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Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves

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Abstract

Particle feeding on suspended and deposited material is a common mode of food collection among many groups of the Metazoa. In particular, many members of the Mollusca, most notably the bivalves, have specialized in particle feeding. Because suspension- and deposit-feeding activities often play significant roles in ecosystem processes, particular attention has been given to the mechanisms of particle feeding by these molluscs, and to the impacts of environmental factors upon these mechanisms.

Early studies of the feeding organs of bivalve molluscs were descriptive and emphasis soon was placed upon the actual uptake of particulate material from the environment and identification of this material. Introduction of electronic particle counters led to a better understanding of the rates and efficiencies at which particle removal occurred, and the interface between food availability in the ocean and responses of these animals to temporal and spatial variability. While some early workers inferred the capabilities of these animals to select particles, it was the introduction of more advanced technologies (e.g., flow cytometry, video endoscopy, confocal microscopy) that allowed more detailed studies of the mechanisms associated with particle uptake and selection by these animals. These techniques have provided a more comprehensive analysis which clearly demonstrate that the mechanisms associated with particle feeding and selection are complex, with species-specific processes based upon both physical and chemical characteristics of the particles. In this review, we summarize prior research on particle selection in suspension- and deposit-feeding bivalve molluscs, discuss current theory and controversy regarding these processes, and propose areas for further study. In particular, more research is needed to elucidate the mechanisms responsible for particle selection, particulate characteristics that impact selection, and the intrinsic and extrinsic factors that mediate these processes.

Keywords: Metazoa; Particle feeding; Molluscs

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1. Introduction

From coastal waters, to estuaries, to inland rivers and lakes, particle-feeding molluscs are often found in large populations that profoundly impact pelagic and benthic processes. In estuaries, particle-feeding molluscs often dominate the macrobenthos and play significant roles in ecosystem processes. Through suspension- and deposit-feeding activities they can cycle large amounts of particulate matter within the environment, converting some of it into flesh and gametes, depositing varying amounts to the benthos and cycling complex molecules into inorganic forms. Populations of particle feeders have been shown to mediate the flux of organic material to the benthos (Doering and Oviatt, 1986; Newell, 1988; Navarro and Thompson, 1997; Chauvaud et al., 2000), recycle biogenic silica (Chauvaud et al., 2000), and contribute to bioturbation and sediment re-working (Rhoads, 1963). In particular, suspension-feeding bivalves contribute significantly to benthic-pelagic coupling processes (summarized in Dame, 1996). Dense populations of bivalves interact strongly with coastal water columns, removing phytoplankton, depositing feces and pseudofeces, and cycling dissolved nutrients (e.g., Kautsky and Evans, 1987; Dame, 1993; Smaal and Prins, 1993; Prins et al., 1998). Tight coupling may lead to stimulation of phytoplankton blooms (Lewin et al., 1975; McLachlan, 1980; Asmus and Asmus, 1991), depletion of phytoplankton populations (Cloern, 1982; Officer et al., 1982; Frechette and Bourget, 1985; Doering and Oviatt, 1986; Asmus and Asmus, 1991) or more complex effects (Dame et al., 1984; Newell, 1988; Vanderploeg et al., 2002). Bivalves can exert top-down control on phytoplankton production, reducing the amount of suspended organic carbon available to stimulate anoxia. Grazing of particulates also reduces turbidity, thereby increasing light availability to the bottom and enhancing the growth of benthic seagrasses (Newell and Ott, 1999). The disappearance of, or colonization by, large populations of bivalves has been concomitant with major reorganizations of near-shore water column communities (Newell, 1988; Jackson et al., 2001; Vanderploeg et al., 2002). Finally, many particle-feeding molluscs are commercially important, playing crucial roles in the local economies of many states, provinces and countries. Given their ecological and economical importance, it is not surprising that particle-feeding molluscs have been extensively studied.

Aquatic particle feeders are confronted with a wide range of living and non-living material. The seston consists of plankton of a wide range of sizes and palatability, material re-suspended from the benthos, as well as aggregates consisting of high molecular weight substances, detritus, fecal pellets and microorganisms (e.g., Alldredge and Gotschalk, 1989; Crocker and Passow, 1995; Passow et al., 1994). Particulate matter in the benthic environment is dominated by mineral grains of various sizes, mixed with a variety of organic matter including material derived from the plankton, benthic microalgae, feces, detritus, protozoa and bacteria (Newell, 1965; Lopez and Levinton, 1987). Over the past 30 years, emphasis has been placed on understanding how benthic particle feeders operate under conditions of natural particulate sources, and research on the mechanisms of particle selection and rejection have become a major area of biological oceanographic research (e.g., Bayne, 1976; Taghon et al., 1978; Jumars et al., 1982; Lopez and Cheng, 1983; Doering and Oviatt, 1986; Shimeta and Jumars, 1991; Yen et al., 1991; Chauvaud et al., 2000). Combined with studies of digestion (e.g., Penry and Jumars, 1987), this research has provided an understanding of interactions between fluctuations in natural food availability and responses of particle feeders to this temporal and spatial variability. Changes in rates and efficiencies of particle feeding, including the degree to which particles are captured, ingested or rejected, can affect ecosystem processes (described above) and mediate the quantity and quality of material that is cycled back to the water column, deposited into the sediment (e.g., Deslous-Paoli et al., 1992; Smaal and Prins, 1993; Prins et al., 1998; Vanderploeg et al., 1996; Baker et al., 1998), or converted into molluscan flesh.

Particle-feeding molluscs rely heavily on muco-ciliary processes for some or all aspects of food collection (i.e., ciliary feeders of Morton, 1960). Differences in food collection methods, however, do exist and molluscs can be separated into two broad categories based on the mechanism of particle uptake and processing: (1) those that utilize mucous nets or strings (external to, or within the mantle cavity) to collect material and (2) those that rely on ciliated structures (proboscides, ctenidia) for particle collection, transport and processing. There are also a few molluscs that rely on both of these mechanisms for particle collection. Molluscs that utilize mucous nets or strings are predominantly in the class Gastropoda, and include several families of mesogastropods and opisthobranchs. Molluscs that rely on ciliated structures for particle collection include the protobranchiate bivalves, which mostly deposit feed using a pair of palp proboscides, and the lamellibranchiate bivalves which use the ctenidia to capture suspended or deposited material. Members of the Scaphopoda can be considered deposit feeders, collecting food by means of ciliated captacula (specialized tentacles) that terminate in a ciliated sticky bulb.

This review focuses on selection of particulate matter by juvenile and adult bivalve molluscs, including the suspension-feeding lamellibranchs (many members of the subclasses: Pteriomorphia, Palaeoheterodonta, Heterodonta, some members of the Anomalodesmata), the deposit-feeding lamellibranchs (some members of the subclass Heterodonta, superfamily: Tellinacea) and the deposit-feeding protobranchs (i.e., order: Nuculoida; Fig. 1). We have structured our review to highlight the three major feeding stages: selective retention/uptake, preingestive processing and postingestive processing. At each of these stages, there are opportunities for particle selection based upon quantitative and qualitative aspects of the particles. We take a mechanistic approach to the particle-selection phenomenon and argue that both passive and active processes work in concert to enable particle-feeding molluscs to reject low quality or unwanted material selectively, thus optimizing their energy intake.

2. Anatomy and functional-morphology of feeding organs and particle selection

Early students of molluscan biology discovered that the feeding organs of bivalves (e.g., ctenidia, proboscides, labial palps, stomach) were extremely complex with numerous folds, ridges and ciliated tracts (Alder and Hancock, 1851; Drew, 1899; Orton, 1912; Kellogg, 1915; Yonge, 1923; Elsey, 1935). Anatomical studies using dissected animals, isolated feeding organs or juveniles with transparent shells described the ability of some ciliated feeding organs to collect and transport particles toward the mouth and eliminate unwanted material from the pallial cavity (Kellogg, 1903, 1915; Yonge, 1923, 1926, 1949). Researchers inferred particle sorting and selection capabilities from observations of particle

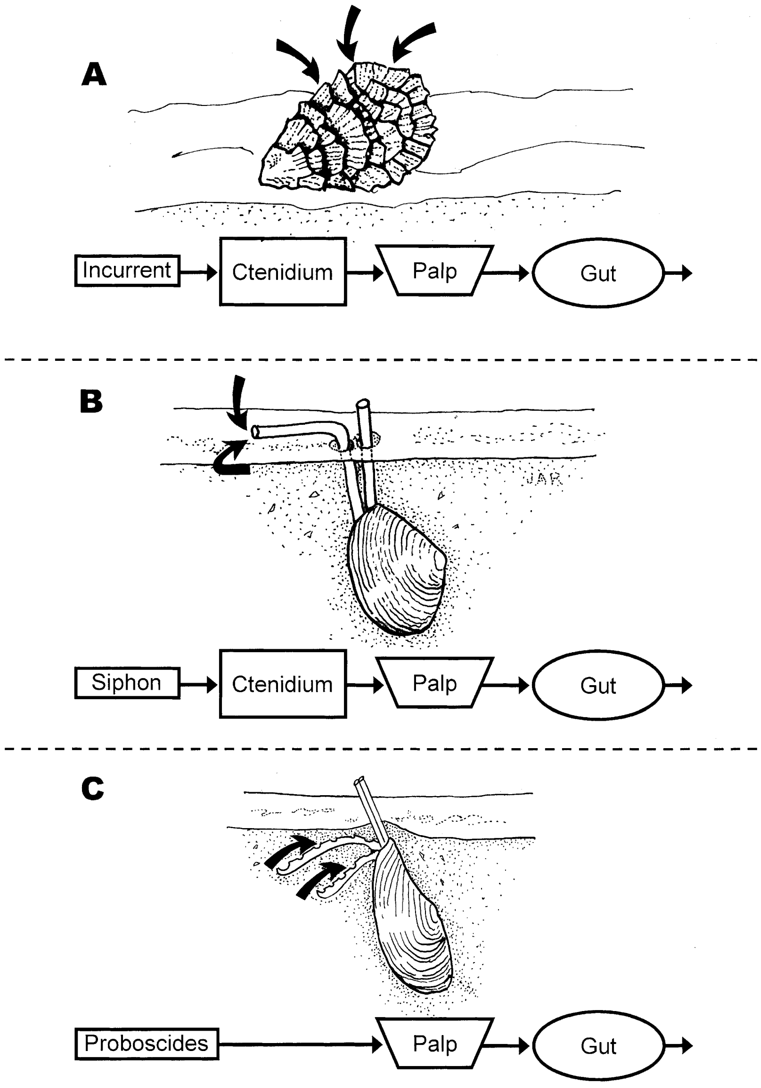

Fig. 1. Diagram of the major modes of food collection in the Bivalvia (arrows). Flow charts demonstrate uptake and movement of particles from the environment (left) through the main feeding compartments: (A) suspension feeding via an inhalant aperture or siphon and the ctenidia (e.g., *Crassostrea* sp.); (B) deposit/interface/suspension feeding by means of an inhalant siphon and the ctenidia (e.g., *Macoma* sp.); (C) deposit feeding by means of palp proboscides (e.g., *Yoldia* sp.). Flow charts adapted from Levinton et al. (1996).

movement on a manifold of ciliated tracts that carried material in opposite or oblique directions (Nelson, 1923; Yonge, 1926; Atkins, 1937a,b). Lotsy (1895), Grave (1916) and Allen (1921) were probably the first scientists to suggest that certain bivalves had the capacity to select particles based on food value. Their speculation was based on a comparison of phytoplankton found in the stomach with that found in the surrounding water. But most researchers were of the opinion that selection was more of a mechanical sorting process based solely on quantitative factors of the particles—larger, heavier particles and masses being rejected and smaller, lighter particles being ingested. The possibility that bivalves could select nutritive components of their diet from the relatively large quantities of inorganic material in the water column became a contentious issue debated by scientists in the early twentieth century. The work of Fox (1936), Loosanoff (1949), Loosanoff and Engle (1947) and later Nelson (1960) provided additional evidence that at least some bivalves had the ability to discriminate food particles based on qualitative factors.

It was not until the application of electronic particle counters and flow cytometers to the questions of particle selectivity that more definitive answers began to emerge. With these techniques, researchers began gathering data on the preferential uptake of particulate matter in molluscs and other invertebrates (e.g., Vahl, 1972a; Shumway et al., 1985, 1990). These data, along with the confirmed complexity of the feeding organs (e.g., Ribelin and Collier, 1977; Barillé, 1994), demonstrated that sorting and selection of particles based on size, quality and perhaps other factors were important components of feeding and energetics in the Bivalvia.

3. Preferential capture of particles

Uptake of particles from the environment is the first step in a sequence of events that ultimately leads to ingestion of food (Fig 1). In general, particle feeding is characterized by efficient uptake, ingestion and assimilation of particulate matter. The capture of particles by feeding structures is the product of particle encounter and retention (Shimeta and Jumars, 1991). Strong selection of particles at this stage would improve the quality of material subjected to subsequent particle sorting processes, potentially increasing efficiency of pre- and postingestive particle sorting. For lamellibranchs, the distinction between suspension-feeding and deposit-feeding is somewhat artificial, as some suspension feeders collect food particles at the sediment–water interface, and some deposit feeders rely partially or completely on suspended food, depending on environmental conditions (see below). It is not our intention to review the literature pertaining to mechanisms of particle capture and we refer the interested reader to previous reviews on the subject (Rubenstein and Koehl, 1977; LaBarbera, 1984; Shimeta and Jumars, 1991; Riisgård and Larsen, 2000a). Rather, we will examine data concerning capture efficiency (i.e., product of encounter rate and retention efficiency) and the factors that mediate this process.

3.1. Suspension-feeding bivalves

These active suspension feeders employ upstream mechanisms to encounter, retain and transport particles on the ctenidium. The lateral cilia on the ctenidial filaments create a current of water that flows into the inhalant aperture or siphon (Fig. 1a), through the interfilamentary spaces of the ctenidia, into the suprabranchial cavity and out the exhalant aperture or siphon. Particles suspended in this flow are captured by the ctenidium and transported to the ventral or dorsal margins by frontal ciliary tracts. Typically, particles are then transported by marginal tracts toward the mouth in either a cohesive mucous string (ventral), or less cohesive mucus–water slurry (dorsal) (Ward, 1996; Ward et al., 1993). Although the exact mechanisms of particle capture are still controversial (Ward et al., 1998b, 2000; Riisgård and Larsen, 2000b), capture occurs as particles encounter and are retained by the frontal surfaces of the ctenidial filaments. Currents produced by the action of the laterofrontal cilia or cirri of the ctenidia facilitate this process by redirecting particles from the through current, laterally onto the filaments (Riisgård et al., 1996; Ward et al., 1998b). This cirral-trapping mechanism (sensu Riisgård and Larsen, 2000a) greatly increases the particle-retention efficiency of the ctenidia, which varies according to size and complexity of the laterofrontal cilia of the filaments (cilia, small cirri or large cirri; see below). Studies in which the laterofrontal cirri of blue mussels, *Mytilus edulis*, are inactivated by serotonin (5-hydroxytryptamine; 10^{-5} to 10^{-4} M concentrations) demonstrate the importance of cirri to the capture process (Jørgensen, 1976; Ward et al., 1998b). When the laterofrontal cirri are inactivated, capture efficiency drops significantly, but does not fall to zero, suggesting that other mechanisms in addition to cirral trapping are involved in particle capture (Ward et al., 1998b).

Numerous workers have examined capture efficiency of the bivalve ctenidium in relation to particle size, using either direct or indirect methods. In direct methods, the exhalant aperture or siphon is physically isolated from the inhalant water, and absolute capture efficiency is determined by comparing particle concentration in the two separated water masses (e.g., Loosanoff and Engle, 1947; Tammes and Dral, 1955; Hildreth and Mallet, 1980; Wilson, 1983). These techniques, however, have been criticized because of potential disturbances to experimental bivalves (Bayne et al., 1976). Most researchers have used variations of the indirect method to examine capture efficiency. It is based upon the proportion of particles of different sizes that are removed from the water in a flowing or static condition. This method provides a relative value, with capture efficiencies of specific particle-size classes reported as a percentage of the particle size that is removed with the greatest efficiency (Palmer and Williams, 1980; Williams, 1982).

In general, capture efficiency increases non-linearly with increasing particle size to a maximum. Early work suggested that bivalves could efficiently capture particles in the sub-micron range (e.g., colloids; Fox and Coe, 1943; Fox et al., 1937; Korringa, 1952). These studies were based upon uptake of vital dyes, soluble starch, or pen ink that were removed during experimentation. However, all of these colloidal substances strongly adsorb to mantle and ctenidial tissue, suggesting that their removal was not due to suspension-feeding mechanisms. Because of these methodological uncertainties, such results were questioned by later workers. The elegant study by Tammes and Dral (1955) demonstrated that *M. edulis* could not efficiently capture particles <2.5 μm in diameter. Using a variety of organic and inorganic particles (e.g., cow-blood cells, starch, clay, carbon black), these authors showed that capture was dependent upon the diameter of particles, and that in mixed suspensions of particles of different size, each component is removed as if it were separate. Tammes and Dral (1955) suggested that the capture process involved a sieving mechanism by the laterofrontal cirri.

Later studies using electronic particle counters better defined the capture efficiency of bivalves in relation to particle size (e.g., Haven and Morales-Alamo, 1970; Jørgensen, 1975). Vahl (1972a,b,c, 1973) studied capture efficiency of four species of bivalves

(*Cardium edule*, *Chlamys opercularis*, *Chlamys islandica*, *M. edulis*) delivered natural particles and cultured phytoplankton. He found that efficiency increased with particle diameter and that capture efficiency of small particles (<7 μm) was species-specific. Møhlenberg and Riisgård (1978) studied retention efficiency of 13 species of bivalves by sampling water from the inhalant and exhalant regions of bivalves fed mixtures of natural particles and cultured phytoplankton. They found that retention efficiency decreased with particle size, but that the degree to which efficiency changed, and the particle diameter at which inefficient retention began were species-specific. All bivalves studied could capture particles greater than about 6 μm in diameter with near 100% efficiency, and some species, such as the ocean quahog, *Arctica islandica*, could retain 1 μm particles with an efficiency of 60–70%. In a similar study, Riisgård (1988) used mixtures of natural particles and cultured phytoplankton to examine capture efficiency of six species of bivalves. Species that possessed large laterofrontal cirri (i.e., *Geukensia demissa*, *Spisula solidissima*, *Brachidontes exustus*, *Mercenaria mercenaria*) retained all particles >4 μm in diameter with an efficiency of 100%, whereas those species with small or lacking laterofrontal cirri (i.e., *Crassostrea virginica*, *Argopecten irradians*) retained 4-μm particles with an efficiency of about 75–85%. The results of Møhlenberg and Riisgård (1978) and Riisgård (1988) suggest that retention efficiency is dependent, in part, on the morphology of the laterofrontal cilia of the ctenidium. Bivalves with complex laterofrontal cirri retained particles >4 μm with almost 100% efficiency (see Jørgensen, 1989; Jørgensen et al., 1984).

Palmer and Williams (1980) studied the effect of particle concentration on the capture efficiency of the bay scallop, *A. irradians*, and the eastern oyster, *C. virginica*. They found that scallops were much less efficient than oysters at capturing particles <7 μm. Oysters removed 50% of the 1.7-μm particles (at 1.45 mg l^{-1} phytoplankton), whereas scallops removed only 1.5% of particles this size (at 0.88 mg l^{-1} phytoplankton). Palmer and Williams also found that capture efficiency of scallops for particles between 1.7 and 3.4 μm increased with increasing concentration of phytoplankton (from 0.88 to 6.08 mg l^{-1}). The authors suggested that the change in capture efficiency was due to an increase in mucus production by the scallop ctenidia; however, no indication was made as to whether aggregation of phytoplankton occurred at the higher concentration.

The studies summarized above and those of other workers (e.g., Wright et al., 1982; Stuart and Klumpp, 1984; McHenery and Birkbeck, 1985; Langdon and Newell, 1990) demonstrate that capture efficiency of bivalves increases non-linearly with particle diameter and that some species are more efficient at capturing small particles than others (Fig. 2). Such differences are probably related to interspecific variation in the complexity of the laterofrontal cilia or cirri (Table 1) and perhaps the ctenidial form (filibranchiate, pseudolamellibranchiate, eulamellibranchiate). Capture, however, is not merely a mechanical sieving process by the laterofrontal ciliary tracts. This perspective is supported by several lines of evidence. First, calculation of Reynolds number at the site of laterofrontal cilia and cirri are 1 (Ward et al., 1998b), and it is unlikely that these structures act as sieves under such viscous flow. Second, mechanical sieving would result in a high capture efficiency for all particles with a diameter greater than the sieve. In *M. edulis*, the distance between branching cilia of the laterofrontal cirri varies from about 1.0 to 1.7 μm (Jørgensen, 1975) and would mean a near 100% capture of all particles down to >2 μm. Clearly, this is not the case (Fig. 2). Instead, the laterofrontal cilia/cirri probably act as paddles to re-direct

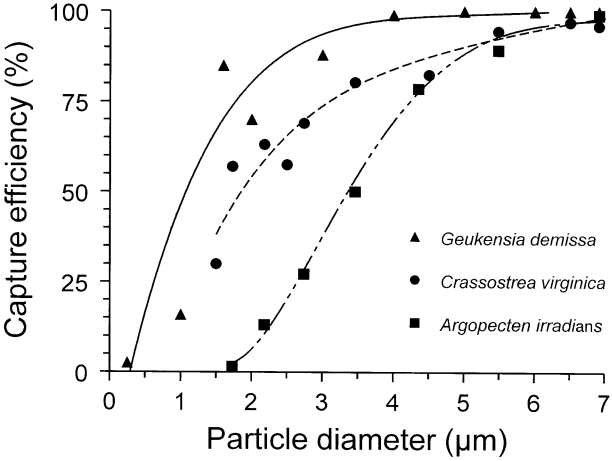

Fig. 2. Relationship between capture efficiency and particle diameter in three species of bivalves representing those with large and small laterofrontal cirri (*G. demissa* and *C. virginica*, respectively) and simple laterofrontal cilia (*A. irradians*). Curves of best fit obtained by replotting combined data from Haven and Morales-Alamo (1970), Vahl (1972a), Møhlenberg and Riisgård (1978), Palmer and Williams (1980), Riisgård (1988) and Langdon and Newell (1990). See also Table 1 and Jørgensen (1989).

flow towards the frontal surfaces of the filament. Species-specific differences in capture efficiency probably relate to the efficiency with which this lateral flow is produced (Ward et al., 1998b).

The spectrum of particles that are captured by a particular species of bivalve may be an adaptation to exploit the local resources available in the water column. For example, Wright et al. (1982) demonstrated that the saltmarsh mussel, *G. demissa*, more efficiently captures bacterioplankton than *M. edulis* or the softshell clam, *Mya arenaria*. Langdon and Newell (1990) reported that the capture efficiency of *G. demissa* was 15.8% on free bacteria (ca. 1 μm diameter), whereas capture efficiency by *C. virginica* was only 5% on free bacteria. The authors calculated that at their study site, bacteria (unattached and attached to detritus) could contribute 70.6% of the metabolic nitrogen requirement of mussels during the

Table 1
Examples of efficiencies of particle capture in relation to the type of laterofrontal cilia or cirri in four species of suspension-feeding bivalves

Species (type of laterofrontal tacts)	Particle diameters (μm)	
	90% retention	50% retention
Geukensia demissa (large cirri)	2.6	1
Mytilus edulis (large cirri)	3.2	1.2
Crassostrea virginica (small cirri)	5	1.8
Argopecten irradians (simple cilia)	5.2	3.3

Values obtained by replotting data from Haven and Morales-Alamo (1970), Vahl (1972a), Møhlenberg and Riisgård (1978), Palmer and Williams (1980), Riisgård (1988) and Langdon and Newell (1990). See also Fig. 2 and Jørgensen (1989). Large laterofrontal cirri are 20–30 μm in length and composed of 22–26 pairs of cilia each; small laterofrontal cirri are 14–25 μm in length and composed of 6–11 pairs of cilia each, and simple cilia are 10–17 μm in length (Atkins, 1938; Owen and McCrae, 1976; Ribelin and Collier, 1977; Owen, 1978).

summer months. The green mussel, *Perna perna*, can capture latex particles of 0.46 μm diameter (Berry and Schleyer, 1983). Such particles correspond approximately to the mean diameter of free-living coccoid bacteria that occur in the natural habitat, which may comprise a potentially significant food resource for the mussels. More recently, Pile and Young (1999) demonstrated that the cold-seep mussel, *Bathymodiolus childressi*, can efficiently retain and utilize ultraplankton (<5 μm) including bacteria. Interestingly, capture efficiency significantly increased with size of the mussel, with 27-mm mussels capturing about 20% of the bacteria and 84-mm mussels capturing about 80% of the bacteria. Pile and Young (1999) calculated that the nitrogen obtained by feeding on ultraplankton was similar to that obtained by symbionts, suggesting that ultraplankton may be an important component in the nutritional requirements of cold-seep mussels.

Although it is widely accepted that particle size is an important parameter that affects capture efficiency, qualitative factors can also influence particle capture. Shumway et al. (1985) and Cucci et al. (1985) were the first scientists to apply flow-cytometric (FCM) techniques to particle selection in bivalves. Shumway et al. (1985) reported that the European oyster, *Ostrea edulis*, preferentially captured the dinoflagellate, *Prorocentrum minimum* (clone Exuv) compared to the diatom, *Phaeodactylum tricornutum* (clone Phaeo) and flagellate, *Chroomonas salina* (clone 3C). Since all phytoplankton were of similar size, the authors suggested that preferential capture was based on properties other than the size of cells (see also Shumway and Cucci, 1987). Similar results have been reported for juvenile scallops (<2 mm shell height; Shumway et al., 1997). *Placopecten magellanicus* cleared the phytoplankton *Amphidinium carterae* (clone Amphi), and *Patinopecten yessoensis* cleared the phytoplankton Amphi and Phaeo in preference to similar sized and smaller phytoplankton. Using FCM techniques, Newell et al. (1989) examined feeding by *M. edulis* on natural assemblages of particles and found that at seston concentrations less than 20,000 particles ml^{-1}, mussels cleared fluorescent particles at a rate significantly higher than that of non-fluorescent particles. Higher clearance efficiency for fluorescent particles occurred at all size ranges (3–15 μm), suggesting that preferential clearance was not based on size alone. Using cultured phytoplankton and natural silt particles, Newell and Shumway (1993) reported similar results; mussels cleared phytoplankton particles at a higher rate than silt particles at total concentrations of less than 20,000 particles ml^{-1}. The mechanisms involved in discrimination of food particles with equivalent spherical diameter by the bivalve ctenidium have not been elucidated. One possibility is that some types of particles are more efficiently retained by the ctendium resulting in a higher capture rate (encounter rate × retention efficiency). Enhanced retention could be a consequence of specific interactions between the extracellular matrix of living cells, and cilia and mucus of the bivalve ctenidia. The amount of sugar-containing compounds on the cell surfaces of marine diatoms varies among species, potentially affecting cell stickiness (Waite et al., 1995). Particles with low stickiness, such as detritus, silt or certain types of phytoplankton, may not be retained as well as particles with higher stickiness. In one of the few studies to examine the effects of surface properties on particle uptake, Hernroth et al. (2000) manipulated the electrostatic charge on the cell surfaces of cultured, radiolabelled bacteria (ca. 1 μm). The researchers then fed bacteria with low and high electrostatic charges to *M. edulis* and found that bacteria with reduced negative surface charge were ingested at a significantly higher level than those with a higher negative surface charge. Their results suggest that interactions between the surface properties of cells and feeding structures of bivalves is a factor that can mediate capture and transport of particles.

Even more perplexing are reports of lower capture efficiency of large particles compared to small particles. Using FCM and mixed phytoplankton suspensions, Lesser et al. (1991) reported that juvenile scallops, *P. magellanicus*, cleared the toxic dinoflagellate, *Alexandrium tamarensis* (clone GT 429; 30–45 μm) at a significantly lower rate than three other phytoplankton species (all less than ca. 16 μm diameter). Pile and Young (1999) showed that bacteria were captured by cold-seep mussels, *B. childressi*, at a higher efficiency than significantly larger protozoans. *M. edulis* has been shown to capture the diatom, *Phaeodactylum* sp. in preference to smaller and larger diameter natural particles (Bayne et al., 1977). Similarly, *Crassostrea gigas* captures the diatom, *Nitzschia closterium*, preferentially when compared to phytoplankton of larger diameter (Bougrier et al., 1997). Such results, that smaller particles are captured more efficiently than larger particles, are difficult to explain given the current knowledge of suspension-feeding in bivalves (e.g., Riisgård and Larsen, 2000a; Riisgård et al., 1996; Ward et al., 1998b). One explanation is that differences in cell shape or flexibility significantly influence particle capture. In particular, elongated or tri-radiated cells may be more efficiently retained than spherical particles of the same volume (Bayne et al., 1977). Because electronic counters (e.g., Coulter) determine particle size as equivalent spherical diameter, effects due to differences in particle shape cannot be evaluated in studies that use these instruments to enumerate particles. Another possibility is that actively swimming cells interact with the ctenidium of some bivalve species in a fundamentally different way. Several reports support this idea. Bricelj et al. (1998) used video endoscopy to study capture and transport of toxic and non-toxic phytoplankton by the ctenidia of two bivalve species. One interesting finding was the difference in how the diatom, *Thalassiosira weissflogii* (11 μm diameter) and toxic and non-toxic strains of the dinoflagellate (*Alexandrium* spp.; 35 μm length) were handled by the ctenidium of *O. edulis*. In contrast to diatoms, dinoflagellates were not retained on the frontal surface of the ctenidium, but were entrained in the anteriorly directed slurry in the dorsal ciliated tract. At the dorsal ctenidium-labial-palp junction, dinoflagellates were not transferred to the palps, but accumulated as a dispersed mass between the surrounding ctenidial lamellae. Periodically, this mass of freely suspended dinoflagellate cells would be ejected from the pallial cavity when the oyster adducted its valves. Shumway (unpublished) observed similar behavior when *C. virginica* was fed the dinoflagellate *Cochlodinium* sp. Thus, dinoflagellate cells were captured and transported by the ctenidium, but were rejected as, in essence, unconsolidated pseudofeces. Sampling and analysis of water surrounding a bivalve exhibiting such rejection would yield a higher depletion rate of smaller diatoms compared to the larger dinoflagellates. Baker et al. (1998) and Vanderploeg et al. (2001) reported similar findings with the zebra mussel, *Dreissena polymorpha*, feeding on mixtures of cultured and natural phytoplankton. Certain species of phytoplankton were selectively rejected in loosely consolidated pseudofeces that were easily re-suspended, potentially allowing viable phytoplankton to return to the water column for continued growth. Therefore, the potential for rejection of unconsolidated pseudofeces from the pallial cavity and resuspension of particles in feces (Hildreth, 1980) should be considered in future experiments in which changes in the concentration of different types of phytoplankton are analyzed to determine capture efficiency.

Capture efficiency of bivalves can also be responsive to environmental factors. Stenton-Dozey and Brown (1992) studied the rock-pool clam, *Venerupis corrugatus*, monitoring changes in particle concentration in rock pools over a tidal cycle, and exposing clams to natural rock-pool water in the laboratory. The researchers found that at low tide, particles with a diameter between 5 and 9 μm were captured with maximum efficiency (70–100%), whereas at high tide particles between 8 and 13 μm diameter were captured with maximum efficiency (75–100%). The shift in efficiency of particle capture coincided with an increase in the size range of particles that contained the greatest organic content. The authors suggested that capture efficiency of clams was adjusted to utilize the size spectra of particles that yield the most food material per liter of water. Several other species of bivalves have been shown to adjust capture efficiency in response to changes in ambient particle concentration. Capture efficiency of sea scallops, *P. magellanicus*, for particles less than 8 μm, decreases in the presence of bentonite clay at concentrations higher than 2 mg l^{-1} (Cranford and Gordon, 1992). *O. edulis* demonstrates a decrease in capture efficiency for phytoplankton, *Isochrysis galbana*, as cell concentrations increase from about 2,000 to 480,000 cells ml^{-1} (Wilson, 1983). Using different mixtures of silt and phytoplankton, Barillé et al. (1993) showed that *C. gigas* adjusted its capture efficiency in response to seston quantity, but not quality. In field experiments at high seston concentrations (64.4 mg l^{-1}) oysters could only capture particles >12 μm at 100% efficiency. The authors suggest that *C. gigas* controls the interfilamentary spaces of the ctenidium as a compensatory response to high sestonic loads. Similar trends have been reported for the oyster, *C. virginica* (Palmer and Williams, 1980). An intriguing corollary to adjustments of ctenidal morphology to affect capture efficiency relates to possible compensations over longer temporal scales (months, years). The mass of the ctenidium and the ctendium-to-labial-palp ratio of *C. gigas* is variable over time (Honkoop et al., 2003). Oysters from high-turbidity regions of the French Atlantic coast have smaller ctenidia and larger labial palps than individuals from low-turbidity regions (Barillé et al., 2000). Length of the laterofrontal cirri of ordinary filaments tended to be longer in oysters from high-turbidity regions, but no significant differences were found. Such morphological plasticity of *C. gigas* may result in functional changes in capture efficiency, clearance rate and particle selection in response to ambient seston concentrations.

Conversely, laboratory studies indicate that there is no correlation between capture efficiency and concentration of suspended phytoplankton to which *M. edulis* is exposed (Davids, 1964; Hildreth and Mallet, 1980). Efficiency of capture remains constantly high even at particle concentrations that stimulate abundant pseudofeces production. Similar findings have been reported under more natural conditions. Lucas et al. (1987) compared the capture efficiency of *M. edulis* from an estuarine site and from an open coastal site in Cornwall, UK. Although the particle concentration was higher at the estuarine site, with about three times the carbon and nitrogen resources as the open coastal site, relative particle-capture efficiencies of the two mussel populations were the same. Capture efficiency on natural bacterioplankton (ca. 0.5 μm) was only 28%, leading the authors to conclude that the contribution of free-living bacteria to the energy budget of mussels is small. Interestingly, *M. edulis* can respond within months to changes in turbidity by altering the area of its ctenidia and palps (Essink et al., 1989); mussels living in turbid habitats develop large palps and small ctenidia (Theisen, 1977). How such phenotypic plasticity affects particle capture is unclear, but seasonal changes in capture efficiency of mussels have been reported (Bayne et al., 1977).

The extent to which bivalves can alter their capture efficiency, the interspecific differences in their ability to respond, and the temporal scale over which they compensate for changing seston concentration is fertile area for future research. Selective grazing, based on size or other cell properties (Targett and Ward, 1991; Hernroth et al., 2000), could significantly impact phytoplankton species composition in near-shore waters. Knowledge of the types of phytoplankton that bivalves do and do not remove from the water column is important for a full understanding of the degree to which these suspension feeders couple the benthic and pelagic realms, exert top-down control on phytoplankton populations and impact food web dynamics of near-shore waters (see Dame, 1996).

3.2. *Deposit-feeding bivalves*

Preferential uptake or capture of particulate matter by deposit-feeding bivalves has been studied less than particle capture in suspension-feeding species. Capture and collection of particles in deposit-feeding bivalves is accomplished either by siphon to ctenidia transfer (i.e., Tellinacea: eulamellibranchs; Fig. 1b), or via tentaculate, palp proboscides (i.e., Nuculoida: protobranchs; Fig. 1c). Members of the Nuculoida (e.g., *Yoldia* spp.) collect food material using extensible, highly ciliated, U-shaped palp proboscides which transport material directly to the labial palps (Kellogg, 1915; Stasek, 1965). Although some suspended particles can be captured by the primitive ctenidium and transported to the palps (Stasek, 1961, 1965; Davenport, 1988; Levinton et al., 1996), the contribution of suspension feeding to the overall energy budget of these protobranchs is probably small (Stead et al., 2003). To feed, the proboscides are extended beyond the margins of the shell and inserted into or on the sediment. Material is collected in the ciliated troughs and directed proximally toward the labial palps. Stasek (1961) suggested that some selection of particles based on size may occur on the palp proboscides. This perspective was based on observations of the ciliated rejection tracts on the crests of the walls of the troughs. In addition, it is possible that mechanical selection at the point of particle collection, based on differences in particle diameter and strength of adhesion to mucus on the palp proboscides, could be occurring (Taghon, 1982; Jumars et al., 1982). Although such mechanisms have been demonstrated for other deposit-feeding invertebrates (see Jumars, 1993), for protobranchs quantitative evidence for preferential uptake of particles based on size or specific gravity is lacking (Self and Jumars, 1988).

The tellinaceans are eulamellibranchs with mobile, separate siphons. In some species, the inhalant siphon reaches a length of up to four to five times that of the shell (Yonge, 1949). The inhalant siphon can move independently of the exhalant siphon and is used to collect material from the bottom. The lateral cilia of the ctenidia produce a strong inhalant current that causes material beneath, on or just above the sediment surface to be sucked into the pallial cavity and onto the frontal surfaces of the ctenidia (Yonge, 1949; Hughes, 1969; Levinton et al., 1996). In essence, capture of deposit material by the ctenidia is functionally similar to removal of suspended material, although the ctenidium of tellinaceans have special adaptions to handle large masses of material (Atkins, 1937b; Stasek, 1961). Collection of deposited material seems to be entirely indiscriminate, with no indication of selection or rejection of material that is collected and drawn down the siphonal tube (Yonge, 1949; Hughes, 1969; Hylleberg and Gallucci, 1975; Self and Jumars, 1988). Large quantities of material, even sand grains up to 250 μm in diameter, are captured by the ctenidium and transported toward the labial palps (Hughes, 1975; Levinton et al., 1996). In *Abra tenuis*, size of particles entering the pallial cavity is simply controlled by the diameter of the inhalant aperture (Hughes, 1973). Particles larger than the opening are excluded and not collected.

In contrast to the deposit-feeding protobranchs (above), there is good evidence that some tellinacean species can obtain food resources from suspension feeding activities (Brafield and Newell, 1961; Hylleberg and Gallucci, 1975; Rae, 1979; Ólafsson, 1986). *Macoma balthica*, for example, can switch from deposit feeding to suspension feeding when the flow regime is high and may predominately feed on suspended matter in habitats with sandy sediments (Ólafsson, 1986). The tellinid, *Scrobicularia plana*, can capture and ingest suspended particles >4 μm in diameter with about 100% efficiency (Hughes, 1969). Using high concentrations of kieselguhr and *Phaeodactylum* cells (5×10^5 to 1.2×10^6 particles ml^{-1}), Hughes (1975) reported that *A. tenuis* can capture suspended particles of 1 μm in diameter with about 100% efficiency. It is possible, however, that the high concentrations of fine particles he used led to aggregation and formation of larger flocs. Other tellinacean species seem to obtain food primarily through deposit feeding (Hylleberg and Gallucci, 1975). Also, there are a few bivalve species that utilize the foot to collect surface and subsurface deposits (e.g., *Fimbria fimbriata*; Morton, 1983). Little is known, however, about their abilities to discriminate among particles.

4. Preingestive particle processing on the pallial organs

Post-capture particle processing is the next step in the sequence of events that leads to ingestion of food. Preingestive sorting leads to the formation of pseudofeces, i.e., material rejected prior to ingestion (Fig. 3). Strong selection of particles at this stage in the feeding process would enhance the quality of material ingested, potentially increasing efficiency of postingestive particle sorting in the stomach. As mentioned above (Section 2), the possibility that bivalves could discriminate among particles was keenly debated by scientist in the early twentieth century. This debate was fueled by differences in experimental results obtained by researchers using different populations or species of bivalves. Such divergent results were probably due to several factors. First, many early studies were conducted on surgically altered specimens or isolated structures, techniques that could have produced artifacts arising from abnormal behavior and excess mucus production (Ward et al., 1991, 1993). Second, the production of pseudofeces is not necessarily indicative of particle selection. Material that is captured but exceeds the ingestive capacity of a bivalve can be rejected with little or no sorting (Foster-Smith, 1975b; Beninger et al., 1992). As seston concentration increases, bulk rejection of material as pseudofeces also increases (e.g., Foster-Smith, 1975b; Kiørboe et al., 1980; Bayne et al., 1993; Barillé et al., 1994). Third, particle selection is not 100% efficient, and selection processes can be affected by the quantity and quality of material that is captured from the seston (e.g., Robinson et al., 1984; Urban and Kirchman, 1992; Bayne et al., 1993;

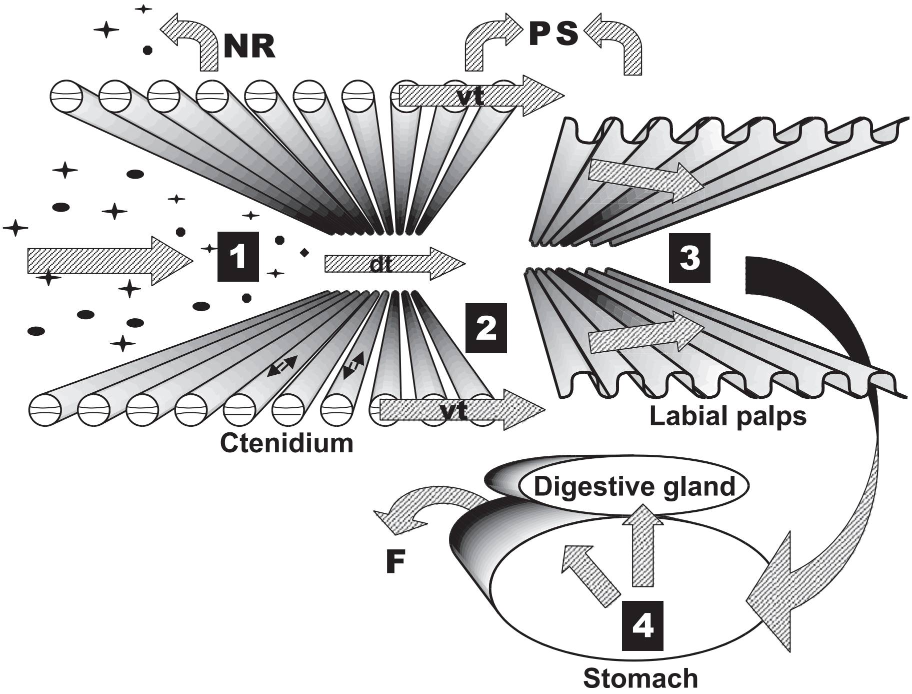

Fig. 3. Diagram showing opportunities for particle selection in lamellibranchiate bivalves. Arrows indicate general movement of particulate matter from the environment (left) through the feeding and digestive organs. (1) Preferential capture by the ctenidium resulting in some particles not being retained (NR); (2) selection and differential transport by the ctenidium resulting in some particles being rejected as pseudofeces (PS); (3) selection by the labial palps resulting in preferential ingestion of some particles and production of PS; and (4) selection in the stomach and preferential transport of some particles to the digestive diverticula. Unabsorbed material egested as feces (F). Note: not all bivalve species transport particles on both ventral (vt) and dorsal tracts (dt) of the ctenidium, or demonstrate all sorting loci.

MacDonald and Ward, 1994). Finally, there can be interspecific differences in the efficiency of selection due to differences in ctenidium and labial palp morphology, or physiological compensation (Ward and MacDonald, 1996; Bacon et al., 1998; Bayne, 2002; Honkoop et al., 2003). Intraspecific differences may also arise due to adaptations or compensations to specific environmental conditions (e.g., changes in ctenidim to palp ratio; Essink et al., 1989; Barillé et al., 2000).

4.1. Suspension-feeding bivalves

Early work of Fox (1936), Loosanoff (1949), Loosanoff and Engle (1947), Purchon (1955), Ballantine and Morton (1956), Nelson (1960) and Morton (1969) provided some evidence that bivalves could discriminate among food particles based upon size and qualitative factors. Subsequent studies, however, produced conflicting results, shedding doubt on the idea that preingestive sorting of particles occurred (Ansell, 1961; Bernard, 1974; Foster-Smith, 1975a; Foster-Smith, 1978). One of the strongest arguments against particle selection was the observation that captured particles were transported along the ctenidia and labial palps embedded in mucous masses or strings (see Foster-Smith, 1975c, 1978; Beninger, 1991). How then could individual particles be sorted and preferentially ingested if all particles were embedded in cohesive mucus? Foster-Smith (1978) observed pallial organ function in 19 species of bivalves through holes cut in the shell and mantle that were covered with pieces of glass. Based on these observations, he argued that pseudofeces was produced to control ingestion and rid the animals of excess mucus. Foster-Smith (1978) concluded that evidence for particle selection, other than early observational work on surgically altered specimens or isolated structures, was either weak (e.g., Ballantine and Morton, 1956), or lacking. The inability to reconcile purported particle-selection capabilities of bivalves with observed pallial organ function was a major conceptual impediment that scientists had to overcome.

In the next stage of particle-selection studies on suspension-feeding bivalves, researchers used more natural mixtures of particles and focused on selection between different phytoplankton species, phytoplankton cells and detrital particles, or organic and inorganic material. Kiørboe et al. (1980) and Kiørboe and Møhlenberg (1981) studied particle selection in several species of bivalves using mixtures of the diatom, *P. tricornutum*, and natural silt. They compared chlorophyll *a* content in the inhalant water with that in the pseudofeces and found that in all cases, bivalves were able to ingest phytoplankton selectively and reject silt. Selection efficiency (SE), however, differed significantly among species. The selective capabilities of *M. edulis* were not affected by silt concentration between 2 and 56 mg l^{-1}, with phytoplankton being enriched in the ingested ration by a factor of 3–30 at the lowest and highest silt concentration, respectively (Kiørboe et al., 1980). The authors concluded that bivalves can compensate for the dilution of food by inorganic material by selecting high quality material on the pallial organs and rejecting more inorganic material in pseudofeces. Bricelj and Malouf (1984) reported that the quahog (=hard clam), *M. mercenaria*, could selectively ingest phytoplankton from a mixed phytoplankton-silt suspension. Using mixtures of phytoplankton and natural silt, and natural seston and silt, Newell and Jordan (1983) studied preferential ingestion of organic material by the eastern oyster, *C. virginica*. At phytoplankton and silt concentrations ranging from ca. 4 to 12 mg l^{-1}, they found that oysters consistently rejected significantly less fluorescent material in the pseudofeces compared to the delivered food. Similarly, with natural seston and silt concentrations between ca. 5 and 20 mg l^{-1}, the pseudofeces of oysters had significantly less energy (Joules), less nitrogen and, at some concentrations, less carbon than the food. Size of particles was examined and found not to be a major factor in the selection process. Importantly, these researchers hypothesized a mechanism that could explain the paradox between selection of individual particles and transport of such particles in mucous masses or strings by the pallial organs. They postulated that ciliary action on the ridged surfaces of opposing palp lamellae reduces mucous viscosity, liberating particles that can then be sorted individually. Excess mucus is taken to the free edges of the palps where mechanical action stops and the mucus regains its cohesive viscosity.

In the following years, numerous workers examined particle selection in a variety of bivalves species, reporting that most had the capacity for particle selection (Table 2). Using flow cytometry, Cucci et al. (1985) and Shumway et al. (1985) demonstrated

Table 2
Examples of studies (post 1980) demonstrating post-capture particle selection in bivalves

Bivalve species	Particle types (diameters[a]/length)	Particle concentration (units)	Measured parameter	Selection comments	Reference
Acanthocardia echinata	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
Aequipecten opercularis	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
Arca zebra	natural seston (2–30 µm)	3–13 mg l^{-1}	PN, POC	PF	Ward and MacDonald (1996)
Arctica islandica	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
	3C (9–12 µm) Exuv (8–15 µm) Phaeo (12–23 µm)	10^4 cells ml^{-1}	fluorescence (FCM)	PF	Shumway et al. (1985)
Cerastoderma edule	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
	Phaeo (12–23 µm), silt (n.g.)	20×10^3 cells ml^{-1}, 20–120 mg l^{-1}	chlorophyll *a*	PF	Prins et al. (1991)
Corbula gibba	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
Crassostrea gigas	Phaeo (12–23 µm), silt ($\bar{x}$=9.6 µm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
	natural seston (1.2–200 µm)	20–175 mg l^{-1}	chlorophyll *a*, *c* phaeophorbides	PF	Pastoureaud et al. (1996)
	mixed phytoplankton (4–9 µm)	7–15 mg l^{-1}	fluorescence (FCM)	PF	Bougrier et al. (1997)
	Rhodo (6–13 µm), *Spartina* detritus (3–20 µm)	10^3, 10^4, 10^5 particles ml^{-1}	fluorescence (FCM)	CT	Ward et al. (1998a,b)
Crassostrea virginica	Tetra (8 µm) silt (n.g.)	4–12 mg l^{-1}	chlorophyll *a*	PF	Newell and Jordan (1983)
	natural seston silt (2–38 µm)	5–20 mg l^{-1}	Joules, PN, POC	PF	Newell and Jordan (1983)

	T-Iso (4 μm), rice starch (n.g.)	1.8 mg l^{-1}, 20 mg l^{-1}	^{14}C and ^{3}H label	PF	Urban and Kirchman (1992)
	Rhodo (6–13 μm), *Spartina* detritus (3–20 μm)	10^{3}, 10^{4}, 10^{5} particles ml^{-1}	fluorescence (FCM)	CT	Ward et al. (1998a)
Dreissena polymorpha	natural seston (10–95 μm)	n.g.	size and morphology	PF	Ten Winkel and Davids (1982)
	diatoms (6–18 μm), chlorophytes (6–25 μm), *Typha* detritus (<20 μm)	10^{5} particles ml^{-1}	fluorescence (FCM)	PF	Ten Winkel and Davids (1982)
	Micro (4 μm), diatoms (6–18 μm), chlorophytes (6–25 μm), *Typha* detritus (<20 μm), clay (<20 μm)	10^{5} particles ml^{-1}	fluorescence (FCM)	PF	Baker et al. (1998)
Ensis directus	3C (9–12 μm), Exuv (8–15 μm), Phaeo (12–23 μm)	10^{4} cells ml^{-1}	fluorescence (FCM)	PF	Shumway et al. (1985)
Mercenaria mercenaria	Pseudoiso (4 μm), sediment (3–44 μm)	0.5–1.5×10^{5}, 5–40 mg l^{-1}	(cells ml^{-1}) chlorophyll *a*	PF	Bricelj and Malouf (1984)
	Pseudoiso (4 μm), chlorophytes (n.g.), cyanobacteria (n.g.)	5–10×10^{4} cells ml^{-1}	^{14}C and ^{51}Cr label	Gut-Ret	Bricelj et al. (1984)
Musculus niger	Phaeo (12–23 μm), silt ($\bar{x}$=9.6 μm)	10–30×10^{3} cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
Mya arenaria	Phaeo (12–23 μm), silt ($\bar{x}$=9.6 μm)	10–30×10^{3} cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
	3C (9–12 μm), 3H (3–4 μm), Exuv (8–15 μm)	10^{5} cells ml^{-1}	fluorescence (FCM)	PF	Shumway and Cucci (1987)

(continued on next page)

Table 2 (*continued*)

Bivalve species	Particle types (diameters[a]/length)	Particle concentration (units)	Measured parameter	Selection comments	Reference
Mytilus edulis	Phaeo (12–23 μm), silt ($\bar{x}$=9.6 μm)	10×10^3 cells ml^{-1}, 0–55 mg l^{-1}	chlorophyll *a*	PF	Kiørboe et al. (1980)
	Phaeo (12–23 μm), silt (n.g.)	20×10^3 cells ml^{-1}, 3–80 mg l^{-1}	chlorophyll *a*	PF	Prins et al. (1991)
	silica beads (5–37 μm)	51, 105, 171 mg l^{-1}	size and volume	PF	Defossez and Hawkins (1997)
	Pav (4.6 μm), Tetra (8.3 μm), Skel (9.0 μm)	7–15 mg l^{-1}	fluorescence (FCM)	PF	Bougrier et al. (1997)
	polystyr. beads[b] (10 μm), silica beads[b] (10 μm), alumina beads[b] (10 μm)	2×10^4 particles ml^{-1}	color/visual	PF	Ward and Targett (1989)
	clay[b] (4–8 μm), iron oxide[b] (4–8 μm), silica[b] (4–8 μm)	n.g.	radioactivity	Gut-Ret	Gagnon and Fisher (1997)
Mytilus trossulus	Rhodo (6–13 μm), *Spartina* detritus (3–20 μm)	10^3, 10^4, 10^5 particles ml^{-1}	fluorescence (FCM)	PF	Ward et al. (1998a)
Ostrea edulis	3C (9–12 μm), 3H (3–4 μm), Exuv (8–15 μm)	10^5 cells ml^{-1}	fluorescence (FCM)	PF	Shumway and Cucci (1987)
Pinctada imbricata	natural seston (2–30 μm)	3–13 mg l^{-1}	PN, POC	PF	Ward and MacDonald (1996)
Pinctada margaritefera	natural seston (1–30 μm)	n.g.	pigments /morphology	PF	Loret et al. (2000)
Placopecten magellanicus	3C (9–12 μm), Exuv (8–15 μm), Phaeo (12–23 μm)	10^4 cells ml^{-1}	fluorescence (FCM)	PF	Shumway et al. (1985)

	3C (9–12 μm), 3H (3–4 μm), Exuv (8–15 μm)	10^5 cells ml^{-1}	fluorescence (FCM)	PF	Shumway and Cucci (1987)
	Tetra (8–12 μm), bentonite (20–60 μm)	1, 0.5–10 mg l^{-1}	chlorophyll *a* POC, organics	PN, PF	Cranford and Gordon (1992)
	natural seston (2–60 μm), Chaet (4–6 μm), silt (2–20 μm)	2–15 mg l^{-1}	chlorophyll *a*	PF	MacDonald and Ward (1994)
Placopecten magellanicus	Exuv (12–19 μm), poly. beads (16–18 μm)	5×10^3, 5×10^3 cells ml^{-1}	^{14}C and ^{51}Cr label	Gut	Brillant and MacDonald (2002)
	Chlorella (killed, 5 μm)	2×10^4 cells ml^{-1}	^{14}C label	Gut-Ret	Brillant and MacDonald (2003)
Ruditapes philippinarum	SiO_2 spheres (5–37 μm)	51, 105, 171 mg l^{-1}	size and volume	PF	Defossez and Hawkins (1997)
Spisula subtruncata	Phaeo (12–23 μm), silt ($\bar{x}$=9.6 μm)	$10–30\times10^3$ cells ml^{-1}, 10–20 mg l^{-1}	chlorophyll *a*	PF	Kiørboe and Møhlenberg (1981)
Tapes decussatus	SiO_2 spheres (5–37 μm)	51, 105, 171 mg l^{-1}	size	PF	Defossez and Hawkins (1997)

PF—preingestive selection determined by comparing composition of particulate matter in the pseudofeces with that of the seston, site of selection (ctendium or labial palps) was not determined; CT—preingestive selection determined by comparing composition of particulate matter on the ctenidium with that of the seston, ctendium involved in particle selection; Gut—postingestive selection determined by comparing composition of material in the stomach, digestive diverticula and/or feces with that of the seston; Gut-Ret—postingestive selection determined by comparing gut-retention time of different types of particulate matter.

3C=*Chroomonas salina*, FCM=flow cytometric analysis, 3H=*Thalassiosira pseudonana*, PN=particulate nitrogen, Chaet=*Chaetoceros muelleri*, POC=particulate organic carbon, Exuv=*Prorocentrum minimum*, n.g.=not given, Micro=*Microcystis aeruginosa*, Pav=*Pavlova lutheri*, Phaeo=*Phaeodactylum tricornutum*, Pseudoiso=*Pseudoisochrysis paradoxa*, Skel=*Skeletonema costatum*, Tetra=*Tetraselmis suecica*.

[a] Equivalent spherical diameter or length; largest dimension given.

[b] Particles with and without an organic coating.

that *M. edulis*, *A. islandica* (ocean quahog), *Ensis directus* (razor clam) and *P. magellanicus* (sea scallop) preferentially rejected the diatom, *P. tricornutum* (2.5–3.5×12–23 μm) compared to the similar sized cryptomonad flagellate, *C. salina* (6–7.5×9–12.5 μm) and dinoflagellate, *P. minimum* (5–6×9–12×12.5–15 μm). Subsequent studies corroborated these results, indicating that several species of bivalves could select among different species of phytoplankton, some of which were similar in size (Shumway and Cucci, 1987). The cockle, *Cerastoderma edule*, and mussel, *M. edulis*, from an estuary in the Netherlands were shown to ingest particles containing chlorophyll *a* selectively from mixtures of phytoplankton and silt over a range of particle concentrations (Prins et al., 1991). Additionally, Bougrier et al. (1997) reported that *M. edulis* can selectively ingest the phytoflagellate, *Tetraselmis suecica* (8.3 μm), in preference to the diatom, *Skeletonema costatum* (9.0 μm), and the phytoflagellate, *Pavlova lutheri* (4.6 μm). These authors also reported that *C. virginica* could sort and differentially select among several phytoplankton species of similar size. Baker et al. (1998) demonstrated that the invasive zebra mussel, *D. polymorpha*, can select among cyanobacterium (*Microcystis* sp.), several diatom species, cattail detritus and clay particles. Diatoms were preferentially rejected by mussels in loosely consolidated pseudofeces that were easily resuspended, whereas *Microcystis* sp. was ingested. The authors suggest that particle selection by large populations of zebra mussels could have ecosystem level effects. In particular, the recent rise in dominance of diatoms in the Hudson River could be caused by the selective rejection of these phytoplankton in the pseudofeces that are resuspended and return to the water column for continued growth (also see Vanderploeg et al., 2001).

Studies focussing on the physiological ecology of bivalves demonstrate that selective ingestion of high-quality, organic material is an important component of feeding physiology and scope for growth of many species (Bayne et al., 1989; Cranford and Gordon, 1992; Iglesias et al., 1992, 1996; Navarro and Iglesias, 1993; Urrutia et al., 1996; Barillé et al., 1997; Hawkins et al., 1998; MacDonald et al., 1998; Ibarrola et al., 2000; Bayne, 2002). Food quality has usually been measured in terms of particulate organic matter or chlorophyll content. Compensation or benefit indices have been published which consider not only the change in quality of material rejected, but amount rejected and thus cumulative impact on the quality of material ingested. When delivered diets of phytoplankton and silica, *P. magellanicus* can improve the organic content of ingested matter by 10–20% at seston qualities of >50% organic matter and seston quantities between 3 and 14 mg l^{-1}. In contrast, *M. arenaria* improves the quality of material ingested by only 2–10% at the same seston qualities and quantities (Bacon et al., 1998). *P. magellanicus* can also significantly enhance the amount of chlorophyll-containing particles ingested by between 10 and 86% ($\bar{x}$=40%) when feeding on natural seston at 2–4 mg l^{-1} (MacDonald and Ward, 1994). In both studies, the proportional enhancement of material ingested decreased asymptotically with increasing clearance rates. When feeding on natural seston and resuspended bottom material (ca. 13 mg l^{-1}, C/N ratio of 25), the turkey wing, *Arca zebra*, can ingest 17% less carbon and 23% more nitrogen, enhancing the C/N ratio of ingested food by 31%. However, when feeding under the same conditions, the Atlantic pearl-oyster, *Pinctada imbricata*, rejects material to control ingestion, but demonstrates no significant selection for suspended particles (Ward and MacDonald, 1996). When feeding on seston concentrations between 3 and 21 mg l^{-1} and seston qualities between 5% and 40% organic matter, the cockle, *C. edule*, can enhance the quality of organic material ingested by 10–45% and chlorophyll-containing particles ingested by 20–65% (Iglesias et al., 1992; Urrutia et al., 2001). Taken together, these results not only support the concept of preingestive particle sorting in bivalves, but demonstrate interspecific differences in selection capabilities.

Many of the studies above also address important questions concerning the degree to which particle selection is affected by short-term variations in the quality and quantity of the seston. Particle-selection efficiency is mediated in some bivalves by seston quality (e.g., organic content). The efficiency with which the cockle, *C. edule*, selects and preferentially ingests organic matter (i.e., SE) increases with the organic quality of the seston to a maximum at about 40% organic content, and then decreases at higher qualities (Fig. 4; Iglesias et al., 1992, 1996; Navarro and Iglesias, 1993; Urrutia et al., 1996, 2001). *M. edulis* demonstrates a similar trend, with maximum SE (ca. 40%) occurring at seston qualities around 40% organics (Bayne et al., 1993; Hawkins et al., 1996). Organic SE in *P. magellanicus* also increases with increasing organic content of the seston (Bacon et al., 1998). Selection efficiency based on other qualitative factors of the seston, such as chlorophyll *a*, has been examined in a few studies. When organic content of the seston increases above 40%, *C. edule* demonstrates a decrease in SE for chlorophyll-containing particles that mirrors the decrease in SE for organic matter (Fig. 4; Urrutia et al., 1996, 2001; Iglesias et al., 1996). When organic content of the seston falls below 40%, SE for chlorophyll-containing particles either increases or decreases with decreasing organic content (Fig. 4). When feeding on diets supplemented with

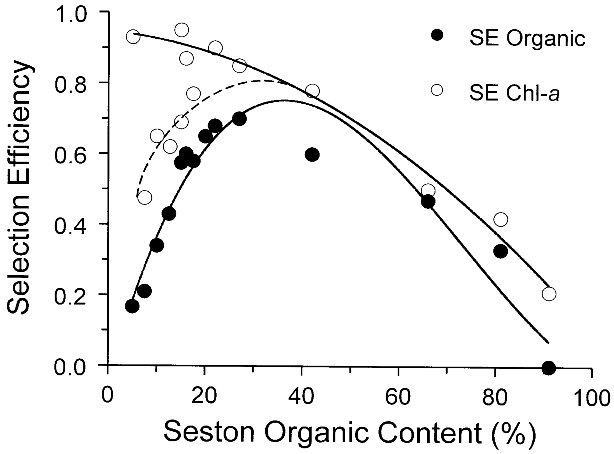

Fig. 4. Relationships between pre-ingestive selection efficiency (SE) and organic content of the seston (POM/TPM) obtained from published studies on the cockle, *C. edule*. Solid symbols (●) indicate SE for organic matter from studies that used prepared diets. Open symbols (○) indicate SE for chlorophyll-containing particles from studies that used natural seston (- - -) and prepared diets (—). Higher values indicate higher selection for chlorophyll-containing or organic particles. Data obtained from Urrutia et al. (1996, 2001).

cultured phytoplankton, *C. edule* demonstrates an increase in SE to a maximum of about 90% with decreasing seston organics (Iglesias et al., 1996; Urrutia et al., 2001). When feeding on natural seston, however, *C. edule* demonstrates a decrease in SE with decreasing seston organics (Urrutia et al., 1996), although under such conditions SE was variable. Similarly, MacDonald and Ward (1994) showed that SE of *P. magellanicus* for chlorophyll-containing particles decreased with decreasing seston quality, as measured by the chlorophyll content of the seston (0.3–6.9 μg chl-*a* mg seston^{-1}). Efficiencies at the low seston quality, however, were variable suggesting that intraspecific variation was high.

The decrease in SE of bivalves in response to increasing organic content of the seston (above ca. 40%) may be due to a limitation of the selection process. Particle selection is a process of rejection, which is not 100% efficient. As the proportion of non-organic particles in the seston decreases (i.e., high organic qualities), selectively rejecting the few poor-quality particles may be difficult. This effect, along with the observation that the amount of rejected material decreases with increasing organic content, results in a drop in SE. The decrease in organic SE in response to decreasing seston organics (below ca. 40%) may also reflect limitations of the selection process due to loss of heterogeneity of a mixed particle suspension (Iglesias et al., 1992; MacDonald and Ward, 1994). However, it may also be due to the proportionally higher contribution of pseudofecal mucus to the overall organics rejected. If pseudofecal mucus constitutes an approximate constant fraction of rejected matter, then it would represent an increasing proportion of the organic component of pseudofeces as organic quality of the seston decreases. In other words, when seston characteristics are such that bivalves are rejecting a large amount of filtered material of low organic content, pseudofecal mucus represents the main organic component of this rejected matter (Iglesias et al., 1992; Urrutia et al., 2001). Considering that proportionally more pseudofeces are produced when bivalves are exposed to low quality diets, the above situation would bias estimates of efficiency yielding lower SE with decreasing seston organic content (Iglesias et al., 1992, 1996; Bayne et al., 1993). Consequently, reduction in SE of organic matter observed at seston qualities of less than 40% organics may be an "artefact caused by the mucus content of the pseudofeces and not from a real loss of efficiency of preingestive sorting processes" (Urrutia et al., 2001, p. 185). Similar arguments could be made for SE that are based on particulate organic carbon and nitrogen. The release of organics in rejected mucus may also be why SE for a species based on chlorophyll tends to be higher than SE based on organics (Fig. 4; MacDonald and Ward, 1994; Iglesias et al., 1996; Urrutia et al., 1996, 2001; Bacon et al., 1998). Therefore, SE values based on organics, and perhaps nitrogen and carbon, should be considered net efficiencies. If the carbon, nitrogen and organic content of pseudofecal mucus is quantified, then gross SE could be calculated. Determination of SE based on chlorophyll eliminates problems associated with pseudofecal mucus discussed above. Interestingly, when cockles (*C. edule*) and scallops (*P. magellanicus*) feed on natural seston, SE for chlorophyll containing particles decreases and becomes highly variable with decreasing seston quality (MacDonald and Ward, 1994; Iglesias et al., 1996; Urrutia et al., 1996). These results suggests that SE may be limited when high quality particles are scarce.

Changes in selection efficiency in response to changes in seston quantity are more difficult to summarize. Many studies have demonstrated that the percentage of captured material which is rejected as pseudofeces increases with increasing seston concentration (e.g., Hildreth, 1980; Deslous-Paoli et al., 1992; Bayne et al., 1993; Stenton-Dozey and Brown, 1994; Urrutia et al., 1996; Hawkins et al., 1998), until a seston load at which feeding is inhibited (Barillé et al., 1997). The efficiency of selection is also affected by changing seston concentration. For example, several species of bivalves show a slight increase in SE for organic and chlorophyll-containing particles with increasing seston loads between 1 and 15 mg l^{-1} (Fig. 5A). At higher seston concentrations, trends are more difficult to discern (Fig. 5B). Urban and Kirchman (1992) reported that exposing *C. virginica* to 20 mg l^{-1} of kaolinite significantly decreases its ability to sort phytoplankton from rice starch. Natural seston loads higher than about 25 mg l^{-1} also cause a reduction in the efficiency with which *C. gigas* selects living phytoplankton from detritus (Pastoureaud et al., 1996). In contrast, similar increases in natural seston elicit an increase in SE for organic material (Hawkins et al., 1998; Fig. 5B). These results suggest that at higher seston loads, the dilution of high quality material with inorganic matter has a differential effect on the ability of *C. gigas* to discriminate and ingest chlorophyll-containing particles compared to organic particles. Interspecific differences in response to seston quantity are also apparent. *C. edule* demonstrates a decrease in organic SE with increasing natural seston concentration, whereas SE of *M. edulis* changes little above 20 mg l^{-1} (Hawkins et al., 1998). Although the exact concentrations that elicit changes in SE are likely species-specific, it appears that in some bivalve species the selection process can become saturated or overloaded when the pallial organs process and reject large amounts of particulate matter.

Some of the apparent conflicting data concerning selection efficiency and seston quantity is due to the different responses obtained when bivalves are fed laboratory prepared diets, consisting of cultured phytoplankton, compared to when they are delivered natural suspensions of material (see Hawkins et al., 1996). In addition, seston quantity per se is probably not the mediating factor. Rather it is filtration rate, or product of seston quantity and clearance rate (volume of water cleared of particles time^{-1}) that probably affects SE. On a functional basis, filtration rate should be the mediating factor, because the concentration of seston to which a bivalve is exposed is less important than the quantity of material actually captured and processed by the pallial organs. This hypothesis was tested by Hawkins et al. (1996, 1998), with three species of bivalves (*C. edule*, *C. gigas*, *M. edulis*) from the bay of Marennes-Oléron (France). These researchers demonstrated that when exposed to different concentrations of natural seston, SE for organic particles significantly increased (*C. gigas*, *M. edulis*) or remained constant (*C. edule*) with increasing filtration rate (Fig. 6). Although some constraints to particle processing exist (Milke and Ward, 2003; Ward et al., 2003), the above results demonstrate the capacity of some bivalves for selection at high rates of particle feeding. The exact relationship between filtration rate and SE, however, is likely to exhibit interspecific differences (cf. MacDonald and Ward, 1994), as well as intraspecific variations due to adaptations to environmental conditions (e.g., Essink et al., 1989).

Although results from numerous studies support the perspective that bivalves can sort and ingest certain types of particles preferentially over others, little is known about the

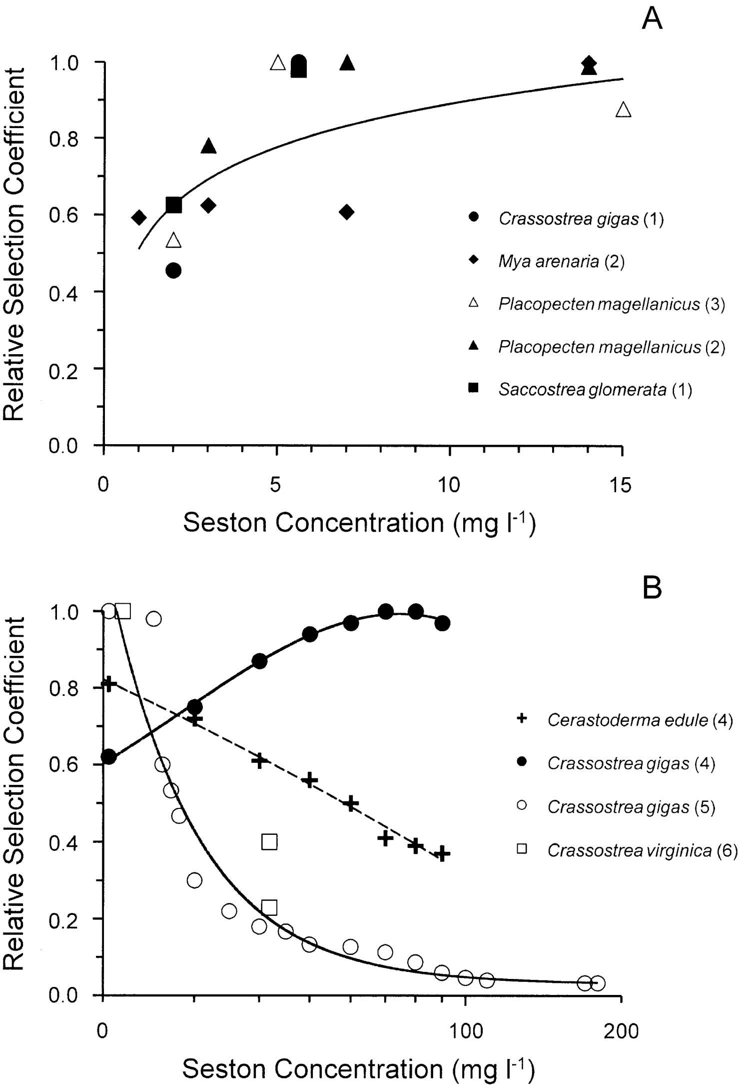

Fig. 5. Relationship between pre-ingestive selection efficiency (SE) and seston concentration obtained from published studies on bivalves. For comparison among studies, a relative selection coefficient was calculated by standardizing all SE values for a given species, under a given set of experimental conditions to the highest efficiency obtained for that study. Solid symbols indicate SE for organic matter, whereas open symbols indicate SE for chlorophyll-containing particles. Higher values indicate higher selection for chlorophyll-containing or organic particles. (A) Changes in SE in response to seston concentration less than 15 mg l^{-1}; (B) changes in SE in response to seston concentration greater than 20 mg l^{-1}. Notice that, for *C. gigas*, there are clear differences in how SE for organic matter and SE for chlorophyll-containing particles change with seston load. Data obtained from: (1) Bayne (2002), (2) Bacon et al. (1998), (3) MacDonald and Ward (1994), (4) Hawkins et al. (1998), (5) Pastoureaud et al. (1996), (6) Urban and Kirchman (1992).

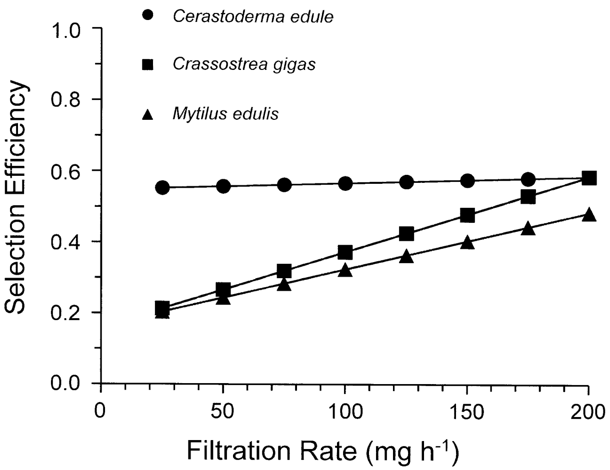

Fig. 6. Relationship between pre-ingestive selection efficiency (SE) and filtration rate (FR) for three species of bivalves exposed to natural seston. Data obtained from regression equations given by Hawkins et al. (1998).

mechanisms of particle sorting and the contribution of the main feeding organs (ctenidium, labial palp) to the selection process. As mentioned above, early objections to the contention that bivalves could select particles were based on observations that material was transported along the pallial organs embedded in mucous masses and strings. Such transport seemed incongruous with selection of individual particles. But these early studies were largely conducted on surgically altered specimens or isolated structures. In the early 1990s, Ward et al. (1991) developed the technique of video endoscopy to examine particle processing on the pallial organs of living, intact bivalves. Results from these studies shed light on some of the major conceptual hurdles concerning particle transport and selection by the pallial organs. Findings revealed this in some species particles are transported along the dorsal ciliated tracts of the ctenidium suspended in a mucus–water slurry (e.g., scallops), not in mucous strings. In other species, captured particles are transported predominately in the ventral ciliated tract incorporated in a cohesive mucous string (e.g., mussels); and in others, particles are transported in both ventral strings and dorsal slurries (e.g., oysters; Fig. 3). Particles delivered to the labial palps via dorsal tracts can be handled individually, because the mode of transport is a slurry. Particles delivered to the palps in a mucous string (via ventral tracts) can still be handled individually, because the action of opposing palp lamellae reduces the cohesiveness of mucus, allowing embedded particles to be dispersed (Ward et al., 1993, 1994b; Beninger and St-Jean, 1997a; Beninger et al., 1997). The observed mechanical fluidization of mucus by the palps supports the hypothesis of Newell and Jordan (1983), and explains how selection of individual particles is possible. Finally, after being processed by the labial palps, particles are ingested in a mucous slurry, not in a continuous mucous string as was traditionally thought (see Ward et al., 1994b).

The mechanisms of particle processing in bivalves were further explained by the studies of Beninger and co-workers who linked observations of function with histological data. By mapping the number and types of mucocytes on the pallial organs, these workers provided links among the biochemical properties, cohesive characteristics, and functional role of mucus in the feeding process (Beninger and Dufour, 1996; Beninger and St-Jean, 1997a; Beninger et al., 1993, 1997). In summary, cohesive acid or acid-dominant mucopolysaccharides (MPS) are used when particle transport occurs on surfaces exposed directly to inhalant flow (e.g., in the ventral groove, on the frontal surfaces of the ordinary filaments), or on surfaces leading to areas exposed directly to flow. Mixed MPS of lower cohesiveness are used when particle transport is on an enclosed or semi-enclosed surface (e.g., in the dorsal tracts, on the principal filaments). Neutral MPS are found in regions where reduction of mucous cohesion is important, such as ridged areas of the labial palps (Beninger and St-Jean, 1997a,b). The above studies demonstrate the interrelationship between different modes of particle transport and types of mucus secreted to make such transport possible. These studies also suggest that fluidization of mucus-particle strings and masses by opposing palp lamellae may have a biochemical component, as highly cohesive mucus (e.g., acid dominant MPS) is diluted by less cohesive mucus (e.g., neutral MPS; Beninger and St-Jean, 1997b); a process that is a necessary prerequisite to particle selection.

Preingestive selection is based on the premise that the pallial organs (ctenidium, labial palp) are responsible for particle sorting. The degree to which each pallial organ is involved in the selection process, however, has been debated for many years (Nelson, 1923, 1960; Yonge, 1926; Atkins, 1937b; Menzel, 1955; Newell and Jordan, 1983). Early morphological work demonstrated that the ctenidial filaments of some species bear two tracts of frontal cilia that beat in opposite directions. Other species possess heterorhabdic ctenidia with ciliated principal and ordinary filaments that transport particles in opposite directions. Sorting of particles based on size and other criteria was inferred from differential movement of material, either ventrally or dorsally, that was placed on different ciliated tracts (Allen, 1921; Atkins, 1937a,b,c; Nelson, 1960; Ribelin and Collier, 1977; Barillé, 1994). Manipulative studies with juvenile oysters with transparent shells, surgically altered adults, or isolated ctenidia, however, produced conflicting results concerning particle selection by the ctenidium (cf. Allen, 1921; Nelson, 1923; Menzel, 1955; Bernard, 1974), and conclusive data regarding the locus of particle selection were lacking. Ward et al. (1997, 1998a) combined video endoscopy and flow cytometry to study the site of particle selection in two species of bivalves. Using the endoscope to direct a micropipette within the pallial cavity of living specimens, these workers sampled the dorsal and ventral ctenidial tracts of *C. virginica*, *C. gigas* and *Mytilus trossulus* delivered a mixture of phytoplankton and similar sized detrital particles. They found that the ctenidium of oysters could select between two particle types, transporting proportionally more phytoplankton to the dorsal tracts and more detritus to the ventral grooves. No such selection was found on the ctenidium of *M. trossulus*, but pseudofeces from mussels contained proportionally more detritus indicating that selection by the labial palps occurred. Another possible means of selection on the ctenidium is to control entry of particles into the ventral ciliated groove. Particles that enter the groove proper are transported to the labial palps for further processing, whereas particles that remain on the marginal tracts bordering the groove are removed by mantle rejection tracts or distal extremities of the palp. This two-layer transport at the ventral margin has been described for several bivalve species (e.g., *Pinna fragilis*, Atkins, 1937b; *D. polymorpha*, Baker et al., 2000), but the composition of material in the groove and on the margin has not been analyzed for qualitative differences. Therefore, we cannot yet determine if such transport is a mechanism to control the quantity or quality of material delivered to the labial palps.

Although particle selection by the ctenidia of two oyster species has been demonstrated, histological studies and observations of surgically altered specimens suggest that the labial palps are important organs of particle selection in most bivalve species (Kellogg, 1915; Menzel, 1955; Nelson, 1960; Galtsoff, 1964; Jørgensen, 1966; Morton, 1969), including those species that utilize the ctenidium for particle selection (Ward et al., 1994b, 1998a). The role of the labial palps in particle sorting can also be inferred from studies which show that relative palp size, within and among species, is positively correlated with SE (Kiørboe and Møhlenberg, 1981), and is related to turbidity of the environment (Ansell, 1961; Nelson, 1960; Theisen, 1982; Essink et al., 1989). Kiørboe et al. (1980), for example, found that *M. edulis* from the Wadden Sea have relatively larger palps and higher SE than those from the Øresund Sound, and suggested that this was an adaptation to high particulate loads in the Wadden Sea. Oysters, *C. gigas*, from high-turbidity regions of the Atlantic coast of France have 66% greater palp area than those from low-turbidity regions (Barillé et al., 2000). Kiørboe and Møhlenberg (1981), however, did not find a clear relationship between palp size and sediment loads of a species' habitat. Nevertheless, the above studies suggest that larger palps are associated with more efficient processing of particulate matter and are indeed a major site of particle selection. Numerous questions concerning the responses of bivalves to high turbidity, in terms of changes in palp size and function, remain and are interesting topics for future research.

4.2. Deposit-feeding bivalves

As with preferential uptake of particles, post-capture selection by deposit-feeding bivalves has been studied less than selection by suspension-feeding species. This is due, in part, to the broad size spectrum and complexity of particulate matter available to deposit feeders, and the difficulty in examining selection based on presumed food particles. Most studies, therefore, have focused on size-specific particle selection because of the assumption that more food is associated with smaller particles with higher surface area particles. For example, based on differential movement of particles on the feeding structures of dissected specimens or isolate organs, Stasek (1965) and Davenport (1988) reported size-dependent selection among particles by the palp proboscides, ctenidium, and labial palps of several *Yolida* species (protobranchs). In vivo studies with an endoscope have shown that extensive processing and re-processing of deposited material occurs on the labial palps of *Y. limatula* (Levinton et al., 1996), which often reject up to 95% of material collected by the palp proboscides (Bender and Davis, 1984). One of the few studies to examine quantitatively particle selection by protobranchs was conducted by Lopez and Cheng (1983). In laboratory studies, these researchers fed natural, radiolabeled sediments (^{51}Cr and ^{14}C) and associated bacteria (^{14}C) to the nutclam, *Nucula annulata*

(=*proxima*). They found that *N. annulata* ingested organic and bacterial fractions selectively from sediments, and that selectivity was independent of ingestion rate. Taken together, the above studies suggest that preingestive particle processing in protobranchs greatly reduces the quantity and increases the quality of material that is ingested. Given the potential importance of some protobranchs to the ecology of the benthos (Rhoads, 1963; Bender and Davis, 1984), more studies are needed to understand how these deposit-feeding bivalves process a wide range of particulate matter, and the degree to which they conform to models established for other tentaculate deposit feeders (see Jumars, 1993).

The ability of some deposit-feeding lamellibranchs to deal with large quantities of material on the ctenidia and transport this material to the labial palps is well known (e.g., tellinaceans; Yonge, 1949; Levinton et al., 1996). In some species, pseudofeces production can exceed fecal production by 30–300 times (Hughes, 1969; Hylleberg and Gallucci, 1975). Qualitative examinations of pseudofeces and stomach content of tellinaceans collected in the field suggest that these bivalves can preferentially ingest certain particle types (Hughes, 1969; Reid and Reid, 1969). Evidence from laboratory studies show that *Macoma nasuta* can select among particles based on size, and preferentially ingest protein- and pigment-containing particles <80 μm in diameter (Hylleberg and Gallucci, 1975). In sediment with a range of particle diameters (15–330 μm), both *Abra alba* and *A. nitida* selectively ingest finer particles compared to coarser particles (Hughes, 1975). Species such as *Macoma secta*, however, regularly ingest sand grains as large as 300 μm in diameter (Kellogg, 1915; Reid and Reid, 1969). Hughes (1973, 1975) compared the frequency of silica particles (0.5–300 μm) in experimental sediments with that in the stomach of *A. tenuis* and found no evidence of size selection by the pallial organs. Larger silica particles (50–200 μm) without microbial colonies, however, were partially rejected compared to natural particles that were colonized by microbes (Hughes, 1975). The author suggested that *A. tenuis* is able to detect the microbial content of particulate matter.

Taghon (1982) pointed out some of the methodological problems inherent in studying particle selection in deposit feeders, and designed a series of field experiments that controlled the physical and chemical characteristics of particles. He used glass microbeads of known size and density as tracers to examine particle feeding in 10 species of deposit feeders, including the deposit-feeding bivalve *Macoma balthica*. Taghon (1982) compared the proportion of different size microbeads delivered to the sediment with the proportion of beads in the stomach of each species after feeding. He showed that *M. balthica* ingests smaller microbeads (13–20 μm) in preference to larger ones (20–44 μm), and ingests protein-coated microbeads (44–53 μm) in preference to uncoated beads irrespective of their density. Strongest selection occurred for the protein coated beads, suggesting that adhesion between organic coatings and mucus on the feeding structures is an important mechanism by which some deposit feeders select organic from inorganic particles (see also Jumars, 1993).

5. Postingestive particle processing

The final opportunity for particle selection in bivalves is postingestive sorting in the stomach (Fig. 3). As with other particle-selection processes, early work on the functioning of the stomach focused on comparative anatomy and observations of particle movement in isolated or dissected organs (Yonge, 1923, 1926, 1939, 1949; Graham, 1949; Owen, 1955, 1956; Reid, 1965). As so elegantly established by these workers, the action of the rotating crystalline style (or protostyle) and teeth of the gastric shield triturate material entering from the esophagus, breaking apart large particles and particle aggregates. Enzymes liberated from the dissolving head of the style, mix with this particle slurry which is then subjected to ridged sorting areas of the stomach and stomach pouches. Lighter organic particles and particle fragments enter the ducts of the digestive diverticula, whereas more dense material passes into the intestinal groove and transported to the mid-gut where it mixes with other undigested material and is incorporated into fecal pellets. The demonstration that the digestive diverticula were sites of intracellular digestion led to the hypothesis that the stomach functioned in particle selection, directing the most nutritious particles and particle fragments into the diverticula for more complete intracellular digestion. Many researchers soon embraced the idea that selective processes in the stomach, along with changes in gut passage time, could alter absorption efficiency of ingested material, allowing bivalves to optimize further food energy obtained from the environment. Few studies, however, addressed potential selective processes in the stomach of living bivalves, and many questions remained regarding the ability of bivalves to postingestively select particles based on physical or qualitative factors.

One approach to studying postingestive processes is to feed bivalves different types of particles and then determine the time period over which these are egested to calculate a gut-retention time (GRT). The hypothesis underlying these studies is that higher quality material should be retained in the gut for a longer period of time than poorer quality material. A long GRT indicates that material is subjected to extensive extracellular digestion and, perhaps, transported to the digestive diverticula for more complete intracellular digestion. A short GRT indicates that material is subjected to little extracellular digestion and transported to the intestine for rapid egestion. This approach was applied by Bricelj et al. (1984), who used a dual tracer technique to label the cell contents (^{14}C) and cell wall (^{51}Cr) of several species of phytoplankton which were then fed to the quahog, *M. mercenaria*. When quahogs were fed the phytoplankton *Pseudoisochrysis paradoxa*, ^{14}C was retained significantly longer in the gut than ^{51}Cr. These results suggested that extracellular digestion in the stomach ruptured the phytoplankton, allowing cell contents to be transported to the digestive diverticula and cell walls to be transported to the intestine for more rapid egestion. In another set of experiments, Bricelj et al. (1984) found that, for certain chlorophytes and cyanobacteria, egestion rates of ^{14}C and ^{51}Cr were the same, and GRT of ^{14}C significantly lower than that for *P. paradoxa*. The authors suggested that inefficiently absorbed phytoplankton species (i.e., chlorophytes, cyanobacteria) were egested more rapidly than phytoplankton that were absorbed more efficiently (i.e., *P. paradoxa*). Similarly, suspended sediments with an organic coating have a longer GRT in *M. edulis* compared to sediments without a coating (Gagnon and Fisher, 1997). The bivalves *Potamocorbula amurensis* and *Macoma balthica*, however, retain 15-µm latex beads in their gut for approximately the same amount of time as smaller marine bacteria (Decho and Luoma, 1991). Although the above results suggest that postingestive selection of particles can occur, the different types of particles used in these studies were fed to bivalves sequentially, not simultaneously. Therefore, the animals were not presented with a choice and did not actually discriminate among particles.

More convincing evidence of postingestive discrimination among particles comes from studies in which different particles were delivered simultaneously. For example, when the oysters, *C. virginica* and *Ostrea equestris*, are fed a mixture of phytoplankton and carmine particles, they pass carmine out of the stomach faster than the plankton (Menzel, 1955). Foster-Smith (1975a) reported that, when three bivalve species (*M. edulis*, *C. edule*, *Venerupis pullastra*) were fed a mixture of *P. tricornutum* (29 μm diameter) and alumina particles (7.5–31.5 μm diameter), bivalves egested a predominance of alumina after 1 h, but after a further hour a greater proportion of *P. tricornutum* was egested. Hughes (1977) showed that, in the tellinacean, *A. tenuis*, little sorting of sediments occurred in the stomach, but some particle selection occurred in the combined caecum and ducts leading to the digestive diverticula.

Additional support for postingestive selection comes from studies that delivered bivalves a mixture of particles, but controlled for differences in size. Shumway et al. (1985) studied feeding activities of several species of bivalves exposed to a mixed suspension of three species of phytoplankton, *P. tricornutum* (clone Phaeo), *P. minimum* (clone Exuv) and *C. salina* (clone 3C). Analysis of fecal samples with flow cytometry demonstrated that differential absorption in the gut occurred. The bivalves *A. islandica*, *O. edulis* and *P. magellanicus* preferentially ingested the phytoplankton *P. minimum* and *C. salina*, but only *C. salina* was efficiently digested, as a significantly higher proportion of whole *P. minimum* cells were egested in the feces. *C. virginica* ingested all three phytoplankton species in about the same proportions, but egested significantly more whole *P. tricornutum* and *P. minimum* in the feces. Similar results were reported for the mussel, *M. edulis* (Cucci et al., 1985). Although *C. salina* is probably easier to digest because of its cell-wall structure, the poorly digested cells were egested within 4 h after cessation of feeding, suggesting that some degree of postingestive selection occurred in the stomach (also see Shumway and Cucci, 1987). Additionally, because all three species of microalgae were of similar size, selection may have been based on qualitative factors. Cognie et al. (2001) fed four species of pennate, benthic diatoms to the oyster, *C. gigas*, and collected feces within 2 h after feeding commenced. They found that oysters egested a significantly higher proportion of two intermediate size diatoms (35–45 μm length) compared to the smallest (22 μm length) and largest (60 μm length) diatom. The two diatom species that were retained in the gut also were preferentially ingested compared to the other species (see Section 4.1 above). These results suggest that factors other than size, such as extracellular digestibility or qualitative sorting, affect postingestive particle processes.

The most comprehensive study of postingestive selection was carried out by Brillant and MacDonald (2000, 2002, 2003) using the sea scallop, *P. magellanicus*. In their first study, Brillant and MacDonald (2000) showed that GRT for 20-μm polystyrene beads was significantly longer than for 5-μm beads, and GRT of polystyrene beads (1.05 g ml^{-1}, 9 μm) was significantly longer than for similar size glass beads of a higher density (2.5 g ml^{-1}, 8 μm). Histological observations of the tubules of the digestive diverticula indicated that beads were not phagocytized by digestive cells, suggesting that differential treatment of beads was caused by increased retention of larger and lighter particles in the stomach. Polystyrene particles could not be fragmented extracellularly, so the 20-μm beads remained in the stomach longer than the smaller beads because they probably were too large to enter rejection grooves efficiently. This idea was supported by results from their experiments with beads of different densities. Nonetheless, differential treatment of particles in the gut based on particle size and particle density was shown.

In a related study, Brillant and MacDonald (2002) used two different experiments to further examine postingestive selection in the gut of scallops. In the first experiments they labeled the dinoflagellate, *P. minimum*, with ^{14}C, and similar size polystyrene beads (dvb; 16–18 μm) with ^{51}Cr. Scallops were fed labeled cells and beads for 1 h, and radioactivity quantified in the stomach, digestive gland, and feces over an additional 5-h period. Results indicated that a higher proportion of dinoflagellate material was transported to the digestive gland, whereas a higher proportion of beads were rejected to the intestine (fecal samples). In the second set of experiments, the workers tested the effects of protein-coated (covalently bonded), flourescent, polystyrene beads (yellow; 5.5 μm) on GRT. These beads were mixed with non-coated, flourescent beads (pink; 5.7 μm) and fed to scallops for 1hr, after which time feces were collected for a 144-h period to calculate GRT. Their results indicated a slight, but significant increase in GRT of protein-coated beads compared to uncoated beads. The authors concluded that scallops have the capability of sorting organic from inorganic particles in the gut, and discriminating among physically identical particles solely on the basis of their surface chemistry.

Brillant and MacDonald (2003) continued studying postingestive processes in scallops by examining discrimination between living and heat-killed phytoplankton. Cultures of the green alga *Chlorella* sp. were labeled with ^{14}C and used in feeding experiments, or heat-killed and then used. Heat treatment significantly reduced the chlorophyll *a*, carbon and nitrogen content of the cells, but did not alter their size or integrity. Scallops were fed equal concentrations of live and heat-killed *Chlorella* sp. cells for 2 h, after which time feces were collected for a 144-h period to calculate GRT. Their data indicated that live *Chlorella* sp. was retained significantly longer than heat-killed *Chlorella* sp. (ca. 11 and 8 h, respectively). This was the first demonstration that a bivalve could postingestively select among cells that were morphologically identical, but that differed in their chemical composition. Taken together, the works of Brillant and MacDonald (2000, 2002, 2003) support the contention that some bivalves can discriminate among particles in the gut based on size, density and chemical properties. Whether the results of Brillant and MacDonald (2000, 2002, 2003) can be generally applied to other bivalve species, especially those with different feeding modes, is an interesting area for future research.

6. The mechanistic bases of particle selection

Although it is now generally accepted that the pallial organs and stomach of many bivalve molluscs can select among different types of particulate matter (Table 2), the criteria that they use to differentiate among particles remain undefined. In general, the basis of selection in particle feeders can be described as being either passive or active.

Passive or mechanical selection can be thought of as autonomous processes operating on the feeding organs as a consequence of their structures and morphology. Selection of small particles over large and spherical particles over angular, regardless of qualitative differences, would be an example of passive selection. Interactions between the surfaces of particles and feeding organs, such as adhesion of stickier particles, is also a form of passive selection. In contrast, active or behavioral selection is initiated by subtle changes in the shape or movement of feeding organs (e.g., muscular contractions), or changes in the activity of cilia or cirri covering these organs. Such changes are stimulated by qualitative aspects of particles (e.g., epicellular metabolites), and presence or absence of such cues allows the animal to redirect particles to acceptance or rejection tracts. That is, decisions are made concerning the acceptability of different particles as they are transported by feeding structures. Although a rich literature base exists concerning mechanisms of diet selection and their influence on optimal foraging and ingestion in several benthic phyla (Jumars, 1993; Jumars et al., 1982; Taghon, 1982; Taghon and Jumars, 1984; Shimeta, 1996), much less is known about the bases of selection in particle-feeding bivalves.

For planktonic suspension feeders, there is evidence for discrimination based on both physical properties and chemical signatures of food particles (see Targett and Ward, 1991 for review). Although it is instructive to examine mechanistic corollaries between pelagic and benthic organisms, the spatial and temporal scale at which benthic particle feeders interact with particulate matter is very different from that of their planktonic counterparts. Unlike planktonic suspension feeders that handle tens of particles per minute (e.g., Wilson, 1980), benthic particle feeders can capture and process hundreds to thousands of particles per second (e.g., Winter, 1978; Foster-Smith, 1975b). Therefore, the factors that influence particle selection in bivalves are most likely different from those of planktonic animals (e.g., Sierszen and Frost, 1992). So what are the mechanisms upon which bivalves rely to discriminate among particles? The work outlined below suggest that both passive and active selection may be operating.

Early studies on the basis of selection suggested that density was a controlling factor in particle selection by the pallial organs of bivalves (Yonge, 1923). Later studies, however, indicated that bivalves could preingestively select particles in any orientation, and rejecta of the palps often moved in an upwards direction (Bernard, 1974; Newell and Jordan, 1983). In addition, Ward and Targett (1989) reported that *M. edulis* ingested 10-μm polystyrene beads in the same proportion as more dense silica beads of the same size. Although sedimentation of large dense particles (specific gravity of 2.6, >14 μm diameter) might occur in the mantle cavity prior to encountering the ctenidia (Bernard, 1974), particle density probably plays a minor role in preingestive particle selection, especially in suspension-feeding species. Brillant and MacDonald (2000), however, reported that the scallop, *P. magellanicus*, retained less dense, polystyrene beads (1.05 g ml^{-1}, 9 μm) in the gut for a significantly longer time than similar sized glass beads of a higher density (2.5 g ml^{-1}, 8 μm). The different effects of density on pre- and postingestive selection could be due to the mechanisms by which particles are processed. Preingestive processing of particles occurs predominately on the surfaces of feeding organs, whereas postingestive processing involves the mixing of a particle slurry in the lumen of the stomach (Reid, 1965; Purchon, 1987; Ward et al., 1994b). Suspended material is circulated by the action of the rotating crystalline style and cilia on the stomach wall. This ‘‘off surface’’ processing might be affected more by density, as heavier particles settle more readily into rejection grooves of the stomach. Such a mechanism may be an adaptation to rid the stomach of small, dense particles that are ingested (e.g., silt).

Studies have also examined how particle size affects selection. In a paper on theoretical considerations of particle selection in bivalves, Defossez and Daguzan (1996) suggest that, even when no selection for organic material occurs, an apparent selection can be measured because of geometric relations between particle size and either weight or volume. They argue that if bivalves are delivered a wide size range of inorganic particles (e.g., 5–45 μm diameter) and a narrow range of organic particles (ca. 15 μm), a 50% rejection of all particle sizes will yield pseudofeces with a higher inorganic content. Their example and calculations, however, are difficult to interpret (their Fig. 1). Using the diameter and mass ranges given in their paper, the initial diet of 20 organic particles and 70 inorganic particles yields an organic content of ca. 13% by weight. A 50% rejection of all particle sizes (inorganic and organic) yields a pseudofeces organic content of about 13%. Obviously this outcome is not biased toward inorganic particles. Nonetheless, if larger and heavier inorganic particles are rejected preferentially by the bivalve, then a decrease in pseudofeces organics (by weight) would occur without the preferential ingestion of organic matter. Therefore, the authors’ recommendation that particle size distributions of pseudofeces and food be carefully checked is valid. In a related paper, Defossez and Hawkins (1997) demonstrated size-dependent rejection of large inorganic particles by the bivalves *M. edulis*, *Ruditapes philippinarum* and *Tapes decussatus*. At all inorganic particle concentrations tested, there was a significant increase in relative abundance of larger particles in pseudofeces compared with that in the food suspension. The authors suggest that size-dependent rejection of larger particles could be an adaptive strategy in environments where smaller organic particles are abundant.

Size is probably one of the criteria used by bivalves to discriminate among particles; but simply selecting for smaller sized particles may not be advantageous under all conditions. For deposit-feeding bivalves there would be an advantage to discriminating among particles according to size, because in sediments food value is inversely related to particle size, at least down to that which approaches the cell size of bacteria (see Jumars, 1993). Foraging theory, therefore, predicts that deposit feeders should be adapted for feeding on small particles (Taghon et al., 1978). For suspension-feeding bivalves, the advantage of selecting for smaller particles is less clear, because food value often scales with volume (larger phytoplankton cells have higher digestible components). Foraging theory predicts that suspension feeders should be adapted for feeding on particles larger than the most abundant size (e.g., Lehman, 1976). Results from studies with particle-feeding marine annelids support this perspective (e.g., Levinton et al., 1984; Shimeta, 1996). Data for bivalves are scarce, but a few studies suggest that selection is not simply biased toward the smallest particles. Zebra mussels, *D. polymorpha*, positively select for particles with diameters between 15 and 45 μm in the pallial cavity and stomach, rejecting particles smaller and larger than this size range (Ten Winkel and Davids, 1982). Similarly, when fed four species of pennate diatoms, the oyster, *C. gigas*, ingests the smallest (22 μm length) and largest (60 μm length) diatom preferentially compared to two other intermediate size diatoms (35–45 μm length; Cognie et al., 2001).

Some studies suggest that bivalves also use chemical criteria to distinguish particles (e.g., Loosanoff, 1949; Kiørboe and Møhlenberg, 1981; Ten Winkel and Davids, 1982). Often, however, it is difficult to determine if selection based on chemical constituents is actually occurring, because researchers fail to factor out selection based on differences in size, shape and surface characteristics among the various particles. But a few studies strongly suggest that some bivalve species discriminate among particles based on epicellular or intracellular metabolites. These include studies that have demonstrated selection by examining qualitative factors (e.g., fluorescence, chlorophyll *a*, nitrogen, carbon) and have compared the size distribution of particles retained or ingested with those in the pseudofeces (e.g., Newell and Jordan, 1983; MacDonald and Ward, 1994; Ward et al., 1998a; Levinton et al., 2002). Studies reporting discrimination among different phytoplankton species of similar size, delivered at similar concentrations (e.g., Shumway et al., 1985), also support the idea that selection can be based on factors other than particle size. Although the aforementioned studies removed particle size as a potential factor in the selection process, differences in shape and surface properties still existed which could have affected particle sorting.

To control for a range of physical characteristics, Ward and Targett (1989) adsorbed metabolites from six species of microalgae onto lipophilic and hydrophilic microspheres (10 μm), and delivered them to *M. edulis*. Mussels either rejected or preferentially ingested metabolite-treated spheres depending upon the type of spheres tested and species of phytoplankton used to treat them. By using uniform microbeads, these researchers removed particle size and shape as a factor in the selection process. Their study was the first to provide evidence that *M. edulis* could ingest or reject particles preferentially based solely upon epiparticulate chemical compounds produced by phytoplankton. Although selection based on chemical properties of particles was determined, the above study sheds little light on the question of passive versus active selection. The possibility exists that surface properties of the particles (e.g., electrostatic charge, wettability, stickiness) affected their interactions with the feeding structures resulting in positive or negative selection without behavioral mediation. The electrostatic charge of particles has been shown to affect capture efficiency in bivalve larvae (Gallager et al., 1988; Solow and Gallager, 1990), and in adult mussels (*M. edulis*, Hernroth et al., 2000). In addition, sugar-containing compounds on the surfaces of phytoplankton cells (Waite et al., 1995) and organic coatings of particles can affect adhesive interactions with mucus-covered feeding organs (Taghon, 1982). Such mechanical selection is emerging as a major mechanism that enables some deposit feeders to select organic over inorganic particles (Jumars, 1993). Interestingly, in a related preliminary study, Ward et al. (1994a) found no effect of density, electrostatic charge, or wettability of the microbeads used by Ward and Targett (1989) on particle selection in two species of bivalves.

One piece of indirect evidence that would support arguments for active selection would be the identification of sensory cells on the feeding organs. The existence of putative sensory cells on the smooth surfaces of the labial palps of *C. virginica* has been reported (Dwivedy, 1973), but the methodology and results of this study have been criticised (Beninger, 1991; Beninger et al., 1990). Although other researchers have attempted to identify chemosensory cells on the feeding organs of bivalves, no conclusive evidence for such structures has been published (Beninger, 1991; Beninger et al., 1990). More research and data concerning active versus passive selection in bivalves is needed before general rules for the bases of particle discrimination can be developed.

Several conclusions can be drawn from the reports summarized above. First, experimentally distinguishing between passive and active particle selection is often difficult because qualitative differences, which could stimulate an active response, often are concomitantly associated with differences in surface properties, which could produce passive selection. Second, many particle-feeding bivalves may rely on both passive and active selection depending upon specific particle regimes and environmental conditions to which they are exposed. Finally, with respect to optimal energy acquisition by the bivalve, it may not matter whether selection is behaviorally mediated or based on passive mechanisms. Passive selection of particles can yield positive results in terms of increased uptake of organics and energy (Jumars, 1993). However, determining the bases of selection is important in understanding the impacts of particle feeding at an ecosystem level, especially considering that under some conditions non-nutritious or toxic particles are ingested (Shumway and Cucci, 1987; Strychar and MacDonald, 1999). Therefore, in order to predict the types of particles that bivalves are likely to ingest and those they are likely to reject back to the water column and benthos, the mechanisms of selection need to be better defined.

7. Conclusions and future directions

A diet of relatively dilute, heterogenous particles presents challenges that have been overcome by numerous adaptations in members of the Bivalvia (Morton, 1960). One of the many problems is the fact that such diets usually contain a high proportion of non-nutritive material. Because bivalves rely almost entirely on ciliary transport to conduct material along feeding organs and through the gut, as opposed to muscular contractions, non-selective ingestion of large volumes of dense particles would be difficult to process. Consequently, few bivalves simply encounter and engulf particulate matter. Rather there is a large body of evidence which suggests that particles can be rapidly sorted based on physical and chemical factors, with material of higher quality being ingested and digested preferentially over that of lower quality (Table 2). This capability for selection is probably unsurpassed by any other particle-feeding group. As with the development of different modes of digestion (Morton, 1960; Owen, 1974; Reid and Reid, 1969), different types of diets are likely to have given rise to different capacities for particle selection among the various species of deposit- and suspension-feeding bivalves (e.g., Boltovskoy et al., 1995). Why do particle-feeding bivalves demonstrate such a capacity for particle selection? Comparison of the function and morphology of the gut of particle-feeding molluscs may shed some light on this intriguing question.

The molluscan gut is a highly plastic organ of digestion, with differences and similarities having more functional rather than phylogenetic basis (Morton, 1960). The entire gut is well supplied with ciliated epithelial cells, and material is moved through the gut, primarily, by means of muco-ciliary transport (e.g., Yonge, 1923). As mentioned above, suspension-feeding lamellibranchs possess complex guts with a crystalline style, well-developed sorting regions, several typhlosoles, a large digestive diverticula and, often, one or two food-sorting caeca. The guts of deposit-feeding lamellibranchs (e.g., tellinaceans) are similarly complex, but have modifications that are probably related to the ingestion of larger, coarser material of very low quality (often 95% inorganics; Lopez and Levinton, 1987). These modifications include a large postero-dorsal caecum which serves to temporarily store particles that enter the stomach, a more robust crystalline style, a larger gastric shield with massive teeth (Morton, 1960) and, in some species, reduced sorting areas on the stomach walls (Hughes, 1977). In both of these lamellibranch groups, the stomach displays a propensity for sorting particles before the digestible fraction is transferred to the diverticula for intracellular digestion (Morton, 1960). The guts of deposit-feeding protobranchs are less modified, resembling those of the primitive archaeogastropods, with a simple sorting area in the stomach and absence of a food-sorting caecum (Morton, 1960; Owen, 1966, 1974). Although protobranchs demonstrate intracellular digestion in the diverticula, they rely heavily on extracellular digestion in the stomach and intestine (Owen, 1973, 1974). Given such differences in stomach morphology, several workers have suggested that there is a relationship between digestive processes and particle selection capabilities. Owen (1956) suggested that less-selective deposit feeders should rely more on extracellular digestion. Since much of the ingested material is inorganic, it would be inefficient and possibly harmful for digestive cells to phagocytize and attempt to assimilate such material. Other workers have proposed that there is an evolutionary trend in bivalves towards more efficient extracellular digestion of large food particles. Such a trend would be advantageous, because it would increase the rate of digestive processes and reduce the volume of cells devoted to intracellular digestion (see Morton, 1983). Whether such trends are wide-spread among the Bivalvia is difficult to determine. Nonetheless, most particle-feeding bivalves rely heavily on phagocytosis of particles and intracellular digestion.

Intracellular digestion is an adaptation to the functional needs of processing an almost continuous stream of fine particles that enter the stomach (Owen, 1966), but presents constraints associated with a discontinuous digestive process. Phagocytic digestive cells within tubules of the digestive diverticula, demonstrate phasic uptake of food material and release of excretory products (Morton, 1983). The time frame associated with this intracellular digestive cycle varies among bivalve species, but can be on the order of hours (2–20 h; Owen, 1966, 1974; Morton, 1977; Foster-Smith, 1975a). Although the filling and emptying of digestive tubules is staggered, this process represents a discontinuous aspect of feeding not encountered in molluscs that rely on more continuous, extracellular digestion (e.g., neogastropods; Owen, 1966). This perspective is supported by reports of reduced absorption efficiency in bivalves fed increasing concentrations of seston (Thompson and Bayne, 1972; Foster-Smith, 1975a). These data suggest that digestive tubules can approach saturation, resulting in a greater proportion of material being transported directly to the mid-gut without being subjected to intracellular digestion. In addition, the energetic demands of subjecting material to the digestive process can be high, comprising about 17% of energy expenditure in *M. edulis* (Widdows and Hawkins, 1989). Therefore, pre- and postingestive particle selection probably evolved as a means to supply the digestive diverticula, and their associated phagocytic cells, with the most nutritive material for intracellular digestion. Doing so ensures that digestive processes and products (phagocytosis, enzymes, etc.; Hawkins et al., 1990) are not wasted on indigestible material, thus optimizing energy gain.

The energetic cost of particle selection has been debated, but data concerning this subject are scarce. Bivalves do not forage in a traditional sense, although some tellinaceans move along the sediment surface during high tide (Brafield and Newell, 1961). Instead, bivalves rely on physical processes (e.g., currents, advection, resuspension, deposition) and microbial activity (e.g., disaggregation and colonization of fecal pellets) to provide food particles to their ambit (sensu Jumars, 1993). The energetic costs of capturing and transporting these particles are low, being less than 2% of metabolic energy expenditure in *M. edulis* (Jørgensen et al., 1986). It is likely that ciliary mechanisms are used not only to capture and transport material, but to discriminate among particles as well. Therefore, if certain ciliary tracts are involved in both transport and particle selection, then separating the energetic costs of these two functions may be impossible.

Like other feeding processes, the rate and efficiency of particle selection in many bivalves is affected by extrinsic factors, including the quantity and quality of suspended or deposited particulate matter. It is likely that selection is also mediated by the way in which the particular bivalve species modulates ingestion, either by reducing clearance rate, increasing pseudofeces production or both (Widdows et al., 1979; Bricelj and Malouf, 1984; Iglesias et al., 1992). Consequently, behavioral mediation of feeding rates interacts with selective mechanisms to optimize energy gain. Models for optimal foraging, ingestion and digestion for bivalves and other particle feeders have been developed and their implications discussed, and we refer the interested reader to reviews by Lehman (1976), Taghon et al. (1978), Lopez and Levinton (1987), Willows (1992) and Jumars (1993).

The potential impact of particle selection is both broad and significant. On an individual level, particle sorting can enhance the quality of material ingested thus optimizing energy acquisition (Barillé et al., 1997; Urrutia et al., 2001) and, in some species, may reduce the uptake of harmful substances (Shumway and Cucci, 1987; Bendell-Young and Arifin, 2004). On an ecosystem level, particle selection can impact the quantity and quality of material deposited to the benthos (Chauvaud et al., 2000), affect phytoplankton abundance (Smaal and Prins, 1993) and, potentially, species composition in the overlying water column. While technological advances have provided numerous tools for the experimental study of bivalve molluscs, we believe that future studies on particle selection should integrate experimental manipulations and careful study of functional morphology. Researchers should be aware of the various artifacts that can arise in particle-selection studies due to the following effects: (1) rejection of suspended and loosely consolidated pseudofeces on apparent retention, (2) rejection of larger inorganic particles on gravimetric measures of organic or chlorophyll content of pseudofeces (especially in environments with an abundance of dense, inorganic particles) and (3) influence of pseudofecal mucus on carbon, nitrogen or organic content of the pseudofeces (especially at low seston qualities). The bases for selection also need additional research, with studies that control for differences in size, shape, density and surface properties of the particles. Whether selection is based on physical or chemical properties of the particles is not completely known, and whether the importance of these properties changes under different conditions of food quantity and quality has not been determined. Studies addressing the bases of selection, passive versus active, are also needed, as is research that address ontogenetic changes in selective mechanisms. Such information will improve our ability to predict the degree of selection and its impact under varying environmental conditions, especially considering that under some conditions non-nutritious or toxic particles are preferentially ingested (Shumway and Cucci, 1987; Strychar and MacDonald, 1999).

Finally, although they are often considered and studied separately, all of the feeding organs are involved in processing particulate matter (Foster-Smith, 1978; Fig. 3). The feeding mechanisms can be viewed as a series of interdependent steps that collectively determine the fate of particles drawn into the pallial cavity (Levinton et al., 1996; Ward, 1996), including: (a) encounter and selective retention by the ctenidia; (b) sorting and differential transport by the frontal ciliary tracts of ordinary and principal filaments; (c) incorporation in mucus with different cohesive properties; (d) anterior transport on the ctenidial margins and interaction with rejection tracts of the mantle; (e) subtle interactions between the ctenidia and labial palps during material transfer; (f) reduction in the cohesiveness of mucous masses and strings by the labial palps; (g) complex sorting on the ridged surfaces of the palps with off-surface transport anteriorly or posteriorly in a slurry; (h) ingestion and sorting in the stomach and gut caeca; and (i) transfer of material to the digestive diverticula for final digestion and absorption. Given the complexity of the deposited and suspended food source, none of these steps result in perfect selection, but collectively they function to sequentially improve the quality of material subjected to digestive processes. It is likely that all of these processing steps can respond to physical, quantitative and qualitative aspects of the particulate matter (e.g., Milke and Ward, 2003; Ward et al., 1993), as well as being affected by intra- and interspecific differences in feeding-organ morphology. The potential for fine scale variation is immense, and the establishment of general rules for suspension- and deposit-feeding bivalves is complex. Yet the impetus for studying the intrinsic and extrinsic factors that mediate particle selection comes from a growing understanding of the impacts of this process on the benthic and planktonic realms, and its implication for processes ranging from the individual to ecosystem level. Understanding the bases for these impacts is a fertile area for future study.

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References

Alder, J., Hancock, A., 1851. On the branchial currents in *Pholas* and *Mya*. Ann. Mag. Nat. Hist. 8 (2nd series).

Alldredge, A.L., Gotschalk, C., 1989. Direct observations of the mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep-Sea Res. 36, 159–171.

Allen, W.R., 1921. Studies of the biology of freshwater mussels. Biol. Bull. 40, 210–241.

Ansell, A.D., 1961. The functional morphology of the British species of Veneracea (Eulamellibranchia). J. Mar. Biol. Assoc. U.K. 41, 489–515.

Asmus, R.M., Asmus, H.A., 1991. Mussel beds: limiting or promoting phytoplankton? J. Exp. Mar. Biol. Ecol. 148, 215–232.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of lamellibranchs: Part I. New observations on sorting mechanisms. Q. J. Microsc. Sci. 79, 181–308.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of lamellibranchs: Part II. Sorting devices on the gills. Q. J. Microsc. Sci. 79, 339–373.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of lamellibranchs: Part III. Types of lamellibranch gills and their food currents. Q. J. Microsc. Sci. 79, 375–420.

Atkins, D., 1938. On the ciliary mechanisms and interrelationships of lamellibranchs: Part VII. Latero-frontal cilia of the gill filaments and their phylogenetic value. Q. J. Microsc. Sci. 80, 345–436.

Bacon, G.S., MacDonald, B.A., Ward, J.E., 1998. Physiological responses of infaunal and epifaunal bivalves to variations in the concentration and quality of suspended particles: I. Feeding activity and selection. J. Exp. Mar. Biol. Ecol. 219, 105–125.

Baker, S.M., Levinton, J.S., Kurdziel, J.P., Shumway, S.E., 1998. Selective feeding and biodeposition by zebra mussels and their relation to changes in phytoplankton composition and seston loads. J. Shellfish Res. 17, 1207–1213.

Baker, S.M., Levinton, J.S., Ward, J.E., 2000. Particle transport in the zebra mussel, *Dreissena polymorpha* (Pallas). Biol. Bull. 199, 116–125.

Ballantine, D., Morton, J.E., 1956. Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra*. J. Mar. Biol. Assoc. U.K. 35, 241–274.

Barillé, L., 1994. Observations des éléments structuraux intervenant dans les mécanismes de nutrition préingestifs chez l'huître japonaise *Crassostrea gigas*. Haliotis 23, 125–137.

Barillé, L., Prou, J., Heral, 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* á l'aide de navicules bleues *Haslea ostrearia* (Simonsen) de différentes tailles. Oceanol. Acta 17, 201–210.

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

Barillé, L., Haure, J., Cognie, B., Leroy, A., 2000. Variations in pallial organs and eulatero-frontal cirri in response to high particulate matter concentrations in the oyster *Crassostrea gigas*. Can. J. Fish. Aquat. Sci. 57, 837–843.

Bayne, B.L., 1976. *Marine Mussels*: their Ecology and Physiology. Cambridge Univ. Press, Cambridge. 506 pp.

Bayne, B.L., 2002. A physiological comparison between Pacific oysters *Crassostrea gigas* and Sydney rock oysters *Saccostrea glomerata*: food, feeding and growth in a shared estuarine habitat. Mar. Ecol. Prog. Ser. 232, 163–178.

Bayne, B.L., Thompson, R.J., Widdows, J., 1976. Physiology: I. In: Bayne, B.L. (Ed.), *Marine Mussels*: their Ecology and Physiology. Cambridge Univ. Press, Cambridge, pp. 121–206.

Bayne, B.L., Widdows, J., Newell, R.I.E., 1977. Physiological measurements on estuarine bivalve molluscs in the field. In: Keegan, B.F. et al., (Eds.), Biology of Benthic Organisms, Pergamon, pp. 57–68.

Bayne, B.L., Hawkins, A.J.S., Navarro, E., Iglesias, I.P., 1989. Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. Mar. Ecol. Prog. Ser. 55, 47–54.

Bayne, B.L., Iglesias, J.I.P., Hawkins, A.J.S., Navarro, E., Heral, M., Deslous-Pauli, J.M., 1993. Feeding behavior of the mussel *Mytilus edulis*: responses to variations in quantity and organic content of seston. J. Mar. Biol. Assoc. U.K. 73, 813–829.

Bendell-Young, L.I., Arifin, Z., 2004. Application of a kinetic model to demonstrate how selective feeding could alter the amount of cadmium accumulated by the blue mussel (*Mytilus trossulus*). J. Exp. Mar. Biol. Ecol. 298, 21–33.

Bender, K., Davis, W.R., 1984. The effect of feeding by *Yoldia limatula* on bioturbation. Ophelia 23, 91–100.

Beninger, P.G., 1991. Structures and mechanisms of feeding in scallops: paradigms and paradoxes. In: Shumway, S.E. (Ed.), An International Compendium of Scallop Biology and Culture. J. World Aquac. Soc., Baton Rouge, pp. 331–340.

Beninger, P.G., Dufour, S.C., 1996. Mucocyte distribution and relationship to particle transport on the pseudolamellibranch gill of *Crassostrea virginica* (Bivalvia: Ostreidae). Mar. Ecol. Prog. Ser. 137, 133–138.

Beninger, P.G., St-Jean, S.D., 1997a. Particle processing on the labial palps of *Mytilus edulis* and *Placopecten magellanicus* (Mollusca: Bivalvia). Mar. Ecol. Prog. Ser. 147, 117–127.

Beninger, P.G., St-Jean, S.D., 1997b. The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles. Mar. Biol. 129, 389–397.

Beninger, P.G., Auffret, M., Le Pennec, M., 1990. Peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure and implications for feeding. Mar. Biol. 107, 215–223.

Beninger, P.G., Ward, J.E., MacDonald, B.A., Thompson, R.J., 1992. Gill function and particle transport in *Placopecten magellanicus* (Mollusca: Bivalvia) as revealed using video endoscopy. Mar. Biol. 114, 281–288.

Beninger, P.G., St-Jean, S., Poussart, Y., Ward, J.E., 1993. Gill function and mucocyte distribution in *Placopecten magellanicus* and *Mytilus edulis* (Mollusca: Bivalvia): the role of mucus in particle transport. Mar. Ecol. Prog. Ser. 98, 275–282.

Beninger, P.G., Dufour, S.C., Bourque, J., 1997. Particle processing mechanisms of the eulamellibranch bivalves *Spisula solidissima* and *Mya arenaria*. Mar. Ecol. Prog. Ser. 150, 157–169.

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

Berry, P.F., Schleyer, M.H., 1983. The brown mussel *Perna perna* on the Natal coast, South Africa: utilization of available food and energy budget. Mar. Ecol. Prog. Ser. 13, 201–210.

Boltovskoy, D., Izaguirre, I., Correa, N., 1995. Feeding selectivity of *Corbicula fluminea* (Bivalvia) on natural phytoplankton. Hydrobiologia 312, 171–182.

Bougrier, S., Hawkins, A.J.S., Héral, M., 1997. Preingestive selection of different microalgal mixtures in *Crassostrea gigas* and *Mytilus edulis*, analysed by flow cytometry. Aquaculture 150, 123–134.

Brafield, A.E., Newell, G.E., 1961. The behaviour of *Macoma balthica* (L.). J. Mar. Biol. Assoc. U.K. 41, 81–87.

Bricelj, V.M., Malouf, R.E., 1984. Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar. Biol. 84, 155–165.

Bricelj, V.M., Bass, A.E., Lopez, G.R., 1984. Absorption and gut passage time of microalgae in a suspension feeder: an evaluation of the ^{51}Cr:^{14}C twin tracer technique. Mar. Ecol. Prog. Ser. 17, 57–63.

Bricelj, V.M., Ward, J.E., Cembella, A.D., MacDonald, B.A., 1998. Application of video-endoscopy to the study of bivalve feeding on toxic dinoflagellates. In: Reguera, B. et al. (Eds.), Harmful Microalgae, Proceedings of the VIII Intern. Conf. on Harmful Algae, Xunta de Galicia and IOC of UNESCO, pp. 453-456.

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

Brillant, M.G.S., MacDonald, B.A., 2002. Postingestive selection in the sea scallop (*Placopecten magellanicus*) on the basis of chemical properties of particles. Mar. Biol. 141, 457–465.

Brillant, M.G.S., MacDonald, B.A., 2003. Postingestive sorting of living and heat-killed *Chlorella* within the sea scallop, *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 290, 81–91.

Chauvaud, L., Jean, F., Ragueneau, O., Thouzeau, G., 2000. Long-term variation of the Bay of Brest ecosystem: benthic-pelagic coupling revisited. Mar. Ecol. Prog. Ser. 200, 35–48.

Cloern, J.E., 1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? Mar. Ecol., Prog. Ser. 9, 191–202.

Cognie, B., Barillé, L., Rincé, Y., 2001. Selective feeding of the oyster *Crassostrea gigas* fed on a natural microphytobenthos assemblage. Estuaries 24, 126–131.

Cranford, P.J., Gordon, D.C., 1992. The influence of dilute clay suspensions on sea scallop (*Placopecten magellanicus*) feeding activity and tissue growth. Neth. J. Sea Res. 30, 107–120.

Crocker, K.M., Passow, U., 1995. Differential aggregations of diatoms. Mar. Ecol. Prog. Ser. 117, 249–257.

Cucci, T.L., Shumway, S.E., Newell, R.C., Selvin, R., Guillard, R.L., Yentsch, C.M., 1985. Flow cytometry: a new method for characterization of differential ingestion, digestion and egestion by suspension feeders. Mar. Ecol., Prog. Ser. 24, 201–204.

Dame, R.F., 1993. The role of bivalve filter feeder material fluxes in estuarine ecosystems. In: Dame, R.F. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO., ASI Ser., vol. G 33, Springer-Verlag, Berlin, pp. 245–269.

Dame, R.F., 1996. Ecology of Marine Bivalves: an Ecosystem Approach CRC Press, Florida.

Dame, R.F., Zingmark, R.G., Haskin, E., 1984. Oyster reefs as processors of estuarine materials. J. Exp. Biol. Ecol. 83, 239–247.

Davenport, J., 1988. The feeding mechanism of Yolida (=*Aequiyoldia*) *eightsi* (Courthouy). Proc. R. Soc. Lond., B 232, 431–442.

Davids, C., 1964. The influence of suspension of micro-organisms of different concentrations on the pumping and retention of food by the mussel (*Mytilus edulis*). Neth. J. Sea Res. 2, 233–249.

Decho, A.W., Luoma, S.N., 1991. Time-courses in the retention of food material in the bivalves *Potamocorbula amurensis* and *Macoma balthica*: significance to the absorption of carbon and chromium. Mar. Ecol. Prog. Ser. 78, 303–314.

Defossez, J.M., Daguzan, J.D., 1996. About preferential ingestion of organic matter by bivalves. J. Molluscan Stud. 62, 394–397.

Defossez, J.M., Hawkins, A.J.S., 1997. Selective feeding in shellfish: size-dependent rejection of large particles within pseudofaeces from *Mytilus edulis, Ruditapes philippinarum* and *Tapes decussatus*. Mar. Biol. 129, 139–147.

Deslous-Paoli, J.-M., Lannou, A.-M., Geairon, P., Bougrier, S., Raillard, O., Héral, M., 1992. Effect of the feeding behaviour of *Crassostrea gigas* (bivalve molluscs) on biosedimentation of natural particulate matter. Hydrobiological 231, 85–91.

Doering, P.H., Oviatt, C.A., 1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. Mar. Ecol. Prog. Ser. 31, 265–275.

Drew, G.A., 1899. The anatomy, habits, and embryology of *Yolida limatula* Say. Johns Hopkins Biol. Mem. 4, 1–39.

Dwivedy, R.C., 1973. A study of chemo-receptors on labial palps of the American oyster using microelectrodes. Proc. Natl. Shellfish. Ass. 63, 20–26.

Elsey, C.R., 1935. On the structure and function of the mantle and gill of *Ostrea gigas* (Thunberg) and *Ostrea lurida* (Carpenter). Trans. R. Soc. Can. Sect. 5, 131–160.

Essink, K., Tydeman, P., de Koning, F., Kleef, H.L., 1989. On the adaptation of the mussel *Mytilus edulis* L. to different environmental suspended matter concentrations. In: Klekowski, R.Z. et al., (Eds.), Proc. 21st European Mar. Biol. Symp., Polish Acad. of Sci., Inst. Oceanol., Gdansk, 41–51.

Foster-Smith, R.L., 1975a. The effect of concentration of suspension and inert material on the assimilation of algae by three bivalves. J. Mar. Biol. Assoc. U.K. 55, 411–418.

Foster-Smith, R.L., 1975b. The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). J. Exp. Mar. Biol. Ecol. 17, 1–22.

Foster-Smith, R.L., 1975c. The role of mucus in the mechanism of feeding in three filter-feeding bivalves. Proc. Malacol. Soc. Lond. 41, 571–588.

Foster-Smith, R.L., 1978. The function of the pallial organs of bivalves in controlling ingestion. J. Molluscan Stud. 44, 83–99.

Fox, D.L., 1936. The habit and food of the California sea mussel. Bull. Scripps Inst. Oceanogr. Tech. Ser. 1, 1–4.

Fox, D.L., Coe, W.R., 1943. Biology of the California sea-mussel (*Mytilus californianus*): II. Nutrition, metabolism, growth and calcium deposition. J. Exp. Zool. 93, 205–249.

Fox, D.L., Sverdrup, H.H., Cunningham, J.P., 1937. The rate of water propulsion by the California mussel. Biol. Bull. 72, 417–438.

Frechette, M., Bourget, E., 1985. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer. Can. J. Fish. Aquat. Sci. 42, 1166–1170.

Gagnon, C., Fisher, N.S., 1997. The bioavailability of sediment-bound Cd, Co, and Ag to the mussel *Mytilus edulis*. Can. J. Fish. Aquat. Sci. 54, 147–156.

Gallager, S.M., Langdon, C.J., Stolzenbach, K.D., Davis, L., Stoecker, D.K., 1988. High-speed video analysis of particle capture by a ciliated suspension feeder. EOS 69, 1086.

Galtsoff, P.S., 1964. The American oyster, *Crassostrea virginica* (Gmelin). U.S. Fish. Wildl. Serv. Fish. Bull. 64, 1–480.

Graham, A., 1949. The molluscan stomach. Trans. R. Soc. Edinb. 61, 737–778.

Grave, C., 1916. The process of feeding in the oyster. Science 44, 178–181.

Haven, D.S., Morales-Alamo, R., 1970. Filtration of particles from suspension by the American oyster *Crassostrea virginica*. Biol. bull. 139 (2), 248–264.

Hawkins, A.J.S., Navarro, E., Iglesias, J.I.P., 1990. Comparative allometries of gut-passage time, gut content and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. Mar. Biol. 105, 197–204.

Hawkins, A.J.S., Smith, R.F.M., Bayne, B.L., Héral, M., 1996. Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. Mar. Ecol. Prog. Ser. 131, 179–190.

Hawkins, A.J.S., Smith, R.F.M., Tan, S.H., Yasin, Z.B., 1998. Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucculata* and *Pinctada margaritifera*. Mar. Ecol., Prog. Ser. 166, 173–185.

Hernroth, B., Larsson, A., Edebo, L., 2000. Influence on uptake, distribution and elimination of *Salmonella typhimurium* in the blue mussel, *Mytilus edulis*, by the cell surface properties of the bacteria. J. Shellfish Res. 19, 167–174.

Hildreth, D.I., 1980. Bioseston production by *Mytilus edulis* and its effect in experimental systems. Mar. Biol. 55, 309–315.

Hildreth, D.I., Mallet, A., 1980. The effect of suspension density on the retention of 5 μm diatoms by the *Mytilus edulis* gill. Biol. Bull. 158, 316–323.

Honkoop, P.J.C., Bayne, B.L., Drent, J., 2003. Flexibility of size of gills and palps in the Sydney rock oyster *Saccostrea glomerata* (Gould, 1850) and the Pacific oyster *Crassostrea gigas* (Thunberg, 1793). J. Exp. Mar. Biol. Ecol. 282, 113–133.

Hughes, R.N., 1969. A study of feeding in *Scrobicularia plana*. J. Mar. Biol. Assoc. U.K. 49, 805–823.

Hughes, T.G., 1973. Deposit feeding in *Abra tenuis* (Bivalvia: Tellinacea). J. Zool., Lond. 171, 499–512.

Hughes, T.G., 1975. The sorting of food particles by *Abra* sp. (Bivalvia: Tellinacea). J. Exp. Mar. Biol. Ecol. 20, 137–156.

Hughes, T.G., 1977. The processing of food material within the gut of *Abra tenuis* (Bivalvia: Tellinacea). J. Molluscan Stud. 43, 162–180.

Hylleberg, J., Gallucci, V.F., 1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. Mar. Biol. 32, 167–178.

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

Iglesias, J.I.P., Navarro, E., Alvarez Jorna, P., Armentia, I., 1992. Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. J. Exp. Mar. Biol. Ecol. 162, 177–198.

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

Jackson, J.B.C. et al., 2001. Historical overfishing and recent collapse of coastal ecosystems. Science 293, 629–637.

Jørgensen, C.B., 1966. *Biology of Suspension Feeding*. Pergamon, Oxford. 357 pp.

Jørgensen, C.B., 1975. On gill function in the mussel *Mytilus edulis* (L.). Ophelia 13, 187–232.

Jørgensen, C.B., 1976. Comparative studies on the function of gills in suspension feeding bivalves, with special reference to effects of serotonin. Biol. Bull. 151, 331–343.

Jørgensen, C.B., 1989. Water processing in ciliary feeders, with special reference to the bivalve filter pump. Comp. Biochem. Physiol. 94A (2), 383–394.

Jørgensen, C.B., Kiørboe, T., Møhlenberg, F., Riisgård, H.U., 1984. Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. Mar. Ecol. Prog. Ser. 15, 283–292.

Jørgensen, C.B., Famme, P., Kristensen, H.S., Larsen, P.S., Møhlenberg, F., Riisgard, H.U., 1986. The bivalve pump. Mar. Ecol. Prog. Ser. 34, 69–77.

Jumars, P.A., 1993. Gourmands of mud: diet choice in deposit feeders. In: Hughes, R.N. (Ed.), Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell, Oxford Univ. Press. Boston, pp. 124–143.

Jumars, P.A., Self, R.F.L., Nowell, A.R.M., 1982. Mechanics of particle selection by tentaculate deposit-feeders. J. Exp. Mar. Biol. Ecol. 64, 47–70.

Kautsky, N., Evans, S., 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. Mar. Ecol., Prog. Ser. 38, 201–212.

Kellogg, J.L., 1903. Feeding habits and growth of *Venus mercenaria*. Bull. N.Y. State Mus. 71.

Kellogg, J.L., 1915. Ciliary mechanisms of lamellibranchs with descriptions of anatomy. J. Morph. 26, 625–701.

Kiørboe, T., Møhlenberg, F., 1981. Particle selection in suspension-feeding bivalves. Mar. Ecol. Prog. Ser. 5, 291–296.

Kiørboe, T., Møhlenberg, F., Nøhr, O., 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia 19 (2), 193–205.

Korringa, P., 1952. Recent advances in oyster biology. Q. Rev. Biol. 27, 266–365.

LaBarbera, M., 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. Amer. Zool. 24, 71–84.

Langdon, C.J., Newell, R.I.E., 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. Mar. Ecol. Prog. Ser. 58, 299–310.

Lehman, J.T., 1976. The filter–feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. 21, 501–516.

Lesser, M.P., Shumway, S.E., Cucci, T., Barter, J., Edwards, J., 1991. Size specific selection of phytoplankton by juvenile filter-feeding bivalves: comparison of the sea scallop *Placopecten magellanicus* (Gmelin, 1791) with *Mya arenarias Linnaeus*, 1758 and *Mytilus edulis Linnaeus*, 1758. In: Shumway, S.E., Sandifer, P.A. (Eds.), An Intl. Compendium of Scallop Biology and Culture World Aquaculture Society.

Levinton, J.S., Bianchi, T.S., Stewart, S., 1984. What is the role of particulate organic matter in benthic invertebrate nutrition? Bull. Mar. Sci. 35, 270–282.

Levinton, J.S., Ward, J.E., Thompson, R.J., 1996. Biodynamics of particle processing in bivalve molluscs: models, data, and future directions. Invert. Biol. 115, 232–242.

Levinton, J.S., Ward, J.E., Shumway, S.E., 2002. Feeding responses of the bivalves *Crassostrea gigas* and *Mytilus trossulus* to chemical composition of fresh and aged kelp detritus. Mar. Biol. 141, 367–376.

Lewin, J.C., Hruby, T., Mackas, D., 1975. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington: V. Environmental conditions associated with blooms (1971 and 1972). Estuar. Coast. Mar. Sci. 3, 229–242.

Loosanoff, V.L., 1949. On the food selectivity of oysters. Science 110, 122.

Loosanoff, V.L., Engle, J.B., 1947. Effects of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). U.S. Fish and Wildl. Serv., Fish. Bull. 51, 31–57.

Lopez, G.R., Cheng, I.-J., 1983. Synoptic measurements of ingestion rate, ingestion selectivity, and absorption efficiency of natural foods in the deposit-feeding molluscs *Nucula annulata* (Bivalvia) and *Hydrobia totteni* (Gastropoda). Mar. Ecol. Prog. Ser. 11, 55–62.

Lopez, G.R., Levinton, J.S., 1987. Ecology of deposit-feeding animals in marine sediments. Q. Rev. Biol. 62 (3), 235–259.

Loret, P., Pastoureaud, A., Bacher, C., Delesalle, B., 2000. Phytoplankton composition and selective feeding of the pearl oyster *Pinctada margaritfera* in the Takapoto lagoon (Tuamotu Archipelago, French Polynesia): in situ study using optical microscopy and HPLC pigment analysis. Mar. Ecol. Prog. Ser. 199, 55–67.

Lotsy, J.P., 1895. The food of the oyster, clam, and ribbed mussel. Report of the U.S. Commission of Fish and Fisheries, 1893, vol. 19, p. 375.

Lucas, M.I., Newell, R.C., Shumway, S.E., Seiderer, L.J., Bally, R., 1987. Particle clearance and yield in relation to bacterioplankton and suspended particulate availability in estuarine and open coast populations of the mussel *Mytilus edulis*. Mar. Ecol. Prog. Ser. 36, 215–224.

MacDonald, B.A., Ward, J.E., 1994. Variation in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca: Bivalvia). Mar. Ecol. Prog. Ser. 108, 251–264.

MacDonald, B.A., Bacon, G.S., Ward, J.E., 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles II. Absorption efficiency and scope for growth. J. Exp. Mar. Biol. Ecol. 219, 127–141.

McHenery, J.G., Birkbeck, T.H., 1985. Uptake and processing of cultured microorganisms by bivalves. J. Exp. Mar. Biol. Ecol. 90, 145–163.

McLachlan, A., 1980. Exposed sandy beaches as semi-enclosed ecosystems. Mar. Environ. Res. 4, 59–63.

Menzel, R.W., 1955. Some phases of the biology of *Ostrea equestris* Say and a comparison with *Crassostrea virginica* (Gmelin). Inst. Mar. Sci. 4, 69–153.

Milke, L.M., Ward, J.E., 2003. Influence of diet on pre-ingestive particle processing in bivalves: II. Pallial cavity residence times and particle handling on the labial palps. J. Exp. Mar. Biol. Ecol. 293, 151–172.

Møhlenberg, F., Riisgård, H.U., 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17, 239–246.

Morton, B.S., 1969. Studies on the biology of *Dreissena polymorpha* Pallas: I. General anatomy and morphology. Proc. Malacol. Soc. Lond. 38, 301–321.

Morton, B.S., 1977. The tidal rhythm of feeding and digestion in the Pacific oyster *Crassostrea gigas* (Thunberg 1793). J. Exp. Mar. Biol. Ecol. 26, 135–151.

Morton, B., 1983. Feeding and digestion in Bivalvia. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), The Mollusca. Physiology, Part 2, vol. 5, Academic Press, New York, pp. 65–340.

Morton, J.E., 1960. The function of the gut in ciliary feeders. Biol. Rev. 35, 92–140.

Navarro, J.M., Thompson, R.J., 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. J. Exp. Mar. Biol. Ecol. 209, 1–13.

Navarro, E.I., Iglesias, J.I.P., 1993. Infaunal filter-feeding bivalves and the physiological response to short-term fluctuations in food availability and composition. In: Dame, R.F. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes, Springer-Verlag, Berlin, pp. 25–56.

Nelson, T.C., 1923. The mechanism of feeding in the oyster. Proc. Soc. Exp. Biol. Med. 21, 166–168.

Nelson, T.C., 1960. The feeding mechanism of the oyster: II. On the gills and palps of *Ostrea edulis, Crassostrea virginica* and *C. angulata*. J. Morphol. 107, 163–203.

Newell, R.C., 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. Lond. 144, 25–45.

Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: are they the result of over harvesting the American oyster, *Crassostrea virginica*? In: Lynch, M.P., Chrome, E.C. (Eds.), Understanding the Estuary: Advances in Chesapeake Bay research, Chesapeake Bay Research Consortium Publication 129, Solomons, Maryland, pp. 536–546.

Newell, R.I.E., Jordan, S.J., 1983. Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 13, 47–53.

Newell, R.I.E., Ott, J.A., 1999. Macrobenthic Communities and Eutrophication In: Malone, TC, NA Smadlaka, A Malej and LW Harding Jr. Ecology and ecosystem function of benthic communities in Chesepeake Bay and the Northern Adriatic Sea In. Land-Use Water quality and fisheries: a comparative ecosystem analysis of the northern Adriatic Sea and the Chesapeake Bay. Coastal and Estuarine comparisons series, American Geophysical Union.

Newell, C.R., Shumway, S.E., 1993. Grazing of natural particles by bivalve molluscs: a spatial and temporal perspective. In: Dame, R.F. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO., ASI Series. vol. G33, Springer-Verlag, Berlin, pp. 85–148.

Newell, C.R., Shumway, S.E., Cucci, T.L., Selvin, R., 1989. The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. J. Shellfish Res. 8, 187–196.

Officer, C.B., Smayda, T.J., Mann, R., 1982. Benthic filter feeding: a natural eutrophication control. Mar. Ecol. Prog. Ser. 9, 203–210.

Ólafsson, E.B., 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. J. Anim. Ecol. 55, 517–526.

Orton, J.H., 1912. The mode of feeding of *Crepidula*, with an account of the current producing mechanism in the mantle cavity, and some remarks on the mode of feeding in gastropods and lamellibranchs. J. Mar. Biol. Assoc. U.K. 9, 444–478.

Owen, G., 1955. Observations on the stomach and digestive diverticula of the Lamellibranchia: I. The Anisomyaria and Eulamellibranchia. Q. J. Microsc. Sci. 96, 517–537.

Owen, G., 1956. Observations on the stomach and digestive diverticula of the Lamellibranchia II. The nuculidae. Q. J. Microsc. Sci. 97, 541–567.

Owen, G., 1966. Digestion. In: Wilbur, K.M., Yonge, C.M. (Eds.), *Physiology of Mollusca*. Academic Press, New York, pp. 53–96.

Owen, G., 1973. The fine structure and histochemistry of the digestive diverticula of the protobranchiate bivalve *Nucula sulcata*. Proc. R. Soc. Lond., B 183, 249–264.

Owen, G., 1974. Feeding and digestion in the Bivalvia. In: Lowenstein, O. (Ed.), Advances in Comparative Physiology and Biochemistry. vol. 5, Academic Press, New York, pp. 1–35.

Owen, G., 1978. Classification and the bivalve gill. Philos. Trans. R. Soc. Lond., B 284, 377–385.

Owen, G., McCrae, J.M., 1976. Further studies on the latero-frontal tracts of bivalves. Proc. R. Soc. Lond., B 194, 527–544.

Palmer, R.E., Williams, L.G., 1980. Effect of particle concentration on filtration efficiency of the bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. Ophelia 19, 163–174.

Passow, U., Alldredge, A.L., Logan, B.E., 1994. The role of particulate carbohydrate exudates in the flocculation of diatom blooms. Deep-Sea Res. 41, 335–357.

Pastoureaud, A., Heral, M., Prou, J., Razet, D., Russu, P., 1996. Particle selection in the oyster *Crassostrea gigas* (Thunberg) studied by pigment HPLC analysis under natural food conditions. Oceanol. Acta 19, 79–88.

Penry, D., Jumars, P.A., 1987. Modeling animal guts as chemical reactors. Am. Nat. 129, 69–96.

Pile, A.J., Young, C.M., 1999. Plankton availability and retention efficiencies of cold-seep symbiotic mussels. Limnol. Oceanogr. 44, 1833–1839.

Prins, T.C., Smaal, A.C., Pouwer, A.J., 1991. Selective ingestion of phytoplankton by the bivalves *Mytilus edulis* L. and *Cerastoderma edule* (L.). Hydrobiol. Bull. 25, 93–100.

Prins, T.C., Smaal, A.C., Dame, R., 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquat. Ecol. 31, 349–359.

Purchon, R.D., 1955. The structure and function of the British Pholadidae (rock-boring Lamellibranchia). Proc. Zool. Soc. Lond. 124, 850–911.

Purchon, R.D., 1987. The stomach in the Bivalvia. Philos. Trans. R. Soc. Lond., B 316, 183–276.

Rae, J.G., 1979. The population dynamics of two sympatric species of *Macoma* (Mollusca: Bivalvia). Veliger 21, 384–399.

Reid, R.G.B., 1965. The structure and function of the stomach in bivalve molluscs. J. Zool. 147, 156–184.

Reid, R.G.B., Reid, A., 1969. Feeding processes of members of the genus *Macoma* (Mollusca: Bivalvia). Can. J. Zool. 47, 649–657.

Rhoads, D.C., 1963. Rates of sediment reworking by *Yolidia limatula* in Buzzards Bay, Massachusetts and Long Island sound. J. Sediment. Petrol. 33 (3), 723–727.

Ribelin, B.W., Collier, A., 1977. Studies on the gill ciliation of the American oyster *Crassostrea virginica* (Gmelin). J. Morph. 151, 439–450.

Riisgård, H.U., 1988. Efficiency of particle retention and filtration rate in 6 species of northeast American bivalves. Mar. Ecol., Prog. Ser. 45, 217–223.

Riisgård, H.U., Larsen, P.S., 2000a. Comparative ecophysiology of active zoobenthic filter feeding, essence of current knowledge. J. Sea Res. 44, 169–193.

Riisgård, H.U., Larsen, P.S., 2000b. A comment on experimental techniques for studying particle capture in filter-feeding bivalves. Limnol. Oceanogr. 45, 169–193.

Riisgård, H.U., Larsen, P.S., Nielsen, N.F., 1996. Particle capture in the mussel *Mytilus edulis*: the role of latero-frontal cirri. Mar. Biol. 127, 259–266.

Robinson, W.E., Wehling, W.E., Morse, M.P., 1984. The effect of suspended clay on feeding and digestive efficiency of the surf clam, *Spisula solidissima* (Dillwyn). J. Exp. Mar. Biol. Ecol. 74, 1–12.

Rubenstein, D.I., Koehl, M.A.R., 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111, 981–994.

Self, R.F.L., Jumars, P.A., 1988. Cross-phyletic patterns of particle selection by deposit feeders. J. Mar. Res. 46, 119–143.

Shimeta, J., 1996. Particle-size selection by *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae) in suspensioin feeding and in deposit feeding: influences of ontogeny and flow speed. Mar. Biol. 126, 479–488.

Shimeta, J., Jumars, P.A., 1991. Physical mechanisms and rates of particle capture by suspension-feeders. Oceanogr. Mar. Biol. Annu. Rev. 29, 191–257.

Shumway, S.E., Cucci, T.L., 1987. The effects of the toxic dinoflagellate *Protogonyaulax tamarensis* on the feeding and behavior of bivalve molluscs. Aquat. Toxicol. 10, 9–27.

Shumway, S.E., Cucci, T., Newell, R.C., Yentsch, C.M., 1985. Particle selection, ingestion, and absorption in filter-feeding bivalves. J. Exp. Mar. Biol. Ecol. 91, 77–92.

Shumway, S.E., Newell, R.C., Crisp, D.J., Cucci, T.L., 1990. Particle selection in filter-feeding bivalve molluscs: a new technique on an old theme. In: Morton, B. (Ed.), *The Bivalvia*. Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986, Hong Kong Univ. Press, Hong Kong, pp. 151–165.

Shumway, S.E., Cucci, T.L., Lesser, M.P., Bourne, N., Bunting, B., 1997. Particle clearance and selection in three species of juvenile scallops. Aquat. Int. 5, 89–99.

Sierszen, M., Frost, T.M., 1992. Selectivity in suspension feeders: food quality and the cost of being selective. Arch. Hydrobiol. 123, 257–273.

Smaal, A.C., Prins, T.C., 1993. The uptake of organic matter and the release of inorganic nutrients by bivalve suspension feeder beds. In: Dame, R.F. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes, Springer-Verlag, Berlin, pp. 271–298.

Solow, A.R., Gallager, S.M., 1990. Analysis of capture efficiency in suspension feeding: application of nonparametric binary regression. Mar. Biol. 107, 341–344.

Stasek, C.R., 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae), with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. Proc. Zool. Soc. Lond. 137, 511–538.

Stasek, C.R., 1965. Feeding and particle-sorting in *Yoldia ensifera* (Bivalvia: Protobranchia), with notes on other nuculanids. Malacologia 2, 349–366.

Stead, R.A., Thompson, R.J., Jaramillo, J.R., 2003. Absorption efficiency, ingestion rate, gut passage time and scope for growth in suspension- and deposit-feeding *Yoldia hyperborea*. Mar. Ecol. Prog. Ser. 252, 159–172.

Stenton-Dozey, J.M.E., Brown, A.C., 1992. Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. Mar. Ecol. Prog. Ser. 82, 175–186.

Stenton-Dozey, J.M.E., Brown, A.C., 1994. Short-term changes in the energy balance of *Venerupis corrugatus* (Bivalvia) in relation to tidal availability of natural suspended particles. Mar. Ecol. Prog. Ser. 103, 57–64.

Strychar, K.B., MacDonald, B.A., 1999. Impacts of suspended peat particles on feeding retention rates in cultured eastern oysters (*Crassostrea virginica*, Gmelin). J. Shellfish Res. 18, 437–444.

Stuart, V., Klumpp, D.W., 1984. Evidence for food-resource partitioning by kelp-bed filter feeders. Mar. Ecol., Prog. Ser. 16, 27–37.

Taghon, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. Oecologia 52, 295–304.

Taghon, G.L, Jumars, P.A., 1984. Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. Ecology 65 (2), 549–558.

Taghon, G.L., Self, R.F.L., Jumars, P.A., 1978. Predicting particle selection by deposit feeders: a model and its implications. Limnol. Oceanogr. 23, 752–759.

Tammes, P.M.L., Dral, A.D.G., 1955. Observations of the straining of suspensions by mussels. Arch. Meerl. Zool. 11, 87–112.

Targett, N.M., Ward, J.E., 1991. Bioactive microalgal metabolites: mediation of subtle ecological interactions in phytophagous suspension feeding marine invertebrates. In: Scheuer, P.J. (Ed.), Bioorganic Marine Chemistry. vol. 4, Springer-Verlag, pp. 91–118.

Ten Winkel, E.H., Davids, C., 1982. Food selection by *Dreissena polymorpha* Pallas (Mollusca: Bivalvia). Freshw. Biol. 12, 553–558.

Theisen, B.F., 1977. Feeding rate of *Mytilus edulis* L. (Bivalvia) from different parts of Danish waters in water of different turbidity. Ophelia 16, 49–63.

Theisen, B.F., 1982. Variation in size of gills, labial palps, and adductor muscle in *Mytilus edulis* L. (Bivalvia) from Danish waters. Ophelia 21, 49–63.

Thompson, R.J., Bayne, B.L., 1972. Active metabolism associated with feeding in the mussel *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 17, 1–22.

Urban, E.R., Kirchman, D.L., 1992. Effect of kaolinite clay on the feeding activity of the eastern oyster *Crassostrea virginica*. J. Exp. Mar. Biol. Ecol. 160, 47–60.

Urrutia, M.B., Iglesias, J.I.P., Navarro, E., Prou, J., 1996. Feeding and absorption in *Cerastoderma edule* under environmental conditions in the Bay of Marennes-Oleron (western France). J. Mar. Biol. Assoc. U.K. 76, 431–450.

Urrutia, M.B., Nararro, E., Ibarrola, I., Iglesias, J.I.P., 2001. Preingestive selection processes in the cockle *Cerastoderma edule*: mucus production related to rejection of pseudofaeces. Mar. Ecol. Prog. Ser. 209, 177–187.

Vahl, O., 1972a. Efficiency of particle retention in *Mytilus edulis* L. Ophelia 10, 17–25.

Vahl, O., 1972b. Particle retention and relation between water transport and oxygen uptake in *Chlamys opercularis* (L.) (Bivalvia). Ophelia 10, 67–74.

Vahl, O., 1972c. Porosity of the gill, oxygen consumption and pumping rate in *Cardium edule* (L.) (Bivalvia). Ophelia 10, 109–118.

Vahl, O., 1973. Efficiency of particle retention in *Chlamys islandica* (O. F. Müller). Astarte 6, 21–25.

Vanderploeg, H.A., Johengen, T.H., Strickler, J.R., Liebig, J.R., Nalepa, T.F., 1996. Zebra mussels may be promoting *Microcystis* blooms in Saginaw Bay and Lake Erie. Bull. North Am. Benthol. Soc. 13, 181–182.

Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish Aquat. Sci. 58, 1208–1221.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.Y., Liebig, J.R., Grigorovich, I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59, 1209–1228.

Waite, A.M., Olson, R.J., Dam, H.G., Passow, U., 1995. Sugar containing compounds on the cell surfaces of marine diatoms measured using concanavalin A and flow cytometry. J. Phycol. 31, 925–933.

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

Ward, J.E., MacDonald, B.A., 1996. Pre-ingestive feeding behaviors of two sub-tropical bivalves (*Arca zebra* and *Pinctada imbricata*): responses to an acute increase in suspended sediment concentration. Bull. Mar. Sci. 59, 417–432.

Ward, J.E., Targett, N.M., 1989. Influence of marine microalgal metabolites on the feeding behavior of the blue mussel *Mytilus edulis*. Mar. Biol. 101, 313–321.

Ward, J.E., Beninger, P.G., MacDonald, B.A., Thompson, R.J., 1991. Direct observations of feeding structures and mechanisms in bivalve molluscs using endoscopic examination and video image analysis. Mar. Biol. 111, 287–291.

Ward, J.E., MacDonald, B.A., Thompson, R.J., Beninger, P.G., 1993. Mechanisms of suspension feeding in bivalves: resolution of current controversies by means of endoscopy. Limnol. Oceanogr. 38, 265–272.

Ward, J.E., MacDonald, B.A., Targett, N.M., Vrolijk, N.H., 1994a. Influence of particle density and surface characteristics on suspension-feeding in two species of bivalves (*Arca zebra* and *Mytilus edulis*). J. Shellfish Res. 13, 305.

Ward, J.E., Newell, R.I.E., Thompson, R.J., MacDonald, B.A., 1994b. In vivo studies of suspension-feeding processes in the eastern oyster *Crassostrea virginica* (Gmelin). Biol. Bull. 186, 221–240.

Ward, J.E., Levinton, J.S., Shumway, S.E., Cucci, T., 1997. Site of particle selection in a bivalve mollusc. Nature 390, 131–132.

Ward, J.E., Levinton, J.S., Shumway, S.E., Cucci, T., 1998a. Particle sorting in bivalves: in vivo determination of the pallial organs of selection. Mar. Biol. 131, 283–292.

Ward, J.E., Sanford, L.P., Newell, R.I.E., MacDonald, B.A., 1998b. A new explanation of particle capture in suspension-feeding bivalve molluscs. Limnol. Oceanogr. 43 (5), 741–752.

Ward, J.E., Sanford, L.P., Newell, R.I.E., MacDonald, B.A., 2000. The utility of in vivo observations for describing particle capture processes in suspension-feeding bivalve molluscs. Limnol. Oceanogr. 45 (5), 1203–1210.

Ward, J.E., Levinton, J.S., Shumway, S.E., 2003. Influence of diet on pre-ingestive particle processing in bivalves: I. Transport velocities on the ctenidium. J. Exp. Mar. Biol. Ecol. 293, 129–149.

Widdows, J., Hawkins, A.J.S., 1989. Partitioning of rate of heat dissipation by *Mytilus edulis* into maintenance, feeding, and growth components. Physiol. Zool. 62, 764–784.

Widdows, J., Fieth, P., Worrall, C.M., 1979. Relationship between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50, 195–207.

Williams, L.G., 1982. Mathematical analysis of the effects of particle retention efficiency on determination of filtration rate. Mar. Biol. 66, 171–177.

Willows, R.I., 1992. Optimal digestive investment: a model for filter feeders experiencing variable diets. Limnol. Oceanogr. 37, 829–847.

Wilson, J.H., 1980. Particle retention and selection by larvae and spat of *Ostrea edulis* in algal suspensions. Mar. Biol. 57, 135–145.

Wilson, J.H., 1983. Retention efficiency and pumping rate of *Ostrea edulis* in suspensions of *Isochrysis galbana*. Mar. Ecol. Prog. Ser. 12, 51–58.

Winter, J.E., 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13, 1–33.

Wright, R.T., Coffin, R.B., Ersing, C.P., Pearson, D., 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. Limnol. Oceanogr. 27, 91–98.

Yen, J., Sanderson, B., Strickler, J.R., Okubo, A., 1991. Feeding currents and energy dissipation by *Euchaeta rimana*, a subtropical benthic copepod. Limnol. Oceanogr. 36, 362–369.

Yonge, C.M., 1923. Studies on the comparative physiology of digestion: I. The mechanism of feeding, digestion, and assimilation in the lamellibranch *Mya*. Br. J. Exp. Biol. 1, 15–63.

Yonge, C.M., 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. J. Mar. Biol. Assoc. U.K. 14, 295–386.

Yonge, C.M., 1939. The Protobranchiate Mollusca; a functional interpretation of their structure and evolution. Philos. Trans. B 230, 79–147.

Yonge, C.M., 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. Philos. Trans. R. Soc. Lond., B 234, 29–76.