# LETTER

# Response of a rocky intertidal ecosystem engineer and community dominant to climate change

Bruce A. Menge,* Francis Chan and Jane Lubchenco

*Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA*
*Correspondence: E-mail: mengeb@oregonstate.edu*

## Abstract

To evaluate how climate change might impact a competitively dominant ecological engineer, we analysed the growth response of the mussel *Mytilus californianus* to climate patterns [El Niño-Southern Oscillation, Pacific Decadal Oscillation (PDO)]. Mussels grew faster during warmer climatic events. Growth was initially faster on a more productive cape compared to a less productive cape. Growth rates at the two capes merged in 2002, coincidentally with a several year-long shift from warm to cool PDO conditions. To determine the mechanism underlying this response, we examined growth responses to intertidal sea and air temperatures, phytoplankton, sea level and tide height. Together, water temperature (32%) and food (12.5%) explained 44.5% of the variance in mussel growth; contributions of other factors were not significant. In turn, water temperature and food respond to climate-driven variation in upwelling and other, unknown factors. Understanding responses of ecosystem engineers to climate change will require knowing direct thermal effects and indirect effects of factors altered by temperature change.

## Keywords

## INTRODUCTION

Disruption of species interactions by climate change is likely to have extensive direct and indirect effects on Earth's biota (Walther *et al.* 2002). For instance, shifts in spring arrival dates may lead to increased nest competition among migratory birds (Both & Visser 2001) and earlier entry into ponds by newts may expose frog larvae to stronger predation (Beebee 1995). Theory and data indicate that such direct effects are likely to ramify indirectly throughout the rest of the community (Yodzis 1988; Abrams *et al.* 1996). The impact of climate change is most simply effected through shifts in temperature regime (McCarty 2001; Parmesan 2006), but evidence suggests that interactions between temperature and other factors are likely to have the most widespread influence on community dynamics (Bale *et al.* 2002; Walther *et al.* 2002; Harley *et al.* 2006; Parmesan 2006). Evidence that climate change has impacted the phenology, abundance, distribution, ranges and other properties of Earth's ecological communities is extensive, particularly in terrestrial habitats (Walther *et al.* 2002; Parmesan 2006). Climate change effects have been documented in several

marine settings (coral reefs, zooplankton and fish communities, rocky intertidal; e.g. Roemmich & McGowan 1995; Sagarin *et al.* 1999; Walther *et al.* 2002; Smith *et al.* 2006), but as with most examples in other habitats, most of these involve changes in abundance, diversity and species composition. Documentation of the impacts of climate change on vital ecological rate processes such as individual growth, mortality and fecundity is rare but invaluable for developing mechanistic and predictive insights into how key species interactions are likely to scale with impending but uncertain ecosystem changes (but see e.g. Bale *et al.* 2002).

Here, our focus is on the response to climate of the growth of an ecologically dominant rocky intertidal mussel *Mytilus californianus* Conrad, 1837. As in many ecologically dominant species such as trees, kelps and macroalgae (Dayton 1975; Dayton *et al.* 1999; Sheil *et al.* 2006), competitive ability of mussels is expressed through an ability to overgrow other interactors (Paine 1994; Robles & Desharnais 2002). Thus, understanding how temperature change and related factors influence growth of individuals offers a potential tool for predicting future consequences of climate change. Useful approaches to gaining such understanding include examining

the response of key components of communities to shorter term climatic variations such as the 3- to 7-year El Niño-Southern Oscillation (ENSO) and multidecadal Pacific Decadal Oscillation (PDO) cycles (Glynn 1988; Francis & Hare 1994; Mantua *et al.* 1997; Holmgren *et al.* 2001; Rodo *et al.* 2002; Chavez *et al.* 2003; Clark *et al.* 2003; Peterson & Schwing 2003). Both cycles involve changes in seawater temperature, with consequent changes in other processes such as upwelling, phytoplankton blooms and coastal currents, also expected to change with warming (e.g. Bakun 1990; Vecchi *et al.* 2006). Hence, responses to shorter term climatic oscillations may serve as a proxy for how systems will respond to climate change.

We address four questions: (1) does growth of *M. californianus* respond to ENSO? (2) Does growth of *M. californianus* respond to PDO? (3) Do these patterns vary among regions? (4) How are these changes related to environmental conditions such as temperature, food availability, sea level and tidal height? We show that growth is highly sensitive to climate variation, responding to food and temperature variation resulting from ENSO and PDO.

## METHODS

### Study system

Rocky intertidal ecosystems have contributed disproportionately to the conceptual development of community ecology. In these well-understood systems, mussels are often central to their dynamics, especially in temperate regions (Seed & Suchanek 1992; Paine 1994; Menge & Branch 2001; Robles & Desharnais 2002). *Mytilus californianus* is a major element of rocky intertidal community structure and dynamics along most of the west coast of North America (Paine 1966, 1974; Menge *et al.* 1994, 2004; Schoch *et al.* 2006; Smith *et al.* 2006). As the primary prey of the keystone predator *Pisaster ochraceus*, a dominant competitor for space, and an ecosystem engineer, *M. californianus* is a determinant of zonation, abundance and diversity in these model ecosystems. Key to this role is its ability to overgrow virtually all other coexisting species. This smothering ability is enabled by growth to large size and its byssal attachment system, which allows glacial movement as it responds to the lateral pressures from growth-induced crowding by adjacent mussels. In the absence of the sea star *P. ochraceus*, this limited movement ability allows mussels to push into the low-intertidal zone where they crowd out seaweeds, other sessile invertebrates and mobile herbivores (Paine 1966, 1974).

### Study sites

To test the hypothesis that food availability explained apparent differences in mussel growth (Menge *et al.* 1994),

we initiated studies in 1991. We initially focused on two contrasting sites on different capes along the Oregon coast, but added new sites over time. Here we analyse the longest time series available, at four to five sites on two capes spanning 8–15 years. Their occurrence during a period of major changes in ENSO and PDO cycles spurred analyses of the response of growth to shifts in climate and thereby to attendant changes in temperature, phytoplankton concentration, tide height and sea level.

Study sites begun in 1990 were Boiler Bay (hereafter BB: 44 49.8 N, 124 03.6 W) on Cape Foulweather (hereafter CF) and Strawberry Hill (hereafter SH: 44 15.0 N, 124 06.6 W) 63 km south on Cape Perpetua (hereafter CP; Menge *et al.* 1994). To increase site replication, over time we added: Fogarty Creek (hereafter FC: 44 50.4 N, 124 03.6 W), a CF site, and Yachats Beach (hereafter YB: 44 19.2 N, 142 06.6 W) and Tokatee Klootchman (hereafter TK, formerly 'Gull Haven': 44 12.0 N, 124 07.2 W), both CP sites. See Menge *et al.* (1994, 2004) for further details on these sites.

### Mussel size

Because growth rates decrease with increasing time out of water (Seed & Suchanek 1992), body size of *M. californianus* varies vertically on the shore, with smaller mussels at the upper edge of the mussel bed and larger mussels at the lower edge. Observations suggested that the size of the largest mussels also varied between capes (B. Menge, personal observation). To quantify this pattern, in 1996 measurements were made of mussel size in mussel patches from mid-shore tide heights [maximum range across sites was *c.* 1.5–2 m above mean lower low water (MLLW) with a total tidal range of *c.* 3.7 m]. The patches had been created by wave disturbance in winter 1995–1996 on benches exposed to severe (exposed) or moderate (intermediate) wave action at FC, BB (CF sites), YB and SH (CP sites). On the edge of each patch, shell length of one or two of the largest mussels was quantified. Patch numbers on a total of eight benches across the four sites ranged from 10 to 50, yielding a total of 166 measurements.

### Mussel growth

Quantification of mussel growth followed a standard protocol (Menge 2000; Blanchette *et al.* 2007). Mussels *c.* 30–40 mm long were collected from a common site (Bob Creek, 1 km south of SH) and held in seawater until use. Prior to transplantation in May, we notched the posterior edge of each mussel. The notch marked initial shell length, and annual growth was measured as the distance between initial and final length. Mussels were placed in previously prepared plots in the mussel bed, all at mid-tide level, *c.* 1.3–2.0 m above MLLW. Plot position was usually the same from year to year,

but some were moved as surrounding mussels filled in the natural gaps we used for the transplants. Mussels ($n$ = 30–50) were placed ventral side down and held in place using plastic mesh fastened with stainless steel screws inserted into wall anchors in previously drilled holes. To encourage stronger attachment through the production of more byssal threads, the mesh was loosened periodically and then removed after *c*. 6 weeks. Size-specific proportional growth rate was estimated as mm shell growth × initial length$^{-1}$ × day$^{-1}$ × 1000. Statistics were done on per plot mean shell growth rates, with five to eight plots per site per year.

### Climatic patterns

The overlap between the mussel growth time series and phases of both ENSO (warm, neutral and cool) and PDO (warm and cool) during the 1990s and 2000s [e.g. Appendix S2 (Fig. S1)] enabled analysis of how mussel growth varied with these climatic patterns. Mussel growth was quantified annually, so we compared growth to ENSO, PDO and oceanographic conditions in the 12 months prior to the collection month. Average annual ENSO and PDO indices were calculated from average monthly indices over the previous 12 months. Not all combinations of ENSO × PDO phases were available with the annual resolution of this data set, so we analysed mussel growth against each index separately. Because it is based on several climatological measures that characterize ENSO cycles (sea level pressure, surface winds, sea surface water and air temperatures, total fraction of cloudy sky), we used the multivariate ENSO index (URL: http://cdc.noaa.gov/ENSO/enso.mei_index). Following standard convention, values >+ 0.5 indicate El Niño (warm water) conditions, −0.5 to + 0.5 indicate neutral conditions and values <−0.5 indicate La Niña (cool water) conditions. PDO index data also were obtained from the web (URL: http://tao.atmos.washington.edu/pdo/). Values > 0 indicate warm-water conditions and values < 0 indicate cool-water conditions.

### Temperature

At each site we deployed temperature loggers in the interface between the low and mid zones, *c*. 0.5–1 m lower than the transplants. We used daily averages to compute the annual averages used in our analyses, and within-day fluctuations in water temperature in particular are small compared to those between days and months (B. Menge, unpubl. data). Loggers were set to record hourly (first Optic StowAways, later TidbiTs; Onset Computer Corporation, Pocasset, MA, USA; precision of ± 0.5 °C). Initially one or two loggers were deployed per site, but starting in 1998, three replicate loggers were deployed at each site. As intertidal loggers record both air and seawater temperatures, we separated these using

a 'detiding' program. We calculated mean hourly air and water temperatures by replicate for each day at each site, and then averaged across replicates to obtain replicate estimates of annual intertidal water and air temperatures. For comparison with mussel growth data which began in late May or June of each year, we defined 1 June to 31 May of the following year as the 'growing season'. Air and water temperatures were highly correlated ($r$ = 0.9) so we used water temperature data in most of our analyses. This correlation and the lack of an association between air temperature and growth (data not shown) suggest that the difference in height between the loggers and the plots is unlikely to have much influence on our results.

### Chlorophyll-*a*

We estimated concentration of phytoplankton, a primary component of the food of filter feeders such as mussels, by quantifying the concentration of chlorophyll-*a* (Chl-*a*) in bottle samples taken from shore at each site (Leslie *et al.* 2005; Barth *et al.* 2007). At low tide, replicate ($n$ = 3 to 5) acid-washed opaque plastic 250-mL bottles (high density polyethylene, HDP) were filled at a depth of 30–50 cm below the surface. Fifty millilitres of water was filtered through 25-mm pre-combusted Whatman GF/F glass-fibre filters with a pore size of 0.7 μm. Chl-*a* concentration was determined using a Turner Designs TD-700 fluorometer after extraction in 90% HPLC acetone for 12 h in the dark at −20 °C. Prior calibrations of the fluorometer were done using pure Chl-*a* standards.

Samples were taken daily to monthly, primarily during the upwelling season (April–September). We calculated monthly mean Chl-*a* using each sample date as a replicate and averaged across months to obtain overall annual upwelling season means for each site. Use of upwelling season average Chl-*a* concentrations assumes that this value is correlated with total annual food availability (i.e. is a constant fraction of total particulate availability for the year). Chl-*a* is on average low in winter (2.1 ± 0.7 and 3.7 ± 0.7 mg L$^{-1}$ at CF and CP, respectively; $n$ = 27) compared to summer (7.1 ± 0.5 and 24.5 ± 1.9 mg L$^{-1}$; $n$ = 282 and 357), winter measurements were sparse, and CP was always > CF, so it seemed reasonable to use upwelling season estimates. Earlier estimates of detritus indicate that these correlate strongly to Chl-*a* concentrations, further supporting Chl-*a* as a proxy for mussel food (Menge 2000).

### Tide height

To test the effect of tide height, we determined the tide heights of mussel transplant plots several times (1993, 1999, 2000, 2006) during the 8- to 15-year study. Heights of mussel bed disturbances in which mussel size was sampled

were determined in 1996. We used a surveyor's level and stadia rod to measure heights, using the level of the low tide mark on a calm day as our reference point. The height of the reference mark for that day was determined using tide tables (http://tidesonline.nos.noaa.gov).

## Sea level

To evaluate the influence of sea level fluctuation on mussel growth we obtained data from the Joint Archive for Sea Level (JASL; http://uhslc.soest.hawaii.edu/uhslc/jasl). We used monthly data from South Beach, Oregon (44.38° N, 124.03° W), centrally located between CF and CP, to generate an annual sea level measure for each year of the study.

## Data analysis

We used two-way analysis of variance to test the effects of cape, site nested within cape and wave exposure, analysed as fixed factors, on mussel length. Analysis of raw data vs. ln-transformed data gave nearly identical results, but ln-transformed analyses detected no outliers so we used transformed data. Levene's test indicated that variances were homogeneous ($P \geq 0.34$).

Two-way analysis of variance with tide height or sea level as covariates tested the effects of ENSO and cape, and PDO and cape, respectively on mussel growth. Variances were homogeneous except for the effects of ENSO (Levene's test, $P = 0.023$), but the data were normal and effects were statistically strong, an indication of robustness (Underwood 1997), so we proceeded with the analysis. We used one-way ANOVA to test for differences among sites and between capes in tide height and sea level.

Repeated measures analysis of variance tested the effect of cape on mussel growth, Chl-$a$ and temperature across years. Levene's test indicated that variances were homogeneous in all years but 2001 for mussel growth, 2000 for Chl-$a$ and in several years for temperature. In all cases, analysis without the heteroscedastic data gave the same results, so we present analyses including these years.

Finally, multiple regression evaluated the relative contributions to mussel growth variability of Chl-$a$, growing season temperature and either tide height of plots or growing season mean sea level. In all cases, residuals in probability plots indicated data were normally distributed with exceptions noted in table captions (see Appendix S1).

## RESULTS

## Mussel size

As suggested by qualitative observations, *M. californianus* were larger at sites on CP (YB and SH) than were mussels at
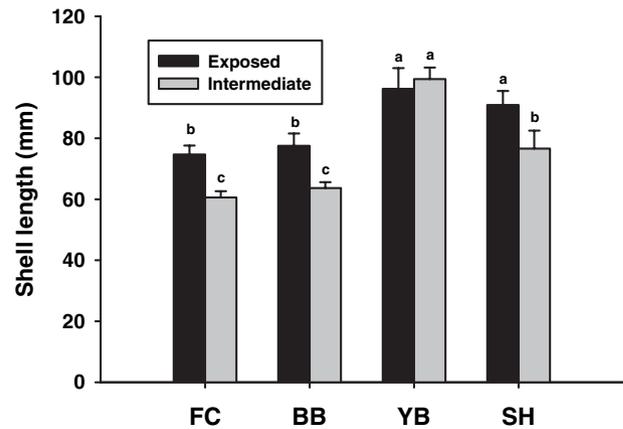


**Figure 1** Mussel length (mean ± 1 SE in this and all subsequent figures) at two exposures at each of four sites on the Oregon coast, listed from left to right from north to south. Sites were Fogarty Creek, Boiler Bay (Cape Foulweather), Yachats Beach and Strawberry Hill (Cape Perpetua); wave exposures were exposed and intermediate. Linear contrasts were used to test differences among sites and exposures; bars sharing the same letter are not different at $P > 0.05$, bars with different letters are different at $P < 0.05$.

sites on CF (FC and BB; Fig. 1, linear contrasts). Between-cape differences had the greatest effect on size, but size varied also with wave exposure (two-way nested ANOVA: cape effect, $F = 46.7$, $P < 0.0001$; exposure effect, $F = 11.2$, $P = 0.001$, 1, 160 d.f., $r^2 = 0.26$; interaction not significant). Mussels varied among sites within capes as well (two-way nested ANOVA; site(cape), $P = 0.03$) a difference attributable to the relatively large sizes at YB regardless of wave exposure (Fig. 1, linear contrasts).

## Mussel growth

Mussel growth varied greatly, both in space and time (Fig. 2). In the 1990s through 2000–2001, growth rates were higher on CP [Appendix S1 (Table S1); one-way tests by year, 1997–1998 to 2000–2001, $P < 0.001$]. This pattern was initially based on just one site on each cape, but with additional sites it became clear that growth differences occurred at the cape scale [Fig. 2, Appendix S1 (Table S1): RM ANOVA 1998–2006; between-subjects cape effect, $F = 15.99$, $P = 0.001$]. Starting in 1998–1999, however, growth rates at the slower growing CF sites increased annually, while mussels on CP changed relatively little in growth compared to prior trends. By 2001–2002, between-cape differences in mussel growth had disappeared as CF growth rates became statistically indistinguishable from CP rates [Fig. 2, Appendix S1 (Table S1): within-subjects year × cape interaction, $P < 0.0001$; one-way tests by year, $P > 0.05$ or more].
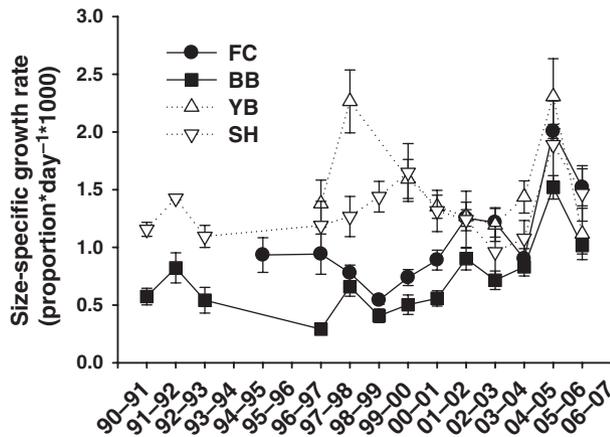
**Figure 2** Size-specific mussel growth at four sites on two capes (Fogarty Creek = FC and Boiler Bay = BB on Cape Foulweather, shown in solid symbols and solid lines, and Yachats Beach = YB and Strawberry Hill = SH on Cape Perpetua, shown in open symbols and dotted lines). We show the full time series, but repeated measures analysis (on ln-transformed growth rates) was done only for years in which we had data from three or more replicate plots for all four sites (1998–2006). Abscissa shows annual growing seasons (i.e. June through the following May). For example, 90–91 refers to experiments started in June 1990 and replaced in May–June 1991.

After this convergence, CF and CP mussels grew at similar but temporally variable rates, with a notable peak in 2004–2005 (Fig. 2).

## Climatic patterns

ENSO effects on growth varied by cape [Fig. 3, Appendix S1 (Table S2): two-way ANOVA, ENSO × cape effect, $P = 0.01$ with tide height as a covariate, $P = 0.02$ with sea level as a covariate]. PDO effects on growth also varied with cape with tide height as a covariate [Fig. 3, Appendix S1 (Table S2): two-way ANOVA, PDO × cape effect, $P = 0.007$], but with sea level as a covariate, PDO and cape effects on growth were independent [Appendix S1 (Table S2): two-way ANOVA, PDO effect, $P = 0.004$, cape effect, $P < 0.0001$]. Neither tide height nor sea level influenced mussel growth in these analyses. The ENSO × cape interaction was manifested in a more strongly negative effect of La Niña on mussel growth at CF than at CP (Fig. 3a). As indicated by overall patterns (Fig. 2), growth was faster at CP than at CF, but was faster during warm-water El Niño (1997–1998) conditions than during neutral conditions or cool-water La Niña (1998–1999) conditions, at least at CF. Similarly, warm-phase conditions of PDO were associated with elevated mussel growth (Fig. 3b).
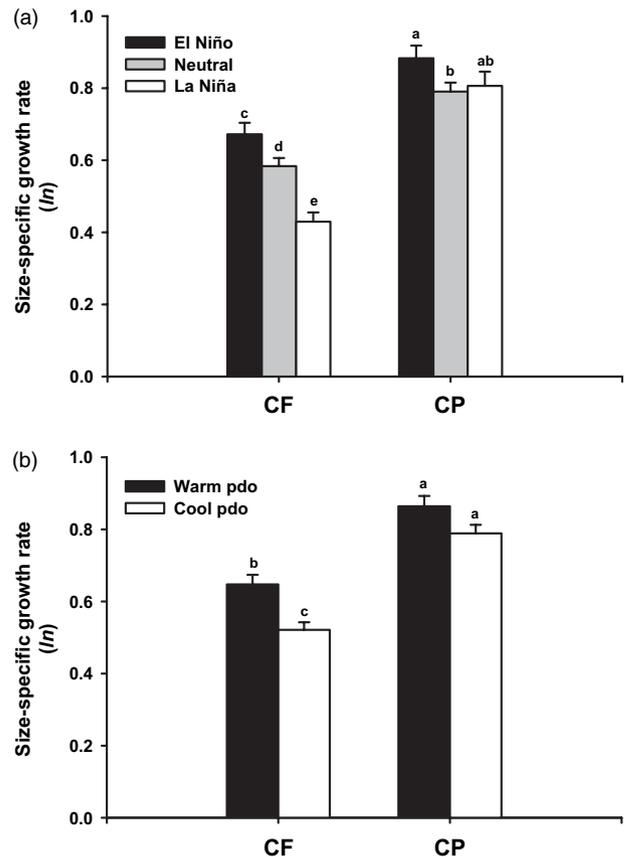


**Figure 3** Variation in effects of (a) ENSO phases and (b) PDO phases on size-specific growth rate of *Mytilus californianus* at sites on Cape Foulweather (CF) and Cape Perpetua (CP). See Table S2 for analyses of variance tests. Linear contrasts were used to determine differences among means. Bars sharing letters are not different at $P = 0.05$.

## Temperature

Mean growing season water temperature varied between capes, with warmer temperatures on CP in some years [Fig. 4, Appendix S1 (Table S3): between-subjects cape effect, $P = 0.002$]. These differences occurred primarily from 1999–2001 (Fig. 4). Changes among years were more striking, with exceptionally high temperatures in 1997–1998, an El Niño year, and elevated values also in 2004–2005 [Fig. 4, Appendix S1 (Table S3): within-subjects year effect, $P < 0.0001$]. Temperatures were cooler from 1998–1999 (a La Niña event) to 2002–2003, with the lowest values in 2001–2002.

## Chlorophyll-*a*

Phytoplankton concentration was greater at CP than CF [Fig. 5, Appendix S1 (Table S4): between-subjects cape
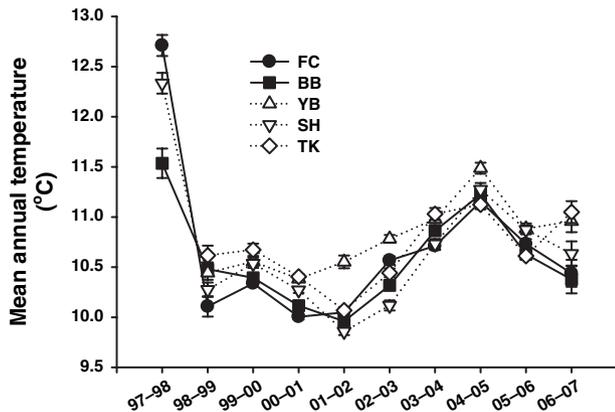
**Figure 4** Mean annual growing season temperature (1 June to 31 May) by site and cape. We show the full time series but repeated measures analysis was done only for years when we had data for all five sites. We omitted from analysis 1997–1998 which were missing data for two sites and 2006 because they included only summer data. One-way analysis of variance testing the effect of cape by year indicates that temperature was greater at Cape Perpetua in 1999 (98–99 in Fig. 4) and 2000 (99–00 in Fig. 4) with no difference in other years (1998, 2001, 2003, 2005; Bonferroni correction: $P = 0.05/6$, yielding a significant $P = 0.0083$).
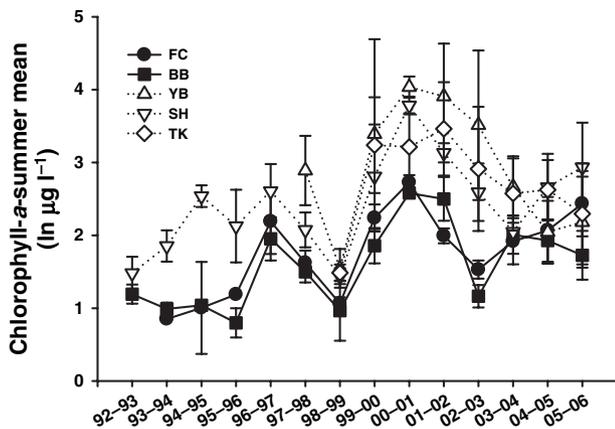


**Figure 5** Chlorophyll-*a* time series, 1993 through summer 2006. Means are based on data from May–August each year or 'summer chlorophyll-*a*'. In addition to sites coded by cape as indicated in Fig. 2 caption, data from a fifth site located on Cape Perpetua (Tokatee Klootchman = TK) are included. We show the full time series but repeated measures analysis (on ln-transformed data) was done only for years in which we had data for all five sites, 1998–2006. One-way analysis of variance testing the effect of cape by year indicates that chlorophyll-*a* was greater at Cape Perpetua in 2001 and 2003, with no difference in other years (Bonferroni correction: 0.05/9, yielding a significant $P = 0.0056$).

effect, $P = 0.004$]. However, the convergence seen in 2001–2002 in mussel growth was not matched by patterns of phytoplankton concentration; patterns at capes did not vary

differentially through time [Fig. 5, Appendix S1 (Table S4): within-subjects year × cape interaction was not significant].

Phytoplankton concentration varied dramatically through time [Fig. 5, Appendix S1 (Table S4): within-subjects year effect, $P < 0.0001$]. Notable shifts were a sharp drop in 1998–1999, which coincided with a strong La Niña, and large increases from 2000–2001 through 2002–2003 (Fig. 5). The latter changes were associated with shifts from warm to cool PDO and an unusually large intrusion of cold subarctic water in 2002 (Peterson & Schwing 2003).
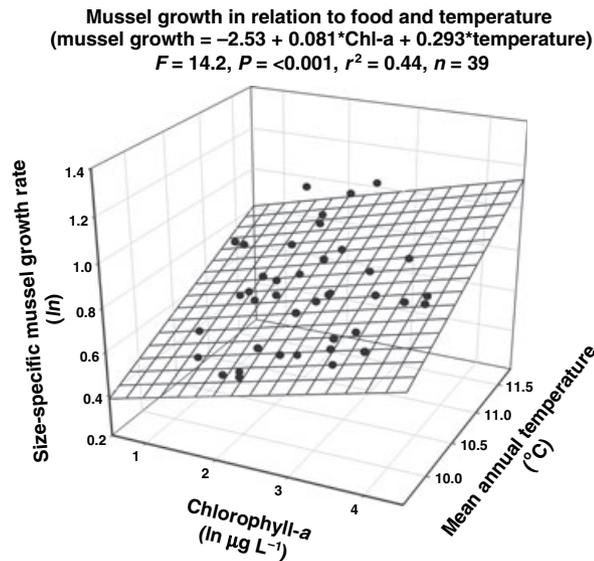
## Tide height

Although tide height did not contribute to growth variation in the context of climatic pattern and cape differences (see above), plot height varied among sites [Appendix S2 (Fig. S2), Appendix S1 (Table S5); $P < 0.0001$]. Overall, plots were higher on the shore at CP sites (1.79 ± 0.05 m) than at CF sites (1.50 ± 0.04 m). Increased tide height should decrease growth (e.g. Seed & Suchanek 1992), but in this case growth actually increased with height [Appendix S2 (Fig. S3); linear regression of growth vs. tide height, $P = 0.01$, 1, 59 d.f.]. Height explained only 11% of the variance in growth. Analysis by cape with tide height as a covariate indicates that despite having higher plots, growth at CP (1.4 ± 0.07 mm day$^{-1}$ initial length$^{-1}$ × 1000) was almost twice that at CF [0.83 ± 0.08; Appendix S1 (Table S6): one-way ANOVA; cape, $F = 16.9$, $P = 0.0001$, 1, 55 d.f., $r^2 = 0.32$; tide height, $P = 0.73$].

## Sea level

Mean monthly sea level did not vary among years from 1991 to 2005 ($P = 0.31$; 14, 165 d.f.), but mussel growth increased slightly with increases in annual sea level [Appendix S2 (Fig. S4): linear regression, slope = 0.00083, $F = 5.22$, $P = 0.02$, 1, 318 d.f.]. The relationship was weak, however ($r^2 = 0.016$), suggesting that sea level change had little impact on mussel growth. As sea level was monitored only at a central site in our study region, we could not analyse site- or cape-related effects of sea level on mussel growth.

## Multivariate effects on growth

What are the mechanisms underlying the response of mussel growth to ENSO and PDO climatic variation? The above analyses suggest that variation in seawater temperature, phytoplankton concentration, tide height, and weakly, sea level were associated with variation in mussel growth. We used multiple regression to sort out the relative impacts of all these factors but tide height on mussel growth. Our model included effects of ENSO (mean annual MEI index), PDO (mean annual PDO index), growing season water

**Mussel growth in relation to food and temperature**
**(mussel growth = −2.53 + 0.081*Chl-a + 0.293*temperature)**
**$F = 14.2$, $P = $ <0.001, $r^2 = 0.44$, $n = 39$**



**Figure 6** Influence of food availability (proxied by chlorophyll-*a*) and temperature (mean annual growing season, June through the following May) on growth of *Mytilus californianus*. Statistics are from a multiple least squares regression test.

temperature (ln °C), Chl-*a* (ln mean summer Chl-*a*) and sea level (annual mean). We excluded tide height because of its paradoxical effect (faster growth at higher levels) and annual mean air temperature because it was highly correlated to water temperature (see above). Stepwise backward regression eliminated sea level from the model ($P = 0.74$), leaving water temperature, Chl-*a*, ENSO and PDO as explanatory variables (multiple regression, $F = 8.9$, $P < 0.0001$, $r^2 = 0.51$). Testing the effects of ENSO and PDO, both expressed through sea surface temperature, confounds the effect of water temperature (both are correlated with water temperature; $P = 0.004$ for ENSO and $P = 0.0003$ for PDO) so we dropped these from the regression as well. The resulting model suggests that water temperature and Chl-*a* are the basis for the effects of cape, ENSO and PDO on mussel growth (Fig. 6). Mussel growth was maximized under conditions of high food availability and warmer water temperatures. Analysis of variance components (e.g. Underwood 1997) indicates that temperature and Chl-*a* were responsible for 32 and 12.5%, respectively, of the total variance (44.5%) explained by the model.

## DISCUSSION

### Growth response to climate pattern

Our analysis suggests that mussel growth tracks annual changes in ENSO and PDO, varying at 3–7 years, and multidecadal scales, respectively. This response seems driven

by sea surface temperature and food abundance, evidently the primary factors underlying between-cape variation in size structure and growth rates of *M. californianus*. Hence, secondary production of mussels and their spatial and temporal variation in competitive ability appears to be markedly sensitive to among-year changes in climate forcing.

The mechanisms underlying these responses seem conflicting. Acceleration of metabolism by increasing temperature doubtless explains the positive association between growth and temperature (e.g. Coe & Fox 1942; Seed & Suchanek 1992; Blanchette *et al.* 2007). Up to a point (Somero 2002), through Q10 effects, warmer temperatures should favour faster physiological rates and all else being equal, enhance growth. But in coastal upwelling systems, warm temperatures are also indicative of low nutrients (e.g. Dayton *et al.* 1999) and thus of low phytoplankton concentration (Corwith & Wheeler 2002), so might be expected to have negative effects on mussel growth through reduced food abundance. Our analysis (Fig. 3) thus suggests that overall, direct thermal effects on growth rate trump the apparent opposing indirect effects of warm events on food.

### Link between growth and climate

The response of mussel growth to climatic shifts seems to be an integrated response to temperature and food, the relative importances of which vary in space and through time. But how are these linked to ENSO and PDO? We suggest that this link operates through climatic effects on upwelling strength. In the Bakun upwelling index, expressed as m³ of water transported × second$^{-1}$ × 100 m of coastline$^{-1}$, positive values reflect upwelling (cooler water) and negative values reflect downwelling (warmer water) (http://www.pfeg.noaa.gov). Regressing upwelling vs. ENSO or PDO indices indicates that, at latitudes spanning the study region (44.5° N to 42.5° N), both climate indices are inversely related to upwelling at time lags of 1 to 5 months, with the strongest relationship at a time lag of 4 months [Appendix S1 (Table S8)]. Although other factors also are important ($r^2$ values are low even for significant relationships), stronger upwelling tends to be associated with cool events and weaker upwelling with warm events occurring a few months earlier. Thus, upwelling-induced variation in the thermal environment may explain growth-rate differences associated with ENSO and PDO (Fig. 3).

### Between-cape differences

In contrast to the apparent larger scale dominance of thermal effects on growth, food differences seem the most likely explanation of between-cape differences (Fig. 3). On average, growth was faster at CP than at CF, regardless of which climate phase prevailed at the time. As noted earlier,

and as reflected in Fig. 5, Chl-*a* concentration was always higher at CP, both in summer and winter. The consistency in this effect reflects circulation differences between these two regions. Currents tend to be strongly advective and seaward, and upwelling is stronger at CF, while currents are weaker and more retentive, and upwelling is weaker at CP (Barth & Wheeler 2005; Fabian Tapia *et al.* unpubl. data). As phytoplankton are passive drifters, and blooms take *c.* 3 days to develop, the lower food at CF may reflect a higher rate of advection of phytoplankton away from the coast than at CP, where phytoplankton may accumulate and be more persistent.

## Temporal and spatial variation in growth

In the 1990s, patterns of growth at the two capes were consistently different but in the 2000s these differences disappeared (Fig. 2). This contrasts to changes in the food supply, which increased dramatically in the 2000s compared to the 1990s but relatively evenly across sites (Fig. 5; two-way ANOVA; decade, $P < 0.0001$; site, $P < 0.0001$; decade × site, $P = 0.53$; $r^2 = 0.36$, $n = 610$ samples). Thus, despite higher food availability in the 2000s at all sites, and higher food at CP, only mussels at CF sites increased their growth (Fig. 2). Although overall temperatures were cooler during years of growth convergence (2000–2002), CF temperatures were never greater than CP temperatures (Fig. 4). Further, high growth rates in 2004–2005 (Fig. 2) were associated with higher temperatures (Fig. 4), not higher food abundance (Fig. 5).

So why didn't growth keep pace with food? The answer likely lies in physiological limitations in food processing. The capacity of mussels to consume particulates increases with increasing concentrations, but above some threshold concentration, the mussel's digestive capacity can be saturated and excess food is rejected in 'pseudofaeces' (e.g. Hawkins & Bayne 1992). Thus, we hypothesize that CP mussels are often at or above this threshold, and that the very high concentrations of phytoplankton in 2001–2004 were above the saturation level at CP but not at CF. As suggested above, the spike in growth at both capes in 2004–2005 indicates that temperature effects can modulate the food effect, perhaps through changes in physiological capacity to process food.

## Implications for community dynamics

Prior analyses have yielded mixed evidence for effects of climate patterns such as ENSO or PDO on intertidal community structure (e.g. Paine 1986; Smith *et al.* 2006). In the present example, growth and thus presumably biomass of the dominant ecosystem engineer in this system, the California mussel, appears sensitive to variation in both ENSO and PDO climatic shifts. Such changes are subtle

and seem less likely to be reflected in abundance (i.e. per cent cover or density) of mussels, and indeed, we have seen little change in per site mussel cover in our 25 + years of working in these communities.

Similarly, the role of *M. californianus* as a provider of habitat for a diverse assemblage of invertebrates (Seed & Suchanek 1992; Smith *et al.* 2006) would presumably be unaffected by variable growth rates. Yet mussel bed diversity at 22 sites along the California coast was dramatically lower in 2002 than in historic studies carried out in the 1960s and 1970s (Smith *et al.* 2006). This change was postulated to be related to drops in productivity associated with the PDO warm phase that began in 1976 (Smith *et al.* 2006), but links to mussel growth rate remain unexplored.

Variation in mussel growth seems most likely to influence its competitive ability. Increased growth is likely to increase the lateral pressures within a mussel bed (e.g. Robles & Desharnais 2002). This could have two consequences. First, increased lateral pressure could potentially weaken the attachment strength of the mussel bed to the underlying rock as mussels in the middle of the bed respond by losing their attachment as they are pushed away from the surface by lateral pressures (Seed & Suchanek 1992). Such mussels would likely reattach to neighbouring mussels, increasing the load on the mussels beneath that are still attached and leading to increased layering of the mussel bed. Mussel beds are well-known to vary in thickness, ranging from monolayer to multilayer beds (Seed & Suchanek 1992; P. Halpin *et al.* unpubl. data). In Oregon, mussel beds tend to be thicker at more productive CP sites, to recover from disturbance more quickly, and possibly to have greater susceptibility to disturbance than at less productive CF sites (Guichard *et al.* 2003; P. Halpin *et al.* unpubl. data). Mussel bed dynamics seem strongly dependent on mussel growth rates.

A second likely consequence of variable growth rates is the effect on mussels 'cascading' down the shore, which should be faster where growth is higher (Robles & Desharnais 2002). This is a major part of the mechanism by which mussels displace and outcompete other sessile invertebrates and macrophytes that normally occupy the zone below the mussel bed, a process that is prevented by the keystone predator *P. ochraceus* (Paine 1966, 1974; Menge *et al.* 1994; Robles & Desharnais 2002). Thus, higher secondary productivity from growth should increase prey inputs to predators, potentially leading to changes in prey distribution or in predator abundance or shifts in predator size structure. Sea stars are in fact more abundant and larger at CP sites (Menge *et al.* 1994, 2004), although higher prey recruitment at CP sites (Menge *et al.* 1994, 2004) seemingly confounds a possible simple effect of higher prey growth rates. In Robles & Desharnais (2002) model of this process, however, recruitment and growth work in concert to cause variation in the rate of downshore cascading.

## Response to climate change

The apparent sensitivity of mussel growth to climate variations through ENSO and PDO effects on food and temperature suggests that up to a point, warming can have a positive effect on mussel populations along the west coast of North America. Mussels are highly sensitive to environmental stress, however (Somero 2002; Dahlhoff 2004; Petes *et al.* 2007) and increased warming implies increased thermal stress during low tide. Warming could thus depress the upper limit of mussels to lower levels on the shore. Further, increases in sea level with global warming are likely to increase the vertical range of sea star predators and warmer waters will likely increase sea star predation rates, perhaps raising the lower limit of the mussel bed (Sanford 1999). Consistent with this, the lower edge of mussels at CP, with higher predation rates, is higher on the shore than at CF, with lower predation rates (Menge *et al.* 1994). The net effect of increased mortality at lower and upper edges of the bed would be to constrict the vertical range of mussels, perhaps ultimately eliminating them. Thus, despite the benefits of warmer temperatures on growth rates, on balance increased warming does not bode well for mussel populations.

This conclusion is confounded by possible alternative influences of oceanography, however. Some (Bakun 1990) have predicted that global warming may increase upwelling intensity, thus causing cooler not warmer water temperatures in coastal zones. If coastal waters cool, then mussel growth should slow, thus reversing most of the predictions listed under a warming scenario. Which change will prevail should become clear as further climate modelling resolves how warming will impact coastal upwelling.

## Lessons learned

Growth rates of most organisms are both temperature and resource dependent, so it seems likely that aspects of these results will relate to many other dominant, habitat-forming organisms such as trees. In marine and terrestrial systems, the ecological impacts of climate change have been perhaps best resolved for long-lived organisms such as trees and corals whose structural architecture provides simultaneous records of both climate variability and individual growth rates (Barber *et al.* 2000; Goodkin *et al.* 2005). For organisms that lack such feasible means of climate and vital rates reconstruction, the functional response of organisms and communities to climate variability remains poorly resolved. This uncertainty appears particularly strong for ecosystem engineers whose population fluctuations can have direct and indirect consequences for ecological communities. A number of efforts to date that have sustained long-term and spatially explicit monitoring efforts have revealed important climate–ecology linkages that can be direct but also difficult to forecast *a priori* (Biondi *et al.* 2001; Clark *et al.* 2003; Kratz *et al.* 2003). Further, too few examples of mechanistic understanding of climate–ecosystem linkages are available to provide insight on cross-system generality of climate effects. Our study on the geographically dependent response of a marine ecosystem engineer to over almost two decades of climate variability highlights the important role that cross-scale, long-term monitoring efforts will continue to play in the understanding and forecasts of climate–ecosystem linkages. The initiation and continuation of such time series will undoubtedly remain key to resolving both the pathways of climate forcing on ecological communities and the propagation of climate signals through complex interaction webs.

## CONCLUSION

Mussels responded strongly to both short-term (ENSO) and long-term (PDO) climatic patterns with increased growth during warm water events and decreased growth during cool water events. The mechanisms appear to be direct effects of temperature on metabolic rates and indirect responses of food to coastal geomorphology and upwelling intensity, with modulating influences of limitations in mussel food-processing capability. The ecological consequences seem varied and complex. We suggest that with varying recruitment, variable growth rates will primarily impact intraspecific competitive ability of mussels. In turn, variation in intraspecific competition is likely to influence rates of disturbance and recovery from disturbance, and the rate at which mussels are pushed downshore into the foraging range of sea stars. Likely long-term consequences under a warming scenario include both positive (increased growth with warmer conditions) and negative effects (increased susceptibility to stress, increased exposure to predation). Finally, we note that these changes coincided with two novel oceanographic events along the Oregon coast; the advent of hypoxia in 2002 (Grantham *et al.* 2004) which has persisted to present (Chan *et al.* unpubl. data), and extreme variation in seasonal upwelling intensity (Barth *et al.* 2007). Are these changes all harbingers of climate change-induced shifts in coastal ecology?

## REFERENCES

Abrams, P., Menge, B.A., Mittelbach, G.G., Spiller, D. & Yodzis, P. (1996). The role of indirect effects in food webs. In: *Food Webs: Integration of Pattern and Dynamics* (eds Polis, G.A. & Winemiller, K.O.). Chapman and Hall, New York, pp. 371–395.

Bakun, A. (1990). Global climate change and the intensification of coastal upwelling. *Science*, 247, 198–201.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. et al. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.*, 8, 1–16.

Barber, V.A., Juday, G.P. & Finney, B.P. (2000). Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405, 668–673.

Barth, J.A. & Wheeler, P.A. (2005). Introduction to special section: coastal advances in shelf transport. *J. Geophys. Res.*, 110, C10S01, doi:10.1029/205JC003124.

Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R. et al. (2007). Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc. Natl Acad. Sci. USA*, 104, 3719–3724.

Beebee, T.J.C. (1995). Amphibian breeding and climate change. *Nature*, 374, 219–220.

Biondi, F., Gereshunov, A. & Cayan, D.R. (2001). North Pacific decadal climate variability since 1661. *J. Clim.*, 14, 5–10.

Blanchette, C.A., Helmuth, B.S.T. & Gaines, S.D. (2007). Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *J. Exp. Mar. Biol. Ecol.*, 340, 126–148.

Both, C. & Visser, M.E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411, 296–298.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. & Niquen, C.M. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, 299, 217–221.

Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. (2003). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Natl Acad. Sci. USA*, 100, 5852–5857.

Coe, W.R. & Fox, D.L. (1942). Biology of the California sea mussel (*Mytilus californianus*). I. Influence of temperature, food supply, sex and age in rate of growth. *J. Exp. Zool.*, 90, 1–30.

Corwith, H.L. & Wheeler, P.A. (2002). El Niño-related variations in nutrient and chlorophyll distributions off Oregon. *Prog. Oceanogr.*, 54, 361–380.

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

Dayton, P.K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.*, 45, 137–159.

Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1999). Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Monogr.*, 69, 219–250.

Francis, R.C. & Hare, S.R. (1994). Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanogr.*, 3, 1–13.

Glynn, P.W. (1988). El Niño-Southern Oscillation 1982–83: nearshore population, community and ecosystem responses. *Annu. Rev. Ecol. Syst.*, 19, 309–345.

Goodkin, N.F., Hughen, K.A., Cohen, A.L. & Smith, S.R. (2005). Record of Little Ice age sea surface temperatures at Bermuda using a growth-dependent calibration of coral Sr/Ca. *Paleoceanography*, 20, PA4016, doi: 4010.1029/2005PA001140.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A. et al. (2004). Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the Northeast Pacific. *Nature*, 429, 749–754.

Guichard, F., Halpin, P., Allison, G.W., Lubchenco, J. & Menge, B.A. (2003). Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. *Am. Nat.*, 161, 889–904.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S. et al. (2006). The impacts of climate change in coastal marine systems. *Ecol. Lett.*, 9, 228–241.

Hawkins, A.J.S. & Bayne, B.L. (1992). Physiological interrelations and the regulation of production. In: *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture* (ed Gosling, E.). Elsevier, Amsterdam, pp. 171–222.

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J.R. & Mohren, G.M.J. (2001). El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.*, 16, 89–94.

Kratz, T.K., Deegan, L.A., Harmon, M.E. & Lauenroth, W.K. (2003). Ecological variability in space and time: insights gained from the US LTER program. *BioScience*, 54, 57–67.

Leslie, H.M., Breck, E.N., Lubchenco, J. & Menge, B.A. (2005). Hotspots of barnacle reproduction associated with nearshore ocean conditions. *Proc. Natl Acad. Sci. USA*, 102, 10534–10539.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.*, 78, 1069–1079.

McCarty, J.P. (2001). Ecological consequences of recent climate change. *Conserv. Biol.*, 15, 320–331.

Menge, B.A. (2000). Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.*, 250, 257–289.

Menge, B.A. & Branch, G.M. (2001). Rocky intertidal communities. In: *Marine Community Ecology* (eds Bertness, M.D., Gaines, S.D.

& Hay, M.E.). Sinauer Associates, Inc., Sunderland, MA, pp. 221–251.

Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A. & Yamada, S.B. (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.*, 64, 249–286.

Menge, B.A., Blanchette, C.A., Raimondi, P., Freidenburg, T.L., Gaines, S.D., Lubchenco, J. *et al.* (2004). Species interaction strength: testing model predictions along an upwelling gradient. *Ecol. Monogr.*, 74, 663–684.

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Paine, R.T. (1974). Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)*, 15, 93–120.

Paine, R.T. (1986). Benthic community-water column coupling during the 1982–83 El Niño. Are community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.*, 31, 351–360.

Paine, R.T. (1994). *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective.* Ecology Institute, Oldendorf/ Luhe, Germany.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637–669.

Peterson, W.T. & Schwing, F.B. (2003). A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.*, 30, 1896, doi:10.1029/2003GL017528.

Petes, L.E., Menge, B.A. & Murphy, G.D. (2007). Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *J. Exp. Mar. Biol. Ecol.*, 351, 83–91.

Robles, C. & Desharnais, R. (2002). History and current development of a paradigm of predation in rocky intertidal communities. *Ecology*, 83, 1521–1536.

Rodo, X., Pascual, M., Fuchs, G. & Faruque, S.G. (2002). ENSO and cholera: a nonstationary link related to climate change. *Proc. Natl Acad. Sci. USA*, 99, 12901–12906.

Roemmich, D. & McGowan, J. (1995). Climatic warming and the decline of zooplankton in the California current. *Science*, 267, 1324–1326.

Sagarin, R.D., Barry, J.P., Gilman, S.E. & Baxter, C.H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.*, 69, 465–490.

Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, 283, 2095–2097.

Schoch, G.C., Menge, B.A., Allison, G.W., Kavanaugh, M. & Wood, S. (2006). Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California current. *Limnol. Oceanogr.*, 51, 2564–2585.

Seed, R. & Suchanek, T.H. (1992). Population and community ecology of *Mytilus*. In: *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture* (ed. Gosling, E.). Elsevier, Amsterdam, pp. 87–169.

Sheil, D., Salim, A., Chave, J., Vanclay, J. & Hawthorne, W.D. (2006). Illumination-size relationships of 109 coexisting tropical forest tree species. *J. Ecol.*, 94, 494–507.

Smith, J.R., Fong, P. & Ambrose, R.F. (2006). Dramatic declines in mussel bed community diversity: response to climate change? *Ecology*, 87, 1153–1161.

Somero, G.N. (2002). Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.*, 42, 780–796.

Underwood, A.J. (1997). *Experiments in Ecology.* Cambridge University Press, Cambridge, UK.

Vecchi, G.A., Soden, B.J., Wittenberg, A.T., Held, I.M., Leetmaa, A. & Harrison, M.J. (2006). Weakening of tropical Pacific atmospheric circulation due to anthropogenic forcing. *Nature*, 441, 73–76.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.

Yodzis, P. (1988). The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, 69, 508–515.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Tables of statistical analyses.
- **Table S1** Repeated measures analysis of variance (RMANOVA) testing effect of cape and time on mussel growth, 1998-2006.
- **Table S2** Two-way analyses of variance testing effects on size specific proportional mussel growth ($ln$ mm d$^{-1}$ initial length$^{-1}$ * 1000) of ENSO and PDO climate patterns with tide height of plots ($ln$ m above MLLW) or sea level (mm) as covariates.
- **Table S3** Repeated measures analysis of variance (RMANOVA) testing effect of cape and time on sea water temperature, 1999-2005.
- **Table S4** Repeated measures analysis of variance (RMANOVA) testing effect of cape and time on chlorophyll-*a*, 1998-2006.
- **Table S5** One-way ANOVA on variation in tide height among five study sites (FC, BB, YB, SH and TK).
- **Table S6** Analysis of effect of cape on mussel growth with tide height ($ln$ meters) as a covariate.
- **Table S7** Analysis of effect of cape on mussel growth with annual mean sea level (mm) as a covariate.
- **Table S8** Summary of linear regression analyses of the Bakun upwelling index (http://www.pfeg.noaa.gov) on ENSO (multiple ENSO index; http://www.cdc.noaa. gov/ENSO/enso.mei_index) and PDO (Pacific Decadal Oscillation index; http://www.jisao.washington. edu/pdo/) indices.

**Appendix S2** Supplementary figures.
- **Figure S1** Variations in ENSO, as indexed by the multivariate ENSO index (A.) and PDO (B.).
- **Figure S2** Height of mussel transplant plots above MLLW at five study sites, Fogarty Creek, Boiler Bay, Yachats Beach, Strawberry Hill and Tokatee Klootchman.

- **Figure S3** Relationship between growth rate and tide height.
- **Figure S4** Relationship between sea level and mussel growth rate.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01135.x

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.