

132835

Comparative physiological energetics of two suspension feeders: polychaete annelid *Lanice conchilega* (Pallas 1766) and Pacific cupped oyster *Crassostrea gigas* (Thunberg 1795)

Michel Ropert ^{a,b,*}, Philippe Goulletquer ^c

^a Muséum National d'Histoire Naturelle, Lab. Biol. Inv. Mar. Malac., 57 rue Cuvier, 75231 Paris Cedex 05, France

^b Lab. Ressources Aquacoles, IFREMER, B.P. 32, 14520 Port-en-Bessin, France

^c Shellfish Aquaculture Research Laboratory of Poitou-Charentes, IFREMER, B.P. 133, 17390 La Tremblade, France

Accepted 11 May 1999

Abstract

Feeding competition between the Pacific cupped oyster *Crassostrea gigas* and the polychaete *Lanice conchilega* was studied by assessing the polychaete suspension feeding activity. Retention efficiency was estimated by comparing particle size distributions at the output of experimental chambers containing the species and controls. Although particles ranging from 4 to 12 μm were collected by *L. conchilega*, no upper threshold or maximum retention rate was reached within this range. In contrast, *C. gigas* showed retention starting at 2 μm , and reaching an upper threshold at 6 to 8 μm . Based on our results, feeding competition is likely to occur between *C. gigas* and *L. conchilega*. Standardised filtration rates reached $0.225 \text{ l h}^{-1} \text{ g dmw}^{-1}$ (± 0.08) for *L. conchilega* and $2.43 \text{ l h}^{-1} \text{ g dmw}^{-1}$ *C. gigas* for animals of 1 g dry meat weight (dmw). Assimilation rates, 0.44 for *L. conchilega* and 0.49 for *C. gigas*, were similar for the two species. Respiration rates were estimated at 0.113 and 0.68 $\text{ml O}_2 \text{ h}^{-1}$ for *L. conchilega* (Allometric coefficient = 0.534) and *C. gigas* respectively. Therefore polychaete scope for growth (SFG) ($4.01 \text{ J h}^{-1} \text{ g dmw}^{-1}$) was significantly lower when compared with *C. gigas* SFG ($61.96 \text{ J h}^{-1} \text{ g dmw}^{-1}$). The impact of the *L. conchilega* population on that of cultivated oysters was evaluated from these results and field population assessment of both species. Based on field population estimates, *L. conchilega* was responsible for a 19% decrease in the carrying capacity and 30% of the oxygen depletion from the total activity of both species. However, *L. conchilega* SFG was only 16% of that of the

* Corresponding author

C. gigas population. Several hypotheses regarding population interactions are discussed. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Lanice conchilega*; *Crassostrea gigas*; Suspension feeding; Trophic competition

1. Introduction

Many benthic marine species have either exclusively deposit or suspension feeding strategies. Certain species are capable of both however, obtaining food at the sediment surface or from the water column depending on the environmental conditions (Miller et al., 1992). It was long thought that the induction of suspension feeding behaviour was solely due to the presence of particles in suspension (Taghon et al., 1980; Dauer et al., 1981). Several works have since shown strong relationships between suspension feeding activity and hydrodynamic characteristics of the bottom layer (Dauer et al., 1981; Frechette et al., 1989; Eckman and Duggins, 1993). According to Bock and Miller (1997), the concentration of particulate organic matter in the water column is the most important factor inducing change in feeding mode from deposit to suspension feeding. The particles in suspension offer a nutritional value 15 to 40 times higher than those found in the sediment layer (Bock and Miller, 1995) which would favour the choice of suspension feeding over deposit feeding when hydrodynamic conditions and suspension of particles allowed.

The annelid tubeworm *Lanice conchilega* was considered as a deposit feeder for a long time, but is in fact capable of modifying its feeding strategy according to its situation by changing from deposit to suspension feeding (Buhr, 1976; Fauchald and Jumars, 1979). Buhr and Winter (1977) suggested that a density-dependant process played a role in inducing the transition. At low densities (several dozen individuals per square metre), *L. conchilega* would be preferentially deposit feeding while at high densities (several thousand individuals per square meter), competition at the sediment surface would force animals to adopt a suspension feeding mode.

Since 1985, an intertidal population of *L. conchilega* has colonised the eastern side of the Bay of Veys (in the west of the Seine bay, English Channel, France). The species has proliferated in the area and densities can exceed 7000 ind m⁻² (Ropert, 1996). A feature of this population is that it is strictly geographically limited to a shellfish production area of around 200 ha. Although the increase in the *Lanice* population has not had a major impact on the quality of the shellfish produced, it does pose the question of whether competition for food resources is occurring with the cultivated Pacific cupped oyster *Crassostrea gigas*.

The feeding behaviour of *C. gigas* has been studied by several groups (e.g., Gerdes, 1983; Barillé et al., 1993, 1994; Raillard et al., 1993) while only Buhr (1976) and Buhr and Winter (1977) quantified and analysed feeding behaviour in *L. conchilega*. The objective of the present study was to examine diets and physiological energetics of *L. conchilega* and *C. gigas* in order to investigate any potential ecological relationship between the species. In vitro experiments were conducted in parallel on oysters and annelids in order to: (1) determine the spectrum of particle size retained by *L.*

conchilega and *C. gigas*; (2) evaluate filtration efficiency in the two species; (3) make a comparison of growth potential between the two species based on respiration measurements, food retention, biodeposit production and estimation of the assimilation rate; (4) evaluate competition between the two species by extrapolation to their biomass in the natural environment.

2. Materials and methods

2.1. Sampling and conditioning of *L. conchilega*

Individuals were sampled from the central area of the intertidal population located in the mesolittoral zone. The animals were sampled using a TASM corer (Souza Reis et al., 1982; Sylvand, 1995) of 0.02 m² area to a depth of 30 cm. The samples were carefully washed in seawater on a 1-mm mesh and brought to the laboratory. On arrival at the laboratory, the sand tubes were separated from the animals which were then deposited on a clean sediment surface of 250–500 µm sized particles. After 48 h, each individual had embedded itself in the sediment and developed a new tube and sandy fringe of about 20 cm. The animals were washed once again on mesh and put into fine plastic tubes ($L = 15$ cm, $\phi = 7$ mm) which could be introduced individually into the experimental apparatus. All the tubes containing the worms were then put into an aquarium with an open circuit and temperature varying between 13°C and 17°C. From the first hours in the aquarium, the worms became active and their tentacles appeared outside the sandy fringe. The animals were kept in the aquarium conditions for at least a week before experiments were carried out.

2.2. Sampling and conditioning of *C. gigas*

Adult Pacific cupped oysters were collected from professional tray culture within the intertidal area, then carefully washed in seawater and brought to the laboratory for acclimation. Oysters were initially cleaned and carefully brushed to remove fouling organisms, then maintained at 17°C in a flow-through system with natural seawater from three outside basins of 300 m³. During acclimation, which lasted at least two weeks, oysters were fed an algal mixture, containing numerous natural phytoplanktonic species from these basins.

2.3. Experimental equipment in the retention study

The technical equipment used to study the particle size spectrum retained by *L. conchilega* was constructed following recommendations for energetic test studies (IFREMER, 1987) and the work of Barillé et al. (1993) on the Pacific cupped oyster *C. gigas*. This equipment is based upon lateral flow chambers in an open circuit supplied with seawater of controlled quality (e.g., particulate load) (Fig. 1). The animals were placed individually into the chambers of 100 ml volume for *L. conchilega* and 500 ml volume for *C. gigas*. A chamber of each size was left vacant to serve as a control for sedimentation. Seawater was distributed from a 3 m³ tank equipped with a stirring system to homogenize the whole volume. The flow across each chamber was measured with a flowmeter (Fig. 1).

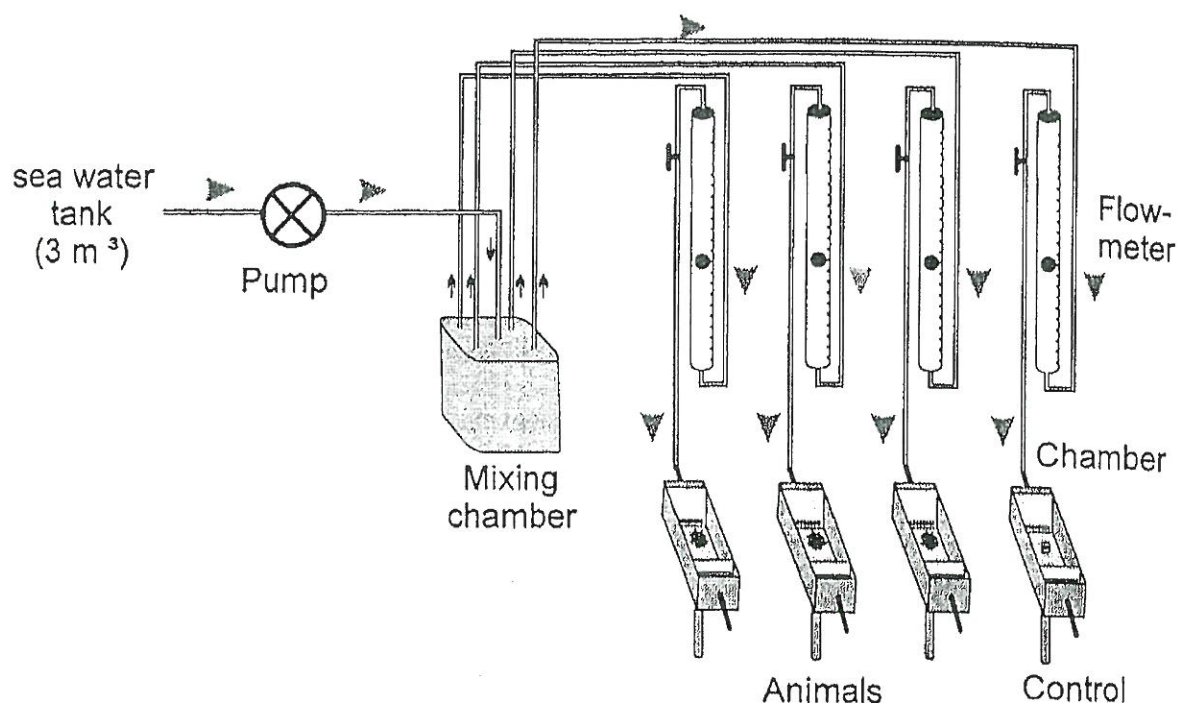


Fig. 1. Experimental set up for Scope For Growth (SFG) assessment study. The apparatus consists of a set of lateral flow chambers connected in parallel. These either contain animals or serve as controls. The respective chamber volumes used were 100 ml and 500 ml for *L. conchilega* and *C. gigas*. During experimentation, seawater was pumped from the 3 m³ tank into a mixing chamber and then conveyed to each chamber. Three experimental diets were supplied to the system via the same route. The flow speed across each chamber was measured with a flowmeter and samples for particle content analysis were taken at each outflow. Arrow represents flow direction.

The animals were transferred to the apparatus 12 h before the start of the experiment. During this phase the system was supplied with filtered (0.5 µm) seawater, in order to avoid sedimentation in the chambers before the start of the experiment. At the end of this acclimation phase, all the chambers therefore had the same water quality. All experiments were carried out at 17°C and 33 ppt seawater temperature and salinity respectively. Three types of nutrient solution (diets) were then used for the experiment (Fig. 2). To begin with, the system was supplied with natural seawater from three outside basins of 300 m³ in which numerous phytoplankton species were growing. Following this, the system was supplied with enriched seawater containing two selected species of phytoplankton: *Isochrysis galbana*, a motile single cell, 3 to 4 µm in size, which is much used in hatcheries and has already been used in tests with *C. virginica* (Palmer and Williams, 1980), and *Tetraselmis suecica*, also motile, which was chosen for its larger size of 9 to 10 µm. The difference in size between the two species used, provided a size range with two distinct peaks (Fig. 2). The third and last mixture tested in the system was made up exclusively with oyster biodeposits (faeces and pseudofaeces) filtered at 125 µm and resuspended in solution.

The flow rate across each chamber, established by using a flowmeter, was verified before each sampling by measuring the volume of output over a minute. A sample of approximately 50 ml was then taken at the outflow of the chamber. The size spectrum of particles in each sample was then determined using a Coultronics Multisizer[®] with 256

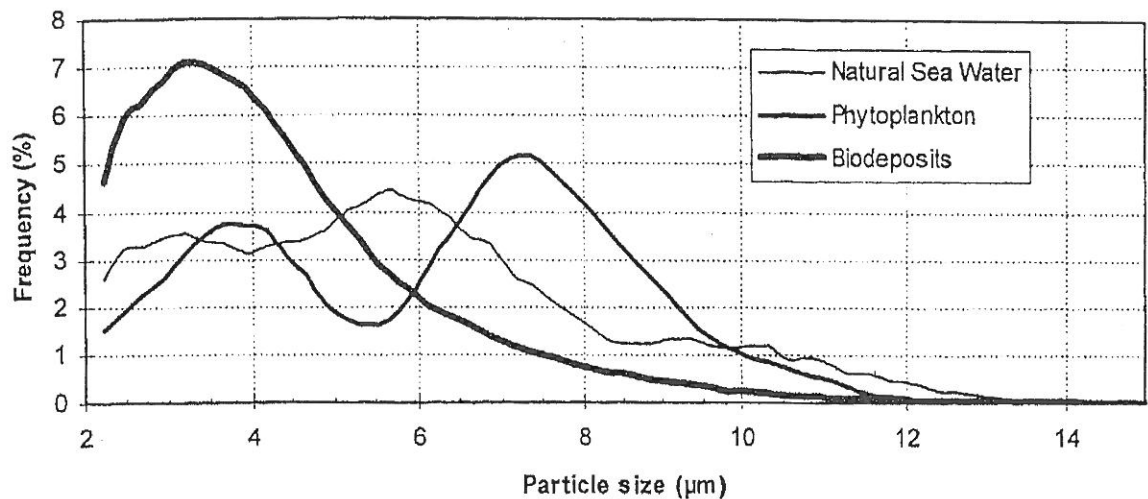


Fig. 2. Particle size composition of the diets (percent frequency). Each diet has a characteristic profile, biodeposits having the smallest particles in general and phytoplankton displaying a decrease in frequency around 5 μm between two peaks representing the two algal species used in the mix.

channels. The probe used, calibrated at 100 μm , allows detection and measurement of particles from 2.21 μm to 62 μm in 256 size classes (linear progression). Experimental measurement was made at a constant volume of 500 μl , giving a coefficient of coincidence (the chance of two particles being measured as one) of less than 8%. The result was recorded directly by a

PC microcomputer using the "AccuComp[®] Coulter[®] Multisizer" program. Retention was considered to be taking place as long as the spectrum of particles from the

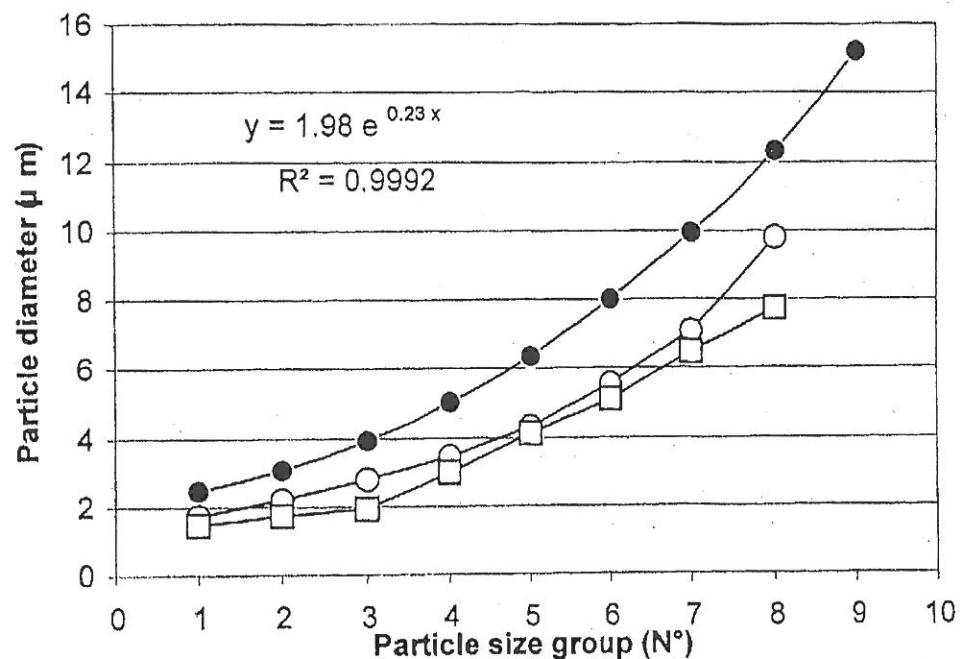


Fig. 3. Particle size classes used in the present experiment compared with two previous studies. The form of the relation between size and class is basically the same as in the previous studies though the present study uses a slightly greater range and larger particles (●: present work; ○: Palmer and Williams, 1980; □: Vahl, 1972).

control chamber was significantly higher than that from the test chamber. This was tested with a non-parametric Mann–Whitney test (Scherrer, 1984).

For each of the 256 channels, the mean number of particles (\bar{X}), from 4 to 6 consecutive counts, and the standard deviation (σ) were calculated. The standard error ($Es = \sigma / \sqrt{n - 1}$) for each channel was expressed as a percentage of the mean (Es / \bar{X}). When counts were below 30 particles, the standard error of the machine became too great ($> 10\%$) and the number of countable particles was no longer considered significant. The spectrum was therefore restricted to between 2.21 and 9 to 14 μm depending on the diet. This size range represents approximately 40–50 channels. Vahl (1972) and Palmer and Williams (1980) reduced their particle spectrum to 8 size classes in the range 2–10 μm . We defined 9 size classes following an exponential progression of the form ($\emptyset \text{ part.}$) = $1.98 \times e^{0.23 \times (n^\circ \text{ class})}$ (Fig. 3).

3. Measurements

3.1. Retention efficiency

Retention efficiency of different sized particles was calculated as the difference between the fraction consumed by the animal and the result from the control chamber. For each recording, the retention efficiency was calculated for each of 9 size classes following the formula (IFREMER, 1987):

$$R_i = \frac{[\nu]_{\text{con}} - [\nu]_{\text{meas}}}{[\nu]_{\text{con}}} \times 100 \quad (1)$$

Where R_i is retention efficiency for particle size class i , $[\nu]_{\text{con}}$ is the particulate volume measured at the output of the control chamber and $[\nu]_{\text{meas}}$ is the particulate volume measured at the output of the experimental chamber.

For each diet, the calculated retention values were analysed across all the individuals tested. The retention spectrum was determined using a non-parametric Wilcoxon test (Scherrer, 1984) over the 9 classes of particle size defined. Once this had been done, a comparative analysis was made with the results from the oysters so as to qualitatively determine the potential competition for food resources between the two species.

With these results and knowing the flow rate across the experimental chambers, it was possible to estimate the filtration rate. From this, the volume of water 100% purified of particles in the animal's range per time unit was quantified for each individual (Buhr 1976, IFREMER, 1987). Vahl (1972) calculated filtration rate using the following formula:

$$F_{\text{ind}} = D \times \frac{[\nu]_{\text{con}} - [\nu]_{\text{meas}}}{[\nu]_{\text{con}}} \quad (2)$$

Where F_{ind} is the filtration rate in $\text{l h}^{-1} \text{ ind}^{-1}$, D is the flow measured across the experimental chamber, in l h^{-1} , $[\nu]_{\text{con}}$ is the particulate volume measured at the output

of the control chamber and $[\nu]_{\text{meas}}$ is the particulate volume measured at the output of the experimental chamber.

To take allometric criteria into account, filtration rate was calculated per unit dry meat weight (dmw). Barillé et al. (1993) standardised filtration rate to an individual of 1 g dmw using the formula by Bayne and Newell (1983) and Bayne et al. (1987):

$$F_s = (W_s/W_e)^b \times F_e \quad (3)$$

Where F_s is the filtration rate of the standard animal, W_s is the dry meat weight of the standard animal (1 g), W_e is the measured dry meat weight of the animal, b is the allometric coefficient and F_e is the uncorrected filtration rate in $l\ h^{-1}\ ind^{-1}$.

An allometric factor of 0.4 was used for *C. gigas* (Barillé et al., 1993; Raillard et al., 1993). In *L. conchilega*, the size range tested did not allow a good estimation of an allometric coefficient. We used the relationship of filtration rate and dry meat weight defined by Buhr (1976):

$$\log(\text{Filtration}) = 0.3159 \times \log(\text{Dry meat weight}) + 0.8766$$

Giving $b = 0.3159$ as the allometric coefficient of filtration in *L. conchilega* that was used.

3.2. Assimilation rate

Measurement of assimilation efficiency was made by supplying the system with natural seawater containing oyster biodeposits, phytoplankton and mineral particles (silt). The method used followed Conover (1966) and required the collection of seston in the nutrient solution, plus enough faeces from the animal to analyse dry weight and ash-free dry weight. The faeces were sampled with a pipette after the animal had been supplied with the selected diet for 24 h. Food and faeces were sampled and analysed in a similar way. Each sample was deposited onto a Whatman GF/C filter, samples were dried at 50°C for 24 h, and then the filter was burnt off by heating to 450°C for 2 h. Mineral and organic matter concentrations were estimated by difference between dry weight and ash dry weight. Assimilation rate (AR) is given by the following formula (Conover, 1966; Bayne and Newell, 1983):

$$AR = (F - E)/(1 - E) \times F \quad (4)$$

Where F = ash free dry weight: dry weight ratio (fraction of organic matter) in the food; E = ash free dry weight: dry weight ratio in the faeces.

3.3. Respiration rate

Respiration rate was recorded individually in a confined environment, a 50 ml chamber for *L. conchilega*, and a 500 ml one for *C. gigas*, for 60 min using a WTW oxygen probe. Control measurements were made using empty chambers. In order to maintain the animals in a stress-free environment, respiration experiments were limited to 25% oxygen desaturation. Individual measurements were standardised to an individual of 1 g dry weight following Bayne et al. (1987). The allometric coefficient used for

C. gigas was 0.80 (Bougrier et al., 1995). For *L. conchilega* this was determined from the relationship between oxygen consumption and freeze-dried (36 h) weight of tested individuals.

3.4. Energetic assessment-growth potential

Energetic assessment was made from the results for assimilation, filtration and respiration. The growth potential (scope for growth: SFG) represents the potential energy available for all metabolism. It is calculated as the difference between energy assimilated (anabolism) and energy lost by excretion and catabolism in respiration. Excretion was considered negligible and was not taken into account in the assessment calculation. The growth potential was calculated from the following formula (Bayne and Newell, 1983) and expressed in $\text{J h}^{-1} \text{g dmw}^{-1}$:

$$\text{SFG} = \text{AR} \times C - R \quad (5)$$

Where SFG is the production rate, AR is the assimilation rate (%), C is the energy consumed and R is the energy lost by respiration. The physiological components were converted into energy terms in the following way:

$$C = F \times P^{-b_f} \times \text{POM} \times E_{\text{POM}} \quad (6)$$

$$R = \text{OR} \times P^{-b_o} \times E_R \quad (7)$$

Where F is the filtration rate, P is the individual dry weight, b_f is the allometric filtration coefficient, POM is the level of particulate organic matter (mg l^{-1}), E_{POM} is the POM energetic coefficient (J mg POM^{-1}), OR is the respiration rate ($\text{ml O}_2 \text{ h}^{-1} \text{g dmw}^{-1}$), b_o is the allometric respiration coefficient and E_R is the energetic respiration coefficient (J ml O_2^{-1}).

The energetic conversion coefficients used were:

$$E_R = 20.08 \text{ J ml O}_2^{-1} \text{ (Bayne and Newell, 1983)}$$

$$E_{\text{POM}} = 10 \text{ J mg POM}^{-1} \text{ (Goulletquer et al., 1989; Haure, pers. comm.)}$$

Feeding competition between the two species can be visualised by the extrapolation of these results to a field situation. Oyster biomass, expressed as dry tissue weight per square meter, was estimated from IFREMER oyster stock assessment data for Bay of Veys leasing grounds (Kopp et al., 1997). Mean biomass of the annelid was estimated from a population monitoring study, started in June 1994. By evaluating the relative respiration and filtration rates of the two populations from standardised results, interspecific competition between *C. gigas* and *L. conchilega* can be estimated.

4. Results

4.1. Retention spectra and filtration efficiency

One hundred and twelve measurements were made in total over the three diets. Because differences were found in the particulate charge, two series of measurements were recorded with natural seawater at different flow rates (351 ml h^{-1} and 740 ml h^{-1}).

h^{-1}). At the end of the experiments, only 48 measurements indicated animal filtration activity (significance in a Mann–Whitney test) and were retained for analysis.

When the flow rate was over 500 ml h^{-1} , particle retention by *L. conchilega* was significant, for particles above $3.9 \mu\text{m}$ diameter, for all three diets tested (Table 1 (A) (C) (D)). For natural seawater with a low particulate charge, retention was significant from $2 \mu\text{m}$ diameter upwards. Retention increased with particle size up to 25–48% for particles of $10\text{--}15 \mu\text{m}$, depending upon seston charge and flow rate.

C. gigas showed 18–40% retention efficiency from $2 \mu\text{m}$ particle diameter for all three diets (Table 1). Retention increased up to 85% for $12 \mu\text{m}$ particles in natural seawater but only attained 47% for the biodeposit diet.

Whatever the diet supplied, individual filtration showed that *L. conchilega* retains particles from sizes greater than $4 \mu\text{m}$ (20 to $125 \text{ ml h}^{-1} \text{ ind}^{-1}$) (Fig. 4). Above this, filtration efficiency increases in a quasi-linear manner with increasing particle size on the natural seawater and the biodeposit diets. With the phytoplankton diet, a decrease in retention was observed for particles between 5.64 and $7.12 \mu\text{m}$. This corresponds to the decrease in particle numbers in this range due to the population composition of the diet (Fig. 2). For the largest classes of particle size studied (greater than $12 \mu\text{m}$), the filtration rate becomes greater than $120 \text{ ml h}^{-1} \text{ ind}^{-1}$ whatever the diet fed (Fig. 4).

Individual filtration is significant for oysters throughout the particle size range and is systematically higher than in *L. conchilega*. Filtration rate is between 1 and $1.5 \text{ l h}^{-1} \text{ ind}^{-1}$ for particles of 2 to $3 \mu\text{m}$ and though the rate increases with larger particles, it stabilises at 2 to $4 \text{ l h}^{-1} \text{ ind}^{-1}$ above 7 to $8 \mu\text{m}$. Despite differences observed in filtration rate, both species are capable of retaining particles from the same range ($> 4 \mu\text{m}$). The difference with *C. gigas* is that filtration rate reaches a plateau whereas in *L. conchilega* it appears to continue above the range of particle size studied.

Rates of filtration were calculated for each individual, over the whole of the significant particle size range, then standardised per gram dry tissue weight (Table 2). These results show that *C. gigas* has a greater particle retention efficiency (46–80%) than *L. conchilega* (12–28%) over the total spectrum.

A similar trend is also observed for individual filtration rates (Table 2). The values calculated for *L. conchilega*, standardised to an individual of 1 g dmw (mean = $0.225 \pm 0.08 \text{ l h}^{-1} \text{ g dmw}^{-1}$) represent only 7% (natural seawater) to 14% (phytoplankton) of those of *C. gigas* (mean = $2.43 \pm 0.71 \text{ l h}^{-1} \text{ g dmw}^{-1}$).

4.2. Assimilation rate

Assimilation measurements were made by supplying the system with natural seawater enriched with phytoplankton and mineral seston. Organic particles represent on average 30% of the total sestonic charge. *L. conchilega* had a mean assimilation rate of 44%, while *C. gigas* had a 49% rate (Table 3).

Taking into account the sestonic charge of the seawater used (21.23 mg l^{-1}), and the standardised filtration rates determined for the two species, the quantity of seston retained by *L. conchilega* represents $4.77 \text{ mg h}^{-1} \text{ g dmw}^{-1}$. Under the same conditions, *C. gigas* retained $51.58 \text{ mg h}^{-1} \text{ g dmw}^{-1}$. At equivalent biomass, retention activity in *L. conchilega* is therefore 9.2% of that achieved by *C. gigas*. The fraction of food assimilated out of that which was retained represents $25.27 \text{ mg h}^{-1} \text{ g dmw}^{-1}$ for *C.*

Table 1
Retention efficiency (\pm standard deviation) of different particle sizes by *Lanice conchilega* and *Crassostrea gigas* supplied with 3 experimental diets ****: Wilcoxon probability less than 5%; “.”: number of particles is not significant (Scherrer, 1984)

Group (N°)	Particle size group (μm)	Central value (μm)	Retention efficiency (%)					
			(A) Natural sea water		(B) Natural sea water		(C) Phytoplankton	
			<i>Lanice conchilega</i>	<i>Crassostrea gigas</i>	<i>Lanice conchilega</i>	<i>Crassostrea gigas</i>	<i>Lanice conchilega</i>	<i>Crassostrea gigas</i>
1	2.21–2.70	2.46	–0.19 (± 5.8)	42.60 ** (± 7.9)	10.49 ** (± 6.8)	18.32 (± 19.1)	–2.32 (± 4.8)	18.99 ** (± 8.9)
2	2.70–3.44	3.07	–1.07 (± 6.3)	46.33 ** (± 8.8)	12.53 ** (± 7.7)	16.61 ** (± 10.9)	0.34 (± 4.2)	26.69 ** (± 12.5)
3	3.44–4.42	3.93	–0.48 (± 8.2)	54.80 ** (± 7.1)	15.93 ** (± 9.7)	17.42 (± 25.9)	3.06 ** (± 4)	37.28 ** (± 17)
4	4.42–5.64	5.03	6.39 ** (± 6.8)	60.60 ** (± 8.3)	22.54 ** (± 11.4)	25.66 ** (± 25.6)	7.96 ** (± 5.7)	44.28 ** (± 21)
5	5.64–7.12	6.38	10.46 ** (± 5.4)	74.02 ** (± 4.5)	30.05 ** (± 9.8)	44.85 ** (± 14.4)	13.18 ** (± 7.1)	47.78 ** (± 23.1)
6	7.12–8.84	7.98	10.08 ** (± 3.8)	81.12 ** (± 3.2)	34.93 ** (± 13.7)	56.90 ** (± 9.3)	15.41 ** (± 7.5)	48.67 ** (± 23.5)
7	8.84–11.05	9.95	16.34 ** (± 4.8)	80.51 ** (± 3.5)	45.36 ** (± 14.5)	56.45 ** (± 20.7)	22.38 ** (± 9.6)	49.09 ** (± 25.5)
8	11.05–13.51	12.28	25.20 ** (± 4.6)	84.65 ** (± 8.3)	43.65 ** (± 16.5)	65.34 ** (± 15.7)	30.72 ** (± 13.9)	47.35 ** (± 25.5)
9	13.51–16.94	15.23	–	–	48.91 ** (± 9.7)	–	–	–
Mean flow (ml l^{-1})								
			740	5160	351	5985	550	4680
Particle Volume (μm^3) in 500 μl			1 565 000		409 330	3 800 000	2 443 000	
Seston (mg l^{-1})					8.22	19.94		
POM (mg l^{-1})					1.57 [19.21]	2.99 [15.01]		
Number of data			14	3	10	4	11	3

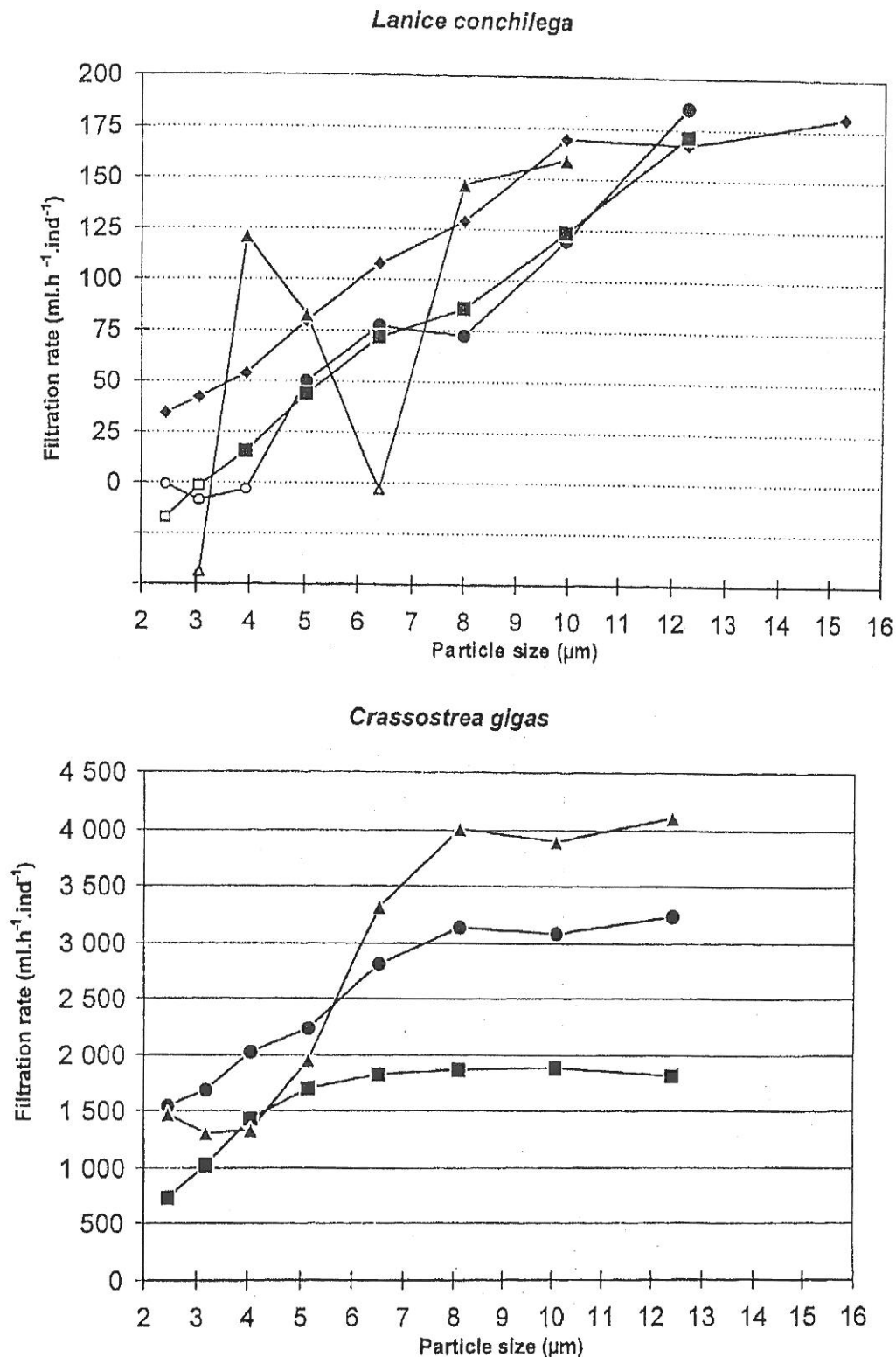


Fig. 4. Individual filtration rate of *Lanice conchilega* and *Crassostrea gigas* according to particle size and three experimental diets. ●: Natural sea water (A); ◆: Natural sea water (B); ▲: Phytoplankton; ■: Biodeposits; The blank symbols indicate no significant retention: $p > 0.05$ (Wilcoxon).

gigas and $2.10 \text{ mg h}^{-1} \text{ g dmw}^{-1}$ for *L. conchilega*, or 7.7% of the total food assimilated by both species.

Table 2

Overall retention efficiency and standardised filtration rates for *Lanice conchilega* and *Crassostrea gigas* on the experimental diets (mean \pm standard deviation)

Diet	Retention efficiency (%)		Filtration rate (ml h ⁻¹ ind ⁻¹)		Std filtration rate (l h ⁻¹ dmw ⁻¹)	
	<i>Lanice Conchilega</i>	<i>Crassostrea gigas</i>	<i>Lanice Conchilega</i>	<i>Crassostrea gigas</i>	<i>Lanice Conchilega</i>	<i>Crassostrea gigas</i>
(A) Natural sea water	13.2 (\pm 3.6)	80.5 (\pm 3.6)	97.05 (\pm 22.89)	4 141.96 (\pm 626.89)	0.23 (\pm 0.06)	4.14 (\pm 0.63)
(B) Natural sea water	28.3 (\pm 11.2)	–	103.57 (\pm 62.22)	–	0.20 (\pm 0.15)	–
(C) Phytoplankton	12.8 (\pm 4.9)	49.7 (\pm 10.2)	108.09 (\pm 58.46)	3 012.68 (\pm 823.87)	0.33 (\pm 0.14)	3.01 (\pm 0.82)
(D) Biodeposits	13.3 (\pm 6.7)	46.1 (\pm 1.1)	73.91 (\pm 44.06)	2 156.75 (\pm 250.69)	0.14 (\pm 0.08)	2.16 (\pm 0.25)
Mean	16.9 (\pm 7.6)	58.8 (\pm 18.9)	95.66 (\pm 15.19)	3 103.80 (\pm 995.74)	0.23 (\pm 0.08)	2.43 (\pm 0.71)

Table 3
Assimilation rate in *Lanice conchilega* and *Crassostrea gigas* measured by the ratio method of Conover (1966)

	Experimental diet			<i>Lanice conchilega</i>				<i>Crassostrea gigas</i>			
	Dry weight (\pm SD)(mg l ⁻¹)	POM (\pm SD) (%)	Faeces products		Faeces products		Assimilation rate [AR]	Faeces products		Assimilation rate [AR]	
			Ind. number	Dry weight (mg l ⁻¹)	POM (%)	Assimilation rate [AR]		Ind. number	Dry weight (mg l ⁻¹)	POM (%)	
1	26.7 (\pm 0.94)	27.8 (\pm 5.2)	Lc01	14.79	22.79	0.23	Cg1	57.31	19.70	0.36	
			Lc02	14.56	21.77	0.28					
			Lc03	10.95	23.55	0.20					
			Lc04	12.41	24.09	0.17					
2	19.5 (\pm 0.7)	29.9 (\pm 1.2)	Lc01	10.06	20.67	0.39	Cg2	46.74	15.00	0.59	
			Lc02	10.35	19.91	0.42					
			Lc03	8.58	23.31	0.29					
			Lc04	9.54	24.54	0.24					
3	17.3 (\pm 1.2)	33.5 (\pm 2.1)	Lc05	9.06	21.41	0.46	Cg3	31.71	21.54	0.36	
			Lc06	12.29	18.31	0.56					
			Lc07	12.27	17.76	0.57					
			Lc08	11.74	17.98	0.57					
4	17.3 (\pm 1.2)	33.5 (\pm 2.1)	Lc09	19.26	15.52	0.64	Cg4	29.83	23.30	0.40	
			Lc10	10.79	21.31	0.46					
			Lc11	14.47	19.91	0.51					
			Lc12	12.41	20.22	0.50					
5	18.7 (\pm 1.8)	31.8 (\pm 0.03)	Lc13	11.98	20.03	0.50	Cg5	24.76	22.54	0.42	
			Lc14	11.26	18.74	0.51					
			Lc15	23.32	11.02	0.73					
			Lc16	10.18	20.52	0.45					
			Lc17	14.25	16.91	0.56	Cg6	53.31	15.72	0.60	
			Lc18	13.51	17.47	0.55					
							Cg7	66.18	16.02	0.59	

4.3. Respiration rate

The allometric relationship for respiration in *L. conchilega* was based on ninety measurements. This takes the form $R = 0.115 \times W^{0.534}$ ($r^2 = 0.60$), where R is oxygen consumption and W is the individual dry meat weight (Fig. 5). This relationship allows the allometric coefficient to be calculated for *L. conchilega* giving $b = 0.534$.

The standardised respiration rate for *L. conchilega* varied from 0.06 to 0.193 ml O₂ h⁻¹ g dmw⁻¹ overall with a mean of 0.113 ml O₂ h⁻¹ g dmw⁻¹. The measurements made on *C. gigas* show a mean consumption of 0.68 ml O₂ h⁻¹ g dmw⁻¹.

4.4. Growth potential

For *L. conchilega*, assimilation efficiency is calculated at 44% for a filtration rate of 0.225 l h⁻¹ g dmw⁻¹. The quantity of particulate organic matter (POM) present in the nutrient supply is 6.35 mg l⁻¹ and the energetic conversion coefficient for POM is 10 J mg POM⁻¹. The assimilated fraction therefore represents 14.29 J h⁻¹ g dmw⁻¹. As the mean standardised respiration rate is 0.113 ml O₂ h⁻¹ g dmw⁻¹ and energy catabolised by respiration represents 2.27 J h⁻¹ g dmw⁻¹, using an energetic conversion coefficient of 20.08 J ml O₂⁻¹, the rate of production obtained for *L. conchilega* with these results was 4.01 J h⁻¹ g dmw⁻¹.

In *C. gigas*, with an assimilation efficiency measured at 49% and a standardised filtration rate of 2.43 l h⁻¹ g dmw⁻¹, the fraction of food assimilated represents 154.31 J h⁻¹ g dmw⁻¹ in energetic terms. Loss of energy to respiration (0.62 ml O₂ h⁻¹ g dmw⁻¹) is estimated at 12.45 J h⁻¹ g dmw⁻¹. The rate of production obtained for *C. gigas* from these results is 61.96 J h⁻¹ g dmw⁻¹.

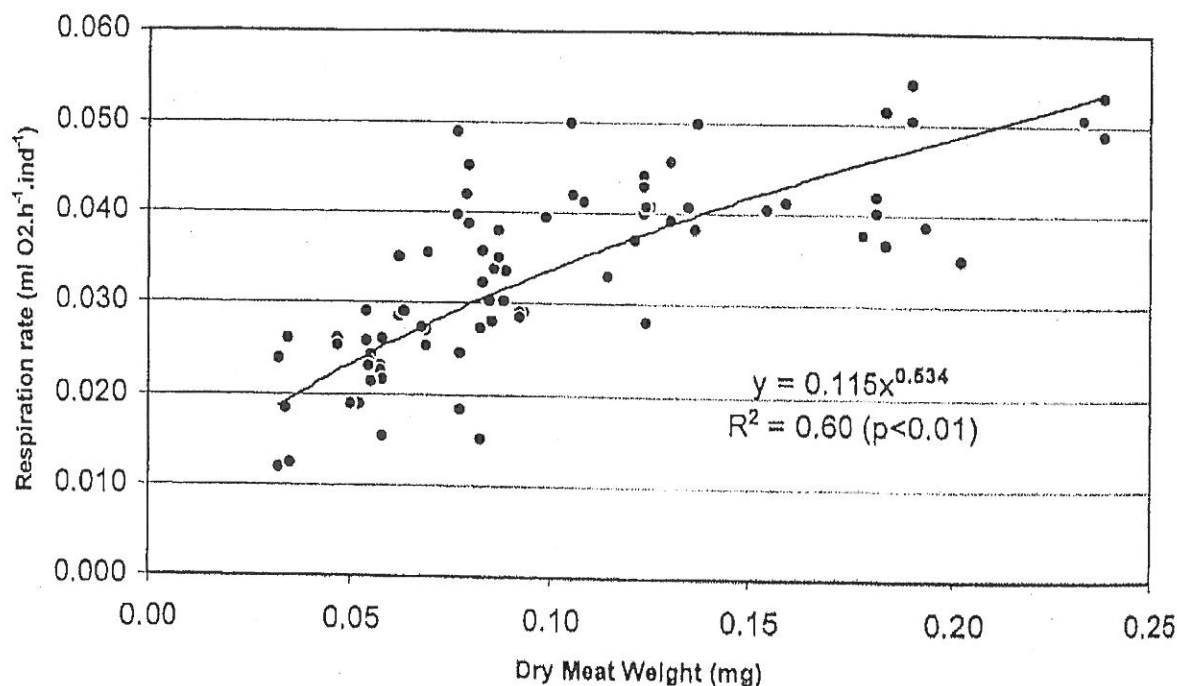


Fig. 5. Determination of the allometric relationship between respiration rate and individual dry meat weight (DMW) for *Lanice conchilega*.

5. Discussion

Whatever the type of diet supplied in our experiments, *L. conchilega* demonstrates the ability to collect particles in suspension. Retention takes place from particle sizes around 4 μm and upwards. Negative retention values obtained below 4 μm do not necessarily demonstrate output of particles by the animals. Similar phenomena were observed by Vahl (1972) on *Mytilus edulis* for particles below 2 μm . Vahl (1972) suggested that this apparent emission of particles was due to particle aggregation or mucus production. The process of retention in polychaetes and more precisely in *L. conchilega* has only been previously examined by Buhr (1976). This author demonstrated retention with particles of the phytoplankton *Dunaliella marina* which are of about 7 μm diameter. Our present results show that *L. conchilega* is capable of retaining smaller particles.

Above 4 μm , retention efficiency appears to increase linearly with size of particles. However, on the phytoplankton diet, a gap in retention was observed in the range 5.6 to 7.1 μm . This particle size class corresponds with a decrease in frequency of particles in the size range between the two species of phytoplankton used (Fig. 2). The results appear to show preferential retention of particles representing these two groups. It should therefore be asked if selection is made for which particles are retained out of those in suspension. A selective process has already been demonstrated in *C. gigas* (Razet et al., 1990; Deslous Paoli et al., 1992; Barillé et al., 1993) but this has never been studied in *L. conchilega*.

The retention results obtained with *C. gigas* confirm those in the literature (Palmer and Williams, 1980; Barillé et al., 1993). Oysters are capable of retaining particles from 2 μm size. Retention efficiency increases progressively with particle size, reaching a maximum between 6 and 8 μm . This pattern is not repeated in *L. conchilega*, where retention efficiency appears to continue to increase beyond the range of size of particles studied.

Overall, our results show that *L. conchilega* can retain suspended particles of the same range as those retained by *C. gigas* and therefore that competition for food is potentially occurring.

Using individuals of a similar size to those in the present study, Buhr (1976) quantified individual filtration rates in the order of 87 $\text{ml h}^{-1} \text{ ind}^{-1}$ using a diet composed entirely of the phytoplankton *D. marina* ($7.5 \times 5.0 \mu\text{m}$). For the same range of particle size, our results give a filtration rate of 50 to 90 $\text{ml h}^{-1} \text{ ind}^{-1}$ depending on the diet type. Our results therefore support the previous study, despite the differences in methodology.

Filtration values are very different between the species when standardised to an animal of 1 g dry weight. For *C. gigas*, filtration rate was 1.78 to 3.19 $\text{l h}^{-1} \text{ g dmw}^{-1}$ and for *L. conchilega* it was 0.14 to 0.33 $\text{l h}^{-1} \text{ g dmw}^{-1}$. Deslous Paoli et al. (1992) determined a standard filtration rate of 2 $\text{l h}^{-1} \text{ g dmw}^{-1}$ for *C. gigas*. This value was used by Raillard et al. (1993) to model *C. gigas* feeding behaviour. Barillé et al. (1993) determined a mean filtration rate of 2.21 $\text{l h}^{-1} \text{ g dmw}^{-1}$. The values we obtained in the present study are therefore in accordance with previous results. For *L. conchilega*, no values are available in the literature with which to make a comparison. The large

difference with *C. gigas* is not surprising however because *C. gigas* feeds solely by filtration whereas *L. conchilega* cannot be considered as a strict filter feeder. Suspension feeding was demonstrated in *L. conchilega* by Buhr (1976), so the animal must be considered a semi-active suspension feeder. Our behavioural observation on *L. conchilega* in the aquarium and experimental chambers indicated that animals extend their mucus covered tentacles around their sandy fringes to catch particles present in the passing water. Mucus production and ciliary movements along the length of the tentacles also indicate their active role in particle retention.

Given the differences in retention strategy between the two species, it would seem logical to expect a significant difference between their filtration efficiencies. But, under the defined experimental conditions, our estimates of filtration rate, standardised to animals of 1 g dry weight, show that *L. conchilega* still attains a level of activity corresponding to 14% that of *C. gigas*.

Assimilation rate measured in *C. gigas* agrees with values reported in the literature (Raillard et al., 1993). Our results for *L. conchilega* vary from 0.17% to 0.73% which is slightly lower than those of Buhr (1976) who obtained AR = 43.3% to 90.2%. However, the phytoplankton (*D. marina*) enriched diet used by this author led to a high degree of assimilation (94.4% POM compared with 30% in our study). Due to the rarity of relevant data in the literature, it was not possible to compare our results with those of other authors. Respiration rates measured on *L. conchilega* under our experimental conditions allowed us to establish an allometric relationship between oxygen consumption and individual dry weight. There are only a few studies on polychaetes in this area (Gremare et al., 1989; Riisgard, 1989; Riisgard and Ivarsson, 1990). Only the latter, in a study on *Sabella penicillus*, made an allometric study of respiration [$R = 0.13 \times W^{0.66}$]. Our results do not basically differ from those of these authors ($[R = 0.115 \times W^{0.536}]$).

C. gigas displays a much higher metabolic profile than *L. conchilega*, $61.96 \text{ J h}^{-1} \text{ g dmw}^{-1}$ versus $4.02 \text{ J h}^{-1} \text{ g dmw}^{-1}$ respectively. This difference is related to the fact that *C. gigas* is particularly well adapted to active filtration while in *L. conchilega*, this feeding method is facultative and likely to be secondary in importance. Field studies have shown however that in terms of biomass, the extent of the *L. conchilega* population far exceeds that of cultivated oysters (Ropert, 1996, 1998 unpublished). Interestingly, the Bay of Veys is the only site in France showing such outbreak of *L. conchilega* population, spatially overlaying oyster leasing grounds, with densities per square metre exceeding 7000 individuals. This precise overlay is likely due to both at a global scale, the current pattern facilitating recruitment from the *L. conchilega* subtidal population, and at a local scale, the relationship between recruitment process and the hydrodynamics affected by the oyster growout facilities (iron tables). Estimation of biomasses in the sampling area gave dry weights of 278 g dmw m^{-2} ($n = 403$, s.e. = 5.6 g) for *C. gigas* (after Kopp et al., 1997), and 717 g dmw m^{-2} (mean density = 3500 ind^{-2} $n = 473$, s.e. = 15.1 g) for *L. conchilega* (Table 4). This corresponds to a biomass ratio between the species of approximately 2.6 in favour of *L. conchilega*. These results can be extrapolated to give filtration rates per square meter per species. The rates, $677 \text{ l h}^{-1} \text{ m}^{-2}$ for *C. gigas* and $161 \text{ l h}^{-1} \text{ m}^{-2}$ for *L. conchilega* show that, at these population levels, *L. conchilega* attains 25% of the oyster filtration rate and that therefore there is potential feeding competition between the species.

Table 4

Scope for growth estimates of *Lanice conchilega* and *Crassostrea gigas* populations based upon field estimates (value \pm standard deviation)

	<i>Lanice conchilega</i>	<i>Crassostrea gigas</i>
Stock field assessment (g dmw m ⁻²)	716.72 (\pm 15.11)	278.64 (\pm 5.62)
Filtration rate (l h ⁻¹ m ²)	161.26 (\pm 3.4)	677.13 (\pm 13.65)
Respiration rate (ml O ₂ h ⁻¹ m ⁻²)	78.84 (\pm 1.66)	172.76 (\pm 3.48)
Scope for Growth (J h ⁻¹ m ⁻²)	2870 (\pm 61)	17265 (\pm 348)

Oxygen consumption by *L. conchilega* (78.8 ml O₂ h⁻¹ m⁻²) represents close to 45% that of cultivated oysters (172.8 ml O₂ h⁻¹ m⁻²). Adding together the total activity of both species, *L. conchilega* represented a 19% decrease in the total carrying capacity and 30% of oxygen depletion (Table 4).

Although suspension feeding has been clearly demonstrated in *L. conchilega*, it has only been quantified under laboratory conditions. Future experiments should take into account variability of environmental conditions (e.g., temperature, sestonic charge, available food resources). Such data would considerably complement the results of the present study.

Equally, within the framework of an overall approach to the biology of *L. conchilega*, it would be interesting to examine the nature of the factors responsible for the change in feeding behaviour and to verify feeding competition in situ. Frechette et al. (1992), working on *M. edulis*, showed a relationship between biomass and density that helped optimise production densities and identify the nature of limiting factors (space or food). Buhr (1976) proposed the hypothesis that the change in feeding behaviour from deposit to suspension feeding was density dependant and therefore a purely physical factor. The role of food availability in the environment must also be examined however, in particular the influence of oyster biodeposit production (Dinet et al., 1990). Enrichment of the water column with organic particles in the oyster production zone could be an important factor in the choice of feeding behaviour in *L. conchilega*. According to Sornin (1981), daily biodeposit output from the biomass of oysters in production represents 14–20 tonnes (dry weight) per hectare for production conditions similar to those in Bay of Veys. For the sum of all the production leasing grounds in the area, this output would be 2000 to 3000 tonnes per day or 3 to 4 times the biomass of the *L. conchilega* population (714 tonnes dry weight, Ropert unpub.).

Studying the relationship linking *L. conchilega* and *C. gigas* and understanding the phenomenon of proliferation in *L. conchilega* will allow the environmental impact to be predicted. It appears that the most important factors for the growth of molluscs are temperature, sestonic charge, organic matter and phytoplankton biomass (Héral et al., 1986). Apart from direct feeding competition from *L. conchilega*, this annelid is also likely to cause particle resuspension (Carey, 1983) and therefore modify the composition of the water column. *L. conchilega* can therefore have a direct impact on food availability for *C. gigas* solely by its presence. In addition, as we have shown in the present work, competition is not solely at the feeding level. Competition could also be occurring for oxygen. We need to ask what the influence of the *L. conchilega*

population would be under conditions of extreme oxygen desaturation. Such situations are not unusual in the Bay of Veys area in summer and also coincide with a high level of mortality in cultivated oysters. The role of the *L. conchilega* population in the occurrence of these low oxygen periods should therefore be examined as well the indirect impact these have on survival of aquacultural species in the Bay of Veys.

Acknowledgements

The authors wish to thank to Dr. H. McCombie for useful comments, and the translation of this paper. Special thanks are extended to P. Geairon for his technical assistance. This work was supported by funds from the Regional Council of Basse-Normandie, 'Agence de L'Eau', and the Normandy Shellfish Farmers Association of Normandie (SRC).

References

- Barillé, L., Prou, J., Héral, M., Bougrier, S., 1993. No influence of food quality, but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* 171, 91–106.
- Barillé, L., Bougrier, S., Geairon, P., Robert, J.M., 1994. Alimentation expérimentale de l'huître *Crassostrea gigas* à l'aide de navicules bleues *Haslea ostrearia* (Simonsen) de différentes tailles. *Oceanol. Acta* 17, 201–210.
- Bayne, B.L., Newell, R.C., 1983. Physiological energetics of marine molluscs. In: Wilbur, K.M., Saleuddin, S.M. (Eds.), *The Mollusca*, 4 (1). Academic Press, London, UK, pp. 407–515.
- Bayne, B.L., Hawkins, A.J.S., 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.
- Bock, M.J., Miller, D.C., 1995. Storm effects on particulate food resources on an intertidal sandflat. *J. Exp. Mar. Biol. Ecol.* 187, 81–101.
- Bock, M.J., Miller, D.C., 1997. Particle-bound organic matter as a cue for suspension feeding in tentaculate polychaetes. *J. Exp. Mar. Biol. Ecol.* 215, 65–80.
- Bougrier, S., Geairon, P., Deslous Paoli, J.M., Bacher, C., Jonquière, G., 1995. Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture* 134, 143–154.
- Buhr, K.J., 1976. Suspension feeding and assimilation efficiency in *Lanice conchilega* (polychaeta). *Mar. Biol.* 38, 373–383.
- Buhr, K.J., Winter, J.E., 1977. Distribution and maintenance of a *Lanice conchilega* association in the Weser Estuary (GFR), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. In: Keegan, B.F., Ceidigh P.O., Boaden, P.J.S. (Eds.), *Biology of Benthic Organisms*. 11. European Symposium on Marine Biology, Galway (Eire), Pergamon, 5 Oct 1976, pp. 101–113.
- Carey, D.A., 1983. Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.* 40, 301–308.
- Conover, R.J., 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* 11, 338–345.
- Dauer, D.M., Maybury, C.A., Ewing, R.M., 1981. Feeding behavior and general ecology of several spionid polychaetes from Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 54 (1), 21–38.
- Deslous Paoli, J.M., Lannou, A.M., Geairon, P., Bougrier, S., Raillard, O., Héral, M., 1992. Effects of the feeding behaviour of *Crassostrea gigas* (bivalve molluscs) on biosedimentation of natural particulate matter. *Hydrobiologia* 231 (2), 85–91.
- Dinet, A., Sornin, J.M., Sablière, A., Delmas, D., Feuillet Girard, M., 1990. Influence de la biodéposition de bivalves filtreurs sur les peuplements meiobenthiques d'un marais maritime. *Cah. Biol. Mar.* 31, 307–322.

- Eckman, J.E., Duggins, D.O., 1993. Effects of flow speed on growth of benthic suspension feeders. *Biol. Bull. Mar. Biol. Lab., Woods Hole* 185, 28–41.
- Fauchald, K., Jumars, P., 1979. The diet of worms: a study of polychaete feeding guilds. *Ocean Mar. Biol. Ann. Rev.* 17, 193–284.
- Frechette, M., Butman, C.A., Geyer, W.R., 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol. Oceanogr.* 34, 19–36.
- Frechette, M., Aitken, A.E., Page, L., 1992. Interdependence of food and space limitation of a benthic suspension feeder: consequences for self-thinning relationships. *Mar. Ecol. Prog. Ser.* 83, 55–62.
- Gerdes, D., 1983. The Pacific oyster *Crassostrea gigas*: Part 1. Feeding behaviour of larvae and adults. *Aquaculture* 31, 195–219.
- Goulletquer, P., Héral, M., Deslous Paoli, J.M., Prou, J., Garnier, J., Razet, D., Boromthananat, W., 1989. Ecophysiologie et bilan énergétique de la palourde japonaise d'élevage *Ruditapes philippinarum*. *J. Exp. Mar. Biol. Ecol.* 132, 85–108.
- Gremare, A., Amouroux, J.M., Amouroux, J., 1989. Modelling of consumption and assimilation in the deposit-feeding polychaete *Eupolyornia nebulosa*. *Mar. Ecol. Prog. Ser.* 54, 239–248.
- Héral, M., Deslous Paoli, J.M., Prou, J., 1986. Dynamiques des productions et des biomasses des huîtres creuses cultivées (*Crassostrea angulata* et *Crassostrea gigas*) dans le bassin de Marennes-Oléron depuis un siècle. *International Counc. for the Exploration of the Sea, Mariculture Committee*, CM 1986/F:41, 21 p.
- IFREMER, 1987. Bilan énergétique chez les mollusques bivalves. *Workshop on Shellfish Ecophysiology. Vie Marine H.S.* 7, 1–68.
- Kopp, J., Joly, J.P., Le Gagneur, E., Ruelle, F., 1997. Biomasses ostréicoles et mytilicoles de Normandie en 1995. IFREMER, Rapp. Int. DRV/RA/RST/97-07, 65 p.
- Miller, D.C., Bock, M.J., Turner, E.J., 1992. Deposit and suspension feeding in oscillatory flows and sediment fluxes. *J. Mar. Res.* 50, 489–520.
- Palmer, R.E., Williams, J.G., 1980. Effect of the particle concentration on filtration efficiency of the Bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. *Ophelia* 19, 163–174.
- Raillard, O., Deslous Paoli, J.M., Héral, M., Razet, D., 1993. Modélisation du comportement nutritionnel et de la croissance de l'huître japonaise *Crassostrea gigas*. *Oceanol. Acta* 16, 73–82.
- Razet, D., Héral, M., Prou, J., Legrand, J., Sornin, J.M., 1990. Variations des productions de biodépôts (feces et pseudofeces) de l'huître *Crassostrea gigas* dans un estuaire macrotidal: Baie de Marennes-Oléron. *Haliotis* 20, 143–161.
- Riisgard, H.U., 1989. Properties and energy cost of the muscular piston pump in the suspension feeding polychaete *Chaetopterus variopedatus*. *Mar. Ecol. Prog. Ser.* 56, 157–168.
- Riisgard, H.U., Ivarsson, N.M., 1990. The crown-filament pump of the suspension-feeding polychaete *Sabella penicillus*: filtration, effects of temperature, and energy cost. *Mar. Ecol. Prog. Ser.* 62, 249–257.
- Ropert, M., 1996. Particularités du recrutement et du renouvellement d'une population de *Lanice conchilega* (Polychaeta, Terebellidae) associée à la conchyliculture en baie des Veys (Baie de Seine occidentale). *J. Rech. Oceanogr.* 21 (2–3), 118–125.
- Scherrer, B., 1984. Biostatistiques. Gaëtan Morin Editeur, Québec, 850 pp.
- Sornin, J.M., 1981. Processus sédimentaires et biodéposition liés à différents modes de conchyliculture. Baie de Cancale, Anse de l'Aiguillon et Bassin de Marennes-Oléron. Thèse de Doct. 3ème cycle, 188 pp.
- Souza Reis, C.D., Monteiro Marques, V., Calvarion, J., Marques, J.C., Melo, R., Santo, R., 1982. Contribuição para o estudo dos povoamentos (substrato móvel) da costa ocidental portuguesa. *Oceanol. Acta* 6, 91–105.
- Sylvand, B., 1995. La Baie des Veys, 1972–1992: structure et évolution à long terme d'un écosystème benthique intertidal de substrat meuble sous influence estuarienne. Thèse de Doct. d'Etat.: Université de Caen, 409 pp.
- Taghon, G.-L., Nowell, A.R., Jumars, P.A., 1980. Induction of suspension feeding in spionid polychaetes by high particulates fluxes. *Science* 210, 562–564.
- Vahl, O., 1972. Efficiency of particle retention in *Mytilus edulis* L. *Ophelia* 10, 17–25.