**ORIGINAL ARTICLE**

# Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea*

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## ABSTRACT

**Aim** We evaluate the stability of the range limits of the rocky intertidal limpet, *Lottia gigantea*, over the last *c.* 140 years, test the validity of the abundant centre hypothesis, and test indirectly the roles played by recruitment limitation and habitat availability in controlling the range limits. Because this species is size-selectively harvested, our results also allow us to assess conservation implications.

**Location** The Pacific coast of North America, from northern California to southern Baja California (41.74° N–23.37° N), encompassing the entire range of *L. gigantea*.

**Methods** The historical and modern distributions of *L. gigantea* were established using museum data and field observations. Overall and juvenile abundances of local populations were estimated at 25 field sites. The spatial distribution of abundance was evaluated statistically against the predictions of five hypothetical models. The availability of habitat was estimated by measuring the percentage of unavailable sandy beach within cumulative bins of coast across the range of *L. gigantea*.

**Results** The northern limit of *L. gigantea* has contracted by *c.* 2.4° of latitude over recent decades (after 1963), while the southern limit has remained stable. The highest abundances of *L. gigantea* occur in the centre of its geographic range. Habitat availability is ample in the centre and northern portions of its range, but is generally lacking in the southern range. The northern range is only sparsely populated by adults, with sharp declines occurring north of Monterey Bay (36.80° N). In the southern range, abundance drops precipitously south of Punta Eugenia (27.82° N), coinciding with the region where suitable habitat becomes sparse.

**Main conclusions** Support for the abundant centre hypothesis was found for *L. gigantea*. Northern populations are characterized as being recruitment-limited, demographically unstable and prone to local extinctions, while southern populations are suggested to be habitat-limited. The abundant centre is suggested to result partly from a combination of the indirect effects of human harvesting, generating denser populations of smaller individuals, and larval recruitment from well-protected offshore rocky islands primarily found in the range centre.

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## INTRODUCTION

The abundance and distribution of a species across its geographic range result from multiple ecological and evolutionary processes, including rates of dispersal, demography, competition, habitat availability/quality, climate and human impacts (Brown, 1995). The effect that these processes have on the range-wide distribution and abundance of a species is a cornerstone of biogeography, macroecology and conservation biology (Gaston, 2003, 2009; Sagarin et al., 2006; Gaines et al., 2009). However, studies that cover the entire range of a species are rare, limiting our ability to answer basic biogeographic questions. Despite this, certain range-wide characteristics are often assumed to be general features exhibited across species. For example, the abundance of a species across its geographic range is classically assumed to be highest in the centre of the range and to decline towards the edges. This abundant centre hypothesis (ACH) assumes that central populations are living at optimal physical and biotic conditions and that individual success is high and is reflected by high abundances (Brown, 1984; Guo et al., 2005). The few studies that have tested this hypothesis are, however, equivocal on the subject (Sagarin & Gaines, 2002; Gaston, 2003; Sagarin et al., 2006; Samis & Eckert, 2007; Tuya et al., 2008; Rivadeneira et al., 2010).

The geographic constraint of most studies also limits our understanding of the causes of range limits, which is a central question in biogeography (Holt & Keitt, 2005; Gaston, 2009; Sexton et al., 2009). Habitat quality, competitive interactions, physical/climatic barriers to dispersal, and the influence of dispersal variability on the genetic potential for local adaptation of peripheral populations are among the more commonly proposed mechanisms for range limits (Holt et al., 2005; Gaston, 2009; Sexton et al., 2009; Dawson et al., 2010). However, how these and other mechanisms differentially affect species at opposite ends of their range (e.g. southern and northern limits) and how they relate to abundance and population structure across the range is not generally known (but see Gross & Price, 2000). Furthermore, geographic patterns of abundance and distribution alone may offer only little information on their underlying physical and biotic causes.

Emergent patterns (or lack thereof) of the causes of abundance and range limits are not likely to arise unless more studies are aimed at measuring relevant traits (e.g. abundance, population structure, habitat availability, population genetics) across the ranges of species. These types of observational studies are needed not only to inform our understanding of basic biogeographic processes, but also to assess the conservation status of species and ecosystems (Sagarin et al., 2006; Sagarin & Pauchard, 2010). Several authors have suggested that the abundance and range limits of species may be geographically reflected by population structure (e.g. the presence of recruits), life history, and genetic traits (Gilman, 2005, 2006; Gaston, 2009; Dawson et al., 2010; Rivadeneira et al., 2010). For example, low abundances near range limits may be a result of recruitment limitation, potentially caused by long distances between reproductive populations due to habitat variability, or of low survival of larvae or juveniles because of other physical factors (e.g. temperature stress, ocean currents, etc.; Zacherl et al., 2003; Gilman, 2005, 2006; Sanford et al., 2006). Alternatively, high abundances near range limits may correspond to abrupt physical barriers to dispersal (Brown, 1984; Dawson et al., 2010). From a population-genetic perspective, the flow of maladapted alleles from central to marginal populations could hinder local adaptation and cause range limits, as recently suggested by Dawson et al. (2010) for a barnacle with a temporally fluctuating range limit along the west coast of North America.

Because abundance and distribution vary not only geographically but also through time, modern 'snapshot' studies of abundance and range limits do not reflect their temporal variation. While it is generally difficult to attain information on past local abundances of a species, natural history museum collections can sometimes provide a solid baseline for the historical distribution (i.e. range limits) of a species (Suarez & Tsutsui, 2004; Johnson et al., 2011). Thus, to have some understanding of the causes of the abundance and range limits of a species throughout its range, it is important to link these data with population-level traits (e.g. recruitment), physical data (e.g. geographic patterns of habitat availability), temporal information (e.g. historical distribution) and human impacts.

Coastal species are particularly amenable for such large-scale studies owing to the geometry of their geographic ranges and the relative ease with which relevant traits can be measured (Sagarin et al., 2006). Along the west coast of North America, for example, species restricted to rocky intertidal habitats essentially have one-dimensional (north–south), short-width (< 0.1 km) geographic ranges, with one point representing the range centre and two representing the range edges (Sagarin et al., 2006). These traits, along with the widespread availability of geographic software (e.g. GIS, Google Earth), make it possible to broadly quantify relevant factors that may affect abundance and range limits, such as distances between available rocky intertidal habitats present within the range of a species. Furthermore, many species are temporally and geographically well represented in natural history museum collections, allowing for a historic baseline of geographic distribution.

Here, we present the results of a range-wide study on the abundance (overall and juveniles), range limits (past and present) and habitat availability of a species of conservation concern along the west coast of North America. The owl limpet, Lottia gigantea (Sowerby, 1834), is a large patellid gastropod species (Lindberg et al., 1998), capable of attaining lengths greater than 100 mm. It has a range from northern California (c. 39.4° N) to southern Baja California (c. 26.1° N) along the Pacific rocky intertidal coast, including all the coastal islands within that latitudinal range. Individuals inhabit multiple rock types in the mid to high intertidal zone (Sagarin et al., 2007), where larger individuals (mostly female; L. gigantea is protandrous) territorially defend their algal grazing area (Stimson, 1970; Shanks, 2002). Recently, it has

been shown that *L. gigantea* populations from California are genetically homogenous, suggesting high rates of gene flow in this portion of its geographic range (Fenberg *et al.*, 2010).

Previous studies aimed at analysing range-wide abundance and the causes of range limits in marine organisms have largely focused on non-harvested species (Sagarin & Gaines, 2002; Gilman, 2005, 2006; Rivadeneira *et al.*, 2010). Humans have size-selectively harvested *L. gigantea* for thousands of years (Lindberg *et al.*, 1998; Erlandson *et al.*, 2011), but the harvesting of this species is more intense and wide-ranging today than the subsistence collecting of the past (Roy *et al.*, 2003; Sagarin *et al.*, 2007). The largest size classes have been declining over the past 100 years in many locations in southern California (Roy *et al.*, 2003). The cascading effects of size-selective harvest include reduction in biomass, reduction in the amount of grazing area individuals occupy (territorial space), reduction in reproductive output and changes in local abundance (Kido & Murray, 2003; Fenberg, 2008).

Our goals were: (1) to evaluate the stability of the range limits of *L. gigantea* over the last *c.* 140 years; (2) to establish the geographic pattern of abundance of *L. gigantea*, testing the validity of the ACH for this species; and (3) to test indirectly the role played by recruitment limitation and habitat availability as determinant factors of the range limits. Because of the human impacts of size-selective harvesting, the test of the ACH will be highly conservative: if humans are affecting abundance patterns, then it should be more difficult to validate the ACH, or, at least, the ACH should be masked by human-induced impacts. However, by combining abundance data with modern and historical distributions, range-wide habitat availability, and human impacts, our study will allow us to broadly assess some of the range-wide physical and biotic controls on the biogeography of *L. gigantea* and to discuss how this information may affect the conservation biology of this species.

## MATERIALS AND METHODS

### Range dynamics

We recorded the geographic locality and the year of collection for every mainland specimen of *L. gigantea* present in the collections of the five major natural history museums in California (San Diego Natural History Museum, Los Angeles County Museum of Natural History, Santa Barbara Museum of Natural History, University of California Museum of Paleontology, and California Academy of Sciences) as well as in the National Museum of Natural History, Washington, D.C. Each specimen was checked by a single observer (P.B.F.) to confirm the taxonomic identification. The resulting database consists of 1850 occurrences in 138 georeferenced localities dating back to 1869. These data were used to create a baseline of historical geographic distribution and to serve as a guide for the selection of field sites.

To establish the modern distribution of *L. gigantea* across its geographic range, we recorded the presence/absence of this species at 34 rocky intertidal field sites along the mainland
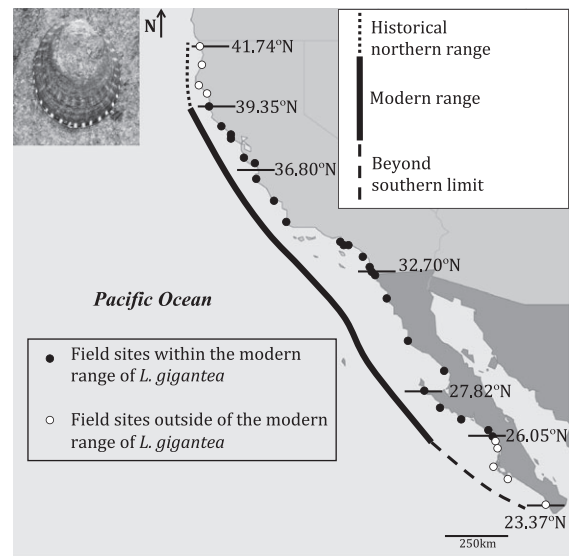


**Figure 1** Map of sampled field sites along the mainland Pacific coast of California and Baja California, encompassing the modern geographic range of *Lottia gigantea* (39.35° N–26.05° N). The historical northern range of *L. gigantea* refers to the observation that this species was collected at 41.74° N at Crescent City, CA (by four individual collectors between 1889 and 1963) but was not seen here or at three sites further south during exhaustive searches (see text). The latitudes 36.80° N, 32.70° N, 27.82° N and 23.37° N correspond to Monterey Bay, the modern range centre of *L. gigantea*, Punta Eugenia and our southernmost field site, respectively.

Pacific coast of California and Baja California (41.74° N–23.37° N) from 2003 to 2007 (Fig. 1 and see Appendix S1 in Supporting Information). *Lottia gigantea* individuals were identified *in situ* by a single observer (P.B.F.). Of these 34 sites, 22 of them occur as *L. gigantea* collection localities at natural history museums. We spent a minimum of 90 min searching each field site for *L. gigantea*, with considerably more time at sites where *L. gigantea* was abundant. Two sites outside the modern range of *L. gigantea* in southern Baja California, at Cabo San Lazaro (24.81° N) and Punta Tosca (24.30° N), were searched as a part of a separate study on rocky intertidal biodiversity (Chuck Baxter, Hopkins Marine Station, Stanford, pers. comm.).

### Geographic patterns of abundance

We define the modern geographic range of *L. gigantea* as the latitudinal span of all locations where individuals are found, and the range limits as the northern and southernmost locations where individuals have been located. We measured the abundance of individuals at sites where *L. gigantea* was present – at 25 out of 34 sites. Once *L. gigantea* individuals were found, we placed belt transects of metre-square quadrats and counted the number of individuals. Because individuals of this species are non-randomly distributed across the rocky intertidal, we did not sample quadrats that fell on areas

unoccupied by *L. gigantea*. Therefore, the lowest number of individuals possible within a quadrat in the dataset is one. We sampled most populations over the course of two successive days. In total, we counted 7615 individuals from 25 field sites for this study. All of our field surveys were carried out by one person (P.B.F.), reducing the possibility of observer bias.

Abundances were averaged across all metre-square quadrats at each site (hereafter 'average' abundance). Using calipers, we took special care to find all individuals of *L. gigantea* over 10 mm in order to obtain an unbiased estimate of abundance at each of our field sites (individuals below 10 mm cannot be distinguished visually from other species of limpet found within the same habitat). In doing so, we were able to obtain a conservative estimate of the number of juveniles present in each quadrat. We define a juvenile as an individual below 25 mm in length, corresponding to an individual of about 2 years of age and not yet sexually mature (see Fenberg, 2008). Therefore, the average percentage of individuals per square metre above 10 mm and below 25 mm gives us a conservative snapshot of recruitment success for each local population.

Recently, numerous local *L. gigantea* populations from central and southern California have been qualitatively categorized according to their relative vulnerability to harvest pressure (Sagarin *et al.*, 2007). These vulnerability categories range from 1 (most vulnerable) to 3 (least vulnerable) and are based on levels of physical accessibility and observations of harvesting events. The only sites with a category 3 are those on the Channel Islands, which we did not sample for this study; thus, we have assigned our 10 southern and central California sites as either 1 (high vulnerability) or 2 (low vulnerability)

using the metrics outlined in Sagarin *et al.* (2007). We overlay these categories with our field data to test the relationship between harvesting pressure and abundance.

## Testing the abundant centre hypothesis

We tested the ACH using the expression proposed by Enquist *et al.* (1995): $RI = 2(L-S)/R$, where RI is the range index, or the relative position of each site across the range (varying between $-1$ and 1: $-1$ = southern edge; 0 = centre of the range; 1 = northern edge), $L$ is the site location (in degrees of latitude), $S$ is the latitudinal midpoint of the species' range, and $R$ is the latitudinal range (in degrees of latitude). Latitudinal limits of distribution were determined using field observations.

Spatial patterns of variation of abundance were fitted to five hypothetical models (Fig. 2). Although many other models may be envisaged, these models encompass the patterns previously reported for other species (Sagarin & Gaines, 2002; Gaston, 2003; Sagarin *et al.*, 2006; Rivadeneira *et al.*, 2010). In the first model (normal, Fig. 2a), abundance follows a normal distribution. The second model (inverse quadratic, Fig. 2b) also assumes that the maximum abundance is reached at the centre of the distribution, declining towards the edges, but the decline is much more gradual than in the normal model. The abundant edge model (Fig. 2c) assumes the inverse pattern, with maximum abundances observed towards the edges of the range, whereas minimum values are observed in the centre. The two remaining models (ramped north, ramped south, Fig. 2d,e) assume that the maximum abundances decline from one range limit to the other and that intermediate abundances are reached at the centre of the range.
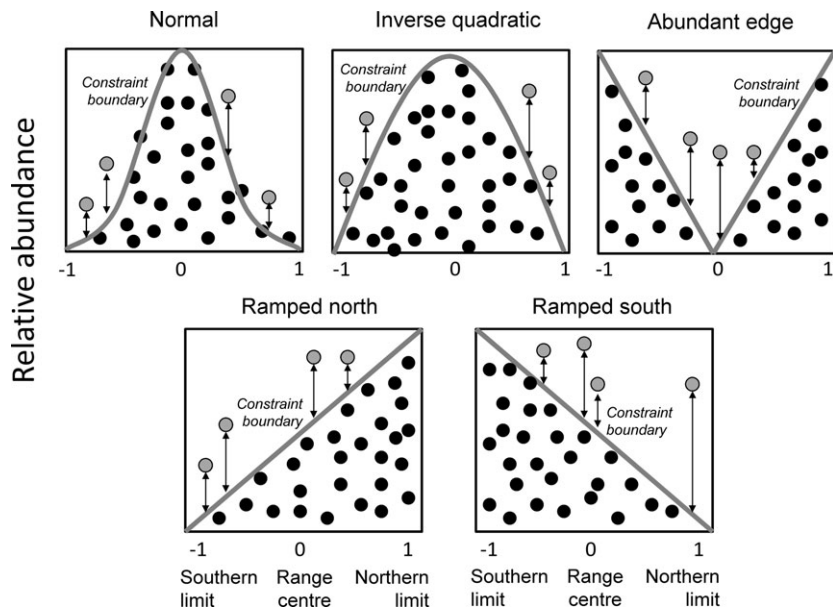


**Figure 2** Five hypothetical models describing the variation of abundance across the geographic range of *Lottia gigantea*. The degree of fit of each model to the observed data was evaluated by calculating the residual sum of squared deviations (RSS, deviations indicated by arrows) for sites exceeding the constraint boundary (grey dots).

The degree of fit of each model to the observed data was evaluated by calculating the residual sum of squared deviations (RSS) for sites exceeding the constraint boundary generated by each model (Fig. 2). Small values of RSS indicate a good fit between the model and the observed data. The significance of the observed RSS values was evaluated by generating $10^6$ randomized values of RI and relative abundance. The fit of the model was considered significant when the observed RSS value was lower than the 5th percentile of the randomized distribution. The degree of support for each model was evaluated by calculating the Akaike's information criterion (AIC), selecting all models with Akaike weights > 0.25. Analyses were carried out using a script written in R (v. 2.11; Appendix S2).

## Habitat availability

We measured the total amount of rocky intertidal habitat present throughout the geographic range of *L. gigantea* (and beyond) using the software program Google Earth (v. 4.1). We traced around the contours of the Pacific coastline of California and Baja California in cumulative 48-km (*c.* 30-mile) sections at a constant elevation of 500 m, from 23.16° N to 41.96° N, encompassing the range of *L. gigantea* (starting in the south and working our way north). Within each section, we measured the amount of coastline that consisted of unsuitable sandy beach habitat. To do this, we measured the length of sandy beach coastline that achieved lengths greater than 1.6 km (1 mile). We then added the lengths of each sandy stretch in a section and divided the sum by the total length of each coastline section (48 km) to calculate a percentage of unsuitable habitat per section. We repeated this protocol for more than the entire mainland range of *L. gigantea* and plotted the percentage of sandy beach per successive 48-km bin for the total length of shoreline. For example, a value of 50% means that *c.* 24 km of shoreline within a particular section is made up of uninhabitable sandy beach and the other 24 km consists mostly of rocky shore (i.e. suitable *L. gigantea* habitat). Our field observations along with the fact that historical museum records of *L. gigantea* are represented at all latitudes within its range (see Results) indicate that individuals will generally live on all rock types found along the California and Baja coastline (also see Sagarin *et al.*, 2007). Thus, our measurements should be a fairly accurate representation of the geographic variation in the amount of habitat available to *L. gigantea* (and to other rocky intertidal species with similar ranges). It is important to note that our measurements are for the mainland range of *L. gigantea* only and do not include measurements for the coastal islands that this species also inhabits. These coastal islands are predominantly lined by rocky shore and therefore increase the amount of habitat available to *L. gigantea* throughout its range. Interestingly, these islands tend to be situated off sandy stretches of the mainland coast towards the middle of the range of *L. gigantea*.

Finally, we tested for correlations between the local abundance (overall and juveniles) and the percentage of unsuitable habitat by matching the abundance data from sampled sites to the nearest latitudinal habitat measurement bin. Correlations were carried out using Pearson's product moment, with *P*-values corrected for spatial autocorrelation using Dutilleul's method (Dutilleul, 1993) implemented in the software program SAM (v. 4.0; Rangel *et al.*, 2010). We tested for correlations for the entire range and then for the northern and southern ranges separately (i.e. from the range centre to the respective range limits).

## RESULTS

### Range shifts

Based on the database of museum occurrences, the historical geographic distribution of *L. gigantea* ranges from 41.74° N to 26.23° N (Fig. 3a). The southern range limit is located at Punta Pequeña in Baja California Sur (one lot from 1979), while the northern limit is located at Crescent City, California (four lots from 1889 to 1963).

Field surveys of 34 localities show that the present geographic distribution of *L. gigantea* ranges from 39.35° N to 26.05° N. At the southern end, we were able to locate *L. gigantea* 0.18° further south than the museum-based range limit. *Lottia gigantea* was not found at five localities directly south of 26.05° N (Fig. 1; see Appendix S1), despite an exhaustive search. In contrast, the discrepancy between museum data and field surveys for the northern range limit is 2.4°. We exhaustively searched four rocky intertidal localities north of 39.35° N, including three separate searches (in 2003, 2005 and 2011) of the museum-based northern limit at Crescent City (41.74° N), but were not able to locate any individuals of *L. gigantea* (Fig. 1; see Appendix S1). The historical occurrence of *L. gigantea* at Crescent City is not likely to be an artefact because four individual collectors found *L. gigantea* at this locality between 1889 and 1963. Misidentification is not likely because P.B.F. personally confirmed each lot from Crescent City. We cannot completely rule out the possibility that the localities were mislabelled, but this is unlikely because these collectors also collected *L. gigantea* specimens at five other locations within its modern range. In addition, one of the collectors, G. P. Kanakoff, was a well-respected researcher and curator at the Los Angeles County Museum of Natural History. These observations suggest that the northern range limit of *L. gigantea* has contracted by *c.* 2.4° in the last few decades (sometime after 1963).

We cross-referenced our presence/absence data with data collected by the Biosurvey team at the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) and found no discrepancies between datasets for the northern range limit (PISCO did not survey the region containing the southern range limit for *L. gigantea*).

### Geographic patterns of abundance

*Lottia gigantea* is clearly most abundant within local populations near the range centre for this species, in southern and central
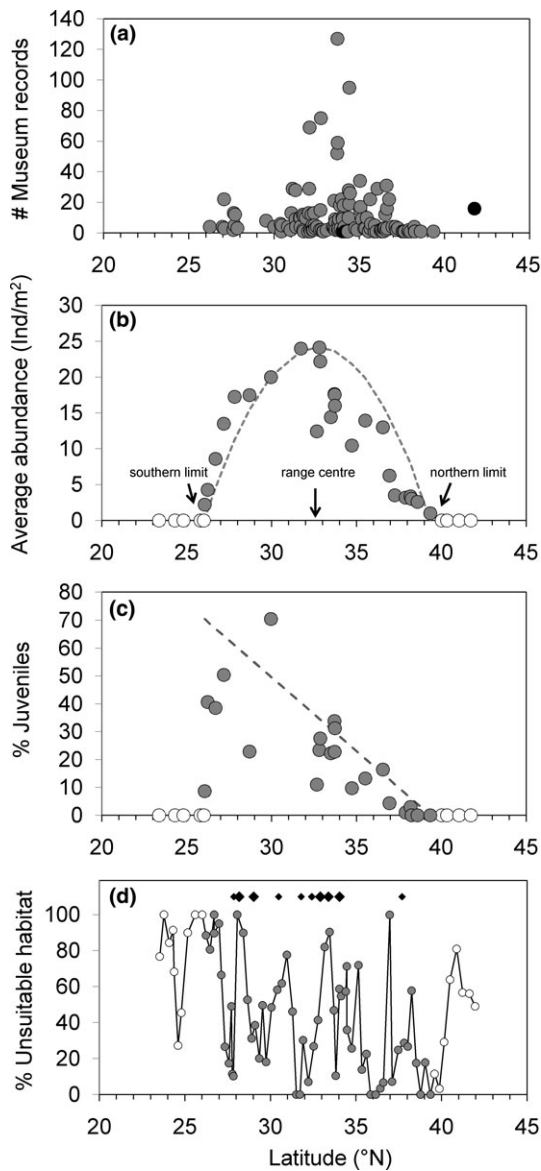
**Figure 3** (a) Number of museum occurrences of *Lottia gigantea* collected at 138 localities along the mainland Pacific coast of California and Baja California from 1869 to 1997 (see text for further details). The black dot corresponds to Crescent City, CA, outside the modern northern range. (b) Average abundances per m$^2$ of *L. gigantea* throughout its geographic range. (c) Average percentage of juveniles (< 25 mm) per m$^2$ at sampled local populations of *L. gigantea*. The empty circles represent sites where exhaustive searches for *L. gigantea* revealed that no individuals were present. The dashed grey line depicts the best-fitting model (see Table 1, Fig. 2 and text for details). (d) Percentage of long stretches of unsuitable habitat (sandy beach) within successive 48-km (30-mile) bins across the range of *L. gigantea* and beyond. A value close to 0 indicates that most of the shoreline within that particular bin consists of rocky shore (vice versa for a value near 100). The empty circles represent sites outside the modern range of *L. gigantea*. The locations of offshore islands are represented by black diamonds, with their relative size indicated by the size of the symbol [large (*n* = 5) or small (*n* = 5)].

California and northern Baja California, declining towards the northern and southern edges of its distribution (Fig. 3b). This pattern of abundance was significantly fitted by the normal, inverse quadratic and ramped south models (i.e. low RSS values; Table 1). However, the best fit was provided by the inverse quadratic model (Akaike weight *c*. 1; Table 1; Fig. 3b).

The highest local abundance of *L. gigantea* was measured in San Diego County at 32.82° N, with an average of 24.14 individuals per m$^2$. The middle portion of the range (from northern Baja to central California) is also characterized by large variations in local abundance, but does not reach levels below an average of 10.44 individuals per m$^2$ (Vandenberg Air Force Base). At the northern end of the range, local abundances notably drop off north of Monterey Bay (36.80° N) and do not reach mid-range levels again. In fact, average local abundance drops by more than half from 13.0 individuals per m$^2$ at the southern end of the bay (Pebble Beach; 36.56° N) to 6.27 individuals per m$^2$ at the northern end of the bay (Long Marine Lab; 36.94° N). Individuals of *L. gigantea* are present further north for another 2.4° but only sparsely and at very low abundances (3 individuals per m$^2$ and lower). Towards the southern end of the range, local abundances drop off precipitously south of Punta Eugenia (27.82° N) and do not reach mid-range levels again. In only 1.77° of latitude, local abundances of *L. gigantea* drop monotonically from 17.25 (Punta Eugenia) to 2.22 individuals per m$^2$ (La Bocana; 26.05° N; southern range limit; Fig. 3b).

We have categorized three southern and central California sites as being subject to low harvest pressure (category 2) and seven as being highly vulnerable to harvest pressure (category 1) based on Sagarin *et al.* (2007). Although detailed statistical analyses are precluded because of the low sample size of protected sites, it should be noted that sites in category 2 (low vulnerability) consistently reached lower abundances than did sites in category 1 (high vulnerability; Fig. 4; Appendix S1).

## Geographic patterns of juvenile abundance

The geographic pattern of the average percentage of juveniles per local population (per m$^2$) largely matches the geographic pattern of abundance for *L. gigantea* across its range, but slight differences are evident (Fig. 3c). The highest value occurs near the range centre at Punta Baja (29.96° N; northern Baja), where the average percentage of juveniles per m$^2$ is a staggering 70.49%. On average, 25.4% of individuals from our sampled sites in the middle of the range are juveniles (southern and central California and northern Baja; *n* = 12). In contrast, only 1.3% of individuals from our sampled sites at the northern end of the range are juveniles (northern California; *n* = 6). The overall geographic pattern of juvenile abundance was fitted only by a ramped-south model (Akaike weight *c*. 1; Table 1; Fig. 3c), which indicates that they are generally more abundant in the southern range.

**Table 1** Degree of fit of each hypothetical model to the observed abundance of *Lottia gigantea* across 25 sampled sites along the mainland Pacific coast of California and Baja California (average number of individuals per m$^2$) and to juvenile abundance (average percentage of individuals < 25 mm per m$^2$ at 23 sites). Significant values are in bold.

| Model | No. of parameters | All individuals | | | Juveniles | | |
|---|---|---|---|---|---|---|---|
| | | RSS | AIC | Akaike weight | RSS | AIC | Akaike weight |
| Normal | 2 | **1.66** | −63.86 | 0.00 | 1.50 | −66.37 | 0.00 |
| Inverse quadratic | 2 | **0.18** | −119.05 | 1.00 | 0.60 | −89.17 | 0.00 |
| Abundant edge | 4 | 4.11 | −37.14 | 0.00 | 0.86 | −76.20 | 0.00 |
| Ramped north | 2 | 2.03 | −58.73 | 0.00 | 1.49 | −66.56 | 0.00 |
| Ramped south | 2 | **1.12** | −73.67 | 0.00 | **0.09** | −136.43 | 1.00 |

RSS, residual sum of squares; AIC, Akaike's information criterion.
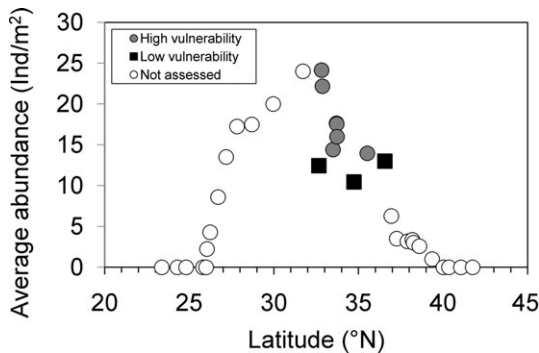


**Figure 4** Average abundances per m$^2$ of *Lottia gigantea* throughout its geographic range with sites in southern and central California labelled for vulnerability to human harvesting according to Sagarin *et al.* (2007). Note that low-vulnerability sites have consistently lower local abundances than high-vulnerability sites (see text for further details).

Like the overall abundance pattern, Monterey Bay (36.80° N) appears to be a geographic demarcation for the abundance of juveniles towards the northern range edge. The percentage of juveniles that make up local populations drops from 16.44% at the southern end of the bay (Pebble Beach; 36.56° N) to 4.36% at the northern end of the bay (Long Marine Lab; 36.94° N) and never reach levels higher than 3% thereafter. We found the three northernmost sampled populations to be only sparsely populated by adults; that is, there are no juveniles present from 38.25° N to the northern limit at 39.35° N.

The average percentage of juveniles that make up sampled local populations (*n* = 4) at the southern end of the range (*c.* 27.8° N–26.05° N) is 34.6%. The general pattern is one of southerly decline, with the southern limit consisting of 8.64% juveniles. These populations, however, never reach a level where zero juveniles are present, as found for the northern populations.

### Habitat availability

There is *c.* 2768 km of shore length within the range of *L. gigantea*. Of this, *c.* 1618 km is suitable rocky intertidal

habitat (58.5%). Figure 3(d) shows the proportion of unsuitable sandy shoreline within successive 48-km bins across the entire geographic range of *L. gigantea* and beyond both range limits. There is a significant equatorward latitudinal gradient in the proportion of unsuitable sandy shoreline (*r* = −0.43, *n* = 75, *P* < 0.0001); that is, long stretches of sandy beach are more common in the region containing the southern limit (southern Baja) than along the extensive rocky coast of northern California towards the opposite range limit. Habitat in the middle of the range is highly variable and not characterized by comparably long stretches of sandy beach (southern limit) or rocky shore (northern limit). Neither average local abundance nor percentage of juveniles was correlated with the amount of unsuitable habitat (*r* = −0.04, *n* = 25, *P* = 0.82, and *r* = −0.39, *n* = 22, *P* = 0.31, respectively). However, different trends were observed when we analysed the southern and northern sections of the latitudinal range (i.e. from the centre to the limits) separately; the correlation between unsuitable habitat and average local abundance was negative and significant in the southern section (*r* = −0.90, *n* = 9, *P* = 0.02), but non-significant in the northern section (*r* = 0.47, *n* = 16, *P* = 0.38). The percentage of juveniles was not correlated with unsuitable habitat in either the northern or the southern section (*r* = 0.59, *n* = 15, *P* = 0.26, and *r* = −0.32, *n* = 7, *P* = 0.28, respectively).

### DISCUSSION

The abundance and distribution of a species is temporally and geographically variable due to a combination of its unique evolutionary history and wide array of physical, biotic and anthropogenic factors encountered across its range (Brown *et al.*, 1996; Davis & Shaw, 2001; Hellberg *et al.*, 2001; Gaston, 2003; Sexton *et al.*, 2009). In order to distinguish among the causes of abundance patterns and range limits, however, studies such as ours should minimally take into account temporal changes in distribution, measures of population structure (e.g. patterns of juvenile abundance), some aspect of the geographic variation of range-wide habitat availability, and an assessment of human impacts on the species in question. While these are by no means the only factors that affect

abundance and range limits, they may serve as a platform for inferring their cause and to assess conservation implications.

## Central range

Our results show that *L. gigantea* individuals are most common in the centre of their geographic range, where habitat availability is ample and juveniles comprise approximately a quarter of measured individuals. Natural history museum data indicate that individuals from central populations have been collected from numerous localities for more than 100 years (Fig. 3a). Previous research indicates not only that local central populations are highly dense and contain high numbers of juveniles, but also that individuals can reach ages of *c.* 20 years and that sex ratios are steady at *c.* 30% female (i.e. 70% male or juvenile; Fenberg, 2008). In addition, population-genetic analyses using both microsatellites (Fenberg *et al.*, 2010) and mitochondrial DNA (Dawson, 2001; P.B. Fenberg, unpublished data) indicate that *L. gigantea* individuals from southern and central California are genetically indistinguishable from one another, suggesting widespread larval exchange among populations. This result is consistent with the pattern seen in other Californian coastal marine invertebrates with planktonic larvae, where low population differentiation and high gene flow are commonly reported (Dawson, 2001; Gruenthal *et al.*, 2007; Kelly & Eernisse, 2007; Lee & Boulding, 2007; Addison *et al.*, 2008).

Although we did not sample populations living on the Channel Islands, which occur within the central portion of the range of *L. gigantea*, previous work shows that these island populations have relatively high local abundances and that individuals reach large sizes owing to their low vulnerability to harvest pressure (Pombo & Escofet, 1996; Sagarin *et al.*, 2007). The high reproductive potential of large individuals coupled with regional oceanographic processes suitable for larval exchange with the mainland (Harms & Winant, 1998; Winant *et al.*, 2003; Shanks & Eckert, 2005) probably result in heavy larval recruitment from these offshore island populations to the mainland – contributing to the high local abundances seen in the range centre (Fig. 3b).

Given these observations, we suggest that *L. gigantea* adheres to the basic assumptions of the ACH, namely that central populations are living at optimal physical and biotic conditions and that individual success is high (Brown, 1984). However, individuals from central populations are size-selectively harvested in many locations (Roy *et al.*, 2003; Sagarin *et al.*, 2007; Fenberg, 2008), which may affect overall patterns of abundance and population structure – possibly contributing to the abundant centre seen in this species (see below).

## Processes shaping the northern edge of the distribution

A main assumption of the ACH is that individual success and abundance should drop off towards the range limits owing to the reduced quality of living conditions. Accordingly, individ-

uals of *L. gigantea* found at range-edge populations are less dense overall and it appears that northern populations are demographically unstable and prone to local extinctions. Along with our field observations, historical museum data suggest that the northern limit of *L. gigantea* contracted by *c.* 2.4° of latitude sometime after 1963, from Crescent City (41.74° N) to Point Cabrillo (39.35° N), while the southern limit has historically remained stable. By themselves, these observations provide little information as to their causes, but important insights are revealed when they are coupled with the abundance, juvenile and habitat data.

There is ample rocky intertidal habitat in northern California: approximately 69% of the coastline north of Monterey Bay (36.80° N) to Crescent City (41.74° N) is rocky. In fact, only one coastline bin within the modern range of *L. gigantea* (see Materials and Methods) consists of more than 50% sandy beach, making this region the rockiest section of coastline within its range. The fact that *L. gigantea* used to occur 2.4° north of its modern limit suggests that habitat is not a strong factor in limiting its northern distribution. Rather, the northward decline in abundance (overall and juveniles) suggests that northern local populations of *L. gigantea* are more likely to be constrained by causes apart from habitat limitation.

Individuals undergo a single spawning event in the winter months, typically in January or February, possibly coinciding with rough seas and downwelling events, which may be conducive to larvae being swept out of the surf zone (Daly, 1975; Shanks, 1998; Fenberg, 2008). Larvae are pelagic and, according to laboratory research on other north-eastern Pacific *Lottia* species (*L. digitalis* and *L. asmi*), metamorphic competence (at 13 °C) occurs about 5.5 days after fertilization (Kay & Emlet, 2002); however, a longer time to competence is likely with cooler water temperatures during the winter. Although dispersal dynamics can only be inferred for this species, given the lack of genetic differentiation between populations, coastal circulation patterns in southern and central California (in the range centre of *L. gigantea*) are generally northward-flowing during the winter spawning season (Winant *et al.*, 2003; Shanks & Eckert, 2005). *Lottia gigantea* larvae sourced from island and mainland populations entrained within these coastal currents could potentially be transported long distances northwards. Northern *L. gigantea* individuals are therefore likely to be sourced from more southerly and abundant populations, even if they arrive only sporadically during favourable conditions. These dispersal dynamics have also been suggested for another species with a similar early life history and geographic range, the California red abalone, *Haliotis rufescens* (Gruenthal *et al.*, 2007).

Sharp breaks in both overall and juvenile abundance occur north of Monterey Bay (36.80° N; Fig. 3b,c), which has been suggested to be a phylogeographic and biogeographic boundary (Dawson, 2001; Blanchette *et al.*, 2008; Gaines *et al.*, 2009), possibly owing to the difficulty that larvae have escaping from an eddy interrupting long-shore flow (Paduan & Rosenfeld, 1996; Dawson, 2001). Genetically speaking, however, there are

no statistical differences between populations north of Monterey Bay and in the rest of the Californian range of this species, as revealed by microsatellites and mitochondrial DNA (Dawson, 2001; Fenberg *et al.*, 2010; P.B. Fenberg, unpublished data). For long-lived species, unidirectional but sporadic recruitment events can, however, have lasting genetic and demographic effects on a local population (Gruenthal *et al.*, 2007). Given that *L. gigantea* individuals can reach ages of 20 years or more (Fenberg, 2008), recruitment events on the decadal scale may be all that is needed to maintain genetic homogeneity and the existence of these northern fringe 'populations'. This scenario would also be consistent with northern range contractions (i.e. local extinctions) and subsequent expansions over time, simply as a result of chance alone. The historical range contraction, as revealed by the museum data, is good evidence that northern *L. gigantea* populations are demographically unstable and prone to local extinctions. Although indirect, this is supported by the fact that we found virtually no juveniles north of Monterey Bay to its range limit (six field sites), an expanse of 2.41° (484 km of coastline). Furthermore, the northernmost 1.1° (242 km of coastline) is only sparsely populated by adults (ages 3+).

Other rocky intertidal species show evidence of recruitment limitation at their northern/poleward range limits (Zacherl *et al.*, 2003; Herbert *et al.*, 2009; Rivadeneira *et al.*, 2010). Most notably, *Collisella scabra* (sometimes *Lottia scabra*) has a similar geographic range, habitat preference and juvenile life history compared to its relative, *L. gigantea* (Nakano & Ozawa, 2004; Gilman, 2005). Both species monotonically decline in abundance and show strong evidence of recruitment limitation at northern latitudes (Gilman, 2006). Gilman (2006) suggests that the most likely explanation for recruitment limitation in *C. scabra* is an increase in distance between populations at the range margin due to a reduction in habitat availability. However, rocky intertidal habitat is ample north of the modern range limit of *L. gigantea* to Crescent City (385 km of coast, of which 56% is rocky) and in the region south of the limit to Monterey Bay (484 km of coast, of which 72% is rocky), suggesting that reduced abundances and the overall dearth of juveniles for northern *L. gigantea* populations are not reduced because of habitat limitation (Fig. 3). Unfortunately, Gilman (2005, 2006) did not measure abundance or recruitment data for *C. scabra* populations in central or southern portions of its geographic range (i.e. southern California and Baja), so further comparisons are not possible. However, as above, we suggest that the most likely cause of the temporally fluctuating northern limit, reduced abundances and an almost complete lack of juveniles is sporadic larval supply sourced from highly abundant island and mainland populations south of Monterey Bay.

## Processes shaping the southern edge of the distribution

The southern range limit of *L. gigantea* occurs at 26.05° N and according to historical museum records has remained stable near this latitude for the past few decades. Interestingly, this region [i.e. between Punta Eugenia (27.82° N) and Magdalena Bay (24.60° N)] also contains the southern range limit for many rocky intertidal species and has long been known to be a distinct biogeographic region (Magdelanan) for rocky intertidal species, with Punta Eugenia representing the northern boundary (Valentine, 1966; Blanchette *et al.*, 2008; Gaines *et al.*, 2009). The cause of this boundary is not understood but we suggest that habitat limitation is one possible explanation.

The region near the southern limit of *L. gigantea* differs from the rest of its geographic range in that it is an exceptionally sandy area of the coast (Fig. 3d). Of the 292 km of coastline from our site at 27.18° N (San Roque, just south of Punta Eugenia) to the southern range limit of *L. gigantea* (26.05° N), 92% consists of uninhabitable sandy beach (270 km); the remaining 8% is rocky, but sparsely scattered along the coast. In addition, there are no coastal islands within this latitudinal span (Fig. 3d). South of the limit of *L. gigantea*, the coast is flanked by nearly 150 km of coastal dunes and beach until the rocky Cabo San Lazaro (24.81° N), at the northern end of Magdalena Bay. Thus, exceptionally long stretches of sandy beach separate the area to the south and north of the range limit of *L. gigantea* and other rocky intertidal species.

The combination of a reduction in the frequency of suitable habitat and the associated long distances between populations has been predicted as a mechanism of range limits in theoretical models (Holt & Keitt, 2000; Holt *et al.*, 2005). If suitable habitat changes abruptly, then one would expect to find a sharp decline in overall abundance in the region precisely where this change occurs (Brown, 1984). In accordance with this, sandy beach begins to predominate the Pacific side of the Baja California peninsula just south of Punta Eugenia, exactly where the sharp decline in overall and juvenile abundance of *L. gigantea* occurs (Fig. 3b,c). This observation is supported by a significant negative correlation between local abundance and habitat availability from the range centre to the southern limit. The long distances between southern local populations should be sufficient to serve as a dispersal barrier and cause reductions in local abundances, and ultimately, in the range limit. However, this would depend on the dispersal ability of *L. gigantea*, which is unknown and can only be inferred from data for other species. With such a low percentage of rocky shore south of Punta Eugenia (27.82° N), it is relatively easy to understand why the area south of this point to Magdalena Bay (24.60° N) constitutes a distinct biogeographic region, at least among rocky shore molluscs (Valentine, 1966; Blanchette *et al.*, 2008; Gaines *et al.*, 2009).

In addition to habitat limitation, another factor possibly contributing to low abundances and the southern range limit of *L. gigantea* and other species could be a low tolerance to the undoubtedly high temperatures of the rocky substrate in southern Baja. Laboratory thermal stress experiments show that the lethal limits of *L. gigantea* range between 30 and 42 °C (Miller *et al.*, 2009). These low tide temperatures should occur

more frequently towards the southern end of the distribution of *L. gigantea* and may therefore contribute to high mortality rates and, hence, lower abundances. In addition, high temperatures may cause differential mortality rates among individuals, affecting large individuals more than small ones because of their lower surface area to volume ratio. This may be a reason for the relative paucity of larger individuals observed in the southern range of *L. gigantea* (Fig. 3c). This is supported by experimental studies by Helmuth (1998), showing that, at low tide, larger mussels of the species *Mytilus californianus* become warmer under constant conditions than do smaller ones. However, the scarcity of large individuals in the southern range may also result from size-selective harvesting, which is common for this species in Baja California (Pombo & Escofet, 1996). Alternatively, hurricanes sometimes hit the coast in this region, and the wave action may be sufficient to cause high but sporadic mortality (Denny & Blanchette, 2000). However, these alternative hypotheses have yet to be tested empirically, owing to the lack of studies along this isolated section of the coast.

## Conservation implications

*Lottia gigantea* is size-selectively harvested throughout much of its geographic range, particularly in the range centre (Pombo & Escofet, 1996; Lindberg *et al.*, 1998; Kido & Murray, 2003; Roy *et al.*, 2003; Sagarin *et al.*, 2007). Because information on past abundances is not available for this species, it is difficult to tell how harvesting may have changed the range-wide patterns of abundance and distribution. However, previous work suggests that size-selective harvesting may indirectly increase the density of individuals in local populations (Fenberg, 2008). As larger limpets occupy more space, from which they exclude conspecifics (Stimson, 1970; Fenberg, 2008), the number of individuals physically able to occupy a given area will be higher for harvested populations because small- to medium-sized individuals have smaller home ranges/territories and are not generally harvested. Therefore, harvested populations should have a higher density of individuals compared with populations that do not experience the effects of harvesting.

Using the vulnerability categories outlined in Sagarin *et al.* (2007), our results show that well-protected central populations with large individuals are less dense than populations that do not receive protection from harvesting (Fig. 4). Thus, central populations may not have been as locally dense prior to experiencing the effects of modern size-selective harvesting. This suggests that the abundant centre pattern seen for *L. gigantea* may be partly a result of the indirect effect of human harvesting causing an increase in the density of small- to medium-sized individuals in local central populations.

Our results also have important conservation implications for the northern portion of the geographic range of *L. gigantea*. Given that the northern range of *L. gigantea* is demographically unstable and prone to local extinctions (see above), any

harvesting or other human disturbance that occurs in this region is likely to have a more pronounced demographic effect on a local population than it would in the centre of its range. With sporadic and limited recruitment at northern latitudes, it would take longer for these populations to recover from human impacts. Although northern populations may be sinks and contribute limited recruits to other populations, they make up a substantial portion of the overall geographic range of *L. gigantea* and should therefore receive appropriate levels of protection from human impacts.

## Concluding remarks

*Lottia gigantea* reaches its highest local abundance in the centre of its range and drops off towards both range limits in accordance with the abundant centre hypothesis. Interestingly, human size-selective harvesting may be contributing to the abundant centre pattern by reducing age and size and thus increasing the local density at a site level because smaller individuals are not harvested and have smaller home ranges than larger (i.e. preferentially harvested) individuals. The abundant centre is also likely to be partly a result of high larval recruitment from well-protected offshore islands to mainland populations in the range centre. Habitat availability is common throughout the species' geographic range except towards the southern end, which we suggest to be a likely cause of its range limit. The northern range limit of *L. gigantea* is probably controlled by recruitment limitation, resulting in sparsely populated sites that consist almost solely of adults. Along with the observed historical northern range contraction, these results suggest that northern *L. gigantea* populations (i.e. north Monterey Bay) are demographically unstable and prone to local extinctions.

By including data on range-wide abundance (overall and juveniles), habitat availability, historical distribution, and human impacts, we were able to infer the underlying causes for both range limits of *L. gigantea* and how they relate to overall abundance and population structure patterns. Future studies on other species should include not only the types of data from this study, but also information on genetics, life history and other physical factors that may influence range-wide patterns of abundance and range limits. Such studies may provide valuable insights into the conservation status of species and ecosystems.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Geographic coordinates of the 34 field sites, and overall and juvenile abundances for each population of *Lottia gigantea* sampled.
**Appendix S2** R-script to fit spatial patterns of abundance to five hypothetical models (see Fig. 2).

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## BIOSKETCHES

**Phillip B. Fenberg** is broadly interested in marine biogeography, historical ecology, life history evolution and conservation biology.

**Marcelo M. Rivadeneira** is interested in marine biogeography, macroecology, palaeoecology and conservation.

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