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Mussel zonation in New Zealand: an integrative eco-physiological approach

Bruce A. Menge[1,*], Bryon A. Daley[2], Eric Sanford[3], Elizabeth P. Dahlhoff[4], Jane Lubchenco[1]

[1]Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914, USA
[2]Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850, USA
[3]Section of Evolution and Ecology, University of California Davis, Bodega Marine Laboratory, Bodega Bay, California 94923, USA
[4]Department of Biology and Center for Environmental Studies, Santa Clara University, Santa Clara, California 95053, USA

ABSTRACT: Environmental stress and productivity models for community dynamics assume that the ecological responses of species are based on sub-organismal (physiological, cellular, molecular) mechanisms. Early tests of these models did not incorporate evaluation of physiological responses. Advances in remote sensing and molecular biology now allow more mechanistic and integrative approaches. In this study, we employed between-zone translocation experiments to test the effects of environmental stress and feeding time on the zonation of 2 species of mussel on rocky shores in New Zealand. Response variables were survival, shell growth, relative tissue mass, and short-term capacity for protein synthesis (indexed by RNA:DNA ratios). We predicted that the ecological and physiological performance of both mussels should increase with depth on the vertical tidal axis, but that the low-zone-dominant *Perna canaliculus* should perform relatively better than the mid-zone-dominant *Mytilus galloprovincialis* lower on the shore and at the more wave-exposed site. In contrast, we predicted that mid-zone-dominant *M. galloprovincialis* should perform relatively better than *P. canaliculus* higher on the shore and at the less wave-exposed site. Collectively, the ecological and molecular responses supported many, but not all of our predictions. As expected, *P. canaliculus* outperformed *M. galloprovincialis* in the more wave-swept and lower shore habitats, and showed lower tolerance of the stressful conditions that prevail higher on the shore, suggesting that the zonation pattern was based on differential responses to stress and food environments.

KEY WORDS: Mussels · New Zealand · Zonation · Eco-physiology · Field experiments · Molecular indices

INTRODUCTION

Understanding the patterns of space occupancy of organisms in ecological communities requires the integrated study of how the organisms respond to species interactions and to gradients in the environment (Menge & Sutherland 1987). Two major environmental gradients occurring across landscapes and seascapes are those of environmental stress and productivity (Oksanen et al. 1981, Menge & Sutherland 1987, Menge & Olson 1990). On rocky shores, for instance, environmental stress and food concentration can vary across vertical (tidal height) and horizontal (wave exposure) gradients. With increasing tidal elevation, thermal and desiccation stress increase, and feeding time for suspension feeders decreases. Along horizontal gradients, desiccation stress may increase in wave-protected habitats as wave forces and spray decrease. Although food concentration gradients along horizontal clines are less well documented, flow decreases with decreasing wave exposure (Denny 1988). Thus, rates of delivery of particulates may also decline along

*Email: mengeb@oregonstate.edu

this gradient (Sanford et al. 1994, Leonard et al. 1998), but see Judge et al. (1992).

On the Banks Peninsula of the east coast of the south island of New Zealand, the mussels *Mytilus galloprovincialis* (the blue mussel) and *Perna canaliculus* (the green-lipped mussel) are dominant space occupants on rocky shores (Knox 1953, Menge et al. 1999). *P. canaliculus* (*Mytilus canaliculus* in Knox 1953) is more abundant lower on the shore and at somewhat greater wave exposures, whereas *M. galloprovincialis* (*M. planulatus* in Knox 1953) is more abundant in the mid-zone and at lesser wave exposures (Knox 1953, Menge et al. 1999). Although these differences in abundance along the vertical tidal gradient are visually clear, the boundary between the species is not abrupt, and individuals of each species occur both above and below this relatively indistinct interspecies boundary.

What are the causes of this zonation pattern? In other intertidal systems, analogous patterns are produced by interspecific interference competition. For example, in Scotland, Connell (1961) demonstrated that interspecific barnacle–barnacle competition determined the zonal boundary between 2 species. The space-occupying dominant lower on the shore, *Semibalanus balanoides*, crushed and overgrew individuals of the higher shore *Chthamalus stellatus*, thereby excluding them from the *S. balanoides* zone. Connell (1961) suggested that *S. balanoides* was intolerant to physical conditions above the upper edge of its distribution, and thus that *C. stellatus* persisted as the high-shore dominant as a consequence of its broader range of tolerance to environmental stress. Similar examples on the coasts of New England and Washington state suggested barnacle–mussel competition-determined patterns of zonation. In New England, the mussel *M. edulis* settled upon, overgrew, and smothered *S. balanoides*, thereby excluding the barnacle from the mid-intertidal mussel bed zone (Menge 1976). *S. balanoides* persisted in the high zone, presumably because *M. edulis* either could not survive or did not settle at this level. In Washington state, Dayton (1971) showed that the mussel *M. californianus* outcompeted *Balanus glandula* by overgrowing and smothering the barnacles.

Thus, one hypothesis is that the zonation between *Perna canaliculus* and *Mytilus galloprovincialis* on Banks Peninsula is the result of interspecific, mussel–mussel interference competition for space. Several observations suggested that space-mediated competition was an incomplete explanation, however. First, as noted above, individuals of each species can occur intermingled with the other species at their respective levels on the shore. Second, no evidence of either species crushing the other has been observed during 11 yr of field work in this system (B. A. Menge et al. pers. obs.). Third, although field observations suggest that *P. canaliculus* can grow to larger sizes than can *M. galloprovincialis*, the co-occurring individuals tend to be similar in size. These observations and the differences in relative abundance with decreasing wave exposure suggested that additional or alternative mechanisms might be at work.

The alternative we chose to examine was differing tolerance of physical conditions. We did not test yet another alternative, predation, because field observations were not consistent with this hypothesis. Sea stars, important predators in other habitats, including on the west coast of the south island of New Zealand (Menge et al. 1999), were almost absent at the Banks Peninsula sites. Whelks (e.g. *Haustrum scobina* [formerly *Lepsiella scobina* and *L. albomarginata*; Schiel 2006] and *H. lacunosus* [formerly *Lepsithais lacunosus*; Schiel 2006]) were either relatively scarce (*H. lacunosus*), or abundant only at higher tidal levels (*H. scobina*) (Menge et al. 1999). Further, we saw little evidence of whelk predation (e.g. almost no empty shells with drill holes were recovered), and mussel cover was high from the upper mid-zone to the level of the lowest tides. If sea star predation was important, we expected to see a mussel-free zone in the lower intertidal as has been observed elsewhere (west coast of the USA [Paine 1966, Dayton 1971, Menge et al. 1994] and west coast of the south island of New Zealand [Menge et al. 1999]). Predation by mobile predators (fish, crabs) has a strong effect on small mussels (~10 to 15 mm; Rilov & Schiel 2006), but no evidence is available to suggest that these consumers affect the larger (greater than ~30 mm) mussels making up these mussel beds.

The possibility that environmental stress might affect the zonation pattern, with more severe effects on *Perna canaliculus*, was suggested by the domination of the low zone and more wave-exposed sites by the green-lipped mussel. Fewer *P. canaliculus* (and more *Mytilus galloprovincialis*) higher on the shore and in more wave-sheltered areas could result from lower tolerance of thermal or desiccation stress. Differing nutritional requirements might also contribute to these patterns of zonation. The reduced abundance of *P. canaliculus* in wave-protected habitats and higher tidal heights might suggest that this species requires longer periods of immersion and feeding. That is, the niche of *P. canaliculus* might be narrower than that of *M. galloprovincialis*, such that the ecophysiological performance of the green-lipped mussel is greater at lower tidal levels and under more turbulent conditions. Under this scenario, *M. galloprovincialis* would dominate at higher shore levels and in less turbulent conditions because of a broader tolerance range and, thus, relatively superior ecophysiological performance than

P. canaliculus in marginal conditions. In the absence of *P. canaliculus*, we would expect *M. galloprovincialis* to do increasingly well with increasing submersion (i.e. lower on the shore, where wave splash is greater); its gradual dominance with increasing shore height would thus result from a disproportionately smaller decline in its ecophysiological performance compared to that of the green-lipped mussel.

Environmental stress models for community dynamics suggest how ecological processes vary along gradients of environmental stress (Menge & Sutherland 1987, Menge & Olson 1990, Bruno et al. 2003). In rocky intertidal habitats, the sharpest gradient is the vertical, tidal gradient, along which thermal and desiccation stress increases and feeding time decreases with increasing height on the shore. The horizontal gradient is more complex, with physical stress from wave forces decreasing and, in theory, thermal and desiccation stress increasing with decreasing wave action. In general, stress effects on intertidal organisms should increase with height on the shore, as both heat and time out of water increase. Along the horizontal gradient, the effects of hydrodynamic forces should decrease and the effects of temperature or desiccation should increase in moving from wave-exposed headlands to wave-sheltered coves.

Species characteristics might modify responses along these gradients. As noted earlier, *Perna canaliculus* is more characteristic of lower shore and more wave-exposed habitats, and thus might be expected to show superior performance to *Mytilus galloprovincialis* in these places. *M. galloprovincialis*, which can occur across a broader range of physical conditions, but is more abundant in wave-sheltered and higher shore habitats, might be expected to show a relatively superior performance to *P. canaliculus* in these areas. However, since low-shore and more wave-exposed conditions are also likely to favor this mussel, we might also expect it to do better in general and perhaps to do at least as well as *P. canaliculus* in lower shore and more wave-exposed areas, at least when *P. canaliculus* is absent.

These considerations suggest several predictions. (1) Along the horizontal gradient, both mussels should survive better, grow faster, and have higher relative tissue mass at the more wave-exposed site than at the wave-protected site. Further, (2) RNA:DNA ratios, an index of short-term growth, should be higher at the former site than at the latter. Alternatively, (3) if *M. galloprovincialis* is better adapted to calmer waters, it might be expected to survive worse, grow slower, have lower relative tissue mass, and have lower RNA:DNA ratios at the more wave-exposed site. Expectations are clearer along the vertical gradient. Lower shore mussels should suffer less stress than higher shore mussels, so on the low shore (4) mortality should be lower, (5) growth should be faster, (6) relative tissue mass should be greater, and (7) RNA:DNA ratios should be higher.

We recognize that additional factors or interactions among factors might complicate these simple predictions. Predictions for the relative proportion of tissue mass, for example, may be less straightforward than those listed above. Although high-shore mussels should have lower food intake, it is possible that due to the demands of reproduction, the reduced volume of food leads to reduced shell growth rather than reduced tissue, in which case relative tissue mass might not vary consistently along horizontal or vertical gradients. Further, RNA:DNA ratios are shorter term responses, which may reflect only recent conditions and not the average conditions over the past several months. For example, in Oregon, the RNA:DNA ratio of the mussel *Mytilus californianus* seemed to respond to phytoplankton fluctuations on temporal scales of a month or less (Menge et al. 1997).

Here, we present the results of a study initiated to investigate these alternatives. Using translocation experiments, we studied survival and growth of marked mussels on mid- and low-zone shores at 2 sites on Banks Peninsula, one somewhat more exposed to wave action than the other. In addition, to begin to evaluate the possible sub-organismal molecular and physiological mechanisms that might underlie differences in mussel performance, we quantified levels of RNA:DNA ratios, an index of short-term growth capacity, for each species at each site and tidal level. This biomarker of performance has provided valuable insights into the physiological mechanisms of responses of invertebrates to food concentration (Dahlhoff et al. 2002, Dahlhoff 2004). To gain insight into thermal and food environments, we also quantified low tide temperatures and concentration of chlorophyll *a* at each site.

MATERIALS AND METHODS

Study sites. The experiment was carried out from October 1994 to March 1995 at 2 sites on the Banks Peninsula, near Taylor's Mistake, a beach adjacent to Christchurch, New Zealand (Menge et al. 1999). The more wave-exposed site, Boulder Bay (hereafter BB), is a rocky reef at the wave-exposed tip of Godley Head, the headland between Taylor's Mistake and the port city of Lyttelton. The less wave-exposed site, Box Thumb (hereafter BT), is a rocky platform on the northern edge of Godley Head about 2 km west of BB. The substratum at BB was more heterogeneous than that at BT, with many outcrops, channels, and pools dissecting the basaltic rock. BT also had a basaltic substratum, but the topography was simpler, with more homogeneous benches and fewer channels and pools.

At both sites, the high zone was dominated by barnacles (*Chamaesipho columna*, *Epopella plicata*) and the small mussel *Xenostrobus pulex* and mid- and low zones were dominated by *Mytilus galloprovincialis* and *Perna canaliculus*, respectively (Menge et al. 1999). The very low and shallow sublittoral zones were dominated by dense covers of the large bull 'kelp' *Durvillea willana*. In total, mussel cover ranged from 65 to 85% in the mid-zone and from 40 to 80% in the low zone. Observations made periodically since 1994/1995 (1997, 1999 to 2006) indicate that little change in patterns of abundance occurred between 1994 and 2000, but, since 2000, total mussel cover at BT has diminished to about 35% (B. A. Menge et al. unpubl. data). Knox's (1953) observations at some of these same sites suggest that these general patterns of mussel zonation have persisted for at least 50 yr.

Mussel survival and growth. We used translocation experiments to quantify survival and growth in relation to tidal height and site. The mussel sources were the populations at each site; translocations were thus within site. Individuals were collected from the approximate middle of the combined mussel bed, in the band of overlap between the species. Methods of translocation were identical to those used previously (Menge 1992, Menge et al. 1994, 1999, 2004). Mussels ranging in shell length from 3 to 5 cm were notched with a file at the posterior (growing) end of the shell, and each cage included mussels spanning the full range of shell lengths. Using a 20 × 20 cm plastic mesh cage, the marked mussels were then held ventral side down against the rock in gaps in the mussel bed in the mid-, *Mytilus galloprovincialis*–dominated zone and the low, *Perna canaliculus*–dominated zone.

Mussels were caged until all had firmly reattached byssal threads to the rock surface, usually ~3 to 6 wk, whereupon the cages were removed. Mussel survival was determined by counting live mussels periodically during the experiment. The shells of dead mussels were removed when discovered; virtually all were recovered with little or no loss. The experiment began when cages were removed in December 1994 and was terminated in February 1995, whereupon samples were processed as described below. Due to different initiation and termination dates, experimental duration among replicates varied from 103 to 134 d.

For survival, growth, and relative tissue mass the full experimental design thus included 2 sites (BB and BT), 2 zones (mid and low), and 2 species (*Mytilus galloprovincialis* and *Perna canaliculus*). With 5 replicates per combination of factors, the total number of translocated mussel clumps was 2 (sites) × 2 (zones) × 2 (clumps; *M. galloprovincialis* alone, *P. canaliculus* alone) × 5 replicates, or 40 clumps. At ~30 mussels per clump, a total of 1200 mussels were translocated.

After termination, we quantified shell length and growth increment. For each replicate, we also determined wet shell and wet flesh mass of up to 13 individuals. Tissue was removed and drained with the empty shells on a paper towel, and both tissue and shell were weighed to 0.01 g. To obtain tissue samples for quantification of RNA:DNA ratios, we field-dissected posterior adductor muscle and gill from 8 to 10 haphazardly selected individuals and flash froze tissues on dry ice. Frozen samples were kept on dry ice or in a –80°C freezer until they were processed in the laboratory in Corvallis, Oregon, USA.

RNA:DNA ratios. RNA:DNA ratios, an indirect measure of protein synthetic capacity, are routinely used as an index of dietary status and growth, both in vertebrates and invertebrates (Foster et al. 1993, Dahlhoff & Menge 1996, Dahlhoff 2004). Concentrations of RNA and DNA in adductor muscle and gill tissue were determined by ethidium bromide fluorescence following the method of Bentle et al. (1981) as modified by Dahlhoff & Menge (1996). Samples were thawed on ice, weighed, and homogenized in 30 vol of 2 M NaCl with a hand-driven glass homogenizer (Kontes Duall). From each sample, 50 µl was incubated in 1.5 ml of 0.005 mg ml^{-1} ethidium bromide and 0.10 mg ml^{-1} Proteinase K at 37°C for 90 min. After incubation, 0.5 ml buffer (80 mM Tris-Cl, pH 7.5 at 20°C) was added, and fluorescence was recorded at 365 nm excitation and 590 nm emission using a Perkin-Elmer LS-5B luminescence spectrofluorometer. RNA and DNA concentrations were estimated from a standard curve calculated using known quantities of RNA and DNA (Sigma calf thymus DNA, 1 to 4 µg; Sigma calf liver RNA, Type IV, 2 to 8 µg).

Temperature. To quantify temperatures at both sites, we installed Onset StowAway temperature loggers (Onset Computer) in the lower mid-zone, approximately at the *Mytilus galloprovincialis*–*Perna canaliculus* distributional interface (Menge et al. 1999). Loggers recorded hourly temperatures. Here, we report only maximum daytime air temperatures taken at low tide, the times of which were obtained from New Zealand tide predictions (Lamont 1996). Thus, although there are 2 low tides per day, we used only the one occurring in daylight, or, if there were low tides in the morning or evening, we used the tide having the highest air temperatures. To check the possibility of unusual readings skewing results, we compared this measure to an average of the 3 hourly temperatures around low tide and obtained similar results (data not shown).

Chlorophyll *a*. Phytoplankton concentration, quantified as chlorophyll *a* (chl *a*), was determined monthly in replicated (n = 3) bottle samples taken at 2 separate sectors at each site, plus another more

shoreward site, Black Point (~0.5 km from BT). Samples were collected from shore in opaque HDPE plastic bottles (250 ml), put on ice, and taken to the laboratory for analysis. Processing followed established techniques (Parsons et al. 1984). Using a hand pump to apply low vacuum pressure (≤180 mmHg), we filtered a subsample (50 ml) through 25 mm combusted Whatman glass fiber filters with a pore size of 0.7 µm. Chl *a* was extracted from filters in 90% HPLC acetone for 12 h in the dark at –20°C and then frozen for later transport to our laboratory in Corvallis for analysis. Chl *a* concentration was determined using a Turner Designs Model 10 fluorometer that had been calibrated using a pure chl *a* standard (Sigma Chemical).

Data analysis. Data were analyzed using SYSTAT Version 10.0 (SPSS) and JMP Version 4.01 (SAS). To analyze survival data, we calculated the slope of a linear regression between the proportion of each species surviving versus days for each replicate under each set of conditions (site, zone, and treatment). The slope was then used as our measure of survival rate and analyzed using a 3-way ANOVA with site, zone, and species. Growth was quantified as millimeters of new shell added per day and was also analyzed using 3-way ANOVA, with the average growth of all surviving mussels per replicate as the response variable. We also analyzed differences in tissue mass, quantified as the proportion of total mass (flesh + shell) using 3-way ANOVA with the same factors as for growth and survival. RNA:DNA ratios were analyzed with a 4-way ANOVA with site, zone, species, and tissue (gill, adductor) as factors.

In all cases, data were transformed when visual examination of residuals indicated that the assumptions of normality (probability plot) or independence of error terms (scatterplots of residuals vs. estimated values) were violated. In most cases, Cochran's *C*-test (Winer et al. 1991) indicated that variances were homogeneous. Data were transformed using $\ln(x + 1)$ for mortality, growth, and RNA:DNA ratio. Flesh mass was transformed using the arcsine transformation. We used linear contrasts to determine effect sizes of significant effects, expressed as the magnitude of the difference between least squares means of the transformed data. To determine the variability of magnitude differences, we used the estimate and its standard error from each linear contrast analysis to calculate 95% confidence intervals.

Temperature differences between sites were tested using a paired *t*-test (Sokal & Rohlf 1995). We analyzed chl *a* data using nested multivariate ANOVA, with monthly chl *a* values (log transformed) as the response variables and site and sector nested within site as factors.

RESULTS

Mortality

Mortality rates of mussels differed between species (Figs. 1 & 2) and were context dependent, with different responses across site and zone (Table 1: site × zone interaction; Fig. 3). Highest mortality rates were for *Mytilus galloprovincialis* in the mid-zone at BB and lowest mortality rates were for *Perna canaliculus* in the low zone at BB (Figs. 1 & 2). Mortality rates were generally lower for *P. canaliculus* than for *M. galloprovincialis* in the mid-zone and in the low zone at BB (Fig. 1). Mortality in the 'worst' habitat, the mid-zone at BT for *M. galloprovincialis*, was far higher, 9.9-fold (95% confidence range: –2.5 to 22.4-fold), than was mortality in the 'best' habitat, the low zone at BB for *P. canaliculus* (Fig. 1, linear contrasts, $p < 0.0001$).

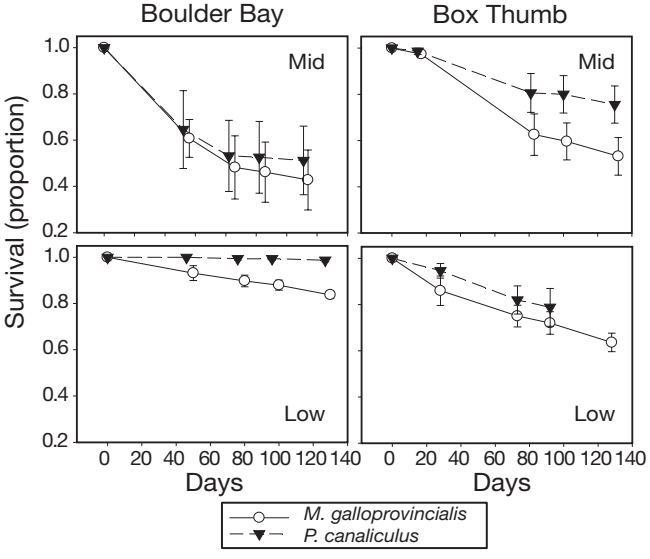

Fig. 1. *Perna canaliculus* and *Mytilus galloprovincialis.* Survival (mean proportion ± 1 SE) over time of the mussels in translocation experiments in the mid- and low zones at Boulder Bay and Box Thumb, Godley Head, South Island, New Zealand

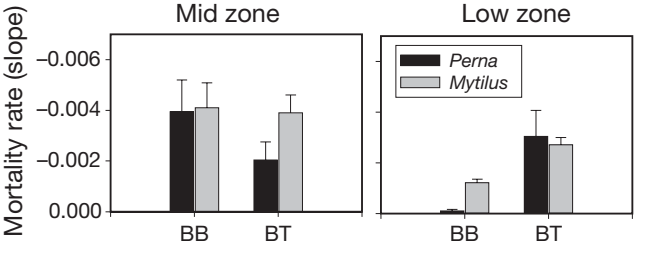

Fig. 2. *Perna canaliculus* and *Mytilus galloprovincialis.* Mortality rates (mean +1 SE), estimated as the average slope of the per-plot survival curves, of mussels in translocation experiments at Boulder Bay (BB) and Box Thumb (BT)

Table 1. Three-way ANOVA testing the effect on mussel mortality of site, zone, and species. Mortality rate was estimated as the slope of a linear regression of the proportion of mussels surviving vs. days. Proportional survival data were arcsine transformed for analysis. Three outliers were removed for this analysis. Significant p-values in bold

Source of variation	df	MS	*F*	p
Site	1	1.9844×10^{-5}	9.01	**0.005**
Zone	1	2.5257×10^{-5}	11.48	**0.002**
Species	1	2.5130×10^{-5}	11.42	**0.002**
Site × Zone	1	3.1505×10^{-5}	14.31	**0.0007**
Site × Species	1	0.0670×10^{-5}	0.30	0.58
Zone × Species	1	0.0049×10^{-5}	0.02	0.88
Site × Zone × Species	1	0.3211×10^{-5}	1.46	0.24
Error	29	0.2201×10^{-5}		

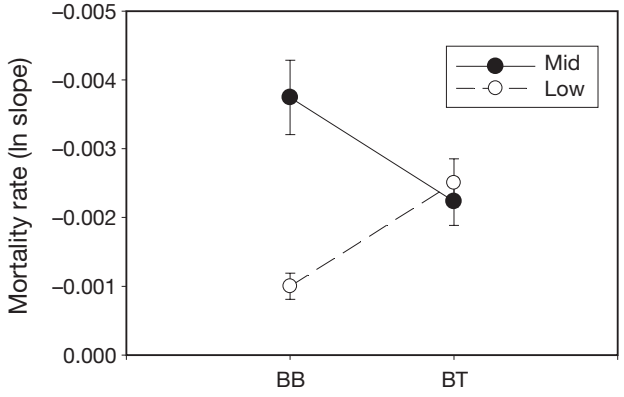

Fig. 3. *Perna canaliculus* and *Mytilus galloprovincialis.* Analysis of 2-way interaction (Table 1) between site and zone in mussel mortality (mean ± 1 SE). BB: Boulder Bay; BT: Box Thumb

Table 2. *Perna canaliculus* and *Mytilus galloprovincialis.* Summary of results, comparing predicted or expected effects with observed effects of different factors (site, zone) on the measures of performance of mussels. Bold indicates observed results that were consistent with expectations. BB: Boulder Bay; BT: Box Thumb; M: mid; L: low

Measure	Species	Site			Zone		
		Expected	Zone	Observed	Expected	Site	Observed
Mortality rate	*Perna*	BB<BT	Mid	BB=BT	M>L	BB	**M>L**
			Low	**BB<BT**		BT	M=L
	Mytilus	BB≥BT	Mid	**BB=BT**	M>L	Both	**M>L**
			Low	BB<BT			
Growth rate	*Perna*	BB>BT	Mid	BB<BT	M<L	Both	**M<L**
			Low	BB≤BT			
	Mytilus	BB≤BT	Mid	**BB<BT**	M<L	Both	**M<L**
Relative tissue mass	*Perna*	BB>BT	Mid	BB<BT	M<L	Both	**M<L**
			Low	BB≤BT			
	Mytilus	BB≤BT	Both	**BB<BT**	M<L	Both	**M<L**
RNA:DNA	*Perna*	BB>BT	Both	**BB>BT**	M<L	Both	M=L
	Mytilus	BB≤BT	Both	**BB<BT**	M<L	Both	M=L

Between zones. For *Perna canaliculus* mortality at BB was greater in the mid-zone (slope = –0.0066) than in the low zone (slope = –0.00058, p = 0.01, n = 10), but at BT did not differ between zones (p = 0.51). For *Mytilus galloprovincialis* mortality across both sites was greater in the mid-zone (slope = –0.006) than in the low zone (slope = –0.004, p = 0.01, n = 20).

Between sites. For *Perna canaliculus*, between-site mortality in the mid-zone did not differ (Figs. 1 & 2; linear contrasts, p = 0.26), but in the low zone the mortality rate of *P. canaliculus* at BT (slope = –0.0053) was 6.5-fold higher (95% confidence range: –2.5 to 15.5-fold) than at BB (slope = –0.00058) (linear contrasts, p = 0.028, n = 10). For *Mytilus galloprovincialis*, between-site mortality in the mid-zone also did not differ (Figs. 1 & 2; linear contrasts, p = 0.96), but in the low zone mortality was also higher at BT (slope = –0.0049) than at BB (slope = –0.0032, p = 0.02, n = 10). Combining both species, mortality rates in the mid-zone at BB were approximately twice those at BT.

For *Perna canaliculus*, these data suggest that from a survival standpoint conditions were best in the low zone at BB, were less favorable in both mid-zones, and were least favorable at BT in the low zone (Fig. 2). For *Mytilus galloprovincialis*, the data indicate that the mid-zone was least favorable and the low zone was most favorable, independent of site. Thus, as expected relatively wave-sheltered conditions and living higher on the shore may be less favorable for survival of the green-lipped mussel (Table 2). *M. galloprovincialis* mortality was also greater higher on the shore as predicted, but contrary to expectation, the blue mussel survived better, not worse, in the low zone at the more wave-exposed site (Fig. 2, Table 2).

Growth

Growth rates of the mussels varied by site and zone, but did not vary between species (Fig. 4). Mussel growth rate in the low zone was 3.3-fold higher (0.7- to 6.0-fold) than in the mid-zone (linear contrasts, p < 0.0001). Overall, growth rates were greater at BT than BB.

Between zones. For *Perna canaliculus* the growth rate was slower in the mid-zone than in the low zone (Fig. 4; linear contrasts, p = 0.0006, n = 17). For *Mytilus galloprovincialis*, between-site growth in the mid-zone also was less at BB than at BT (Fig. 4; linear contrasts, p < 0.0001, n = 9). Growth was slower across both sites in the mid-zone than

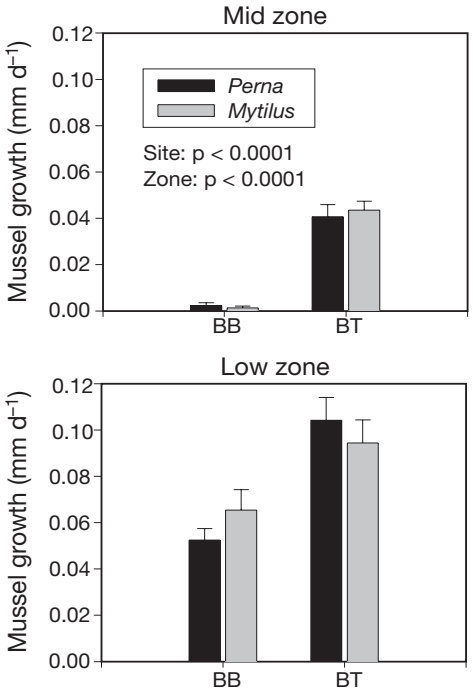

Fig. 4. *Perna canaliculus* and *Mytilus galloprovincialis.* Growth rates (mean + 1 SE) (mm d^{-1}) of mussels in the translocation experiments at Boulder Bay (BB) and Box Thumb (BT). Data were ln(x + 1) transformed for analysis, n = 34. Data were analyzed with a 3-way ANOVA; the effect of species and all interactions were not significant at α = 0.05

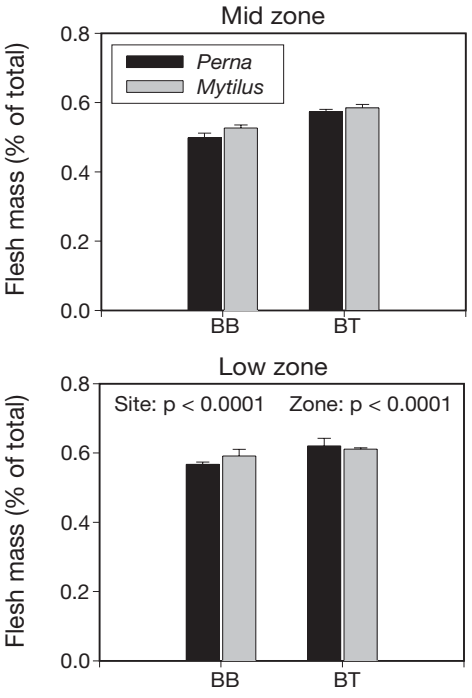

Fig. 5. *Perna canaliculus* and *Mytilus galloprovincialis.* Proportion of total mass consisting of tissue of mussels (mean + 1 SE) in the translocation experiments at Boulder Bay (BB) and Box Thumb (BT). Proportion data were arcsine-transformed for analysis, n = 33. Data were analyzed with 3-way ANOVA; the effect of species and all interactions were not significant at α = 0.05

in the low zone (Fig. 4; linear contrasts, p = 0.0002, n = 18). Note that average growth rates of the 2 mussel species by zones across sites were nearly identical.

Between sites. For *Perna canaliculus*, growth at BT was 2.3-fold faster (0.7- to 4.0-fold) than at BB. Growth in the mid-zone was greater at BT (linear contrasts, p < 0.0001, n = 9) than at BB, but, despite a similar trend in the low zone, sites did not differ (p = 0.08). For *Mytilus galloprovincialis* growth at BT was 1.8-fold faster (0.7- to 2.9-fold) than at BB. Growth in the mid-zone was greater at BT (linear contrasts, p < 0.0001, n = 17) than at BB, but as with *P. canaliculus* the similar trend in the low zone was not significant (p = 0.07). The consistently lower growth at BB and in the mid-zone suggests that, at least as reflected in shell growth rates, the low zone was the more favorable zone, and BT was the more favorable site.

Relative tissue mass

Trends similar to those seen for growth were seen with relative tissue mass (RTM; Fig. 5). As reflected by the proportion of the total mass consisting of tissue, RTM varied by site and zone, but not species (Fig. 5). RTM at BT low was 1.06-fold (0.9- to 1.16-fold) that at BT mid, 1.06-fold (0.96- to 1.19-fold) that at BB low, and 1.20-fold (0.96- to 1.55-fold) that at BB mid (linear contrasts, p < 0.01 or less). The tissue fraction at BT mid was 1.13-fold (0.96- to 1.40-fold) that at BB mid (linear contrasts, p < 0.0001). Thus, as indexed by RTM, the BB mid-zone was least favorable, and the BT low zone was most favorable for both mussels. Not surprisingly, differences in growth rate evidently translate into differences in mussel condition, as reflected in the proportion of tissue to the total mass.

RNA:DNA ratios

The capacity for protein synthesis, a measure of short-term growth indexed by RNA:DNA ratios, varied by tissue (Fig. 6; 4-way ANOVA, p < 0.0001) and by species, but differently by site (Fig. 6; 4-way ANOVA, p = 0.0003). Ratios did not differ between zones. RNA:DNA ratios were 1.62-fold higher (0.85- to 2.84-fold) in adductor tissue than in gill tissue (linear contrasts, p <0.0001). Focusing on adductor tissue, which appeared more sensitive to between-site and species differences (Fig. 6), species RNA:DNA ratios varied by site (Fig. 6). Ratios for *Perna canaliculus* at BB were not different from those for *Mytilus galloprovincialis* at BT

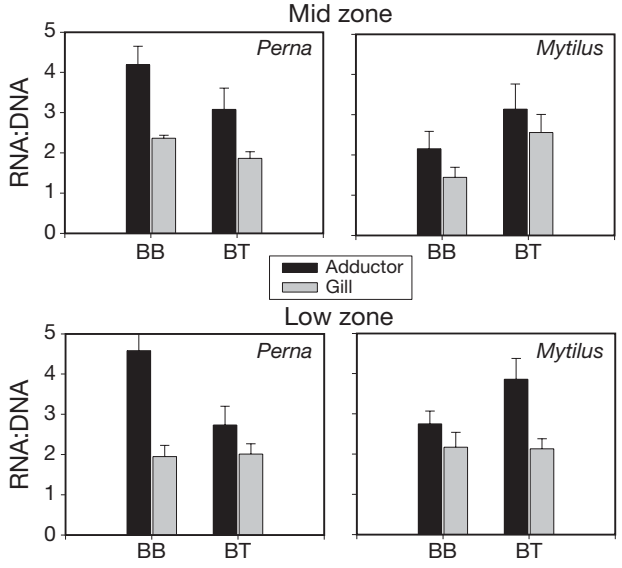

Fig. 6. *Perna canaliculus* and *Mytilus galloprovincialis*. RNA:DNA ratios (mean + 1 SE) of mussels in translocation experiments at Boulder Bay (BB) and Box Thumb (BT). Tissues sampled were adductor muscle and gill. Data were ln(x + 1) transformed for analysis, n = 147. Data were analyzed with 4-way ANOVA (site, zone, species, tissue); tissue was significant as a main effect ($p < 0.0001$), but the zone effect and all interactions but site × species ($p = 0.0003$) were not significant at $\alpha = 0.05$

(linear contrasts, p = 0.41), but were 1.24-fold higher (0.8- to 1.82-fold) than ratios for *P. canaliculus* at BT (linear contrasts, p = 0.043) and 1.52-fold higher (0.87- to 2.48-fold) than ratios for *M. galloprovincialis* at BB (linear contrasts, $p < 0.0001$). Ratios for *M. galloprovincialis* at BT did not differ from those for *P. canaliculus* at BT (linear contrasts, p = 0.21), but were 1.41-fold greater (0.84- to 2.21-fold) than ratios for *M. galloprovincialis* at BB (linear contrasts, p = 0.001). RNA:DNA ratios of *P. canaliculus* at BT did not differ from those of *M. galloprovincialis* at BB (linear contrasts, p = 0.07). Surprisingly, ratios did not differ between zone for either mussel (p = 0.23 or more). Given that ecological performance (mortality, growth, RTM) varied between zones, it is unclear why no difference in RNA:DNA ratios was observed with zone.

Temperature

Air temperatures were higher at BB than at BT in December and January, but not in February (Fig. 7; *t*-tests). Although temperatures were sometimes higher at one site and at other times higher at the other, at BB there were a number of several-day-long periods in which temperatures were often substantially

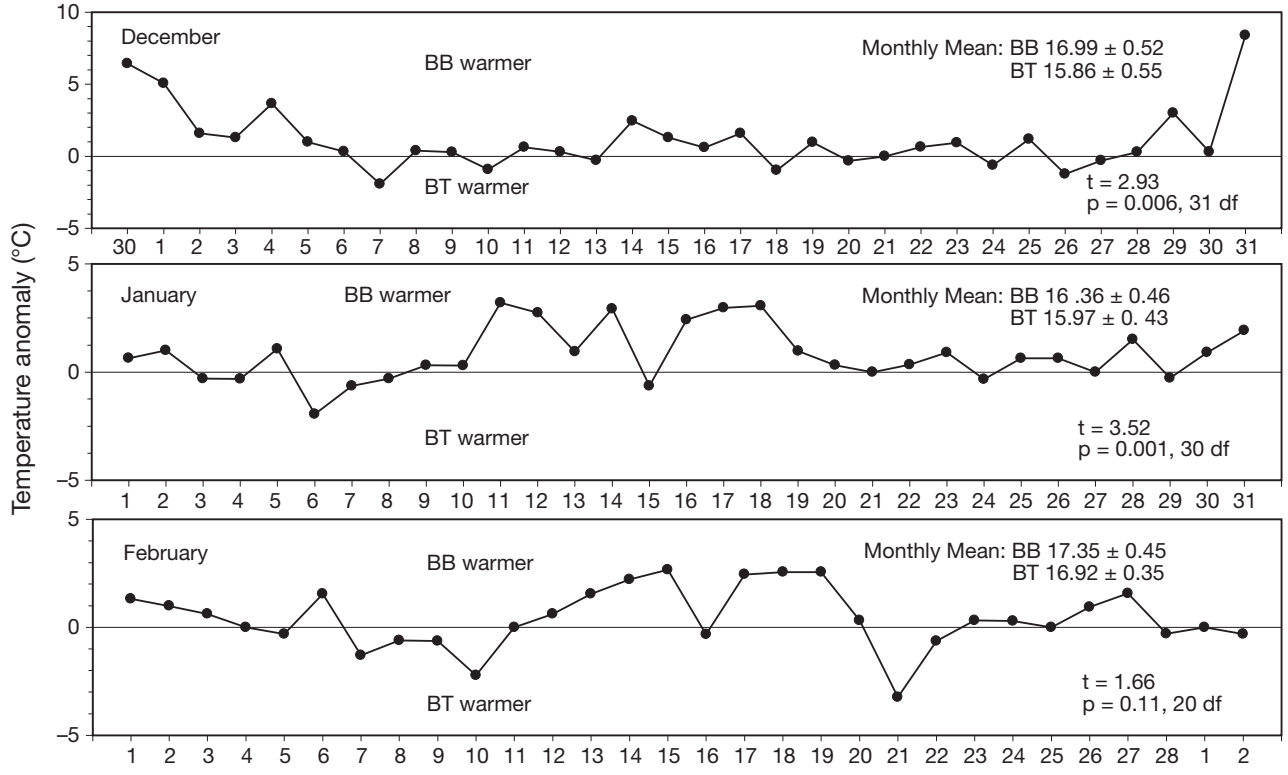

Fig. 7. Daytime low tide air temperature 'anomalies' at Boulder Bay (BB) and Box Thumb (BT) in December 1994, and January and February 1995. Values above the 0 line indicated that BB was warmer, and values below the line indicate that BT was warmer. Monthly means are averages (± SE) across all daily measurements for the month

higher (e.g. 3 to 9°C) during low tide. Such periods at BT were fewer, shorter, and rarely reached differences of comparable magnitude. Although such measures are crude and may not accurately reflect the body temperature of intertidal invertebrates (Helmuth & Hofmann 2001), these data suggest that BB can be more stressful during low tide.

Chl *a*

Phytoplankton (chl *a*) concentration did not vary among sites or between sectors within sites in November or December (Fig. 8, Tables 3 & 4). In contrast, in January and February, chl *a* concentration varied among sites and between sectors within sites (Tables 3 & 4). However, the absolute magnitude of chl *a* was generally low (usually $<2 \times$ g l^{-1}) and among- and within-site variation was relatively inconsistent, suggesting that ecologically no strong gradient in food concentration occurs within the ~2 km extent of the study region.

DISCUSSION

Factors underlying mussel responses: horizontal vs. vertical gradients

The relatively high mortality in the low zone at BT of *Mytilus galloprovincialis* and especially of *Perna canaliculus* was unexpected (Fig. 1). This could be a consequence of predation, but on balance this seems unlikely. Recent studies have shown that fish and crab predation on small mussels (~10 to 15 mm) can be intense at this site in particular and is generally higher where there are subtidal rocky reefs that harbor fish and crab populations (Rilov & Schiel 2006). Arguing against this possibility, however, the mussels used in our experiments were large (40 to 60 cm) and thus probably beyond the handling size range of the mobile predators. Further, large mussels are naturally abundant from the low to upper mid-zone at both sites, suggesting that predation, on large mussels at least, is weak (e.g. Menge et al. 1999). The mechanisms underlying the high mortality of mussels in the low zone at BT remain unclear.

As expected (Table 2), both mussels grew faster in the low zone than in the mid-zone (Fig. 4). These patterns were mirrored by RTM differences. Mussel growth was 3.1-fold greater in the low than the mid-zone. In the mid-zone growth was 17- to 33-fold greater at BT than at BB, a much greater difference than the 1.4- to 1.8-fold between-site difference in the

Table 3. Univariate ANOVA in chlorophyll *a* concentrations at Boulder Bay, Box Thumb, and Black Point. Bold: Bonferroni-corrected (p = 0.05/4 = 0.0125) significant univariate tests

Source	df	MS	*F*	p
Effect site				
Nov	2	0.0091	0.15	0.86
Error	12	0.0611		
Dec	2	0.0336	4.73	0.03
Error	12	0.0070		
Jan	2	0.0282	10.80	**0.002**
Error	12	0.0026		
Feb	2	0.0479	36.67	**0.000008**
Error	12	0.0013		
Effect site (sector)				
Nov	3	0.0700	1.14	0.37
Error	12	0.0611		
Dec	3	0.0213	3.00	0.07
Error	12	0.0071		
Jan	3	0.0337	12.91	**0.0005**
Error	12	0.0026		
Feb	3	0.1517	116.17	**<0.000001**
Error	12	0.0013		

Table 4. Multivariate nested ANOVA in chlorophyll *a* concentrations at Boulder Bay, Box Thumb, and Black Point. Bold: Bonferroni-corrected (p = 0.05/4 = 0.0125) significant multivariate tests

Source	Wilks' λ	*F*	df	p
Effect site				
Error	0.0550	7.35	8.18	**0.0002**
Effect site (sector)				
Error	0.0061	11.8	12.24	**<0.000001**

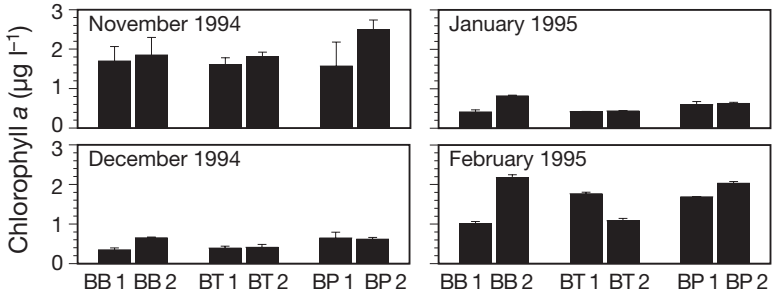

Fig. 8. Chlorophyll *a* in November and December 1994 and January and February 1995 at Boulder Bay (BB), Box Thumb (BT), and Black Point (BP). BB1 and BB2, BT1 and BT2, and BP1 and BP2 indicate the averages (+ 1 SE) for the 2 sectors nested within each site

low zone. The between-site differences in the mid-zone were clearly due to the very slow growth in BB mid-zone plots. These observations on growth and RTM suggest that, for both mussels, conditions for growth were better at the less wave-exposed site and in the low zone compared to in the mid-zone.

Despite somewhat higher temperatures at BB than at BT in December 1994 and January 1995 (Fig. 7), there was no between-site difference in survival in the experiments, at least in the mid-zone (Fig. 2). The mid-zone growth rate, in contrast, was sharply reduced at BB compared to BT (Fig. 4). Since food abundance varied little among sites (Fig. 8), the difference in growth may be attributable to thermal stress. Another factor is the angle of inclination of the substratum. BB surfaces were steep compared to BT surfaces, and water drained more quickly off the rock at this site as a result, likely leading to faster drying of the biota.

RNA:DNA patterns suggest that, at least as indexed by this measure, short-term growth conditions were generally more favorable for *Perna canaliculus* at BB and more favorable for *Mytilus galloprovincialis* at BT. Since food concentrations did not differ between sites, this result suggests that a short-term capacity for growth is an integrated result of food, stress, and possibly other differences between sites. We do not know why no difference occurred between zones. It is possible that mussels transplanted to the upper edge of the mussel bed had acclimated to conditions at this shore level by the end of the experiment.

More recent results provide further insight into the responses of these mussels to vertical stress gradients. In 2002 and 2003 at BT (B. A. Menge et al. unpubl. data), we sampled mussels of both species from the upper and lower edges of their range of overlap in the mussel zone and quantified heat-shock proteins (Hsp). Hsps are molecular chaperones found in all cells that are used to repair proteins that have been damaged by any of a variety of stresses, including thermal, pH, anoxia, or heavy-metal contamination (Feder & Hofmann 1999, Dahlhoff 2004). Hsps refold partially denatured proteins, and thus enhance the ability of the cell machinery to recover normal physiological function. Hsps come in 2 'isoforms', stress-inducible Hsp70 and constitutive Hsp70. The former is an up-regulated form that responds to sublethal stresses, while the latter is always present, and is involved in normal protein synthesis (Dahlhoff 2004, Halpin et al. 2004). In our studies, inducible Hsp was higher overall in *Mytilus galloprovincialis* than in *Perna canaliculus* (linear contrasts in 3-way ANOVA, main effect of species; 1.11 ± 0.04 (SE) vs. 0.96 ± 0.04 relative density units, respectively; $F_{1,100} = 6.10$, p = 0.015). For both species, inducible Hsp was greater in mussels from the upper edge than from the lower edge (linear contrasts in 3-way ANOVA, species × zone interaction: upper vs. lower *M. galloprovincialis* = 1.37 ± 0.06 vs. 0.84 ± 0.06, $F_{1,100} = 39.3$, p < 0.0001; upper vs. lower *P. canaliculus* = 1.10 ± 0.06 vs. 0.82 ± 0.06, $F_{1,100} = 10.7$, p = 0.001). Further, inducible Hsp was greater in upper level *M. galloprovincialis* than in upper level *P. canaliculus* (linear contrasts in 3-way ANOVA, species × zone interaction: $F_{1,100} = 10.1$, p = 0.002), but did not differ between species at the lower level (p = 0.8) (B. A. Menge et al. unpubl. data). No differences were seen in constitutive Hsp between species (p = 0.18), while this isoform was marginally higher in upper zone mussels (p = 0.046). Higher levels of inducible Hsp are an indication that the species endured a stronger stress event and also may have a greater ability to repair damage after stress (Dahlhoff 2004, G. Somero pers. comm.). Hence, these data suggest that *M. galloprovincialis* may be better able to deal with elevated temperatures than is *P. canaliculus*, at least at BT.

The implications of this physiological response for the relative tolerances of each species to stress were supported by field observations at BT of mortality differences between the species after an extreme temperature event (Petes et al. 2007). In January 2005, 3 straight days of +30°C temperatures were recorded at the lower edge of the mussel bed, with a maximum of 36.9°C recorded on 15 January. From 2002 to 2004, the highest average weekly temperature at low tide was 23°C. Immediately after this thermal event, we observed that many *Perna canaliculus* near the upper edge of the mussel bed were dead, as indicated by gaping shells with bits of decaying mussel tissue still attached to the shells. We quantified the number of dead mussels of each species in 0.25 m^2 quadrats (n = 5 per zone) at the upper and lower edges of their range of overlap within the bed, and found no dead mussels at the lower edge (0% mortality), but, at the higher edge, 3.4 ± 1.2% of *Mytilus galloprovincialis* and 35.4 ± 5.0% of *P. canaliculus* were dead (Petes et al. 2007). These observations are consistent with the conclusion that *P. canaliculus* is less tolerant to thermal stress at higher levels on the shore than is *M. galloprovincialis*.

Comparison between expected and observed patterns

For differences between zones for both mussels, 6 of 9 observed patterns were as expected (Table 2), 3 of 5 for *Perna canaliculus* and 3 of 4 for *Mytilus galloprovincialis*. The primary surprises were that: (1) *P. canaliculus* grew slower, not faster than *M. galloprovincialis*; (2) *P. canaliculus* had lower, not higher RTM at BB than *M. galloprovincialis*; (3) that for both mussels, the short-term capacity for growth did not vary by zone; and (4) that *P. canaliculus* had higher survival in the mid-zone at BT

than did *M. galloprovincialis*. For differences between sites for both mussels, 6 of 12 observed patterns were as expected (Table 2). For *P. canaliculus*, only 2 of 7 possible outcomes (in 3 cases, mid- and low-zone patterns were different) met our expectations based on how this mussel, most abundant in low zones and at more wave-exposed locations, might respond to gradients of food, wave exposure, and environmental stress. In contrast, *M. galloprovincialis* performed as expected in 4 of 5 cases. These trends are consistent with our suggestion that the vertical tidal gradient generates stronger, more contrasting differences in conditions for mussels than do the differences along the horizontal wave-exposure gradient.

Thus, in general, it appears that overall ecological performances are consistent with the idea that *Perna canaliculus* performs best in low, wave-exposed habitats (as indicated by survival in experiments and after the thermal event, growth, Hsp, and RTM in the low zone). With respect to wave exposure, *Mytilus galloprovincialis* proved to be more of a habitat generalist than expected, showing better performance in some respects at the wave-exposed area (survival), but otherwise showing reduced performance at the wave-exposed site (growth, RTM, RNA:DNA). Its poorer performance in the mid- than in the low zone was expected, and, as indicated by RNA:DNA ratios, Hsp, and survival of the thermal stress event (but not survival in the transplant experiment), it performed relatively better higher on the shore than did *P. canaliculus*. For RNA:DNA, the inverse pattern of ratios for *P. canaliculus* (high at BB, low at BT) and *M. galloprovincialis* (low at BB, high at BT) are consistent with the hypothesis that growth conditions are better for each mussel at the site at which each does better ecologically (survival for *P. canaliculus* at BB, growth for *M. galloprovincialis* at BT).

CONCLUSIONS

In general, these results suggest that environmental conditions are important to mussel physiology and perhaps distribution. *Perna canaliculus* seems to enjoy superior ecological and physiological performance at the more wave-exposed and lower shore portions of the intertidal habitat, while *Mytilus galloprovincialis* seems to tolerate a broader range of conditions, but to perform less well than *P. canaliculus* in the ecologically and, in some respects, physiologically more favorable environmental conditions.

Thus, the simplest interpretation of the distributional patterns of these mussel species is one of differential tolerances to physical conditions along the horizontal and vertical environmental gradients. *Perna canaliculus* performed better in the low zone, growing faster and having higher RTM, and surviving best in experiments at the low, more wave-exposed BB. The higher Hsp in high *P. canaliculus* and particularly the exceptionally high mortality of *P. canaliculus* observed during the extreme stress event in 2005 relative to that of *Mytilus galloprovincialis* (Petes et al. 2007) suggest that the relative scarcity of the green-lipped mussel on the upper shore is due to intolerance of sporadic and unpredictable extremes in thermal stress. The higher RNA:DNA ratios at BB are also consistent with this being the more optimal habitat for *P. canaliculus*. Growth and tissue mass data, in contrast, suggest that in these measures the more protected site favors better individual performance of the green-lipped mussel. Thus, the upper limit of *P. canaliculus* may fluctuate as conditions fluctuate between the usual relatively benign conditions that normally occur and the rare extreme thermal events that kill a high fraction of those *P. canaliculus* that colonize this part of their range.

Similar patterns were observed for *Mytilus galloprovincialis*, although BT, the less wave-exposed site, was more consistently the 'better' site for this mussel. The Hsp and surviving extreme thermal stress results suggest that this mussel has a broader tolerance of stressful conditions than does the green-lipped mussel, and thus can occupy a higher level of the shore. The primary unanswered question in this study is why, if the low zone is the better habitat for *M. galloprovincialis* (as suggested by the survival, growth, and tissue fraction data), this mussel is less abundant in the low than the mid-zone? Answering this question will probably require longer term field experimentation, testing species interactions coupled with more intensive analyses of the physiological mechanisms in relation to organismal responses to environmental gradients. We conclude that integrating ecological field experiments with physiological and molecular measurements is a promising approach for increasing our mechanistic understanding of how species performance and interactions vary along environmental gradients.

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LITERATURE CITED

Bentle LA, Dutta S, Metcoff J (1981) The sequential enzymatic determination of DNA and RNA. Anal Biochem 116:5–16

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18: 119–125

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723

Dahlhoff EP (2004) Biochemical indicators of stress and metabolism: applications for marine ecological studies. Annu Rev Physiol 66:183–207

Dahlhoff EP, Menge BA (1996) Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. Mar Ecol Prog Ser 144:97–107

Dahlhoff EP, Stillman JH, Menge BA (2002) Physiological community ecology: variation in metabolic activity of ecologically important rocky intertidal invertebrates along environmental gradients. Integr Comp Biol 42:862–871

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41: 351–389

Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NY

Feder ME, Hofmann GE (1999) Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. Annu Rev Physiol 61:243–282

Foster AR, Houlihan DF, Hall SJ (1993) Effects of nutritional regime on correlates of growth rate in juvenile Atlantic cod *Gadus morhua*: comparisons of morphological and biochemical measurements. Can J Fish Aquat Sci 50: 502–512

Halpin PM, Menge BA, Hofmann GE (2004) Experimental demonstration of plasticity in the heat shock response of the intertidal mussel *Mytilus californianus*. Mar Ecol Prog Ser 276:137–145

Helmuth BST, Hofmann GE (2001) Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. Biol Bull 201: 374–384

Judge ML, Coen LD, Heck KL Jr (1992) The effect of long-term alteration of *in situ* currents on the growth of *Mercenaria mercenaria* in the northern Gulf of Mexico. Limnol Oceanogr 37:1550–1559

Knox GA (1953) The intertidal ecology of Taylor's Mistake, Banks Peninsula. Trans R Soc NZ 81:189–220

Lamont IC (1996) New Zealand nautical almanac. Hydrographic Office of the Royal New Zealand Navy, Auckland, and GP Publications, Wellington

Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecol Monogr 46:355–393

Menge BA (1992) Community regulation: Under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130: 730–757

Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol Monogr 64:249–286

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997) Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proc Natl Acad Sci USA 94:14530–14535

Menge BA, Daley BA, Lubchenco J, Sanford E, Dahlhoff E, Halpin PM, Hudson G, Burnaford JL (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecol Monogr 69:297–330

Menge BA, Blanchette C, Raimondi P, Freidenburg T and 6 others (2004) Species interaction strength: testing model predictions along an upwelling gradient. Ecol Monogr 74: 663–684

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York

Petes LE, Menge BA, Murphy GD (2007) Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. J Exp Mar Biol Ecol (in press)

Rilov G, Schiel DR (2006) Seascape-dependent subtidal–intertidal trophic linkages. Ecology 87:731–744

Sanford E, Bermudez D, Bertness MD, Gaines SD (1994) Flow, food supply and acorn barnacle population dynamics. Mar Ecol Prog Ser 104:49–62

Schiel DR (2006) Guide to common intertidal species of the South Island, New Zealand. Marine Ecology Research Group, University of Canterbury, Christchurch

Sokal RR, Rohlf FJ (1995) Biometry. WH Freeman, New York

Winer BJ, Brown DR, Michels KM (1991) Statistical principles in experimental design, 3rd edn. McGraw-Hill, New York

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