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RESEARCH ARTICLE

Ecological impacts on the limpet *Lottia gigantea* populations: human pressure over a broad scale on island and mainland intertidal zones

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Abstract Here long-term monitoring data taken at 33 sites in southern and central California coast and islands were used to evaluate the size structure of the large intertidal limpet, *Lottia gigantea* in restricted-access and in easily accessible intertidal zones that encompass a wide range of ecological variables. Using multi-dimensional analysis of population size structures, we found that sites on islands and strictly protected mainland sites have significantly larger median limpet sizes and a greater range of limpet sizes than unprotected mainland sites, while no pattern occurs in latitudinal or regional comparison of sites. Although intertidal predators such as oystercatchers were not the primary focus of the monitoring efforts, extensive natural history notes taken during sampling visits support the argument that predation was not a primary cause for the size structure differences. Finally, substratum differences were determined not to have biased the observation of larger limpets in protected sites. In regard to human interactions with limpets, we conclude that the degree of enforcement against poaching is the better predictor of limpet size structure than proximity to population centers or visitation to intertidal sites.

Introduction

Separating the effects of human impacts, ecological interactions, and environmental variability on population parameters is an important goal in applied ecology. Key questions about whether or not species are responding to climate change, where to situate habitat reserves and how to manage fisheries depend on identifying forces driving population dynamics. These drivers may be extremely difficult to study in a controlled fashion across a wide range of sites, due to the complexity of interacting factors (e.g., climate-related changes to upwelling regimes affecting species interactions,

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(see Sanford 1999) non-linear responses of populations to environmental factors (Welch et al. 1998) and the occurrence of rare, high-impact events (such as a single intensive poaching episode). Moreover, because these driving forces may vary spatially and temporally in strength, even the most carefully controlled study carried out at one or a few sites may fail to identify the factors affecting population dynamics over a large part of a species range. This problem is especially pressing because environmental change and human pressures on populations act at regional and in some cases global scales, rather than the local scale at which most field experiments are conducted.

The historical descriptive approach, which relies on observational data to test multiple alternative hypotheses, has been used increasingly to study population dynamics over broad spatial scales, including for example, changes in fishery populations (Francis and Hare 1994) and species responses to climate change (McGowan et al. 1998; Sagarin et al. 1999). A historical descriptive approach is particularly appropriate where unpredictable and highly variable historical contingencies have likely affected study populations (Francis and Hare 1994). This approach is greatly strengthened when data are available from multiple locations with different environmental characteristics so that multiple hypotheses can be tested simultaneously (Francis and Hare 1994; Sagarin 2001).

Population size structures, which are affected by environmental change, ecological interactions, and in many cases, human exploitation, are an important indicator of population status that can be used comparatively across sites and through time to identify forces controlling population dynamics (Lewis et al. 1982; Cowen 1985; Zacherl et al. 2003). They can also be used to track losses of large individuals from populations, which are often the target of exploitation by humans (Haedrich and Barnes 1997; Rochet and Trenkel 2003).

The large intertidal limpet *Lottia gigantea* (Sowerby 1834) is a species whose ecological role is strongly affected by body size. Large *L. gigantea* are territorial grazers that "farm" home areas, estimated in one study to average 1,000 cm^2, to maintain a cover of microalgae to support growth and reproduction (Stimson 1970). Large limpets are able to exclude smaller conspecifics, other limpets, and predatory gastropods from their home territories. Moreover, this limpet is protandrous, meaning that individuals change from male to female with maturity (Wright and Lindberg 1982; Lindberg and Wright 1985), resulting in the tendency for larger individuals to be female (Kido and Murray 2003). Thus, even in the absence of significant changes in limpet density, a loss of large individuals can result in loss of reproductive output and encroachment of habitat by algae, mussels and other invertebrates, and bring about dramatic and lasting effects on intertidal communities (Lindberg et al. 1987, 1998; Kido and Murray 2003).

Recent work performed at a limited number of sites in southern California and northern Mexico has demonstrated that human access to intertidal sites is strongly correlated with reductions in the numbers of large *L. gigantea*, suggesting a response to size-selective human foraging (Pombo and Escofet 1996; Kido and Murray 2003; Roy et al. 2003). Although persuasive, these studies leave unanswered three critical questions. First, what role do geographic differences due to environmental conditions play in shaping *L. gigantea* population size structures? Second, if humans are affecting the structure of *L. gigantea* populations, are impacts most likely related to the cumulative activities of human visitors to intertidal sites or due to a small subset of visitors who actively poach larger *L. gigantea* individuals? Third, what role do non-human predators play in affecting the size structure of limpet populations? Answering the first question will provide a spatially complete understanding of variations in *L. gigantea* population structure, while answering the second and third questions will enable onsite managers to develop improved management structures for protecting coastal marine habitats.

We address these questions by comparing the size structures of owl limpet populations from 33 intertidal sites spread across the southern and central California mainland and the offshore Channel Islands (Fig. 1). These data, obtained by the Multi-Agency Rocky

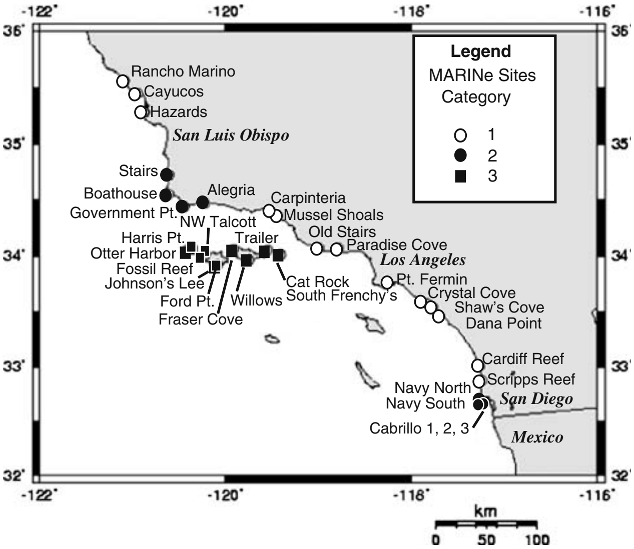

Fig. 1 Map of intertidal study sites, labeled by vulnerability to poaching. Vulnerability is rated from 1 (most vulnerable) to 3 (least vulnerable); see Materials and methods for details

Intertidal Network (MARINe) monitoring program in over 500 sampling visits, are used to evaluate the importance of the following hypotheses to explain site-to-site differences in the size structures of *L. gigantea* populations:

Geographic gradients

Differences in population size structures due to environmental variation across the latitudinal range encompassed by our sites might be expected for two reasons. First, latitudinal gradients in size have been observed in many taxa (Gaston and Tim 2000). Second, our sites span Pt. Conception, a breakpoint between biogeographic provinces marked by sharp differences in nearshore temperature, nutrient availability, wave action, and current flow (Murray and Littler 1981; Doyle 1985; Wares et al. 2001; Zacherl et al. 2003) Pt. Conception is known to separate intraspecific phenotypes (Blanchette et al. 2002) and intertidal community structures (Murray et al. 1980; Murray and Littler 1981; Seapy and Littler 1982; Doyle 1985).

Effects of human foraging

Limpets have been exploited for food by humans on the west coast of North America since prehistoric times (Lindberg et al. 1998; Roy et al. 2003). Humans leave a distinctive foraging signal on limpet size structures because they tend to select the largest individuals in a population. If human foraging is affecting an intertidal population, we would expect to see reductions in the numbers of large individuals in populations inhabiting sites vulnerable to poaching, but not at sites where intertidal resources are protected through enforced restrictions against access or the taking of living resources.

Impacts from intertidal visitation

Visitation to intertidal sites by large numbers of people is a cause for increasing concern among ecologists. Heavily visited sites or areas have been shown to have lower population densities, lower diversity, and lower algal cover than less visited control sites (Murray et al. 1999; Tenera 2003; Ambrose and Smith 2005). A correlation between human visitation to intertidal sites and reduced sizes of intertidal invertebrates, including *L. gigantea*, has been observed (Kido and Murray 2003; Ambrose and Smith 2005). However, this correlation could arise not only as a result of the cumulative activities of large numbers of visitors (e.g., through trampling, dislodging animals, or habitat modification), but also because highly visited sites are also most often frequented by poachers who actively forage for *L. gigantea*. The diversity of our 33 study sites allows us to separate and contrast sites that are heavily visited but protected from collecting and poaching from those sites that are vulnerable to poaching regardless of the level of visitation. If human visitation in general, rather than poaching in particular, primarily affects size structures, we would expect to see the greatest differences between heavily visited and lightly visited sites, rather than between sites that are vulnerable to poaching and those that are protected.

Biological interactions

The black oystercatcher *Haematopis bachmanii* forages on intertidal limpets, including *L. gigantea* (Lindberg et al. 1987). It is not known, however, whether oystercatchers differentially consume the largest limpets in a population, as do human foragers. If oystercatchers have similar foraging effects as humans, we would expect to see similar size structures in owl limpet populations at both sites with high oystercatcher abundance and sites with high vulnerability to poaching. These are typically different sites in our study because oystercatchers strongly avoid areas frequented by humans (Lindberg et al. 1998). Hence, our least vulnerable sites to human foraging, which occur on the Channel Islands, also are the sites with the highest oystercatcher densities. Intertidal communities may also be affected by other limpet predators and by deposition of bird guano, as has been demonstrated in South Africa (Bosman and Hockey 1986). Limpet populations could be affected by guano negatively through toxic effects, or positively, though enhancement of micro-algal growth within limpet habitats.

Sampling biases

Our fixed sample plots are neither randomly selected nor exact replicates of one another, raising concerns about potential biases. An unacceptable bias that affects only a subset of the sites, and thus would affect our conclusions here, could occur if plots were set up at some sites in optimal limpet habitat but not in others. Moreover, changes within the plots through time (e.g., invasion by mussels or erosion of plot substratum) could change the nature of sampling biases. Encroachment by mussels at the time of plot selection or subsequently, for example, is likely to result in a shift in size structure favoring smaller *L. gigantea* (Kido and Murray 2003).

Materials and methods

The MARINe is a consortium of 23 state, federal, university and private organizations that monitors intertidal populations biannually at 34 mainland sites and 23 island sites in 6 different counties in southern and central California. Here, we examine 22 mainland and 11 island sites where the number and shell lengths of *L. gigantea* were determined within three to six fixed, 3.14 m^2 circular plots (most sites have five plots) each spring and fall for 1–15 years, depending on the site (Table 1, Fig. 1). Fixed plots were initially located in optimal *L. gigantea* habitat as indicated by the presence of large numbers and large sizes of owl limpets. A 1 m length of line was attached to a marked center bolt and arced around to form each circular plot. Plots were thoroughly searched and the maximum shell length of each *L. gigantea* encountered was measured to the nearest millimeter using calipers, and then marked with a crayon to avoid scoring duplication. Limpets were never removed from the rock during assessments. Only limpets >15 mm shell length were sampled because of difficulties in consistently distinguishing small *L. gigantea* from other small limpet species that occur in these habitats. We do not expect the omission of limpets <15 mm shell length to bias our analysis because this was done at all sites. In addition to limpet counts and shell length measurements, notes on site and plot conditions and presence and activities of birds, humans, dogs and marine mammals were made during each site visit.

Table 1 Sites in MARINe network used for limpet size sampling

Site name (Abbreviation)	Sampling group[a]	County or island	Latitude (N)	Longitude (W)	First sample	Legal take?[b]
Alegria (ALEG)	UCLA	Santa Barbara	34.47	120.23	Fall 1992	Yes
Boathouse (BOA)	UCSC	Santa Barbara	34.55	120.61	Spring 1992	Yes
Cabrillo I (CAB1)	CNM	San Diego	32.67	117.25	Spring 1990	No
Cabrillo II (CAB2)	CNM	San Diego	32.67	117.25	Spring 1990	No
Cabrillo III (CAB3)	CNM	San Diego	32.67	117.24	Spring 1990	No
Cardiff Reef (CARE)	UCSB	San Diego	33.00	117.28	Fall 1997	No
Carpinteria (CARP)	UCLA	Santa Barbara	34.39	119.52	Fall 2001	No
Cat Rock (ANCR)	CINP	Anacapa Is.	34.01	119.42	Fall 1988	No
Cayucos (CAY)	UCSC	San Luis Obispo	35.45	120.95	Fall 1995	Yes[c]
Crystal Cove (CRCO)	CSUF	Orange	33.57	117.84	Fall 1996	No
Dana Point (DAPT)	CSUF	Orange	33.46	117.71	Fall 1996	No
Ford Point (SRFP)	CINP	Santa Rosa Is.	33.92	120.09	Spring 1988	No
Fossil Reef (SRFR)	CINP	Santa Rosa Is.	33.99	120.24	Spring 1999	No
Fraser Cove (SCFC)	CINP	Santa Cruz Is.	34.06	119.92	Fall 1998	No
Government Point (GPT)	UCSC	Santa Barbara	34.44	120.45	Spring 1992	Yes
Harris Point (SMHP)	CINP	San Miguel Is.	34.07	120.36	Spring 2000	No
Hazard's (HAZ)	UCSC	San Luis Obispo	35.28	120.88	Spring 1996	No
Johnson's Lee (SRJL)	CINP	Santa Rosa Is.	33.91	120.1	Spring 1988	No
Mussel Shoals (MUSH)	UCLA	Ventura	34.36	119.44	Spring 2002	Yes
Navy North (NANO)	UCSB	San Diego	32.69	117.25	Spring 1995	Yes
Navy South (NASO)	UCSB	San Diego	32.68	117.25	Spring 1995	Yes
NW Talcott (SRNW)	CINP	Santa Rosa Is.	34.01	120.22	Spring 1993	No
Old Stairs (OLDS)	UCLA	Ventura	34.07	119.00	Fall 1994	Yes
Otter Harbor (SMOH)	CINP	San Miguel Is.	34.05	120.41	Spring 1988	No
Paradise Cove (PCOV)	UCLA	Los Angeles	34.07	118.79	Fall 1994	Yes
Point Fermin (PTFM)	UCLA	Los Angeles	33.71	118.29	Fall 2002	No
Rancho Marino (RMR)	UCSC	San Luis Obispo	35.56	121.09	Spring 2002	Yes
S Frenchy's Cove (ANSFC)	CINP	Anacapa Is.	34.01	119.41	Fall 1994	No
Scripps Reef (SCRE)	UCSB	San Diego	32.87	117.25	Fall 1997	No
Shaws Cove (SHCO)	CSUF	Orange	33.54	117.78	Fall 1996	No
Stairs (STA)	UCSC	Santa Barbara	34.72	120.61	Spring 1992	Yes
Trailer (SCTR)	CINP	Santa Cruz Is.	34.05	119.55	Fall 1998	No
Willows Anchorage (SCWA)	CINP	Santa Cruz Is.	33.96	119.75	Fall 1998	No

[a] Sampling groups: *CINP* Channel Islands National Park, *CNM* Cabrillo National Monument, *CSUF* California State University Fullerton, *UCLA* University of California Los Angeles, *UCSB* University of California Santa Barbara, *UCSC* University of California Santa Cruz

[b] Legal Take: sites with legal take allow 35 individuals to be taken per day for sport

[c] Sport take was legal at the time of sampling

Analysis of changes in the size structures of monitored *L. gigantea* populations showed no strong or consistent trends (MARINe unpublished data, http://www.marine.gov) through time, so we focused primarily on site to site differences in size structures aggregated over time. Size structures for each site were generated using the mean number of limpets assigned to each 1 mm size bin across all samples at that site. However, traditional statistical approaches to test for site differences among these size structures are limited for several reasons. First, reducing the data to summary statistics such as median or mean sizes avoids some of the statistical limitations, but greatly reduces the information available to make comparisons. Moreover, as with many ecological impact data (Clarke and Warwick 2001), the assumptions for parametric statistics are not met with our data, which have severe departures from normality and equal variances due to the very types of impacts we are trying to study. Finally, the non-parametric two sample Kolmogorov–Smirnov test, which is often used to compare size frequency distributions, is limited to pairs of comparisons and can only determine if two distributions differ, providing no more specific information on the nature of differences between size structures from various pairs of sites (Pacheco and Henderson 1996).

Here we use multivariate statistics in the PRIMER (Version 6) statistical package (Primer-E, Ltd.) to test for significant differences in size structures between sites and between groups of sites. Mean limpet numbers in each size bin were first standardized and compiled to create a cumulative size curve for each site. A similarity matrix based on Euclidean distances was generated based on the curves for each pair of sites using PRIMER. Non-metric multi-dimensional scaling (MDS) was then used to plot centroids representing site population size structures in ordination space. Analysis of similarity (ANOSIM) (Clarke and Green 1988; Clarke and Warwick 2001), a permutation test, was then used to test hypotheses about site to site differences in limpet size structure profiles after grouping sites by relevant categories (e.g., vulnerability to poaching, substratum type, etc., Table 2).

Non-metric multi-dimensional scaling and ANOSIM were used to test the alternative hypotheses described in the Introduction:

Geographic gradients

Two comparisons were used to assess the role of geographical gradients on limpet size structure. First we compared size structures from all mainland sites using the “RELATE” function in Primer 6, which contrasts the similarity matrix created from each site’s size structure (and ordered sequentially from south to north) to a seriation model in which sites closest to one another are the most similar. Second, to assess any effect of crossing the biogeographic boundary at Pt. Conception, we grouped sites into four categories: island sites, mainland sites north of Pt. Conception, mainland sites south of Pt. Conception to Los Angeles and mainland sites south of Los Angeles to the Mexico border and assessed group differences using ANOSIM.

Effects of human poaching

Illegal harvest of limpets (poaching) is likely at many of our sites for several reasons. Based on California Department of Fish and Game regulations and legal designations of our sites, recreational collecting of *L. gigantea* is legal at only 11 of our sites (Table 1), with a daily bag limit of 35 individuals. Commercial harvest of *L. gigantea* is illegal throughout California. Yet multiple observations have been made of people taking far greater than 35 individuals (see Discussion). Moreover, previous studies show that even at intertidal sites designated as habitat reserves, collection activity is common where adequate enforcement is lacking (Murray et al. 1999). Thus, legal status is not a good indicator of sites where *L. gigantea* is most likely to be collected.

Accordingly, we used a qualitative, but objective, three-category scheme to classify the vulnerability of our sites to human foraging based on physical and *enforced* legal limits on collection activity (Fig. 1, Table 2) and used these categories to test for differences in *L. gigantea* size structures using ANOSIM.

> Category 1: sites where extensive collection is possible because access is not restricted by physical (e.g., gates), geological (e.g., steep cliffs) or enforced legal barriers (e.g., law enforcement patrols, gated communities). Some of these sites are close to dense human populations, whereas others are fairly remote. Yet even are remote sites where collection is not enforced and few barriers to access exist, large-scale collection events have been reported (Don Canestro, personal communication from Rancho Marino).
> Category 2: sites on the mainland with little to no expected collection due to well enforced access with gates, enforced collection restrictions, or extreme difficulty of access.
> Category 3: sites on the Channel Islands, which feature almost no resident humans, and in many cases, enforced restrictions against collection or extreme difficulty of access.

Table 2 Categories used for ANOSIM analyses

Site name (Abbreviation)	Region	Vulnerability[a]	Likely visitation	Oystercatchers?[b]	Substratum type[c]
Alegria (ALEG)	Pt C. South	2	Low	Occasional	Soft
Boathouse (BOA)	Pt. C. North	2	Low	Occasional	Soft
Cabrillo I (CAB1)	So. Cal.	2	High	None	Mixed
Cabrillo II (CAB2)	So. Cal.	2	High	None	Mixed
Cabrillo III (CAB3)	So. Cal.	2	High	Rare	Mixed
Cardiff Reef (CARE)	So. Cal.	1	High	None	Hard
Carpinteria (CARP)	Pt. C. South	1	Medium	None	Soft
Cat Rock (ANCR)	Island	3	Island	Common	Hard
Cayucos (CAY)	Pt. C. North	1	Low	Occasional	Soft
Crystal Cove (CRCO)	So. Cal.	1	High	None	Soft
Dana Point (DAPT)	So. Cal.	1	High	None	Conglomerate
Ford Point (SRFP)	Island	3	Island	Common	Soft
Fossil Reef (SRFR)	Island	3	Island	Common	Soft
Fraser Cove (SCFC)	Island	3	Island	Common	Hard
Government Point (GPT)	Pt. C. North	2	Low	Occasional	Soft
Harris Point (SMHP)	Island	3	Island	Common	Conglomerate
Hazard's (HAZ)	Pt. C. North	1	Low	Occasional	Soft
Johnson's Lee (SRJL)	Island	3	Island	Common	Soft
Mussel Shoals (MUSH)	Pt. C. South	1	Medium	None	Hard
Navy North (NANO)	So. Cal.	2	High	Rare	Soft
Navy South (NASO)	So. Cal.	2	High	Rare	Soft
NW Talcott (SRNW)	Island	3	Island	Common	Soft
Old Stairs (OLDS)	Pt. C South	1	High	None	Hard
Otter Harbor (SMOH)	Island	3	Island	Common	Hard
Paradise Cove (PCOV)	Pt. C. South	1	Medium	None	Soft
Pt. Fermin (PTFM)	Pt. C. South	1	High	None	Soft
Rancho Marino (RMR)	Pt. C. North	1	Low	Common	Soft
S Frenchy's Cove (ANSFC)	Island	3	Island	Occasional	Hard
Scripps Reef (SCRE)	So. Cal.	1	High	None	Hard
Shaws Cove (SHCO)	So. Cal.	1	High	None	Conglomerate
Stairs (STA)	Pt. C. North	2	Low	Occasional	Hard
Trailer (SCTR)	Island	3	Island	Common	Hard
Willows Anchorage (SCWA)	Island	3	Island	Occasional	Conglomerate

[a] Vulnerability: *1* unprotected mainland sites, *2* protected mainland sites, *3* protected island sites

[b] Oystercatcher abundance: Rare (observed <25% of sample days), occasional (25–75%), common (>75%)

[c] Substratum: Hard (granitic, meta-volcanic and hardened sedimentary), Soft (sandstone, shale and mudstone), Mixed (plots are mixed between sandstone and meta-volcanic), Conglomerate (Breccia)

Although there are no recent reports of major collecting events from the protected sites for the period of study, we suspect that none of these sites is immune to human exploitation of intertidal resources. In fact, poaching has been observed on mainland sites (Murray et al. 1999), and occasionally even on the Channel Islands (D. Richards personal observation), Cabrillo National Monument (Engle and Davis 2000; B. Becker, personal communication) and restricted-access mainland sites (Lindberg et al. 1998; M. Miner, personal communication). Rather than absolute differences, then, the categories 1–3 approximate a decreasing long-term likelihood of collecting intensity by incorporating increasing hurdles to collection through law enforcement, patrolled property barriers, distance and water. Based on their extensive experience with the sites, all MARINe PIs came to consensus in the assignment of our sites to the three vulnerability categories prior to data analysis.

Effects of intertidal visitation

We attempted to separate effects of human foraging from effects of heavy visitation to intertidal sites in two ways. First, we categorized sites by their likely visitation based on proximity to population centers, specific site traits, and observations of human use of sites, and used these categories as factors in ANOSIM analysis. We initially divided sites into one island category (where the resident human population is zero and visitation relatively low) and three mainland categories based on 2000 U.S. Census data for county population density. Mainland visitation categories were thus: High (county population >1.5 M), Medium (500,000–1.5 M), and Low (<500,000). Although their sizes vary, San Diego, Orange, and Los Angeles Counties (the source of our "High" visitation sites) also have the highest population densities and the greatest concentrations of highly populated coastal cities. These categories are in accordance with our extensive observations of human visitation during our site visits as well as available published visitation surveys (Murray et al. 1999; Ambrose and Smith 2005), which suggest that there is a strong relationship between proximity to population centers and visitation to intertidal sites in southern California. However, based on our observations of individual site characteristics, we adjusted the categories of two sites prior to analysis. Carpinteria, although located in a relatively sparsely populated county, was moved from the Low to Medium category because the site lies in a frequently visited state park. Cabrillo 3, which is adjacent to highly visited sites in a highly populated county, was moved from High visitation to Low because it is part of a human exclusion experiment where visitors are actively restricted by Cabrillo National Monument personnel. Because some of our sites that are vulnerable to poaching are in sparsely populated areas, our proximity categories are not the same as our vulnerability categories (Table 2), allowing a contrast between visitation and vulnerability. Thus, if heavy visitation per se primarily affects size structures, we would expect to see a stronger pattern of difference between sites of high and low visitation categories than between sites of different vulnerability.

Second, we augmented this method with a more fine-scale approach by comparing size structures at two pairs of sites that feature strictly enforced regulations against collection and are difficult to access for the purposes of poaching. In each site pair, one site was heavily visited by tourists and school groups and the other site was rarely visited. One pair of sites within the Cabrillo National Monument on mainland California includes a site (CAB1) where annual visitation is in the tens of thousands of visitors per year (Engle and Davis 2000; Tenera 2003), and a nearby site (CAB3), actively patrolled by park rangers during low tides, where a human exclusion experiment has been conducted since 1996. At all sites within the Monument, prohibitions on collection are actively enforced by park rangers and volunteer docents during operational hours. Access to the sites after park hours is difficult because the monument is part of an active U.S. Navy base and intertidal sites are several kilometers from a controlled gate on the seaward end of a narrow peninsula. The second pair of sites, located within 1 km of one another on Anacapa island, includes South Frenchy's Cove, a landing site that receives approximately 3,000 visitors annually (mostly school groups), and Cat Rock, a site with similar wave exposure and rock type. The Cat Rock site has been used as a control site by Channel Islands National Park officials to test the effects of visitors on intertidal biota at South Frenchy's Cove. No other equivalent pairs of well-protected sites with vastly different levels of human visitation were available among the 33 sites examined in this study.

Biological interactions

We were unable to control for the potential effects of non-human predators on *L. gigantea* populations. However, ANOSIM was used to test for differences in size structures between sites with different densities of oystercatchers based on our extensive site notes (Table 2). Other predators that have been suggested for *L. gigantea* include sea stars, sea gulls, octopus and lobster, but these have not been directly studied in relation to *L. gigantea* at our sites. The study was also not designed to directly address the potential role of guano on limpet populations, so discussion of this hypothesis is based on comparative observations of bird populations at our sites.

Sampling biases

We screened for potential biases in several ways. We factored substratum type into multivariate analyses under the hypothesis that all else being equal, limpets would reach larger sizes on softer surfaces such as sandstone and mudstone where they can more easily carve out home depressions and which support thicker microalgal films, than on harder surfaces such as granite or irregular conglomerate rock such as breccia. We used our site notes to identify changes in permanent plots due to erosion or mussel encroachment that might bias our results from the above analyses. Changes through time also were addressed using the RELATE procedure in PRIMER 6 by comparing the similarity matrix for our overall analysis of size structures to a similarity matrix created from size structures at each site taken at the first sample date for that site. The RELATE procedure directly contrasts similarity matrices using a randomization procedure similar to ANOSIM. Significant differences in these matrices may be indicative of population changes at a limited subset of sites. In addition, analysis of MDS plots for the first sample date for each site gives us a sense of the relative condition of populations from different sites when permanent plots were established.

Results

Geographic analysis

We found no evidence of a latitudinal gradient in sizes nor significant differences between sites solely based on their position relative to Pt. Conception. Seriation analysis of sites ordered by their position along the coast was non-significant (RELATE procedure: R=0.049, P=0.23). ANOSIM analysis showed no significant differences between regions on the mainland or between mainland regions and the islands (Table 3).

Effects of human poaching

Results strongly supported the expectations of the hypothesis that humans affect owl limpet size structures by taking large individuals. Histograms of population size structures showed clear differences between vulnerability categories, with Category 1 (most vulnerable) sites showing a complete lack of larger limpets (Fig. 2). The global ANOSIM test revealed significant differences in size structures among the three site categories (R=0.33; P<0.001; Table 4). Further, pairwise ANOSIM analyses showed significant differences between Categories 3 and 1, and Categories 2 and 1, but not between the more protected Categories 2 and 3 (Table 4). Maximum, mean and median shell lengths increased with greater protection of sites (Table 5). Moreover, a wider range of size classes was found at less vulnerable sites. This was revealed by comparing standard deviation, skewness, and kurtosis values for the three site categories (Table 5). Standard deviation around the mean size became greater at more protected sites. While all sites showed significant right-hand skew, probably due to the truncation of observations of limpets <15 mm, skewness was much lower at the more protected Category 2 and 3 sites. More protected sites also were more platykurtic (showing more even frequency distribution of sizes), with Category 2 and 3 sites showing significantly negative kurtosis values. The proportion of limpets in the smallest size class (≤20 mm) was similar across Categories, with slightly higher percentages of small limpets at Category 1 sites (Table 5). Differentiation between individual sites and between groups was visualized with an MDS plot, which in this case separates sites and vulnerability categories according to limpet size (Fig. 3). Category 1 sites with greater accessibility to human visitors uniformly grouped on one side of the MDS plot, opposite Category 3 sites, with Category 2 sites tending to be intermediate. Bubble plots, constructed from median shell lengths for each site, clearly demonstrated a relationship between site position in the MDS diagram and the size structure of the limpet populations. Populations with greater median sizes were almost exclusively found at Category 3 sites, whereas smaller median shell lengths almost always occurred at Category 1 sites (Fig. 3).

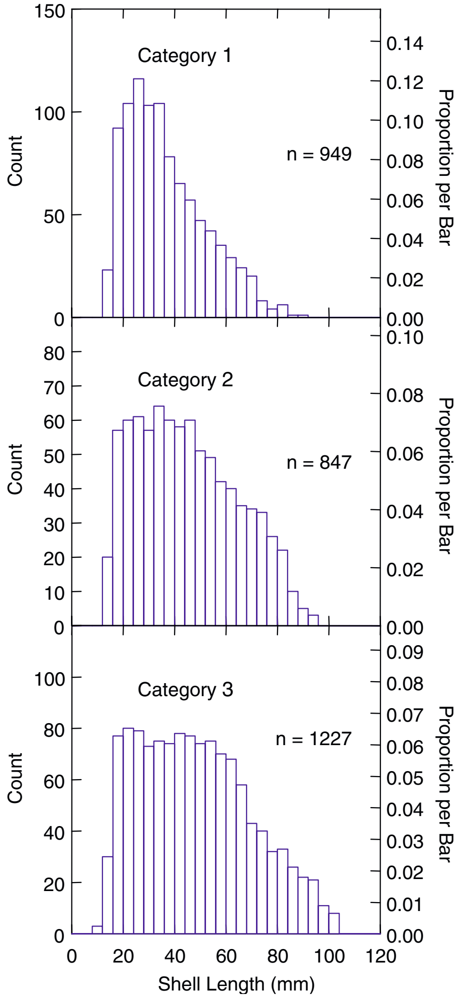

Fig. 2 Size frequency histograms for observations of *Lottia gigantea* in three vulnerability categories

Table 3 ANOSIM tests for differences between size distributions of *Lottia gigantea* from mainland sites in three regions

Test (Categories)	R	P
Global	0.02	0.33
Pt. Conception South vs. Southern California	−0.03	0.51
Pt. Conception South vs. Pt. Conception North	−0.01	0.37
Pt. Conception South vs. Islands	0.18	0.07
Southern California vs. Pt. Conception North	−0.12	0.95
Southern California vs. Islands	0.07	0.14
Pt. Conception North vs. Islands	−0.006	0.39

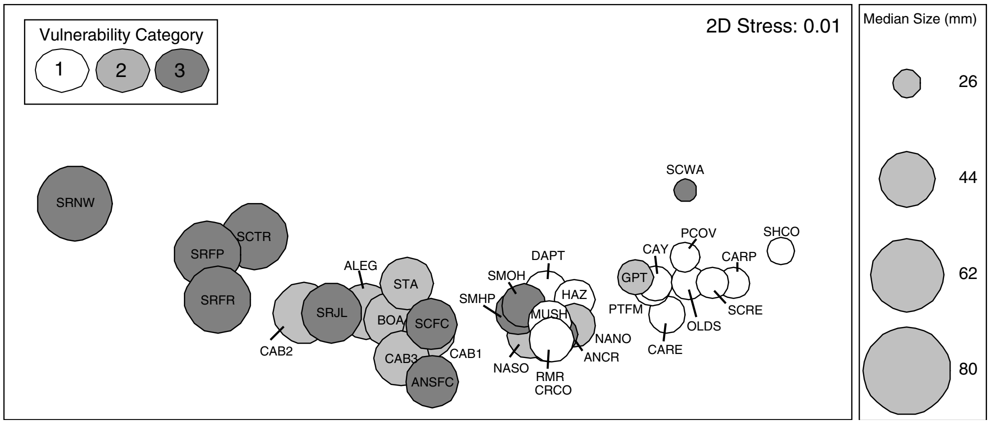

Fig. 3 Non-metric MDS ordination of *Lottia gigantea* size distributions based on mean sizes in each 1 mm size bin from all sample periods. Site abbreviations are listed in Table 1. Bubble sizes are proportional to median size of limpets for all samples at that site, and are used for illustrative purposes: MDS ordinations were created from similarity matrices based on the entire distribution of sizes at each site

Table 4 ANOSIM tests for differences between size distributions of *Lottia gigantea* from groups of sites based on vulnerability to poaching

Test	*R*	*P*
Global	0.33	<0.001
1 vs. 2	0.50	<0.001
1 vs. 3	0.43	<0.001
2 vs. 3	−0.03	0.57

Table 6 ANOSIM tests for differences between size distributions of *Lottia gigantea* from groups of sites based on likelihood of visitation

Test	*R*	*P*
Global	0.06	0.13
Low vs. high	0.02	0.29
Low vs. medium	0.16	0.12
Low vs. islands	−0.02	0.51
High vs. medium	−0.18	0.84
High vs. islands	0.17	0.02
Medium vs. islands	0.20	0.11

Effects of intertidal visitation

Impacts from high levels of visitation on owl limpet size structures were not apparent. The ANOSIM test failed to detect a significant difference between sites proximal or distant from population centers on the mainland (Table 6). Islands sites, however, were significantly different from urban mainland sites (R=0.17; P=0.02). Visitation by school groups and tourists did not appear to impact owl limpet size structures because little difference was observed between high and low visitation sites at Cabrillo National Monument, both of which are well protected from human foraging (Fig. 4a). Even robust Kolmogorov–Smirnov tests for differences between size distributions at these sites were non-significant (P>0.39). Interestingly, the paired Anacapa Island sites at South Frenchy's Cove and Cat Rock did show significantly different size distributions (Fig. 4B; K–S test P<0.002). However, higher visitation was not a factor in reducing the proportion of larger owl limpets because larger maximum, mean, and median sizes were found at South Frenchy's Cove, the more visited site.

Biological interactions

We did not observe foraging of *L. gigantea* by oystercatchers or other predators in our plots during any of

Table 5 Summary statistics for *Lottia gigantea* sizes by vulnerability categories for all samples

Vulnerability Category	*n*	*n*≤20 (%)	Max (mm)	Median (mm)	Mean (mm)	SD	Skew	SE Skew	Kurtosis	SE Kurtosis	Kurtosis type
1	959	142 (15%)	90	33	36.24	15.30	0.78[a]	0.08	−0.05	0.16	NS
2	847	93 (11%)	95	42	44.63	19.39	0.37[a]	0.08	−0.83[b]	0.17	Platykurtic
3	1,229	132 (11%)	103	46	47.68	21.70	0.40[a]	0.07	−0.68[b]	0.14	Platykurtic

[a] Skewness is considered significant when its absolute value is greater than 2*SE of Skewness

[b] Kurtosis is considered significant when its absolute value is greater than 2*SE of Kurtosis

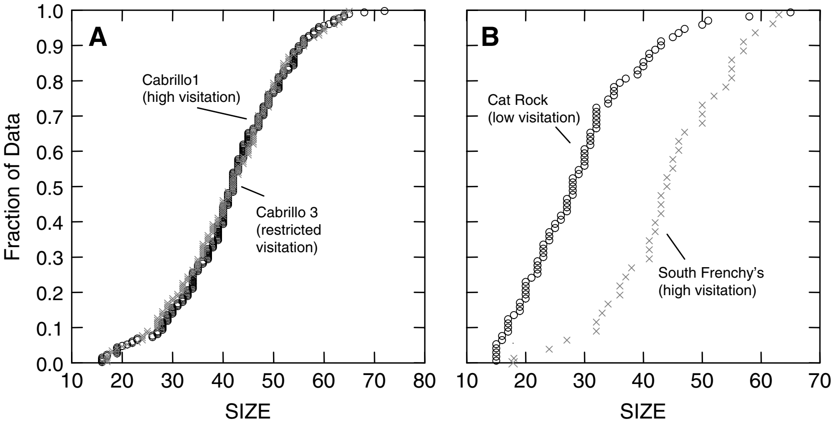

Fig. 4 Quantile plots for distribution of sizes of *Lottia gigantea* in Fall 2002 at two pairs of well-protected sites. **a** Two sites at the Cabrillo National Monument. **b** Two sites on Anacapa island

our intertidal visits. A significant difference in size structure between sites of varying oystercatcher abundance was found in the global ANOSIM test, yet pairwise comparison of sites grouped by oystercatcher abundance found significant differences only between sites where oystercatchers were most common and those where oystercatchers were absent (Table 7).

Sampling biases

We observed no pattern in owl limpet size structures at our sites attributable to variations in rock type (Table 8). Softer sedimentary formations expected to present more favorable environmental conditions for limpets were found at mainland and island sites and across all vulnerability categories whereas harder, more irregular formations such as breccia made up the primary substratum in a small number of Category 1 and 3 sites. Notably, Willows Anchorage (SCWA), a Category 3 site, which anomalously showed the smallest median sizes in the first sample (Fig. 5), is a breccia-dominated site.

Table 7 ANOSIM test for differences between size distributions of *Lottia gigantea* from groups of sites based on observed frequency of oystercatchers

Test	*R*	*P*
Global	0.12	0.04
Occasional vs. none	0.04	0.27
Occasional vs. rare	−0.12	0.71
Occasional vs. common	0.08	0.16
None vs. rare	0.07	0.30
None vs. common	0.29	< 0.01
Rare vs. common	−0.12	0.75

Table 8 ANOSIM test for differences between size distributions of *Lottia gigantea* from groups of sites based on substratum type

Test	*R*	*P*
Global	−0.04	0.66
Conglomerate vs. soft	−0.03	0.50
Conglomerate vs. hard	−0.01	0.47
Conglomerate vs. mixed	0.52	0.06
Soft vs. hard	−0.08	0.98
Mixed vs. soft	−0.05	0.54
Mixed vs. hard	0.04	0.33

Although the availability of owl limpet habitat changed through time in some plots at our sites due to mussel encroachment, there was no evidence of a systematic bias due to this factor. Cardiff Reef (Vulnerability Category 1), Government Point (Category 2), and Fraser Cove, Harris Point, Otter Harbor, Willows Anchorage (Category 3), for example, are sites with plots established in areas of mussel encroachment. Indeed, MDS ordination using data from the first sampling season (Fig. 5) revealed that three of these sites (all from Category 3) had smaller size structures relative to others in this category. Reports of increasing mussel encroachment into limpet plots through time occurred most often at more southerly Category 1 sites (Dana Point, Shaw's Cove, Cardiff Reef, Crystal Cove). Such encroachment could be a natural process or could be an effect of the removal of larger territorial limpets from these sites.

Size structures in the overall comparison based on means calculated over several sampling seasons were not significantly different from size structures based only on the first site sampling period (the hypothesis of non-similarity, tested in the RELATE procedure, was rejected: R=0.86, P<0.01). However, erosion forced investigators to shift the location of study plots at Cabrillo National Monument, Stairs, Navy North and Navy South, all Category 2 sites. Because plots were originally targeted in areas of high densities of large, conspicuous limpets, however, any changes in these plots would be expected to produce shifts towards smaller limpets, which is opposite the pattern observed at these well-protected (Category 2) mainland sites.

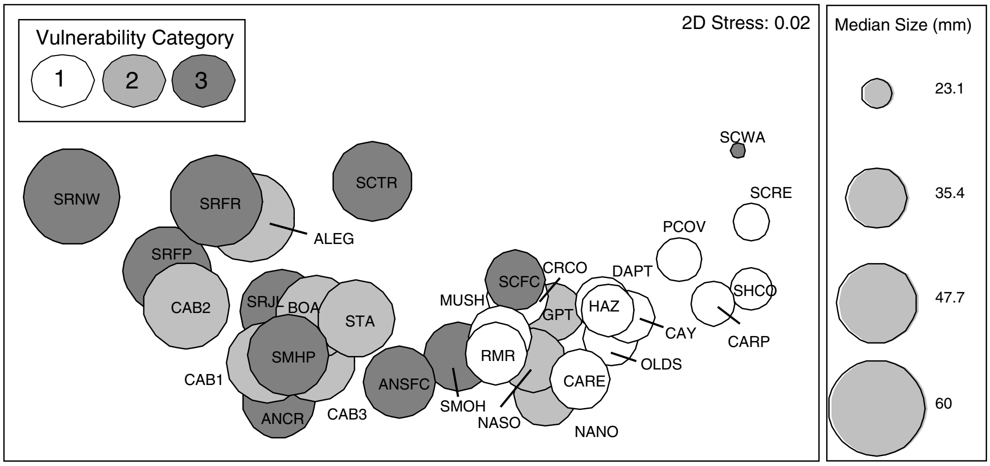

Fig. 5 Non-metric MDS ordination for limpet size distributions from each site's first sample period. Bubble sizes are proportional to median size of limpets for that sample period

Discussion

The strongest signal in our analysis of *L. gigantea* population structures is that of greatly truncated numbers of larger limpets at sites that are least protected from poaching. We argue here that while several alternative mechanisms could be responsible for this signal, foraging by humans is the most parsimonious explanation. While other studies have come to similar conclusions for *L. gigantea* (Pombo and Escofet 1996; Kido and Murray 2003; Roy et al. 2003), a large data set from multiple sites across a broad range is necessary to effectively evaluate alternative hypotheses and separate at a finer scale the factors responsible for depletion of large owl limpets from many Californian populations.

Notably, reduction in frequencies of large limpets does not seem to be related merely to large numbers of human visitors. While past studies of human foraging from Chile and South Africa have stressed the relationship between foraging intensity and proximity to population centers (Siegfried et al. 1985; Hockey and Bosman 1986; Oliva and Castilla 1986), our multivariate comparison of limpet sizes at multiple sites places new emphasis on the role of enforcement in protecting against poaching effects. In our comparative analysis, sites on the Channel Islands, which are the least accessible among our sites to human visitors, showed no significant differences in owl limpet size structure from those at mainland sites where enforcement against poaching is strongest (Table 4), even when these mainland sites lie in close proximity to large population centers and are highly visited. On the mainland, ANOSIM analysis (Table 6) showed no significant difference between the most populous and least populous sites, and additionally our regional analysis showed no significant difference between sites from populous (e.g., southern California) and sparsely populated (north of Pt. Conception) geographic regions (Table 3). In these analyses, groups of sites separated by region or proximity to human population centers contained both protected and unprotected sites. Thus, differences between sites near and far from urban centers only become evident when their vulnerability to poaching is considered (e.g., Table 4).

Finer-scale analyses of paired protected sites showed that even extremely high human visitation could not be related to reductions in owl limpet size structures. This lends further support to the idea that visitation per se is not primarily responsible for the absence of large owl limpets. Observations by Lindberg et al. (1998) demonstrating large populations of *L. gigantea* at heavily visited but protected sites in Santa Cruz, California and observations by Zedler (1978) showing larger sizes and a greater range of sizes of *L. gigantea* at Cabrillo National Monument compared to an unprotected nearby site provide some additional evidence of patterns we observed here. Where sites are protected from collection for food or bait, large *L. gigantea* may be buffered from the typical effects of visitation because they are relatively drab and thus less likely to be removed for observation or plucked by casual souvenir collectors and because they often occupy angled rock faces where they are unlikely to be trampled upon.

The effects of other biological interactions, such as predation or enhancement of algal food sources by guano, appear to be less important than human foraging, especially in reducing the density of the largest limpets. We often found largest limpets in our plots on vertical and steeply sloped surfaces where oystercatchers cannot perch and remove limpets (Hockey and Branch 1984; Lindberg et al. 1998). Although the variable orientation of our plots suggests that our study design could not adequately sample actual oystercatcher foraging, we can at least conclude that large limpets can thrive even where oystercatchers are common and relatively undisturbed by humans. Our data cannot rule out the possibility that oystercatchers have impacts on limpet populations outside our study plots, or that there are indirect benefits to large limpets through oystercatcher foraging on smaller limpets. However, we did not observe a decrease in frequency of small or medium limpets at sites where oystercatchers are common.

The effect of other potential predators such as sea stars, octopuses, terrestrial mammals and sea gulls on *L. gigantea* populations is less certain. Although natural history accounts suggest that there are other *L. gigantea* predators (Morris et al. 1980), no study has quantified size preference or potential effects of these predators on owl limpet populations. The predatory sea star *Pisaster ochraceus* was rarely observed in upper mid intertidal habitats occupied by *L. gigantea* during our study, and none of the potential predators was observed foraging at our sites.

The role of guano on intertidal populations was outside the scope of our sampling program, so our conclusions are based on comparisons of bird population densities, distributions and habitat characteristics at the sites studied here relative to sites where guano has been shown to have a large effect (e.g., Bosman and Hockey 1986). In Saldanha Bay, South Africa, where Bosman and Hockey found significant effects of bird guano, roosting bird populations were very dense, guano deposition was heavy enough to be harvested commercially and study slopes were gentle, not steep. By contrast there are no major bird roosting locations at our sites and substantial guano deposition is not seen at any of the sites. Moreover, our study plots tend to be located on steep or vertical walls where guano deposition is expected to wash away quickly. Although the larger number of oystercatchers on the Channel Islands relative to the mainland raises the concern of differential effects of guano between island and mainland sites, Bosman and Hockey (1986) considered deposition by non-roosting birds to be insignificant and overall bird densities on the islands are much lower than those reported from impacted South African sites.

When relying on a comparative approach dependent on historical, descriptive data, there is always a concern that interpretations may be biased in some way by factors that weren't recorded (Dayton et al. 1998). Nevertheless, we believe that our conclusions about the effect of humans on *L. gigantea* populations are conservative, and that given more information we might find evidence for even a more dramatic shift toward smaller sizes at sites vulnerable to human collection. For instance, several southern California rocky intertidal sites where collection pressure is likely to be high were not sampled in our program, and thus our data are believed to overestimate the sizes of limpets in unprotected sites as a whole. Indeed, reported mean shell lengths of *L. gigantea* ranged from 26.2 to 31.2 mm for five heavily accessed and unprotected Orange County sites not represented in our study (Kido and Murray 2003), from 25.3 to 31.6 mm for unprotected Los Angeles County sites (Ambrose and Smith 2005), and was 31 mm at an unprotected San Diego site (Zedler 1978). All of these sizes are smaller than the mean sizes found for any of our site categories. Additionally, large changes in the size structures of limpets and other shelled invertebrates are known to have occurred before the period of our study (Roy et al. 2003). Thus, as has been well documented in fisheries studies, we are faced with a shifting baseline that results in the underreporting of the loss of large individuals in a coastal marine population (Dayton et al. 1998; Jackson 2001).

If human foraging is an important contributor to owl limpet size structure, one might ask why not study and quantify foraging directly or experimentally? Experimental removals, which have been used in the past to test ecological effects of foraging (Lindberg et al. 1998; Sharpe and Keough 1998), may not accurately capture the timing, intensity or long-term effects of foraging pressure, and experimental treatments may themselves be compromised by stochastic poaching events (see Lindberg et al. 1998). Some natural comparative studies from Chile and northern and southern Africa, which compared exploited and protected sites, have successfully demonstrated both the direct and indirect effects of human foraging (Hockey and Bosman 1986; Oliva and Castilla 1986; Ortega 1987; Duran and Castilla 1989; Castilla 1999; Branch and Odendaal 2003; Guerra-Garcia et al. 2004). This approach, however, requires the existence of fully protected reserves, which are typically limited to a very small number of sites. Moreover, this approach might not be suitable for supporting robust studies of resource exploitation because of limited site features (e.g., don't span wide latitudinal ranges) or the absence of appropriate matched control sites. Comparing only one or a few protected sites to an equally small number of unprotected sites not only limits power of statistical tests (Keough et al. 1993), but also potentially confounds causal variables due to environmental variability (Lasiak 1993).

Direct observations leading to the quantification of foraging activity also are problematic. Because collecting is an unpredictable and often surreptitious activity, designing a sampling scheme that would have a strong probability of accurately assessing collection pressures at a site might not be possible. This would be especially true if the majority of collection pressure occurs in infrequent, high intensity sessions. Past attempts to assess intertidal collection activity have largely relied on daytime monitoring of visitors (Murray et al. 1999; Kido and Murray 2003; Tenera 2003; Ambrose and Smith 2005). Although these studies have demonstrated a positive correlation between visitation and broadly defined collection activity, daytime surveys can miss the most intensive foraging, and fail to document illegal collecting activities (poaching) that occur under cover of darkness. Even the presence of researchers may affect the behavior of would-be collectors if such activities are illegal. Thus, Kingsford et al. (1991) recommend that the most accurate way to determine the effects of humans on nearshore ecosystems is to compare multiple protected and unprotected areas, as we have done here.

Our observational approach, however, cannot determine whether the population level effects we observed are due to continual foraging pressures or infrequent high-intensity collection events. Occasional chance observations suggest that high intensity *L. gigantea* collection events do occur. Lindberg et al. (1998) accidentally observed the effects of a large scale poaching event on a mainland site in Santa Cruz, California and estimated that >300 owl limpets were taken, including all accessible limpets >25 mm in shell length. Rancho Marino reserve manager Don Canestro, who lives on the reserve full time, observed collectors on four occasions illegally transporting large bags of *L. gigantea*, which were estimated on one occasion to contain 2,500 limpets (D. Canestro, personal communication, September 12, 2004). Staff at Cabrillo National Monument also have cited people for collecting “sackfulls of owl limpets”, although these incidents are believed to be rare (Engle and Davis 2000). Most recently, Steven Lee observed a family collecting between 50 and 100 owl limpets at White’s Point, a site near Pt. Fermin in Los Angeles County (S. Lee, personal observation, April 23, 2005).

A final question is whether illicit foraging on the scale suggested by the depleted size structures observed at our most impacted sites is likely to have substantial and long-lasting ecological effects at these exploited sites or, more broadly, on *L. gigantea* populations extending out from these sites? Human foraging of intertidal invertebrate resources has occurred since prehistoric times (Ortega 1987; Mannino and Thomas 2002). Despite shifts away from the use of intertidal populations as primary food resources, improved technology for accessing sites far from home and increases in human population densities have provided the means for these impacts to continue today (Siegfried et al. 1985; Hockey and Bosman 1986; Pombo and Escofet 1996; Castilla 1999), and they are expected to increase in the future (Thompson et al. 2002). Yet, there is evidence that the intertidal zone is resilient to the effects of foraging documented here and elsewhere for three reasons. First, sizes of intertidal invertebrates are larger within the boundaries of present day reserves than in museum records and observations from the mid twentieth century (Roy et al. 2003). Second, exclusion experiments have revealed dramatic recoveries of exploited species in marine reserves, even when protection only has been enforced for 2–10 years (Hockey and Bosman 1986; Ortega 1987; Moreno 2001; Thompson et al. 2002), although studies of prosobranch limpets (Ortega 1987) suggest mixed recovery and the suggestion has been made that *L. gigantea* will not recover as quickly (Kido and Murray 2003). Third, in the present study young limpets still appear to recruit into populations lacking large, and presumably more fecund, individuals (Table 5). This suggests that planktonic larvae of *L. gigantea* from sites where large reproductive adults are present are able to replenish depauperate sites (see Catterall and Poiner 1987; Pombo and Escofet 1996). Genetic analysis of *L. gigantea* showing little population structure (see Dawson 2001) lends empirical support to the assumption that this species disperses widely throughout the region. Nonetheless, if protected populations are important in maintaining recruitment to heavily foraged populations, our study raises the concern that legal status of sites and restrictions on take are inadequate if there is no enforcement of the regulations.

Moreover, direct and indirect effects of the loss of large adult limpets may occur regardless of changes in overall limpet density, and lead to a loss of reproductive potential in owl limpet populations. Indirect losses could occur due to encroachment of optimal limpet territories by mussels, algae, or high densities of smaller limpets once large limpets are removed, whereas direct losses could occur due to loss of large, older females (Kido and Murray 2003). Although the relationship between size and age in limpets is not known precisely, recent studies from fisheries have shown that exploitation of larger and older females can have disproportionate effects on populations (Berkeley et al. 2004; Palumbi 2004). Hence, larval recruitment from large individuals residing in refuge sites might not be sufficient to establish natural population size structures under continual foraging pressures. Without a better understanding of the degree of connectedness between intertidal zones along the coast, we cannot determine whether these local site-specific effects will affect *L. gigantea* or coastal intertidal communities in general. The uncertainty regarding the scope of future foraging pressure and its effects across interconnected intertidal sites underscores the value of large-scale monitoring programs for documenting changing baselines and the decline and recovery of intertidal systems.

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