A physiological comparison between Pacific oysters *Crassostrea gigas* and Sydney Rock oysters *Saccostrea glomerata*: food, feeding and growth in a shared estuarine habitat

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ABSTRACT: This field study had 2 objectives: (1) to test predictions from laboratory studies on growth and feeding behaviour in a comparison of 2 oyster species from the same estuary in NSW, Australia; and (2) to compare the feeding behaviour of these oysters with published accounts of other bivalve species from elsewhere. The predictions were that Pacific oysters *Crassostrea gigas* would feed and grow more quickly along with a greater metabolic efficiency than Sydney Rock oysters *Saccostrea glomerata*. Measurements were made at 3 sites in the Port Stephens estuary, NSW, and the predicted differences between species were confirmed. For both species, growth was quicker from March to May than from May to July (1999). Feeding was also faster in March and May than in July. Absorption efficiency was maintained at a relatively constant level over the experimental period by a compensatory response to changes in the organic content of the ingested material. Selection and absorption efficiencies for nitrogen altered over time, holding nitrogen absorption relatively independent of the nitrogen content of the food. Simple equations were fitted to the data to describe feeding behaviour as a function of properties of the diet, and these equations used to compare these oysters with relationships for other bivalves in the literature. A few such equations may be used to predict net absorption of food energy by oysters in the field, based on measurements of food only. At one rather coarse level, there are basic similarities between bivalve suspension feeders regarding feeding behaviour and its relation to growth. At a more detailed level, differences in physiological responses to diet may help in the interpretation of differences in growth, such as have been observed here for 2 oyster species growing in the same habitat. The competitive advantage enjoyed by *C. gigas* over *S. glomerata* is due to faster rates of feeding, particularly at higher food concentrations, and greater metabolic efficiencies of both feeding and growth.

KEY WORDS: Oysters · Feeding · Growth · Metabolism · Carbon · Nitrogen

INTRODUCTION

The Sydney Rock oyster, now recognised as *Saccostrea glomerata* (formerly *S. commercialis*; Buroker et al. 1979, Anderson & Adlard 1994), is native to estuarine areas on the coast of New South Wales (NSW), Australia. The systematic cultivation of this species first began in 1870. Production increased rapidly from the 1930s to a peak in the 1970s (Malcolm 1987, Nell 1993). Nell (1993) reported a subsequent decline in production, from around 170 million oysters per annum in the 1970s to 100 million in 1996–1997. The Port Stephens estuary, NSW (32° 45′ S, 152° 10′ E) is at the centre of this species' range and is an important area for its cultivation.

One likely cause for a decline in Rock oyster production at Port Stephens is increased cultivation of the Pacific oyster *Crassostrea gigas*. Pacific oysters first appeared in large numbers at Port Stephens in the

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summer of 1984–1985 (Nell 1993) and, although first treated as a 'noxious species', approval to farm Pacific oysters was passed in 1991. This species is thought to grow more rapidly than the Sydney Rock oyster (Nell 1991) and with a greater fecundity, thus posing a threat to the native species (Holliday & Nell 1985, Mason & Nell 1995).

In a recent study, Honkoop & Bayne (2002) confirmed earlier observations that both species grew in whole body weight throughout the year (Nell 1991), although an uncoupling of growth between the shell and the dry tissue resulted in a seasonal pattern in tissue growth that differed between the species. Somatic tissue growth, for example, was positive in *Saccostrea glomerata* during the spring (September to November 1999) and autumn (February to June 2000), but positive only during the autumn for *Crassostrea gigas*. In the autumn, growth of the Pacific oysters was faster than that of the Rock oysters. Both species lost tissue weight in the summer (November 1999 to February 2000), possibly related to the annual reproductive cycle, particularly spawning. Mason & Nell (1995) observed that Pacific oysters in Port Stephens spawned in October; Sydney Rock oysters spawned later, during December and January (i.e. summer in Australia).

An interest in genetic correlates of growth prompted a number of laboratory experiments to explore relationships between various physiological traits and rates of growth of these 2 species (Bayne 1999a, Bayne et al. 1999). When these data were reduced to a similar body size (Bayne 1999b) Pacific oysters were found to 'out-perform' Rock oysters by their faster rates of both feeding and growth. This comparison was constrained, however, by the very different origins of the experimental specimens of the 2 species (the Pacific oysters came from Tasmania, the Rock oysters from NSW), and by the limited environmental conditions used in the experiments. As the introduction of Pacific oysters into NSW provides a good example of bringing 2 related species into close proximity and potential competition for resources, a physiological comparison under field conditions was considered timely.

This comparison of feeding and growth was therefore done to test hypotheses based on the earlier laboratory studies, specifically: (1) Pacific oysters would grow faster than Sydney Rock oysters; (2) Pacific oysters would also feed more rapidly than Rock oysters; (3) the 2 species would have similar feeding efficiencies; and (4) Rock oysters would have faster metabolic rates than Pacific oysters, and greater metabolic expenditures per unit of absorbed energy.

In recent years, our understanding of the feeding behaviour of bivalve molluscs under natural conditions of food availability, and the consequences for growth, has improved substantially (Bayne et al. 1989, 1993,

Navarro et al. 1992, 1994, Cranford & Hargrave 1994, Clausen & Riisgärd 1996, Grant 1996, Hawkins et al. 1996, 1998, 1999, Iglesias et al. 1996, 1998, Soletchnik et al. 1996, Urrutia et al. 1996, Arifin & Bendell-Young 1997, Barillé et al. 1997, Cranford et al. 1998, Wong & Cheung 1999, Babarro et al. 2000, Pouvreau et al. 2000, Ren et al. 2000). These and other studies have led to the derivation of formal relationships between rates and efficiencies of feeding, and the quantity and quality of the available food. Such studies have also demonstrated a flexibility of feeding behaviour in these suspension-feeders (Bayne 1998). Previous feeding history and the endogenous metabolic demands of growth and reproduction (Hawkins & Bayne 1992, Kreeger 1993, Kreeger et al. 1995, Cranford 1998) are significant determinants of feeding behaviour and should be considered, together with environmental factors, in analyses of feeding and growth. When taken together with earlier research (reviews by Winter 1978, Bayne & Newell 1983, Griffiths & Griffiths 1987), this large body of information greatly facilitates further comparative studies of the physiological energetics of bivalves.

In evaluating predictions about growth and feeding in 2 oyster species in NSW, Australia, therefore, a secondary aim was to compare the observed food/feeding relationships with the findings of other published studies on mussels *Mytilus edulis*, cockles *Cerastoderma edule*, scallops *Placopecten magellanicus* and other species. The following features, comprising the main elements of feeding behaviour, were considered: (1) filtration rates of suspended particles as a function of particle concentration; (2) the efficiency with which relatively organic-rich particles are selected for ingestion; (3) relations controlling the efficiency of absorption; (4) how some of these rates and efficiencies differ when considered in terms of total nitrogen in the food compared with relations for total organic matter; and (5) the precision with which information on available food may be used to predict patterns of feeding and growth.

The study was done at 3 sites in the Port Stephens estuary (Fig. 1) over a period of 5 mo during autumn and winter (March to July). The design was not appropriate for a rigorous comparison of sites and any 'seasonal' element in the data is preliminary in the absence of adequate replication. Rather, the aim was to compare the performance of the 2 oyster species and to relate feeding behaviour to simultaneous measurements of growth and to properties of the available food. The results were expected to shed some light on the physiology of 2 similar species that now share a common habitat, and to contribute to an understanding of the role of a variable food supply in determining the growth of bivalves.
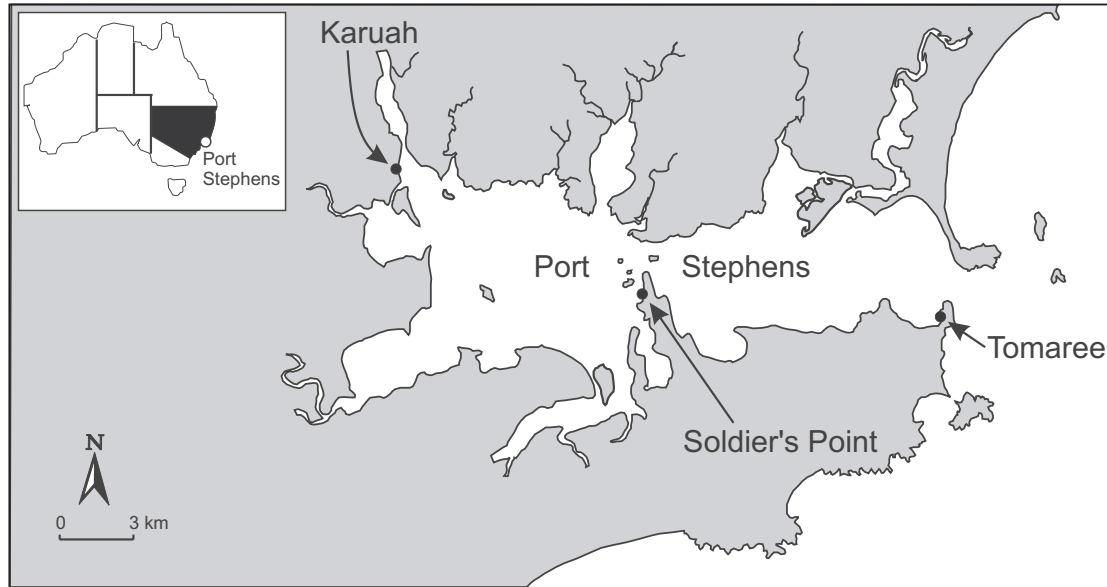
Fig. 1. A map of the study sites in the Port Stephens estuary 250 km north of Sydney, NSW

MATERIALS AND METHODS

The Port Stephens Research Centre of NSW Fisheries provided the oysters. Individuals of each species were from natural recruitment within the Port Stephens estuary and had been maintained in cages on a commercial oyster lease. When acquired for this experiment, the Pacific oysters *Crassostrea gigas* weighed 29.4 ± 1.4 g whole body weight (shell plus all soft tissues including pallial fluid; mean ± standard error for n = 20). The Rock oysters *Saccostrea glomerata* were slightly smaller at 26.1 ± 0.8 g. The Pacific oysters weighed 0.69 ± 0.04 g dry tissue (tissue dried for 24 h at 80°C); the Rock oysters weighed 0.44 ± 0.03 g.

A total of 96 oysters of each species were tagged for identification using plastic 'shellfish tags' glued to the shell. Sixteen individuals of each species were then placed in each of 6 plastic oyster trays ($40 \times 60 \times 8$ cm^3) for deployment of 2 trays subtidally at each of 3 sites within the estuary (Fig. 1). At Karuah, the cages were attached to wooden pilings at the end of a pier. The area in the immediate vicinity of this pier is used for commercial cultivation of oysters. At Soldier's Point, the cages were suspended below a wharf which is part of a small marina. This site is also within a larger area used for commercial oyster production. There was some risk of these oysters being affected by operations at the marina, but this risk was considered small. The third site was at Tomaree, where the oyster trays were suspended from a small jetty. This site was more exposed than the other 2 to prevailing winds and wave fetch, and is not used for commercial production. The cages at Tomaree were lost to the weather sometime between May (the time of the second site visit) and July (the third site visit and the end of the experiment).

The sites were visited in March, May and July 1999, when: (1) water temperature and salinity were recorded, and samples taken for measurement of food concentrations; (2) trays were recovered for cleaning and all oysters were air-dried and weighed (= whole-body weight); (3) 12 oysters of each species were selected for measurement of feeding behaviour; and (4) these oysters were subsequently dissected, the soft tissues dried at 80°C for 24 h, and then weighed (= dry flesh weight): at Soldier's Point, in March and July, 10 individuals were used for measurement of oxygen consumption rates. Only those oysters actively feeding (i.e. with shells open, and producing biodeposits) were measured for feeding behaviour. This resulted in 8 individuals of each species being used to calculate feeding traits per feeding trial. Each site visit lasted 1 d. Sites were visited in random order.

Availability of food. On 3 occasions during each visit, at each site, 2l of seawater were filtered, in duplicate, through numbered glass-fibre (GF/C) filters, washed in distilled water, dried, ashed and weighed. The filters were kept on ice until returning to the laboratory where they were dried (80°C, 24 h) and weighed. One

duplicate set was then ashed at 450°C for 4 h and weighed again. The second duplicate was analysed for carbon and nitrogen content using a Perkin Elmer series II (2400) CHN Analyser, with acetanilide as standard. The following were then calculated: the total particulate matter in suspension (TPM, mg l^{-1}); the particulate inorganic matter (PIM; weight after ashing) and, by difference, the particulate organic matter (POM) in suspension (mg l^{-1}); the percent carbon and nitrogen content by weight of the TPM and the C:N mass ratio of the particulates.

Similar procedures were used in a parallel study of suspended particulates in Port Stephens, at a site close to Soldier's Point (B.L.B. unpubl. data) and the results were used to provide a reference for the measurements made for this experiment (see 'Results').

Feeding behaviour and oxygen consumption. Feeding rates and efficiencies (see Table 1 for abbreviations) were measured using the 'biodeposition method' as described by Iglesias et al. (1998), Hawkins et al. (1998) and Bayne et al. (1999). Oysters were placed individually in specially constructed feeding trays and directly supplied with water pumped from the immediate vicinity of the experimental trays. The feeding trays measured 37 × 16 × 6 cm^3, and were painted white to facilitate collection of biodeposits and designed to minimise turbulent flows of water through the tray (water inflow baffled; multiple outflow ports). Flow rates were controlled at 500 ± 48 ml min^{-1} and the trays were shaded during the measurements. The oysters were left undisturbed until they were open, feeding and producing biodeposits (faeces and pseudofaeces), requiring between 30 and 60 min. Any oysters not feeding after 60 min were not considered further. All deposited material was then pipetted from the trays, which were left undisturbed for a further 60 min. The faeces and pseudofaeces deposited during this time were separately and quantitatively collected by pipette, briefly suspended in ca. 30 ml of filtered seawater and then filtered through GF/C filters. In March and July, but not in May, the oysters were then left undisturbed for a further 30 min, after which biodeposits were collected for analysis of their carbon and nitrogen contents.

On return to the laboratory, the filters from the first 60 min period were treated as described for the food samples. The filters for carbon and nitrogen analysis were dried, weighed and analysed using the CHN Analyser. The feeding traits listed in Table 1 were then calculated for each oyster individually. The dry flesh of the oysters was subsequently weighed. All physiological rates were related to a standard body size of 1 g dry tissue using the procedure described by Bayne & Newell (1983). This uses an exponent that relates the measured physiological rates to the oyster's dry body mass; the exponents quoted in Bayne (1999b) were used.

Oxygen consumption rates were determined by incubation of individual oysters within respirometer flasks of ca. 1 l volume, fitted with Strathkelvin oxygen electrodes and monitored with a Strathkelvin model 928 oxygen analyser (Bayne 1999b). The oysters were left for a minimum of 30 min before recording was started, and consumption rates calculated only whilst the concentration of oxygen in the flasks was >75% of the air-saturation value. The consumption rates (ml O$_2$ h^{-1}) were then calculated for a standard body size of 1 g dry tissue.

Growth. The protocol for estimating the growth of individuals was as follows. (1) In March, all oysters were weighed for whole-body weight. In addition, 12 individually tagged oysters of each species, from each site, taken at random from the 2 trays, were measured for dry flesh weight. These were the same oysters that had, earlier in the site visit, been used for determinations of feeding behaviour. (2) A regression analysis of dry flesh weight as a function of whole-body weight for these 36 individuals yielded a regression equation that was then used to estimate the weight of dry tissue of the remaining oysters in each tray, at each site. (3) In May, a further 12 oysters of each species were used from each site for physiological determinations, then measured for whole-body and dry tissue weights, and these data also analysed by regression (n = 36). The estimated dry tissue weights of these particular oysters from the March sample (i.e. estimated from the whole-body/dry tissue weight regression in March) were taken as the starting (t_0) values, for comparison with the measured values in May (t_1). The whole-body weights of all remaining oysters were measured again and assigned an estimated dry flesh weight from the above regression for May. (4) In July, a final sample of 12 oysters of each species was weighed as before (whole-body and dry tissue) and the result used as the t_2 sample, for comparison with the estimated dry tissue weight, in May, of these same oysters. In both March and May, unlabelled oysters of similar size were used to replace those removed for measurement, in order to maintain a constant stocking density in the trays.

Changes in body weight per day were calculated for 2 periods, from March to May and from May to July, 1999. These data were then checked by regression analysis for any dependence on body size. In no case was the calculated growth, either as whole-body or dry tissue weight, significantly dependent on initial body size (p > 0.05). This was subsequently confirmed by covariance analysis, with initial body size as the covariate. All growth data are therefore presented as change in body size per day for the 2 growth periods of the experiment. Growth rates were also calculated as 'average relative growth' (ARG), where ARG = ln(W_t/W_{t-1})/Δt, where W is body weight and t is time, for comparison with previously published data.

Table 1. Terms used to describe feeding behaviour in 2 oyster species, and their measurement. Abbreviations which refer to measurements on the suspended particulate matter (the food; see text) are: TPM, total particulate matter (mg l^{-1}); PIM, particulate inorganic matter (mg l^{-1}); OC, organic content of the TPM (fraction); TPMNC, nitrogen content of the TPM (fraction)

Measured variable and its abbreviation	Derived variable and its abbreviation	Description (and units)
Total faeces production; FP		Faeces dried at 80°C (mg h^{-1})
Faecal inorganic matter; FIM		Faeces ashed at 450°C (mg h^{-1})
	Faecal organic matter; FOM	FP – FIM (mg h^{-1})
Total pseudofaeces production; PsP (= Rejection rate; RR)		Pseudofaeces dried at 80°C (mg h^{-1})
Pseudofaecal inorganic matter; PsIM		Pseudofaeces ashed at 450°C (mg h^{-1})
	Pseudofaecal organic matter; PsOM	PsP – PsIM (mg h^{-1})
	Pseudofaecal organic content; PsOC	PsOM/PsP (fraction)
	Filtration rate; FR	(FIM+PsIM) $\times$ (TPM/PIM) (mg h^{-1})
	Selection efficiency; SE	1 – (PsOC/OC) (fraction)
	Ingestion rate; IR (or, net organic ingestion rate, NOIR)	(FR $\times$ OC) – PsOM (mg h^{-1})
	Organic content of ingested matter; OCI	IR/(FR – PsP) (fraction)
	Absorption rate; AR (or, net organic absorption rate, NOAR)	IR – FOM (mg h^{-1})
	Absorption efficiency; AE (or, net absorption efficiency for ingested organics, NAEIO)	AR/IR (fraction)
Faecal nitrogen content; FNC		Proportion of nitrogen in true faeces (fraction)
Pseudofaecal nitrogen content; PsNC		Proportion of nitrogen in pseudofaeces (fraction)
	Filtration rate for nitrogen; FR_N	FR $\times$ TPMNC (mg h^{-1})
	Pseudofaeces nitrogen production; PsP_N (or, rejection rate for nitrogen; RR_N)	RR $\times$ PsNC (mg h^{-1})
	Selection efficiency for nitrogen; SE_N	1 – (PsNC/TPMNC) (fraction)
	Nitrogen ingestion rate; IR_N	FR_N – PsP_N (mg h^{-1})
	Nitrogen absorption rate; AR_N	IR_N – (FP $\times$ FNC) (mg h^{-1})
	Absorption efficiency for nitrogen; AE_N	AR_N/IR_N (fraction)

Data analysis. The primary purpose of this study was to evaluate whether the 2 species grew at different rates when held under similar conditions, and whether physiological differences would reflect any such differences in growth rate (see 'Introduction'). It became clear, however, that there were large differences in growth rates between times of sampling (see 'Results'). A secondary purpose was therefore incorporated to equate any physiological differences also due to these apparent seasonal effects. The hypotheses to be tested were therefore that physiological performance, particularly in feeding behaviour, would correlate positively with growth rate, and that both physiological performance and growth would be greater for the Pacific oysters than for the Sydney Rock oysters.

Statistical analyses were performed with SYSTAT Version 6.0 (SPSS). All data were first checked for normality by examining normal probability and residual plots (Wilkinson 1996). ANOVA was then used to evaluate differences between species and between months, and the 'species $\times$ month' interaction, with different sites treated separately and pooled. Regression analysis was used to explore relations between feeding traits and the properties of the available food.

RESULTS

Temperatures, salinities and food

Water temperature and salinity did not differ significantly between sites in any of the 3 mo of measurements. Average values (± standard error) were as follows: temperature (°C): March 25.4 ± 0.6, May 20.2 ± 0.4, July 15.8 ± 0.4; salinity (‰): March 35.0 ± 2.0, May 33.3 ± 2.6, July 27.0 ± 2.7.

On average, concentrations of TPM differed between sites in the order Karuah > Soldier's Point >

Table 2. Concentrations of total particulate matter (TPM) and particulate organic matter (POM) at 3 experimental sites in Port Stephens; values are mg l^{-1} ± standard error. OC%, C% and N% are organic content, carbon and nitrogen, respectively, all as percent of TPM. C:N is the mass ratio for carbon:nitrogen in the total particulates

Site	Month (1998)	TPM	POM	OC%	C%	N%	C:N
Karuah	Mar	15.7 ± 3.0	2.69 ± 0.57	17.3 ± 1.6	7.5 ± 0.5	2.1 ± 0.2	3.6 ± 0.1
	May	6.5 ± 0.7	1.17 ± 0.16	17.9 ± 1.6	8.5 ± 0.4	1.3 ± 0.1	6.8 ± 0.6
	Jul	8.5 ± 1.3	1.13 ± 0.18	13.2 ± 0.7	8.3 ± 0.7	0.8 ± 0.2	10.6 ± 0.5
Soldier's Point	Mar	5.6 ± 0.4	2.02 ± 0.33	36.1 ± 4.7	9.1 ± 0.6	2.0 ± 0.1	4.5 ± 0.3
	May	4.3 ± 0.3	0.80 ± 0.13	18.1 ± 2.1	8.1 ± 0.7	1.4 ± 0.1	5.7 ± 0.1
	Jul	3.1 ± 0.1	0.59 ± 0.02	19.6 ± 1.2	12.1 ± 0.6	1.2 ± 0.1	9.9 ± 0.3
Tomaree	Mar	1.9 ± 0.2	0.69 ± 0.05	38.7 ± 4.7	14.5 ± 0.3	3.9 ± 0.3	3.8 ± 0.4
	May	3.9 ± 0.7	0.94 ± 0.16	25.2 ± 2.5	10.9 ± 0.4	1.7 ± 0.1	6.8 ± 0.6

Tomaree (Table 2) and between months, not including Tomaree, in the order March > May > July; differences due both to sites and to months were statistically significant (p < 0.05). The full range of TPM values was from 1.9 to 15.7 mg l^{-1}. Concentrations of POM (range from 0.59 to 2.69 mg l^{-1}) varied between sites and months in the same order as TPM, and represented an organic content (OC) of the particulates of between 13 and 39% (Table 2; OC%).

These values for TPM and POM were typical for the Port Stephens estuary (Fig. 2). This figure compares the values used in this study with independent measures taken at a site close to Soldier's Point over an 11 mo period from March 1998 to January 1999.

The OC of the particulates was considered a measure of food quality and was, on average across the 3 sites, largest in March. The other measure of food quality was the C:N mass ratio (Table 2), which also showed a strong seasonal pattern, with lowest values in March (overall average 4.0 ± 0.18), greater in May (6.4 ± 0.32) and greatest in July (10.1 ± 0.27). Large C:N values were coincident with reduced OC of the particulates.

Growth

When measured either as total weight or as dry tissue weight, Pacific oysters grew more quickly than Rock oysters over both time periods (Table 3). Growth in both species was faster between March and May than between May and July. A similar trend, both between species and over time, was evident for growth in dry tissue when estimated as average relative growth (Table 3). The data therefore strongly support the species difference hypothesis regarding growth rate.

Feeding

Comparing species

Where there were significant differences in feeding behaviour, the Pacific oysters had faster rates than the Sydney oysters. This partially supports the 'feeding-rate' hypothesis. However, this species difference did not occur on all occasions (Tables 4 & 5). One possible explanation concerns the feeding responses of the oysters to different levels of total particulate matter. In March, for example, when temperatures at the 3 sites were similar, filtration rates (FR) by Rock oysters were significantly reduced compared with those for Pacifics at the highest level of TPM (as experienced at Karuah),
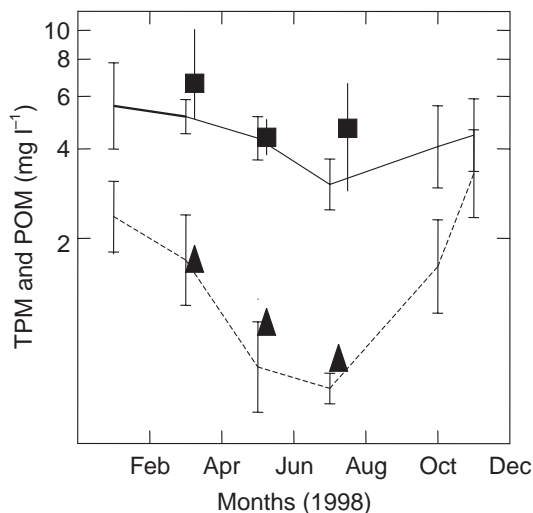

Fig. 2. Concentrations of total particulate matter (TPM; solid line) and particulate organic matter (POM; dashed line) in suspension in the Port Stephens estuary, NSW (values are means ± standard error for variable sample sizes between 9 and 18). The ■ (TPM) and ▲ (POM) are the mean values measured for the present study (see Table 2)

Table 3. Growth rates of Pacific (*Crassotrea gigas*) and Sydney Rock (*Saccostrea glomerata*) oysters over 2 periods in 1999 and at 2 sites in Port Stephens. Values are means ± 95% CI for n = 12 in all cases. ARG is 'average relative growth' (see text). In all cases except ARG for May to July, the differences between species were highly significant (p < 0.001), with *C. gigas* values > *S. glomerata*. Differences between sites in the period March to May were all highly significant (Soldier's Point > Karuah); site differences May to July were not significant. Rates of growth between March and May were all significantly faster than between May and July

Species	Site	Whole-body growth: mg d^{-1}		Dry tissue growth: mg d^{-1}		ARG ($\times 10^{-3}$)	
		Mar–May	May–Jul	Mar–May	May–Jul	Mar–May	May–Jul
Crassotrea	Karuah	219 ± 55	74.8 ± 43.5	7.55 ± 1.43	2.58 ± 1.47	6.5 ± 1.3	1.8 ± 0.9
gigas	Soldier's Point	341 ± 72	97.5 ± 36.1	10.90 ± 2.28	3.12 ± 1.16	9.0 ± 1.6	2.0 ± 0.9
Saccostrea	Karuah	40.8 ± 14.9	14.9 ± 8.7	1.84 ± 0.61	0.67 ± 0.39	2.0 ± 1.0	1.3 ± 1.1
glomerata	Soldier's Point	71.9 ± 11.9	28.0 ± 11.8	3.23 ± 0.53	1.26 ± 0.53	2.5 ± 0.4	0.9 ± 0.7

a difference not evident at the lowest TPM concentration (at Tomaree; Fig. 3). The species differences in feeding behaviour were most marked when the oysters were processing a larger mass of particulate matter.

The data did not entirely support the 'feeding-efficiency' hypothesis of no differences between species (Table 5). Pacific oysters had greater selection efficiencies (SEs) than Rock oysters at 1 of 3 sites (Karuah) and greater absorption efficiencies (AEs) at 2 (Karuah and Soldier's Point). SE in Rock oysters was greater at Tomaree. In the Rock oysters, although not in the Pacifics, SE was sensitive to the OC of the food, increasing from near zero at a particulate OC% of approx. 12%, to a maximum 0.45 at the higher OC% values of ca. 40%. SE did not vary with the FR in either

species. Absorption efficiency was positively related to POC (see below and Fig. 4).

Comparing months

When feeding behaviour varied significantly between months (Tables 4 & 5), measured rates were in the order March > May > July, with the exception of FR at Tomaree where rates in May were higher than in March, in both species. It is not possible to discriminate rigorously between the effects of temperature and food in these comparisons between months. There appeared, however, to be a variable influence of temperature on feeding rates, as measured by an index of temperature dependence, Q_{10}. For example, at Soldier's Point,
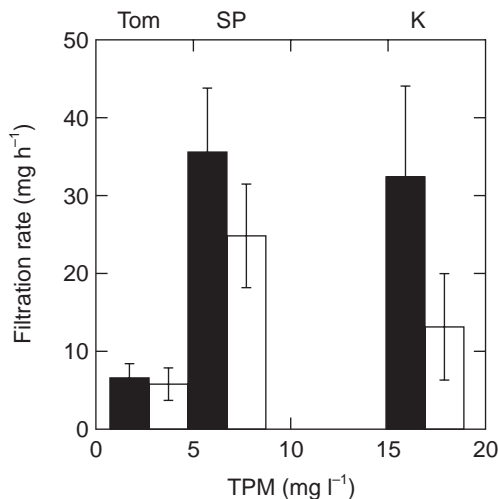

Fig. 3. Rates of filtration by 2 species of oyster related to the concentrations of TPM in suspension at Port Stephens in March, 1999. Black bars, Pacific oysters; White bars, Rock oysters. Values are means ± 95% CI; n = 8 for each histogram. The data are for 3 sites: Tom: Tomaree (the species difference was not significant); SP: Soldier's Point (species difference significant at p < 0.05); K: Karuah (species difference significant at p < 0.001)
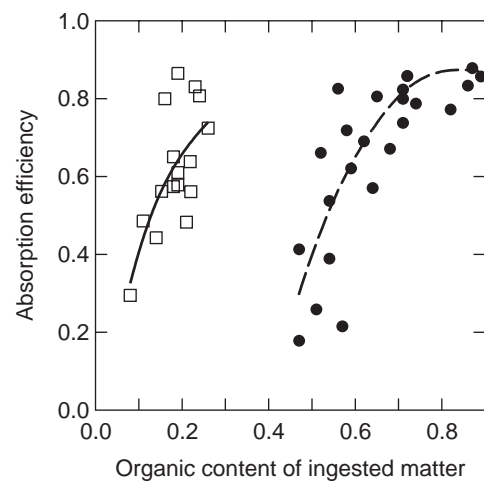

Fig. 4. *Crassostrea gigas*. Absorption efficiency (AE) related to the organic content of the ingested (OCI) matter, in March (●) and in July (□). The curves are fitted as follows (parameter values ± standard error): March: AE = $0.90 ± 0.12[1-e^{6.54 ± 3.29(OCI - 0.41 ± 0.04)}]$ (r^2 = 0.64); July: AE = $0.78 ± 0.23[1-e^{11.2 ± 8.8(OCI - 0.03 ± 0.05)}]$ (r^2 = 0.45)

Table 4. Filtration (FR), ingestion (IR) and absorption (AR) rates, and selection (SE) and absorption (AE) efficiencies in 2 oyster species at 3 sites, during 3 mo, in Port Stephens. Values for feeding rates are mg g^{-1} h^{-1} ± 95 % CI (n = 8). The efficiency values are fractions (also ±95 % CI and n = 8). The results of statistical analyses are shown in Table 5

Species	Site	Month	FR	IR	AR	SE	AE
Crassostrea gigas	Karuah	Mar	32.4 ± 9.1	4.2 ± 1.4	3.0 ± 1.2	0.40 ± 0.10	0.71 ± 0.11
		May	19.2 ± 6.3	3.7 ± 0.7	2.4 ± 0.7	0.46 ± 0.04	0.64 ± 0.13
		Jul	22.1 ± 6.1	1.2 ± 0.4	0.7 ± 0.3	0.21 ± 0.08	0.57 ± 0.14
	Soldier's Point	Mar	35.6 ± 6.4	12.4 ± 3.9	10.2 ± 3.6	0.44 ± 0.12	0.81 ± 0.06
		May	19.1 ± 5.6	1.4 ± 0.9	1.0 ± 0.8	0.24 ± 0.07	0.69 ± 0.12
		Jul	5.7 ± 1.9	1.1 ± 0.6	0.7 ± 0.5	0.33 ± 0.12	0.64 ± 0.12
	Tomaree	Mar	6.6 ± 1.4	2.8 ± 1.2	1.0 ± 0.3	0.20 ± 0.10	0.45 ± 0.20
		May	23.2 ± 7.8	4.0 ± 2.3	2.4 ± 2.0	0.15 ± 0.06	0.49 ± 0.20
Saccostrea glomerata	Karuah	Mar	13.1 ± 5.3	2.0 ± 1.7	0.9 ± 0.8	0.30 ± 0.09	0.46 ± 0.17
		May	15.1 ± 3.4	1.0 ± 0.3	0.5 ± 0.2	0.32 ± 0.05	0.53 ± 0.11
		Jul	12.3 ± 2.4	0.7 ± 0.3	0.3 ± 0.1	0.10 ± 0.04	0.39 ± 0.10
	Soldier's Point	Mar	24.8 ± 5.2	9.7 ± 3.0	5.9 ± 2.2	0.48 ± 0.10	0.60 ± 0.10
		May	8.8 ± 4.7	1.3 ± 0.8	0.8 ± 0.4	0.39 ± 0.09	0.58 ± 0.13
		Jul	7.3 ± 3.0	0.7 ± 0.3	0.3 ± 0.2	0.30 ± 0.09	0.45 ± 0.10
	Tomaree	Mar	5.8 ± 1.6	2.5 ± 0.9	1.1 ± 0.5	0.30 ± 0.09	0.46 ± 0.12
		May	30.5 ± 5.8	5.1 ± 2.5	1.6 ± 1.2	0.34 ± 0.09	0.32 ± 0.21

where TPM concentrations were relatively invariant over the 3 mo (Table 2), the Q_{10} for FR was high for the temperature change between May and July (5.3 and 4.8 for Pacific and Rock oysters, respectively, for a temperature change from 15.8 to 20.2°C). Between March and May, however, Q_{10} was significantly less (2.2 and 1.3, for a temperature change from 20.2 to 25.4°C). The 2 species had similar apparent sensitivities to temperature changes over the full range from 15.8 to 25.4°C. This comparison is, however, provisional, due to the confounding between food quantity, food quality and temperature between mo.

The relationship between AE and the OC of the diet (Fig. 4) varied between months, in both species. In July, when the organic content of ingested matter (OCI; see Table 1) was small, the curve for AE as a function of OCI was displaced to the left, relative to March. The curves in Fig. 4 are drawn according to the equation

Table 5. Levels of significance for the effects of 'species', 'mo' and their interactions, in analyses of variance for measures of FR, IR, AR, and SE and AE by 2 oyster species, at 3 sites and over 3 mo in Port Stephens (see Table 4). Note that measurements at the Tomaree site were made only in March and May. P: Pacific oysters; R: Rock oysters; *: p < 0.05; **: p < 0.005; ***: p < 0.001; ns: not significant. In all cases, including those where the interaction term was significant, the rank order of month was the same for both species

Site	Variable	Comparing species	Comparing mo	Interaction (species × months)
Karuah	FR	***P > R	*Mar > May = Jul	*
	IR	***P > R	***Mar > May > Jul	ns
	AR	***P > R	***Mar > May > Jul	*
	SE	***P > R	***Mar = May > Jul	ns
	AE	**P > R	ns	ns
Soldier's Point	FR	***P > R	***Mar > May > Jul	**
	IR	ns	***Mar > May > Jul	ns
	AR	*P > R	***Mar > May > Jul	*
	SE	ns	**Mar > May > Jul	ns
	AE	**P > R	**Mar > May > Jul	ns
Tomaree	FR	ns	***May > Mar	ns
	IR	ns	*May > Mar	ns
	AR	ns	ns	ns
	SE	***R > P	*Mar > May	ns
	AE	ns	ns	ns

Table 6. Ingestion (IR_N) and absorption (AR_N) rates for nitrogen, and selection (SE_N) and nitrogen absorption (AE_N) efficiencies in 2 oyster species at 3 sites, during 2 mo, at Port Stephens. At Tomaree, measurements were made only in March. Values for feeding rates are mg N g^{-1} h^{-1} $\pm 95\%$ CI (n = 8). The efficiency values are fractions (also $\pm 95\%$ CI and n = 8). For the results of a statistical analysis of these data see Table 7

Species	Site	Mo	IR_N	AR_N	SE_N	AE_N
Crassostrea gigas	Karuah	Mar	0.78 ± 0.07	0.73 ± 0.07	0.23 ± 0.05	0.93 ± 0.02
		Jul	0.23 ± 0.08	0.12 ± 0.07	0.61 ± 0.07	0.46 ± 0.13
	Soldier's Point	Mar	1.13 ± 0.26	1.08 ± 0.25	0.33 ± 0.09	0.96 ± 0.05
		Jul	0.25 ± 0.08	0.12 ± 0.06	0.55 ± 0.08	0.44 ± 0.08
	Tomaree	Mar	0.32 ± 0.07	0.27 ± 0.08	0.28 ± 0.09	0.83 ± 0.04
Saccostrea glomerata	Karuah	Mar	0.41 ± 0.16	0.36 ± 0.17	0.11 ± 0.03	0.84 ± 0.05
		Jul	0.11 ± 0.04	0.04 ± 0.01	0.42 ± 0.17	0.44 ± 0.12
	Soldier's Point	Mar	0.91 ± 0.11	0.86 ± 0.11	0.32 ± 0.11	0.94 ± 0.02
		Jul	0.27 ± 0.15	0.14 ± 0.09	0.58 ± 0.15	0.51 ± 0.15
	Tomaree	Mar	0.12 ± 0.04	0.09 ± 0.04	0.19 ± 0.08	0.71 ± 0.12

(Bayne et al. 1987): $AE = a(1-e^{-b(OCI-c)})$, where *a*, *b* and *c* are fitted parameters representing, respectively, maximal AE, the rate at which this is reached relative to increasing OCI, and the value for OCI at which AE is 0. The shift in this relation over time (March to July) is expressed particularly in the value for *c*, which declines, for Pacific oysters, from 0.41 ± 0.04 in March to 0.03 ± 0.05 in July. A similar shift in the AE/OCI relation occurred in the Rock oysters. As overall AE remained relatively invariant over time (Tables 4 & 5), this suggests a physiological compensation for temporal changes in the OC of the diet. These findings are consistent with the expectation that feeding behaviour would be faster and more efficient when growth rates were most rapid (i.e. March to May).

Feeding on nitrogen

Results presented thus far have been in terms of POM. The feeding traits were also measured, in March and July, in units of nitrogen (Table 6). Differences between species were significant for IR and absorption of nitrogen at 2 sites (Table 7). Where these differences were significant, Pacific oysters were more active than Rock oysters. Feeding rates were faster in March than in July.

Generally, SE and AE for nitrogen did not differ between species (the exception is for SE_N at Karuah, where Pacifics had a higher efficiency than Rocks). For both species, SE for nitrogen increased with increase in the C:N ratio of the available food (Fig. 5). AE for nitrogen was greater in March than July (Table 7) and

Table 7. Levels of significance in the effects of 'species', 'mo' and their interactions in analyses of variance in measures of IR_N and AR_N, and SE_N and AE_N by 2 oyster species, at 3 sites and during 2 mo, in Port Stephens (see Table 6 for the actual data). Measurements at Tomaree were made in March only. P: Pacific oysters; R: Rock oysters; *: $p < 0.05$; **: $p < 0.005$; ***: $p < 0.001$; ns: not significant. In all cases for Karuah and Soldier's Point, including those where the interaction term was significant, the rank order between mo was the same for both species

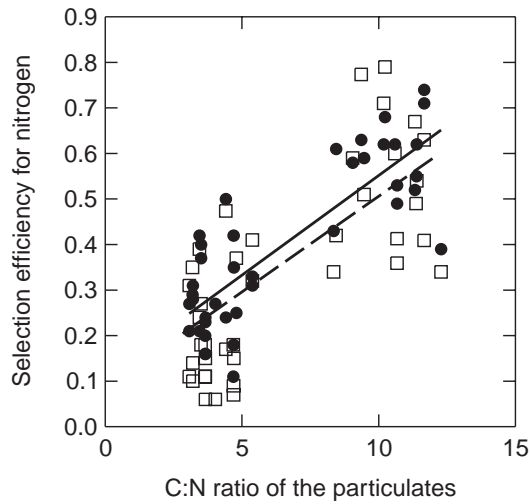| Site	Variable	Comparing species	Comparing month	Interactions (species × month)
Karuah	IR_N	***P > R	***Mar > Jul	*
	AR_N	***P > R	***Mar > Jul	**
	SE_N	**P > R	***Jul > Mar	ns
	AE_N	ns	***Mar > Jul	ns
Soldier's Point	IR_N	ns	***Mar > Jul	ns
	AR_N	ns	***Mar > Jul	ns
	SE_N	ns	***Jul > Mar	ns
	AE_N	ns	***Mar > Jul	ns
Tomaree	IR_N	***P > R	–	–
	AR_N	***P > R	–	–
	SE_N	ns	–	–
	AE_N	*P > R	–	–

Fig. 5. Selection efficiencies for nitrogen (SE_N) related to the carbon:nitrogen ratio of the suspended particulates, for 2 oyster species at Port Stephens. ●: *Crassostrea gigas*; □: *Saccostrea glomerata*. The regressions are fitted as follows (parameter values ± standard error; no significant species differences): *Crassostrea gigas*: $SE_N = 0.15 \pm 0.05 + 0.037 \pm 0.006 \times CN$ ($r^2 = 0.41$); *Saccostrea glomerata*: $SE_N = 0.12 \pm 0.05 + 0.043 \pm 0.006 \times CN$ ($r^2 = 0.50$)

increased with increased percentage nitrogen in the food.

During May and July, there was evidence of differential absorption of nitrogen from the food (Fig. 6; data for Pacific oysters were similar). The data points fall predominantly above the 45° line in the graph. As the food quality declined from March to July, AE for nitrogen increased, whereas the AE for carbon was maintained approximately the same, resulting in an increase in relative absorption of nitrogen.

Oxygen consumption and metabolic efficiency

Oxygen consumption rates (VO_2) were measured at Soldier's Point in March and July (Table 8). The differences between species were not significant, but the

Table 8. Oxygen consumption rates by 2 oyster species, at Soldier's Point, Port Stephens, in March and July, 1999. n = 10 in all cases. Differences between species were not significant; differences between mo were highly significant (p < 0.001)

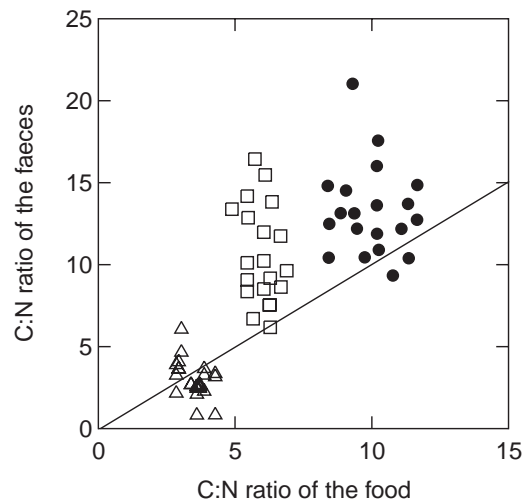| Species	Month	O_2 consumption (ml O_2 g^{-1} h^{-1})
Crassostrea gigas	Mar	0.658 ± 0.086
	Jul	0.192 ± 0.037
Saccostrea glomerata	Mar	0.647 ± 0.052
	Jul	0.201 ± 0.040

Fig. 6. *Saccostrea glomerata*. The carbon:nitrogen ratio of the faeces plotted against the carbon:nitrogen ratio of the food. The line is drawn at 45°. The data are for 3 mo: △, March; □, May; and ●, July 1999

seasonal differences for VO_2 were highly significant (p < 0.001), with faster rates of consumption in March.

Measured oxygen consumption rates (ml O_2 h^{-1}) were converted to energy equivalents by multiplying by 20.08 J ml^{-1} O_2 (Gnaiger 1983); absorption rates were converted assuming 20 J mg^{-1} organic matter ingested (Fig. 7). Rock oysters expended more energy per unit energy absorption than Pacific oysters. Aver-
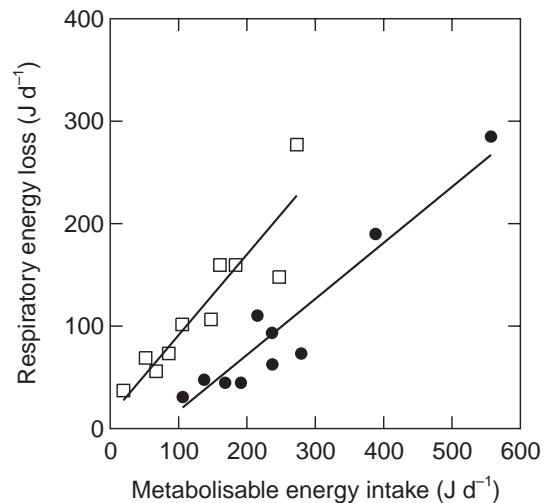

Fig. 7. Respiratory energy loss as a function of metabolisable energy intake (MEI) in 2 oyster species, in Port Stephens in July 1999. □: Sydney Rock oysters; ●: Pacific oysters. Energy loss is calculated as oxygen consumption rate (ml O_2 h^{-1}) × 20.08 J ml^{-1} O_2. MEI is absorption rate (mg organic matter h^{-1}) × 20.0 J mg^{-1}. The slopes of the fitted regressions are not significantly different, but the elevations of the lines differ at p < 0.001

age values for the months of March and July were, respectively: Pacific oysters: 0.09 ± 0.01 and 0.38 ± 0.04; Rock oysters: 0.18 ± 0.03 and 0.83 ± 0.06.

These differences between species were highly significant, confirming the 'metabolic efficiency' hypothesis. The difference between mo may be exaggerated here, by the use of a single and very approximate conversion factor for the food (20 J mg^{-1}). Nevertheless, for both species, the balance between energy uptake and loss was evidently more efficient in March than in July.

DISCUSSION

Comparisons between species at Port Stephens

The size range of oysters used in this experiment was relatively small. Taking mean values, whole-body weight increased from 29.4 to 51.2 g for the Pacific oysters, and 26.1 to 30.8 g for the Sydney Rock oysters. Over these size ranges, there was no discernible effect of body size on the measured growth rates. Mason et al. (1998) derived the parameters of a regression model to describe growth of Rock oysters as a function of temperature and body size. Using their model, daily ARG of 0.0029 and 0.0018 are predicted for the conditions of the present experiment, over the periods of March to May and May to July, respectively. These compare with observed values of 0.0023 and 0.0011. ARGs for the Pacific oysters were significantly faster, 0.0075 and 0.0019. Clearly, the Pacific oysters *Crassostrea gigas* grew faster than the Rock oysters *Saccostrea glomerata* throughout this field experiment.

Growth was faster between March and May than between May and July. This finding was consistent with higher temperatures and better quality of food (measured as OC and C:N ratio) in March than in May. It also agrees with the seasonal growth pattern reported by Mason et al. (1998) for Rock oysters in Port Stephens. Honkoop & Bayne (2002) observed faster growth in dry tissue, for both oyster species, over the period February to June in the Port Stephens estuary when compared with other seasons.

Results from laboratory experiments (see 'Introduction') suggested that Pacific oysters would also feed more rapidly than Sydney Rock oysters. This was only partly confirmed in the field, although there was a clear trend in support of the prediction. Of the 8 comparisons for FR, the species difference was significant on 4 occasions. In all of these, Pacifics fed more quickly than Sydney Rocks. For the absorption rate, 5 of these 8 comparisons were significant and in all of these, also, the Pacific oysters showed faster rates than the Rock oysters.

Given the effects of concentration of total particulates (TPM) on FR (Fig. 3), species differences in feeding behaviour are more exaggerated at higher particle levels. A similar conclusion applies to the ingestion and absorption of nitrogen. Of the 5 comparisons possible (Table 6), 3 showed a significant species difference in the absorption rate of nitrogen. In all of these, Pacific oysters performed faster than Rock oysters.

A further suggestion from laboratory studies was that there would be no species differences in feeding efficiencies, either in selection or absorption. This was not confirmed, although the results were equivocal. Selection within the pallial cavity between organic-rich (or nitrogen-rich) and organic- or nitrogen-poor particles is a complicated function of ciliary and mucus-based processes on the ctenidia and labial palps (Ward 1996, Beninger & St.-Jean 1997, Beninger et al. 1997, Ward et al. 1998). These processes have not been described for oysters of the genus *Saccostrea*, in contrast to the many studies on *Crassostrea* (Bernard 1974, Ward et al. 1993, 1994, Beninger & Venoit 1999). Indeed, the relationships between the morphology of the feeding and rejection tracts, and the physiological traits of SE and rejection efficiency at different levels of TPM and particulate OC have not yet been described for any bivalve mollusc.

Whereas FRs and rejection may bear a relatively simple relationship to the sizes of the ctenidia and the labial palps (Kiørboe et al. 1980, Pouvreau et al. 1999), the likely functional morphology of selection and rejection from a complex mixture of natural particles is more difficult to establish. AE, on the other hand, is a property of gut passage time and the balance between the digestive enzymes and the biochemical composition of the diet (Ibarrola et al. 1996, 2000a,b). Results of the present study suggest that both of the relevant efficiencies, selection and absorption, may be adjusted to the available diet, resulting in reduced variability relative to the variability in the associated rates of filtration and absorption. The seasonally variable relation between AE and the OCI (see Fig. 4 for *Crassostrea gigas*) supports this argument. With a reduction in OC of TPM between March and July, the AE/OCI relation shifted in a manner consistent with physiological compensation, maintaining a relatively invariant AE as food quality declined.

The results of laboratory experiments also predicted that Pacific oysters would use less oxygen per unit of energy absorption than Rock oysters. Although absolute levels of oxygen consumption did not differ between the 2 species, Pacific oysters, by virtue of their faster feeding rates, were more metabolically efficient in their feeding than Rock oysters. The Pacifics expended between 9 and 38% of metabolisable energy intake as metabolic loss, compared with 18 to 83% for Sydney

Rock oysters. A species difference was evident also in respiratory expenditure relative to growth. For *Crassostrea gigas*, total metabolic energy loss was between 1.2 and $1.9 \times$ the energy equivalent of growth in soft tissues (see Tables 2 & 8). For *Saccostrea glomerata* the equivalent ratio was between 2.4 and 2.6.

These conclusions confirm earlier studies on growth in these 2 species (Nell 1991) and provide a partial physiological explanation for the differences. The differences in metabolic efficiencies seem particularly striking, given the very similar body plan and similarities between the species in other aspects of feeding physiology such as selection and absorption. A capacity for faster feeding and growth, at higher levels of metabolic efficiency, should indeed contribute to a competitive advantage for Pacific oysters over Sydney Rock oysters.

Feeding and the available food: comparisons with other species

A wider set of questions concerns the relationships between feeding traits and the available food, for bivalves generally, and the extent to which such relations may be used to predict growth in the field. If knowledge of feeding behaviour is to be used routinely to predict the performance of oysters in cultivation, then this must be formulated around an easily acquired suite of measurements allied with a few robust relations between behaviour and the ambient food.

The feeding relationships that are most likely to contribute to an accurate prediction of growth are: FR as a function of the concentration of TPM in suspension (i.e. food quantity); selection of material for ingestion, as a function of some measure of food quality (such as C:N ratio, OC, or chl *a* content); ingestion of selected material, as a function of FR and SE; and absorption of organic matter as a function of ingestion and food quality. A number of recent studies have described such relationships, and others, for a variety of bivalve species feeding on natural particles (see 'Introduction'). A primary aim of some of these studies has been to predict feeding behaviour from knowledge of food abundance and quality only, avoiding the need for difficult physiological determinations in the field.

The FR of particles from suspension has long been considered to increase monotonically to some maximum value with increased particle concentration, and then to decline as a result of overloading of the filtration apparatus (Winter 1978, Widdows et al. 1979). Results for *Crassostrea gigas* and *Saccostrea glomerata* are consistent with this model (Fig. 3), and suggest that inhibition of filtration occurs in *S. glomerata* at a comparatively low concentration of particles, between 10 and 15 mg l^{-1}. This compares with inhibition in *C. gigas*

at ca. 100 mg l^{-1} (Barillé et al. 1997; but see Ren et al. (2000) suggesting a higher threshold), *Cerastoderma edule* at ca. 300 mg l^{-1} (Navarro & Widdows 1997) and *Perna canaliculus* at >1000 mg l^{-1} (Hawkins et al. 1999). When taken through the origin (i.e. where both FR and TPM are 0), the relation between FR and TPM can be described by a simple quadratic equation. For Rock oysters in this study, FR = $2.1 \pm 1.0 \times$ TPM – $0.09 \pm 0.05 \times$ TPM^2 ($r^2 = 0.63$); for Pacific oysters, FR = $3.4 \pm 1.6 \times$ TPM – $0.08 \pm 0.09 \times$ TPM^2 ($r^2 = 0.84$). As discussed above, Rock oysters showed significantly reduced FRs, relative to Pacific oysters, at greater TPM concentrations.

FR by *Crassostrea gigas* in this study is compared in Fig. 8 with predictions for similar TPM values derived from Barillé et al. (1997) and Soletchnik et al. (1996; as analysed by Hawkins et al. 1998) and Ren et al. (2000). All data are corrected to a body size of 1 g dry tissue wt, at similar temperatures. The experiments of both Barillé et al. and Soletchnik et al. were done on oysters from Marennes-Oléron Bay in France, but at different times. The comparison illustrates the variability to be expected of physiological traits when measured using similar procedures but in different environments. It identifies the challenge in moving from site-specific to more general statements on feeding behaviour, when based only on empirical relations between variables.

From this filtered material, organically enriched particles are selected for ingestion with a certain efficiency (SE). SE in bivalves may vary with the OC of the diet and/or with the FR (Hawkins et al. 1998). In the present study, Rock oysters varied SE with dietary OC, but not with FR. This resembles the behaviour of the
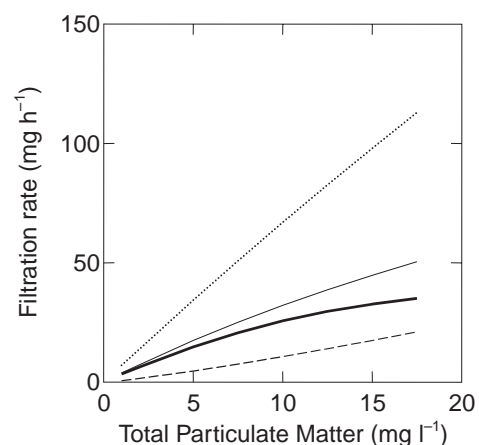

Fig. 8. *Crassostrea gigas*. Filtration rates related to the concentration of particulate matter in suspension. Data from the present experiment, as fitted by a simple quadratic as discussed in the text, are shown as a heavy solid line. The results of fitting equations from the literature to TPM data from Port Stephens are also shown: Barillé et al. (1997), dotted line; Hawkins et al. (1997), dashed line; Ren et al. (2000), thin solid line

European cockle *Cerastoderma edule* in the bay of Marennes-Oléron in France, where the effect of FR on SE is minor relative to the positive effect of increased OC (Urrutia et al. 1996; see also Ibarrola et al. 2000a). In contrast, Pacific oysters did not increase SE with increased OC. This, too, is similar to the behaviour of this species in France where, at slow FRs such as those observed in Port Stephens, there was no effect of OC on selection efficiency for organic matter. The small range of FRs by both species of oysters in Port Stephens (e.g. 6 to 35 mg h^{-1} for Pacific oysters, compared with rates up to 200 mg h^{-1} in the bay of Marennes-Oléron) signifies that the effects of FR on SE are likely to be small and difficult to detect (see analysis by Hawkins et al. 1998, of original data by Soletchnik et al. 1996).

IR in bivalves has been described as a power function of TPM, weighted for some species by the OC of the TPM (Hawkins et al. 1998); and as a Type 2 functional response incorporating both TPM and OC (Ren et al. 2000). In the present study, both TPM and OC are necessary for a statistically significant fit to measured IRs. The relevant equations are: Rock oysters, IR = 8.8 ± 3.2 × TPM × OC$^{2.90 \pm 0.53}$ (r^2 for 'predicted' vs 'observed' = 0.53) and Pacific oysters, IR = 7.6 ± 1.6 × TPM × OC$^{2.17 \pm 0.22}$ (r^2 = 0.62). These equations take no account of differences related to temperature, which appear to be rather small. The equation quoted for *Crassostrea gigas* by Hawkins et al. (1998) predicts similar values to those observed here (5.24 vs 5.57 mg h^{-1}, at 10 mg TPM l^{-1} and an OC of 30%). The model fitted by Ren et al. (2000) predicts an IR of 4.31 mg h^{-1}. It is clear from these statistical models that IR is sensitive not just to total seston, but also to its nutritional quality.

The efficiency with which this ingested material is absorbed (AE) may be related to the OCI by an exponential asymptotic model (see legend to Fig. 4; Bayne et al. 1987, Navarro et al. 1992, Cranford 1995, Navarro & Widdows 1997). Hawkins et al. (1998, 1999) used a simple hyperbolic of the form: AE = *a* – *b* × (1/OCI), where *a* and *b* are fitted parameters. The present study has shown that this relationship is variable, with a seasonal shift coincident with a change in the ambient OC of the suspended particles. This occurred in both species and has been observed in other bivalves, albeit over shorter time-scales, e.g. *Placopecten magellanicus* in the field (Cranford 1995), and in laboratory experiments with mussels (Bayne et al. 1993) and European cockles *Cerastoderma. edule* (Ibarrola et al. 2000a).

An ability to adjust digestive processes to compensate for changes in food quality is indicated for these suspension feeders. For example, between March and July the mean OC of the material ingested by *Crassostrea gigas* declined from 0.65 to 0.19 (–70%), but the mean AE was maintained between 0.61

and 0.66. Coincidentally, between March and July the respiratory energy expended per unit of metabolisable energy intake increased from 0.09 to 0.38. The relationships, if any, between the processes underlying metabolic efficiency and AE are not known for bivalves. The suggestion, however, that an increase in metabolic rate per unit of absorbed energy may contribute to compensatory absorption processes when food quality declines, is of some interest.

Grant & Bacher (1998) have demonstrated how sensitive the modelled growth of bivalves is to small changes in AE. In future computer modelling of growth in these species, it will be important to include robust relations between AE and food quality, including compensatory responses to changes in food quality. Research on post-ingestive processes in bivalves (e.g. Cranford et al. 1998, Brillant & MacDonald 2000, Ibarrola et al. 2000b) is therefore timely.

AR can be modelled, on average, as dependent on TPM and its OC. In the present study, this required quadratic equations with 4 parameters, as follows: Rock oysters: AR = −4.9 ± 1.1 + 10.6 ± 1.8 × OC + 0.95 ± 0.26 × TPM − 0.04 ± 0.01 × TPM^2 (r^2 = 0.46); Pacific oysters: AR = −10.5 ± 2.0 + 20.3 ± 3.3 × OC + 2.04 ± 0.44 × TPM − 0.09 ± 0.02 × TPM^2 (r^2 = 0.44).

When the values for AR predicted from these equations are compared with mean observed values for each of the 8 grouped sets of data (Fig. 9), the agreement is statistically acceptable (p < 0.05) although the
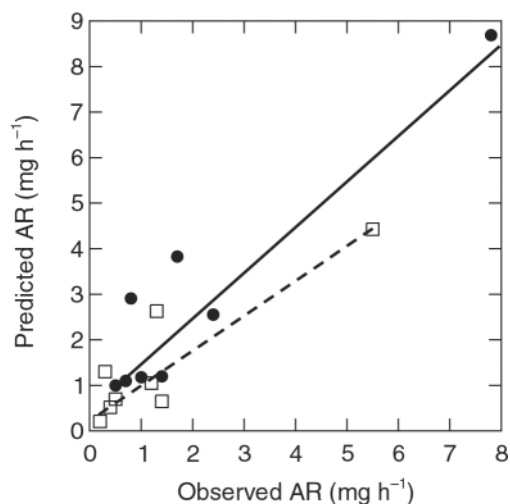

Fig. 9. Rates of absorption of organic matter (AR) by Pacific (● and solid line) and Sydney Rock (□ and dashed line) oysters. The plot compares values predicted by polynomial equations of the form AR = a + b × OC + c × TPM − d × TPM^2, where TPM and OC are the quantity and quality of the available food, respectively, with average observed values measured at 3 sites on 3, 3 and 2 occasions, at Port Stephens. The fitted slopes ± standard error (and r^2) for the regression lines are: Pacific oysters, 1.18 ± 0.12 (0.90); Rock oysters, 0.86 ± 0.17 (0.87)

analysis is biased by the larger values, measured at Soldier's Point in March.

This analysis has been based on the organic matter available to the oysters. Measurements were made also on the nitrogen content (and C:N ratio) of the suspended particles and associated feeding behaviour. Both SE and AE for nitrogen were related to nitrogen content. Both oyster species expressed greater nitrogen SE when the food was relatively depleted of nitrogen; but nitrogen AE was greatest when food particles were relatively rich in nitrogen. The net result was an absorption rate for nitrogen, per unit nitrogen filtered, which was independent of the nitrogen content of the particulates ($p > 0.05$) but highly site-dependent ($p < 0.001$). For Pacific oysters at Karuah, for example, only $5 \pm 3.5\%$ of filtered nitrogen was absorbed, over a range of particulate C:N ratios from 3.6 to 10.6. At Soldier's Point, however, over a similar range of C:N (4.5 to 9.9), on average $32 \pm 5.3\%$ of filtered nitrogen was absorbed.

Presumably, features of food quality not measured by total nitrogen content alone were important in determining overall feeding efficiency for nitrogen (e.g. chl *a* content: Hawkins et al. 1999, Babarro et al. 2000). Nevertheless, a balance between SE and AE ensures a degree of constancy of nitrogen extraction over a range of C:N values (or percent nitrogen) for food particles of similar type. Seasonal endogenous factors are particularly significant in determining the balance between carbon and nitrogen absorption (Grant & Cranford 1991, Hawkins & Bayne 1992, Kreeger et al. 1996). The present study suggested a seasonal component for both species, by a quantitative shift in the relation between the C:N ratio of the faeces and the food (see Fig. 6 for *Saccostrea glomerata*).

This study has provided, in part at least, a physiological explanation for observed growth differences in 2 closely similar oyster species sharing a common estuarine habitat. It has also demonstrated similarities between the feeding behaviours of these oysters and other bivalves from different geographical regions. There are some clear pointers to gaps in our knowledge of bivalve suspension feeding, but this is coupled with some evidence that quantitative predictions of growth are possible, when based on a few simple but robust relationships between feeding, and the quantity and quality of the food available.

LITERATURE CITED

Anderson TJ, Allard RD (1994) Nucleotide sequence of rDNA internal transcribed spacer supports synonymy of *Saccostrea commercialis* and *S. glomerata*. J Molluscan Stud 60:196–197

Arifin Z, Bendell-Young LI (1997) Feeding response and carbon assimilation by the blue mussel *Mytilus trossulus* exposed to environmentally relevant seston matrices. Mar Ecol Prog Ser 160:241–253

Babarro JMF, Fernández MJ, Labarta U (2000) Feeding behaviour of seed mussel *Mytilus galloprovincialis*: environmental parameters and seed origin. J Shellfish Res 19:195–201

Barillé L, Prou J, Héral M, Razet D (1997) Effects of high natural seston concentrations on the feeding, selection and absorption of the oyster *Crassostrea gigas* (Thunberg). J Exp Mar Biol Ecol 212:149–172

Bayne BL (1998) The physiology of suspension feeding by bivalve molluscs: an introduction to the Plymouth 'TROPHEE' workshop. J Exp Mar Biol Ecol 219:1–19

Bayne BL (1999a) Relations between variable rates of growth, metabolic costs and growth efficiencies in individual Sydney rock oysters (*Saccostrea commercialis*). J Exp Mar Biol Ecol 251:185–203

Bayne BL (1999b) Physiological components of growth differences between individual oysters (*Crassostrea gigas*) and a comparison with *Saccostrea commercialis*. Physiol Biochem Zool 72:705–713

Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: Wilber KM, Saleuddin AS (eds) The mollusca, Vol 4. Academic Press, New York, p 407–515

Bayne BL, Hawkins AJS, Navarro E (1987) Feeding and digestion by the mussel *Mytilus edulis* L (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. J Exp Mar Biol Ecol 111:1–22

Bayne BL, Hawkins AJS, Navarro E, Iglesias JIP (1989) Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. Mar Ecol Prog Ser 55:47–54

Bayne BL, Iglesias JIP, Hawkins AJS, Navarro E, Héral M, Deslous-Pauli JMD (1993) Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. J Mar Biol Assoc UK 73:813–829

Bayne BL, Svensson S, Nell JA (1999) The physiological basis of faster growth in the Sydney rock oyster, *Saccostrea commercialis*. Biol Bull 197:377–387

Beninger PG, St.-Jean SD (1997) The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles. Mar Biol 129:389–397

Beninger PG, Veniot A (1999) The oyster proves the rule: mechanisms of pseudofaeces transport and rejection on the mantle of *Crassostrea virginica* and *C. gigas*. Mar Ecol Prog Ser 190:179–188

Beninger PG, Lynn JW, Dietz TH, Silverman H (1997) Mucociliary transport in living tissue: the two-layer model confirmed in the mussel *Mytilus edulis* L. Biol Bull 193:4–7

Bernard FR (1974) Particle sorting and labial palp function in the Pacific oyster *Crassostrea gigas* (Thunberg, 1795). Biol Bull 146:1–10

Brillant MGS, MacDonald BA (2000) Postingestive selection in the sea scallop, *Placopecten magellanicus* (Gmelin): the role of particle size and density. J Exp Mar Biol Ecol 253:211–227

Buroker NE, Hershberger WK, Chew KK (1979) Population genetics of the family Ostreidae. I. Intraspecific studies of *Crassostrea gigas* and *Saccostrea commercialis*. Mar Biol 54:157–169

Clausen I, Riisgärd HU (1996) Growth, filtration and respiration in the mussel *Mytilus edulis*: no evidence for physiological regulation of the filter pump to nutritional needs. Mar Ecol Prog Ser 141:37–45

Cranford PJ (1995) Relationships between food quantity and quality and absorption efficiency in sea scallops *Placopecten magellanicus* (Gmelin). J Exp Mar Biol Ecol 189:124–142

Cranford PJ (1998) Temporal perspectives on food acquisition by suspension-feeding bivalves: *Placopecten magellanicus* and *Mytilus edulis*. PhD thesis, Dalhousie University, Halifax, Nova Scotia

Cranford PJ, Hargrave BT (1994) In-situ time-series measurements of ingestion and absorption rates of suspension-feeding bivalves: *Placopecten magellanicus*. Limnol Oceanog 39:730–738

Cranford PJ, Emerson CW, Hargrave BT, Milligan TG (1998) In situ feeding and absorption responses of sea scallops *Placopecten magellanicus* (Gmelin) to storm-induced changes in the quantity and composition of the seston. J Exp Mar Biol Ecol 219:45–70

Gnaiger E (1983) Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. In: Gnaiger E, Forstner H (eds) Polarographic oxygen sensors. Springer-Verlag, Berlin, p 337–345

Grant J (1996) The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J Exp Mar Biol Ecol 200:239–256

Grant J, Bacher C (1998) Comparative models of mussel bioenergetics and their validation at field culture sites. J Exp Mar Biol Ecol 219:21–44

Grant J, Cranford PJ (1991) Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus*. J Mar Biol Assoc UK 71:437–450

Griffiths CL, Griffiths RJ (1987) Bivalvia. In: Pandian TJ, Vernberg FJ (eds) Animal energetics, Vol 2. Bivalvia through Reptilia. Academic Press, New York, p 1–88

Hawkins AJS, Bayne BL (1992) Physiological processes, and the regulation of production. In: Gosling E (ed) The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier Science Publishers, Amsterdam, p 171–222

Hawkins AJS, Smith RFM, Bayne BL, Héral M (1996) Novel observations underlying fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. Mar Ecol Prog Ser 131:179–190

Hawkins AJS, Bayne BL, Bougrier S, Héral M, Iglesias JIP, Navarro E, Smith RFM, Urrutia MB (1998) Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. J Exp Mar Biol Ecol 219:87–103

Hawkins AJS, James MR, Hickman RW, Hatton S, Weatherhead M (1999) Modelling of suspension-feeding and growth in the green-lipped mussel *Perna canaliculus* exposed to natural and experimental variations of seston availability in the Marlborough Sounds, New Zealand. Mar Ecol Prog Ser 191:217–232

Holliday JE, Nell JA (1985) Concern over Pacific oysters in Port Stephens. Aust Fish 44:29–31

Honkoop PJC, Bayne BL (2002) Stocking density and changes in total and somatic mass of the Pacific oyster (*Crassostrea gigas*) and the Sydney rock oyster (*Saccostrea glomerata*). Aquaculture (in press)

Ibbarola I, Iglesias JIP, Navarro E (1996) Differential absorption of biochemical components in the diet of the cockle *Cerastoderma edule*: enzymatic responses to variations in seston composition. Can J Zool 74:1887–1897

Ibbarola I, Navarro E, Urrutia MB (2000a) Acute and acclimated digestive responses of the cockle *Cerastoderma edule* (L) to changes in food quality and quantity. I. Feeding and absorption of biochemical components. J Exp Mar Biol Ecol 252:181–198

Ibbarola I, Etxeberria M, Iglesias JIP, Urrutia MB, Angulo E (2000b) Acute and acclimated digestive responses of the cockle *Cerastoderma edule* (L) to changes in the food quality and quantity. II. Enzymatic, cellular and tissue responses of the digestive gland. J Exp Mar Biol Ecol 252:199–219

Iglesias JIP, Urrutia MB, Navarro E, Alvarez-Jorna P, Larretxea X, Bougrier S, Héral M (1996) Variability in feeding processes in the cockle *Cerastoderma edule* (L) in response to changes in seston concentration and composition. J Exp Mar Biol Ecol 197:121–143

Iglesias JIP, Urrutia MB, Navarro E, Ibarrola I (1998) Measuring feeding and absorption in suspension-feeding bivalves: an appraisal of the biodeposition method. J Exp Mar Biol Ecol 219:71–86

Kiørboe T, Møhlenberg F, Nøhr O (1980) Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia 19:193–205

Kreeger DA (1993) Seasonal patterns in utilisation of dietary protein by the mussel *Mytilus trossulus*. Mar Ecol Prog Ser 95:215–232

Kreeger DA, Hawkins AJS, Bayne BL, Lowe DM (1995) Seasonal variation in the relative utilisation of dietary protein for energy and biosynthesis by the mussel *Mytilus edulis*. Mar Ecol Prog Ser 126:177–184

Kreeger DA, Hawkins AJS, Bayne BL (1996) Use of dual-labelled microcapsules to discern the physiological fates of assimilated carbohydrate, protein carbon and protein nitrogen in suspension-feeding organisms. Limnol Oceanog 41:208–215

Malcolm WB (1987) The Sydney rock oyster. Department of Agriculture, report Agfact F3.1.1, Sydney, NSW

Mason CJ, Nell JA (1995) Condition index and chemical composition of meats of Sydney rock oysters (*Saccostrea commercialis*) and Pacific oysters (*Crassostrea gigas*) at four sites in Port Stephens, NSW. Mar Freshw Res 46:873–881

Mason CJ, Reid DD, Nell JA (1998) Growth characteristics of Sydney rock oysters *Saccostrea commercialis* in relation to size and temperature. J Exp Mar Biol Ecol 227:155–168

Navarro JM, Widdows J (1997) Feeding physiology of Cerastoderma edule in response to a wide range of seston concentrations. Mar Ecol Prog Ser 152:175–186

Navarro E, Iglesias JIP, Ortega M (1992) Natural sediment as a food source for the cockle *Cerastoderma edule* (L): effect of variable particle concentration on feeding, digestion and the scope for growth. J Exp Mar Biol Ecol 156:69–87

Navarro E, Iglesias JIP, Ortega M, Larretxea X (1994) The basis for a functional response to variable food quantity

and quality in cockles *Cerastoderma edule* (Bivalvia, Cardiidae). Physiol Zool 67:468–496

Nell JA (1991) Comparative growth study of Sydney Rock oysters *(Saccostrea commercialis)* and Pacific oysters (*Crassostrea gigas*) in Port Stephens, NSW. Report to Fisheries Research and Development Corporation, Australia; FIRTA 86/66; DAN 11Z

Nell JA (1993) Farming the Sydney rock oyster (*Saccostrea commercialis*) in Australia. Rev Fish Sci 1:97–120

Pouvreau S, Jonquières G, Buestel D (1999) Filtration by the pearl oyster, *Pinctada margaritifera*, under conditions of low seston load and small particle size in a tropical lagoon habitat. Aquaculture 176:295–314

Pouvreau S, Bodoy A, Buestel D (2000) In situ suspension feeding behaviour of the pearl oyster, *Pinctada margaratifera*: combined effects of body size and weather-related seston composition. Aquaculture 181:91–113

Ren JS, Ross AH, Schiel DR (2000) Functional descriptions of feeding and energetics of the Pacific oyster *Crassostrea gigas* in New Zealand. Mar Ecol Progr Ser 208:119–130

Soletchnik P, Goulletquer P, Héral M, Razet D, Geairon P (1996) Évaluation du bilan énergétique de l'huître creuse, *Crassostrea gigas*, en baie de Marennes-Oléron (France). Aquat Living Resour 9:65–73

Urrutia MB, Iglesias JIP, Navarro E, Prou J (1996) Feeding and absorption in *Cerastoderma edule* under environmental conditions in the bay of Marennes-Oléron (Western France). J Mar Biol Assoc UK 76:431–450

Ward JE (1996) Biodynamics of suspension-feeding in adult bivalve molluscs: particle capture, processing and fate. Invertebr Biol 115:218–231

Ward JE, MacDonald BA, Thompson RJ, Beninger PG (1993) Mechanisms of suspension feeding in bivalves: resolution of current controversies by means of endoscopy. Limnol Oceanogr 38:265–272

Ward JE, Newell RIE, Thompson RJ, MacDonald BA (1994) In vivo studies of suspension-feeding processes in the eastern oyster *Crassostrea virginica* (Gmelin). Biol Bull 186:221–240

Ward JE, Sanford LP, Newell RIE, MacDonald BA (1998) A new explanation of particle capture in suspension-feeding bivalve molluscs. Limnol Oceanogr 43:741–752

Widdows J, Fieth P, Worrall CM (1979) Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis.* Mar Biol 50:195–207

Wilkinson L (1996) SYSTAT 6.0 for Windows. SPSS, Chicago

Winter JE (1978) A review of knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13:1–33

Wong WH, Cheung SG (1999) Feeding behaviour of the green mussel, *Perna viridis* (L): responses to variation in seston quantity and quality. J Exp Mar Biol Ecol 236:191–207