



Predicting consequences of climate change for ecosystem functioning: variation across trophic levels, species and individuals

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ABSTRACT

Aim Maintenance of ecosystem function under climate change may depend on variation in the way species within functional guilds and individuals within species respond to changes in temperature. What level of variation among and within species do we need to understand, and is it predictable from distribution and trait data?

Location Northern California, USA.

Methods We used a mesocosm experiment and a set of feeding trials to test the ability of a guild of marine invertebrate grazers to control benthic algal blooms along a local temperature gradient. We investigate links between the locally disjunct distributions of these species, their temperature tolerance traits and the temperature dependence of their population growth and grazing rates.

Results We found that the effect of increased temperature on population growth rates is independent of species interactions, but strongly species specific. This variation among herbivores is only partly predictable from differences in species distributions and traits, but translated into large differences in their ability to control macroalgae. Further, these species effects were amplified at warmer temperatures. Finally, we found evidence for a strong response to temperature in the feeding rates of the most important consumer over the course of the experiment, resulting in almost as much variation in grazing rates within one species as the average difference between species.

Main conclusions These results illustrate the importance of understanding the variation in responses to temperature among species within a trophic level, among populations within key species and potentially within populations over time. However, this variation is not easily predicted. Further research is needed to uncover links between individuals' thermal optima and their current and future temperature niche.

Keywords

acclimation, algae, distribution, grazers, plasticity, population growth, temperature.

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INTRODUCTION

Climate change has been forecast to impact a wide range of important ecological variables (Montoya & Raffaelli, 2010). As a result, there is considerable interest in understanding species' and communities' responses to environmental conditions (Blois *et al.*, 2013; Poloczanska *et al.*, 2013) and using these to prioritize management and conservation decisions

that mitigate these impacts (Pearson *et al.*, 2014). Given this objective, one of the central questions in climate change research is about the amount of complexity and variation among and within those species and communities we must account for to make predictions about the ecological impacts of changes in temperature.

There are two key components to this question. First, how do indirect effects mediated by species interactions compare

to direct effects of temperature? Several recent studies have focused on predicting the independent and direct effects of environmental change on individual species using trait and distribution information. For example, impacts of climate warming on both terrestrial and marine ectotherms has been shown to be predictable from their latitudinal distribution (Deutsch *et al.*, 2008; Sunday *et al.*, 2011; Diamond *et al.*, 2012a), life history traits (Pearson *et al.*, 2014), or physiological traits and evolutionary history (Diamond *et al.*, 2012a, b). At the same time, other studies and reviews have pointed out that changing environmental conditions may have large indirect effects on community composition and function by strengthening or weakening interactions between species that respond differently to environmental changes (Petchey *et al.*, 1999; Schweiger *et al.*, 2008; Tylianakis *et al.*, 2008; Barton *et al.*, 2009; Van der Putten *et al.*, 2010; Kordas *et al.*, 2011). If indirect effects are important, then data on variation in both physiological tolerances and interaction strengths (e.g. competitive abilities and predation susceptibility) may be necessary to predict community outcomes.

Second, at what level of biological organization can we generalize without missing important variation in response to temperature? At the most general level, both theoretical work and empirical work have shown that understanding only trophic structure within a community can provide substantial predictive power. For example, given fundamental differences in the temperature sensitivity of photosynthesis and respiration, non-lethal temperature increase can have predictable effects on the relative biomass of producers and consumers, regardless of species composition within those trophic levels (Allen *et al.*, 2005; O'Connor, 2009; O'Connor *et al.*, 2011). In addition to these differential effects on metabolic rates, trophic level can also predict vulnerability to lethal effects and consequent extinction (Petchey *et al.*, 1999). However, community response is not determined by trophic level alone; variation in both ecological impact and environmental tolerance among species within a trophic level can lead to large impacts if those traits align (Harley *et al.*, 2006; Russell *et al.*, 2012).

At an even finer scale, there can also be substantial variation among populations of the same species in their response to temperature (Franssen *et al.*, 2011; Manyak-Davis *et al.*, 2013), and in their potential to adapt to changing conditions (Sanford & Kelly, 2011; Kelly *et al.*, 2012). Even in the absence of genetic differentiation among populations, plastic responses within and across generations can cause individuals of the same species to show different responses to changing conditions (Salinas & Munch, 2012). This raises the potential for local and/or rapidly developed variation in individual responses to changing temperature and is consistent with previous work showing that temperature can affect individual variability in response strongly enough to alter net grazing effects even in the absence of temperature effects on either grazer population growth or mean grazing rates (O'Connor, 2009).

In this paper, we seek to understand the joint effects of temperature and species interactions on both the current

distribution and the ecological impact of a guild of marine herbivores. These mesograzers play a key role in controlling blooms of benthic algae and facilitating the growth of seagrasses, which are key habitat providers in coastal and estuarine systems (Duarte, 2002; Valentine & Duffy, 2006; Best & Stachowicz, 2012; Whalen *et al.*, 2013). All six of the herbivorous amphipod species we studied here are found in microhabitats dominated by ephemeral green macroalgae (*Ulva* spp.) and/or seagrasses, and they consume *Ulva* in feeding trials (Fig. 1a). Despite this apparent overlap in resource niche, half of these species are found in protected, soft-sediment environments of Bodega Harbor, and half are found in rocky habitats on the exposed coast immediately outside the harbour (these habitat types are separated by less than 1 km). With spring and summer temperature extremes up to 10 °C higher in the harbour, temperature tolerance is one possible reason for these disjunct local distributions. However, the species from the outer coast can survive in increased water temperatures (25 °C, nearing the maximum temperatures reached at shallow harbour sites at low tide) for longer than several species that are currently found in Bodega Harbor, including both native species and successful exotic colonists (Best & Stachowicz, 2013; data summarized in Fig. 1a). Given their ability to consume *Ulva* and their moderate tolerance of increased water temperature, we hypothesized that these species might be restricted from colonizing harbour habitats because of interactive effects of water temperature and feeding rates and specifically that competition for *Ulva* with other species adapted to warmer water temperatures might prevent successful establishment.

We used a mesocosm experiment paired with a set of feeding trials to answer three questions. First, we tested whether temperature and/or competition between these related species could explain their adjacent but separate distributions in marine habitats surrounding Bodega Harbor, California. Second, we examined how variation in temperature adaptation among these species predicts the effects of water temperatures on their population growth rates and ability to control algal biomass. Third, beyond variation between trophic levels (macroalgae and grazers) and among species (six species of amphipods), we tested for a third level of possible variation in temperature response by assessing feeding rates in individuals of the same species that grew to adulthood in contrasting temperature regimes.

METHODS

Study system

In our study region in Northern California, USA (38°19.110'N, 123°04.294'W), the macroalgae *Ulva* spp. (hereafter *Ulva*) grows on both protected, soft-sediment habitats within Bodega Harbor and exposed, rocky substrates on the open coast. Protected by a ~2 km sand spit, Bodega Harbor includes both shallow mudflats (at 0 to 0.7 m above mean lower low water [MLLW]) and deeper eelgrass (*Zostera*

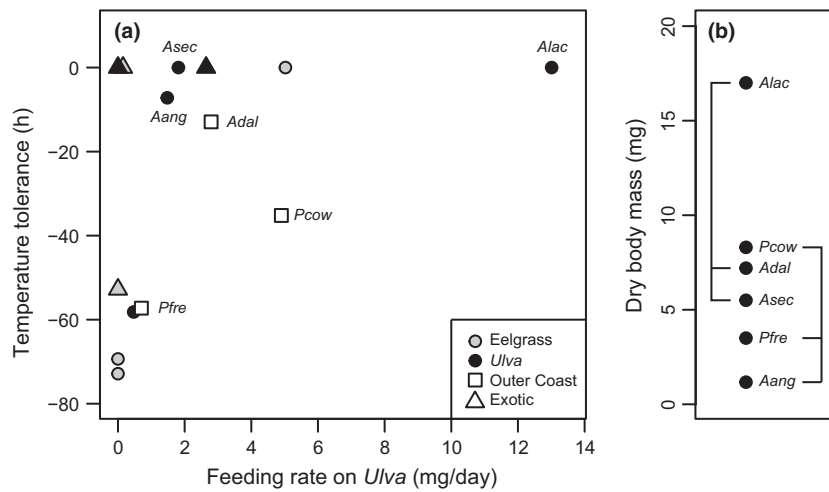


Figure 1 Grazer traits. (a) Temperature tolerance and feeding rates on *Ulva* macroalgae for 16 amphipod and isopod grazers from Bodega Harbor, CA. Temperature tolerance is the change in survival time when exposed to maximum (25 °C) vs. mean (12–15 °C) summer water temperatures. Feeding rates are from trials using *Ulva* from the harbour, but additional feeding trials with *Ampithoe dalli* (outer coast) and *A. lacertosa* (harbour) found similar grazing rates on *Ulva* from the outer coast (both choice and no-choice trials, M.N. Stone unpublished data). Species found within Bodega Harbor (11 amphipods and 2 isopods) are shown with their primary habitat within the harbour (*Ulva* or eelgrass beds), and their origin (exotic versus native). Squares represent the 3 amphipod species found on the outer coast but not in the harbour. Species from the outer coast are within the range of temperature tolerances and feeding rates of species already found in the harbour. Note: 3 species overlap at (0, 0), including two native species found in eelgrass and one exotic species found in *Ulva* on mudflats. (b) Individual body mass (dry weight) and phylogenetic groupings (left = *Ampithoe*, right = Talitroidea) for the six species used in this study, which are labelled in both panels (harbour: Aang = *Allorchestes angusta*, Alac = *Ampithoe lacertosa*, Asec = *Ampithoe sectimanus*; outer coast: Adal = *Ampithoe dalli*, Pcow = *Parallorchestes cowani*, Pfre = *Protohyale frequens*). All data are from previously published trait assessments (Best & Stachowicz, 2013).

marina) beds (at 3 to 0 m below MLLW). Inside the harbour, what is most likely *Ulva lactuca* covers the mudflats between the spring and fall, providing above-sediment habitat structure and food where it is otherwise lacking, and also intermixes with eelgrass in deeper, colder water (Olyarnik & Stachowicz, 2012; Best & Stachowicz, 2014). Immediately outside of the harbour, *Ulva* of the same and/or additional species also blooms in spring and summer in the rocky intertidal-zone of the outer coast, where it is the most widespread ephemeral, both forming monotypic patches and intermixing with perennial macroalgae.

In all of these habitats, *Ulva* provides food and habitat for several species of herbivorous amphipods. In Bodega Harbor, eleven amphipods and two isopods are distributed across mudflat and eelgrass habitats in a manner consistent with species' water temperature tolerance and ability to feed on *Ulva* macroalgae. Particularly during low tides, mudflat communities experience higher water temperatures than deeper harbour habitats or the outer coast (Fig. 2a), and species found in these mudflat habitats have higher tolerance of those warmer temperatures and share an ability to directly consume *Ulva* (Fig. 1a; Best & Stachowicz, 2014). On the outer coast, three different species of amphipods are commonly found in *Ulva* and surfgrass (*Phyllospadix* spp.), and can also consume *Ulva* (Fig. 1a). Species from the harbour and outer coast also overlap in size and are closely related; each of two separate clades is represented in both of these environments (Fig. 1b). For this experiment, we selected the

three outer coast species (*Ampithoe dalli* Shoemaker, 1938; *Parallorchestes cowani* Bousfield & Hendrycks, 2002; and *Protohyale frequens* Stout, 1913) and three common species found in *Ulva* in the harbour (*Ampithoe lacertosa* Bate, 1858; *Ampithoe sectimanus* Conlan & Bousfield, 1982; and *Allorchestes angusta* Dana, 1856) from these two matching taxonomic groups (Fig. 1). The three Ampithoids share an ability to build tubes within *Ulva*, a habit which reduces susceptibility to fish predation (Best & Stachowicz, 2012). The three remaining species (two on the outer coast and one in the harbour) are all members of the Talitroidea superfamily and share similarities in rapid swimming behaviour.

Mesocosm experiment

To test the effects of water temperature and interspecific competition on grazer population growth and *Ulva* biomass, we conducted a mesocosm experiment at the Bodega Marine Laboratory between 8 July 2013 and 2 September 2013 (8 weeks). We constructed 114 mesocosms from 2.4-L clear plastic buckets with two 9 × 10 cm panels of 500 µm mesh to allow water flow and placed half of these mesocosms into each of two large outdoor concrete raceways, each 0.9 × 4.6 m in area and filled 25 cm deep with seawater (enough to cover the mesocosms by ~10 cm). Each raceway received an equal and constant flow of filtered seawater from the adjacent outer coast. We kept one raceway at ambient ocean temperatures (daily average of 12–16 °C

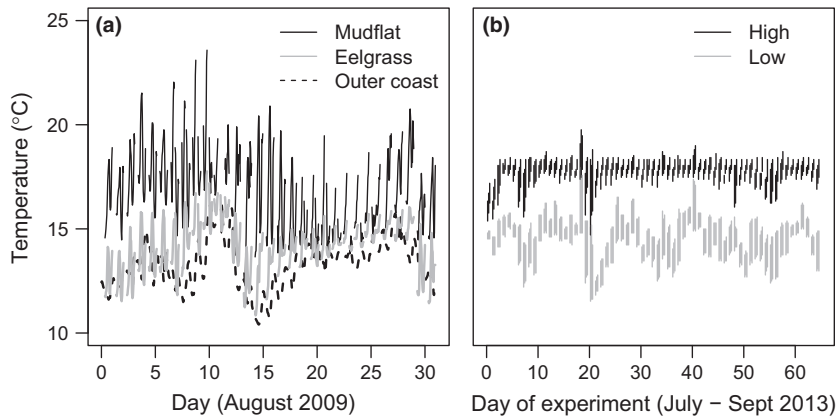


Figure 2 Seawater temperature variation within and between (a) habitats in the field and (b) treatments in the mesocosm experiment. In (a), data for mudflat and eelgrass habitats are hourly averages recorded by HOBO Pendant temperature and light loggers (Onset Computer Corp, Pocasset, MA) anchored approximately 5 cm from the sediment surface. Data for the outer coast are hourly averages recorded by the Bodega Ocean Observing Node shoreline sensor at the Bodega Marine Laboratory (data provided by the University of California, Davis, Bodega Marine Laboratory, available at <http://bml.ucdavis.edu/boon>). In (b), data are daily ranges recorded by 3 HOBO loggers deployed per experimental raceway and placed among the mesocosms. For each day, the 3 adjacent vertical lines indicate the similarity in temperature range experienced at the three different locations within that raceway. Light levels recorded by these loggers differed within but not between raceways: average \pm 1 standard deviation mid-day (11:00 to 14:00) illuminance (in lux) in low temperature: 527 ± 260 , 580 ± 299 and 386 ± 199 ; in high temperature: 522 ± 402 , 538 ± 230 and 389 ± 308 ; random effects of day and individual logger ($P < 0.0001$); and no fixed effect of raceway ($P = 0.58$).

depending on upwelling), and in the other raceway, we increased the temperature to 18 ± 1 °C using two 1000 W titanium heaters with horizontal heating cylinders 28 cm in length (Aquatic Eco-Systems, Apopka, FL, USA). We selected these temperatures to simulate the upper end of average water temperatures currently experienced in mudflat habitats (Fig. 2a) and refer to the temperature treatments as low (L) versus high (H). Although variation at the scale of days to weeks is higher in the low temperature treatment due to periodic upwelling of colder water, the daily variation is much closer in magnitude (Fig. 2b). To ensure adequate water circulation and heat distribution, we used water pumps at identical locations in both raceways and covered both raceways with shade cloth to reduce light levels to natural conditions.

We acknowledge that this design manipulates temperature at the level of the raceway, rather than the individual mesocosm. However, we treat the mesocosms as independent for analyses for several reasons. First, we had a constant flow of water at approximately 216 L h^{-1} , which we reset every 1–2 days in both raceways (only minor adjustment necessary, no periods of substantially reduced or increased flow). This prevented systematic differences in water flow and resulted in a residence time of only 4.8 h, meaning that pH and nutrient concentrations should reflect the characteristics of the laboratory seawater, rather than raceway-specific processes. Second, we randomized the position of the mesocosms and cleaned the outside of the screens of epiphytic algae every two to three days to prevent any differential build-up of microalgae. Third, the raceways were immediately adjacent and so received equivalent solar input (see Fig. 2 legend for data).

For each temperature treatment, we established a total of 18 grazer treatments plus a no-grazer control. The grazer treatments included monocultures of all species (6), all possible pairings of an outer coast species with a harbour species ($3 \times 3 = 9$) and all possible pairings of a harbour species with another harbour species (3). These combinations were chosen to investigate species interactions within the harbour, so pairs involving only outer coast species were not used. Each species was initially represented in both monocultures and polycultures by six adults, with three males and three females to ensure equal potential for population growth. We used additive species densities in the pair treatments to maintain constant initial reproductive potential within a species across treatments and to simulate the invasion of one species when another is already present. Each combination had three replicates per temperature except for the no-grazer controls (six) and three treatments involving less abundant species, for which we had only two (*Ampithoe sectimanus* and *A. dalli* in monoculture and combination). Amphipods were collected from either *Ulva* in Bodega Harbor or *Ulva* and surfgrass on the outer coast adjacent to the Bodega Marine Laboratory.

Four days prior to adding the grazers, each mesocosm was stocked with 10 ± 0.5 g wet weight of *Ulva* collected from the harbour. We cleaned the *Ulva* of all grazers, trimmed it into pieces of roughly equivalent size and shape and added two randomly chosen pieces to each mesocosm. For 8 mesocosms in which all *Ulva* was completely consumed before the end of the experiment (starting week 5), we added an additional ~ 1 g piece of *Ulva* every two to three days to avoid grazer population crash before the final census (range of total additional *Ulva*: 1.5–7.5 g). At the end of the

experiment, we cleaned the *Ulva* of all grazers and recorded its final wet biomass. Grazers were separated by species, and after the use of some individuals in feeding trials (below), all were preserved in ethanol and size-sorted using stack of nesting sieves with mesh sizes of 8, 5.6, 4, 2.8, 2, 1.4, 1, 0.71 and 0.5 mm. Numbers per size class were used to estimate ash-free biomass via regression equations (Edgar, 1990).

Statistical analysis of the mesocosm experiment

We analysed the effects of temperature and competition on final grazer population size and biomass using two levels of mixed models. First, we combined the response (either final abundance or biomass) of each stocked species in each mesocosm in a single model with the fixed effects being the main and interactive effects of species, the presence of a potential competitor (monoculture or pair) and temperature (low or high), and the random effect being the unique grazer composition treatment (18 levels). To test for positive non-independence between the two responses from a single species-pair mesocosm, we also ran this model for the pair treatments only with the individual mesocosm identity as an additional random effect, but found no evidence for this ($P = 1$). Second, to test these effects using only one response per mesocosm, we repeated the model for each species separately, using the same fixed and random effects minus the effect of species. In all cases, we log-transformed both grazer abundance and biomass to obtain residuals that were normally distributed with equal variance.

To test the effects of temperature and grazing on the change in *Ulva* biomass over the course of the experiment, we used a mixed model with interactive effects of temperature and final grazer biomass, plus the grazer composition (18 levels) as a random factor, and square root-transformed the final grazer biomass to obtain a linear relationship with the change in *Ulva* biomass (final *Ulva* minus total *Ulva* added to the mesocosm). We conducted these analyses in R (R Core Team, 2014) using the lmer function in the lme4 package.

Feeding trials

Immediately following the mesocosm experiment, we conducted feeding trials to measure the effect of both short- and long-term temperature exposure on feeding rates. For each of the three harbour species, we crossed the temperature at which an individual hatched and grew to adulthood (rearing temperature: low or high) with the temperature at which feeding was tested (feeding temperature: low or high), using 6–10 adult individuals for each of the four combinations. The outer coast species were not sufficiently abundant at the end of the experiment, and so were excluded. We placed each individual into a 118-mL plastic cup with a mesh lid and placed these cups back into the same raceways used for the mesocosm experiment. After 24 h without food, we added to each cup ~55 mg wet biomass of *Ulva* grown in

the corresponding temperature (harvested from control mesocosms for each temperature after final biomass was recorded). We then measured change in *Ulva* biomass over 4 days (96 h). The replicates were spread over two separate 4-day periods in the week following the mesocosm experiment. For each temperature treatment during each period, we included 10 control cups with no grazer to measure *Ulva* growth.

Statistical analysis of feeding trials

We used the 10 control measurements of *Ulva* growth during each time period and at each temperature to characterize the distribution (mean and standard deviation) of proportional growth rates in the absence of grazing. To account for this growth in the cups with grazers, we randomly drew a value from this distribution for each replicate at the corresponding time and temperature. We used that value to adjust the initial biomass of *Ulva* (initial amount + amount due to growth) and then calculated the total amount of *Ulva* consumed by that individual over the four days of the experiment. We used an ANOVA to test for interactive effects of grazer species (*Ampithoe lacertosa*, *A. sectimanus* or *Allorchestes angusta*), feeding temperature and rearing temperature on the log-transformed amount consumed. We then repeated the entire procedure 1000 times, each time drawing a new value from the control distribution of algal growth for each grazer cup and running the model again.

RESULTS

Effects on grazers

Overall, grazers were not affected by the presence of a competitor (Table 1), but had clear species-specific responses to increased seawater temperature (significant Species \times Temperature interaction for both final grazer abundance and final grazer biomass in Table 1, Fig. 3). While the abundance of all three harbour species (*Ampithoe lacertosa*, *Ampithoe sectimanus* and *Allorchestes angusta*) increased with increased temperatures, the effect was much larger for *A. lacertosa* and was only marginally significant for *A. sectimanus* (Fig. 3, note log scale, P -values are from species-specific models, see Table S1 in Supporting Information). The effect of temperature on biomass was again strong for *A. lacertosa* ($P < 0.0001$) and non-significant for the others ($P = 0.12$ for *A. sectimanus*, 0.53 for *A. angusta*, again from species-specific models). One important caveat to these findings is that we did discover over the course of the experiment that just-released juveniles of the smallest species, *A. angusta*, were able to escape through the mesh of at least some of the mesocosms and re-colonize others, although at low abundances (on average less than 25% of the biomass of this species where it was originally stocked). This means that our final population size for this species is underestimated, but should not preclude our ability to detect a

Table 1 Statistical results for all models used to analyse the mesocosm experiment and feeding trials. Denominator degrees of freedom and *P*-values for fixed effects were obtained using the Satterthwaite approximation, and random effects were tested with likelihood ratio tests (both carried out in the lmerTest package (Kuznetsova *et al.*, 2012). Boldface indicates effects with *P* < 0.05

Fixed effect	d.f.	<i>F</i>	Pr > <i>F</i>	Random effect	Pr > χ^2
Mesocosms: Final grazer abundance*					
Temperature	1, 103.4	6.7	0.011	Grazer treat.	1
Species	4, 26.5	97.2	< 0.0001		
Diversity	1, 17.1	0.3	0.61		
Temp. × Species	4, 103.4	10.9	< 0.0001		
Temp. × Diversity	1, 103.4	2.7	0.10		
Species × Diversity	4, 26.5	1.8	0.17		
Temp. × Species × Diversity	4, 103.4	0.9	0.47		
Mesocosms: Final grazer biomass*					
Temperature	1, 93.2	2.2	0.14	Grazer treat.	1
Species	4, 21.4	87.6	< 0.0001		
Diversity	1, 14.1	0.2	0.70		
Temp. × Species	4, 100.6	15.6	< 0.0001		
Temp. × Diversity	1, 93.2	0.6	0.44		
Species × Diversity	4, 21.4	1.0	0.42		
Temp. × Species × Diversity	4, 100.6	0.9	0.48		
Mesocosms: Change in <i>Ulva</i> biomass					
Temperature	1, 66.1	3.3	0.073	Grazer treat.	0.02
Grazer biomass	1, 26.7	172.6	< 0.0001		
Temp. × Grazer biomass	1, 97.4	0.5	0.49		
Feeding trials: <i>Ulva</i> consumption†					
Species	2, 88.8	125.9	< 0.0001	Mesocosm	1
Feeding temperature	1, 97.5	0.3	0.667		
Rearing temperature	1, 89.9	0.9	0.471		
Species × Feeding temp.	2, 97.7	0.7	0.584		
Species × Rearing temp.	2, 94.7	6.6	0.006		
Feeding temp. × Rearing temp.	1, 97.8	0.3	0.671		
Species × Feeding temp. × Rearing temp.	2, 97.6	0.6	0.589		

*Results from full model using one response per species per mesocosm (two for each pair mesocosm). In a model for pair treatments only, mesocosm identity as a random effect explained no variation (*P* = 1). In species-specific models using only one response per mesocosm, results were consistent with those reported here (no effect of diversity except for a marginally positive effect on *Ampithoe lacertosa* abundance at low temperatures only [Temp. × Diversity interaction *P* > 0.06] and variable effects of temperature across species). Full results of all species-specific models are reported in Table S1.

†Feeding trial results were analysed using 1000 repeated draws of potential control values for *Ulva* growth. All values given here are averages across those 1000 trials, and there was very little variation among trials. Species was significant (*P* < 0.05) in 100% of trials, Species × Rearing temp. was significant in 99% of trials, and all other effects were significant in 1% or fewer.

temperature effect. It is also very unlikely that this additional number of grazers, if present in their original mesocosms, could have approached anywhere near *A. lacertosa* in terms of mean population size or impacts on *Ulva* abundance (see below).

In addition to the variation in the magnitude of response among the harbour species, one of the outer coast species, *Parallorchestes cowani*, responded negatively to increased temperature (*P* ≤ 0.0001 for both abundance and biomass). Beyond this negative effect of temperature on one outer coast species, all three of these species responded poorly to experimental conditions overall. *Protohyale frequens* was present only as a single juvenile in a single mesocosm, and both *Ampithoe dalli* and *Parallorchestes cowani* were at low abundance (Fig. 3).

Effects on *Ulva*

Examining first the effect of temperature on *Ulva* growth in the control mesocosms, we found no significant effect (*P* = 0.11), with a trend towards lower rather than higher biomass in increased temperature (Fig. 4b). Further, to rule out any possibility that temperature failed to affect *Ulva* growth due to self-shading within the mesocosms, we conducted an additional growth experiment in the same temperature raceways following the mesocosm experiment, with lower starting biomass. Again using six replicates per temperature, but only 2 g wet biomass of *Ulva*, we found significant growth over a 10-day period (*P* = 0.01), but no effect of temperature on growth (*P* = 0.6).

While temperature had no direct effect on *Ulva*, the biomass of grazers had a very strong effect (Table 1, Fig. 4a). In

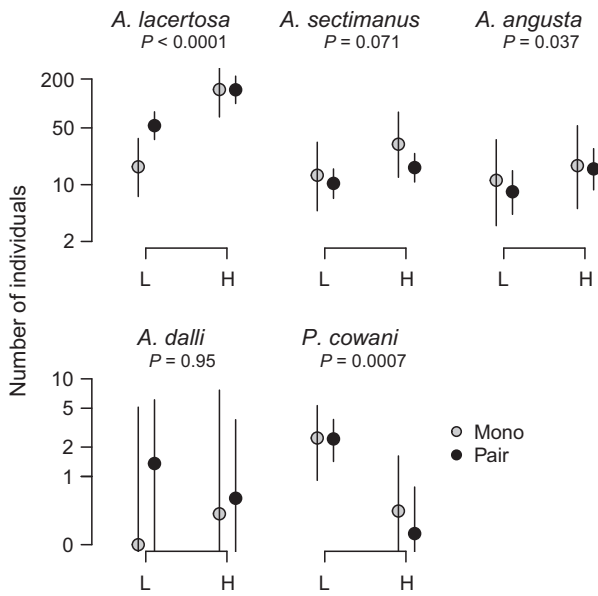


Figure 3 Effects of temperature (low [L] versus high [H]) and diversity (monoculture versus pair of species) on final amphipod abundance by species. Error bars are 95% confidence intervals. Data were log-transformed for analysis and are shown on a log scale. Note that the lower row shows the outer coast species on a different scale because they were less abundant (the third species, *Protohyale frequens*, was effectively absent at the end of the experiment so is not included). P-values are for the effect of temperature in individual models for each species (see Table S1).

particular, *Ampithoe lacertosa*, the species with the largest body size (Fig. 1b) and the largest increase in population growth in response to increased temperature, had the clearest effect on *Ulva* abundance. In nearly all mesocosms with *A. lacertosa* present, *Ulva* consumption outweighed *Ulva* growth, and in all mesocosms without *A. lacertosa* present, growth outweighed consumption (Fig. 4a). Within mesocosms containing *A. lacertosa*, the large effect of temperature on *Ulva* biomass was clearly mediated by the effect of temperature on *A. lacertosa* biomass (Fig. 4a) and perhaps grazing rate (see below).

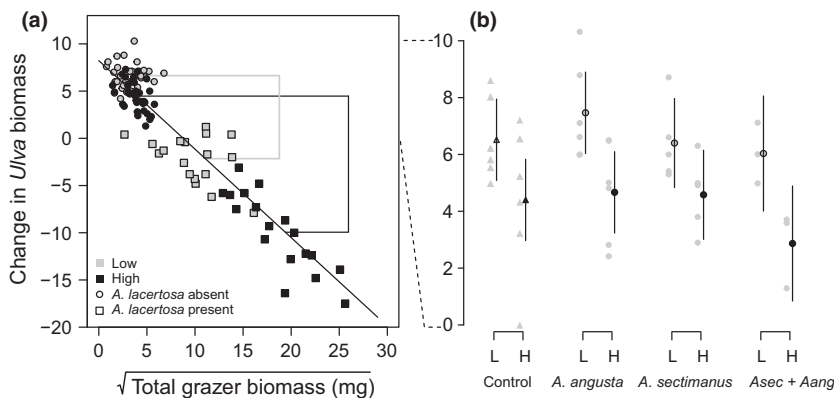


Figure 4 Effects of temperature and grazers on *Ulva* abundance. In (a), grazer biomass was the dominant predictor of *Ulva* growth or consumption and temperature had no effect (see Table 1). In (b), compared to controls (triangles), harbour species other than *Ampithoe lacertosa* had little impact on *Ulva* biomass when in monocultures. A slightly larger effect appeared with the two grazer species in combination. Error bars are 95% confidence intervals.

In contrast to the ability of *A. lacertosa* to control *Ulva*, the other grazers had little effect on algal biomass. This difference among species in their grazing response to temperature led to an amplified species effect at higher temperatures (Fig. 4a). To further assess the ability of the other harbour species to control *Ulva* on their own, we pooled their monocultures with mesocosms in which they were paired with *Protohyale frequens*, which failed to survive. Neither *Ampithoe sectimanus* nor *Allorchestes angusta* significantly reduced the biomass of *Ulva* relative to controls, but the mesocosms with these two species in combination had slightly lower final biomass of *Ulva* (Fig. 4b).

Feeding trials

In the feeding trials following the mesocosm experiment, grazing rates differed substantially among the three harbour species and were also differentially affected by rearing temperature (Table 1). *Ampithoe lacertosa* showed substantially increased feeding rates when reared at the higher temperature, while the other two species were generally unaffected (Fig. 5). The temperature at which feeding rates were assessed had no effect on either the mean feeding rate (Table 1) or the variation in feeding rate across individuals.

DISCUSSION

We predicted that species' differences in optimum temperature might interact with competition for a shared resource to determine species distributions, population growth rates and contributions to the control of macroalgae. Such joint effects of temperature and competition have previously been shown to control species distributions in damselflies (Nilsson-Örtman *et al.*, 2013) and *Daphnia* (Fey & Cottingham, 2012) and have been predicted for brown trout (Hein *et al.*, 2013) and sessile marine invertebrates (Sorte & White, 2013). However, in this study, we found a wide range of direct effects of temperature on population growth rate but no effect of interactions among amphipod species. We also found substantial variation among individuals of a single species resulting from acclimation and/or selection. This within-species

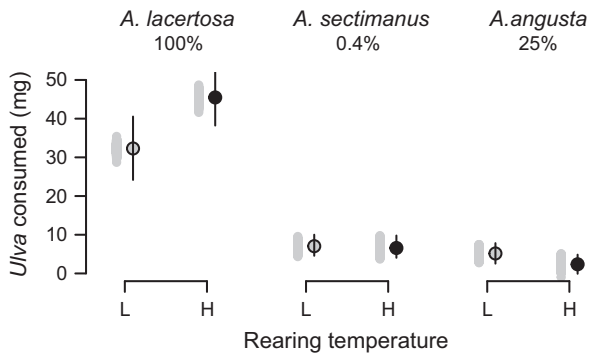


Figure 5 Feeding rates for harbour amphipod species reared in low (L) versus high (H) water temperatures. Grey bars show the range of mean feeding rates for each species and temperature across the 1000 analytical trials (random draws of control values for each replicate), and circles with error bars show the average of these trials, along with the average width of the 95% confidence interval. To show relative effects within and across species and to show average variation across analytical trials, we show means and variances calculated for each species individually, where no transformation was necessary. For full analysis of species by temperature interactions, data were log-transformed to account for large differences in mean and variance between species. Percentages below the species name give the percentage of 1000 trials that showed a significant ($P < 0.05$) effect of an increased rearing temperature on feeding rate in that species. Full distributions of P -values are given in Fig. S1. This effect was positive for *Ampithoe lacertosa*, non-significant for *Ampithoe sectimanus* and either non-significant or negative for *Allorchestes angusta*. When reared at low temperature, individuals of all three species significantly reduced *Ulva* mass: feeding rates were significantly greater than zero for *Ampithoe lacertosa* ($P < 0.0001$), *Ampithoe sectimanus* ($P = 0.002$) and *Allorchestes angusta* ($P = 0.02$). When reared at higher temperature, feeding rates were greater than zero for *Ampithoe lacertosa* ($P < 0.0001$) and *A. sectimanus* ($P = 0.004$), but not *Allorchestes angusta* ($P = 0.13$).

difference emerged either across generations (> 1 month) or over the life span of an individual (weeks), not within the time frame of a feeding trial (days). Below, we compare our results to previous work across levels of trait variation and discuss the implications for predicting whole-community responses to increased temperatures.

Variation in response across trophic levels

Metabolic theory predicts that a non-lethal increase in water temperature should increase both producer growth rates and consumer feeding rates, but that the latter should increase more steeply with temperature, leading to stronger top-down control (Allen *et al.*, 2005; O'Connor *et al.*, 2009, 2011). Experimental evidence from a range of systems has demonstrated the predicted increase in top-down control (Barton *et al.*, 2009; O'Connor, 2009; Kratina *et al.*, 2012; Carr & Bruno, 2013; Werner & Matthiessen, 2013). This is consistent with our finding that for one grazer species, higher tempera-

ture did have a strong indirect negative effect on *Ulva* biomass via a positive effect on grazer biomass (Fig. 4a). At the same time, however, results in both this experiment and several others demonstrate substantial variation in the component responses of producer versus consumer trophic levels.

We found positive effects of temperature on the population growth (Fig. 3) and feeding rates (Fig. 5) of some but not all amphipod species, and no direct effect of temperature on algae growth (Table 1: Change in *Ulva* biomass). Previous mesocosm experiments with comparable temperature manipulations (+ 2–6 °C) have shown variable effects on both algal producers and invertebrate consumers. Direct effects on algae have been neutral or positive depending on experimental duration (O'Connor, 2009); strongly positive, resulting in a doubling of algal biomass (Eklöf *et al.*, 2012); positive for microalgae but not macroalgae (Blake & Duffy, 2012); or either positive or negative for different species in the same functional group (Olabarria *et al.*, 2012). Direct effects on grazer population growth have also been neutral (O'Connor, 2009), or neutral or negative depending on the species (Blake & Duffy, 2012; Eklöf *et al.*, 2012).

Variation among grazer species

Across the six grazer species, we saw large differences in population growth and its response to temperature (Fig. 3), which could be partly due to underlying variation in thermal optima between harbour and outer coast species. Although outer coast species can survive for multiple days at the maximum harbour temperature (Fig. 1a), here we found that at least one of those species (*P. cowani*) may be negatively affected by even the 18 °C average temperature on the harbour mudflats where much of the *Ulva* is found (Fig. 3). This experiment did exclude the variation around this mean that would naturally be found in the harbour, and such variation can have important consequences for survival and feeding rates (Sanford, 2002; Clusella-Trullas *et al.*, 2011; Marshall & McQuaid, 2011). However, in our previous measurements of temperature tolerance, we found high correspondence between effects of constant high temperature and tidal-scale temperature variation (Best & Stachowicz, 2013). This suggests that our focus on mean differences does provide a relevant predictor of temperature stress, but there are clearly additional possible dimensions of variation between species in their strategies for feeding and activity levels during fluctuating temperatures. Also, the very low survival of all three outer coast species regardless of temperature or competition suggests that there are other components of the mesocosm (and perhaps harbour) environment that favoured only the harbour species. These could include water flow and dissolved oxygen concentrations, which are doubtless much higher in the surf zone of the outer coast than in either the harbour or the experimental raceways.

Within the harbour species, the variation in response to temperature could clearly not be predicted from our previous short-term assessment of temperature tolerance: the

survival of both *Ampithoe lacertosa* and *A. sectimanus* is unaffected by maximum harbour temperatures (Fig. 1a), but *A. lacertosa* showed a much larger proportional increase in population growth under increased temperatures (Fig. 3) as well as a strong response in feeding rate (Fig. 5). The third species, *Allorchestes angusta*, had slightly lower temperature tolerance in our previous assay but an intermediate response in population growth here. This variation among species is also not predictable from their distributions within the harbour. While we have shown previously that there is a strong correlation between species temperature tolerance and prevalence on warm, shallow mudflats within the harbour (Best & Stachowicz, 2014), variation among the species capable of passing that filter was not predictable. *Ampithoe lacertosa* is frequently found across all habitats and temperatures in Bodega Harbor and had a strong response to higher temperatures, while the other two species are found almost exclusively in the warmest harbour habitat, yet had much weaker responses to the warmer temperatures characteristic of this environment.

Variation within a grazer species

Ampithoe lacertosa showed large increases in feeding rates when reared at higher temperature, but no short-term response to the temperature at which feeding was measured. Because feeding trials in the two temperatures used *Ulva* grown at those temperatures, feeding rates were not affected by any temperature-induced differences in *Ulva* palatability or nutritional content, as has been found for phytoplankton (De Senerpont Domis *et al.*, 2013) and terrestrial plants (Lemoine *et al.*, 2013). Instead, the intraspecific variation in feeding rates due to temperature appears because of plasticity within or across generations, and/or selection. Time-scales longer than the 1-week feeding trails may have been necessary for acclimation or developmental changes within a generation (3–6 weeks) to increase ingestion efficiency to keep up with metabolism (Lemoine & Burkepile, 2012). Alternatively, adults experiencing increased temperatures may have provisioned their offspring for optimum feeding at those temperatures (Salinas & Munch, 2012), or there may have been differential survival of individuals with different feeding rates.

Along with increased population growth under higher temperatures, the increased consumption rates with temperature has important implications for our understanding of the way ecosystem function (such as control of algae blooms) can be affected by temperature. Even if we know which species are the largest mean contributors to ecosystem function, populations of those species may differ in their effect depending on ambient temperature. This is especially likely for these direct-developing benthic species associated with host plants, which are relatively poor swimmers and may frequently spend their entire life in a single habitat with a particular temperature regime. *Ampithoe lacertosa* is found in both deep eelgrass beds and shallow mudflats, but stable

isotope signatures clearly distinguish individuals from the two habitats, indicating that they are not frequently moving between the two to feed (R.J. Best unpublished data).

Implications for predicting community responses

In combination, results from the mesocosm experiment and feeding trials have two important implications for our ability to predict community responses to changes in water temperature. First, we found that even closely related species with overlapping feeding traits and body sizes responded to temperature in very different ways and that effects of temperature on population growth and consumption rates were not predictable from temperature effects on survival. Second, we found substantial condition-dependent variation in feeding rates within one species with high ecological impact. This unexplained within-trophic level and within-species variation poses a major challenge for predicting community-level response to temperature, even if such responses are independent of interactions among community members. It also suggests that particularly valuable avenues of future research might seek to identify physiological links between ecological impact and the mean and variance of the temperature niche and to determine whether they are jointly or independently subject to plastic and/or genetic differentiation on small or large spatial scales.

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SUPPORTING INFORMATION

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

Table S1 Results of species-specific statistical models.

Figure S1 Distributions of *P*-values for feeding trials.

BIOSKETCHES

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