



Influence of diet on pre-ingestive particle processing in bivalves

I: Transport velocities on the ctenidium

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Abstract

Suspension-feeding bivalve molluscs can assume a large ecological role by linking benthic and pelagic ecosystems. Therefore, a knowledge of the factors that influence feeding rates and processes at the level of the individual is important in understanding bivalve-dominated environments. We examined the roles of diet quality and concentration on particle processing by the ctenidia of four species of bivalves: the mussels *Mytilus edulis* L. and *Mytilus trossulus* Gould, and oysters *Crassostrea virginica* (Gmelin) and *Crassostrea gigas* (Thunberg). Bivalves were delivered diets of three different qualities at three different concentrations ($1-2 \times 10^3$, 10^4 , 10^5 particles ml^{-1}). The high-quality diet consisted of the cryptophyte *Rhodomonas lens* Pascher et Ruttnr; the low-quality diet consisted of particles prepared from ground *Spartina* sp. detritus; the medium-quality diet consisted of a 50:50 mixture (by particle number) of both particle types. Particle transport velocities on the ventral groove and dorsal tracts were then measured by means of video endoscopy. Ventral-groove transport velocities of *M. edulis* were the most responsive, demonstrating a significant increase with increasing diet quality, and a significant decrease with increasing diet concentration. Transport velocities in the ventral groove and dorsal tracts of *C. virginica* were not significantly affected by changes in diet quality, but significantly increased with increasing diet concentration. Transport velocities of *M. trossulus* and *C. gigas* demonstrated little change with diet quality or concentration, indicating that responses are species specific. Our data suggest that differential control of particle transport on the bivalve ctenidium is one of the underlying mechanisms that contribute to compensatory feeding responses exhibited by the entire organism.

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1. Introduction

Dense populations of suspension-feeding bivalve molluscs, such as oysters and mussels, play dominant roles in the ecology of coastal ecosystems. Bivalves not only convert heterogenous mixtures of suspended material into animal flesh that can be used by higher trophic levels, but also are one of the strongest interactors in shallow water benthic–pelagic coupling (Dame, 1993a,b, 1996). Through suspension-feeding activities, bivalves can strongly affect pelagic and benthic processes by removal of phytoplankton, deposition of feces and pseudofeces, and cycling of dissolved nutrients to the water column. Tight coupling may lead to stimulation of phytoplankton blooms (Lewin et al., 1975), depletion of phytoplankton (Cloern, 1982; Officer et al., 1982), changes in phytoplankton composition (Baker et al., 1998), or more complex ecosystem level effects (Dame et al., 1984; Newell, 1988; McKee, 2002).

Bivalve molluscs are exposed to a suspended food supply that varies in size, concentration, and quality, over both spatial and temporal scales. The food source includes material supplied directly from the water column or by resuspension events (Frechette et al., 1989; Judge et al., 1993). The way in which bivalves mediate benthic–pelagic processes is complicated by the fact that very few particle feeders are so simple that they merely encounter particles, engulf them, and excrete metabolic end products. Rather, in bivalves there is strong evidence that changes in the content of non-nutritive particles elicit compensatory feeding responses (Bayne et al., 1987, 1993; Iglesias et al., 1992; Barille et al., 1993; Bacon et al., 1998; Hawkins et al., 1998; Cranford and Hill, 1999; Levinton et al., 2002). Studies have also indicated differential handling of particles by bivalve pallial organs (Ward et al., 1997, 1998a) and qualitative selection (Newell and Jordan, 1983; Prins et al., 1991; MacDonald and Ward, 1994; Bougrier et al., 1997; Defosse and Hawkins, 1997; Ward et al., 1998a; Brilliant and MacDonald, 2000), even of similar-sized particles (Shumway et al., 1985, 1997; Ward and Targett, 1989; Ward et al., 1997). Therefore, the way in which bivalves deal with the heterogenous mixture of suspended particles could affect the quantity and quality of material that is cycled back to the water column or delivered to the benthos via pseudofeces and feces.

In order to understand the issue of particle processing in relation to water column supply, it is crucial to have a mechanistic understanding of the feeding activities of bivalves, including clearance rates, organic and inorganic particle sorting, ingestion capacities, digestion efficiencies, and the potential feedback mechanisms that integrate and coordinate these feeding functions. Equally important is an understanding of how changes in concentration and quality of suspended material affects the coordination of suspension-feeding mechanisms and the ability of bivalves to respond to changing particle regimes to optimize energy intake. Although a large body of data exists concerning the behavioral and physiological responses of bivalves to changing environmental conditions (e.g., Hawkins and Bayne, 1992; and see papers in Dame, 1993a; Bayne and Warwick, 1998), the underlying mechanisms accountable for these responses are largely unknown. In particular, there is a paucity of information on how the major feeding organs, ctenidia and labial palps, respond to changing particle regimes or gut fullness. This includes little information on the factors that mediate the velocity at which material is transported along the ctenidia. From the few studies that do exist (Beninger et al., 1992; Levinton et al.,

1996; Richoux and Thompson, 2001), there is compelling evidence that changes in particle collection and transport may serve as a mechanism to regulate the amount of material delivered to the labial palps and ultimately to the mouth for ingestion.

Studies using tools such as endoscopic examination and confocal microscopy have provided unique insights into the fine-scale feeding processes of bivalves (Ward et al., 1993, 1994, 1998b, 2000; Tankersley, 1996; Beninger et al., 1997; Baker et al., 2000), and conceptual models of particle capture and processing have been developed (Levinton et al., 1996, 2001; Ward, 1996; Ward et al., 1998b). In this study, we used video-endoscopy to examine how changes in the quantity and quality of suspended material affect particle transport velocities within the ventral grooves and dorsal tracts of the ctenidia of four species of suspension-feeding bivalves. The goal of our research was to begin quantifying the rate functions associated with particle handling and feeding to obtaining data on feeding processes at the scale of the pallial organs. A knowledge of the mechanisms of particle processing at the level of the individual could contribute to a better understanding of processes at the population level (Dame, 1993b).

2. Materials and methods

Four species of bivalve molluscs were examined in our study; two from the east coast and two from the west coast of the United States. On the west coast, the Pacific oyster, *Crassostrea gigas* (Thunberg), and the foolish mussel, *Mytilus trossulus* Gould, were obtained from Westcott Bay Farms (San Juan Island, WA) during the months of July and August. Bivalves were transported to facilities at the University of Washington's, Friday Harbor Laboratories (San Juan Island, WA) where experiments were conducted. On the east coast, eastern oysters, *Crassostrea virginica* Gmelin, were obtained from the Cornell Cooperative Extension Hatchery (Southold, NY) during the months of May, June, July, and October. Blue mussels, *Mytilus edulis* L., were collected from local populations in Long Island Sound near the University of Connecticut's, Avery Point campus (Groton, CT) during the months of February, May, June, and July. Oysters and mussels were transported to the Department of Marine Sciences' laboratory at Avery Point where experiments were conducted. In all cases, bivalves were acclimated to experimental conditions in unfiltered, flowing seawater and maintained on a diet of naturally occurring particles supplemented with cultured phytoplankton.

Particle transport velocities on the ctenidia of bivalves were examined by means of video-endoscopy (Ward et al., 1991). Adult oysters (9 to 15 cm in shell height) and mussels (6 to 8 cm in shell length) were prepared for endoscopy using methods described previously (Ward et al., 1993, 1998a). Specimens were cleaned of debris and encrusting organisms, and a small section of shell was trimmed from the inhalant margin of the upper and lower valves without damaging the underlying mantle margins. Trimming produced a narrow opening in the shell that provided more freedom of movement for the optical insertion tube (OIT) of the endoscope, and prevented the shell edges from damaging the OIT when the specimen adducted its valves. Bivalves were allowed to recover for at least 1 day after preparation, and they usually began repairing their shells shortly after the recovery period.

Bivalves were fed diets of three different qualities at three different concentrations ($1-2 \times 10^3$, 10^4 , 10^5 particles ml^{-1}). The low-quality diet consisted of particles prepared from ground leaves and stems of *Spartina* sp. ($<20 \mu\text{m}$), a major constituent of detritus in many coastal environments on the east coast of the United States; the high-quality diet consisted of the cryptophyte *Rhodomonas lens* Pascher et Ruttner ($6-13 \mu\text{m}$), a microalga the bivalves readily consume (Ward et al., 1998a); and the medium-quality diet consisted of a 50:50 mixture (by particle number) of both particle types (=Mixed). *R. lens* was grown in batch culture on f/2 media. Aged *Spartina* sp. detritus was collected from wrack in the supratidal zone, which probably had spent months or more decomposing. Particles were prepared by grinding dried leaves and stems of *Spartina* sp. in a laboratory blender for approximately 5 min, and then collecting particles which passed through a $20\text{-}\mu\text{m}$ sieve (Ward et al., 1997, 1998a). This procedure produced a range of particles that overlapped with that of the *R. lens* culture (Ward et al., 1998a,b).

Suspensions of each diet at each concentration were prepared and then delivered to bivalves in transport velocity assays. For an assay, one bivalve was placed in the aerated, assay chamber (1.0 l) filled with one of the three diet suspensions at one of the three concentrations. Bivalves were allowed to open and feed on the diets for at least 15 min before endoscopic observations were made. A few drops of a tracer-particle suspension ($10 \mu\text{m}$ yellow, polystyrene microspheres) were then added and observations of the appropriate ctenidial food tracts made on animals that were feeding normally (i.e., extended mantle edges or siphons, drawing particles into the pallial cavity). Recordings were made periodically over a 10- to 15-min period. Particle concentration in the assay chamber was monitored during the exposure period using an electronic particle counter, and the chamber was flushed with additional volumes of the appropriate suspension when needed. Each bivalve was exposed to each diet by concentration treatment for 0.5 to 1.5 h depending on the feeding activity of the specimen. When observations were complete, the same bivalve was exposed to another concentration of the same quality diet. To control for changes in gut fullness as the bivalves were exposed to successive particle concentrations, the order of delivery of the three concentrations was changed for every other specimen. To increase particle concentration, the assay chamber was flushed with the next higher concentration diet. To decrease particle concentration, the assay chamber was first flushed with $0.45 \mu\text{m}$ filtered seawater before the next lower concentration was added. After exposure to all three concentrations, the bivalve was removed, another individual added to the assay chamber, and the process repeated. Six replicate bivalves of each species were used for each of the three different quality diets, except for *M. edulis* that were fed the *Spartina* sp. diet, where five individuals were used. Transport velocity assays were conducted on the west coast at a water temperature of 12 to 14 °C for mussels, and 13 to 16 °C for oysters. On the east coast, assays were conducted at a water temperature of 16 to 18 °C for both mussels and oysters.

Recorded images were used to determine particle transport velocities in the ventral groove and dorsal tract of the ctenidia. Particle velocities were determined by counting the number of frames required for a particle (i.e., *R. lens* cell, detritus, or tracer) to traverse a known distance along the ctenidium (e.g., several filaments, or entire plica; Ward, 1996; Richoux and Thompson, 2001). Distances were determined by isolating the ctenidia of several specimens of each species and measuring the width of various structures (e.g.,

filaments, plicae) with a calibrated ocular micrometer under a compound microscope. Recording speed was 30 frames/s (NTSC format). Nine to twenty velocity determinations were made on the ctenidium of each individual and averaged to give one velocity value per specimen for each condition. For mussels, only ventral-groove transport velocities were determined, because little if any material is transported in the dorsal tracts (Atkins, 1937; Ward et al., 1993). For oysters, transport velocities in both the ventral groove and the dorsal tracts of the ctenidia were determined.

A two-way, repeated measures analysis of variance (ANOVAR) was used to analyze transport velocity data with diet concentration as the repeated factor (within-subject), and diet quality as the independent factor (between-subject). Data were analyzed for normality using a one-sample, Kolmogorov–Smirnov test (Lilliefors option; SYSTAT, 1999). Homogeneity of variance was evaluated using Greenhouse and Geiser's epsilon index (for repeated measures; LaTour and Miniard, 1983). If the index indicated departures from homogeneity, and the Greenhouse–Geiser and Huynh–Feldt corrected significance levels did not agree, then a multivariate repeated measures analysis was used to examine the within-subject effects (Potvin et al., 1990). If the model indicated a significant effect of diet concentration, diet quality, or their interaction, a posteriori contrasts were performed to examine differences among the within-subject and between-subject levels (SYSTAT, 1999). In some cases, within-subject effects (concentration) were further analyzed using a one-way ANOVAR.

Finally, in order to compare data trends between *M. edulis* and *C. virginica*, transport velocities of individuals of each species were normalized to the highest velocity obtained for that species, for a given ctenidial location (ventral or dorsal). Normalized data were arcsine-transformed and analyzed statistically using ANOVAR procedures outlined above.

3. Results

3.1. Qualitative observations

All bivalve species readily fed on the *R. lens* and Mixed diets, and were less active when delivered the *Spartina* sp. diet. This was particularly evident for the mussels, which often required an hour or more to open and begin feeding on *Spartina* sp. diet, especially at 10^5 particles ml^{-1} . Once feeding, however, all species actively cleared all particle types as was evidenced by the amount of material observed being transported by the ctenidia.

As has been described previously (Ward, 1996; Ward et al., 1993), material in the ventral grooves of all bivalve species in all treatments was carried in a cohesive mucous string. Material in the dorsal tracts was carried in suspension. Because of this difference in transport mode (Ward et al., 1994; Beninger and Dufour, 1996), material in the dorsal tracts was transported at a velocity about two to four times higher than material in the ventral tracts (Table 1). Observations of the relative amount and type of material in the ventral grooves and dorsal tracts of the oysters support previous reports (Ward et al., 1998a). Low-quality material, such as *Spartina* sp. particles, was predominantly transported in the ventral grooves, whereas high quality material, such as *R. lens* cells, was predominantly transported in the dorsal tracts. Finally, we intermittently observed the following changes

Table 1

Mean (\pm S.D.) transport velocities on the ctenidia of four species of bivalve molluscs exposed to different diet concentrations (within-subject effects) and qualities (between-subject effects)

Species	Temperature (°C)	Location	Within-subject rates		Between-subject rates	
			Diet concentration (particles ml ⁻¹)	Velocity ($\mu\text{m s}^{-1}$)	Diet quality	Velocity ($\mu\text{m s}^{-1}$)
<i>M. edulis</i>	16–18	Ventral	10 ³	482 (57) ^C	<i>Spartina</i> sp.	444 (82) ^a
					Mixed	478 (26) ^a
					<i>R. lens</i>	518 (33) ^a
		Ventral	10 ⁴	452 (91) ^D	<i>Spartina</i> sp.	356 (79) ^a
					Mixed	490 (57) ^b
					<i>R. lens</i>	496 (72) ^b
		Ventral	10 ⁵	364 (96) ^E	<i>Spartina</i> sp.	271 (54) ^a
					Mixed	402 (99) ^b
					<i>R. lens</i>	404 (71) ^b
<i>M. trossulus</i>	12–14	Ventral	10 ³	356 (61) ^C	<i>Spartina</i> sp.	341 (44) ^a
					Mixed	356 (66) ^a
					<i>R. lens</i>	372 (77) ^a
		Ventral	10 ⁴	390 (90) ^C	<i>Spartina</i> sp.	371 (64) ^a
					Mixed	346 (99) ^a
					<i>R. lens</i>	454 (77) ^a
		Ventral	10 ⁵	359 (59) ^C	<i>Spartina</i> sp.	331 (57) ^a
					Mixed	371 (62) ^a
					<i>R. lens</i>	374 (57) ^a
<i>C. virginica</i>	16–18	Ventral	10 ³	329 (80) ^C	<i>Spartina</i> sp.	305 (31) ^a
					Mixed	324 (61) ^a
					<i>R. lens</i>	357 (123) ^a
		Ventral	10 ⁴	379 (110) ^D	<i>Spartina</i> sp.	344 (57) ^a
					Mixed	346 (96) ^a
					<i>R. lens</i>	446 (144) ^a
		Ventral	10 ⁵	406 (127) ^D	<i>Spartina</i> sp.	357 (54) ^a
					Mixed	361 (59) ^a
					<i>R. lens</i>	501 (180) ^a
		Dorsal	10 ³	1244 (293) ^C	<i>Spartina</i> sp.	1382 (330) ^a
					Mixed	1191 (190) ^a
					<i>R. lens</i>	1157 (329) ^a
Dorsal	10 ⁴	1415 (307) ^D	<i>Spartina</i> sp.	1327 (159) ^a		
			Mixed	1439 (304) ^a		
			<i>R. lens</i>	1478 (435) ^a		
Dorsal	10 ⁵	1425 (331) ^D	<i>Spartina</i> sp.	1367 (301) ^a		
			Mixed	1538 (234) ^a		
			<i>R. lens</i>	1370 (453) ^a		
<i>C. gigas</i>	13–16	Ventral	10 ³	594 (125) ^C	<i>Spartina</i> sp.	538 (179) ^a
					Mixed	630 (61) ^a
					<i>R. lens</i>	613 (108) ^a
		Ventral	10 ⁴	622 (155) ^C	<i>Spartina</i> sp.	511 (176) ^a
					Mixed	653 (101) ^a
					<i>R. lens</i>	700 (129) ^a
Ventral	10 ⁵	630 (155) ^C	<i>Spartina</i> sp.	499 (150) ^a		
			Mixed	749 (121) ^b		
			<i>R. lens</i>	642 (80) ^{a,b}		

Table 1 (continued)

Species	Temperature (°C)	Location	Within-subject rates		Between-subject rates	
			Diet concentration (particles ml ⁻¹)	Velocity (µm s ⁻¹)	Diet quality	Velocity (µm s ⁻¹)
<i>C. gigas</i>	13–16	Dorsal	10 ³	1001 (351) ^C	<i>Spartina</i> sp.	885 (258) ^a
					Mixed	958 (329) ^a
		<i>R. lens</i>	1160 (441) ^a			
	Dorsal	10 ⁴	1087 (312) ^C	<i>Spartina</i> sp.	822 (175) ^a	
				Mixed	1059 (239) ^a	
				<i>R. lens</i>	1380 (232) ^b	
	Dorsal	10 ⁵	1110 (358) ^C	<i>Spartina</i> sp.	855 (243) ^a	
				Mixed	1202 (464) ^a	
				<i>R. lens</i>	1272 (204) ^a	

Six replicates of each species were used for each concentration × quality mean, except for *M. edulis* fed the *Spartina* sp. diet where five replicates were used. Means designated with different capital letters indicate significant within-subject differences (within a species), whereas means designated with different lowercase letters indicate significant between-subject differences (within a species, within a concentration). Quality designations are: *Spartina* sp. = low-quality diet; Mixed = medium-quality diet; *R. lens* = high-quality diet (see text for details).

in the way in which material was transported in the dorsal tracts of oysters: (a) anterior transport of particles would stop, (b) the amount of material being transported would noticeably decrease over a few seconds time leaving little material moving in the tract, or (c) material would reverse direction and be transported posteriorly for a few seconds; this transport reversal was associated with partial or complete valve adductions. In contrast, there was little change in the way in which material was transported in the ventral grooves. On a few occasions, transport of material in the groove would slow or stop. This change usually occurred when an anterior portion of the mucous string dislodged from the ventral groove after a rapid adduction. The dislodged portion would form a dense mass that would temporarily jam movement of the posterior portion of the string.

3.2. *M. edulis* transport velocities

Mean ventral-groove transport velocities ranged from 271 to 518 µm s⁻¹, and were significantly affected by both diet quality and diet concentration (two-way ANOVA, $p < 0.01$ for both effects; Table 1). There was no significant interaction effect on transport velocities ($p > 0.1$). Between-subject comparisons indicated that there was a significant decrease in transport velocities at the lowest quality diet (*Spartina* sp.) at 10⁴ ($p < 0.01$), and 10⁵ particles ml⁻¹ ($p < 0.05$; Fig. 1). At 10³ particles ml⁻¹, transport velocities of mussels delivered *Spartina* sp. were lower than the other two diet qualities, but no significant difference could be detected ($p > 0.05$; Table 1). There were no significant differences between the Mixed and *R. lens* diets at any concentration ($p > 0.05$). Within-subject comparisons indicated that there was a significant decrease in transport velocities with increasing diet concentration (Fig. 1). Overall, velocities of mussels delivered 10³ particles ml⁻¹ were significantly higher than velocities of mussels delivered 10⁴ particles ml⁻¹ ($p < 0.05$), which were significantly higher than those of mussels delivered 10⁵

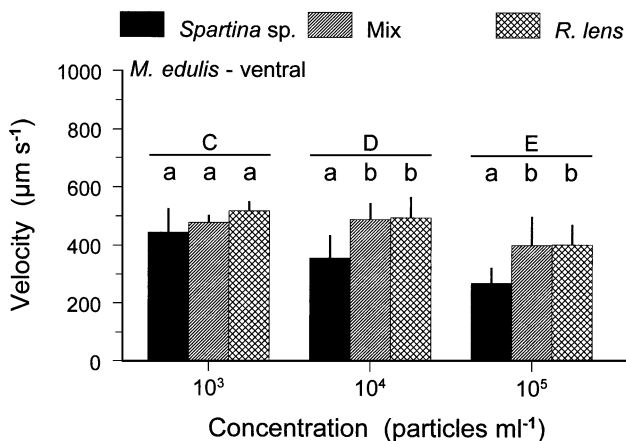


Fig. 1. Mean (\pm S.D.) particle transport velocities in the ventral groove of *M. edulis* delivered diets of three different qualities at three different concentrations. The high-quality diet consisted of *R. lens* (*R. lens*; 6–13 μm); the low-quality diet consisted of particles prepared from ground, dried leaves and stems of *Spartina sp.* (<20 μm); and the medium-quality diet consisted of a 50:50 mixture of both particle types (Mixed). Capital letters indicate within-subject contrasts comparing velocity among the three diet concentrations across all qualities. Groups of means with different capital letters are significantly different from each other. Lowercase letters indicate between-subject contrasts comparing velocity among the three diet qualities at a given diet concentration. Means with different lowercase letters within a concentration are significantly different from each other. For all comparisons, an alpha level of 0.05 was used (see text for actual *p* values).

particles ml^{-1} ($p < 0.05$). This effect was particularly strong in the *Spartina sp.* and the *R. lens* treatments (one-way ANOVA, $p < 0.01$ and $p < 0.05$, respectively; Table 1).

3.3. *M. trossulus* transport velocities

Mean ventral-groove transport velocities ranged from 331 to 454 $\mu\text{m s}^{-1}$, and were not affected by diet quality or diet concentration (two-way ANOVA, $p > 0.1$ for both effects; Table 1; Fig. 2). In addition, there was no significant interaction effect on transport velocities ($p > 0.05$).

3.4. *C. virginica* transport velocities

Mean ventral-groove transport velocities ranged from 305 to 501 $\mu\text{m s}^{-1}$, and were unaffected by diet quality, but were significantly affected by diet concentration (two-way ANOVA; $p > 0.1$ and $p < 0.01$, respectively; Table 1). There was no significant interaction effect on transport velocities ($p > 0.1$). Within-subject comparisons indicated that there was a significant increase in transport velocities with increasing diet concentration (Fig. 3A). Overall, velocities of oysters delivered 10^3 particles ml^{-1} were significantly lower than velocities of oysters delivered 10^4 particles ml^{-1} ($p < 0.01$), and 10^5 particles ml^{-1} ($p < 0.01$). This effect was particularly strong in *R. lens* treatment (one-way ANOVA, $p < 0.05$; Table 1). No significant difference in transport velocities was found between oysters delivered 10^4 and 10^5 particles ml^{-1} ($p > 0.1$; Fig 3A).

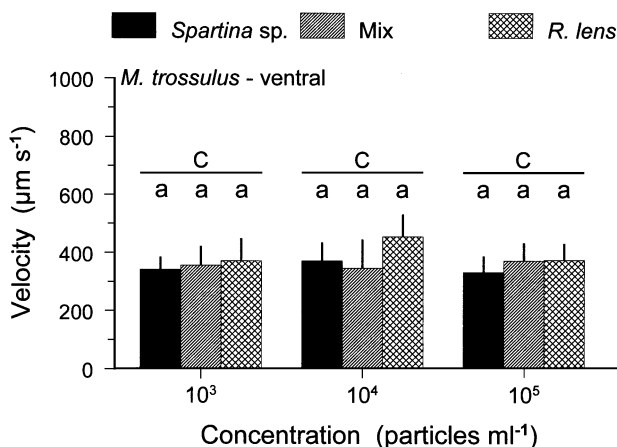


Fig. 2. Mean (\pm S.D.) particle transport velocities in the ventral groove of *M. trossulus* delivered diets of three different qualities at three different concentrations. See Fig. 1 for description of diet quality. Capital letters indicate within-subject contrasts comparing velocity among the three diet concentrations across all qualities. Groups of means with different capital letters are significantly different from each other. Lowercase letters indicate between-subject contrasts comparing velocity among the three diet qualities at a given diet concentration. Means with different lowercase letters within a concentration are significantly different from each other. For all comparisons, an alpha level of 0.05 was used (see text for actual p values).

Mean dorsal-tract transport velocities ranged from 1157 to 1538 $\mu\text{m s}^{-1}$, and also were unaffected by diet quality, but were significantly affected by diet concentration (two-way ANOVA; $p > 0.1$ and $p < 0.05$, respectively; Table 1). There was no significant interaction effect on transport velocities ($p > 0.05$). Within-subject comparisons indicated that there was a significant increase in transport velocities with increasing diet concentration (Fig. 3B). Overall, velocities of oysters delivered 10^3 particles ml^{-1} were significantly lower than velocities of oysters delivered 10^4 particles ml^{-1} ($p < 0.01$), and 10^5 particles ml^{-1} ($p < 0.01$). This effect was particularly strong in the Mixed diet treatment (one-way ANOVA, $p < 0.05$; Table 1). No significant difference in transport velocities was found between oysters delivered 10^4 and 10^5 particles ml^{-1} ($p > 0.1$; Fig 3B).

3.5. *C. gigas* transport velocities

Mean ventral-groove transport velocities ranged from 499 to 749 $\mu\text{m s}^{-1}$, and were not affected by diet quality, or diet concentration (two-way ANOVA; $p > 0.05$ and $p > 0.1$, respectively; Table 1). There was, however, a significant diet-quality-by-concentration interaction effect on transport velocities ($p < 0.05$). Further analysis revealed that at 10^5 particles ml^{-1} , oysters in the Mixed diet treatment had transport velocities significantly higher than those in the *Spartina sp.* treatment ($p < 0.01$; Fig. 4A). No significant differences in velocities were found between oysters in the *Spartina sp.* and *R. lens* treatments ($p > 0.05$), or between oysters in the *R. lens* and Mixed diet treatments ($p > 0.1$). No other between-subject effects were found for ventral transport velocities (Table 1). Within-subject comparisons also indicated that in the Mixed diet treatment, transport

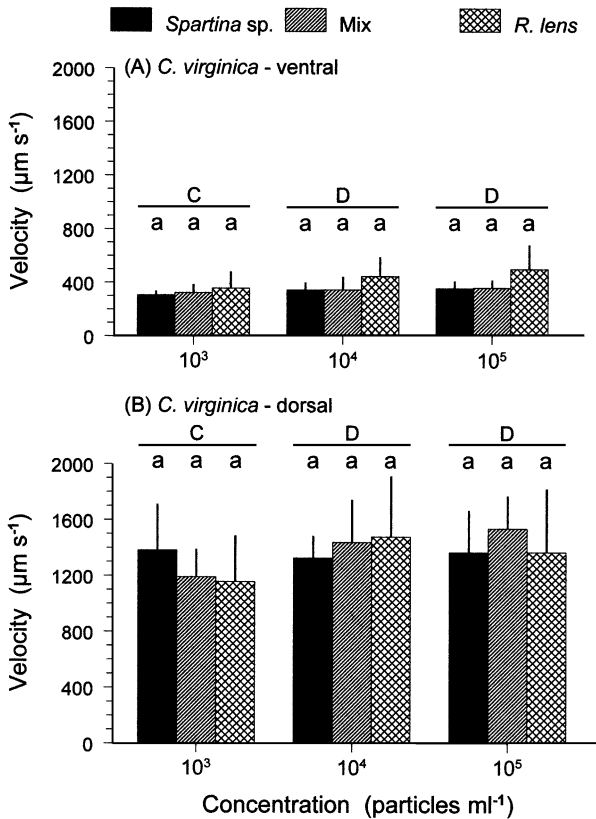


Fig. 3. Mean (\pm S.D.) particle transport velocities in the ventral groove (A) and dorsal tract (B) of *C. virginica* delivered diets of three different qualities at three different concentrations. See Fig. 1 for description of diet quality. Capital letters indicate within-subject contrasts comparing velocity among the three diet concentrations across all qualities. Groups of means with different capital letters are significantly different from each other. Lowercase letters indicate between-subject contrasts comparing velocity among the three diet qualities at a given diet concentration. Means with different lowercase letters within a concentration are significantly different from each other. For all comparisons, an alpha level of 0.05 was used (see text for actual p values).

velocities of oysters delivered 10^5 particles ml^{-1} were significantly higher than those of oysters delivered the two lower concentrations (one-way ANOVA; $p < 0.05$). No other within-subject effects were found.

Mean dorsal-tract transport velocities ranged from 822 to $1380 \mu\text{m s}^{-1}$, and were not affected by diet quality, or diet concentration (two-way ANOVA; $p = 0.053$ and $p > 0.1$, respectively; Table 1). There was no significant interaction effect on transport velocities ($p > 0.05$). Although no significant effects were found, there was a clear trend of increasing transport velocities with increasing diet quality at all concentrations (Fig. 4B). Between-subject comparisons supported this assertion, demonstrating a significant difference in oyster transport velocities between *R. lens* and the Mixed diet ($p < 0.05$), and between *R. lens* and *Spartina* sp. diet ($p < 0.01$) at the 10^4 particles ml^{-1} treatment. The high variation

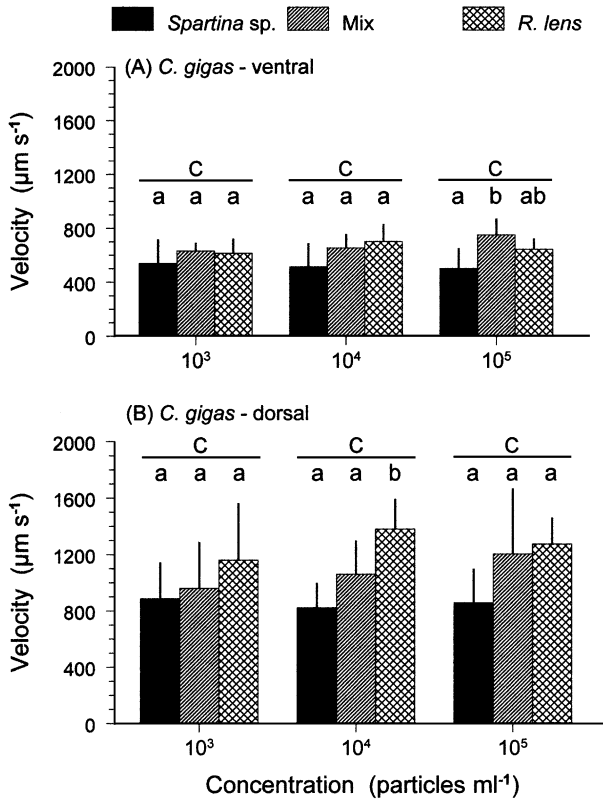


Fig. 4. Mean (\pm S.D.) particle transport velocities in the ventral groove (A) and dorsal tract (B) of *C. gigas* delivered diets of three different qualities at three different concentrations. See Fig. 1 for description of diet quality. Capital letters indicate within-subject contrasts comparing velocity among the three diet concentrations across all qualities. Groups of means with different capital letters are significantly different from each other. Lowercase letters indicate between-subject contrasts comparing velocity among the three diet qualities at a given diet concentration. Means with different lowercase letters within a concentration are significantly different from each other. For all comparisons, an alpha level of 0.05 was used (see text for actual *p* values).

in dorsal-tract transport velocities among replicates, however, obscured significant differences in the other concentration treatments, and in the overall model ($p = 0.053$; Table 1).

3.6. Normalized transport velocities

Normalized, ventral-groove transport velocities of *M. edulis* increased significantly with increasing diet quality ($p < 0.01$), whereas ventral-groove transport velocities of *C. virginica* demonstrated no significant increase with diet quality ($p > 0.05$; Fig. 5A). In addition, ventral-groove velocities of *M. edulis* decreased significantly with increasing diet concentration ($p < 0.01$), whereas ventral-groove velocities of *C. virginica* increased significantly with increasing diet concentration ($p < 0.01$; Fig. 5B). Normalized, dorsal-tract transport velocities of *C. virginica* showed trends similar to those of the ventral

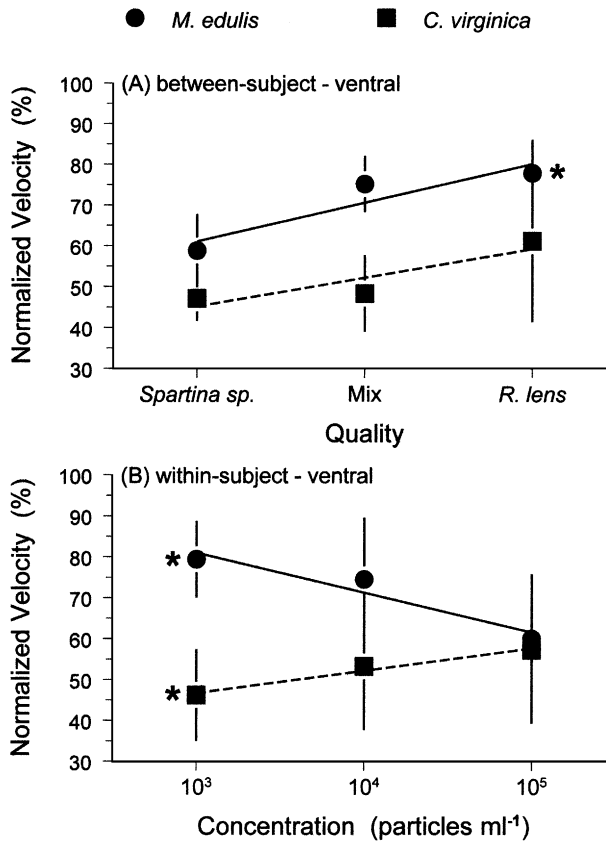


Fig. 5. Normalized, particle transport velocities in the ventral groove of *M. edulis* and *C. virginica* as a percentage of the highest rate obtained for that species. Data are presented as means \pm S.D. (A) Between-subject comparisons of the effects of diet quality on velocity. (B) Within-subject comparisons of the effects of diet concentration on velocity. Normalized, dorsal tract velocities of *C. virginica* show similar relationships with diet quality and concentration (not shown). Data trends marked with asterisks (*) are significant at an alpha level of 0.05 (see text for actual *p* values).

groove, showing no significant increase with diet quality ($p > 0.05$), but increasing significantly with increasing diet concentration ($p < 0.01$).

4. Discussion

Analyses of ctenidial-transport velocity data suggest that the way in which bivalves respond to the quantity and quality of particulate food is species dependent. Previous studies have demonstrated species-specific responses to changes in particulate food regimes, including differences in feeding rates, particle rejection and selection processes, and digestive processes (e.g., Foster-Smith, 1975; Langdon and Newell, 1990;

Ward and MacDonald, 1996; Bougrier et al., 1997; Cranford and Hill, 1999). Considering the results from the above studies, differential control of transport velocities on the ctenidia, one of the main feeding organs of suspension-feeding bivalves, could be one underlying mechanism for the reported behavioral and physiological responses of bivalve species to changes in the quantity and quality of food (see also Milke and Ward, 2003).

The ctenidia of *M. edulis* was the most responsive to changes in diet quality and concentration. Overall, transport velocities significantly increased with increasing diet quality, especially at the higher diet concentrations (10^4 and 10^5 particles ml^{-1}), and significantly decreased with increasing particle concentration, especially at the lowest diet quality (*Spartina* sp.). Our results are similar to those of Richoux and Thompson (2001) who studied *M. edulis* from Newfoundland. These researchers found that at 14 °C, transport velocities in the ventral groove of the ctenidia decrease with increasing microalgal concentration (from ca. 1×10^4 to 1.7×10^5 particles ml^{-1}). Using the line equation given by Richoux and Thompson (2001, their Fig. 3), we determined the predicted decrease in transport velocities for the range of particle concentrations used in our study (note: equation given by Richoux and Thompson, 2001, should read, Log velocity = $-0.0025 \times \text{particle concentration} + 2.63$). Predicted values range from $424 \mu\text{m s}^{-1}$ at 10^3 particles ml^{-1} to $240 \mu\text{m s}^{-1}$ at 10^5 particles ml^{-1} , representing about a 43% decrease in transport velocities. Measured values obtained in our study range from $482 \mu\text{m s}^{-1}$ at 10^3 particles ml^{-1} to $364 \mu\text{m s}^{-1}$ at 10^5 particles ml^{-1} (all particle types combined; Table 1), representing about a 24% decrease in transport velocities. Maximum decrease in ventral-groove transport velocities occurred when mussels were delivered the *Spartina* sp. diet. Under this condition, transport velocities decreased 39% from $444 \mu\text{m s}^{-1}$ at 10^3 particles ml^{-1} to $271 \mu\text{m s}^{-1}$ at 10^5 particles ml^{-1} , suggesting that mussels reacted more strongly to the poorest-quality particles. Slight differences between our results and those of Richoux and Thompson (2001), may be due to differences in tolerance of the two populations (Newfoundland vs. Connecticut) to suspended particulate loads. Nevertheless, these studies demonstrate that the velocity at which material is transported in the ventral groove of the ctenidia is affected by changes in the quantity and quality of particles in suspension.

Ventral-groove transport velocities on the ctenidia of *M. trossulus* were unaffected by changes in diet quality and concentration. Transport velocities tended to increase with increasing diet quality, but no significant differences were detected. Transport velocities in *M. trossulus* were also consistently lower than in *M. edulis* (Table 1), even though clearance rates of *M. trossulus* can be higher than those of *M. edulis* (Mooney et al., 1999). Differences in the response of the two mussel species could be partially due to differences in experimental temperature, which was about 4 °C colder in *M. trossulus* assays. Changes in temperature not only affect particle transport velocities in bivalves (Richoux and Thompson, 2001; Milke and Ward, 2003), but can also diminish the response to changes in food quantity and quality. Richoux and Thompson (2001) reported that ventral-groove transport velocities were unaffected by particle concentration at 5 °C, but significantly decreased with increasing concentration at 14 °C. Similarly, Milke and Ward (2003) found a significant effect of particle concentration on particle-handling times by the labial palps of *M. edulis* at 20 °C, but no effect at 5 °C.

Ventral-groove and dorsal-tract transport velocities of *C. virginica* were not affected by changes in diet quality. Similar results were obtained for *C. gigas*, although in the dorsal tract there was a clear trend of increasing transport velocity with increasing diet quality, which was significant in the 10^4 particles ml^{-1} treatment. Transport velocities in the ventral grooves and dorsal tracts of *C. virginica* increased significantly with an increase in diet concentration from 10^3 to 10^4 particles ml^{-1} . Ward et al. (1994) observed that cilia on the lips of *C. virginica* were inactive in seawater with low particle concentration, but could be stimulated with the addition of the diatom *Chaetoceros muelleri*. Taken together, these results suggest that particle transport and handling rates in the pallial cavity of *C. virginica* are stimulated by an increase in particle concentration. In contrast, ventral-groove and dorsal-tract transport velocities of *C. gigas* did not change significantly with increasing diet concentration.

Both west-coast species were less responsive to changes in diet quality and quantity than the east-coast bivalves. The reasons for this are not clear. As mentioned above, the lower experimental temperatures could have had some diminishing effect on the responses of west-coast bivalves. In addition, *M. trossulus* and *C. gigas* most likely encounter particle regimes that are very different than those used in this study. In the Puget Sound, most detrital particles are probably derived from kelp rather than angiosperms such as *Spartina* sp. (Duggins and Eckman, 1997). The lack of a significant response of west-coast bivalves in our study may reflect an inability to detect, select, and process *Spartina* sp. detritus or the *Rhodomonas lens* cells.

Significant responses to changes in diet quality and concentration were demonstrated by the two east-coast bivalves, *M. edulis* and *C. virginica*. Normalized velocities allow for a better comparison of the differences in the magnitude and direction of responses between these two species (Fig. 5). For example, mussels demonstrated a significant decrease in ctenidial-transport velocities with increasing diet concentration, whereas oysters demonstrated a significant increase in transport velocities (both ventral groove and dorsal tract) with increasing concentration. We suggest that the different ctenidial responses of mussels and oysters to changes in particle concentration may be linked to differences in feeding behavior of these two bivalves.

Both mussels and oysters modulate their clearance rates in response to seston loads, maintaining high rates of feeding at elevated seston concentrations (Newell and Langdon, 1996). There are, however, differences in the range of seston concentrations that mediate their feeding response. At a very low seston concentration, mussels exhibit low feeding (Newell et al., 1998). As particle concentration increases (1 to 4 mg l^{-1}), mussels exhibit increased feeding rates, and demonstrate maximum clearance rates at seston concentrations of 3 to 10 mg l^{-1} (e.g., Widdows et al., 1979; Kiørboe et al., 1980; Newell et al., 2001). At even higher seston concentrations, however, clearance rates rapidly decline (Kiørboe et al., 1980; Newell and Shumway, 1993; Richoux and Thompson, 2001). In oysters, continuous feeding also does not occur below 1 mg l^{-1} , and maximum clearance rates are obtained at seston concentrations of 5 to 10 mg l^{-1} (Newell and Langdon, 1996). Clearance rates of oysters, however, remain near maximum up to 25 mg l^{-1} , and oysters have been reported to actively feed in a concentration exceeding 100 mg l^{-1} (Nelson, 1960; Mathers, 1974). The above differences in clearance rates at high seston concentrations result in a large difference

in the amount of material filtered from suspension by these bivalves. For example, at a seston load of 50 mg l^{-1} , *M. edulis* has a filtration rate of about $50 \text{ mg h}^{-1} \text{ g dry weight}^{-1}$ (calculate from data in Widdows et al., 1979), whereas *C. gigas* has a filtration rate of about $270 \text{ mg h}^{-1} \text{ g dry weight}^{-1}$ (Barillé et al., 1997).

Clearly, the way in which mussels and oysters respond to increasing seston concentrations is different. The specific responses of these two bivalve species may be a result of differences in the complexity of their ctenidia (Ward et al., 1994), which has led to different strategies for controlling the transfer of material to the labial palps. On the ctenidia of mussels, almost all particles are carried to the four ventral grooves for transport to the labial palps, whereas in oysters material can be divided between the four ventral grooves and five dorsal tracts of the ctenidia (Ward et al., 1994, 1997, 1998a). In addition, particle selection in mussels takes place only on the labial palps, whereas in oysters the ctenidia play a large role in sorting particulate matter. Therefore, mussels probably have a lower capacity than oysters to transport material to the labial palps for selection (less than 1/5 the capacity at 50 mg l^{-1} ; see above), and saturation of the ventral groove and ctenidia–palp transfer regions of mussels probably occurs at lower particle concentrations. Although the labial palps of mussels have more sorting surfaces than oysters (Milke and Ward, 2003), delivery of a large concentration of unprocessed material anteriorly could saturate the sorting capacity of the palps leading to a reduction in selection efficiency. We suggest that decreasing ctenidial-transport velocities in response to increasing seston concentration is another mechanism that allows mussels to regulate the flux of material to the labial palps. The combined action of reducing clearance rate, decreasing particle-transport velocities along the ctenidia, and selecting particles on the palps is an effective way to regulate the quantity and quality of material ultimately ingested. In contrast, oysters have a higher capacity to transfer material along the ctenidia to the labial palps. Low-quality or unwanted material in the ventral tract can be bulk rejected without being delivered to the palps (Ward et al., 1994), at the same time that higher-quality material in the dorsal tracts is delivered to the labial palps for processing and ingestion. Selection of particles and high rates of particle transport on the ctenidia may be mechanisms that allow oysters to rapidly deliver high quality material to the labial palps, and may explain the ability of oysters to feed at high seston concentrations. However, the high rate of transfer of material to the labial palps imparts a measurable time-cost associated with particle processing by this pallial organ (Milke and Ward, 2003).

In contrast to the responses to diet concentration, the way in which *M. edulis* and *C. virginica* responded to changes in diet quality was similar (Fig. 5A). On the ctenidia of mussels, particle-transport velocities increased significantly with increasing diet quality. Oysters demonstrated a similar, although nonsignificant, trend with diet quality. These results suggest that high-quality food is transported more rapidly to the labial palps for further processing, and may be linked with other physiological responses. For example, Richoux and Thompson (2001) demonstrated a significant positive correlation between increasing clearance rates and increasing ventral-groove transport velocities of *M. edulis*. Such responses could be energetically favorable to bivalves that are exposed to patchy, suspended food regimes.

Changes in particle transport velocities in response to changes in diet quality and concentration could be due to mechanical inhibition of ciliary activity, stimulation of

ciliary activity (numbers and frequency of beat), or changes in the type of mucus incorporated in transport grooves and tracts. For all bivalves, we observed an increase in the amount of material transported by the ventral grooves and dorsal tracts as diet concentration increased. In mussels, an increase in the concentration of particles and associated mucus in ventral grooves could have increased resistance to the effective stroke of the transport cilia. If ciliary activity was at a maximum, increased resistance would decrease the speed of the effective stroke, reduce propulsion efficiency (Sleigh, 1982; Sleigh et al., 1988), and retard mucociliary processes such as particle transport velocity.

Although this mechanical resistance model can explain decreases in transport velocities with increasing diet concentration, it cannot explain other changes observed in our study. For example, in *M. edulis*, the velocity of transport of Mixed and *R. lens* diets was significantly higher than that of *Spartina* sp. at both 10^4 and 10^5 particles ml^{-1} . These enhanced velocities were associated with more active feeding and larger more voluminous mucous strings in the ventral grooves of mussels feeding on the Mixed and *R. lens* diets. In *C. virginica*, transport velocities in both the ventral groove and dorsal tracts increased significantly with an increase in diet concentration and the associated increase in amount of material carried along the ctenidia. Our results suggest that other mechanisms contribute to the observed changes in particle transport velocities such as stimulation of ciliary activity and changes in the type of mucus produced.

Mechanical stimuli can activate the lateral and abfrontal cilia of *M. edulis* (Murakami and Machemer, 1982; Stommel and Stephens, 1988), and mucus-propelling cilia of other animals (see Sleigh et al., 1988). Therefore, in oysters an increase in the amount of particles and mucus carried in the dorsal tracts and ventral grooves probably stimulated ciliary activity, thereby increasing propulsive effort and transport velocity (Sleigh, 1982). Dissolved and epiparticulate phytoplankton compounds can also stimulate feeding activities in bivalves (Ward and Targett, 1989; Ward et al., 1992). For both mussels and oysters, an increase in the concentration of phytoplankton cells, associated with an increase in diet quality, could have activated transport cilia and enhanced transport velocity. In addition, changes in the type of mucopolysaccharides produced by mucocytes on the ctenidia could alter the viscosity of transport mucus and thus resistance to the cilia. For example, the ctenidia of *M. edulis* possess nearly equal densities of mucocytes that produce neutral (less viscous) and acid-dominant (more viscous) mucopolysaccharides (Beninger et al., 1993; Beninger and St-Jean, 1997). Changes in the ratio of these secretions could alter the final viscosity of the mucous string transported in the ventral food groove. Therefore, increases in transport velocity of material along the ctenidia in response to an increase in diet quality (e.g., *M. edulis*, *C. gigas*) or diet concentration (e.g., *C. virginica*) are probably due to physiological compensations by the pallial organs, potentially linked to particle processing by the labial palps (Milke and Ward, 2003), or post-ingestive feedback from the gut.

Previous studies have demonstrated that with increasing seston concentration many bivalves regulate the quantity of material ingested by reducing clearance rate and increasing pseudofeces production (e.g., Iglesias et al., 1996). Our data suggest that some bivalves can also regulate the link between capture and rejection/ingestion processes by altering rates of particle transport along the ctenidia. Changes in clearance and transport velocities would allow bivalves to finely regulate the quantity or flux of

material delivered to the labial palps. We suggest that in bivalves the flux of material to the palps is a function of filtration rate (i.e., mg time^{-1}), time spent feeding, transport velocity along the ctenidial margins, and length of the marginal tracts. By modulating the flux of material to the palps and bulk rejecting material at the ctenidia–palp junction, bivalves can mediate the quantity and, in species that sort particles on the ctenidia (e.g., oysters, Ward et al., 1998a,b; zebra mussels, Baker et al., 2000), quality of material transported to the palps for further processing and ingestion. Ultimately, these processes may affect the efficiency with which bivalves select among particles and optimize the quality of material ingested.

5. Conclusions

Our results demonstrate that some bivalve species can respond to changes in diet concentration and quality by changing the velocity at which material is transported along the ctenidia. For example, ventral-groove transport velocities of *M. edulis* increased by about 38% to 49% when diet quality increased. Transport velocities decreased in *M. edulis* by about 24% when diet concentration changed from 10^3 to 10^5 particles ml^{-1} , although larger differences were observed depending on diet quality. In contrast, transport velocities in both the ventral grooves and dorsal tracts of *C. virginica* increased by about 23% and 15%, respectively, when diet concentration changed from 10^3 to 10^5 particles ml^{-1} , although larger differences were observed depending on diet quality. The changes we observed in transport velocities cannot be fully explained by mechanical processes brought about by changes in mucus concentration. We suggest that physiological responses by the bivalves are involved which are manifested as changes in ciliary beat frequency, number of active cilia, or type of mucus produced by the ctenidia resulting in changes in particle-transport velocity. Considering the differences in feeding rates and particle-handling processes between mussels and oysters, different transport-velocity responses might reflect species-specific adaptations that help modulate the flux of material to the labial palps and optimizing energy intake. A full understanding of how ctenidial and palp processes are coordinated to optimize ingestion will require more information on other feeding-related factors that differ between mussels and oysters. For example, factors such as the ratio between filtration capacity and area of the ctenidia, and the quantity of material that is actually transported in the ventral grooves compared to the dorsal tracts need to be considered.

Our research is the first study to compare rate functions on the pallial organs of several bivalve species. These rate functions are not constant and can change with changes in diet concentration and quality. Such information could be used to generate numerical models of pallial-cavity processes that could help to refine carrying capacity models for bivalve populations in near-shore waters. Finally, our data do not support the hypothesis that feeding is “automatized” with no capacity for response to changes in food regimes (Jørgensen, 1996). Rather, our results add to the body of evidence which suggest that “bivalve suspension feeding is a complex synergy between behavioural, physiological and morphological traits which are responsive to variations in available food” (Bayne, 1998).

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