

Feeding adaptations of the pearl oysters *Pinctada margaritifera* and *P. maxima* to variations in natural particulates

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ABSTRACT: The tropical pearl oysters *Pinctada margaritifera* (Linnaeus) and *P. maxima* Jameson are suspension feeders of major economic importance. *P. margaritifera* occurs in coral reef waters characterised by oligotrophy and low turbidity. *P. maxima* habitats are generally characterised by high terrigenous sediment and nutrient inputs, and productivity levels. These differences in habitat suggest that *P. margaritifera* will feed more successfully at low food concentrations, while *P. maxima* will cope with a wider range of food concentrations and more silty conditions. The effect of varying concentrations of natural suspended particulate matter (SPM) on clearance rate (CR), pseudofaeces production, absorption efficiency (abs. eff.), respired energy (RE) and excreted energy (EE) was determined for *P. margaritifera* and *P. maxima*. The resultant scope for growth (SFG) was determined and related to habitat differences between the oysters. There was no selective feeding on organic particles in either species. *P. margaritifera* had higher CR at low SPM concentration (<2 mg l⁻¹), while *P. maxima* had higher CR under turbid conditions (SPM: 13–45 mg l⁻¹). The latter species produced less pseudofaeces in relation to its filtration rates; consequently, this species ingested more SPM than *P. margaritifera*. *P. maxima* had positive SFG over a wider range of SPM concentrations (up to 30–40 mg l⁻¹) while *P. margaritifera* maximised SFG under low SPM conditions (<3 mg l⁻¹). Thus feeding responses and energy balance reflected the typical habitats of each species. *P. margaritifera* retained smaller particles than *P. maxima*, enabling it to consume a wider particle size range of SPM at low food levels. *P. maxima* was adapted to its environments of greater SPM load through greater ingestion rates and higher digestive ability. The optimum SPM concentrations and particle size range for *P. margaritifera* (SPM < 5 mg l⁻¹, size > 3 µm) and *P. maxima* (SPM = ca 3 to 15 mg l⁻¹, size > 4 µm) may be used for selection of optimum pearl culture sites.

KEY WORDS: Suspended particulate matter · Turbidity · *Pinctada margaritifera* · *Pinctada maxima* · Suspension-feeding · Scope for growth

INTRODUCTION

The quantity and quality of suspended particulate matter (SPM) in inshore waters fluctuate depending on oceanographic and meteorological factors such as tidal currents, wind-driven waves, storms and floods. Turbid water contains substantial fractions of inorganic particles, and this has been considered a disadvantage, in bioenergetic terms, for suspension feeding ani-

mals dwelling in such waters. However, some adaptive strategies by temperate and subtropical suspension feeding bivalves, such as preferential ingestion of organic-rich particles and an effective digestive mechanism, act to maximise energy gain under turbid conditions (e.g. Hawkins et al. 1996, Ward & MacDonald 1996, Barillé et al. 1997, Navarro & Widdows 1997).

The black-lip pearl oyster *Pinctada margaritifera* (Linnaeus) and the silver-lip pearl oyster *P. maxima* Jameson (Pteriidae: Bivalvia) are typical filter-feeders in tropical waters. They are relatively fast growing bivalves (*K* values 0.2 to 0.5; Gervis & Sims 1992), and

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are commercially important as the basis of the Indo-Pacific cultured pearl industries, producing black and silver pearls, respectively. As a key to economic development, the pearl industry has had a rapid expansion in Asia and Oceania over the last decades. Consequently, substantial areas of bays and coral reef atoll lagoons in these regions have been used for pearl culture. Recently, this situation has required more comprehensive environmental management to achieve sustainable development because pearl culture sites and local ecosystems tend to be fully exploited and deteriorate due to the intensive pearl culture. Knowledge of optimal habitat conditions for the pearl oysters is essential for an adequate management scheme.

The natural habitats of *Pinctada margaritifera* and *P. maxima* are quite different (Gervis & Sims 1992). *P. margaritifera* is typically found in coral reef waters characterised by oligotrophy and low turbidity. It lives attached by byssal threads to hard substrata on the coral reef. It is most abundant in the atoll lagoons of eastern Polynesia (e.g. 5 million in Penrhyn lagoon and 2 million in Manihiki lagoon, Cook Islands; Sims 1992). On the other hand, Kailola et al. (1993) found that *P. maxima* inhabits a variety of substrata, from mud, sand, gravel, seagrass beds to deepwater 'reefs', living beside sponges, soft corals and whip corals. The habitats in which this latter species is most abundant are generally characterised by substantial amounts of terrigenous sediments combined with high nutrient inputs and productivity levels (Gervis & Sims 1992, Sims 1993). Adult *P. maxima* release their hold on substrata by losing their byssal threads, and become free-living on the sea bed.

The ecological differences between *Pinctada margaritifera* and *P. maxima* suggest that these 2 species would differ in their feeding strategies. For example, *P. maxima* should possess superior ability for coping with high particulate loads, including substantial amounts of inorganic particles. This ability may derive from selective ingestion of organic particles, greater rates of filtration and ingestion, and more efficient digestion in turbid environments. In contrast, *P. margaritifera* should maximise energy gain under environments of low concentrations of SPM.

In laboratory studies, Yukihiro et al. (1998b) revealed that *Pinctada maxima* had higher clearance rates (CR) than *P. margaritifera* at relatively high concentrations of pure microalgae, *Dunaliella primolecta* and *Isochrysis* aff. *galbana* (T-Iso). *P. maxima* also had higher absorption efficiencies throughout most of the range of food concentrations (range: 0.1 to 11 mg l⁻¹). The resultant energy balance of *P. maxima* was maintained positive over wider ranges of food concentration than that of *P. margaritifera*. These results indicated that *P. maxima* was better adapted to waters with

greater particulate loads than *P. margaritifera*. However, Yukihiro et al. (1998b) also showed that different food species (*D. primolecta* and T-Iso) variously affected the ingestion, absorption and respiration of these 2 species of pearl oysters.

Growth or feeding rates of some temperate bivalve species under natural conditions are often considerably different from the results obtained from laboratory experiments. Thus, application of laboratory results to field situations has been questioned (review by Jørgensen 1996). The black mussel *Choromytilus meridionalis* produced no pseudofaeces when feeding on natural food over the range ca 3 to 17 mg l⁻¹, for which average food absorption efficiency (abs. eff.) was 40%. In contrast, mussels fed on a pure algal diet of *Dunaliella primolecta* had zero abs. eff. at ca 4 mg l⁻¹, and produced pseudofaeces from ca 6 mg l⁻¹ (Griffiths 1980a). Griffiths (1980a,b) concluded that experiments using *D. primolecta* were not directly applicable to the field. Riisgård (1991) suggested that the comparatively low growth rates of *Mytilus edulis* in laboratory studies using pure algal diets may be due to the use of unnaturally high algal concentrations that lead to suboptimal conditions (valve closure, reduced metabolism and reduced growth). Navarro et al. (1996) found that the occurrence of inorganic particles in the ingesta of mussels *M. galloprovincialis* enhanced absorption of microalgae in the field.

These results suggest that pearl oysters feeding on natural SPM may also show different patterns of feeding and energy budgets to those found in laboratory studies. Therefore, it was important to extend our laboratory experiments on feeding and energetics to conditions with natural SPM, considering the crucial aspect of comparative effects of inorganic particles on feeding in the 2 species.

The aims of this study were, therefore: (1) to quantify and compare feeding (filtration, pseudofaeces production, selective feeding on organic particles, and absorption), respiration, ammonia excretion and resultant energy budgets (= scope for growth) of *Pinctada margaritifera* and *P. maxima* feeding on natural food particles, including effects of natural fluctuations in food quantity and quality; (2) to relate these results to habitat differences between the 2 species of pearl oyster.

MATERIALS AND METHODS

Pearl oysters. *Pinctada margaritifera* (126 to 146 mm shell height, 5.5 to 8.8 g dry soft tissue, n = 15) were obtained from a floating long-line at Orpheus Island Research Station and *P. maxima* (111 to 150 mm shell height, 2.3 to 5.5 g dry soft tissue, n = 15) were obtained from a pearl culture company located at

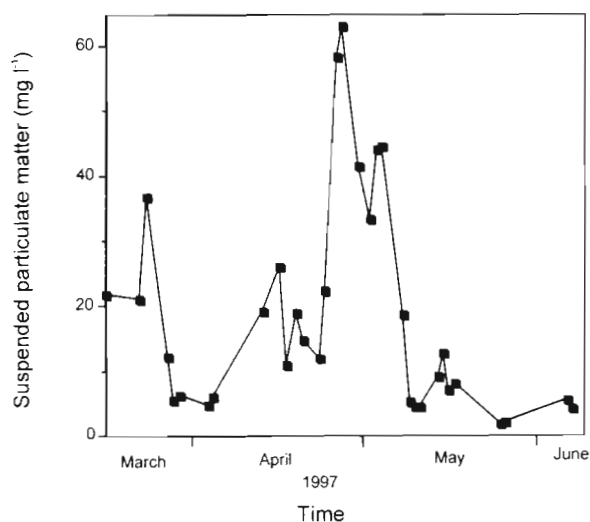


Fig. 1. Variation in amount of suspended particulate matter (SPM) in the water column at the Australian Institute of Marine Science (AIMS) pontoon site from March to June 1997

nearby Hinchinbrook Channel, North Queensland. Oysters were kept suspended in pocket nets (see Gervis & Sims 1992, Fig. 6F) at 1.5 m depth beneath a pontoon located in Bowling Green Bay, North Queensland, near the Australian Institute of Marine Science (AIMS). They were acclimated there for at least 2 wk before use in experiments.

Experimental design. Experiments were mainly conducted at the above pontoon. Ambient water was continuously pumped from the acclimation site into a 200 l experimental tank at a rate of ca 900 l h⁻¹. The lowest concentration of suspended particulate matter (SPM, mg l⁻¹) recorded at the pontoon site during the study was 1.95 mg l⁻¹ (Fig. 1). Therefore, lower SPM concentrations (0.80 to 3.57 mg l⁻¹) were obtained by conducting additional experiments in the AIMS aquarium system, which uses pre-settled Bowling Green Bay water. Water temperature ranged between 23 and 28°C during the pontoon and aquarium experiments.

Three individuals of each oyster species were thoroughly cleaned of epibiota and transferred to the 200 l experimental tank 2 d before experiments began. Oysters were used 3 or 4 times over a week for a series of physiological measurements, and then replaced with a fresh set of oysters from the pontoon site. Faeces and pseudofaeces that had been ejected by oysters were carefully removed from the tank using a siphon, then a plastic tray (25 cm width × 30 cm length × 9 cm height) was slipped beneath each oyster. A piece of plastic attached to the inside of each tray effectively separated the deposited faeces and pseudofaeces. The faeces appeared as dark grey ribbons or fragile pellets and were deposited close to the exhalent opening. The

pseudofaeces were ejected from the anterior to ventral margin and were mucus-like, light grey, and fragile masses. Water samples were collected from the region surrounding the inhalent opening of the oysters and from the outlet of the experimental tank for measurement of SPM volume using a Coulter Multisizer. The water in the tank was thoroughly mixed by the inflowing seawater; hence differences in SPM volume between inhalent openings of oysters and the tank outlet were small (less than 10%). Experiments lasted for 2 to 3 h depending on the production rate of faeces and pseudofaeces. At the end of the experiment, faeces and pseudofaeces of each oyster were separately collected. The above techniques are based on Hawkins et al. (1996).

Availability of natural suspended particulate matter. Gut transit times were monitored in 6 individuals of each species that had been fed on natural SPM and kept undisturbed for at least 2 h in the experimental tank. They were fed a 20 min pulse of dry alga *Tetraselmis suecica* as a marker and then supplied with more natural running seawater (= time A). Gut transit time was defined as the time between time A and reappearance of natural dark grey faeces after all the yellow-green algal faeces of *T. suecica* had been defaecated. Gut transit times for *Pinctada margaritifera* and *P. maxima* were 42 ± 10 (SE) and 56 ± 11 (SE) min, respectively. Assuming that pseudofaeces are produced immediately after filtration (i.e. 0 min after filtration), 2 water samples of 2 l were collected from the outlet of the tank about 25 min (= [(42 + 0) ÷ 2 + (56 + 0) ÷ 2] ÷ 2) before each experiment commenced, and another 2 samples of 2 l about 25 min before the completion of experiments. The water samples (n = 4) were filtered onto separate pre-rinsed, ashed and weighed Whatman GF/C filters. All filters were dried at 60°C and weighed, then ashed at 450°C for 5 h and re-weighed to provide organic content (OC, fraction) and particulate organic matter (POM, mg l⁻¹) of each sample.

Three individuals of each species were placed in the 200 l experimental tank with water of low SPM concentration (1.9 mg l⁻¹) and left undisturbed for at least 2 h. Water samples were then collected from the vicinity of the inhalent opening and from inside the exhalent opening using a siphon at a low suction rate (<90 ml min⁻¹). Concentrations of particles (by volume) from each of 13 particle size classes spanning the range between 1.4 and 10.0 µm mean diameter were determined using a Coulter Multisizer. The volume of each sample counted was 12 ml. The fraction of each size class retained by the oysters was calculated as retention efficiency, 1 - C_e/C_i, where C_e and C_i are the concentration of particles in the exhalent and inhalent water, respectively. Production of faecal and other particles via the exhalent siphon was controlled by coinci-

dent measurements of the particles generated by oysters kept in 0.45 µm filtered seawater, following Klumpp et al. (1992).

To determine the SPM particle size composition (by volume), a 2 l water sample was collected from the acclimation site under different conditions of low (2 mg l⁻¹) and high (29 and 44 mg l⁻¹) SPM concentration. Analyses of size composition by volume of SPM ranging from 1.4 to 44.4 µm mean diameter were undertaken using the Coulter Multisizer.

Feeding. Samples of faeces and pseudofaeces were analysed for dry weight and organic fraction in the same manner as described above to quantify SPM concentration, OC and POM. Clearance rates (CR, l h⁻¹) were calculated using the expression: CR = (mg inorganic matter egested both as faeces and pseudofaeces h⁻¹) ÷ (mg inorganic matter available l⁻¹ seawater), (Hawkins et al. 1996).

Oysters were sacrificed at the end of experiments. Their soft tissues were dried at 60°C and then weighed. CR and rejection rate (RR = mg total pseudofaeces ejected h⁻¹, mg h⁻¹) were size-standardised to those for an equivalent individual of 10 g dry soft tissue wt as follows:

$$Y_s = (W_s/W_e)^b Y_e \quad (\text{Navarro et al. 1991})$$

where Y_s is the size-standardised physiological rate, W_s is the standard size (10 g dry tissue weight), W_e is the dry tissue weight of experimental oyster, b is the size exponent: 0.61 (Yukihira et al. 1998a), and Y_e is the uncorrected physiological rate.

Respiration and ammonia excretion. Respiration rates (R, ml O₂ h⁻¹) were determined in sealed chambers (2.3 l), 3 containing an experimental oyster and 2 serving as a control without an oyster. Oxygen was measured with YSI dissolved oxygen electrodes (Model 55). Three individuals from each pearl oyster species were kept in the tank used for the feeding experiments for at least 2 h before measuring respiration. After this, each oyster was placed into a sealed chamber filled with seawater from the flow-through tank. Water in each chamber was thoroughly mixed by a magnetic stirrer, which was separated from the oyster by a mesh partition. Oxygen concentration in each chamber was monitored at 5 min intervals for 10 or 15 min after initial equilibration in the chamber. Measurements of R were conducted over conditions of 10 different SPM concentrations (1 to 63 mg l⁻¹). R was determined after Bayne et al. (1985) and size-standardised to 10 g soft tissue dry wt using the size exponents, 0.439 for *Pinctada margaritifera* and 0.543 for *P. maxima* (Yukihira et al. 1998a). Respired energy (RE, J h⁻¹) was calculated assuming 1 ml O₂ = 20.33 J.

The rate of ammonia excretion (E, µg NH₄-N h⁻¹) was determined for all oysters as follows. On comple-

tion of each feeding experiment, 2 oysters of each species were placed individually in chambers containing 1 l of 0.45 µm filtered seawater. The 4 chambers with oysters and the 2 control chambers containing only filtered seawater were left undisturbed for 60 min. Duplicate 10 ml water samples were collected from each chamber, passed through a 0.45 µm filter and analysed for ammonia using the phenol-hypochlorite method (Solorzano 1969). E was determined following Bayne et al. (1985) and size-standardised to 10 g soft tissue dry wt using the size exponents, 0.642 for *Pinctada margaritifera* and 0.789 for *P. maxima* (Yukihira et al. 1998a). Excreted energy (EE, J h⁻¹) was calculated assuming 1 mg NH₄-N = 24.87 J.

Scope for growth. The energy content of absorbed organic matter was 11.8 J mg⁻¹, as determined from water samples collected in summer and winter (Yukihira 1998). Hence, absorbed energy (AE) of standard 10 g oysters was calculated as AE (J h⁻¹) = 11.8 (J mg⁻¹) × organic matter absorbed (mg h⁻¹). Scope for growth (SFG, J h⁻¹), the energy oysters have available for growth and reproduction, was calculated as in Bayne et al. (1985) and Warren & Davis (1967):

$$\text{SFG} = \text{AE} - \text{RE} - \text{EE}$$

Statistical analysis. Selective feeding on organic particles was examined by comparing mean organic fraction in pseudofaeces with OC of SPM using a 2-way ANOVA. The relationships between SPM concentration and each of the parameters, CR, pseudofaeces production, abs.eff., AE, RE and EE were determined using regression analyses. When the regressions for both oyster species were linear, the similarity in slopes and intercepts were tested by ANCOVA. When the relationships were otherwise (e.g. logarithmic vs exponential regressions), then the mean values for each comparable SPM concentration were compared between species using a 2-way ANOVA. Data were tested for normality before being subjected to parametric statistics.

RESULTS

Suspended particulate matter

SPM at the experimental site (AIMS) fluctuated greatly from 1.95 to 63.2 mg l⁻¹ (Fig. 1). The organic fraction (OC) of SPM as a measure of food quality varied between 0.63 and 0.13. The relation between SPM concentration and organic fraction at the experimental site (Fig. 2a) was expressed by the equation:

$$\text{OC} = 0.354 \times \text{SPM}^{-0.253} \quad (r^2 = 0.53, n = 31, p < 0.001)$$

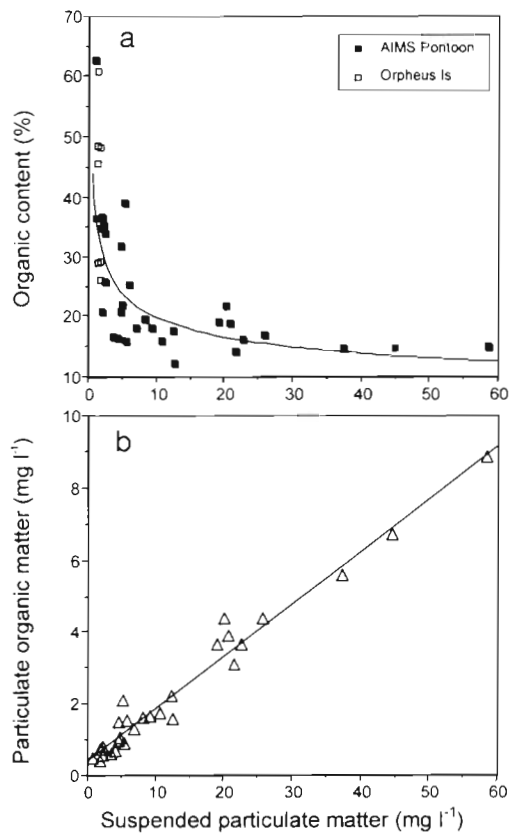


Fig. 2. (a) Organic content and (b) particulate organic matter in relation to amount of suspended particulate matter in the water column at the AIMS pontoon (■, ▲) and at Orpheus Island (□, △) (a typical habitat of *Pinctada margaritifera*). Regression equations are in the text

SPM concentrations and OC ($n = 9$) over a 14 mo period at Orpheus Island, a habitat of *Pinctada margaritifera* in the Great Barrier Reef, did not fluctuate widely, and never exceeded 2 mg l^{-1} (Fig. 2a). The relationship between OC and SPM concentration at Orpheus Island did not differ significantly (ANCOVA $p > 0.05$) from that at the AIMS experimental site over similar SPM levels (0.8 to 3 mg l^{-1} ; $n = 6$). Therefore, it was assumed that conditions of low SPM (i.e. $\text{SPM} < 2 \text{ mg l}^{-1}$) at the AIMS site approximated the natural habitat of *P. margaritifera* in terms of organic fraction.

Particulate organic matter (POM, mg l^{-1}) increased significantly with increasing SPM concentration (Fig. 2b):

$$\text{POM} = 0.408 + 0.145 \times \text{SPM} \\ (r^2 = 0.97, n = 31, p < 0.001)$$

Thus, the increase in turbidity in the water (SPM concentration) corresponded with an increase in the absolute amounts of POM, but with a decline in the organic fraction.

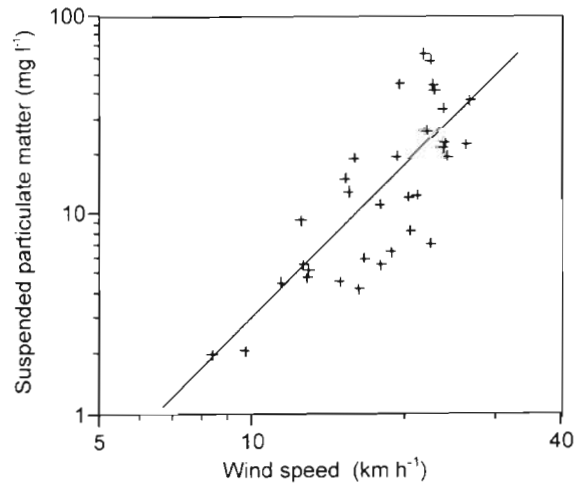


Fig. 3. Relationship between amount of suspended particulate matter in the water column and wind speed. The regression equation is in the text

The high SPM concentrations at AIMS did not coincide with spring tides and there was no major discharge from rivers. However, high SPM concentrations coincided with waves generated by strong winds (Fig. 3, $r^2 = 0.61$, $n = 33$, $p < 0.001$). Therefore, turbid water conditions during the study period are attributable mainly to wind activity, causing resuspension of benthic materials, such as silt, benthic algae and deposited detritus.

Retention efficiency

Pinctada margaritifera and *P. maxima* retained particles larger than 3 and 4 μm , respectively, with over 90% efficiency, but the efficiencies decreased rapidly for smaller particles (Fig. 4). *P. margaritifera* had significantly higher retention efficiencies of particles $< 3 \mu\text{m}$ than *P. maxima* (ANOVA $p < 0.05$).

Fig. 5 shows the size composition of SPM by volume under clear (2 mg SPM l^{-1}) and turbid (29 and 44 mg SPM l^{-1}) water conditions. Turbid water tended to contain greater percentages of particles $> 7 \mu\text{m}$ diameter than clear water. In turbid waters of 29 and 44 mg l^{-1} SPM, 83 and 90% of particles, respectively, were larger than 4 μm diameter on a volumetric basis. The clear water, in comparison, contained mainly particles smaller than 6 μm and only 64% of all SPM was larger than 4 μm diameter.

Feeding selectivity

Organic fractions of pseudofaeces were similar in the 2 species (Fig. 6), and there was no significant differ-

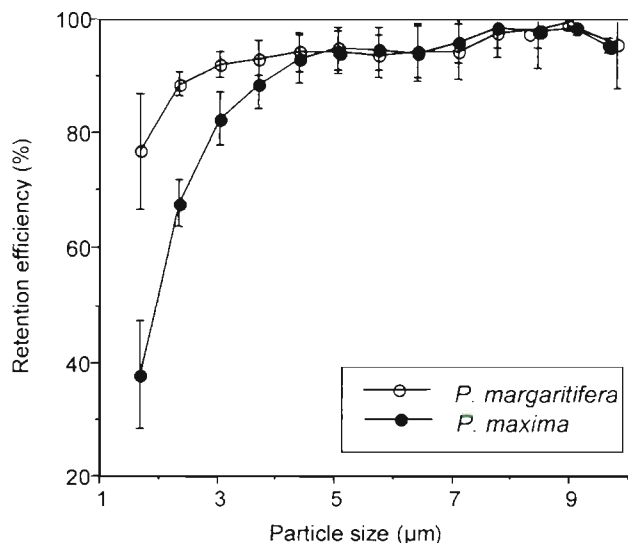


Fig. 4. *Pinctada margaritifera* and *P. maxima*. Retention efficiency (mean \pm SE) by oysters for different-sized particles present in the water column (SPM, 2 mg l⁻¹)

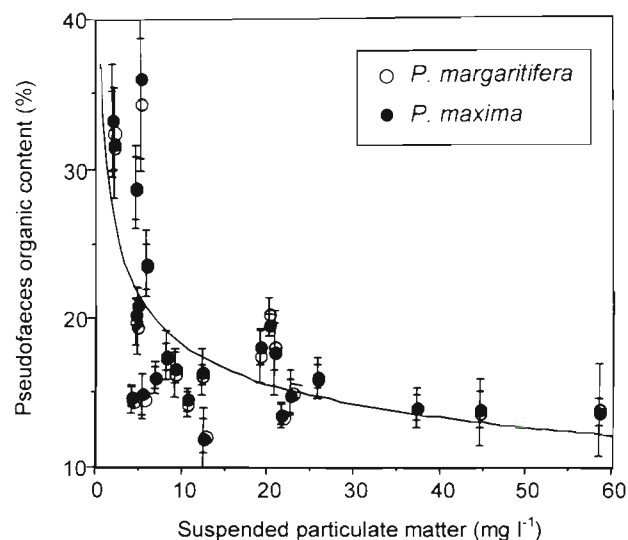


Fig. 6. *Pinctada margaritifera* and *P. maxima*. Feeding selectivity, as reflected in organic content (mean \pm SE) in pseudo faeces of oysters, at various SPM concentrations

ence between the organic fraction of SPM and of pseudo-faeces (ANOVA $p > 0.05$). This indicates that there was no feeding selectivity in either species of pearl oysters. The relationship between SPM concentration and organic fractions in pseudo-faeces (OFP) of both species was identical (Table 1).

Since there were clear relationships between the OC and POM of natural particles and SPM concentration (Fig. 2), and there was no evidence of selective feeding; hereafter, total mass of SPM was considered the food of pearl oysters. This declines in quality with increasing quantity (Fig. 2).

Clearance rate

Clearance rate (CR, l h⁻¹) was significantly associated with SPM concentration, and the relationship for each species (Fig. 7) is outlined by the functions in Table 1. CR decreased with increasing SPM concentration, especially so in *Pinctada margaritifera*. Mean CR values for *P. margaritifera* under conditions of low SPM concentration (< 2.0 mg l⁻¹) were higher than those of *P. maxima*. Under turbid conditions (SPM: 12.7 to 44.7 mg l⁻¹) the latter species always had higher CR (ANOVA $p < 0.05$).

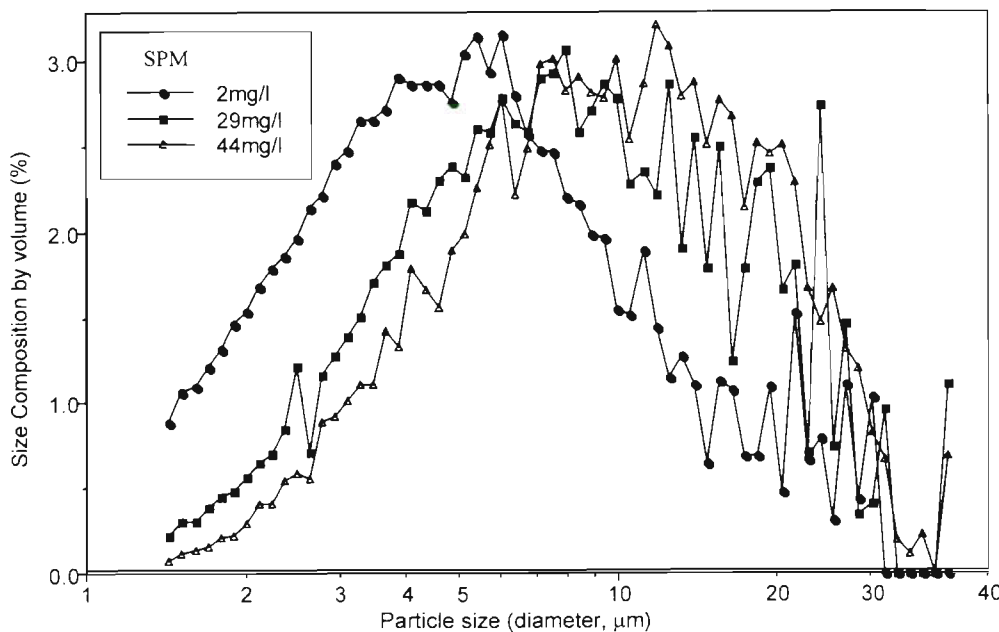


Fig. 5. Particle-size distribution in the water column at the AIMS pontoon site under different SPM conditions

Table 1. *Pinctada margaritifera* and *P. maxima*. Relationships between feeding selectivity, clearance rate (l h^{-1}), pseudofaecal fraction (proportion of particles filtered), ingestion rate (mg h^{-1}), absorption efficiency (%), absorbed energy and respired energy (J h^{-1}), and level of natural suspended particulate matter (SPM, mg l^{-1}); and between pseudofaeces production rate (mg h^{-1}) and filtration rate (FR)

Function	<i>Pinctada margaritifera</i>	<i>Pinctada maxima</i>
Feeding selectivity (organic fraction in pseudofaeces, OFP)	$\text{OFP} = 0.305 \text{ SPM}^{-0.224}$ ($r^2 = 0.47$, $n = 48$, $p < 0.001$)	$\text{OFP} = 0.305 \text{ SPM}^{-0.224}$ ($r^2 = 0.47$, $n = 48$, $p < 0.001$)
Clearance rate (CR)	$\text{CR} = 103.1 \text{ SPM}^{-0.904}$ ($r^2 = 0.91$, $n = 30$, $p < 0.001$)	$\text{CR} = 38.5 \times 10^{(-0.0187 \text{ SPM})}$ ($r^2 = 0.95$, $n = 30$, $p < 0.001$)
Pseudofaeces production rate (rejection rate, RR)	$\text{RR} = -29.8 + 0.457 \text{ FR}$ ($r^2 = 0.44$, $n = 26$, $p < 0.001$)	$\text{RR} = -13.2 + 0.182 \text{ FR}$ ($r^2 = 0.61$, $n = 24$, $p < 0.001$)
Pseudofaecal fraction (PF)	$\text{PF} = 0.44 (1 - e^{-0.090(\text{SPM}-1.3)})$ ($r^2 = 0.78$, $n = 26$)	$\text{PF} = 0.20 (1 - e^{-0.11(\text{SPM}-2.6)})$ ($r^2 = 0.73$, $n = 24$)
Ingestion rate (IR)	$\text{IR} = (10\,559/\text{SPM})e^{(-13.25/\text{SPM})}$ ($r^2 = 0.80$, $n = 29$)	$\text{IR} = (2130/\text{SPM})e^{(-5.416/\text{SPM})}$ ($r^2 = 0.68$, $n = 29$)
Absorption efficiency (abs. eff.)	$\text{abs. eff.} = 0.652 \text{ SPM}^{-0.340}$ ($r^2 = 0.83$, $n = 29$, $p < 0.001$)	$\text{abs. eff.} = 0.630 \times 10^{-0.0147 \text{ SPM}}$ ($r^2 = 0.92$, $n = 29$, $p < 0.001$)
Absorbed energy (AE)	$\text{AE} = 220.5 - 23.8 \text{ SPM} + 1.16 \text{ SPM}^2 - 0.0244 \text{ SPM}^3 + 0.000178 \text{ SPM}^4$ ($r^2 = 0.87$, $n = 29$, $p < 0.001$)	$\text{AE} = 30.2 - 72.0 \text{ SPM} - 8.24 \text{ SPM}^2 + 0.404 \text{ SPM}^3 - 0.0101 \text{ SPM}^4 + 0.0000124 \text{ SPM}^5 - 0.000000602 \text{ SPM}^6$ ($r^2 = 0.70$, $n = 29$, $p < 0.001$)
Respired energy (RE)	$\text{RE} = 70.0 \text{ SPM}^{-0.159 (\pm 0.060)}$ ($r^2 = 0.47$, $n = 10$, $p < 0.001$)	No significant relationship with SPM

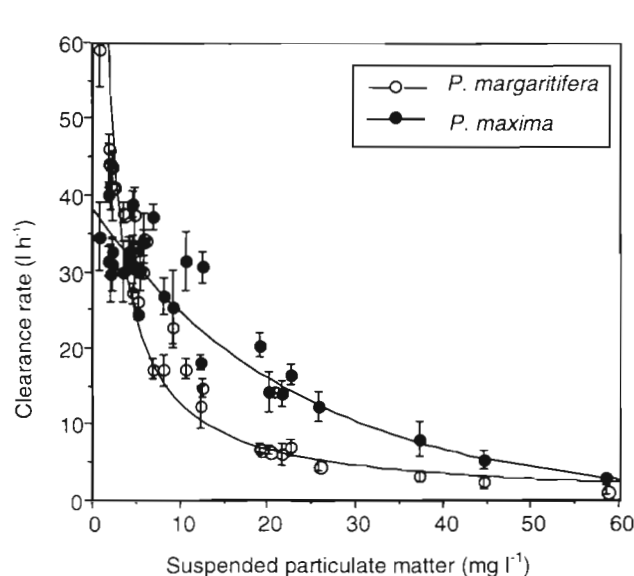


Fig. 7. *Pinctada margaritifera* and *P. maxima*. Relationships between clearance rate (mean \pm SE) of oysters and SPM concentration. Regression equations are in Table 1

Pseudofaeces production

The rejection rate (RR, mg pseudofaeces ejected per h) of both species was positively associated with filtration rate (FR = CR \times SPM concentration) (Fig. 8, Table 1). Slopes of these regression lines were signifi-

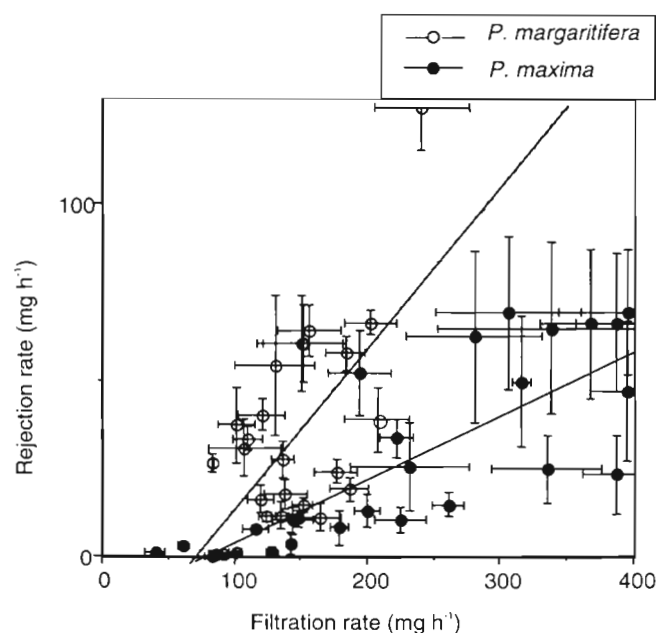


Fig. 8. *Pinctada margaritifera* and *P. maxima*. Relationships between rejection rate (mean \pm SE) (pseudofaeces production rate) and filtration rate of oysters. Regression equations are in Table 1

cantly different between species (ANCOVA $p < 0.01$), indicating that *Pinctada margaritifera* produces significantly greater amounts of pseudofaeces for a given amount of filtered material than *P. maxima*.

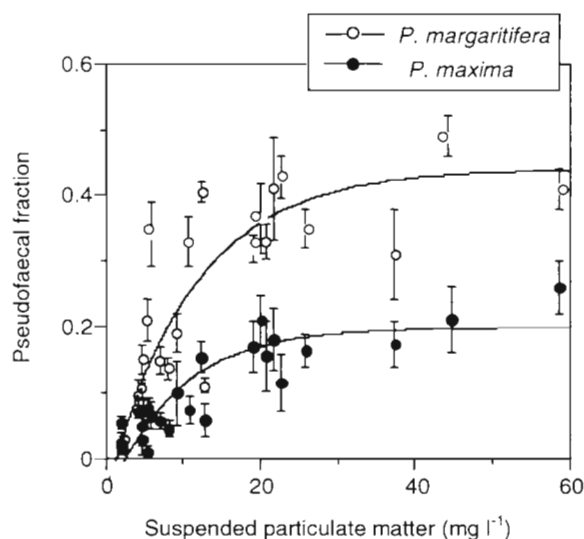


Fig. 9. *Pinctada margaritifera* and *P. maxima*. Relationships between pseudofaecal fraction (mean \pm SE) in oysters and SPM concentration. Regression equations are in Table 1

The pseudofaecal fraction ($PF = RR \div FR$) of both species increased significantly with increasing SPM concentration (Fig. 9, Table 1). The maximum pseudofaecal fraction of *Pinctada margaritifera* (0.4) was approximately twice that of *P. maxima*. The mean pseudofaecal fraction of the former species was significantly higher ($p < 0.05$) than the latter species at SPM above 19.1 mg l^{-1} .

Ingestion and absorption

Fig. 10 shows the ingestion rates (IR, mg h^{-1}) as a function of SPM concentration. The relationship between IR and SPM concentration for each species was expressed by the equations in Table 1. The form of the equations is after Kjørboe et al. (1985). *Pinctada margaritifera* had relatively high IRs for SPM between 2 and 15 mg l^{-1} while *P. maxima* displayed high IRs over SPM of 5 to 50 mg l^{-1} . IRs of *P. maxima* were consistently higher under turbid conditions ($SPM > 10 \text{ mg l}^{-1}$) than those of *P. margaritifera*, and the maximum IR recorded for *P. maxima* was about twice as high as that of *P. margaritifera*.

Since there was no significant difference between organic fraction of food and organic content in pseudofaeces in both species of oysters, abs.eff. was simply calculated using the Conover ratio (Conover 1966): $\% \text{ abs.eff.} = 100(f - e)/(1 - e)f$, where f and e are the fractions of SPM and faeces lost on ashing, respectively. The relations between abs.eff. and SPM concentration are shown in Fig. 11 & Table 1. The abs.eff. of both species decreased with increasing SPM concen-

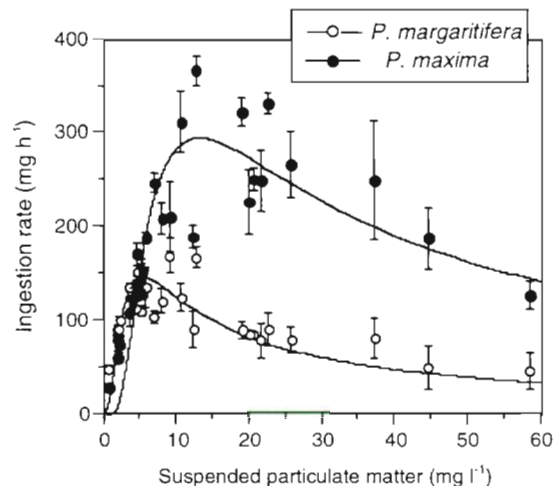


Fig. 10. *Pinctada margaritifera* and *P. maxima*. Relationships between ingestion rate (mean \pm SE) of oysters and SPM concentration. Regression equations are in Table 1

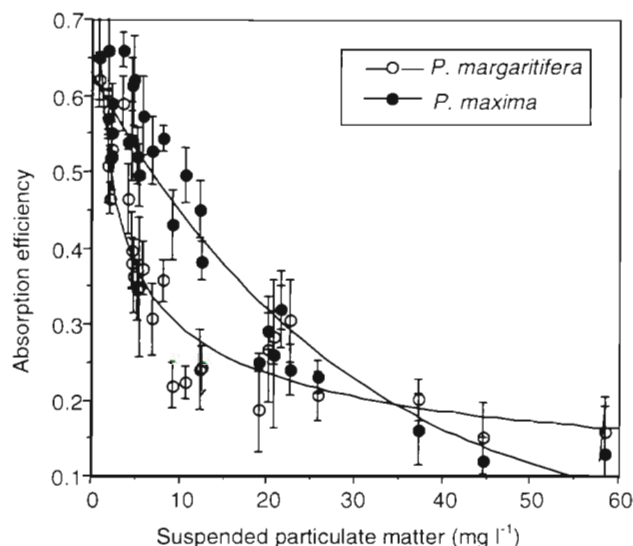


Fig. 11. *Pinctada margaritifera* and *P. maxima*. Relationships between absorption efficiency (mean \pm SE) in oysters and SPM concentration. Regression equations are in Table 1

tration. This decrease was more marked for *Pinctada margaritifera*. The mean abs.eff. values of *P. maxima* were consistently higher when SPM was within the range 7 to 12 mg l^{-1} (ANOVA $p < 0.05$).

The relationships between absorbed energy (AE, J h^{-1}) and SPM concentration were best expressed by polynomial regressions (Fig. 12, Table 1). *Pinctada maxima* had maximum AE when SPM was between 5 and 15 mg l^{-1} , while *P. margaritifera* had maximum AE for SPM below 5 mg l^{-1} . The mean AE values for SPM from 5.3 to 25.8 mg l^{-1} were highest for *P. maxima*, while *P. margaritifera* had a higher mean AE at the

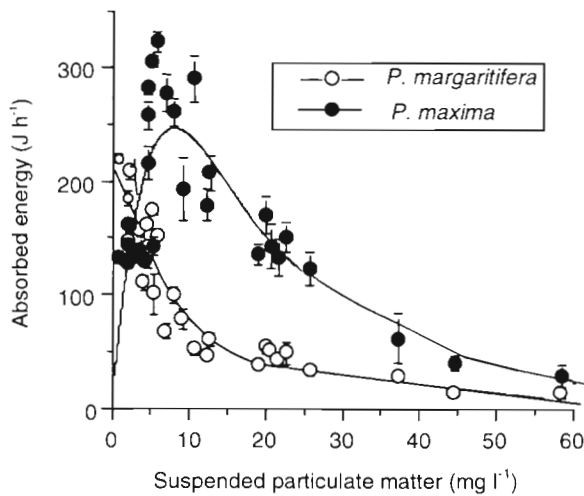


Fig. 12. *Pinctada margaritifera* and *P. maxima*. Relationships between absorbed energy (mean \pm SE) in oysters and SPM concentration. Regression equations are in Table 1

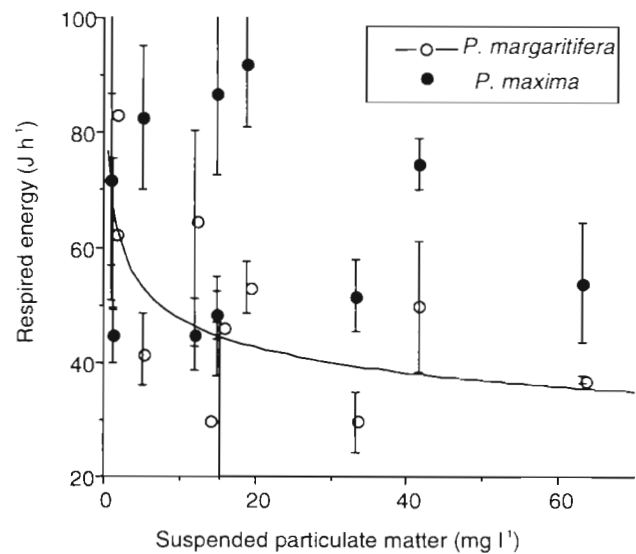


Fig. 13. *Pinctada margaritifera* and *P. maxima*. Relationships between respired energy (mean \pm SE) in oysters and SPM concentration. Regression equation is in Table 1

lowest SPM concentration (0.8 mg l^{-1} ; ANOVA at $p < 0.01$). The predicted AE and 95% confidence limits (CL) in response to different SPM conditions were calculated using the equations and are shown in Table 2.

Table 2. *Pinctada margaritifera* and *P. maxima*. Calculated mean values \pm 95% confidence limits of absorbed energy (AE), respired energy (RE), excreted energy (EE) and resultant scope for growth (SFG = AE – RE – EE) of oysters in relation to different levels of suspended particulate matter

Species		SPM (mg l^{-1})							
		3	5	7	10	15	20	30	40
AE (J h^{-1})	<i>P. margaritifera</i>	158	127	103	76	53	47	41	24
		143	114	88	59	37	28	15	-11
		173	140	118	93	69	66	67	58
	<i>P. maxima</i>	180	227	245	240	194	150	99	55
		150	197	215	201	147	111	24	-31
		210	259	277	280	241	190	175	142
RE (J h^{-1})	<i>P. margaritifera</i>	59	54	51	49	46	43	41	39
		46	41	38	35	32	30	28	26
		73	69	67	65	62	61	58	57
	<i>P. maxima</i>	65	65	65	65	65	65	65	65
		52	52	52	52	52	52	52	52
		78	78	78	78	78	78	78	78
EE (J h^{-1})	Both species	6	6	6	6	6	6	6	6
SFG (J h^{-1})	<i>P. margaritifera</i>	94	67	46	22	2	-2	-5	-21
		64	39	15	-12	-31	-38	-49	-73
		121	93	74	52	31	30	34	26
	<i>P. maxima</i>	109	156	174	169	123	79	28	-16
		66	113	131	117	63	27	-60	-115
		152	201	219	222	183	132	117	84

Respiration

Respired energy (RE, J h^{-1}) of *Pinctada maxima* did not vary with SPM concentration, but RE of *P. margaritifera* decreased significantly with increasing SPM concentration (Fig. 13, Table 1). Using this regression, predicted RE values and 95% CLs of *P. margaritifera* in response to different SPM concentrations were calculated (Table 2). The mean RE value \pm 95% CL for *P. maxima* was $65.1 \pm 13.2 \text{ J h}^{-1}$ ($n = 10$) over all SPM levels.

Excreted energy

Excreted energy (EE, J h^{-1}) in both pearl oyster species was not affected by SPM concentration (Fig. 14). There was no significant difference in mean EE between the 2 species (ANOVA $p > 0.05$). Therefore, all EE values were pooled and a common mean value (\pm 95% CL) was calculated for both species ($5.83 \pm 0.65 \text{ J h}^{-1}$, $n = 26$).

Scope for growth

Table 2 shows the calculated scope for growth (SFG = AE – RE – EE, J h^{-1}). *Pinc-*

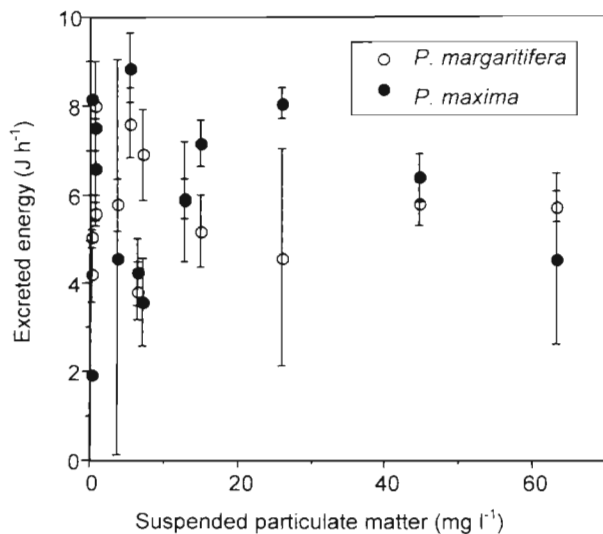


Fig. 14. *Pinctada margaritifera* and *P. maxima*. Excreted energy (mean \pm SE) in oysters in relation to SPM concentration

tada margaritifera had a high mean SFG at low SPM concentration ($< \text{ca } 3 \text{ mg l}^{-1}$), but mean SFG fell to zero at $\text{ca } 10$ to 20 mg l^{-1} . *P. maxima* had highest mean SFG at $\text{ca } 10 \text{ mg SPM l}^{-1}$ and maintained positive values of SFG up to 40 mg l^{-1} . Considering lower and upper 95% CL values for AE and RE, SFG of *P. maxima* was always higher than *P. margaritifera* over the SPM concentration range of 5 to 15 mg l^{-1} .

DISCUSSION

Feeding and food utilisation in the pearl oysters *Pinctada margaritifera* and *P. maxima* were affected by variations in both quantity and quality of natural SPM. Oysters responded to increases in turbidity (SPM concentration), and corresponding declines in the quality of particulates (lowered organic fraction) by reducing their CR, and absorption efficiency, and by increasing the PF. Comparing both species, *P. maxima* had higher CR, ingestion rate, food absorption and lower PF, and thus greater AE under a wide range of field conditions. Of the 2 species, *P. maxima* is clearly a more efficient suspension feeder at high concentrations of SPM.

Similarly, when feeding on pure algal diets, *Pinctada maxima* was more efficient than *P. margaritifera* at gaining energy at high cell concentrations (Yukihira et al. 1998b). However, there were several differences between the feeding and energy budgets of pearl oysters supplied with mono-specific algal diets (Yukihira et al. 1998a,b) and those fed natural SPM. For example, SFG was much higher on the natural diet at all particle concentrations, and also the thresholds of particulate

Table 3. *Pinctada margaritifera* and *P. maxima*. Threshold concentration (mg l^{-1}) above which the scope for growth of oysters falls below zero when feeding on 2 microalgal diets, *Dunaliella primolecta* and Tahitian *Isochrysis galbana* (T-Iso), and natural suspended particulate matter (SPM). (Data for the microalgal diets from Yukihira et al. 1998b)

	<i>D. primolecta</i>	T-Iso	SPM
<i>P. margaritifera</i>	5	7	10 – 20
<i>P. maxima</i>	7	9	30 – 40

concentrations above which SFG fell below zero were far higher on the natural diet than on cultured algal diets (Table 3). These differences result from higher CR and food absorption, and lower PF under conditions of high SPM concentration. The results agree with the conclusions reached by Griffiths (1980b), Riisgård (1991) and Jørgensen (1996) for mytilids. One reason for the difference suggested by Griffiths (1980b) might be that cultured algal diets are extremely concentrated food resources that are never experienced in natural habitats (natural SPM includes substantial inorganic fraction) and this adversely affects feeding functions (i.e. filtration, pseudofaeces production and absorption). The comparatively high SFG we observed for pearl oysters fed natural particles may also be due to the presence of inorganic particles. Griffiths (1980b) and Navarro et al. (1996) reported that particulate inorganic matter enhanced absorption of algal food. Similarly, Urban & Langdon (1984) demonstrated that the addition of kaolinite to algae/yeast diets improved oyster growth. Jørgensen (1990) showed that the presence of silt in a microalgal diet resulted in higher growth rate of *Mytilus edulis*.

A number of temperate and tropical bivalve species have been found to selectively ingest organic material and reject inorganic or unfavourable material in the pseudofaeces to cope with high fractions of inorganic particles in turbid water conditions (Navarro et al. 1992, Bayne et al. 1993, Hawkins et al. 1996, 1998, Barillé et al. 1997). However, there was no evidence of selective feeding on organic particles as a pre-ingestive strategy in either *Pinctada margaritifera* or *P. maxima*. This was also demonstrated in the sub-tropical pearl oyster *P. imbricata* (Ward & MacDonald 1996) and in *P. margaritifera* in Malaysia (Hawkins et al. 1998). On the basis of gut analysis, Gervis & Sims (1992) have also suggested an absence of food selection in *Pinctada* species. Low feeding rates are generally associated with more efficient processes of particle selection (Sierszen & Frost 1992, MacDonald & Ward 1994, Ward & MacDonald 1996). *P. margaritifera* and *P. maxima* have relatively high pumping rates compared with other bivalve species (Yukihira et al. 1998a).

Thus, the lack of selective feeding may be at least partially explained by their high CR. Some anatomical features, such as gill and labial palp structures may also be associated with non-selective feeding of these species. Adaptation of *P. maxima* to relatively turbid environments appears to be explained by its greater ingestion rate and higher digestibility.

Even though SPM in inshore waters includes a substantial fraction of inorganic matter, these waters are high in particulate organic matter (POM). This is a potentially rich source of food to filter feeders such as *Pinctada maxima*. By contrast, in oligotrophic coral reef waters, neither SPM nor POM are abundant. However, *P. margaritifera* filters smaller particles more efficiently than *P. maxima*, and filters particles larger than 3 μm at high efficiencies (>90%) under conditions of low SPM concentration (2 mg l^{-1}). Dufour & Torr  ton (1996) also found that *P. margaritifera* was able to filter particles smaller than 3 μm , and they suggested that this species uses bacterial aggregates as a supplemental food source. Small particles were dominant in clear water conditions (<2 mg SPM l^{-1}) compared to turbid conditions at the 2 Great Barrier Reef sites of this study. Similarly, EVAAM (1996, cited by Anonymous 1997) reported that POM in Takapoto Lagoon, French Polynesia, a habitat of *P. margaritifera*, consisted predominantly (75%) of particles less than 3 μm . In Takapoto Lagoon there was no seasonal pattern of variation in the quantity of SPM: it varied according to water agitation from wind and swell and increased by 54% when the lagoon waters were disturbed. Taken overall, the capability of filtering smaller sized food particles for *P. margaritifera* may be a vital adaptation to maximise energy gain in environments of low SPM concentration.

Differences in patterns of energy gain and consumption between the 2 species relate well to differences in their habitats. *Pinctada maxima* feeds most efficiently and thus gains the greatest energy from natural SPM under relatively turbid conditions: particularly within the SPM range of ca 3 to 15 mg l^{-1} (Table 2). Adult *P. maxima* detach their byssal threads and come to rest on the substratum where the environment is characterised by high amounts of terrigenous sediments, nutrient inputs, high productivity levels and fast water currents (Gervis & Sims 1992). Grant et al. (1990) suggested that resuspended bottom material could be a valuable food supplement for cultured bivalves, and a positive relationship between bivalve growth and food particles supplied from the benthos has been reported for *Macoma balthica* (Thompson & Nichols 1988), *Mytilus edulis* (Rhoads et al. 1984) and *Ostrea edulis* (Grant et al. 1990). While a severe reduction in food quality due to wind-driven resuspension was observed in this study, the absolute amount of POM steadily

increased as water became turbid. Its habitats and feeding responses under turbid conditions indicate that *P. maxima* uses resuspended sediments as valuable additional food, and potentially grows and reproduces even under relatively high turbidity conditions (up to SPM concentrations of ca 30 to 40 mg l^{-1}). In contrast, *P. margaritifera* maximises energy gain under low SPM concentrations (<3 mg l^{-1}), which represent conditions of coral reef waters, and which coincided very well with SPM concentrations observed in a typical natural habitat of *P. margaritifera* (1 to 2 mg l^{-1} at Orpheus Island).

Comparing feeding behaviour in 5 tropical bivalve molluscs supplied with natural seston in a relatively turbid mangrove estuary, Hawkins et al. (1998) concluded that *Pinctada margaritifera* had the lowest rate of absorption from POM. SPM varied from 10 to 23 mg l^{-1} during their short-term study of *P. margaritifera*; however, our findings show these are the least optimal conditions for efficient energy acquisition in this species. In its optimal environment, such as on coral reefs (<3 mg l^{-1}), *P. margaritifera* should absorb some 3 to 4 times more energy from POM than in turbid waters (see AE data in Table 2). Hawkins et al. (1998) also suggested that the low nutrient acquisition they observed for *P. margaritifera* was a partial explanation for slow growth in the *Pinctada* group. They based this hypothesis on growth data for the Japanese pearl oyster *P. fucata martensii*. In comparison, tropical pearl oysters such as *P. margaritifera* are fast-growing bivalves (Gervis & Sims 1992, Yukihira 1998, see 'Introduction').

Studies of physiological energetics in mussels have demonstrated that SFG over a wide food concentration range corresponds well with measured growth and reproductive output (Bayne & Worrall 1980, van Erkom Schurink & Griffiths 1992). Of the 2 pearl oysters, *Pinctada maxima* reaches a larger size in terms of both shell length and soft tissue. The maximum body size (including byssal threads) recorded for *P. maxima* and *P. margaritifera* in these studies was 27 and 19 g soft tissue dry wt, respectively (Yukihira 1998). Given that the SFG values in this study were calculated for 10 g tissue dry wt oysters, and both oyster species are sexually mature at this size, the greater maximum SFG recorded for *P. maxima* suggests why it grows to a larger body size.

This study provides information that may be used for ecologically sustainable developments in the rapidly expanding pearl oyster industry. In general, suspension feeding activities by cultured bivalves under conditions of slow water exchange tend to cause depletion of natural food particles (Newell 1990, Fr  chette & Grant 1991, Navarro et al. 1991, Grant 1996) and affect bottom environments due to biodeposition of faeces

and pseudofaeces from the bivalves (Kusuki 1977, 1978, Kaspar et al. 1985, Baudinet et al. 1990, Deslous-Paoli et al. 1992, Bacher et al. 1995, Gilbert et al. 1997). Consequently, intensive bivalve aquaculture may have substantial environmental impacts on local ecosystems (Ito & Imai 1955, Kusuki 1977, 1978, Hatcher et al. 1994, Bacher et al. 1995, Kishi & Uchiyama 1995).

There have been several cases of environmental degradation associated with pearl culture. Recent mass mortalities of the Japanese pearl oyster *Pinctada fucata martensii* in culture grounds of Japan were due to the synergistic effects of dense culture and environmental degradation (e.g. harmful red tides), (Nagai et al. 1996, Shinomiya et al. 1997, Tanaka 1997). Similarly, mass mortalities of the tropical black-lip pearl oyster *P. margaritifera* during 1985 to 1986 in Takapoto lagoon, French Polynesia (Vacelet et al. 1996, Charpy et al. 1997) were attributed to the depletion of natural food particles by densely cultured *P. margaritifera*.

Both *Pinctada margaritifera* and *P. maxima* maintain high feeding rates over a wide range of environmental conditions (Yukihira 1998): their ecological roles in energy transfer and environmental impacts on ecosystems as suspension feeders can be of considerable importance. Therefore the stocking densities of cultured pearl oysters should be managed, taking account of water replacement conditions. Before launching pearl farming in an area, it would be wise to conduct trophic modelling and environmental impact assessment at the appropriate stocking densities of cultured pearl oysters, as has been undertaken for mussel farming (e.g. Rodhouse & Roden 1987, Grant 1996).

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