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The Impacts of Human Visitation on Mussel Bed Communities Along the California Coast: Are Regulatory Marine Reserves Effective in Protecting These Communities?

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Abstract Rocky intertidal habitats frequently are used by humans for recreational, educational, and subsistence-harvesting purposes, with intertidal populations damaged by visitation activities such as extraction, trampling, and handling. California Marine Managed Areas, particularly regulatory marine reserves (MRs), were established to provide legal protection and enhancement of coastal resources and include prohibitions on harvesting intertidal populations. However, the effectiveness of MRs is unclear as enforcement of no-take laws is weak and no regulations protect intertidal species from other detrimental visitor impacts such as trampling. The goal of this study was two-fold: (1) to determine impacts from human visitation on California mussel populations (*Mytilus californianus*) and mussel bed community diversity; and (2) to investigate the effectiveness of regulatory MRs in reducing visitor impacts on these populations. Surveys of mussel populations and bed-associated diversity were compared: (1) at sites subjected to either high or low levels of human use, and (2) at sites either unprotected or with regulatory protection banning collecting. At sites subjected to higher levels of human visitation, mussel populations were significantly lower than low-use sites. Comparisons of mussel populations inside and outside of regulatory MRs revealed no consistent pattern suggesting that California no-take regulatory reserves may have limited effectiveness in protecting mussel communities. In areas where many people visit intertidal habitats for purposes other than collecting, many organisms will be affected by trampling, turning of rocks, and handling. In these cases, effective protection of rocky intertidal communities requires an approach that goes beyond the singular focus on collecting to reduce the full suite of impacts.

Keywords Marine reserves · Anthropogenic disturbance · Rocky intertidal · *Mytilus californianus* · Mussel bed community · Trampling · Collecting

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Introduction

Natural disturbances of marine communities are important for maintaining biological diversity and ecosystem functioning, especially within the rocky intertidal zone (e.g., Dayton 1971; Sousa 1979a, 1979b; Paine and Levin 1981). Anthropogenic perturbations, however, disrupt natural ecosystem functioning and are a major threat to coastal communities (Suchanek 1994; Fraschetti and others 2001; Jackson 2001; Jackson and others 2001). In California, flora and fauna populations on wave-exposed rocky shores are subjected to perturbations from a large number of people who visit intertidal zones for recreational or education purposes, or to collect intertidal species for food, fish bait, or ornamentation (Smith 1993; Addessi 1994; Murray 1998; Ambrose and Smith 2005). The impacts of visitor activities, including collecting, trampling, rock

turning, and handling of intertidal species, can result in loss or damage to flora and fauna and cause alterations of community processes (e.g., Ghazanshahi and others 1983; Castilla and Duran 1985; Castilla and Bustamante 1989; Brown and Taylor 1999; Schiel and Taylor 1999). Human disturbance along the California coast, particularly in southern California due to the dense human population near the coastline, can be very high and persistent throughout the year, with usage at some high traffic sites yielding over 1400 persons at approximately a 500–m length of coast within a single afternoon low tide (Murray and others 1999) and over 50,000 visitors on a 100-m shoreline in a year (Ambrose and Smith 2005).

Disturbance from human visitation can have direct effects, such as loss of individuals through collecting (e.g., Castilla and Bustamente 1989; Fairweather 1991; Keough and others 1993; Roy and others 2003) and the dislodgement or crushing of individuals by trampling (e.g., Beauchamp and Gowing 1982; Bally and Griffiths 1989; Povey and Keough 1991; Brosnan and Crumrine 1994; Smith and Murray 2005; Casu and others 2006). Human activities also may result in morphological damage that can affect other physiological or reproductive processes, thus reducing overall fitness (Keough and Quinn 1998; Schiel and Taylor 1999; Denis 2003). In addition, harvesting of intertidal flora and fauna can directly affect the size structure of a population (Branch 1975; McLachlan and Lombard 1981; Moreno and others 1984; Castilla and Duran 1985; Ortega 1987; Lasiak 1991; Pombo and Escofet 1996; Kido and Murray 2003; Sagarin and others 2007) because humans tend to select the largest specimens.

In addition to direct impacts of visitation, human activities can cause indirect effects on intertidal flora and fauna. For example, shifts in the size structure of a population towards smaller and younger individuals may result in a disproportionate decrease in the reproductive ability of the population because the reproductive potential (i.e., gonad volume in invertebrates) increases exponentially with size (Branch 1974, 1975; Creese 1980; Levitan 1991; Tegner and others 1996). For species with long-lived pelagic larval stages, declines in reproductive output can affect both local and regional recruitment. Human activities can also result in cascading effects such as alteration of community processes through the disruption of the ecological balance of competitors, predators, and/or food supply (e.g., Duran and Castilla 1989) or through alterations of habitat provision such as declines in the abundance of an ecosystem engineer (Brown and Taylor 1999; Schiel and Taylor 1999).

To preserve marine ecosystem integrity and protect the resources and natural diversity of marine habitats, including rocky shores, many areas in California and elsewhere are regulated as Marine Managed Areas (MMAs) under one of many protective designations depending on their objectives (i.e., State Park or Beach, Marine Life Refuge, Area of Special Biological Significance). For rocky intertidal zones, protection is often afforded through legislative regulatory means where removal of intertidal flora and fauna are prohibited by law. Within some MMAs, a list of numerous species may be available for legal harvest by recreational or commercial collectors but, for the purposes of this study, only protective designations that include bans on harvesting of intertidal species, particularly the study species, will be discussed and will be referred herein as regulatory marine reserves (MRs). Despite the strong goals of protecting and enhancing marine populations within MRs, their effectiveness for rocky intertidal communities is under debate because California MR status, unlike other regions such as Chile (Castilla 1999), does not limit visitor access and thus does not protect intertidal populations from foot traffic associated with recreational and educational activities (Murray 1998). In addition, enforcement of MR regulations in California appears to be weak as collecting continues to occur (Murray 1998; Murray and others 1999; Ambrose and Smith 2005; Ambrose and Smith personal observation 2002), although the magnitude of collecting in comparison to nonreserves is unknown.

The goal of this study is two-fold: (1) to determine population and community-level impacts from human visitation on rocky-shore mussel communities; and (2) to investigate the effectiveness of regulatory marine reserves in reducing impacts from human activities on these communities. Mussels (*Mytilus californianus* Conrad) and their associated communities were chosen for this study because they are a major component of the mid stratum of the exposed rocky intertidal zone along the eastern coast of the north Pacific and are considered to be an extraordinarily diverse micro-habitat, with previously reported richness measures of 300 species within a site and 750 species within the Southern California Bight (Ricketts and others 1968; Kanter 1980; Suchanek 1992). Mussel populations are particularly vulnerable to human use; they are susceptible to damage by trampling (Brosnan and Crumrine 1994; Smith and Murray 2005) and are commonly collected for food (Smith personal observation 2002) and as fish bait by recreational shore fishers (Murray and others 1999). Direct effects of crushing mussels underfoot and removing individuals are only two components of the loss. Further loss occurs indirectly as these activities weaken the attachment strength of surrounding mussels, making them susceptible to loss from wave activity and more sensitive to future human activities (Brosnan and Crumrine 1994; Smith and Murray 2005). Because mussels are an important habitat-forming species providing food, space, and shelter for its associated community, investigating the effects human impacts on mussel populations may provide insight into cascading effects on associated species.

Methods

Site Selection

Impacts of Human Visitation

To investigate impacts from human visitors, we measured mussel population and community composition at several sites over approximately 1000 km of the California coast. We selected pairs of sites located on rocky headlands, with each pair having a site receiving a lower and a higher level of human use that were as close together as possible (Fig. 1). When comparing these sites along the entire coast, a paired design minimized site-to-site differences due to factors other than human use, such as temperature, exposure to wave activity, or biogeographic location. Ten matched pairs (Fig. 1, Table 1) were used to investigate the impact of humans on mussels; nondestructive measures of mussel populations were taken at all ten pairs of sites while additional destructive harvest sampling was conducted at five of the paired sites. Four of the ten pairs contained a higher and lower-use site within a single area. In two cases, there was higher-use site near an access point paired with a lower-use site farthest from the access. In the other two cases, lower human use portions of the area were located on isolated outer rocks that were difficult to reach. We attempted to match the remaining pairs with sites in close proximity but also with similar topography, exposure, and geology (Smith 2005).

In southern California, appropriate sites receiving low levels of human use were difficult to find; in northern California, sites with high levels of human use were difficult to find. Therefore, some sites within matched pairs were not always ideal but were the most comparable sites available. The weakest of the pairs were Carlsbad/Ocean Beach and Government Point/Coal Oil Point. Within these pairs, the sites were of different geologic origin and with sharply different slopes. In addition, Coal Oil Point is much more sand-influenced than Government Point. Despite these differences, these pairs showed similar trends as observed in the stronger site pairs. Analyses included all paired sites for a more inclusive understanding of human impacts along a large geographic extent.

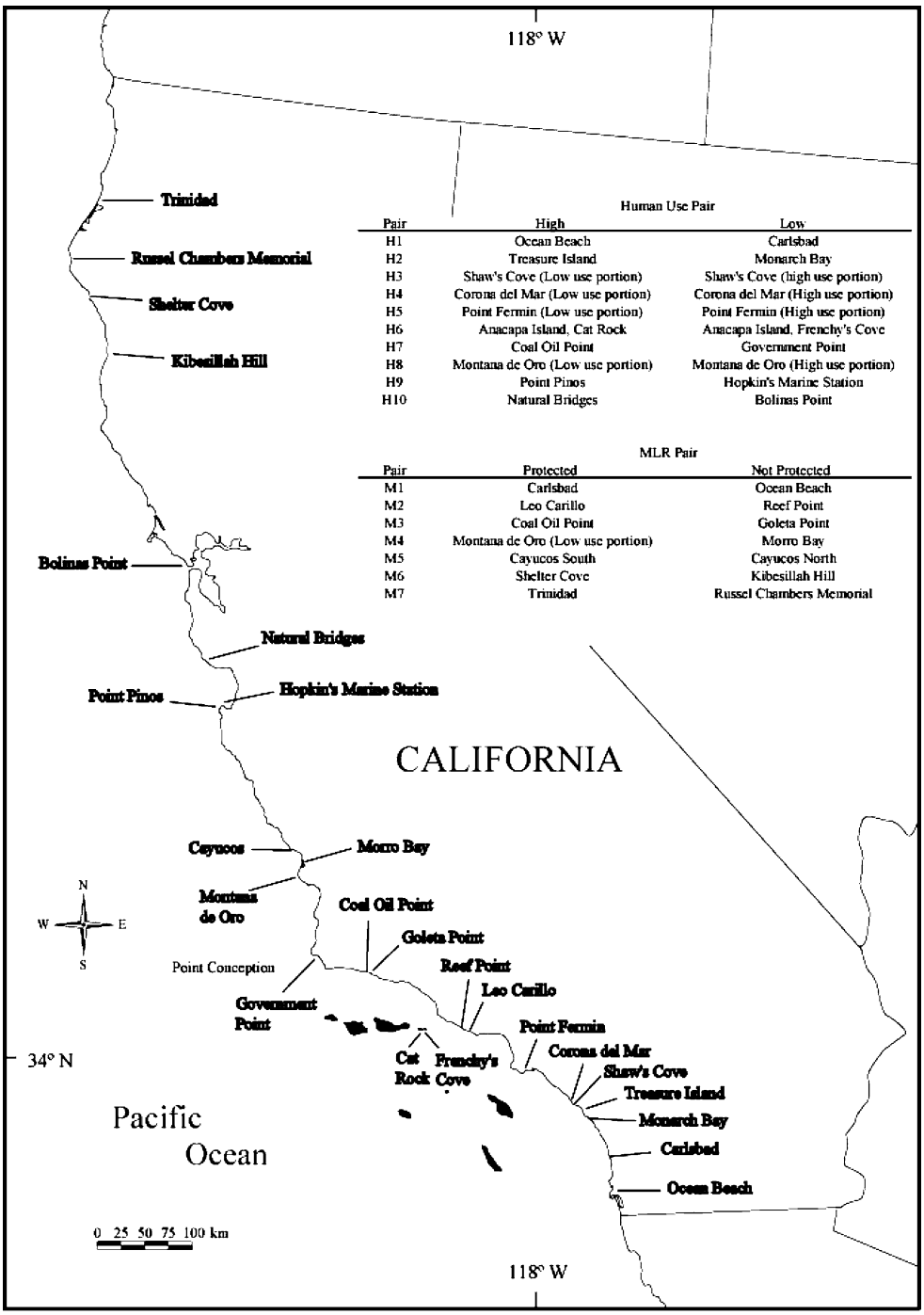
We estimated the degree of human activity by developing scales for three main factors: (a) estimated level of use from site observations, personal experience, or existing data where available; (b) the number of people on site when sampled; and (c) measurements of accessibility (Table 1, scale of use). The estimated level of use was scaled from one (low human use) to five (very high human use) from personal experience and from existing data including studies investigating human use at Monarch Bay, Treasure Island, and Shaw's Cove in Orange County (Kido and Murray 2003), Point Fermin and Leo Carillo in Los Angeles County (Ambrose and Smith 2005), and Point Pinos in Monterey (Tenera 2003). The number of persons on site was counted during sampling and scaled from one (none observed on site) to five (over 20 individuals on site at one time). Accessibility was based on five scaled components that were averaged for one accessibility value: public access rights (e.g., if the only access is through private land; no access = one, full access = five), parking availability (number of spaces, cost, distance from site; parking difficult and/or expensive = one, parking easy with no cost = 5), physical effort required to reach the site (difficult = one, easy = five), distance from large populated areas (far = one, close = five), and topography of shore in allowing for easy tidepooling/collecting (difficult = one, easy = 5).

Although this scaled value was subjective, it provided, in our opinion, a strong characterization of general usage at a site. Recording actual numbers of visitors over time was beyond the realm of this study as it would have required simultaneous and repeated surveys of usage at each of the sites. Nevertheless, repeated visits (once per month) and observations of usage at seven of the sites after the scaled level of human use was determined were consistent with the estimate of use during one-time visits. Due to the imprecision of qualitative data of human use, sites were divided into two main categories, higher and lower-usage.

Because of difficulty in finding low-use sites in southern California and high-use sites in northern California, in some cases the scaled human-use values for sites put into different use categories in two different regions were similar (Table 1). For example, 2.8 was classified as low use at Pt. Fermin in Los Angeles County, but 2.5 was high use at Pt. Pinos in Monterey County. However, pairing the sites corrects for any error this may cause. Furthermore, comparisons of human use scales for higher and lower-use sites revealed significantly different scales (Paired t-test, $t = 12.9$, df $= 9$, $p < 0.001$).

MR Effectiveness

To assess whether regulatory MRs protect or enhance the abundance of intertidal mussels and their associated species, we compared mussel populations and communities in sites protected from harvesting by law to those in non-protected sites. Although some MMAs are not regulatory in nature, this study investigated MRs where collecting of mussels is banned by law and included a University of California Reserve, a State Marine Conservation Area, and numerous State Parks or Beaches. The year of establishment of these MRs varied but most were established before



Human Use Pair

Pair	High	Low
H1	Ocean Beach	Carlsbad
H2	Treasure Island	Monarch Bay
H3	Shaw's Cove (Low use portion)	Shaw's Cove (high use portion)
H4	Corona del Mar (Low use portion)	Corona del Mar (High use portion)
H5	Point Fermin (Low use portion)	Point Fermin (High use portion)
H6	Anacapa Island, Cat Rock	Anacapa Island, Frenchy's Cove
H7	Coal Oil Point	Government Point
H8	Montana de Oro (Low use portion)	Montana de Oro (High use portion)
H9	Point Pinos	Hopkin's Marine Station
H10	Natural Bridges	Bolinas Point

MLR Pair

Pair	Protected	Not Protected
M1	Carlsbad	Ocean Beach
M2	Leo Carillo	Reef Point
M3	Coal Oil Point	Goleta Point
M4	Montana de Oro (Low use portion)	Morro Bay
M5	Cayucos South	Cayucos North
M6	Shelter Cove	Kibesillah Hill
M7	Trinidad	Russel Chambers Memorial

Fig. 1 Map of the California coast with sites sampled for both human use comparisons and MR effectiveness. Sites were paired in the human use study with a low and high-use site within each pair. Some pairs had both a low and high human use area within one site. Sites to study MR effectiveness were paired with a site protected by law from collecting and an unprotected site within each pair

the 1970s and thus have been protected for several decades. Seven pairs of sites (Fig. 1, Table 1) in close proximity to each other were matched, with one site being protected as a MR while the other site was not afforded protection. Nondestructive field measurements were taken at all seven pairs of sites, and plots were harvested at four pairs. Sites were paired so that access and the level of human use within a pair was similar (paired t-test, $t = 0.11$, df $= 6$, $p = 0.915$). This was done to ensure that we did not compare, for example, an unprotected site that was difficult to access with a protected site that was easy to access and thus had high human visitation. This type of comparison would bias the results towards MRs being ineffective.

Similar to the selection of sites comparing human use, it was difficult to find pairs that were very similar in topography, exposure, and geology as well as accessibility. Therefore, some site pairings were not ideal, but were the most comparable available. The weakest of the site pairs were Carlsbad/Ocean Beach and Coal Oil Point/Goleta Point, as described above.

Table 1 Site name, abbreviation, location, county, and scaled level of human use of sampled sites

Site name	Site abbreviation	Location		County	Scale of use	Level of use	Protection status	Pair code	Harvest sampling
Ocean Beach	OCB	32.4438	117.1519	San Diego	4.7	High	Unprotected	H1, M1	*
Carlsbad State Beach	CBD	33.0645	117.2041	San Diego	2.5	Low	Protected[a]	H1, M1	*
Monarch Bay	MON	33.2903	117.4356	Orange County	2.3	Low		H2	
Treasure Island	TRE	33.3048	117.4533	Orange County	4.9	High		H2	
Shaw's Cove	SHW-L	33.3242	117.4757	Orange County	2.2	Low		H3	
Shaw's Cove	SHW-H	33.3242	117.4757	Orange County	5.0	High		H3	
Corona Del Mar	CDM-L	33.3524	117.5207	Orange County	2.2	Low		H4	*
Corona Del Mar	CDM-H	33.3524	117.5207	Orange County	4.8	High		H4	*
Point Fermin	PTF-L	33.4220	118.1717	Los Angeles	2.8	Low		H5	
Point Fermin	PTF-H	33.4226	118.1709	Los Angeles	5.0	High		H5	
Leo Carillo State Park	LEO	34.0237	118.5559	Los Angeles	3.9		Protected[a]	M2	
Reef Point	RPT	34.0356	118.5944	Ventura	3.8		Unprotected	M2	
Anacapa Island, Frenchy's Cove	ANFC	34.0025	119.2436	Ventura	2.9	High		H6	
Anacapa Island, Cat Rock	ANCR	34.0019	119.2509	Ventura	1.4	Low		H6	
Goleta Point	GOL	34.2417	119.5037	Santa Barbara	4.3		Unprotected	M3	
Coal Oil Point	COP	34.2424	119.5241	Santa Barbara	3.9	High	Protected[b]	H7, M3	*
Government Point	GOV	34.2660	120.2739	Santa Barbara	1.3	Low		H7	*
Montana de Oro State Park	MDO-L	35.1636	120.5324	San Luis Obispo	2.3	Low	Protected[a]	H8, M4	*
Montana de Oro State Park	MDO-H	35.1633	120.5322	San Luis Obispo	4.9	High		H8	*
Morro Bay	MBY	35.2201	120.5210	San Luis Obispo	1.7		Unprotected	M4	
Cayucos South State Beach	CAS	35.2626	120.5417	San Luis Obispo	2.8		Protected[a]	M5	
Cayucos North	CAN	35.2626	120.5417	San Luis Obispo	2.1		Unprotected	M5	
Point Pinos	PTP	36.3706	121.5401	Monterey	2.5	High		H9	
Hopkin's Marine Lab	HMS	36.3706	121.5401	Monterey	1.3	Low		H9	
Natural Bridges	NAT	36.5656	122.0344	Santa Cruz	3.4	High		H10	*
Bolinas Point	BOL	37.5413	122.4334	Marin	1.6	Low		H10	*
Kibesillah Hill	KEB	39.3614	123.4719	Mendocino	1.9		Unprotected	M6	
Shelter Cove	SHC	40.0166	124.0440	Humboldt	2.4		Protected[c]	M6	
Russel Chambers Memorial	RCM	40.2051	124.2152	Humboldt	1.8		Unprotected	M7	
Trinidad State Beach	TRI	41.0214	124.0705	Humboldt	2.2		Protected[a]	M7	

For those sites testing the effects of human use, sites were categorized into low or high levels of use within a pair. For those sites testing the effectiveness of regulatory marine reserves (MRs), the protection status and designation are given. Study sites are coded based on the pair number and whether the site was used as a human use pair (H) or a MR pair (M). As indicated, a number of the sites were sampled with a harvest method to determine the mussel biomass, densities of adult and juvenile mussels, mussel length, and diversity of fauna associated with the bed

[a] State Park or Beach; [b] UC Reserve; [c] State Marine Conservation Area

Data Collection

Mussel cover and bed thickness were measured nondestructively at all sites. At each location, one to three transects of varying length were haphazardly placed inside the boundaries of mussel beds, avoiding the lower and upper limits of the bed to avoid edge effects. Ten 0.5 × 0.7-m quadrats were randomly placed along the transect lines and mussel cover estimated using a point intercept method in which mussel presence beneath 100 uniformly distributed points on a grid in each quadrat was recorded. Depending on the size of the mussel bed and time available for sampling, up to an additional 46 more quadrats were randomly placed within the mussel bed and the percent cover measured. We chose five of the original ten quadrats with the highest mussel cover for further measurements. We targeted quadrats with highest mussel cover to ensure that further measurements regarding the mussel bed and its community were taken where mussels were present (as opposed to gaps in the mussel bed). However, at some sites with many gaps within the mussel bed, this could not be avoided. In the five chosen quadrats, mussel bed thickness was measured by pushing a steel pin through the bed until it reached the understory rock in twenty grid

points haphazardly chosen within a plot. The mean thickness of the 20 points was calculated for each of the 5 plots.

To measure further mussel population variables and to quantify bed-associated diversity of macroinvertebrates, we destructively harvested a 300-cm^2 plot directly in the center of each of the previously chosen five quadrats at a portion of the sites. Harvest sampling was approved by the California Department of Fish and Game and the MR or State Park or Beach managers when applicable. During harvest sampling, all fauna as well as sediment and debris from each plot were collected and fixed in 10–15% formalin seawater. Mussel biomass (wet weight of shell and tissue) was measured after all organisms attached to the shell of the mussel were removed and any excess water within the shell drained. The density of adult mussels (≥15-mm shell length) and density of juvenile mussels (<15-mm shell length) was determined. The shell lengths of all adult mussels were measured and size frequency distributions were constructed. In addition, we quantified the diversity of macrofauna associated with the mussel bed by counting and identifying, to the lowest taxonomic level possible, all sessile and mobile macroinvertebrates that were visible with the naked eye; microfauna were not quantified. Although quantified, amphipods were removed from analyses as they were likely under sampled due to their highly mobile nature and difficulty in capturing them. Macroalgae were not quantified as it was difficult to determine if seaweeds were attached or loose pieces that were present in the mussel bed. Shannon-Wiener and Pielou's species diversity indices were calculated using macroinvertebrate densities (Pielou 1975).

Statistical Analyses

Statistical analyses were conducted using Minitab 13.2 software. The mean of each variable was calculated for each site and analyzed using a Paired *t*-test with either human use or protection status as the fixed factor. Size frequency distributions were compared using Kolmogorov-Smirnov tests for each pair.

Results

Impacts of Human Visitation

In every case, percent cover of mussels was lower in sites subjected to higher levels of use compared to lower-use sites within a pair (Fig. 2a). Mean cover at the higher use sites was significantly lower than the lower use site (Table 2a). Bed thickness was also lower in the higher-use sites in all but one of the matched pairs (Fig. 2b) and was found to be significantly different (Table 2a).

Biomass of mussels was always lower at sites receiving higher levels of human visitors within a pair, with differences in biomass among sites within a matched pair ranging from 11.6 kg m^{-2} to 48.5 kg m^{-2} (Fig. 3a). In four of five matched pairs, density of adult mussels within a pair was lower at sites receiving higher levels of human disturbance (Fig. 3b). Both biomass and adult densities were significantly lower at the high-use sites as compared to the low-use sites (Table 2a). In contrast, the density of juvenile mussels (<15 mm) was similar among all sites except Carlsbad, which had an extremely high density of juveniles (Fig. 3c). Juvenile densities were similar between low and high-use sites (Table 2a).

Mean length of mussels measured within harvested plots was smaller in higher-use sites in 4 of 5 paired comparisons, though differences were small and not significant (Fig. 3d; Table 2a). Because individual sizes often are not normally distributed, mean length is often not sensitive to differences in size distributions. Examination of the size frequency distributions revealed that the lower human use sites had a higher frequency of larger individuals as compared to the higher-use site within a pair (Fig. 4). Kolmogorov-Smirnov tests showed significant ($p < 0.05$) differences in size distributions for all five pairs.

In contrast to mussel population measures, the diversity of species associated with the mussel bed was not affected by level of human use; the level of human use was not significant for any of the three diversity measures (Table 2a). Species richness was low for most sites (approximately 20 species), particularly at Government Point (14 species, Fig. 3e). Pielou's Evenness and the Shannon-Wiener diversity index showed a large difference only for the weakest matched pair at Government Point and Coal Oil Point (Fig. 3f, g).

MR Effectiveness

Field measures of mussel cover and bed thickness were not significantly different between regulatory Marine Reserves and unprotected sites (Table 2b). Mussel cover was similar for most site pairings except for two pairs (Fig. 5a). In one of these pairs, cover was higher at the protected site while the other pair showed the opposite pattern. Mussel bed thickness was higher in the protected sites in three of the seven pairs while it was lower in two of the pairs (Fig. 5b).

Lab measures of mussel population variables were consistent with the field results, with all measures similar in both protected and unprotected sites (Table 2b). Although there are large differences in biomass and both adult and juvenile densities within some pairings, there was no consistent pattern (Fig. 6a, b, c). Size frequency distributions yielded a weak pattern with a significantly higher

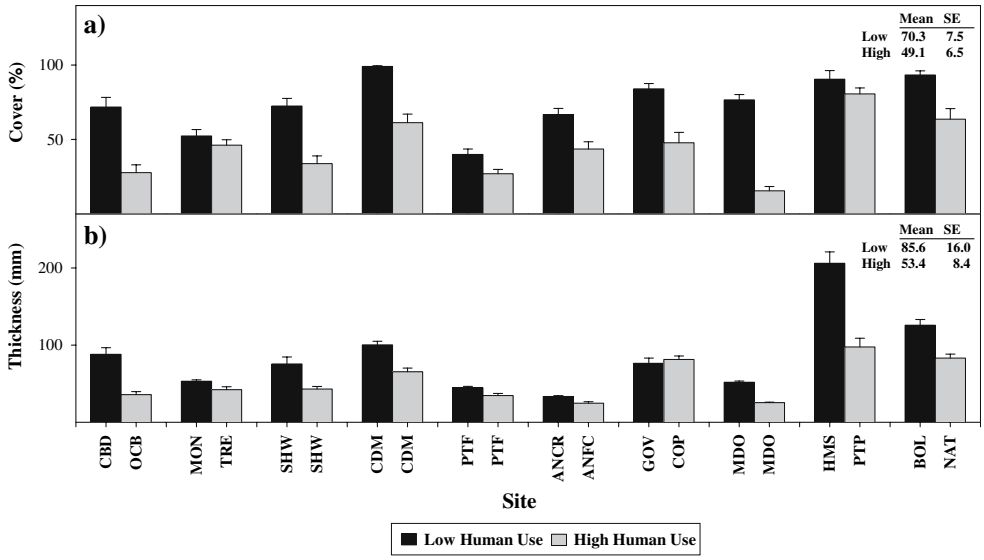


Fig. 2 Comparison of field measures (mean ± SE) of (**a**) mussel cover (%) and (**b**) bed thickness (mm) at paired low and high-use sites along the coast of California. Mean variables (± SE) are indicated for grouped low and high-use sites in which paired *t*-tests where conducted (cover and thickness $p < 0.05$). Site abbreviations are located in Table 1

Table 2 Paired *t*-test results testing: (**a**) the impacts of human visitation and (**b**) the effectiveness of regulatory marine reserves on mussel population variables and community diversity

	(**a**) Impacts of human use (H-L)				(**b**) MR effectiveness (MR-NP)			
	p-value	*t*-Value	95% CI for mean difference	df	*p*-value	*t*-Value	95% CI for mean difference	df
Mussel cover (%)	0.042	−2.38	−41.3, −1.0	9	0.787	−0.28	−25.8, 20.5	6
Mussel bed thickness (mm)	0.011	−3.18	−55.1, −9.3	9	0.604	0.55	−25.7, 40.5	6
Mussel biomass (kg/m^2)	0.023	−3.60	−42.1, −5.4	4	0.776	0.31	−46.4, 56.4	3
Density adult mussels (≥15 mm)	0.044	−2.90	−2390, −50	4	0.676	−0.46	−4537, 3388	3
Density juvenile mussels (<15 mm)	0.593	−0.58	−8731, 5712	4	0.760	−0.33	−18028, 14599	3
Mussel length (mm)	0.075	−2.40	−16.1, 1.2	4	0.534	0.70	−15.5, 24.2	3
Species richness	0.305	1.20	−2.0, 4.9	4	0.641	−0.52	−8.1, 5.8	3
Pielou's evenness	0.722	−0.38	−0.25, 0.19	4	0.143	−1.98	−0.25, 0.06	3
Shannon-Wiener Diversity index	0.870	−0.17	−0.25, 0.22	4	0.159	−1.86	−0.38, 0.10	3

Sites within close proximity were paired together with: (**a**) one site subjected to high levels of human use (H) and one site with low human use (L) or (**b**) one site protected by law from harvesting (MR) and one site unprotected (NP). Mean variables were calculated for each site in the paired analysis

frequency of larger individuals within protected sites at 3 of 4 pairs (Kolmogorov-Smirnov tests, $p < 0.05$; Fig. 7), while one pair revealed a significantly higher frequency of larger individuals within the unprotected site (Kolmogorov-Smirnov test, $p < 0.05$; Fig. 7).

Although some differences in species richness were present among sites within a pair, there was no consistent pattern (Fig. 6e). Species richness was not significantly different between protected and unprotected sites (Table 2b). The diversity of species within the mussel bed, measured as Pielou's Evenness and Shannon-Wiener Diversity Index, were often higher in sites not protected from collecting within a pair (Fig. 6f, g). However, a Paired *t*-test (Table 2b) yielded non significant differences between MRs and unprotected sites.

Discussion

Our data indicate that human use of rocky intertidal zones over a large geographic scale had markedly detrimental impacts to mussels. Higher-use sites located over approximately 1000 km of the California coast had significantly lower mussel population variables (cover, bed thickness, mussel biomass, and mussel abundance) than lower-use sites and exhibited a shift in the size structure of the populations towards smaller individuals. Previous work in many locations around the world investigating the impacts of human activities (McLachlan and Lombard 1981; Beauchamp and Gowing 1982; Castilla and Bustamante 1989; Pombo and Escofet 1996; Brown and Taylor 1999; Ambrose and Smith 2005), in conjunction with our results,

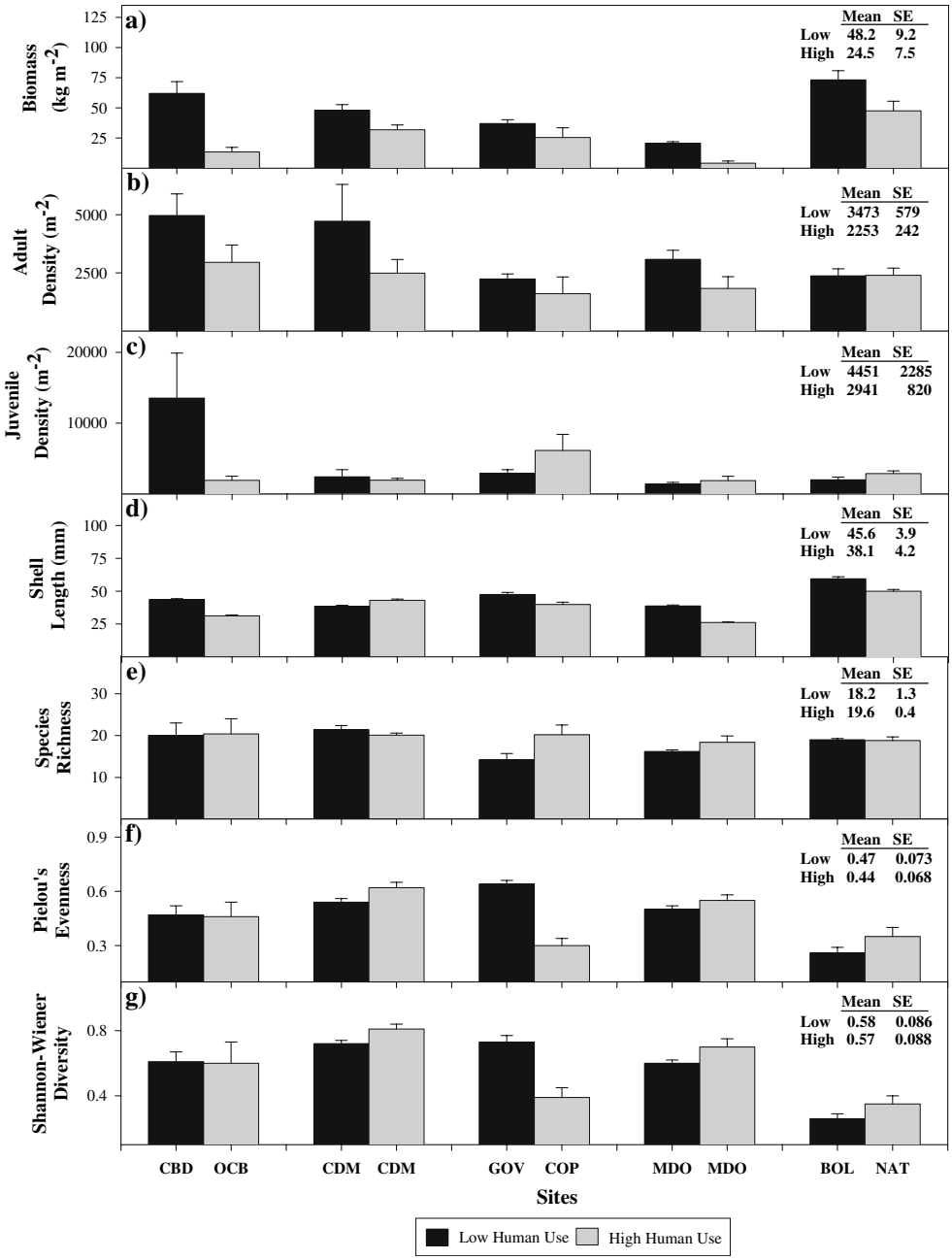


Fig. 3 Comparison of (**a**) mussel biomass (kg m^{-2}); (**b**) density of adult (≥15 mm) and (**c**) juvenile (<15 mm) mussels (m^{-2}); (**d**) mussel length (mm); (**e**) species richness; (**f**) Pielou's Evenness; and (**g**) Shannon-Wiener Diversity Index collected from harvested plots at paired low and high-use sites. Species richness and diversity indices were calculated from invertebrate densities. Mean variables (± SE) are indicated for grouped low and high-use sites in which paired *t*-tests where conducted (biomass, adult density $p < 0.05$, juvenile density, length, richness, Pielou's, Shannon-Wiener $p > 0.05$). Site abbreviations are located in Table 1

demonstrates a strong association between human activities and reduced abundance and size structure of marine populations.

For most intertidal species negatively affected by human activities, depleted populations are usually linked to one type of activity or another. For example, trampling has been shown to reduce cover of seaweeds (Zedler 1978; Povey and Keough 1991; Keough and Quinn 1998; Brown and Taylor 1999; Schiel and Taylor 1999; Denis 2003) and abundances of certain invertebrates (Zedler 1978; Brosnan and Crumrine 1994; Casu and others 2006) while collecting reduces certain target species of value (Branch 1975; McLachlan and Lombard 1981; Castilla and Duran 1985; Fairweather 1991; Lasiak 1991; Keough and others 1993; Pombo and Escofet 1996). Mussels are unique in that they are affected by a number of different human activities. Mussels, a large and conspicuous element of rocky intertidal communities, are preferred for both human consumption and fishing bait (Smith personal observation 2002; Murray and others 1999; Ambrose and Smith 2005), so they are commonly targeted for harvesting. Although their shells are resistant to wave forces, they also can be crushed when trampled (Brosnan and Crumrine 1994; Smith and Murray 2005). In addition, a compounded

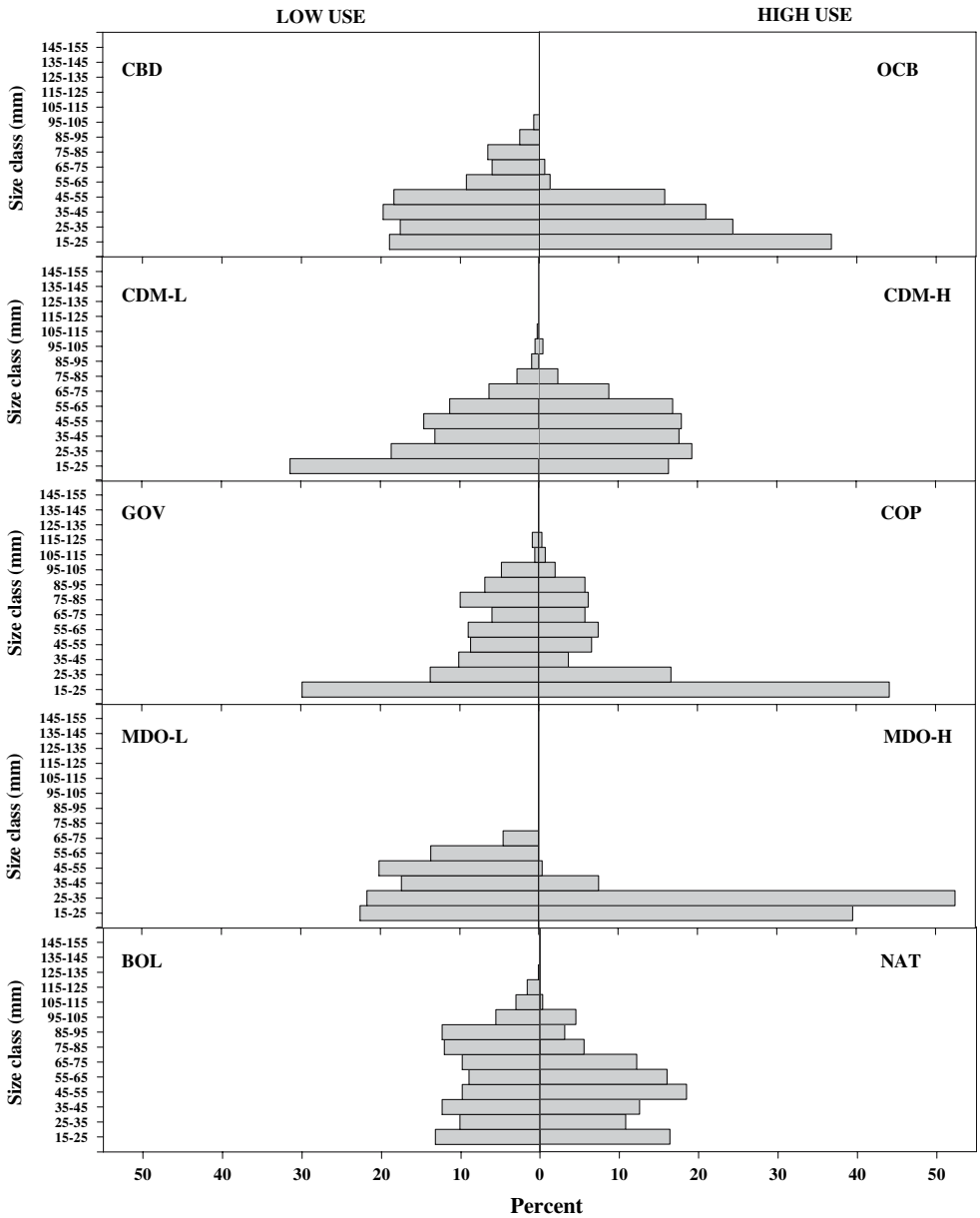


Fig. 4 Size frequency distributions of mussels measured from harvested plots at 10 sites along the California coast. Figures are paired with a site subjected to low human use next to its paired high human use site. Site abbreviations are located in Table 1. All pairs were separately analyzed using a Kolmogorov-Smirnov test and were significantly different ($p < 0.05$ for each pair)

indirect effect of removal or crushing results in losses of neighboring mussels due to the weakening of the attachment strengths of surrounding individuals (Smith and Murray 2005). Their location also makes them vulnerable to human activities, since they are frequently found at relatively high intertidal heights on easily accessible rocky benches. Thus, various aspects of mussel biology and human behavior make mussels vulnerable to multiple and frequent human activities in the rocky intertidal.

Reduced abundances of a particular species also may have indirect, cascading effects on other species and cause shifts in the structure of the community (Moreno and others 1984; Duran and Castilla 1989). For example, in areas where the abundance of an intertidal limpet was reduced because of over collecting, the intertidal zone community shifted to one dominated by macroalgae (Moreno and others 1984). Mussels are important ecosystem engineers, providing food, shelter, refuge from predators, and space for settlement for a large number of associated species (Kanter 1980; Suchanek 1992). The well-known dependence of hundreds of species on mussels would suggest that a reduction in mussel populations would result in impacts to mussel-associated species. Somewhat surprisingly, we did not find that reductions in mussel populations in high-use areas led to less diverse mussel-associated communities. Biodiversity within thick beds at lower-use sites were similar to those in thin, patchy beds at higher-use sites.

The lack of a detected indirect effect of human use contradicts previous findings that biodiversity in this community is directly related to complexity of the bed

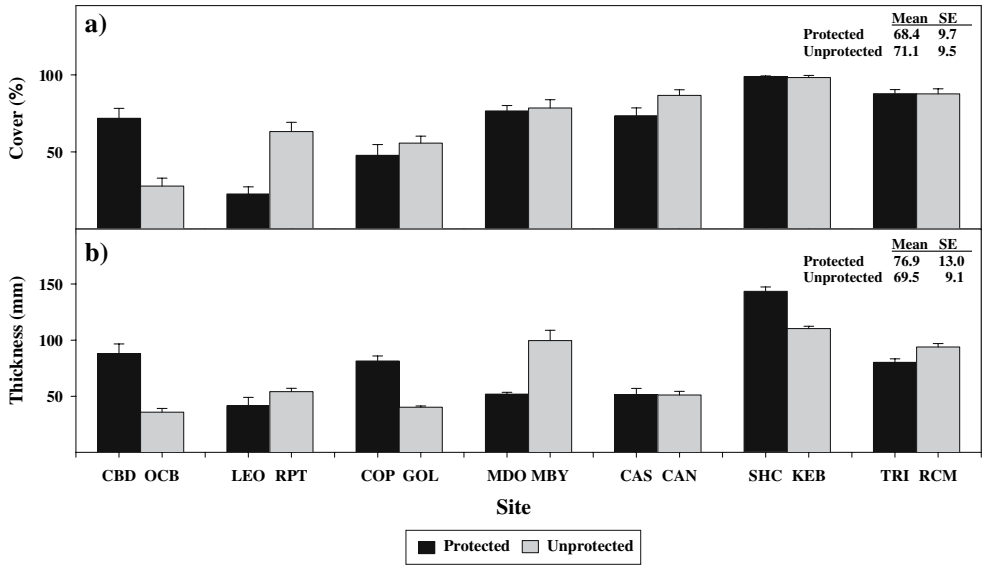


Fig. 5 Field measurements of (**a**) mussel cover (%) and (**b**) bed thickness (mm) at paired protected and unprotected sites along the coast of California. Mean variables (± SE) are indicated for grouped protected and unprotected sites in which paired *t*-tests where conducted (cover and thickness $p > 0.05$). Site abbreviations are located in Table 1

(Kanter 1977), and statistically and positively correlated with mussel bed thickness (Kanter 1979) and biomass (Smith 2005). However, the relationship between biomass and richness was recently found to be weakened as mussel biomass declined, with the relationship disappearing in beds with a biomass lower than 40 kg m^{-2} (Smith 2005). Since mussel beds measured in this study often had biomass less than 40 kg m^{-2}, cascading effects on bed associated biodiversity declines were not present. In addition, studies previously noting the relationship between biodiversity and the complexity or thickness of the bed (Kanter 1977, 1979) were conducted in the mid 1970s, when species richness of the bed was much higher than that found during the same sampling period as this study (Smith and others 2006). Because diversity of species within a mussel bed in this study was already heavily reduced, species richness may have been too low to detect further effects of human activities.

No-take Marine Protected Areas (MPAs) or, in this case regulatory marine reserves, are widely viewed as an effective management tool for protecting biodiversity and intensely harvested species (Ticco 1995; Agardy 1997). The population density, biomass, and size of subtidal fish and invertebrates are often higher in no-take reserves than outside (see Halpern 2003), including locations within southern California (Tetreault and Ambrose 2007). Rocky intertidal marine reserves in Chile (Moreno and others 1984; Castilla and Duran 1985; Moreno and others 1986; Oliva and Castilla 1986; Castilla and Bustamante 1989; Duran and Castilla 1989; Godoy and Moreno 1989: see summary Castilla 1999), Australia (Keough and others 1993), and South Africa (Lasiak 1991) also have been shown to be effective, with higher densities and sizes of target populations in reserves as compared to outside reserves. In contrast, we found little difference in mussel populations found in reserves compared to non-reserves, despite the MRs used in this study being established several decades ago, theoretically allowing ample time for recovery from pre-protection depletion from anthropogenic use. The discrepancy with other studies is most likely related to two factors: enforcement of reserve regulations and the range of human activities that were restricted.

Although there are regulations prohibiting harvesting of intertidal species in the MRs we studied, other studies have concluded that southern California marine reserves, as currently designed and patrolled, may not be effective in protecting and enhancing rocky intertidal marine life (Murray 1998; Murray and others 1999; Ambrose and Smith 2005). These studies indicate that, within urban southern California, there is little enforcement of regulations prohibiting collection so collecting continues to occur to some degree (Murray 1998; Murray and others 1999; Ambrose and Smith 2005; Ambrose and Smith personal observation 2002). Although it is documented that collecting continues to occur, it is unclear if the frequency of collecting is similar within MRs and non-reserves; several studies have characterized and quantified human activities in rocky intertidal zones in southern California (Murray 1998; Murray and others 1999; Ambrose and Smith 2005), yet collecting rates inside and outside of MRs have not been directly compared.

Additionally, and possibly more importantly, current regulations for the marine reserve we studied do not protect

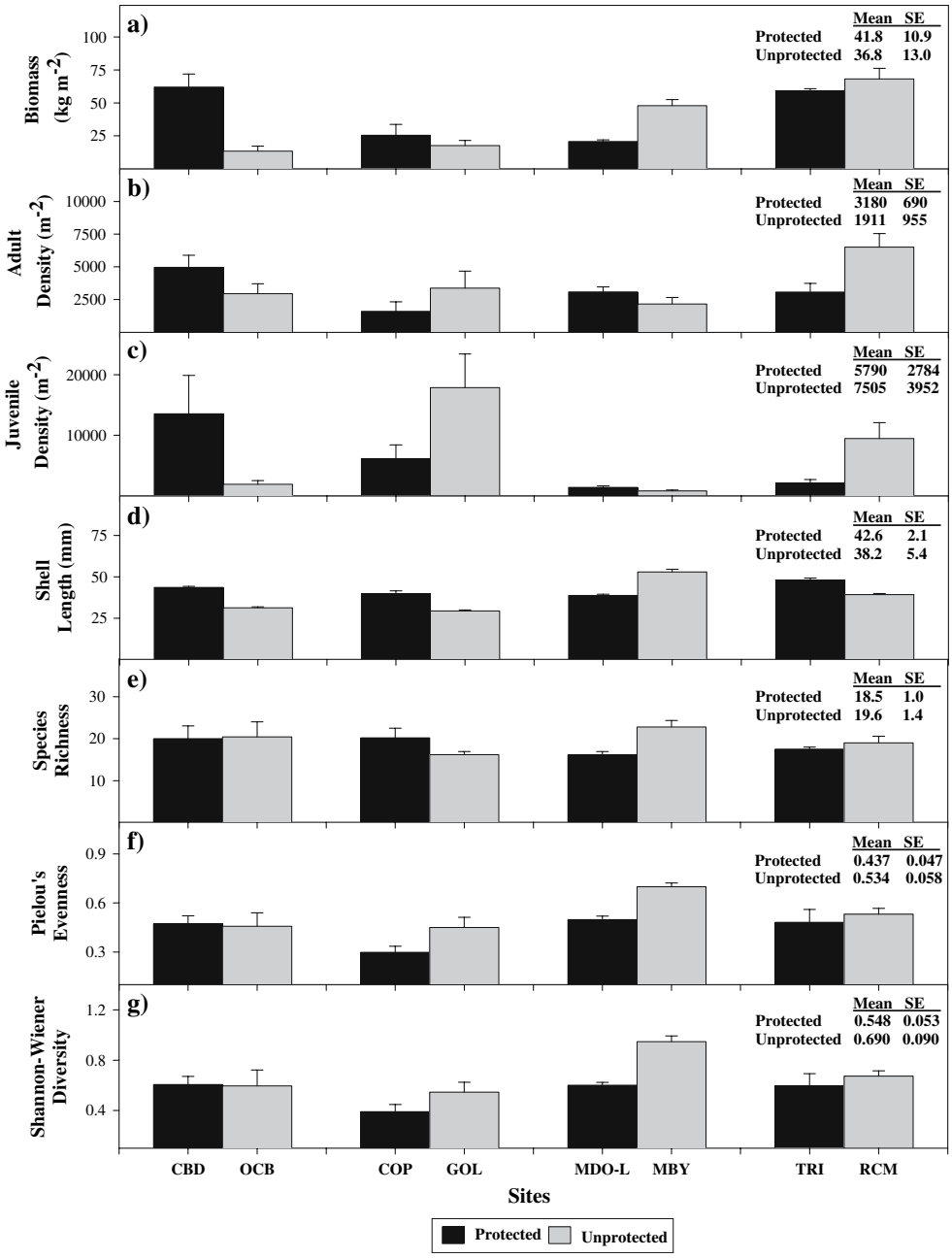


Fig. 6 Measures of (**a**) mussel biomass (kg m^{-2}); (**b**) density of adult (≥15 mm) and (**c**) juvenile (<15 mm) mussels (m^{-2}); (**d**) mussel length (mm); (**e**) species richness; (**f**) Pielou's Evenness; and (**g**) Shannon-Wiener Diversity Index collected from harvested plots at paired protected and unprotected sites along the coast of California. Species richness and diversity indices were calculated from invertebrate densities. Mean variables (± SE) are indicated for grouped protected and unprotected sites in which paired *t*-tests where conducted (biomass, adult density, juvenile density, length, richness, Pielou's, Shannon-Wiener $p > 0.05$). Site abbreviations are located in Table 1

intertidal biota from anthropogenic disturbances such as trampling and handling. In our study, both reserves and nonreserves had open access and relatively similar levels of human visitation; even if collecting intensity was reduced, there would be similar amounts of trampling and handling. Nonharvesting activities have been shown to negatively affect a number of rocky intertidal species (Beauchamp and Gowing 1982; Bally and Griffiths 1989; Povey and Keough 1991; Brosnan and Crumrine 1994; Brown and Taylor 1999; Schiel and Taylor 1999; Smith and Murray 2005). In contrast to the reserves we studied, reserves in Chile and Australia that were effective in enhancing intertidal populations completely excluded humans. In these cases, the reserves were effective in enhancing intertidal populations because all perturbations from direct human activities were completely absent.

Although reserves can be effective tools for protecting and managing marine populations, their effectiveness depends on the regulations matching the cause of the impacts. When harvesting is the main source of perturbation, such as in subtidal areas not subjected to other detrimental impacts such as trampling, then harvest restrictions can be sufficient to enhance populations with the reserve boundaries (Halpern 2003). Allison and others (1998) recognized that marine reserves may be insufficient if they are not isolated from other perturbation. For

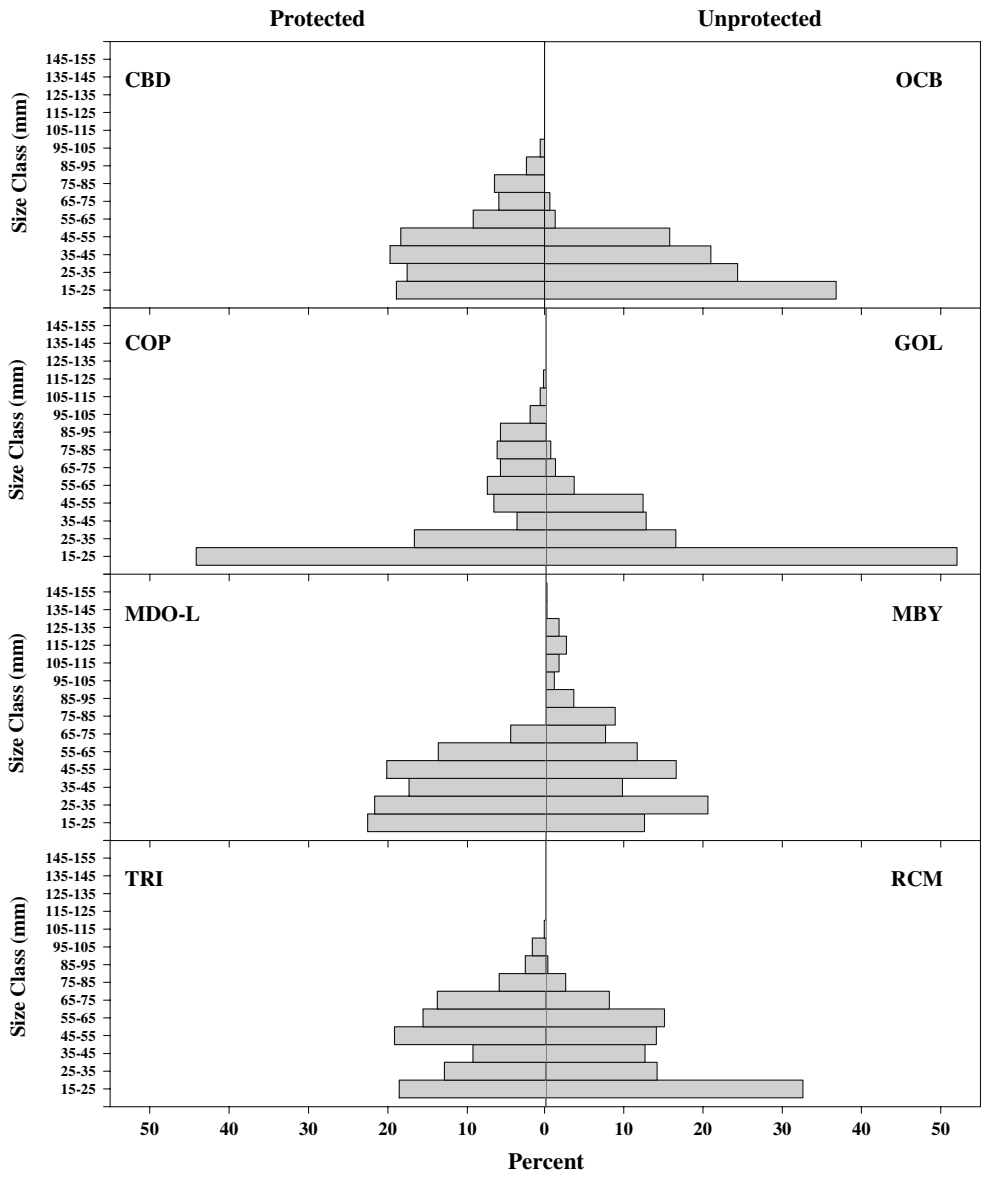


Fig. 7 Size frequency distributions of mussels measured from harvested plots at 8 sites along the California coast. Figures are paired with a protected site next to its paired unprotected site. Site abbreviations are located in Table 1. All pairs were separately analyzed using a Kolmogorov-Smirnov test and were significantly different ($p < 0.05$ for each pair)

example, coral reef populations in no-take reserves are still threatened by damage from tourist activities such as snorkeling that are not regulated under reserve regulations (Plathong and others 2000). In addition, subtidal bryozoan populations in a Mediterranean Marine Protected Area were negatively affected by the unintentional abrasive impacts caused by recreational divers (Garrabou and others 1998). When the main sources of perturbation for rocky intertidal systems include trampling as well as harvesting, then reserve status will only be effective if all of those activities are restricted, as has occurred in Chile and Australia (Keough and others 1993; Castilla 1999). This is particularly evident on the shores of Australia, where reserve status was effective when intertidal populations were protected both by legislation and by mechanical barriers resulting in exclusion (Keough and Quinn 2000); removal of the mechanical barrier was followed by decreases in the size of target populations, despite the continued legal protection, suggesting that exclusion, not legislative protection, was the dominant force in protecting intertidal flora.

The current regulatory marine reserve system in California needs to be re-evaluated and improved. With few exceptions, intertidal reserves in California aim to protect intertidal populations and diversity through prohibitions of manual harvesting of intertidal organisms. Our results show that this approach is not sufficient to protect mussel populations, and Murray and others (1999) have shown that this is a problem for other species as well. In areas where many people visit intertidal habitats for purposes other than collecting (Murray and others 1999; Ambrose and Smith 2005), many organisms will be affected by trampling,

turning of rocks, and handling. In cases such as these, effective protection of rocky intertidal communities will require an approach that goes beyond the singular focus on collecting to reduce the full suite of impacts on intertidal organisms.

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