

Abundance, growth and recruitment of *Mytilus galloprovincialis* on the west coast of South Africa in relation to upwelling

Bárbara M. Xavier^{1,2}, George M. Branch^{2,*}, Evie Wieters²

¹Departamento de Biologia Animal, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

²Marine Biology Research Institute and Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

ABSTRACT: Upwelling has the potential to influence the structure of intertidal populations and communities by enhancing productivity and thereby food supplies, and by influencing the transport and abundance of propagules. We investigated alongshore variability in *Mytilus galloprovincialis* populations in relation to upwelling intensity at 11 sites spread across ~1000 km of the west coast of South Africa. Mussels grew faster at upwelling centres than at downstream sites characterized by weaker upwelling, presumably due to greater availability of food supply provided by organic material from nearshore subtidal kelp beds and/or phytoplankton. Maximum sizes reached by mussels were correlated with growth rate. Large among-site variability existed in mussel recruitment, density, percentage cover, biomass, mean size, condition and shell thickness. However, contrary to predictions of bottom-up regulation, none of these differences were consistent with differences in upwelling intensity. High growth rates did not, therefore, influence local population structure. In general, where densities were low, mean size was larger and shells were thinner. This implies that although upwelling influences growth rate and maximum size of *M. galloprovincialis*, these effects are overridden by other factors such as recruitment and intraspecific competition so that fast growth does not translate into greater abundance, biomass, cover or improved condition at upwelling sites.

KEY WORDS: Alien species · *Mytilus galloprovincialis* · Mussels · Nearshore oceanography · Rocky intertidal · South Africa · Upwelling

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Recent studies on the effects of large-scale variations in oceanographic conditions on nearshore productivity suggest that bottom-up effects strongly influence the structure and dynamics of benthic marine populations and communities by influencing supplies of nutrients, particles and propagules (see Menge 2000 for review). Nutrients can modify benthic rocky-shore communities by (1) invigorating productivity of phytoplankton which, in turn, fuels growth of sessile filter feeders (e.g. Duggins et al. 1989, Sanford and Menge 2000), or (2) directly stimulating local benthic algal productivity (see references

in Menge 2000). Water transport can alter the onshore supply of particles and determine rates of larval settlement of benthic invertebrates (Wing et al. 1995, and see Shanks 1995 for review), thereby controlling local prey availability (e.g. Raimondi 1990, Robles et al. 1995). Elevated productivity of basal trophic groups can accelerate grazing and predation, indirectly supporting higher consumer abundance and biomass (see Menge 2000 for review). Thus, the factors that produce spatial and temporal variation in individual growth and recruitment of basal species are critical for an understanding of the dynamics of benthic systems. Moreover, the extent to which growth and recruitment are coupled may ultimately

*Corresponding author. Email: george.branch@uct.ac.za

offer insight into whether (or where/when) benthic food-web dynamics depend more on nutrient input or transport of propagules.

The world's most productive coastal ocean regions lie along eastern boundaries of ocean basins, where wind-induced upwelling drives nutrient influx and phytoplankton productivity in surface waters. In terms of food supply for filter feeders, there is, however, a trade-off associated with upwelling. On the one hand, upwelling enhances nutrient levels, stimulating phytoplankton and macrophyte growth (Bustamante et al. 1995, Bustamante & Branch 1996a, Nielsen & Navarrete 2004, Wieters 2005). On the other hand, offshore advection of nutrients and particles during upwelling can produce phytoplankton-poor waters close inshore at upwelling centres (Andrews & Hutchings 1980, Field et al. 1980, Brown & Field 1985, Menge et al. 1997a, Wieters et al. 2003). The exported, aged water may be pushed onshore during relaxation of upwelling, bringing with it greater chl *a* concentrations (e.g. Pitcher et al. 1998). Likewise, larvae of many invertebrates can be entrained in offshore-moving, newly-upwelled waters, so that their delivery and settlement onshore occur when upwelling relaxes (Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995). Since surface waters are subject to along-shore and alternating offshore–onshore advection, larvae and/or phytoplankton-rich fronts are likely transported further downstream and collide with the shore where upwelling is weaker between upwelling centres (Wieters et al. 2003). This introduces the idea that there may be distinct zones of upwelling and production intensity, viz. upwelling centres where water is colder and nutrient rich, but poor in chl *a* and particulate organic matter (POM), and adjacent downstream zones that are warmer, relatively nutrient-poor, but richer in chl *a* and POM (Graham & Largier 1997, Wieters et al. 2003). Recent studies are beginning to show that such differences can manifest into important among-site differences in nutrient, particle and propagule supply to onshore benthic communities (Menge et al. 1997a,b, Wieters et al. 2003).

Nearshore benthic habitats support a large biomass of filter feeders, which can act as an important benthic-pelagic link since field studies have shown that (1) supply of food (phytoplankton and POM) in surface waters can regulate filter-feeder growth, size, and adult distribution (Duggins et al. 1989, Bertness et al. 1991, Bustamante & Branch 1996b), (2) larval settlement and recruitment are often leading determinants of population dynamics (Connell 1985, Gaines et al. 1985, Raimondi 1990), and (3) filter-feeder productivity can lead to greater abundances of key predators and/or intensify their influences (e.g. Menge et al. 1994, 1999, Robles et al. 1995, Robles 1997, Navarrete et al. 2005).

Moreover, growth and/or recruitment often determine mussel competitive ability and size-related escapes from predation (e.g. Paine 1974, Griffiths & Hockey 1987), thereby magnifying community consequences of variation in the productivity of these bivalves.

In comparisons across oceanic regimes or entire continents such as those contrasting the east and west coasts of South Africa and New Zealand, large differences in filter-feeder growth and/or recruitment have been documented and attributed to the intensity of coastal upwelling (Harris et al. 1998, Menge et al. 1999, Phillips 2005, Blanchette et al. 2006). Sharp regional-scale discontinuities in recruitment of filter feeders may also be produced by differences in the persistence and frequency of upwelling, which appear to regulate opportunities for larvae to return to shore (Connolly et al. 2001, Navarrete et al. 2005). While recruitment often differs substantially among sites that are only 10s to 100s of km apart (Menge et al. 1994, Connolly et al. 2001, Navarrete et al. 2005), descriptions of mesoscale differences in filter-feeder growth rates are scarcer. However, recent studies comparing 2 sites along the Oregon coast found that at the site with higher phytoplankton concentrations, filter feeders had faster rates of growth and greater recruitment, which were attributed to mesoscale differences in upwelling intensity and/or retention of phytoplankton and larvae (Menge et al. 1997a, Sanford & Menge 2000).

The west coast of South Africa, lying within the southern Benguela region, is dominated by seasonally-pulsed wind-driven upwelling, with winds maximally favouring upwelling in spring-summer (Shannon 1985). When equator-ward winds begin to blow, effects of upwelling are quickly felt close inshore (e.g. Field et al. 1980) and even in the intertidal zone (Bustamante et al. 1995). Nearshore, low chlorophyll and high nutrient concentrations are consistently associated with newly-upwelled water in the euphotic zone (Andrews & Hutchings 1980, Field et al. 1980, Brown & Field 1985). Moreover, frontal phytoplankton blooms are associated with onshore movement of maturing upwelled waters, suggesting that nearshore increases of particles occur during relaxation events following upwelling (Pitcher et al. 1998). Indeed, phytoplankton blooms often occur during reversals of strong winds that favour upwelling (Shannon & Pillar 1986, Pitcher et al. 1998). Considerable alongshore variations in sea surface temperature and nutrient availability over scales of few to 10s of km characterize the southern region of the Benguela system, with well-described upwelling centres focused at prominent capes (Shannon 1985). Whether this mesoscale variation in intensity of upwelling leads to differences in productivity of benthic basal trophic groups is not

known, but recent evidence suggests that growth of mussels may be regulated by food availability (Bustamante & Branch 1996b, Steffani & Branch 2003a).

Here we examine the links between coastal upwelling and productivity of the filter-feeding mussel *Mytilus galloprovincialis* Lamarck by quantifying local individual growth and recruitment at 11 sites spanning ~1000 km across the southern Benguela system, and differing in their proximity to upwelling centres. *M. galloprovincialis* invaded the west coast of South Africa in the 1970s and is now the dominant mussel species on rocky shores there (Branch & Steffani 2004). *M. galloprovincialis* has a competitive advantage over native intertidal mussels because of its relatively fast growth rate, higher fecundity and higher tolerance to desiccation (Hockey & van Erkom Schurink 1992, van Erkom Schurink & Griffiths 1993). Moreover, it displaces native limpets from the primary substratum (Steffani & Branch 2003b, Branch & Steffani 2004). Because it generates a multi-layered and structurally heterogeneous matrix, *M. galloprovincialis* supports a unique infauna (Hammond & Griffiths 2006). Both recruitment and growth of *M. galloprovincialis* are greatest on wave-exposed, as opposed to sheltered shores, and as a result, its effects are not uniform (Steffani & Branch 2003a, Branch & Steffani 2004). Local wave-action thus influences the population dynamics of *M. galloprovincialis*, and we deliberately confined our studies to exposed shores to exclude the effects of different intensities of wave action, thus allowing us to focus on the effects of upwelling.

Our goal was to determine spatial variation in production of this invasive mussel, specifically asking whether patterns in growth and recruitment are spatially coupled and can be related to local differences in upwelling conditions. In addition, we asked whether patterns in production explain variation in overall mussel abundance, size, or condition.

MATERIALS AND METHODS

Study areas. The study was conducted within the southern portion of the Benguela ecosystem on the west coast of South Africa, where mesoscale variation in sea surface temperature caused by localized upwelling characterizes the region and is easily observed in thermal imagery

(Fig. 1). Eleven study sites were selected (Fig. 1), 6 within well-described upwelling centres (Cape Hangklip, Kommetjie, Llandudno, Cape Columbine, Hondeklipbaai and Brazil), and 5 downstream of upwelling cells (Fish Hoek, Blouberg, Melkbos, Elandsbaai and Port Nolloth), where upwelling is either absent or weaker (Shannon 1985, Andrew & Hutchings 1988). Within this region, upwelling occurs largely in summer (Shannon 1985), so we undertook our observations and measurements during the austral summer and ensuing months (November to June). All sites studied had similar slopes (<30°) and similar intensities of wave exposure (in the range of 10 000 to 15 000 N m⁻²; Steffani & Branch 2003b).

Sea surface temperature. To characterize the physical environment and upwelling intensity onshore, sea surface temperature (SST) was recorded *in situ* at the 8 southernmost sites (Fig. 1). Optic Stowaway®

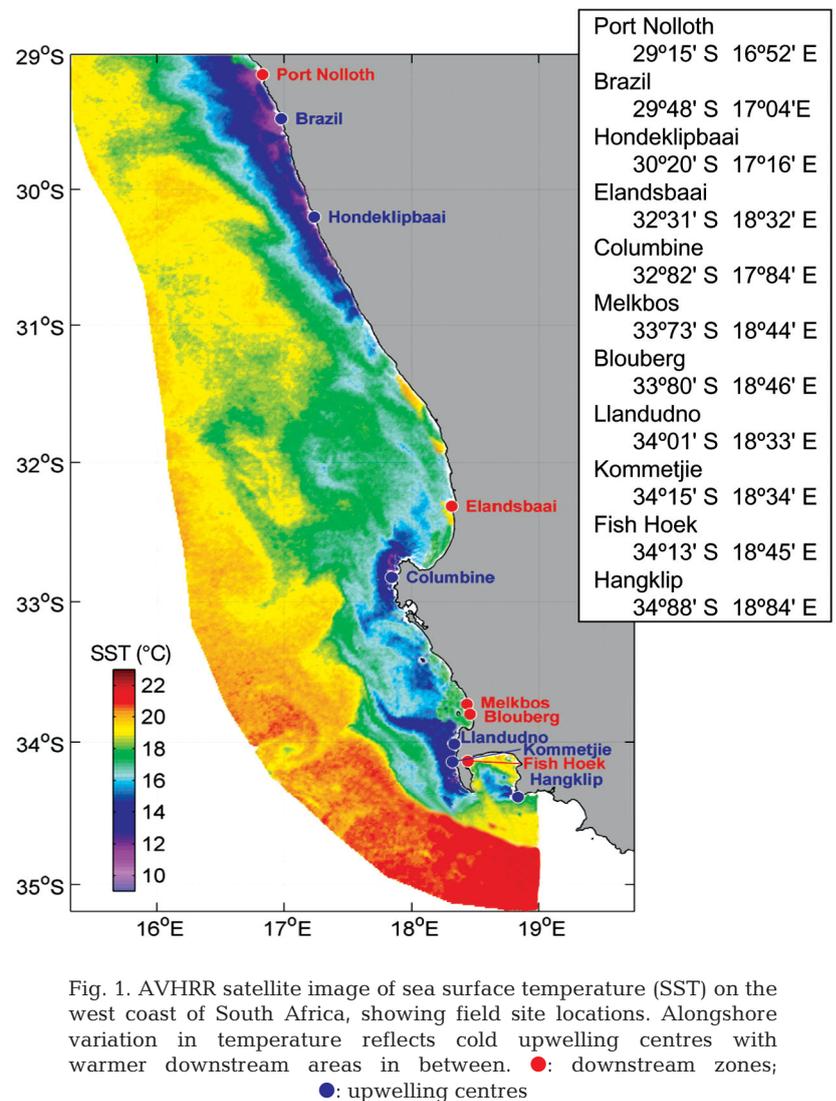


Fig. 1. AVHRR satellite image of sea surface temperature (SST) on the west coast of South Africa, showing field site locations. Alongshore variation in temperature reflects cold upwelling centres with warmer downstream areas in between. ●: downstream zones; ●: upwelling centres

temperature loggers (Onset Computer Corp.; $\pm 0.1^\circ\text{C}$ precision) were set to record every 5 min and were submersed at ~ 1 m depth below the lowest low tide at each site. These data were used to compare temperatures at sites in upwelling centres with their adjacent downstream sites and to calculate the frequencies of rapid cooling events (defined as a decline in mean daily temperature of $\geq 1^\circ\text{C}$ in a 24 h period), and the number of successive days of cooling in each event. Advanced Very High Resolution Radar (AVHRR) satellite imagery (1 km resolution) helped to categorize upwelling condition at all sites, and we relied solely on this for the 3 northern sites, where it was logistically impractical to maintain temperature loggers. Based on 17 daily images encompassing 4 upwelling events (from initiation to relaxation) that occurred during our study, we calculated the mean difference between onshore SST (pixel closest to shore) and offshore SST (pixel corresponding to 25 km perpendicularly offshore) at each site. Upwelling conditions were assumed to be represented by onshore waters being cooler than those observed offshore, and site categorization was based on residuals after removing the latitudinal trend by fitting LOWESS regression using SAS software. These data were taken from analyses conducted by Wieters (2006) for 35 sites across this same region and followed the methods of Broitman et al. (2001) and Navarrete et al. (2005).

Geographic variation in population variables. To quantify among-site differences in mussel abundance, 8 to 10 quadrats (50×50 cm, each with a grid of 10×10 cm squares) were haphazardly placed along transects oriented parallel to the shore in the middle of the mussel zone. Percentage cover of mussels was visually estimated to an accuracy of 4% cover. Density and biomass were measured at each site in eight 10×10 cm quadrats randomly placed between low and mid-tidal heights along 20 m stretches of shore in areas with 100% mussel cover. For each quadrat, all mussels were removed, counted and weighed to the nearest 5 g. The shell lengths of the first 60 mussels encountered in each sample were measured to the nearest 0.5 mm. Size structure at each site was based on the lengths of ~ 480 mussels, with the 5 largest averaged to estimate maximum size.

Indices of mussel condition and shell shape were calculated for 50 mussels collected randomly from low to mid-tidal heights at each site. Shell lengths, widths and heights were measured to nearest 0.5 mm using vernier calipers. The flesh was removed and oven-dried at 80°C for 72 h, then weighed to the nearest 0.0001 g. Cleaned dry shells were weighed separately. These data were used to calculate the following condition index (CI), derived from Davenport & Chen (1987):

$$\text{CI} = [\text{dry flesh mass (mg)} / \text{dry shell mass (mg)}] \times 100$$

As a shell thickness index (STI), we used a modification of Raubenheimer & Cook's (1990) equation:

$$\text{STI} = \text{dry shell mass (mg)} / [\text{length (mm)} \times \text{height (mm)}]$$

Mussel growth rates and recruitment. At each site, eight 15×10 cm plots were randomly selected from the middle of the mussel bed between the low- and mid-tide levels and marked with marine epoxy (Quickset Putty, Pratley®). In each plot, 50 mussels from 10 to 40 mm in length were randomly chosen and their shells notched with a triangular file at the posterior-ventral margin (see Steffani & Branch 2003a). The mussels were marked during the austral summer of 2003 to 2004 but, for logistical reasons, separate (but overlapping) time periods were required for the southern and northern regions; mussels at southern sites were marked in November, whereas mussels at northern sites were marked in February.

After 4 to 5 mo, marked mussels were collected and their increments in shell length measured. Shells were measured with Vernier calipers to the nearest 0.05 mm from the anterior end of the shell to the base of the notched mark (initial length) and from the anterior end of the shell to the posterior ventral margin (final length). Ford-Walford plots were derived by regressing final length (L_t) against initial length (L_{t_0}):

$$L_t = mL_{t_0} + i$$

where L_{t_0} = initial shell length, L_t = shell length after 5 mo growth for the southern sites and after 4 mo for the northern sites; m = slope and i = intercept on the y -axis. Constants from Ford-Walford plots were used to determine parameters for the von Bertalanffy growth curves, which are appropriate for fast-growing bivalves (Seed 1980):

$$L_t = L_\infty (1 - e^{-Kt})$$

where L_t = length at the age t , L_∞ = asymptotic length ($i/(1 - m)$), K = growth coefficient based on 5-monthly (for southern sites) and 4-monthly (for northern sites) growth calculated by $-\ln m$. In using growth measurements for portions of the year to determine annual growth, it was assumed that *Mytilus galloprovincialis* has a constant rate of growth throughout the year on the west coast of South Africa, as indicated in previous studies (Steffani & Branch 2003a).

To characterize among-site variation in recruitment rates of mussels, we deployed artificial substrata (7 cm diameter plastic-mesh scrub pads) that mimicked the natural filamentous matrices to which settling mussel larvae attach. Five replicate pads were placed in the mid-zone of each of our 8 southern sites and replaced monthly for 29 mo. In the

laboratory, all recruits that had settled in the pads were counted and identified with the aid of a dissecting microscope.

Data analyses. All data were analysed using Statistica 6 for Windows (StatSoft) and were tested for normality and homogeneity of variances by Kolmogorov-Smirnov and Levene tests, respectively. If necessary, data were log transformed (density, size and shell thickness) or arcsine transformed (percentage cover) to meet these assumptions. Results for most population variables were analysed using a nested ANOVA. Upwelling condition (upwelling centre versus downstream) was considered a fixed factor, whereas site (replicates) was considered a random factor nested within upwelling condition. Growth rate (increment in shell length d^{-1}), condition and shell thickness were analysed with a nested ANCOVA after testing for the assumption of homogeneity of slopes. Site was nested

within upwelling condition and initial shell length was used as the covariate nested within Site and Upwelling. Mean monthly recruitment rates of mussels were analysed using 1-way ANOVA, with upwelling condition considered as a fixed factor. Spatial correlations among the populations and individual variables were quantified using Pearson product moment.

RESULTS

Sea surface temperature

Onshore SST was characterized by substantial high-frequency variation at intervals of hours to days, but pronounced differences occurred among sites (Fig. 2). Upwelling sites (Hangklip, Kommetjie, Llandudno and Columbine) all exhibited consistently colder conditions

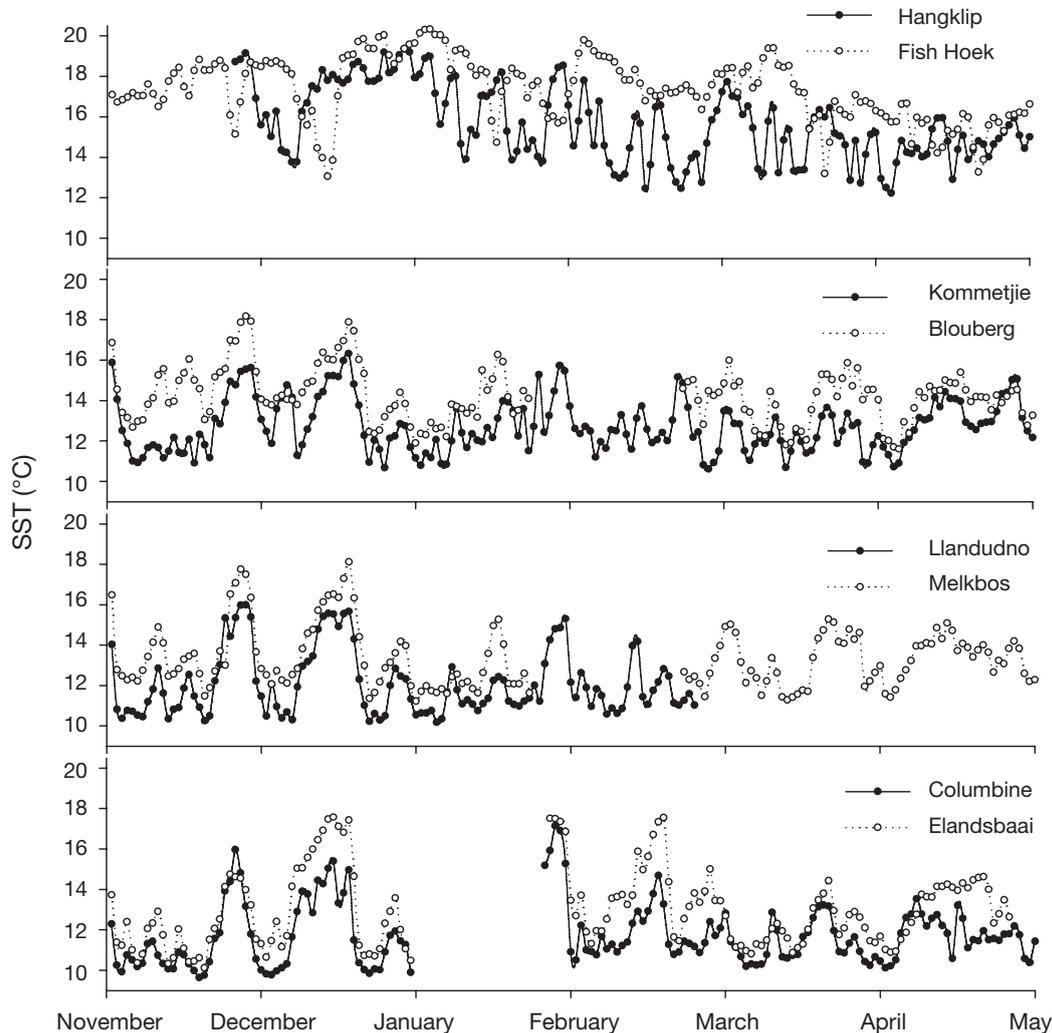


Fig. 2. Mean daily *in situ* sea surface temperatures (SST) at the 8 southernmost sites derived from onshore loggers for the period during which growth experiments were conducted. No data for some sites for certain periods due to equipment failure

by an average of 2.2°C less than at their proximate downstream sites (Fish Hoek, Blouberg, Melkbos and Elandsbaai) where rapid cooling events were less frequent and of shorter duration. At upwelling cells, rapid cooling took place on 17.9% of the days versus 9.7% at downstream sites, and the durations of successive days with cooling, respectively, averaged 3.71 d (± 0.24 SE) versus 2.67 d (± 0.20 SE). These differences matched well with alongshore variation observed in AVHRR images (Fig. 1), which further illustrate the clear association between meso-scale spatial structure in SST and shoreline topography and coastal orientation. Confirmation of our initial classification of northern sites was more difficult as we were unable to place temperature loggers there due to their isolation. Satellite imagery did confirm that Hondeklipbaai and Brazil both lay in an upwelling centre (Fig. 1), as described by Andrews & Hutchings (1980) and Shannon (1985). The status of Port Nolloth was more difficult to determine, and likely represents intermediate conditions. However, because residuals of differences between offshore and onshore temperatures (after removing the regional trend) were negative there and thus resembled the residuals of other downstream sites (Fig. 3), we maintained our original classification of this site as a downstream site with relatively weak upwelling. Moreover, to ensure that our analyses and conclusions were conservative, we ran all our upwelling-downstream comparisons both with and without the northern sites. As both approaches led to the same conclusions, we are confident that our categorization of sites was robust.

Biomass, abundance, size, condition and shell shape

Large and significant among-site variation was observed for all population and individual characteristics, but differences did not follow any trend in relation to upwelling intensity (Table 1, Fig. 4).

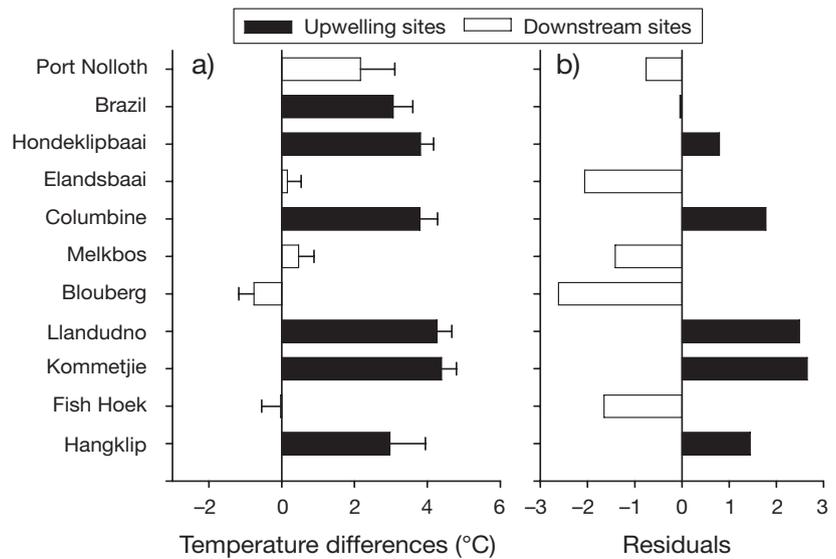


Fig. 3. (a) Mean (\pm SE) daily difference in sea surface temperature between pixels 25 km offshore from each study site and pixels 2 km offshore, and (b) data after removing the regional trend using LOWESS regression (residuals). Positive values indicate water nearshore was colder than offshore

Table 1. *Mytilus galloprovincialis*. Nested ANOVA and ANCOVA tests in relation to among-site differences and upwelling intensity at 11 sites

	df	MS	F	p
Biomass				
Upwelling	1	40671.8	1.13	0.32
Site (Upwelling)	9	36645.1	6.52	<0.0001
Density				
Upwelling	1	0.02	0.09	0.77
Site (Upwelling)	9	2.26	7.741	<0.0001
Percentage cover				
Upwelling	1	2.84	3.03	0.12
Site (Upwelling)	9	0.86	7.85	<0.0001
Mean size				
Upwelling	1	139.3	1.89	0.20
Site (Upwelling)	9	94.9	91.91	<0.0001
Mean maximum size				
Upwelling	1	0.50	3.52	0.09
Site (Upwelling)	9	0.14	76.22	<0.0001
Condition				
Upwelling	1	22.34	0.92	0.36
Site (Upwelling) & random	9	28.63	8.17	<0.0001
Initial length	1	0.035	0.01	0.92
Model	11	25.47	7.27	<0.0001
Error	179	3.503		
Shell thickness [log (thickness + 1)]				
Upwelling	1	0.735	2.239	0.165
Site (Upwelling) & random	9	0.381	4.667	<0.0001
Initial length	1	0.501	6.152	0.014
Model	11	0.387	4.756	<0.0001
Error	179	0.0815		
Growth increments				
Upwelling	1	0.021	10.25	<0.01
Site (Upwelling) & random	9	0.003	23.31	<0.0001
Initial length	1	0.007	55.71	<0.0001
Model	11	0.005	45.59	<0.0001
Error	1098	0.00012		

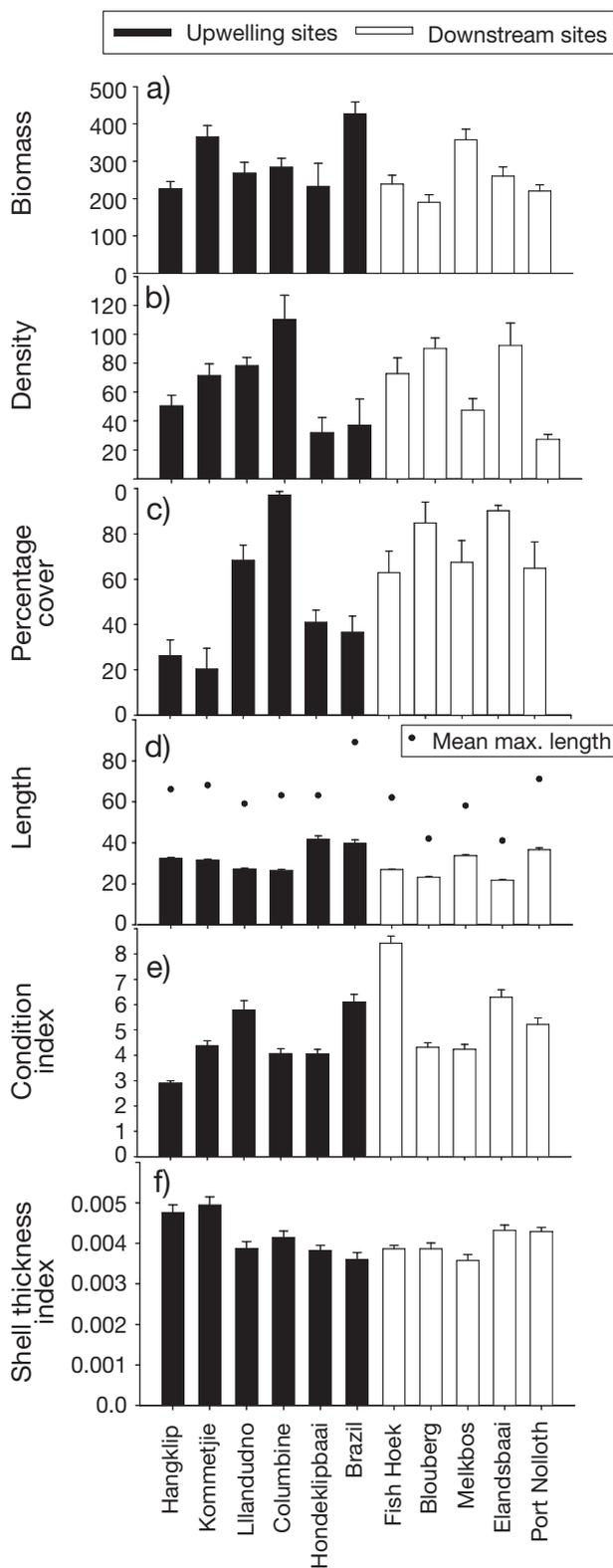


Fig. 4. *Mytilus galloprovincialis*. (a) Biomass ($\text{g } 100 \text{ cm}^{-2}$), (b) density ($\text{ind. } 100 \text{ cm}^{-2}$), (c) percentage cover, (d) mean size and mean max. size (mm), (e) condition index, and (f) shell thickness index at the 11 sites. Sites listed from south to north within the 2 categories. All values are means + SE

Significant, negative spatial correlations were found between density and mean size and density and maximum size (Pearson = -0.89 , $p < 0.001$ and Pearson = -0.60 , $p = 0.05$, respectively). Sites characterized by low mussel density supported the largest mussels (Fig. 4b,d), and therefore no significant relationships were observed between the cover or density of mussels and local biomass (Pearson = 0.005 , $p > 0.5$ and Pearson = -0.17 , $p > 0.5$; Fig. 4a–c). Moreover, those sites with larger mussels also had thin-shelled individuals (Fig. 4d,f; Pearson = 0.65 , $p < 0.05$), but mussel condition (Fig. 4e) was not significantly correlated with any of the other variables ($p > 0.5$ in all cases).

Mussel growth rates and recruitment

The von Bertalanffy growth curves differed considerably between upwelling and downstream sites (Fig. 5, Table 2). Growth was faster at upwelling sites, and mussels there obtained larger maximum sizes (Pearson correlation = 0.87 ; $p < 0.0005$).

Differences between the 2 intensities of upwelling were most easily visualized and analysed using the regressions between growth increments and initial length (Fig. 6, Table 2). There were significant differences between upwelling conditions, among sites within upwelling conditions, and among initial lengths (Table 1, Growth increments). There was a significant interaction between sites and initial length, which was attributable to one site lacking small mussels (Brazil), but no significant interaction between initial length and upwelling condition (Table 1, Growth increments).

Mean monthly recruitment rates did not vary consistently in relation to upwelling condition (Fig. 7; $F_{1,6} = 0.21$, $p = 0.66$). Rather, recruitment increased stepwise from south to north. There was no correlation between recruitment rates and growth rates (Pearson = 0.14 , $p = 0.72$), indicating a lack of any coupling between these 2 sources of productivity, but a significant, positive correlation did exist between recruitment rate and mussel density (Pearson = 0.84 , $p = 0.018$).

DISCUSSION

Filter-feeding invertebrates dominate most nearshore habitats world-wide, but the factors influencing their abundance over broad scales have only recently received attention, despite their obvious relevance to conservation and management. Our study is the first to describe the effects of prevalent coastal upwelling variability on geographic patterns of productivity (recruitment and growth) and population structure of a

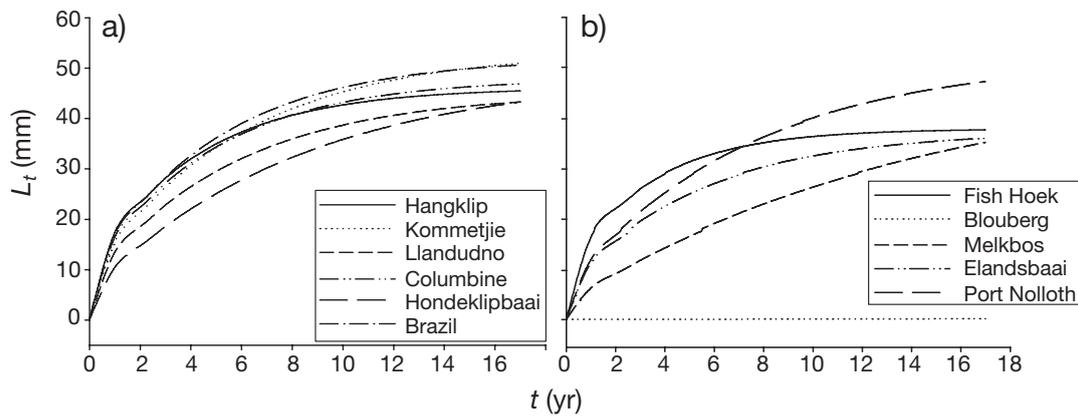


Fig. 5. *Mytilus galloprovincialis*. Von Bertalanffy growth curves for (a) upwelling sites and (b) downstream sites. Growth curve for Blouberg is indicated as zero because mussels there had a negative growth coefficient (Table 2). L_t : final length

benthic filter feeder on the west coast of South Africa. Making *a priori* predictions about the mesoscale spatial effects of upwelling on benthic filter feeders is not simple because upwelling constitutes a 2-edged sword, viz. increased nutrient supply may enhance local primary production, but advective upwelling may reduce on-shore delivery of larvae and particulate food (Menge et al. 1997a,b, Sanford & Menge 2000, Wieters et al. 2003, Nielsen & Navarrete 2004). In addition, upwelling variation may qualitatively influence the outcome of complex predatory, grazing and competitive interactions that operate between species. For example, Wieters (2005) found that differences in the intensity of upwelling in central Chile regulate the height of algal turfs, in turn dictating levels of mussel recruitment. The net effect is thus difficult to forecast. While establishing mechanisms is beyond the scope of this study, the patterns revealed here differ from those observed in most other upwelled systems. In contrast to comparable work

along the US west coast (Menge et al. 1997a,b, Sanford & Menge 2000, Phillips 2005, Blanchette et al. 2006, 2007), our study revealed that (1) the 2 main sources of production (growth and recruitment) were not spatially coupled, with growth but not recruitment being upwelling-dependent, (2) growth rates were higher at upwelling centres and (3) population structure was unrelated to upwelling intensity. In general, although our results indicate that mussels at upwelling centres grow faster than downstream, the consequences of this for local population structure were limited, due to the more important influences of recruitment rates and intraspecific competition.

Sea surface temperature

All of the sites we examined fall within the southern Benguela region in which overall productivity and

Table 2. *Mytilus galloprovincialis*. Constants of the Ford-Walford growth regressions and the von Bertalanffy growth curves. m = slope, i = intercept at y-axis, r^2 = coefficient of determination, L_∞ = asymptotic length (mm), K = growth coefficient (5-monthly growth for southern sites and 4-monthly growth for northern sites)

Site	Ford-Walford			von Bertalanffy	
	m	i	r^2	L_∞	K
Upwelling centres					
Hangklip	0.8212	8.2511	0.8721	46.1471	0.1970
Kommetjie	0.8674	7.0917	0.8756	53.4819	0.1423
Llandudno	0.8633	6.1788	0.8676	45.1997	0.1470
Columbine	0.8398	7.6921	0.7924	48.0156	0.1746
Hondeklipbaai	0.9234	3.7542	0.9501	49.0104	0.0797
Brazil	0.8769	6.4188	0.7887	52.1430	0.1314
Downstream sites					
Fish Hoek	0.7856	8.1817	0.7432	38.1609	0.2413
Blouberg	1.0031	0.0065	0.9968	-2.0968	-0.0031
Melkbos	0.9438	2.7914	0.9463	49.6690	0.0578
Elandsbaai	0.8579	5.3445	0.9355	37.6108	0.1533
Port Nolloth	0.9156	4.4256	0.9312	52.4360	0.0881

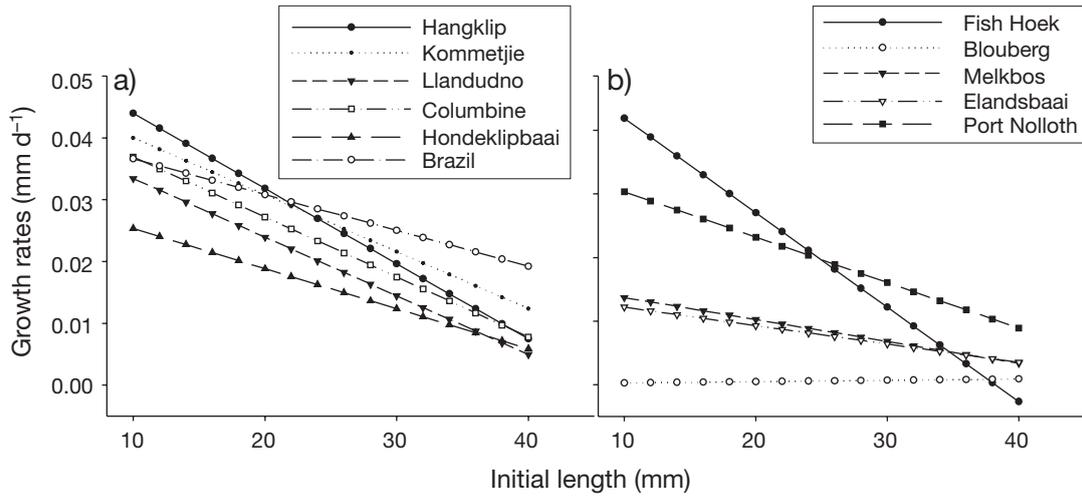


Fig. 6. *Mytilus galloprovincialis*. Regressions between initial sizes and growth increments at (a) upwelling sites and (b) downstream sites

biomass are high compared with the south and east coasts of South Africa, but taxonomic diversity is low (Bustamante et al. 1995, Bustamante & Branch 1996a). Our concern, however, was with intra-regional effects at mesoscales, specifically differences between upwelling cells and downstream sites.

The combination of temperature loggers and AVHRR satellite thermal imagery showed that the 6 sites we classed as upwelling centres were, on average, 2.2°C cooler than adjacent downstream sites, and had longer and more intense periods of low temperatures. Nevertheless, all sites experienced frequent and large fluctuations of temperature linked with the

roughly weekly periodicity of wind-induced upwelling events characteristic of the southern Benguela system (Fig. 2).

We had to rely on satellite imagery and existing literature to classify the 3 northernmost sites. Both sources confirm that Hondeklipbaai and Brazil fall within an upwelling cell, but classifying Port Nolloth was more problematic. It lies at the northern end of the same upwelling cell as Hondeklipbaai and Brazil, and could perhaps have been considered as an upwelling site. However, we retained our initial classification of it as ‘downstream’ based on local differences between onshore and offshore temperatures (Fig. 3). This decision is also conservative. Had we reversed it and considered Port Nolloth as part of the upwelling cell, this would have strengthened our conclusions about growth rate being faster at upwelling cells, and left our conclusions about the influence of upwelling on other population parameters unaltered.

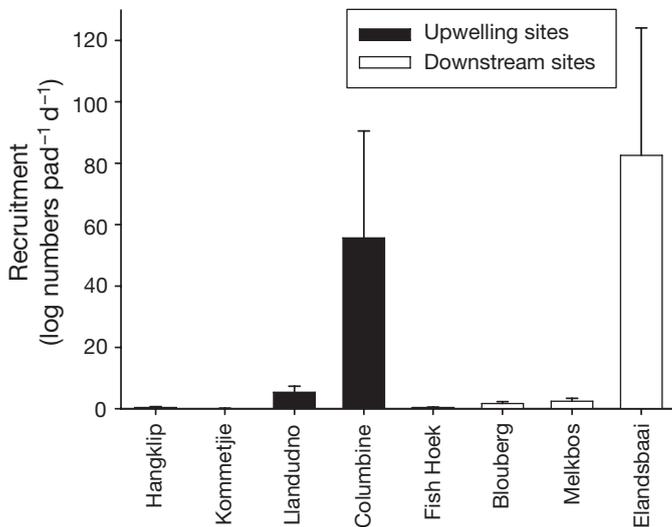


Fig. 7. *Mytilus galloprovincialis*. Number of recruits settling in artificial pads at upwelling and downstream sites among the 8 southernmost sites examined, listed from south to north within each category of upwelling

Effects of upwelling on mussel growth and recruitment

Our results revealed a strong relationship between upwelling intensity and *Mytilus galloprovincialis* growth rates. What we had not predicted was that mussels at upwelling locations would have faster growth than those downstream, because previous authors have recorded faster mussel growth associated with areas of weaker upwelling and higher temperatures (Menge et al. 1997a,b, Sanford & Menge 2000, Phillips 2005, Blanchette et al. 2006, 2007), which are also often characterized by greater onshore concentrations of chl a (Menge et al. 1997a,b, Sanford

& Menge 2000, Wieters et al. 2003). Phytoplankton is, however, not the only potential source of food for filter feeders; POM derived from kelp is an important supply of food for them on the west coast of South Africa (Bustamante & Branch 1996b). Faster growth of mussels at upwelling cells may thus have 2 explanations: (1) upwelling centres may be associated with greater amounts of kelp, enhancing local supplies of POM, or (2) alongshore advection of upwelled water may be weak enough for phytoplankton to be retained within upwelling centres where it is generated, rather than being exported to downstream sites. The latter seems less plausible than the former because satellite imagery and *in situ* measurements reveal a scarcity of chl *a* close inshore within upwelling cells, relative to downstream localities (Brown & Field 1985, Shannon & Pillar 1986). Moreover, Cliff's (1982) observations that in the intertidal zone only 14% of suspended organic material comprises phytoplankton, even during peaks of upwelling, led him to argue that intertidal filter feeders depend largely on detritus generated from seaweeds rather than phytoplankton. The kelps *Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria pallida* Grev. form dense nearshore subtidal beds on the west coast of South Africa, and Bustamante & Branch (1996b) found that mussel diet is largely composed of kelp detritus. Unlike phytoplankton, kelp is fixed in position, so advection does not remove kelp plants in the way that it exports phytoplankton. Kelp particles will therefore be concentrated where kelp productivity is highest. Duggins et al. (1989) also consider kelp to have a substantial impact on filter-feeder assemblages. In Chile, abundance of intertidal kelp and algal growth rates vary consistently with upwelling (Broitman et al. 2001, Nielsen & Navarrete 2004, Wieters 2005). Thus, upwelling may indirectly influence mussel growth by regulating kelp growth and detritus shedding.

In addition to food availability, there are other factors that potentially influenced the relative growth rates of *Mytilus galloprovincialis*. First, the 2 southernmost sites, Hangklip and Fish Hoek, lie in False Bay to the east of the boundary between the cool-temperate Namaqua and the warm-temperate Agulhas biogeographic provinces (Emanuel et al. 1992) and are warmed by the tail end of the Agulhas Current (Shannon 1985). Indeed, SSTs there were consistently about 2°C warmer than at the west coast sites, theoretically contributing to the faster growth rates there. There was, however, no indication of a latitudinal trend in growth rate on the west coast. Overall, the clearest pattern was that upwelled sites had faster growth rates than downstream sites. This outcome is the reverse of that predicted if higher temperatures boost growth, for highest growth actually occurred at the sites with

lower temperatures. Secondly, differences among sites could have arisen from differences in the patterns of upwelling. Sites in the north fell in a zone where upwelling covers a greater but more diffusely defined geographic extent and is more sustained throughout the year. In the south, upwelling is sharply focused at well-defined cells, but it is intermittent. Despite this, no simple differences emerged between growth rates in the south and north; the pervasive pattern remained one of differences between upwelled versus downstream sites.

No difference in recruitment emerged between upwelled and downstream sites, but recruitment increased in a stepwise manner northwards, suggesting that there may be a strong regional-scale discontinuity or latitudinal gradient in larval settlement and subsequent recruitment. It is noteworthy that the sharp change in recruitment rates that we observed coincides with a change in coastal topography, orientation and the width of the continental shelf, which may influence advection or retention nearshore. *Mytilus galloprovincialis* was introduced to the west coast of South Africa at Saldanha Bay (immediately south of Cape Columbine) in the later 1970s, and has spread faster northwards than southwards (G. M. Branch unpubl. data). Our results suggest that this differential rate of colonization is largely due to differences in recruitment rates, and may be linked to prevailing wind-driven water movements. McQuaid & Phillips (2000) have previously shown that larval dispersal of *M. galloprovincialis* on the south coast of South Africa is related to prevailing winds.

Population dynamics of mussels

Of all the variables examined, only growth rate correlated with upwelling intensity. Recruitment, abundance, size, condition and shell thickness all varied strongly among sites, but not in a manner consistent with upwelling intensity. There were also no obvious trends from north to south, so latitudinal differences were not masking upwelling effects. Thus, differences in growth rate may have been important in terms of the reproductive output of individuals, but at the level of the population they did not translate into differences in biomass, density or other population parameters.

Differences in physical conditions between upwelling cells and downstream sites may be too subtle to influence the abundance and biomass of mussels, and the high levels of settlement may swamp any influences of growth rate on abundance. However, at a larger scale around the entire coast of southern Africa, the presence or absence of upwelling is profoundly

correlated with mussel population dynamics. Bustamante et al. (1995) and Bustamante & Branch (1996a) demonstrated that filter-feeder biomass declines from the west to the south and east coasts of South Africa as upwelling, nutrient levels and productivity decline. Within the west coast region, other factors unrelated to mesoscale variation in upwelling, such as recruitment levels and intraspecific competition for food or space may overwhelm any influences of bottom-up effects related to upwelling.

Correlations among parameters across sites provided some insight into potential trade-offs caused by intraspecific competition. Sites with lower densities supported larger mussels, possibly because individuals gained (1) more food, or (2) more space, which could enhance survivorship either by fast growth to a large size at which predation is diminished or by reducing self-thinning that would otherwise deplete numbers in a size-dependent manner (Griffiths & Hockey 1987) respectively. However, greater shell length does not necessarily mean increased flesh mass, as this depends on the allometry of growth (condition index) and morphology (shell thickness index) (Seed 1980). It is possible that at high-growth sites more energy is put into shell growth than into tissue growth and reproductive output, which is a common trade-off in mussels. Fast growth to large size does have important benefits (i.e. escape from predators, larger eventual reproductive output), but fast growth may also postpone reproduction. An alternative explanation for the negative correlation between density and size may be differences in recruitment; indeed, the large average size of mussels at low-density sites was partially explained by the lack of small mussels (10 to 20 mm), inferring low recruitment.

Overall, density and biomass are set by recruitment and growth versus post-recruitment mortality. Elsewhere, correlations have been demonstrated between growth rate and recruitment of mussels (Menge et al. 1997a, 1999). However, we found that recruitment was not coupled with growth rate or with upwelling, and this is probably the central reason why fast growth associated with upwelling was not manifested in greater abundance. Recruitment was, however, correlated with mussel density, suggesting that it has a pervasive effect on density that overrides any influence of upwelling. Settlement of *Mytilus galloprovincialis* is extremely dense on the west coast of South Africa, reaching 20 000 settlers 100 cm^{-2} (Harris et al. 1998). At settlement levels this high, intraspecific competition is a major cause of mortality, due to self-thinning (Griffiths & Hockey 1987), and fast growth will merely intensify thinning. Competition thus sets limits on cover and biomass, overriding the potential effect of growth rate.

A combination of bottom-up and top-down effects is likely to affect space occupiers such as filter feeders (e.g. Menge 2000). The major predators on mussels in intertidal communities of the west coast of South Africa are whelks (*Nucella* species) and birds (mainly *Haematopus moquini*), and *Mytilus galloprovincialis* is able to escape these predators with large size (Griffiths & Hockey 1987, Branch & Steffani 2004). Predators with direct development (i.e. no planktonic life history stages) such as these whelks are expected to respond numerically to local prey availability via reproduction (Hockey & van Erkom Schurink 1992), and therefore areas of higher prey production (recruitment) may also experience higher predation rates. Among-site differences in mussel size and density may, therefore, reflect variation in predation intensity. Griffiths & Hockey (1987) suggest that predation accounts for 50 to 90% of mussel mortality in the intertidal zone, but at present there are no experimental studies testing the effects of predators on *M. galloprovincialis* or descriptions of among-site variability in predator population size. In some locations, human harvesting could influence abundance of mussels, but this is unlikely along the west coast because it is sparsely inhabited and mussel harvesting is minimal.

CONCLUSIONS

Overall, the intensity of upwelling had a clear-cut influence on mussel growth but this was not manifested in differences in parameters such as percentage cover and biomass.

Our findings are important because recent papers have emphasised the effects that local upwelling may have on population dynamics and community composition (Menge et al. 1999). Striking differences in biomass and the relative representation of different trophic groups have been correlated with differences in productivity around the southern African coastline (Bustamante & Branch 1996a). Within the region that we examined, however, the central message is that local upwelling is unlikely to have profound effects on mussel populations unless there is congruence in the responses of both recruitment and growth to upwelling.

Acknowledgements. We thank H. N. Cabral, T. B. Robinson and C. L. Griffiths for their comments and help in designing the experiment and M. de Ponte, C. Holness and R. Borges for hours spent on field and laboratory work collecting and measuring mussels. Funding was received from the National Research Foundation, the Andrew Mellon Foundation and the University of Cape Town.

LITERATURE CITED

- Andrews WRH, Hutchings L (1980) Upwelling in the southern Benguela Current. *Prog Oceanogr* 9:1–88
- Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 75:91–100
- Blanchette C, Broitman B, Gaines SD (2006) Intertidal community structure and nearshore oceanography around Santa Cruz Island, California, USA. *Mar Biol* 149:689–701
- Blanchette CA, Helmuth B, Gaines SD (2007) Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic boundary at Point Conception, California, USA. *J Exp Mar Biol Ecol* 340:126–148
- Branch GM, Steffani CN (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *J Exp Mar Biol Ecol* 300:189–215
- Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation of south eastern Pacific intertidal communities. *Mar Ecol Prog Ser* 224:21–34
- Brown PC, Field JG (1985) Factors limiting phytoplankton production in a nearshore upwelling area. *J Plankton Res* 8:55–68
- Bustamante RH, Branch GM (1996a) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *J Biogeogr* 23:339–351
- Bustamante RH, Branch GM (1996b) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *J Exp Mar Biol Ecol* 196:1–28
- Bustamante RH, Branch GM, Eekhout S, Robertson LB and 7 others (1995) Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102:189–201
- Cliff G (1982) Seasonal variation in the contribution of phytoplankton, bacteria, detritus and inorganic nutrients to a rocky shore ecosystem. *Trans R Soc S Afr* 44:523–538
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11–45
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813
- Davenport J, Chen X (1987) A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L.). *J Molluscan Stud* 53:293–297
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Emanuel BP, Bustamante RH, Branch GM, Eekhout S, Odenaal FJ (1992) A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *S Afr J Mar Sci* 12:341–354
- Farrell TM, Bracher D, Roughgarden J (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol Oceanogr* 36:279–288
- Field JG, Griffiths CL, Linley EA, Carter RA, Zoutendyk P (1980) Upwelling in a nearshore marine ecosystem and its biological implications. *Estuar Coast Mar Sci* 11:133–150
- Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272
- Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Cont Shelf Res* 17:509–532
- Griffiths CL, Hockey PAR (1987) A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. *S Afr J Mar Sci* 5:547–556
- Hammond W, Griffiths CL (2006) Biogeographic variation in community composition of mussel bed infauna along the southern African coast. *Afr Zool* 41:123–130
- Harris JM, Branch GM, Elliott BL, Currie B, Dye A, McQuaid CD, Tomalin B, Velasquez C (1998) Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *S Afr J Zool* 33:1–11
- Hockey PAR, van Erkom Schurink C (1992) The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Trans R Soc S Afr* 48:123–139
- McQuaid CD, Phillips T (2000) Limited wind-driven dispersal of intertidal mussel larvae: *in situ* evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Mar Ecol Prog Ser* 201:211–220
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J Exp Mar Biol Ecol* 250:257–289
- Menge BA, Berlow EL, Blanchette C, 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, Strub PT (1997a) Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnol Oceanogr* 42:57–66
- Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997b) 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 JJ (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol Monogr* 69:297–330
- Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top down control. *Proc Natl Acad Sci USA* 102:18046–48051
- Nielsen KJ, Navarrete SA (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecol Lett* 7:31–41
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principle predator. *Oecologia* 15:93–120
- Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Mar Ecol Prog Ser* 295:79–85
- Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Mar Ecol Prog Ser* 172:253–264
- Raimondi P (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol Monogr* 60:283–309
- Raubenheimer D, Cook P (1990) Effects of exposure to wave action on allocation of resources to shell and meat growth by the subtidal mussel, *Mytilus galloprovincialis*. *J Shellfish Res* 9:87–93
- Robles CD (1997) Changing recruitment patterns in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* 78:1400–1414

- Robles C, Sherwood-Stephens R, Alvarado M (1995) Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76:565–579
- Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. *Acta Oecol* 12:35–51
- Sanford E, Menge BA (2000) Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Mar Ecol Prog Ser* 209:143–157
- Seed R (1980) Shell growth and form in the Bivalvia. In: Rhoads DC, Lutz RA (eds) *Skeletal growth of aquatic organisms: biological records of environmental change*. Plenum Press, New York, p 23–61
- Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward L (ed) *Ecology of marine invertebrate larvae*. CRC Press, New York, p 323–367
- Shannon LV (1985) The Benguela ecosystem Part I. Evolution of the Benguela, physical features and processes. *Oceanogr Mar Biol Annu Rev* 23:105–182
- Shannon LV, Pillar SC (1986) The Benguela ecosystem Part III. Plankton. *Oceanogr Mar Biol Ann Rev* 24:65–170
- Steffani CN, Branch GM (2003a) Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Mar Ecol Prog Ser* 246:197–209
- Steffani CN, Branch GM (2003b) Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *Afr J Mar Sci* 25:195–212
- van Erkom Schurink C, Griffiths CL (1993) Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109:257–273
- Wieters E (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Mar Ecol Prog Ser* 301:43–54
- Wieters EA (2006) Benthic-pelagic coupling: rocky intertidal communities and nearshore oceanographic conditions across multiple scales. PhD thesis, University of Cape Town
- Wieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen KJ, Véliz F (2003) Alongshore and temporal variability in chl *a* concentration in Chilean nearshore waters. *Mar Ecol Prog Ser* 249:93–105
- Wing SR, Largier J, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region *Limnol Oceanogr* 40:316–329

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: December 11, 2006; Accepted: April 3, 2007
Proofs received from author(s): September 6, 2007*