Environmental stress decreases survival, growth, and reproduction in New Zealand mussels

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Abstract

To test the effects of environmental stress on mussel growth and reproduction, reciprocal transplants of two New Zealand mussel species, *Mytilus galloprovincialis* and *Perna canaliculus*, were performed between the high (high-stress) and low (low-stress) elevation edges of an intertidal mussel bed in New Zealand. Mussels transplanted to the high edge of the mussel bed exhibited slower growth, lower mass of reproductive tissue, and stress-induced spawning, indicating that stress impairs the ability of these organisms to grow and reproduce. *P. canaliculus* grew more quickly than *M. galloprovincialis* but allocated less relative energy towards reproduction. An anomalous high aerial temperature event led to differential mortality of the two mussel species in the field, indicating that *P. canaliculus* is less thermotolerant than *M. galloprovincialis*. These results suggest that the abundance of *P. canaliculus*, the competitive dominant on New Zealand rocky shores, may decrease in the face of increasing aerial temperatures predicted under global climate change scenarios, drastically altering intertidal community structure.
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1. Introduction

Global temperatures have risen 0.6 °C during the past century and are predicted to continue rising by 1.4–5.8 °C over the next century (Houghton et al., 2001). Expected alterations to the physical environment under climate change scenarios include potential sea level rise, warming of both air and water temperatures, alterations to oceanic circulation, and increasing frequency and

severity of storms (e.g. Lubchenco et al., 1993; Houghton et al., 2001). Climate change may also lead to numerous biological consequences for organisms, including phenological shifts and alterations to species ranges (Parmesan and Yohe, 2003). Marine systems such as coral reefs (Hoegh-Guldberg, 1999), kelp forests (Schiel et al., 2004), and the rocky intertidal zone (Sagarin et al., 1999) have already exhibited shifts in community structure as a result of warming water and air temperatures. It is likely that environmental stress will increase under scenarios of climate change, as increasing frequency and severity of aerial temperature events are predicted to occur (Houghton et al., 2001).

The rocky intertidal zone is an ideal model system for examining the effects of environmental stress, as the

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physical environment is inherently stressful to the biota that live in this habitat. Intertidal organisms are exposed to both terrestrial and marine conditions on a daily basis, and timing of aerial exposure varies with the tidal cycle (Denny and Paine, 1998; Helmuth, 1999; Helmuth et al., 2002). Upper distributional limits in the intertidal zone are thought to be determined primarily by desiccation and temperature stress, whereas lower limits are typically established by species interactions (e.g. Connell, 1961; Paine, 1966; Paine, 1974; Lubchenco, 1980). While environmental stress in the upper limit of the rocky intertidal zone is driven by a synergistic combination of temperature, desiccation, and decreased food supply that potentially result from exposure at low tide, high aerial temperatures appear to cause the most dramatic sublethal (e.g. Helmuth and Hofmann, 2001) and lethal (Tsuchiya, 1983) physiological consequences for intertidal organisms.

Mytilid mussels are dominant space-occupiers on temperate rocky shores throughout the world (e.g. Seed and Suchanek, 1992) and span the entire vertical area between the low zone, an area of relatively low temperature and desiccation stress, and the high zone, a potentially high-stress environment. High aerial temperatures during low tide can lead to protein damage (e.g. Helmuth and Hofmann, 2001; Halpin et al., 2004), reduced growth (e.g. Menge et al., 2002), and mass mortality (Tsuchiya, 1983) in mussels at the upper edge of the mussel bed. However, very little is known about the effects of environmental stress on intertidal mussel reproduction.

Reproduction can be inhibited by sublethal environmental stress, because animals reallocate energy away from gamete production and towards defense and repair mechanisms (e.g. Michalek-Wagner and Willis, 2001). Timing of reproduction can be modulated under an altered thermal regime, potentially having consequences of asynchrony and overall decreased fertilization and recruitment success (Walther et al., 2002; Philippart et al., 2003). All of these factors can lead to a decreased number of propagules that supply adult populations and communities.

On the east coast of the South Island of New Zealand, rocky shores are dominated by mussels in the mid-zone of the rocky intertidal zone (Knox, 1953; Menge et al., 1999). The two dominant species are *Perna canaliculus* Gmelin and *Mytilus galloprovincialis* Lamarck (Knox, 1953; Menge et al., 1999). Both species undergo gametogenesis throughout the year and exhibit both late winter and late summer spawning events (Kennedy, 1977; Buchanan, 2001). Both mussel species span the vertical gradient between the low zone and the high zone, and *P. canaliculus* appears to be the competitive

dominant, growing large (∼15 cm) at the lower edge of its distribution. However, in the very extreme upper edge of the mussel bed, this species is found only in crevices, suggesting that it is less thermotolerant than *M. galloprovincialis* (Kennedy, 1976).

The purpose of this study was to determine the effects of environmental stress on two intertidal mussel species. We predicted that under conditions of high stress, mussels would exhibit decreased growth and energy allocation towards reproduction. We also predicted that *P. canaliculus* would show the greatest responses to sublethal stress. Species-specific responses to stress could provide insight into future alterations to intertidal community structure under warming aerial temperatures predicted from global climate change scenarios.

2. Materials and methods

This study was conducted on the east coast of the South Island of New Zealand, specifically at "Box Thumb" (43°34′ S, 172°48′ E) on Godley Head of the Banks Peninsula near Christchurch. Box Thumb is a small peninsula with a basaltic substrate. Macroalgae and *P. canaliculus* dominate the low zone, *M. galloprovincialis* and *P. canaliculus* dominate the mid-zone, and barnacles dominate the high zone (Menge et al., 1999; Menge et al., in press). Tides are semidiurnal, and low tides often occur during the daytime throughout the summer season, providing the potential for high thermal and desiccation stress.

2.1. Temperature recording

Two TidbiT temperature loggers (Onset Computer Corp., Pocahassett, MA, USA) were deployed in the intertidal zone: one logger was placed above the high edge of the mussel bed ("high-zone logger") and the other was placed in the middle of the mussel bed ("mid-zone logger") on October 26, 2001; these loggers recorded hourly temperatures (air or water depending on tidal cycle) during the summers (October–February) from 2001 to 2005.

2.2. Surveys of mussel reproduction

Surveys of reproduction in natural mussel populations were conducted monthly during the experiment (Dec. 2004–Feb. 2005). Mussels of both species (*M. galloprovincialis* and *P. canaliculus*) were haphazardly collected from the lower edge (∼+1.0 m above MLLW; "low edge") and upper edge (∼+2.0 m above MLLW; "high edge") of the mussel bed (*n*=50 of both species, both edges; total mussels per month=200). All
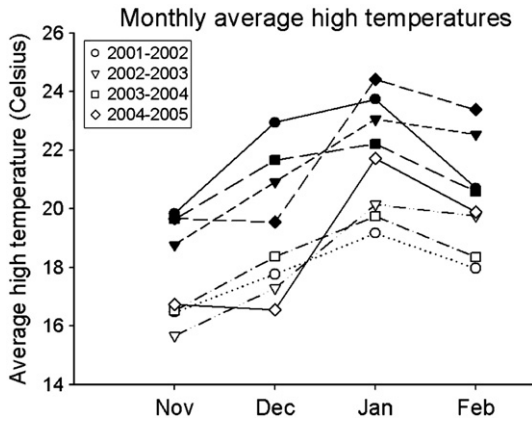
Monthly average high temperatures

Fig. 1. Average monthly high temperatures in high-zone (dark symbols) and mid-zone (open symbols) temperature loggers from November–February of 2001–2005.

mussels collected were in the same size class (approximately 5–7 cm in length) to minimize the influence of size variation.

In a subsample of mussels ($n = 10$ of both species, both edges; total mussels each month = 40), gonadal tissues and somatic tissues (including gills, hepatopancreas, and adductor muscles) were separated and weighed. From these tissues, a gonadosomatic index (GSI; e.g. Roff, 1992) was calculated:

$$GSI = (gonadal\ tissue\ weight)/ \\ (gonadal + somatic\ tissue\ weight)$$

Gonadal tissue from each mussel was collected and placed into 10% formalin in seawater for fixation prior to histological processing to assess spawning activity.

2.3. Histological processing and analyses

Gonadal tissues were dehydrated, embedded in paraffin wax, sliced to 7 μm thickness, and stained with Mayer's haemalum and eosin according to Luna (1968). Each slide was examined under a compound

a. Daily maximum temperature
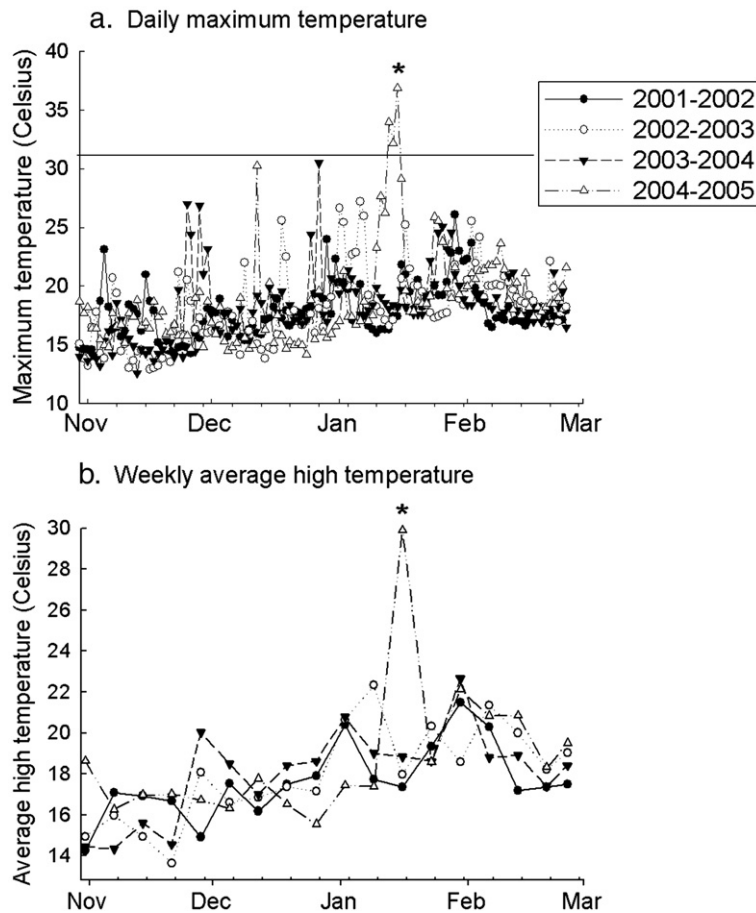

b. Weekly average high temperature

Fig. 2. (a) Daily maximum temperatures (horizontal line indicates 31 °C) and (b) average maximum weekly temperatures for mid-zone temperature logger from October–February of 2001–2005. Asterisks denote heat stress event in Jan. 2005.

Table 1
Spawning activity (% of mussels spawned-out) for surveys of high and low edges of the mussel bed ($n = 9$–10 mussels) from Dec. 2004 to Feb. 2005

Treatment	Species	8-Dec	7-Jan	5-Feb
High edge survey	*M. galloprovincialis*	20%	50%	60%
	P. canaliculus	10%	0%	20%
Low edge survey	*M. galloprovincialis*	0%	20%	10%
	P. canaliculus	10%	10%	10%

microscope (Leica DMLS, Leica Microsystems, Inc., Bannockburn, IL, USA) to look for evidence of spawning. Spawned-out mussels were identified by lack of gametes and only lipid storage tissue remaining.

2.4. Field transplantation and sampling

Mussels of both species were collected haphazardly from the low and high edges of the mussel bed at Box Thumb on October 23, 2004. All mussels collected were between 5 and 7 cm in length. Prior to transplantation, the posterior margin of the shell of each individual was notched with a file; a scar forms at the site of notching, and new shell growth can subsequently be measured from this point (Menge et al., 2004). Growth rate (mm new growth per day) was calculated as:

$$\text{Growth rate} = (\text{New shell growth}/\text{Initial length})/$$
$$(\text{Days since experiment initiation})$$

Mussels were transplanted on the same day as collection into mixed-species plots of 40 individuals (20 *M. galloprovincialis* and 20 *P. canaliculus* per plot). The mussels were reciprocally transplanted between edges and within edges of the mussel bed ($n = 4$ plots per transplant treatment). Between-edge transplants were conducted from low-to-high ("LH") and high-to-low ("HL") edges of the mussel bed. Within-edge transplants were conducted from low-to-low ("LL") and high-to-high ("HH") edges to control for the effect of transplantation stress. Mussels were placed ventral-side down against the rocks to allow for byssal thread attachment using plastic-mesh cages $\sim 20 \times 20$ cm with 10-cm-wide borders (Menge et al., 1994). Mussels were held under mesh for 6 weeks to allow for firm attachment prior to mesh removal, which occurred on December 8, 2004.

Monthly sampling was conducted three times from Dec. 2004–Feb. 2005. Each month, a subsample of four mussels of each species was removed from each plot. For every individual, growth rate was measured, GSI was calculated, and gonadal tissue was fixed for histological processing and analyses as described above.

2.5. Mortality event

In January 2005, high aerial temperatures occurred in Christchurch. During this event, high mussel mortality was discernible in the intertidal zone by the presence of gaping mussels with bits of tissue remaining at Box Thumb. To quantify this event, the numbers of dead and alive mussels of both species were counted in five 0.25 m² quadrats in the low and high edges of the mussel bed. The event also led to high mortality of experimental mussels in the high-edge plots, and as a consequence, individuals from these treatments were unavailable for collection during the February sampling date.

2.6. Statistical analyses

All analyses were performed using JMP 6.0 (SAS Institute Inc., Cary, NC, USA, 2005). For the surveys of reproduction, gonadosomatic index (GSI) data were analyzed as a 3-factor ANOVA, with time, edge, and
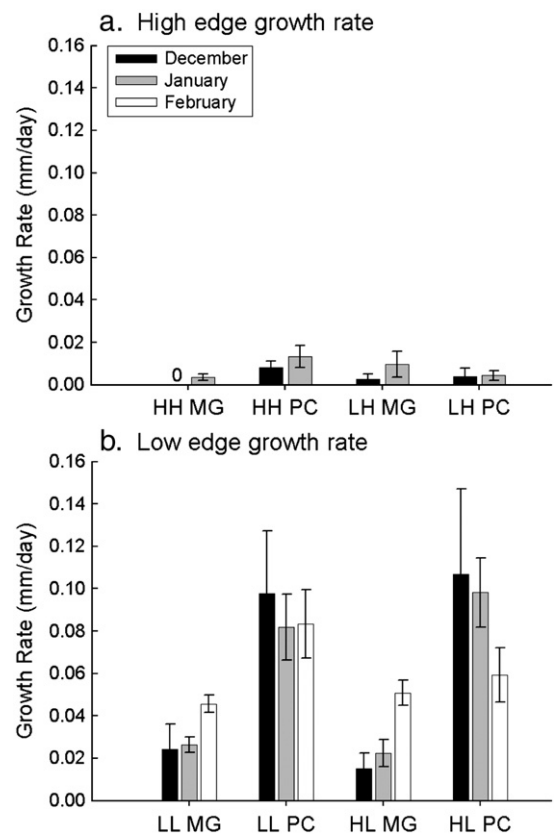

Fig. 3. Growth rates of two mussel species for (a) high-edge and (b) low-edge treatments. Mussels: MG = *Mytilus galloprovincialis*, PC = *Perna canaliculus*; transplant treatments: HH = high-to-high, LH = low-to-high, LL = low-to-low, HL = high-to-low edge. Error bars = standard error. Zero denotes no growth.

Table 2
Results of repeated-measures MANOVA tests for growth, GSI, and percentage of mussels spawned-out

Response variable	Comparison	Parameter	df	F	p
Growth rate	Between edges	Species	1,28	194.60	**<0.0001**
		Edge	1,28	71.49	**<0.0001**
		Edge × species	1,28	12.30	**0.002**
		Time	1,28	5.00	**0.04**
	Within high edge	Species	1,12	1.77	0.21
		Treatment	1,12	0.28	0.61
		Time	1,12	12.83	**0.004**
	Within low edge	Species	1,12	24.01	**0.0004**
		Treatment	1,12	0.09	0.77
		Time	2,11	0.84	0.46
		Time × species	2,11	6.02	**0.02**
Gonadosomatic index (GSI)	Between edges	Species	1,28	45.39	**<0.0001**
		Edge	1,28	22.12	**<0.0001**
		Time	1,28	9.72	**0.004**
		Time × species	1,28	3.56	0.07
	Within high edge	Species	1,12	88.74	**<0.0001**
		Treatment	1,12	19.77	**0.0008**
		Time	1,12	14.41	**0.002**
		Time × treatment × species	1,12	7.37	**0.02**
	Within low edge	Species	1,12	33.82	**<0.0001**
		Treatment	1,12	1.67	0.22
		Time × species	2,11	3.08	0.09
		Time × treatment	2,11	10.21	**0.003**
Percentage of mussels spawned-out	Between edges	Species	1,28	1.44	0.24
		Edge	1,28	13.91	**0.0009**
	Within high edge	Species	1,12	0.57	0.47
		Treatment	1,12	5.85	**0.03**
	Within low edge	Species	1,12	1.80	0.20
		Treatment	1,12	3.87	0.07
		Time	2,11	6.99	**0.01**

Comparisons were performed between edges and subsequently within edges. All results for $p<0.10$ are displayed. Results of interaction terms with $p>0.10$ are not shown. Values for $p<0.05$ are bolded.

species as explanatory variables. For experimental mussels, growth rate, GSI, and percentage of mussels spawned-out were analyzed with RM-MANOVA, and species, edge, and species × edge interactions were investigated for these parameters in December and January. Treatment comparisons were subsequently performed using RM-MANOVA within an edge for Dec.–Feb. for low-edge treatments (LL and HL), and Dec.–Jan. for high-edge treatments (HH and LH). Data were examined for normality and the presence of outliers. To meet the assumption of normality, growth rate data were square root transformed, and percentage of mussels spawned-out were arcsine-square root transformed.

3. Results

3.1. Temperature

Temperatures were consistently higher above the high edge of the mussel bed than in the mussel bed (Fig. 1),

showing that temperatures were higher on average with increasing tidal height in the intertidal zone. While temperatures recorded by these loggers may deviate slightly from mussel body temperatures (e.g. Helmuth and Hofmann, 2001), the recorded temperatures accurately represented aerial temperatures recorded by the New Zealand government for this location and time period (NIWA, 2004, 2005) and capture the magnitude of the temperature event. Extreme high temperatures occurred in mid-January 2005 both in the intertidal zone (Fig. 2) and in the city of Christchurch (NIWA, 2005). The mid-zone temperature logger recorded a high of 36.9 °C in the mussel bed during low tide on Jan. 15, 2005 (Fig. 2a). For 3 days in a row (Jan. 13–15), this logger recorded temperatures above 31 °C, and this was the only time period that this temperature was reached in the four months of temperature recording. In addition, in the previous 3 years, 31 °C had never been reached in the same location during these months (Fig. 2a). Whereas the highest weekly average temperature for 2001–2004

was 23 °C, a weekly average high temperature of 30 °C was reached the week of Jan. 10–16, 2005, indicating the extreme and prolonged heat wave (Fig. 2b). This heat event followed below-average temperatures in late Dec. 2004 through early Jan. 2005 (Fig. 2b, NIWA, 2004).

3.2. Mussel reproduction surveys

Surveys conducted on both mussel species from Dec.–Feb. at the high and low edges of the mussel bed adjacent to experimental plots indicated that *M. galloprovincialis* had higher gonadosomatic indices (GSI) than *P. canaliculus* (ANOVA: $F_{1,108}=113.73$, $p<0.0001$), indicating more relative energy allocation towards reproduction. High-edge mussels had higher overall GSI than the low-edge mussels ($F_{1,108}=13.97$, $p=0.0003$), but a time × edge interaction ($F_{2,108}=3.71$, $p=0.03$) reflected that high-edge mussels had an overall decrease in GSI over the summer sampling period. Spawning activity was higher in the high edge of the mussel bed in *M. galloprovincialis* than *P. canaliculus*, and the drop in GSI over the summer likely resulted from loss of gametes through spawning (Table 1).

3.3. Experimental results: mussel growth rate

Regardless of their origin, growth rates of experimental mussels were higher in low-edge (LL and HL) treatments than high-edge (LH and HH) treatments ($F_{1,28}=71.49$, $p<0.0001$; Fig. 3; see Table 2 for MANOVA results). Growth was faster in *P. canaliculus* than in *M. galloprovincialis* ($F_{1,28}=194.60$, $p<0.0001$; Fig. 3). There was also an edge × species interaction ($F_{1,28}=12.30$, $p=0.002$), indicating that growth rate was dependent on both species and location, with low-edge *P. canaliculus* growing the fastest, followed by low-edge *M. galloprovincialis*, high-edge *P. canaliculus*, and finally high-edge *M. galloprovincialis* growing the slowest. In addition, growth rate marginally increased over time ($F_{1,28}=5.00$, $p=0.04$). Within the high-edge treatments, growth rates did not vary between species ($F_{1,12}=1.77$, $p=0.21$), and HH and LH growth rates were the same ($F_{1,12}=0.28$, $p=0.61$), but growth rate increased over time ($F_{1,12}=12.83$, $p=0.004$). Within the low-edge treatments, growth rates were the same in LL and HL mussels ($F_{1,12}=0.09$, $p=0.77$), but growth was faster in *P. canaliculus* than in *M. galloprovincialis* ($F_{1,12}=24.01$, $p=0.0004$). Overall, growth rate did not change with time ($F_{2,11}=0.84$, $p=0.46$); however, a time × species interaction ($F_{2,11}=6.02$, $p=0.02$) indicated that growth rate decreased in *P. canaliculus* between January and February and increased in *M. galloprovincialis* during the same time period.

3.4. Experimental results: gonadosomatic index (GSI)

Gonadosomatic indices (GSI) were higher in *M. galloprovincialis* than in *P. canaliculus* ($F_{1,28}=45.39$, $p<0.0001$; Fig. 4; see Table 2 for MANOVA results) in both the high ($F_{1,12}=88.74$, $p<0.0001$) and low ($F_{1,12}=33.82$, $p<0.0001$) edges of the mussel bed. The low-edge treatments had higher GSI than the high-edge treatments ($F_{1,28}=22.12$, $p<0.0001$; Fig. 4). GSI decreased between December and January ($F_{1,28}=9.72$, $p=0.004$). In the high edge, the HH treatment mussels had higher GSI than the LH treatment ($F_{1,12}=19.77$, $p=0.0008$). GSI decreased with time in the high edge ($F_{1,12}=14.41$, $p=0.002$), and a time × treatment × species interaction ($F_{1,12}=7.37$, $p=0.02$) showed that GSI decreased in LH *M. galloprovincialis* between December and January. In the low-edge treatments, GSI was higher in HL mussels than LL mussels in February ($t_{1,12}=7.77$, $p<0.0001$).
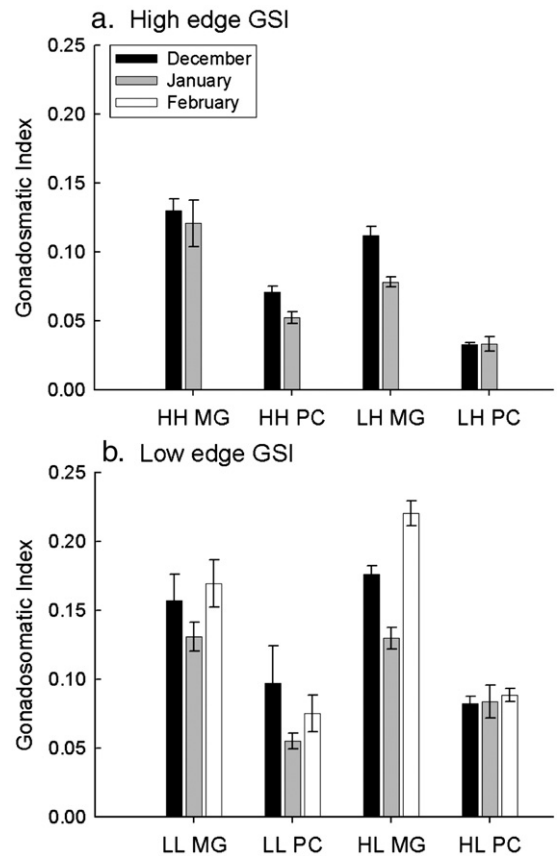

Fig. 4. Gonadosomatic indices (GSI) for (a) high-edge and (b) low-edge treatments. Mussels: MG = *Mytilus galloprovincialis*, PC = *Perna canaliculus*; transplant treatments: HH = high-to-high, LH = low-to-high, LL = low-to-low, HL = high-to-low edge. Error bars = standard error.

3.5. Experimental results: spawning in mussels

Histological analyses indicated that a higher percentage of mussels were spawned-out in the high-edge treatments than in the low-edge treatments ($F_{1,28}$=13.91, p=0.0009; Fig. 5; see Table 2 for MANOVA results). The two mussel species did not differ in spawning activity ($F_{1,28}$=1.44, p=0.24; Table 2), and time did not affect spawning ($F_{1,28}$=1.75, p=0.20). Within the high edge, spawning activity was higher in the LH treatment than the HH treatment ($F_{1,12}$=5.85, p=0.03), suggesting that spawning may occur as a response to increased environmental stress. It is also possible that low-edge mussels could have had more energy available for spawning than high-edge mussels. Within the low edge, there were no species ($F_{1,12}$=1.80, p=0.20) or treatment ($F_{1,12}$=3.87, p=0.07) effects, but spawning activity increased over the course of the summer ($F_{2,11}$=6.99, p=0.01).
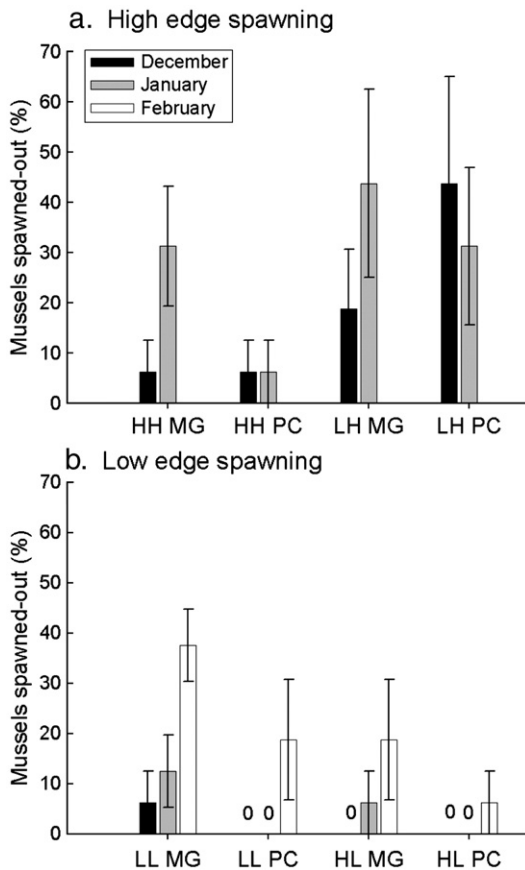

Fig. 5. Percentage of spawned-out mussels for (a) high-edge and (b) low-edge treatments. Mussels: MG = *Mytilus galloprovincialis*, PC = *Perna canaliculus*; transplant treatments: HH = high-to-high, LH = low-to-high, LL = low-to-low, HL = high-to-low edge. Error bars = standard error. Zeros indicate no spawned-out mussels.

3.6. Temperature-related mortality event

No mortality (0%) of either mussel species resulted at the low edge of the mussel bed from the natural temperature stress event between Jan. 13–15, 2005 in Christchurch. However, in the high edge, 35.4% (±5.0% s.e.) of *P. canaliculus* and 3.4% (±1.2% s.e.) of *M. galloprovincialis* were found dead and gaping.

4. Discussion

In the New Zealand rocky intertidal system, environmental stress led to decreased growth rates, reduced energy allocation towards reproduction, and increased spawning activity in two species of mussels. While environmental stress in the high intertidal zone is likely driven by multiple factors, including temperature, desiccation, and reduced feeding time, evidence from this study suggests that exposure to high aerial temperatures has a large, negative effect on intertidal mussels, which is consistent with the results of previous studies (e.g. Helmuth and Hofmann, 2001; Tsuchiya, 1983). One species (*P. canaliculus*) was more negatively affected by thermal stress and suffered mortality as a result. At the lower edge of the mussel bed, *P. canaliculus* dominates due to its rapid growth rate and high competitive ability (Menge et al., in press). However, under extreme high temperatures, survival of *P. canaliculus* higher on the shore was reduced, in contrast to the minimal effect on *M. galloprovincialis*. This result strongly suggests that *M. galloprovincialis* is more tolerant of temperature and desiccation stress. The allocation of more energy towards reproduction, indicated by higher gonadosomatic indices (GSI), further indicates that *M. galloprovincialis* is less sensitive to environmental stress. The complementary tradeoff strategies, faster growth by *P. canaliculus* and greater stress tolerance in *M. galloprovincialis*, may underlie the coexistence of these two species in the rocky intertidal zone.

Effects of transplantation revealed a plastic, inducible response to stress. Growth rates of both mussel species transplanted from the low to high edge of the mussel bed decreased and were identical to control mussels (HH treatment), indicating that environmental stress in the higher intertidal zone led immediately to slower growth rates. Differences in growth rate were likely due to both increased exposure to aerial temperatures and reduced feeding time. A high percentage of mussels (44% of *M. galloprovincialis* and 31% of *P. canaliculus*) transplanted from the low to the high edge (LH treatment) had spawned all of their gametes by January. This is in contrast to the within-low-edge (LL) treatment, in which

few mussels (13% of *M. galloprovincialis* and 6% of *P. canaliculus*) had spawned gametes by the same month. Stress affects many aspects of reproduction, including timing of spawning, gamete quality, and fertilization success (e.g. Schreck et al., 2001). It is possible that in this system, earlier spawning time could be a response to increased stress. High-edge mussels may be releasing gametes to reallocate energy away from reproduction and towards defense and repair mechanisms that increase their likelihood of survival.

The predictions of global climate change scenarios are complex and include alterations to oceanic circulation, increasing frequency and severity of storms and aerial temperature events, and sea level rise (e.g. Lubchenco et al., 1993; Houghton et al., 2001). All of these factors could potentially affect intertidal communities. This study documented strong sublethal (growth and reproduction) and lethal effects of temperature on intertidal mussels. Warming temperatures likely resulting from climate change have already been shown to affect reproduction and recruitment in bivalves (Philippart et al., 2003) and may have already affected mussel bed community diversity (Smith et al., 2006). Although releasing gametes in response to sudden increases in stress, as documented here, has potential adaptive value, temperature-dependent spawning of bivalves can lead to a mismatch with phytoplankton blooms, leaving larvae food-deficient and potentially decreasing larval survivorship (Philippart et al., 2003). Hence, spawning induced by environmental stress in New Zealand mussels could possibly lead to increased larval mortality and lower recruitment rates.

In the face of potential increases in environmental stress under global climate change scenarios (Houghton et al., 2001), species will likely be differentially affected by warming temperatures (e.g. Schiel et al., 2004). Many marine animals are already living close to their physiological thermal tolerance limit (Stillman and Somero, 2000; Somero, 2002). The upper distributional limit of mussel beds fluctuates with long-term patterns of emersion time and could move down under scenarios of increasing aerial temperatures (Denny and Paine, 1998; Harley et al., 2006). The anomalous temperature event in this study surpassed the tolerance limit of *P. canaliculus* living at the upper edge of their distribution, killing approximately one-third of the population. While we recognize that the sublethal and lethal responses of organisms in this study were not a direct response to climate change, the findings reveal potential consequences of high aerial temperature events on a community-dominant group. As a result of future high temperature events, alterations in community structure could occur, as *P. canaliculus* distribution in the intertidal zone could shift lower along the vertical stress gradient, and *M. galloprovincialis* would subsequently dominate the upper edge of the mussel bed even more strongly.

Under increasing global temperatures and particularly higher variance in temperature (Houghton et al., 2001), it is predicted that the number of acute aerial temperature events will increase. The high temperature on the day of the mortality event in this study was the 3rd highest January temperature for this area of New Zealand since records began in 1939 (NIWA, 2005). This followed immediately after the coldest December in Christchurch since temperature measurements started in 1953 (NIWA, 2004). As documented from the mortality event in this study, it is likely that some species will be unable to adapt quickly enough to defend themselves from a rapidly changing and unpredictable climatic regime (Houghton et al., 2001). This study provides some insight into potential alterations in species interactions that could potentially arise as a consequence of global climate change.

Acknowledgements

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