of each species (*a*=20–30%, *b*=10–20%, *c*=5–10%, *d*=1–5%, *e*=present but <1%, – or blank=0%). The first letter in each bay site column represents percent cover in June 2000; the second letter, November 2000. Open-coast sites were sampled only in August 2000

	FP	OB	SI		HI		EP		CV	
			Exp	Pro	Exp	Pro	Exp	Pro	Exp	Pro
Open coast only										
<i>Endocladia muricata</i> (B)	e									
<i>Zonaria</i> spp. (B)	d									
<i>Pelvetia fastigiata</i> (B)	d									
<i>Nienburgia andersoniana</i> (R)	d									
<i>Ceramium</i> spp. (R)	e	e								
<i>Phyllospadix</i> spp. (S)	d	c								
Bay										
<i>Plocanium cartilagineum</i> (R)	e	e	e, –							
<i>Egregia menziesii</i> (B)	e	d	e, –							
<i>Dictyota binghamiae</i> (B)	d	e	–, e	d, d		–, e				
<i>Corallina</i> spp. (R)	d	b	b, c	e, d	d, c		d, –			
<i>Mazzaella</i> spp. (R)	e	e	e, –		e, –		e, e			
Gelidiaceae (R)	d	d	e, e		–, d		e, e			
<i>Gigartina</i> spp. (R)	e		e, –		e, e		e, –			
<i>Prionitis filiformis</i> (R)		e			–, e					
<i>Laurencia</i> spp. (R)	d	b					–, e			
<i>Colpomenia sinuosa</i> (B)		e	e, d	e, –	d, d		d, e	d, e		
<i>Sargassum</i> spp. (B)	d		d, d	d, –	e, d	–, e	d, c		d, –	d, –
<i>Ulva</i> spp. (G)	c	c	e, e		d, e		e, d		a, c	d, c
<i>Zostera marina</i> (S)									c, –	
<i>Polysiphonia</i> spp. (R)									e, –	e, e
<i>Enteromorpha</i> spp. (G)									c, –	b, c
Unidentified algae	d	d	e, e	e, d	c, c		d, d	e, –	d, b	d, c

Table 3. Percent cover of emergent intertidal fauna at two open-coast sites (August 2000) and eight San Diego Bay riprap sites (June and November 2000). Taxa are listed in approximate order of occurrence in the system, from open coast to the back of the bay.

Following each scientific name is an identifying common name or code (*B* bivalve; *BR* bryozoan; *C* barnacle; *G* non-limpet gastropod; *L* limpet; *S* sponge; *T* tunicate). See Table 2 for site abbreviations and percent cover codes

	FP	OB	SI		HI		EP		CV	
			Exp	Pro	Exp	Pro	Exp	Pro	Exp	Pro
Open coast only										
<i>Pagurus samuelis</i> (crab)	e									
<i>Tegula eiseni</i> (G)	e									
<i>Roperia poulsoni</i> (G)	e									
<i>Nucella emarginata</i> (G)	e									
<i>Tegula funebris</i> (G)	d	e								
<i>Pollicipes polymerus</i> (C)		e								
Bay										
<i>Fissurella volcano</i> (G)			e, e							
<i>Collisella digitalis</i> (L)	e	d	e, e	e, -	e, e					
<i>Littorina planaxis</i> (G)	e	e	-, e			e, -				
<i>Serpulorbis squamigerus</i> (G)		e		d, e	d, d	d, d	e, e			
<i>Littorina scutulata</i> (G)	d	d	d, e	e, e	e, -		e, -			
<i>Chthamalus fissus</i> (C)	b	d	b, a	d, c	b, d	d, d	d, d			
<i>Collisella scabra</i> (L)	d	d	e, d	-, e	e, e	e, -	d, d			
<i>Tetraclita rubescens</i> (C)		e	d, d		d, e	e, -	e, e			
<i>Nuttilina fluxa</i> (chiton)	e	e	e, -		-, e		e, e			
<i>Lottia gigantea</i> (L)		e	e, e		e, -		e, -			
<i>Pachygrapsus crassipes</i> (crab)	e	e	e, -				e, -			
<i>Collisella strigatella</i> (L)	e	e	-, e				d, -			
<i>Anthopleura</i> spp. (anemone)	e	e			e, -		-, e			
<i>Bulla gouldiana</i> (G)					e, -					
<i>Collisella limatula</i> (L)	d		e, e		e, d	-, e	d, d	e, e		
<i>Balanus glandula</i> (C)			d, d	e, e	d, d	e, e	d, d	d, d		
<i>Ostrea lurida</i> (B)		e	e, d	d, d	d, d	c, c	d, d	d, c	d, d	e, d
<i>Mytilus</i> spp. (B)		e	d, d	-, e	e, e	d, -	e, d	e, -	-, e	e, e
<i>Pseudochama exogyra</i> (B)			e, -	e, -	e, -	e, -	e, e	-, e	-, e	e, e
<i>Styela</i> spp. (T)			-, e	e, e	e, e	e, e	e, e	e, e	e, e	e, d
<i>Aplysina fistularis</i> (S)			-, d		d, d	-, d	-, c		-, c	e, d
Sponges-other			e, d		d, -	e, -	d, -	e, -	d, -	e, -
<i>Crepidula onyx</i> (G)				e, e		e, e		e, -	e, -	
Serpulid worms				-, d				-, e		e, e
<i>Watersipora</i> spp. (BR)				e, c		d	e, e	e, -	e, e	-, e
Bryozoans-other				-, e	e, e	-, e	e, e	e, e		-, e
<i>Leucetta</i> spp. (S)								-, e	e, -	-, e
<i>Botrylloides</i> spp. (T)								e, -		
<i>Musculista senhousia</i> (B)								-, e		
<i>Botryllus</i> spp. (T)						e, -		e, e	e, e	-, e
<i>Crucibulum spinosum</i> (G)						e, -	-, e	-, e	e, e	e, -
<i>Balanus amphitrite</i> (C)							d, -		b, b	b, c
Ophiuroids (brittle stars)									e, -	
Anemones-other								e, e	e, -	e, e

identified to species, this number is an underestimate of species richness. For example, macroalgae of the highly speciose *Pterocladia* and *Gelidium* genera were grouped into one category in this study. At least five genera of Bryozoa were grouped together.

A total of 22 species of fish were recorded during high-tide snorkeling surveys of the eight San Diego Bay intertidal riprap sites, and an additional four species were observed during non-survey times (Table 4). Only one fish, the California clingfish (*Gobiesox rhesodon*), was ever observed in the intertidal zone of a riprap seawall at low tide (a non-survey time). Probably due to its cryptic habitat, it was never recorded during snorkeling surveys.

These species lists (Tables 2, 3, 4) only reflect species measured using the two types of sampling surveys.

Several groups of species also observed at the sites but absent from surveys include: motile intertidal species that tended not to remain in quadrats during sampling (most crabs), species using only crevices or undersides of rocks (e.g. brittle stars, clingfish, octopus), relatively rare species (e.g. urchins, seastars), and those species too small to be identified using the quadrat method (e.g. amphipods, isopods, some algae).

Horizontal distribution within the bay

Intertidal emergent and fish species were not distributed uniformly among riprap sites in the bay. Some species occurred only near the bay mouth; others occurred only in the back. Some species occurred only at exposed sites;

Table 4. High-tide fish abundance in July 2000 at eight intertidal riprap sites at four locations in San Diego Bay (SI Shelter Island; HI Harbor Island; EP Embarcadero Park; CV Chula Vista), listed in order of increasing distance from the bay mouth); both protected (Pro) and exposed (Exp) sites at each location were sampled. Fish

species are listed in approximate order of those that occur near the mouth to those that occur in the back of the bay. Abundance of each species is calculated as the number per meter of transect length (transects were approximately 2 m wide). Species observed at a site but not recorded during transects are indicated with “x”

	Common name	SI		HI		EP		CV	
		Exp	Pro	Exp	Pro	Exp	Pro	Exp	Pro
<i>Hypsypops rubicundus</i>	Garibaldi	0.01	0.11						
<i>Seriphus politus</i>	Queenfish		x						
<i>Clinocottus analis</i>	Woolly sculpin	0.13	0.01	0.01					
<i>Paralabrax clathratus</i>	Kelp bass	x	x	x					
<i>Cymatogaster aggregata</i>	Shiner surfperch	0.02		0.04					
<i>Hypsoblennius gilberti</i>	Rockpool blenny	0.02		0.01					
<i>Hypsoblennius gentilis</i>	Bay blenny	0.01		0.01					
<i>Scorpaena guttata</i>	Spotted scorpionfish	0.01		0.01					
<i>Hypsoblennius jenkinsi</i>	Mussel blenny			x					
<i>Gobiesox rhesodon</i>	California clingfish		x		x				
<i>Gibbonsia elegans</i>	Spotted kelpfish	0.05		0.01		0.01			
<i>Girella nigricans</i>	Opaleye	1.31	0.09	0.06	0.22	0.04	0.30		
<i>Embiotosa jacksoni</i>	Black surfperch	0.12	0.20	0.03		0.01	0.04		
<i>Paralabrax nebulifer</i>	Barred sandbass			0.02			0.02		
<i>Heterostichus rostratus</i>	Giant kelpfish			0.01					
<i>Oxyjulis californica</i>	Senorita	x					0.02		
<i>Atherinops affinis</i>	Topsmelt	1.44	0.03	60.60	1.67	1.62	0.92	4.41	2.80
<i>Atherinopsis affinis</i>	Jacksmelt	0.01			0.28	0.97	0.38	0.17	0.28
<i>Urolophus halleri</i>	Round stingray		0.01				0.01	0.02	0.06
<i>Micrometrus minimus</i>	Dwarf surfperch					0.17			
<i>Paralabrax maculatofasciatus</i>	Spotted sand bass					0.01			
<i>Phanerodon furcatus</i>	White surfperch					0.18			
<i>Clevelandia ios</i>	Arrow goby				1.78		0.94	0.01	0.19
<i>Fundulus parvipinnis</i>	California killifish							0.57	1.15
<i>Umbrina roncadior</i>	Yellow croaker							0.01	
<i>Mugil cephalus</i>	Striped mullet								0.03

others, only at protected sites (Tables 2, 3, 4). In general, exposed sites were more speciose than protected sites (paired *t*-test, $t_4 = 3.09$, $P = 0.053$) (Fig. 2). Species richness decreased with increasing distance from the bay mouth at exposed sites (regression analysis, $n = 4$, $r^2 = 0.97$, $P = 0.016$), but not at protected sites ($r^2 = 0.01$, $P = 0.925$).

Most taxa (23 of 34 analyzed) differed significantly in percent cover both among locations (SI, HI, EP, and CV) and between exposure levels, with significant interaction between location and exposure (Table 5). Significant interaction terms indicate that differences between exposed and protected sites at each location

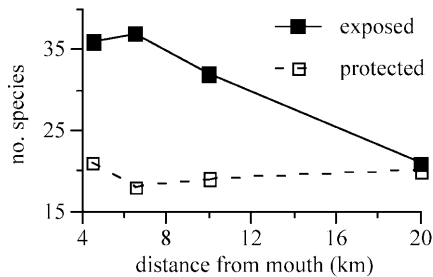


Fig. 2. Total number of emergent species and fishes (combined) in four San Diego Bay study locations in June and August 2000 as a function of distance from the mouth of San Diego Bay. Data are shown separately for exposed and protected sites at each location

were not consistent, but that some locations had greater differences between exposed and protected sites than others. The smallest differences between exposed and protected sites were measured at CV (e.g., Fig. 2), where energetic and other physical differences between “exposed” and “protected” sites were less pronounced.

Not all taxa followed the same abundance pattern. Some, including snails of the genus *Littorina*, the barnacles *Chthamalus fissus* and *Tetraclita rubescens*, the tube snail *Serpulorbis squamigerus*, mussels of the genus *Mytilus*, bryozoans of the genus *Watersipora*, and coralline algae exhibited higher percent cover near the mouth (at SI) than at other sites. Others, such as the limpets *Collisella limatula* and *C. scabra*, the chiton *Nuttilina fluxa*, the oyster *Ostrea lurida*, the slipper snail *Crepidula onyx*, anemones of the genus *Anthopleura*, colonial *Botryllus tunicates*, the brown alga *Colpomenia sinuosa*, and non-coralline red algae had highest cover in the middle of San Diego Bay, at either HI or EP. Taxa such as the slipper snail *Crucibulum spinosum*, barnacles of the genus *Balanus*, the sponge *Aplysina fistularis*, and the green algae *Ulva* spp. and *Enteromorpha* spp. had highest cover in the back of the bay, at CV.

Most taxa (25) differed in percent cover between exposed and protected sites; however, the effect of exposure was modified by location, as indicated by the significant interaction between location and exposure for all 25 taxa (Table 5). Of these, 18 were more abundant

Table 5. Results of three-way ANOVAs testing for differences in species' percent cover among locations (*Loc*), between exposures (*Exp*), and between months. *P*-values for each of the three terms and four interactions are listed. When significant differences between location, exposure, or month were found (*bold print*), letters were used to indicate whether percent cover was higher at the mouth (*M*), center (*C*), or back (*B*) of the bay; at exposed (*E*) or protected (*P*) sites; or in June (*J*) or November (*N*). Taxa are listed

Taxa	Location	Exposure	Month	Loc×Exp	Loc×Month	Exp×Month	Loc×Exp×Month
<i>Tetraclita rubescens</i>	< 0.001 M	< 0.001 E	0.028 J	< 0.001	0.384	0.162	0.364
Serpulid worms	< 0.001 M	< 0.001 P	< 0.001 N	< 0.001	< 0.001	< 0.001	< 0.001
Limpets-other	< 0.001 C	< 0.001 E	< 0.001 J	< 0.001	< 0.001	0.001	< 0.001
<i>Balanus</i> spp.	< 0.001 B	0.017 E	0.016 J	0.009	0.893	0.310	0.203
<i>Enteromorpha</i> spp.	< 0.001 B	< 0.001 P	0.001 J	< 0.001	< 0.001	0.272	0.311
<i>Aplysina fistularis</i>	< 0.001 B	< 0.001 E	< 0.001 N	0.075	0.016	< 0.001	0.096
<i>Leucetta</i> spp.	0.001 B	< 0.001 P	< 0.001 N	0.015	0.015	< 0.001	0.001
<i>Styela</i> spp.	0.036 B	0.190	< 0.001 N	0.934	0.148	0.108	0.487
Sponges-other	0.347	< 0.001 E	< 0.001 J	0.034	0.002	0.066	0.048
<i>Sargassum</i> spp.	0.052	< 0.001 E	0.011 J	0.001	0.016	0.731	0.104
<i>Littorina</i> spp.	< 0.001 M	0.001 E	0.967	0.018	0.342	0.916	0.395
<i>Fissurella volcano</i>	< 0.001 M	0.007 E	0.148	< 0.001	0.098	0.148	0.098
<i>Chthamalus fissus</i>	< 0.001 M	< 0.001 E	0.797	< 0.001	0.027	0.154	0.803
Corallines	< 0.001 M	< 0.001 E	0.526	< 0.001	0.018	0.577	< 0.001
<i>Mytilus</i> spp.	0.003 M	< 0.001 E	0.710	0.001	0.278	0.563	0.334
<i>Watersipora</i> spp.	< 0.001 M	< 0.001 P	0.139	< 0.001	0.185	0.807	0.212
<i>Collisella limatula</i>	< 0.001 C	< 0.001 E	0.245	< 0.001	0.343	0.995	0.395
<i>Collisella scabra</i>	< 0.001 C	< 0.001 E	0.783	< 0.001	0.020	0.765	0.608
All other reds	< 0.001 C	< 0.001 E	0.180	< 0.001	0.748	0.001	0.006
<i>Colpomenia sinuosa</i>	< 0.001 C	< 0.001 E	0.829	< 0.001	0.254	0.017	0.009
<i>Nuttalina fluxa</i>	0.002 C	0.001 E	0.432	0.002	0.449	0.432	0.449
<i>Anthopleura</i> spp.	0.014 C	0.007 E	0.175	0.014	0.002	0.175	0.002
<i>Botryllus</i> spp.	< 0.001 C	0.011 P	0.350	< 0.001	0.344	0.585	0.773
<i>Crepidula onyx</i>	0.011 C	0.007 P	0.241	< 0.001	0.090	0.475	0.612
<i>Ulva</i> spp.	< 0.001 B	< 0.001 E	0.168	0.002	0.001	< 0.001	< 0.001
Anemone-other	< 0.001 B	< 0.001 P	0.878	< 0.001	0.978	0.625	0.921
<i>Serpul. squamigerus</i>	< 0.001 M	0.377	0.800	< 0.001	0.783	0.253	0.494
<i>Dictyota binghamiae</i>	0.005 M	0.127	0.346	0.395	0.822	0.783	0.331
<i>Ostrea lurida</i>	< 0.001 C	0.092	0.062	0.074	0.552	0.246	0.160
Bryozoa-other	0.007 C	0.148	0.589	0.867	0.355	0.103	0.980
<i>Crucibulum spinosum</i>	< 0.001 B	0.694	0.746	< 0.001	0.191	0.007	0.001
<i>Pachygraps. crassipes</i>	0.217	0.066	0.066	0.217	0.217	0.066	0.217
<i>Pseudochama exogyra</i>	0.324	0.513	0.842	0.343	0.053	0.520	0.467
Encrusting corallines	0.417	0.189	0.067	0.290	0.557	0.104	0.186

in the following order: those different between months, those different between exposures, those different only among sites, and those that did not differ by any of the three factors. Taxa names depend on level of identification in the field. For example, a group listed as "limpets-other," indicates that more specific limpet groups appear elsewhere on the list. Group degrees of freedom (*df*): three for Site, Site×Exp, Site×Month, and Site×Exp×Month, one for Exp, Time, and Exp×Month. Error *df*: 48

at exposed sites, and 7 were more abundant at protected sites (Table 5). All seven taxa in the latter group, which included the slipper snail *Crepidula onyx*, sponges of the genus *Leucetta*, bryozoans of the genus *Watersipora*, tunicates of the genus *Botryllus*, and green algae of the genus *Enteromorpha*, were absent from the open coast, emphasizing community differences between protected sites and the open coast. Of the 18 taxa more abundant at exposed sites, which included the barnacles *Tetraclita rubescens* and *Balanus* spp., the limpets *Collisella scabra* and *C. limatula*, *Littorina* snails, the chiton *Nuttalina fluxa*, and others, all but the sponge *Aplysina fistularis* were found on the open coast.

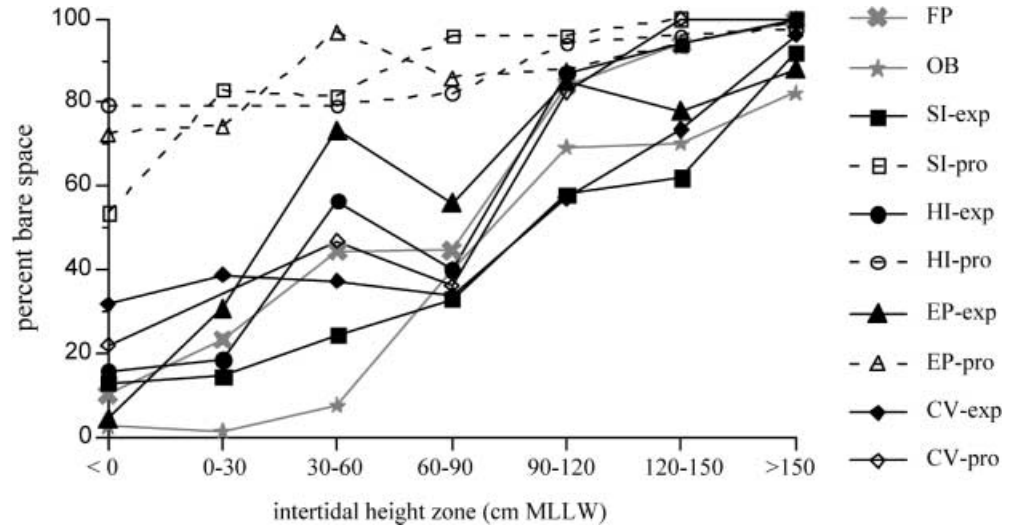
Only 10 of the 34 taxa had different percent cover between June and November 2000 (Table 5), suggesting that spatial variation in the environment is more important than temporal variation. Of the ten, six were more abundant in June (including *Tetraclita rubescens*, *Balanus* spp., *Enteromorpha* spp., and brown algae of the genus *Sargassum*), and four were more abundant in

November (including two sponges and solitary tunicates of the genus *Styela*).

Vertical zonation

Vertical zonation of the emergent biota differed between exposed and protected sites, as indicated by differences in tidal height of empty space (Fig. 3). Low and middle intertidal height zones (−30 to +90 cm MLLW) of protected sites had more empty space (71 ± 6%) than low and middle zones of exposed sites (33 ± 5%), with CV again an exception (two-way ANOVA, exposure: $F_{1,24} = 33.1$, $P < 0.001$, site: $F_{3,24} = 2.8$, $P = 0.062$, site×exposure: $F_{3,24} = 3.9$, $P = 0.021$). At the highest zones, however, protected and exposed sites were more similar in amount of empty space (94 ± 2% protected, 79 ± 5% exposed), although still significantly different (exposure: $F_{1,24} = 10.0$, $P = 0.013$, site and site×exposure: $F_{3,24} < 1.5$, $P > 0.4$).

Fig. 3. Percent cover of bare space in seven 30-cm wide intertidal height zones in June 2000. Relationships were similar in November 2000 and are not shown. See Table 1 for site abbreviations



For species that occurred in two or more transects at both the exposed and protected sites at a location, intertidal heights were compared between exposure levels. In June, eight, five, five, and five species occurred at both sites of SI, HI, EP, and CV, respectively. Of these, eight had significantly higher intertidal height at the exposed site, and five were higher at the protected site (Table 6). In November, six, six, four, and six species occurred at both sites of SI, HI, EP, and CV, respectively (Table 6). All 10 significant differences reflected species that occurred higher at the exposed site. Of all 45 comparisons, there were three to four times as many cases of species occurring higher at the exposed site (18) than the protected site (5). However, there were few consistent patterns within species. For example, the barnacles *Chthamalus fissus* and *Balanus* spp. were sometimes higher at the exposed site, sometimes at the protected site.

The question of whether intertidal height changed with distance from the bay mouth could only be addressed for those species present at all four locations: tunicates of the genus *Styela*, the oyster *Ostrea lurida*, mussels of the genus *Mytilus*, the sponge *Aplysina fistularis*, green algae of the genus *Ulva*, and brown algae of the genus *Sargassum*. None of these taxa displayed a relationship between intertidal height and distance from the mouth (regression analysis, $n=4$, $P>0.05$). Low sample size contributes to the lack of statistical significance, and we acknowledge that the present design is not ideal for testing this question.

Sea level was 4.5 cm higher in November than June 2000 (calculated for 30 days prior to sampling from data at <http://uhslc.soest.hawaii.edu>). Intertidal heights of many species were also significantly higher in the intertidal zone in November than June (Table 7). Of 22 taxa abundant enough for analysis, 12 occurred higher in November and one occurred higher in June. These 22 taxa can be grouped based on their expected response to seasonal shifts in sea level. Of the six motile invertebrates capable of responding through individual movement, three were significantly higher in November

(Table 7). All four upper-intertidal (average height >30 cm MLLW), non-motile species occurred higher in November. Of the lower-intertidal (<30 cm MLLW), non-motile invertebrates, none were higher in November, and one was higher in June. Five of six algal species occurred higher in November.

Community composition

Principal component analyses (PCA) of emergent species revealed four site clusters: (1) CV sites, (2) exposed sites (excluding CV), (3) protected sites (excluding CV), and (4) open coast (Fig. 4A). PCA of fishes, which were not measured on the open coast, revealed CV and protected site clusters, but exposed sites did not cluster together (Fig. 4C). For emergent species, the exposed site at a particular location was more similar to the exposed site at another location (excluding CV) than to its corresponding protected site (Fig. 4B), an observation supported by comparison of Bray-Curtis similarity values between pairs of sites (Table 8). For example, the mean (± 1 SE) similarity between pairs of exposed sites (SI-exposed and HI-exposed, HI-exposed and EP-exposed, SI-exposed and EP-exposed) in June was $66 \pm 3\%$, significantly higher than the average similarity between exposed and protected sites in the same location ($34 \pm 2\%$) ($t_4=9.56$, $P<0.001$). Similarity of fishes did not exhibit a similar trend (pairs of exposed sites: $34 \pm 6\%$; exposed vs. protected: $38 \pm 9\%$, $P>>0.05$), and CV displayed the opposite trend. The exposed site at CV was only $32 \pm 4\%$ similar (emergent taxa) and $38 \pm 4\%$ similar (fishes) to the exposed sites of the other three locations, but was 69% (emergent taxa) and 80% (fishes) similar to the protected CV site (Table 8).

Comparison to open coast

Of 49 emergent taxa, 21 (17 invertebrates, 3 algae, and 1 seagrass) were found only in the bay and not on the

Table 6. Comparison of a taxon's intertidal height between exposed and protected sites. Average heights of each taxon at exposed (*Exp*) and protected (*Pro*) sites are listed in centimeters above or below MLLW. For differences in height that were significant (*bold print*), the site of higher intertidal height is indicated (*E* exposed; *P* protected). See Tables 2 and 3 for taxonomic information

Taxon	June			November		
	Exp	Pro	High site	Exp	Pro	High site
Shelter Island						
<i>Colpomenia sinuosa</i>	2	-52	E			
<i>Dictyota binghamiae</i>				-12	-18	
<i>Sargassum</i> spp.	1	-52	E			
Coralline algae	-16	-43	E	-1	-18	E
Other red algae	-24	-51	E			
<i>Collisella scabra</i>				76	-18	E
<i>Serpul. squamigerus</i>	20	-15	E	1	-1	
<i>Ostrea lurida</i>	18	-20	E	3	-2	
<i>Chthamalus fissus</i>	80	70	70	103	124	
<i>Balanus glandula</i>	48	69	69			
Harbor Island						
<i>Aplysina fistularis</i>	-3	-9		-23	-18	
<i>Serpul. squamigerus</i>	24	64	P	2	-3	
<i>Ostrea lurida</i>	25	23		34	12	E
<i>Balanus</i> spp.	52	88	P			
<i>Chthamalus fissus</i>	80	121	P	106	103	
<i>Styella</i> spp.				14	-12	E
Embarcadero Park						
<i>Colpomenia sinuosa</i>	-8	-3	3	28	-2	
<i>Aplysina fistularis</i>	-18	-3	P			
<i>Collisella limatula</i>				65	40	
<i>Ostrea lurida</i>	17	11		32	-8	E
<i>Mytilus</i> spp.	54	-9	E			
<i>Balanus</i> spp.	113	94		126	87	E
Chula Vista						
<i>Enteromorpha</i> spp.	76	-3	E			
<i>Ulva</i> spp.	-9	32	P	68	53	
Other red algae				54	24	E
<i>Aplysina fistularis</i>	-20	1		33	12	
<i>Ostrea lurida</i>	-15	18		46	17	E
<i>Balanus</i> spp.	70	66		124	91	E
<i>Styela</i> spp.				15	-12	E

open coast. An additional 12 taxa (6 invertebrates, 5 algae, and 1 seagrass) were found only on the open coast and not in San Diego Bay (Tables 2, 3). Of taxa found both in the bay and on the open coast, five (*Littorina* snails, the limpet *Collisella scabra*, the brown alga *Egrecia menziesii*, non-coralline red algae, and total seagrass) were significantly more abundant on the open coast than in the bay (ANOVA $P < 0.05$). None was more abundant inside than outside the bay, a result consistent with the greater amount of bare space found in the bay ($F_{1,4} = 7.53$, $P = 0.052$). This difference in amount of bare space is attributable mainly to the protected bay sites, especially at lower intertidal heights, and not to exposed sites (Fig. 3). Exposed bay sites and open-coast sites had similar amounts of bare space. We must acknowledge that some differences between the riprap and open-coast sites may be due to the 2-month gap between sampling or to the distance of the open-coast sites from the bay mouth.

Similarity of emergent community composition to the two open-coast communities was highest for exposed riprap sites closest to the bay mouth, decreasing with distance from the mouth (Fig. 5). These relationships were significant for the exposed, but not for the pro-

ected sites. Exposed sites at the four locations were more similar to the open-coast sites than the protected sites (two-way ANOVA, exposure: $F_{1,24} = 5.9$, $P = 0.032$, open-coast site: $F_{1,24} = 0.4$, $P = 0.541$, exposure \times site: $F_{1,24} = 0.2$, $P = 0.675$).

Comparison of intertidal height of species at the bay riprap sites to open-coast sites was made difficult by the large variability in average intertidal height of a taxon between the two open-coast sites (Fig. 6). Of the five taxa occurring in enough locations for analysis (*Littorina* snails, the barnacle *Chthamalus fissus*, the limpet *Collisella scabra*, the green algae *Ulva* spp., and coralline algae), none were significantly different in height between bay (grouped together, $n = 2, 3$, or 4) and open coast ($n = 2$) (t -tests, $P > 0.05$, Fig. 6).

Discussion

The addition of artificial riprap habitat to San Diego Bay has had several ecological consequences. The hard substrate has provided habitat to open-coast species, stretching the influence of the open coast into the bay. However, the hard substrate has also provided habitat

Table 7. Comparison of a taxon's intertidal height between June and November. Average intertidal heights of each taxon in the two different months are listed in centimeters above or below MLLW. *P*-value of the month factor in two-way ANOVAs (for species that occurred at two or more sites) and one-way ANOVAs (for species

that occurred at only one site) is listed for each species. For significant results (*bold print*), the month of higher intertidal height is indicated (*N* November; *J* June) (*B* brown algae; *G* green algae; *R* red algae)

Taxon	Height (cm MLLW)			No. of sites	<i>P</i>
	Jun	Nov	High month		
Algae					
<i>Ulva</i> spp. (<i>G</i>)	13	52	N	4	< 0.001
<i>Colpomenia sinuosa</i> (<i>B</i>)	-10	14	N	4	0.001
Corallines (<i>R</i>)	-16	0	N	3	0.001
Other red algae	-7	19	N	4	0.001
<i>Enteromorpha</i> spp. (<i>B</i>)	4	31	N	1	0.008
<i>Sargassum</i> spp. (<i>B</i>)	-15	-2		2	0.095
Motile invertebrates					
<i>Collisella scabra</i> (limpet)	51	84	N	3	0.004
<i>Nuttalina fluxa</i> (chiton)	17	63	N	1	0.007
Anemone	-8	14	N	1	0.042
<i>Littorina</i> spp. (gastropod)	129	114		1	0.267
<i>Crepidula onyx</i> (gastropod)	-25	-14		1	0.438
<i>Collisella limatula</i> (limpet)	66	69		2	0.645
Non-motile, high-intertidal invertebrates					
<i>Chthamalus fissus</i> (barnacle)	86	112	N	4	< 0.001
<i>Balanus</i> spp. (barnacle)	73	95	N	6	0.001
<i>Tetraclita rubescens</i> (barnacle)	42	65	N	3	0.006
<i>Mytilus</i> spp. (bivalve)	35	50	N	3	0.033
Non-motile, low-intertidal invertebrates					
<i>Serpul. squagimerus</i> (gastropod)	17	-2	J	4	0.003
<i>Watersipora</i> spp. (bryozoan)	-3	15		1	0.080
<i>Aplysina fistularis</i> (sponge)	-31	-9		1	0.121
<i>Botryllus</i> spp. (tunicate)	-8	-20		1	0.413
<i>Ostrea lurida</i> (bivalve)	14	17		8	0.539
<i>Styela</i> spp. (tunicate)	-2	15		1	0.673

to non-coastal species, especially at protected sites in man-made marinas. The influence of the open coast was most apparent at exposed sites close to the mouth for both emergent species (Fig. 5) and fishes (Table 4; Davis 2000). Sites farther from the mouth and more protected inside marinas resembled open-coast communities less.

Exposure to wave energy plays a role in the structure of communities in rocky, open-coast systems (e.g. McQuaid and Branch 1985; Debrot 1990; Bustamante and Branch 1996; Dalhoff and Menge 1996; Robles 1997). In the same way, this factor may serve to structure communities on artificial hard substrate in bays and estuaries. Although wave energy regimes within these sheltered environments tend to be much quieter than even the most protected locations of the open coast, wave energy gradients in bays may account for spatial variability in intertidal community structure. An increase in wave height stretches the vertical range of the upper intertidal and splash zones, essentially providing more space for intertidal biota and perhaps allowing species to occupy wider and higher intertidal ranges. Higher wave energy is associated with increased water flow and circulation, which can affect organisms and populations both negatively and positively. Higher flow can provide a greater rate of nutrient, food, and recruit delivery (Leonard et al. 1998), enhancing growth and survivorship of individuals (Dalhoff and Menge 1996) and populations (Debrot 1990; Robles 1997). Higher

energy can also affect the temperature regime and flush pollutants more quickly out of a location.

However, higher energy can lead to decreased handling efficiency of food particles, lower settlement success (Mullineaux and Garland 1993), higher energy cost necessary to maintain position on the substrate (e.g. Stebbins 1988; Trussell 1997), and damage to biota by debris (Debrot 1990). Sediment is swept away, clearing space for hard-substrate species. Space cleared through disturbance negatively impacts individuals already present but makes room for opportunists. At sites close to the mouth, the benefits and drawbacks of increased exposure interact with higher flushing rates of water coming from outside San Diego Bay (Chadwick and Largier 1999). Nutrients, food, and larvae in this water have a greater open-coast signal.

Community structure

In San Diego Bay, spatial and exposure differences among sites were more important than time of year in determining emergent community structure of riprap habitats. Some species, especially those that tended to be absent from the open coast, were more abundant at protected than exposed sites in San Diego Bay. These may be predominantly bay species, adapted to less energetic, more turbid, or more productive environments.

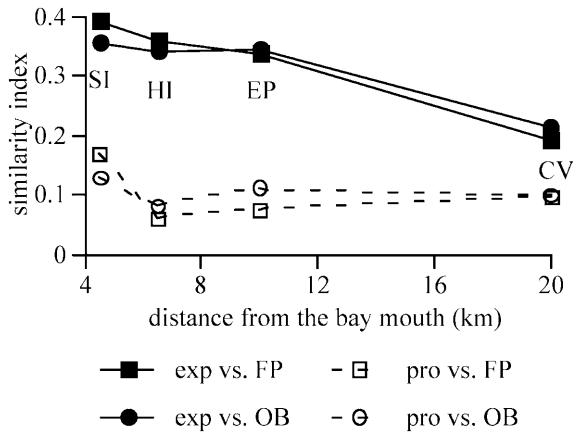


Fig. 5. Relationship between similarity of emergent fauna to the open coast and distance from bay mouth for exposed and protected sites at four San Diego Bay locations. Relationships were significantly negative for exposed sites ($n=4$, $r^2=0.92$, $P=0.042$ when compared to Ocean Beach; $r^2=0.98$, $P=0.012$ when compared to False Point) but not for protected sites ($P > 0.05$). See Table 1 for site abbreviations

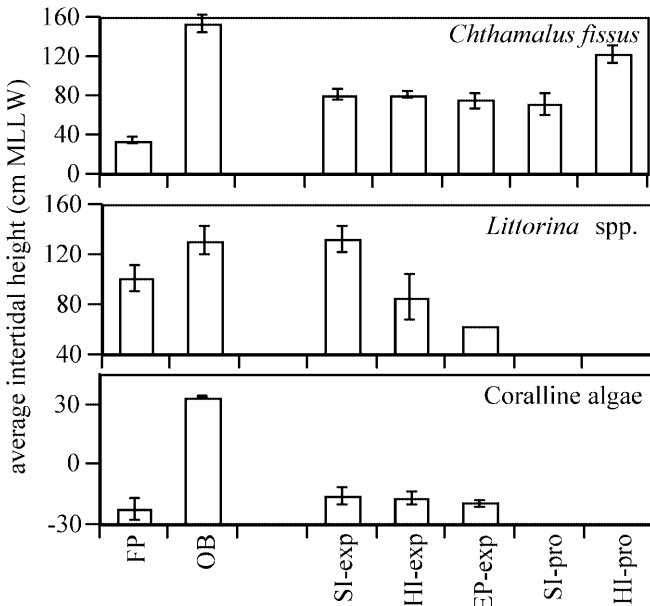


Fig. 6. Examples of the comparison of emergent species' intertidal height between the two open-coast sites (False Point and Ocean Beach) and the San Diego Bay sites. *T*-tests revealed no significant differences between height at the open coast and the bay ($P > 0.05$) for any taxa. See Table 1 for site abbreviations

Although riprap habitats, especially those that were exposed and close to the mouth, permitted the extension of open-coast species ranges into the bay, not all open-coast species were found at exposed riprap sites. Noticeably absent were large gastropods such as *Tegula eiseni*, *T. funebris*, *Nucella emarginata*, and *Roperia paulsani*. Other factors than lower energy in the bay may contribute to their absence. Most rocky-intertidal species have a planktonic larval stage (Shanks 1995), and

many have ontogenetic habitat shifts after settlement. Although bay riprap may provide suitable adult habitat, lack of juvenile habitat may exclude these species from San Diego Bay. For example, *N. emarginata* juveniles cannot survive any degree of desiccation (Gosselin and Chia 1995). Because riprap seawalls have no tidepools, and also often do not extend far into the subtidal zone, intertidal species requiring extensive rocky-subtidal or permanently wet nursery habitats (Moreno et al. 1993; Gosselin and Chia 1995) would not survive the juvenile phase.

When compared to other habitats in San Diego Bay (intertidal un-vegetated and vegetated, deep channel), intertidal riprap serves a unique function. Several fishes found nowhere else in the bay (Pondella 1998), such as *Gobiesox rhessodon*, *Hypsoblennius gilberti*, and *Clino-cottus analis*, use riprap (Table 4). Intertidal tidepools on the open coast are the primary habitat for all three of these fishes (Davis 2000). In addition, intertidal bay riprap indirectly affects other bay habitats, and as a result, has become part of the bay system. Highly motile fishes, especially *Girella nigricans*, *Paralabrax* spp., and surfperches, were observed to feed on riprap organisms at high tide (Walther and Davis, personal observations). These fishes use other parts of the bay (Pondella 1998), transporting production among riprap and other habitats. Birds were observed to forage on the riprap walls at low tide, and may similarly connect bay habitats through food webs.

Vertical zonation

Less attention has been directed to the effects of exposure and wave energy on intertidal height of biota. In San Diego Bay, many species that occurred at both exposed and protected sites occurred higher in the intertidal zone at exposed sites. This result is consistent with the hypothesis that the vertical ranges of the intertidal zone are extended upward through splash in higher wave energy regimes. This hypothesis has not often been tested [but see Pannacciulli and Relini's (2000) study of intertidal Mediterranean barnacles]. Results of the present study, however, were not consistent with the extension of this hypothesis to the open coast. We predicted that species would occur higher on the open coast than in the bay due to higher wave energy and exposure. However, differences in intertidal height between the two open-coast sites were greater than the differences between the bay and the open coast. Intra-open-coast differences may be due to differences in energy and/or rock type between the two sites described above, or to other physical or oceanographic differences separating the sites.

Even less is known about effects of seasonal shifts in sea level on species' vertical zonation. Sea level in San Diego is usually about 16 cm higher in the fall than the spring (Davis 2000), influencing the vertical extent of the influence of wave energy within the intertidal zone. In

the present study, most species, especially algae and non-motile, high-intertidal invertebrates, occurred significantly higher in the intertidal zone in November than in June, when sea level was about 4.5 cm higher than it was June.

A similar vertical shift in intertidal height was observed for San Diego rocky-intertidal fishes (Davis 2000). Unlike the fishes, however, which probably accomplished seasonal shifts through vertical movement by individuals (Davis 2000), shifts for most species in the present study, because they are sessile, cannot be attributed to individual movement. We expected seasonal height shifts to be most pronounced in motile species, but only half of the motile species changed their distributions between June and November. The taxa whose heights changed most consistently were algae and non-motile, high-intertidal species.

Several possible mechanisms, such as seasonal mortality in and recruitment to either the low or high edge of a species' height range, may explain these vertical shifts. Individuals may die of desiccation in the upper part of their species' vertical range when sea level is low during the spring. They may re-recruit to these upper areas in the late summer and fall, when sea level rises to inundate these areas again. This hypothesis could not be tested in the present study, as individual age was not measured. Predation by birds and other nonaquatic predators may also play a role. These predators have increased access to the intertidal zone in the spring, when sea level is lower, and may reduce abundances of their prey species in the higher zones. Observed shifts may also be responses to other cues that change seasonally, such as temperature or light (Davis 2000).

Conclusions

Riprap seawalls in San Diego Bay provide habitat for open-coastal, rocky-intertidal species as well as non-open-coastal species. Although the presence of riprap and its replacement of soft-sediment habitat are inherently unnatural, there may be ways to make more natural or otherwise improve the ecological functions of riprap in areas where alternative methods of shoreline stabilization are not successful. For example, should the enhancement of bay species be desired, structures like terraces to trap soft sediment (Simenstad and Thom 1992) might be added to riprap in protected locations. Should the extension of open-coast communities into the bay be desired, ways to add tidepools to riprap in exposed locations might be explored. As world-wide development of bay shoreline continues and natural bay shoreline is lost, managers may be forced to consider the ecological roles of shoreline stabilization structures and find ways to integrate ecological function with anthropogenic needs.

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