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SELECTIVE CAPTURE AND INGESTION OF PARTICLES BY SUSPENSION-FEEDING BIVALVE MOLLUSCS: A REVIEW

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ABSTRACT Suspension-feeding bivalve molluscs are foundation species in coastal intertidal systems. The selective feeding capabilities of these animals can have a large influence on phytoplankton communities and nutrient flow to the benthos. Particle selection, including the types of particles chosen for ingestion and the possible mechanisms mediating selection, has been studied extensively and reported in the literature. To date, however, the possible mechanisms mediating these selective processes have remained elusive. Generally, the focus on a few key commercial species, and their demonstrated range of selective capabilities, has made it difficult to design studies that elucidate the mechanisms behind particle selection. This review focuses on key research that has been carried out in the last 20 y toward better understanding the mechanism that underlays selective capture and ingestion of particles in this important group of animals. Recently, work has been completed which has advanced the field in pointing to a passive mechanism as a mediator of selection, with the interactions between the physicochemical properties of particles and the mucus covering the pallial organs most likely mediating food choice. Although no strong evidence for an immediate, active mechanism which underlies particle selection was found, avenues for future research are suggested in this review. The possible mechanisms that control capture, including qualitative precapture selection, are also summarized and discussed in depth. Methodological considerations for rigorous experiments to advance the field are also discussed, including suggestions of general guidelines for experimental designs, which will allow better comparison of findings across studies.

KEY WORDS: mussel, oyster, particle selection, *Crassostrea*, *Mytilus*, physicochemical properties

INTRODUCTION

Suspension-feeding bivalve molluscs are among the most important nearshore groups of animals, often dominating the macrobenthos and contributing significantly to benthic-pelagic coupling and the structure of benthic food webs (Dame & Olenin 2003). These contributions are affected by the ability of bivalves to ingest particles selectively, rejecting some and ingesting others as food. The pre-ingestive sorting process of bivalves has been extensively studied for the past century in an effort to determine what types of particles these organisms select (e.g., microalgae, zooplankton, and detritus), the factors that control the sorting process, and the mechanism(s) involved in selection.

Early research on particle selection focused on commercially important species, such as the eastern oyster (*Crassostrea virginica* [Gmelin, 1791]) and their food preferences (Dean 1887, Lotsy 1896, Kellogg 1910). Analysis of gut contents of the blue mussel (*Mytilus edulis* [Linnaeus, 1758]) by Field (1911) found that diatoms were the primary phytoplankton ingested by mussels, similar to what had been previously reported for *C. virginica*. The relative importance of phytoplankton versus detrital particles as the main food source for suspension-feeding bivalves was a point of disagreement in the literature. Blegvad (1914) reported on gut-content analyses of more than 40 bivalve species, which he claimed showed that detritus was their main food source; a claim supported by other works (Petersen 1908, Petersen & Jensen 1911). Subsequent and more thorough studies of the gut contents of more than 200 bivalve species (Hunt 1925, Martin 1925, Nelson 1927, 1947, Galtsoff 1964) suggested a different concept and affirmed the importance of phytoplankton, particularly diatoms, as the primary food source of bivalves. Contemporaneously, morphological work by Yonge (1923) and Nelson (1924) demonstrated the role of the pallial organs in feeding, and the relative importance of organic matter as the primary food source in these organisms. With this base of information, scientists were able to better design experiments to examine feeding physiology, particularly selective feeding, in bivalves.

Feeding in bivalves generally is understood to be physiologically plastic, with animals responding to changes in seston composition and particle loads (Bayne 1976, Bayne et al. 1976, 1977, Iglesias et al. 1992, Bacon et al. 1998, Beninger et al. 2008a, Bayne 2009). To process the bulk of particulate material they encounter, suspension feeders can either reduce particle clearance rate (CR) or select between particles and increase production of pseudofeces (PF) (captured material that is not ingested). The presence of this highly selective, pre-ingestive sorting mechanism serves as a way to optimize energy gain (Taghon et al. 1978, Kiørboe & Møhlenberg 1981, Newell et al. 1989, Iglesias et al. 1992, Grizzle et al. 2001, Ward & Shumway 2004) by enabling bivalves to ingest particles with a higher nutritive quality. For example, bivalves have been shown to ingest microalgae preferentially (*Rhodomonas lens* and *Phaeodactylum tricornutum*) over detrital particles (ground *Spartina* sp. and suspended bottom material, respectively; Ward et al. 1997, Levinton et al. 2002) and select between different microalgal species (Shumway et al. 1985), including algae of the same size (Lesser et al. 1991, MacDonald & Ward 1994, Shumway et al. 1997).

The process of particle selection by bivalves has been described as either active or passive (see reviews by Jørgensen 1996, Ward & Shumway 2004). Active selection, if present, would be dependent on an immediate physiological response by

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the cilia or feeding organs to feeding stimuli (see Ward & Shumway 2004). Passive selection, on the other hand, would be dependent on the physicochemical interactions between the particles and the feeding organs, with factors such as particle size and shape possibly serving as bases for sorting (i.e., larger particles preferentially selected over smaller particles, see Bayne et al. 1977). Importantly, the distinction between passive and active refers to the mechanism(s) responsible for the selection, not the factor(s) that elicits the mechanism(s). For example, the adhesion of different types of carbohydrates to ctenidial (= gill) mucus via lectin binding may be a qualitative factor of a microalgal cell but the mechanism is passive if the particle is moved one direction or the other as a consequence of mucus binding and there is no behavioral change in the shape or movement of feeding organs (e.g., muscular contractions), or changes in activity of cilia covering these organs. Qualitative factors can stimulate an active selection response, but qualitative factors can also be involved in passive selection.

Although some headway has been made recently regarding the mechanisms that underlay particle selection, there still is much to be explored. Some of the unknowns include whether there are baseline passive processes in place that may result in some particles being more likely than others to be ingested or rejected based on physicochemical characteristics. If present, such a process could be linked to a basic default mechanism wherein most particles are accepted, and changes in seston quality and quantity induce rejection (MacDonald & Ward 1994). Alternatively, although less likely, the default mechanism could be that all captured particles are rejected, and changes in seston quantity and quality induce ingestion. Furthermore, it is unknown if there is an immediate response (= active component) that could trigger this shift in the sorting mechanism. Particle fate is dependent on encounter with ctenidial filaments and subsequent retention and discrimination by the pallial organs. Understanding the mechanisms that underlie selection during each of these steps (pre and postcapture) would help to elucidate how they act in concert to determine the material ultimately ingested.

Early work regarding particle selection by bivalves has been extensively reviewed (see Ward & Shumway 2004), and the current review focuses on advances made in the last two decades. In particular, this review summarizes recent research examining selection at time of particle capture (termed "pre-capture selection"), and selection after particle capture, but before ingestion (termed "pre-ingestive selection"). For a literature review of the process of postingestive selection, readers are referred to the review of Ward and Shumway (2004) and papers by Brillant and MacDonald (2000, 2002, 2003). For a review of particle selection by deposit-feeding bivalves, readers are referred to Ward and Shumway (2004).

BACKGROUND

Pumping, Clearance Rate, and Filtration Rates

Suspension-feeding bivalves filter water and capture particles from the seston during feeding activities. The amount of water flowing through the ctenidia per unit time (L h^{-1}) is known as the pumping rate. This flow is a direct result of water currents produced by the lateral cilia located on the ctenidial filaments (Table 1). It scales with the size of the ctenidium and can be described using allometric equations (e.g., Vahl 1972,

TABLE 1.

Index of common terms used in the literature to describe feeding morphology of bivalves. For source definitions see Yonge 1923 and Atkins 1937.

Structure	Definition
Pallial (= mantle) cavity	Area enclosed by the mantle but exterior to the visceral mass. Ctenidia and LP are found within this cavity.
Ctenidia	The paired gills composed of filaments (ordinary and/or principal) joined together by ciliary or tissue connections.
Ordinary filaments	Tube-shaped filaments that make up most of the ctenidium.
Principal filaments	Modified, U-shaped filaments that are found between adjacent plicae of heterorhabdic ctenidia. These filaments form the "troughs" of the plicate ctenidium.
Heterorhabdic ctenidia	Ctenidia composed of at least two different types of filament (e.g., ordinary, principal).
Homorhabdic ctenidia	Ctenidia composed of only one type of filament.
Filibranch	Adjacent ctenidial filaments joined by ciliary tufts.
Eulamellibranch	Adjacent ctenidial filaments joined by tissue connections with openings (= ostia) through which water flows.
Pseudolamellibranch	Adjacent ctenidial filaments joined by less extensive interfilamentar junctions, found in members of the Ostreidae.
Frontal cilia	Cilia present on the incurrent-facing surface of the filaments, which transport mucus and captured particles along the ctenidia.
Lateral cilia	Cilia present along the sides of the filaments, which create currents that pull water into the pallial cavity, drive it through the interfilamentar spaces or ostia of the ctenidia, and out the exhalant siphon or aperture.
Laterofrontal cilia & cirri	Cilia located between the frontal and lateral ciliary tracts. The presence of simple cilia or compound cirri is species-specific, but both facilitate particle capture.
Labial palps (LP)	Paired accessory feeding structures surrounding the mouth. The palps are heavily ciliated and typically have a ridged inner surface that faces the opposing palp,and a smooth outer surface. These structures are important in particle sorting and ingestion.

1973, Meyhöfer 1985, Jones et al. 1992). Clearance rate, also measured in volume per unit time, is an indication of the volume of water cleared of particles as a result of suspension feeding (Table 2). If all particles entering the bivalve are retained, then CR is equivalent to pumping rate. If particles are not cleared with 100% efficiency, then pumping rate and CR are not comparable (Coughlan 1969). Clearance rate is sometimes used interchangeably with filtration rate, which is a measurement of the mass of particles cleared per unit time (e.g., mg h^{-1}). It is not the intention of this review to go in depth into the specifics of pumping and filtration by bivalves. Readers interested in the physiological considerations and constraints on bivalve suspension feeding are referred to reviews by Cranford et al. (2011) and Riisgård et al. (2015).

Clearance rate has been posited as being physiologically plastic, with suspension feeders being able to adjust this rate as a response to environmental factors (Bayne & Newell 1983, Cranford & Grant 1990, Bacon et al. 1998, Baker et al. 1998, Bayne 2004). The ability to adjust CR allows bivalves to optimize particle selection (Hawkins et al. 1999), with some bivalves increasing CR as seston loads increase. Experiments on the feeding behavior of filter-feeding zooplankton have shown that these animals can maximize their net energy intake if they control both the rate of filtration and the structural properties (i.e., shape and sieve size) of the filter unit (Lehman 1976, Bayne et al. 1977, Jørgensen et al. 1986, Shimeta & Jumars 1991, Iglesias et al. 1992). The premise is that by doing so, zooplankton can increase the range of particles that can be efficiently collected and ingested. If similar adjustments can be made by suspension-feeding bivalves, e.g., dynamic changes in ciliary activity and the spacing of ctenidial filaments, both rate and efficiency of capture could be adjusted to maximize energy intake. Several studies have reported differences in CR by bivalves depending on the seston composition. Bayne et al. (1988) reviewed the early literature on feeding and digestion in bivalves and discussed the available information within the scope of physiological compensations. They provided evidence of an immediate and active compensatory response in CR and filtration rate to decreases in food quantity and quality, or after periods of emersion in the case of the intertidal blue mussel (*Mytilus edulis*). Factors that can elicit a CR response include variations in seston loads (Foster-Smith 1975a, Palmer & Williams 1980, Iglesias et al. 1996, Ward & MacDonald 1996, Cranford et al. 2005, Strøhmeier et al. 2009), presence of phytoplankton metabolites (Bricelj & Malouf 1984, Birkbeck et al. 1987, Shumway & Cucci 1987, Ward et al. 1992, Silverman et al. 1995), seston composition (Dionisio Pires et al. 2004, Li et al. 2009), and temperature (Richoux & Thompson 2001, Kittner & Riisgård 2005, Specht & Fuchs 2018).

Many bivalve species have physiological control over the lateral cilia and consequently, the rate at which water is pumped (Paparo 1972, Jørgensen 1976, 1982, Catapane 1983, Frank et al. 2015). Temperature also has an effect on ciliary activity and consequently the CR of particles (Aiello 1960, Malanga et al. 1981, Richoux & Thompson 2001, Specht & Fuchs 2018). Kittner and Riisgård (2005) studied the effects of temperature on filtration rates of *Mytilus edulis* and reported a linear relationship between temperature and filtration rate, with no evidence of temperature acclimation by the mussels. Results should be interpreted with caution; however, as the authors used several mussels in one tank, estimated how many were feeding based on valve gape, and calculated an individual rate by dividing total clearance by the number of active animals. Furthermore, the rates were based on filtration of a monoalgal diet, which can result in underestimations compared with filtration of natural seston (e.g., Wright et al. 1982, MacDonald et al. 2011). Work by Riisgård and Larsen (2007) on blue mussels (*M. edulis*) suggests that the warmer water temperature itself does not influence ciliary beat by affecting physiological processes, but rather temperature alters the viscosity of water and affects fluid mechanics. In particular, increasing temperature decreases water viscosity and reduces drag on the cilia,

TABLE 2.

Common functions and equations used in the literature to quantify particle capture and selection in suspension-feeding organisms. Efficiencies and indices have no units and can be presented as either a proportion (0–1) or a percentage (0%–100%).

Function	Equation	Terms	Reference
CR (L h^{-1}) static system	$\mathrm{CR} = \frac{v}{t}\ln(\frac{C_t}{C_O})$	v = chamber volume, t = time of trial, C_t = final concentration, and C_0 = initial concentration	Coughlan 1969
CR (L h^{-1}) flow-through system	$\mathrm{CR} = \left[\frac{(C_{\mathrm{in}} - C_{\mathrm{out}})}{C_{\mathrm{in}}}\right] \times F$	C_{in} = concentration entering chamber, C_{out} = concentration exiting chamber, and F = flow rate	Hildreth and Crisp 1976
CE	$\mathrm{CE} = 1 - \frac{C_{\mathrm{out}}}{C_{\mathrm{in}}}$	C_{in} = concentration entering chamber or inhalant siphon/aperture and C_{out} = concentration exiting chamber or exhalent siphon/aperture	Vahl 1972
SE	$\mathrm{SE} = 1 - \frac{S}{W}$	S = proportion of food type in sample and W = proportion of food type in water (diet)	Iglesias et al. 1992
Electivity index (EI)	$\mathrm{EI} = \frac{S - W}{(S + W) - (2SW)}$	See SE	Jacobs 1974 (modified from Ivlev's 1961)
Chesson's alpha (α) index	$\alpha_i = F_i\left(\sum_{i=1}^{m} F_i\right)^{-1}$	F_i = filtration efficiency of ith particle type (see CE), m = number of particle types	Chesson 1983

which results in higher rates of ciliary beating. Recently, Specht and Fuchs (2018) examined the effects of temperature on ciliary activity and clearance by the northern quahog (hard clam) (*Mercenaria mercenaria* [Linnaeus, 1758]) and reported that, unlike with *M. edulis*, the effects of temperature are purely physiological. The authors report that in isolated gill preparations, ciliary beat was not affected by changes in water viscosity, but was affected by temperature changes. To date, however, no clear consensus has been reached regarding the apparent effects of physiology versus viscosity on ciliary movement and consequently particle CR (Fuchs & Specht 2018, Riisgård & Larsen 2018).

Bivalves also adjust feeding rate in response to the quantity and quality of particles in some environments (Bayne et al. 1988, Barillé et al. 1993, Baker et al. 1998, Cranford & Hill 1999, Cranford et al. 2005, Beninger et al. 2008a). Strøhmeier et al. (2009), however, demonstrated that both mussels (*Mytilus edulis*) and scallops (*Pecten maximus* [Linnaeus, 1758]) from oligotrophic environments continued to feed at low seston concentrations (0.15 mg L^{-1}), a finding that contradicts some previous reports of cessation of feeding under low particle loads. Their data indicate that current concepts of functional responses of bivalves in oligotrophic environments need reexamination. These workers also reported little short-term variability in mean CR of the mussels (4.2 ± 2.2 L h^{-1}, $n = 144$) and scallops (28.2 ± 12.7 L h^{-1}, $n = 132$). The CR of scallops was negatively correlated with chlorophyll *a* concentration, but not with temperature, supporting previous findings by MacDonald and Ward (1994) for *Placopecten magellanicus* (Gmelin, 1791; but see MacDonald & Ward 2009 for daily fluctuations in temperature and scallop CR). These and other findings (e.g., Li et al. 2009, Strøhmeier et al. 2009) support the concept that behavioral responses in CR are important components of bivalve feeding.

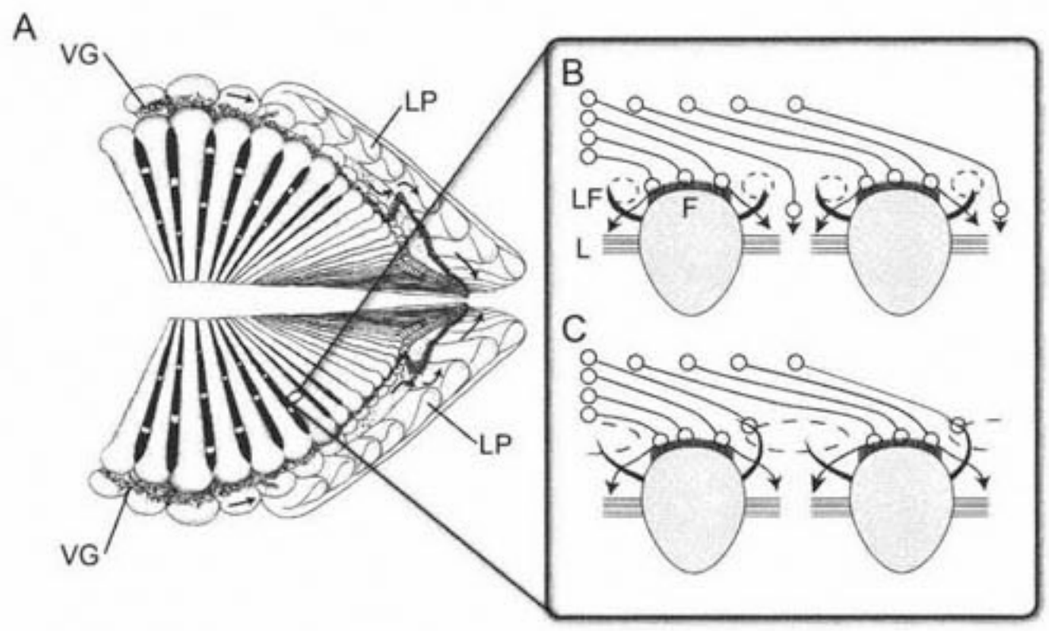

Figure 1. (A) Diagram of a bivalve ctenidium with a homorhabdic structure composed of ordinary filaments, as observed using video endoscopy (orientation: ventral foreground and dorsal background). The ctenidium is inserted between the LP to the right, and particles trapped in a cohesive mucus string are being transported toward the palps in the ventral groove (VG). Offset panel shows a cross section of two ordinary filaments, three major ciliary tracts (F = frontal, LF = laterofrontal, and L = lateral), and particle movement at the time of capture. (B) Representation of bivalves that possess small laterofrontal cilia (e.g., scallops), creating a smaller area of hydrodynamic particle entrainment (dashed oval), resulting in lower CE for small particles. (C) Representation of bivalves that possess larger laterofrontal cirri (e.g., mussels), creating a larger area of hydrodynamic particle entrainment (dashed oval), resulting in higher CE for small particles (see Ward et al. 1998 for full explanation). Arrows show the direction of water flow across and between filaments. Open circles represent particles before and after being captured by the filaments. Figures adapted after Ward (1996) and Ward et al. (1998).

PRECAPTURE SELECTION

Particle Capture Efficiency (CE)

Particle capture is the first step in the feeding process and is a consequence of encounter with, and retention on, the ctenidial filaments. The processes of capture and subsequent transport are facilitated by the mucus produced by the ctenidia (Foster-Smith 1975b, Beninger et al. 1992, 1993, Ward et al. 1998). Particles suspended in water enter the inhalant aperture or siphon via currents generated by the action of lateral cilia located on the sides of ctenidial filaments (Fig. 1). Particles entering the pallial cavity are either directly intercepted by the frontal surface of the filaments or trapped by currents created by the laterofrontal cilia/cirri and then directed onto the frontal surface (Atkins 1937, Jørgensen 1981, Ward 1996, Beninger et al. 1997, Ward et al. 1998, Riisgård & Larsen 2010). Diffusional deposition of particles is also possible (Shimeta 1993), as are mechanisms involving inertial forces when Reynolds number at the filaments exceed 0.1 (Shimeta & Jumars 1991, Ward 1996). In some species with heterorhabdic ctenidia, particles also can be hydrodynamically entrained on the principal filaments (Owen 1974, Jørgensen 1976, Owen & McCrae 1976, Ward et al. 1998). Water, and particles not retained by the ctenidia, is directed out the exhalent aperture or siphon.

Although postcapture, pre-ingestive selection has been well studied, much less is known about selective retention during particle capture. Particle encounter efficiency relates to the proportion of particles that come into contact with the ctenidial filaments, whereas retention efficiency is the proportion of encountered particles that are actually retained (see Shimeta & Jumars 1991). Although previous workers have used the term "retention efficiency" to describe particle CE in bivalves (Riisgård 1988, MacDonald & Ward 1994, Cranford & Hill 1999, Strøhmeier et al. 2012), unless *in vivo* techniques are used to differentiate the number of particles that encounter the ctendial filaments from those that are actually retained (Ward et al. 1998), retention efficiency cannot be determined. Therefore, the term CE should be used in place of retention efficiency to describe the process accurately that is typically being measured. In some cases, CR has been used interchangeably with CE. Capture efficiency and CR, whereas related, are not the same. Capture efficiency is not a rate, and is independent of volume of water filtered or time. Furthermore, CR of particles of different sizes can only be compared if all particles are captured with 100% efficiency. For the purposes of this review, and to avoid confusion, the terminology used in the cited publications will be used, with appropriate comments as to whether the findings reflect CE. For an explanation of methods used to measure CE, readers are referred to **Differential Capture** of this review.

Early research on suspension-feeding processes reported that most bivalves capture particles greater than 6 µm at close to 100% efficiency, with capture decreasing nonlinearly for particles of smaller size (Table 3; Vahl 1972, Palmer & Williams 1980, Riisgård 1988). Vahl (1972) examined CE in blue mussels (*Mytilus edulis*) using a flow-through system with a common

head tank and measured particle concentrations several times over the course of the experiment. He reported "negative" CE values at the smallest size class (1–2 μm), which he attributed to recirculation of water in the chambers. Further experiments to minimize recirculation also resulted in a few negative values at the smallest size classes. The author concluded that the mussels themselves were releasing small particles or breaking up larger aggregates, resulting in a higher number of small particles in the chambers with animals compared with control chambers (without animals). These findings demonstrated an effective CE of zero for the smallest sized particles, though they may also be indicative of the methodological limitations of accurately enumerating small particles. A decade later, Wilson (1983) examined the CE of the European oyster (*Ostrea edulis* [Linnaeus, 1758]) fed suspensions of *Isochrysis galbana* (T-Iso strain, ~4 μm). Using a rubber sleeve to capture all of the exhalent flow, he found that as the concentration of *I. galbana* cells increased, the CE of oysters decreased according to a parabolic curve ($R^2 = 0.84$). Interestingly, for the long-term experiments (~56 h), there was variation in CE at the different algal concentrations examined, though no pattern was found to explain the observed differences in CE over time.

Studies examining the mechanisms of particle capture in suspension feeders have demonstrated that the surface properties of particles can have an effect on CE. Particles with a charged surface, for example, were demonstrated to be more readily captured than particles with a neutral charge by both the brittle star (*Ophiopholis aculeata* [Linneaus, 1767] (LaBarbera 1978) and larvae of the northern quahog (= hard clam) (*Mercenaria mercenaria*) (Solow & Gallager 1990). In other marine invertebrates, particle capture has been shown to be mediated by surface hydrophobicity. For example, hydrophilic particles are retained at a higher proportion than hydrophobic particles by the crustacean (*Daphnia magna* [Straus, 1820]) (Gerritsen & Porter 1982). Characterization of the surface properties of bacterial species found that they tend to be more hydrophilic (Grasland et al. 2003) than several microalgal species (Ozkan & Berberoglu 2013a, Rosa et al. 2017). This difference may account for the relatively higher efficiency at which bacteria are captured by several bivalve species, such as the clam (*Venus verrucosa* [Linneaus, 1758]), ribbed mussel (*Geukensia demissa* [Dyllwin, 1817]), and the blue mussel (*Mytilus edulis*), compared with particles of similar size (Amouroux 1986, Langdon & Newell 1990, Hernroth et al. 2000; respectively). Conova (1999) examined the role of hydrophobicity in particle capture by the suspension-feeding mole crab (*Emerita talpoida* [Say, 1817]). She reported that as small particles (0.5–10 μm) were made more hydrophilic, their adhesion to the capture organ generally decreased. Interestingly, for particles 15–25 μm in size, particle hydrophobicity did not affect capture rates. Recently, Dadon-Pilosof et al. (2017) examined the surface properties of several planktonic, free-living bacteria in the SAR 11 Clade and found that they have a more hydrophilic surface than most other bacteria in the seston. Interestingly, the SAR 11 microorganisms are captured less efficiently than similarly sized bacteria and polystyrene microspheres (0.3 μm) by suspension-feeding ascidians. This result is the opposite of what has been observed for some bivalves. In *M. edulis*, small hydrophilic particles (2–3 μm) are generally captured at higher rates than their hydrophobic counterparts (Rosa et al. 2017). The tropical bivalve (*Leiosolenus* [*Lithophaga*] *simplex* [Iredale, 1939]) preferentially captured the photosynthetic bacteria *Synechococcus*, part of the SAR 11 family, at higher rates than similarly sized bacteria (Yahel et al. 2009). Thus, hydrophobicity appears to play a role in capture only in the smaller size range of particles, and these effects could be species dependent.

Capture efficiency of small particles (e.g., <6 μm) varies by species, and likely is dependent on ctenidial architecture and laterofrontal cilia/cirri microstructure. Mussels, for example, have a filibranchiate homorhabdic ctenidium with large compound laterofrontal cirri (Atkins 1938, Owen 1978) that could account for the reported high CE of particles in the 4- to 10-μm size range (Riisgård 1988, Rosa et al. 2015). Scallops have a filibranchiate heterorhabdic ctenidial structure with a single row of laterofrontal cilia (Atkins 1938, Owen & McCrae 1976, Beninger 1991) that seem to be inefficient at entraining particles not directly intercepted by the frontal surface. Generally, scallops have been reported to have low CE for 2–7 μm particles (Møhlenberg & Riisgård 1978, Riisgård 1988). Oysters have a pseudolamellibranchiate heterorhabdic ctenidium with developed laterofrontal cirri that are less complex than those of mytilids (Owen & McCrae 1976, Ribelin & Collier 1977) but generally have higher CE for particles greater than 3 μm than mussels.

Because of the known mechanical limitations of the bivalve ctenidium with regard to particle capture, feeding studies have generally focused on capture and ingestion of particles or microalgae larger than ~5 μm, with fewer papers examining the contributions of smaller particles to the bivalve diet. Palmer and Williams (1980) were some of the earliest workers to examine effects of particle concentration on CE of different sized particles. These authors preconditioned scallops (*Argopecten irradians* [Lamarck, 1819]) and oysters (*Crassostrea virginica*) by feeding them a monoalgal diet of 4- or 10-μm-size algae at six different cell concentrations (0.88–6.54 mg wet weight L^{-1}). They found no effect of this preconditioning on CE, suggesting that the size of microalgae available in the seston did not affect efficiency of particle capture. Interestingly, for scallops fed the 4-μm algae, CE was found to increase with increasing particle concentration, which the authors posited could be a result of increased mucus production in response to higher seston loads. The same effect was not found for oysters, and there was considerable variability in CE throughout the experiments at the different cell concentrations. The authors suggested that more research was needed to determine if bivalves could alter "efficiency of gill response" to any changes in the size class particles dominating the seston. Silverman et al. (1995) were among the few early investigators that examined the uptake of bacteria by bivalves. They found that freshwater mussels were able to uptake and use laboratory-cultured *Escherichia coli* with relatively high CR. On a weight-specific basis, the zebra mussel (*Dreissena polymorpha* [Pallas, 1771]) was able to ingest the smallest bacteria (1.7–2.9 μm) at rates 30–100 times faster than the other two mussel species [*Corbicula fluminea* (O.F. Müller, 1774) and *Toxolasma* (*Carunculina*) *texasensis* (Lea, 1857)] studied. The higher ingestion rate by *D. polymorpha* was attributed to a higher CE for the bacteria and a higher pumping rate, a consequence of a higher number of laterofrontal cirri and larger ctenidia, respectively, in this mussel compared with the other two species. In a later study, Hernroth et al. (2000) manipulated the cell surface characteristics (= charge) of bacterium *Salmonella typhimurium* cells (~1 μm) and fed them to mussels

TABLE 3.

Reported capture efficiencies (CE, 0–1) for particles 0.25–4 μm in size. Variability in CE reported between bivalve species and within species is provided depending on methods used. Efficiencies calculated based on reported values, unless the CE was provided in the referenced paper. Overall, some bivalve species have relatively high CE for small particles (0.25–4 μm), and not all capture efficiencies of small particles are effectively zero as has been reported in the early literature.

Bivalve species	Particle type	Size (μm)	CE	Method for calculating CE	Notes	Reference
Cardium echinatum	Seston + supplemental algae	1–4	0.50–0.98	Direct	Measurements averages on single counts of 4–9 individuals	Møhlenberg and Riisgård 1978
Cardium edule			0.35–0.90			
Venruptis pullastra			0.60–1.0			
Mytilus edulis			0.45–0.98			
Modiolus modiolus			0.55–1.0			
Musculus niger			0.45–0.90			
Arctica islandica			0.70–1.0			
Mya arenaria			0.20–1.0			
Cultellus pellucidus			0.50–0.90			
Hiatella striata			0.60–1.0			
Ostrea edulis			0.05–0.80			
Pecten opercularis			0.10–0.30			
Pecten septemradiatus			0.20–0.40			
Argopecten irradians	Microalgal suspension	1.7–4.3	~0.35	Flow-through	Approximated values based on reported CE of animals fed at low algae concentrations (0.88 mg wet algal wt mL^{-1})	Palmer and Williams 1980
Crassostrea virginica			~0.76			
Ostrea edulis	*Isochrysis galbana* (T. iso)	~4	0.98	Direct	High CE at algal concentrations below 10^5 cells mL^{-1}, at higher concentrations exponential decrease in CE.	Wilson 1983
Venus verrucosa	*Lactobacillus* sp. (bacterium)	0.5–5	~0.95	Static	Four animals per chamber used, difficult to determine individual CE	Amouroux 1986
Geukensia demissa	Seston + *I. galbana* (T. iso)	2–4	0.60–1.0	Static	Mean based on a single measurement of 2–5 animals	Riisgård 1988
Crassostrea virginica			0.50–0.80			
Mercenaria mercenaria			0.40–0.90			
Brachidontes exustus			0.30–0.70			
Argopecten irradians			0.10–0.80			
Spisula solidissima			0.50–0.90			
Crassostrea virginica	Bacteria	0.25–1.6	0.05	Flow-through		Langdon and Newell 1990
Geukensia demissa			0.15			
Placopecten magellanicus	Seston	3	0.41	Flow-through		MacDonald and Ward 1994
		4	0.41			
		5	0.60			
		6	0.70			
Dreissena polymorpha	*Escherichia coli*	2.3 L		Static		Silverman et al. 1995
Corbicula fluminea						
Carunculina texasensis						
Placopecten magllanicus	Seston	2–50	0.45	Biodeposition		Cranford and Hill 1999
Mytilus edulis		2–50	0.75			Hernroth et al. 2000
Lithophaga simplex	Seston (free bacteria fraction)	~0.4–0.9	0.41–0.69	Direct		Yahel et al. 2009
Mytilus edulis	Seston	1–4	~0.28–0.40	Flow-through	Mean calculated from reported seasonal CE	Strøhmeier et al. 2012

continued on next page

TABLE 3.

continued

Bivalve species	Particle type	Size (μm)	CE	Method for calculating CE	Notes	Reference
Mytilus edulis	Seston	1–4	0.27–0.60	Flow-through	Mean calculated from reported seasonal CE	Rosa et al. 2015
	Polystyrene particles	2	0.30	Direct	Mean calculated from reported values across seasons	
Mytilus edulis	Picophytoplankton	0.2–2.0	0.20	Static	Used natural seston and size fractonization of particles using FCM	Sonier et al. 2016

Data ordered by date of publication. See Particle Capture Efficiency for full discussion. Direct = bivalves' inhalant and exhalant flows are directly sampled; flow-through = animals are placed in chambers with flow-through water during sampling; Static = animals are placed in a closed container with no water exchange during sampling.

(*Mytilus edulis*). The bacteria with the manipulated surface charge were retained with the same efficiency as the larger control polystyrene particles (10 μm) and at a higher efficiency than the nonmanipulated bacteria.

In recent years, there has been an increase in research examining the contributions of picoplankton and other small particles (<4 μm) to bivalve growth. These studies have been driven by new technologies that allow for more precise quantification of small particles and collection of more robust data. Picoplankton are operationally defined as particles ranging from 0.2 to 2-μm in size, including the cyanobacteria and small eukaryotes that can numerically dominate the seston. Yahel et al. (2009) studied particle capture and selection by the burrowing bivalve (*Leiosolenus* [*Lithophaga*] *simplex*) in a semi-oligotrophic environment. Particle loads were low at this study site (~0.1 mg L^{-1} of POC) and ultraphytoplankton (2–8 μm) dominated the seston. Despite these conditions, bivalves were found to ingest some bacteria (*Synechococcus* and eukaryotic algae; Chesson's alpha = 0.5 and 0.3, respectively) preferentially over others (*Prochlorococcus* and nonphotosynthetic bacteria; Chesson's alpha = 0.2 and 0, respectively). More striking, the mean CE for the small photosynthetic bacteria *Synechococcus* (~0.9 μm) and *Prochlorococcus* (~0.4 μm) were 69% (±14 SD) and 41% (±19 SD), respectively. These findings demonstrate that *L. simplex* has higher CE for submicron particles than previously reported. LeBlanc et al. (2012) developed a method for quantifying isotopic-labeled proteins in the byssus threads of *Mytilus edulis* using chromatography and tandem mass spectrophotometry. To determine isotope uptake in tissue, mussels were fed a diet with labeled *Nannochloropsis* sp. and the assimilation of this diet into the protein fibers studied. Mussels were found to uptake nutrients efficiently from the microalgae (~2 μm) and with a relatively high capture rate explaining the observed incorporation. Sonier et al. (2016) also examined the contribution of picoplankton (0.2–2 μm) to the growth of the blue mussel (*M. edulis*) in field studies. The CE of mussels fed picoplankton ranged from 3% to 37%, with an average CE of 20% [2% sorting efficiency (SE)]. Estimates of the CE of the 2- to 20-μm particles were higher, ranging from 19% to 81% with an average CE of 60% (3.5% SE). The findings of Sonier et al. (2016) demonstrate that mussels can have a higher CE for particles less than ~3 μm than previously reported (e.g., Vahl 1972, Riisgård 1988). In the same study, Sonier et al. (2016) modeled the contribution of smaller particles to the mussel diet, and, for the first time, showed that picoplankton could be a significant proportion of the total net intake and contribute 13%–28% of the energy needed for tissue and shell growth in mussels. Similarly, *in situ* studies by Strøhmeier et al. (2012) reported mean a CE of 14%–43% for *M. edulis* feeding on 1-μm particles, with CE varying seasonally. Together, the aforementioned studies suggest that the contribution of small organic particles to bivalve energetics is likely higher than previously reported. Therefore, the importance of these small particles to bivalve diets should be reassessed, especially in environments where most sestonic particles are in the picoplankton size range.

Particle aggregation (flocculation) scavenges smaller particles, such as picoplankton and bacteria (Waite et al. 2000), which increases their bioavailability to suspension feeders. Marine aggregates (also known as. flocs) range widely in size, with the largest (marine snow) being greater than 500 μm in size, and can be broken apart by the ctenidia and labial palps (LP). Aggregates have also been shown to increase the ingestion efficiency of picoplankton by the scallop (*Placopecten magellanicus*) (Cranford et al. 2005) and enhance the uptake of dissolved matter by the scallop (*Argopecten irradians*) (Alber & Valiela 1995), and mussels (*Geukensia demissa* and *Mytilus edulis*) (Alber & Valiela 1994). Kach and Ward (2008) used picoplankton-sized particles (fluorescently labeled microspheres & *Escherichia coli*) in feeding studies with several suspension-feeding molluscs (*Mercenaria mercenaria*, *M. edulis*, *Crassostrea virginica*, *A. irradians*, and *Crepidula fornicate* [Linnaeus, 1758]). Microspheres and cells were delivered to the animals as free suspensions or incorporated into aggregates. Results indicated that except for the suspension-feeding snail (*C. fornicata*), all bivalves ingested significantly more of the aggregate-bound particles than the freely suspended particles. Thus, aggregation and floc formation serves as a mechanism for the efficient uptake of picoplankton and bacteria that are generally captured with lower efficiencies.

Less work has been conducted on the maximum size of particles that can be captured and ingested by suspension-feeding bivalves. Karlsson et al. (2003) carried out experiments on the cockle (*Cerastoderma edule* [Linneaus, 1758]) using different flow speeds and found that these bivalves could capture and ingest polystyrene and synthetic cellulose microspheres

between 100 and 500 μm in diameter. Capture efficiency for the larger particles increased with flow velocity, and the authors suggested that differences in capture were a matter of availability, that is, the higher flow rates resuspended the larger particles. Other studies also have suggested that bivalves can capture and ingest large particles and zooplankton. For example, the oyster (*Crassostrea virginica*) can capture and ingest polystyrene microspheres between 10 and 370 μm in diameter but the efficiency of ingestion decreases rapidly with particle size to less than 10% for 370-μm particles (Tamburri & Zimmer-Faust 1996). Interestingly, in the same study oysters ingested larvae of nine different invertebrate species, measuring between 100 μm and greater than 500 μm in length, at efficiencies of about 80%. The ability to capture larger particles means that bivalve grazing could affect zooplankton communities (Davenport et al. 2000, 2011), including aquaculture farms where bivalves are suspended in the water column in high numbers. A study by Shumway et al. (1987) examined the food sources of nearshore and offshore populations of the scallop (*Placopecten magellanicus*). Through gut content analysis these workers demonstrated that scallops are opportunistic feeders that prey on available seston. Species found in the gut ranged in size from 8 to 250 μm and included zooplankton tests and ciliates. The presence of some of the larger forms in the gut, however, may be indicative of their indigestibility, and the authors suggested that the contribution of large zooplankton to the bivalve diet is minimal. In a similar study, Peharda et al. (2012) examined grazing by four bivalve species (*Ostrea edulis*, *Mytilus galloprovincialis* [Lamarck, 1819], *Modiolus barbatus* [Linneaus, 1758], and *Arca noae* [Linneaus, 1758]) in the Adriatic Sea. Animals were collected monthly and stomach contents analyzed and compared with seston samples collected at the same time. Zooplankters were found in all bivalve species, with the cultured species (*O. edulis* and *M. galloprovincialis*) having higher abundances in their stomach than the native benthic species (*M. barbatus* and *A. noae*). Bivalve larvae were the most abundant zooplankton in all samples, followed by tintinnids and copepods. The methodology used in the study, which relied on gut contents for identification of ingested plankton, was limited because counts of species that are more easily digested could be underestimated. The aforementioned findings indicate that the effective size range of seston that suspension-feeding bivalves can capture is large and can be influenced by availability of the plankton.

Differential Capture

As described previously, historically CE has been attributed solely to particle size, with particles greater than some threshold size being captured at similar high efficiency (>95%; e.g., Ward & Shumway 2004). Some studies suggest, however, that particles of the same size can be differentially captured by bivalves, especially those that are less than 2 μm in size. These findings raise the question of whether observed pre-ingestive selection patterns are a consequence of, at least to some extent, differential capture. In other words, are some particles more likely to be captured than others and is this differential capture responsible for the differences in particle ratios between biodeposits (i.e., PF and feces) and the water column? If differential capture occurs, based on size (mechanistic) or the physicochemical properties of the particles, it could result in over- or underestimation of the postcapture selection response. The use of flow cytometric techniques (FCM) was an important advance in allowing scientists to examine the capture of similarly sized particles such as microalgae. Shumway et al. (1985) applied FCM to study particle capture in the European oyster (*Ostrea edulis*) and demonstrated that this species preferentially captured the dinoflagellate (*Prorocentrum minimum*) over a similarly sized diatom and flagellate (*Phaeodactylum tricornutum* and *Chroomonas salina*, respectively). The authors suggested that properties other than cell size resulted in the differences in capture. Differential capture was also demonstrated in the blue mussel (*Mytilus edulis*) (Cucci et al. 1985, Newell et al. 1989) and juvenile scallops (*Placopecten magellanicus*) (Shumway et al. 1997). Other studies have found no difference in the capture of similar size particles even when they differ in quality. Cranford and Grant (1990), for example, fed scallops a mixed diet of *Isochrysis galbana* (~5 μm), *Chaetoceros gracilis* (4–10 μm), macroalgal detritus (kelp 2–40 μm), and sediment organic matter (2–40 μm) and calculated the CE and CR of the various size classes. They found that CE was the same for similar-sized particles regardless of particle type. In addition, there are a few studies that have reported that smaller particles can be captured more efficiently than larger particles (Bayne et al. 1977, Lesser et al. 1991, Bougrier et al. 1997, Pile & Young 1999, Strøhmeier et al. 2012). For particles that are equal to or greater in size than the theoretical maximum CE, the mechanism(s) that would allow the ctenidium to capture particles of the same diameter differentially or capture small particles more efficiently than large particles have not been described. In fact, such results run counter to the current knowledge of the hydrosol filtration mechanism used by suspension-feeding bivalves (e.g., Riisgård et al. 1996, Ward et al. 1998, Riisgård & Larsen 2000, Riisgård et al. 2015). Rosa et al. (2015) examined this possibility with the mussel (*M. edulis*) using natural seston and microspheres of uniform shape and defined sizes. They found that microspheres greater than or equal to 4 μm in diameter were always captured at the same high efficiency regardless of variations in CE of natural particles. The authors suggested that the apparent inverse difference in CE (i.e., smaller particles being captured at a higher efficiency than larger particles) is a result of one or more of the following confounding factors; (1) instrument artifacts that can arise as a result of the way in which laser and electronic particle counters calculate equivalent spherical diameter to estimate particle size; (2) disaggregation of flocculent material collected from control chambers; (3) postcapture escape of highly motile microalgal cells from the infrabranchial cavity; (4) qualitative factors of the particles that could affect capture; or (5) mathematical happenstance of calculating CE on particle size classes that contain widely different numbers of particles.

Advances in the analysis of natural suspended particulate matter less than 2 μm in size (e.g., *in situ* laser analysis, portable flow cytometer, and next-generation DNA sequencing) have allowed researchers to probe the efficiency at which bivalves capture picoplankton (0.2–2 μm). Yahel et al. (2009), for example, examined *in situ* feeding in the tropical bivalve (*Leiosolenus* [*Lithophaga*] *simplex*) using a direct technique (InEx system) to sample ambient water before it entered the inhalant aperture and as it exited the exhalent siphon. They then used flow cytometry to differentiate between particle types and calculate CE for the particles. They found that *L. simplex*

preferentially retained the photosynthetic bacteria *Synechococcus* and larger eukaryotic algae. A small proportion of non-photosynthetic bacteria, sharing a size overlap with the retained photosynthetic bacteria, were not captured as efficiently. Similarly, Jacobs et al. (2015) reported differences in CE between particles of similar size. Picophytoplankton between 0.7 and 1 μm in diameter were found to be cleared at higher rates than bacteria (~0.6 μm in size) by *Mytilus edulis*, further suggesting that factors other than size affected capture. In their study, the authors reported that "optimal retention" plateaued for particles larger than 6 μm in diameter, with nanophytoplankton (~6 μm) and ciliates (10–200 μm) being cleared at similar rates. These findings indicate size-independent preferential capture, at least for particles less than 4 μm, and suggest that surface characteristics may contribute to particle CE. The process of differential capture based on qualitative factors of the particles would be a form of passive selection and understanding its mechanistic basis worthy of further exploration. It is important to note that the best evidence for differential capture is for particles below the size of maximum CE for a particular bivalve species (e.g., picoplankton), whereas data demonstrating differential capture of particles greater than 4 μm currently is inconclusive.

Shifts in CE

Several reports suggest that particle CE of bivalves can shift in response to changes in seston composition and concentration, and thus is physiologically plastic. Field studies by Stenton-Dozey and Brown (1992) on the clam (*Venerupis corrugate* [Gmelin, 1791]) demonstrated an effect of tides on CE. The clams captured particles 5–9 μm in size with the highest efficiency during low tide and particles 8–13 μm in size during high tide. Barillé et al. (1993) conducted laboratory and field experiments on the oyster (*Crassostrea gigas* [Thunberg, 1793]) to examine the effects of variable seston quality and quantity on CE. These workers found no effect of food quality on CE in laboratory or field experiments. They did, however, find an effect of seston loads on CE. At the lowest particle concentration, *C. gigas* captured particles larger than ~3 μm with an efficiency of ca. 70%. At the higher seston concentrations, CE was lower for particles ~3 μm in size (ca. 20%) and the highest for particles larger than 12 μm (ca. 100%). More recent efforts have focused on seasonal field experiments to examine variations in CE. Naddafi et al. (2007) used delayed fluorescence excitation spectroscopy to examine feeding selectivity by zebra mussels (*Dreissena polymorpha*) continuously over a period of several months (April to November). These workers calculated CR and used it as a proxy for CE (see section 3.1). During the months when food concentrations were low they found that the rate at which different phytoplankton groups were cleared did not vary. When food concentrations were high, mussels cleared dinoflagellates (37–200 μm) at significantly higher rates than the other available phytoplankton groups. The authors reported lower CR for cyanobacteria (9–900 μm) during the summer (July to August) and lower rates during the fall (September to October). Mussels preferentially cleared and ingested cryptophytes (9–50 μm) compared with chlorophytes (6–650 μm) and dinoflagellates (37–250 μm). This study demonstrated that zebra mussels can shift the rate at which certain cells are captured, presumably in response to food availability. The authors argued that the mussels regulate selectivity in response to food size. Based on their methods and experimental design, however, it is not clear if they could differentiate the effects of cell size versus other particle characteristics on capture and selection. Because the size of the rejected microalgae (e.g., chlorophytes and dinoflagellates) overlapped, it is likely that selection was based, at least in part, on cell properties of the algal species.

Strøhmeier et al. (2012) reported a seasonal variation in particle retention efficiency (= CE) in the mussel (*Mytilus edulis*). They used a flow-through method to simulate *in situ* conditions and calculated RE and CR based on the size distribution and concentration of available particles. Animals were reused at two sampling sites, with samples being collected six times between May and August. In late summer (August) when small particles (ca. 4 μm) dominated the seston, the workers reported a shift in CE with smaller particles being captured more efficiently than larger particles. Strøhmeier et al. (2012) concluded that mussels have the capacity to control particle retention mechanisms in response to a shift in seston composition. As described in **Particle Capture Efficiency**, however, these results are counter to the current understandings of the hydrosol filtration system used by bivalves, and the authors did not propose a mechanistic explanation for the observed shifts in CE. In a similarly designed study, Rosa et al. (2015) examined apparent seasonal shifts in CE of natural seston in *M. edulis*. During each sampling period (six times over 1 y), the researchers also simultaneously delivered uniform microspheres of different sizes as a control to the mussels. They reported that the capture of microspheres greater than or equal to 4 μm in diameter was consistently high across all sampling months, with only the 2-μm particles being captured at a lower efficiency than particles of greater size. The results for microspheres were different from those for natural seston, which did demonstrate apparent shifts in CE seasonally. Rosa et al. (2015) concluded that the CE of mussels is not physiologically plastic, at least for particles that are captured near 100% efficiency, and provided alternate explanations for the purported shifts in CE of natural seston over time (see **Differential Capture**).

In another study, Lopes-Lima et al. (2014) examined selective feeding by the freshwater uninoid (*Anodonta cygnea* [Linneaus, 1758]). They found that in the winter months, cyanobacteria made up a large portion of the gut contents (cells g^{-1}) even though these cells were less abundant in the seston. The authors suggested that seasonal and nutritional demands elicit a CE response by *A. cygnea*. Although intriguing, only a few specimens were collected at each sampling date ($n = 6$), and no data were presented on the surface properties of the cyanobacteria or whether these properties changed with season. Therefore, a physiologically mediated change in CE cannot be conclusively demonstrated. Taken together, the reports outlined previously provide little conclusive data that the CE in bivalves is physiologically plastic and responsive to shifts in seston composition. To better determine if bivalves can regulate CE, studies should include appropriate controls to ensure methodological artifacts or other confounding factors are not responsible for the apparent patterns in particle capture over time (Rosa et al. 2015, Cranford et al. 2016).

PRE-INGESTIVE SELECTION

Functional Morphology of Pallial Organs

After particles are captured by the ctenidia, the next step in the feeding process involves the transport of material toward

the mouth for ingestion. Both hydrodynamic and mucociliary transport mechanisms can be involved (Ward 1996). During transport, pre-ingestive particle selection occurs on the ctenidia and/or LP depending on the ctenidial architecture of the species (Fig. 2). Bivalves with homorhabdic ctenidia have only one type of ctenidial filament and generally demonstrate unidirectional transport of captured particles (no selection on the ctenidia). In some bivalve species with homorhabdic ctenidia, such as those belonging to the genus *Arca*, bidirectional transport on the ctenidia does occur (Atkins 1937). Although mechanistically possible, selection on the ctenidia by these species has not been conclusively demonstrated. In most homorhabdic species studied to date, captured particles are transported to the LP, where selection occurs. Bivalves with heterorhabdic ctenidia have at least two different types of filaments (e.g., ordinary and principal) and demonstrate bidirectional transport of captured particles. Material is transported either ventrally or dorsally on the ctenidia and then to the LP, where further selection is possible (see Ward 1996, Ward et al. 1997). Particle size and shape can affect particle selection on the ctenidia of these species. The orientation of large particles as they are captured by the ctenidia, for example, can preclude entrance into the principal filaments in *Crassostrea gigas* and *Crassostrea virginica* (Cognie et al. 2003, Mafra et al. 2009). When this happens the larger particles are sent to the LP, where they are rejected.

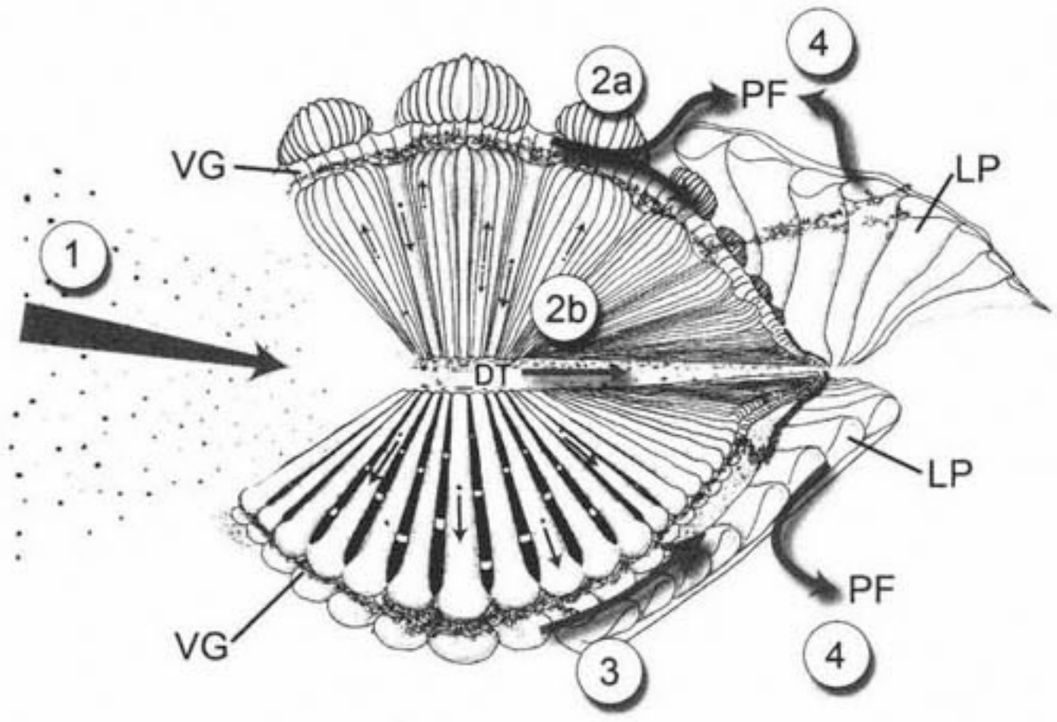

Figure 2. Composite diagram of bivalve ctenidia as observed using video endoscopy (orientation: ventral foreground and dorsal background). Upper ctenidium represents a heterorhabdic condition (e.g., oyster), whereas lower ctenidium represents a homorhabdic condition (e.g., mussel). Suspended particles enter the pallial cavity (1) and are captured by the ctenidium at an efficiency that depends on laterofrontal ciliary structure (see Fig. 1) and particle size. Once captured, particles are transported to the margins of the ctenidium by frontal cilia. In an oyster (top), bidirectional transport and particle selection on the ctenidium is possible. Particles are transported to the VG only on the ordinary filaments, whereas particles are transported to the dorsal tract on the principal filaments or on the ordinary filaments. Material in the VG (2a) is transported in a cohesive mucous string and can be rejected directly from the groove, forming PF or directed onto the LP for further processing. Particles in the dorsal tract are transported in a mucous slurry to the LP for further processing (2b). In a mussel (bottom), almost all particles are transported to the VG by the ordinary filaments (little, if any, bidirectional transport). Material in the VG (3) is transported in a cohesive mucous string to the LP for further processing. In both oysters and mussels, particle selection on the LP results in material either being rejected as PF (4), or ingested. Figure adapted after Ward (1996).

Particle sorting is mediated by the organs of selection, for example, ctenidia alone, or ctenidia and LP (Kiørboe & Møhlenberg 1981, Lesser et al. 1991, Bougrier et al. 1997, Bacon et al. 1998, Beninger et al. 2007, Rosa et al. 2013). Several studies have demonstrated the ability of bivalves to alter the area of the pallial organs in response to changes in seston composition and particle load concentration. Some bivalve species with populations living in turbid environments have been found to have larger ctenidium and LP areas than populations living in less turbid environments, including the blue mussel (*Mytilus edulis*) (Theisen 1982), the oyster (*Crassostrea gigas*) (Barillé et al. 2000), and the arcid bivalve (*Anadara* [*Scapharca*] *kagoshimensis* [Tokunaga, 1906]) (Yoshino et al. 2013). A study by Dutertre et al. (2009) used a combination of morphological biometrics and video endoscopy to demonstrate that differences in the size of pallial organs of the pacific oyster (*C. gigas*) had a functional effect on particle feeding. They found a morphological plasticity in the ratio of ctenidium to LP area that was correlated with the environmental turbidity to which the oysters were exposed. Palp size, but not ctenidial area, increased with higher levels of suspended particulate matter. In the laboratory, oysters from two different sites (high and low turbidity) were exposed to two concentrations of microalgae and clay. For oysters from both sites, selection occurred only on the ctenidia, and CR was positively related to ctenidial area at low particle concentrations. At high particle concentrations, oysters with smaller ctenidia (lower ctenidium to palp ratio) exhibited CR and SE that were positively correlated with LP area. Oysters with larger ctenidia exhibited lower CR, but without an effect on SE. These biometric measurements indicate that differences in ctenidial and palp size can influence pre-ingestive selection.

Garrido et al. (2012) carried out endoscopic examinations of two different bivalve species (*Mulinia edulis* [King, 1832] and *Mytilus chilensis* [Hupé, 1854]) both with homorhabdic ctenidia, and unable to select on this organ, that occupy different intertidal zones. The infaunal, siphonate spisulid clam (*M. edulis*) has a constriction at the tip of each LP, allowing articulation at the distal region and rotation about its axis. The motility of the palps allows it to manipulate rejected particles into a mucus-bound ball that is stored at the base of the inhalant siphon and expelled intermittently. Heavy ciliation of the mantle tract, which aids in PF elimination, was also found. The epifaunal, asiphonate bivalve (*M. chilensis*) was found to have shorter LP, which are heavily folded in the face directly contacting the ctenidial filaments. This morphology allows for the processing of coarse sediments that this bivalve encounters. When the suspended sediment load is high, PF is eliminated continuously via the inhalant aperture. By contrast, the LP morphology of *M. edulis* allows for processing of the finer material that this bivalve encounters. Together, the aforementioned findings further demonstrate plasticity in the morphology of the pallial organs of bivalves as a function of their habitat, even in animals with similar ctenidial architectures. Most importantly, this plasticity allows bivalve species to more efficiently process particles in environments with variable seston loads.

Mucus and Its Role in Particle Selection

Beyond the morphological differences in pallial organs, the production and composition of the mucus covering the ctenidia

and LP can vary between species and within a particular pallial organ. The role of mucus in particle capture and selection has been widely debated (see Ward & Shumway 2004 for an in-depth review), with early reports disregarding the role of mucus and suggesting direct ciliary activity was responsible for particle capture (e.g., Jørgensen 1966, 1975). Other early points of contention included how bivalves could select particles that were imbedded in mucus during the capture and transport processes. The role of ctenidial mucus in particle capture, transport, and selection was elucidated over several years via a series of experiments (see Foster-Smith 1978, Newell & Jordan 1983). The introduction of video endoscopy allowed for a better assessment of suspension-feeding processes (Ward et al. 1991, Beninger et al. 1992, Ward et al. 1993, Ward 1996) and confirmed the role of mucus in the feeding process. Direct endoscopic observations by Ward et al. (1998) also demonstrated that particles are captured by direct interception with the ctenidial filaments, and that retention of particles is likely enhanced by mucus present on the frontal surfaces or ordinary filaments. Further confirmation of mucociliary transport on the frontal surface of ordinary filaments (*Mytilus edulis*) was reported by Beninger et al. (1997) using confocal laser microscopy. The presence of mucus has also been demonstrated to aid in the uptake of viruses from the surrounding water. Di Girolamo et al. (1977) studied the adhesion of *Vibrio* species to mucus collected from *Crassostrea gigas*, *Ostrea lurida*, and *Mercenaria mercenaria*. These workers found that ionic or hydrogen bonding is responsible for the binding and rapid adherence of different virus species to the bivalve mucus. The combined results of *in vivo* examinations and mucocyte distribution studies clearly demonstrated the roles of mucus in particle capture and transport in bivalves (Beninger et al. 1992, Ward et al. 1993).

Complementing the nonspecific physicochemical interactions between mucus and captured particles, specific chemical constituents of mucus (e.g., agglutinins = lectins; Fisher & DiNuzzo 1991) also seem to be involved in particle discrimination. Work by Pales-Espinosa et al. (2010a) demonstrated that interactions occur between lectins in the mucus of pallial organs and carbohydrates present on the surfaces of microalgal cells. In several studies, these workers isolated mucus from the ctenidia and LP of oysters (*Crassostrea virginica*) (Pales-Espinosa et al. 2009) and mussels (*Mytilus edulis*) (Pales-Espinosa et al. 2010b), and measured specific lectin activity. Mucous extracts were able to agglutinate cells of several different species of microalgae, indicating binding to carbohydrates on the cell surface. Furthermore, treating microalgal cells with mucus from the pallial organs disrupted the ability of the bivalves to select between different species of microalgae. These studies suggest that a carbohydrate–lectin interaction is involved in mediating particle sorting in both *C. virginica* and *M. edulis*. Pales Espinosa and Allam (2013) examined the factors that affected gene expression of a mucosal lectin (MeML) on the ctenidia and LP of *M. edulis*. Transcript levels were found to vary seasonally in both pallial organs. In the ctenidia, the lowest levels were found in May (ripening of gonads in gametogenic cycle) and the highest levels found in November (associated with somatic growth). This trend was maintained regardless of the preconditioning diet to which mussels were exposed, suggesting endogenous factors in MeML transcript regulation. With regard to the palps, the opposite was observed when the mussels were exposed to a high quality diet, with higher levels in May and lower levels in November. Poorly fed mussels did not exhibit this seasonal trend in transcript expression, although there was an upregulation of MeML during some of the months. Sorting efficiencies were significantly correlated with MeML expression in the LP but not the ctenidia. These findings indicate that although bivalves have the capacity to alter lectin profiles in response to different food qualities, a factor that can change spatially, this response is not always immediate and may shift seasonally.

Physicochemical Properties of Particles

Physicochemical surface properties of particles, such as electrostatic charge and hydrophobicity (= wettability), are a set of factors that have been suggested to play a role in the particle sorting mechanism of bivalves (Newell et al. 1989, Beninger 1991). The physicochemical surface properties of organic and inorganic particles have been well studied as a way to explain the aggregation and flux of materials to the benthos. Tangentially, these studies have identified factors that may be used by suspension feeders in particle discrimination. Surface properties of phytoplankton have been reported to contain a relatively wide range of surface characteristics. Neihof and Loeb (1972) reported that organic particles of the seston (a mixture of bacteria, algae, and detritus) generally have a negative charge. Inorganic particles (e.g., glass, resin, and clay) also have a negative charge but had a lower range of surface charges. These charges were not correlated with particle size or aggregation. There are few reports of positively charged particles in seawater. Particles that have been reported to have a positive charge were typically inorganic marine sediments (Pravdic 1970) composed of clay, quartz, and iron in the 2- to 200-μm size range (+32 mV in seawater of salinity 36). The authors reported that the positive charge affects deposition and agglomeration, as surface charge reverses from a negative value in freshwater, to the measured positive value in estuarine water. The differences in charges between organic and inorganic particles have been partially explained by adsorbed organic constituents (Neihof & Loeb 1974). The surface chemistry of natural particles in seawater is controlled largely by the adsorption of organic matter (Abramson et al. 1942, Neihof & Loeb 1974, Hunter 1980), with carboxylic acid (-COOH) and phenolic (-OH) groups being some of the major ionizable functional groups identified in organic films (Hunter 1980).

Ozkan and Berberoglu (2013a) characterized various physical and chemical properties of five species of marine and freshwater microalgae. They reported variations in zeta potential (a proxy for surface charge) among species, although no consistent trends in properties among classes were found. In a follow-up study, Ozkan and Berberoglu (2013b) studied 10 different marine and freshwater microalgal species and six different inorganic substrate materials. They examined cell-to-cell and cell-to-substrata interactions, quantifying total interactive energy as a linear sum of the Van der Wall's interactions (attractive), electrostatic interactions (repulsive), and acid–base interactions (attractive in hydrophobic interactions and repulsive in hydrophilic interactions). Results demonstrated that the total interactive energy is a function of the distance between the interacting surfaces, with a negative interactive energy indicating adhesion and a positive interactive energy indicating

repulsion. These workers also noted that cells with larger diameters experienced larger attractive or repulsive forces than smaller cells under the same ambient conditions.

Given the range of physicochemical surface properties of suspended particles, speculation arose regarding whether these characteristics can be used by suspension feeders to differentiate between particles. In subsequent years, researchers examined the influence of surface properties on particle capture and selection by a range of pelagic and benthic suspension feeders (Hughes 1975, LaBarbera 1978, Gerritsen & Porter 1982, Hernroth et al. 2000, Rosa et al. 2013). Their findings helped define the interactions between particles (e.g., microalgae and detritus) and the capture units (e.g., setae, ctenidial filaments, and pharyngeal bars), and allowed for the design of experiments to better assess the underlying mechanisms of particle selection in bivalves.

Particle Discrimination—Passive Mechanisms

Once captured, particles can either be rejected before ingestion, or ingested and subjected to digestion. Early work on feeding selectivity demonstrated that bivalves can preferentially ingest some particles over others including selecting organic over inorganic material (Newell & Jordan 1983), microalgae over detritus (Ward et al. 1997, 1998), living over dead cells (Beninger et al. 2008b), and one type of microalgae over others (Shumway et al. 1985, 1997, Cognie et al. 2003, Mafra et al. 2009). This body of work showed that selection could be mediated by particle size, shape, surface properties, and other undefined characteristics (see Ward & Shumway 2004 and the following paragraphs). From an energetics point of view, this is advantageous as bivalves have generally been shown to have low absorption efficiency for detrital material, meaning that more energy is spent capturing and ingesting such particles than what the animal receives from digestion (Bricelj & Malouf 1984, Cranford & Grant 1990).

Most work on preingestive particle selection has demonstrated a passive sorting mechanism, even if the authors argue otherwise. As it is difficult to factor out selection based on differences in size, shape, and surface characteristics among various particles, specific and nonspecific passive interactions could be occurring between the particles and the pallial organs. Nonetheless, many examples of passive selection by a range of bivalve species exist and readers are referred to the review by Ward and Shumway (2004) for literature published before 2004. More recent work adds to the body of knowledge regarding passive selection mechanisms, but it also demonstrates that differences exist in the selection response between bivalve species exposed to the same mixture of particles. Thus, it is likely that the particle characteristics that mediate selection are species dependent. For example, Beninger and Decottignies (2005) used live and dead cells of the diatom (*Coscinodiscus perforatus*), whose epicellular frustules had been left intact and uncleaned, and found that all cells were handled similarly for the bivalve (*Pecten maximus*). Because no selection was noted between the live and dead cells of this diatom, the authors suggested that the organic casing (= frustule) and any associated organic molecules were factors mediating selection by the scallop, perhaps by being an indication of food quality. When the same experiments were repeated with *Crassostrea gigas*, the oyster was able to select between the diatom cells, rejecting the heat-killed diatom cells (Beninger et al. 2008b). These findings suggest that cellular status acts as a quality factor for selection in *C. gigas* but not in *P. maximus*. Similarly, Dutertre et al. (2007) found that *C. gigas* demonstrated preferential rejection of heat-killed *Tetraselmis suecica* over live cells and over the chain-forming diatom *Skeletonema costatum*. Kasai et al. (2004) used stable isotope techniques to compare seston and the tissues of two species of clams (*Ruditapes philippinarum* [Adams & Reeve, 1850] and *Mactra* [*veneriformis*] *quadrangularis* [Reeve, 1854]). Based on C^{13} and N^{15} isotopic signatures, most of the diet (90%) of these estuarine bivalves was of marine origin, with only 10% being of terrestrial origin. In the surrounding tidal flat, POM had higher levels of terrestrial constituents; therefore, tissue signatures were a result of selective feeding on both phytoplankton and marine detritus over terrestrial particles. In a mesocosm study by Frau et al. (2016), feeding selectivity in the mussel (*Limnoperna fortune* [Dunker, 1857]) was examined during exposure to natural phytoplankton assemblages. When rotifers were added to the diet, patterns of selection among different phytoplankton species were maintained even though rotifers were preferentially ingested by the mussels. The authors suggested that selection of the phytoplankton was because of a combination of cell shape and quality. Some cell types (belonging to the Volvocales, Cyptophyceae, and *Trachelomonas* sp.) were strongly rejected. This and other studies (Ward & Targett 1989, Rosa et al. 2013, 2017) show that patterns of selection are not fixed, and in some cases, selection can change depending on the type of particle delivered to the animals.

Although the authors of many past studies suggested that qualitative "cues" of the particles elicit a selection response by the bivalve, physicochemical surface properties were not determined and differences in these characteristics among particles were unknown. Therefore, an active selection response cannot be conclusively implicated (see section 4.5). To define further the influence of physicochemical properties of particles on selection, Rosa et al. (2013) experimentally assessed the effects of wettability and surface charge on pre-ingestive particle selection by the eastern oyster (*Crassostrea virginica*) and blue mussel (*Mytilus edulis*). The authors quantified the surface properties of several types of synthetic microspheres composed of polystyrene, silica, and alumina. They delivered the microspheres in different pairings to individual animals, determined the number of each sphere type in collected biodeposits, and calculated a selection index. Results from this study demonstrated that both bivalve species could discriminate between particles of the same size based on the quantified surface properties. For example, highly wettable (= hydrophilic surface) alumina microspheres were consistently and strongly rejected by both species of bivalve regardless of the specific particle pairing used. The authors also characterized the surface properties of several detrital particles and a microalga to determine if differences in surface properties were observed among particles regularly encountered by bivalves under natural seston conditions. The results indicated that further characterization of microalgae and detrital particles were needed to explore fully the role of surface properties as determinants of selection in suspension feeders.

In a follow-up study, Rosa et al. (2017) demonstrated that both physical (charge and wettability) and chemical (carbohydrates) surface properties of microalgae affect the selection processes of *Mytilus edulis* and *Crassostrea virginica*. Distinct surface property profiles were reported for 10 different

microalgal species, with a wide range of surface charges and hydrophobicity. Further, some lectins (e.g., *Pisum sativum* agglutinin) strongly bound to the sugars on the cell surfaces of all tested microalgal species, and other lectins had high specificity for the sugars on the cell surfaces of one or two algal species only. The bivalves were found to use distinct surface properties to discriminate between microalgal species resulting in strong preferential ingestion or rejection. Most commonly, microalgae with a midrange of surface charges, hydrophobic surfaces, and cell surfaces generally rich in glucose and mannose sugar residues were preferentially ingested. Data from microalgal characteristics and feeding experiments were used to generate statistical models for predicting selection in both bivalve species. Notably, there were differences between the particle selection models generated for mussels and oysters, which the authors attributed to the loci of selection, which are different in these two species of bivalve. In a similar study, Pales Espinosa et al. (2016) determined lectin-binding profiles of different species of microalgae and fed them in pairs to *M. edulis* and *C. virginica* to model food selection in these species. They too found differences in lectin-binding activity depending on microalgae species, and results indicated that the microalgal species preferentially ingested by the bivalves had cell surfaces generally rich in glucose and mannose sugar residues. These workers then generated statistical models of particle selection by mussels and oysters, using lectin profiles to predict the likelihood of a particle being selected. Although predictive models were generated, the results of Pales Espinosa et al. (2016) should be interpreted with caution as these workers pooled data obtained for *M. edulis* and *C. virginica* to generate one classification model. Given the clear differences in the way in which mussels and oysters handle particles, such an approach is problematic and yields a model with questionable applicability to either species. Results of the experiments outlined previuosly all indicate that specific physicochemical properties of particles are factors that mediate selection, suggesting that specific and nonspecific interactions between particles and feeding organs underlay particle selection.

Particle Discrimination—Active Mechanisms

Active particle selection would depend on a chemosensory response to food stimuli that elicits a change in ciliary action of the feeding organs. Bivalves can detect and respond to dissolved chemicals (Loosanoff & Engle 1947, Birckbeck et al. 1987, Shumway & Cucci 1987, Ward et al. 1992, Ganesan et al. 2012), and the presence of distance chemoreception in many species is well documented. The ability of bivalves to perceive chemical cues of particles once they are captured has not been demonstrated. Numerous neurobiological studies have found that lateral ctenidial cilia can be stimulated via mechanical and chemical means (Aiello 1960, 1970, Jørgensen 1975, Malanga 1975, Davenport & Fletcher 1978, Malanga et al. 1981, Catapane 1983, Carroll & Catapane 2007, Frank et al. 2015) and are innervated. Studies examining stimulation of the frontal cilia have not found that they are innervated (Aiello 1970). One prerequisite for an active selection response would be the "recognition" of particles of different quality followed by translocation from one transport tract (e.g., acceptance tract) to an adjacent one (e.g., rejection tract; see Ward & Shumway 2004). In most suspension-feeding bivalves, such a process would likely occur via ciliary mechanisms on the frontal surface of ctenidial filaments and inner surface of the LP. Endoscopic observations of particle movement demonstrate that, in most cases, particles transported by these cilia are within micrometers of the ciliated surface (<5 μm), so changes in beat angle or frequency would translate to changes in particle movement (Ward 1996).

For contact chemoreception by the ctenidia and LP to be possible, bivalves would need both receptors and innervated cilia and epithelium. Chemoreceptors and ciliary innervation have been found in some pallial organs. Hodgson and Fielden (1984) found three types of ciliary receptors in the siphons and mantle edge of two species of bivalves. The authors suggested that the cilia function as chemoreceptors. Morphological investigations of the mantle and siphons of several bivalve species have demonstrated that these tissues have sensory organs, with the degree of ciliation varying between species (Fishelson 2000). To our knowledge, only one study has attempted to determine the presence of chemoreceptors on the feeding organs of bivalves. Dwivedy (1973) examined the presence of chemoreceptors on the LP of *Crassostrea virginica* by using microelectrodes attached to the tissue and exposing the whole animal to chemicals known to stimulate taste receptors, specifically sodium chloride (NaCl), hydrochloric acid (HCl), quinine sulfate, and sucrose. He reported that different concentrations of these substances resulted in a change in receptor potential, suggesting that oysters were probably able to discriminate between the different chemicals. Results of this experiment have been questioned, however, because of methodological errors. In particular, the size of the electrodes Dwivedy (1973) used (20 μm) was larger than the receptor cells, which would lead to a pseudo-response with any physical movement of the receptor. This means that the author could not definitively show that a signal was a result of a chemosensory response, a point that the author acknowledged. Although it is possible that bivalves use contact chemoreception to mediate particle selection, to date there are few, if any, data that support the involvement of such an active selective mechanism.

The response by the frontal ctenidial cilia to dissolved extracellular and intracellular metabolites from phytoplankton was experimentally assessed by Rosa (2016). *In vivo* assays were carried out to examine particle transport by the frontal cilia of the eastern oyster *Crassostrea virginica* when exposed to exudates and extracts of *Tetraselmis chui* cells. Oysters are known to select particles on the gill (Bougrier et al. 1997, Ward et al. 1997, 1998, Beninger et al. 2008b), with those directed ventrally more likely to be rejected than those directed dorsally (Ward et al. 1994). Addition of metabolites had no significant effect on the transport, either dorsally or ventrally, of particles captured on the frontal surface of the ctenidia. Furthermore, microspheres with covalently bound neoglycoproteins (D-mannose or N-acetyl-glucosamine), which altered the physicochemical properties of these particles, resulted in a selection response. When given a choice, the N-acetyl-glucosamine microspheres were generally ingested, and the D-mannose microspheres were generally rejected. Although contact chemoreception could not be completely ruled out, these findings further indicate that physicochemical properties of particles, and not an active behavioral response (i.e., chemoreception of dissolved metabolites), mediate particle selection in bivalves. Although the process of pre-ingestive particle selection has been well studied

and demonstrated, the actual mechanism(s) involved in discriminating among particles and the mechanism(s) that allows different types of particle to be guided to different ciliary tracts (i.e., acceptance, rejection) remain elusive.

METHODOLOGICAL CONSIDERATIONS

In examining the literature on particle capture and selection in bivalves, it is apparent that between-study differences in measured parameters are sometimes high. Although some of these variations can be ascribed to seasonal conditions and individual variation, differences in applied methodologies and experimental designs likely are responsible for a portion of the interstudy differences. Summarized in the following paragraphs are some of the methodological challenges that should be considered when planning feeding experiments with bivalves, and several "best practices" for future studies are suggested. Static, flow-through, and biodeposition methods have been used to determine CR. Cranford et al. (2011) provided a comprehensive review of the literature regarding these methods as they relate to CR calculations, and the reader is referred to that paper. Capture efficiency has also been measured using static and flow-through methods and to a lesser extent the biodeposition method (e.g., Cranford et al. 2005). Generally, CE is measured indirectly, with the efficiency determined as particles are depleted from a constant volume (static system) or constant flow (flow-through system) of water. Most experiments that assess particle capture (71% of the articles in this review) used the indirect method. In a static system, animals are placed in a closed beaker and particle depletion is measured over time. In such systems, recirculation of water can yield errors in CE, as several passes of water over the ctenidia will result in a higher removal of particles than would otherwise be observed (see Williams 1982). In a flow-through system, a set water flow rate is used, generally more than 100 mL min^{-1} (see Widdows 1985), and particle depletion calculated over time (Table 2). If flow rate is too slow or feeding behavior is flow dependent, this method may yield incorrect CE. Recently, the direct method for measuring CE has gained traction. In this method, particles of interest are directly delivered to the inhalant aperture/siphon and water exiting the exhalent aperture/siphon sampled at the source (e.g., InEx system, Yahel et al. 2005). This method generally allows for a more accurate count of all the particles in the water that are not captured. As with the measurement of CR, there are several sources of error that need to be considered when calculating CE. Bivalves use a hydrosol filtration mechanism to capture particles (Shimeta & Jumars 1991, see **Background**); therefore, any particle will have a probability of being trapped on the ctenidial filament regardless of size. In a static system, larger particles (e.g., >10 μm) will be captured more efficiently and removed from suspension faster compared with smaller particles (e.g., <3 μm). A portion of the smaller particles will then be available for refiltration and additional removal (Williams 1982). Given that pumping rates of many bivalve species are on the order of several liters per hour (per gram dry tissue mass), in a small chamber (e.g., 1 L) an adult bivalve could reprocess the entire volume of water many times in 1 h. This circumstance would lead to an overestimation of the CE of small particles because they will have been processed by the ctenidia several times. Therefore, when determining CE in a static system the following best practices, outlined previously for CR measurements (Coughlan 1969, Williams 1982), should be followed: (1) chambers need to be well mixed, (2) expected pumping rate of the bivalve species needs to be considered, and (3) the time course over which samples are collected should be adjusted accordingly so that water is processed only once. The CE of different size particles should then be standardized to the particle size with the highest efficiency (see in the following paragraphs). With regard to measuring CE in flow-through chambers, two general techniques have been used. In the first method, water entering and exiting the chamber are sampled and the particle size distribution determined (e.g., MacDonald & Ward 1994). In the second method, samples are taken directly from the inhalant and exhalant flow produced by the animal and particle distribution determined (e.g., InEx method of Yahel et al. 2005). In the first method, as long as there is minimal recirculation of filtered water, reliable CE can be calculated. As it is virtually impossible for all of the water flowing through the chamber to be accessed by the bivalve, only relative CE can be calculated. Efficiencies can be standardized, however, by dividing the relative CE of each particle size by the highest relative efficiency, thus setting the highest efficiency to 100% (Cranford & Grant 1990, Cranford & Gordon 1992, MacDonald & Ward 1994). By contrast, the InEx method allows for a direct measure of CE because water is sampled from the inhalant and exhalant feeding currents produced by the bivalve. Care must be taken to adjust the sampling rate (mL/min) to match as closely as possible the rate of flow of the feeding currents. By doing so, the amount of ambient water sampled can be minimized.

Comparing the results of CE experiments conducted in flow-through chambers using indirect (chamber inflow and chamber outflow) and direct (InEx) techniques, differences are apparent. Some of the variation could be a result of the two different sampling techniques and some could be a result of the types of particles used to determine CE (see in the following paragraphs). The results from experiments using a direct sampling method (e.g., Yahel et al. 2009, Strøhmeier et al. 2012, Rosa et al. 2015) indicate that mean CE of 2–4 μm particles can range from 40% and 80% for mussels, and 20% and 60% for scallops. By contrast, results obtained using indirect methods have reported the CE for similar sized particles to be between 20% and 60% for mussels, and 0% and 20% for scallops (e.g., Møhlenberg & Riisgård 1978, Palmer & Williams 1980, Riisgård 1988, Newell et al. 1989) Confounding attempts to identify the source of this variation is the fact that most studies which used direct techniques have been carried out with natural seston, whereas many studies that used indirect techniques have used monoalgal cultures. Field studies have shown that the use of natural seston assemblages can lead to results that differ from those obtained using mixed microalgal diets in the laboratory. For example, data published by Barillé et al. (1993) showed that the CE of the Pacific oyster (*Crassostrea gigas*) calculated based on field experiments were lower than those calculated for concurrent laboratory experiments using the same seawater spiked with microalgae, even though the particle loads were similar. The capture efficiency ranged from 43% to 70% for the 3-μm particles in the laboratory experiments, whereas in the field experiments the CE ranged from 10% to 27% for the same sized particles. Similar differences in retention efficiencies and CR between field and laboratory studies have also been reported (Barillé et al. 1993, Petersen et al. 2004, respectively). By contrast, some studies using bacterial

cultures and natural seston assemblages have reported a higher CE of 1- to 2-μm particles (e.g., Hernroth et al. 2000, Rosa et al. 2015). If bivalves indeed capture smaller natural particles (e.g., picoplankton) at higher efficiencies than previously reported, both the methods used to determine the CE and the contribution of these particles to molluscan energetics may warrant reexamination.

Another source of variation in determining CE can be attributed to the type of particle analyzer used to size and enumerate experimental particles. Recently, Rosa et al. (2015) demonstrated that the use of different particle counters can result in differences in calculated CR and CE. In a seasonal study on the mussel (*Mytilus edulis*), these workers analyzed the same water samples by means of both an electronic particle counter (Coulter Multisizer IIe) and laser *in situ* scattering transmissometry (LISST-100x; Sequoia Inc.). They found that CR ranged between 0.67 and 3.34 L h^{-1} and were similar to rates reported previously for *M. edulis* of similar size (MacDonald & Ward 2009, Cranford et al. 2011). More importantly, Rosa et al. (2015) reported that in two of the months (September and December) data collected by the LISST-100x indicated a significant decrease in the CE of particles within the 11–25 μm size class compared with smaller sizes between 4 and 10 μm but no significant differences in CR between these two size classes. Conversely, data collected using the Coulter Multisizer in September indicated no significant difference in the CE between particles in the 11- to 25-μm and 4- to 10-μm size classes but a significantly lower CR for the smaller size particles. In addition, for many of the months studied (e.g., May, September, December, and March 2014), CR calculated from data generated by the LISST was significantly different than that generated by the Multisizer. These findings demonstrate that the instrument used to analyze samples may yield different results, even when using the same experimental design and water samples, and therefore affect the conclusions of the study.

With regard to pre-ingestive particle selection, differences in selection responses of bivalves between field and laboratory experiments have also been reported. One possible explanation for this discrepancy is the use of static versus flow-through systems to measure physiological traits. The amount of PF produced by some bivalves is partially dependent on particle concentration (Bayne et al. 1977), meaning rapidly declining particle concentrations in static systems can result in small amounts of PF being produced (e.g., Pales Espinosa et al. 2016). Lower PF productions in turn lead to difficulties in accurately quantifying the number of each particle type in the collected samples and a less reliable instantaneous assessment of selection. By contrast, a flow-through system delivers a constant concentration of particles over a longer period of time, and under constant conditions, a greater quantity of PF may be produced. In selection studies, a flow-through system allows for a more accurate determination of the ratio of particles in food and PF and more robust time-averaged assessment of selection (e.g., Petersen et al. 2004, Rosa et al. 2017). Such methods ultimately lead to stronger models and more consistent results than experiments that used a static system with decreasing particle concentration over a short period of time.

In summary, the aforementioned studies demonstrate that for a more comprehensive understanding of particle feeding and selection in bivalves to be realized, more standardized methodologies need to be used. It is suggested that the most accurate measures of CR, CE, and particle selection efficiency will be obtained using flow-through chambers, direct sampling of inhalant and exhalant water, and natural assemblages of particles and cells. Attention should also be paid to the instrument used to quantify the particle size distribution with consideration of the experimental design.

CONCLUSIONS AND FUTURE DIRECTIONS

In the past century, particle selectivity in suspension-feeding bivalve molluscs has been extensively studied (see Ward & Shumway 2004 and references therein). Researchers have independently examined the types of particles captured, rejected, and ingested by this group of organisms in an effort to understand the types of particulate matter used as food. The extensive extant literature has shown that, generally, where selection occurs, bivalves select organic and living particles over inorganic and detrital material (Bayne et al. 1977, Kiørboe et al. 1980, Iglesias et al. 1992, Ward et al. 1997, Safi et al. 2007, Beninger et al. 2008b). Bivalves can discriminate between different microalgal species, preferentially ingesting some over others. This discrimination, however, is not 100% as particles that are less desirable are still ingested but in lower quantities (Shumway et al. 1985, Cucci et al. 1985, Ward et al. 1997, Baker et al. 1998). Furthermore, at low particle concentrations, bivalve species "dampen" their selection response and ingest most of the particulate material available (Newell et al. 1989, Iglesias et al. 1996, Hawkins et al. 1999, Beninger et al. 2008a). Differences in selective capabilities between species of bivalves have been demonstrated (e.g., Lesser et al. 1991, Bougrier et al. 1997, Bacon et al. 1998, Levinton et al. 2002, Beninger et al. 2007, Pales Espinosa et al. 2010b, Rosa et al. 2013), suggesting that not all bivalve species rely on the same physicochemical factors for selection. Some of the differences in SE between mussels and oysters, two of the most studied bivalve species, may be a result of the different ctenidial architectures they possess and the loci of selection (Ward et al. 1997, 1998). Other species demonstrate a range of capabilities. The lack of general "rules" for particle selection has made it more difficult to design studies that elucidate the mechanisms behind particle selectivity.

Most published studies suggest that a passive selection mechanism directs particle discrimination, with the physicochemical properties of different particles interacting with the mucus covering the pallial organs directing particle fate. To date, few studies support an active contact chemoreception component. The lack of evidence, however, does not mean such a mechanism is nonexistent, and more definitive studies are needed and will undoubtedly require development of new techniques and technologies. Clearly it is difficult to separate active responses from passive effects but research focused on a paracrine signaling, a form of cell-to-cell communication where one cell produces a signal to induce a response in a nearby cell, could shed light on the issue.

As new technologies (e.g., FITC and isotopic labeling, field-based particle analyzers) and methods for studying particle capture and selection in suspension-feeding bivalves arise, older reports and assumptions need to be revisited. In particular, the underlying causes for differences in the feeding responses of bivalves under field and laboratory conditions need to be better defined, as does the CE of picoplankton which may be higher than previously reported. The effects of particle

surface properties, including epicellular chemicals, on CE and SE is another area that requires further investigation. For CE, such factors may be particularly important at the lower size class threshold (e.g., ≤4 μm) and, if so, the contribution of picoplankton as a food resource for bivalves may be greater than previously recognized.

Although the process of pre-ingestive particle selection has been well studied and demonstrated, the actual mechanism(s) involved in discriminating among particles and the mechanism(s) that allows different types of particles to be guided to different ciliary tracts (i.e., acceptance, rejection) remain elusive. Recent studies offer strong evidence for the role of passive mechanisms in mediating selection. Essential to the selection process are the interactions, both specific and nonspecific, between the surface properties of particles and the constituents of mucus produced by the feeding organs (e.g., Rosa et al. 2013, Pales Espinosa et al. 2016, Rosa et al. 2017). Further defining these mechanisms and determining the role, if any, of an active selection mechanism are fertile areas for future research.

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