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Site-related differences in the feeding physiology of the green mussel *Perna viridis*: a reciprocal transplantation experiment

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ABSTRACT: Differences in the feeding physiology of the green mussel *Perna viridis* between 2 aquaculture sites with contrasting hydrographies in Hong Kong were demonstrated. One site, Kat O, is oceanic and characterized by low seston concentrations and high organic contents. The other, Ma Wan, is under the influence of the Pearl River Estuary, hence the water is more turbid and has a low organic content. To determine the extent to which differences in mussel feeding responses were caused by environmental factors, a reciprocal transplantation experiment between the 2 sites was undertaken. Feeding rates (clearance rate, rejection rate, absorption rate and absorption efficiency) and enzyme activities (amylase and cellulase) were determined at various times, up to 8 mo post-transplantation. Complete acclimatization of the physiological responses of transplanted mussels occured 30 d post-transplantation. Transplanted individuals also showed complete morphological acclimatization in terms of palp area and palp:ctenidial area ratio 150 d post-transplantation, with higher ratios being obtained at Kat O, where suspended solid levels were lower, which is in contrast to other mytilids. The physiological differences between the 2 populations are thus largely environmentally induced.

KEY WORDS: Mussels · *Perna viridis* · Feeding rate · Digestive enzymes · Palp:ctenidial area ratio · Transplantation

INTRODUCTION

Suspension-feeding bivalves living in shallow waters are exposed to large fluctuations in food supply, both in terms of composition and concentration. Variations may be associated with seasonal events such as the seasonal availability of phytoplankton, or short-term events such as the resuspension of sediment caused by wave and/or tidal action (Bayne 1993, Navarro & Iglesias 1993). To cope with such a variable food environment, and to optimize ingested energy, various feeding strategies have evolved in suspension-feeding bivalves. These include regulation of feeding rates and enzymatic activities, and production of pseudofaeces (Bayne & Newell 1983, Navarro & Iglesias 1993). Compared with considerable scientific research on *Mytilus* spp. in temperate waters, much less work has been done on tropical and subtropical species (Ward & MacDonald 1996, Hawkins et al. 1998a, Yukihira et al. 1999), particularly the warm-water species *Perna viridis* (L.), though it is of high ecological significance (Seed & Richardson 1999) and has aquaculture value (Guo et al. 1999).

The green mussel *Perna viridis* widely distributed in the Indo-Pacific region, from the Persian Gulf to the SW Pacific longitudinally, and from southern Japan to Papua New Guinea latitudinally (Siddall 1980). It has recently been introduced into coastal areas of the western hemisphere, such as Venezuela, Trinidad, Jamaica, and Florida in the United States (Ingrao et al. 2001). It is one of 5 mussel species cultured commercially in Guangdong and other southern provinces in China (Guo et al. 1999), and is an inexpensive protein source in Southeast Asia. After China, Thailand is the

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second largest producer of mussels in Asia and *P. viridis* yields the highest net profit of any bivalve cultured in the country (Chalmermwat & Lutz 1989). In Hong Kong, *P. viridis* is distributed widely, from oceanic to estuarine waters, and is a dominant subtidal species with highest densities recorded from Victoria Harbour (246 m^{-2}) and Tolo Harbour (>1000 m^{-2}) (Huang et al. 1985).

Reciprocal transplantation is commonly used to examine the plasticity of bivalve physiological responses, and also the extent to which measured differences in native populations may be environmentally induced (i.e. phenotypic) rather than genetically determined characteristics (i.e. genotypic) (Worrall & Widdows 1983). This technique has been applied successfully to studying inter-site differences in feeding rates, growth, energetics and metal accumulation in mussels (Widdows et al. 1984, Kautsky et al. 1990, Tedengren et al. 1990, Okumus & Stirling 1994, Riget et al. 1997). In one experiment, *Perna viridis* was transplanted from Tolo Harbour to various locations in Hong Kong, with highest and lowest growth being obtained in eastern and western waters, respectively (Cheung 1991). Such inter-site differences in growth, reproduction and energetics of *P. viridis* were reported to be largely determined by environmental factors (Lee 1986, Cheung 1991).

Spatial and temporal variations in the feeding physiology of *Perna viridis* were studied for 1 yr at 2 sites in Hong Kong (Wong & Cheung 2001a, 2003). These 2 sites, Kat O and Ma Wan, are located in the eastern and western waters of Hong Kong, respectively. Kat O is characterized by low seston concentrations and high organic contents. In contrast, under the influence of the Pearl River, which is the third largest river in China, Ma Wan is estuarine and characterized by high seston concentrations and lower organic contents (Morton & Morton 1983). Feeding responses, including clearance rate, absorption rate and efficiency, and digestive enzyme activities (amylase and cellulase), were correlated with food availability (Wong & Cheung 2001a, 2003). Inter-site differences in feeding responses, however, were still discernible. For example, pseudofaeces production was interpreted as a selective behaviour which enhances the ingestion of particulate organic matter (POM) for individuals of *P. viridis* at Ma Wan, but not at Kat O. Such inter-site differences in feeding behaviour may be environmentally induced or caused by genetic differences. Differences in allelic and genotypic frequencies have been observed between *P. viridis* populations at 2 other sites in Hong Kong, Victoria Harbour and Tolo Harbour, and among the 9 genotypic classes studied, 6 occurred more frequently in the Victoria Harbour samples, while 3 occurred more frequently in the Tolo Harbour samples (Chan 1992). In the present study, native populations of *P. viridis* at Kat O and Ma Wan (Fig. 1) were transplanted reciprocally, and the feeding responses of transplanted individuals were compared with those of native ones to determine to what extent inter-site differences are environmentally induced in the physiological responses of *P. viridis*.

MATERIALS AND METHODS

Perna viridis. Kat O is located in the northeastern oceanic waters of Hong Kong, which are characterized by low total particulate matter (TPM) and high organic contents (*f*). In contrast, Ma Wan is located in the central waters of Hong Kong and is characterized by high TPM and low *f* values. Salinity at Ma Wan, particularly in summer, is also lower than at Kat O (Fig. 1). Feeding and absorption by *Perna viridis* varied with both season and site and were postulated to be the result of food availability (Wong & Cheung 2001a, 2003). A reciprocal transplantation experiment was also undertaken at the 2 study sites. On 5 February 1998, individuals of *P. viridis* were collected from Kat O and separated into 2 size categories, small (S) and large (L), each containing 160 individuals. Half of each group (80 individuals) was then cultured in cages at the same site

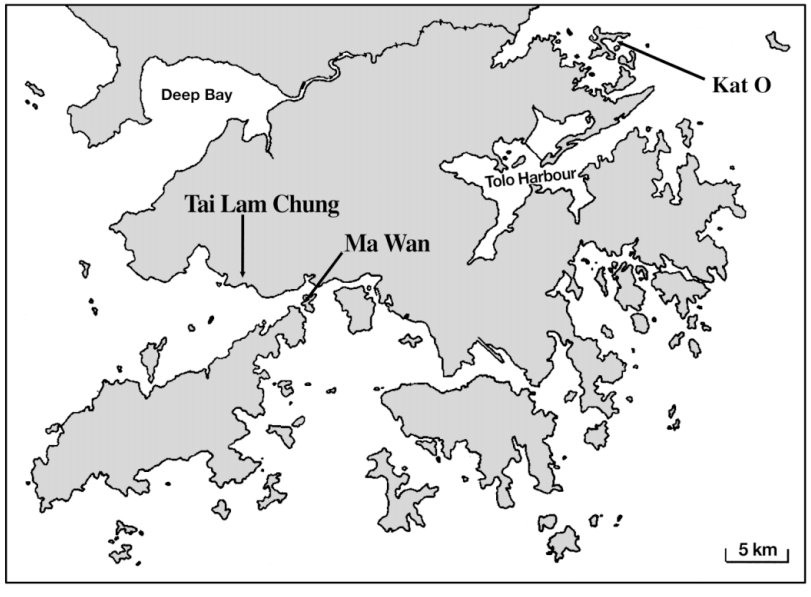

Fig. 1. Map of Hong Kong showing Kat O and Ma Wan, the experimental sites for reciprocal transplantation

and referred to as KO. Another half was transplanted to Ma Wan on the same date and referred to as KO→MW. On the same date, individuals of *P. viridis* were also collected from Ma Wan and divided into 2 size groups. Half of these were then cultured in cages at Ma Wan (MW), and the other half transplanted to Kat O (MW→KO). Individuals were kept out of water, but in a moist environment, for 4 h during transportation between the 2 sites. Native individuals were kept under the same conditions for 4 h before being put into experimental cages. Initial sizes among the 4 experimental groups were not significantly different for either small (1-way ANOVA, F = 0.06, df = 3, 24, p = 0.98) or large individuals (1-way ANOVA, F = 1.24, df = 3, 24, p = 0.32) (see Fig. 4).

Hydrographic parameters. Temperature, salinity, dissolved oxygen and seston characteristics, and feeding responses of *Perna viridis*, were determined on 5 occasions at each site. These were: 15 to 20 February, 5 to 10 March, 5 to 10 May, 5 to 10 July and 5 to 10 October 1998, i.e. ~10, 30, 90, 150 and 240 d post-transplantation, respectively.

Seston characteristics. TPM (mg l^{-1}), POM (mg l^{-1}), particulate inorganic matter (PIM: mg l^{-1}) and organic fraction of seston (f) of the seawater were determined. This was done by collecting a water sample of 300 ml at a time interval of ca. 30 min from the outflow of the empty container (control) (see 'Physiological measurements'). Each water sample was filtered onto ashed and pre-weighed 25 mm GF/C filters (Whatman) and rinsed with distilled water. Instead of using isotonic ammonium formate, distilled water was used to remove salts because a preliminary test showed that there was no significant difference in the results obtained by these 2 methods (Wong & Cheung 1999). The samples were dried in an oven (110°C for 24 h), weighed, and ashed in a muffle furnace (450°C for 6 h) before final weighing. Thus, concentrations of TPM and PIM were measured. POM concentration was estimated by subtracting PIM from TPM. The organic content of suspended matter was computed as f = POM/TPM.

Physiological measurements. Physiological responses, which included rejection and clearance rates, and absorption efficiency and rate, were determined ~10, 30, 90, 150 and 240 d post-transplantation. During each visit, 7 individuals of *Perna viridis* from each size group of the 4 treatments were placed in separate plastic containers (250 ml) into which natural seawater (10 cm below the sea surface) was pumped from the sea via a multi-channel peristaltic pump (Wong & Cheung 2001a, 2003). One vessel containing no mussels was used as a control to determine the characteristics of natural seawater. A preliminary experiment was undertaken to determine the optimum flow rate for the experiment. Seven individuals with shell lengths between 42 and 65 mm were placed in separate containers and received a continuous flow of fresh seawater. Five flow rates were tested for suitability in the experiment (50, 100, 150, 200 and 250 ml min^{-1}), and the clearance rate at 50 ml min^{-1} was found to be significantly different from the others. A flow rate of 100 ml min^{-1}, therefore, was used, and the depletion of particle concentration produced by the filtering activity of *P. viridis* at this flow rate was <40%, as determined by an electronic Coulter Counter. To minimize the problem of recirculation, the position of each *P. viridis* in the chamber was adjusted such that the inflow tube of the chamber (at the bottom) was facing an individual's inhalant aperture, and exhalant apertures faced the out-flow tube (at the top) (Riisgård 1977). Individuals were left in separate trays with flowing seawater for ca. 1 h prior to experimentation to evacuate the gut. Subsequently, all pseudofaeces and faeces produced in the first hour were removed using an autopipette. Between 1.5 and 2 h later, faeces and pseudofaeces were collected separately. They can be differentiated by their appearance, in that particles in pseudofaeces are loosely held by mucus, whereas faeces are more tightly packed. As seawater used in the experiment was pumped directly from just below the sea surface where the bivalves were held, the seston collected during the feeding experiments was a good representation of the material that the bivalves had fed on ca. 6 to 9 h (a complete digestive cycle including both extracellular and intracellular digestive phases) prior to the experiments. The effect of tidal cycles on seston composition was minimized by undertaking the experiment during neap tides in each month, when temporal variations in seston quantity and quality were small (Wong & Cheung 2001b).

During each site visit, feeding rates were determined for 7 individuals from each size group. A sample size of 7 was used, as it was found to be adequate for significant results in a previous study on the feeding behaviour of this species (Wong & Cheung 1999). Faeces and pseudofaeces were collected with an autopipette and treated in the same way as the seston particles, described previously. Measured parameters included: rejection rates (in mg h^{-1}), as pseudofaeces of the total (RR), organic (ORR) and inorganic (IRR) particulate matter; and egestion rates (in mg h^{-1}), as true faeces of the total (ER), organic (OER) and inorganic (IER) particulate matter. Assuming that absorption of the inorganic matter through the digestive system is negligible, the sum of IRR and IER was considered to represent the rate of inorganic matter filtration (IFR) and, hence, clearance rates (CR: l h^{-1}) were estimated as CR = IFR/PIM (Iglesias et al. 1996). The filtration rate (in mg h^{-1}) of TPM (FR) was calculated as FR = CR × TPM and that of POM (OFR) as OFR = CR × POM. Ingestion

rates (in mg h^{-1}) of total (IR) and organic (OIR) particulate matter were estimated as IR = FR – RR and OIR = OFR – ORR, respectively. The rate of food absorption (AR: mg h^{-1}) was calculated as AR = OIR – OER, and absorption efficiency (AE) as AE = AR/OIR. Energy absorbed was calculated from AR using a conversion factor of 20.78 J mg^{-1} POM (Crisp 1971).

Amylase and cellulase activities. Owing to logistic problems, enzyme activities in the digestive diverticula and crystalline style could only be determined on Days 90, 150 and 240 post-transplantation. Since amylase and cellulase activities are highest among all the carbohydrases in the digestive diverticula of *Perna viridis*, and lipase and protease activities are low (Teo & Sabapathy 1990), only those of α-amylase and cellulase were studied in the present experiment. The digestive diverticula and crystalline style were collected *in situ*, placed in liquid nitrogen, transported to the laboratory and stored at –30°C for *in vitro* enzyme assays. Wet weights of the digestive diverticula and crystalline styles were recorded before enzyme assays. Either 1 digestive diverticulum or 2 crystalline styles were homogenised in cold 20 mM phosphate buffer (pH 6.9 and 6.5, respectively) containing 20 mM NaCl and centrifuged for 15 min (4000 × *g*). The clear supernatants were used to determine amylase and cellulase activities using the Nelson-Somogyi method (Nelson 1944, Somogyi 1952). Standard calibration curves were determined with glucose. The substrata for the determination of amylase and cellulase were starch (1%) and carboxymethylcellulose (1%), respectively, and they were made up with appropriate phosphate buffers for the digestive diverticula and crystalline styles, respectively (Ibarrola et al. 1998a). Diverticula and crystalline style masses were estimated as mg of protein using the method of Lowry et al. (1951), and a standard calibration curve for measuring protein was set up using bovine serum albumin (BSA). Enzyme activity was expressed in mg glucose h^{-1} per mg protein.

On Day 150 post-transplantation, *Perna viridis* was collected from each of the 4 experimental groups (KO, MW, KO→MW, MW→KO). Shell length of each individual was measured to the nearest 0.01 mm using calipers. Ctenidial area was estimated by measuring the area of the ascending lamella of the outer demibranch, and palp area was estimated as the average of the surfaces of the right and left labial palps. Estimations of ctenidial and palp areas were made to the nearest 0.1 mm^2, by measuring the outlines of magnified images obtained by a fixed high-resolution camera with a calibration scale (Leica Model: Quantimet 500+) of relevant organs (excised from live mussels under a stereomicroscope and placed in a dish of seawater, allowing them to expand to a maximum extent, which occurred within a few minutes). This method was modified from the technique adopted by Jones et al. (1992) and Payne et al. (1995a). Both ctenidial and palp areas were measured in mm^2. The ratio between palp area (P) and ctenidial area (C) was calculated as $P/C \times 100$ (Payne et al. 1995a).

Statistical analyses. Feeding responses and enzymatic activities among different groups were compared using 1-way ANOVA followed by multiple-comparison procedures. The relationship between seston quantity and quality was analyzed by nonlinear regression. Linear regression was used in relating shell length and ctenidial and labial palp areas (log-transformed data), and elevations and intercepts of different regression lines were compared using ANCOVA. Since no significant differences were found for either initial or final shell length among the 4 experimental groups (see Fig. 4), no size standardization was conducted prior to between-group comparisons. Because a series of ANOVA or ANCOVA for variables that are not independent of each other were employed, a Bonferroni adjustment was used to correct for Type I errors, and significance for each ANOVA was evaluated against $\alpha = 0.05$ divided by the number of comparisons being made (Sokal & Rohlf 1995). All statistical methods used were according to Zar (1984).

RESULTS

Hydrography of the 2 study sites

Temporal variations in hydrographical parameters, including temperature, salinity, dissolved oxygen and food availability (TPM, POM, PIM, f), of the 2 experimental sites are shown in Fig. 2. Temperature changes at the 2 sites were similar, with low values in February and March and higher values in July and October (Fig. 2A). Salinity and dissolved oxygen values at Ma Wan, however, were consistently significantly lower than at Kat O (Fig. 2B,C). TPM and PIM concentrations were significantly higher ($t = -9.25$, df = 295, $p < 0.001$; and $t = -9.17$, df = 295, $p < 0.001$, respectively) but organic content was significantly lower ($t = 6.47$, df = 295, $p < 0.001$) at Ma Wan (TPM: 10.63 to 13.97 mg l^{-1}; PIM: 6.79 to 10.51 mg l^{-1}, f: 0.22 to 0.43) than at Kat O (TPM: 5.71 to 10.68 mg l^{-1}; PIM: 3.60 to 6.21 mg l^{-1}, f: 0.38 to 0.46) (Fig. 2D–G).

The organic fraction of seston was a negative power function of TPM for both sites, and the relationships were best described by the 2 equations shown in Fig. 3.

Physiological measurements

Both size groups of all treatments increased in length at the end of the experiment (Fig. 4), and mean shell

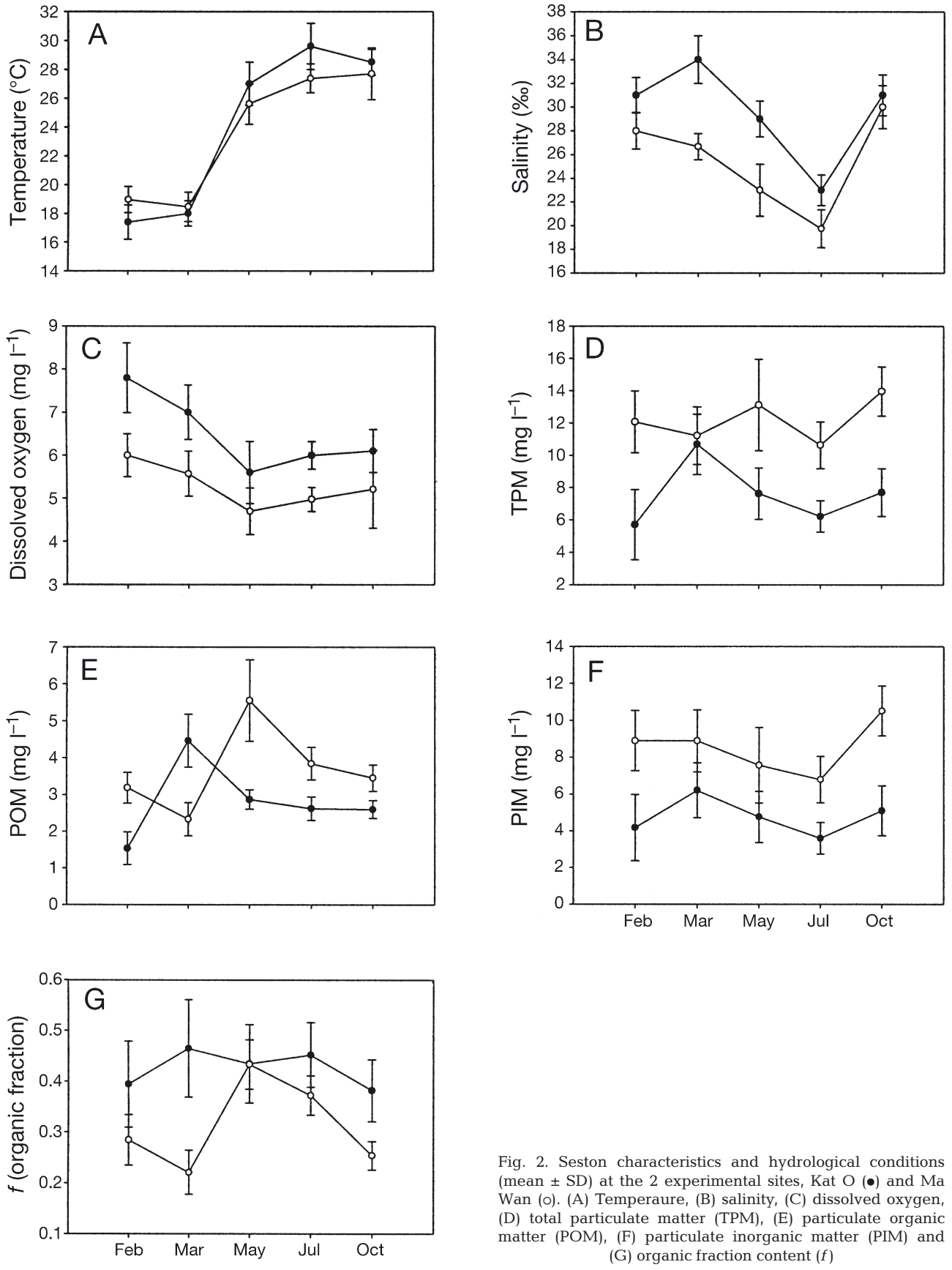

Fig. 2. Seston characteristics and hydrological conditions (mean ± SD) at the 2 experimental sites, Kat O (●) and Ma Wan (○). (A) Temperaure, (B) salinity, (C) dissolved oxygen, (D) total particulate matter (TPM), (E) particulate organic matter (POM), (F) particulate inorganic matter (PIM) and (G) organic fraction content (*f*)

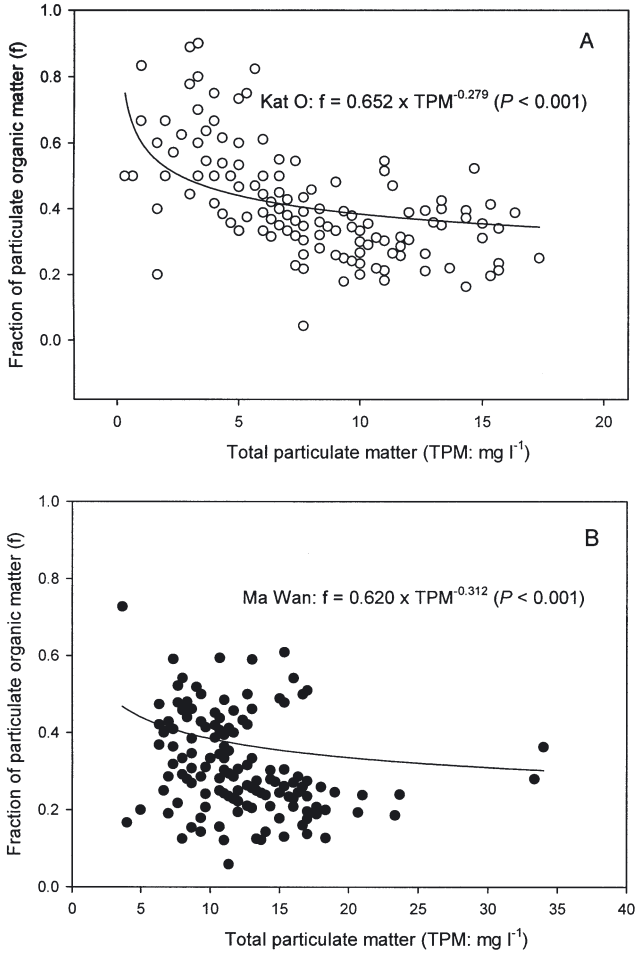

Fig. 3. Relationships between organic fraction content (f) and total particulate matter (TPM) at the 2 experimental sites, (A) Kat O and (B) Ma Wan

length of S groups increased from ca. 35 to 65 mm, and L groups from ca. 52 to 75 mm. Differences in final length of the same size-group of different treatments, however, were insignificant for both small (1-way ANOVA, F = 1.67, df = 3,23, p = 0.20) and large mussels (1-way ANOVA, F = 1.68, df = 3,24, p = 0.20). No pseudofaeces were produced by individuals of KO and MW→KO throughout the experiment. MW individuals, however, produced pseudofaeces between all 5 visits (Fig. 5). For KO→MW, pseudofaeces were produced by all size groups on all occasions except for Group L individuals in May. Rejection rate of MW was significantly higher than that of KO→MW. The difference, however, diminished as time elapsed. Clearance rate of the transplanted group of MW→KO was significantly lower than that of the native group KO, ~10 d post-transplantation (Fig. 6), although the difference diminished as time elapsed. Clearance rate of KO→MW, however, was comparable to that of MW throughout the experiment. Both native and transplanted individuals at Ma Wan had a consistently higher clearance rate than those at Kat O. Approximately 10 d post-transplantation, for the small mussels, the assimilation efficiency of transplanted individuals of MW→KO was lower than that of native individuals (KO), while no difference was found between the transplanted (KO→MW) and native (MW) mussels at Ma Wan (Fig. 7A). This difference, however, was diminished on Day 30 post-transplantation until the end of the experiment. For Group L, the difference in assimilation efficiency between native and transplanted individuals persisted almost throughout the experiment, especially for individuals cultured at Kat O (Fig. 7B). Similar to clearance rate, assimilation efficiency at Ma Wan was consistently higher than at Kat O, for both native and transplanted individuals. Absorption rate of transplanted and native individuals was similar for both size groups (Fig. 8), with higher values being obtained at Ma Wan than at Kat O.

There was no significant difference in amylase and cellulase activity in the crystalline style and cellulase in the digestive diverticula between transplanted and native individuals at either site (Table 1). Amylase activity in the digestive diverticula of *Perna viridis* of KO and MW→KO was similar, whereas amylase activity of MW was either higher or similar to that of KO→MW. Site-related differences in enzyme activity were observed, e.g. amylase activity in the digestive diverticula of small individuals of MW was higher than that of KO in May and October; such differences, however, were inconsistent.

ANCOVA showed significant differences in allometric relationships between shell length and palp

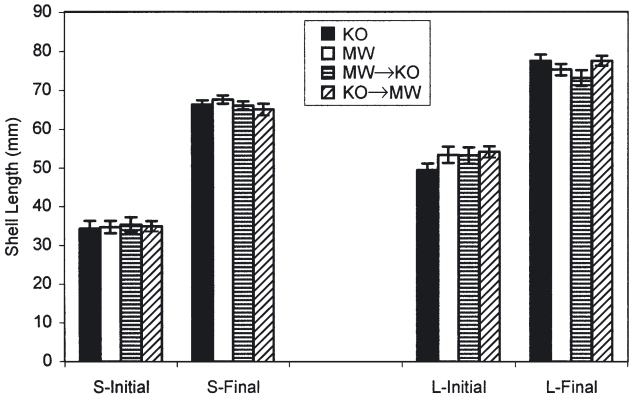

Fig. 4. *Perna viridis*. Initial and final shell length (±SD) of the 4 experimental groups, KO (Kat O), MW→KO (Ma Wan to Kat O transplant), MW (Ma Wan) and KO→MW (Kat O to Ma Wan transplant). S-Initial and S-Final, and L-Initial and L-Final mean initial and final measurements of small and large individuals (N = 7)

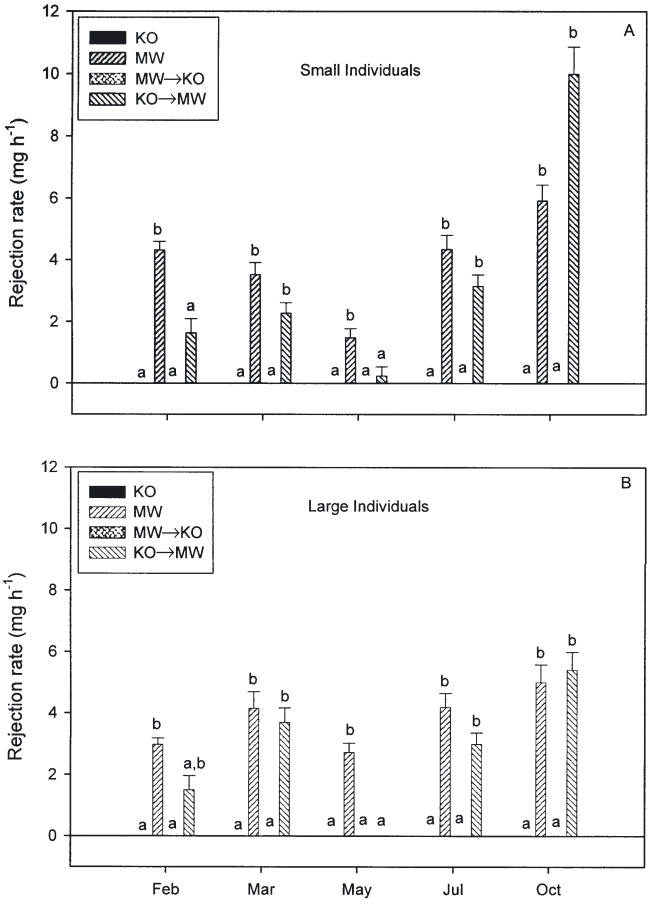

Fig. 5. *Perna viridis*. Rejection rate (RR: mg h^{-1}) (±SD) of (A) small and (B) large individuals from February to October 1998 (N = 7), of the 4 experimental groups, KO (Kat O) , MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). At each time point, treatment-means followed by different letters are significantly different ($p < 0.005$ after Bonferroni adjustment)

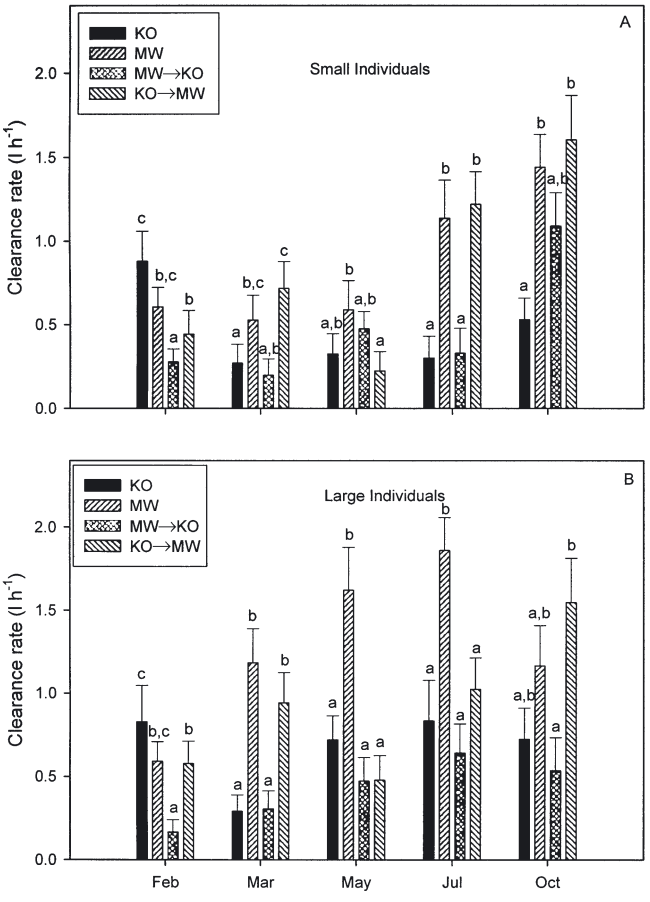

Fig. 6. *Perna viridis*. Clearance rate (CR: l h^{-1}) (±SD) of (A) small and (B) large individuals from February to October 1998 (N = 7), of the 4 experimental groups, KO (Kat O) , MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). At each time point, treatment-means followed by different letters are significantly different ($p < 0.005$ after Bonferroni adjustment)

area, but not between shell length and ctenidial area (Table 2). For regressions relating palp area and shell length, no difference was found among the slopes, but there was a significant difference in elevations between KO and MW, while the 2 transplanted groups did not show any difference to their original stocks (MW→KO vs MW and KO→MW vs KO), or the stocks they were transplanted to (MW→KO vs KO and KO→MW vs MW). There was no significant relationship ($p > 0.05$) between the *P*:*C* ratio and shell length for all 4 groups and, therefore, mean ratios were calculated for each one. The KO *P*:*C* ratio was significantly higher than the other 3 groups (1-way ANOVA, $p < 0.05$). Differences between the native and transplanted groups at both sites, however, were not significant (KO = MW→KO, MW = KO→MW) (Table 3).

DISCUSSION

We found marked physiological differences (RR, CR, AR and AE) between native groups of *Perna viridis* at Ma Wan and Kat O, with higher values being obtained for the former. Ma Wan is estuarine, with a significantly higher TPM concentration and lower organic content than Kat O. To cope with high seston levels, *P. viridis* growing at Ma Wan produced pseudofaeces: an adaptation for life within estuarine and shallow coastal habitats where seston levels are frequently high. By preferential rejection of inorganic matter as pseudofaeces, a degree of sorting is effected, by which material relatively enriched in organic content is selected for ingestion (Bayne 1993, Ward et al. 1997, Wong & Cheung 1999). Bayne et al. (1993) estimated a 35% increase in the ingestion rate for POM over values

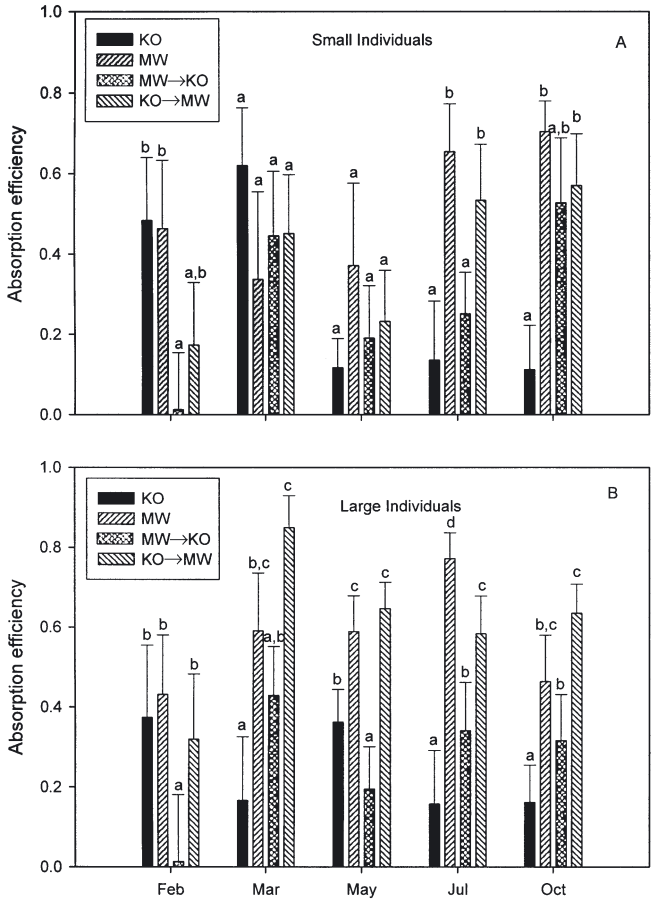

Fig. 7. *Perna viridis*. Absorption efficiency (AE) (±SD) of (A) small and (B) large individuals from February to October 1998 (N = 7), of the 4 experimental groups, KO (Kat O), MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). At each time point, treatment-means followed by different letters are significantly different ($p < 0.005$ after Bonferroni adjustment)

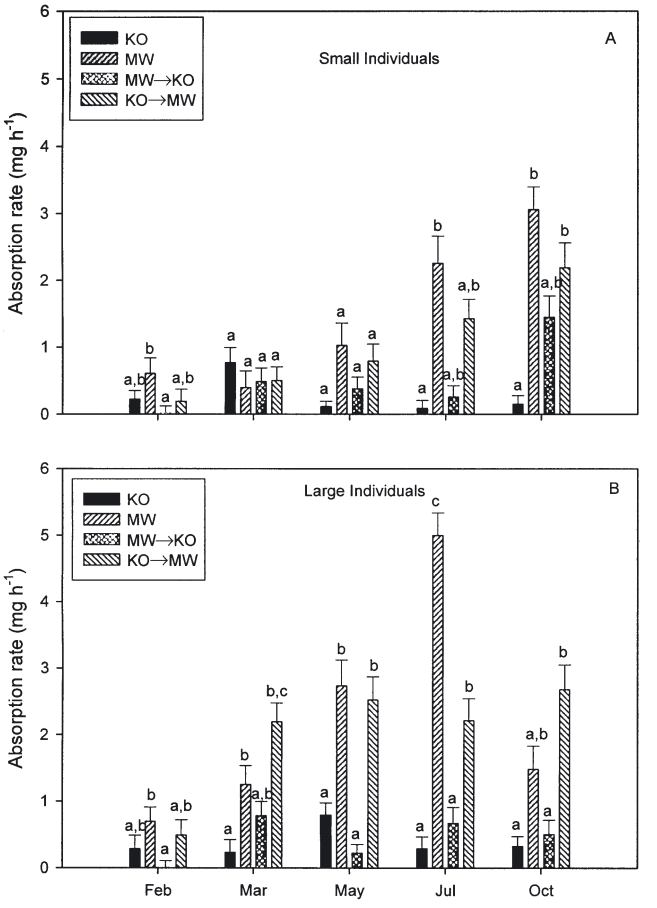

Fig. 8. *Perna viridis*. Absorption rate (AR: mg h^{-1}) (±SD) of (A) small and (B) large individuals from February to October 1998 (N = 7), of the 4 experimental groups, KO (Kat O), MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). At each time point, treatment-means followed by different letters are significantly different ($p < 0.005$ after Bonferroni adjustment)

which would be expected if no compensation for reduced diet quality occurred. Such selection has been widely reported for temperate species such as *Mytilus edulis* and *Cerastoderma edule* (Ward et al. 1997, Hawkins et al. 1998b) and tropical species such as *P. viridis* and *Pinctada margaritifera* (Hawkins et al. 1998a). The production of pseudofaeces is commonly observed when a threshold concentration of TPM is reached (Bayne et al. 1976). This helps explain why both native and transplanted mussels cultured at Kat O did not produce pseudofaeces, as particulate concentrations at this site may be below the production threshold. Similar results were obtained in an annual study of feeding responses of *P. viridis* at Kat O, of which pseudofaeces were produced only in 1 out of 12 mo (Wong & Cheung 2001a). By ingesting all filtered particles, instead of selecting only nutritious ones, and producing pseudofaeces, energy intake by *P. viridis* could be maximized, although absorbed energy was still lower than that at Ma Wan, where POM concentration was much higher.

Transplanted individuals of *Perna viridis* acclimatized to their new environments within 1 mo, inter-site differences in physiological responses, therefore, were largely environmentally induced, i.e. phenotypic. The rate of acclimatization depends on a number of factors, and may be prolonged when environmental conditions differ markedly, or reproductive state differs (Worrall & Widdows 1983). In a transplantation experiment between 3 populations of *Scrobicularia plana*, acclimatization was still incomplete after a transplant period of 3 mo (Worrall & Widdows 1983). In contrast, rapid adaptation (<6 wk) was shown by *Mytilus edulis* following reciprocal transplantation between 2 physio-

Table 1. *Perna viridis*. Amylase activity and cellulase activity (mg glucose h^{-1} mg $protein^{-1}$) of each size group (S: small; L : large) from the 4 experimental groups, KO (Kat O) , MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant) from May to October 1998. Note: within columns, treatment-means followed by different letters are significantly different ($p < 0.0042$ after Bonferroni adjustment)

	Groups	Amylase		Cellulase	
		S	L	S	L
May					
Digestive diverticula	KO	$3.65 \pm 0.40^{a,b}$	$3.56 \pm 0.54^{a,b}$	1.46 ± 0.28^{a}	2.15 ± 0.47^{a}
	MW	$5.52 \pm 0.47^{b,c}$	6.02 ± 0.61^{b}	1.92 ± 0.33^{a}	1.79 ± 0.36^{a}
	MW→KO	2.64 ± 0.48^{a}	$2.58 \pm 0.36^{a,b}$	1.44 ± 0.34^{a}	1.90 ± 0.26^{a}
	KO→MW	7.01 ± 0.60^{c}	2.12 ± 0.42^{a}	3.90 ± 0.34^{b}	0.81 ± 0.25^{a}
Crystalline style	KO	2.38 ± 0.20^{a}	2.01 ± 0.24^{a}	1.52 ± 0.24^{a}	1.32 ± 0.18^{a}
	MW	6.42 ± 0.60^{a}	6.55 ± 0.72^{a}	1.41 ± 0.37^{a}	1.51 ± 0.45^{a}
	MW→KO	2.00 ± 0.53^{a}	2.45 ± 0.53^{a}	1.20 ± 0.44^{a}	1.24 ± 0.31^{a}
	KO→MW	3.26 ± 0.76^{a}	3.49 ± 0.13^{a}	1.56 ± 0.29^{a}	1.33 ± 0.18^{a}
July					
Digestive diverticula	KO	4.93 ± 0.48^{a}	3.78 ± 0.44^{a}	4.00 ± 0.40^{b}	3.27 ± 0.35^{a}
	MW	3.66 ± 0.36^{a}	4.98 ± 0.38^{a}	2.03 ± 0.16^{a}	3.25 ± 0.23^{a}
	MW→KO	5.94 ± 0.36^{a}	5.12 ± 0.35^{a}	$3.43 \pm 0.27^{a,b}$	3.67 ± 0.31^{a}
	KO→MW	5.63 ± 0.44^{a}	4.75 ± 0.35^{a}	3.73 ± 0.34^{b}	4.11 ± 0.24^{a}
Crystalline style	KO	5.07 ± 0.73^{a}	4.46 ± 0.54^{a}	2.69 ± 0.18^{a}	2.14 ± 0.33^{a}
	MW	2.86 ± 0.28^{a}	3.57 ± 0.41^{a}	1.87 ± 0.48^{a}	0.74 ± 0.22^{a}
	MW→KO	5.22 ± 0.74^{a}	1.63 ± 0.53^{a}	3.28 ± 0.51^{a}	1.63 ± 0.38^{a}
	KO→MW	4.38 ± 0.78^{a}	3.73 ± 0.67^{a}	2.16 ± 0.35^{a}	2.09 ± 0.38^{a}
October					
Digestive diverticula	KO	4.02 ± 0.36^{a}	$4.89 \pm 0.28^{a,b}$	$1.91 \pm 0.22^{a,b}$	2.19 ± 0.19^{a}
	MW	7.89 ± 0.56^{b}	7.39 ± 0.65^{b}	$1.67 \pm 0.25^{a,b}$	1.87 ± 0.24^{a}
	MW→KO	4.12 ± 0.28^{a}	3.79 ± 0.27^{a}	2.04 ± 0.14^{b}	2.23 ± 0.29^{a}
	KO→MW	4.16 ± 0.37^{a}	3.81 ± 0.36^{a}	1.41 ± 0.20^{a}	1.66 ± 0.25^{a}
Crystalline style	KO	4.11 ± 0.20^{a}	4.27 ± 0.25^{a}	1.68 ± 0.27^{a}	1.36 ± 0.14^{a}
	MW	3.07 ± 0.57^{a}	4.31 ± 0.51^{a}	1.96 ± 0.50^{a}	1.66 ± 0.27^{a}
	MW→KO	2.87 ± 0.62^{a}	2.93 ± 0.34^{a}	1.22 ± 0.33^{a}	1.25 ± 0.22^{a}
	KO→MW	3.68 ± 0.70^{a}	2.83 ± 0.70^{a}	1.64 ± 0.47^{a}	1.55 ± 0.25^{a}

logically different populations (Widdows et al. 1984). The present study did not show any inter-site differences in acclimatization rates of feeding responses, with complete acclimatization being obtained 30 d post-transplantation. Complete acclimatization of amylase and cellulase activity in transplanted mussels was observed 90 d post-transplantation. As this was the first occasion post-transplantation when enzyme activities were determined, it is uncertain whether 90 d or a shorter period was required for complete acclimatization. Studies on other bivalves have shown that adjustment can take place in a short period of time. For example, the cellulase activity adjustment within the digestive diverticula is an acute (3 d) physiological response of the cockle *Cerastoderma edule* to increased food organic content (Ibarrola et al. 1996, 1998a). Bayne (1993) also pointed out that at least 15 d were required for the digestive system of *M. edulis* to significantly modify digestive-enzyme levels. Ibarrola et al. (1998a,b) concluded that short-term digestive adjustments to seasonally changing food availability is a continuous process that determines the seasonal cycle of enzyme activities in the digestive diverticula of cockles. Apart from the effects of food on digestive enzyme activities, it was also found that specific cellulase and laminarinase activities in the digestive diverticula of cockles were correlated with the volumetric fraction of basophilic cells, and specific protease activity was highly correlated with lysosomal volume density (Ibarrola et al. 2000). This kind of digestive enzyme acclimation may also be influenced by other factors, such as temperature (Newell & Branch 1980), salinity (Fang & Chiou 1989) and pH (Sajiki & Sato 1996).

The relative size of ctenidia and labial palps is another adaptation to the prevailing supply of suspended matter (Theissen 1982, Payne et al. 1995a,b). Bivalves usually have smaller ctenidial areas and larger palp areas in a siltier environment (Essink et al. 1989, Mettam 1992). Contrary to these studies, the native *Perna viridis* at Ma Wan, where suspended solid levels were higher, was characterized by a smaller

Table 2. *Perna viridis*. Regression and comparison of palp and ctenidial areas of the 4 experimental groups, KO (Kat O), MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). Note: the α-value for each regression line was 0.0063 after Bonferroni adjustment. Within columns, treatment means followed by different letters are significantly different ($p < 0.025$ after Bonferroni adjustment)

Regressions	Groups	Linear regression ($y = ax + b$)				
		a	b	n	R^2	p
Palp area (log) on shell length (log)	KO	2.473	−2.734[a]	14	0.600	<0.0063
	MW	1.138	−0.453[b]	18	0.707	<0.0063
	KO→MW	2.247	−2.401[a,b]	19	0.661	<0.0063
	MW→KO	2.247	−2.341[a,b]	14	0.669	<0.0063
Ctenidial area (log) on shell length (log)	KO	2.278	−1.663	14	0.869	<0.0063
	MW	2.354	−1.795	18	0.829	<0.0063
	KO→MW	1.762	−0.709	19	0.833	<0.0063
	MW→KO	1.804	−0.787	14	0.884	<0.0063

palp:ctenidium ratio than the other group (KO). The discrepancy between the present study and those on other bivalves may be attributed to morphological differences in the feeding apparatus between *P. viridis* and other mytilids, in that the feeding apparatus of the former deviates significantly from the standard mytilid plan (Morton 1987). The dorsal edges of the outer and inner labial palps of *P. viridis* are united with the mantle or the visceral mass, respectively, for more than $^2/_3$ of their lengths, and both have only a small ventral sorting area, restricted to a thin line of ridges along the inner ventral margin. There are strong rejectory tracts in the mantle margins and on the visceral mass, resulting in relatively small ctenidial collection areas (Morton 1987). Palps in *P. viridis*, therefore, are assumed not to have such an important rejectory function as in other mytilids. Rather, the ctenidia and other organs of the mantle cavity are more important both in food acquisition and material rejection. Individuals of *P. viridis* growing in a siltier environment, therefore, should be expected to have a lower *P*:*C* ratio, results which were in contrast to other bivalves (Table 3). This helps explain why a smaller *P*:*C* ratio and higher feeding rates were obtained for individuals cultured at Ma Wan where the water is turbid. Given the fact that a significant change in ctenidium area, such as the *P*:*C* ratio, occurred in *P. viridis* following transplantation from their original stocks (e.g. KO→MW close to MW but not KO, see Table 3), relative palp size is suggested to be largely environmentally determined. Similar results were obtained for *Mytilus edulis*, in that after 4 mo transplantation, the relatively smaller ctenidia of Wadden Sea individuals did attain larger relative dimensions after being transferred to the low particle environment of the North Sea, and the larger relative ctenidium area of North Sea individuals decreased when transferred to the more turbid Wadden Sea (Essink et al. 1989).

The present study demonstrated that inter-site differences in growth of *Perna viridis* in Hong Kong, reported upon in previous studies, are largely attributed to food availability. A slower growth has been recorded for *P. viridis* at Tai Lam Chung in the western waters of Hong Kong (salinity: 19 to 31‰), as compared with Kat O in the east (salinity: 24 to 34‰), and was postulated to result from salinity stress and/or a poorer food quality due to dilution by the sediment, especially in summer (Lee 1986, Cheung 1991). Although both Ma Wan and Tai Lam Chung are located in western waters, the growth of *P. viridis* at Ma Wan was comparable to that at Kat O in the present study (Fig. 4). Clearance rate, absorption rate, and absorption efficiency were also higher at Ma Wan than at Kat O. Salinity, therefore, should not be a major factor limiting growth in *P. viridis*. Sundaram & Shafee (1989) also reported that *P. viridis* could live well in salinities as low as 16‰. After acclimation to reduced salinity (as low as 13‰) for 44 d, *M. edulis* was able to regulate shell growth independent of a wider range of salinities (Widdows 1985). Inter-site differences in growth of *P. viridis* in Hong Kong, therefore, are more likely caused by food availability. Laboratory experiments have demonstrated that particulate organic concentration is correlated with absorption rate in *P. viridis* (Wong & Cheung 1999). Food availability was higher at Ma Wan and resulted in a higher POM concentration and organic content (*f*) as compared with Tai Lam Chung, i.e. TPM at Ma Wan varied from 5.5 to 10.55 mg l^{-1} and *f* varied from 0.2 to 0.43, whereas TPM at Tai Lam Chung was similar (11.02 to 12.66 mg l^{-1}) but *f* was 25 to 40% lower (0.15 to 0.26 mg l^{-1}) than at Ma Wan. During summer and autumn, when growth of *P. viridis* was most rapid, *f* at Tai Lam Chung could be as low as 0.06 to 0.13 (Cheung 1991). Although actual growth of *P. viridis* at Kat O and Ma Wan was comparable, the

Table 3. *Perna viridis*. Comparison of palp to ctenidial area (*P*:*C*) ratio between the 4 experimental groups, KO (Kat O), MW (Ma Wan), MW→KO (Ma Wan to Kat O transplant) and KO→MW (Kat O to Ma Wan transplant). Note: values followed by different letters are significantly different ($p < 0.05$)

Groups	*n*	*P*:*C* ratio
KO	14	19.63[b]
MW	18	15.62[a]
KO→MW	19	15.18[a]
MW→KO	14	17.21[a,b]

discrepancy between absorption rate and true growth may be due to mucus production from large pallial glands (Morton 1987). Excessive mucus production may cause a net loss of carbon, and this was most clearly observed when animals were fed diets with a low organic content (Prins & Smaal 1989). Urrutia et al. (2001) suggested that underestimation of 'true' rates of organic ingestion and absorption of dietary organic matter in *Cerastoderma edule* may be as high as 46 and 98.6%, respectively, as a result of the assumption that the presence of mucus in the pseudofaeces is negligible. Davies & Hawkins (1998) estimated that 1 to 68% of the energy consumed may be expended on mucus production in molluscs. A relatively larger quantity of mucus was produced in the present study as a result of high PIM concentration in the seston at Ma Wan. In contrast, Kat O was characterized by low TPM and high *f*-values, and energy loss through mucus secretion, therefore, should be lower (Wong & Cheung 2001a).

The data of our reciprocal transplantation experiment showed that differences in feeding physiology of *Perna viridis* between 2 experimental sites in Hong Kong with contrasting hydrographies were mainly induced by environmental factors. Complete acclimatization of the physiological responses of transplanted mussels was demonstrated 30 d post-transplantation and that of morphology, in terms of palp area and *P*:*C* area ratio, was demonstrated 150 d post-transplantation. The acclimatization of this species becomes more ecologically important with its recent invasion into many other areas world wide (Ingrao et al. 2001). The invasions of exotic bivalves into other water bodies have resulted in major reorganizations in planktonic and benthic communities (Carlton & Geller 1993). In San Francisco Bay, USA, for example, the invasion of the clam *Potamocorbula amurensis* was associated with the decline in abundance of 3 common estuarine copepod species, probably owing to the consumption of naupliar stages (Kimmerer et al. 1994). Therefore, it can be predicted that the invasiveness of the green mussel *P. viridis* and its adaptation to new environments can bring potential impacts to those aquatic ecosystems, and studies on population dynamics, and its consequence to the water columns of this species, should be monitored continuously.

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