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The effects of temperature on producers, consumers, and plant–herbivore interactions in an intertidal community

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Abstract

Although global warming is acknowledged as a primary threat to populations and communities, the impact of rising temperature on community structure remains poorly understood. In this study, we investigated the direct and indirect effects of temperature on epilithic primary producers (micro- and macroalgae) and an abundant consumer, the rough limpet *Lottia scabra*, in the rocky intertidal zone in central and northern California, USA. We factorially manipulated temperature and limpet abundance in the field to determine the effects of temperature on herbivore growth and mortality, algal abundance, and the strength of plant–herbivore interactions. Microalgal growth was positively affected by shading at both locations, and negatively affected by limpet grazing at Pacific Grove but not at Bodega Bay. Macroalgae were only abundant at Bodega Bay, where changes in abundance were negatively related to grazing and independent of temperature. Despite temperature-related changes in microalgal food supply, there were no direct or indirect effects of temperature manipulation on *L. scabra* growth or mortality. Furthermore, temperature did not alter the importance of herbivory at either site. These results indicate that the influence of increasing temperature, as is predicted with climate change, will have differential effects on producers and consumers. However, thermal effects at one trophic level do not necessarily propagate through the food web to other trophic levels.

Keywords: Herbivory; *Lottia* (Collisella) *scabra*; Macroalgae; Microalgae; Thermal stress; Top-down vs. bottom-up effects

1. Introduction

It has been widely recognized that global temperatures are rising (IPCC, 2001). It is predicted that by the 2050s, average air temperatures relevant to rocky coastal platforms may be up to 2.1 °C higher than at present (Hiscock et al., 2004; IPCC, 2001). Sea surface temperatures may be up to 2.5 °C higher than in 2000 (Hiscock et al., 2004). However, because the ecological impacts of climate change can depend on interactions among species (e.g. Sanford, 1999), the ecological consequences of climatic warming are still largely unclear. In marine systems, one major challenge lies in understanding how interactions among species will ameliorate or enhance the effects of temperature change (Harley et al., 2006).

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Rocky intertidal environments are extremely physiologically stressful habitats; temperatures can fluctuate swiftly and can reach lethal extremes during low tide (Hiscock et al., 2004; Helmuth and Hofmann, 2001). Because many intertidal organisms already live very close to their thermal tolerance limits (Somero, 2002), temperature has an important and pervasive influence on the distribution and abundance of organisms via its effects on physiological processes (Dahlhoff et al., 2001; Somero, 2002). Organisms living in the rocky intertidal zone are therefore considered to be good indicators of climate change impacts (Helmuth and Hofmann, 2001; Helmuth et al., 2002). Predicting ecological responses to climate change, however, requires information on how abiotic changes are mediated by interspecific interactions. For example, thermal conditions influence the importance of biological interactions such as predation, competition, and facilitation (Sanford, 1999; Leonard, 2000). To date, studies which simultaneously manipulate abiotic and biological variables remain rare.

Biological communities are structured by both top-down and bottom-up processes (e.g., Nielsen, 2001), and temperature may influence both of these processes (Thompson et al., 2004). For example, the abundance of intertidal microflora depends on herbivory, local variation in light and temperature, and seasonal changes in environmental conditions (Nicotri, 1977; Cubit, 1984). Specifically, environmental conditions during the winter are sufficiently benign to allow microalgal production to outpace consumption (Cubit, 1984). Temperature is also known to affect macroalgae (e.g., Allison, 2004; Keser et al., 2005), and the combined influence of temperature and herbivory can determine the distribution and abundance of macroalgae via disproportionately strong impacts on that trophic level (Harley, 2003). Taken together, these results suggest that rising temperatures and associated physiological stress can decrease primary and secondary production and alter the relative importance of herbivory.

In this study we simultaneously investigated the effects of temperature and an abundant consumer, the rough limpet *Lottia scabra* (Gould) (formerly *Collisella scabra* and *Macclintockia scabra*; see Gilman, 2007 for the most recent treatment of the taxonomy of this species) on community dynamics in the rocky intertidal zone in California, USA. Temperature was manipulated with experimental shades. Limpet enclosures and exclosures were used to investigate the effect of limpets on their algal food source in different temperature treatments (shaded and non-shaded treatments). The main focus of this research was to determine the effect of thermal stress on high-intertidal micro- and macroalgae, grazing limpets, and plant–herbivore interactions. We hypothesized that increased thermal stress would reduce limpet growth and increase limpet mortality. We further hypothesized that thermal stress would reduce microalgal biomass, but that this reduction would be partially or fully offset by reduced grazing rates.

2. Materials and methods

2.1. Study sites and organisms

Experiments were conducted during the spring and summer of 2005 at two different locations along the coast of California, USA (Fig. 1): the Bodega Marine Laboratory in Bodega Bay (38° 20′N, 123° 4′W), and the Hopkins Marine Station in Pacific Grove (36° 37′N, 121° 54′W). The Californian rocky intertidal zone is ideal for addressing questions regarding thermal stress and species interactions. Air temperatures are expected to rise in California, but sea surface temperatures may not, due to steady or enhanced upwelling (see Bakun, 1990). Therefore, examination of thermal stress at low tide is realistic in terms of expected future changes in the environment.

The intertidal substratum at both study sites is granite, and both locations are wave exposed, although some sites at each location are protected to varying degrees by the peculiarities of the topography. The tides in the region are mixed semi-diurnal, with two unequal high and two unequal low tides each day. During March, April, and May, lower low tides occur during the middle of the day and may be associated with high thermal stress for intertidal organisms at both locations (Sutherland, 1970; Helmuth et al., 2002). From June through September, the lower low tides shift to the early morning hours, reducing the likelihood of thermal stress during low tide. In addition, coastal fog is common during the summer months, further ameliorating thermal stress. However, occasional calm, sunny days may result in physiological stress at either location at any time during the spring and summer (e.g., Wolcott, 1973). Mean daily maximum air temperatures during the spring and summer typically range from 16 to 21 °C at the Bodega Marine Laboratory (Wolcott, 1973; Bodega Ocean Observing Node dataset), and from 20 to 24 °C at the Hopkins Marine Station (M. Denny; unpublished data).

Bodega Bay has a fairly high biodiversity in the high rocky intertidal. Mobile gastropods are abundant, and include limpets (mainly *L. scabra* and *L. digitalis*), littorine snails (predominantly *Littorina plena*, but also *Littorina keenae* and *L. scutulata*) and black turban

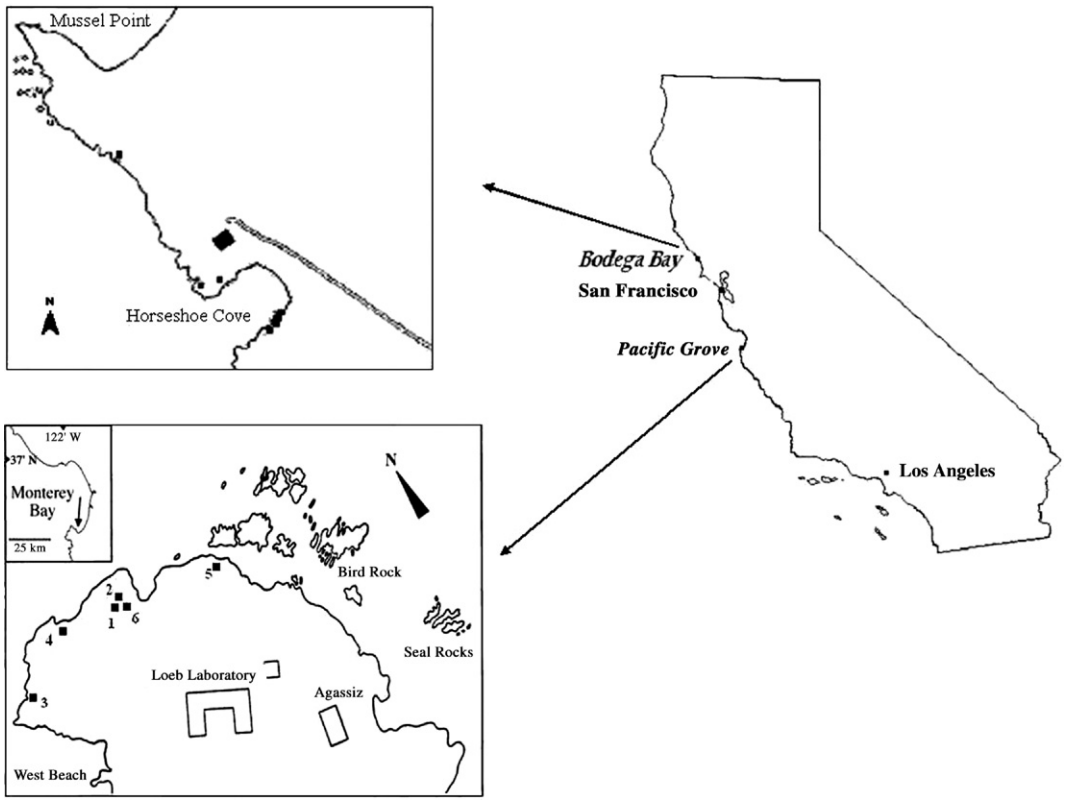

Fig. 1. Map of California with the locations of the two research sites: Bodega Bay and Pacific Grove. The top-left inserted map shows the Bodega Bay research site at the Bodega Marine Reserve, with the locations of the 8 experimental sites. The research site in Pacific Grove, at the Hopkins Marine Station, Stanford University, is shown in the bottom left insertion (adjusted map from Sagarin et al., 1999), along with the locations of the 6 experimental sites.

snails (*Tegula funebralis*). There is also a diverse macroalgal assemblage featuring *Porphyra perforata*, *Mastocarpus papillatus*, *Endocladia muricata*, and *Pelvetiopsis limitata* as the most abundant species. *L. scabra* is also abundant in high-intertidal communities in Pacific Grove. However, Pacific Grove differs from Bodega Bay in that it has a higher abundance of the owl limpet *Lottia gigantea* in the high-intertidal zone and a much greater abundance of *L. keenae* in the splash zone. Unlike Bodega Bay, there is very little macroalgae in areas occupied by *L. scabra* in Pacific Grove.

In this study, we focused on the impacts of temperature on communities dominated by the limpet *L. scabra*. *L. scabra* occupies shore levels from the mid-intertidal zone to the splash zone (Sutherland, 1972; Haven, 1973; Sept, 2002). Larger (adult) animals are most abundant in or just above the uppermost zone of macroalgae on rocky shores (Sutherland, 1972; Gilman, 2005). The snail shows homing behavior, returning to its home scar nearly every low tide (Jessee, 1968; Connor and Quinn, 1984; Sommer, 1982). *L. scabra* is a generalist grazer, feeding on epilithic microalgal film (Sutherland, 1970; Branch, 1981). *L. scabra* populations are known to be vulnerable to thermal stress: a mass mortality event was observed at Bodega Bay in the spring of 1967 when consecutive hot days coincided with late morning low tides (Sutherland, 1970). Another thermally-mediated mortality event reduced *L. scabra* populations at Bodega Bay in the spring of 2004 (Harley, unpubl. data). This encouraged us to investigate the possible effects of thermal stress on this abundant consumer with regard to potential future climate change.

2.2. Field experiments

At Bodega Bay, experiments were initiated in March, 2005. A total of eight experimental sites were selected in areas where *L. scabra* were abundant. Six of the sites were situated within a south-west facing cove, with five sites on the south side and one site on the north side. The remaining two sites were on fully exposed, south-west

facing benches (Fig. 1; top left insertion). Selection of sites ensured within-site similarity of substratum orientation and limpet abundance, yet allowed for among-site differences in substratum orientation. The intertidal height of the selected sites varied from 1.92 m to 2.70 m (mean ± standard deviation: 2.21 m ± 0.26 m) above Mean Lower Low Water. Plots within sites were within 39 vertical cm of one another. Experiments in Pacific Grove were initiated in April, 2005. At that location only six sites were established. Again, sites were selected for high *L. scabra* abundance and consistent within-site substrate orientation. The sites at Pacific Grove ranged from 1.78 m to 3.08 m (2.43 ± 0.52) above MLLW. Plots within sites were within 27 vertical cm of one another.

At each site within each of the two locations, six 15 × 15 cm plots were selected. This plot size was chosen according to the limpets' foraging behavior, which is generally confined to within 10 cm of individual home scars (Sutherland, 1970). In four of those plots, cages (15 × 15 cm, 3 cm tall; constructed out of 6 × 6 mm stainless steel wire mesh) were placed by drilling holes into the rocky substratum, and using wall anchors, stainless steel washers, and screw bolts to attach the cage to the rock. Two of the plots were left without caging, but were marked 15 × 15 cm with screw bolts or Z-spar Epoxy Putty (A-788 Splash Zone Compound; Z-spar Los Angeles, CA, USA) and used as controls. Z-spar Epoxy Putty was also used to close off the corners of cages when they could not be attached tightly to the rock by the bolts.

The plots at every site were assigned to two different temperature treatments: two caged plots and one open plot received no shading, the other two caged plots and open plot were shaded. The shades were made of heavy-duty Vexar™ mesh (opening size 6 × 6 mm) strapped to a PVC-coated galvanized steel welded cloth (opening size 25 × 25 mm) with cable ties. The shades were attached to the rock by means of stainless steel screw eyes anchored into the rock with wall anchors and cable ties. Shades were open on two sides, and the "roof" was ~ 7 cm above the substratum. To minimize the hydrodynamic influences, shades were placed in such way that the waves surged parallel to the shade's two walls (i.e. water surged directly through the open sides rather than through the walled sides, see Harley, 2002). Similar shades reduced light levels by 60–65%, depending on ambient conditions (Harley, 2002). Our experiments were conducted in spring and summer when irradiance was expected to be high enough to prevent light limitation (see, e.g., Rasmussen et al., 1983). Procedural controls for shading (e.g. wire mesh lacking vexar) were not attempted because mesh cages and other "shade controls" can also have a considerable effect on substrate temperature (Hayworth and Quinn, 1990; Harley and Lopez, 2003).

We placed iButton® temperature loggers (Dallas Semiconductor, Dallas, Texas, USA) next to every shaded and non-shaded fenceless control plot (i.e. a total of two loggers per block) to keep the record of the rock temperature (shaded or non-shaded) over time. Loggers were placed immediately adjacent to the plots, such that they did not interfere with the experimental area yet were still covered by the shade structure in shaded plots. To be able to place them, we chiseled off enough rock to create a small depression and used Epoxy putty (Sea Goin' Poxy Putty, Heavy Duty; Permalite Plastics Corporation, Costa Mesa, California, USA) to both attach and completely cover the loggers. The temperature loggers were wrapped in parafilm before insertion into the epoxy putty for protection and easier removal of the loggers at the end of the experiment. To mimic the surface albedo of the surrounding rock, fine dark beach sand was pressed into the setting epoxy (Harley and Helmuth, 2003). The body temperature of a limpet is very similar to the temperature of the rock upon which it sits; the latter is thus an excellent proxy for the former (Wolcott, 1973; Denny and Harley, 2006). The iButtons recorded temperature at 60-minute intervals from the end of March through the end of July 2005 at Bodega Bay and from the end of April through the end of July at Pacific Grove.

At every site, limpet exclusion treatments were assigned to two of the caged plots (a shaded and a non-shaded plot, randomly chosen), which were then cleared of limpets and other grazers. In the remaining plots, there were an average of 9.7 ± 0.8 (mean ± standard error) *L. scabra* per plot at Bodega Bay (excluding site #7; see below), and 11.6 ± 0.8 *L. scabra* per plot at Pacific Grove. Initial limpet densities did not vary among treatments ($p > 0.3$ in all cases). All the limpets in the non-exclusion plots were tagged (only at Bodega Bay), using small numbered adhesive tags and glue (Super Glue, liquid; Loctite, Dist. By Henkel Consumer Adhesives, Inc., Avon, Ohio, USA) for identification purposes, and their shell size was measured with a pair of dividers, the gape of which was measured with digital calipers. This was done at the start and at the end of the experiment to determine individual growth over the four-month period. Other grazers (if present) were removed from the plots, except from the "open" control plots.

Microalgal biomass in the plots was estimated by measuring benthic chlorophyll *a*. Preliminary analyses

indicated that rock chips were a poor proxy for benthic chlorophyll because the rock tended to crumble and it was difficult to measure the true surface area of a sample. Therefore, we used 1 × 1 cm ceramic tiles (Mosaic Basics, Atlanta, GA), which eliminated any a priori spatial variation in benthic chlorophyll and provided an easily quantified surface for microalgal growth. Two replicate tiles were placed in the center of every plot with the unglazed side facing up. The unglazed surface was roughened with coarse sand-paper prior to deployment to better mimic the rock surface and create more favorable conditions for microalgal settlement. The tiles were attached to the rocky substrate using Sea Goin' Poxy Putty (Heavy duty), to estimate microalgal biomass/development inside the plots. Sea Goin' Poxy Putty is nontoxic after it has set and is readily colonized by invertebrates and algae (Harley, 2002). At the end of the experiment the tiles were removed and taken back to the laboratory to determine the chlorophyll *a* content on the tiles. Every tile was put into an individual test tube with 10 mL 90% HPLC acetone. All samples were then vortexed and stored in the freezer (−4 °C) in the dark for 24 h. After this (passive) extraction time, samples were vortexed again and centrifuged for 5 min (6000 rpm) and then measured by means of a fluorometer (TD-700, Tuner Designs) using the method of Welschmeyer (1994). The two measurements from every plot were averaged to obtain a single estimate of chlorophyll *a* per plot.

Digital photos were taken of all the plots at the start and end of the experiment to determine changes in grazing activity/algal abundance, behavioral changes (change of home scars, migration), mortality, and recruitment, besides observations in the field. In Bodega Bay, additional photos were taken at the mid-way point of the experiment. At the end of the experiment, limpet lengths were measured again to determine growth over the four-month period. Time limitations prevented us from tagging limpets in Pacific Grove; hence, limpet growth was not measured at that site. Limpet mortality/absence and limpet recruitment were also recorded. Macroalgal percentage cover was determined in the field and from photos at the start, middle and end of the experiment in Bodega Bay, and at the start and end of the experiment in Pacific Grove. Because macroalgal species composition was highly variable among blocks, analyses of individual macroalgal species were uninformative due to limited power. Therefore, we present analyses of total macroalgal cover.

2.3. Statistics

Data were analyzed using JMP 5.1 (SAS institute). Prior to statistical analysis, chlorophyll *a* data were log transformed and proportional limpet mortality data were arcsine square-root transformed to meet the assumption of normality. Site number 7 at Bodega Bay was not included in limpet growth and survival analyses because this site contained only small individuals which were impossible to tag individually. To determine macroalgal responses to experimental treatments, we used change in percent cover as a response metric. The raw data conformed to the assumptions of an ANOVA during the second half of the experiment (May–July), but not during the first half. No transformation was able to remedy this problem. Thus, macroalgal results (based on untransformed data) from April–late May should be interpreted with caution.

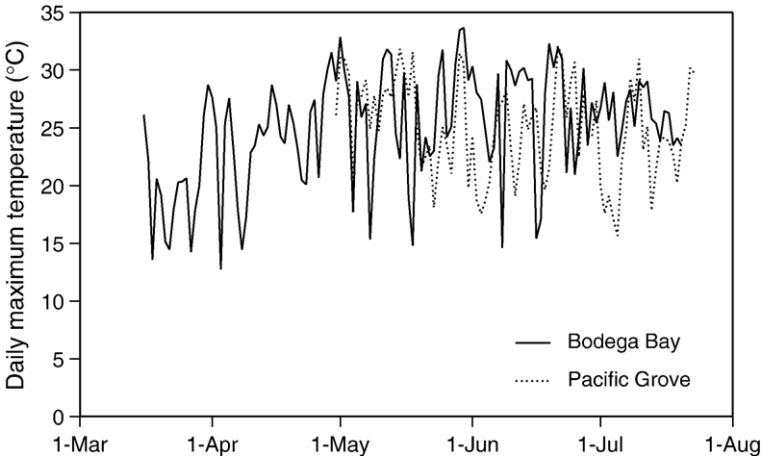

Fig. 2. A: Daily maximum rock temperature in the non-shaded treatments at Bodega Bay (mean of eight loggers) and Pacific Grove (mean of five loggers) during spring/summer 2005.

3. Results

3.1. Temperature

The spring and summer of 2005 had no distinct heat waves or extremely hot days (Fig. 2). Instead, it was foggy for most of the experimental period. Owing to temperature logger failures at Pacific Grove, only four shaded and five non-shaded thermal time series were usable.

To investigate location and shade effects on substratum temperature, we collapsed the time series for each temperature logger into an average daily maximum value (literally the mean of all daily maxima within a given thermal time series) and performed statistical analyses on those metadata. During the time that loggers were deployed at both sites (30 April–21 July, 2005), the effect of shading on average daily maximum temperatures was highly significant (2-way ANOVA, shade effect $F_{1,21}=30.1$, $p < 0.001$), with shaded plots remaining several degrees cooler than unshaded plots (Fig. 3). The effect of location (Bodega Bay vs. Pacific Grove), and the shading × location interaction, had no significant effect on substratum temperature (2-way ANOVA, location effect $F_{1,21}=0.01$, $p=0.942$; shading × location interaction $F_{1,21}=2.52$, $p=0.127$). Although the interaction term was not significant, shades at Bodega Bay lowered rock temperatures slightly more

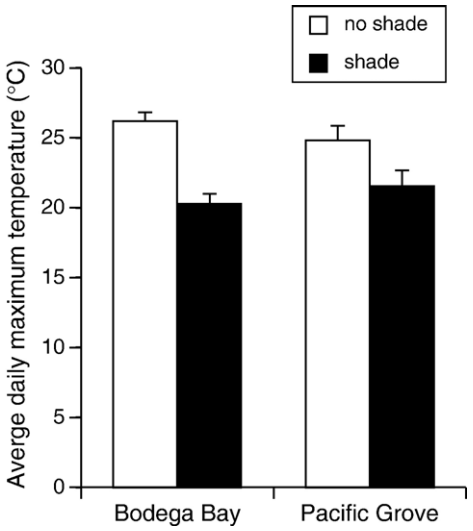

Fig. 3. Average daily maximum rock temperature over the course of the experiment. Daily maximum temperature data were averaged within each time series, and means and standard errors were generated using these averages ($N=8$ time series for Bodega Bay shaded and unshaded, $N=4$ for Pacific Grove unshaded, and $N=5$ for Pacific Grove shaded). See text for statistical analyses.

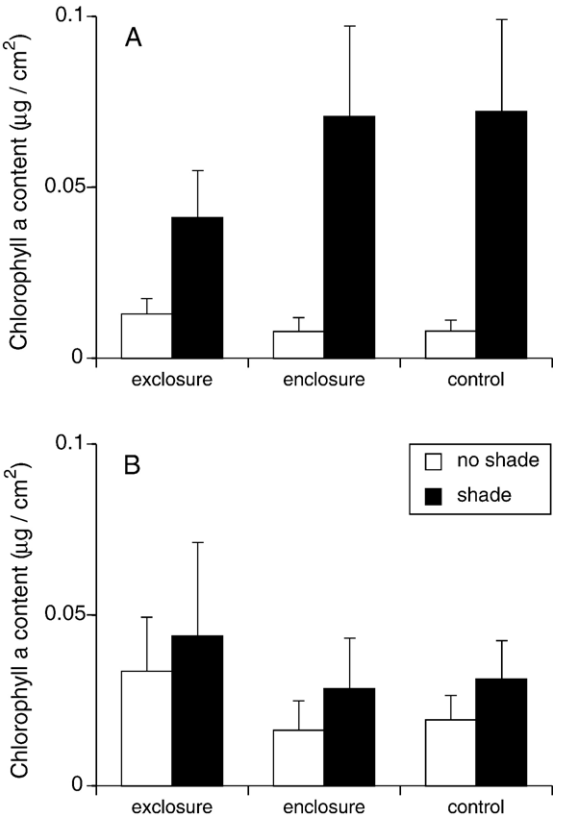

Fig. 4. The chlorophyll *a* content on tiles in the experimental plots at (A) Bodega Bay and (B) Pacific Grove. The effect of shading is significant at both locations, and the effect of limpet grazing is significant at Pacific Grove. Note that the significant main effects at Pacific Grove are obscured in this graph by the highly significant block effect (see Table 1 for details). Enclosure with limpets, no other grazers; Exclosure without any grazers; Control: open plots, with limpets and possibly other grazers (not fenced). Error bars are standard errors.

than at Pacific Grove (~ 5.9 °C vs. ~ 3.3 °C, respectively). By comparison, Harley and Lopez (2003) showed a difference of 4 °C in earlier research with a similar shade design.

3.2. Chlorophyll a

In Bodega Bay, there was a strong effect of shading on chlorophyll *a* content (Fig. 4, Table 1); shaded plots had a higher chlorophyll *a* content than non-shaded plots. Neither limpets nor the limpet × shading interaction had any effect on the chlorophyll *a* content on the substratum (Table 1). In Pacific Grove, by contrast, there were effects of limpets, shading, and block (site) on benthic chlorophyll *a* (Fig. 4, Table 1). In experimental plots in which limpets were present, the chlorophyll *a* content on the ceramic tiles was lower than in plots in

Table 1
Results of two-factor ANOVA (shade and limpet presence) on chlorophyll *a* content at Bodega Bay and Pacific Grove

Effect	Bodega Bay			Pacific Grove		
	df	*F*	*p*	*df*	*F*	*p*
Shade	1	54.6	**<0.001**	1	9.86	**0.004**
Limpets	2	0.01	0.991	2	6.31	**0.006**
Shade × limpets	2	1.92	0.161	2	0.39	0.684
Block	7	1.89	0.102	5	27.0	**<0.001**
Error	35			25		

Significant effects ($p<0.05$) in boldface type.

which limpets were excluded. Furthermore, as we observed in Bodega Bay, the shaded plots in Pacific Grove contained more chlorophyll *a* than the non-shaded plots. Finally, the strong block effect indicates that the location and orientation of the experimental sites influenced the chlorophyll content in the plots.

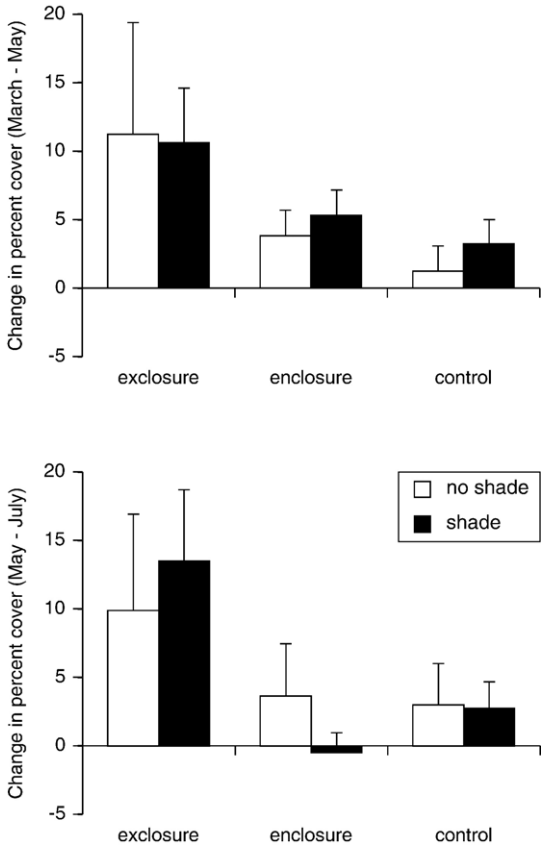

Fig. 5. Change in macroalgal percent cover at Bodega Bay during the first and second halves of the experiment (April–May and May–July, respectively). Labels as in Fig. 4. Error bars are standard errors. See Table 2 for statistical analyses.

3.3. Macroalgal cover

The cover of macroalgal species in Bodega Bay was low and variable among plots (means ± standard deviation during the May sampling: *Porphyra* sp. 5.1 ± 10.2, *M. papillatus* 3.9 ± 5.3, *P. limitata* 1.1 ± 2.9, all others < 1% cover). Therefore, macroalgal cover was analyzed in aggregate. Macroalgal percent cover generally increased over the course of the experiment, particularly in the limpet exclusion plots (Fig. 5). During the first half of the experiment, the increase of macroalgal cover was weakly but significantly related to limpet abundance, with larger macroalgal increases in limpet exclosures. There was no significant effect of shading or of the limpet × shade interaction (Table 2). However, because the assumption of normality could not be met during this time period, these results must be interpreted cautiously. During the second half of the experiment in Bodega Bay, increases in macroalgal cover continued to be highest in limpet exclosures, and the limpet effect was again significant (Table 2) despite the loss of macroalgal data from half of the unshaded inclusion and exclusion plots due to a procedural error. The blocking factor (site) was also significant at both sampling dates. Macroalgae were extremely rare in experimental plots in Pacific Grove, precluding formal analyses.

In Bodega Bay, we found no relationship (facilitation or inhibition) between microalgal chlorophyll (log transformed) at the end of the experiment and macroalgal cover in May (linear regression: $F_{1,46}=1.71$; $p=0.198$) or macroalgal cover at the end of the experiment (linear regression: $F_{1,38}=3.13$; $p=0.085$; note the loss of 8 plots). Furthermore, macroalgal cover at either time point was not a significant covariate when

Table 2
Results two-factor ANOVA (shade and limpet presence) on changes in macroalgal percent cover during the first and second halves of the experiment at Bodega Bay

Effect	Cover change (April–May)			Cover change (May–July)		
	df	*F*	*p*	*df*	*F*	*p*
Shade	1	0.12	0.733	1	0.01	0.932
Limpets	2	3.48	**0.042**	2	4.88	**0.023**
Shade × limpets	2	0.08	0.920	2	0.60	0.559
Block	7	3.18	**0.010**	3	3.45	**0.044**
Error	35			15		

Significant effects ($p<0.05$) in boldface type. Note that the assumption of normality was violated in the April–May interval; thus, the results from that time period should be interpreted with caution. Data from four blocks were lost during the May–July time period; thus, the statistical analysis was conducted on the remaining four blocks.

Table 3
Results of two-factor ANCOVA on limpet growth at Bodega Bay

Effect	*df*	*F*	*p*
Shade	1	0.0093	0.9240
Fence	1	4.2307	0.0517
Shade × fence	1	1.2093	0.2834
Intertidal height	1	7.7644	**0.0108**
Average initial limpet length	1	6.8946	**0.0154**
Error	22		

The "fence" effect refers to fenced vs. unfenced (control) plots. Intertidal height and average initial limpet length are treated as covariates in the analysis. Significant effects ($p<0.05$) in boldface type.

included in an exploratory, full factorial analysis of chlorophyll *a* ($p > 0.05$, full results not shown).

3.4. Limpet mortality

The total number of limpets in experimental plots in Bodega Bay at the start of the experiment was 208 (roughly 7.4 per non-exclusion plot in the seven blocks where limpet abundance was tracked). At the end of the experiment this number had decreased by 14.9% to 177. In Pacific Grove, the total number of limpets at the start of the experiment was 279 (roughly 11.6 per non-exclusion plot). At the end 242 limpets were still present (a 13.3% decrease). Because we cannot distinguish mortality from emigration at Pacific Grove (where limpets were not individually tagged), we restrict our analysis of limpet mortality to fenced enclosure plots. There was no effect of shading on limpet mortality at either site. At Bodega Bay, percentage limpet mortality under shades (mean ± standard error of raw data: 20.9 ± 6.6) was statistically similar to mortality in unshaded plots (9.6 ± 4.7) (blocked ANOVA, shade effect $F=1.72$, $p=0.238$). At Pacific Grove, percentage mortality in shaded and unshaded plots (9.5 ± 4.5 and 4.8 ± 2.2, respectively) was also statistically indistinguishable (blocked ANOVA, shade effect $F=0.47$, $p=0.524$).

In case a shading effect was obscured by among-site variation in temperature, we examined the direct effect of temperature on limpet mortality. Rock temperature (in the adjacent unfenced plots) had no effect on limpet mortality in limpet inclusion plots at Bodega Bay (linear regression, $N=14$, $F=0.36$, $p=0.562$) or Pacific Grove (linear regression, $N=9$, $F=0.81$, $p=0.258$).

3.5. Limpet growth

Both the intertidal height ($F_{1,25}=7.8386$; $R^2_{adj.}=0.388$; $p=0.0097$) and the initial length of the limpets ($F_{1,25}=7.0605$; $R^2_{adj.}=0.388$; $p=0.0135$) influenced average growth of the limpets in each plot. Small limpets grew significantly faster than larger conspecifics, and those found lower on the shore grew faster than those found higher on the shore. When we included 'Intertidal Height' and 'Average Initial Limpet Length' as covariates, we found that both influenced limpet growth, even after accounting for shading, limpet manipulation (fenced enclosures vs. unfenced controls), and the interaction term (Table 3). None of the latter variables were significant (Table 3). There was also no direct relationship between substratum temperature and limpet growth, even after accounting for initial limpet length ($p > 0.8$).

To further investigate potential bottom-up effects on limpet growth at Bodega Bay, we compared limpet growth in enclosures to benthic chlorophyll in exclosures. There was no significant relationship between the two variables (ANCOVA, shade effect $F=0.13$, $p=0.728$; chlorophyll effect $F=1.22$, $p=0.293$). When the non-significant shade term was dropped from the analysis, there was still no relationship between benthic chlorophyll and limpet growth (linear regression, $N=14$, $F=2.79$, $p=0.121$). Similar analyses between limpet growth and macroalgal productivity (i.e. change in macroalgal cover from April through late May) were also non-significant ($p > 0.1$ in all cases).

4. Discussion

Intertidal environments often feature sharp thermal gradients and experience extreme temperature variation, by which organism distribution and abundance can be greatly affected (Newell, 1979). Temperature is also known to influence the rates of per capita interactions in the intertidal (Sanford, 1999). As a result of its impacts on abundance and per capita interaction strength, temperature plays a major role in structuring intertidal communities (Sanford, 1999; Harley, 2003; Harley and Lopez, 2003; Schiel et al., 2004).

Our experiments were designed to interpret the effects of thermal stress on high-intertidal microalgae, grazing limpets, and plant–herbivore interactions. We hypothesized that increased thermal stress would directly affect limpet feeding rates, growth, and mortality, and both directly and indirectly affect microalgal biomass. Unfortunately, the spring and summer of 2005 did not feature any notable thermal stress events along the Central and Northern California coastline. Instead, upwelling-related fog prevailed during this period. Despite the moderate thermal conditions, our manipulations did create thermal differences between treatments, and our results indicate that temperature is an important factor in our study system.

4.1. Temperature and bottom-up effects

Both macroalgae and microalgae are susceptible to thermal stress (Matta and Chapman, 1995; Blanchard et al. 1997). Although we found no evidence of thermal effects on macroalgae, there were distinct differences among shading treatments in terms of microalgal chlorophyll. Benthic microalgal production is strongly influenced by temperature (Grant, 1986; Migné et al., 2004). In general, benthic microalgal photosynthetic rates increase with temperature to an optimum between 15 °C and 30 °C, depending on the study (Rasmussen et al., 1983; Blanchard et al., 1997). Above this optimum, photosynthetic rates decrease (Rasmussen et al., 1983; Blanchard et al., 1997). In our experiment, shaded, and thus cooler, treatments contained higher microalgal chlorophyll than the non-shaded plots at both experimental locations, suggesting that temperatures in unshaded plots (which regularly exceeded 30 °C) were higher than optimal for microalgal production. If this trend holds true for future climatic regimes, this could lead to a suppression of microalgal production as temperatures rise. Epilithic biofilms play a key role in marine ecosystems, and they represent the main fraction of biomass produced and directly consumed *in situ* on exposed rocky shores (Thompson et al., 2004). Thus, a reduction in the microalgal food supply could have profound effects on intertidal community structure via limitation of herbivore density or growth (e.g. Harley, 2002; Thompson et al., 2004).

Contrary to our expectations, *L. scabra* growth in our experiment was not correlated with epibenthic chlorophyll. Previous work in Northern California has shown that microalgal food supply, as estimated by benthic chlorophyll, is an important determinant of *L. scabra* growth, although complex interactions exist between chlorophyll and temperature (Gilman, 2006a). Because *L. scabra* grows faster during the winter than during the summer (Sutherland, 1970), it is possible that we did not record a growth signal due to very low summer growth rates. However, there was a significant relationship between growth and intertidal height (see below), which indicates that growth differences are measurable even during the summer. Our results suggest that some other factor, such as available foraging time or sublethal stress, limited *L. scabra* growth during our experiment (see below).

4.2. Temperature and top-down effects

Temperature has been shown to influence *L. scabra* in two ways. First, extreme thermal stress results in massive mortality of this limpet (Sutherland, 1970). Second, in the absence of severe stress, warmer temperatures tend to favor *L. scabra* growth (Gilman, 2006b). Contrary to these previous findings, temperature had no measurable effect on *L. scabra* growth or mortality during our experiment. The lack of mortality is not surprising, given the lack of severe thermal stress. Rock temperatures at Bodega Bay in the spring of 2004, for example, exceeded 40 °C in several areas occupied by *L. scabra* (Harley, unpublished data). The maximum temperature we recorded during the spring/summer of 2005 was 38.5 °C. The absence of a temperature effect on limpet growth could result from counteractive thermal effects on the food supply, an offsetting of thermal benefits by sublethal thermal stress, or high variability and low sample size.

L. scabra had a strong, negative effect on microalgal chlorophyll at Pacific Grove but not at Bodega Bay. However, this top-down effect was not influenced by temperature (i.e. the shade × limpet interaction term was not significant). *L. scabra* at Bodega Bay had a weak but consistent negative effect on macroalgal abundance. Although *L. scabra* is thought to feed only on microalgae (Sutherland, 1972), it is likely that the microscopic stages of macroalgae are also consumed by *L. scabra*, which may explain the negative interaction between the limpet and the development of macroscopic stages. However, as with microalgal suppression at Pacific Grove, macroalgal suppression at Bodega Bay was independent of temperature.

Although we did not demonstrate a thermal effect on rates of herbivory, we cannot rule out a thermally-triggered cascade under more stressful conditions. Temperature-related *L. scabra* mortality events have been observed in the past (Sutherland, 1970, Harley unpublished data), and thermal stress greater than that which we observed over the course of our study may reduce limpet populations to the point where algal cover and abundance would increase in response. The exact nature of such a cascade would depend on the relative resistance and resilience of producer and consumer populations during and following a thermal stress event. In our study, the absence of temperature-related limpet mortality precluded the development of such density-mediated indirect effects.

4.3. Shore-level effects

L. scabra living lower on the shore grew faster than conspecifics living higher up, which agrees with previous results from this site during the late spring/early summer (Sutherland, 1970). Sutherland (1970)

also showed that limpet populations higher in the intertidal exhibited more seasonal growth rates, which presumably resulted from externally induced changes in food availability. Indeed, microalgal production decreases, and the seasonality of production increases, with increasing shore level (Nicotri, 1977). Although it is tempting to conclude that higher limpet growth rates at lower shore levels in our study are attributable to higher primary production, we found no link between limpet growth and indicators of micro- or macroalgal productivity. Alternatively, lower shore animals may have avoided some of the energetic costs of sub-cellular thermal protection and repair functions (e.g. Somero, 2002). However, we found no relationship between limpet growth and average daily maximum temperature. Limpets at lower shore levels may simply have had more time available for foraging, and growth may thus be limited by foraging time rather than by thermal stress or the availability of algal biomass. It is also possible that patterns in limpet growth rates are complicated by spatial variation in intraspecific competition (Sutherland, 1970).

4.4. Differences between locations

Bodega Bay and Pacific Grove were generally similar in their thermal environments during the course of our study. However, the importance of limpets varied between sites; limpets suppressed macro- but not microalgae at Bodega Bay, whereas the reverse was true at Pacific Grove. This may be related to the differences in the algal assemblage between the two locations, i.e. Bodega Bay featured a diverse macroalgal assemblage while Pacific Grove lacked macroalgae at our study sites. Thus, the diet of *L. scabra* may vary between locations, depending on the local availability of small macroalgal life stages. Additionally, limpet density was higher at Pacific Grove (11.6 per plot vs. 7.4 per plot at Bodega Bay), suggesting that density-mediated processes could be important in the suppression of microalgae (see, e.g., Ruesink, 1998). Given that *L. scabra* density declines dramatically north of Bodega Bay (Gilman, 2005), it is likely that their impacts as herbivores also decline with increasing latitude.

4.5. Caveats

Applying our results to the issue of climate change requires several caveats regarding the timing and method of thermal manipulation. Owing to the difficulty of experimentally increasing temperatures in the intertidal zone, we were constrained to use artificial shades to experimentally decrease temperature. Although shading is a highly effective way to manipulate organismal temperature at low tide (Harley and Lopez, 2003), shades have very little if any influence on body temperature at high tide due to the rapid transfer of heat between organisms and moving water. Our results are thus specific to the effects of temperature during low tide (i.e. atmospheric warming) but not at high tide (i.e. oceanic warming). The high-intertidal community studied here is underwater for a relatively small proportion of the time, suggesting that air temperature may be more biologically relevant than water temperature; water temperature is more closely tied to limpet body temperatures in the low intertidal zone (Denny et al., 2006). Nevertheless, previous research has shown that both air and water temperatures influence the success of grazing intertidal invertebrates (Gilman, 2006a), suggesting that plant–herbivore interactions may depend on temperature during both emersion and immersion.

Our experiment was conducted during the spring and summer, when high temperature stress was most likely to be important. We therefore cannot shed any light on the ecological significance of thermal changes during the winter. Much of the warming in California over the past half century has been an increase in winter minimum temperatures (Nemani et al., 2001). Like the effects of increased sea surface temperature, winter warming is unlikely to exceed the thermal tolerance of intertidal species. However, like warming water temperature, changes in winter temperatures could impact other aspects of organismal performance such as metabolic rate, growth, and reproduction.

Finally, our experimental shades may have had unintended ecological effects stemming from alteration of the light environment. The shade design used here reduces light levels by approximately 60–65% (Harley, 2002). Therefore, it is possible that algae in unshaded plots were subject to damaging UV radiation and/or photoinhibition while algae in shaded plots were not. High-intertidal macroalgae appear to be highly tolerant to UV radiation (Gómez et al., 2004). Although photoinhibition at solar noon is common in intertidal macroalgae, most species recover rapidly in the afternoon and regain full photosynthetic capacity (Gómez et al., 2004). In a heroic experiment which simultaneously manipulated light, temperature, and desiccation, Matta and Chapman (1995) found interactive effects of temperature and desiccation on photosynthetic performance of an emersed intertidal brown alga (*Colpomenia perigrina*), but no effect of light intensity. This evidence, along with the lack of a shading

effect on macroalgae in our study, suggests that light did not play a large role as a confounding variable with regards to macroalgal cover in our experiment.

It is also possible that UV damage and photoinhibition influenced the microalgae in our experiment. Although artificially elevated levels of UV radiation can negatively impact benthic microalgae on mudflats, ambient levels of UV radiation have no significant effects on benthic microalgal chlorophyll *a* concentrations (Sundbäck et al., 1996; Underwood et al., 1999). Photoinhibition has been documented in the microphytobenthos following long exposures to very high irradiance (Blanchard et al., 2004); however, several field studies failed to find evidence for photoinhibition in temperate zone sand- and mudflat microflora (Rasmussen et al., 1983; Grant, 1986; Barranguet et al., 1998; Migné et al., 2004). Furthermore, in studies that have simultaneously examined the effects of irradiance and temperature on benthic microalgae, thermal effects tend to explain most of the variation in photosynthetic parameters (Rasmussen et al., 1983; Grant, 1986; Migné et al., 2004). Given these results, plus the fact that temperatures in our unshaded plots exceeded optimal temperatures for benthic microalgal production (see, e.g., Blanchard et al., 1997), it seems reasonable to assume that temperature was more important than irradiance in driving benthic chlorophyll patterns in our experiment. However, we are not aware of controlled manipulations of both light and temperature with regards to epilithic microphytobenthos, and the exact determination of the relative importance of temperature and light in driving microalgal production on hard substrata awaits further experimentation.

4.6. Conclusions

In intertidal systems, there is a strong potential for temperature to disproportionately impact populations at different trophic levels and thus alter bottom-up and top-down interactions (Sanford, 1999; Harley, 2003; Harley and Lopez, 2003). In the present study, we found that microalgae were indeed more susceptible to thermal stress than were herbivorous limpets. However, thermal impacts on microalgae did not propagate up the food chain to indirectly influence *L. scabra*. Furthermore, although limpets had exerted strong top-down control of specific algal functional groups at specific locations, the strength of top-down control did not change with temperature. Our results suggest that changes in thermal stress, such as those accompanying climate change, may disproportionately affect specific trophic levels, but that these direct impacts will not necessarily propagate via interspecific interactions to other members of the community.

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