

R. Beiras · A. Pérez Camacho · M. Albentosa

## Comparison of the scope for growth with the growth performance of *Ostrea edulis* seed reared at different food concentrations in an open-flow system

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**Abstract** Oyster (*Ostrea edulis* L.) seed was reared on five rations of *Isochrysis galbana* Parke: 10, 30, 100, 200 and 300 cells  $\mu\text{l}^{-1}$ , in an open-flow system. Physiological parameters such as clearance, ingestion, absorption and respiration rates were measured, and the scope for growth (SFG) calculated from these parameters was compared with actual growth over 20 d. Actual growth was negligible at 10 cells  $\mu\text{l}^{-1}$  (daily maintenance ration=2.5% organic wt) and maximum (growth rate=13.64  $\text{d}^{-1}$ ) at 200 cells  $\mu\text{l}^{-1}$  (daily ration=43% organic wt), which also supported the maximum gross and net growth efficiencies ( $K_1=50\%$ ,  $K_2=85\%$ ). Ingestion rate was directly correlated to cell concentration up to maximum of  $\sim 100$  cells  $\mu\text{l}^{-1}$ , but further increases failed to support higher ingestions. Absorption efficiency decreased with increasing algal concentration from 95% down to 60%. Due to the costs of growth, respiration rate significantly increased when food was added above maintenance levels; however, metabolic costs associated with feeding activity were undetectable. The scope for growth calculated from these physiological parameters agreed with the long-term growth performance, validating the physiological energetics method as a valuable tool for predicting long-term growth performance under constant environmental conditions.

### Introduction

The measurement of physiological parameters, such as rates of feeding, digestion and metabolism, and their inte-

gration by means of physiological energetics, have been used to provide insight into the growth process and how it may be affected by environmental variables (e.g. Widdows and Johnson 1988). The growth expected under particular conditions or the scope for growth (SFG) can thus be calculated from the energy balance equation developed by Ivlev (1945), Winberg (1956) and Warren (1971):  $SFG=I-F-M=A=M$ , where  $I$ =ingestion,  $F$ =faecal loss,  $M$ =total metabolic costs and  $A$ =absorption.

Food availability in the natural environment or rations provided in a hatchery are, along with temperature, the governing factors of growth rate. Many short-term studies have focused on the effect of the food level on SFG in bivalves (Thompson and Bayne 1972, 1974; Widdows 1978 a,b; Griffiths and King 1979; Griffiths 1980; Navarro and Winter 1982; Winter et al. 1984; and reviews by Winter 1978; Bayne and Newell 1983; Hawkins and Bayne 1990). Although Bayne and Worrall (1980) found that growth estimations based on size-class analysis agreed with physiological measurements, none of the studies compared the SFG with measurements of actual growth. This approach has been undertaken by Riisgård and Randløv (1981) using *Mytilus edulis*, and they concluded that only when the relationship between estimated and actual growth has been convincingly described does it seem proper to use SFG as a physiological indicator of suitability of the environment. Despite the considerable amount of research that focuses on molluscan physiological energetics, experimental approaches in this direction are still lacking.

In addition, the influence of particulate food concentration on feeding rates should be studied in an open-flow system where the filtering activity of the bivalve can be measured under stable conditions (Widdows and Johnson 1988).

The aim of the present research was to evaluate the effect of food ration using (1) the energy budget calculated from the integration of physiological parameters, and (2) the actual growth performance under the same constant environmental conditions to test the utility and accurateness of SFG as a growth predictor and indicator of physiological condition.

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R. Beiras<sup>1</sup> (✉) · A. Pérez Camacho · M. Albentosa  
 Instituto Español de Oceanografía,  
 Centro Costero de A Coruña,  
 Apartado 130, E-15080 A Coruña,  
 Spain

<sup>1</sup> Present address: IFREMER Station d'Arcachon, Quai Silhouette, F-33120 Arcachon, France

## Materials and methods

Experiments were carried out in 1991 using young postmetamorphic oysters (*Ostrea edulis* L.) obtained from the hatchery at the Instituto Español de Oceanografía, with an initial live weight (LW) of 0.58 mg [0.39 mg dry weight (DW), 1.47 mm length (L)]. Duplicate groups of 200 specimens were arranged into 250 ml filtering flasks and were continuously fed using a 13 channel dosing pump (Ismatec mp13). This pumped from five 30-litre tanks, each containing 10, 30, 100, 200 and 300 *Isochrysis galbana* Parke cells  $\mu\text{l}^{-1}$ , which is equivalent to 0.3, 0.6, 2, 4 and 6 mg matter particulate organic litre $^{-1}$ . Details on the open-flow system has been previously described in Beiras et al. (1993). Temperature inside the flasks was  $20 \pm 1 \text{ }^\circ\text{C}$ .

Food concentration in the tanks was checked daily using an electronic particle Coulter Counter (TAII model). Every 2 d, inflow ( $c_i$ ) and outflow ( $c_o$ ) concentrations and flow ( $f$ ) through the experimental chambers were recorded to calculate the ingestion rate (IR) and the clearance rate (CR), following the equations (Widdows and Bayne 1971; Wilson 1980):  $\text{IR} = f(c_i - c_o)$  and  $\text{CR} = f[(c_i - c_o)/c_i]$ . Ingested ration was calculated from the organic weight of *Isochrysis galbana* in initial exponential phase ( $0.024 \text{ mg } 10^6 \text{ cells}^{-1}$ ; Beiras et al. 1993).

Absorption efficiency (AE) was measured by the ratio method of Conover (1966):  $\text{AE} = F - E / (1 - E) F$ , where  $F$  and  $E$  = the organic content in the food and faeces. For this purpose, twice throughout the experiment faeces that had accumulated within several hours were decanted, seed was retained in a coarse nylon net filter, and the remainder was filtered through ashed and pre-weighed glass-fibre filters (GFC Whatman) set in a Millipore kit. All samples were rinsed with isotonic ammonium formate (0.1 M), dried for 24 h at  $90 \text{ }^\circ\text{C}$ , and ashed in a muffle furnace at  $450 \text{ }^\circ\text{C}$  to constant weight to calculate the percentage of organic matter.

The absorption ( $A$ ) was calculated using:  $A = I \text{AE}$ , where  $I$  = ingested ration.

Respiration rate was measured by the rate of decline in oxygen partial pressure recorded by means of oxygen electrodes (YSI BOD 5270A) connected to oxygen meters (YSI Model 57). The oysters were transferred from the open-flow system to 250 ml flasks (3 to 4 replicates per treatment) filled with air-saturated sea water, and sealed with Parafilm. One of the replicates per treatment was sealed with an oxygen electrode fitted to a perforated stopper to monitor oxygen decrease. The design of the experiment assumes that the metabolic condition of the oysters exposed to different food levels remains constant throughout the experimental period (6 h maximum). The rate of oxygen consumption ( $V_{\text{O}_2}$ ) was calculated as follows:  $V_{\text{O}_2} = V/nt (c_o - c_i)$ , where  $V$  = volume of the respirometer,  $n$  = number of individuals,  $t$  = measurement period, and  $c_o$  and  $c_i$  = the initial and final oxygen concentrations.

Individual physiological rates were converted to mass-specific rates and to energy equivalents (Widdows and Johnson 1988) to estimate the SFG using the energy balance equation rearranged as:  $\text{SFG} = (I \text{AE}) - R$ . The energy calculations assume that 1 mg of both algae and oyster organic matter is equivalent to 5 cal (=21 J), based on general calorimetric experiments concerning both bivalves and microalgae (Hughes 1970; Widdows and Bayne 1971; Dame 1972; Bayne and Worrall 1980; Navarro and Winter 1982; Heral and Deslous-Paoli 1983; Winter et al. 1984).

Growth ( $G$ ) was measured gravimetrically as both LW and AFDW (ash-free dry wt) increase (see details in Beiras et al. 1993). Growth rates (GR) were calculated following the expression:  $\text{GR} = (\ln LW_f - \ln LW_0) / 100t$ , where  $LW_0$  and  $LW_f$  = initial and final live weights, respectively, and  $t$  = time in days. Gross ( $K_1$ ) and net ( $K_2$ ) growth efficiencies were calculated using the equations modified from Ivlev (1945):  $K_1 = G/I$  and  $K_2 = G/A$ .

Analysis of variance (ANOVA) (Sokal and Rohlf 1969) was used to test the effect of food concentration on the physiological traits (CR, IR, AE and  $V_{\text{O}_2}$ ). Regarding AE, organic content of the feces was the variable tested, after arcsine of the square-root transformation. Multiple-range analyses for 95 and 99% confidence intervals, provided by Statgraphics computer statistical package, were applied to identify homogeneous groups.

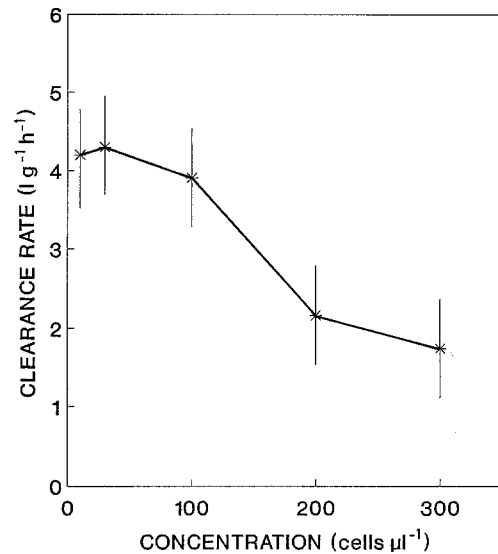


Fig. 1 *Ostrea edulis*. Clearance rate of oyster seed as a function of algal cell (*Isochrysis galbana*) concentration. Bars represent 95% confidence intervals

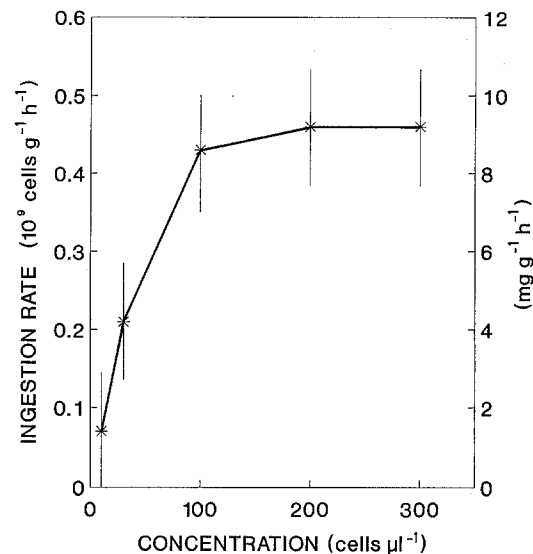
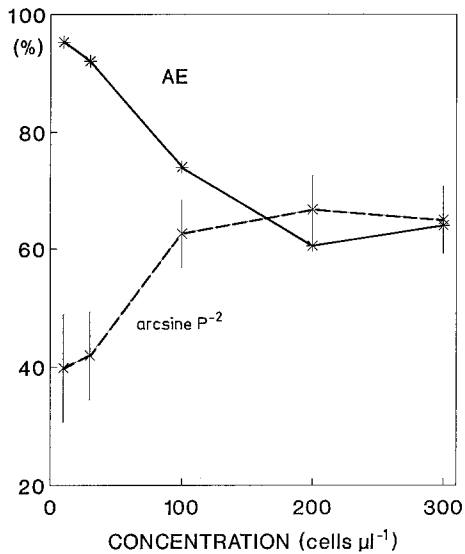


Fig. 2 *Ostrea edulis*. Ingestion rate of oyster seed as a function of algal cell (*Isochrysis galbana*) concentration. Ingestion is expressed both in number of cells (left ordinate) and as organic weight (right ordinate). Bars represent 95% confidence intervals

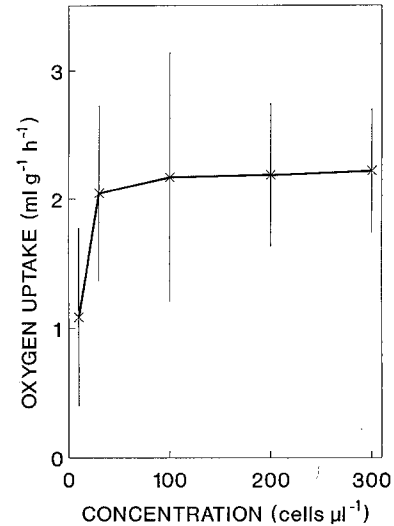
## Results

### Feeding rates

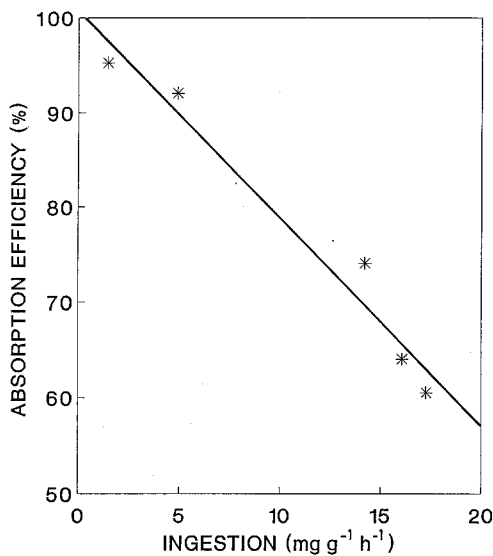
The variation in particulate food concentration significantly affected both CR and IR ( $p < 0.0001$ ) of *Ostrea edulis*. CR was maximum at low cell concentrations and decreased as food ration increased (Fig. 1). Conversely, IR was directly related to cell concentration up to a maximum of  $\sim 100 \text{ cells } \mu\text{l}^{-1}$ , but further ration increases failed to support substantially higher ingestion (Fig. 2).



**Fig. 3** *Ostrea edulis*. Organic content of faeces ( $P$ ) and corresponding absorption efficiencies ( $AE$ ) as a function of algal cell (*Isochrysis galbana*) concentration. Bars represent 95% confidence intervals



**Fig. 5** *Ostrea edulis*. Oxygen consumption rate of oyster seed as a function of algal cell (*Isochrysis galbana*) concentration. Bars represent 95% confidence intervals



**Fig. 4** *Ostrea edulis*. Inverse correlation between ingestion rate and absorption efficiency in oyster seed (see "Results – Absorption" for regression equation)

### Absorption

In general, an increase in the food ration caused an increase in the organic content of the faeces, and therefore, a lower absorption efficiency (Fig. 3). An ANOVA detected highly significant differences ( $p < 0.0001$ ) in organic content of the faeces, and therefore in AE, between rations. Two homogeneous groups could be separated at the 99% confidence level: the 10 and 30 cells  $\mu\text{l}^{-1}$  treatments and the remaining treatments (100, 200 and 300  $\mu\text{l}^{-1}$ ). At 10 cells  $\mu\text{l}^{-1}$ , defined as the maintenance ration (see subsection "Energy balance and growth" below), about 40% of organic matter

remained in the faeces from an initial 94% in the food. This indicates, following the Conover ratio, an AE as high as 95%. Conversely, at 200 cells  $\mu\text{l}^{-1}$ , which supported the maximum amount ingested, faeces retained 80 to 90% of organic matter and AE decreased to ~60%.

Fig. 4 shows the inverse correlation between ingestion rate and percentage of organic matter from the ingested ration absorbed in the digestive tube. This relationship is defined by the linear regression (SE of the parameters in parentheses):  $P = 35.4 (\pm 1.64) + 1.84 (\pm 0.131) I$ ;  $r = 0.992$ ;  $p < 0.0001$ ; where  $P$  = the transformed organic content of the faeces and  $I$  = the ingestion rate ( $\text{mg g}^{-1} \text{h}^{-1}$ ). Therefore, the amount of food ingested explained 98.5% of the variability in AE found in the experiment.

### Respiration

Oxygen consumption rate (Fig. 5) was  $\sim 2 \text{ ml g}^{-1} \text{ AFDW h}^{-1}$  ( $0.15 \text{ ml g}^{-1} \text{ DW h}^{-1}$ ) at medium and high food levels, but only  $1 \text{ ml h}^{-1}$  at the lowest food ration (10 cells  $\mu\text{l}^{-1}$ ), and the difference was statistically significant ( $p < 0.05$ ). At this lowest food ration, growth was almost zero. Therefore, the total metabolic energy expenditure in oyster seed could be partitioned into the costs associated with maintenance metabolism, covered with a  $V_{\text{O}_2} = 1 \text{ ml g}^{-1} \text{ h}^{-1}$ , and the energy expenditure increment associated with growth, which enhanced the respiration rate by an additional  $1 \text{ ml g}^{-1} \text{ h}^{-1}$ .

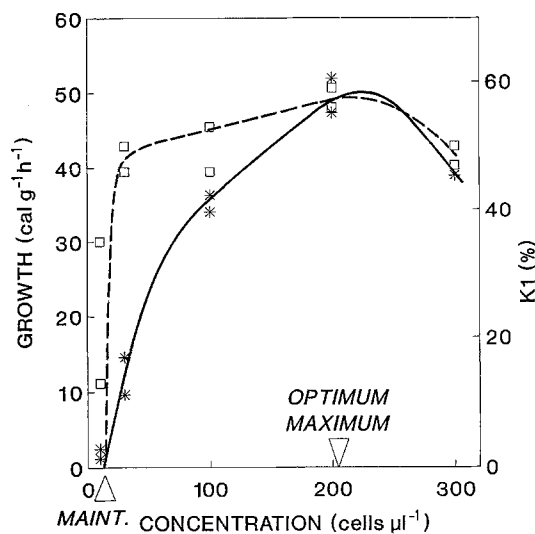
### Energy balance and growth

Table 1 summarizes the physiological parameters integrated in the SFG as well as the actual growth performance, both expressed in the same energy unit for direct compar-

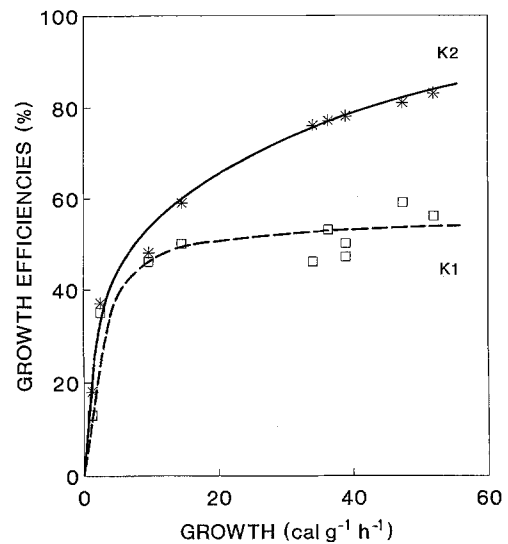
**Table 1** *Ostrea edulis*. Energy budget and actual growth in oyster seed reared at different algal concentrations in an open-flow system. (See Figs. 1–3 and Fig. 5 for 95% confidence intervals of physiological rates) ( $K_1$ ,  $K_2$  gross and net growth efficiency, respectively)

Concentration (cells $\mu\text{l}^{-1}$ )	Ingestion (cal $\text{g}^{-1} \text{h}^{-1}$ )	Absorption efficiency (%)	Absorp- tion (cal $\text{g}^{-1}$ $\text{h}^{-1}$ )	Respira- tion (cal $\text{g}^{-1}$ $\text{h}^{-1}$ )	Scope for growth			Actual growth			Growth rate $\text{d}^{-1}$
					(cal $\text{g}^{-1}$ $\text{h}^{-1}$ )	$K_1$ (%)	$K_2$ (%)	(cal $\text{g}^{-1}$ $\text{h}^{-1}$ )	$K_1$ (%)	$K_2$ (%)	
10 <sup>a</sup>	7.1 7.4	95	6.7 7.1	5.4	1.3 1.7	(18) (23)	(19) (24)	2.5 1.2	(35) (13)	(32) (18)	0.89
30 <sup>b</sup>	28.7 20.3	92	26.4 18.7	10.2	16.2 8.5	(56) (42)	(61) (45)	14.5 9.6	(50) (46)	(59) (48)	4.73
100 <sup>c</sup>	68.4 73.8	74	50.6 54.6	10.8	39.8 43.8	(58) (59)	(79) (80)	36.3 34.0	(53) (46)	(77) (76)	10.83
200 <sup>d</sup>	80.3 92.2	61	49.0 56.2	10.9	38.1 45.3	(47) (49)	(78) (81)	47.3 51.9	(59) (56)	(81) (83)	13.64
300 <sup>c</sup>	83.3 77.3	64	53.3 49.5	11.1	42.2 38.4	(51) (50)	(79) (78)	38.9 38.9	(47) (50)	(78) (78)	11.64

a, b, c, d Actual homogeneous growth groups for  $p < 0.05$



**Fig. 6** *Ostrea edulis*. Actual growth (\*, left ordinate) and gross growth efficiency,  $K_1$  ( $\square$ , right ordinate), in oyster seed as a function of algal cell (*Isochrysis galbana*) concentration. Estimated maintenance, optimum and maximum food rations are also shown. Curves fitted by eye



**Fig. 7** *Ostrea edulis*. Net ( $K_2$ ) and gross ( $K_1$ ) growth efficiencies as a function of actual growth in oyster seed reared at different food rations. Curves fitted by eye

ison. There is remarkable agreement between actual growth and SFG, except for the 200 cells  $\mu\text{l}^{-1}$  ration where actual growth exceeded the prediction of the SFG. The effect of ration on the actual growth was, as expected, highly significant ( $p < 0.0001$ ), and a multiple-range test for 95% confidence intervals identified the following homogeneous groups: (10), (30), (100, 300), (200 cells  $\mu\text{l}^{-1}$ ). Average daily growth rates are also shown. The 200 cells  $\mu\text{l}^{-1}$  treatment corresponded to the maximum ration, since it supported the highest growth rate. On the other hand, at 10 cells  $\mu\text{l}^{-1}$ , the maintenance ration was approached, for growth was almost zero.

Fig. 6 plots actual growth and  $K_1$  against food concentration. Variations in the form of the curves do occur, according to environmental conditions and species; however,

the general form and indicated parameters are indisputable (Brett 1979). Elliott (cited by Brett 1979) tried unsuccessfully to find a suitable linear transformation for these relations, and resorted to smooth-curve-fitting by eye. As shown in Fig. 6, maintenance ration ( $G=0$ ) was attained at  $\sim 10$  *I. galbana* cells  $\mu\text{l}^{-1}$  ( $0.2 \text{ mg l}^{-1}$ ). This food concentration supported a daily ingested ration of 2.5% (algal AFDW:oyster AFDW), equivalent to 0.2% DW. Growth rate increased linearly with increasing food concentration up to 100  $\mu\text{l}^{-1}$  ( $2 \text{ mg l}^{-1}$ ), and reached a maximum at 200  $\mu\text{l}^{-1}$  ( $4 \text{ mg l}^{-1}$ ). Therefore, the maximum ration was 43% AFDW daily (3% DW). This ration is also regarded as the optimum ration since it corresponds to maximum values of  $K_1$ . Further increases in the food level resulted in a significantly decreased growth rate.

As growth increased, the  $K_2$  asymptotically approached a maximum of 85% (Fig. 7), while  $K_1$  remained fairly constant around 50%, except for very low growth rates, which showed decreased gross efficiencies.

## Discussion

At low levels of food availability, filter-feeding bivalves show maximum and constant filtration rates and therefore increasing particle concentration resulting in enhanced ingestion rates. However, at high food concentrations, ingestion capacity is saturated and a functional response occurs decreasing the filtration rates in order to keep the ingested ration at maximum level, avoiding obstruction of the feeding mechanisms (Walne 1972; Schulte 1975; Foster-Smith 1975, 1976a; Widdows et al. 1979; Navarro and Winter 1982; Gerdes 1983; Bricelj and Malouf 1984; see also Figs. 1 and 2 of present study). Ingestion can also be regulated by increased rejection of filtered particles as pseudofaeces (Foster-Smith 1975; Navarro et al. 1992). Cockles were demonstrated to resort to pseudofaeces production when fed diets consisting of particles low in food value; conversely, ingestion was mainly regulated by adjusting clearance rates when, as in the present experiment, the animals were fed organically rich diets (Iglesias et al. 1992).

Jørgensen (1990) disputed the assumed ability of bivalves to regulate water pumping-rates according to nutritional needs. From his standpoint, filter-feeding is a highly automatized process, and retention of particulate matter is determined by physical properties of the pump and food concentration rather than by physiological regulation at the organismic level. Independent of the cause, the present study on *Ostrea edulis* shows a clear limitation of the ingestion rate at high particle concentrations concomitant with a marked decrease in filtration rate.

The ingestion rate was the simple physiological parameter that correlated best with the actual growth. This is in agreement with previous studies, which found that the effect of different environmental variables such as hydrocarbon pollution (Widdows et al. 1990) or natural sediment availability (Navarro et al. 1992) on the ingestion rate also accounted for most of the variation in the integrated SFG.

Ingested food is digested and absorbed with an efficiency inversely correlated to ingested ration (see review in Bayne and Newell 1983). At very low particle concentrations, all ingested material is digested in the digestive gland with high efficiency and the remaining unassimilated matter is rejected as glandular faeces (Widdows et al. 1979); however, as the seston concentration increases, the excess of material entering the stomach bypasses the digestive gland and is rejected undigested as intestinal faeces (Van Weel 1961). Hawkins et al. (1983), found digestive rhythms, with alternating periods of greater faecal deposition and high AE, corresponding to glandular faeces being highly affected by intracellular digestion, and periods of lower faecal egestion representing relatively undigested material which was transported directly into the hind-gut.

Absorption efficiency in previously starved molluscs could be enhanced by increasing the gut residence time (Calow 1975; Hawkins and Bayne 1984); the longer the gut residence-time, the higher the AE (Bayne et al. 1987). The null or even negative values of AE found in adult mussels by Thompson and Bayne (1972, 1974), Griffiths and King (1979) and Griffiths (1980) were not found in the present study. Since ingestion is limited, the decrease in AE reaches a minimum at very high food levels and further decreases in AE were not expected (Widdows 1978 a, b; Navarro and Winter 1982; Bricelj and Malouf 1984). Further, negative values of AE are incompatible with the energy budget of a healthy growing specimen.

In this study, growing oysters fed above the maintenance ration showed a metabolic rate independent of food concentration, indicating that the costs of pumping water and processing retained particulate material are negligible compared to the total metabolic expenditure. In contrast, the metabolic rate of oysters fed at the maintenance ration decreased by half. A very economic system of capture and transport of particles based on ciliary movements has frequently been stated to account for only 1 to 2% of the total metabolic expenditure (Jørgensen 1955; Foster-Smith 1976 b; Silvester and Sleight 1984; Jørgensen et al. 1986; Clemmesen and Jørgensen 1987); this is of adaptive significance in continuous feeders such as mussels and oysters. Widdows (1973) found doubled metabolic rates (called active rates) in fed mussels compared to standard rates in unfed specimens. Famme and Kofoed (1980) proved that oxygen consumption could be increased by water perfusion through the mantle cavity, and concluded that the short-term response of increased oxygen consumption in well-fed mussels is due to increased ventilation rate rather than to enhanced costs of activity. In the present study on *Ostrea edulis*, we also found two different metabolic states: a low metabolic rate in oysters fed at maintenance ration, and a doubled metabolic rate in growing individuals fed above the maintenance ration. Since the experimental oysters were kept under constant food-level conditions, a long-term physiological response seems to be involved. Widdows and Hawkins (1989) divided the total metabolic expenditure of well-fed mussels into costs of maintenance, digestion-absorption and growth in the proportion 3:1:2. Therefore, costs of growth, and especially protein biosynthesis, considerably enhanced the metabolic rate, while costs associated with water pumping were again undetectable (<3% of total metabolic expenditure).

In conclusion, limits to energy gain in bivalve filter-feeders are set by the amount of food available at low food levels and by constraints in the ingestive and digestive capacity at high particle concentrations. No appreciable extra metabolic costs are originated by the mechanism of capture and transport of particles at increased food levels. As a consequence, growth rate is directly correlated to the food ration offered up to a saturation point (maximum ration) and further increases in food level fail to enhance growth performance.

The SFG, derived from the integration of the physiological parameters involved in the energy budget, showed

a striking agreement with actual growth (see Table 1). This confirms that the physiological energetics method is a valuable tool for predicting long-term growth performance under constant and specific environmental conditions. In the present experiment, only at a ration of 200 cells  $\mu\text{l}^{-1}$  did the SFG underestimate the actual growth, due to a relatively low theoretical absorption efficiency (61%). The Conover ratio method for calculating AE is highly sensitive to deviations when food very rich in organic matter, such as a pure algal culture, is used, due to the inherent assumption that inorganic matter remains unaltered during digestion (Jørgensen 1990).

We have previously found (Beiras et al. 1993) a close correlation between clam (*Venerupis pullastra*) seed growth and absorbed ration calculated from the physiological energetic parameters. Estimated metabolic rates (growth minus absorption), assuming the suitability of the energy partition upon which the SFG calculation is based, were predicted to show constant values at high and medium food levels and a substantial decrease at lower food rations. This general trend has been confirmed in the present study, which directly measured respiration rates. Riisgård and Randløv (1981) have also demonstrated a reasonable agreement between actual growth at different algal cell concentrations and the energy budget, although they resorted to values of assimilation efficiency from the literature to estimate the SFG, since they regard the Conover (1966) ratio method as unreliable.

From an aquaculture standpoint, the maximum ration of 200 *Isochrysis galbana* cells  $\mu\text{l}^{-1}$  (3% DW daily), is the target food ration to maximize biomass increase. High food rations that support high growth rates are required, despite their negative effects on absorption efficiency. In addition, this relatively high food level (200 *I. galbana* cells  $\mu\text{l}^{-1}$ ) was also the optimum ration, since it corresponded to the maximum efficiency of conversion of food into oyster biomass ( $K_1$ ). Industrial seed rearing should attempt to embrace both economic and physiological criteria, with the main goal being a high growth rate to enable enhanced production.

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## References

- 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* 3: 1–22
- Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: Saleuddin, ASM, Wilbur KM (eds) *The Mollusca*. Academic Press, New York
- Bayne BL, Worrall CM (1980) Growth and production of mussels *Mytilus edulis* from two populations. *Mar Ecol Prog Ser* 3: 317–328
- Beiras R, Pérez Camacho A, Albentosa M (1993) Influence of food concentration on energy balance and growth performance of *Venerupis pullastra* seed reared in an open-flow system. *Aquaculture*, Amsterdam 116: 353–365
- Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish physiology*. Vol 8. Academic Press, New York
- Bricelj VM, Malouf RE (1984) Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. *Mar Biol* 84: 155–165
- Calow P (1975) Defecation strategies of two freshwater gastropods, *Ancylus fluviatilis* Müll. and *Planorbis contortus* Linn. (Pulmonata) with a comparison of field and laboratory estimates of food absorption rate. *Oecologia* 20: 51–63
- Clemmesen B, Jørgensen CB (1987) Energetic costs and efficiencies of ciliary filter feeding. *Mar Biol* 94: 445–449
- Conover RJ (1966) Assimilation of organic matter by zooplankton. *Limnol Oceanogr* 2: 338–354
- Dame RF (1972) The ecological energies of growth, respiration and assimilation in the intertidal American oyster *Crassostrea virginica*. *Mar Biol* 17: 243–250
- Famme P, Kofoed LH (1980) The ventilatory current and ctenidial function related to oxygen uptake in declining oxygen tension by the mussel *Mytilus edulis* L. *Comp Biochem Physiol* 66: 161–171
- Foster-Smith RL (1975) The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L. *Cerastoderma edule* (L.) and *Venerupis pullastra* (Mendegu). *J exp mar Biol Ecol* 17: 1–22
- Foster-Smith RL (1976a) Some mechanisms for the control of pumping activity in bivalves. *Mar Behav Physiol* 4: 41–60
- Foster-Smith RL (1976b) Pressures generated by the pumping of some ciliary filter-feeders. *J exp mar Biol Ecol* 25: 199–206
- Gerdes D (1983) The Pacific oyster, *Crassostrea gigas*. Part I. Feeding behaviour of larvae and adults. *Aquaculture*, Amsterdam 31: 195–219
- Griffiths CL, King JA (1979) Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Mar Biol* 51: 141–149
- Griffiths RJ (1980) Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis*. *Mar Ecol Prog Ser* 3: 63–70
- Hawkins AJS, Bayne BL (1984) Seasonal variation in the balance between physiological mechanisms of feeding and digestion in *Mytilus edulis* (Bivalvia: Mollusca). *Mar Biol* 82: 233–240
- Hawkins AJS, Bayne BL (1990) Physiological interrelations, and the regulation of production. In: Gosling E (ed) *The mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier, Amsterdam
- Hawkins AJS, Bayne BL, Clarke KR (1983) Co-ordinated rhythms of digestion, absorption and excretion in *Mytilus edulis* (Bivalvia: Mollusca). *Mar Biol* 74: 41–148
- Heral M, Deslous-Paoli JM (1983) Valeur énergétique de la chair de l'huitre *Crassostrea gigas* estimée par mesures micro-alorimétriques et par dosages biochimiques. *Oceanol Acta* 6: 193–199
- Hughes RN (1970) An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa). *J Anim Ecol* 39: 357–381
- Iglesias JIP, Navarro E, Alvarez Jorna P, Armentia I (1992) Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. *J exp mar Biol Ecol* 162: 177–198
- Ivlev VS (1945) The biological productivity of waters. *Usp sovrem Biol* 19: 98–120. [In Russ] [Transl *J Fish Res Bd Can* 23: 1727–1759 (1966)]
- Jørgensen CB (1955) Quantitative aspects of filter feeding in invertebrates. *Biol Rev* 30: 391–454
- Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Denmark
- Jørgensen CB, Famme P, Kristensen HS, Larsen PS, Møhlenberg F, Riisgård HU (1986) The bivalve pump. *Mar Ecol Prog Ser* 34: 69–77

- Navarro E, Iglesias JIP, Ortega MM (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 JM, Winter JE (1982) Ingestion rate, assimilation efficiency and energy balance in *Mytilus chilensis* in relation to body size and different algal concentrations. *Mar Biol* 67: 255–266
- Riisgård HU, Randløv A (1981) Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. *Mar Biol* 61: 227–234
- Schulte EH (1975) Influence of algal concentration and temperature on the filtration rate of *Mytilus edulis*. *Mar Biol* 30: 331–341
- Silvester NR, Sleigh MA (1984) Hydrodynamic aspects of particle capture by *Mytilus*. *J mar biol Ass UK* 64: 859–879
- Sokal RR, Rohlf FJ (1969) *Biometry. The principles and practice of statistics in biological research.* WH Freeman & Co, San Francisco
- Thompson RJ, Bayne BL (1972) Active metabolism associated with feeding in the mussel *Mytilus edulis* L. *J exp mar Biol Ecol* 9: 111–124
- Thompson RJ, Bayne BL (1974) Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. *Mar Biol* 27: 317–326
- Van Weel PB (1961) The comparative physiology of digestion in molluscs. *Am Zool* 1: 245–252
- Walne PR (1972) The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J mar biol Ass UK* 52: 345–374
- Warren CE (1971) *Biology and water pollution control.* Saunders, Philadelphia
- Widdows J (1973) Effect of temperature and food on the heart beat, ventilation rate and oxygen uptake of *Mytilus edulis*. *Mar Biol* 20: 269–276
- Widdows J (1978 a) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J mar biol Ass UK* 58: 109–124
- Widdows J (1978 b) Physiological indices of stress in *Mytilus edulis*. *J mar biol Ass UK* 58: 125–142
- Widdows J, Bayne BL (1971) Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *J mar biol Ass UK* 51: 827–843
- Widdows J, Burns KA, Menon NR, Page, DS, Soria S (1990) Measurement of physiological energetics (scope for growth) and chemical contaminants in mussels (*Arca zebra*) transplanted along a contamination gradient in Bermuda. *J exp mar Biol Ecol* 138: 99–117
- Widdows J, Fieth P, Worrall CM (1979) Relationship between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar Biol* 50: 195–207
- Widdows J, Hawkins AJS (1989) Partitioning of rate of heat dissipation by *Mytilus edulis* into maintenance, feeding and growth components. *Physiol Zoöl.* 62: 764–784
- Widdows J, Johnson D (1988) Physiological energetics of *Mytilus edulis*: scope for growth. *Mar Ecol Prog Ser* 46: 113–121
- Wilson JH (1980) Particle retention and selection by larvae and spat of *Ostrea edulis* in algal suspensions. *Mar Biol* 57: 135–145
- Winberg GG (1956) Rate of metabolism and food requirements of fishes. Belorussian State University, Minsk. [In Russ] [Transl: *Transl Ser Fish Res Bd Can* 194: 1–202 (1960)]
- Winter J (1978) A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial systems. *Aquaculture, Amsterdam* 13: 1–33
- Winter JE, Acevedo MA, Navarro JM (1984) Quempillén estuary, an experimental oyster cultivation station in southern Chile. Energy balance in *Ostrea chilensis*. *Mar Ecol Prog Ser* 20: 151–164