Particle selection in the ribbed mussel *Geukensia demissa* and the Eastern oyster *Crassostrea virginica*: Effect of microalgae growth stage

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ABSTRACT

We studied particle selection in the ribbed mussel *Geukensia demissa*, an important suspension-feeding inhabitant of estuaries and intertidal zones of salt marshes along the Atlantic coast of North America. Adult mussels were fed on several mixtures of microalgal cultures (1) in exponential or (2) in stationary phase of growth, and the proportional occurrence of algal species in pseudofeces was examined by flow cytometry. The Eastern oyster, *Crassostrea virginica*, was chosen as a reference. Results showed that both mussels and oysters were able to selectively ingest or reject our experimental microalgae. Moreover, the pre-ingestive particle selection was affected by microalgal growth phase, particularly in mussels. For instance, the sorting efficiency index increased significantly in mussels fed with a blend made of *Nitzschia closterium*, *Isochrysis* sp. and *Tetraselmis suesica* harvested in stationary growth phase, as compared to the same blend made with microalgae in exponential growth phase. *Isochrysis* sp. and *T. suesica* were preferentially ingested by both bivalves whereas *N. closterium*, was preferentially rejected in pseudofeces. These results demonstrate particle selection in ribbed mussel and underline the effect of algae growth phase on the sorting mechanisms.

1. Introduction

The Atlantic ribbed mussel *Geukensia demissa* inhabits estuaries and intertidal zones of salt marsh along the Atlantic coast of North America. In wetlands, this suspension-feeding mollusk is often found in large populations (Jordan and Valiela, 1982; Franz, 2001) affecting benthic-pelagic coupling and marsh ecosystems. As a result, the ecological roles of *G. demissa* have been emphasized in many studies. Through suspension-feeding activities, the presence of dense ribbed mussel beds is known to reduce turbidity by filtering water and physically trapping and stabilizing substantial quantities of suspended particles (Bertness and Grosholz, 1985). Thus, large amounts of organic material can be deposited to the benthos or cycled into inorganic forms (Jordan and Valiela, 1982; Langdon and Newell, 1990). Suspension-feeders such as *G. demissa*, have been shown to strongly interact with phytoplankton and phytobenthos populations (Kreeger and Newell, 2001). They remove a significant portion of microalgae as food, and in return, the grazing process cycles dissolved nutrients, reduces turbidity, increases light in the bottom and as a result stimulates microalgae growth (Dame, 1996). This species is well adapted to use resources available in salt marsh, where seston composition is extremely variable (Huang et al., 2003b). For instance, *G. demisa* has the ability to exploit a wide variety of food sources such as detrital cellulose from vascular plants (Charles and Newell, 1997), small-sized bacteria (Kemp et al., 1990; Newell and Krambeck, 1995; Kreeger and Newell, 1996), heterotrophic protists (Kreeger and Newell, 1996), microphytobenthos, cyanobacteria and phytoplankton (Riisgard, 1988; Kemp et al., 1990). Moreover, the digestive physiology of ribbed mussels can respond to seasonal variation in dietary composition of marsh water (Kreeger and Newell, 2001) and to the limited time available for feeding associated with living high in the intertidal zone (Charles and Newell, 1997).

To enhance the nutritive value of consumed particles and to optimize energy gain, several suspension feeding bivalves, such as the eastern oyster *Crassostrea virginica* (Shumway et al., 1985), are able to select food, typically by passing the water over their gills and, from it, straining suspended matter and food particles. Through this mechanism, suspension feeders preferentially ingest particles of interest while undesirable particles are rejected in pseudofeces (Loosanoff and Engle, 1947; Morton, 1960). In this manner, the impact of suspension-feeding bivalves on aquatic ecosystems is significantly amplified by their ability to select and ingest specific particles. Although *Geukensia demissa* is known to have developed physiological adaptations to address challenging environmental conditions, such as long emersion in high intertidal areas of salt marsh (Charles and Newell, 1997; Franz, 2001 and references therein; Kreeger and Newell, 2001), to our knowledge,

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there is no prior investigation of ribbed mussel's ability to sort its food particles. However, Kemp et al. (1990) suspected this ability after measuring filtration rates in *G. demissa* and finding that the mussels were able to remove some particle types with greatly differing effectiveness. This mytilid species is characterized by a filibranch homorhabdic ctenidia and other marine members of this family are known to sort particles, including *Mytilus edulis* (Cucci et al., 1985; Ward and Targett, 1989; Bougrier et al., 1997), *Mytilus trossulus* (Ward et al., 1998), *Mytilus chilensis* (Velasco and Navarro, 2002), and *Perna viridis* (Ke and Wang, 2002). The freshwater mussels *Dreissena polymorpha* (Dreissenidae) (Baker et al., 1998), as well as *Margaritifera margaritifera*, *Amblema plicata* and *Pyganodon cataracta* (Unionidae) (Baker and Levinton, 2003), were found to select particles as well. However, saltwater and freshwater mussels are not closely related (separate subclasses) and have different gill structure, making inappropriate any extrapolation from one group to another.

Particle selection mechanism in suspension-feeders is controlled by diverse physical, chemical, and biological factors in the environment and many previous studies have shown that changes in size, density, electrostatic charges or concentration of particles can affect selection (Iglesias et al., 1996; Barillé et al., 1997; Bougrier et al., 1997; Cognie et al., 2001; Ward and Shumway, 2004). Some studies have also demonstrated that chemical cues represent important factors mediating particle selection mechanisms in bivalves (Shumway et al., 1985; Ward and Targett, 1989; Pales Espinosa et al., 2007, 2008). Chemical cues identified during these studies include extracellular phytoplankton metabolites (Ward and Targett, 1989; Pales Espinosa et al., 2007) and carbohydrates coating microalgae cell-surfaces (Pales Espinosa et al., 2008). Interestingly, both ectocrines and cell-surface membrane markers change during the cell cycle of cultured microalgae, suggesting various outcomes for their interactions with suspension-feeders at different life stages. Thus, production and excretion of secondary metabolites (fatty acids, carbohydrates, pigments, or toxins) by microalgae often increased during stationary phase of algal growth and nutrient depletion (Targett and Ward, 1991; Harker et al., 1996; Fidalgo et al., 1998; Uronen et al., 2005). Likewise, the glycoconjugate composition on the cell surface of several microalgae can also vary depending on the physiological state of growth (Waite et al., 1995; Aguilera and Gonzalez-Gil, 2001; Kremp and Anderson, 2004).

The purpose of this study was to evaluate the ability of *Geukensia demissa* to sort food particles compared to the well-known sorting capacity of the Eastern oyster, *Crassosstrea virginica*. This comparison is particularly relevant since the habitat of both species overlaps in some low tidal marsh areas with *Spartina alterniflora* coverage (Borrero, 1987) potentially leading to interspecific competition for nutritional resources. Moreover, we used these two estuarine bivalves to study the effect of microalgal growth phase on particle sorting efficiency.

2. Materials and methods

2.1. Microalgal cultures

The microalgal strains investigated (Table 1) were supplied by Dr Gary Wikfors (Milford Marine Laboratory, CT, USA). Despite the fact that they present major differences (taxonomic group, shape, size), these microalgae species were chosen to conduct the feeding experiments since they are well known to be differentially selected by several bivalves; thus *Isochrysis* sp. and *Tetraselmis suesica* are preferentially ingested whereas *Nitzschia closterium* is preferentially rejected by oysters *Crassostrea gigas* and other bivalves (Pales Espinosa et al., 2007 and several references within). Algae were separately grown in F/2 medium (Guillard, 1982) at 15 °C under 14-h light/10-h dark cycle. Diets were prepared just prior to the

Table 1
List of the microalgae species used in the feeding experiments

Species	Abbreviation used	Class	Size (μm)
Isochrysis sp.	Is	Prymnesiophyceae	5–6
Nitzschia closterium	Nc	Diatom (pennate)	17–20
Tetraselmis suesica	Ts	Prasinophyceae	10–18
Thalassiosira pseudonana	Tp	Diatom (centric)	5–6
Thalassiosira weissflogii	Tw	Diatom (centric)	25–27

feeding experiments to obtain approximately equal cell proportions (33.3% of each species) with a final total concentration of 10^4 cells mL^{-1} in each mixture. All microalgae species larger than 5 μm are retained by *Crassostrea virginica* and *Geukensia demissa* gills with an efficiency of 100% (Riisgard, 1988). Diet 1 (*N. closterium*, *Isochrysis* sp., *T. suesica*) and Diet 2 (*N. closterium*, *Thalassiosira pseudonana*, *Thalassiosira weissflogii*) were made of microalgae cultures in exponential phase of growth. Diet 3 was identical to Diet 1, but was prepared with cultures in stationary phase.

2.2. Feeding experiments

The design of the feeding experiments was inspired from prior studies investigating particle selection in bivalves (Shumway et al., 1985; Ward et al., 1998; Pales Espinosa et al., 2007). *Geukensia demissa* (Dillwyn) were collected from the Maurice River estuary (Port Norris, NJ, USA). *Crassostrea virginica* (Gmelin), harvested in Delaware Bay, were obtained from a commercial source (Bivalve Packing Inc., Port Norris, NJ, USA). Bivalves were scrubbed to remove all epiphytes and encrusting organisms from their shells. All animals were acclimated in the laboratory for a minimum of 1 week (fed daily with cultured *Isochrysis* sp., 28 salinity, 21 °C), then purged in filtered (0.22 μm) seawater for a day prior to being used in the feeding experiments.

Bivalves were placed in individual trays, each supplied with 3 L of filtered seawater containing one of the tested diets. A control tray with empty oyster shells was used to measure microalgal sedimentation. Microalgae were kept in suspension using a magnetic stirrer (gentle stirring to avoid spreading pseudofeces). Experiments lasted for 2 h during which water samples were taken for flow cytometry analyses at 0, 60 and 120 min to determine sedimentation. Pseudofeces were collected from each individual and their algal composition was determined using flow cytometry. Prior to the analysis, pseudofeces samples were vortexed to disrupt particle aggregates and filtered through a Nitex net (64 μm).

2.3. Flow cytometry analysis

Flow cytometry was used to discriminate and enumerate different microalgae species in diets and pseudofeces. Prior to the experiment, each algal species was processed by the flow cytometer to identify its distinguishing characteristics. All particles were discriminated based on their optical and autofluorescence properties by means of a Coulter EPICS C flow cytometer/sorter equipped with a 2000 mW, 488 nm argon ion excitation laser and interfaced with the standard computer. The algae were detected by the simultaneous measurements of their forward light scatter (FLS), which is correlated to the size of each cell, and the fluorescence of their chlorophyll pigments (log red fluorescence or LRFL collected at 660 nm). Gains and photomultiplier high voltage settings were adjusted to include all cells on the two-parameter display plot. List-mode data were collected for at least 5000 particles in each sample. The proportion of each algae species was calculated using bitmaps (electronic outlining) on the two-parameter plots.

2.4. Data analysis

A series of goodness-of-fit tests (*G* test) was performed using raw counts to compare the proportion of each type of microalgae in diet and pseudofeces samples. The null hypothesis was that the proportion of each type of microalgae was the same in diet and pseudofeces. In addition to the comparison of raw data, a sorting efficiency (SE) index was calculated in order to examine particle selection (Iglesias et al., 1992). This index was defined as:

$$SE = 1 - (P/D)$$

where *P* and *D* represent the proportion of the particle of interest in the pseudofeces and diet, respectively. A positive SE for a given particle type indicates that it is preferentially ingested (particle type is depleted in the pseudofeces, compared to diet), a negative SE indicates rejection (particle type is enriched in the pseudofeces compared to diet), and zero indicates the absence of active selection. After confirming their normal distributions, calculated SEs were compared to zero using a one sample *t*-test (two-tailed). The null hypothesis was that the selection efficiencies were equal to zero (i.e. no selection). In all statistical tests, results were considered significant if $p < 0.05$.

3. Results

Although the targeted proportion of each microalgae was 33%, *a posteriori* counts revealed the following proportions in the feeding blends: Diet 1, $39.8 \pm 1.1\%$ (mean $\pm$ SD) of *Nitzschia closterium*, $29.1 \pm 1.1\%$ of *Isochrysis* sp. and $31.1 \pm 2.2\%$ of *Tetraselmis suesica*; Diet 2, $37.3 \pm 2.1\%$ of *N. closterium*, $28.8 \pm 2.3\%$ of *Thalassiosira pseudonana* and $33.8 \pm 1.2\%$ of *Thalassiosira weissflogii*; Diet 3, $33.9 \pm 2.4\%$ of *N. closterium*, $29.4 \pm 3.6\%$ of *Isochrysis* sp. and $37.2 \pm 3.9\%$ of *T. suesica* (Fig. 1). These proportions remained stable over the entire duration of the experiment indicating that differential settling of microalgae did not occur.

3.1. Selection of algae in exponential phase of growth

The proportion of *Nitzschia closterium* and *Tetraselmis suesica* in mussel pseudofeces fed with Diet 1 decreased slightly from $39.8 \pm 1.1\%$ in the diet to $35.6 \pm 2.8\%$ and from $31.1 \pm 2.2\%$ to $30.4 \pm 4.9\%$, respectively (Fig. 1). At the same time, the percentage of *Isochrysis* sp. increased from $29.1 \pm 1.1\%$ in Diet 1 to $34.0 \pm 5.0\%$ in mussel pseudofeces. Differences in the proportions of each algal species between Diet 1 and mussel pseudofeces were statistically significantly ($G = 150$, $n = 10$, $p < 0.0001$). Results obtained with oysters were more pronounced ($G = 1904$, $n = 12$, $p < 0.0001$). The proportion of *N. closterium* increased significantly from $39.8 \pm 1.1\%$ in Diet 1 to $50.1 \pm 2.7\%$ in oyster pseudofeces (Fig. 1). The percentage of *Isochrysis* sp. decreased from $29.1 \pm 1.1\%$ in Diet 1 to $18.5 \pm 4.4\%$ in oyster pseudofeces, while the proportion of *T. suesica* did not change.

Results obtained using Diet 2 were slightly different. For instance, the proportion of *Nitzschia closterium* increased significantly from $37.3 \pm 2.1\%$ in the diet to $43.4 \pm 1.1\%$ in mussel pseudofeces (Fig. 1). The proportions of *Thalassiosira pseudonana* and *Thalassiosira weissflogii* decreased slightly from $28.8 \pm 2.3\%$ to $25.9 \pm 2.1\%$ and from $33.8 \pm 1.2\%$ to $30.7 \pm 1.6\%$, respectively. These changes in the proportions of each algae species were significantly different ($G = 317$, $n = 12$, $p < 0.0001$). Changes were more dramatic in oyster pseudofeces, as the proportion of *N. closterium* increased significantly from $37.3 \pm 2.1\%$ in the diet to $55.8 \pm 1.1\%$. At the same time, the proportions of *T. pseudonana* and *T. weissflogii* decreased significantly from $28.8 \pm 2.3\%$ in diet to $17.2 \pm 1.1\%$ in pseudofeces and from $33.8 \pm 1.2\%$ to $27.0 \pm 1.9\%$, respectively ($G = 477$, $n = 11$, $p < 0.0001$).
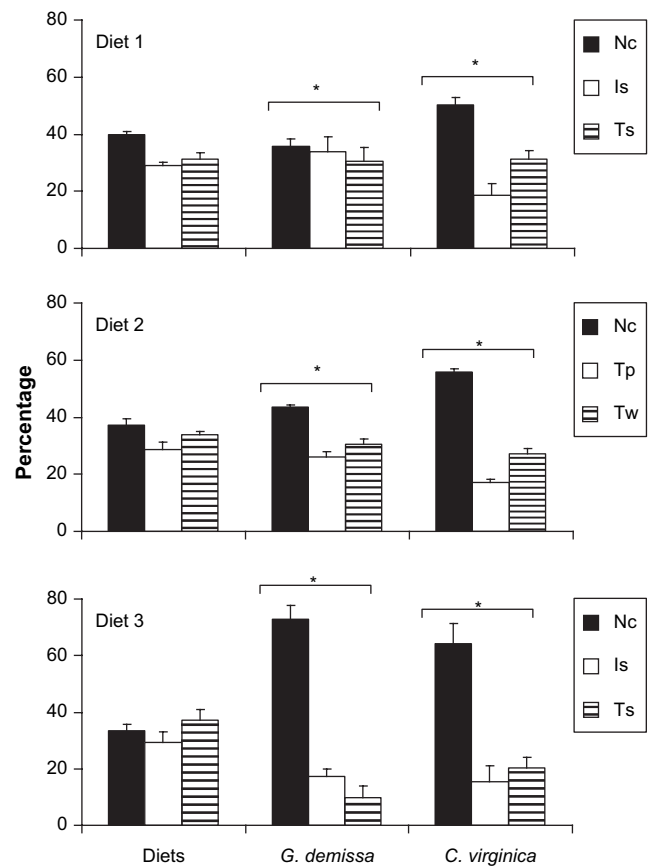

Fig. 1. Percentage (mean $\pm$ SD) of each microalgae in food supply (Diets) and pseudofeces of *Geukensia demissa* and *Crassostrea virginica*. See Table 1 for abbreviations. *Significant difference in species composition between each experimental diet and pseudofeces (goodness-of-fit *G* test, $p < 0.001$).

Calculated selection indices highlighted differences in microalgal processing between mussels and oysters. For instance, sorting efficiencies were generally lower in mussels than those determined for oysters when fed with microalgae in exponential phase (Fig. 2). Considering both diets, indices varied from -0.17 (*Isochrysis* sp.) to 0.10 (*Nitzschia closterium*) for *Geukensia demissa* whereas indices calculated for *Crassostrea virginica* varied from -0.50 (*N. closterium*) to 0.40 (*Thalassiosira pseudonana*). Selection indices were not statistically significant in mussels fed Diet 1 and were only significant for *N. closterium* (rejection) and *T. pseudonana* (acceptance) in Diet 2 (Student's *t*-test, $p < 0.05$). In contrast, oysters significantly rejected *N. closterium* both in Diet 1 and Diet 2 whereas *Isochrysis* sp. (Diet 1), *T. pseudonana* and *Thalassiosira weissflogii* (Diet 2) were preferentially accepted.

3.2. Selection of algae in stationary phase of growth

Diet 3 had the same species composition as Diet 1 but only cultures in stationary phase of growth were used. Results show a significant impact of algae phase of growth on particle selection. For instance, the proportion of *Nitzschia closterium* increased from $33.4 \pm 2.4\%$ in Diet 3 to $72.8 \pm 5.1\%$ in mussel pseudofeces and to $64.4 \pm 6.9\%$ and in oyster pseudofeces (Fig. 1). Similarly, the percentages of both *Isochrysis* sp. and *Tetraselmis suesica* decreased significantly in mussel and oyster pseudofeces when compared to their proportions in the diet. From $29.4 \pm 3.6\%$ in the diet, the proportion of *Isochrysis* sp. decreased to $17.3 \pm 2.7\%$ and $15.3 \pm 5.8\%$ in mussel and oyster pseudofeces, respectively. Similarly, the proportion of *T. suesica* decreased from $37.2 \pm 3.9\%$ to $9.9 \pm 4.1\%$
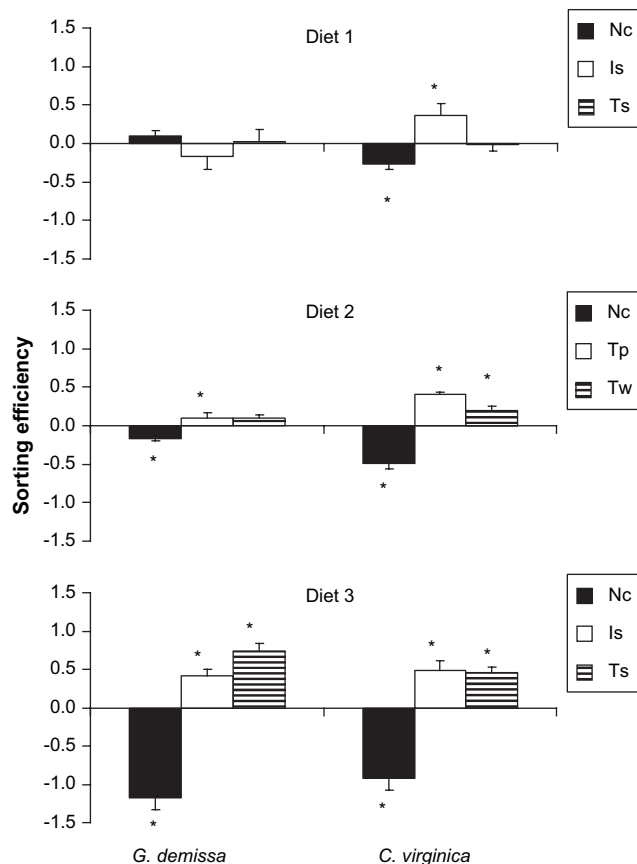
Fig. 2. Sorting efficiency (mean ± SD) of microalgae by *Geukensia demissa* and *Crassostrea virginica*. See Table 1 for abbreviations. Positive values indicate a microalgal depletion in pseudofeces while negative values indicate a microalgae rejection. *Significant ingestion or rejection (Student's *t*-test, $p < 0.05$). Sorting efficiencies in Diet 3 are significantly different from those calculated in Diet 1 for all algae species in both bivalves except for *Isochrysis* sp. in oysters.

(mussel pseudofeces) and 20.3 ± 3.6% (oyster pseudofeces). Changes in the proportions of each algae species between Diet 3 and mussel and oyster pseudofeces were significantly different ($p < 0.0001$; $G = 4165$, $n = 11$ and $G = 7782$, $n = 10$, respectively).

Calculated selection indices clearly show the differences in microalgal processing by mussels and oysters between exponentially growing algae and those in the stationary stage. Both mussels and oysters selectively ingested *Isochrysis* sp. (sorting efficiencies of 0.41 and 0.48 respectively) and *Tetraselmis suesica* (0.73 and 0.45 respectively) in stationary phase (Fig. 2). In addition, both mussels (−1.18) and oysters (−0.93) significantly rejected *Nitzschia closterium* in pseudofeces. Significant differences were observed for both bivalves and for all algae species between sorting efficiencies obtained with Diet 3 and those calculated with Diet 1, except for *Isochrysis* sp. in oysters (Student *t*-test, $p < 0.01$).

4. Discussion

The estuarine environment exhibits huge temporal and spatial variation in concentration and biochemical composition of suspended particulate food resources (Langdon and Newell, 1990; Huang et al., 2003a). During periods of low phytoplankton abundance or in areas with short periods of immersion (Charles and Newell, 1997), detrital cellulose, bacteria or protists can be an important source of food for omnivore species such as *Geukensia demissa* (Kreeger and Newell, 2001). Thus, the direct utilization of cellulose and bacteria can account for 40% of the summer metabolic carbon requirement of mussels inhabiting marshes dominated by

the marshgrass *Spartina alterniflora* in Delaware Bay (Langdon and Newell, 1990). Under the same conditions, bacteria also supplied 71% of the mussel's metabolic nitrogen requirements. This characteristic allows ribbed mussels to inhabit environments, such as high intertidal salt marshes, that might be considered inhospitable to a filter-feeding bivalve. Their ability to use a wide range of trophic resources raised the question about whether they have the same ability to select their food particles as other filibranch homorhabdic mussel species and what benefit this might offer. Results obtained in this study show that the ribbed mussel *G. demissa* is able to sort food particles, especially when fed with microalgae in stationary growth phase. Algal sorting was significantly less marked when mussels were fed with microalgae in exponential growth phase.

In bivalves, gills and labial palps are the principal structures involved in particle selection. *Geukensia demissa* has a nonplicate (flat) and homorhabdic (one type of filament) ctenidium (Morton, 1979). This gill architecture is common to several other Mytilidae, which have the ability to select particles (Bougrier et al., 1997; Ward et al., 1998). Interestingly, visual observations (endoscopy associated or not with histology) led to the conclusion that in *Mytilus edulis* (Beninger and St Jean, 1997) and *Mytilus trossulus* (Ward et al., 1998), the ctenidia seem to play little or no role in particle selection whereas labial palps could be the main sorting organ. Even though we did not find a description of the structure of *G. demissa* labial palps, it is likely that their morphology and function are closely related to those of *M. edulis* palps, as described by Beninger et al. (1995) and Beninger and St Jean (1997). Thus, based on taxonomic classification and morphological resemblance, *G. demissa* was expected to be able to select particles like other Mytilidae members (i.e. *M. edulis*). However, the fact that particle selection in mussels and oysters varies with microalgae growth phase was unexpected, and to our knowledge, a finding that has not been reported before in adult bivalves.

Although it is now shown that many bivalve mollusks can select among different types of particulate matter, the criteria used to differentiate between particles remain undefined. Among several theories, some studies have supported the idea that bivalves can use chemical cues to discriminate among particles (Kiørboe and Møhlenberg, 1981; Newell and Jordan, 1983; Shumway et al., 1985; Ward and Targett, 1989; Pales Espinosa et al., 2007). In fact, chemical communication is widely distributed in the marine environment and thousands of organic metabolites have been identified in seawater. In numerous physiological processes, marine organisms interact with each other using chemical signals (Hay, 1996 and references therein). Microalgal species are known to produce (Hodgson et al., 1991; Fidalgo et al., 1998) and excrete (Schmidt and Hansen, 2001; Fistarol et al., 2005; Uronen et al., 2005) metabolites during their life cycle. Metabolites released by microalgae, including polysaccharides, nitrogenous substances, amino acids, fatty acids and vitamins (Shimizu, 1996) can be recognized by grazers and influence their feeding behavior (Shaw et al., 1995; Tillmann and John, 2002; Leising et al., 2005 and numerous references therein). In the case of the interactions between suspension-feeding bivalves and microalgae, Ward and Targett (1989) demonstrated that mussels, *M. edulis*, are able to select and preferentially ingest synthetic beads coated with metabolites produced by microalgal species at the end of their exponential growth phase. Several authors, using blends of algae similar in size, have assumed that chemoselection in bivalves is based on microalgal exudates (Shumway et al., 1985; Baldwin, 1995). More recently, we demonstrated that microalgae selection in oysters (*Crassostrea gigas* and *Crassostrea virginica*) involves extracellular metabolites (Pales Espinosa et al., 2007), as well as glycoconjugates coating algal cells (Pales Espinosa et al., 2008).

Extracellular metabolites and glycoconjugates on microalgal cell surfaces are not constant in quality and quantity during different

growth stages. Thus, ectocrines are produced and excreted by microalage especially in stationary phase of growth when media are depleted in nutrient (Fidalgo et al., 1998; Uronen et al., 2005). Moreover, it has been shown that glycoconjugate composition of microalgal cell surfaces changes significantly between different growth stages (Waite et al., 1995; Aguilera and Gonzalez-Gil, 2001), sometimes in relation to nutrient depletion (Kremp and Anderson, 2004). Thus, the amount of glycoconjugates on the cell surface of the diatom *Thalassiosira pseudonnana* increased in early stationary phase under nutrient depletion (Waite et al., 1995). In the present study, the sorting efficiency of *Geukensia demissa* and *Crassostrea virginica* increased dramatically when fed with microalgae in the stationary growth phase, probably due to a variation in quality or quantity of compounds involved in the (positive or negative) selection process, including cell surface glycogonjugates.

Our results show that *Isochrysis* sp. and *Tetraselmis suesica* were preferentially ingested whereas *Nitzschia closterium* was preferentially rejected in pseudofeces of both bivalves. These results are supported by previous studies, describing *T. suesica* as a good diet for *Crassostrea gigas*, the flat oyster, *Ostrea edulis* and the Manila clam, *Ruditapes decussatus*, especially in combination with other algal species (Walne, 1970; Langdon and Waldock, 1981; Robert et al., 2001; Pales Espinosa et al., 2007). Moreover, *Isochrysis* spp. are considered as the industry standard for supporting bivalve growth (Ponis et al., 2003) as well as positive controls in numerous feeding studies (Bricelj and MacQuarrie, 2007; Padilla et al., 2006). Thus, *Isochrysis galbana* induced the best growth and lowest mortality rates in juvenile hard clams *Mercenaria mercenaria* when compared to several commercial diets (Pales Espinosa and Allam, 2006). In contrast, the diatom *N. closterium* is known to produce high rates of biodeposition by *Crassostrea virginica* (Tenore and Dunstan, 1973) and in *C. gigas* (Barillé et al., 2003). *Niztschia closterium* was also clearly rejected in the pseudofeces of *Mytilus edulis* (Bougrier et al., 1997), *C. gigas* (Bougrier et al., 1997; Pales Espinosa et al., 2007) and *C. virginica* (Pales Espinosa et al., 2008). The reasons why bivalves from different groups respond similarly to different algae species are intriguing and require further investigations.

5. Conclusion

Geukensia demissa lives in a high-intertidal environment where food supply varies considerably in quality and quantity (Huang et al., 2003a). Under environmental conditions where the quality of available food items is similar (i.e., no abundance of high-quality food), it was suggested that selection costs may outweigh any advantages of selective feeding, thus favoring the success of non-selectors (Sierszen and Frost, 1992). However, *G. demissa*, seems to be well adapted to low food availability and, in fact, grows better in intertidal than in subtidal zones where food is always accessible (Gillmor, 1982). Our results suggest that when the nutritional value of food particles is high enough to overcome the costs of selection process, *G. demissa* is able to become "selective". The role of ectocrines produced by microalgae during their life cycle and the carbohydrate moieties present at their cell surface should be further investigated since they are suspected to play an important role in the selection mechanism.

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