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REPORT

Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California

Kaustuv Roy[1]*, Allen G. Collins[1], Bonnie J. Becker[2], Emina Begovic[3] and John M. Engle[4]
[1]Section of Ecology, Behaviour and Evolution, Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093-0116, USA
[2]National Park Service and Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA
[3]Department of Integrative Biology, University of California, Berkeley, CA 94720, USA
[4]Marine Science Institute, University of California, Santa Barbara, CA 93106, USA
**Correspondence: E-mail: kroy@biomail.ucsd.edu*

Abstract

The diverse fauna and flora of rocky intertidal ecosystems are being impacted by the activities of rapidly increasing coastal populations in many regions of the world. Human harvesting of intertidal species can lead to significant changes in body sizes of these taxa. However, little is known about the temporal trajectories of such size declines and more importantly, the long-term effects of chronic human impacts. Furthermore, it is unclear whether sizes of species not directly targeted for harvesting are also declining through indirect effects. Here we use historical (extending back to 1869) and field survey data covering 200 km of mainland southern California coast to show that human activities have led to significant and widespread declines in body sizes of rocky intertidal gastropod species over the last century. These declines, initiated several decades ago, are continuing and contrary to expectation, they are not restricted to species harvested for human consumption. Data from the only national park in this area, where conservation laws are strictly imposed, demonstrate that negative ecological impacts can be ameliorated if existing laws are enforced.

Keywords

Body size, gastropods, human impacts, Southern California.

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INTRODUCTION

The diverse biota of southern California's rocky intertidal communities is increasingly under threat from a human population that has more than doubled over the past 4 decades (Forstall 1996; Anonymous 2001). Human activities such as trampling (Murray *et al.* 1999; Schiel & Taylor 1999), legal and illegal harvesting for food, fish bait, aquaria and other uses (Eekhout *et al.* 1992; Addessi 1994; Griffiths & Branch 1997; Kyle *et al.* 1997), and removing rocks and dead shells that serve as habitats for many animals (Addessi 1994) may be negatively impacting on biological diversity of rocky shores (Littler 1980; Murray & Bray 1994; Lindberg *et al.* 1998; Murray *et al.* 1999), but quantifying their effects on individual species and populations has been difficult. Easy access and lack of enforcement of existing collecting laws have allowed for relatively unimpeded human activities at virtually every rocky intertidal habitat along the southern California coastline over many decades (Murray *et al.* 1999). Hence, it is difficult to determine the long-term effects of exploitation using current communities as ecological baseline. Historical data collected over the last century and archived in museums, however, can provide a long-term baseline appropriate for quantifying ecological consequences of anthropogenic impacts on rocky intertidal populations (Jackson *et al.* 2001). In this study, we investigate how size structures of four intertidal gastropod species in southern California have been affected by human activities over the last century by comparing old museum collections with extensive field samples.

When rocky intertidal species are harvested by humans, larger individuals are often preferentially collected, resulting in altered size structures of the exploited populations (Castilla & Duran 1985; Branch & Moreno 1994; Lindberg *et al.* 1998; Jackson & Sala 2001). Moreover, body sizes of species that are not direct targets of harvesting may also decline because of indirect effects (Jackson & Sala 2001; but see Keough *et al.* 1993). To examine how human activities have affected size structures of southern California rocky intertidal species, both directly and indirectly, we use four species of gastropods that differ in life habits and body sizes. *Lottia gigantea*, the owl limpet, is a large gastropod extensively collected as a food item (Pombo & Escofet 1996; Lindberg *et al.* 1998); *Fissurella volcano* is a small species not known to be harvested that lives primarily on the undersurface of rocks; *Tegula aureotincta* is herbivorous and occasionally harvested and *Acanthinucella spirata* is carnivorous and not a known food item in California.

METHODS

Museum data

For each of the four species used in this study, we examined collections from southern California (Los Angeles to San Diego; Fig. 1) at the California Academy of Sciences, University of California Museum of Palaeontology, Los Angeles County Museum of Natural History, San Diego Natural History Museum, Santa Barbara Museum of Natural History and Scripps Institution of Oceanography Benthic Invertebrate Collection. In these collections, we measured every individual of our target species that were over species-specific size thresholds (for *A. spirata* and *F. volcano*, individuals with lengths greater than 20 mm; for *L. gigantea*, those with lengths more than 50 mm and for *T. aureotincta*, individuals with a maximum diameter greater than 20 mm). We focused on large individuals of each species because past studies have suggested that an important effect of anthropogenic impacts on intertidal invertebrates is a significant decrease in body size in the exploited populations (Castilla & Duran 1985; Keough *et al.* 1993; Branch & Moreno 1994; Pombo & Escofet 1996; Griffiths & Branch 1997). For every measured individual we recorded the year it was collected. For specimens whose date of collection was not available, we estimated the latest possible date of collection based on information about the collector, as described in http://www.biology.ucsd.edu/labs/roy/CBRISC/search.html. Our estimated collecting dates are the latest possible, rendering our trends conservative.

These data provide a historical time series extending from 1869 to 1981 for *F. volcano*, 1896–1975 for *T. aureotincta*, 1869–1960 for *L. gigantea* and 1903–1985 for *A. spirata*. As

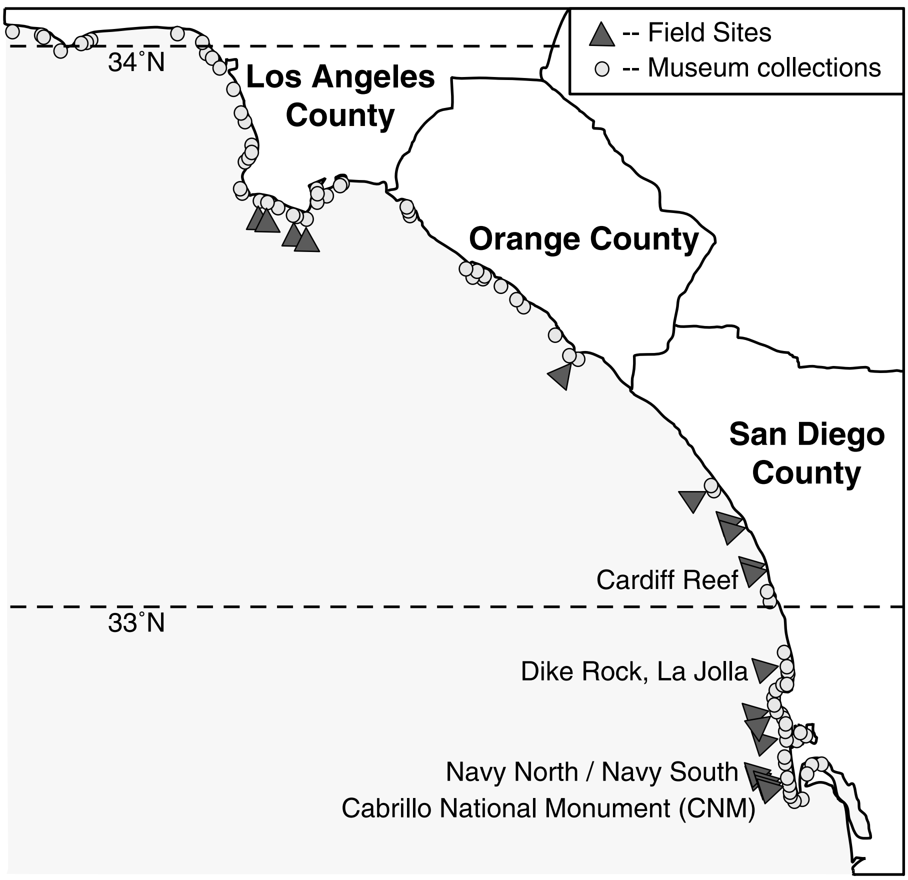

Figure 1 Map of southern California coastline showing field sites and spatial coverage of museum collections. The names shown are for sites where multi-year quadrat-level data were also available (see text).

past collecting methods are unknown, we cannot assume that these data are unbiased representations of past body size distributions, smaller individuals are under-represented in museums because collectors often favour larger specimens. However, even with this bias, historical data provide a baseline against which present body size distributions can be compared; under-representation of certain size classes today that are known to have been common in the past is direct evidence for changes in population size structure.

Field survey data

To quantify size structures of living populations, we sampled 14 rocky intertidal localities in southern California (Fig. 1). About 71% of these sites are also present in the museum data although not all our species occur at all the sites. These sites include state ecological reserves – where collecting of intertidal invertebrates is prohibited in principle – and non-reserve sites, but exclude the only national park on the coastline (see below). We used a sampling design aimed at finding the largest individuals of each species because our goal is to determine whether individuals in the larger size classes known to have lived in southern California are still present there. Timed searches were used to locate and measure individuals of each of the four species during low tides; we ignored all individuals below the species-specific size threshold used in compiling the museum data and explicitly searched for the largest individuals. At each site we carefully searched for individuals of our target species, ignored juveniles and subadults but measured all adults encountered with a pair of calipers; lengths of only those adults that were at or above the size threshold were recorded. We measured both live and dead individuals encountered because time-averaged death assemblages of marine molluscs provide more comprehensive representations of the regional populations than possible from living individuals alone (Kidwell & Flessa 1995; Kidwell 2001). The number of minutes spent searching for a given species at a particular locality varied depending on local abundance of the species and the proportion of large adults present. Total minutes spent in searching for large individuals were 198, 271, 598 and 200 for *A. spirata*, *F. volcano*, *L. gigantea* and *T. aureotincta*, respectively.

Statistical analyses

We analysed temporal patterns of body size changes using standard nonparametric statistics and quantile regressions. Quantile regressions minimize the sum of absolute deviations of a function from the observed values of a specified quantile and are appropriate for investigating body size trends (McClain & Rex 2001). We used the software BLOSSOM (Midcontinental Ecological Science Center, http://www.mesc.usgs.gov/) to perform quantile regressions of SIZE as a function of YEAR for the 50th, 80th and 90th quantiles for the museum plus field data and for the 50th and 80th quantiles for just the museum data. In addition, BLOSSOM was used to test if the estimated slopes were significantly different from zero using regression quantile rank-score tests.

RESULTS AND DISCUSSION

As the human population of coastal southern California counties has doubled since 1960 (Forstall 1996; Anonymous 2001), we combined all individuals of each species collected up to 1960 to construct our first historical baseline, and all collections between 1961 and 1980 to create a second, more recent, baseline. The second baseline was not constructed for *L. gigantea* because of small sample sizes. Figure 2 compares sizes of individuals collected in the field (2001–2002) with those from earlier time intervals. For all four species, adults collected prior to 1960 are significantly larger compared with those collected in the field or between 1961 and 1980 (Fig. 2). Similar trends also emerge when the data are binned differently (e.g. 1940 as a cut-off date instead of 1960) indicating that the patterns are robust to bin selection.

We also analysed the museum and field data using quantile regression, which obviates the need for binning data. Quantile regressions of shell length on date of collection reveal significant declining temporal trends for all four species (Table 1). Significant declines are evident in median sizes (50th quantile) and among the largest individuals (80th and 90th quantiles) (Table 1). This temporal trend is also present when the museum data are analysed by themselves for each species. Although museum data for *L. gigantea* were too sparse between 1960 and 1980 to construct a second baseline for the binned analysis (Fig. 2), quantile regression reveals a significant decline in size among the largest individuals of this species (80th quantile) prior to 1960 (Table 1).

The decline in body size revealed in these analyses most likely resulted from human activities, but comparisons of museum and field data by themselves are not conclusive tests of this hypothesis. Non-anthropogenic factors such as climate change could potentially have driven the decrease in size (e.g. Yom-Tov 2001). To test the anthropogenic hypothesis, we sampled size distributions of the four species at Cabrillo National Monument (CNM) using the same protocol as the rest of our field surveys. The CNM is located on the southern tip of Point Loma, a peninsula at the mouth of San Diego Bay, and extends for *c.* 1.5 km along the south-western coast of the point. It is the only intertidal reserve in southern California where collecting

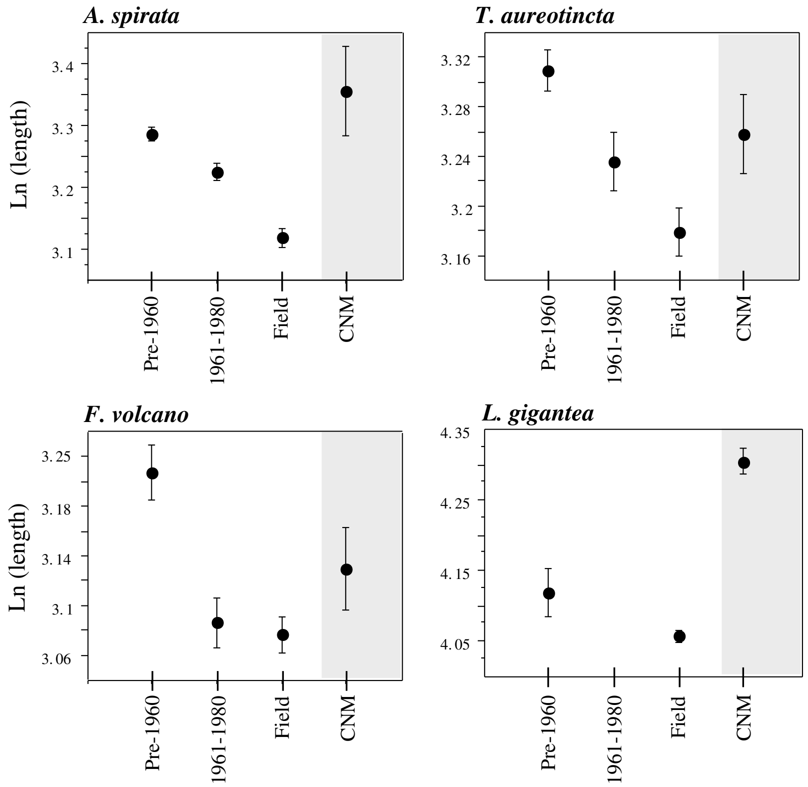

Figure 2 Mean sizes (log-transformed) of each species (with 95% confidence intervals) in individual temporal bins described in the text. The shaded area represents data from the only well-protected intertidal reserve in California (see text). As a result of small sample size, the second baseline was not calculated for *Lottia gigantea*. For *Fissurella volcano*, data are for San Diego County only. All pairwise comparisons of baselines, field samples and Cabrillo National Monument (CNM) reveal significant differences at 0.05 level or better (Kolmogorov–Smirnov tests with sequential Bonferroni corrections (Rice 1989), with the exception of Field−2nd Baseline ($P = 0.90$) and Field–CNM ($P = 0.06$) for *F. volcano*.

Table 1 Significance of temporal trends in size: *P*-values resulting from quantile regression rank-score tests, which are used to evaluate whether the slope of YEAR against SIZE, which is negative in all cases, likely differs from zero. N_1, N_2 – numbers of individuals, museum plus field and museum, respectively

	Museum plus field data			Museum data only	
Species (N_1, N_2)	50%	80%	90%	50%	80%
Acanthinucella spirata (1675, 1456)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Fissurella volcano (322, 238)	<0.0001	<0.0001	<0.0001	<0.0001	<0.01
Lottia gigantea (570, 91)	0.083	<0.0001	<0.0001	0.073	<0.05
Tegula aureotincta (610, 497)	<0.0001	<0.0001	<0.01	<0.05	0.136

laws have been strictly enforced for the last few decades, and the only one in the region with a human exclusion zone. If human impacts were the major cause of size decline seen in our data, then individuals from CNM should be larger than those from other sites. As shown in Fig. 2, for all four species, individuals found at CNM are indeed significantly larger than those from our other field sites. For *L. gigantea* and *A. spirata*, CNM individuals are actually larger than museum specimens collected before 1960, suggesting that our museum-derived historical baseline is conservative. Thus, the observed size decline over the last century is most likely the result of anthropogenic impacts. In addition, data from CNM, where we spent much less time in searching for each of the species (minutes spent searching for large individuals at CNM were 51, 140, 60 and 70 for *A. spirata*, *F. volcano*, *L. gigantea* and *T. aureotincta*, respectively), show that our field methods are adequate to find large individuals if they are present at a site and not compromised by some seasonal, habitat-related or other unknown bias. This conclusion is further supported by the fact that significant size declines are present in quantile regressions of museum data by themselves (Table 1).

As a final test of our hypothesis that anthropogenic impacts are the primary cause of size decline in rocky intertidal species in southern California, we used independently collected quadrat-scale data to compare size distributions of *L. gigantea* between CNM and four other sites where the populations of this species are either unprotected (Cardiff Reef) or minimally protected (Navy North and South, and Scripps Coastal Reserve) from poaching. Sites on the naval base are within 3 km of the boundary of CNM while the other two are within 30 km. All individuals of *L. gigantea* (≥15 mm) within fixed quadrats were measured each spring and fall from 1990 to 1999 at CNM except for spring 1996, and from spring 1995 to spring 2002, except for spring 1996 at Navy North and South sites. Scripps and Cardiff were sampled from fall 1997 to spring 2002. The median size of *L. gigantea* from CNM (45 mm) is larger than that from the other sites combined (32 mm) and the size-frequency distributions differ significantly (Fig. 3). Specifically, the unprotected sites are depauperate in larger size classes relative to CNM (Fig. 3), consistent with size selective human predation (Keough *et al.* 1993; Branch & Moreno 1994; Pombo & Escofet 1996; Griffiths & Branch 1997).

In combination, our analyses come to a clear conclusion – human activities have profoundly altered size structures of rocky intertidal gastropod populations throughout southern California. The decline in body size is evident in century-scale comparisons covering 200 km of coastline and in quadrat-scale data collected over multiple years. In addition, these declines are pervasive, at least among intertidal gastropods, lending empirical support to the notion that chronic anthropogenic impacts have negative effects that extend beyond species commonly harvested for human consumption (Griffiths & Branch 1997; Castilla 1999; Jackson & Sala 2001). The correlation of body size with many different aspects of species life histories (Peters 1983) suggests that size reductions documented here may have profound ecological and evolutionary consequences. For example, the loss of large individuals is particularly troublesome for species like *L. gigantea*, which is characterized by protandric hermaphroditism, a sequential change of sex from male to female, with large size classes being mainly female (Wright & Lindberg 1982). Thus, impacted populations of this species are likely to be preferentially losing females over males. The positive correlation between body size and fecundity in ectotherms (Peters 1983) suggests that the size decline could also be affecting the reproductive output of the impacted populations. Additionally, limpets such as *L. gigantea* are important components of trophic cascades and changes in their densities and size structures can substantially alter the organization of intertidal communities (Lindberg *et al.* 1998).

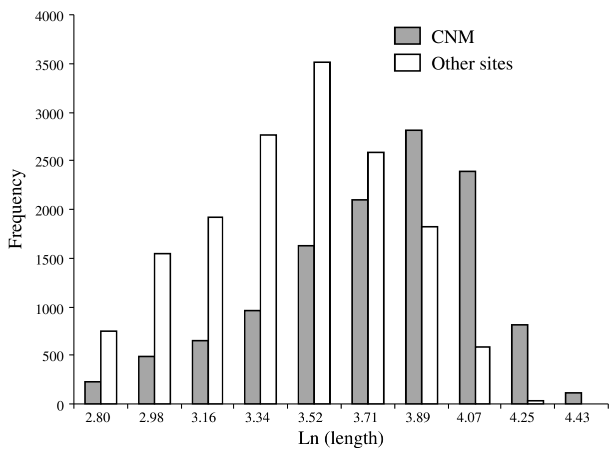

Figure 3 Size distributions of *Lottia gigantea* measured at fixed replicate quadrats over multiple years at Cabrillo National Monument (CNM) and less protected sites (see text). The distributions are significantly different ($P < 0.0001$ Kolmogorov–Smirnov test).

Much remains to be learned about mechanisms underlying the disappearance of large gastropods from southern California rocky shores. For species that are already known to be commonly harvested, differential removal of large adults is likely to be the main cause but it is unclear why sizes of small, rather cryptic species such as *F. volcano*, or small predators such as *A. spirata* have also declined. One possibility is that the small species are also being harvested, either directly or as bycatch. Currently we lack quantitative data on illegal harvesting practices along the California coast but discussions with law enforcement personnel suggest that rather than selective harvesting of certain species almost every organism living in the intertidal habitats is being collected for human use (Lt. D. Sforza, Bonnie J. Becker, personal communication). A second possibility is that post-settlement growth rates and/or longevities of individuals are being impacted because of trampling and other chronic disturbances. Testing these alternatives will require better information about patterns of human exploitation along the California coast and accurate measurement of growth rates and population age structures of intertidal species.

Our results strongly support the growing concern that intertidal species all over the world are being impacted by human activities (Castilla & Duran 1985; Keough *et al.* 1993; Branch & Moreno 1994; Griffiths & Branch 1997; Castilla 1999) and that historical data are of crucial importance in quantifying the nature and magnitude of such impacts on marine ecosystems (Pauly 1995; Jackson *et al.* 2001; Wares *et al.* 2002). In addition, concerns about shifting baselines (Pauly 1995; Jackson 1997) are just as relevant for temperate rocky intertidal species as they are for marine fisheries or coral reefs. For the four gastropods studied here, museum drawers are full of individuals belonging to size classes that intertidal ecologists only rarely see today on southern California rocky shores. Also we cannot reject the possibility that even our historical baseline may represent an 'unnatural' state compared with pre-European times when some of these species were abundant and commonly exploited by the Native Americans (e.g. Byrd 1998). On the other hand, our results confirm that demonstrably large and widespread negative effects of human activities may also be reversible in some situations (Halpern & Warner 2002). Data from CNM show that existing conservation laws, if properly enforced, can help protect the intertidal biota from some anthropogenic impacts. California has a long history of establishing coastal marine reserves (Murray *et al.* 1999) and strict enforcement of existing laws within them would go a long way towards restoring the intertidal invertebrate communities of southern California closer to their unimpacted states.

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