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Sarah E. Gilman

Life at the edge: an experimental study of a poleward range boundary

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Abstract Experimental studies of biogeographic processes are important, but rarely attempted because of the logistical challenges of research at large spatial scales. I used a series of large-scale transplant experiments to investigate the mechanisms controlling species abundance near a poleward range boundary. The intertidal limpet *Collisella scabra* experiences a 100-fold decline in abundance over the northernmost 300 km of its range. Temperature and food supply both strongly influenced individual survival, growth, and maturation. Regression analysis also revealed significant interactions among these conditions: the effect of one could not be predicted without knowing the level of the other. But these relationships could not explain geographic abundance patterns. Instead, individual limpets were highly successful at sites with relatively low abundance. These results suggest that, even though temperature is important to the success of individual *C. scabra* populations, the primary effect of warming temperatures under climate change may not be a shift in geographic distribution.

Keywords *Collisella scabra* · *Macclintockia* · Geographic range limit · Temperature · Intertidal

Introduction

Geographic range boundaries are challenging to study because of the inherently large spatial scales involved. Experimental techniques used to study distributions at smaller spatial scales are difficult to implement over hundreds to thousands of kilometers. Biogeographic studies of species range boundaries commonly use a combination of observational data and statistical techniques to associate range boundaries with specific causal factors (Gaston 2003; Parmesan et al. 2005). These studies are often criticized on several grounds, including an over-reliance on untested assumptions, high frequency of spurious associations, and limited mechanistic insight (Hengeveld 1990; Davis et al. 1998; Samways et al. 1999; Lawton 2000; Gaston 2003; Hampe 2004; Parmesan et al. 2005). In particular, a mechanistic understanding of range boundaries is critical for predicting future distributions, such as under climate change or after a species introduction (Samways et al. 1999; Lawton 2000; Gaston 2003; Hampe 2004), and for understanding evolutionary dynamics at range boundaries (Hoffmann and Blows 1994). These fields require integrating experimental and manipulative approaches into biogeographic studies (Samways et al. 1999; Lawton 2000; Hampe 2004; Parmesan et al. 2005). Yet such studies are exceedingly rare and mostly limited to terrestrial plants (Gaston 2003).

Intertidal invertebrates along north–south running coastlines, such as the Pacific coast of North America, are well suited for experimental studies at the geographic scale. Because these species are restricted to narrow bands of habitat along coastal margins, their geographic distributions can be treated as linear (Sagarin and Gaines 2002). Intertidal communities have a long history of use in experimental ecology (e.g., Connell 1961; Paine 1966), and are amenable to experimental research at large spatial scales (e.g., Pennings et al. 2003). Thus, they present a unique opportunity for large-scale experimental studies of range boundaries.

Because temperature is often invoked as a cause of range boundaries for both marine and terrestrial species (Brown and Lomolino 1998; Gaston 2003), many are expected to shift their geographic distributions poleward in response to expected warming under global climate change (Lubchenco et al. 1993; Walther et al. 2002).

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S. E. Gilman
Section of Evolution and Ecology, and, Center for Population Biology, University of California, Davis, CA 95616, USA

Present address: S. E. Gilman (✉)
Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, WA 98250, USA
E-mail: gilmans@u.washington.edu
Tel.: +1-360-3782165
Fax: +1-206-5431273

Temperature changes have been associated with abundance changes for intertidal invertebrates in both the eastern Atlantic (Southward et al. 1995) and eastern Pacific (Barry et al. 1995; Sagarin et al. 1999). Yet, the connection between these mostly local responses and geographic-scale changes in species distributions is often tenuous (Root 1988). In particular, Helmuth et al. (2002) report latitudinal heterogeneity in the body temperature of the intertidal mussel *Mytilus californianus* in the northeastern Pacific. They argue that because higher latitude sites are not always colder, future temperature changes could cause scattered extinctions throughout the species range without a coherent geographic range shift. Missing from these studies is evidence that temperature, or any abiotic stressor likely to change under future climate change, is directly responsible for differences in either local abundance or individual success among populations across a species' distribution. If temperature does not directly control abundance, responses to climate change may be even more complex than anticipated (Davis et al. 1998).

The intertidal limpet "*Collisella*" *scabra* (see Lindberg 1986; S. E. Gilman, in review, for taxonomic issues) is found along the Pacific coast of North America (Fig. 1) from central Baja California, Mexico ($<28°$N; Morris et al. 1980; Lindberg 1981), to approximately the California–Oregon border in the United States ($\sim$42°N, Gilman 2005). In northern California abundance declines from 435 individuals/m^2 at Fort Bragg, California (39.2820°N 123.8030°W) to <3 individuals/m^2 at Brookings, Oregon (42.0420°N 124.2902°W) (Fig. 2a; see also Gilman 2005). Sagarin et al. (1999) identified *C. scabra* as one of 12 species which increased in abundance in Monterey Bay, California, in conjunction with a regional warming in water temperature, and interpreted their observations as evidence of thermally mediated geographic range shifts. Additionally, three other observations suggest that *C. scabra*'s poleward range boundary is controlled by an abiotic factor like temperature. First, poleward range boundaries are generally controlled by abiotic stress (MacArthur 1972; Brown et al. 1996). Second, the gradual decline in abundance near its poleward range boundary (Fig. 2a) is characteristic of a range boundary determined by the organism's physiological tolerance of an abiotic factor (Brown 1984; Caughley et al. 1988; but see Carter and Prince 1981). Finally, no known competitor, predator, parasite, or disease of *C. scabra* appears or increases in abundance along this stretch of the coast (Gilman 2003), suggesting that a species interaction is unlikely to determine the range boundary.

Yet, there are at least two reasons why one should not expect *C. scabra*'s poleward range boundary to be controlled by abiotic stress. First, dispersal limitation is a more common cause of marine range boundaries than physiological limitation (Briggs 1974; Lewis 1986; Gaylord and Gaines 2000). Many marine species are obligate dispersers, and ocean currents control access to habitats. Although patellogastropod larvae have relatively short

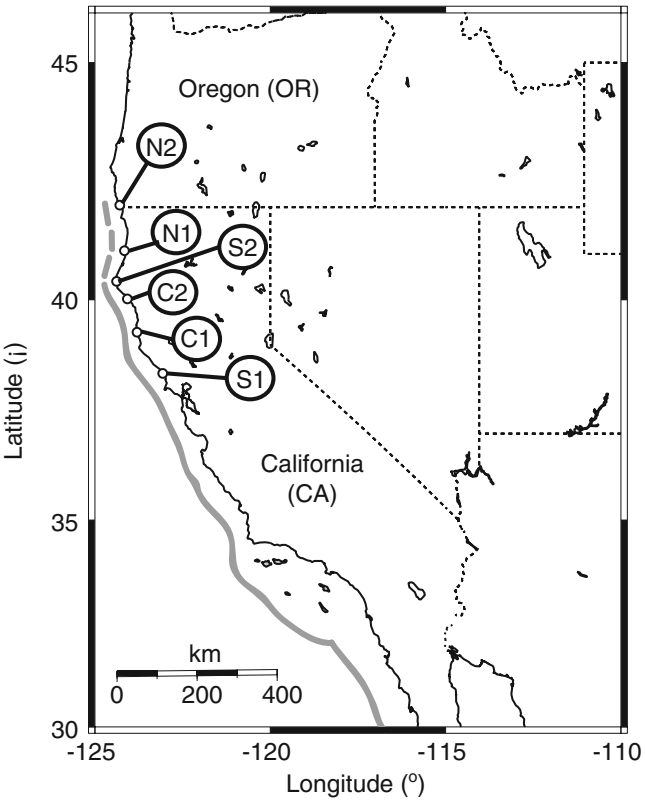

Fig. 1 Known geographic distribution of *Collisella scabra* (*gray line*) and study sites. *Circled numbers* indicate location of source populations [Sonoma Coast State Beach, California (38.3650°N 123.0700°W) (*S1*) and Devil's Gate, California (40.4006°N 124.3819°W) (*S2*)] or transplant destination [Mendocino, California (39.2820°N 123.8030°W) (*C1*); Shelter Cove, California (40.0220°N 124.0737°W) (*C2*); College Cove, California (41.0680°N 124.1543°W) (*N1*); Brookings, Oregon (42.0420°N 124.2902°W) (*N2*)]. *Dashed gray line* indicates region of declining abundance near poleward range boundary

planktonic duration (<14 days; Bowman and Lewis 1986; Strathmann 1987), the decline in *C. scabra*'s abundance between Fort Bragg, California and Brookings, Oregon might reflect an oceanographic dispersal barrier (Gaylord and Gaines 2000). Second, environmental conditions are often heterogeneous at small spatial scales in intertidal systems (Foster 1990; Steele 1991; Helmuth and Hofmann 2001). Climatic differences between sites separated by a few meters may be as extreme as those observed across latitudes (Edney 1953; Helmuth and Hofmann 2001). High levels of local environmental heterogeneity are likely to select for broadly tolerant individuals contrary to that shown by conceptual models of physiological limitation at range boundaries (e.g., Kirkpatrick and Barton 1997).

Here I report the results of a transplant experiment to determine if abiotic conditions limit abundance near the poleward range boundary of *C. scabra*. There are two main objectives to this study. The first is to determine if performance is reduced in northern, low-density sites, relative to more central portions of the range. To test this, I transplanted limpets from two source populations

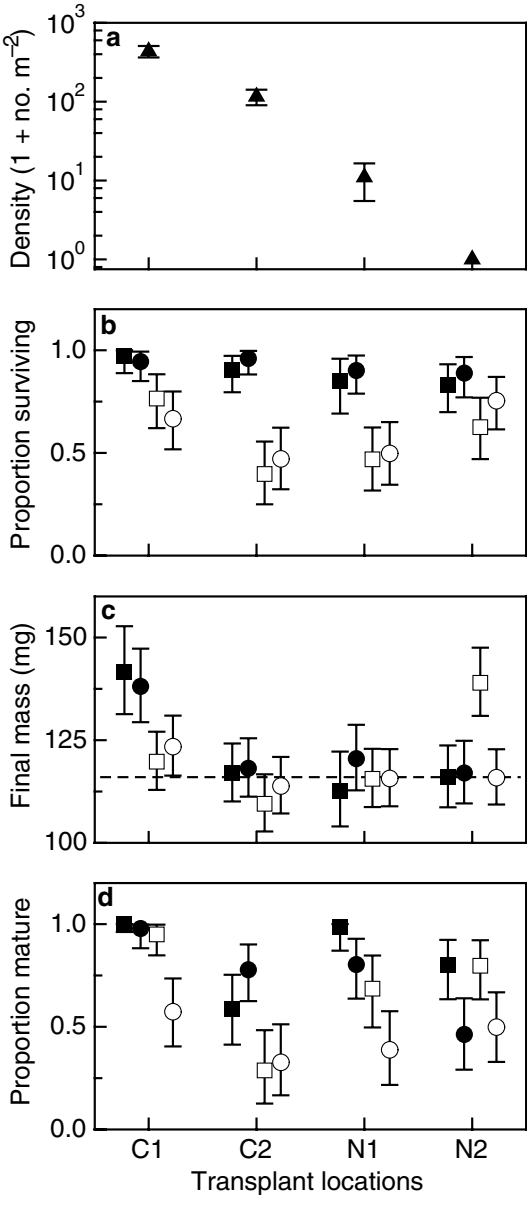

Fig. 2 **a** Density of *C. scabra* by latitude, from Gilman (2005), for the four transplant destinations (C1, C2, N1, N2). The four transplant sites were selected along a continuous gradient of limpet density from low to high latitude (Gilman 2005). See Fig. 1 for study site locations. Performance of limpets transplanted to the four sites (C1, C2, N1, N2): **b** survival, **c** final mass, and **d** maturation [least squared means (LSM) ± SE calculated from models presented in Table 1]. Limpets were transplanted during winter (*filled symbols*) or summer (*open symbols*) from source population S1 (*squares*) or S2 (*circles*). See Fig. 1 for location of source populations. Final mass was calculated for an average initial mass of 116 mg, indicated by the *dashed line*, and for an average density of 5.56 limpets per cage. Data are staggered slight along the *x*-axis in **b**–**d** for clarity

to four locations spanning a 100-fold decline in abundance at *C. scabra*'s poleward margin (Fig. 1). I selected limpets from two source populations to control for the possibility of inter-population differences in physiological tolerances. The second objective tests two alternate hypotheses suggested by Sagarin et al. (1999) and Helmuth et al. (2002), respectively: that cold temperatures limit individual success in northern populations, or that temperature is too spatially heterogeneous to control the range boundary.

Materials and methods

Site descriptions and the geographic range of *C. scabra*

C. scabra is a high intertidal herbivorous gastropod common along much of the Californian coastline. In a detailed survey of the Californian and Oregon coasts (Gilman 2003) I identified a pattern of a 100-fold decline in abundance along 300 km from approximately Fort Bragg (123.803°W, 39.282°N) to the Oregon border (Fig. 2a) centered at approximately Cape Mendocino, California (CPM; 40.450°N, 124.400°W). I have avoided labeling a specific geographic location for *C. scabra*'s range boundary because, as Gaston (2003) notes, literal edges of geographic ranges do not exist. The processes controlling the range boundary should be more evident over this region of declining abundance than at some point farther north occupied by the northernmost individual.

Limpets were collected from two source locations (Fig. 1): Devil's Gate (S2) in Humboldt County, ~5 km south of CPM; and Sonoma Coast State Beach (S1), ~200 km farther south and well inside *C. scabra*'s geographic range. Both sites are semi-protected outer coasts (sensu Ricketts et al. 1985), and consist primarily of small rocky outcrops interspersed with boulders, cobbles, and sand. I transplanted limpets to four sites spaced at ~100-km intervals along the coast, two each at high-density sites inside the species range [Mendocino, California (39.2820°N 123.8030°W) (C1); Shelter Cove, California (40.0220°N 124.0737°W) (C2)] and low-density sites north of CPM [College Cove, California (41.0680°N 124.1543°W) (N1); Brookings, Oregon (42.0420°N 124.2902°W) (N2)] (Fig. 1). The four sites are semi-protected outer coasts, and are similar in wave exposure, slope, and community composition (Gilman 2003).

Transplant design

I conducted four transplant experiments, one each in the winters (approximately October–January) and summers (approximately March–July) of 2000 and 2001. Each experiment lasted 12–14 weeks. For each experiment, I collected approximately 700 limpets by hand from mid-intertidal environments (mainly barnacle and *Pelvetiopsis* beds, ~1.5 m above mean lower low water) from each of the two source populations. Limpets were roughly 50–200 mg at the start of the experiment, corresponding to 1–2 years of age. The lower size limit was set by the diameter of the cage

mesh. The upper limit was set by the size of limpets likely to show measurable growth over the duration of the experiment (Sutherland 1970). I tagged each limpet with a numbered bee tag (Bee Works, Orilla, ON, Canada) and a small dot of paint (TexPen Industrial Marker; ITW Dymon, Olathe , KS) to distinguish the two source populations.

I transplanted limpets to field sites in 15-cmx15-cmx7.5-cm cages, consisting of 0.64-cm Vexar diamond mesh (Norplex Plastics, Seattle, WA), built around an unglazed terra cotta tile, glued to a plywood base. Although cage size may affect growth in some limpet species (Quinn and Keough 1993), such cage effects can be excluded by using a fixed cage size in all experiments. At least 2 weeks before each experiment, I incubated the cages under dripping seawater and natural sunlight (e.g., Lindberg and Pearse 1990). I added the limpets to the cages at least 24 h before transplanting. The total number of limpets assigned to each cage before the start of each experiment varied by experiment, and ranged from eight to 11. Each cage contained limpets from only one of the two source populations.

At each of the four transplant destination sites described earlier, I placed cages at five replicate subsites, separated by at least 0.5 m. The maximum distance between subsites was approximate 10 m. Each subsite consisted of four cages, two each containing limpets from one source population. I located the subsites in the intertidal at the upper vertical limit of macroalgae (usually *Pelvetiopsis* sp.), which is the zone of greatest natural abundance of *C. scabra*.

I censused cages every 2 weeks for at least the first 4 weeks of each experiment and then every 4 weeks thereafter. To maintain limpets at constant densities across all treatments, new limpets were added to each cage at each census interval. These ''replacement'' limpets were not included in survival or growth analyses. Even with the replacements some treatments experienced high mortality that precluded constant density across treatments. I used the census data to estimate an average density per cage: the harmonic mean of the census densities, weighted by the length of the interval between census points. Preliminary analysis indicated that the harmonic mean of the census densities gave a better fit than the arithmetic or geometric mean.

Measures of performance

I used three measures of performance: survival, growth, and maturation. Although these may seem relatively coarse measures of physiological stress, the ability of *C. scabra* to maintain a stable population depends on maintaining high levels of all three measures. Survival was defined as the fraction of limpets within a cage that remained alive for 10 weeks after the first census point. This excluded initial mortality, which may reflect handling stress (Lindberg et al. 1998; S. E. Gilman, personal observation). To quantify individual growth, I measured the mass (to the nearest 0.001 g) of each limpet at the start and end of each experiment. Maturation was the fraction of limpets remaining in each cage at the end of an experiment that showed evidence of a developed gonad upon dissection (Sutherland 1970).

Temperature

A data logger recorded temperatures at 20-min intervals from a single subsite within each destination site (HOBO H8; Onset Computer, Bourne, Mass.). The data logger was housed in a white opaque PVC waterproof case. The daily temperature minima were used to explore potential site differences in cold stress. Because the thermal properties of these loggers differ from a live limpet (e.g., Fitzhenry et al. 2004), the minima should be considered a relative index of temperatures at different sites, rather than measurements of the exact temperatures experienced by *C. scabra* at low tide. Water temperature, which I calculated from temperature logger observations at high tide, is directly comparable with the limpet body temperatures during immersion.

Chlorophyll measurements

C. scabra is a generalist grazer of algal films on rock surfaces (Sutherland 1970; Branch 1981), thus chlorophyll (Chl) concentration on rock substrates is a proxy for food availability (Nicotri 1977). During the winter and summer 2001 transplant experiments, I measured Chl concentration in periphyton samples taken from each subsite. At week 6 in winter 2001 and week 0 in summer 2001, at each of the five subsites within each site, I established a fifth cage that contained 25 replicate 2.54-cmx2.54-cm tile squares. At subsequent census intervals I removed two tiles per cage, in a predetermined order, for Chl quantification. To quantify Chl abundance I used the fluorometric method described in Eaton et al. (1995), with the modifications discussed in Gilman (2003), on a Turner Model AU-10 fluorometer (Turner Designs, Sunnyvale, Calif.).

Statistical analyses

All statistical analyses were performed in the mixed procedure of SAS v6.12 (SAS Institute, Cary, N.C.). Both the survival and maturation data were arcsine square root-transformed to meet the assumptions of normality. I also weighted these fractions by the number of limpets in the sample to reflect the greater confidence in mean responses from larger sample sizes. For multiple comparisons among levels or treatments, all *P*-values were adjusted using the Tukey–Kramer method (Westfall et al. 1999). I used a log-likelihood statistic to test significance of random effects (Littell et al. 1996). Because mortality and cage loss during the experiments

led to an unbalanced design, I used the Satterthwaite option to calculate denominator *df* (Littell et al. 1996). To test for a relationship between performance and transplant destination, I tested for significant differences among source populations, destination sites, and season using ANOVA (survival, maturation) and analysis of covariance (ANCOVA; growth). In the growth model, both initial size and mean density per cage were included as covariates. I also estimated variance components for the size model.

To test the hypotheses relating temperature, Chl, and location, I compared differences among sites in daily minimum and daily water temperature for each of the four experiments using ANCOVA, with the previous day's observation as the covariate to remove autocorrelation of the errors. I calculated least square means (LSM) within each experiment. I similarly tested for significant differences in Chl concentration among sites and between experiments in 2001 using ANCOVA, with sampling date as the covariate. I used variance components analysis to estimate the distribution of variation in Chl concentration among experiments, sites and subsites, and sampling day. I also used the Chl data from 2001 to generate a regression to estimate Chl concentrations for the first two experiments from temperature data [$\ln(\text{Chl}) = \text{sub} + 2.787 \times \text{mean} - 1.113 \times \text{maximum} + 0.086 \times \text{mean} \times \text{maximum}$ ($R^2 = 0.835$, $P = 0.0029$), where sub refers to a separate intercept term for each of the 20 subsites and mean and maximum are daily temperature statistics].

To characterize the relationships between performance, environment, and population I regressed performance against LSM for the emersed and water (immersed) temperatures and against LSM or predicted values for Chl. In fitting the regression models, I used a backward elimination approach, starting with a model that included all possible interactions.

Results

Geographic variation in performance

For all three measures (survival, growth, maturation), performance at the two northern sites by both source populations equaled or exceeded that at the central transplant sites (Fig. 2b–d). In most cases there was little difference in performance among the source populations. Full model results are presented in Table 1.

When pooled across both seasons, limpets transplanted to C1 had significantly higher survival than at C2 or N1 ($P < 0.05$ in both cases), with animals at N2 falling intermediate to the other two groups. This pattern is clearest in the summer transplants (Fig. 2b, open symbols), but after correcting for multiple comparisons, there were no significant differences among sites within either season. Survival was also equivalent for S2 and S1 limpets (62% vs. 60%). Survival was generally higher in the winter experiments than in the summer (Fig. 2b), but comparison across seasons for each site separately (i.e., effect slices) revealed that this difference was only significant at C2 ($F_{1,234} = 8.94$, $P = 0.0030$) and N1 ($F_{1,234} = 4.55$, $P = 0.0339$).

Limpets transplanted to C1 had higher growth, particularly in the winter experiments, than those at nearly all other sites for both source populations across both seasons (Fig. 2c). However, one of the largest increases in mass occurred in S1 limpets transplanted to the N2 site in the summer experiments, which accounts for the significant three-way interaction among source population, transplant, and season in the ANCOVA (Table 1). The variance components analysis revealed that most of the variance in growth occurred at the smallest spatial scales of the experiment. Site effects explained only 4.01% of the variance in size. In contrast, subsite

Table 1 ANOVA of the effects of source population, transplant season, and transplant site on three measures of performance. *n* Total number of observations in the model

	Survival		Growth		Maturation	
	df	*F*	*df*	*F*	*df*	*F*
Source population	1, 222.00	0.84	1, 132.0	0.13	1, 178	9.48**
Season	1, 2.04	4.56	1, 2.4	0.17	1, 2	4.23
Transplant site	3, 227.00	3.49*	3, 65.1	4.25**	3, 17	3.90*
Season×source	1, 222.00	0.05	1, 134.0	1.41	1, 178	0.47
Season×site	3, 227.00	3.09*	3, 64.9	2.85*	3, 178	2.75*
Source×site	3, 223.00	0.95	3, 132.0	2.63	3, 178	2.91*
Season×source×site	3, 223.00	0.05	3, 132.0	2.76*	3, 178	0.35
Starting weight[a]	N/A		1, 683.0	5,304.31***	N/A	
Within cage density[a]	N/A		1, 208.0	13.39**	N/A	
		χ^2		χ^2		χ^2
Year (season) (R)[b]	1	21.511*	1	19.568****	1	2.774*
Subsite (site) (R)[b]	1	4.87****	1	288.536****	1	12.558**
Cage (year, subsite) (R)[b]	N/A		1	240.84****	N/A	
n	252		880		213	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$

[a]Only included as covariates in the growth model

[b]Calculated from the log-likelihood of the model with and without the term, as recommended by Littell et al. (1996)

explained 17.88% and cage explained 30.60% of the variance in growth.

Limpets matured at greater rates at the C1 site across most combinations of source population and season (Fig. 2d), as reflected in the significant site effect in the geographic model. After correcting for multiple comparisons only one pair of sites significantly differed from each other (C1 vs. C2, $P < 0.05$). In nearly all cases, S1 limpets also showed greater overall maturation than S2 limpets, but there was also a significant source by site interaction (Table 1). At the C2 site, S2 limpets had greater maturation than S1 limpets, but not significantly so (56.0% vs. 43.5%; effect slice: $F = 0.892$, $P = 0.346$). More limpets matured in the winter than in the summer experiments, but the pattern was not significant and was reversed at the N2 site.

Environmental differences among study sites

The southernmost transplant site, C1, was consistently the coldest of the four transplant sites (Fig. 3a). C1 had significantly lower minimum daily temperatures in all four experiments ($P < 0.05$). The northernmost site at N2 was often the warmest site during both emersion and immersion. But the pattern is not clinal, as the C2 site was often as warm or warmer than N2. Daily immersion (water) temperatures were much less variable (Fig. 3b). They tended to decrease with latitude in the winter, but increase with latitude in the summer.

For Chl density, the C2 and N1 sites tended to have lower average densities than the other two sites (Fig. 3c), but there was no statistical difference among sites ($F_{3,16} = 2.39$, $P = 0.1073$). This may be explained in part by the large within-site variation in Chl. Subsite effects contributed twice as much to the variance as site effects did (11.74% vs. 4.39%), although the between-season difference (13.51%) was even larger. Overall, Chl concentrations were significantly higher in winter than in summer ($F_{1,36} = 31.81$, $P < 0.0001$).

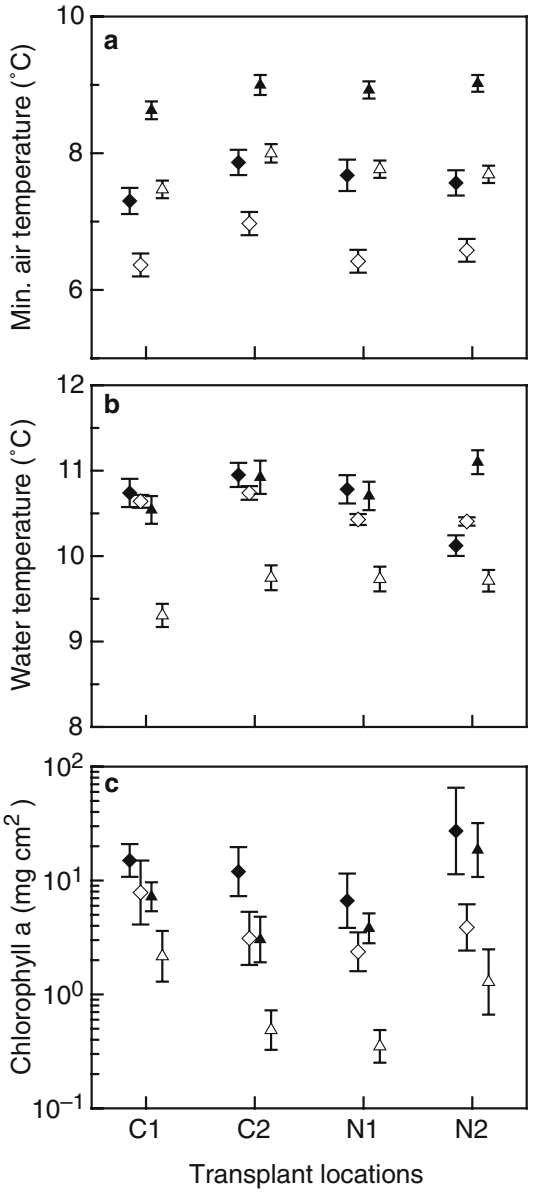

Fig. 3 **a** Daily minimum (*Min.*) air temperature, **b** water temperature, and **c** chlorophyll *a* (Chl) density (LSM ± SE) at the four transplant sites during winter (*filled symbols*) and summer (*open symbols*) of 2000 (*diamonds*) and 2001 (*triangles*). As in Fig. 2b–d, data are staggered slightly along the *x*-axis for clarity. For other abbreviations, see Figs. 1 and 2

Individual performance in response to food and temperature

Environmental conditions were strongly associated with all three measures of performance (Table 2). Both survival and maturation were greatest at colder emersion and water temperatures, although the effects were not always significant. All three measures of performance were also positively associated with Chl density. Each measure of performance also showed unique patterns of significant higher order interactions.

The response of survival to any of the three environmental conditions depended on the values of the other two, as evidenced by the significant three-way interaction in the regression model (Table 2). Survival was generally lowest at warm air temperatures and low Chl, regardless of water temperature; and was highest at cold air temperatures, regardless of water or Chl levels (Fig. 4a). Thus at low Chl, increasing temperatures decreased survival. This association also held at high Chl levels, but only with warmer water temperatures. There was no significant difference between the two source populations.

Limpets only showed positive growth at high Chl levels (Fig. 4b). The effects of temperature on growth were complicated by a significant three-way interaction between source population, emersion temperature, and water temperature (Table 2). S1 limpets showed greatest

Table 2 Results of regression analyses of the effects of source population, air temperature, water temperature, and chlorophyll *a* (*Chl*) density on three measures of performance. *Not estimated* Terms not included in the final model for one of the measures, *N*/*A* not applicable

Term	Survival			Growth			Maturation		
	Estimate	Error	*F*-ratio	Estimate	Error	*F*-ratio	Estimate	Error	*F*-ratio
Source population	1.256	1.347	0.87	0.007	0.011	0.41	−6.144	2.022	9.24**
Air temperature	−15.055	4.811	9.79**	0.006	0.037	0.02	−0.424	7.087	0.00
Water temperature	−3.741	2.662	1.97	0.004	0.019	0.04	−2.117	3.790	0.31
Chl density	16.061	3.492	21.15****	0.169	0.025	44.27****	34.701	5.768	36.24****
Source×air	Not estimated			0.053	0.034	2.41	Not estimated		
Source×water	Not estimated			0.016	0.017	0.91	8.438	3.292	6.55*
Air×water	−6.842	8.422	0.66	−0.014	0.058	0.06	−19.280	12.783	2.28
Air×Chl	26.194	11.819	4.91*	Not estimated			58.452	18.744	9.73
Water×Chl	−1.518	6.094	0.06	Not estimated			19.453	9.043	4.62
Source×air×water	(Not estimated)			−0.132	0.057	5.36 *	Not estimated		
Air×water×Chl	−41.427	17.546	5.57*	Not estimated			−60.137	28.769	4.37*
Starting weight	N/A			0.873	0.012	5308.43 ****	N/A		
Within-cage density	N/A			1.849	0.374	24.42****	N/A		

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$

growth when both water and emersion temperatures were cold, while S2 limpets showed the greatest growth when at least one was warm (Fig. 4b).

Maturation showed complex responses that depended on all three environmental variables, and the source population (Fig. 4c). Maturation was always greatest at high Chl, except at the coldest air and water temperatures, where there was no effect of Chl. At low Chl, maturation decreased with increasing air temperature, regardless of water temperature or source population. The significant interaction between source population and water temperature (Table 2) is evident mainly in the different responses of the two populations when both air and water temperatures were cold: S1 limpets had greater maturation than S2, regardless of Chl.

Discussion

This experiment provides little evidence that physiological tolerance to abiotic conditions is limiting in low-density populations at *C. scabra*'s poleward geographic range boundary. Transplanted limpets showed no consistent pattern of reduced performance at high latitude sites (N1, N2) relative to more central portions of the species' range (C1, C2), in spite of the fact that natural densities at N1 and N2 are 50- to 100-fold lower. This result is consistent with a separate study of natural populations at five sites from C1 to N2 which found that growth and survival of native individuals generally increased with latitude (S. E. Gilman, in review). Surprisingly, given the relatively high performance at high latitude sites, there was a strong negative relationship between temperature and performance.

This study considered temperature as a possible factor limiting adult success because of earlier work by the author and collaborators (Barry et al. 1995; Sagarin et al. 1999) that suggested a relationship between temperature and changes in species distribution of many intertidal invertebrates in California. This study is consistent with the earlier work in that both air and water temperature influenced survival, growth, and maturation. Warmer temperatures, particularly under limiting food conditions, were associated with both higher mortality and lower maturation. This effect was stronger for air than water temperature, as predicted by Helmuth et al. (2002). Although warm temperature limitation is unexpected near a poleward range boundary, it should not be surprising given the importance of desiccation stress in intertidal systems (Sousa 2001). When combined with the observed spatial thermal heterogeneity, this sensitivity to warm temperatures suggests that future temperature changes will change local abundance, but that the changes will be felt unevenly across the species distribution and may reduce populations at many high latitude sites.

Responses to temperature were strongly influenced by food availability, as reflected in the significant associations between Chl and all three measures of performance in the regression models. Most notably, growth only occurred at high levels of Chl. For survival and maturation, air and water temperatures that reduced performance under low Chl conditions were less detrimental under high Chl. Such patterns should be expected for ectotherms, because warmer temperatures should raise metabolic rates, increasing demand for food (Cossins and Bowler 1987; Dahlhoff et al. 2001; Sanford 2002). Thus, the negative effects of warm temperatures are strongest under limited food supplies. In endotherms, a similar interaction occurs at cold temperature stress and is thought to control the poleward range limits of some birds and mammals (Kendleigh 1934; Hersteinsson and Macdonald 1992; Gross and Price 2000; Canterbury 2002). Importantly, these interactions may complicate predictions of species' responses to climate change, particularly if food supply is controlled by factors other than temperature. For example, in inter-

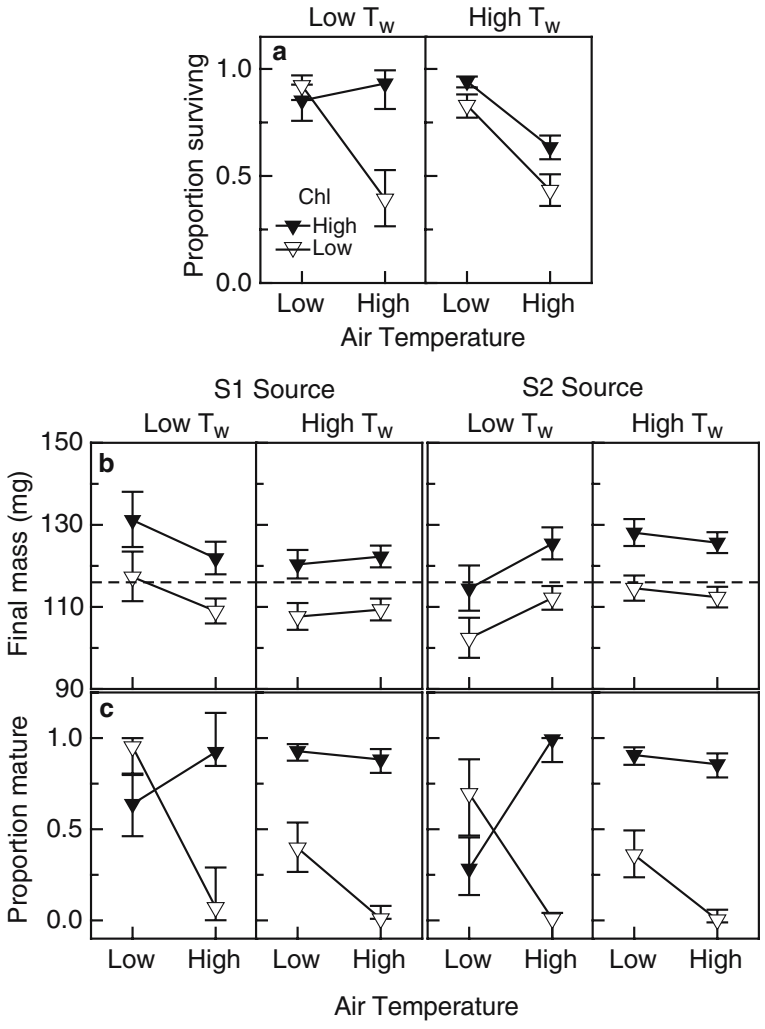

Fig. 4 Effects of environmental conditions (air temperature, water temperature, and chlorophyll *a* (*Chl*) density) on: **a** survival, **b** final mass, and **c** maturation of transplanted limpets from the two source populations (S1, S2). Each point is the LSM ± SE, calculated from models presented in Table 2. Note that the source populations are combined in panel **a**. For air temperature, 25th percentile (*Low*) = 6.96°C and 75th percentile (*High*) = 8.63°C. For water temperature (T_w), Low = 9.75°C and High = 10.74°C. Data points represent Chl density, Low (*open symbols*, 0.399 mg m^{-2}) and High (*closed symbols*, 10.18 mg m^{-2}). The *dashed line* in panel **b** indicates the average initial size, of 116 mg. All growth values were calculated for average density of 6.17 individuals per cage. For other abbreviations, see Figs. 1, 2 and 3

tidal systems, benthic algal growth is negatively correlated with coastal upwelling (Nielsen et al. 2002), which may also be altered under climate change (Bakun 1990; Diffenbaugh et al. 2004).

The conclusion that abiotic conditions do not control the poleward range boundary should be tempered by the relatively short time-period of this study. Incorporating a greater temporal range might have revealed responses consistent with abiotic control of the range boundary, if either the years of this study were somehow atypical of normal abiotic conditions along the California and Oregon coastlines, or if abundance is limited by more extreme abiotic conditions that occur infrequently. The strongest argument against this hypothesis comes from a separate comparison of size frequency distribution in *C. scabra* (Gilman 2005). Limpets at high latitude sites such as N1 and N2 show similar or larger mean sizes than in more central portions of *C. scabra*'s distribution, suggesting that individuals in these populations are experiencing either longer life-spans or faster growth rates, and that these conditions have held over at least the past 10–20 years. Yet there is some evidence that conditions were warmer than normal across much of the western United States, particularly in the two spring experiments (Lawrimore et al. 2001; Waple et al. 2002). By the same measure, temperatures in the winter experiments were normal to slightly below normal. In either case, the absence of a relationship between latitude and temperature still precludes a role for temperature in the range boundary.

A second caveat concerns the spacing of sites and subsites in the experimental design. The subsites sampled a small area (< 10 m^2) relative to the distance between sites (≥100 km). If the chosen sites were somehow atypical of surrounding environmental conditions, these experiments could present an incomplete picture of how performance varies across the northern margin of *C. scabra*'s distribution. Yet this seems highly unlikely given that the natural density and size-frequency of *C. scabra* at each of the four transplant destinations is typical of densities in the surrounding 5–10 km (Gilman 2005).

Rather than adult performance, northern populations may be limited by recruitment. A separate study

revealed significantly lower per capita and per area recruitment into sites north of S2 (S. E. Gilman, in review), suggesting poor success of larval or post-settlement stages. Although abiotic conditions could limit post-settlement survival, this seems unlikely given the spatial patterns of adult performance observed in this study. More likely, larval dispersal or survival is limited, either because of a dispersal barrier (Gaylord and Gaines 2000) or because of an increase in distance between suitable habitats at the range boundary (Carter and Prince 1981; see also S. E. Gilman, in review).

Climate change is frequently predicted to cause poleward range extensions in a variety of organisms. In the case of *C. scabra*, although temperature strongly influenced local success, a poleward range extension is highly unlikely. Accurately predicting range shifts under climate change requires a mechanistic understanding of the processes driving geographic distributions. Large-scale manipulations, such as this one, must become more common if we are to fully understand biogeographic processes and the potential impacts of climate change.

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