Variation in owl limpet *Lottia gigantea* population structures, growth rates, and gonadal production on southern California rocky shores

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ABSTRACT: The size structures of *Lottia gigantea* populations were studied at 8 southern California sites, 4 of which were longstanding Marine Protected Areas (MPAs). Greater mean sizes and higher frequencies of larger individuals occurred at sites with lowest human visitation. Mean *L. gigantea* shell lengths (SLs) were negatively correlated with the number of visitors and collectors per 10 m of shoreline. Limpets never achieved SLs greater than 79.0 mm at any of our 8 sites, a size well below the maximum for this species. Mean SLs were comparable to sizes at other sites where *L. gigantea* is intensely collected. The presence of collectors, small mean SLs, and the absence of large limpets suggest that *L. gigantea* populations are affected by humans at our sites. Lower densities and higher frequencies of larger limpets were found in a subpopulation living on open-rock surfaces compared with a subpopulation occupying smaller, patch habitats within mussel beds. Larger limpets were mostly female and gonadal mass increased exponentially with SL in both subpopulations. Limpets <40 mm SL exhibited highly variable growth rates; however, limpets in patch habitats grew slower and produced less gonadal mass than limpets inhabiting open rocks, despite the availability of more microalgal food. Ages of the largest limpets in the open-rock subpopulation were estimated to be >8 yr. Given the age of larger limpets and the potential for collectors to remove larger individuals and shift populations towards smaller size structures, effective MPAs may take decades to reverse the effects of human impacts on *L. gigantea* populations in southern California.

KEY WORDS: Owl limpets · Reproduction · Growth · Population structure · Marine protected areas · Human impact · Rocky intertidal · Southern California

INTRODUCTION

Humans collect vulnerable intertidal species mainly for use as food or fishing bait or for their shells. Effects of over-collecting can cause reductions in population density and, because humans prefer to collect larger animals, decreases in the number of larger individuals. Such changes in the structures of exploited intertidal invertebrate populations have been reported in Australia (Catterall & Poiner 1987, Keough et al. 1993), Baja California, Mexico (Pombo & Escofet 1996), California, USA (Zedler 1978, Addessi 1994, Roy et al. 2003), Chile (Moreno et al. 1984, Castilla & Durán 1985, Oliva & Castilla 1986, Durán & Castilla 1989),

Costa Rica (Ortega 1987), South Africa (Branch 1975, McLachlan & Lombard 1981, Hockey & Bosman 1986, Lasiak & Dye 1989) and Tanzania (Newton et al. 1993). Through reductions in density and shifts toward smaller individuals, human exploitation also can decrease the reproductive output of intertidal invertebrate populations in which there is an increase in individual fecundity with body size (Seapy 1966, Branch 1974, 1975, Creese 1980a, Levitan 1991, Tegner et al. 1996). This is especially true for broadcast spawners such as limpets, trochid snails, and urchins that depend on high gamete concentrations to increase the probability for successful fertilization (Hockey & Branch 1994).

The owl limpet *Lottia gigantea* is the largest limpet in North America, reaching sizes >100 mm in shell length (Lindberg et al. 1998). *L. gigantea* is confined to upper, mid-intertidal zone habitats from Washington to Baja California (Abbott & Haderlie 1980), where it maintains grazing territories (Stimson 1970) and is an important 'space occupier' (Lindberg et al. 1998). By repeatedly grazing the same area, *L. gigantea* limits the recruitment and incursion of other space-occupying organisms into its territories, and therefore, its grazing activities can alter the structure of mid-intertidal communities (Stimson 1970, 1973, Lindberg et al. 1998). Owl limpets are often collected by humans for use as food or fishing bait because of their large muscular foot (Pombo & Escofet 1996, Lindberg et al. 1998). Also, owl limpets can be strongly preyed upon by the American black oyster-catcher *Haematopus bachmani*, a territorial shorebird that can exert sufficient predation pressure to influence limpet abundances and *L. gigantea*'s utilization of microhabitat (Lindberg et al. 1987, 1998). However, American black oystercatchers are very sensitive to human presence (Sowls et al. 1980, Frank 1982, Lindberg et al. 1987, 1998) and are essentially absent from heavily populated, urban coastlines.

Humans strongly exploit larger limpets and, as a result, *Lottia gigantea* populations become dominated by smaller animals in areas subjected to human predation (Pombo & Escofet 1996, Lindberg et al. 1998, Roy et al. 2003). Such human-induced shifts in the size structure of owl limpet populations may be of concern due to the reproductive strategy of this species. *L. gigantea* is a broadcast spawner and is protandrous, i.e. animals change from male to female with age (Wright & Lindberg 1982). Hypothetically, larger, older individuals are mostly female and collecting or other sources of mortality that selectively concentrate on larger animals can alter male-to-female ratios. Previous studies (Lindberg et al. 1987, 1998) have shown that both American black oystercatcher predation and human exploitation of *L. gigantea* can have profound effects on owl limpet populations and the structure of rocky intertidal communities.

The purpose of this study was to examine variations in the structure of *Lottia gigantea* populations over regional (among-site) and local (within-site) scales in urban southern California habitats, where human presence is high and the ecological influence of American black oystercatchers is absent or negligible. Based on historical museum specimens and current field surveys, Roy et al. (2003) reported that human activities have resulted in a significant decline in owl limpet body sizes in the southern California region over the last century. Hence, an additional goal of this study was to determine whether regional, urban Marine Protected Areas (MPAs) protect owl limpets and support *L. gigantea* population size structures characteristic of those from unexploited habitats. Populations were studied at 8 southern California sites, 4 of which were longstanding MPAs that hypothetically protect intertidal animals from human collection. Our sites were located along a heavily populated section of coastline where we have not seen American black oystercatchers for the last 10 yr. The population size structures of *L. gigantea* at these urban sites were compared with those reported for owl limpet populations from other southern Californian and Mexican locations, some of which are known to receive intense human exploitation.

Lottia gigantea populations occupy a range of intertidal habitat types that vary in the nature and size of the substratum available for grazing. For example, in southern California, *L. gigantea* is found in habitats ranging from large, smooth open-rock platforms or boulders, where they can potentially establish large grazing territories, to small, topographically heterogeneous patches located within mussel beds. Qualitative observations revealed that larger limpets were often found on large, open-rock surfaces, where they are easily visible to humans and predatory shorebirds but were rare or absent from smaller, patchy habitats that appeared to support higher densities of small-sized limpets. Because the removal of larger, territorial owl limpets can reduce the exclusion of encroaching organisms, collecting pressure also can result in the modification of habitat available to support natural *L. gigantea* population structures (Lindberg et al. 1998). Hypothetically, exploited populations become packed into smaller habitat patches where grazing territories are smaller and more limited due to encroachment of mussels or other organisms. This change in habitat availability may also cause modified population structures. Hence, we examined within-site differences in the characteristics of *L. gigantea* subpopulations occupying open-rock surfaces and smaller patch habitats. This comparison is unique because past studies on *L. gigantea* appear to have been concentrated on sub-populations occupying large, open-rock surfaces. Because smaller habitats contain less grazing territory, we predicted that the density, size structure, growth rates, and gonadal production of owl limpet subpopulations occupying patch habitats would differ from subpopulations occupying open-rock surfaces. We also hypothesized that the majority of larger individuals of this protandrous limpet would be females in both habitats if sex change occurs in *L. gigantea* irrespective of the maximum achieved size of limpets in a subpopulation.

MATERIALS AND METHODS

Study sites. Eight study sites were established in topographically similar rocky intertidal habitats located along 15.5 km of southwest-facing Orange County coastline in southern California (Fig. 1). Sites were separated by stretches of sandy beach and were located on most of the workable headlands or outcrops along this stretch of shoreline. With the exception of Crystal Cove, all sites consisted of substrata of similar geologic origin (Table 1). The collection of limpets and other intertidal invertebrates has been prohibited for more than 25 yr at 4 of the 8 sites (Crystal Cove, Shaw's Cove, Monarch Bay, and Dana Point), which were established as MPAs between 1969 and 1971 (McArdle 1997); the other 4 sites (Woods Cove, Victoria Beach, Treasure Island, and Thousand Steps) were accorded MPA protection in January 1994, 3 yr prior to the initiation of our study (Fig. 1).

Oceanographic conditions vary little among sites along this short stretch of coastline. Local annual sea temperatures from 1997 to 1999 ranged from 11 to 23°C and salinity from 30 to 34‰ (NEMO Oceanographic Data Server for Newport Beach, California; http://nemo.ucsd.edu). All study sites are largely shielded from prevailing swell patterns by the offshore Channel Islands (Hickey 1993). Based on measurements of maximum wave force using field transducers (Table 1), greater wave action occurs at Woods Cove, Victoria Beach, and Treasure Island. Sand periodically accumulates on rock surfaces at most of our study sites (Table 1), but greatest sand influence is found at Thousand Steps and Monarch Bay. The study sites support *Lottia*
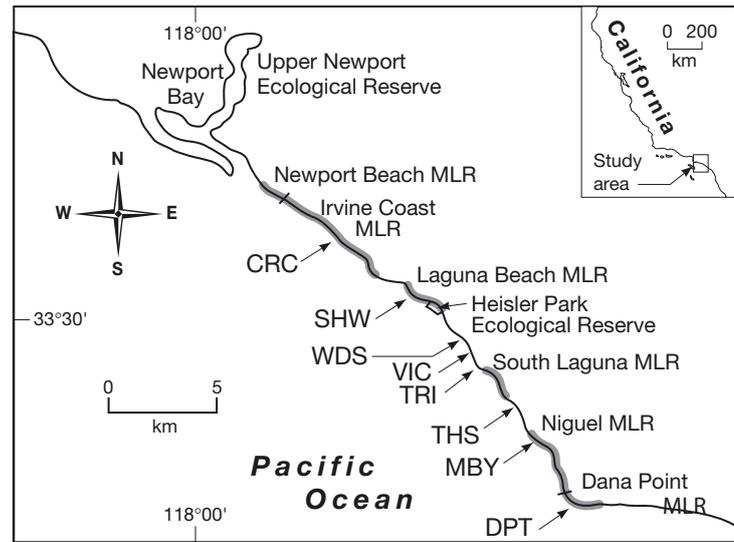

Fig. 1. Map of the 8 southern California study sites. CRC: Crystal Cove, SHW: Shaw's Cove, WDS: Woods Cove, VIC: Victoria Beach, TRI: Treasure Island, THS: Thousand Steps, MBY: Monarch Bay, DPT: Dana Point. Shaded areas represent boundaries of local MPAs (California Marine Life Refuges [MLRs] and Ecological Reserves) established prior to 1994 in which collecting of invertebrates is prohibited

gigantea populations at similar, mid-shore tidal elevations on flattened rock benches, large boulders, and on patches of rocky habitat often associated with mussel communities. American black oystercatchers were never observed at these sites during the study.

The 8 study sites differed in the amount of human use and disturbance. Recent studies (Murray 1998, Murray et al. 1999) have shown that human visitation can be high and that intertidal invertebrates are routinely collected at all of our study sites, including the 4 longstanding MPAs (Table 2). These reports were

Table 1. Study-site characteristics, including latitude and longitude, substratum geology (Tm = Monterey Formation in the Tertiary Period; Tso = San Onofre Breccia in the Tertiary Period), maximum wave force (mean ± SE; n = 10–36), and sand cover (mean ± SE; n = 20) for 0.15 m^2 plots located in adjacent *Silvetia compressa* zone. Maximum daily wave force was determined using field transducers (Bell & Denny 1994); wave-force and sand-cover measurements were taken during autumn 1996 and spring 1997 (see Sapper & Murray 2003 for additional details). [a]Sites located within intertidal MPAs designated between 1969–1972. Remaining sites were accorded similar MPA status in 1994 but sites were not signed and the public was largely unaware of this change in status during the study. See Fig. 1 for site locations

Study site (abbreviation)	Latitude, longitude	Geologic formation	Maximum wave force (m s^{-1})	Sand cover (%)
Crystal Cove (CRC)[a]	33° 34′ 13″ N, 117° 50′ 15″ W	Tm	4.89 ± 0.08	16.3 ± 3.8
Shaw's Cove (SHW)[a]	33° 32′ 42″ N, 117° 47′ 57″ W	Tso	4.86 ± 0.17	10.9 ± 2.9
Woods Cove (WDS)	33° 31′ 42″ N, 117° 46′ 05″ W	Tso	7.22 ± 0.57	0.5 ± 0.9
Victoria Beach (VIC)	33° 31′ 11″ N, 117° 45′ 52″ W	Tso	6.84 ± 0.34	14.4 ± 4.8
Treasure Island (TRI)	33° 30′ 48″ N, 117° 45′ 33″ W	Tso	6.23 ± 0.25	1.6 ± 2.3
Thousand Steps (THS)	33° 29′ 55″ N, 117° 44′ 35″ W	Tso	4.93 ± 0.14	20.4 ± 4.4
Monarch Bay (MBY)[a]	33° 29′ 03″ N, 117° 43′ 56″ W	Tso	5.17 ± 0.21	21.8 ± 3.0
Dana Point (DPT)[a]	33° 27′ 35″ N, 117° 42′ 52″ W	Tso	5.15 ± 0.27	16.5 ± 3.5

Table 2. *Homo sapiens* and intertidal invertebrates. Patterns of human visitation and collecting at the study sites. Human visitation reported as the mean monthly number of low-tide visitors per 10 min observation period for 10 m of shoreline. Data are averages of monthly low-tide observations made during lower low water from February 1995 through January 1996 (see text for explanation), and they are believed to represent the intensities of visitation and collection at the study sites. Reported are the annual mean number of visitors and collectors calculated per 10 m of shoreline and the maximum monthly mean number of site visitors (plus month observed) recorded during the 10 min observation periods. Collectors are included as a component of annual mean visitor numbers. [a]Sites located within intertidal MPAs designated between 1969–1972

Site	Shoreline span at site (linear m)	Maximum mean monthly number of visitors (month)	Annual mean number of visitors per 10 m shoreline	Annual mean number of collectors per 10 m shoreline	Site ranks for visitor and collecting disturbance
Crystal Cove[a]	87.8	9.7 (Jan)	0.30	0.034	Visitation (5), Collecting (5)
Shaw's Cove[a]	209.4	21.8 (Nov)	0.35	0.029	Visitation (4), Collecting (6)
Woods Cove	78.2	16.6 (Sep)	0.95	0.051	Visitation (1), Collecting (3)
Victoria Beach	100.4	7.4 (Apr)	0.44	0.110	Visitation (3), Collecting (2)
Treasure Island	61.7	5.7 (Dec)	0.49	0.113	Visitation (2), Collecting (1)
Thousand Steps	53.9	5.4 (Sep)	0.30	0.037	Visitation (5), Collecting (4)
Monarch Bay[a]	73.5	1.3 (Feb)	0.05	0.014	Visitation (8), Collecting (7)
Dana Point[a]	321.0	34.2 (Apr)	0.27	0.009	Visitation (7), Collecting (8)

based on data obtained during extensive 1995–96 surveys, which determined the number of low-tide visitors and collectors over a prescribed section of shoreline at each of the 8 sites (Table 2; S.N.M. unpubl. data). In performing these surveys, observations were made for five 10 min intervals spaced evenly over 2 h during low tides ($\leq$ +0.3 m with reference to MLLW) occurring between dawn and dusk at each site 4 times mo^{-1} (twice on weekdays and twice on weekend days) for 12 consecutive mo. The mean monthly numbers of visitors and collectors per 10 min period were then determined for the year. In southern California, lowest low tides occur in the late morning and afternoon during autumn and winter and during pre-dawn and early morning hours from late spring through summer. The number of shore visitors is much greater during the daytime low tides that characterize autumn and winter and much less during summer (Murray 1998; Table 2). Collection of intertidal invertebrates was observed at all 8 study sites, including the longstanding MPAs, and enforcement of collecting regulations was essentially non-existent during these surveys (Murray 1998, Murray et al. 1999). Based on these data, the greatest numbers of human visitors and collectors per 10 m stretch of shoreline were recorded at Woods Cove, Treasure Island, and Victoria Beach (Table 2). In contrast, less human visitation and fewer collectors were observed at the other study sites, and this appeared to be correlated with access difficulties and the presence of site managers. For example, public access is regulated and officials routinely patrol the site at Crystal Cove, a State Park, and long or difficult walks are required to reach the study areas at Thousand Steps, Monarch Bay, and Dana Point.

Among-site differences in population size structure. *Lottia gigantea* populations were sampled during

spring 1997 to test for differences in mean size and size-frequency profiles among the 8 study sites. Using digital calipers, the longest shell length (± 0.1 mm) of 200 to 500 individuals was determined for each site population. Shell length (SL) measured along the maximum dimension often has been used as the parameter of choice for analyzing the size structures of limpet populations (e.g. Stimson 1973, Branch 1975, Daly 1975, Hockey & Bosman 1986, Pombo & Escofet 1996). Measurements were made on all limpets >15 mm encountered during thorough searches of all habitat types occupied by *L. gigantea*. Limpets <15 mm were excluded from these surveys because individuals of this size could not be quickly and consistently distinguished in the field from other small limpet species by all observers. Size-frequency distributions were developed for each population after sorting measured limpets into 5 mm size classes. In addition, the mean size (± 1 SE) was determined for each population.

Within-site analyses of patch and open-rock subpopulations. We hypothesized that the *Lottia gigantea* subpopulations occupying larger, open-rock and smaller, patch habitats would exhibit different densities, size structures, age distributions, growth rates, sex ratios and reproductive potentials. To test these hypotheses, we initiated studies on *L. gigantea* subpopulations occupying these 2 habitat types at our Monarch Bay study site (Fig. 1, Table 1). The patch habitat consisted of small gaps (0.25 to 0.50 m^2) of rocky substrata occurring within mussel communities that ranged in size from approximately 6 to 20 m^2. Open-rock study areas were established on large, smooth, fixed boulders or flat rock benches that provided mostly open surfaces of variable size (0.35 to 3 m^2).

Density, grazing area, and size structure. *Lottia gigantea* densities were determined every 3 to 4 mo

between March 1997 and February 1998 for both the open-rock and patch habitat subpopulations at Monarch Bay using 11 to 14 fixed plots (0.25 m^2: 0.5 × 0.5 m). We established plot locations by placing a series of potential plots in *L. gigantea* habitat, and then we randomly selected a subset for study. Assessments of the available grazing area within each plot were made by a point contact method using a grid containing 30 equally spaced points. Grazing area was defined as the percentage of substratum consisting of rock surfaces occupied primarily by microalgae.

Shell lengths were determined for all sampled limpets in subpopulations occurring in the patch (n = 222) and open-rock (n = 284) habitats during January 1997. All encountered limpets were measured following thorough searches of patch habitats in a minimum of 3 different mussel communities and 10 open-rock habitats at our Monarch Bay site. Care was taken during this portion of the study to include smaller, identifiable *Lottia gigantea* (<15 mm) occurring in cryptic habitats, including those residing on or beneath mussels. Measurement methods and handling of size structure data were performed as described previously.

Growth rates and age determination. Growth rates of limpets occupying the patch and open-rock habitats were determined by measuring the SLs of marked individuals every 3 to 4 mo over an 11 mo period. Limpets were double marked with numbered electrical wire tags (GC Electronics) or plastic bee tags (Graze Bienenzucht Geräte) fixed to shells with polyacrylamide super glue (GC Electronics). A total of 70 limpets in the patch habitat and 64 limpets in the open-rock habitat of various initial sizes (patch = 22.0 to 38.0 mm; open rock = 24.0 to 68.0 mm) were selected for growth-rate determinations and tagged during March 1997. Relationships between limpet SL and age were established for the open-rock subpopulation from growth rate data using the von Bertalanffy (1957) growth model. This procedure has been used successfully to obtain model parameters in past limpet growth-rate studies (Daly 1975, Balaparameswara Rao 1976, Branch 1981). The maximum limpet size used in the model was the largest measured individual in the subpopulation, since a Ford-Walford plot (Walford 1946) predicted a slightly smaller maximum size. Similar relationships and estimates of age for limpets from the patch habitat could not be made with confidence because of the high variation in individual growth rates recorded for this subpopulation.

Chlorophyll *a* content of grazing territories. Because limpet growth rates may vary based on differences in food resource availability, the chlorophyll *a* (chl *a*) content of grazing surfaces was assessed for the 2 habitat types during April and September 1997. Small (1.5 to 4.8 cm^2), flat rock samples were chipped

from surfaces of patch (n = 13) and open-rock (n = 10) habitats immediately adjacent to fixed plots using a hammer and chisel. Rock chips were placed in vials, returned to the laboratory in darkened coolers and stored in the dark at −80°C until they were analyzed. The exposed surface area of each rock chip was determined from magnified video projections using a Delta-T Area Meter (Decagon Devices). Rock chips were submerged in 90% acetone in 15 ml disposable centrifuge tubes for 48 h, the minimum time required for complete chlorophyll extraction. All extractions were performed in the dark at 10°C and under constant agitation. Following extraction, samples were centrifuged at 15°C for 5 min at 3000 rpm (2060 × *g*) in a Beckman GS-6R refrigerated centrifuge. The absorbance of the supernatant was measured at 730, 664, 647, and 630 nm using a Beckman DU-50 spectrophotometer, where the absorbance at 730 nm was used to correct for any turbidity. Total chl *a* concentrations were then determined using equations from Jeffrey & Humphrey (1975) and converted to µg chl *a* cm^{-2} using measurements of exposed rock surface area.

Sex ratio and reproductive potential. Daly (1975) concluded that *Lottia gigantea* at Punta Banda, Mexico, located ca. 300 km south of our study area, experiences a single major spawning event between December and January. Several limpets were initially collected from our study area and determined to be gravid during autumn. Therefore, we collected 42 specimens between the sizes of 16 and 68 mm from the open-rock habitat and 51 specimens between the sizes of 13 and 34 mm from the patch habitat during October 1997 to assess gonadal production. These individuals represented the range of limpet sizes occurring in each habitat type and were collected to establish relationships between limpet size and gonadal mass and to construct profiles of total gonadal production for each subpopulation. Collected limpets were placed in a 7% MgCl$_2$-seawater solution for approximately 30 min and then fixed in 10% formalin-seawater. The shell was removed, the SL measured, and the body (excluding shell) blotted to remove excess water and weighed. The gonadal mass was dissected away from the body, examined for the presence of eggs or sperm, and weighed. A gonadal somatic index (GSI = gonad weight/[body weight − gonad weight] × 100) was calculated for each limpet and means for each subpopulation determined. Specimens were also assigned to 5 mm size classes as described previously, and the percentages of immature, female, and male limpets and the gonadal wet mass (g) for each size class were determined. Mean gonadal wet weight per size class, March 1997 limpet densities (m^{-2}), and size structure data were then used to estimate the total gonadal production per unit area for each subpopulation.

Statistical analyses. Size profiles for limpet populations from the 8 sites and from the patch and open-rock habitats at Monarch Bay were analyzed using a *G*-test procedure described by Zar (1999, p. 505). To perform these analyses, limpets ≥60 mm SL were combined into a single size class, and an arbitrary value (0.01) was assigned to each frequency cell to eliminate zeros so that logs could be calculated. Data for the remaining among-site and within-site comparisons were analyzed using either ANOVA or *t*-test statistical procedures. For analyses using ANOVA models, data sets were first examined for heterogeneity of variances using Cochran's test, transformed if necessary, and then subjected to ANOVA procedures. ANOVA is robust to non-normality (Underwood 1997); therefore, departures from normality were not considered a reason to reject the parametric procedure. When the homoscedasticity criterion could not be met by transformation and variance departures were judged to be large, randomization tests were used to test the null hypothesis of no difference among groups. As suggested by Manly (1997), random reassignment of the data was repeated 1000 times for setting α at 0.05. Randomization tests were used to test for significant differences in mean *Lottia gigantea* SLs among our 8 sites and the gonadal production among size classes in each habitat. Following significant results, differences among means were examined *a posteriori* using the Student-Newman-Keuls' multiple comparison test (ANOVA) or Dunn's multiple range test (randomization tests).

Because fixed plots were used to determine limpet densities and available grazing area, data were analyzed by a 2-way ANOVA with repeated measures to test for differences between subpopulations and among sampling periods. Three plots were randomly eliminated from the patch samples to achieve equal sample sizes, a requirement for this analysis. In this model both subpopulations and sampling periods were treated as fixed factors. Because separate rock pieces for each sampling period were used in determining the chl *a* content of grazing territories, data were analyzed using a 2-way ANOVA to test for differences between chl *a* in the 2 habitat types and among sampling periods.

Calculated annual growth rates of limpets from both subpopulations were plotted as a function of initial SL and subjected to regression analysis to determine growth-rate functions for subpopulations from the 2 habitat types. Analysis of covariance (ANCOVA) was performed to test whether growth rates of limpets in the 2 habitats differed with the initial SL of monitored individuals set as the covariate. Using only limpets <40 mm SL, growth-rate data for both subpopulations were subjected to separate 1-way ANOVAs to test for differences in growth rates among sampling periods for the 2 subpopulations. Preliminary analysis of these data by ANCOVA, revealed no significant effect of initial SL on the annual growth of limpets <40 mm SL in either habitat. Separate 1-way ANOVAs were performed for each habitat type instead of a crossed model because sample sizes varied greatly between the 2 subpopulations.

To determine whether size structures, gonadal mass, and the gonadal somatic index differed between the subpopulations occupying the 2 habitat types, each data set was subjected to a 2-tailed *t*-test. Because of differences in group variances, Welch's approximate *t*-test, a more conservative and reliable
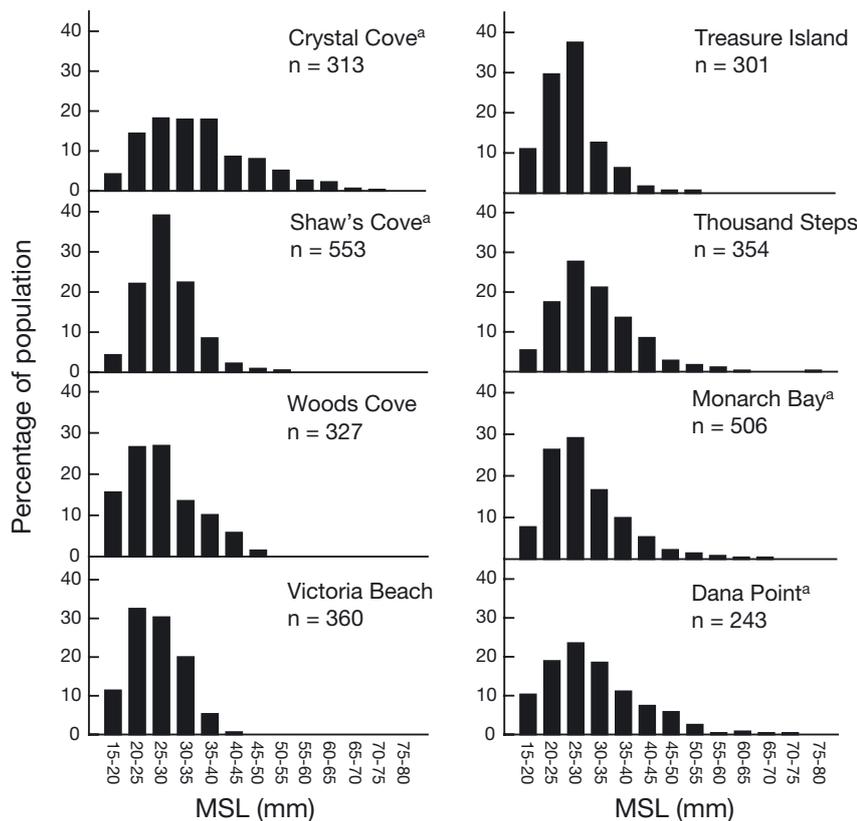

Fig. 2. *Lottia gigantea*. Size-frequency distributions (maximum shell length) of populations at the 8 sites. Values are sorted into 5 mm size classes and based on the indicated sample sizes (n). [a]Sites located within MPAs established between 1969 and 1971 where regulations have prohibited the collection of *L. gigantea* except for scientific purposes. Size-frequency distributions differed significantly among sites

Table 3. *Lottia gigantea*. Maximum shell length (mm; mean ± 1 SE) and size of the largest sampled individual for populations at the 8 study sites. Mean values are based on the indicated sample sizes (n). [a]Sites located within intertidal MPAs designated between 1969 and 1972 where regulations have prohibited the collection of *L. gigantea* except for scientific purposes for more than 25 yr at the time of the study. A randomization test procedure revealed highly significant differences among site mean SLs (p ≪ 0.001). Mean values followed by the same letter (a–d) belong to the same subset based on results of the Dunn's multiple range test

Site	n	Population	Largest limpet
Crystal Cove[a]	313	35.2 ± 0.6 a	73.2
Shaw's Cove[a]	553	28.5 ± 0.2 b	53.6
Woods Cove	327	27.4 ± 0.4 c	49.2
Victoria Beach	360	26.2 ± 0.3 c	41.9
Treasure Island	301	26.6 ± 0.4 c	53.4
Thousand Steps	354	31.2 ± 0.4 e	79.0
Monarch Bay[a]	506	29.1 ± 0.4 b	67.6
Dana Point[a]	243	31.3 ± 0.7 e	70.0

test than the traditional *t*-test under these circumstances (Quinn & Keough 2002), was employed. Gonadal mass was also plotted against SL for limpets in both subpopulations and regression analysis used to describe the relationship between gonadal mass and limpet size.

RESULTS

Among-site differences in population size structure

The mean SL (p ≪ 0.001) and size-frequency distributions (G = 121.29; df = 70; p < 0.001) of *Lottia gigantea* populations differed significantly among the 8 study sites (Fig. 2, Table 3). The largest mean SL (35.2 mm) and highest frequency of larger-sized limpets were recorded for the Crystal Cove MPA population. The largest limpet SLs found at the 8 sites ranged from 41.9 to 79.0 mm; the largest measured individual was obtained at Thousand Steps, a difficult to access, newly-established MPA. The smallest mean SLs, fewest numbers of larger-sized limpets, and the smallest SLs occurred at Victoria Beach, Treasure Island, and Woods Cove (newly-established MPAs).

Within-site analyses of patch and open-rock subpopulations

Density and size structure

The densities of *Lottia gigantea* subpopulations at Monarch Bay differed significantly (2-way ANOVA)

between habitat types (p < 0.001) and over time (p < 0.001); a significant interaction also was found between habitat and time (p < 0.01) (Table 4). *L. gigantea* densities in the patch habitats were more than twice those obtained for the subpopulation occupying open-rock surfaces during each of the 4 assessment periods. Densities of *L. gigantea* were lower in March and July 1997 than in October 1997 and February 1998 in both habitats. However, as supported by the significant interaction, the patch subpopulation exhibited a greater increase in density over time compared with the open-rock subpopulation, presumably due to greater recruitment or the migration of juveniles from nearby crevices or other cryptic microhabitats.

The mean SLs (p ≪ 0.001) and size-frequency distributions (G = 49.12; df = 10, p < 0.001) of the *Lottia gigantea* subpopulations differed greatly between habitat types (Fig. 3, Table 5). Fewer larger-sized limpets and a smaller mean SL were found in the patch habitat subpopulation. More than 75% of individuals occupying patch habitats fell within the 20–25 and 25–30 mm SL size classes, in contrast with the open-rock subpopulation where more than 55% of the individuals exceeded 30 mm SL. Nearly 10% of the limpets comprising the open-rock subpopulation reached sizes between 45–70 mm SL, whereas no limpets in the patch subpopulation exceeded 45 mm SL (Fig. 3).
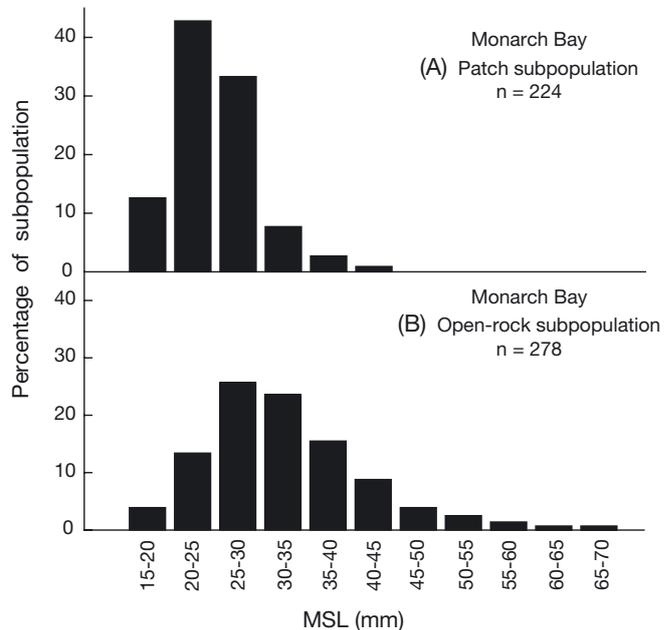

Fig. 3. *Lottia gigantea*. Size-frequency distributions (maximum shell length) of subpopulations occupying (A) patch and (B) open-rock habitats. Values are sorted into 5 mm size classes and based on the indicated sample sizes. Size-frequency distributions differed significantly among subpopulations

Table 4. *Lottia gigantea*. Density and available grazing area in patch and open-rock habitats by sampling period. Density and grazing area cover were determined quarterly throughout the sampling program (March 1997 to February 1998). Values reported are means ± 1 SE based on assessments of fixed plots (n = 11)

Season	Density (no. m^{-2})		Grazing area (% cover)	
	Patch	Open rock	Patch	Open rock
Mar 1997	46.2 ± 4.8	22.9 ± 3.1	36.5 ± 4.0	70.7 ± 2.7
Jul 1997	49.5 ± 4.5	22.2 ± 2.8	38.0 ± 3.7	75.2 ± 2.4
Oct 1997	57.5 ± 5.2	27.3 ± 3.7	17.2 ± 1.4	59.1 ± 3.7
Feb 1998	64.7 ± 5.8	26.2 ± 4.0	31.1 ± 2.2	79.1 ± 2.9
Results of 2-way ANOVA with repeated measures				
	df	MS	*F*	
	df	MS	*F*	
Habitat type	1, 20	19560.7	23.4***	1, 20	35742.1	138.3***
Season	3, 60	599.5	12.5***	3, 60	1614.6	35.9***
Habitat type × sampling period	3, 60	230.3	4.8**	3, 60	200.9	4.5**

**p < 0.01; ***p < 0.001

Shell growth rates and age determination

Shell growth rates of *Lottia gigantea* differed between habitat types (Fig. 4, Table 5) and over time (Table 6). Shell growth rates also were much more variable and poorly related to limpet size in individuals with initial lengths <40 mm SL in both habitat types (Fig. 4). Regressions of shell growth on initial SL for limpets <40 mm SL were not significant for either the patch ($r^2 = 0.03$, df 1, 27, $F = 0.827$, p = 0.37) or open-rock ($r^2 = 0.07$, df 1, 13, $F = 0.961$, p = 0.34) subpopulations. Nevertheless, the mean annual growth rate of individuals < 40 mm SL was more than 4 times greater in open-rock than in patch habitats (Fig. 4, Table 5). When all limpets in the open-rock subpopulation were considered, a significant linear relationship was detected between annual growth and initial SL ($r^2 = 0.57$, df 1, 35, $F = 46.289$, p ≪ 0.001), and shell growth rates decreased strongly with limpet size (Fig. 4). Using the von Bertalanffy growth function, the age of the largest

limpet in the open-rock habitat (67.7 mm) was estimated to be 8.5 yr (Fig. 5). After applying age estimates to the limpets used in the size-frequency distributions, over 80% of the limpets <45 mm SL in the open-rock subpopulation were ≤2 yr old (Fig. 6). Mean shell growth rates also varied over time for limpets <40 mm SL in both habitat types (Table 6). Greatest shell growth occurred in the spring and early summer (March to July 1997) and least growth in autumn and winter (October 1997 to February 1998), the period when limpets were believed to be accumulating gonadal material.

Table 5. *Lottia gigantea*. SL (mm) and the gonadal somatic index (GSI) of entire subpopulations, and shell growth rates (mm yr^{-1}) of individuals <40 mm in patch and open-rock habitats. Data are means ± 1 SE based on the indicated sample sizes (n). Statistical analyses by Welch's approximate *t*-test procedure

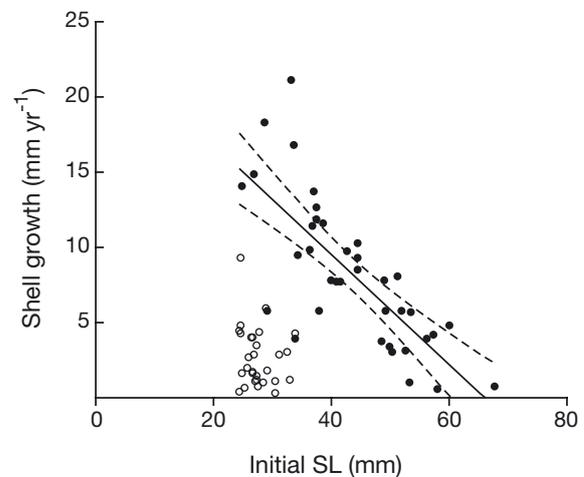| Parameter	Patch	Open rock	Statistical test results
Shell length (mm)	24.7 ± 0.3 (n = 224)	32.8 ± 0.5 (n = 278)	*t* = 12.81; df = 435 p ≪ 0.001
GSI	11.5 ± 0.8 (n = 48)	12.8 ± 1.7 (n = 40)	*t* = 0.715; df = 57 p = 0.52
Growth rates (mm yr^{-1}) in limpets < 40 mm SL	2.7 ± 0.4 (n = 29)	12.1 ± 1.2 (n = 15)	*t* = 7.315; df = 16 p ≪ 0.001

Fig. 4. *Lottia gigantea*. Annual shell growth as a function of initial shell length in the patch (○) and open-rock (●) habitats. Growth rates of limpets <40 mm SL were highly variable regardless of subpopulation. Regression line (±95% CI) is for the entire open-rock subpopulation ($y = 24.16 - 0.366x$; $r^2 = 0.57$). Regression line (and equation) not given for the patch subpopulation because the regression relationship was weak and not significant. Limpets in the open-rock habitats showed much higher growth rates than limpets occupying the patch habitats (ANCOVA; df 1, 63; $F = 125.257$; p ≪ 0.001)

Table 6. *Lottia gigantea*. Mean shell growth rates (mm mo^{-1}) of subpopulations occupying patch and open-rock habitats for the 3 sampling periods. Mean increases in SL ± SE for individuals <40 mm. Statistical analysis by 1-way ANOVA for each subpopulation. Values followed by the same letter (a–c) belong to the same subset based on Student-Newman-Keuls *a posteriori* multiple-comparison tests. ***p $\ll$ 0.001

Season	Patch (n = 32)	Open rock (n = 14)
Mar–Jul 1997	0.44 ± 0.08 a	1.92 ± 0.19 a
Jul–Oct 1997	0.21 ± 0.07 b	0.88 ± 0.13 b
Oct 1997–Feb 1998	−0.04 ± 0.06 c	0.30 ± 0.14 c

Results of 1-way ANOVA

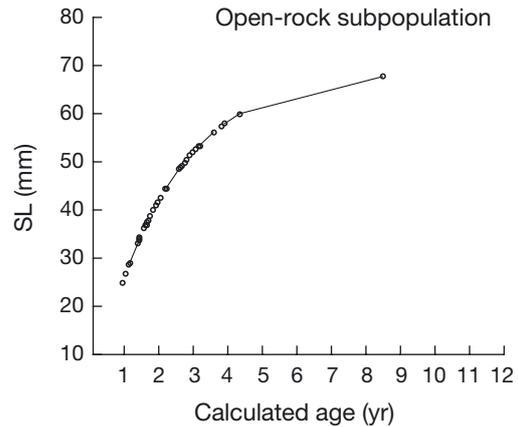| df	MS	F	df	MS	F
2,95	1.88	12.2***	2,41	9.45	27.3***

Fig. 5. *Lottia gigantea*. Relationship between shell length (mm) and age for the open-rock (n = 38) subpopulation. Relationships were established using the von Bertalanffy (1957) growth function. The calculated growth coefficient (*K*) was 0.18 for the open-rock subpopulation. Relationships between SL and age were not performed for the patch subpopulation because a significant relationship between shell growth and SL was not detected

Area and chl *a* content of grazing territories

Grazing territory, defined as the percentage of rock surfaces occupied primarily by microalgae, differed markedly (2-way ANOVA) between habitat types (p < 0.001) and over time (p < 0.001) and a significant interaction (p < 0.01) was found between habitat type and time (Table 4). The amount of grazing territory in the open-rock habitat was twice that in the patch habitat. Grazing territory varied little in both cases throughout the year, with the exception of October 1997, when grazing area decreased in both habitats due to an increase in the cover (6.4 to 11.0%) of barnacles *Chthamalus* spp. and *Balanus glandula* in the open-rock and articulated coralline algae *Corallina* spp. in both the patch (1.6 to 25.0%) and open-rock (0.5 to 4.9%) habitats. Within the open-rock habitat, coralline algae and barnacle cover decreased between October 1997 and February 1998, opening up more available grazing area compared with the patch habitat over the same time period.

Availability of microalgal food, defined in terms of chl *a* concentrations in the grazing territories (µg cm^{-2}), varied significantly (2-way ANOVA) between habitat types (p < 0.05) and over time (p < 0.05); a significant interaction between habitat type and time was not detected (Fig. 7). Chl *a* content per unit area in patch habitats was twice that found in open-rock habitats. However, because of the higher densities of owl limpets found in the patch habitats, the chl *a*:owl-limpet ratio for patch habitats (397 µg chl *a* limpet^{-1}) was less than half that determined for open-rock habitats (815 µg chl *a* limpet^{-1}), largely because open-rock habitats were less densely occupied. September chl *a* concentrations in both habitats were twice as large as those observed in April.

Gender, and gonadal production

As predicted for protandrous limpets, females fell within the larger size classes in both subpopulations (Fig. 8). In the patch subpopulation, 60% of the females were larger and 71% of the males were smaller than the mean SL (24.7 mm). Similarly, in the open-rock subpopulation 64% of the females were larger and 62% of the males were smaller than the mean limpet SL (32.8 mm). The open-rock habitat supported a slightly greater proportion of males to females (2.6 to 1) compared with the patch habitat (2.0 to 1). The gonadal somatic index of limpets <40 mm SL did not differ significantly (p = 0.52) between the 2 sub-
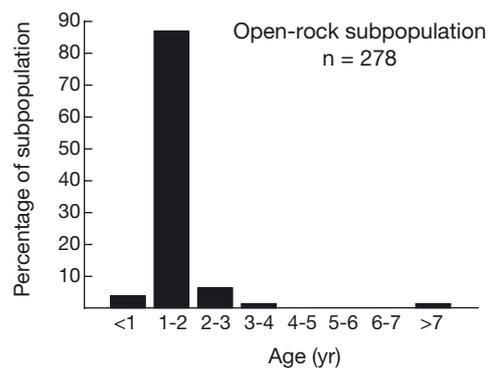

Fig. 6. *Lottia gigantea*. Age-frequency distributions of subpopulations occupying open-rock habitats, estimated using growth data and the von Bertalanffy function. Proportions are based on the indicated sample size
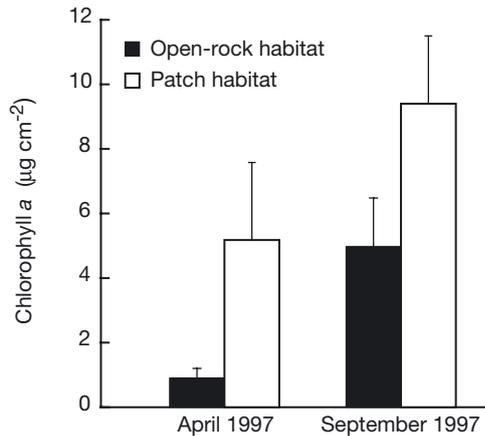
Fig. 7. Chl *a* in open-rock and patch habitats occupied by *Lottia gigantea*. Data are means (+1 SE). Results of 2-way ANOVA (n = 9 for all comparisons): habitat: df 1,16, MS = 172.5, *F* = 5.91, p < 0.05; season: df 1,16, MS = 157.0, *F* = 5.4, p < 0.05; habitat × season: df 1,16, *F* = 0.0, MS = 0.0, p > 0.90 (not significant)
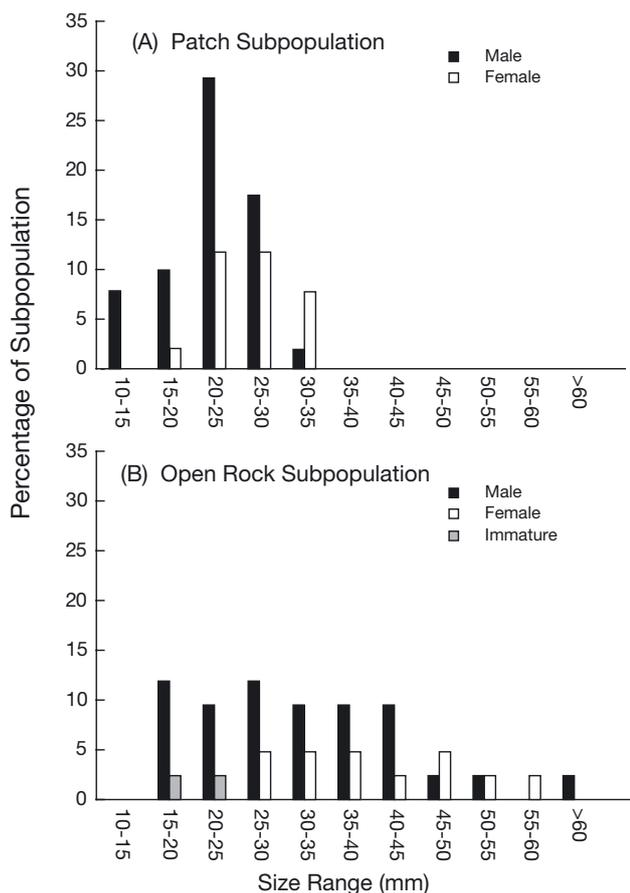

Fig. 8. *Lottia gigantea*. Percentage of the (A) patch subpopulation (n = 51) and (B) open-rock subpopulation (n = 42), categorized into 5 mm size classes, that were identified as male, female, and sexually immature

populations (Table 5). Therefore, smaller limpets in both habitats produced similar amounts of gonadal mass with respect to their body mass. As expected for many invertebrates, gonadal mass increased exponentially and showed a significant regression versus SL in both the patch ($r^2 = 0.66$ for log gonad mass vs SL; df 1,46; *F* = 89.975; p ≪ 0.001) and open-rock ($r^2 = 0.82$; df 1,38; *F* = 179.465; p ≪ 0.001) subpopulations (Fig. 9). Even though fewer limpets were found per unit area of open-rock surface, the total estimated gonadal production for this subpopulation was still much greater (5.50 g m^{-2}) than the patch (3.42 g m^{-2}) subpopulation (Table 7). Limpets >40 mm SL accounted for 58% (3.19 of 5.50 g m^{-2}) of the gonadal production in the open-rock subpopulation despite being less numerous and accounting for only 18% (4.1 of 22.9 m^{-2}) of limpet densities.

DISCUSSION

Because humans are known to selectively remove larger individuals, collecting activity can shift the size structure of exploited populations towards those dominated by smaller limpets (Branch 1975, Griffiths & Branch 1997). In fact, the degree of exploitation by humans seems to be related to declines in size structures and densities of targeted populations of limpets (Moreno et al. 1984, Hockey & Bosman 1986, Oliva & Castilla 1986, Ortega 1987, Lindberg et al. 1998, Roy et al. 2003), other gastropods (McLachlan & Lombard 1981, Castilla & Durán 1985, Moreno et al. 1986, Durán & Castilla 1989, Newton et al. 1993), mussels (Hockey & Bosman 1986) and even algae (Castilla & Bustamante 1989).

Human exploitation of *Lottia gigantea* along the California and Mexican coasts has taken place for over 13 000 yr (Vedder & Norris 1963, Abbott & Haderlie 1980, Lindberg et al. 1998, Roy et al. 2003) and continues to occur throughout most of this species' range (Pombo & Escofet 1996, Lindberg et al. 1998). Collecting activity on urban, southern California shores continues today, even within MPAs (Murray 1998, Murray et al. 1999; Table 2), and appears to have affected the size structures of *L. gigantea* populations in this heavily populated region, where the ecological effects of American black oystercatchers are essentially absent. The reduced status of *L. gigantea* populations is of concern because these and other limpet species strongly influence the structure of rocky intertidal communities by serving as herbivores, prey, and space dominators (Underwood 1979, Branch 1981, Lubchenco & Gaines 1981, Lindberg et al. 1998). In the absence of *L. gigantea* or other large grazers, smaller limpets and sessile organisms such as algae, barnacles, mussels, and anemones
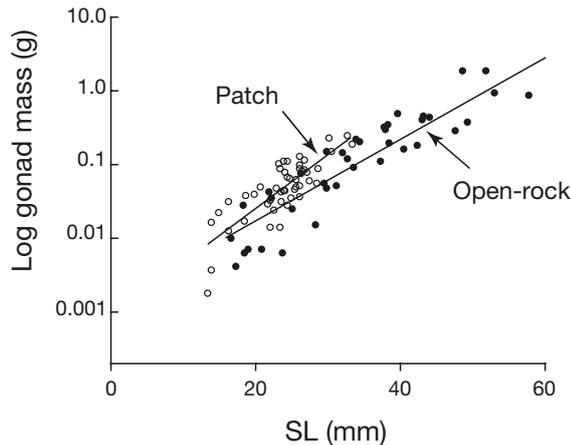
Fig. 9. Plot showing exponential increase in gonadal mass with SL. Log gonadal wet mass plotted against SL for *Lottia gigantea* in patch (○) and open-rock (●) habitats. Significant regressions were found for both the open-rock ($y = -2.87 + 0.055x$) and the patch ($y = -3.06 + 0.073x$) subpopulations

can increase their abundance in intertidal communities (Stimson 1973, Underwood 1980, 1984, Underwood & Jernakoff 1981, Creese 1982, Lindberg et al. 1998).

Our results are consistent with previous reports (Pombo & Escofet 1996, Lindberg et al. 1998, Roy et al. 2003), which have implicated humans in declining body sizes of owl limpets and other rocky intertidal gastropods on southern California shores. Among our 8 sites, *Lottia gigantea* mean and maximum SLs were generally smaller where human visitation and collecting pressure was greater (i.e. Woods Cove, Treasure Island, and Victoria Beach; Tables 2 & 3) and larger at sites that received less human disturbance (i.e. Monarch Bay, Thousand Steps, Crystal Cove, and Dana Point). Limpets reaching SLs > 70 mm were found at only 3 of our sites (Table 3). However, these maximum SLs (70 to 79 mm) were still well below the maximum

reported size (>100 mm) for *L. gigantea* (Lindberg et al. 1998), and below the largest body sizes found at sites receiving effective protection from human impacts (Roy et al. 2003). Correlation analyses provide further support for a relationship between human activities and *L. gigantea* population structures at our study sites. Significant negative rank correlations (Spearman) were found between mean *L. gigantea* SL and the number of visitors per 10 m of shoreline (r = −0.71; p = 0.048) and between mean SL and the number of collectors per 10 m of shoreline (r = −0.71; p = 0.046). Significant rank correlations were not observed between *L. gigantea* SLs and either sand cover (r = 0.60; p = 0.118) or wave force (r = −0.67; p = 0.070), although for both parameters a trend towards either positive (sand) or negative (wave action) correlations with SL was found. Under the semi-protected conditions at our study sites, however, owl limpet SLs would be expected to increase not decrease in habitats subject to greater wave action because the largest *L. gigantea* individuals are known (Ricketts et al. 1985) to occur under more wave swept conditions. Additionally, it is unlikely that larger limpet sizes would occur in more sand-scoured habitats, because sand can erode *L. gigantea* shells and bury rock substrata covering feeding territories.

With the exception of Thousand Steps, a site with intermediate levels of visitation and collecting pressure, the largest mean and maximum limpet SLs were found at sites (Crystal Cove, Monarch Bay, and Dana Point) designated as MPAs for more than 25 yr, and the smallest mean and maximum SLs at historically non-MPA sites (Woods Cove, Victoria Beach, and Treasure Island). However, collecting of invertebrates was observed at all sites, regardless of MPA status (Table 2; Murray 1998, Murray et al. 1999), and the size structures of *Lottia gigantea* populations at all our sites appear to be similar to sites where owl limpets are

Table 7. *Lottia gigantea.* Density, and individual and subpopulation gonadal mass (GM) of all size classes in patch and open-rock habitats at Monarch Bay. Data are based on January 1997 population size structures, March 1997 limpet densities, and mean gonadal wet weights for each 5 mm size class

Size class (mm)	Patch				Open rock			
	Density (no. m^{-2})	Ind. GM (g)	Subpopulation GM		Density (no. m^{-2})	Ind. GM (g)	Subpopulation GM	
			(g m^{-2})	(%)			(g m^{-2})	(%)
15–20	5.8	0.028	0.16	4.7	0.9	0.011	0.01	0.2
20–25	19.8	0.053	1.05	30.7	3.1	0.023	0.07	1.3
25–30	15.4	0.075	1.16	33.9	5.9	0.074	0.44	8.0
30–35	3.6	0.200	0.72	21.1	5.4	0.139	0.75	13.6
35–40	1.2	0.200[a]	0.25	7.3	3.5	0.294	1.04	18.9
40–45	0.4	0.200[a]	0.08	2.3	2.0	0.328	0.66	12.0
45–50	–	–	–	–	0.9	0.845	0.76	13.8
50–70	–	–	–	–	1.2	1.458	1.77	32.2
Total	46.2		3.42	100.0	22.9		5.50	100.0

[a]To determine patch subpopulation GM, the ind. GM of the 30–35 mm size class was used as a conservative estimate, because no actual data were available

extracted by humans. For example, *L. gigantea* SLs at our study sites, including those designated MPAs, were smaller than mean limpet sizes (30.6 mm) found at Sunset Cliffs in San Diego, a site characterized by high human visitation (Zedler 1978) and were comparable to SLs of *L. gigantea* populations found at Mexican sites, where collection occurs nearly on a daily basis (Pombo & Escofet 1996). In addition, *L. gigantea* mean SLs at our sites were smaller than mean SLs found in Santa Barbara, California, 24 yr ago (Stimson 1973) and smaller than those found in unexploited and difficult to access areas from central and southern California (Raimondi et al. 1999, Roy et al. 2003). Thus, our data are consistent with the premise that humans have affected the size structures of *L. gigantea* populations at our study sites, and they indicate that MPA designation has only minimally protected these populations from anthropogenic impacts.

Removal of larger limpets from open-rock surfaces provides opportunities for recruitment and the encroachment of adjacent populations of other sessile and mobile organisms. Therefore, size-selective human predation on *Lottia gigantea* can result in habitat modifications that may have lasting indirect effects on the population structure of this territorial species. Lindberg et al. (1998) suggested that the characteristically dense populations of smaller limpet species in California exist mainly because in the past humans have exploited *L. gigantea.* At Monarch Bay, we observed higher densities of smaller-sized owl limpets concentrated in small territories in patch habitats compared with subpopulations found occupying open rocks (Table 4). Mussel shells, such as those adjacent to our patch habitats, provide greater grazing surface area and refuge for small limpets (Creese 1982, Tablado et al. 1994) and increase settlement and survival of limpet larvae and juveniles (Lewis & Bowman 1975, Choat 1977, Creese 1982). Larger *L. gigantea* individuals, however, require larger open-rock surfaces to establish grazing territories with sufficient amounts of food (Stimson 1970, 1973). We recorded higher numbers of large limpets in the open-rock habitat at Monarch Bay, where there was more grazing territory and greater availability of microalgal food per limpet (Fig. 7, Table 4). Moreover, higher shell growth rates were observed for limpets inhabiting open-rock habitats compared with the similarly sized limpets found in smaller, patch habitats, where densities were higher (Table 5), and intra- and interspecific competition was likely more intense (Stimson 1973, Lewis & Bowman 1975, Choat 1977, Creese 1980b, 1982, Turon et al. 1995).

As expected for this protandrous limpet, male *Lottia gigantea* dominated the smaller size classes and were numerically dominant (2.0–2.6 to 1) in both habitats, similar to reports for protandrous South African patellids (Branch 1974). Females were almost exclusively found within the larger size classes (Fig. 8), a finding which supported our hypothesis that the majority of larger limpets would be females in both habitats irrespective of the size structures of the 2 subpopulations. An exponential relationship between gonadal weight and body size also was found for *L. gigantea* (Fig. 9), comparable to previous reports for other limpet species (Branch 1974, 1975, Creese 1980a). For example, Branch (1975) concluded that a decrease of only 20 mm SL resulted in as much as 90 % less gonadal production in the South African limpet *Patella concolor*. Larger individuals (SLs > 40 mm) from the open-rock subpopulation accounted for greater gonadal mass (3.19 g m^{-2}) and presumably gamete production than the total gonadal mass (2.31 g m^{-2}) contributed by the more numerous, smaller limpets from the open-rock habitat and nearly equivalent to the total gonadal production of the more dense limpet subpopulation (3.52 g m^{-2}) from the patch habitat (Table 7). Thus, although limpet densities were lower in the open-rock habitat, the amount of gonadal mass produced by this subpopulation was still greater than that in the patch subpopulation because of the higher numbers of larger, more fecund limpets. This is additional evidence that shifts in population structure towards higher frequencies of smaller individuals can lead to less gonadal production and lower reproductive success in *L. gigantea* and other free-spawning invertebrates where high concentrations of gametes are required for fertilization (Levitan 1991, Levitan et al. 1992, Tegner et al. 1996).

Previous researchers (MacGinitie & MacGinitie 1968, Stimson 1973, Daly 1975, Abbott & Haderlie 1980) have reported that *Lottia gigantea* may live for more than 30 yr. However, few investigators have attempted to determine the ages of limpets (see Balaparameswara Rao 1976), probably because age determination in most intertidal invertebrates is a difficult task and is usually accomplished by estimating age from growth rates (Murray 2002). Perhaps because smaller individuals have less consistent access to food resources due to intraspecific competition, shell growth rates were highly variable and poorly related to size in limpets < 40 mm SL in both habitat types (Fig. 4). Thus, age determination from growth-rate data could be estimated only for the open-rock subpopulation, which was comprised of many limpets > 40 mm SL. According to our estimates, the largest limpets in the open-rock subpopulation were > 8 yr old. However, these limpets may be even older than our estimates, because the slower growth rates together with shell erosion of larger *L. gigantea* make actual increases in SL difficult to determine. Nevertheless, our age estimates are consistent with those of MacGinitie & MacGinitie (1968), who believed that owl limpets live at least 10 to 15 yr. As a result, if MPA protection were able to reverse the

effects of long-term, size-selective human impacts, effective MPAs would take decades to change the size structure of *L. gigantea* populations based on the age of larger limpets and the potential for direct or indirect, human-induced modifications of limpet habitats.

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