



Dynamic filter-feeding responses in fouling organisms

P. L. Pascoe*, H. E. Parry, A. J. S. Hawkins

Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, UK

ABSTRACT: Filter-feeding responses were studied in 2 ascidians, *Ciona intestinalis* and *Asciidiella aspersa*, and a bryozoan *Membranipora membranacea* to suspensions of *Isochrysis galbana* at concentrations between 1000 and 100 000 cells ml⁻¹, and to a mixture of *I. galbana* and inorganic silt (0.36 to 36 µg l⁻¹ chlorophyll *a*; 0.5 to 15 mg l⁻¹ total particulate matter), thus simulating a wide range of food availabilities. Clearance rates (CR) varied significantly, reaching maxima of 4.61 l g⁻¹ h⁻¹ at about 5000 cells ml⁻¹ in *C. intestinalis* and 5.26 l g⁻¹ h⁻¹ above about 10 000 cells ml⁻¹ in *A. aspersa*. Between 1000 and 25 000 cells ml⁻¹, CR in a standardised 1000 mm² colony of *M. membranacea* increased from 0.50 to 1.23 l h⁻¹, the maximum equating to 0.36 ml zooid⁻¹ h⁻¹. At 100 000 cells ml⁻¹, CR in *M. membranacea* reduced dramatically to 0.11 l h⁻¹, associated with satiation and the cessation of feeding. Apart from this one observation of satiation in *M. membranacea*, ingestion rates increased linearly with cell concentration in all 3 species. Assessing the selective retention of particles between 2 and 5.5 µm in diameter in the *I. galbana* and silt mixture, *C. intestinalis* showed a significant decrease in retention efficiency for all particles above 4.5 µm, and *M. membranacea* exhibited positive selection for algal particles over inorganic silt, whereas *A. aspersa* showed similar retention of all particles. Collective findings indicate that functional dependencies of CR and retention efficiency upon food quantity and quality should be included within dynamic models of feeding and growth in these and other suspension-feeding species.

KEY WORDS: Ascidian · Bryozoan · Clearance rate · Retention efficiency · Filter feeding · Fouling

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The role and impact of filter-feeders on ecosystem function and dynamics has become an important area of study over the last decade, particularly with respect to sustainable aquaculture development and ecosystem modelling (McKindsey et al. 2006, Gibbs 2007). Whilst most previous work on filter-feeding in marine species has concentrated on bivalve molluscs, as many are of commercial importance and are cultured worldwide, there has been growing interest in interspecific competition for space and food by fouling communities (Lesser et al. 1992, Riisgard & Larsen 2000, Mazouni et al. 2001).

Lesser et al. (1992) assessed the interspecific competition for food between cultured mussels and suspension-feeding fouling taxa and found that although there were some differences in particle selection, blue

mussels *Mytilus edulis* L. showed a higher clearance rate for all particle types and size classes. They concluded that where the food supply does not limit the ability of mussels to sustain high feeding rates, interspecific competition from fouling organisms should not affect the commercial yield. Their results showed *Ciona intestinalis* to exhibit the highest clearance rate of the fouling organisms examined and some selection against large non-chlorophyll particles (>16 µm), estimating that it would take 3 *C. intestinalis* (mean dry wt = 0.22 g) to match the clearance rate of 1 mussel (mean dry wt = 0.83 g). In addition, Petersen & Riisgard (1992) highlighted temperature dependent changes in filtration rate (FR) in *C. intestinalis* compared to mussels, and concluded that the large numbers of ascidians in Kertinge Nor, Denmark would have an important grazing impact on the phytoplankton during summer and early fall.

*Email: plp@pml.ac.uk

A slightly different perspective is shown for oysters *Crassostrea gigas* and ascidians in the Thau Lagoon, France, where food resource-partitioning is suggested between these species, thus limiting competition (Mazouni et al. 2001). Ascidians feed on the high levels of picophytoplankton ($< 1 \mu\text{m}$) in this lagoon, some of which are released in their faeces and pseudofaeces, and subsequently made available to the oysters. Mazouni et al. (2001) assume that this positive trophic interaction supports the rapid oyster growth shown in the lagoon, citing the observations of farmers, who note that the presence of ascidians on the ropes is predictive of a good harvest. Similar trophic interactions have been reported for great scallop *Pecten maximus* cultivation off the Isle of Man (Ross et al. 2002).

However, in many cases, heavily fouled ropes, nets, or cages will inevitably reduce the food particles reaching the cultured species, if only by forming a physical barrier. Removal of the fouling organisms is labour-intensive and, thus, expensive, and is an ongoing problem for shellfish farmers. To help counter this problem, Ross et al. (2004) investigated the biological control of fouling in great scallop *Pecten maximus* culture by introducing sea urchins (*Echinus esculentus* and *Psammechinus miliaris*) and hermit crabs *Pagurus* spp. to scallop nets. This proved an effective method for removing hydroids and tunicates, in some cases leading to increased scallop growth, and it is suggested that this could form a commercially viable form of polyculture. Similar conclusions were reached using sea urchins as a biocontrol for fouling in pearl oyster *Pinctada imbricata* culture in Venezuela (Lodeiros & Garcia 2004).

For ascidians and bryozoans, a decline in clearance rate (CR), or FR with increasing food availability has been repeatedly demonstrated (Robbins 1983, Petersen et al. 1995, Riisgaard & Larsen 2000, Lisbjerg & Petersen 2001, Sigsgaard et al. 2003), thus giving a relatively constant ingestion rate (IR). However, experiments to date have not been designed to define responses over the full range of natural food availabilities found in oligotrophic open water and turbid nearshore environments (e.g. estuaries) where bivalve culture frequently occurs. Here we investigate feeding responses in 3 common species of fouling organisms over a 100-fold range from 0.36 to $36 \mu\text{g l}^{-1}$ chlorophyll *a*, including from 0.5 to 15mg l^{-1} total particulate matter. These responses will be of use for dynamic simulations of interrelations between these and other suspension-feeding species, and between those species and their environment (J. G. Ferreira et al. in press).

MATERIALS AND METHODS

Three species of common filter-feeding fouling organisms were investigated; the solitary ascidians

Ciona intestinalis (L.) and *Ascidella aspersa* (O. F. Muller, 1776), and the encrusting cheilostome bryozoan *Membranipora membranacea* (Linnaeus, 1767). All fouling organisms were collected from marina pontoons in the vicinity of Plymouth Sound (South Devon, UK) before being maintained in a system of natural recirculating seawater at $17.5 \pm 1^\circ\text{C}$ and $34 \pm 1 \%$. To provide a maintenance food ration, the water was supplemented with a suspension of cultured *Isochrysis galbana* (3.5 to $5.5 \mu\text{m}$) to give a concentration of around $3000 \text{ particles ml}^{-1}$, equating to approximately $1 \mu\text{g l}^{-1}$ chlorophyll *a* (chl *a*).

Feeding responses of 8 replicate individuals or colonies of each species were measured, during exposure to a range of food quantities and qualities, in separate glass beakers containing 5 l of seawater at $17.5 \pm 1^\circ\text{C}$. In preparation for these measurements, the bases of individual ascidians were glued to small stones to act as stability anchors. Colonies of *Membranipora membranacea* encrusting on the fronds of kelp (*Laminaria* sp.) were inspected to ensure the lophophores were living and feeding, and then cut into squares to be suspended by cotton threads in each beaker. Two squares with a total area of 1682 mm^2 ($29 \times 29 \text{ mm}$) were used in each, and the number of zooids per unit area determined from counts made from photographs. For the ascidians, 2 beakers containing seawater only were used as controls. For the bryozoans, 2 similar squares of kelp, without the encrusting bryozoans, were placed in 2 control beakers. Gentle aeration through Pasteur pipettes was applied to each beaker to maintain food particles in suspension. Food quantity was varied by additions of cultured *Isochrysis galbana* cells to give a range of concentrations between 1000 and 100 000 cells ml^{-1} (0.36 to $36 \mu\text{g l}^{-1}$ chl *a*). To assess the differential selection of food particles in these animals, we measured their responses to mixtures of *I. galbana* and inorganic silt (natural estuarine sediment that was ashed, crushed and sieved to $60 \mu\text{m}$). Before experiments, a measured volume of silt was suspended in filtered seawater, allowed to settle for 10 min, and then the uppermost portion (mostly comprising particles $< 20 \mu\text{m}$) was siphoned off for use. The mixture was designed to comprise equal volumes of algae and silt particles, and to produce approximately $10\,000 \text{ particles ml}^{-1}$ when added to each beaker. Although, ideally, this type of investigation is better conducted using a totally natural food source, it is impossible to achieve such a large range of quality and quantity of food rations, in a limited time period, allowing use of the same animals, without resorting to cultured microalgae. This also facilitates comparisons with the numerous other studies which have adopted similar strategies.

Individuals or colonies were acclimated in beakers for 30 min before the addition of food particles. After a

further 10 min, 20 ml samples of the waters were analysed with a Coulter® Multisizer for particle number and volume over a range of 2 to 30 μm , to give the initial (C_0) values in each beaker. In trials, sampling at 30 min intervals, we found that there was often a lag-phase in the initial feeding response of each species. We therefore adopted a protocol where particle concentrations were measured each hour over a 3 h period, when at each sampling point, any depletion in cells was replenished to the original value and another sample measured to give the initial concentration for the next period. Thus, for each food ration, 3 hourly measures of CR (l of water cleared of particles h^{-1}) were obtained. The calculation of CR in a static system is given by $Vt^{-1} \times (\ln C_0 - \ln C_1)$, which is equivalent to that integrated by Coughlan (1969), where V = volume of water (l), t = time interval (h), and C_0 and C_1 are the concentrations of particles at the start and end of the interval (no. ml^{-1}). In ascidians, values were standardised for an equivalent animal of 1 g dry wt using the formula $Y_s = (W_s/W_e)^b \times Y_e$, where Y_s is the standardised parameter, W_s and W_e are the standard weight (1 g) and the weight of the animal, respectively, Y_e is the uncorrected parameter, and b the exponents of 0.68 derived for *Ciona intestinalis* (Petersen & Riisgard 1992) and 1.05 for *Ascidiella aspersa* (Randlov & Riisgard 1979). In *Membranipora membranacea*, CR values were standardised to represent a colony area of 1000 mm^2 , and from the zooid counts could also be calculated as a rate per zooid. Concentrations of chl *a* at each food ration were measured through conventional filtration, acetone extraction and analysis on a Turner Designs fluorometer.

Ingestion rates (IR, no. of particles consumed min^{-1}) were estimated as $\text{IR} = \text{CR} \times C_0$, assuming all particles cleared were ingested. Retention efficiencies (RE) for a

given size range of particles over any time period were calculated as a percentage by $\text{RE} = 100 \times [1 - (C_2 - C_1)]$, where C_1 and C_2 are the concentrations of particles at the start and finish of the period, and then expressed as a relative percentage, using the most-retained size class as 100% (Møhlenberg & Riisgård 1978, Jørgensen et al. 1984). The time between measurements, the original food concentration and the aeration/mixing were standardised throughout the experiments. It was found that RE values for particles larger than 5.5 μm were highly variable due to the relatively low particle numbers at this size. Hence, RE results given are restricted to particles of 5.5 μm and below.

For statistical analyses, the relationships between CR and food concentration, and between IR and food concentration were analysed using 2-way ANOVA and multiple range tests (Tukey).

RESULTS

Clearance rate

In initial trials, where CRs were also measured after the first 30 min, there was evidence of a significant initial lag-phase in all species. For example, in *Membranipora membranacea*, only the 2 and 3 h measures were not significantly different (Fig. 1A) ($p < 0.01$). The only other noteworthy difference observed between the hourly measures of CR was at the highest concentration (100 000 cells ml^{-1}) in *M. membranacea*, where a significant reduction in CR between each hourly measurement was seen (Fig. 1B) ($p < 0.01$). Thus, to give a better representation of the adjusted CR at each algal concentration, we used the mean values from our 2 and 3 h measures (Fig. 2). CR values in the controls of each species

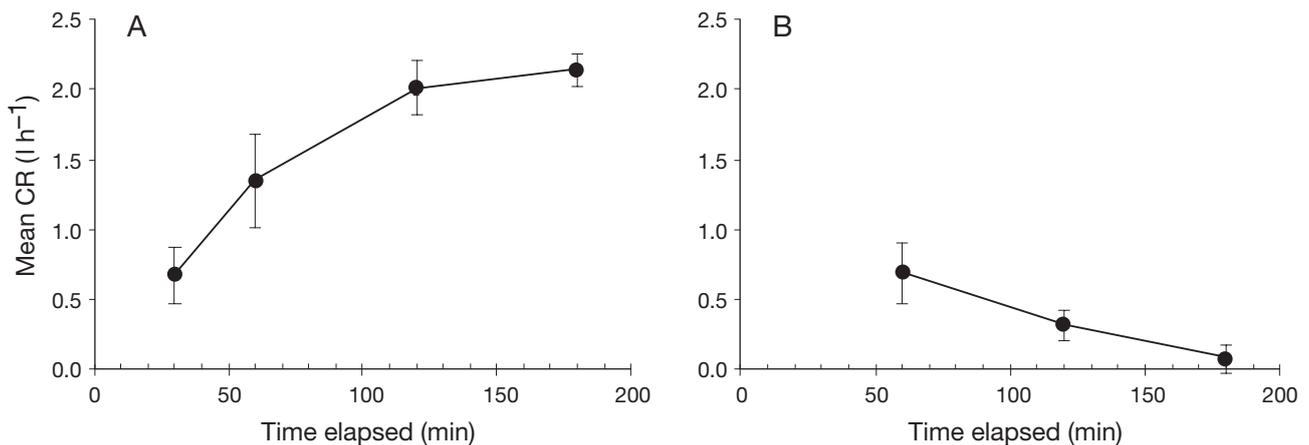


Fig. 1. *Membranipora membranacea*. Mean clearance rates (CR) of 8 colonies feeding on *Isochrysis galbana* at (A) 5000 cells ml^{-1} and (B) 100 000 cells ml^{-1} . Error bars: ± 2 SE

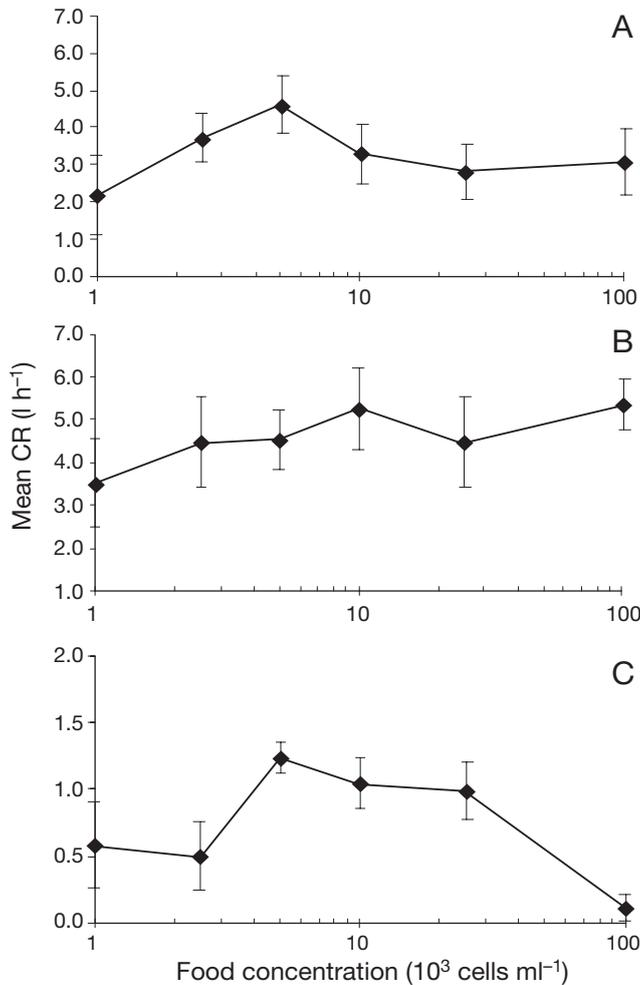


Fig. 2. Mean clearance rates (CR) of 3 fouling species after feeding on *Isochrysis galbana* for 2 and 3 h. (A) *Ciona intestinalis*, (B) *Ascidiella aspersa*, and (C) *Membranipora membranacea*. Error bars: ± 2 SE

were not significantly different from zero. A bell-shaped curve as reported in bivalve species (e.g. Hawkins et al. 2001) was clear in *M. membranacea* (Fig. 2C), showing a peak around 5000 to 10 000 cells ml⁻¹. A maximum CR was also evident in *Ciona intestinalis*, increasing from 2.2 l h⁻¹ at 1000 cells ml⁻¹ to 4.61 l h⁻¹ at 5000 cells ml⁻¹ ($p < 0.05$), followed by a significant decrease to around 3 l h⁻¹ at the higher concentrations (Fig. 2A) ($p < 0.05$). Alternatively, *Ascidiella aspersa* (Fig. 2B) showed a weak positive correlation between CR and cell concentration (CRs = $3.604 + 0.285x$, $R^2 = 0.067$), with a significant difference between the lowest and highest concentration ($p < 0.05$), but not within the mid-range ($p > 0.05$). Maximal CRs in *C. intestinalis* and *A. aspersa*, standardised to an organism of 1 g dry wt, were 4.61 l h⁻¹ at 5000 cells ml⁻¹ and 5.26 l h⁻¹ at 10 000 cells ml⁻¹, respectively, whereas the minimal values, both at 1000 cells ml⁻¹, were 2.2 and 3.51 l h⁻¹, respectively. The CR values

for the standardised 1000 mm² colony of *M. membranacea* reached a maximum of 1.23 l h⁻¹ at around 5000 cells ml⁻¹ and remained high (around 1 l h⁻¹) through to 25 000 cells ml⁻¹. These concentrations of *Isochrysis galbana* represented chl *a* concentrations of approximately 2 to 12 $\mu\text{g l}^{-1}$, and the colony CR of 1 l h⁻¹ equates to 0.29 ml zooid⁻¹ h⁻¹. As mentioned above, the CR of *M. membranacea* at the highest concentration, 100 000 cells ml⁻¹, showed a dramatic reduction to 0.11 l h⁻¹ (Fig. 2C).

Plots of mean IR against cell concentration (Fig. 3) showed a linear relationship over the concentrations used here in both species of ascidian. Alternatively, in *Membranipora membranacea*, a similar trend was seen up to a concentration of 25 000 cells ml⁻¹, but a distinct and significant decrease in IR ($p < 0.01$) was observed at the higher concentration of 100 000 cells ml⁻¹. This

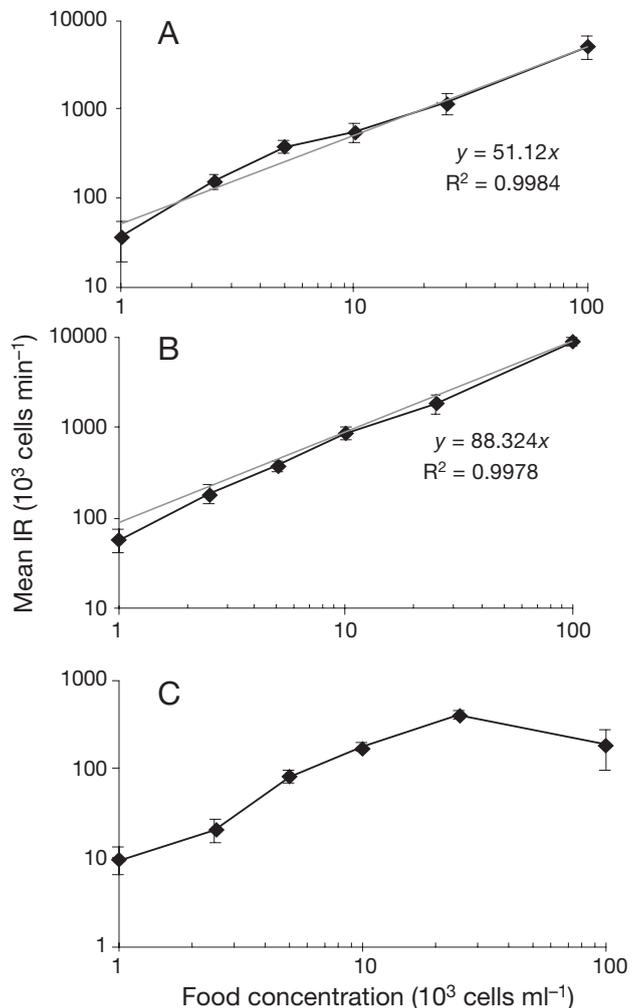


Fig. 3. Mean ingestion rates (IR) for 8 individuals of the 3 fouling species after feeding on *Isochrysis galbana* for 2 and 3 h. (A) *Ciona intestinalis*, (B) *Ascidiella aspersa*, and (C) *Membranipora membranacea*. Error bars: ± 2 SE

reduced IR was associated with the marked reduction in CR at the same concentration, and which is assumed to reflect satiation upon exposure to this high food ration for over 2 h.

Retention efficiency

Particle size spectra of the *Isochrysis galbana* and silt mixture are shown in Fig. 4, comparing spectra for beakers with and without animals of each species after 1 h feeding for the ascidians and 2 h feeding for *Membranipora membranacea*. *I. galbana* cells ranged in

size from around 3.5 to 5.5 μm with a peak at 4.5 μm , and the silt particles ranged from 2 to >10 μm , but with very reduced numbers as particle size increased above 7 μm . Reduced concentrations suggest a fairly uniform retention efficiency of particles throughout the size range in the 2 ascidians, but illustrate in *Membranipora membranacea* a precise coincidence of increased RE over the size range of the algal cells. Fig. 5 shows mean percentage RE of particles between 2 and 5.5 μm for 8 animals or colonies of each species over 1 or 2 h periods (see legend), using the individual size channels as recorded on the Multisizer. *Ciona intestinalis* exhibited a RE of around 60% for particles up to

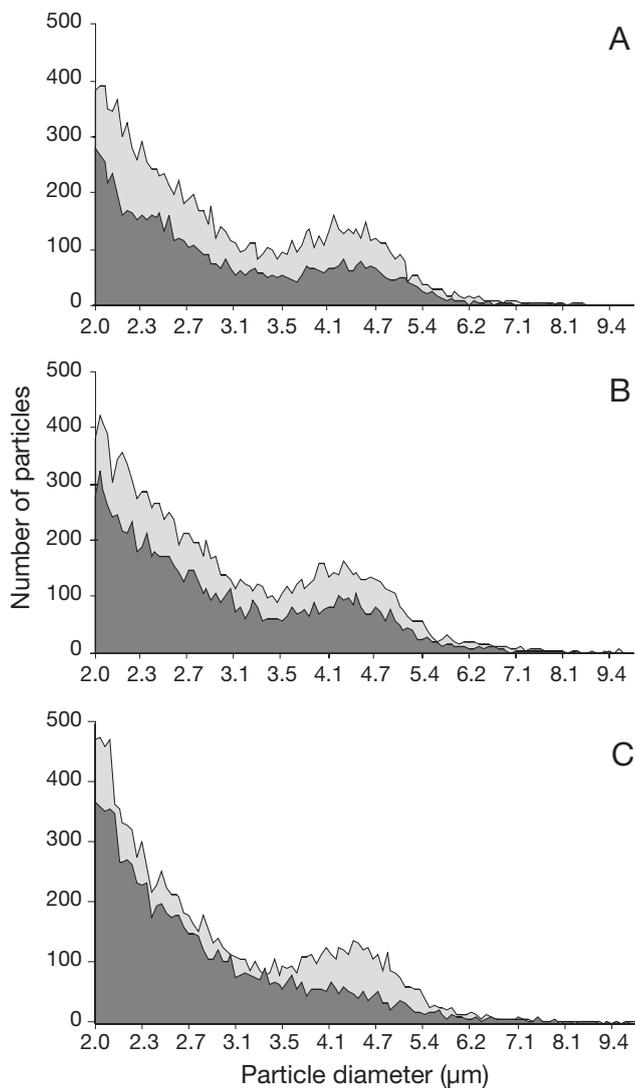


Fig. 4. Particle size spectra of mixtures of *Isochrysis galbana* and silt, before and after 1 h feeding by (A) *Ciona intestinalis* and (B) *Asciidiella aspersa*, and 2 h feeding by (C) *Membranipora membranacea*. The lighter area represents particles before feeding and the darker area those remaining after feeding

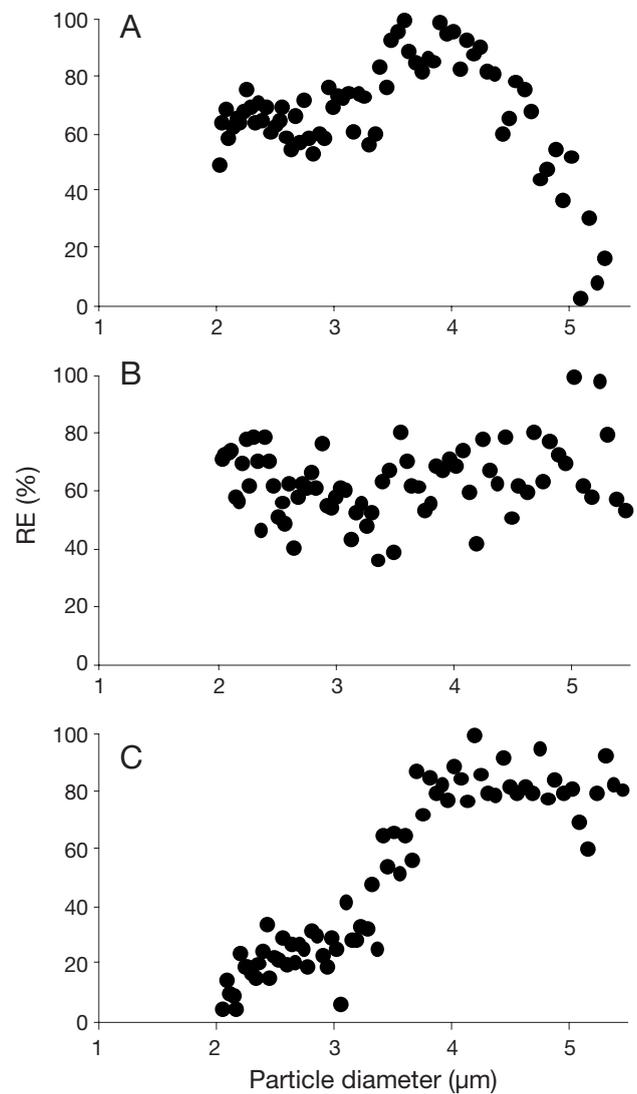


Fig. 5. Relative retention efficiencies (RE) for particles from 2 to 5.5 μm diameter in a mixture of cultured *Isochrysis galbana* and inorganic silt after feeding for 1 h by (A) *Ciona intestinalis* and (B) *Asciidiella aspersa*, and 2 h by (C) *Membranipora membranacea*

3.5 μm , which was predominantly silt, then an increase to around 95% at 4 μm , which were mainly algal cells, followed by a significant decrease (Fig. 5A). *Asciidiella aspersa* demonstrated rather variable RE values of around 50 to 80% across the full particle size range, with no notable selectivity (Fig. 5B). In contrast, as discussed above, findings for *M. membranacea* exhibited very low REs for the smallest particles (<10%) but values increased sharply (mostly >75%) for particles from 3.5 to 5.5 μm which are predominantly algal cells (Fig. 5C).

DISCUSSION

Ascidians

Regulation of feeding rate

Previous reports on feeding in common fouling species are varied and at times somewhat contradictory. Published relationships between body size and maximal CR (equivalent to filtration rate F , ml min^{-1}) in ascidians show considerable variation: for example, $F = 46.4 W_{\text{total}}^{0.84}$ at 10°C in *Ciona intestinalis* and $F = 54.4 W_{\text{total}}^{1.05}$ at 20°C in *Asciidiella aspersa*, where W_{total} = total body wt (test and organs) (Randlov & Riisgard 1979); but $F = 40 W_{\text{organ}}^{0.65}$ (Robbins 1983; W_{organ} = dry wt or organs [without test]) and $F = 118 W_{\text{total}}^{0.68}$ (Petersen & Riisgard 1992) for *C. intestinalis* at 15°C. It has also been reported that ciliary beat frequency is proportional to water flow through *C. intestinalis* and that any changes in pumping caused by temperature and food concentration are under nervous control or related to enzyme kinetics rather than to physico-mechanical properties (Petersen et al. 1999). The relationship combining body weight (W) and temperature (T) is summarised by Petersen & Riisgard (1992) as $F = (8.3T - 6.9) W_{\text{total}}^{0.68}$.

Most previous studies on feeding in these species found that CR decreased with increasing particle concentration, both for algal cells and inorganic particles (Robbins 1983, Petersen & Riisgard 1992, Petersen et al. 1995, 1999, Sigsgaard et al. 2003). In a study of *Ciona intestinalis* and *Asciidiella scabra* feeding on 3 types of inorganic particulate suspensions, Robbins (1983) found that FR decreased with increasing concentrations in such a way that IR soon became constant and maximal, which now seems to be the general consensus among scientists. A non-mathematical model of filter-feeding in ascidians relating to gut and seston volumes was proposed (Robbins 1983). This contrasts markedly with our results, which suggest there is some regulation of CR with varying food quantity, illustrated by a bell-shaped response in *C. intestinalis* and a gen-

eral increase in CR with increasing food ration in *A. aspersa* (Fig. 2). At 6 cell concentrations of *Isochrysis galbana*, ranging from 1000 to 100 000 cells ml^{-1} , *C. intestinalis* exhibited mean CR of between 2.20 and 4.61, and *A. aspersa* from 3.51 to 5.35 $\text{l h}^{-1} \text{g}^{-1}$ total dry wt. There is little evidence in our results of the major decreases in CR with increasing food concentration shown in the previous studies above. Most importantly, the CR values for both ascidians throughout the range of concentrations in this study translate into positive linear relationships for ingestion rate. Most other studies have shown IR becoming maximal at relatively low concentrations of algal cells.

Our results concur, however, with those reported by Petersen & Riisgard (1992) for larger *Ciona intestinalis* specimens (0.1 to 0.24 g dry wt). They found that CR (= FR) reached a constant maximum of around 35 $\text{ml min}^{-1} \text{ind}^{-1}$, equivalent to over 8.4 $\text{l h}^{-1} \text{g}^{-1}$ dry wt, at concentrations of *Rhodomonas* sp. between 2000 and 20 000 cells ml^{-1} for a period of 5 h. However, at their highest concentration of 30 000 cells ml^{-1} , CR of the large fouling organisms reduced to <20 $\text{ml min}^{-1} \text{ind}^{-1}$ after feeding for 200 min, due to possible satiation. A significant lag phase of 1 to 2 h after the addition of algal cells was seen in large and small fouling organisms at virtually all concentrations, but which may have been a consequence of starvation before the experiment, as the lag-phase duration found in the present study was less than 1 h for ascidians. The *C. intestinalis* used in the present study were even larger (mean 0.39 g dry wt) than those used by Petersen & Riisgard (1992). In addition, they were fed over a shorter period and were not starved before the experiment, which may explain the limited lag-phase and lack of satiation even at *Isochrysis galbana* cell concentrations of 100 000 cells ml^{-1} . However, the considerable difference in size and volume of *I. galbana* cells (4.5 μm) compared to *Rhodomonas* sp. (6 μm) may be an explanatory factor. Clearance rates measured here for these large specimens are comparatively low at 2.2 to 4.61 $\text{l h}^{-1} \text{g}^{-1}$ dry wt.

Particle retention efficiency

In studies on particle RE in 4 species of ascidian, including the 2 studied here, Randlov & Riisgard (1979) compared inhaled and exhaled water to show that particles down to 2 to 3 μm were completely retained, and only for 1 μm particles did RE reduce to 70%. Others concur with this observation (Robbins 1984, Stuart & Klumpp 1984), and even particles as small as 0.25 μm (sepia ink) are filtered by *Ciona intestinalis* (Bone et al. 2003). However, other authors have observed some variation in particle retention, relating to size, quality

and also sediment load. For example, Lesser et al. (1992) found that the clearance rates of natural planktonic assemblages tended to increase with particle size; those $>16\ \mu\text{m}$ were filtered at twice the rate of those at $5\ \text{to}\ 16\ \mu\text{m}$, and almost 4 times those at $3\ \text{to}\ 5\ \mu\text{m}$. Some selection against large ($>16\ \mu\text{m}$) non-chlorophyll particles was also shown. In another study on the ascidian *Pyura stolonifera*, some selectivity was shown between organic kelp particles and *Dunaliella primolecta* cells, with respective assimilation efficiencies of 75 and 42% (Klumpp 1984). Also, the results of a study on *Halocynthia pyriformis* (Armsworthy et al. 2001) indicate that with increasing sediment concentration, IR increased to a constant level, absorption rates increased linearly despite a logarithmic decrease in absorption efficiencies, and the retention of small particles ($2\ \text{to}\ 5\ \mu\text{m}$) increased, while retention of larger particles ($5\ \text{to}\ 15\ \mu\text{m}$) decreased with increasing sediment. They concluded that *H. pyriformis* appeared to compensate for episodic changes in the quantity and quality of available food particles to maintain constant CR by altering siphon-opening diameter, squirting frequency, the structure and transport of mucus, and retention efficiency.

RE in the 2 species in the present study, when exposed to a mixture of *Isochrysis galbana* and silt, suggests some differences in selectivity (Fig. 5). *Ciona intestinalis* shows high retention for all particles up to $4.5\ \mu\text{m}$, particularly for *I. galbana*, but a distinct decrease in RE above this size possibly due to the higher proportion of silt. In contrast, *Asciidiella aspersa* shows similar relative ability to retain both *I. galbana* and silt particles. The wide variation in RE values shown in *Asciidiella* across the particle size range (Fig. 5B) is somewhat enhanced by standardising to 100% (see 'Materials and methods'), as the retention of most particles was generally low.

Bryozoans

Regulation of feeding rate

Research on the biology and feeding of bryozoans has been plentiful in the last 3 decades as they are recognised as important filter-feeders within the coastal zone (Woollacott & Zimmer 1977, Okamura 1990, Hayward et al. 1994, Riisgard & Manriquez 1997, Larsen & Riisgard 2002). Food capture in bryozoans is by means of a funnel of ciliated tentacles, the lophophore, a method termed 'impingement feeding' by Bullivant (1968). Most studies suggest that bryozoans are capable of adjusting to fluctuations in the abundance of suitable food. The variety of morphology and mechanisms also suggest that some degree of special-

ization has occurred (Winston 1977). Variations in measured feeding or CR can relate to different mechanisms that include cilia beat frequency affecting current velocity through the lophophore, tentacle flicking, periodic retraction of the lophophore, and particle selectivity (Lisbjerg & Petersen 2001). Best & Thorpe (1994) reviewed earlier studies on bryozoan feeding and concluded that: (1) feeding current velocity is not independent of particle size; (2) feeding efficiency can vary considerably and relates to the 'natural feeding strategy' of bryozoans, which has evolved in response to patchiness in food particles; for a hungry colony will feed maximally at first detection of food, then decrease if supply continues, and eventually virtually cease when satiated; (3) overall feeding efficiency will depend on several intrinsic and extrinsic factors, which will affect current/particle speed and IR and, hence, determine feeding efficiency and CR; and (4) under natural conditions there will be other modifying factors such as 'taste', composition, amount of inorganic matter, and mechanical or chemical disturbance.

However, there are some conflicting reports on how bryozoan feeding rates vary with algal cell (or chlorophyll) concentrations. For example, the relationship between mean CR and cell concentration in several species (including *Membranipora membranacea*) is shown to be logarithmic, increasing with concentration (Best & Thorpe 1986), but as a decreasing linear relationship in *Electra crustulenta* (Lisbjerg & Petersen 2001). In the present study we have shown that CR in *M. membranacea* exhibits a bell-shape response to *Isochrysis galbana* cell concentration, but IR has a linear relationship with cell concentration until very high concentrations are reached ($100\ 000\ \text{cells}\ \text{ml}^{-1}$). These variations, as suggested above, usually depend on size and food quality of the particles used, the feeding history of the animals, and the duration of the feeding.

Precise comparisons of CR are often difficult due to the methods of measurement, the food type and other factors. However, CR values are generally given as the maxima measured, and the units which most easily express comparisons are $\text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$. Mean CR values (water-processing rates) for *Membranipora membranacea* in the literature vary from $0.36\ \text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$ using *Tetraselmis suecica* at $1000\ \text{cells}\ \text{ml}^{-1}$, to $0.88\ \text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$ at $100\ 000\ \text{cells}\ \text{ml}^{-1}$, with a measured maximum of $1.51\ \text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$ which occurred at $25\ 000\ \text{cells}\ \text{ml}^{-1}$ (Best & Thorpe 1986). Around $1.3\ \text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$ at 17.5°C was recorded in the study of temperature effects by Sanderson & Thorpe (1996), and $0.93\ \text{ml}\ \text{zooid}^{-1}\ \text{h}^{-1}$ was calculated based on the figures of Riisgard & Manriquez (1997), using *Rhinomonas reticulata*. Pratt (2004) records ingestion rates of polystyrene beads ($10.3\ \mu\text{m}$ diameter) of around $6.5\ \text{beads}\ \text{zooid}^{-1}\ \text{min}^{-1}$, which at the concentration used equates

to 0.36 ml zooid⁻¹ h⁻¹. Our maximal CR for means of the 8 colonies was 0.36 ml zooid⁻¹ h⁻¹ at an *Isochrysis galbana* concentration of 5000 cells ml⁻¹. So although there are many factors influencing CR and several methods of measurement or estimation, there appears to be some consensus for this species.

Particle selection

Studies on particle selection in bryozoans are numerous and come to varying conclusions. Simultaneous clearance of 2 different sized algal cells by *Electra crustulenta* showed that *Rhinomonas reticulata* (6 µm) and *Tetraselmis* sp. (14 µm) are cleared from the water at approximately the same rate, whereas the removal of 4 µm diameter *Isochrysis galbana* cells is approximately half this rate (Riisgard & Goldson 1997). This is supported by Riisgard & Manriquez (1997) who showed a much lower retention efficiency for algal cells less than 6 µm (i.e. *Isochrysis galbana*, 4.4 µm) compared to *R. reticulata* (6.8 µm) and *Tetraselmis* sp. (8.6 µm) in *Celleporella hyalina*. Lisbjerg & Petersen (2001) found *Electra crustulenta* was capable of retaining and ingesting particles in the range 5 to 30 µm, but smaller particles were less efficiently retained due to the structure of the lophophore, and larger particles due to the size of the mouth (30 µm). Ciliary spacing in different species has also been shown to be a relevant factor (Larsen & Riisgard 2002). Gilmour (1978) showed that *Membranipora* sp. feeds selectively. Fed on a mixture of algae and a low concentration of Sephadex particles (10 to 40 µm), the former were captured and deflected to the mouth while the Sephadex particles were propelled to the tentacle tips and discharged into the outgoing water currents. A mixture with a high concentration of Sephadex particles caused rapid retraction of the lophophore.

Our results generally concur with the above findings on selectivity in bryozoans, as we have shown that retention efficiency in *Membranipora membranacea* increases with particle size, but a preference is shown for algal cells rather than inorganic silt. The overall conclusion is that bryozoan feeding involves complex and highly dynamic mechanisms which respond to several factors, related both to the particulates and the environment.

The results of the present study are relevant to the debate over the physiological control of feeding mechanisms in filter-feeders. It has been suggested that the filter pump is working to capacity in mussels, bryozoans and ascidians, stating that pumping rates are maximal at 'normal' food availabilities, and only decline in response to stress under unnaturally low or unnaturally high food conditions, thus, with no evi-

dence of physiological regulation (Riisgard & Larsen 2000, Riisgard & Goldson 1997, Riisgard 2001). We do not agree that the variations in CR observed in various bivalves (Hawkins et al. 1999, 2001), and here in *Ciona intestinalis*, *Membranipora membranacea* and possibly *Asciidiella aspersa*, are unnatural. The debate possibly hinges on the definition of 'normal' food availabilities. Present findings indicate that functional dependencies of CR and RE upon food quantity and quality will need to be included within dynamic models of feeding and growth in these and other suspension-feeding species.

Acknowledgements. We thank 3 anonymous reviewers for their comments, which have added clarity and substantial improvements to the manuscript.

LITERATURE CITED

- Armstrong SL, MacDonald BA, Ward JE (2001) Feeding activity, absorption efficiency suspension feeding processes in the ascidian, *Halocynthia pyriformis* (Stolidobranchia: Ascidiacea): responses to variations in diet quantity and quality. *J Exp Mar Biol Ecol* 260:41–69
- Best MA, Thorpe JP (1986) Effects of food particle concentration on feeding current velocity in six species of marine Bryozoa. *Mar Biol* 93:255–262
- Best MA, Thorpe JP (1994) Particle size, clearance rate and feeding efficiency in marine bryozoa. In: Hayward PJ, Ryland JS, Taylor PD (eds) *Biology and palaeobiology of bryozoans*. Proc 9th Int Bryozoology Conf, University of Wales, Swansea, 1992. Olsen & Olsen, Fredensborg
- Bone Q, Carré C, Chang P (2003) Tunicate feeding filters. *J Mar Biol Assoc UK* 83:907–919
- Bullivant JS (1968) The rate of feeding of the bryozoan *Zoobotryon verticillatum*. *N Z J Mar Freshw Res* 2:111–134
- Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. *Mar Biol* 2:356–358
- Ferreira JG, Hawkins AJS, Monteiro P, Moore H and others (in press). Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas. *Aquaculture*
- Gibbs MT (2007) Sustainability performance indicators for suspended bivalve aquaculture activities. *Ecol Indicators* 7:94–107
- Gilmour THJ (1978) Ciliation and function of the food-collecting and waste-rejecting organs of lophophorates. *Can J Zool* 56:2142–2155
- 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
- Hawkins AJS, Fang JG, Pascoe PL, Zhang JH, Zhang XL, Zhu MY (2001) Modelling short-term responsive adjustments in particle clearance rate among bivalve suspension-feeders: separate unimodal effects of seston volume and composition in the scallop *Chlamys farreri*. *J Exp Mar Biol Ecol* 262:61–73
- Hayward PJ, Ryland JS, Taylor PD (eds) (1994) *Biology and palaeobiology of bryozoans*. Proc 9th Int Bryozoology Conf, University of Wales, Swansea, 1992. Olsen & Olsen,

- Fredensborg
- Jørgensen CB, Kiørboe T, Møhlenberg F, Riisgard HU (1984) Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. *Mar Ecol Prog Ser* 15:283–292.
- Klumpp DW (1984) Nutritional ecology of the ascidian *Pyura stolonifera*: influence of body size, food quantity and quality on filter-feeding, respiration, assimilation efficiency and energy balance. *Mar Ecol Prog Ser* 19: 269–284
- Larsen PS, Riisgard HU (2002) On ciliary sieving and pumping in bryozoans. *J Sea Res* 48:181–195
- Lesser MP, Shumway SE, Cucci T, Smith J (1992) Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates. *J Exp Mar Biol Ecol* 165:91–102
- Lisbjerg D, Petersen JK (2001) Feeding activity, retention efficiency, and effects of temperature and particle concentration on clearance rate in the marine bryozoan *Electra crustulenta*. *Mar Ecol Prog Ser* 215:133–141
- Lodeiros C, Garcia N (2004) The use of sea urchins to control fouling during suspended culture of bivalves. *Aquaculture* 231:293–298
- Mazouni N, Gaertner JC, Deslous-Paoli JM (2001) Composition of biofouling communities on suspended oyster cultures: an *in situ* study of their interactions with the water column. *Mar Ecol Prog Ser* 214:93–102
- McKindsey CW, Thetmeyer H, Landry T, Silvert W (2006) Review of recent carrying capacity models for bivalve culture and recommendations for research and management. *Aquaculture* 261:451–462
- Møhlenberg F, Riisgard HU (1978) Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* 17(2):239–246
- Okamura B (1990) Particle size, flow velocity, and suspension-feeding by the erect bryozoans *Bugula neritina* and *B. stolonifera*. *Mar Biol* 105:33–38
- Petersen JK, Riisgard HU (1992) Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. *Mar Ecol Prog Ser* 88:9–17
- Petersen JK, Schou O, Thor P (1995) Growth and energetics in the ascidian *Ciona intestinalis*. *Mar Ecol Prog Ser* 120: 175–184
- Petersen JK, Mayer S, Knudsen MA (1999) Beat frequency of cilia in the branchial basket of the ascidian *Ciona intestinalis* in relation to temperature and algal cell concentration. *Mar Biol* 133:185–192
- Pratt MC (2004) Effect of zooid spacing on bryozoan feeding success: is competition or facilitation more important? *Biol Bull (Woods Hole)* 207:17–27
- Randlov A, Riisgard HU (1979) Efficiency of particle retention and filtration rate in four species of ascidians. *Mar Ecol Prog Ser* 1:55–59
- Riisgard HU (2001) On measurement of filtration rates in bivalves—the stony road to reliable data: review and interpretation. *Mar Ecol Prog Ser* 211:275–291
- Riisgard HU, Goldson A (1997) Minimal scaling of the lophophore filter-pump in ectoprocts (Bryozoa) excludes physiological regulation of filtration rate to nutritional needs. Test of hypothesis. *Mar Ecol Prog Ser* 156: 109–120
- Riisgard HU, Larsen PS (2000) Comparative ecophysiology of active zoobenthic filter feeding, essence of current knowledge. *J Sea Res* 44:169–193
- Riisgard HU, Manriquez P (1997) Filter-feeding in fifteen marine ectoprocts (Bryozoa): particle capture and water pumping. *Mar Ecol Prog Ser* 154:223–239
- Robbins IJ (1983) The effects of body size, temperature, and suspension density on the filtration and ingestion of inorganic particulate suspensions by ascidians. *J Exp Mar Biol Ecol* 70:65–78
- Robbins IJ (1984) The regulation of ingestion rate, at high suspended particulate concentrations, by some phleobranchiate ascidians. *J Exp Mar Biol Ecol* 82:1–10
- Ross KA, Thorpe JP, Norton TA, Brand AR (2002) Fouling in scallop cultivation: Help or hindrance? *J Shellfish Res* 21: 539–547
- Ross KA, Thorpe JP, Brand AR (2004) Biological control of fouling in suspended scallop cultivation. *Aquaculture* 229: 99–116
- Sanderson WG, Thorpe JP (1996) Effects of temperature on the feeding activity of some temperate intertidal Bryozoa. In: Gordon DP, Smith AM, Grant-Mackie JA (eds) Bryozoans in space and time. 10th Int Bryozoology Assoc Conf Wellington, New Zealand. National Institute of Water and Atmospheric Research Ltd, Wellington p 271–281
- Sigsgaard SJ, Petersen JK, Iversen JJJ (2003) Relationship between specific dynamic action and food quality in the solitary ascidian *Ciona intestinalis*. *Mar Biol* 143:1143–1149
- Stuart V, Klumpp DW (1984) Evidence for food-resource partitioning by kelp-bed filter feeders. *Mar Ecol Prog Ser* 16: 27–37
- Winston JE (1977) Feeding in marine bryozoans. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York, p 233–271
- Woollacott RM, Zimmer RL (eds) (1977) Biology of bryozoans. Academic Press, New York

Editorial responsibility: Peter Beninger (Contributing Editor), Nantes, France

Submitted: September 22, 2007; Accepted: November 29, 2007
Proofs received from author(s): December 23, 2007