

Comparative effects of microalgal species and food concentration on suspension feeding and energy budgets of the pearl oysters *Pinctada margaritifera* and *P. maxima* (Bivalvia: Pteriidae)

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ABSTRACT: This study aimed to determine the influence of microalgal species and food concentration on various physiological parameters and Scope for Growth (SFG) in adults of 2 pearl oysters, *Pinctada margaritifera* and *P. maxima*. Clearance rate, pseudofaecal production rate, absorption efficiency, respiration rate and excretion rate were determined over a range of food concentrations using 2 microalgal diets, Tahitian *Isochrysis* sp. (T-Iso) and *Dunaliella primolecta* at 28°C. Clearance, pseudofaecal production and respiration rates were significantly affected by microalgal diet. From these results, and because of the higher energy content of T-Iso, pearl oysters feeding on T-Iso had maximum values of SFG that were 1.5 to 2.1 times higher than when feeding on *D. primolecta*. Clearance rate and absorption efficiency were significantly related to food concentration as negative exponential relationships ($p < 0.001$). Generally, pseudofaecal production, respiration and excretion rates were significantly related to food concentration as positive linear relationships ($p < 0.005$). Optimal food concentrations for maximum SFG for *P. margaritifera* and *P. maxima* were 1 to 2 mg l⁻¹ and 2 to 3 mg l⁻¹, respectively. *P. maxima* was better adapted to a wider range of food concentrations. *P. maxima* maintained positive SFG up to 9 mg l⁻¹ food concentration when feeding on T-Iso and up to 7 mg l⁻¹ when feeding on *D. primolecta*, while equivalent values for *P. margaritifera* were 7 mg l⁻¹ and 5 mg l⁻¹, respectively. These results are in accordance with *P. maxima* occurring in a wider range of habitats than *P. margaritifera*, and experiencing greater concentration ranges of suspended particulate matter.

KEY WORDS: Bivalve · *Pinctada margaritifera* · *Pinctada maxima* · Food · Suspension feeding · Scope for Growth · Energy

INTRODUCTION

Food concentration and microalgal diet are major factors influencing the growth and reproduction of suspension feeding bivalves. The relationships between suspension feeding and energy budget versus food concentration and food quality have been well studied in temperate bivalves, but not generally in tropical

bivalves (the exception is giant clams). These studies of temperate bivalves aimed to better understand their ecophysiology and trophic roles in aquatic ecosystems (Tenore & Dunstan 1973a, b, Widdows et al. 1979, Navarro et al. 1992, Hawkins et al. 1996). Some also sought to determine optimum food conditions for aquaculture purposes (Tenore & Dunstan 1973a, b, Kirby-Smith & Barber 1974, Navarro & Winter 1982, Beiras et al. 1993, 1994, Navarro et al. 1996). In particular, energy balances obtained for various microalgal diets and concentrations are of interest for bivalve aquaculture because pure cultures of unicellular microalgae

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are widely used as food for rearing larvae and spat, and for broodstock maturation. However, in spite of comparisons of nutritive values of microalgae (Finlay & Uhlig 1981, Pillsbury 1985, Helm & Laing 1987, Whyte 1987) and growth rates of bivalves (Walne 1970, Helm 1977, Ewart & Epifanio 1981, Langdon & Waldock 1981) on various diets, the way that different microalgal diets influence feeding (filtration, pseudofaeces production, ingestion and digestion) and energy balance has not been fully appreciated. Thus, studies of the influence of microalgal diet and concentration on feeding and energy balance of commercially important bivalve species can provide useful information for both ecology and aquaculture.

Pinctada margaritifera and *P. maxima* are economically important bivalves, as well as being typical suspension feeders occurring in tropical waters. They are among the largest species of pearl oysters (Bivalvia: Pteriidae) and are used extensively in cultured pearl production (Doumenge et al. 1991, Shirai 1994). They tend to occur in different habitats. *P. margaritifera* is found in greatest numbers in the oligotrophic waters of atoll lagoons; it tends to be excluded from turbid waters (Tranter 1959). On the other hand, *P. maxima* inhabits a variety of areas, from seagrass beds to deep-water 'reefs' on substrates varying from mud to sand and gravel (Kailola et al. 1993). Its inshore habitats may have considerable terrigenous sediment, and substantial nutrient inputs and productivity levels (Gervis & Sims 1992). The distribution of *P. maxima* suggests that it will experience a wide range of concentrations of suspended particulate matter (SPM). SPM may also be high in its inshore habitats, with SPM quality depending on meteorological and tidal conditions. The 2 oyster species inhabit such different waters that food particle concentration and food quality should be important factors for their ecology and energetics. The 2 species may correspondingly show different patterns of **energy gain and expenditure over various** food concentrations and types.

Scope for Growth (SFG, $J h^{-1}$) is a measure of the energy available to the animal for growth and reproduction (Warren & Davis 1967, Bayne & Newell 1983, Griffiths & Griffiths 1987). Yukihiro et al. (1998) demonstrated that in simulated oligotrophic conditions ($0.5 mg l^{-1}$ Tahitian *Isochrysis* sp.), *Pinctada margaritifera* and *P. maxima* both had high clearance rates (CR) and high values of SFG compared to most other bivalves, including bivalves feeding on higher food concentrations. It appears that both species are capable of growing and reproducing under conditions of low food supply. This is most notable for *P. maxima* because its habitats may have high levels of SPM. Thus, following on from these findings for a low concentration of one microalga (Yukihiro et al. 1998), it is

appropriate to examine the effects of microalgal species and food concentration on feeding and energy budgets of *P. margaritifera* and *P. maxima*.

Effects of various algal diets and concentrations on feeding rates (Hayashi 1983), larval growth (Nishimura 1980), and spat growth (Wada 1973, Okauchi 1990) have been examined for the Japanese pearl oyster *Pinctada fucata martensii*. However, there has not been a comprehensive study of the effects of food species and concentration on feeding and energy budgets of a *Pinctada* species. The first aim of the present study was therefore to compare the suspension feeding (clearance, pseudofaeces production and absorption rates) and energy budgets (absorbed, respired and excreted energy) of *P. margaritifera* and *P. maxima* feeding on 2 microalgae species over a range of food concentrations. The second was to consider whether the results on feeding and energy budgets are related to differences between habitats of these pearl oyster species. The energy budgets of the pearl oysters were summarised in the parameter Scope for Growth.

MATERIALS AND METHODS

The techniques used in this study were similar to those of Yukihiro et al. (1998). All experiments were carried out at $28 \pm 0.5^{\circ}C$.

Pearl oysters. Large *Pinctada maxima* (132 to 237 mm shell height, $n = 30$) and *P. margaritifera* (121 to 180 mm shell height, $n = 40$) were put into pocket nets (Gervis & Sims 1992) kept at ca 1.5 m depth suspended from a pontoon at Cape Ferguson, Australian Institute of Marine Science, North Queensland ($19^{\circ} 15' S$, $147^{\circ} 05' E$). They were acclimated to these conditions for at least 3 wk before use in all experiments. Water temperature varied from 26.0 to 29.5°C over the study period. The shells of all oysters were thoroughly cleaned of epibiota during the acclimation period and were re-cleaned the day before use in experiments. After the completion of each experiment, shell height (SH, mm), which is the greatest distance from the umbo to the bottom of a finger or growth process, was recorded. Measurements of feeding, respiration, and excretion rates and food absorption efficiency were performed as described below on a sample size of 30 to 40 oysters.

Microalgae. Two unicellular microalgal species, Tahitian *Isochrysis* aff. *galbana* Green (T-Iso) and *Dunaliella primolecta* Butcher, were separately used as food suspensions. These algae were selected for their range of cell size (4 to 8 μm) and because they are used in mariculture, or resemble natural phytoplankton (T-Iso). The energy contents of the microalgae were determined using a Parr 1421 semi-micro oxygen

bomb calorimeter (following Whyte 1987). Experiments were conducted over an algal concentration range between 0 (= no food) and 11 mg dry wt l⁻¹ using algal cells from cultures in their logarithmic growth phase.

Clearance rates. The volume of water each oyster cleared of particulate material (CR, l h⁻¹) was determined using a flow-through system in which 0.45 µm filtered seawater containing a constant concentration of algal food was allowed to run through a set of 4 chambers. Three of these contained an oyster, while the remaining one acted as a control. From the flow rate (F, l h⁻¹), and the concentrations of algae immediately surrounding each oyster (C₀), in the outflow of control chamber (C₁) and in the outflow of each experimental chamber (C₂), clearance rates were calculated from the following equation (after Hildreth & Crisp 1976):

$$CR (l h^{-1}) = F (C_1 - C_2) / C_0$$

Two chamber volumes, 6 and 18 l, were used to hold the oysters according to their size. A constant flow rate between 25 and 35 l h⁻¹ was maintained during the experiment. Oysters were placed in the flow-through chambers and kept undisturbed. Measurements were commenced at least 1 h after they showed enough gape as evidence of feeding. Algal concentrations were measured at 1 h intervals (means of 5 counts) using a high-speed particle counter (Coulter Multi-sizer) with a 140 µm orifice tube. The ration level of each oyster was expressed as a mean value of C₀.

Pseudofaeces. Pseudofaeces is uningested material that is rejected from the labial palps. Both oyster species tended to produce mucus-like, fragile masses of pseudofaeces at the higher food concentrations. These were distinguished by their colour and texture from faeces, which were darker-coloured ribbons or pellets. Deposited pseudofaeces were carefully collected from each chamber during and on completion of experiments. Pseudofaecal production was quantified by filtering samples onto pre-rinsed-and-ashed GF/C filter papers, rinsing with distilled water, drying, and ashing at 450°C for 5 h. Proportion of pseudofaeces to total food filtered (PF, %) was then calculated.

Absorption efficiency. The percentage of food consumed that was then absorbed was determined by comparing the fraction of faeces lost on ashing with that of samples of food suspension treated in the same way. Absorption efficiency (abs. eff., %) was then calculated according to the equation of Conover (1966):

$$\text{abs. eff. (\%)} = 100 \times (f - e) / (1 - e) f$$

where *f* and *e* are the fractions of food and faeces lost on ashing, respectively.

Collection of faeces from the chambers was carried out on completion of the measurements of CR and

excretion rate (see below). Samples were filtered onto pre-rinsed-and-ashed GF/C filter papers, rinsed with distilled water, dried and ashed at 450°C for 5 h. Food samples consisting of 2 l samples of water and algae were collected from the control chamber and treated in the same way.

Respiration rate. Respiration rates (R, ml h⁻¹) were determined in 4 sealed chambers using YSI dissolved oxygen electrodes (Model 55). Three sizes of chambers, 2, 5 and 13 l, were used to hold the oysters, according to size. Before the experiments, oysters were fed the appropriate food concentration for at least 2 h in a 100 l tank with aeration. Then 3 oysters were placed individually into sealed chambers with 0.45 µm filtered seawater and algal food at the appropriate concentration. The fourth chamber served as a control. Water in each chamber was thoroughly mixed by a magnetic stirrer. A mesh platform separated oyster from stirrer bar. Oxygen concentration in each chamber was monitored at 5 min intervals. Preliminary research revealed that both species took at most 15 min to stabilise in the conditions of the respirometer chamber. Since the clearance rates of the oysters were quite high compared to the chamber volumes, which meant that the animals would quickly deplete the food suspension in the chamber, recordings were restricted to the first 10 or 15 min after the initial equilibration period. R was determined after Bayne et al. (1985).

Excretion rate. The rate of ammonia excretion (E, mg NH₄-N h⁻¹) was determined on the completion of CR measurements. Oysters were carefully transferred into another set of 4 chambers containing 0.45 µm-filtered seawater. Three of these contained an oyster, while the remaining chamber acted as a control. Oysters were kept undisturbed for 60 to 90 min according to the volume of water and the oyster's body size. Duplicate samples (10 ml) were collected from each chamber and filtered through a 0.45 µm Sartorius minisart filter and frozen until assaying. Analyses for ammonia content were conducted using the phenol-hypochlorite method of Solorzano (1969).

Size standardisation of CR, R and E. The dry tissue weight of each experimental oyster was calculated from shell height (SH) using the SH-tissue weight relationships determined in a previous study (Yukihira et al. 1998). CR, R and E were standardised to that of a specimen of 10 g dry tissue weight (wt) to allow comparisons according to the equation:

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

where Y_s = size-standardised physiological rate, W_s = standard size (dry tissue weight) = 10 g, W_e = dry tissue wt of animal, *b* = size-weight exponent, and Y_e = uncorrected physiological rate. Table 1 shows *b* values used for the standardisation of CR, R and E of both species.

Scope for growth. Absorbed energy (AE, J h^{-1}) was calculated as follows:

$$\text{AE} = \text{CR}(1 - \text{PF})(\text{abs. eff.})(\text{energy content of the algal food})$$

Relationships between AE and food concentration were expressed by polynomial regression curves. Respired energy (RE, J h^{-1}) and excreted energy (EE, J h^{-1}) were calculated after Bayne et al. (1985). Scope for Growth (SFG, J h^{-1}) was determined using the equation:

$$\text{SFG} (\text{J h}^{-1}) = \text{AE} - (\text{RE} + \text{EE})$$

Data analysis. When the regression analysis showed that CR, PF, R, abs. eff. and E were correlated with increasing food concentration, differences in these parameters between oyster species and microalgal diet were examined using ANCOVA with food concentration as the covariate. Since R of *Pinctada maxima* was independent of ration level, the effect of microalgal diet was tested using 1-way ANOVA. Predicted mean values from regression equations and their 95% confidence limits (95% CL) for AE and RE were used to assess differences in SFG values between the 2 microalgal diets and 2 oyster species.

RESULTS

Microalgae

T-Iso had a mean diameter of ca 4.5 μm and contained 20.27 J mg^{-1} dry wt. *Dunaliella primolecta* was larger (ca 7.0 μm) and contained less energy: 15.06 J mg^{-1} dry wt.

Clearance rates

Clearance rates (CR, l h^{-1}) of both oysters were significantly, negatively correlated with food concentration (Fig. 1). Relationships between CR and food concentration (FC, mg l^{-1} dry wt) were best described by exponential functions (Table 2). Slopes of the regressions of clearance rate on food concentration differed significantly between oyster species and between microalgal diets (Table 3). With increasing food concentration the CR of *Pinctada margaritifera* de-

Table 1. *Pinctada margaritifera* and *P. maxima*. Size-rate exponents (b values) of clearance rate (CR, l h^{-1}), respiration rate (R, $\text{ml O}_2 \text{ h}^{-1}$) and excretion rate (E, $\text{mg NH}_4\text{-N h}^{-1}$) (from Yukihiro et al. 1998)

Species	Weight (g)	CR	R	E
<i>P. margaritifera</i>	0.043–12.83	0.613	0.439	0.642
<i>P. maxima</i>	0.044–20.39	0.613	0.561	0.789

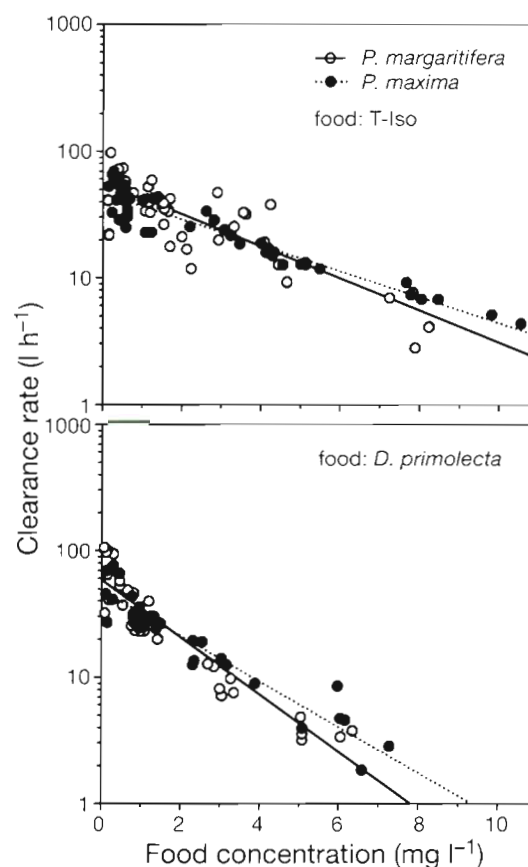


Fig. 1. *Pinctada margaritifera* and *P. maxima*. Clearance rate versus food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

creased significantly more than that of *P. maxima* (Fig. 1, Table 3a). CRs of oysters feeding on *Dunaliella primolecta* decreased significantly more with increasing FC than the CRs of oysters feeding on T-Iso (Fig. 1, Table 3c, d). Thus, the relationships between clearance rate and food concentration reflected both microalgal species and oyster species.

We observed that the shell gape of both oyster species tended to decrease at higher food concentrations, and the gills were never observed to extend beyond the shell margins. (Similarly, Palmer [1980] and Palmer & Williams [1980] found that high clearance rates in scallops at low food concentrations were typically reflected in a wide shell gape.)

Pseudofaecal production

Relationships between pseudofaecal production (PF, % of total food filtered) and FC were described by

Table 2. *Pinctada margaritifera* and *P. maxima*. Relationships between clearance ($l\ h^{-1}$), pseudofaecal production (% of total food filtered), absorption efficiency (%), respiration ($ml\ O_2\ h^{-1}$) and excretion rates ($mg\ NH_4\text{-}N\ h^{-1}$), and food concentration (FC, $mg\ ml^{-1}$ dry wt) of oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) or *Dunaliella primolecta*

Function	Pearl oyster species	
Microalgae species	<i>P. margaritifera</i>	<i>P. maxima</i>
Clearance rate (CR)		
T-Iso	$CR = 56.67 \times 10^{-0.127FC}$ ($r^2 = 0.74$, $n = 50$, $p < 0.001$)	$CR = 47.00 \times 10^{-0.102FC}$ ($r^2 = 0.90$, $n = 43$, $p < 0.001$)
<i>D. primolecta</i>	$CR = 58.31 \times 10^{-0.227FC}$ ($r^2 = 0.89$, $n = 45$, $p < 0.001$)	$CR = 49.81 \times 10^{-0.182FC}$ ($r^2 = 0.91$, $n = 33$, $p < 0.001$)
Pseudofaecal production (PF)		
T-Iso	$PF = 8.52 + 4.39FC$ ($r^2 = 0.26$, $n = 50$, $p < 0.001$)	$PF = -1.80 + 3.78FC$ ($r^2 = 0.68$, $n = 43$, $p < 0.001$)
<i>D. primolecta</i>	$PF = -0.99 + 5.51FC$ ($r^2 = 0.81$, $n = 45$, $p < 0.001$)	$PF = -1.67 + 3.59FC$ ($r^2 = 0.81$, $n = 35$, $p < 0.001$)
Absorption efficiency (abs.eff.)		
T-Iso	$abs.eff. = 67.39 \times 10^{-0.108FC}$ ($r^2 = 0.56$, $n = 49$, $p < 0.001$)	$abs.eff. = 70.20 \times 10^{-0.0720FC}$ ($r^2 = 0.82$, $n = 43$, $p < 0.001$)
<i>D. primolecta</i>	$abs.eff. = 55.29 \times 10^{-0.0566FC}$ ($r^2 = 0.55$, $n = 45$, $p < 0.001$)	$abs.eff. = 78.42 \times 10^{-0.0617FC}$ ($r^2 = 0.76$, $n = 32$, $p < 0.001$)
Respiration (R)		
T-Iso	$R = 2.80 + 0.264FC$ ($r^2 = 0.426$, $n = 24$, $p < 0.001$)	$R = 3.76 + 0.0662FC$ ($r^2 = 0.043$, $n = 28$, ns)
<i>D. primolecta</i>	$R = 1.81 + 0.238FC$ ($r^2 = 0.621$, $n = 23$, $p < 0.001$)	$R = 2.61 + 0.0610FC$ ($r^2 = 0.055$, $n = 22$, ns)
Excretion rate (E)		
T-Iso	$E = 0.294 + 0.081FC$ ($r^2 = 0.25$, $n = 32$, $p < 0.005$)	$E = 0.374 + 0.110FC$ ($r^2 = 0.40$, $n = 37$, $p < 0.001$)
<i>D. primolecta</i>	$E = 0.225 + 0.096FC$ ($r^2 = 0.57$, $n = 29$, $p < 0.001$)	$E = 0.346 + 0.127FC$ ($r^2 = 0.50$, $n = 35$, $p < 0.001$)

Table 3. Summary of ANCOVA testing for similarity in slopes and intercepts of regression lines of clearance rate (CR, $l\ h^{-1}$), pseudofaecal production (PF, % of filtered material), absorption efficiency (abs.eff., %) and excretion rate (E, $mg\ NH_4\text{-}N\ h^{-1}$) versus food concentration ($mg\ l^{-1}$ dry wt) in pearl oyster *Pinctada margaritifera* and *P. maxima*, and food Tahitian *Isochrysis* sp. (T-Iso) and *Dunaliella primolecta*. When there was no significant difference in slope, then difference in intercept was tested. ns: not significant at $p < 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

	CR	PF	abs.eff.	E
(a) Comparison between <i>P. margaritifera</i> and <i>P. maxima</i> feeding on T-Iso				
Slopes	*	ns	*	ns
Intercepts		***	ns	ns
(b) Comparison between <i>P. margaritifera</i> and <i>P. maxima</i> feeding on <i>D. primolecta</i>				
Slopes	**	***	ns	ns
Intercepts			***	ns
(c) Comparison between T-Iso and <i>D. primolecta</i> fed on by <i>P. margaritifera</i>				
Slopes	***	ns	**	ns
Intercepts		**		ns
(d) Comparison between T-Iso and <i>D. primolecta</i> fed on by <i>P. maxima</i>				
Slopes	***	ns	ns	ns
Intercepts		ns	**	ns

linear functions (Table 2). PF, although showing considerable variability, increased significantly with increasing food concentration (Fig. 2). When the 2 oyster species were compared, slopes of the regressions of pseudofaeces production on food concentration were found to be significantly different for *Dunaliella primolecta* but not for T-Iso (Table 3a, b). However, the intercepts differed significantly between the oyster species when feeding on T-Iso (Table 3a). There was a significant difference between the intercepts of the regressions of pseudofaeces production on food concentration for the 2 microalgal diets for *Pinctada margaritifera* (Table 3c), but no significant difference between the regressions of pseudofaeces production on food concentration for the microalgal diets for *P. maxima*.

Pinctada margaritifera produced relatively more pseudofaeces than *P. maxima* at comparable food concentrations. Only in *P. margaritifera* was there a difference between pseudofaecal production with different diets: T-Iso resulted in greater pseudofaecal production than *Dunaliella primolecta* at lower food concentration (Fig. 2).

Absorption efficiency (abs.eff., %)

Relationships between abs.eff. and food concentration (FC) were best described by the exponential functions (Table 2). Abs.eff. declined significantly with increasing food concentration (Fig. 3) Slopes or intercepts of the regressions of abs.eff. on food concentration varied significantly between oyster species and microalgal diets (Table 3). *Pinctada maxima* had higher abs.eff. than *P. margaritifera* regardless of diet. *P. maxima* had higher abs.eff. of *Dunaliella primolecta* compared to T-Iso at all food concentrations. *P. margaritifera* had higher abs.eff. when feeding on *D. primolecta* compared with T-Iso, except at food concentrations below about $2\ mg\ l^{-1}$.

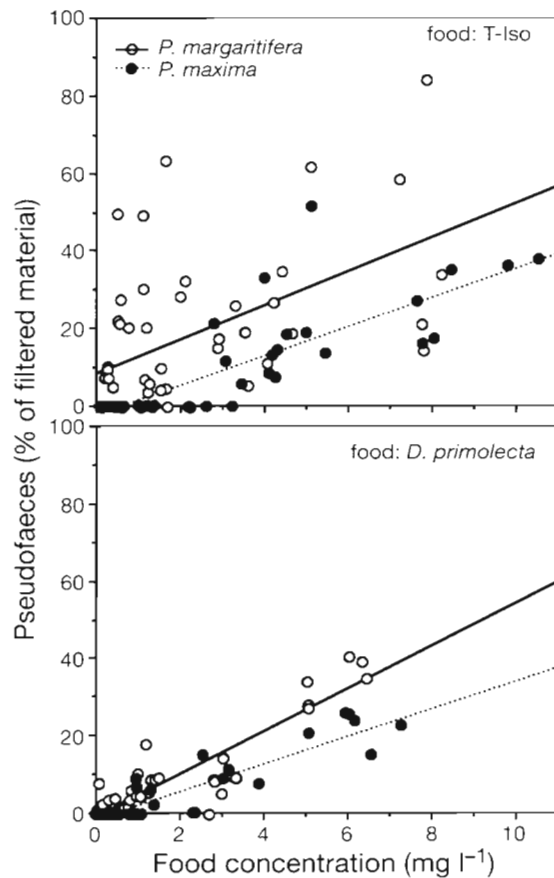


Fig. 2. *Pinctada margaritifera* and *P. maxima*. Pseudofaecal production (% of total food filtered) versus food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

Absorbed energy (AE)

Relationships between AE and FC were best expressed by fourth-power polynomial regressions (Fig. 4).

Pinctada margaritifera (T-Iso)

$$AE = 32.2 + 589.6FC + (-253.2)FC^2 + 37.3FC^3 + (-1.85)FC^4 \quad (1)$$

($r^2 = 0.82$, $n = 49$, $p < 0.001$)

P. margaritifera (*Dunaliella primolecta*)

$$AE = 38.6 + 364.0FC + (-20.43)FC^2 + 39.0FC^3 + (-2.49)FC^4 \quad (2)$$

($r^2 = 0.76$, $n = 45$, $p < 0.001$)

P. maxima (T-Iso)

$$AE = 97.8 + 403.6FC + (-121.0)FC^2 + 12.5FC^3 + (-0.45)FC^4 \quad (3)$$

($r^2 = 0.81$, $n = 43$, $p < 0.001$)

P. maxima (*D. primolecta*)

$$AE = 88.9 + 322.2FC + (-125.0)FC^2 + 16.16FC^3 + (-0.70)FC^4 \quad (4)$$

($r^2 = 0.77$, $n = 33$, $p < 0.001$)

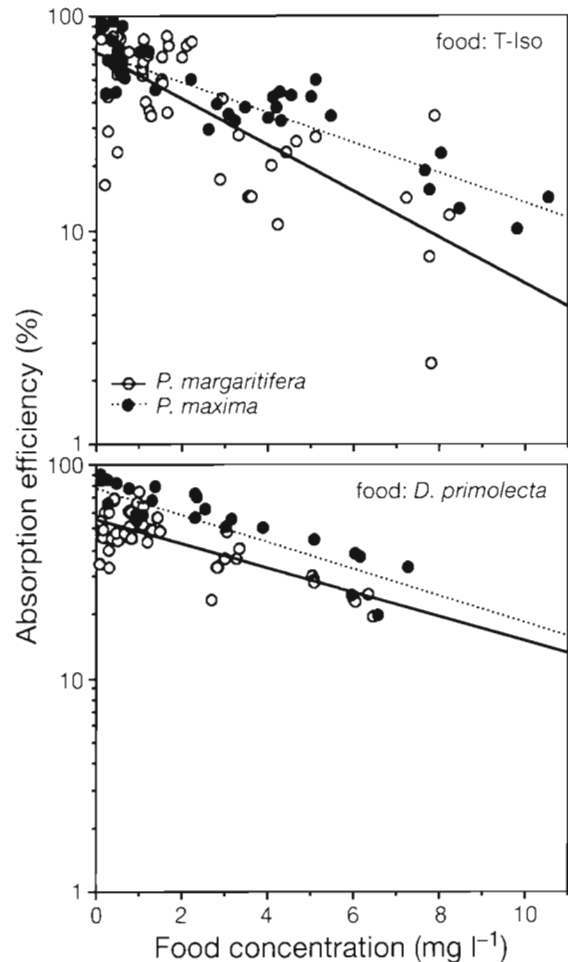


Fig. 3. *Pinctada margaritifera* and *P. maxima*. Absorption efficiency versus food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

Predicted mean values of AE and 95% confidence limits (95% CL) corresponding to 1 to 10 mg FC l⁻¹ are shown in Table 4. Both pearl oysters feeding on T-Iso and *Dunaliella primolecta* displayed maximum values of AE within the range 1 to 3 mg l⁻¹. The 95% CL values show significant effects of food species concentration on AE of both pearl oysters. These effects were: (1) at food concentrations of 0.5 to 4.5 mg l⁻¹ (*Pinctada margaritifera*) and 0.5 to 6.0 mg l⁻¹ (*P. maxima*), pearl oysters feeding on T-Iso had higher AE values than those feeding on *D. primolecta*, and (2) *P. maxima* had higher AE at 2.5 to 6.0 mg l⁻¹ (T-Iso) and 1 to 4.5 mg l⁻¹ (*D. primolecta*) than *P. margaritifera*. Except for these food concentration ranges, there were no significant differences in AE values between oyster species or food species.

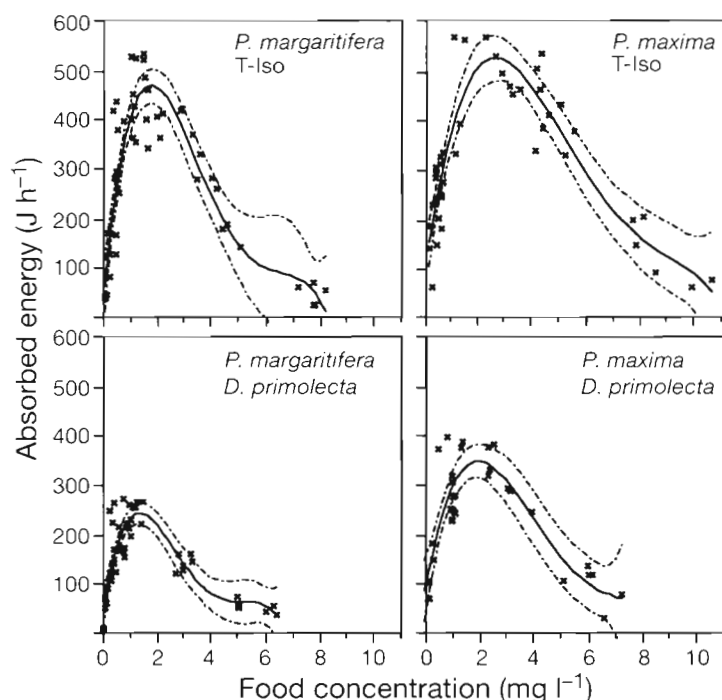


Fig. 4. *Pinctada margaritifera* and *P. maxima*. Relationships (regression curves and 95% confidence curves) between absorbed energy and food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

Respiration

There were linear relationships between respiration (R , $\text{ml O}_2 \text{ h}^{-1}$) and FC (Table 2). Respiration rate of *Pinctada margaritifera* increased significantly with increasing food concentration (Fig. 5, Table 5), but respiration rate of *P. maxima* was not significantly affected. Therefore, the mean R values for *P. maxima* were compared between the microalgal diets. *P. maxima* had significantly higher R when feeding on T-Iso than on *Dunaliella primolecta* (Table 5, ANOVA, $p < 0.01$). These mean values of R were used to calculate RE (J h^{-1}) and 95% CL values for *P. maxima* in Table 4.

Slopes of regression lines of R versus FC for *Pinctada margaritifera* were not significantly different for the 2 diets, but intercepts were significantly different (ANCOVA, $p < 0.01$). Therefore relationships between R and FC for *P. margaritifera* were re-expressed as follows:

$$\text{T-Iso} \\ R = 2.80 (\pm 0.496) + 0.247FC, \quad (5)$$

$$\text{Dunaliella primolecta} \\ R = 1.81 (\pm 0.406) + 0.247FC, \quad (6)$$

where figures in parenthesis are 95% confidence limits (95% CL). These regressions were used to calculate

RE and 95% CL of predicted mean RE for the comparison between microalgal diets.

To compare RE and 95% CL between the oyster species feeding on the same food, the following regressions for *Pinctada margaritifera* were used:

$$\text{T-Iso} \\ R = 2.80 (\pm 0.496) + 0.264 (\pm 0.136)FC \quad (7)$$

$$\text{Dunaliella primolecta} \\ R = 1.81 (\pm 0.406) + 0.238 (\pm 0.084)FC \quad (8)$$

Calculated respired energy (RE , J h^{-1}) and 95% CL are shown in Table 4.

Excretion

Relationships between excretion rate (E , mg h^{-1}) and food concentration were expressed by linear functions (Table 2). E varied considerably, but increased significantly with increasing food concentration (Fig. 6). However, neither slopes nor intercepts of the regressions of E on FC varied significantly between oyster species nor between microalgal diet (Table 3). Therefore, all data were pooled and a common regression was determined:

$$E = 0.306 + 0.110FC \\ (r^2 = 0.42, n = 133, p < 0.001)$$

Excreted energy (EE , J h^{-1}) was calculated using this equation (Table 4).

Scope for Growth

Scope for Growth (SFG) values for *Pinctada margaritifera* and *P. maxima* feeding on T-Iso and *Dunaliella primolecta* were determined from calculated AE , RE and EE values (Table 4). Considering 95% CL for AE and RE , *P. maxima* feeding on T-Iso and *D. primolecta* had distinctly higher SFG than *P. margaritifera* throughout ration levels 3 to 6 mg l^{-1} T-Iso and 2 to 4 mg l^{-1} *D. primolecta*, respectively. *P. margaritifera* and *P. maxima* feeding on T-Iso had higher SFG than when feeding on *D. primolecta* over food concentration ranges 1 to 4 mg l^{-1} and 2 to 6 mg l^{-1} , respectively. *P. margaritifera* and *P. maxima* feeding on T-Iso had 2.1 times ($387/183 \text{ J h}^{-1}$) and 1.5 times ($423/280 \text{ J h}^{-1}$) higher maximum SFG values, respectively, than those feeding on *D. primolecta*. The highest SFGs of *P. margaritifera* and *P. maxima* feeding on the 2 diets were at approximately the following food concentrations:

Table 4. *Pinctada margaritifera* and *P. maxima*. Predicted mean values of absorbed energy (AE), respired energy (RE), excreted energy (EE) corresponding to different food concentrations (1 to 10 mg l⁻¹) and food species, *Isachrysis* sp. Tahitian (T-Iso) and *Dunaliella primolecta*, and resultant scope for growth [SFG = AE - (RE + EE)]. 95% confidence limits (95% CL) are also shown for AE and RE. There was no significant difference in EE between pearl oyster species or with food species. Significant differences in SFG values are indicated by: ^a between oyster species on T-Iso; ^b between oyster species feeding on *D. primolecta*; ^c between food species for *P. margaritifera*; ^d between species for *P. maxima*

Parameter	Species	Source	1 mg l ⁻¹				2 mg l ⁻¹				3 mg l ⁻¹				4 mg l ⁻¹			
			T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>	
AE (J h ⁻¹)	<i>P. margaritifera</i>	Eqs. (1) & (2) 95% CL	404	235	467	222	379	143	253	84								
			(370, 430)	(213, 254)	(430, 501)	(195, 244)	(330, 420)	(111, 173)	(200, 302)	(48, 114)								
<i>P. maxima</i>		Eqs. (3) & (4) 95% CL	392	302	514	351	521	310	461	233								
			(353, 429)	(270, 329)	(465, 562)	(317, 384)	(480, 569)	(263, 358)	(423, 499)	(177, 287)								
RE (J h ⁻¹)	<i>P. margaritifera</i> 1	Eqs. (5) & (6) (RE1) 95% CL	62	42	67	47	72	52	77	57								
			(52, 72)	(34, 50)	(57, 77)	(39, 55)	(61, 82)	(44, 60)	(67, 87)	(49, 65)								
<i>P. margaritifera</i> 2		Eqs. (7) & (8) (RE2) 95% CL	62	42	68	47	73	51	78	56								
			(49, 75)	(32, 52)	(52, 83)	(35, 58)	(55, 91)	(38, 65)	(57, 100)	(47, 71)								
<i>P. maxima</i>		From Table 5 95% CL	81	58	81	58	81	58	81	58								
			(71, 92)	(49, 67)	(71, 92)	(49, 67)	(71, 92)	(49, 67)	(71, 92)	(49, 67)								
EE (J h ⁻¹)	Both species		10	10	13	13	16	16	19	19								
SFG (J h ⁻¹)	<i>P. margaritifera</i>	SFG = AE - RE1 - EE SFG = AE - RE2 - EE SFG = AE - RE - EE	332 ^c 331 301	183 ^c 183 233	387 ^c 387 419 ^d	162 ^c 162 ^b 280 ^{b,d}	292 ^c 291 ^a 423 ^{a,d}	75 ^c 76 ^b 236 ^{b,d}	157 ^c 156 ^a 361 ^{a,d}	9 ^c 10 ^b 156 ^{b,d}								
	<i>P. maxima</i>																	
5 mg l ⁻¹	<i>D. primolecta</i>		7 mg l ⁻¹				8 mg l ⁻¹				9 mg l ⁻¹				10 mg l ⁻¹			
			T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>		T-Iso		<i>D. primolecta</i>	
156	70	114	65	105	64													
(82, 217)	(21, 109)	(-5, 204)	(17, 96)	(-20, 185)	(-45, 114)													
372	157	280	105	201	139													
(329, 421)	(102, 210)	(235, 336)	(48, 159)	(155, 266)	(95, 224)													
82	62	87	67	92	97													
(72, 92)	(54, 70)	(77, 97)	(59, 75)	(82, 102)	(64, 80)													
84	61	89	66	95	100													
(60, 108)	(44, 78)	(63, 116)	(47, 84)	(65, 124)	(50, 91)													
81	58	81	58	81	81													
(71, 92)	(49, 67)	(71, 92)	(49, 67)	(71, 92)	(71, 92)													
21	21	24	24	27	30													
53	-13	3	-26	-14	-62													
51 ^a	-13	1 ^a	-25	-17	-65													
269 ^{a,d}	78 ^d	175 ^{a,d}	23 ^d	93	29													

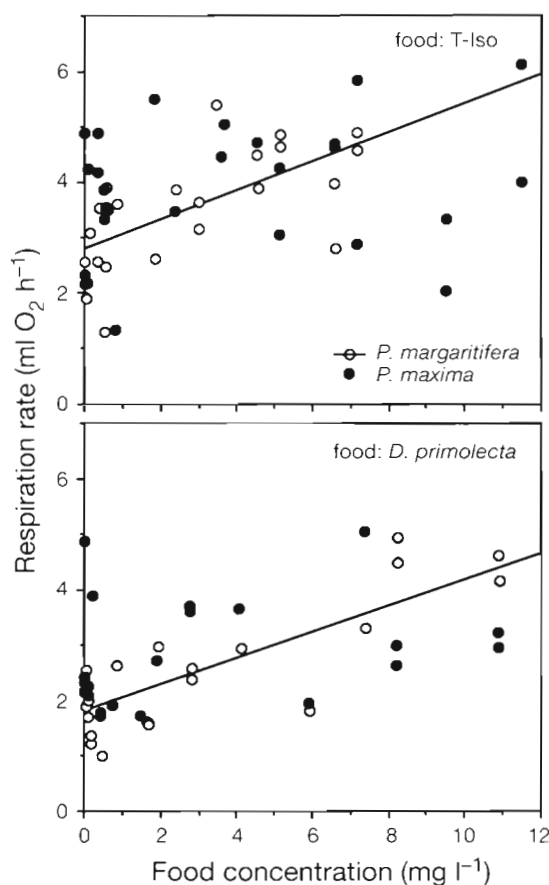


Fig. 5. *Pinctada margaritifera* and *P. maxima*. Respiration rate versus food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

P. margaritifera: 2 mg l⁻¹ (T-Iso), 1 mg l⁻¹ (*D. primolecta*)
P. maxima: 3 mg l⁻¹ (T-Iso), 2 mg l⁻¹ (*D. primolecta*)

Above these peaks, SFG declined to below zero with increasing food ration level. The approximate upper threshold concentrations beyond which SFG values became negative were:

P. margaritifera: 7 mg l⁻¹ (T-Iso) and 5 mg l⁻¹ (*D. primolecta*)
P. maxima: 9 mg l⁻¹ (T-Iso) and 7 mg l⁻¹ (*D. primolecta*)

Table 5. *Pinctada maxima*. Mean respiration rates (R, ml O₂ h⁻¹) and 95% confidence limits (CL) of oysters consuming various concentrations of Tahitian *Isochrysis* sp. (T-Iso) and *Dunaliella primolecta*. Food species has a significant effect on R (ANOVA, $p < 0.01$)

Food species	Food concentration (mg l ⁻¹)	n	R (CL)
T-Iso	0–11.4	28	4.00 (± 0.513)
<i>D. primolecta</i>	0–10.9	22	2.86 (± 0.458)

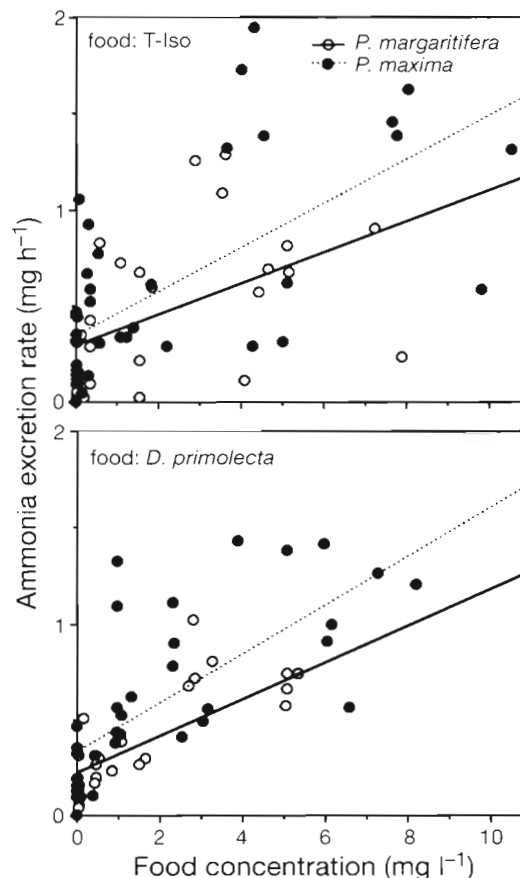


Fig. 6. *Pinctada margaritifera* and *P. maxima*. Excretion rate versus food concentration for oysters feeding on Tahitian *Isochrysis* sp. (T-Iso) (top) and *Dunaliella primolecta* (bottom). Each data point is the rate for a single oyster, standardised to 10 g dry tissue wt. Regression equations are in Table 2

Thus, *Pinctada maxima* maintained positive SFG over a wider range of food concentration than *P. margaritifera*.

DISCUSSION

Effects of food concentration on energetics

At high algal concentrations, suspension-feeding bivalves generally decrease clearance rates (Winter 1978, Griffiths 1980) and absorption efficiency (Van Weel 1961, Thompson & Bayne 1972, Griffiths & King 1979, Griffiths 1980, Bayne et al. 1989, van Erkom Schurink & Griffiths 1992), and increase pseudofaeces production (Foster-Smith 1975, Bayne & Worrall 1980). This study of 2 tropical pearl oysters demonstrated similar trends (Figs. 1, 2 & 3). Consequently, their absorbed energy (AE) was also strongly affected by increasing food concentration (Fig. 4). Both *Pinctada margaritifera* and *P. maxima* controlled the total amount of material in-

gested in varying food environments by a combination of altering their clearance rates and the amount of material rejected in pseudofaeces. This agrees with observations for the sub-tropical pearl oyster *Pinctada imbricata* (Ward & MacDonald 1996).

Pinctada margaritifera and *P. maxima* have distinctly different patterns of feeding and energy budgets. Yuki-hira et al. (1998) demonstrated that *P. maxima* had higher absorption efficiency (abs. eff.) than *P. margaritifera* at low food concentration (0.5 mg l^{-1} T-Iso). There was no difference in clearance rate (CR) at this food level. The present study found that, at higher food concentrations, *P. maxima* had significantly higher abs. eff. and CR than *P. margaritifera*, regardless of algal diet (Figs. 1 & 3, Table 3a, b). Due to this and the lower pseudofaecal wastage of potential food particles in *P. maxima*, this species had higher SFG at food concentrations of 3 to 6 mg l^{-1} (T-Iso) and 2 to 4 mg l^{-1} (*D. primolecta*) (Table 4). Thus, it would appear that *P. maxima* is better adapted to maximise energy gain at higher food concentrations compared with *P. margaritifera*.

Winter (1978) showed that increases in food concentration promote growth rates of bivalves only up to an optimum food concentration beyond which growth rates decline. In terms of maximisation of growth potentiality, optimal concentrations for *P. margaritifera* and *P. maxima* are 1 to 2 mg l^{-1} T-Iso (ca $10\,000$ to $20\,000 \text{ cells ml}^{-1}$) and 2 to 3 mg l^{-1} T-Iso (ca $20\,000$ to $30\,000 \text{ cells ml}^{-1}$), respectively, as indicated by measured SFG (Table 4). These ration levels are in the range of algal concentrations generating the highest SFG or growth rates recorded for other suspension-feeding bivalves (Table 6).

Effects of food species on energetics

The 2 microalgae species used in this study, T-Iso and *Dunaliella primolecta*, significantly influenced the CR, abs. eff. and respiration rate of both pearl oyster species (Table 3), and the pseudofaeces production of

Pinctada margaritifera. *D. primolecta* was not as good a food for pearl oysters as T-Iso at any ration level and the disparity increased at higher ration levels (Table 4). These effects of the microalgal species on the pearl oysters' feeding and metabolism were similar to other studies that demonstrated effects of diet on feeding in bivalves. Tenore & Dunstan (1973b), for example, demonstrated that clearance rate of *Crassostrea virginica* was influenced by different microalgal diets and especially depressed by high concentrations of *Dunaliella tertiolecta* (cf. Fig. 1), while Le Pennec & Rangel (1985) reported that ingestion and digestion of *D. primolecta* by *Pecten maximus* were low and *Isochrysis galbana* was among the best algal diets.

Particle retention efficiency is about 100% in determinations of CR for bivalves filtering particles greater than ca $4 \text{ }\mu\text{m}$ diameter (Bayne et al. 1985). This has been confirmed for *Pinctada margaritifera* and *P. maxima* (Yukihira et al. 1998). Since average diameters of T-Iso and *Dunaliella primolecta* are ca $4.5 \text{ }\mu\text{m}$ and $7.0 \text{ }\mu\text{m}$, respectively, the size difference is unlikely to influence filtration by the pearl oysters. There may be other factors affecting feeding upon different types of food, e.g. chemical stimulants on the surface of food particles. Dwivedy (1973) reported the presence of chemoreceptors, sensitive to different tastes, on the labial palps of the American oyster *Crassostrea virginica*, and Newell & Jordan (1983) inferred chemo-selection of particles by *C. virginica*. Energy used in digesting and absorbing energy from ingested food may be important (Thompson & Bayne 1972, Bayne & Scullard 1977).

The effects of food species on CR, abs. eff. and R resulted in substantial differences in SFG between pearl oysters feeding on the 2 microalgal diets. T-Iso contains 1.3 times more energy than *Dunaliella primolecta* (20.3 and 15.1 J mg^{-1} , respectively), but oysters feeding on T-Iso had 1.5 to 2.1 times higher maximum SFG values than those feeding on *D. primolecta* (Table 4). This was in spite of higher respired energy (RE) for oysters feeding on T-Iso. (The higher oxygen

Table 6. Food levels used for highest Scope for Growth or highest recorded growth rates for filter-feeding bivalves

Species	Food level	Food species	Source
<i>Pinctada margaritifera</i>	$1\text{--}2 \text{ mg l}^{-1}$, ca $10\,000\text{--}20\,000 \text{ cells ml}^{-1}$	Tahitian <i>Isochrysis</i> sp.	This study
<i>Pinctada maxima</i>	$2\text{--}3 \text{ mg l}^{-1}$, ca $20\,000\text{--}30\,000 \text{ cells ml}^{-1}$	Tahitian <i>Isochrysis</i> sp.	This study
<i>Argopecten irradians</i>	$6000 \text{ cells ml}^{-1}$	Tahitian <i>Isochrysis</i> sp.	Cahalan et al. (1989)
<i>Aulacomya ater</i>	ca 3 mg l^{-1}	<i>Dunaliella primolecta</i>	Griffiths & King (1979)
<i>Choromytilus meridionalis</i>	ca 2 mg l^{-1}	<i>Dunaliella primolecta</i>	Griffiths (1980)
<i>Mytilus chilensis</i>	ca $15\,000 \text{ cells ml}^{-1}$	<i>Dunaliella marina</i>	Navarro & Winter (1982)
<i>Mytilus edulis</i>	ca $12\,000 \text{ cells ml}^{-1}$	<i>Tetraselmis suecica</i>	Thompson & Bayne (1974)
<i>Ostrea edulis</i> (juveniles)	$200\,000 \text{ cells ml}^{-1}$	<i>Isochrysis galbana</i>	Beiras et al. (1994)
<i>Venerupis pullastra</i> (juveniles)	$300\,000 \text{ cells ml}^{-1}$	<i>Isochrysis galbana</i>	Beiras et al. (1993)

consumption in pearl oysters feeding on T-Iso at all food concentrations [Table 5] may be due to higher mechanical and physiological costs relating to higher pumping [CR] and also to higher assimilation costs.) The higher energy gain on T-Iso was mainly due to significantly higher CR on T-Iso (Table 3c, d). For the same reason, SFG upper thresholds for *D. primolecta*, i.e. food concentrations beyond which SFG fell below zero, were lower than those for T-Iso in both pearl oysters (Table 4). These results show the importance of energy-rich, ingestible and highly digestible food particles for the energy gain of pearl oysters and other suspension feeders.

The food particles, however, must not only provide the energy needs, but also the nutritional requirements of the pearl oyster. Okauchi (1990) found that, while T-Iso has higher energy and total nitrogen content than *Isochrysis galbana* and *Chaetoceros gracilis*, it was the poorest food species for supporting growth in *Pinctada fucata martensii* spat. The spat showed poorest growth when feeding on T-Iso compared to feeding on *C. gracilis* and *I. galbana*. Okauchi suggested that the low content in T-Iso of eicosapentaenoic acid (EPA), a potentially essential lipid, may be the dietary factor limiting its value for oyster growth (see also Pilsbury 1985, Helm & Laing 1987). For culture of bivalves, T-Iso is generally used in combination with other microalgal species to achieve a diet without nutritional deficiencies. This is currently practised when using T-Iso as food for culturing bivalve larvae, including *P. margaritifera* and *P. maxima* larvae (e.g. Rose & Baker 1994, Southgate & Beer 1997).

Other studies have also demonstrated differences between microalgae species in their ability to support growth of pearl oyster larvae and spat, and differences between microalgae species in the rate at which they are filtered by pearl oysters. Wada (1973) demonstrated that *Pinctada fucata martensii* larvae feeding on pure diets of *Pavlova lutheri* and *Chaetoceros calcitrans* or on a mixture of these 2 algae (1 to 2×10^4 cells ml^{-1}) had higher growth rates than larvae feeding on a pure diet of *Chlorella* sp. or on mixed diets of *Chlorella* sp. with *P. lutheri* or *C. calcitrans*. Nishimura (1980) assessed the influence of *P. lutheri* and *Nitzschia closterium* and ration (20 , 50 and 100×10^3 cells $\text{ml}^{-1} \text{d}^{-1}$) on growth of pearl oyster spat. Better growth rates were obtained with *P. lutheri*, especially at $20\,000$ cells ml^{-1} during the first 20 d, but there were no clear differences in growth at Day 28. Another study of *P. fucata martensii* demonstrated higher filtration rates (percentage of cells removed) when oysters were feeding on *C. calcitrans* (72.6%, at ca $50\,000$ cells ml^{-1}), *C. gracilis* (69.1%, at ca $20\,000$ to $30\,000$ cells ml^{-1}) and *P. lutheri* (56.1 to 68.1%, at ca $40\,000$ cells ml^{-1}) than when oysters were feeding on *Chlorella* sp. (48.4%, at

ca $30\,000$ cells ml^{-1}) and *Olithodiscus* sp. (3.8%, at ca 5000 cells ml^{-1}) (Hayashi 1983).

Broodstock conditioning

Physiological energetics are a valuable tool for predicting long-term growth performance under specific environmental conditions (Beiras et al. 1994). Thus, the present study is relevant to a major aspect of pearl oyster farming, i.e. the maturation of broodstock in tanks using microalgal diets. Hayashi (1980) tested the broodstock maturation of *Punctada fucata martensii* in static indoor tanks using 2 different diets, homogenised rice starch powder and *Pavlova lutheri*, at $50\,000$ to $60\,000$ particles or cells $\text{ml}^{-1} \text{d}^{-1}$. Hayashi reported better maturation of pearl oysters feeding on *P. lutheri*. However, fully mature individuals were not produced in this trial and the feasibility of artificial broodstock conditioning was not demonstrated.

There is no published study on broodstock conditioning of *Pinctada margaritifera* and *P. maxima*. However, our study suggests the potential for using optimum ration levels (i.e. 1 to 2 mg l^{-1} for *P. margaritifera* and 2 to 3 mg l^{-1} for *P. maxima*) of nutritionally rich microalgae, such as a 'balanced' diet containing T-Iso, for broodstock conditioning. If these rations are continuously fed to adult pearl oysters in an appropriate static or flow-through system, they should support gonadal development provided other conditions favour gametogenesis, e.g. temperature regime.

Habitat differences

Jørgensen (1990, 1996) concluded that the capacity for water processing in bivalves is an adaptation to the concentrations of suspended food that prevail in their biotope during the productive seasons of the year. Our studies on comparative feeding ecology of 2 species of tropical pearl oyster support this. Since *Pinctada maxima* processes more water than *P. margaritifera* when feeding in the high particulate range (Fig. 1), *P. maxima* should be better adapted to waters with higher particulate and productivity levels.

Both pearl oyster species occur in the Great Barrier Reef region (GBR), northeast coast of Australia (Hynd 1955, Dayton et al. 1989), but they occur in different habitats, as outlined in the 'Introduction'. *Pinctada margaritifera* tends to occur on coral reefs offshore from the mainland, whereas *P. maxima* occurs on substrates ranging from mud to sand and gravel, but not on coral reefs. *P. maxima* tends to occur in the waters of the inner and middle shelf, where there are greater nutrient inputs and higher productivity levels than in coral reef

habitats. The habitats of *P. margaritifera* are characterised by low levels of suspended particulate matter (SPM); SPM declines significantly from the inner to the outer continental shelf of the GBR (Oliver et al. 1995). Insofar as field data for SPM are available, and one can extrapolate these laboratory energetics data to the field (see below), the optimal food concentrations for *P. margaritifera* (1 to 2 mg l⁻¹) are equivalent to SPM concentrations found in waters of the GBR continental shelf where coral reefs occur (Oliver et al. 1995, Yukihiro unpubl.). For example, the average annual SPM concentration was 1.47 mg l⁻¹ (range: 1.18 to 1.72 mg l⁻¹, n = 21; Yukihiro unpubl.) near a fringing coral reef in Pioneer Bay, Orpheus Island (18° 37' S, 146° 30' E), where *P. margaritifera* is common. The low food concentrations corresponding with the upper threshold of negative SFG of *P. margaritifera* (e.g. 5 mg l⁻¹ for *Dunaliella primolecta* l⁻¹ and 7 mg l⁻¹ for T-Iso) help to explain why this species is excluded from turbid water.

SPM or equivalent data are not available for GBR habitats specifically inhabited by *Pinctada maxima*. However, its terrigenous sediment habitats in the inner to middle shelf region are characterised by turbid water and the SPM concentrations will fluctuate substantially due to river discharge and wind-driven re-suspension of sediment (Furnas et al. 1990, Furnas et al. 1995, Oliver et al. 1995). Reflecting this, at a near-shore site of the inner shelf at Cape Ferguson, the average annual SPM concentration was 12.22 mg l⁻¹ (range: 1.95 to 60.37 mg l⁻¹; n = 72; Yukihiro unpubl.). Although *P. maxima* has not been recorded from this site, it indicates the kind of conditions that this species may encounter at its most inshore distributions. Its higher optimum SFG concentration (2 to 3 mg l⁻¹) and upper threshold for negative SFG (7 or 9 mg l⁻¹) are largely below these field SPM levels, but they are more in accord with these conditions than are the equivalent parameters for *P. margaritifera*. On the other hand, *P. maxima* may experience lower levels of SPM in its offshore, deepwater habitats. It is also well adapted to maintaining a positive SFG at low SPM levels (Table 4, Yukihiro et al. 1998). Thus, *P. maxima* is better adapted than *P. margaritifera* to feeding over a broader range of SPM concentrations and this is reflected in its wider range of habitats.

Unlike the laboratory experiments of this study, where the SPM consisted of pure cultures of microalgae, SPM in the field is a mixture of microalgae species, non-living organic particles and inorganic particles. Much of the field SPM may have no nutritional value for the pearl oyster due to factors such as unmanageable size, indigestibility and no energy content. In considering bivalve feeding and energy budgets, there needs to be caution in extrapolating results from precise levels of SPM in laboratory studies to field situations. This has been recognised by other authors, e.g. Griffiths (1980), Riisgård

(1991), and review by Jørgensen (1996). Thus, a further development of this study will deal with the feeding and energetics of *Pinctada margaritifera* and *P. maxima* supplied with natural suspended particles.

Acknowledgements. We thank Mr Michael Crimp of Indo-Pacific Pearl and Mr Bruce Stevens of Reefarm for providing some of the pearl oyster specimens. We are grateful to Dr Paul Southgate of JCU for constructive criticism of the manuscript. This study was supported in part by an Internal Research Allowance and a Meritorious Research Grant from JCU. H.Y. gratefully acknowledges financial support from the Japan International Cooperation Agency. AIMS contribution number 927

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

Submitted: April 15, 1998; Accepted: July 7, 1998
Proofs received from author(s): September 16, 1998