Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions

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ABSTRACT: Examination of the physiological ecology of 3 sympatrically occurring mytilids (the ribbed, blue and greenshell mussels, *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*, respectively) was carried out during summer and winter at 2 sites which differ markedly in their environmental characteristics (Mahanga Bay inside Wellington Harbour, where mussels are abundant, and Island Bay on the exposed Cook Strait shore, where mussels are absent). Seston components (particle counts per ml in the size range 2.5 to 63 µm, total particulate matter [TPM], particulate organic matter [POM], and percent organic matter [PCOM]) all varied significantly between sites and between seasons. Mahanga Bay seston exhibited characteristics typical of productive temperate coastal waters, whereas Island Bay seston was characterised by low POM and low PCOM values. Weight-standardised clearance rate (CR$_S$), net absorption efficiency (AE) and Scope for Growth (SFG) values were determined for all 3 mussel species at both sites during both seasons. At Island Bay there was no evidence of seasonal differences in CR$_S$ whereas at Mahanga Bay species-specific CR$_S$ values were all highest in the winter. Regardless of season, CR$_S$ estimates for all 3 species were higher at Mahanga Bay than at Island Bay. At both sites, AE estimates were highest in the winter, and AE estimates were higher at Mahanga Bay than at Island Bay during each season. SFG estimates mirrored AE estimates, with SFG at both sites being highest in winter, and higher at Mahanga Bay than at Island Bay during each season. The SFG data support the hypothesis that mussels are absent from sites along Cook Strait shores because they do not enjoy a positive energy balance for long periods of time, consistent with the low seston organic matter levels at such locations. The SFG data also indicate that mussels inside Wellington Harbour can maintain a large, positive net energy balance throughout the year, consistent with the considerable biomass and very large size of all 3 species in this environment.

KEY WORDS: *Aulacomya maoriana* · *Mytilus galloprovincialis* · *Perna canaliculus* · Mussels · Ecological distribution · Physiological energetics · Seston · Scope for Growth

INTRODUCTION

In 1949 the Stephensons published a landmark paper in marine ecology on the universality of patterns of intertidal zonation on temperate rocky shores (Stephenson & Stephenson 1949). Although the universality of this zonation pattern was quickly repudiated, the basic premise remains: temperate rocky shores are characterised by zones of the same groups of organisms from the top of the intertidal region to the sublittoral (myxophysid lichens, littorinid gastropods, barnacles, mussels, kelps), even though the species and genera in question differ from region to region. Thus, mytilid mussels are characteristic of lower midshore regions worldwide and constitute an obvious and important ecological component of temperate intertidal rocky shore communities. The main reason for the lack of true universality of this phenomenon is that, while the majority of temperate rocky shores con-

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form to this pattern, a small number do not. One exam-
ple of this is the wave-exposed shoreline of much of the
Cook Strait which separates New Zealand's North
Island from the South Island. Mussels are mostly or
entirely absent from large stretches of this coast,
despite apparently suitable substrate being available
for colonisation. This is true of large areas of the outer
Marlborough Sounds of the South Island, and also of
the southern-most coast line of the North Island
towards Wellington Harbour (Fig. 1). Wellington Har-
bour itself exhibits the typical characteristics of inter-
tidal zonation described by the Stephensons, including
4 species of mytilids (the little black mussel *Xeno-
strobus pulex*, the blue mussel *Mytilus galloprovin-
cialis*, the endemic ribbed mussel *Aulacomya maori-
ana*, and the endemic greenshell mussel *Perna
canaliculus*) which occur in large and dense beds
wherever suitable substrate occurs. Given that mussels
are defining members of temperate intertidal rocky
shore communities, it is of interest to determine why
mussels do not occur on many Cook Strait shores
but are so abundant in the neighbouring Wellington
Harbour.

J. P. A. Gardner & R. J. Thompson (unpubl.) investi-
gated the physiological energetics of *Perna canaliculus*

at Island Bay (a Cook Strait site at which mussels are
absent) under ambient late-summer conditions of low
seston quality. They reported a mean negative net
absorption efficiency (AE) value of −14.2% for green-
shell mussels fed ambient seston which was charac-
terised by a low organic matter content of ~22%. Con-
sistent with published findings for other mytilid
species, principally *Mytilus edulis*, Gardner & Thomp-
son (unpubl.) suggested that the combined effects of
metabolic faecal loss (MFL) and naturally low levels of
seston organic matter content resulted in the negative
AE estimates, which in turn translated into negative
Scope for Growth (SFG) estimates. It was concluded
that under ambient late-summer conditions mussels
were losing energy faster than they were gaining it, a
state which, for obvious reasons, cannot be sustained
for too long. Gardner & Thompson (unpubl.) hypothe-
sised that the low quality seston along Cook Strait
shores might explain why mussels are absent from
much of this coastline. However, it was noted that con-
firmation for such a conclusion would require the esti-
mation of the net energy balance of more than 1 spe-
cies of mussel in more than 1 time period.

The present paper describes a series of experiments
carried out to compare the physiological energetics
and SFG of 3 sympatrically occurring mussel species.
The purpose of this research was to determine the
importance of seasonal variation in seston quantity
(total particulate matter [TPM]) and quality (particu-
late organic matter [POM], and percent organic matter
[PCOM]) as factors explaining the presence or absence
of mussels at 2 neighbouring sites which are charac-
terised by contrasting environmental conditions. The
experiments were conducted in early summer and
mid-winter at Island Bay on the Cook Strait, where
mussels are absent, and Mahanga Bay in Wellington
Harbour, where mussels are abundant. The findings
indicate that highly significant differences exist in nat-
ural seston characteristics between the 2 sites, and that
such differences effect the SFG of the 3 species in a
manner consistent with the presence of mussels at the
one site and their absence at the other.

MATERIALS AND METHODS

Sample collection and holding conditions. Mussels
(*Aulacomya maoriana*, *Mytilus galloprovincialis* and
Perna canaliculus) were collected from the low inter-
tidal region at Seatoun, inside Wellington Harbour,
during the early austral summer (26 November 1996),
and again during mid-winter (30 June 1997). On both
occasions, mussels were cleared of all epibionts:
approximately 30 individuals of each species were
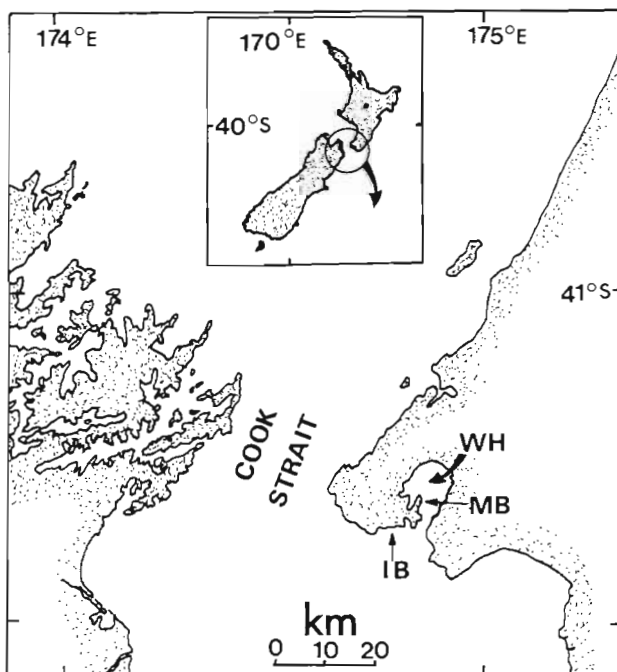held for a minimum of 10 d at the Island Bay Marine

Fig. 1. Geographic location of the experimental sites. Inset
map: the North and South Islands of New Zealand with the
Cook Strait region circled. Main map: Cook Strait region
showing detail of the Marlborough Sounds (northeast end of
the South Island) and the 2 experimental sites, IB = Island Bay
on the exposed Cook Strait coast and MB = Mahanga Bay
inside WH = Wellington Harbour

Laboratory and the same number of each species was transferred to and held for a minimum of 10 d at NIWA's Aquaculture Facility, Mahanga Bay. Both facilities are representative of their 2 respective systems (harbour and open coast) in terms of the biological community along the shore next to the facilities and in terms of the water supply to each laboratory. A wide size (shell length) range of each species was chosen for the experimental work. Mussels held at Island Bay were provided with unfiltered seawater pumped into the Marine Laboratory from the coastal waters of Cook Strait. Mussels held at Mahanga Bay were provided with unfiltered seawater pumped directly into the facility from Wellington Harbour. Seawater intake pipes at both facilities draw water from ~2 m below the surface at mean low water (MLW) and from a few metres offshore. At both Island Bay and Mahanga Bay a comparison was made of seawater flowing through the laboratory with seawater in the immediate vicinity of the intake pipe. Although particle counts and estimates of TPM and POM were lower inside the laboratory than in the sea, the magnitude of the differences was small and reflected the settlement of larger particles (>60 μm) which do not constitute the main food source of suspension-feeding mussels. The following methodology follows that described by Gardner & Thompson (unpubl.).

Seston characteristics. During any 24 h experimental period (see subsequent 'Clearance rates' section) three 2 l water samples were taken from the feeding apparatus overflow pipe to determine seston concentrations. Seston was concentrated on to pre-ashed and pre-weighed Whatman GF/C filters. Seston TPM (60°C for 24 h) and POM (450°C for 24 h) were calculated for each sample to an accuracy of 0.1 mg. Seston PCOM = [(POM/TPM × 100)] was also calculated. Seston particle counts in the size range of 2.5 to 63.0 μm were taken using a Coulter Z1 dual threshold electronic particle counter fitted with a 100 μm aperture.

Clearance rates (CR: l h^{-1}). Eighteen mussels of each species were used to estimate CR (= volume of water cleared of particles mussel^{-1} h^{-1}) at both sites during both seasons. The experimental set-up and protocol followed Bayne et al. (1976) and Gardner & Thompson (unpubl.). It consists of a header tank (maintained at constant pressure with an overflow pipe set so that the volume of the header tank was 20 l) which fed simultaneously into each of 13 chambers through 13 individual flow restrictors. Because CR is a function of body size, chamber geometry, and flow rate (Widdows & Johnson 1988), the flow rate through each chamber was adjusted according to the size of the mussel being tested, and varied between 100 to 500 ml min^{-1}. Outflow from each chamber was via a standpipe at the opposite end of the chamber from the inflow. During

any 24 h experimental period, 6 mussels of 2 separate species, representing a range of different shell lengths, were tested. One mussel was placed in each of 12 chambers while the thirteenth chamber was left empty as a control. The location of the control chamber was varied among experiments, and the flow rate of the control chamber was held at approximately the mean flow rate of the 12 experimental chambers. Mussels were allowed to feed for approximately 1 h before water samples were taken. Before each period of water sampling from the outflow standpipes of the 12 experimental chambers, mussels were checked to ensure that their valves were open, that their mantle tentacles were extended, and that there was evidence of water movement around them consistent with feeding activity. Timed outflow water samples were collected simultaneously from the standpipes of all 13 chambers on 3 occasions throughout each 24 h period. Particle counts were made of unfiltered outflow water of each of the 13 chambers using a Coulter Z1 particle counter fitted with a 100 μm aperture tube which recorded all particles in the size range 2.5 to 63 μm. The volume of seawater sampled by the Coulter counter was set at 1 ml. Particle counts from experimental chambers were always >10% lower than particle counts from the control chamber. CR for each mussel at each time of sampling was calculated as number of particles removed from the water per unit volume by reference to particle levels in the control sample. Mean CR per mussel per 24 h period was calculated and this figure was employed for statistical analyses. At the end of each 24 h experimental period the mussels were shucked, and dried (60°C for 24 to 48 h) and dry body weights were measured to an accuracy of 0.1 mg. CR was standardized to mass-specific rates for mussels of 1 g dry weight. Weight exponents (b in the allometric equation $Y = aX^b$, where Y is the physiological rate process, X is the dry body weight, and a and b are fitted parameters) were determined from log-log plots of CR as a function of dry body weight.

Net absorption efficiency (AE). During each 24 h CR experiment a subsample of faecal material was collected from each of the 12 chambers containing a mussel using a pipette and without disturbing the feeding mussels. The faecal sample was concentrated onto pre-ashed and pre-weighed Whatman GF/C filters for dry weight (dried for 24 h at 60°C) and ash-free dry weight (AFDW — weight loss on ignition at 450°C after 24 h) determinations. No pseudofaecal material was produced by mussels held at Island Bay. Pseudofaecal material was collected from mussels held at Mahanga Bay, but these samples were lost when the freezer in which they were held broke down. AE estimates for mussels from Island Bay are therefore calculated from ingestion of non-enriched

seston because no pseudofaeces were produced, whereas AE estimates for mussels from Mahanga Bay were calculated for an enriched diet following selection against those seston particles rejected as pseudofaeces. Individual net AE values were calculated for all mussels used in the CR experiments according to Conover (1966):

$$AE = (F - E)/[(1 - E) F]$$

where F = AFDW to dry weight ratio of seston supplied to mussels, and E = AFDW to dry weight ratio of mussel faeces. Individual AE values were not weight-standardised because variation in AE was independent of dry body weight for all 3 species.

Scope for Growth (SFG: $J\ g^{-1}\ h^{-1}$). SFG was calculated from the above physiological measurements according to Widdows (1985) and Gardner & Thompson (unpubl.). Because ammonia excretion was not measured, the estimates of SFG will be slightly elevated. Species-specific estimates of oxygen consumption rate (VO_2) were obtained from published values: values employed were 0.17, 0.40 and 0.45 $ml\ O_2\ g^{-1}\ h^{-1}$ for *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*, respectively (Griffiths & King [1979] for Aulacomya ater, Labarta et al. [1997] for *M. galloprovincialis*, Gardner & Thompson [1999] for *P. canaliculus*) and are consistent with unpublished data for these species at these sites (J. G. Helson & J. P. A. Gardner unpubl.). Natural variability in VO_2 values, for example as associated with seasonal physiological condition or the rate of organic absorption, does not ultimately effect the net energy balance of any of the 3 species. All data were standardised to 1 g dry body weight equivalents. Oxygen consumption was converted to energy equivalents according to Gnaiger (1983) such that 1 ml O_2 = 20.08 J. POM was converted to energy equivalents according to Crisp (1971) such that 1 mg POM = 20.78 J. SFG was calculated from the balanced energy equation (without the ammonium excretion term) as follows:

$$C = P + R + F$$

where C = total energy consumed, P = production of somatic and reproductive tissues, R = respiratory energy loss, and F = faecal energy loss. Because the absorbed ration (A) is the product of C and AE, P can be expressed as:

$$P = A - R$$

P is therefore the difference between energy absorbed from the food and energy expenditure due to respiration and excretion. Calculation of C, A and R

(all in $J\ g^{-1}\ h^{-1}$) follows Widdows & Johnson (1988, p. 116):

$$C = CR\ (l\ g^{-1}\ h^{-1}) \times POM\ (mg\ l^{-1}) \times 23\ J\ mg^{-1}\ AFDW$$
$$A = C \times AE$$
$$R = VO_2\ (ml\ O_2\ g^{-1}\ h^{-1}) \times 20.33\ J\ ml^{-1}\ O_2$$

P is referred to as Scope for Growth (SFG) and reflects the overall energy balance of the individual mussel. Because there was no observed pseudofaecal production by mussels held at Island Bay, the calculated SFG values represent estimates of energy gain or loss without consideration of particle selection and loss off the gill, i.e., CR = ingestion rate (IR). However, because pseudofaecal samples were not available for the Mahanga Bay mussels, the SFG values for these mussels are overestimates. Positive SFG values reflect energy which is available for production (somatic and/or reproductive growth) after routine metabolic demands have been met, whereas negative SFG values reflect an overall loss of energy by the individual.

Statistical analyses. Non-parametric ranked ANOVA was carried out to test for the effects of site and season upon the 3 separate dependent variables which define seston quantity and quality, namely TPM, POM and PCOM. Data were not normally distributed (Shapiro-Wilks statistic of Proc Univariate; SAS 1987), so were rank transformed before non-parametric analysis (Conover & Iman 1981). The 2 single effect terms (site and season) and their interaction were tested in each ANOVA model: non-significant terms were dropped from the analysis because they did not explain significant variation in the dependent variable.

ANOVA was employed to test for effects of the independent variables (species, site and season) and all possible interaction terms upon each separate physiological dependent variable (CR_S, AE, SFG). Non-significant terms were dropped from the ANOVA model until only single terms and interactions which explained significant variation in the dependent variable remained in the model. Analyses of CR_S, AE and SFG were carried out by non-parametric ranked ANOVA (Conover & Iman 1981) because the data were not normally distributed, even after transformation (Shapiro-Wilks statistic of Proc Univariate; SAS 1987).

RESULTS

Seston characteristics

Data for TPM, POM, PCOM and particle counts are presented in Table 1. TPM concentrations were lowest at Island Bay in the summer and highest at Island Bay in the winter (ANOVA: R^2 = 0.397, p < 0.0001; site: p =

Table 1. Seston and water characteristics, including temperature (°C), total particulate matter (TPM), particulate organic matter (POM), percent organic matter (PCOM), and particle counts [mean ±SD (n)]

Site	Season	Temperature (°C)	TPM	POM	PCOM	No. of particles in range 2.5–63.0 μm ml^{-1}
Island Bay	Summer	15.8 ±0.49 (15)	9.3 ±3.0 (30)	2.8 ±0.9 (30)	30.07 ±2.31 (30)	8013.9 ±2733.0 (31)
Island Bay	Winter	10.8 ±0.27 (15)	14.0 ±2.4 (15)	3.0 ±0.7 (15)	21.45 ±2.66 (15)	25958.4 ±13919.2 (45)
Mahanga Bay	Summer	15.9 ±0.32 (15)	13.7 ±3.5 (30)	4.0 ±1.1 (30)	28.92 ±1.51 (30)	24109.5 ±6130.8 (40)
Mahanga Bay	Winter	10.4 ±0.31 (15)	11.8 ±1.3 (15)	7.0 ±1.1 (15)	59.17 ±6.44 (15)	20246.9 ±5109.9 (49)

0.0168; season × site: p < 0.0001). At both sites, POM concentrations increased from summer to winter, by ~7 % at Island Bay and by ~75 % at Mahanga Bay (ANOVA: R^2 = 0.690; p < 0.0001; site: p < 0.0001; season: p < 0.0001; site × season: p < 0.0001). POM concentrations were higher at Mahanga Bay than at Island Bay, regardless of season. PCOM decreased from summer to winter by almost 30 % at Island Bay, but more than doubled at Mahanga Bay (ANOVA: R^2 = 0.910; p < 0.0001; site: p < 0.0001; season × site: p < 0.0001). During the summer the PCOM values at both sites were similar at ~30 %, but during the winter the value was almost 3 times higher at Mahanga Bay than at Island Bay (~60 vs 21 %). The number of particles in the range 2.5 to 63.0 μm increased from summer to winter by more than 3-fold at Island Bay but decreased by ~16 % at Mahanga Bay, mirroring the changes observed in TPM concentrations.

Clearance rates (CR)

CR_S values (l g^{-1} h^{-1}) are presented in Table 2. Typically, Aulacomya maoriana exhibited the lowest, and Perna canaliculus the highest, CR_S values regardless of site or season. At Island Bay, season had no apparent effect upon CR_S for any of the 3 species, whereas CR_S values at Mahanga Bay were all higher in the winter than in the summer. CR_S values for all species were higher at Mahanga Bay than at Island Bay regardless of season. ANOVA of CR_S values (Table 3) indicated that a model including 3 single effects and 2 interaction terms explained significant variation in CR_S (R^2 = 0.524, p < 0.0001). Because significant interactions existed among terms it was not possible to determine the significance of the single-term-dependent variables.

Table 2. Values for clearance rate (CR in l g^{-1} h^{-1}) and absorption efficiency (AE) for Aulacomya maoriana, Mytilus galloprovincialis, and Perna canaliculus at both sites during both seasons

Species	Season	Site	CR (mean ± SD)	AE (mean ± SD)
A. maoriana	Summer	Island Bay	1.73 ± 0.78	0.0049 ± 0.2344
M. galloprovincialis	Summer	Island Bay	2.82 ± 0.97	0.0348 ± 0.1127
P. canaliculus	Summer	Island Bay	3.40 ± 1.12	0.0736 ± 0.1370
A. maoriana	Winter	Island Bay	1.73 ± 0.55	0.3406 ± 0.1915
M. galloprovincialis	Winter	Island Bay	2.83 ± 0.93	0.0334 ± 0.2348
P. canaliculus	Winter	Island Bay	3.40 ± 0.97	0.1967 ± 0.2945
A. maoriana	Summer	Mahanga Bay	1.82 ± 0.79	0.2368 ± 0.0851
M. galloprovincialis	Summer	Mahanga Bay	3.58 ± 1.16	0.2702 ± 0.0968
P. canaliculus	Summer	Mahanga Bay	3.51 ± 1.32	0.3300 ± 0.1402
A. maoriana	Winter	Mahanga Bay	2.55 ± 0.92	0.8143 ± 0.0631
M. galloprovincialis	Winter	Mahanga Bay	4.49 ± 0.76	0.7920 ± 0.0368
P. canaliculus	Winter	Mahanga Bay	4.61 ± 1.18	0.8013 ± 0.0665

Table 3. ANOVA testing for the effects of season, site, species and their interactions upon ranked standardised clearance rate (CR_S in $l\ g^{-1}\ h^{-1}$)

Source	df	SS	MS	F-value	p
Model	7	439781.3	62825.9	32.67	0.0001
Error	208	400008.7	1923.1		
Corrected total	215	839790.0			
Season	1	23437.5	23437.5	12.2	0.0006
Site	1	61273.4	61273.4	31.9	0.0001
Species	2	318090.1	159049.0	82.7	0.0001
Site × Species	2	13409.7	6704.9	3.5	0.0324
Season × Site	1	23562.7	23562.7	12.3	0.0006

Net absorption efficiency (AE)

Mean net AE values are presented in Table 2: these values reflect non-enriched (i.e., no pseudofaecal production) and enriched (i.e., pseudofaecal production) seston ingestion at Island Bay and Mahanga Bay, respectively. These data indicate that (1) AE estimates during the summer at Island Bay were positive but low; (2) during the winter at Island Bay AE estimates for *Aulacomya maoriana* and *Perna canaliculus* were moderately high, but the AE for *Mytilus galloprovincialis* remained low and positive; (3) during the summer at Mahanga Bay AE estimates were in the range of 20 to 33%; and (4) during the winter at Mahanga Bay all AE estimates were high (~80%) with low standard deviations. The significant ANOVA model ($R^2 = 0.717$, p < 0.0001) indicated that season, site, species and all three 2-way interactions explained significant variation in AE (Table 4). Mean AE values were higher in winter than in summer, were higher at Mahanga Bay than at Island Bay, and were higher in both *A. maoriana* and *P. canaliculus* than in *M. galloprovincialis*. However, significant interaction terms precluded the identification of significant single term effects.

Scope for Growth (SFG)

Energy consumed (C, $J\ h^{-1}$), energy absorbed (A, $J\ h^{-1}$), energy respired (R, $J\ g^{-1}\ h^{-1}$) and SFG ($J\ g^{-1}\ h^{-1}$) estimates are presented in Table 5. All 3 species exhibited negative SFG estimates under the summer conditions at Island Bay. During the winter at Island Bay, SFG values for *Aulacomya maoriana* and *Perna canaliculus* were moderately high, whereas those for *Mytilus galloprovincialis* were negative. At Mahanga Bay during the summer SFG values for all 3 species were positive and ranged from 34 to 121 $J\ g^{-1}\ h^{-1}$. During the winter at Mahanga Bay the SFG estimates for all 3 species were very high, ranging from 333 to 614 $J\ g^{-1}\ h^{-1}$. ANOVA of SFG values (Table 6) indicated that the 3 single dependent variables and all 2-way interaction terms had a significant effect upon SFG ($R^2 = 0.777$, p < 0.0001). Mean SFG values were higher at Mahanga Bay than at Island Bay, were higher in the winter than in the summer, and were highest in *P. canaliculus* and lowest in *A. maoriana*. Significant interaction terms, however, precluded the identification of significant dependent variables. As previously indicated, it is important to appreciate that the SFG estimates obtained for mussels from Mahanga

Table 4. ANOVA testing for the effects of season, site, species and their interactions upon ranked absorption efficiency, AE

Source	df	SS	MS	F-value	p
Model	9	593514.5	65946.1	57.61	0.0001
Error	205	234665.0	1144.7		
Corrected total	214	828179.5			
Species	2	347569.0	347569.0	303.6	0.0001
Season	1	185099.3	185099.3	161.7	0.0001
Site	1	10031.1	5015.6	4.4	0.0137
Season × Site	1	24917.6	24917.6	21.8	0.0001
Season × Species	2	16791.3	8395.7	7.3	0.0008
Site × Species	2	8266.7	4133.3	3.6	0.0288

Table 5. Components of the energy budget (means ± SD) and Scope for Growth for *Aulacomya maoriana*, *Mytilus galloprovincialis*, and *Perna canaliculus* at 2 sites during 2 seasons

Species	Site	Season	Energy consumed, C $(J\ g^{-1}\ h^{-1})$	Energy absorbed, A $(J\ g^{-1}\ h^{-1})$	Energy respired, R^a $(J\ g^{-1}\ h^{-1})$	Scope for Growth $(J\ g^{-1}\ h^{-1})$
A. maoriana	Island Bay	Summer	136.9 ± 79.7	−1.2 ± 36.9	3.5	−4.7 ± 36.9
M. galloprovincialis	Island Bay	Summer	195.7 ± 109.2	3.2 ± 25.2	8.1	−4.9 ± 25.2
P. canaliculus	Island Bay	Summer	218.5 ± 107.7	7.9 ± 28.5	9.1	−1.3 ± 28.5
A. maoriana	Island Bay	Winter	127.8 ± 39.4	41.7 ± 24.4	3.5	38.2 ± 24.4
M. galloprovincialis	Island Bay	Winter	176.4 ± 69.2	5.4 ± 47.1	8.1	−2.7 ± 47.1
P. canaliculus	Island Bay	Winter	215.8 ± 83.3	34.0 ± 69.4	9.1	24.9 ± 69.4
A. maoriana	Mahanga Bay	Summer	158.3 ± 70.7	37.6 ± 19.7	3.5	34.2 ± 19.7
M. galloprovincialis	Mahanga Bay	Summer	361.6 ± 154.8	95.5 ± 47.2	8.1	87.4 ± 47.2
P. canaliculus	Mahanga Bay	Summer	353.6 ± 182.4	129.8 ± 93.7	9.1	120.6 ± 93.7
A. maoriana	Mahanga Bay	Winter	417.2 ± 160.3	336.9 ± 123.5	3.5	333.5 ± 123.5
M. galloprovincialis	Mahanga Bay	Winter	735.7 ± 119.0	582.9 ± 97.5	8.1	574.8 ± 97.5
P. canaliculus	Mahanga Bay	Winter	778.4 ± 188.7	622.7 ± 162.1	9.1	613.5 ± 162.1

[a]VO_2 values of 0.17, 0.40 and 0.45 ml O_2 g^{-1} h^{-1} were used for *A. maoriana*, *M. galloprovincialis* and *P. canaliculus* respectively; hence standard deviations are not available

Table 6. ANOVA testing for the effects of season, site, species and their interactions upon Scope for Growth (SFG)

Source	df	SS	MS	F-value	p
Model	9	643568.9	71507.7	79.41	0.0001
Error	205	184611.1	900.5		
Corrected total	214	828180.0			
Site	1	446164.5	446164.5	495.4	0.0001
Season	1	143623.4	143623.4	159.5	0.0001
Species	2	5998.1	2999.1	3.3	0.0377
Site × Species	2	22891.9	11445.9	12.7	0.0001
Season × Species	2	7071.4	3535.7	3.9	0.0212
Season × Site	1	16890.6	16890.6	18.8	0.0001

Bay are overestimates because the calculations are based on the assumption that CR = IR, an unrealistic assumption which cannot be corrected for because pseudofaecal samples were lost when a freezer broke down. The SFG estimates for mussels held at Island Bay are correct because no pseudofaecal material was produced, thus CR = IR.

DISCUSSION

Gardner & Thompson (unpubl.) suggested that mussels are absent from Island Bay and other such sites along Cook Strait as a consequence of energy limitation, resulting from low seston quality. If this hypothesis is true then 2 main conditions must be satisfied. First, water column comparisons between the Cook Strait region and Wellington Harbour must be consis-

tent with the hypothesis, and second, the physiological responses of the mussels in the 2 contrasting environments must support the hypothesis.

The observed differences in seston quantity and quality between the 2 sites must be explicable in terms of local hydrographic conditions if site-specific differences in seston quality do influence mussel presence or absence. Several authors have suggested that Wellington Harbour is at least partially isolated from the shelf area immediately outside the harbour entrance (Maxwell 1956, Booth 1975, Harris 1990). The Harbour is a sheltered, well-mixed, nutrient-rich, semi-enclosed body of water (85 km^2 in area) with a flushing time of ~9 d (Maxwell 1956, Brodie 1958, Booth 1975, Heath 1977). By comparison, the south coast shelf system (Cook Strait) is a high-energy, very exposed coastline. Strong surface current movement through Cook Strait (primarily the D'Urville Current)

results in a net flow of oceanic Tasman Sea water down the east coast of the North Island, through Cook Strait, and along Wellington's south coast (Bowman et al. 1983, Harris 1990). This water is generally of low productivity (Bowman et al. 1983) and does not receive significant input of either particulate material (detritus) or dissolved nutrients from riparian flow along this coast (author's pers. obs.). The net result is that primary productivity of the coastal water column is low along Wellington's south coast. Seston quantity (expressed as TPM levels) at both sites during both seasons was moderately high and is not considered to be limiting to mussel growth simply in terms of concentration (Bayne & Widdows 1978, Widdows et al. 1979). When compared with published values from similar environments, seston quality (expressed as PCOM) was very low at Island Bay during the winter, was moderate at both sites during the summer, and was high at Mahanga Bay during the winter. These seston data are consistent with those of Gardner & Thompson (unpubl.), who observed that ambient TPM levels at Island Bay during late summer in 1996 were in the range of published values, but that ambient PCOM levels were low compared with published values for other temperate rocky reef sites. The water column conditions of the 2 contrasting regions are therefore consistent with the hypothesis that mussels are absent from large stretches of Cook Strait because they cannot maintain a positive energy balance when feeding on low quality seston. However, other possible biological and physical explanations for the absence of mussels from Cook Strait shores, such as reduced or absent larval supply, harsh environmental conditions, predation, etc., are also presently being investigated.

If mussels are absent from Cook Strait shores as a consequence of low seston quality then the suite of physiological responses of all 3 mussel species should reflect this under experimental conditions at both sites and during both seasons. CR is the most important component of energy acquisition, often accounting for ~70% of total energy intake (Bayne et al. 1976). In all 3 species CR$_S$ was strongly influenced by seston quality with species-specific CR$_S$ estimates being higher at Mahanga Bay than at Island Bay in all cases. The higher species-specific CR$_S$ values at Mahanga Bay than at Island Bay are reflected in the higher values of energy consumed at the former site compared with the latter, and are consistent with the hypothesis being tested.

AE values are most often calculated to reflect the ratio of organic matter in the seston to that in the faeces. However, in the present study, site-specific differences in AE are confounded to some small extent by the dietary enrichment resulting from pseudofaecal production at Mahanga Bay and the absence of such at

Island Bay. Regardless of this, bivalve AE is strongly dependent upon food quality (Bricelj & Malouf 1984, Bayne et al. 1987, Navarro et al. 1991, Gardner & Thompson unpubl.), in particular, upon the ratio of organic to inorganic matter (Griffiths 1980, Bayne et al. 1987). Net AE values typically range from about –60% up to about 60% (Bayne & Hawkins 1990). Gardner & Thompson (unpubl.) reported negative net AE values for *Perna canaliculus* feeding on ambient seston in late summer at Island Bay, a finding which was interpreted in terms of MFL. In the present study the AE values observed for all 3 species at Island Bay during both seasons (0 to 7% in early summer, 3 to 34% in winter), and at Mahanga Bay during the summer (23 to 33%), are typical of published values, but the AE values observed for all 3 species at Mahanga Bay during the winter are unusually high (79 to 81%). The extent of dietary enrichment by mussels at Mahanga Bay cannot at present be estimated, but the fact that this difference in dietary enrichment exists between the 2 sites highlights the magnitude of the difference in seston quality between them. The AE data for mussels at Island Bay from early summer (Gardner & Thompson unpubl.) and late summer (present study) indicate that all 3 species are barely able to maintain a positive net AE level, which is a requirement if individuals are to enjoy a positive net energy balance.

SFG represents the net energy balance of an individual after energy acquisition and expenditure have been accounted for. Positive SFG values are good predictors of growth potential (Dame 1976, Bayne & Worrall 1980, Bayne & Newell 1983). Negative SFG values usually result because respiratory costs exceed energy absorption, but under certain circumstances SFG can be negative as a result of negative AE values, which can result from MFL (Hawkins & Bayne 1985, 1992, Bayne & Hawkins 1990, Gardner & Thompson unpubl.). SFG is largely independent of temperature within the normal temperature range of the species concerned (Widdows & Bayne 1971, Bayne et al. 1973, Widdows 1978), i.e., SFG is thought to be regulated in intertidal and shallow subtidal species except at temperature extremes. Thus, temperature differences between seasons within a site, or between sites are unlikely to have contributed to differences in SFG between seasons or between sites because the experiments were carried out under ambient conditions.

SFG estimates for the 3 species were generally of a similar magnitude to each other, and tended to mirror the net AE estimates. Under ambient early summer conditions at Island Bay, all 3 species were losing energy at roughly equal rates. Energy loss continued for *Mytilus galloprovincialis* at Island Bay under winter conditions, but the 2 other species both had positive energy balances, typical of values observed in natural

conditions (Widdows & Johnson 1988). Gardner & Thompson (unpubl.) calculated negative SFG values for *Perna canaliculus* under ambient late summer conditions at Island Bay (-18.6 J g^{-1} h^{-1}), indicating that these mussels were, in effect, losing more energy than they were acquiring under these conditions. All 3 species of mussels held at Island Bay under ambient early summer conditions in the present study were losing energy faster than they could acquire it. Additionally, because energy loss as a consequence of ammonium excretion was not measured in the present study, these values are all underestimates of the true net energy balance of each species. Thus, during ambient summer conditions and regardless of species, mussels are in a state of negative energy balance at Island Bay. This in itself does not explain why mussels are absent from many Cook Strait shores, because the duration of time that each species can exist for under such conditions depends to a large extent on how much of an energy reserve can be accumulated during winter conditions, and how efficiently such a reserve can be utilised. For *Aulacomya maoriana* and *P. canaliculus* at Island Bay, ambient winter conditions resulted in a net positive energy balance, with the opportunity to accumulate energy reserves. For these 2 species, the extent of the net energy loss during summer and the net energy gain during winter will be very much dependent upon the duration of the seston conditions associated with these seasons. For *M. galloprovincialis*, however, a negative net energy balance during winter at Island Bay suggests that this species cannot accumulate energy reserves during winter which might be used to offset energy loss at other times of the year. The main reason for the species-specific difference in AE and SFG is attributable to a difference in energy absorbed. For all 3 species at Island Bay, energy consumed is very similar in summer and winter, but energy absorbed changes substantially between the 2 seasons. For *A. maoriana* and *P. canaliculus* the estimated energy absorbed increases from a range of -1.2 to $+7.9$ J h^{-1} to a range of 34.0 to 41.7 J h^{-1}; for *M. galloprovincialis*, the energy absorbed decreases from 3.2 to 0.2 J h^{-1}. The reason for this differential response is unknown and warrants further investigation.

For mussels from Mahanga Bay, the SFG values are overestimates of net energy balance because the calculations make no allowance for energy not ingested but lost as pseudofaeces. However, even allowing for pseudofaecal energy loss levels of 50%, which is consistent with values reported for other mytilids under similar circumstances, the SFG values are all high and indicative of an environment which is well suited to mussel growth. With such high SFG estimates it is clear that the major source of energy loss, namely respiration, can vary quite substantially without influencing to any

great extent the net energy balance of mussels at Mahanga Bay regardless of season. Thus, although the energy loss associated with respiration is an important component of the overall energy budget of each species, it is energy consumption (the product of CR and POM) and energy absorption (the product of energy consumption and AE) which most significantly effect species-specific SFG estimates under the environmental conditions examined in Wellington Harbour.

In their extensive review of molluscan physiology Bayne & Newell (1983, p. 487) note that 'It is probably a commonplace for many bivalve species to be limited in their distribution by seasonally varying conditions that lead to periods of negative growth efficiency.' However, there are very few published reports of food limitation resulting in the absence of mussels from large stretches of otherwise suitable coast. In this context, the high SFG values obtained for all 3 species at Mahanga Bay contrast sharply with the low values obtained for mussels at Island Bay. Under ambient summer conditions at Mahanga Bay, all 3 species maintained a positive and moderately high energy balance, even allowing for the fact that the energetic costs of ammonium excretion have not been taken into consideration. Under ambient winter conditions, the SFG values for all 3 species increased substantially. These positive SFG values for the Mahanga Bay site are reflected in the dense intertidal and shallow subtidal beds of mixed mussel species, and the large sizes that all 3 species can attain in the Harbour ($\sim$7, 9 and 20 cm for *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*, respectively: author's pers. obs.). Under ambient early summer conditions at Island Bay, all 3 species exhibited negative SFG values, consistent with findings for *P. canaliculus* under late summer ambient conditions at Island Bay (Gardner & Thompson unpubl.). By mid-winter, the SFG estimates for *A. maoriana* and *P. canaliculus* were positive and moderately high, indicating a period of net energy acquisition. The SFG estimate for *M. galloprovincialis* was negative, however, indicating a prolonged period of net energy loss. Thus, the SFG estimates are consistent with the hypothesis that mussels are absent from much of the Cook Strait shore as a consequence of some form of seston limitation, most probably low organic matter concentrations.

Future research will focus upon more frequent seston sampling for TPM, POM and PCOM, as well as for particulate C and N and chlorophyll *a* concentrations. This will better address the question of the duration and timing of the availability of seston quantity and quality, and the concomitant duration and timing of periods of net energy loss or gain for all 3 mussel species. It is hoped that this additional information will help to explain the very different bioenergetic re-

sponses of all 3 mussel species during the summer, when seston conditions at Island Bay and Mahanga Bay were apparently relatively similar. With these additional data, bioenergetics models will be developed to more accurately describe the annual energy balance of each species to confirm whether findings from the present study do explain the unusual absence of mussels from many exposed Cook Strait shores.

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