

Bottom-up control of temperate rocky intertidal community structure: evidence from a transplant experiment

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ABSTRACT: Transplantation of mussels *Mytilus galloprovincialis* to Wellington Harbour and Cook Strait (central New Zealand) was carried out to test for bottom-up control (food limitation) of intertidal community structure and scarcity of mussels. Analysis of water-column variables revealed that mean turbidity and chlorophyll a concentrations were 3 and 10 times higher, respectively, in Wellington Harbour than in Cook Strait. The responses of transplanted mussels reflected the water-column properties: mortality of Wellington Harbour mussels was very low whereas mortality of Cook Strait mussels was significantly greater, and all components of shell growth and soft tissue condition were higher for Wellington Harbour than Cook Strait mussels. These results are consistent with bottom-up control of mussel abundance, as mediated by feeding activity, body condition and energy balance. The results demonstrate how pronounced differences in localised coastal conditions may influence temperate rocky intertidal community structure on spatial scales of hundreds of metres, and how this influence may explain differences in community composition on spatial scales of many kilometres.

KEY WORDS: *Mytilus galloprovincialis* · Food limitation · Bottom-up control · Coastal processes · Growth · Condition index · Mortality

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INTRODUCTION

More than 50 yr ago, it was suggested that intertidal community structure on temperate rocky reefs is similar across all regions, with the same functional groups of organisms exhibiting similar patterns of zonation (non-repeating bands of occurrence) from the top of the intertidal region (the supralittoral) to the bottom (infralittoral), and down into the shallow subtidal region (Stephenson & Stephenson 1949, 1972). The processes that give rise to this common pattern of structuring include both physical (e.g. wave exposure, shore aspect, height on the shore) and biological (e.g. predation, competition) processes (Lewis 1961, Dayton 1971, Paine 1974, Menge 1976). More recent research has identified both biogeographic-scale variation, with latitudinal gradients of intertidal community differences in macroalgae and invertebrate community structure (Gaines

& Lubchenko 1982, Bustamante & Branch 1996a, and references therein), and the roles of top-down (e.g. predation) and bottom-up (e.g. food supply, larval supply) processes in contributing to temperate intertidal community structure (Menge 1992, 2000, Menge et al. 2002, Navarrete et al. 2005, McQuaid & Lindsay 2007). Bottom-up processes are often strongly influenced by local coastal geomorphology and hydrography, so factors such as gyres in local bays, upwelling and downwelling, and wave exposure may influence the delivery of seston and larvae to the local shoreline (e.g. Archambault et al. 1999, McCulloch & Shanks 2003, Menge et al. 2003, Wieters et al. 2003, Broitman & Kinlan 2006, Jessopp & McAllen 2008). Although the concepts of top-down (consumer-driven) and bottom-up (resource-driven) effects are most usually considered in marine science in the context of temperate intertidal ecology, they are also relevant at very large spatial scales (e.g.

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North Atlantic ecosystems) and may have direct relevance to fisheries management (Frank et al. 2007).

Variability in seston particle concentrations and types is a common feature of coastal waters (Fréchette & Bourget 1985, Page & Ricard 1990, Witman et al. 1993, Gardner 2002). The extent of temporal and spatial variability of particulate food availability is well documented and the ecophysiological responses of mussels to such variability have long been appreciated (Bayne & Widdows 1978, Starr et al. 1990, Bayne 1993). The widespread distribution of filter-feeding mussels of genera such as *Mytilus*, *Perna* and *Aulacomya* in many parts of the world suggests that evolutionary adaptation to such variability in food supply is likely to exist. That is, mussels living in regions of variable food supply must be able to withstand periods of low or no food supply by utilising stored energy reserves until food supply increases again (Bayne & Worrall 1980, Bayne 1993). Despite this adaptation to a fluctuating food supply, it is probably common for the larvae of many marine bivalve species to be food-limited even if only briefly (Bos et al. 2006) and for the distribution of bivalve suspension-feeding species to be limited by seasonal variation in food supply (Bayne & Newell 1983).

Cook Strait, the body of water that separates New Zealand's North Island from the South Island, has a wave-exposed intertidal region that is characterised by an abundance of bare rock (Morton & Miller 1968, Gardner 2000, Helson & Gardner 2004, 2007). The shoreline is characterised by a low density of winkles (2 species), patchy coverage of barnacles (2 chthamalid species), an almost complete absence of mussels (only occasional individuals of 2 of the 4 main species are found), and a well-developed low intertidal macroalgal fringe. In contrast to this, only 12 km away, Wellington Harbour supports a temperate rocky reef intertidal community characterised by an abundance of winkles (2 littorinid species), barnacles (2 chthamalid species), mussels (4 mytilid species), and a well-developed macroalgal fringe that extends into the sublittoral zone (Gardner 2000, 2008). Cook Strait and Wellington Harbour shores are both largely composed of sedimentary rock (greywacke). The major geomorphological difference between the 2 regions is that Wellington Harbour is a semi-enclosed and reasonably sheltered body of water, whereas Cook Strait is open and exposed. The major environmental difference is that Wellington Harbour receives freshwater supply from the Hutt River and is nutrient- and particulate-rich, whereas Cook Strait receives no riparian input and is nutrient- and particulate-poor (Bowman et al. 1983,

Gardner 2000, 2002, Gardner & Thompson 2001, Helson et al. 2007). These differences arise in large part because of the terrestrial and marine geomorphology of the region and also because the water that flows into Cook Strait arrives from the northwest, which means that it is Tasman Sea (oceanic) water that is funnelled through Cook Strait (net flow is northwest to southeast), creating an environmental gradient in terms of water-column properties (Bowman et al. 1983, Gardner 2000, 2008). This natural environmental gradient is reflected in the biological communities of northern Cook Strait, with a pronounced change from west (entrance to Cook Strait) to east (towards Wellington Harbour) (Pande & Gardner 2009).

Profound differences in intertidal community structure between 2 regions only a few kilometres apart raise questions about the biological and physical processes that contribute to such differences. It has been suggested that mussels may be largely absent from Cook Strait shores for 2 main reasons. First, recruitment limitation (a bottom-up process) may be affecting not just mussels but other species (winkles, barnacles) and this would explain the low densities of most intertidal faunal species and the large amount of bare rock on many Cook Strait shores (e.g. Helson & Gardner 2004). The exact way in which this recruitment limitation is achieved is unclear because winkles *Austrolittorina antipodum* and *A. cincta* are found at low to moderate densities on Cook Strait shores, little black mussels *Limnoperna pulex* and barnacles *Chamaesipho brunnea* and *C. columnata* are found at high densities in isolated patches, and the occasional single mussel *Mytilus galloprovincialis* can be found (Gardner 2008). Clearly, larval supply, settlement and recruitment of taxa with pelagic larval phases are occurring, but, when compared with the situation in Wellington Harbour, they are reduced in extent for species such as *C. brunnea*, *C. columnata* and *L. pulex*, are almost entirely absent for species such as *M. galloprovincialis*, and, as far as it is possible to tell, are completely absent for species such as the New Zealand greenshell mussel *Perna canaliculus* and the ribbed mussel *Aulacomya maoriana*. Second, food limitation may explain the much-reduced densities of filter-feeding species such as barnacles and mussels that usually dominate the mid intertidal zone. Comparisons of seston—(total particulate matter (TPM), particulate organic matter (POM), and percent organic matter (PCOM)—between Cook Strait and Wellington Harbour reveal that levels of POM and PCOM are both low to very low, resulting in a poor-quality diet for suspension-

feeding taxa (Gardner 2000, 2002, Gardner & Thompson 2001, Helson & Gardner 2007, Helson et al. 2007). Again, it is unclear at which life-history stage or stages this form of bottom-up limitation may have effect, as it is possible that food limitation affects the feeding larval stage, the new recruit, the adult or perhaps all of these.

The present study describes a transplant experiment of blue mussels *Mytilus galloprovincialis* among 3 sites in New Zealand—2 in Cook Strait and 1 in Wellington Harbour. In conjunction with the collection of water-quality parameters—temperature, salinity, chlorophyll a (chl a) concentration, turbidity (the latter 2 variables can be thought of as proxies for seston (particulate food) quality and quantity, respectively)—the mussels were sampled on a monthly basis to determine their shell growth, soft tissue condition and survivorship. The expectation was that if food limitation contributes to the near-total absence of mussels on Cook Strait shores, then mussels transplanted to sites on this coastline would exhibit reduced or zero shell growth, would lose condition, and might experience increased mortality compared with mussels transplanted to the Wellington Harbour site.

MATERIALS AND METHODS

Collection of animals and experimental set-up

On 5 September 2005, mussels *Mytilus galloprovincialis* were collected from the intertidal zone at Seatoun, inside Wellington Harbour (Fig. 1). At Victoria University's Island Bay Marine Laboratory (IBML) the mussels were cleaned of epibionts and were sorted into 3 different size categories ('small' <30 mm shell length, 'medium' 30–50 mm, and 'large' >50 mm; sizes are approximations only because at this stage mussels were not measured for shell length). Based on the numbers of individuals collected, mussels were haphazardly assigned according to their proportions within size classes to each of 45 containers. The container consisted of a white plastic tray (31.5 cm length × 13.0 cm width × 5.5 cm height) with holes (approximately 2.4 × 0.8 cm) in the sides and a solid base. With the mussels in the container, a black, plastic netting (gutter guard) was cable-tied over the top of the container to ensure that the mussels could not fall out. Each container held 15 mussels (2 small, 10 medium, 3 large). Each mussel was measured for shell length (to the nearest 1 mm) with callipers. The length of each

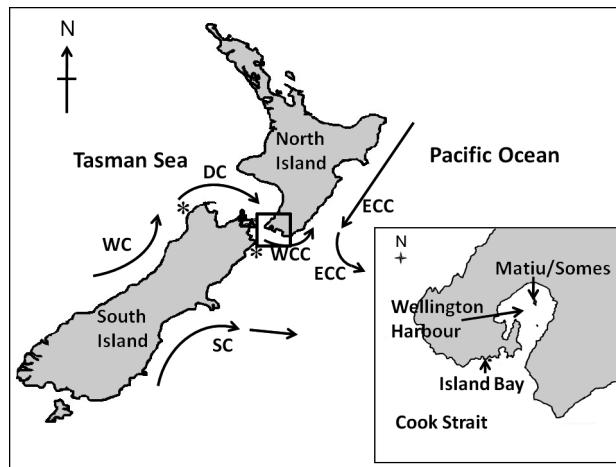


Fig. 1. *Mytilus galloprovincialis*. Map of New Zealand showing major regional currents influencing Cook Strait (modified from Helson et al. 2007). DC = D'Urville Current; ECC = East Cape Current; SC = Southland Current; WCC = Wairarapa Counter Current; WC = Westland Current. Areas of upwelling are indicated by stars. Inset: Wellington Harbour and the Cook Strait coastal region of the North Island with transplant sites (Matiu/Somes and Island Bay)

mussel was etched into the valve of that individual using a diamond-tipped drill bit in a rotary engraving tool. Each container was individually numbered and was assigned at random to 1 of 3 large heavy-duty cages. The use of the container and cage set-up was preferred over other options (e.g. epoxying mussels directly onto the shore) because experience suggested that the cage set-up would probably survive storms much better than individual mussels stuck directly to the shore or wharf, and previous use of marking the shell exterior had worked well (e.g. Gardner & Thomas 1987) and was more likely to last than individually glued tags for the mussels. Before deployment into the field, the mussels were held submerged in constant-flowing unfiltered Cook Strait seawater at IBML. Between collection and deployment mortality rates were very low (3 of 1080 mussels) suggesting that handling stress had no significant impact on mussel survivorship.

The initial experimental design had involved 2 sites inside Wellington Harbour and 2 sites in Cook Strait, but a large storm 2 d after the start resulted in loss of the set-up at one harbour site and substantial damage to the set-up at one Cook Strait site. Because of this, the experimental design was changed within 3 d of the start to include 1 Wellington Harbour, 1 Cook Strait and 1 marine laboratory site. Thus, mussels in containers inside large, protective cages were

deployed at 3 sites (Fig. 1). One plastic cage was attached in the intertidal zone to the wharf at Matiu/Somes Island (hereafter Matiu/Somes) inside Wellington Harbour, another was attached in the intertidal zone at Island Bay in Cook Strait (hereafter IB-intertidal) and as a precaution against losses of experimental equipment at Island Bay an identical experiment was set up at IBML. The IBML mussels (in containers, inside the cage) were placed in a stainless steel tank (~1.5 m length × 0.8 m width × 1.0 m height) that was supplied with unfiltered Cook Strait seawater on a simulated semi-diurnal tidal cycle. An automatic timer was set to supply constantly running seawater for 7 h, after which time the seawater supply was turned off, the tank drained and was left without seawater for 5 h. This 7 h immersed, 5 h emerged cycle was repeated every 12 h to mimic the intertidal conditions of emergence and aerial exposure experienced by the mussels at IB-intertidal and Matiu/Somes, but without the wave exposure component of IB-intertidal. In total, 8 containers were deployed at Matiu/Somes, 10 at IB-intertidal and 8 at IBML. The experiment commenced at the start of the austral spring (September 2005) and finished in the austral autumn (May 2006), covering the period of greatest food availability, warmest water temperatures, and greatest mussel shell growth and body condition. As a final caveat, it is noted that the absence of replication at the level of site may lead to site-level rather than region-level effects, but the magnitude of the differences (see 'Results') and the fact that the responses are consistent with a large body of earlier work (see 'Discussion') indicate that this is not likely to be the case.

Monthly collection and analysis of mussels

An initial sample of $n = 15$ mussels was taken on 5 September 2005 from the Seatoun mass collection. Subsequently, at approximately monthly intervals (see Table 2), 1 container was collected from each cage at each of the 3 sites until March 2006, after which 1 container was collected in April and May for Matiu/Somes mussels, 2 containers were collected in April and 2 in May for IB-intertidal mussels, and 2 containers were collected in April and zero in May for IBML mussels. These site-specific differences in collections at the end reflected high levels of mortality for IB-intertidal and IBML mussels at the end of the experiment (i.e. low sample sizes per container), and concern that any mussels left out in the field at these 2 sites beyond April and May would be dead and lost to

the experiment. Mussels were analysed as follows. The number of surviving mussels per container was recorded at each month to permit estimation of monthly survivorship. Individual initial shell length (engraved on the shell) was recorded, and final shell length was estimated using callipers accurate to ± 0.1 mm. The following estimates of weight were made: whole animal wet weight (after a standardised drying procedure that included leaving all mussels on paper towel for 5 min and blotting dry the shell), dry shell weight, dry weight of gonad, dry weight of soma, dry weight of all soft tissue, ash-free dry weight (AFDW) of gonad, AFDW of soma and AFDW of all soft tissue (defined as AFDW of gonad + AFDW of soma). Dry weights were determined by drying at 60°C for 24 h and AFDWs were determined as weight loss on ignition at 450°C after 24 h (Gardner 2000).

Analysis of water-column variables

To coincide with the transplant experiment, one Richard Brancker CTD sonde (XR 420) with integrated SeaPoint fluorometer and turbidimeter was deployed at Matiu/Somes (Wellington Harbour) and one in the 60 000 l seawater holding tank at IBML (Cook Strait). Seawater is pumped directly from Cook Strait into the IBML holding tank and is not filtered (Gardner 2000, Gardner & Thompson 2001). Unpublished assessments of TPM, POM and PCOM indicate that the seston in the seawater pumped into the marine laboratory is not significantly different from that of Cook Strait seawater at Island Bay. The volume of the tank is replaced approximately every 4 to 8 h, depending on demand at the marine laboratory. The CTD could not be deployed in the sea at Island Bay or other Cook Strait locations because of the absence of suitable anchor points. Data from the CTDs were downloaded at intervals of approximately 1 to 2 mo, at which time the units were cleaned and their batteries replaced. At both locations, 4 water-column variables were recorded: temperature (°C), salinity (PSU), chl a concentration ($\mu\text{g l}^{-1}$) and turbidity (nephelometer turbidity units, NTU). Data from the CTD in the seawater tank at IBML were considered to be representative of the IB-intertidal and IBML sites.

Data analyses

Data analyses were carried out using STATISTICA software (v.7.1 StatSoft Software) or the permutational multivariate analysis of variance (PERM-

ANOVA) add-on for PRIMER (Plymouth Marine Laboratory). Data were tested for normality (probability plots of observed versus expected distribution) and equality of variances (Levene's test and Cochran's C-test). Failure to satisfy the assumption of equality of variances meant that non-parametric statistics (e.g. Mann-Whitney *U*-test or Kruskal-Wallis (KW) ANOVA) were employed. In instances where a 2-way ANOVA design was required and when variances were not equal, a PERMANOVA approach (Anderson 2001) was employed. In this case, for a single variable with 2 factors (e.g. site and month), a similarity matrix was constructed using either the Bray-Curtis similarity index (when the data set contained no zeros) or Euclidean distance (when the data set contained many zeros) and 9999 permutations of the raw data were employed to test for differences among the factors and their interaction term. In the event of a significant overall result, the pairwise testing procedure (post hoc test) was employed to identify the location of the difference.

Mortality

Cumulative mortality was calculated for the full experimental period (8 mo at Matiu/Somes and IB-intertidal and 7 mo at IBM). A permutational RxC test (<http://marksgeneticsoftware.net>) was employed to test for differences in the total number of mortalities for the 7 mo period (October to April, inclusive) at all 3 sites.

Initial shell length

To ensure that no size differences existed among the mussels deployed at the 3 sites at time of set-up, an ANOVA was used to test for differences in initial shell length.

Final shell length

ANOVA was employed to test for differences in final shell length among mussels of the 3 sites for the period October to April.

Growth rate of shell

Growth rate (mm d^{-1}) was calculated as: (final shell length – initial shell length) / total number of days.

KW-ANOVA was employed to test for site-specific differences in growth rate.

Instantaneous growth rate

The instantaneous growth rate (Brody 1964) was calculated according to the following formula and standardized to number of days: $\log_e (\text{final shell length} / \text{initial shell length}) / \text{time in days}$.

von Bertalanffy growth function

The software package VONBIT (www.fao.org/fishery/topic/16078/en) was used to fit von Bertalanffy growth curves to the mark-recapture data for the mussels at each site (Stamatopoulos & Caddy 1989). This approach requires an estimate of initial individual shell length, final individual shell length and duration (time in days). This is a linear regression approach to fitting the von Bertalanffy growth function and may also be used to fit growth functions to tag-recapture data. It is based on the observation that if successive length increments L_1 and L_2 over a period T follow an exponential law of decline of the form $L_2/L_1 = \exp(-KT)$ then for any value of K (the Brody growth coefficient), growth can be described by a simple linear regression whose parameters are any 2 theoretical lengths L_a and L_b . From this observation it follows that the primary parameter in growth is K , trial values of which can each generate a simple linear regression and hence determine the optimal K for which the goodness of fit is maximized. The other 2 parameters, namely asymptotic length L_∞ and age t_0 at which length is zero, are computed at a separate phase as secondary parameters. Comparative tests have shown that this approach has low error and bias (Stamatopoulos & Caddy 1989). The VONBIT software package was used to derive estimates of 3 growth parameters for mussels from each of the 3 sites: K_{opt} , the optimal Brody growth coefficient; L_∞ , the theoretical maximum size of an individual; and t_0 , the age at which length is zero. The coefficient of determination (R^2) was used as a measure of goodness of fit of the growth equation to the observed data.

Condition index

Condition index (CI) was calculated as: $(\text{dry flesh weight} \times 100) / (\text{whole wet weight} - \text{dry shell weight})$ (Hickman & Illingworth 1980). This is an index of the

amount of energy diverted to soft tissue growth as a function of energy diverted to all growth. PERMANOVA (as described above) was employed to test for differences in CI among sites and months.

Gonad condition

Gonad condition (GC) was calculated as: (dry weight of gonad / dry weight of all soft tissue) × 100. This is an index of energy diverted to reproductive growth as a function of energy diverted to soft tissue growth (somatic and reproductive). In the event of periods of starvation, mussels may resorb gonadal material and use that energy for routine metabolism (Villalba 1995, Suárez et al. 2005). Thus, this index may be a useful indicator of mussel condition in food-limited environments. PERMANOVA (as described above) was employed to test for differences in GC among sites and months.

Water-column variables

Data for all CTD deployments were recorded once every hour, with the result that individual CTD files were very large (often many tens of thousands of data points). Data were therefore averaged on a per day basis to reduce data file size. For both sites (Matiu/Somes and IBML), CTD data files covered the period early August 2005 through to mid-May 2006, giving a total of 258 and 263 data points for Matiu/Somes and for IBML and IB-intertidal, respectively (for salinity, these numbers were reduced to 195 and 205, respectively, due to fouling of the conductivity sensor) (Table 1). A Mann-Whitney *U*-test was employed to test for differences between sites

Table 1. *Mytilus galloprovincialis*. Information about time periods of data and number of daily mean points for CTD files (temperature, salinity, chlorophyll *a* concentration, turbidity)

Matiu/Somes CTD files	No. data points (daily mean) file ⁻¹	IBML CTD files	No. data points (daily mean) file ⁻¹
08 Aug–14 Sept 2005	38	10 Aug–20 Sept 2005	42
14 Sept–31 Oct 2005	48	20–26 Sept 2005	7
18 Nov 2005–3 Jan 2006	47	26 Sept–30 Oct 2005	35
13 Jan–15 Mar 2006	62	21 Nov–14 Dec 2005	24
15 Mar–16 May 2006	63	14 Dec 2005–18 Jan 2006	36
Total	258	18 Jan–16 Mar 2006	58
		16 March–16 May 2006	61
		Total	263

(Wellington Harbour and Cook Strait) in all values of the 4 watercolumn variables (temperature, turbidity, chl *a* concentration and salinity). A 2-way PERMANOVA was employed to test for differences in all 4 variables with respect to site and season. For this analysis, values in August to November were classified as spring, December to February as summer, and March to May as autumn.

Linking biological responses with water-column variability

Multiple linear regression (MLR) was employed to test for the effect of the 4 water-column variables on biological responses. Two separate MLRs were employed. In the first, monthly responses of mussels (4 separate dependent variables [DV]: growth rate, instantaneous growth rate, CI, GC) were tested against monthly mean values of the water-column variables (4 independent variables [IV]: temperature, turbidity, chl *a* concentration, salinity). This allowed for a test of the immediate response of the mussels to the most recently experienced environmental variation. In the second MLR, monthly responses of mussels (4 separate DVs) were tested against mean cumulative monthly mean values of the 4 water-column variables (4 IVs). Thus, responses of mussels collected in Month 1 (October) were tested against the mean water-column variables as calculated for Month 1 (October), responses of mussels collected in Month 2 (November) were tested against the mean water-column variables as calculated for Months 1 and 2 (October and November), and so on for the full period of the transplant experiment. This allows for a test of the longer-term responses of the mussels to all of the environmental conditions that they experienced. In all cases, the standardised regression coefficient (β) was used to compare the relative contribution of each IV in the prediction of the DV for each site-specific MLR.

RESULTS

Mortality

Of the 120 tagged mussels collected over 8 mo from Matiu/Somes, only 3 were dead (~2.5% total mortality). At IB-intertidal over an 8 mo period, a total of 36 mussels from 150 were

Table 2. *Mytilus galloprovincialis*. Date of sample collection and cumulative number of mussel mortalities at Matiu/Somes Island (inside Wellington Harbour), Island Bay (IB-intertidal in Cook Strait) and the Island Bay Marine Laboratory (IBML in Cook Strait). na: sample from the IBML site was not available for collection in May

Date	Cumulative number of dead mussels		
	Matiu/Somes	IB-intertidal	IBML
12 Oct 2005	0/15	3/15	1/15
15 Nov 2005	1/30	4/30	1/30
12 Dec 2005	1/45	5/45	2/45
16 Jan 2005	1/60	6/60	3/60
13 Feb 2006	3/75	8/75	5/75
15 Mar 2006	3/90	13/90	10/90
12 Apr 2006	3/105	24/120	26/120
12 May 2006	3/120	36/150	na

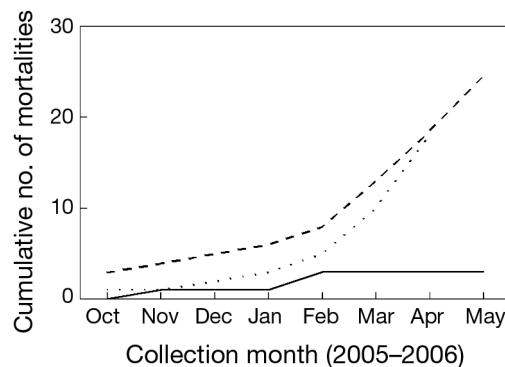


Fig. 2. *Mytilus galloprovincialis*. Cumulative mortalities for mussels transplanted to 3 sites. Numbers were standardised to reflect differences in collection sample sizes in April and May. Matiu/Somes = solid line; IB-intertidal = dashed line; IBML = dotted line

dead (~24 %), whereas at IBML 26 mussels of 120 collected over 7 mo (~22 %) were dead (Table 2). While mortalities at Matiu/Somes were restricted to 2 incidences (1 in November and 2 in February), the rate of mortalities at both IB-intertidal and IBML increased over time (Fig. 2). The RxC permutation test revealed a significant difference among sites in total number of mortalities ($p = 0.0004$, SE = 0.0003), with greatest similarity between IB-intertidal and IBML, and least similarity between these 2 sites and Matiu/Somes.

Initial shell length

ANOVA testing of initial shell length revealed no significant differences among mussels held at the 3

sites. Mean \pm SD initial shell length values (mm) at the 3 sites were: Matiu/Somes 41.26 ± 8.15 , IB-intertidal 39.92 ± 8.17 and IBML 38.66 ± 8.14 ($F_{2,313} = 2.665$, $p = 0.071$).

Final shell length

ANOVA testing of final shell length revealed a significant difference among mussels held at the 3 sites ($F_{2,316} = 57.453$, $p < 0.0001$). Post hoc testing revealed that mussels from Matiu/Somes were significantly longer than mussels from IB-intertidal and IBML. For the period October 2005 to April 2006, the mean \pm SD final shell length values (mm) at the 3 sites were: Matiu/Somes 48.12 ± 7.45 , IB-intertidal 40.68 ± 7.89 and IBML 39.13 ± 7.72 .

Growth rate of shell

At Matiu/Somes, 13 of 115 mussels had zero growth (~1.13 %), 12 of which were in the first sample (October, 37 d after the start of the experiment). At IB-intertidal 65 of 107 mussels (~61 %) had zero growth, and at IBML 70 of 94 mussels (~74 %) had zero growth. KW-ANOVA revealed significant differences in shell growth rate among the mussels of the 3 sites ($H_{(2,316)} = 164.6$, $p < 0.0001$), with mussel growth rate at Matiu/Somes being significantly greater than at IB-intertidal and IBML. For the period October 2005 to April 2006, the mean \pm SD shell growth rate values (mm d^{-1}) at the 3 sites were: Matiu/Somes 0.0496 ± 0.0325 , IB-intertidal 0.0078 ± 0.0116 and IBML 0.0032 ± 0.0062 .

Instantaneous growth rate

KW-ANOVA revealed significant differences among the 3 groups ($H_{2,316} = 150.1$, $p < 0.0001$), with instantaneous growth rate of mussels at Matiu/Somes being greater than at IB-intertidal and IBML. For the period October 2005 to April 2006, the mean \pm SD instantaneous growth rate values at the 3 sites were Matiu/Somes 0.0012 ± 0.0009 , IB-intertidal 0.0002 ± 0.0004 and IBML 0.0001 ± 0.0002 .

von Bertalanffy growth function

The von Bertalanffy growth curves for mussels from the 3 sites were substantially different (Fig. 3).

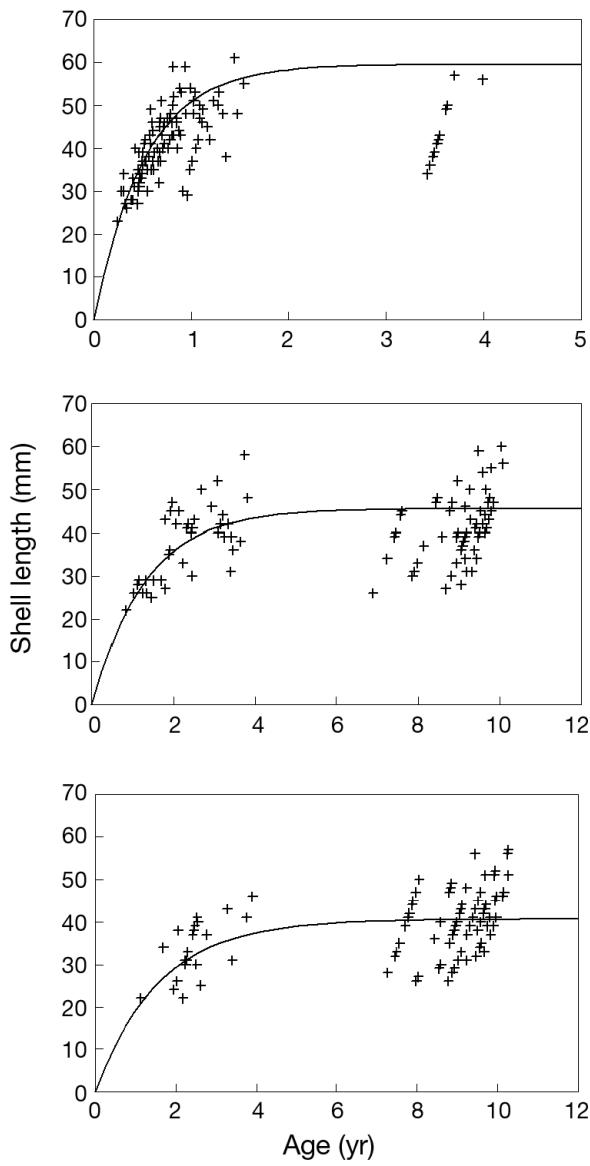


Fig. 3. *Mytilus galloprovincialis*, von Bertalanffy growth curves for tagged mussels transplanted to 3 sites. Matiu/Somes = top panel; IB-intertidal = middle panel; IBML = bottom panel

Mussels at Matiu/Somes had higher values of L_{∞} and K_{opt} than mussels at IB-intertidal, which in turn had values higher than mussels from IBML (L_{∞} values were 59.55, 45.55 and 40.64, respectively; values of K_{opt} were 1.93, 0.77 and 0.64, respectively). There was a good fit for the growth curves for mussels at Matiu/Somes ($R^2 = 0.694$) and for mussels at IB-intertidal ($R^2 = 0.773$), but not so good for the mussels at IBML ($R^2 = 0.428$). In fitting the curve it is necessary to get the $K-L_{\infty}$ plots to have a hyperbola shape: this could not be achieved for the IBML data set, reflect-

ing the zero growth values of ~74 % of the mussels. Nonetheless, all 3 growth plots and growth curve parameters are presented here for comparative purposes.

Condition index

PERMANOVA revealed that site, month and site \times month all explained significant variation in CI ($p < 0.0001$ in all 3 cases). Partitioning of the variation revealed that site explained 65.3 %, month explained 5.4 %, and site \times month explained 11.24 % of the variation in the data set. The CI value of the Seatoun mussels (initial sample collected in September) was 9.82 ± 2.44 (mean \pm SD). Mean \pm SD values of CI for mussels from all 3 sites for the period October 2005 to April 2006 indicated that mussels at Matiu/Somes had substantially higher overall CI values (mean \pm SD (N) Matiu/Somes 13.12 ± 3.95 (98); IB-intertidal 5.23 ± 1.80 (92); IBML 5.36 ± 2.66 (93)) and higher monthly CI values than the mussels at the 2 Cook Strait sites (Fig. 4).

Gonad condition

Of the 101 mussels collected over 8 mo at Matiu/Somes, none had GC values of zero, whereas 7 of 93 mussels at IB-intertidal over 8 mo and 9 of 93 mussels at IBML over 7 mo had GC values of zero. PERMANOVA revealed that site, month and site \times month all explained variation in GC ($p < 0.0001$ for site and site \times month; $p < 0.03$ for month). Partitioning of the variation revealed that site explained 45.5 %, month explained 1.34 %, and site \times month explained 12.2 % of the variation in the data set. The GC value of the Seatoun mussels (initial sample collected in September) was 14.20 ± 9.39 (mean \pm SD). GC values of the mussels from the 3 sites across all time periods were: 30.15 ± 9.45 at Matiu/Somes, 13.58 ± 8.24 at IB-intertidal and 13.78 ± 11.83 at IBML. Mussels at Matiu/Somes had substantially higher monthly GC values than mussels from the 2 Cook Strait sites (Fig. 5).

Water-column variables

Mean values of temperature ($p = 0.017$), turbidity ($p < 0.0001$) and chl a concentration ($p < 0.0001$) were all higher, while salinity was lower ($p < 0.0001$) at Matiu/Somes (Wellington Harbour) than at IBML

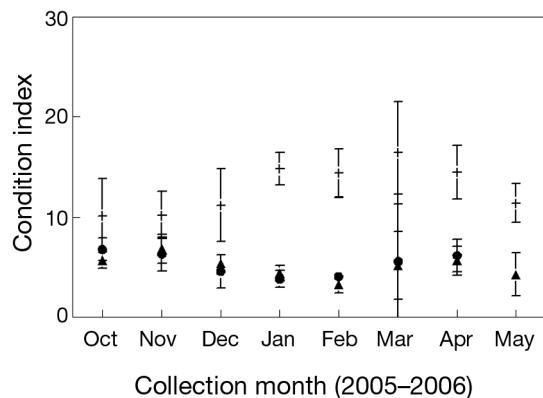


Fig. 4. *Mytilus galloprovincialis*. Monthly condition index values (means \pm SD) of transplanted mussels at 3 sites. Matiu/Somes = +; IB-intertidal = ▲; IBML = ●

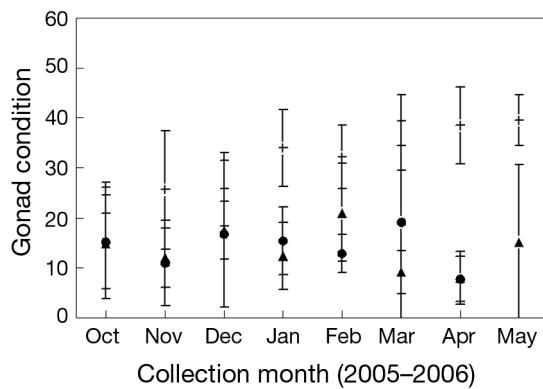


Fig. 5. *Mytilus galloprovincialis*. Monthly gonad condition values (means \pm SD) of transplanted mussels at 3 sites. Matiu/Somes = +; IB-intertidal = ▲; IBML = ●

(Cook Strait). Estimates of temperature ($^{\circ}\text{C}$; mean \pm SD for Wellington Harbour versus for Cook Strait: 15.15 ± 2.14 versus 14.68 ± 1.70) reflected, on average, warmer water compared with Cook Strait, with both regions exhibiting comparable levels of variability during the 9 mo period from late winter to mid-autumn. Turbidity (NTU) was on average 3 times greater in Wellington Harbour than in Cook Strait, and highly variable in both regions (26.57 ± 28.35 versus 9.13 ± 7.51), whereas chl a concentration ($\mu\text{g l}^{-1}$) was almost 10 times higher in Wellington Harbour compared with Cook Strait, being variable at both regions (3.69 ± 2.34 versus 0.39 ± 0.17). Salinity (PSU) was slightly lower in Wellington Harbour than in Cook Strait and was more variable over time (32.52 ± 1.48 versus 34.65 ± 0.44). Overall, these 4 variables characterise 2 bodies of water with small but significant differences in temperature and salinity related to size and depth of the water body

and presence or absence of riparian input, but profound differences in both turbidity and chl a concentrations.

Two-way PERMANOVA tests revealed that site, season and site \times season all explained significant variation in each of the 4 variables ($p < 0.0001$ in all cases). For temperature, variation was explained mostly by season (season = 74.4 %, site = 2.7 % and site \times season = 2.1 % of the variation), whereas for salinity and for chl a concentration, site explained the most variation (site = 61.2 % and 73.6 %, season = 8.1 % and 2.6 %, and site \times season = 8.8 % and 7.1 % of the variation, respectively). For turbidity, the site \times season interaction explained the most variation (site = 15.0 %, season = 8.5 % and site \times season = 19.4 % of the variation).

Linking biological responses with water-column variability

For mussels at Matiu/Somes, the MLR tests of the ability of 4 IVs to predict variation in the 4 separate DVs were all significantly different ($p < 0.0001$) in all 4 cases for both sets of MLR tests, but the model R^2 values were higher in 3 of 4 cases, and the contributions of the IVs were greater in all cases for the monthly mean rather than the cumulative mean IV values (Table 3). Typically, temperature, chl a concentration and salinity had positive effects on biological response, whereas turbidity had a negative effect, when tested on a month-by-month basis (monthly means, Table 3). Such statistical significance was reduced or even absent when the IVs were tested on a cumulative basis (cumulative means, Table 3).

For mussels at both IB-intertidal and IBML, the cumulative monthly IV values explained more variation in the DVs than did the mean monthly IV values. Turbidity was usually, but not always, negatively correlated with biological response, whereas the 3 other IVs were usually, but not always, positively correlated with biological response. For mussels at IB-intertidal, the significance levels of the IVs were more pronounced in the cumulative monthly models than in the mean monthly models, but for mussels at IBML, the IVs were not able to predict the DVs with any degree of accuracy (Table 3). The greater ability of the IVs to predict the DVs at Matiu/Somes compared with IB-intertidal and IBML reflects the pronounced differences in the biological responses in Wellington Harbour when compared with the Cook Strait.

Table 3. *Mytilus galloprovincialis*. Site-specific multiple linear regression (MLR) results for transplanted mussels with respect to environmental variability at Matiu/Somes Island (inside Wellington Harbour), Island Bay (IB-intertidal in Cook Strait) and the Island Bay Marine Laboratory (IBML in Cook Strait). DV: dependent variable. Independent variables (IV): temperature (°C), turbidity (nephelometer turbidity units, NTU), chlorophyll a ($\mu\text{g l}^{-1}$), salinity (PSU). Inst: instantaneous; CI: condition index; GC: gonad condition

Site	MLR test	DV	Model R ²	Model F	p	IV		
						β	p	
Matiu/Somes	Monthly means	Growth rate (mm d ⁻¹)	0.669	40.86	<0.0001	Temp	0.674	<0.0001
						Turbidity	-1.430	<0.0001
						Chl a	1.542	<0.0001
						Salinity	0.07	0.354
		Inst. growth rate	0.379	12.36	<0.0001	Temp	0.564	<0.0001
						Turbidity	-0.449	0.136
						Chl a	0.244	0.394
						Salinity	-0.059	0.568
		CI	0.356	10.9	<0.0001	Temp	0.395	<0.0001
						Turbidity	-1.242	0.0001
						Chl a	1.411	<0.0001
Cumulative means	Growth rate (mm d ⁻¹)		0.473	24.66	<0.0001	Salinity	0.177	0.097
						Temp	0.473	<0.0001
						Turbidity	-1.093	0.0008
						Chl a	1.120	0.0003
						Salinity	0.22	0.043
		Inst. growth rate	0.303	11.94	<0.0001	Temp	0.368	0.005
						Turbidity	-0.85	0.032
						Chl a	0.99	0.006
						Salinity	-0.162	0.234
		CI	0.269	9.95	<0.0001	Temp	0.142	0.338
						Turbidity	-0.26	0.566
						Chl a	-0.039	0.924
IB-intertidal	Monthly means	Growth rate (mm d ⁻¹)	0.239	6.98	<0.0001	Salinity	-0.205	0.192
						Temp	0.701	<0.0001
						Turbidity	0.288	0.533
						Chl a	-0.254	0.542
						Salinity	0.179	0.265
		Inst. growth rate	0.198	5.51	0.0005	Temp	0.457	0.001
						Turbidity	-1.079	0.011
						Chl a	1.111	0.004
						Salinity	0.139	0.345
		CI	0.137	3.3	0.015	Temp	-0.481	0.003
						Turbidity	0.819	0.015
						Chl a	-0.575	0.04
Cumulative means	Growth rate (mm d ⁻¹)		0.137	3.3	0.015	Salinity	0.129	0.271
						Temp	-0.033	0.842
						Turbidity	0.003	0.994
						Chl a	-0.001	0.997
						Salinity	0.222	0.072
						Temp	0.825	0.005

Table 3 (continued)

Site	MLR test	DV	Model R ²	Model F	p	IV	
						β	p
IB-intertidal (continued)	CI	0.236	7.43	<0.0001		Temp	-0.918
						Turbidity	0.684
						Chl a	0.539
						Salinity	0.029
						Temp	-0.4
	GC	0.09	2.41	0.055		Turbidity	0.053
						Chl a	0.868
						Salinity	0.589
						Temp	0.156
						Turbidity	-0.47
IBML	Monthly means	Growth rate (mm d ⁻¹)	0.051	1.02	0.405	Chl a	0.078
						Salinity	0.433
						Temp	0.025
						Turbidity	-0.157
						Chl a	0.698
	Inst. growth rate	0.032	0.62	0.65		Salinity	-0.023
						Temp	-0.109
						Turbidity	0.408
						Chl a	-0.168
						Salinity	0.309
Cumulative means	CI	0.135	2.92	0.027		Temp	-0.076
						Turbidity	0.134
						Chl a	-0.006
						Salinity	0.965
						Temp	-0.376
	GC	0.017	0.32	0.866		Turbidity	0.069
						Chl a	0.723
						Salinity	-0.006
						Temp	-0.098
						Turbidity	0.786

DISCUSSION

There is now a substantial body of evidence from many different locations demonstrating the contribution of bottom-up processes to the structuring of temperate intertidal communities. What has become increasingly of interest is the determination of the scale at which bottom-up processes operate and if all such processes operate at equal rates on all shores, regardless of location. Bottom-up processes, such as the provision of nutrients, food or larvae,

that influence intertidal community structure are generally explained by oceanographic processes that operate at large spatial scales, ~10 to ~100 km (e.g. Navarrete et al. 2005, Barth et al. 2007). This scale of influence can be contrasted with the small, local scale (~10 to ~100 m) of top-down processes, such as predation and competition (e.g. Menge et al. 1999, 2002). Interestingly, recent research has demonstrated that processes at the scale of centimetres can significantly influence water flow and therefore food supply to individual mussels, demon-

strating that not all bottom-up processes operate at large spatial scales (McQuaid & Mostert 2010) and that top-down and bottom-up effects may both operate at the scale of the ecosystem (Frank et al. 2007). Thus, top-down and bottom-up processes may interact across a range of spatial scales to influence community structure in the intertidal zone and also the continental shelf.

Particulate food (seston such as phytoplankton and detritus) that is produced in one area is delivered to one or more distant areas as a consequence of coastal processes such as tidal flow, wind-driven flow and wave action. Suspension-feeding organisms of the intertidal region form an important link between the pelagic productivity of coastal waters and the benthic productivity of the shoreline (Fréchette & Bourget 1985, Hill et al. 2006) such that intertidal community structure is often thought to reflect levels of near-shore primary production (Dahlhoff & Menge 1996, Menge et al. 1997, McQuaid & Lindsay 2000, 2007). Consistent with previous findings (Gardner 2000, Gardner & Thompson 2001, Helson & Gardner 2004, 2007, Helson et al. 2007, Pande & Gardner 2009), the present study highlights the difference between Wellington Harbour and Cook Strait as suitable intertidal and subtidal habitats for many different taxa, including mussels. Profound differences were observed in turbidity and chl a concentrations (3 and 10 times higher in Wellington Harbour than in Cook Strait, respectively). These 2 variables are proxies for the quantity and the quality, respectively, of particulate material available to suspension-feeding organisms such as mussels. The responses of the transplanted mussels reflected these water-column properties and were consistent with bottom-up control of mussel presence and absence as mediated by feeding activity and net energy balance. These findings highlight how changes in environmental conditions over small spatial scales (100s of metres) may influence temperate intertidal community structure, from well developed inside the harbour to depauperate on the open coast.

Wave exposure can have a positive effect on intertidal community structure and/or mussel ecophysiology by increasing the supply of food particles to the shore, where such particles are rapidly assimilated and reflected in increased metabolic processes and ultimately in growth rate and size (e.g. Dahlhoff & Menge 1996, McQuaid & Lindsay 2000, 2007, McQuaid & Mostert 2010). Although wave exposure was not explicitly tested in the present study as a factor explaining mussel presence and absence, food levels at Cook Strait (as measured in terms of turbid-

ity and chl a concentrations) were consistently low throughout the study period (and also at other times: Gardner 2000, Gardner & Thompson 2001, Helson et al. 2007) and therefore suggest that wave action does not promote or retard delivery of particulate food at sufficient concentrations to the Cook Strait intertidal region to enhance or restrict mussel or intertidal community abundance and growth. These findings indicate that food limitation control of the Cook Strait intertidal community is generally a process that it is temporally consistent (particulate material supply to the shore is independent of wave action) and does not exhibit the elevated peak concentrations or the level of variability reported in other studies (e.g. Dahlhoff & Menge 1996, Wieters et al. 2003). Findings from all of these studies across different regions of the world therefore suggest that bottom-up control of intertidal community structure in terms of food limitation is an interaction between the availability of particulate matter (living phytoplankton plus detrital material) and its delivery by wave action to the shore. Both need to exist to promote mussel growth and condition. The relatively low and temporally consistent concentrations of particulate matter in Cook Strait water are sufficient to result in food limitation of mussels and presumably other suspension-feeding taxa in this region, regardless of the wave exposure, and highlights an important difference in the mechanism of bottom-up control between sites in central New Zealand and those on the west coast of USA, South Africa and Chile (Dahlhoff & Menge 1996, McQuaid & Lindsay 2000, 2007, Wieters et al. 2003).

Temperate coastal waters exhibit pronounced temporal and spatial variability in the concentration and composition of suspended particulate material (Bayne & Widdows 1978, Bayne & Worrall 1980). Consistent with previous reports based on direct assessments of particulate matter (e.g. Gardner 2000, 2002, Gardner & Thompson 2001, Helson et al. 2007), the CTD data of the present study highlight the profound difference in suspended particulate food quality and quantity between 2 regions that are ~12 km apart. In addition, the present study highlights the different contributions of the water-column variables to explaining the biological variables. For example, in an area of pronounced growth such as Wellington Harbour, turbidity and chl a concentration explained much more of the biological responses (negatively and positively, respectively) than they did in an area of very low to almost zero growth such as at IB-intertidal (usually, but not always, negatively and positively,

respectively). The importance of the composition of seston as food for suspension-feeding organisms has long been recognised (e.g. Bayne & Widdows 1978, Bayne & Worrall 1980), as has the fact that seston as a food source may be seasonally variable and thereby limiting for some bivalve suspension-feeding species (Bayne & Newell 1983). For example, kelp-derived subsidies have been shown to be very important as a particulate food source for many intertidal suspension-feeding taxa (e.g. Duggins et al. 1989, Bustamante & Branch 1996b, Tallis 2009) and also for continental shelf benthic communities (Harrold et al. 1998). Elsewhere, the composition of the particulate material has been shown to strongly affect mussel growth (e.g. Bracken et al. 2012, present study), in particular in terms of the fatty acid components of the phytoplankton (e.g. Budge et al. 2001, Alkanani et al. 2007). All of these studies point to the conclusion that much more detailed examination of phytoplankton community composition and its seasonal variability will be required for a more complete understanding of the basis of food limitation in temperate intertidal regions across the world.

In conclusion, the present study has provided strong evidence in support of the hypothesis that Cook Strait intertidal communities are affected by food limitation. The natural environmental gradient from the nutrient- and particle-rich harbour to the nutrient- and particle-poor open coast spans only a few 100 metres, but over that distance intertidal community structure changes from well-developed to depauperate. Once outside the harbour, the open coast intertidal community extends for many kilometres along Cook Strait, consistent with a large body of water that is food limiting for rocky reef suspension-feeding taxa. While the pronounced responses of the transplanted mussels, and also the water column variables (in particular the chl *a* concentrations), highlight the role of food limitation in explaining community structure, further research into the particulars of this are required. For example, is particulate food supply limiting simply because food concentration regardless of particle type is too low, or is particle type limiting because the phytoplankton community is composed of the 'wrong' sort of taxa for suspension-feeders? It is answers to these types of questions that will provide insights into the similarity and differences among sites of the mechanistic basis of food limitation as a bottom-up process from regions such as central New Zealand, the west coast of the USA, Chile and South Africa.

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LITERATURE CITED

- Alkanani T, Parrish CC, Thompson RJ, McKenzie CH (2007) Role of fatty acids in cultured mussels, *Mytilus edulis*, grown in Notre Dame Bay, Newfoundland. *J Exp Mar Biol Ecol* 348:33–45
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci* 58:626–640
- Archambault P, McKinsey CW, Bourget E (1999) Large-scale shoreline configuration influences phytoplankton concentration and mussel growth. *Estuar Coast Shelf Sci* 49:193–208
- Barth JA, Menge BA, Lubchenco J, Chan F and others (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc Natl Acad Sci USA* 104:3719–3724
- Bayne BL (1993) Feeding physiology of bivalves: time-dependence and compensation for changes in food availability. *NATO Adv Sci Inst G* 33:1–24
- Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: Saleuddin ASM, Wilbur KM (eds) *The Mollusca, Vol 4: Physiology, Part 1*. Academic Press, New York, NY, p 407–515
- Bayne BL, Widdows J (1978) The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia* 37: 137–162
- Bayne BL, Worrall CM (1980) Growth and production of mussels *Mytilus edulis* from two populations. *Mar Ecol Prog Ser* 3:317–328
- Bos OG, Hendriks IE, Strasser M, Dolmer P, Kamermans P (2006) Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. *J Sea Res* 55: 191–206
- Bowman MJ, Kibblewhite AC, Murtagh RA, Chiswell SM, Sanderson BG (1983) Circulation and mixing in greater Cook Strait, New Zealand. *Oceanol Acta* 6:383–391
- Bracken MES, Menge BA, Foley MM, Sorte CJB, Lubchenco J, Schiel DR (2012) Mussel selectivity for high-quality food drives carbon inputs into open-coast intertidal ecosystems. *Mar Ecol Prog Ser* 459:53–62
- Brody S (1964) *Bioenergetics and growth*. Hafner Publishing, New York, NY
- Broitman BR, Kinlan BP (2006) Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. *Mar Ecol Prog Ser* 327:15–25
- Budge SM, Parrish CC, McKenzie CH (2001) Fatty acid composition of phytoplankton, settling matter and sediments at a sheltered bivalve aquaculture site. *Mar Chem* 76: 285–303
- 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
- Dahlhoff EP, Menge BA (1996) Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Mar Ecol Prog Ser* 144:97–107
- Dayton PK (1971) Competition, disturbance, and community organisation: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41: 351–389
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol Evol* 22:236–242
- Fréchette M, Bourget E (1985) Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. *Can J Fish Aquat Sci* 42:1158–1165
- Gaines SD, Lubchenko J (1982) A unified approach to marine plant-herbivore interactions. II. Biogeography. *Annu Rev Ecol Syst* 13:111–138
- Gardner JPA (2000) Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions. *Mar Ecol Prog Ser* 194:123–132
- Gardner JPA (2002) Effects of seston variability on the clearance rate and absorption efficiency of the mussels *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus* from New Zealand. *J Exp Mar Biol Ecol* 268: 83–101
- Gardner JPA (2008) Where are the mussels on Wellington's south coast? In: Gardner, JPA (ed) *The Taputeranga Marine Reserve*. First Edition Publishers, Wellington, p 288–304
- Gardner JPA, Thomas MLH (1987) Growth, mortality and production of organic matter by a rocky intertidal population of *Mytilus edulis* in the Quoddy Region of the Bay of Fundy. *Mar Ecol Prog Ser* 39:31–36
- Gardner JPA, Thompson RJ (2001) Naturally low seston concentration and the net energy balance of the greenshell mussel (*Perna canaliculus*) at Island Bay, Cook Strait, New Zealand. *N Z J Mar Freshw Res* 35:457–468
- Harrold C, Light K, Lisin S (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnol Oceanogr* 43:669–678
- Helson JG, Gardner JPA (2004) Contrasting patterns of mussel abundance at neighbouring sites: Does recruitment limitation explain the absence of mussels on Cook Strait (New Zealand) shores? *J Exp Mar Biol Ecol* 312: 285–298
- Helson JG, Gardner JPA (2007) Variation in mussel scope for growth: a test of intertidal community structure. *Hydrobiologia* 586:373–392
- Helson JG, Pledger S, Gardner JPA (2007) Does differential particulate food supply explain the presence of mussels in Wellington Harbour (New Zealand) and their absence on neighbouring Cook Strait shores? *Estuar Coast Shelf Sci* 72:223–234
- Hickman RW, Illingworth J (1980) Condition cycle of the green-lipped mussel *Perna canaliculus* in New Zealand. *Mar Biol* 60:27–38
- Hill JM, McQuaid CD, Kaehler S (2006) Biogeographic and nearshore–offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. *Mar Ecol Prog Ser* 318:63–73
- Jessopp MJ, McAllen RJ (2008) Go with the flow: tidal import and export of larvae from semi-enclosed bays. *Hydrobiologia* 606:81–92
- Lewis JR (1961) The littoral zone on rocky shores—a biological or physical entity? *Oikos* 12:280–301
- McCulloch A, Shanks AL (2003) Topographically generated fronts, very nearshore oceanography and the distribution and settlement of mussel larvae and barnacle cyprids. *J Plankton Res* 25:1427–1439
- McQuaid CD, Lindsay TL (2000) Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom up regulation of intertidal populations. *Mar Ecol Prog Ser* 206:147–154
- McQuaid CD, Lindsay TL (2007) Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space. *Mar Biol* 151: 2123–2131
- McQuaid CD, Mostert BP (2010) The effects of within-shore water movement on growth of the intertidal mussel *Perna perna*: an experimental field test of bottom-up control at centimetre scales. *J Exp Mar Biol Ecol* 384: 119–123
- Menge BA (1976) Organisation of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol Monogr* 46:355–393
- Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755–765
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J Exp Mar Biol Ecol* 250:257–289
- Menge BA, Daley B, Wheeler PA, Strub PT (1997) Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnol Oceanogr* 42:57–66
- Menge BA, Daley BA, Lubchenko J, Sanford E and others (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol Monogr* 69: 297–330
- Menge BA, Sanford E, Daley BA, Freidenburg TL, Hudson G, Lubchenko J (2002) Inter-hemispheric comparison of bottom-up effects on community structure: insights revealed using the comparative-experimental approach. *Ecol Res* 17:1–16
- Menge BA, Lubchenko J, Bracken MES, Chan F and others (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proc Natl Acad Sci USA* 100: 12229–12234
- Morton J, Miller M (1968) The New Zealand sea shore. Collins, Auckland
- 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* 102:18046–18051
- Page HM, Ricard YO (1990) Food availability as a limiting factor to mussel *Mytilus edulis* growth in California coastal waters. *Fish Bull* 88:677–686
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120

- Pande A, Gardner JPA (2009) A baseline biological survey of the proposed Taputeranga Marine Reserve (Wellington, New Zealand): spatial and temporal variability along a natural environmental gradient. *Aquat Conserv Mar Freshw Ecosyst* 19:237–248
- Stamatopoulos C, Caddy JF (1989) Estimation of von Bertalanffy growth parameters: a versatile linear regression approach. *J Cons Int Explor Mer* 45:200–208
- Starr M, Himmelman JH, Therriault JC (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247:1071–1074
- Stephenson TA, Stephenson A (1949) The universal features of zonation between tide-marks on rocky coasts. *J Ecol* 37:289–305
- Stephenson TA, Stephenson A (1972) Life between tide-marks on rocky shores. Freeman, San Francisco, CA
- Suárez MP, Alvarez C, Molist P, San Jaun F (2005) Particular aspects of gonadal cycle and seasonal distribution of gametogenic stages of *Mytilus galloprovincialis* cultured in the estuary of Vigo. *J Shell Res* 24:531–540
- Tallis H (2009) Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA). *Mar Ecol Prog Ser* 389:85–96
- Villalba A (1995) Gametogenic cycle of cultured mussel, *Mytilus galloprovincialis*, in the bays of Galicia (NW Spain). *Aquaculture* 130:269–277
- Wieters EA, Kaplan DM, Navarrete SA, Sotomayer A, Largier J, Nielsen KJ, Vélez F (2003) Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters. *Mar Ecol Prog Ser* 249:93–105
- Witman JD, Leichter JJ, Genovese SJ, Brooks DA (1993) Pulsed phytoplankton supply to the rocky subtidal zone: influence of internal waves. *Proc Natl Acad Sci USA* 90: 1686–1690

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