The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses

Sarah E. Gilman

Gilman, S. E. 2006. The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses. – Ecography 29: 709–720.

A decline in abundance towards a species' range boundary is often interpreted as evidence of a decline in individual success, and is usually assumed to reflect a decline in suitable environmental conditions. Gradual declines towards high latitude range boundaries are frequently attributed to limitations on organismal tolerance of cold temperature. Rarely have these two assumptions been empirically tested. The intertidal gastropod *Collisella scabra* declines monotonically in abundance from 435 to <1 m^{-2} over the northern 300 km of its geographic distribution. I examined temperature, adult performance (survival, growth, reproduction), and recruitment at five locations in this region of decline. Mortality ranged from 4.9 to 11.2% per month, but was highest at the lowest latitude study site. Growth rates ranged from 0 to 5.2 mm yr^{-1}, but were generally lower at lower latitude sites. Gonad development was high in the three populations examined, but the possibility of infrequent spawning at high latitude sites could not be excluded. Finally, a comparison of performance differences among populations with temperature revealed clear effects of temperature on both growth and mortality; however, the patterns were not consistent with a hypothesis of cold stress at the range boundary. Overall there was little evidence for either reduced performance or increasing cold stress in low density high latitude populations. Over the same 300 km, recruitment declined monotonically from a mean of six recruits per 625 cm^2 to less than one; suggesting that limitations on recruitment, rather that adult performance, are responsible for low abundance in marginal populations. Several hypotheses for the decline in recruitment are discussed in the paper and the most likely explanation appears to be an increase in the distance between populations at the range margin, reducing the chances that dispersing larvae find suitable habitat for settlement.

S. E. Gilman (gilmans@u.washington.edu), Section of Evolution and Ecology, and Center for Population Biology, Univ. of California, Davis, CA 95616, USA (present address of S. E. G.: Friday Harbor Laboratories, Univ. of Washington, 620 University Road, Friday Harbor, WA 98250, USA).

A classic view of a species' biogeographic distribution is of a gradual decline in density towards the range boundary, reflecting a gradual change in environmental conditions from the center to the edge of the range (Brown et al. 1996, Brown and Lomolino 1998, Case and Taper 2000, Guo et al. 2005). As environmental conditions change over space, organisms become less adapted to their environment, and their performance declines until population growth rates become negative. The term "environmental condition" may encompass any aspect of an organism's Hutchinsonian niche, such as climate, prey items, and other interacting species (Brown and

Lomolino 1998). While the classic view of a geographic range has influenced research in a variety of fields in biology (Lawton 1993, Kirkpatrick and Barton 1997, Channell and Lomolino 2000, Sagarin and Gaines 2002b); empirical evidence supporting it is limited (Sagarin and Gaines 2002b, McGill and Collins 2003). Many species do not show gradual declines in abundance towards their range boundaries (Brown et al. 1995, Blackburn et al. 1999, Sagarin and Gaines 2002b, McGill and Collins 2003). Explanations for these patterns include both the spatial pattern of environmental conditions (Caughley et al. 1988, Bell et al. 1993, Lawton 2000) and local adaptation (Carbonell et al. 2003). Even where abundance does decline gradually, lower density may not indicate lower performance (Van Home 1983, Pulliam 2000, Gonzalez-Guzman and Mehlman 2001), or performance may be reduced only in some years (MacArthur 1972, Holt et al. 2005). The classic view also ignores evidence that range limits can occur in the absence of clear environmental gradients, and may be determined by dispersal dynamics, habitat arrangements, or demographic effects (Hutchins 1947, Carter and Prince 1981, Gaylord and Gaines 2000, Gonzalez-Guzman and Mehlman 2001, Holt et al. 2005). An accurate assessment of the frequency of classic and non-classic patterns in species distributions is limited by the general paucity of empirical studies of range boundaries (Sagarin and Gaines 2002b, Gaston 2003, Parmesan et al. 2005).

Temperature is often implicated as the environmental variable controlling geographic range boundaries, particularly at the poleward edge of species' distributions (Hutchins 1947, MacArthur 1972, Brown et al. 1996). The physiological effects of extreme temperatures on individual performance are well-documented in a wide range of plant and animal taxa (Cossins and Bowler 1987, Gurevitch et al. 2002, Somero 2005), leading to frequent predictions of geographic range shifts in response to climate change (Walther et al. 2002, Parmesan and Yohe 2003). Such shifts have been reported in both terrestrial and marine systems (Southward et al. 1995, Parmesan et al. 1999, Mieszkowska et al. 2006); but, many of the studies purporting to link temperature to species' range boundaries have been criticized for an over-reliance on correlational techniques (Samways et al. 1999, Gaston 2003, Parmesan et al. 2005). Moreover temperatures are not always clinal across a species distribution, creating the possibility that marginal populations may not be the most sensitive to climate change (Halpin 1997, Helmuth et al. 2002).

Intertidal marine species have emerged as model organisms for empirical studies of biogeographic processes because of their near-linear geographic distributions (Sagarin and Gaines 2002a). Eastern Pacific coastlines run approximately parallel to a north-south axis, meaning that they are ideal for studying latitudinal effects on species distributions. Additionally because these species are often believed to live very close to their thermal tolerance limits, they are considered highly sensitive to climate change (Helmuth et al. 2002). "*Collisella*" *scabra* (see Lindberg 1986 and Gilman unpubl. for an explanation of taxonomic issues) is a northeastern Pacific herbivorous gastropod common to the upper intertidal of the California (USA) coast (Fig. 1). It shows a gradual decline in abundance across the northern 300 km of its distribution (Fig. 2A). In earlier studies (Barry et al. 1995, Sagarin et al. 1999) we found *C. scabra* increasing locally in abundance in conjunction with a regional increase in water temperature in Monterey Bay, California, suggesting the species might be sensitive to temperature on a biogeographic scale. However, in a caged transplant study of the northern 300 km of the range boundary, I was unable to detect reduced survival or growth at higher latitude sites near the poleward range boundary (Gilman 2006). Measured environmental conditions (temperature, food availability) also showed no relationship with latitude; although, warmer temperatures were associated with higher mortality and greater growth. Thus despite an apparent link between temperature and population dynamics on a local scale, the measured environmental conditions could not explain the gradual decline in abundance at higher latitudes.
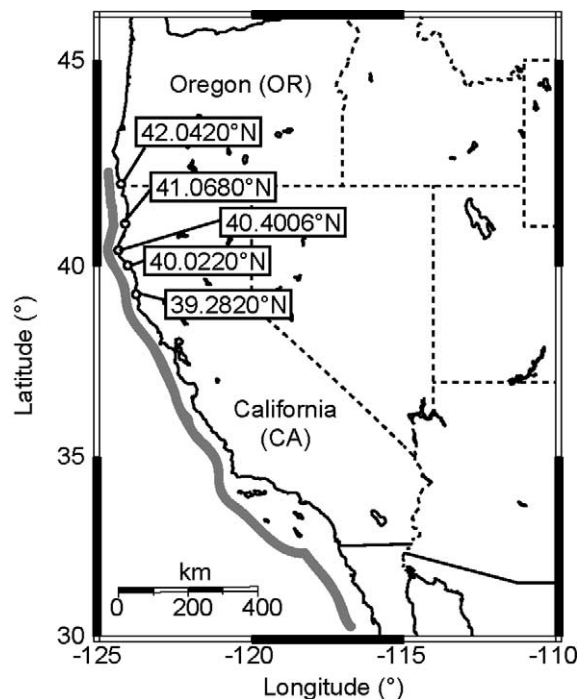

Fig. 1. The geographic distribution of *Collisella scabra* (gray line) and location of study sites (open circles). Each study site is identified by it latitude.
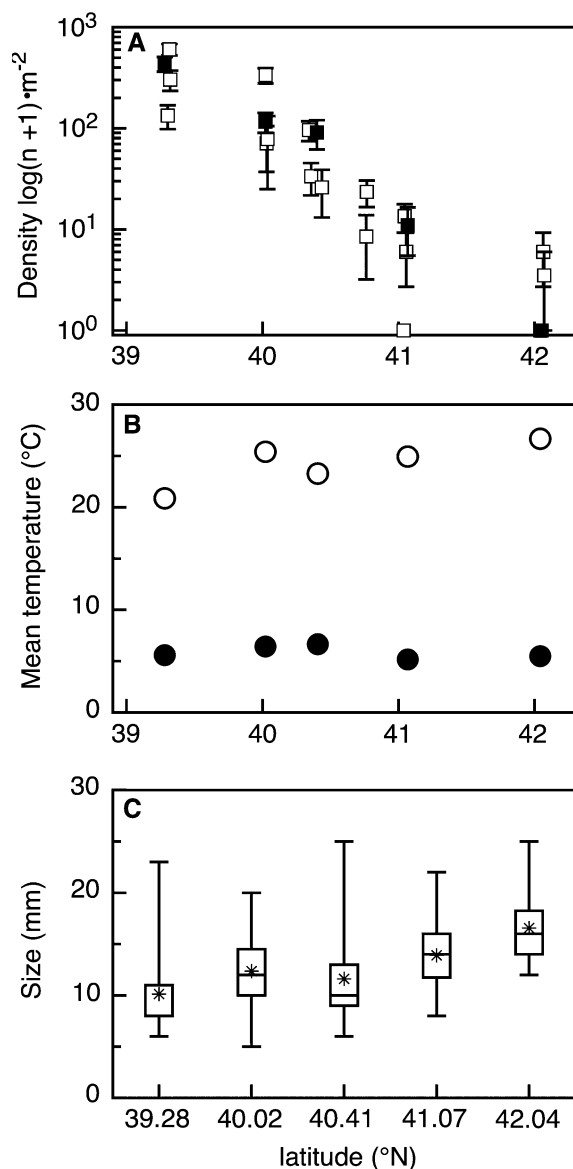
Fig. 2. Patterns of density, temperature, and size across the northern 300 km of *Collisella scabra*'s distribution. (A) The mean density, with standard error bars, of *C. scabra* observed in surveys conducted in *Pelvetiopsis* spp. beds. Data are from Gilman (2005). Filled symbols indicate sites used in this study. (B) The average daily maximum temperature for the warmest month (○) and average daily minimum temperature for the coldest month (●) of the study period. (C) Box plot of 25, 50, and 75%ile with extreme largest and smallest individuals observed in August 2001. Mean size is indicated by the asterisk (*). At 39.282°N, the median and 25%ile sizes coincide.

mance. Such a decline in performance could have been obscured in the earlier transplant experiment by the experimental methods used. Specifically, because limpets were transplanted in cages some local conditions, such as predation and interspecific competition, could not be tested. Other conditions, such as temperature, may have been altered by the cage itself. Alternately, because the transplanted limpets were not from local populations, they may show different responses to local environmental conditions like temperature. These two hypothesis can be tested by comparing individual performance of uncaged local limpets both among populations and with temperature. Second, limiting conditions may occur periodically, and marginal populations could experience reduced performance but just not during the years of the transplant experiment. This should be apparent in marginal populations through demographic comparisons; specifically, marginal populations should be relatively younger than other locations (Lewis et al. 1982, Zacherl et al. 2003). Third, *C. scabra*'s poleward range boundary might not be determined by individual performance at all. Processes that can limit population success independent of individual performance include dispersal dynamics, habitat patchiness, and allee effects (Hutchins 1947, Carter and Prince 1981, Gaylord and Gaines 2000, Gonzalez-Guzman and Mehlman 2001, Holt et al. 2005); and would be evident by a limited supply of new individuals in marginal populations. It should be noted that the second and third of these hypotheses are not traditionally considered within the classic view of range boundaries.

To test these three hypotheses, I conducted a detailed study of uncaged individuals in five populations spanning the northern 300 km of *C. scabra*'s distribution (Fig. 2). I compared three measures of individual performance (mortality, growth, maturation), as well as the rate of recruitment of new individuals into each population. I also measured temperatures at each site. I address four specific questions. First, do present patterns of individual performance in uncaged populations explain the gradual decline in abundance towards the northern range boundary? Second, does temperature influence individual performance in these populations? Third, do age differences among populations suggest that individual performance may have been reduced in previous years? Fourth, do northern populations appear recruitment limited relative to higher density locations?

Materials and methods

Study species and field sites

Collisella scabra is a high intertidal gastropod common to rocky shores of the northeastern Pacific (Fig. 1). *Collisella scabra* is a generalist herbivore, feeding on

Yet there remains a monotonic decline in abundance over the northernmost 300 km of *C. scabra*'s distribution. Three possible hypotheses could explain these observations in the context of the previous studies. First, under the classic view of a species range, this decline should reflect a parallel decline in individual perfor-

microalgae which grow on hard surfaces. *Collisella scabra* has a biphasic life-cycle with a pelagic (swimming) larval phase of less than two weeks (Strathmann 1987) and a benthic (sedentary) adult phase of 10–30 yr (Sutherland 1970). Migration among populations occurs almost exclusively during the pelagic phase. Adults show strong homing tendencies. Individuals return to a specific position and orientation on the rocks at low tide and shells often grow to match the contours of the home scar; thus, adults are unlikely to travel more than a few meters over their lifetime (Sutherland 1970, Hahn and Denny 1989).

The exact delineation of a geographic range boundary is more a conceptual than empirical exercise (Gaston 2003). In this paper I focus upon a 300 km span of coastline over which *Collisella scabra*'s abundance declines 100-fold (Fig. 2A, see also Gilman 2005). While the literal range boundary might be identified by any number of criteria (e.g. the "last" individual), such labels at best only distract from the real processes controlling the range boundary, namely the factors responsible for this 300 km decline in abundance. I surveyed populations at five sites along this 300 km coastline (Fig. 1). All sites are semiprotected outer coast (sensu Ricketts et al. 1985) and were chosen for overall similarity in wave exposure, slope, and community composition. All five sites were used in an earlier survey of limpet abundance (Gilman 2005) and four were used in a separate transplant experiment (Gilman 2006).

Temperature

I recorded temperature at each site at 20 min intervals using a temperature datalogger (HOBO H8, Onset Computer, Pocasset, MA, USA) placed inside an opaque, white PVC waterproof case, near the census quadrats (see below). Temperatures measured in this way may differ considerably from what an individual limpet experiences (Fitzhenry et al. 2004), and thus should be considered an index of relative differences in thermal environments among sites. For each of the intervals between the approximately monthly survey dates (see below), I calculated the average daily minimum and maximum temperatures recorded by the data logger for each site.

Demography

Surveys of *Collisella scabra* abundance across a range of habitats and latitudes (Gilman 2005) revealed that the limpets are most abundant at or just above the uppermost zone of macroalgae in the rocky intertidal (usually *Pelvetiopsis limitata* or other fucoid algae), corresponding to the upper edge of Ricketts et al. (1985) zone 2. At each study site, I established permanent replicate

25×25 cm quadrats in this zone, along ca 25 m of shore. The total number of quadrats was inversely proportional to local abundance, and ranged from 11 at the highest abundance site to 36 at the lowest. This ensured a minimum of 50 limpets at the lowest density site and up to 300 at higher density sites. Quadrats were separated by a minimum of 0.5 m and all contained at least one *C. scabra* at the start of sampling. Because of the extremely low population density at the northernmost site ($42.042°N$), the total length of shore sampled was longer (~ 100 m) and the distance between replicate quadrats was smaller.

I marked the corners of each quadrat with a small amount of paint, but otherwise left quadrats open to recruitment and migration by *C. scabra* and all other species. Within each quadrat, I labeled individuals >4 mm in length using a small numbered tag. Smaller limpets were marked with a small dot of paint until they grew larger. I censused quadrats monthly from June 2000 to September 2001. At each visit I mapped the location of each *C. scabra* within the quadrat onto a 25×25 cm sheet of clear polyethylene film. I then tagged any new individuals, and examined at least a 0.5 m radius surrounding each quadrat for emigrants. I also measured the shell length (maximum aperture diameter) to the nearest 0.5 mm of all marked limpets within or outside the quadrat with a pair of vernier calipers.

Following Sutherland (1970), I classified all new limpets observed in a quadrat as recruits if they were <4.5 mm in length. All other new limpets were considered immigrants. I calculated recruitment per quadrat by summing the total number of recruits observed in quadrat over all months. I calculated recruitment per capita for each site for each month as the total number of recruits observed across all quadrats divided by the total number of adults observed.

Missing limpets were only classified as mortalities if they had been observed in the quadrat for at least the two preceding censuses. Otherwise, they were considered transients. To determine the mortality per capita per month for each site, I divided the number of mortalities at each site by the number of limpets that were present for the two preceding sampling intervals at that site. This is the potential pool of limpets that could have been classified as a "true" mortality if they had disappeared that month.

Fecundity

To follow seasonal patterns of gonad development and spawning, I collected and dissected 10–20 limpets per site at bi-weekly to monthly intervals (November 1999– September 2001) at the three southernmost of the five sites. I could not examine fecundity regularly at the two northernmost sites, because destructive sampling was

not feasible in such low abundance populations. To determine if there was any evidence of gonad maturation at these sites, small samples were collected on 2–3 occasions during times of the year when individual were mature at other locations.

Visually, the gonads of males and females differ only by color, there are no overall differences in size or shape. I classified each limpet into one of two categories, depending on whether there was a visible gonad ("sexable") or not ("neuter"). The sexable limpets I further classified as "ripe" if the gonad filled most of the shell cavity. To identify the number of spawning events at each of the three gonad collection sites, I plotted the time series of "sexable" and "ripe" limpets. Following Sutherland (1970), I visually identified spawning events on these plots as a sharp decline in the frequency of "ripe" limpets between two successive sampling dates.

Statistical analyses

All statistical analyses were conducted in either the GLM or Mixed procedures of SAS statistical software (SAS Inst., Cary, NC). I adjusted the p-values of all multiple comparisons using either a step-down Bonferroni correction or a simulated approximation of the multivariate t distribution (Westfall et al. 1999). Where possible I transformed the data to improve the fit to model assumptions, all results presented have been back-transformed. In some cases substantial heteroscedasticity remained in spite of transformation, and I instead used a heteroscedastic model in Proc Mixed. This model incorporates a separate error variance term for each factor level or treatment (Westfall et al. 1999).

I tested for differences in mortality and recruitment among sites using analysis of variance (ANOVA). I also tested for a relationship between temperature and mortality using regression. In preliminary analyses I examined several different temperature statistics, including minima, mean, and maxima for both one and two months prior to the mortality observation. All models resulted in a positive relationship between mortality and temperature. The strongest relationship was found using the average maximum temperature for the second sampling period before the mortality measurement, and is the model presented here.

To compare overall growth rates among sites, I regressed limpet length in August 2001 against length in August 2000. Incorporating a quadratic effect of length gave a better fit to the data than a strictly linear model (likelihood ratio test, $\chi^2 = 41.237$, df $= 5$, p < 0.001). Because of significant differences in the linear and quadratic temperature terms among sites, there is not a consistent ranking of growth rates among sites across all sizes. Thus, I tested for significant differences

in final length at three different values of initial length, 7, 11, and 15 mm. Assuming that growth between August 2000 and 2001 was typical of size-specific annual growth rates, the parameters of the regression model can be used to estimate the age of a limpet from its size. I used this approach to calculate the number of years it would take for a 1 mm limpet to reach the maximum size observed in August 2001 at each site.

To examine the relationship between growth rate and temperature, I repeated the quadratic regression, using monthly intervals and included the monthly average daily temperature as a regressor variable. A model using one month lagged average daily maximum temperature (not shown) produced similar results. From the model parameters I calculated the net change in size per °C for three different sizes of limpet (7, 11, and 15 mm) for each of the five sites.

Results

Temperature

There is little relationship between latitude and temperature for these study sites (Fig. 2B). The southernmost site consistently showed the coldest daily temperatures, while the northernmost site has some of the warmest maximum and minimum temperatures. The results were similar when extreme events were compared among sites (Gilman 2003). For example, the hottest temperature observed (36.67°C) occurred at the northernmost of the five sites (42.042°N). Monthly minima at the southernmost site (39.282°N) were routinely lower than at all but one of the remaining four sites (41.068°N).

Mortality

Overall, there is little evidence that mortality is greater in low density northern populations. Although per capita mortality differed significantly among sites ($F_{4,52} = 3.17$, p $= 0.0209$), it was greatest at the most southern site (Fig. 3). Mortality at the two northernmost sites did not differ significantly from other sites, after correcting for multiple comparisons by the Tukey method. Regression analysis revealed a significant positive relationship between monthly mortality and monthly average daily maximum temperature ($F_{1,51} = 5.84$, p $= 0.019$, $\beta = 0.356 \pm 0.166$ individuals month^{-1} °C^{-1}).

Growth

Between August 2000 and August 2001, growth varied significantly among sites ($F_{4,365} = 2.57$, p $= 0.0377$). Because both the linear and polynomial effects of initial
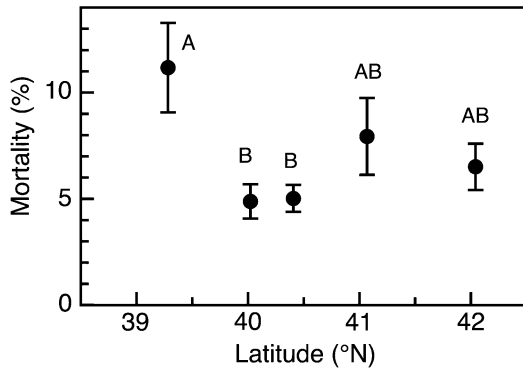
Fig. 3. The average per capita mortality per month. A single mortality rate was calculated across all quadrats for each combination of site and month. Bars indicate standard errors. Letters indicate groups of means that are statistically indistinguishable after correction of p-values for multiple comparisons (p >0.05).

size differed among sites (site × initial Size: $F_{4,371} = 2.77$, $p = 0.0271$; site × initial size^2: $F_{4,379} = 4.21$, $p = 0.0024$), the overall F-test for site is less informative than direct examination of the least squared means of final size at each site for specific initial sizes. The LSMs generally showed greater growth at the two northernmost sites (Fig. 4), particularly at smaller sizes; although few comparisons were significant after correcting p-values for multiple comparisons.

Based on the estimated growth functions from this regression (Table 1) there are large differences in the ages of the largest limpets observed at each site (Fig. 2B), but no decline in age with increasing latitude. The largest individual could have reached its current size in <10 yr at the southernmost site (39.282°N), in 10–12 yr at the two northernmost sites (41.068°N and 42.042°N) and in >20 yr at the two remaining sites (40.022°N and 40.407°N). These estimates are not consistent with a hypothesis of decreased age at the range margin, as might be expected if environments were more stressful in these locations in past years.

The effect of temperature on growth varied with site and initial size (Table 2A). However, in 12 of 15 cases warmer temperatures were associated with increased sizes (Table 2B). The greatest positive effect of temperature was on 7 mm limpets at 40.407°N, where an increase of 1°C increased shell length by 0.077 mm month^{-1}. In only two of fifteen cases did increasing temperature significantly decrease size: 15 mm limpets at 39.282°N and 7 mm limpets at 41.068°N.

Recruitment

Both recruitment per unit area and per capita decreased with increasing latitude (Fig. 5). Recruitment differed significantly among sites in both analyses (per unit area $F_{4,22} = 10.53$, $p = 0.0001$; per capita $F_{4,70} = 8.42$, $p = 0.0001$). After correcting for multiple comparisons (multivariate t-test simulation, Westfall et al. 1999), I identified significant differences between only the northernmost site (42.042°N) and the remaining four. In the per capita analysis, multiple comparison tests (p-values corrected by step-down Bonferroni) revealed three overlapping groups of similarity, ordered by latitude (Fig. 5B). Both recruitment per area and per capita showed strong negative correlations with latitude ($\rho_{area} = -0.421$, $\rho_{capita} = -0.475$, both p <0.0001).
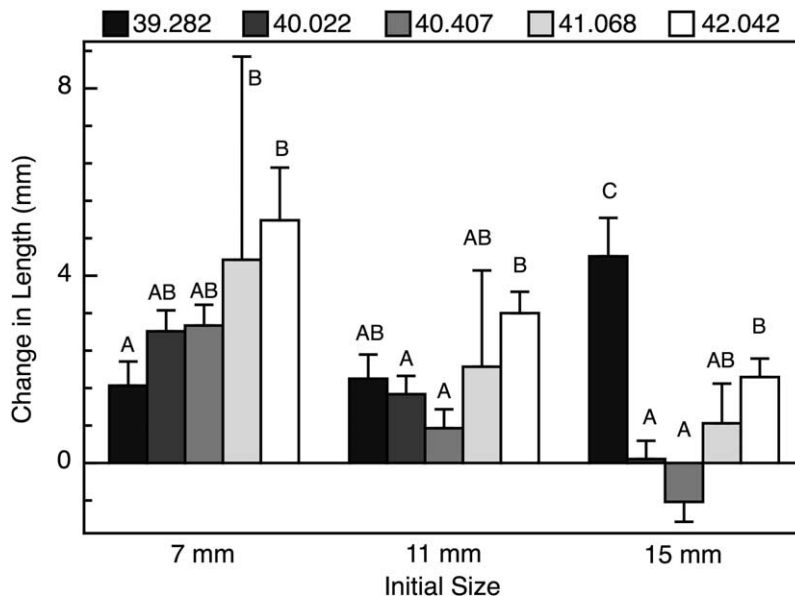

Fig. 4. Average size change by August 2001, with standard errors, of limpets at initial sizes of 7, 11, and 15 mm in August 2000. Data are least square mean estimates from a polynomial fit. Letters indicate groups of means within a size class that are not significantly different from each other, after correction for multiple comparisons (multivariate t-test simulation, Westfall et al. 1999). Limpets >15 mm or <7 mm were not observed in sufficient numbers at all sites for comparisons.

Table 1. Parameter estimate for polynomial regression predicting size in August 2001 from size in August 2000. Regression equations are of the form $Size_{2001} = \beta_0 + \beta_1(Size_{2000}) + \beta_2(Size_{2000})^2$.

Site	β_0	β_1	β_2
42.042	10.142	0.157	0.019
41.068	10.926	−0.176	0.034
40.407	8.263	0.104	0.019
40.042	5.064	0.688	−0.001
39.282	7.330	−0.351	0.077

Fecundity

In both years I observed ripe individuals at all three of the southern sites where *Collisella scabra* was sufficiently abundant to allow destructive sampling (Fig. 6). In 1999–2000, there were at least two spawning events at the two southernmost sites (40.022°N and 39.282°N), and at least one at 40.407°N. In 2000–2001, there was at least one spawning event at 39.282°N, but I was unable to identify a definite spawning event at either 40.022°N or 40.407°N. The populations at 40.022°N and 40.407°N do appear qualitatively different in 2000–2001: the fraction of limpet that were ripe at 40.407°N never exceeded 35%, while at 40.022°N it was over 70% for more than three months. Thus although there is some evidence for reduced fecundity at lower density marginal sites, there is also strong temporal variability in gonad size and spawning among all sites.

Limited gonad data collected for the two northernmost sites also indicate high rates of maturation in individual limpets. Limpets at 42.042°N were sampled on three occasions and at 41.068°N on two occasions. All samples were collected during the winter spawning season, and sample sizes ranged from five to nine limpets. In all five samples the limpets were 100% sexable and at least 50% ripe. However there is not sufficient gonad data at these sites to estimate the frequency of spawning events.

Discussion

Although the density of *C. scabra* declines more than one hundred fold over the northern 300 km of its distribution, adult performance does not. The lowest density populations examined had consistently higher growth and lower mortality than higher density populations in more central parts of the distribution. Thus, *C. scabra* does not conform to the expected pattern of reduced adult performance in low density populations at the range boundary. High adult (benthic) performance in edge populations excludes interspecific competition, predation, and resource (prey) limitation as controlling factors of the range boundary. The survey quadrats were accessible to all interacting species and so an increase in any of these negative species interactions would be reflected in either elevated mortality or reduced

Table 2. (A) Significance of models terms testing the effect of temperature and initial (starting) size on growth. The significant interactions of site with temperature and starting size necessitate an examination of least squared means (LSMs) at three separate initial sizes to determine the site-specific relationship of temperature on growth. These are calculated in (B). Units in (B) are mm month^{-1} °C^{-1} and indicate the monthly change in shell length for each 1°C increase in average daily maximum temperature, for a limpet of the given initial size. Asterisks indicate values significantly different from zero, based on a two-tailed t-test.
(A)

Term	ndf	ddf	F	p
Site	4	8296	5.04	0.0005
Starting size	1	8403	46.12	0.0001
Starting size^2	1	8409	3.62	0.0572
Temperature	1	8407	0.10	0.7503
Site × starting size	4	8338	5.22	0.0003
Site × starting size^2	4	8380	5.66	0.0002
Site × temperature	4	8371	5.61	0.0002
Temperature × starting size	1	8406	0.78	0.3780
Temperature × starting size^2	1	8389	2.98	0.0842
Site × temperature × starting size	4	8360	5.08	0.0004
Site × temperature × starting size^2	4	8377	5.51	0.0002

(B)

Latitude	7 mm	11 mm	15 mm
All latitudes	0.043**	0.031**	−0.001
42.042°N	0.086	0.070*	0.054*
41.068°N	−0.050*	0.035	0.058*
40.407°N	0.077**	0.010	−0.014
40.022°N	0.053***	0.034**	0.039**
39.282°N	0.050**	0.005	−0.144***

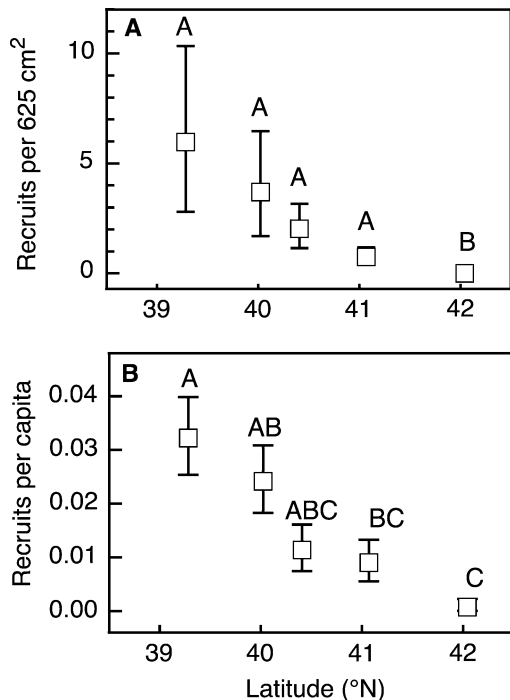*p < 0.05, **p < 0.01, ***p < 0.001.

Fig. 5. Average recruitment of new individuals per site calculated per unit area (A) and per capita (B). Error bars are standard errors of the mean and reflect the variance in the total number of recruits per quadrat summed over all months in (A) and variance in the total number of recruits per capita per month summed across quadrats in (B). Letters indicate groups of sites that are not significantly different from each other, based on a Tukey-HSD test.

individual growth rates in marginal populations; yet, neither was observed in the sampled edge populations.

Based on the age of the largest limpets at each site, the second hypotheses, that performance is limiting in marginal populations only in some years, also seems unlikely. Both mean and maximum sizes increase with latitude among these sites. Even with the observed faster growth rates at the two highest latitude sites (41.068°N and 42.042°N), the ages estimated for these limpets are comparable or slightly older than at the southernmost site (39.282°N), ca 10–12 yr. They suggest that life spans at high latitudes are comparable to those in more central parts of the range and that mortality events (Crisp 1964) are not more frequent at higher latitudes. Additionally, an examination of the past 50 yr of climate records from terrestrial meteorological stations near each site revealed that extreme climate events were not more frequent at higher latitudes (Gilman 2003). In particular, the frequency of freezing events follows the general pattern of temperatures among sites observed in this study. Freezes are least common (< 1 yr^{-1}) at the warmest site (40.022°N) and most common (> 10 yr^{-1}) at the coldest site (39.282°N) rather than the highest latitude site. Because the age and climate data provide only indirect

estimates of historical conditions, I cannot completely rule out the possibility that low abundance at high latitude sites is driven by poor adult performance in some years. Nevertheless the preponderance of larger individuals at higher latitudes strongly suggests that there were no years of poor performance at these sites in the recent past (Lewis et al. 1982).

The reduced rates of recruitment observed in marginal populations are consistent with the hypothesis that *C. scabra*'s range boundary is controlled by a factor that does not operate on performance at all, such as dispersal dynamics or habitat patchiness. Both recruitment per area and per capita were negatively correlated with latitude. The latter particularly suggests that recruitment in edge populations may not be high enough to maintain populations. Moreover the tendency towards greater adult performance in the northern populations is consistent with a hypothesis of reduced intraspecific competition (Boaventura et al. 2003), as might be expected if recruitment is limiting (Lewis et al. 1982). Thus variation in recruitment success is the most likely explanation for both patterns of local abundance and the location of the range boundary. Recruitment or repopulation failure has long been considered a cause of geographic range boundaries in intertidal invertebrates (Hutchins 1947, Lewis et al. 1982, Gaylord and Gaines 2000, Mieszkowska et al. 2006). The underlying mechanism may be biological, such as reproductive failure (Hutchins 1947), or physical, such as oceanographic dispersal limitation (Gaylord and Gaines 2000).

Mechanisms of recruitment limitation

In this study, successful recruitment reflects several steps in *C. scabra*'s life cycle, including fertilization of spawned gametes, survival and dispersal of the planktonic larvae back to shore, and survival and growth of the newly settled larvae to a visible size. At least four different factors could be contributing to reduced recruitment in edge populations: 1) reduced larval production, 2) mortality of larval or post-settlement stages, 3) an oceanographic larval dispersal barrier, or 4) availability of habitat.

1) Reduced larval production. Larval output and supply could be reduced at higher latitudes by: reduced gonad production, fewer spawning events, or reduced fertilization rates. Gonad production appears high at all sites examined in this study, but maturation alone does not ensure reproductive success. Most patellogastropods depend on environmental cues such as temperature or wave action (Lewis 1986, Shanks 1998). If these cues are rare or absent in marginal sites then spawning may be less frequent. Lewis (1986) suggested that a reduction in the length of the spawning season and/or in the frequency of spawning events reduced recruitment

Fig. 6. The frequency of limpets collected showing "sexable" or "ripe" gonads by sampling date at three sites near the northern range limit. Dark and light shaded bars indicate likely and questionable spawning events, respectively. See text for explanation.
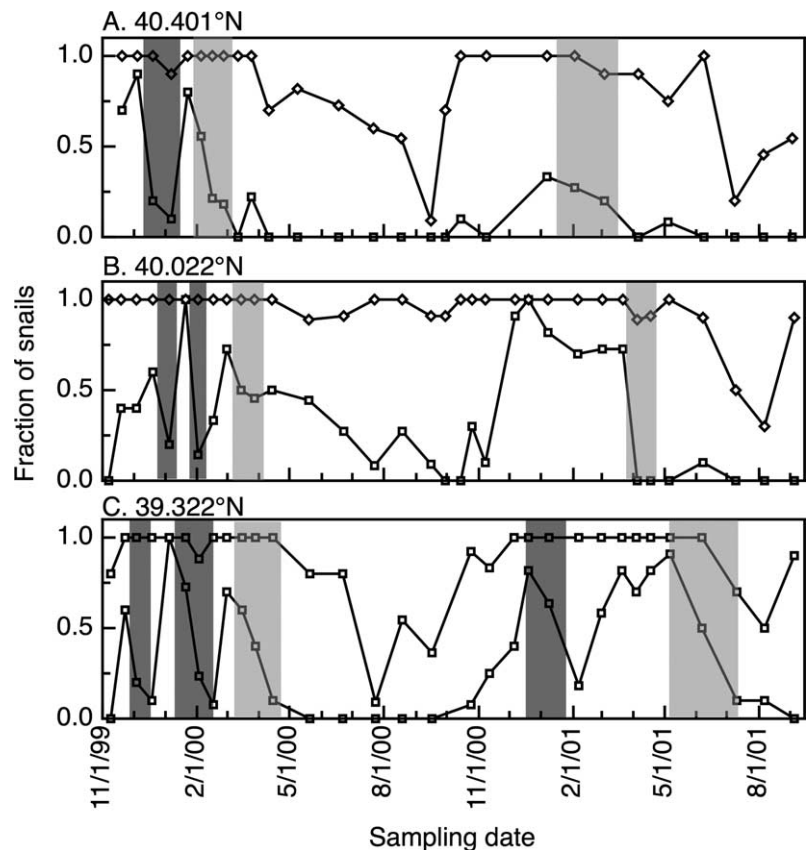
success in poleward-margin populations of several species of gastropods and cirripedes. It appears from this study that individuals at all sites are maturing and are likely spawning. Mass spawning may be slightly less frequent in the more northern of the three populations examined; yet, studies from more central portions of *C. scabra*'s range suggest that 2 or fewer spawnings per year is fairly typical (Fritchman 1961, Sutherland 1970). Additionally, low densities at the two northern sites may reduce the likelihood of successful fertilization during spawning. In other free spawning marine invertebrates, fertilization becomes limited when individuals of the opposite sex are separated by >1 m (Levitan and Sewell 1998). Local densities below two individuals per meter begin to appear around 41°N (Gilman 2005). Thus in extreme northern populations, low adult density may preclude successful reproduction; however, this cannot explain the initial decline in density among sites south of 41°N.

2) Mortality of early life stages. Patellogastropod larvae are generally <1 mm in size when they settle to shore (Bowman and Lewis 1986, Strathmann 1987, Kay and Emlet 2002) and little is known about survival of early life stages. Post-settlement mortality has been indicated as a cause of recruitment failure in high latitude populations of northwestern Atlantic patello-

gastropods (Bowman and Lewis 1986), but these are primarily associated with cold temperature stress which was not evident in this study. Indeed growth rates of the smallest individuals examined (7 mm) showed the strongest signal of increasing growth with latitude, suggesting performance of earlier life stages is also high. Nevertheless these individuals are likely already one year old and the possibility that environmental stressors are greatly different for new settled individuals than juveniles cannot be excluded.

3) Oceanographic dispersal barrier. Ocean currents may act as dispersal barriers for marine invertebrates by preventing larvae from dispersing to otherwise suitable habitat (Hutchins 1947, Lewis 1986, Gaylord and Gaines 2000). Such a mechanism has been proposed for the major biogeographic boundaries on the North American east and west coasts at Cape Hatteras, North Carolina and Pt. Conception, California (Doyle 1985, Gaylord and Gaines 2000, Zacherl et al. 2003); and also for Cape Mendocino, California (Rawson et al. 1999), which is within the present study area. Because such breaks usually co-occur with sharp changes in environmental conditions it has been difficult to establish oceanography as the definite cause of range boundaries (Zacherl et al. 2003, Parmesan et al. 2005). No such environmental breaks appear to occur at Cape Mendocino. However it

seems an unlikely location for an oceanographic boundary, because there are not many other species with range boundaries in this region of the coastline. Unfortunately very little is known of ocean circulation in this region of the northeastern Pacific.

4) Habitat availability. Long distances between populations can also serve as a form of dispersal barrier. The larvae of indirectly developing marine invertebrates such as *Collisella scabra* can potentially disperse tens to hundreds of kilometers before returning to shore (Shanks et al. 2003). Consequently, most of the local production of larvae may disperse and settle away from their natal site; and proximity to other spawning populations may be more important in determining recruitment than local production. Reduced population persistence because of a reduction in the frequency of suitable habitat and an increase in the distance between populations has been predicted as a mechanism of range boundary control in theoretical and conceptual models of range margins (Carter and Prince 1981, Holt and Keitt 2000, Holt et al. 2005) and also in models of marine reserves (Botsford et al. 2001, Gaines et al. 2003, Gerber et al. 2003); yet, the phenomenon has rarely been documented empirically (Carter and Prince 1981, Lewis 1986, Gonzalez-Guzman and Mehlman 2001).

The coastline near and north of Cape Mendocino (CPM, 40.440°N, 124.410°W) is very sandy and the three northernmost populations of this study may be isolated by >50 km from neighboring populations to the north and/or south. Whether these sandy patches of coastline control the range boundary depends on the dispersal ability of *C. scabra* larvae, which is unknown. At a generic mean current speed of 10 cm s^{-1}, a *C. scabra* larva would require more than a week to disperse the 70 km distance between the populations at 40.022°N and 41.068°N. However, Shanks et al. (2003) note that few species disperse as fast as 10 cm s^{-1}. Crisp (1958) reported that a 40–50 km barrier of unsuitable habitat was enough to stop the invasion of the cirripede *Elminius modestus* in Europe, which has a similar larval planktonic duration to *C. scabra* of 1–2 weeks. Data from Hockey and Branch (1994, Fig. 3) suggest that the patellogastropod *Patella aspera*, which has a similar life history to *C. scabra*, rarely disperses >5 km. Thus 50 km of unsuitable habitat may represent a considerable dispersal barrier for *C. scabra*.

Distributional patterns of abundance of other northeastern Pacific limpets suggest that their dispersal may also be limited among populations between 40°N and 42°N. Specifically, the abundance of the closely related species, *Lottia digitalis*, is reduced in this region relative to other parts of California and Oregon (Gilman 2003). *Lottia digitalis* also has a similar larval duration and ecology to *C. scabra*, suggesting that it would respond similarly to either an oceanographic or habitat barrier. However, *L. digitalis* has a much broader geographic distribution than *C. scabra*, extending into Alaska and possibly Japan (Morris et al. 1980, Lindberg 1981). Phylogenetic (Simison 2000) and paleontological (Zullo 1969, Hetherington and Reid 2003) studies suggest that *L. digitalis* and other, more widespread, congeners of *C. scabra* have a long history of occupation of the northeastern Pacific, while *C. scabra* does not; which may explain its more restricted distribution. Thus it may be that the mechanism controlling *C. scabra*'s range boundary also serves to restrict the dispersal between populations north and south of CPM in other patellogastropods.

Temperature and *C. scabra*'s distribution

In all populations examined in this study, I found consistent relationships between temperature and performance. At most sites, both mortality and growth were higher at warmer temperatures, suggesting that the consequences future warming under climate change may be difficult to predict. Because there is little evidence of either reduced performance in marginal populations or strong latitudinal clines in temperature, temperature cannot play a role in determining *C. scabra*'s poleward range boundary. This incongruity between local and geographic scale responses to climate change has been previously suggested (Helmuth et al. 2002, Gilman 2006). It underscores the precariousness of extrapolating the results of local-scale studies to larger scales (Root 1988) and demonstrates why empirical studies are necessary at biogeographic scales (Parmesan et al. 2005).

Conclusions

Several recent studies have questioned the classic view of a geographic range boundary as determined solely by temporally continuous processes acting on individual performance (see discussions in Gonzalez-Guzman and Mehlman 2001, Sagarin and Gaines 2002b, Gilman 2005). In this study, I found no evidence that individual performance of adults was reduced in marginal populations, as expected under the classic view. Instead the results strongly suggest the range boundary is controlled by a process that operates on recruitment rather than performance. Additionally, the observed relationships between temperature and performance suggest that although temperature may limit adult performance in some high latitude populations, it plays a negligible role in determining the location of the poleward range boundary. The paucity of empirical studies of species range boundaries (Gaston 2003, Parmesan et al. 2005) precludes a determination of the generality of either of these two findings. Non-classic processes may ultimately prove the rule for explaining species distributions, rather

than the exception, in species with long-distance passive dispersal (Gaylord and Gaines 2000) or strong Allee effects (Holt et al. 2005). The temperature effects observed here point to the possibility that temperature can play different roles in species dynamics at local and geographic scales. Consequently the effects of climate change need not be concentrated in populations near latitudinal range margins (Halpin 1997, Helmuth et al. 2002). Perhaps more importantly, without detailed empirical studies of species geographic ranges the generality of biogeographic theory, and its usefulness for predicting the consequences of climate change, may ultimately be limited.

References

Barry, J. P. et al. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. – Science 267: 672–675.

Bell, G. et al. 1993. The spatial structure of the physical environment. – Oecologia 96: 114–121.

Blackburn, T. M. et al. 1999. Do local abundances of British birds change with proximity to range edge? – J. Biogeogr. 26: 493–505.

Boaventura, D. et al. 2003. Size matters: competition within populations of the limpet *Patella depressa*. – J. Anim. Ecol. 72: 435–446.

Botsford, L. W. et al. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. – Ecol. Lett. 4: 144–150.

Bowman, R. S. and Lewis, J. R. 1986. Geographical variation in the breeding cycles and recruitment of *Patella* spp. – Hydrobiologia 142: 41–56.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. – Sinauer.

Brown, J. H. et al. 1995. Spatial variation in abundance. – Ecology 76: 2028–2043.

Brown, J. H. et al. 1996. The geographic range: size, shape, boundaries and internal structure. – Annu. Rev. Ecol. Syst. 27: 597–623.

Carbonell, R. et al. 2003. Effects of habitat heterogeneity and local adaptation on the body condition of a forest passerine at the edge of its distributional range. – Biol. J. Linn. Soc. 78: 479–488.

Carter, R. N. and Prince, S. D. 1981. Epidemic models used to explain bio geographical distribution limits. – Nature 293: 644–645.

Case, T. J. and Taper, M. L. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. – Am. Nat. 155: 583–605.

Caughley, G. et al. 1988. The edge of the range. – J. Anim. Ecol. 57: 771–786.

Channell, R. and Lomolino, M. V. 2000. Dynamic biogeography and conservation of endangered species. – Nature 403: 84–86.

Cossins, A. R. and Bowler, K. 1987. Temperature biology of animals. – Chapman and Hall.

Crisp, D. J. 1958. The spread of *Elminius modestus* Darwin in north-west Europe. – J. Mar. Biol. Ass. U.K. 37: 483–520(ed.).

Crisp, D. J. (ed.) 1964. The effects of the severe winter of 1962–1963 on marine life in Britain. – J. Anim. Ecol. 33: 179–210.

Doyle, R. F. 1985. Biogeographical studies of rocky shores near Point Conception, California. – Ph.D. thesis, Univ. of California, Santa Barbara, CA, USA.

Fitzhenry, T. et al. 2004. Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. – Mar. Biol. 145: 339–349.

Fritchman, H. I. 1961. A study of the reproductive cycle in the California Acmaeidae (Gastropoda) Part III. – Veliger 4: 41–47.

Gaines, S. D. et al. 2003. Avoiding current oversights in marine reserve design. – Ecol. Appl. 13: S32–S46.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. – Oxford Univ. Press.

Gaylord, B. and Gaines, S. D. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. – Am. Nat. 155: 769–789.

Gerber, L. R. et al. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. – Ecol. Appl. 13: S47–S64.

Gilman, S. E. 2003. Factors controlling the northern geographic range limit of the intertidal limpet, *Collisella scabra* (Gould). – Ph.D. thesis, Univ. of California, Davis, CA, USA.

Gilman, S. E. 2005. A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). – J. Biogeogr. 32: 1583–1589.

Gilman, S. E. 2006. Life at the edge: an experimental study of a poleward range boundary. – Oecologia 148: 270–279.

Gonzalez-Guzman, L. I. and Mehlman, D. W. 2001. Developmental stability across the breeding distribution of the scissor-tailed flycatcher (*Tyrannus forficatus*). – Ecol. Lett. 4: 444–452.

Guo, Q. F. et al. 2005. Spatial-temporal population dynamics across species range: from centre to margin. – Oikos 108: 47–57.

Gurevitch, J. et al. 2002. The ecology of plants. – Sinauer.

Hahn, T. and Denny, M. 1989. Tenacity-mediated selective predation by oystercatchers on intertidal limpets and its role in maintaining habitat partitioning by *Collisella scabra* and *Lottia digitalis*. – Mar. Ecol. Prog. Ser. 53: 1–10.

Halpin, P. 1997. Global climate change and natural-area protection: management responses and research directions. – Ecol. Appl. 7: 828–843.

Helmuth, B. et al. 2002. Climate change and latitudinal patterns of intertidal thermal stress. – Science 298: 1015–1017.

Hetherington, R. and Reid, R. G. B. 2003. Malacological insights into the marine ecology and changing climate of the late Pleistocene–early Holocene Queen Charlotte Islands archipelago, western Canada, and implications for early peoples. – Can. J. Zool. 81: 626–661.

Hockey, P. A. R. and Branch, G. M. 1994. Conserving marine biodiversity on the African coast: implications of a terrestrial perspective. – Aquat. Conserv. 4: 345–362.

Holt, R. D. and Keitt, T. H. 2000. Alternative causes for range limits: a metapopulation perspective. – Ecol. Lett. 3: 41–47.

Holt, R. D. et al. 2005. Theoretical models of species' borders: single species approaches. – Oikos 108: 18–27.

Hutchins, L. W. 1947. The basis for temperature zonation in geographical distribution. – Ecol. Monogr. 17: 325–335.

Kay, M. C. and Emlet, R. B. 2002. Laboratory spawning, larval development, and metamorphosis of the limpets *Lottia*

digitalis and *Lottia asmi* (Patellogastropoda, Lottiidae). – Invertebr. Biol. 121: 11–24.

Kirkpatrick, M. and Barton, N. H. 1997. Evolution of a species' range. – Am. Nat. 150: 1–23.

Lawton, J. H. 1993. Range, population abundance and conservation. – Trends Ecol. Evol. 8: 409–413.

Lawton, J. H. 2000. Concluding remarks: a review of some open questions. – In: Hutchings, M. J. et al. (eds), The ecological consequences of environmental heterogeneity. Blackwell, pp. 401–424.

Levitan, D. R. and Sewell, M. A. 1998. Fertilization success in free-spawning marine invertebrates: review of the evidence and fisheries implications. – Can. Spec. Publ. Fish. Aquat. Sci. 125: 159–164.

Lewis, J. R. 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. – Hydrobiologia 142: 1–13.

Lewis, J. R. et al. 1982. Some geographical components in population dynamics: possibilities and realities in some littoral species. – Neth. J. Sea Res. 16: 18–28.

Lindberg, D. R. 1981. Acmaeidae: Gastropoda Mollusca. – Boxwood Press.

Lindberg, D. R. 1986. Name changes in the "Acmaeidae". – Veliger 29: 142–148.

MacArthur, R. H. 1972. Geographical ecology. – Princeton Univ. Press.

McGill, B. and Collins, C. 2003. A unified theory for macroecology based on spatial patterns of abundance. – Evol. Ecol. Res. 5: 469–492.

Mieszkowska, N. et al. 2006. Changes in the range of some common rocky shore species in Britain – a response to climate change? – Hydrobiologia 555: 241–251.

Morris, R. H. et al. 1980. Intertidal invertebrates of California. – Stanford Univ. Press.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Parmesan, C. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. – Nature 399: 579–583.

Parmesan, C. et al. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. – Oikos 108: 58–75.

Pulliam, H. R. 2000. On the relationship between niche and distribution. – Ecol. Lett. 3: 349–361.

Rawson, P. D. et al. 1999. Hybridization between the blue mussels *Mytilus galloprovincialis* and *M. trossulus* along the Pacific coast of North America: evidence for limited introgression. – Mar. Biol. 134: 201–211.

Ricketts, E. F. et al. 1985. Between Pacific tides. – Stanford Univ. Press.

Root, T. L. 1988. Energy constraints on avian distributions and abundances. – Ecology 69: 330–339.

Sagarin, R. D. and Gaines, S. D. 2002a. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. – J. Biogeogr. 29: 985–997.

Sagarin, R. D. and Gaines, S. D. 2002b. The 'abundant centre' distribution: to what extent is it a biogeographical rule? – Ecol. Lett. 5: 137–147.

Sagarin, R. D. et al. 1999. Climate-related change in an intertidal community over short and long time scales. – Ecol. Monogr. 69: 465–490.

Samways, M. J. et al. 1999. Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide. – J. Biogeogr. 26: 795–812.

Shanks, A. L. 1998. Apparent oceanographic triggers to the spawning of the limpet *Lottia digitalis* (Rathke). – J. Exp. Mar. Biol. Ecol. 222: 31–41.

Shanks, A. L. et al. 2003. Propagule dispersal distance and the size and spacing of marine reserves. – Ecol. Appl. 13: S159–S169.

Simison, W. B. 2000. Evolution and phylogeography of New World gastropod faunas. – Ph.D. thesis, Univ. of California, Berkeley

Somero, G. 2005. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. – Frontiers Zool. 2: 1–9.

Southward, A. J. et al. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. – J. Therm. Biol. 20: 127–155.

Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. – Univ. of Washington Press.

Sutherland, J. P. 1970. Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). – Ecol. Monogr. 40: 169–188.

Van Home, B. 1983. Density as a misleading indicator of habitat quality. – J. Wildl. Manage. 47: 893–901.

Walther, G.-R. et al. 2002. Ecological responses to recent climate change. – Nature 416: 389–395.

Westfall, P. H. et al. 1999. Multiple comparisons and multiple tests: using the SAS system. – SAS Inst.

Zacherl, D. et al. 2003. The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). – J. Biogeogr. 30: 913–924.

Zullo, V. A. 1969. A late Pleistocene marine invertebrate fauna from Bandon, Oregon. – Proc. Calif. Acad. Sci. 36: 347–361.

Subject Editor: Miguel Araújo.