



A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846)

Sarah Gilman*

Section of Evolution and Ecology and Center
for Population Biology, University of
California, Davis, CA, USA

ABSTRACT

Aim Brown's principle predicts that a species will peak in density near its range centre, and decline gradually towards the margins of its geographical distribution. The decline is assumed to reflect a decrease in individual performance near range margins. I test this abundance–performance hypothesis by comparing patterns in density and size across the northern half of the geographical distribution of the marine patellogastropod *Collisella scabra* (Gould, 1846).

Location *Collisella scabra* is a high intertidal patellogastropod species distributed along the Pacific coast of North America from Cape Mendocino (CA, USA) to southern Baja California (Mexico). I surveyed 11 research sites spanning c. 36–44° N.

Methods In each of the 11 research sites I surveyed four distinct microhabitats, and compared spatial patterns in density and in the size of solitary limpets.

Results Both density and size were highly variable across the species range. Density peaked near the northern range margin, and showed greater variance at small spatial scales (< 10 km) than at large scales (> 100 km). In contrast, large size occurred uniformly across the survey area, and size was strongly associated with microhabitat.

Main conclusion *Collisella scabra* does not show spatial patterns of density or performance that are consistent with Brown's principle. The underlying assumptions of Brown's principle may conflict with specific characteristics of *C. scabra*'s life history and/or patterns of environmental variation across its range. Because such conflicts may be common in a large number of marine and terrestrial species, the generality of Brown's principle is questioned.

Keywords

Abundance, Brown's principle, *Collisella scabra*, environmental heterogeneity, geographical range, *Macdintockia*, North American coast, performance, size.

*Correspondence: Sarah Gilman, Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA.
E-mail: gilmans@biol.sc.edu

INTRODUCTION

Patterns of abundance across a species geographical distribution are frequently used as sources of information about spatial variation in individual performance, population dynamics and the causes of geographical range limits (Van Horne, 1983; Caughley *et al.*, 1988; Brown *et al.*, 1995). Brown's principle (Brown, 1984; Brown *et al.*, 1995; Maurer, 1999) predicts that species show a few sites of high density clustered near their range centre, with declining abundance towards the range margins. Brown's principle relies on two assumptions: (1) individuals are best matched to environmental conditions near the range

centre; and (2) local population density reflects individual success. Thus high abundance sites near the range centre are the locations of greatest individual success. The term 'environmental condition' encompasses any aspect of an organism's Hutchinsonian niche, such as climate, prey items or other interacting species (Brown & Lomolino, 1998). Brown's principle has influenced thinking across a spectrum of biological problems from evolution (Kirkpatrick & Barton, 1997) to conservation (Lawton, 1993; Channell & Lomolino, 2000).

Not all species distributions match Brown's principle. Species may show low density near the centre of their distribution, high density close to a range margin, or more

generally heterogeneous patterns of abundance across their distribution (Blackburn *et al.*, 1999; Ribeiro & Fernandes, 2000; Sagarin & Gaines, 2002a,b). Moreover, high individual success or fitness is not always associated with high abundance (Van Horne, 1983; Gonzalez-Guzman & Mehlman, 2001). These 'exceptions' suggest that more detailed studies of the patterns of abundance and performance across species ranges are needed before Brown's principle can be accepted as a general rule of biogeography.

Because of their near-linear geographical distributions, intertidal invertebrates that occur along north–south running continental margins are considered model species for studying biogeographical processes (Sagarin & Gaines, 2002a). Yet, in a recent survey of 12 north-eastern Pacific intertidal invertebrates, Sagarin & Gaines (2002a) found that only two species showed a pattern of greatest abundance near their range centre. Their results suggest that one or both of the underlying assumptions of Brown's principle are violated in this group.

For a longitudinally restricted species, the first assumption, that habitat suitability peaks near the range centre, implies an association between latitude and environmental conditions. In intertidal systems, many environmental conditions show local or large-scale patterns of heterogeneity that are not well correlated with latitude. These include tidal cycles, temperature, wave exposure, coastal topography and species interactions (Fawcett, 1984; Foster, 1990; Bertness & Ewanchuk, 2002; Helmuth *et al.*, 2002). If position within the geographical range is a poor predictor of local environmental conditions and thus individual success, high abundance may still indicate high individual success. Alternately, processes such as source–sink population dynamics, disturbance, and dispersal behaviour could alter the relationship between local abundance and habitat suitability (Van Horne, 1983; Ebert & Russell, 1988; Pineda & Caswell, 1997; Pulliam, 2000), violating the second assumption of Brown's principle. In this case, even if environmental conditions are most favourable near the range centre, adult abundance may not reflect local environmental conditions. A detailed survey of abundance and individual success in a single species is necessary to distinguish between these two explanations for Sagarin & Gaines' (2002a) results.

Here I report on the results of a geographical survey of abundance and size of the intertidal gastropod '*Collisella*' *scabra* (see below for taxonomic issues), in the context of a broader study of its poleward geographical range limit (Gilman, 2003). *Collisella scabra* is a high intertidal limpet common to the California (USA) coast. I surveyed *C. scabra* at 11 locations across 900 km encompassing approximately the northern half of its geographical distribution, and compared patterns across four microhabitats at each location. I measured both abundance and the size of individual limpets, using size as a proxy for individual performance. I use the survey results to test three specific hypotheses: (1) that spatial patterns of abundance in *C. scabra* match Brown's principle; (2) that spatial patterns of individual performance in *C. scabra* match Brown's principle; and (3) that spatial patterns of abundance differ from patterns of individual performance.

MATERIALS AND METHODS

Study species

Collisella scabra is a high intertidal herbivorous patello-gastropod common to rocky shores of the north-eastern Pacific. While there is some uncertainty over its taxonomy (Lindberg, 1986), both molecular (Simison, 2000) and morphological (Gilman, unpubl. data) evidence suggest it is closely related to the genus *Lottia*. *Collisella scabra* has a biphasic life cycle with a pelagic (swimming) larval phase of probably < 2 weeks (Strathmann, 1987) and a benthic (sedentary) adult phase of 10–30 years (Sutherland, 1970). Maximum dispersal distances during the pelagic phase are unknown, but likely fall between 5 and 50 km (Hockey & Branch, 1994; Shanks *et al.*, 2003). Published range descriptions commonly indicate a northern range limit near Cape Arago, Oregon (43°20' N, Morris *et al.*, 1980; Lindberg, 1981). Published southern range boundaries are more vague, but suggest the snail is common in Baja California Sur, Mexico (< 28° N, Morris *et al.*, 1980; Lindberg, 1981). This survey was conducted as part of a broader study of the processes controlling *C. scabra*'s northern geographical range limit.

Survey

In the summers of 1999 and 2000, I surveyed *C. scabra* individuals in 11 locations in California and Oregon (Fig. 1). Ten of the locations are spaced at c. 100 km intervals along the coast. The eleventh location at Devil's Gate, CA is located about halfway between the Shelter Cove and Trinidad locations (Fig. 1). All sites are classified as 'protected outer coast' *sensu* Ricketts *et al.* (1985), and were visited once in either 1999 or 2000. Additional details on sampling locations are reported in Gilman (2003).

To control for microhabitat effects on abundance, I surveyed the abundance and size of *C. scabra* in four separate habitats at each location. I defined the habitats by the dominant space occupying species, rather than by absolute tidal height, because heights are difficult to measure in the field and are not directly comparable among sites that differ in total tidal range. The four habitats, from highest to lowest, are: (1) bare rock above the highest algal beds, (2) fucoid algal beds (mainly *Pelvetiopsis* spp.), (3) algal turf (primarily *Endocladia muricata* and *Gigartina papillatus*), and (4) mussel beds (*Mytilus* spp.). Relative to the Ricketts *et al.* (1985) zonation scheme for the Pacific Coast, the first habitat falls in zone 1, the second two in zone 2, and the fourth in zone 3.

I surveyed four replicate transects for each combination of habitat and location. The transects were distributed over a length of 5–15 km of coastline in each location, and were separated by at least 0.8 km from other transects sampling the same combination of location and habitat. Replication at this spatial scale allowed for variation in wave exposure, substrate orientation and aspect, and other environmental differences that might affect *C. scabra* abundance but could not be

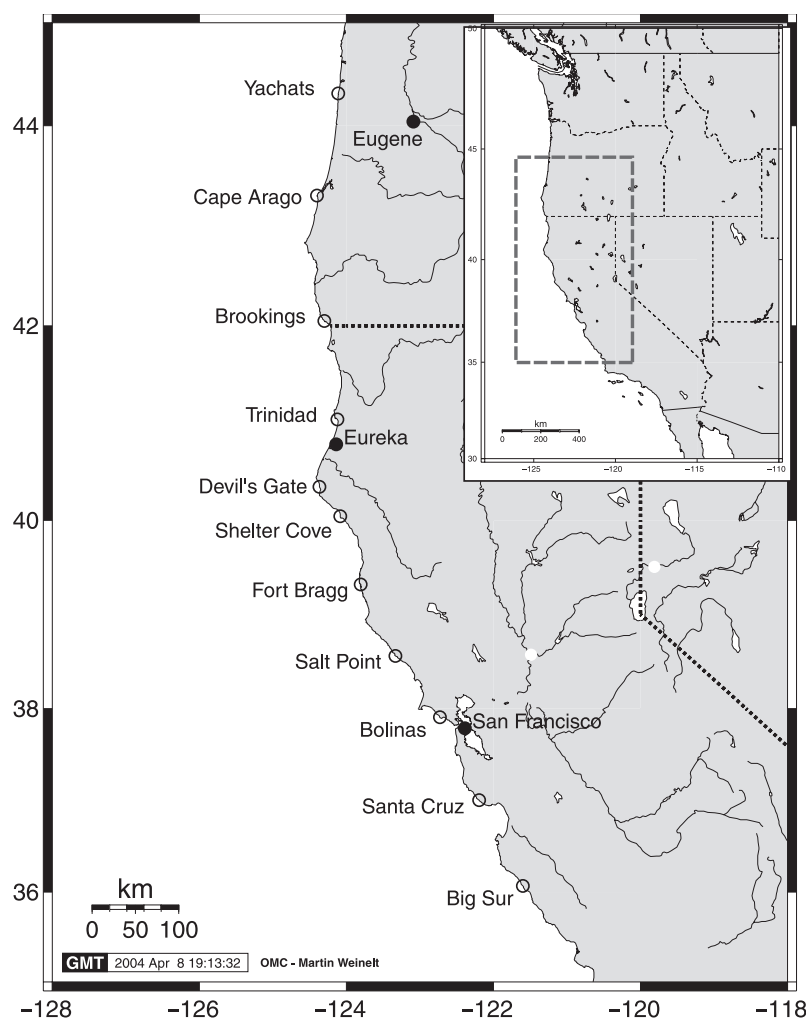


Figure 1 Sampling locations in California and Oregon (USA). Eleven locations were surveyed between Big Sur, CA and Yachats, OR. At every location, I sampled 16 transects, four in each of four habitats.

captured within a single transect. Each transect consisted of 10 replicate $0.2 \text{ m} \times 0.2 \text{ m}$ quadrats spaced at 0.5 m intervals, starting at a randomly chosen point along a horizontal transect line through the vertical centre of the habitat. Preliminary surveys, testing a range of transect lengths and quadrat sizes, found that this design provided a reasonable estimate of *C. scabra* abundance within a reef, relative to the effort required. I recorded the latitude and longitude of each transect by GPS. In each quadrat I counted the total number of *C. scabra* and estimated the length of each snail to the nearest 4 mm using a small piece of 4 mm mesh as a grid.

Size as a measure of performance

In species with indeterminate growth, such as *C. scabra* (Sutherland, 1970), larger sizes within a population can indicate either greater individual growth rates or longer life spans, both of which are consistent with greater individual success. Larger size may also indicate greater fecundity (Kido & Murray, 2003). Thus size is frequently used as a measure of individual performance

(e.g., Carter & Prince, 1985; Lewis, 1986; Ribeiro & Fernandes, 2000; Zacherl *et al.*, 2003). However, growth rate, and hence size, may be influenced by other factors such as temperature (Cossins & Bowler, 1987; Atkinson, 1994) or intraspecific competition (e.g., self-thinning, Silvertown, 1987). Before using size as a proxy for individual performance, the potential effects of these other factors on size should be examined.

In the present study, temperature is unlikely to influence latitudinal patterns in body size, because temperatures are very similar along most of the study area (Gilman, 2003) and there is no consistent latitudinal pattern of temperature in this system (Helmuth *et al.*, 2002; Gilman, 2003). However, particularly because I intend to contrast patterns of size and density, the effect of intraspecific competition on size is a potential concern (Sutherland, 1970) and requires first testing for a negative relationship between density and size. Because I did find evidence for such a pattern (discussed below), I have restricted my analysis of latitudinal size patterns to the 167 sampled quadrats containing only a single individual (hereafter, 'solitary size'). At this extremely low density, intraspecific

competition is unlikely to influence growth rate and thus size can be interpreted as a reflection of the suitability of local environmental conditions. Additionally, because individuals of this species return to a 'home scar' at every low tide, short-term temporal variation in density is negligible (Sutherland, 1970; Gilman, unpubl. data).

Statistical analysis

To examine relationships between latitude, density and size I calculated Pearson correlation coefficients by habitat. For the correlations with latitude, I used the latitude of individual transects within each location. Because there was a large number of zero observations at the quadrat level, I averaged all quadrats within a transect to generate a mean abundance and mean size per transect. Mean size per transect was calculated by weighting the number of individuals in each size class by the midpoint value of the size class. I used variance components analysis to compare the variation in density and size at different spatial scales. All statistical analyses were run in either SAS version 6.12 or JMP version 4.0 for Macintosh (SAS Institute, Cary, NC, USA).

RESULTS

Density

Mean density per transect was negatively correlated with latitude in all habitats (Table 1), suggesting a general pattern of decline in abundance towards the range boundary; however, only one of the correlation coefficients was significantly different from zero. Moreover the plots of abundance do not show a gradual decline in density with increasing latitude (Fig. 2a). The highest abundances observed were near Fort Bragg, California (c. 39° N), which is much closer to the range margin than to the centre. Eighty-four per cent of the transects at sites north of 41° N contained no *C. scabra*, suggesting that these locations are extra-limital. Excluding data from these locations results in positive (but not significant) correlation coefficients at all sites (data not shown). The relative abundance of *C. scabra* among habitats varied by location, but with no clear latitudinal pattern (data not shown).

The variance components analysis revealed substantial heterogeneity in abundance both within and among sites (Table 2). While more than 30% of the variation occurred among latitudinal sites, there was also significant variation at smaller spatial scales. Overall, there was greater variation in

density among the replicate transects of a habitat and location combination (< 15 km) and among the quadrats within a transect (< 5 m) than among sites (100 km).

Size

There was little overall pattern in mean size among latitudes (Fig. 2b, Table 1). Mean size was negatively correlated with density in all habitats (Table 1, Fig. 2c). Although the correlations were only significant in the fucoid and turf habitats, the patterns are consistent with intraspecific competition and suggest that mean size is a biased estimator of performance. Solitary size, which should minimize the effect of intraspecific competition, also showed little overall pattern in size among latitudes (Fig. 3). Large solitary individuals were present at most of the surveyed sites, and not concentrated near the range centre. Solitary size was positively correlated with latitude in the bare rock habitat and negatively correlated in the turf habitat, but only the second was statistically significant ($P < 0.05$). Variation in size was most strongly associated with differences among habitats and with replicate quadrats within a transect (Table 2), although only the inter-quadrat term was significant.

DISCUSSION

Collisella scabra showed highly heterogeneous patterns of abundance over a range of spatial scales and little evidence of a gradual decline in abundance from the range centre to the range margin, both contrary to the predictions of Brown's principle. Moreover, Brown's principle predicts that high abundance sites will be near each other because the environmental conditions controlling abundance are spatially auto-correlated (Brown *et al.*, 1995). Instead, *C. scabra* shows highly variable abundance at extremely small spatial scales. Densities differ as much between quadrats less than a metre apart as between quadrats hundreds of kilometres apart.

Spatial patterns of performance, as reflected in solitary limpet sizes, also do not match Brown's principle. The largest individuals are found at sites from 36 to 42° N, suggesting that high individual success is possible across most of region surveyed in this study and does not decline towards the range margin. This pattern is distinct from the spatial pattern of density, which peaked around 39° N, and suggests that density is a poor predictor of individual success or habitat suitability.

Although the patterns observed in density and performance offer little support for Brown's principle in *C. scabra*, two

Measurements	Bare	Fucoid	Turf	Mussel
Mean density \times latitude	-0.2505 (44)	-0.2995* (44)	-0.2945 (43)	-0.1863 (44)
Mean size \times latitude	0.4452* (24)	-0.1027 (34)	-0.4512* (27)	-0.0181 (30)
Mean size \times mean density	-0.0325 (24)	-0.4062* (34)	-0.4063* (27)	-0.0938 (30)
Solitary size \times latitude	0.3333 (21)	-0.0369 (21)	-0.4623* (21)	0.0122 (24)

* $P < 0.05$.

Table 1 Correlation coefficients among density, size and latitude for each of the four sampled habitats. In all cases, quadrats were averaged across transects before calculating correlations. Numbers in parentheses indicate sample size (number of transects). Sample sizes are reduced for analyses involving size because zero density transects are excluded

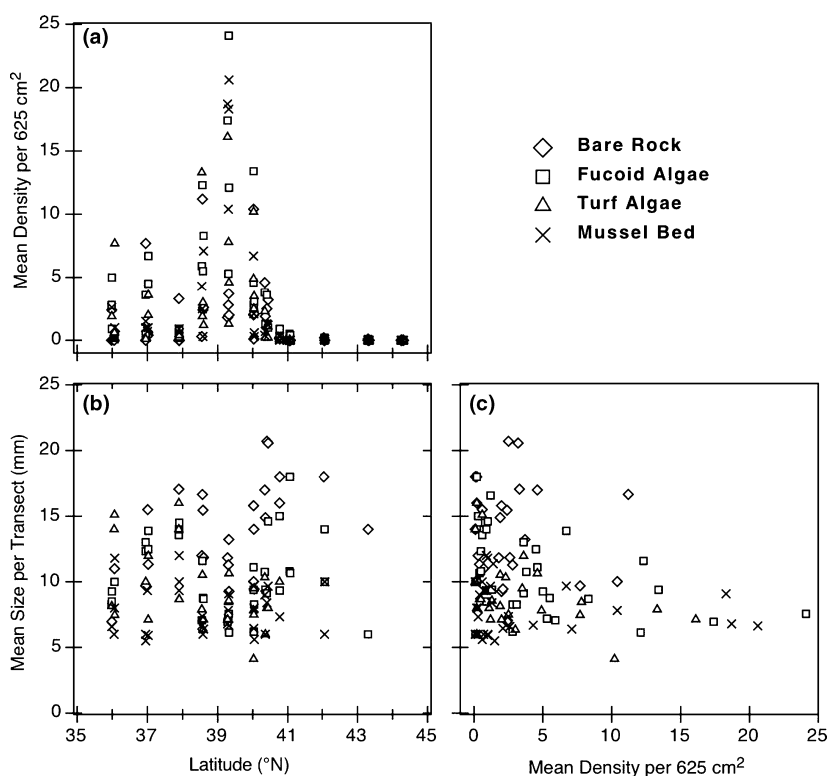


Figure 2 Plots of (a) mean abundance and (b) mean size per transect against the latitude of the transect, and (c) mean size against mean abundance. Symbols indicate the four microhabitats sampled.

Table 2 Variance component analysis for the effects of latitude and habitat on the abundance and size of *Collisella scabra* (Gould 1846). *P*-values are based on a Wald *Z*-test ($H_0: \sigma^2 = 0$). $n = 1750$ quadrats for density and 167 for solitary size.

Term	Density			Solitary size*		
	% Variation	SE %	<i>P</i>	% Variation	SE %	<i>P</i>
Location (north or south of 40° N)	16.50	29.53	0.5764	2.28	10.67	0.8311
Latitude (within location)	18.56	10.44	0.0754	7.98	7.25	0.2709
Habitat	0.69	1.64	0.6742	32.85	28.92	0.2561
Habitat by latitude (within location)	8.64	3.68	0.0188	4.94	6.84	0.4704
Replicate transect (within latitude and habitat)	17.71	2.66	0.0001	7.69	7.19	0.2846
Replicate quadrat (within transect)	37.90	1.35	0.0001	44.27	6.73	0.0001

*Includes only quadrats with a single individual

limitations of this and similar studies should also be considered. First, this study surveyed only the northern half of *C. scabra*'s geographical distribution. Sampling across the entire species range could provide a more complete test of Brown's principle and might change the interpretation of these results (Sagarin & Gaines, 2002b). Yet it is difficult to conceive a pattern of abundance or solitary size across the unsampled regions that would bring these results in line with Brown's principle, as both abundance and performance remained high up to the northern range boundary. Secondly, size patterns, particularly mean size, may be influenced by processes other than individual success and should be interpreted with caution. In the case of *C. scabra*, a separate study of populations at five locations between Fort Bragg, California (39.282° N, 123.803° W) and Brookings, Oregon (42.042° N, 124.290° W) confirmed that limpets in marginal populations

survived and grew at rates comparable to or greater than those from more central portions of the range (Gilman, 2003). Thus even with these caveats, the results of this study are inconsistent with Brown's principle, suggesting that *C. scabra* violates one or both of the underlying assumptions of Brown's principle.

The poor correlation between mean solitary size and latitude suggests a violation of the first assumption: that the most suitable environmental conditions occur near the range centre. The association between solitary size and habitat type or zone indicates that environmental conditions do influence the individual success of *C. scabra*. However, many environmental conditions in intertidal systems, particularly in the north-eastern Pacific, are poorly correlated with latitude. These conditions include temperature, tides, wave forces and species interactions (Foster, 1990; Menconi *et al.*, 1999; Bertness &

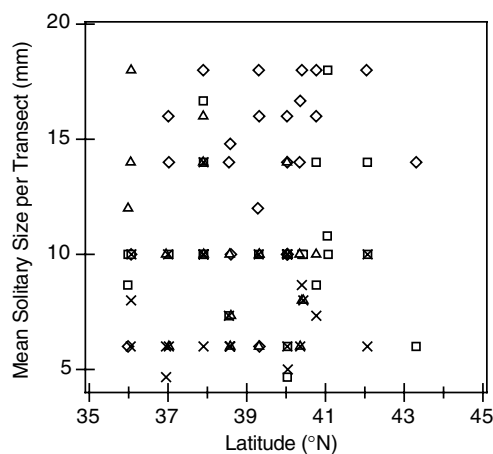


Figure 3 Plot of mean solitary limpet size per transect against latitude. See Fig. 2 for symbol legend.

Ewanchuk, 2002; Helmuth *et al.*, 2002). This environmental heterogeneity may complicate the relationship between position within the species range and individual success.

In contrast to solitary size, habitat type explained very little of the density variation within or among sites, suggesting that environmental conditions have less influence on density. Another factor that may control density is variation in recruitment success. Many intertidal invertebrates, including *C. scabra* and 9 of the 12 species studied by Sagarin & Gaines (2002a), possess an obligate planktonic (ocean-living) larval dispersal stage. In these species, ocean currents (e.g. Ebert & Russell, 1988; Morgan *et al.*, 2000) and larval behaviour (e.g. Pineda & Caswell, 1997) both may disassociate adult success within a location from the subsequent local input of larval recruits, creating high adult density at some sites with less favourable conditions than lower density sites. Similar mechanisms have been proposed in terrestrial species with high rates of postnatal dispersal (Gonzalez-Guzman & Mehlman, 2001). When dispersal is controlled by such processes, the number of recruits to a site may no longer reflect its suitability for adults, violating the second major assumption of Brown's principle. Establishing that dispersal patterns control *C. scabra* adult abundance would require more detailed studies of larval dispersal and post-settlement survival patterns.

This paper is one of many to report patterns contradicting part or all of Brown's principle (Blackburn *et al.*, 1999; Kiflawi *et al.*, 2000; Perez-Tris *et al.*, 2000; Ribeiro & Fernandes, 2000; Gonzalez-Guzman & Mehlman, 2001; Sagarin & Gaines, 2002a,b). In the case of *C. scabra*, it is likely that both environmental heterogeneity and obligate larval dispersal combine to uncouple the relationship between abundance and position within the range. Large solitary sizes suggest that suitable habitats occur near the range boundary and throughout the range; however, dispersal may limit local abundance at the most suitable sites by removing a large portion of the locally produced larvae. Although by itself this study remains a limited refutation of Brown's principle, when considered in conjunction with the growing number of 'exceptions' to Brown's principle it

suggests that the underlying assumptions may be violated by many species. Rather than assuming an *a priori* relationship between density and abundance, biogeographers should consider carefully how aspects of a species life history may influence spatial patterns of abundance. Brown's principle, in fact, may only apply to a select group of species: those with relatively low dispersal, living in environments that change predictably over space, with little temporal heterogeneity.

ACKNOWLEDGEMENTS

I gratefully acknowledge Kelly Batchelor for field assistance. R. Grosberg, S. Gaines, J. Stachowicz, N. Tsutsui, K. Mabry, J. Weston and two anonymous referees provided many helpful comments on earlier drafts of this paper. Financial support was provided by an NSF predoctoral fellowship to S. Gilman and by NSF grant OCE-9906741 to R. Grosberg. This research was performed in partial fulfilment of a PhD at the University of California, Davis.

REFERENCES

- Atkinson, D. (1994) Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.
- Bertness, M.D. & Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, **132**, 392–401.
- Blackburn, T.M., Gaston, K.J., Quinn, R.M. & Gregory, R.D. (1999) Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography*, **26**, 493–505.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer and Associates, Sunderland, MA.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.
- Carter, R.N. & Prince, S.D. (1985) The geographical distribution of prickly lettuce *Lactuca serriola* L. A general survey of its habitats and performance in Britain. *Journal of Ecology*, **73**, 27–38.
- Caughley, G., Grice, D., Barker, R. & Brown, B. (1988) The edge of the range. *Journal of Animal Ecology*, **57**, 771–786.
- Channell, R. & Lomolino, M.V. (2000) Dynamic biogeography and conservation of endangered species. *Nature*, **403**, 84–86.
- Cossins, A.R. & Bowler, K. (1987) *Temperature biology of animals*. Chapman and Hall, London, New York.
- Ebert, T.A. & Russell, M.P. (1988) Latitudinal variation in size structure of the west coast USA purple sea urchin: a correlation with headlands. *Limnology and Oceanography*, **33**, 286–294.
- Fawcett, M.H. (1984) Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology*, **65**, 1214–1230.

- Foster, M.S. (1990) Organization of macroalgal assemblages in the northeast Pacific – the assumption of homogeneity and the illusion of generality. *Hydrobiologia*, **192**, 21–33.
- Gilman, S.E. (2003) *Factors controlling the northern geographic range limit of the intertidal limpet, *Collisella scabra* (Gould)*. PhD Thesis, Population Biology, University of California, Davis, CA.
- Gonzalez-Guzman, L.I. & Mehlman, D.W. (2001) Developmental stability across the breeding distribution of the scissor-tailed flycatcher (*Tyrannus forficatus*). *Ecology Letters*, **4**, 444–452.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science*, **298**, 1015–1017.
- Hockey, P.A.R. & Branch, G.M. (1994) Conserving marine biodiversity on the African coast: implications of a terrestrial perspective. *Aquatic Conservation*, **4**, 345–362.
- Kido, J.S. & Murray, S.N. (2003) Variation in owl limpet *Lottia gigantea* population structures, growth rates, and gonadal production on southern California rocky shores. *Marine Ecology Progress Series*, **257**, 111–124.
- Kiflawi, M., Enquist, B.J. & Jordan, M.A. (2000) Position within the geographic range, relative local abundance and developmental instability. *Ecography*, **23**, 539–546.
- Kirkpatrick, M. & Barton, N.H. (1997) Evolution of a species range. *American Naturalist*, **150**, 1–23.
- Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, **8**, 409–413.
- Lewis, J.R. (1986) Latitudinal trends in reproduction recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia*, **142**, 1–14.
- Lindberg, D.R. (1981) *Acmaeidae: Gastropoda Mollusca*. Boxwood Press, Pacific Grove, CA.
- Lindberg, D.R. (1986) Name changes in the 'Acmaeidae'. *The Veliger*, **29**, 142–148.
- Maurer, B.A. (1999) *Untangling ecological complexity: the macroscopic perspective*. University of Chicago Press, Chicago, IL.
- Menconi, M., Benedetti-Cecchi, L. & Cinelli, F. (1999) Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **233**, 1–23.
- Morgan, L.E., Wing, S.R., Botsford, L.W., Lundquist, C.J. & Diehl, J.M. (2000) Spatial variability in red sea urchin (*Strongylocentrotus franciscanus*) recruitment in northern California. *Fisheries Oceanography*, **9**, 83–98.
- Morris, R.H., Abbott, D.P. & Haderlie, E.C. (1980) *Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
- Perez-Tris, J., Carbonell, R. & Telleria, J.L. (2000) Abundance distribution, morphological variation and juvenile condition of robins, *Erithacus rubecula* (L), in their Mediterranean range boundary. *Journal of Biogeography*, **27**, 879–888.
- Pineda, J. & Caswell, H. (1997) Dependence of settlement rate on suitable substrate area. *Marine Biology*, **129**, 541–548.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Ribeiro, K.T. & Fernandes, G.W. (2000) Patterns of abundance of a narrow endemic species in a tropical and infertile montane habitat. *Plant Ecology*, **147**, 205–218.
- Ricketts, E.F., Calvin, J., Hedgpeth, J.W. & Phillips, D.W. (1985) *Between Pacific tides*. Stanford University Press, Stanford, CA.
- Sagarin, R.D. & Gaines, S.D. (2002a) Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography*, **29**, 985–997.
- Sagarin, R.D. & Gaines, S.D. (2002b) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Shanks, A.L., Grantham, B.A. & Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, **13**, S159–S169.
- Silverton, J. (1987) *Introduction to plant population ecology*. John Wiley & Sons, New York, NY.
- Simison, W.B. (2000) *Evolution and phylogeography of New World gastropod faunas*. PhD Thesis, Integrative Biology, University of California, Berkeley, CA.
- 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*. University of Washington Press, Seattle, WA.
- Sutherland, J.P. (1970) Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). *Ecological Monographs*, **40**, 169–188.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Zacherl, D., Gaines, S.D. & Lonhart, S.I. (2003) The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *Journal of Biogeography*, **30**, 913–924.

BIOSKETCH

Sarah Gilman is a postdoctoral researcher in the Department of Biological Sciences at the University of South Carolina, Columbia. Her research focuses on the processes that control species distributions at local and geographical scales, and in interactions between processes at different spatial scales.

Editor: Philip Stott and David Bellwood