

Chapter 4

Bivalve filter feeding: variability and limits of the aquaculture biofilter

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Introduction

A fundamental knowledge of bivalve feeding behavior is a minimum requirement for understanding how aquaculture interacts with the surrounding ecosystem. The potential environmental effects and ecological services of bivalve culture (Chapters 1 and 9 in this book) are related, in large part, to how the cultured population interacts with the ecosystem by means of suspension feeding. A close interplay between water filtration activity, primary production, seston availability, and hydrodynamics defines the magnitude of many of the ecological services provided by bivalves, as well as the sustainable level of aquaculture for a given area. Shellfish growth is limited primarily by a species' capacity for nutrient

acquisition, which is regulated by feeding activity (Hawkins et al. 1999). Predictions of bivalve growth and the maximum aquaculture yield that can be produced within an area (production carrying capacity) often involve eco-physiological modeling, which includes equations describing how feeding processes (particle capture, selection, and ingestion) are related to population dynamics and environmental changes. Uncertainty or inaccuracy in feeding parameter estimates strongly influence model predictions of bivalve growth and carrying capacity (Dowd 1997).

Suspension feeding always results in some local food depletion. The ecological costs of seston depletion by bivalve aquaculture are of concern only when the depletion zone is persistent and of an ecologically significant

magnitude and spatial scale. Accurate information on how fast resident bivalve stocks can filter a body of water is required to assess the ecological carrying capacity of a region, which is the level of aquaculture that can be supported in the growing environment without leading to significant changes to ecological processes, species, populations, or communities (Gibbs 2007). Beyond the need to understand the potential direct effects of biofiltration, indirect effects on ecosystem processes and structure may result from the by-products of suspension feeding, including ammonia excretion and the egestion of particulate organic materials (feces and pseudofeces) on marine particle transport, energy flow, and nutrient cycling.

Bivalve feeding activity has been studied across a wide range of laboratory and natural conditions and there is a vast literature, particularly on clearance rate, which is the volume of water cleared of particles of a certain size in a period of time. Despite this large research effort, there remains uncertainty in the measurement of clearance rate, which affects our confidence in predictions of individual to community-level feeding rates (Doering and Oviatt 1986; Cranford and Hill 1999; Riisgård 2001a, 2001b, 2004; Cranford 2001; Widdows 2001; Bayne 2004; Petersen et al. 2004). A fundamental understanding of the feeding behavior of individual bivalves provides the foundation for estimating population clearance rate, which is critical to understanding the ecological role of bivalves and environmental interactions with shellfish culture, including the capacity of dense bivalve assemblages to control the phytoplankton at the coastal ecosystem scale (Chapter 5 in this book). Feeding rate measurements must reflect the actual responses of specific species and cultured populations to the multiple physical, chemical, and biological factors that can influence feeding behavior in the natural environment. In this review, we summarize the available literature pertaining to feeding behavior with a focus on ascertaining the pres-

ence of predictive relationships for the clearance rate of key aquaculture species that can be used to help understand both positive and negative interactions between bivalve aquaculture activities and the environment. Our goal was to synthesize knowledge on specific aspects of bivalve feeding behavior relevant to the aquaculture issues outlined above. Several previously published reviews have addressed divergent hypotheses on physiological regulation of feeding activities and autonomous behavior (Jørgenson 1996; Bayne 1998; Riisgård 2001b). Such considerations are not the focus of this review, but it is not possible to address our task without contributing to this long-standing theoretical debate.

Constraints on maximum feeding activity

Suspension-feeding lamellibranchiate bivalves rely on ciliated structures to capture and transport suspended particulate matter for selection and ingestion. The particle capture organ is the ctenidium (Ward et al. 1998), which also serves as the respiratory organ (gill). The asynchronous beating of lateral cilia on gill filaments serves as a pump that creates a water current which flows into the inhalant siphon or aperture, through the spaces between the gill filaments (or ostia) and then out of the exhalant siphon or aperture. Particles suspended in the feeding current are captured on the gill. An in-depth review of food capture, transport, and processing mechanisms in bivalve molluscs is provided by Ward and Shumway (2004).

The ciliary activity of the gill delivers a flow that can be measured as a pumping (= ventilation) rate (P ; $L\ h^{-1}$) by various means such as the constant-level apparatus developed by Galtsoff (1926), the delivery of exhaled seawater into a constant flow of fresh water (Davenport and Woolmington 1982), the laser apparatus developed by Famme et al. (1986),

the use of micro-flow meters (Meyhöfer 1985; Jones et al. 1992), and by the application of particle image velocimetry (Frank et al. 2008). Pumping rate scales with the size of the gill, which is somewhat proportional to the square of shell length (L^2). Tissue dry weight (W) is proportional to L^3 so pumping rate can, at least in theory, be expected to scale with $W^{2/3}$ ($=W^{0.67}$). This translates into a large increase in pumping rate for a small increase in body size (L or W). These relationships are described by the allometric equations

$$P = aW^b \text{ and } P = aL^b, \quad (4.1)$$

where a and b are fitted parameters. The allometric exponent (b) describes how fast the rate increases relative to body size. Jones et al. (1992) reported that maximum pumping rate for *Mytilus edulis* scaled with $L^{2.1}$ (Fig. 4.1) and $W^{0.70}$, and showed that these allometric coefficients were not significantly different from the predicted values.

Clearance rate (C ; Lh^{-1}) is the more generally used measure of water processing than pumping rate, although the two measures are closely related. Some studies use the terms

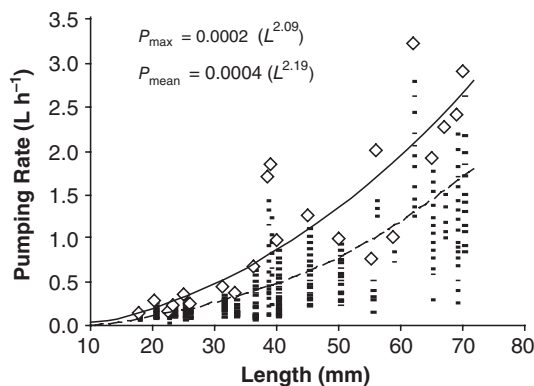


Figure 4.1 Allometric relationship between pumping rate (P) of the mussel *Mytilus edulis* and shell length (L). Multiple individual measurements for each mussel are shown, including the maximum (P_{\max} ; \diamond). Regression lines and equations are shown for average P (P_{mean} ; broken line) and P_{\max} (solid line) values. (Redrawn from Jones et al. 1992.)

clearance rate and filtration rate interchangeably, but the latter term is more often used to define the mass of particles cleared per unit time (e.g., $mg h^{-1}$). Clearance and pumping rates are equal if all particles in the inhalant current are removed from suspension. Small particles ($<2\text{-}\mu\text{m}$ diameter) in natural waters are not effectively retained by most species, but these particles can account for a high proportion of the total suspended particulate matter. Clearance rate, therefore, is measured for a particle size range that is retained by the species with 100% efficiency ($>4\text{-}$ to $7\text{-}\mu\text{m}$ diameter, depending on the presence of eu- or pro-laterofrontal cilia, respectively; reviewed by Riisgård 2001a). While pumping rate can be measured directly by a number of methods, clearance rate is most often determined using indirect methods that involve measuring changes in particle abundance or concentration due to suspension-feeding activity of the bivalves.

Under laboratory conditions, optimal food concentrations have been identified that stimulate the full exploitation of water pumping and particle clearance capacity in many species of bivalves (e.g., 1000–6000 *Rhodomonas* sp. cells mL^{-1} for *Mytilus edulis*; Kittner and Riisgård 2005). Riisgård et al. (2003) reported that under these conditions, the valves of *Cardium edule*, *Mytilus edulis*, and *Mya arenaria* are fully open within an hour after a starvation period of at least 24 h, and maximum clearance rate (C_{\max}) is thereafter maintained. The results of C_{\max} measurements on 13 bivalve species of different sizes from eight studies have been summarized by Riisgård (2001a, 2001b). Reanalysis of the parameters of the allometric relationships reported in these eight studies provide the following average (\pm standard deviation [SD]) relationships for dry tissue weight (W) and shell length (L):

$$C_{\max} (L h^{-1}) = 6.54 \pm 2.41 W^{0.72 \pm 0.09} \quad (4.2)$$

$$C_{\max} (L h^{-1}) = 0.0036 \pm 0.10 L^{1.60 \pm 0.45} \quad (4.3)$$

As noted above, clearance rate is theoretically expected to scale with body geometry (L^2 and $W^{0.67}$), and the above equations generally confirm the assumed constraints of body size on maximum feeding activity. The exponent (b) in Equation 4.3 is lower than expected owing largely to the results of Meyhöfer (1985), which were conducted over a narrow size range. The median b -value of $L^{1.81}$ may therefore be a more accurate estimate.

Fluid dynamic forces can control the ability of shellfish to clear food particles. Uncertainty in the literature regarding the effect of current speed on bivalve feeding (positive vs. negative relationship) appears to stem from experimental conditions (Ackerman 1999). Turbulent conditions tend to result in a negative relationship between feeding activity and current speed, whereas the opposite is generally observed under laminar flow conditions. In general, there appears to be a unimodal functional response to flow: Moderate current speed and laminar flow conditions promote particle clearance rate, whereas high speeds and turbulent conditions inhibit clearance (reviewed by Ackerman 1999). The range of velocities permitting maximal feeding and shellfish growth depends on the species. For example, maximum clearance rate of *Mytilus edulis* was reported at $\sim 25 \text{ cm s}^{-1}$ (Wildish and Miyares 1990) and 80 cm s^{-1} (Widdows et al. 2002), whereas *Mytilus trossulus* and *Mytilus californianus* exhibited peak rates at ~ 18 and 12 cm s^{-1} , respectively (Ackerman and Nishizaki 2004). The scallop *Placopecten magellanicus* exhibited flow inhibition at $20\text{--}25 \text{ cm s}^{-1}$ (Wildish et al. 1987; Pilditch and Grant 1999), while the cockle *Cerastoderma edule* showed no inhibitory effects at 35 cm s^{-1} (Widdows and Navarro 2007). The reduction in feeding rate with increasing flow velocity appears to be a response of epifaunal bivalves to a flow-induced pressure differential between the pressure field in the mantle cavity, created by the ciliary pump, and

the external pressure field caused by flow velocity (Wildish and Kristmanson 1997). Back-pressure on the ciliary pump results in reduced pumping efficiency and valve closure (Jørgenson 1990; Wildish and Saulnier 1993). Similar effects of flow velocity have been observed for infaunal bivalves (Cole et al. 1992), and appear to result from the reduced ability of the bivalve to draw water into the mantle cavity when there is a high cross-flow.

Temperature and salinity also serve as constraints on the maximum feeding rate of suspension-feeders. Temperature effects are related to a combination of mechanical (fluid dynamic) and physiological effects. At a scale of individual cilia, viscous forces dominate cilia and water motion. Water viscosity is inversely related to temperature, and the higher viscosity at lower temperatures has been shown to account for a large fraction of the effect of temperature on water pumping by ciliary filter-feeders, including bivalves (Jørgenson et al. 1990; Podolsky 1994). Viscosity affects the resistance of water flow within the shellfish pump, and the viscosity/temperature relationship therefore limits their maximum clearance rate (Kittner and Riisgård 2005 and references cited therein). Salinity fluctuations also can severely disrupt normal feeding physiology (e.g., Navarro and González 1998; Gardner and Thompson 2001). Some species within the same taxon exhibit increased tolerance to low-salinity environments, resulting in differentiation of some species distributions (Seed 1992).

The maximum capacity for food intake is ultimately limited by the morphological constraint of a limited gut volume and the time required to digest food. Both factors impose a major bottleneck on food uptake that morphological and physiological adaptations (e.g., active regulation of feeding rates) may help to mitigate (Hawkins and Bayne 1992; Bayne 1998).

Shellfish feeding in nature

Shellfish are opportunistic feeders that exploit the diverse nature of suspended particulate matter (the seston). The types of food utilized by shellfish include phytoplankton, ciliates, flagellates, zooplankton, and detritus, which occur within a spatially and temporally diverse mixture that includes inorganic materials (e.g., Trottet et al. 2008). Studies of the natural food available to suspension-feeding bivalves in coastal waters reveal marked short-term to seasonal variations in the concentration, composition, and nutritional value of the seston (e.g., Fegley et al. 1992; Cranford et al. 1998, 2005; Cranford and Hill 1999). Long-term changes in seston abundance and composition in temperate waters arise primarily from the seasonal cycle of primary production. Variability on a scale of days to weeks can result from algal blooms, horizontal phytoplankton patchiness, storm-induced resuspension of bottom deposits, or the spring/neap tidal cycle. In many coastal systems, fine-scale fluctuations in the seston are superimposed on these longer-term trends and result largely from tide-induced resuspension and deposition of bottom deposits and associated organic and inorganic constituents. The increase in the proportion of inorganic particles in the water column during resuspension events has a “dilution” effect on food quality, which is generally defined in terms of the organic and/or elemental content of seston. The challenge to shellfish ecophysiologicalists has been to characterize feeding responses over this wide range of feeding conditions, as well as to other potential mediating factors. The intent of such studies is to provide accurate predictive relationships between changes in food quantity and quality and feeding activity. In this section, we will characterize the range of temporal and spatial variability in clearance rate responses measured across a wide range of natural and experimental conditions prior to discussing

potential reasons for this variability in the following section.

Temporal variability in clearance rate

Water pumping and clearance rate may be actively controlled by changing the activity of the lateral cilia of the gill that create the water flow, and by controlling various musculature that affects shell gape (valve opening), exhalent siphon area (Jørgenson et al. 1988; Newell et al. 2001), and interfilamentary distance of the gill (Jørgensen 1990; Medler and Silverman 2001; Gainey et al. 2003). These mechanisms appear to be uncoupled (Newell et al. 2001; Maire et al. 2007), possibly responding to different stimuli and/or providing different degrees of control over water flow and food acquisition. The capacity of shellfish to actively control clearance rate is a key factor in determining food acquisition, and individual shellfish appear to vary feeding activity continuously. Direct continuous measurements of water pumping rate in *Mytilus edulis* by Davenport and Woolmington (1982) showed that under optimal laboratory conditions (constant algal cell diet) mussels demonstrate relatively low temporal variability in pumping rate, but with irregular and sometimes large interruptions (Fig. 4.2A). Variable diets (periodic starvation), however, induced large fluctuations in pumping rate. The large degree of variability in individual pumping rates is also shown in Figure 4.1B, which includes data on the full range of measurements from mussels of different size, including the maximum rate discussed above (Jones et al. 1992). Studies utilizing natural seston as the food source typically show large short-term variations in clearance rate over time periods ranging from minutes to hours, including periodic cessation of all feeding activity (Fig. 4.2B and Fig. 4.2C). Strohmeier et al. (2009) showed that large variations in

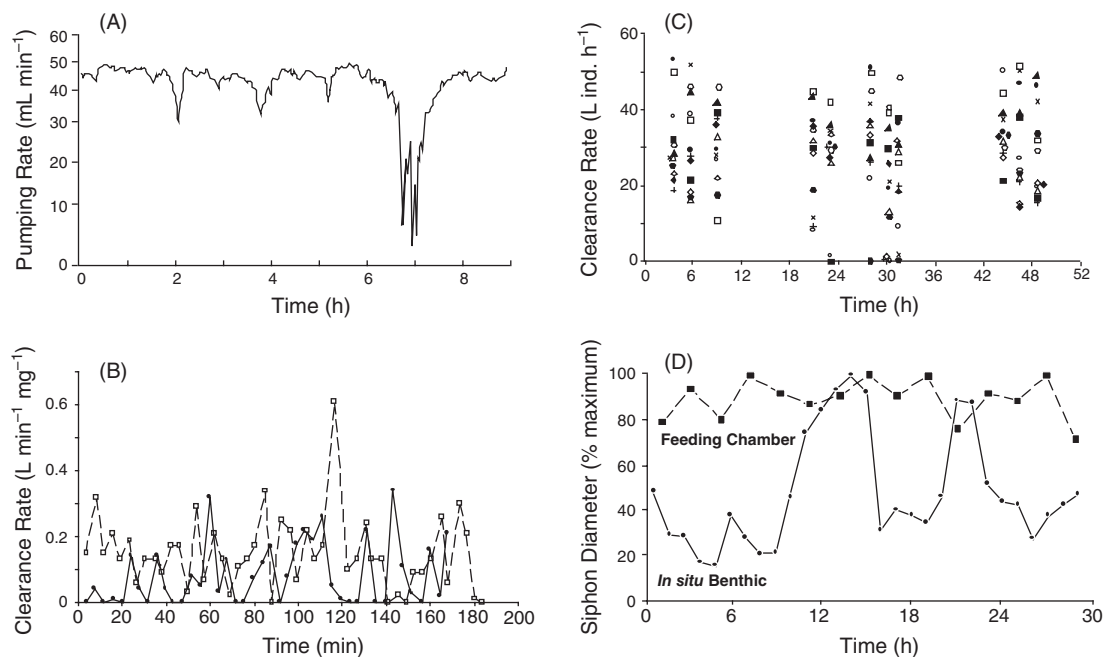


Figure 4.2 Examples of short-term variations in shellfish feeding activity. (A) Continuous direct measurements of pumping rate of one *Mytilus edulis* during constant supply of an algal cell diet (5×10^3 cells mL⁻¹) (Davenport and Woolmington 1982). (B) *M. edulis* clearance rate of natural seston (\bullet , 5.5 mg L⁻¹; \square , 2.5 mg L⁻¹) in flow-through feeding chambers (redrawn from Fr chet and Bourget 1987). (C) Changes in clearance rate of 12 individual queen scallops (*Pecten maximus*; the symbols identify each scallop) feeding on natural seston in flow-through feeding chambers (redrawn from Strohmeier et al. 2009). (D) Percent maximum exhalant siphon area of *M. edulis* measured *in situ* (\bullet) and in feeding chambers (\blacksquare) (Newell et al. 2005).

short-term clearance rate responses of individual *Mytilus edulis* and *Pecten maximus* occur under relatively constant environmental conditions and that this variation was not synchronized with other individuals (Fig. 4.2C).

Observations of shell gape and exhalant siphon area have been used to study feeding behavior under both controlled laboratory conditions (Newell et al. 1998; Riisg rd et al. 2003; Frank et al. 2007; Maire et al. 2007) and naturally variable environmental conditions (Newell et al. 1998, 2005; Dolmer 2000; Saurel et al. 2007). Frank et al. (2007) showed that valve gape accounts for an average of only 25% (range of 2–82%) of the variation in clearance rate in oysters (Frank et al. 2007),

and this relationship can differ between individuals and within an individual over different periods of time. MacDonald et al. (2009) reported that exhalant siphon area explained a maximum of 53% of clearance rate variations in *Mytilus edulis* and that the correlation appeared to differ with mussel size. Valve gape and exhalant siphon area do influence water filtration to varying degrees, but these measurements should not be interpreted as being synonymous with clearance rate. The true value of these measurements is in their utility to provide semicontinuous measurements that can reveal general trends in feeding behavior (Frank et al. 2007; MacDonald et al. 2009).

Newell et al. (2001) demonstrated that exhalent siphon area is more closely related to clearance rate than valve gape (see also Maire et al. 2007), and *in situ* video observations in a benthic mussel population in Maine, USA, showed large short-term variations in mussel feeding activity and feeding rates that were typically less than 50% of the maximum (Fig. 4.2D). Analysis of underwater photos of a mussel population in Limfjorden, Denmark, over a 4-day period showed that between 17% and 69% of the mussels were inactive (closed; Dolmer 2000). The highest percentage of closed mussels corresponded with a period of low food availability ($<0.5 \mu\text{g}$ chlorophyll *a* [Chl]L⁻¹), but a significant fraction of the population was inactive even when sufficient food was present. This study estimated that the gaping mussels were feeding at rates averaging 55% (range: 27–98%) of their maximum capacity. Saurel et al. (2007) used a similar approach to observe mussel feeding behavior in the Menai Strait, UK, and showed that individuals continuously varied feeding activity between zero and maximum over a 48-h period, with an average feeding rate of between 39% and 46% of maximum capacity.

Field studies of temporal variations in clearance rate show a high degree of feeding variability over tidal to seasonal time scales (Fig. 4.3), with the transition between low, medium, and maximum clearance rates sometimes occurring over very short periods (e.g., Bayne and Widdows 1978; Thompson 1984; Deslous-Paoli et al. 1987; Fréchette and Bourget 1987; Cranford and Hargrave 1994; Smaal and Vonck 1997; Smaal et al. 1997; Newell et al. 1998, Cranford et al. 1998; Cranford and Hill 1999; James et al. 2001; Wong and Cheung 2001b; MacDonald and Ward 2009; Strohmeier et al. 2009). These studies, as well as the preponderance of research on bivalve feeding physiology, point to the high flexibility inherent within bivalve species to alter feeding behavior over different temporal scales.

Average standardized clearance rates

Rate standardization and allometries

For comparative purposes, water processing rates of bivalves have generally been standardized to a 1-g (dry tissue weight) individual using the following formula:

$$Y_s = Y_e(1/W_e)^b, \quad (4.4)$$

where Y_s and Y_e are the corrected and experimental physiological rates, respectively, W_e is the weight of the experimental animal, and b is the allometric exponent. Determining the appropriate exponent to use is a critical decision as the accuracy of the standardized value degrades exponentially as the b -value is progressively over- or underestimated. Selection of a b -value from the literature and comparisons between reported values requires some precautions (see below). Utilizing body mass to standardize clearance rate is merely a practical proxy for describing the effect of gill size (surface area). A complication is that seasonal changes in body mass are unrelated to gill size (fluctuations in internal nutrient stores and reproductive tissues fluctuates) and this introduces standardization errors that can complicate clearance rate comparisons both within and between studies. Shellfish condition index, which reflects seasonal cycles in nutritional and reproductive states, should be considered when comparing weight-standardized feeding rates. The true relationship between water processing rate and gill size may be more accurately related to shell length than to body weight (e.g., Filgueira et al. 2008). However, mean annual length/weight relationships can vary greatly between geographic locations and, under this scenario, gill size may be more accurately indicated, for comparative purposes, by animal weight than by shell length. The majority of results presented on the maximum clearance capacity of different shellfish species (above) come from populations in

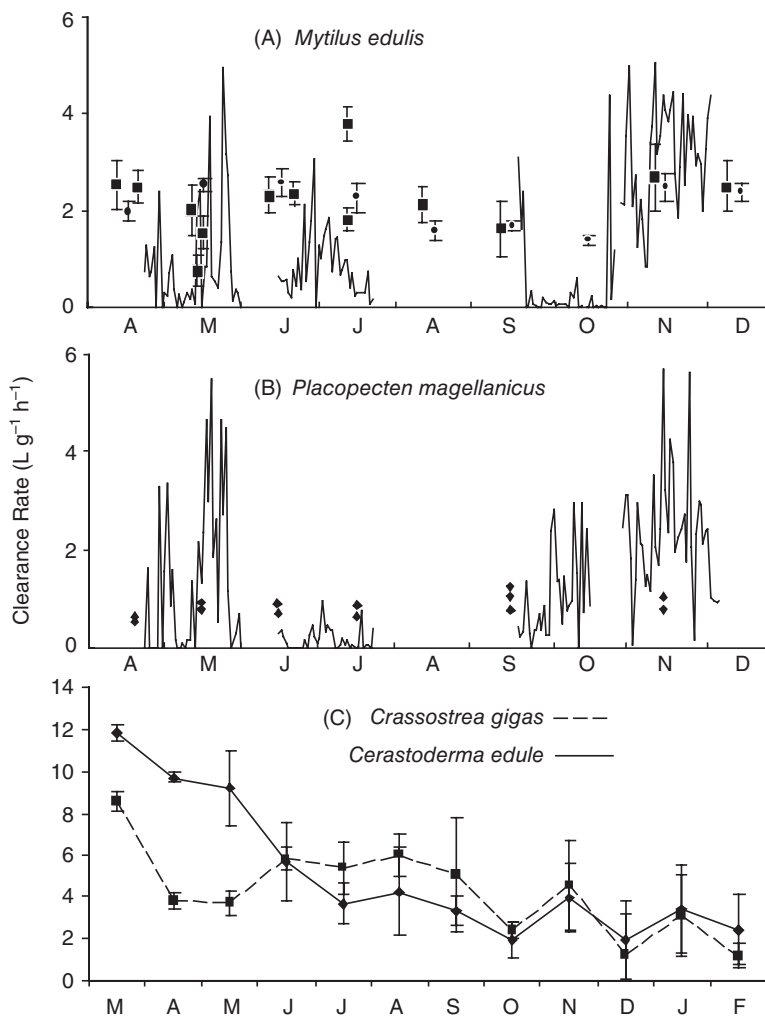


Figure 4.3 Seasonal variation in standardized clearance rate of (A) the blue mussel *Mytilus edulis*, (B) the sea scallop (*Placopecten magellanicus*), and (C) the cockle *Cerastoderma edule* and oyster *Crassostrea gigas*. Solid lines in panels A and B are calculated from data reported in Cranford and Hill (1999). Discrete measurements are from Smaal et al. (1997; ■) and Smaal and Vonck (1997; •) for *M. edulis*, MacDonald and Thompson (1986; ◆) for *P. magellanicus*, and Deslous-Paoli et al. (1987) for *C. edule* and *C. gigas*.

Denmark, which may help to explain the relatively low variability in allometric parameters given in Equations 4.2 and 4.3. We recommend that the selection of a standardization method be based on the specific goals of the study (e.g., understanding spatial vs. temporal variation), and that both the experimental animal weight and length be reported so that

other researchers can more effectively make comparisons between studies.

The allometric relationship between clearance rate and body size of 21 species is summarized in Table 4.1. This summary only includes studies not previously reviewed by Winter (1978) and Riisgård (2001a, 2001b). The values of the allometric exponent for dry

Table 4.1 Clearance and pumping rate (C and P ; Lh^{-1}) as a function of the size of different shellfish species according to the allometric equation $Y = aX^b$, where Y is C or P , and X is dry tissue weight (W ; g) or shell length (L ; mm).

Species and reference	Size	T (°C)	n	Weight relationship	Length relationship
<i>Argopecten purpuratus</i>					
Navarro and González (1998)	0.1–5.7 g	12	15	$C = 2.45W^{0.80}$	
<i>Aulacomya ater</i>					
Stuart (1982)	0.005–2.1 g	12.5	86	$C = 1.48W^{0.59}$	
Van Erkon Schurink and Griffiths (1992)	10–60 mm	15	—	$C = 0.89W^{0.81}$	$C = 8.4 \times 10^{-5}L^{2.29}$
<i>Cerastoderma edule</i>					
Smaal et al. (1986)*	—	9.5–15	53	$C = 2.59 \pm 0.12W^{0.51 \pm 0.02}$	
Smaal et al. (1997)*	0.03–1.4 g	1.4–18.5	134	$C = 1.44W^{0.69}$	
Urrutia et al. (1996)	—	—	—	$C = aW^{0.57}$	
Newell and Bayne (1980)*	10–40 cm	—	68	$C = 0.60W^{0.51}$	
<i>Chlamys islandica</i>					
Vahl (1980)	0.01–7.0 g	3.4	21	$C = 3.9W^{0.60}$	
<i>Choromytilus meridionalis</i>					
Griffiths (1980)	0.02–3.2 g	12, 18	64	$C = 5.37W^{0.60}$	$C = 0.0064L^{1.58}$
Van Erkon Schurink and Griffiths (1992)	10–60 mm	15	—	$C = 3.49W^{1.00}$	$C = 2.0 \times 10^{-5}L^{2.93}$
<i>Crassostrea gigas</i>					
Bougrier et al. (1995)*	0.1–3.0 g	5–25	316	$C = 3.92 \pm 0.84W^{0.50 \pm 0.17}$	
Ren et al. (2000)	0.02–0.4 g	10–13	38	$C = aL^{0.57}$	$C = 0.016L^{1.46}$
Gerdes (1983)	0.05–0.81 g	20	10	$C = 2.28L^{0.73}$	
<i>Mercenaria mercenaria</i>					
Doering and Oviatt (1986)	32–107 mm	13–21	41		$C = 0.0307L^{0.97}$
<i>Mytilus edulis</i>					
Jones et al. (1992); maximum	0.01–2.1 g	10–12	24	$P = 3.16W^{0.72}$	$P = 0.0037L^{2.09}$
Jones et al. (1992); mean	0.01–2.1 g	10–12	24	$P = 1.78W^{0.70}$	$P = 0.0024L^{2.19}$
Smaal et al. (1997)*	0.02–3.90 g	0.4–19	139	$C = 1.66 \pm 0.55W^{0.57 \pm 0.17}$	

Table 4.1 (Continued)

Species and reference	Size	T (°C)	n	Weight relationship	Length relationship
Hawkins et al. (1985)	45–57 mm	—	—	$C = aW^{0.45}$	
Thompson (1984)*	0.07–4.20 g	0–15	128	$C = 1.73 \pm 0.19W^{0.41 \pm 0.08}$	
Smaal et al. (1986)*	0.01–1.17 g	9–15	20	$C = 1.65 \pm 0.79W^{0.61 \pm 0.20}$	
Widdows (1978)	0.01–2.4 g	15	50	$C = 2.65W^{0.38}$	
Bayne and Widdows (1978)					
Lyner*	0.15–2.9 g	7–21	122	$C = 1.98 \pm 0.49W^{0.45 \pm 0.24}$	
Cattewater*	0.13–2.8 g	10–17	105	$C = 1.57 \pm 0.36W^{0.47 \pm 0.11}$	
<i>Mytilus edulis platensis</i>					
Dellatorre et al. (2007)					
Wild mussels	30–85 mm	20	49	$C = 3.89W^{0.56}$	$C = 0.0040L^{1.72}$
Cultured mussels	16–73 mm	20	52	$C = 5.74W^{0.58}$	$C = 0.0022L^{1.97}$
<i>Mytilus chilensis</i>					
Navarro and Winter (1982)	0.02–3 g	12	34	$C = 1.13W^{0.60}$	
<i>Mytilus galloprovincialis</i>					
Filgueira et al. (2008); experiment 1	27–85 mm	—	59	$C = 5.80W^{0.60}$	$C = 0.0035L^{1.72}$
Filgueira et al. (2008); experiment 2	24–86 mm	—	93	$C = 5.02W^{0.50}$	$C = 0.0039L^{1.72}$
Van Erkon Schurink and Griffiths (1992)	10–60 mm	15	—	$C = 4.08W^{1.06}$	$C = 1.7 \times 10^{-5}L^{3.02}$
<i>Ostrea edulis</i>					
Haure et al. (1998)*	0.1–2.7 g	10–30	149	$C = 1.38 \pm 1.15W^{0.83 \pm 0.07}$	
Rodhouse (1978)	0.1–2 g	—	—	$C = aW^{0.48}$	
<i>Ostrea chilensis</i>					
Winter et al. (1984)	0.05–2.3 g	12	16	$C = 1.32W^{0.63}$	
Winter et al. (1984)	0.05–2.3 g	12	12	$C = 0.62W^{0.60}$	
<i>Perna canaliculus</i>					
James et al. (2001)*	20–100 mm	11–17	53	$C = 2.29 \pm 1.05W^{0.75 \pm 0.31}$	$C = 0.001 \pm 0.016L^{1.99 \pm 0.64}$

Table 4.1 (Continued)

Species and reference	Size	T (°C)	n	Weight relationship	Length relationship
<i>Perna viridis</i>					
Wong and Cheung (2001b)*	25–85 mm	18–30	512	$C = 0.81 \pm 0.56W^{0.61 \pm 0.29}$	
<i>Perna perna</i>					
Berry and Schleyer (1983)	10–120 mm	20	97	$C = 8.85W^{0.66}$	$C = 0.0027L^{1.86}$
Van Erkon Schurink and Griffiths (1992)	10–60 mm	15	—	$C = 2.55W^{0.88}$	$C = 6.5 \times 10^{-5}L^{2.54}$
<i>Pinctada margaritifera</i>					
Pouvreau et al. (1999)	0.2–7.5 g	28	43	$C = 25.88W^{0.57}$	
Yukihira et al. (1998)	0.05–20 g	25	52	$C = 12.34W^{0.60}$	
<i>Pinctada maxima</i>					
Yukihira et al. (1998)	0.05–20 g	25	54	$C = 10.73W^{0.62}$	
<i>Placopecten magellanicus</i>					
MacDonald and Thompson (1986); 10 m	5–40 g	5.5–12	61	$C = 0.942W^{0.67}$	
MacDonald and Thompson (1986); 31 m	5–20 g	1–11	56	$C = 0.828W^{0.69}$	
<i>Saccostrea commercialis</i>					
Kesarcodi-Watson et al. (2001)	0.005–3 g	22–25	120	$C = 1.89W^{0.32}$	
<i>Venerupis corrugatus</i>					
Stenton-Dozey and Brown (1994)	0.03–0.87 g	13–18	54	$C = 1.90 - 3.62W^{0.61}$	

Results are from studies not included in the previous reviews identified in the text.

* = mean \pm SD of significant regressions; a = intercept not reported.

body weight averaged 0.62 ± 0.05 (± 2 standard error [SE], $n = 43$). This b -value may be somewhat overestimated owing to the anomalously high values reported by Van Erkon Schurink and Griffiths (1992), which averaged

0.94. When these outlier data are excluded, the mean b -value falls to 0.58 ± 0.04 ($n = 39$), which is equal to the average reported by Winter (1978) for 12 species of bivalves (0.58 ± 0.07 , $n = 25$). Combining these data

sets gives an overall average b -value of 0.58 ± 0.04 . This exponent is less than the theoretical value of 0.67 that assumes proportionality with gill surface area (see above) and is considerably less than the value of 0.72 reported for bivalves feeding at maximum capacity (Eq. 4.2). Although fewer studies have reported relationships between clearance rate and shell length, the allometries summarized in Table 4.1 indicate a mean b -value of 2.04 ± 0.54 ($n = 14$). This average is also weighted toward the high values reported by Van Erkon Schurink and Griffiths (1992), and a more generally applicable b -value is 1.78 ± 0.34 ($n = 10$). Although there is considerable variability between studies, there appears to be a tendency for b -values to be less than the theoretical proportionality between gill area and shell length (L^2).

Meta-analysis of clearance rate responses for different species groups

A meta-analysis was conducted on average clearance rate measurements extracted from 61, 30, 25, and 17 published studies on mytilid, pectinid, oyster, and cockle species, respectively. This was conducted to investigate central tendencies in values reported over a range of experimental conditions and to provide a foundation for discussing methodological viewpoints and the multiple factors potentially controlling the feeding responses of shellfish. Average rates reported using a wide range of direct and indirect clearance rate methodologies are incorporated in this analysis, including laboratory, field, and *in situ* studies with algal cell, seston, and/or mixed diets. The size of the literature dictated setting some limitations, and the studies identified in Table 4.2 (mussels) and Table 4.3 (scallops, oysters, and cockles) include only work with diet concentrations between 0 and 10 mg L^{-1} , salinity greater than 20‰ ppt, and flow conditions less than 15 cm s^{-1} . Potential food concentration, salinity, and water flow effects on

clearance rate are addressed separately. The food concentration limits were set to permit comparisons within a relatively narrow, but commonly studied range of food concentrations. Although shellfish feeding is responsive to low levels of many common anthropogenic contaminants and to toxic phytoplankton, these topics are outside the context of this review and such studies were not included in the meta-analysis, with the exception of utilizing data designated as representing reference (control) conditions. The studies reported represent an extensive, but not an exhaustive, search of the literature. Studies were randomly selected and the results are believed to be representative of the full range of published clearance rate values. Clearance rates reported in graphical form were digitized using Didger 4 software (Golden Software, Golden, CO).

The literature on mussel feeding behavior is particularly extensive and frequency distributions of published average clearance rates for different mussel species of standard dry body weight (1 g) and shell length (60 mm) are presented in Figure 4.4 and summary statistics are given in Table 4.4. Results have generally been presented for mussels of standard weight ($n = 401$), but 72 average values were also reported for mussels of standard length (Fig. 4.4B). Reported clearance rates averaged $2.98 \text{ L g}^{-1} \text{ h}^{-1}$ and 3.23 L h^{-1} or a 60-mm mussel, but ranged widely with a maximum value of $17.5 \text{ L g}^{-1} \text{ h}^{-1}$ (not shown) reported for *Mytilus galloprovincialis* by Maire et al. (2007). The weight standardized distribution is skewed toward lower values, and the median of $2.32 \text{ L g}^{-1} \text{ h}^{-1}$ is substantially lower than the predicted mean of $6.54 \text{ L g}^{-1} \text{ h}^{-1}$ calculated using Equation 4.2 for animals feeding at maximum rates under optimal conditions. In fact, 95% of the reported mean values are below this predicted rate. Standardization by length gave a broad distribution of data (Fig. 4.4B) and the predicted maximum clearance rate of 5.95 L h^{-1} for a 60-mm mussel (Eq. 4.3 using $b = 1.81$) is still higher than the mean of

Table 4.2 Studies included in the meta-analysis of average clearance rate estimates for mytilid species subdivided by methodologies employed.

Flow-through chamber (^a Eq. 4.5 or ^b Eq. 4.6 in text)	Closed system (^a clearance, ^b chemostat, ^c static, or ^d flume)	Biodeposition (^a chamber or ^b <i>in situ</i>)	Consumption (^a tunnel, ^b chamber, or ^c suction)
<i>Aulacomya ater</i>			
Bayne et al. (1984) ^{a, A}	Stuart (1982) ^{c, A}		
<i>Choromytilus meridionalis</i>			
Bayne et al. (1984) ^{a, A}	Griffiths (1980) ^{c, A}		
<i>Mytilus chilensis</i>			
Navarro et al. (2003) ^{a, A}		Velasco and Navarro (2003) ^{a, A, S}	
<i>Mytilus edulis</i>			
Okumus and Stirling (1994) ^{a, S}	Kittner and Riisgård (2005) ^{a, A}	Newell et al. (2005) ^{a, S}	Prins et al. 1994 ^{a, S}
Smaal and Vonck (1997) ^{a, S}	Newell et al. (1989) ^{c, S}	Petersen et al. (2004) ^{a, S}	Prins et al. (1996) ^{a, S}
Fréchette et al. (1991) ^{a, S}	Riisgård (1991) ^{a, A}	Hawkins et al. (1996) ^{a, S}	Bayne et al. (1989) ^{b, A}
Prins et al. (1996) ^{a, S}	Riisgård et al. (2003) ^{a, A}	Cranford and Hill (1999) ^{b, S}	Smaal et al. (1986) ^{a, S}
Newell et al. (2005) ^{a, S}	Riisgård and Møhlenberg (1979) ^{b, A}	Hawkins et al. (1997) ^{a, A}	Zurburg et al. (1994) ^{a, S}
Widdows et al. (1979) ^{a, S}	Widdows et al. (2002) ^{d, A}	Dellatorre et al. (2007) ^{a, S}	Møhlenberg and Riisgård (1979) ^{c, A}
Petersen et al. (2004) ^{a, b, S}	Petersen et al. (2004) ^{c, S}		Kjørboe et al. (1980) ^{c, A}
Smaal et al. (1997) ^{b, S}	Riisgård et al. 2003) ^{a, A}		
Thompson (1984) ^{a, S}	Lucas et al. (1987) ^{c, S}		
Bayne et al. (1987) ^{a, S}	Kjørboe et al. (1981) ^{b, A}		
Bayne et al. (1985) ^{a, b, A}	Clausen and Riisgård (1996) ^{a, A}		
Widdows (1978) ^{a, A}	Bayne et al. (1985) ^{c, A}		
Widdows and Johnson (1988) ^{a, A}			
Smaal and Twisk (1997) ^{a, A}			
Widdows et al. (1984) ^{a, S}			
Newell et al. (1998) ^{b, S}			
Vismann (1990) ^{b, S}			
MacDonald and Ward (2009) ^{a, S}			
Bayne and Widdows (1978) ^{a, S}			

Table 4.2 (Continued)

Flow-through chamber (^a Eq. 4.5 or ^b Eq. 4.6 in text)	Closed system (^a clearance, ^b chemostat, ^c static, or ^d flume)	Biodeposition (^a chamber or ^b <i>in situ</i>)	Consumption (^a tunnel, ^b chamber, or ^c suction)
<i>Mytilus galloprovincialis</i>			
Filgueira et al. (2006) ^{a, A, S}	Maire et al. (2007) ^{a, A}	Iglesias et al. 1996) ^{a, S}	
Filgueira et al. (2008) ^{a, A}	Navarro et al. (1996) ^{a, A}	Navarro et al. (1991) ^{a, S}	
Labarta et al. (1997) ^{a, A}		Pérez Camacho et al. (2000) ^{a, S}	
Navarro et al. (1991) ^{a, S}			
Pérez Camacho et al. (2000) ^{b, A}			
<i>Mytilus trossulus</i>			
	Ackerman and Nishizaki (2004) ^{c, S}		
<i>Mytilus californianus</i>			
	Ackerman and Nishizaki (2004) ^{c, S}		
<i>Perna canaliculus</i>			
James et al. (2001) ^{a, S}	Zeldis et al. (2004) ^{c, S}	Hawkins et al. (1999) ^{a, S}	
<i>Perna perna</i>			
Bayne et al. (1984) ^{a, A}	Resgalla et al. (2007) ^{c, A}		
	Berry and Schleyer (1983) ^{c, A}		
<i>Perna viridis</i>			
		Wong and Cheung (1999) ^{a, A}	
		Wong and Cheung (2001a) ^{a, S}	
		Wong and Cheung (2001b) ^{a, S}	

Note that some studies used several methods and/or species. Superscripts indicate the method and use of algae cell (A) and/or seston diets (S).

3.23 Lh⁻¹ (median = 3.18 Lh⁻¹). The literature clearly shows that the maximum feeding response has only occasionally been observed in mussels and is an extreme condition within a wide and highly variable range of average rates.

One factor contributing to the shape of clearance rate frequency distributions is the variation in the allometric exponent employed in each study, which ranged from 0.2 to 1.1. Relatively few studies determined the *b*-value; instead using a value selected from the litera-

Table 4.3 Studies included in the meta-analysis of average clearance rate estimates for scallop, oyster and cockle species.

Scallop	Oyster	Cockle
<i>Argopecten irradians</i>	<i>Crassostrea gigas</i>	<i>Cerastoderma edule</i>
Bauder et al. (2001) ¹	Bayne (2004) ^{2, 4}	Deslous-Paoli et al. (1987) ⁴
Li et al. (2009); low density only ¹	Bayne (1999) ⁴	Foster-Smith (1975) ⁴
Palmer (1980) ⁴	Bougrier et al. (1995) ⁴	Ibarrola et al. (2000) ²
<i>Argopecten purpuratus</i>	Deslous-Paoli et al. (1987) ⁴	Ibarrola et al. (1998) ⁴
Navarro et al. (2000) ⁴	Zurburg et al. (1994) ⁵	Iglesias et al. 1996 ²
Navarro and González 1998 ⁴	Dupuy et al. (2000) ⁴	Iglesias et al. (1998) ⁴
<i>Argopecten ventricosus-circularis</i>	Lefebvre et al. (2000) ²	Møhlenberg and Riisgård (1979) ⁵
Sicard et al. (1999) ⁴	Ren et al. (2000) ¹	Navarro et al. (1992) ⁴
<i>Argopecten nucleus</i>	Haure et al. (2003) ¹	Navarro and Widdows (1997) ¹
Velasco (2007) ¹	Smaal and Zurburg (1997) ⁵	Newell and Bayne (1980) ¹
<i>Chlamys nobilis</i>	Barillé et al. (2003) ¹	Prins and Smaal (1989) ¹
Li et al. (2001) ⁴	Gerdes (1983) ⁴	Prins et al. (1991) ²
<i>Chlamys opercularis</i>	<i>Crassostrea belcheri</i>	Riisgård et al. (2003) ³
McLusky (1973) ⁴	Hawkins et al. (1998) ¹	Smaal et al. (1997) ¹
<i>Chlamys farreri</i>	<i>Crassostrea iradelei</i>	Urrutia et al. (2001) ²
Jihong et al. (2004) ⁴	Hawkins et al. (1998) ¹	Widdows and Navarro (2007) ⁴
Zhou et al. (2006) ²	<i>Crassostrea virginica</i>	Widdows and Shick (1985) ¹
<i>Chlamys hastata</i>	Palmer (1980) ⁴	
Meyhöfer (1985) ⁵	Pernet et al. (2008) ⁴	
<i>Chlamys islandica</i>	Riisgård (1988) ⁴	
Vahl (1980) ¹	<i>Ostrea edulis</i>	
<i>Nodipecten nodosus</i>	Haure et al. (1998) ¹	
Velasco (2007) ¹	Newell et al. (1977) ⁴	
<i>Placopecten magellanicus</i>	Rodhouse (1978) ⁴	
Bacon et al. (1998) ¹	Wilson (1983) ⁵	
Cranford and Grant (1990) ⁴	Buxton et al. (1981) ⁴	
Cranford and Gordon (1992) ¹	<i>Ostrea chilensis</i>	
Cranford et al. (1998) ²	Dunphy et al. (2006) ⁴	
Cranford and Hill (1999) ²	Chaparro and Thompson (1998) ⁴	
Cranford et al. (2005) ²	<i>Saccostrea commercialis</i>	
MacDonald and Thompson (1986) ¹	Bayne et al. (1999) ⁴	
MacDonald and Ward (2009) ¹	Kesarcodi-Watson et al. (2001) ¹	
Ward et al. (1992) ⁴		

Table 4.3 (Continued)

Scallop	Oyster	Cockle
MacDonald and Ward (1994) ¹		
Pilditch and Grant (1999) ⁴		
Wildish et al. (1992) ⁴		
<i>Pecten maximus</i>		
Strohmeier et al. (2009) ¹		
<i>Pecten furtivus</i>		
Møhlenberg and Riisgård (1979) ⁵		
<i>Pecten opercularis</i>		
Møhlenberg and Riisgård (1979) ⁵		
<i>Pecten irradians</i>		
Chipman and Hopkins (1954) ⁵		

Superscripts indicate the method employed (1 = flow-through; 2 = biodeposition; 3 = clearance; 4 = static; and 5 = other).

ture. Where sufficient data were reported on mussel weight and/or length, the standardized results were converted back to experimental rates using the reported b -value and then standardized again using the average weight and length allometric exponents of 0.58 and 1.8, respectively, determined above. Studies reporting nonstandardized rates were also standardized by this method, which increased the number of length-standardized values from 72 to 361. This procedure increased the median clearance rate to $2.46 \text{ L g}^{-1} \text{ h}^{-1}$ (Table 4.4; Fig. 4.4C) and 3.26 L h^{-1} for a 60-mm mussel (Table 4.4; Fig. 4.4D). The resulting distribution for weight-normalized rates is bimodal with a smaller peak at $\sim 5 \text{ L g}^{-1} \text{ h}^{-1}$ that is attributed to the results of studies designed to stimulate maximum clearance rate through the use of an optimal algal-cell diet. Comparison of Figure 4.4C and Figure 4.4D shows that the distribution of reported clearance rates of mussels of standard weight is more closely constrained than for animals of standard length. This suggests that some of the variability between published rates results from geographic differences in mussel length–weight

relationships and the fact that length is not a particularly good surrogate for weight (Hilbish 1986).

Summaries of mean standardized clearance rates for scallops, oysters, and cockles are presented in Table 4.4 along with the mussel data that were shown in Figure 4.4. Given the bimodal distribution of these data, differences between species groups are examined using median values. Based on reported rates, mussels appear to feed at slightly lower rates relative to the other three groups. Standardization using a constant b -value of 0.58 indicated that oysters appear to have the lowest median clearance rate. In both cases, cockles exhibited the highest clearance rates. A factor having a large effect on the mean rate obtained for each species group is the type of experimental diet provided. Studies utilizing an algal cell-based diet resulted in clearance rates of mussels, scallops, and cockles that were on average 1.7 times higher than rates obtained utilizing a natural seston-based diet (Table 4.4). The only exception was for oysters, where data for seston diets was too sparse ($n = 10$) for an objective comparison. The

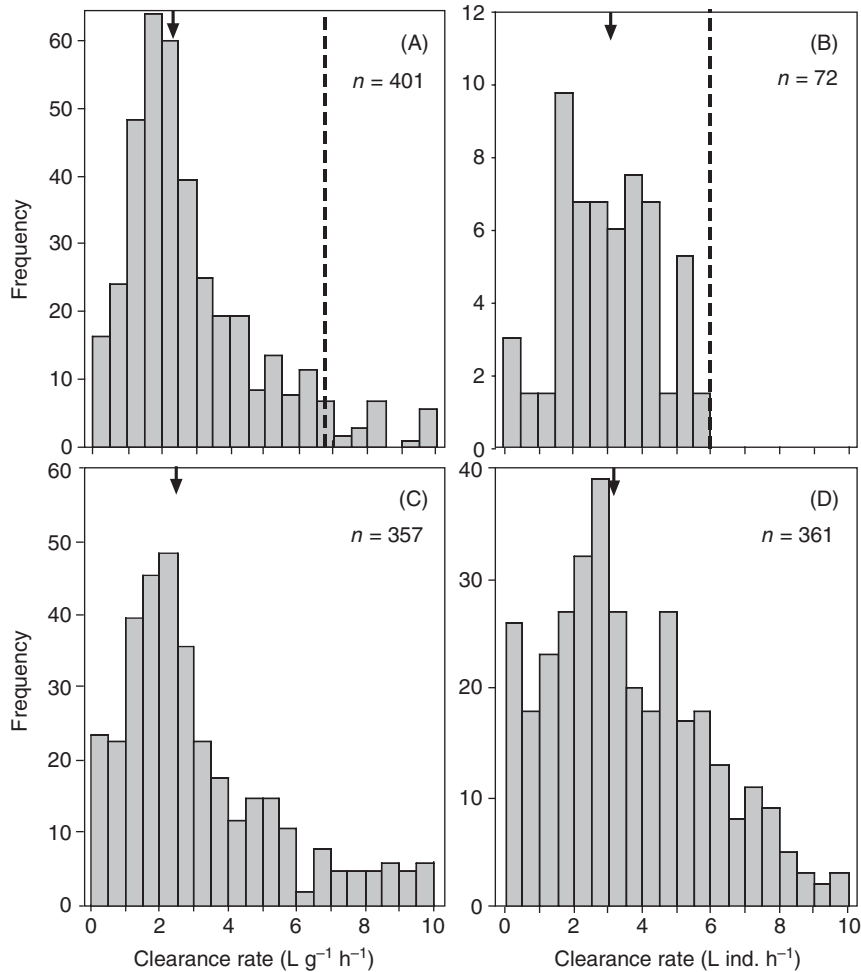


Figure 4.4 Frequency distributions of mussel clearance rate results from the 61 publications listed in Table 4.2. Average rates are standardized by dry weight (A and C; $L g^{-1} h^{-1}$) and shell length (B and D; $L h^{-1}$ for 60mm individual). Plots A and B summarize results as published and plots C and D show the distributions after restandardization using b -values of 0.58 and 1.8 for weight and length, respectively. The arrows indicate median values, and the vertical dashed lines represent the maximum rates predicted by Equations 4.2 and 4.3 for weight- and length-standardized animals, respectively.

generally higher rates obtained for the high-nutritional-quality algal-cell diets was the main reason for the bimodal frequency distribution observed for these species groups. For most aquaculture and wild population predictions requiring clearance rate data, the seston-based results are a logical choice, with mussels, scallops, and cockles feeding at 2.43, 3.49, and $2.81 L g^{-1} h^{-1}$, respectively. The average

rate for oysters feeding on both types of diets ($2.54 L g^{-1} h^{-1}$) is comparable with mussels, and cockles and scallops appear to have a relatively high rate of feeding.

The above comparisons of clearance rates across bivalve species groups are not meant to be conclusive given possible differences in the range of experimental conditions employed in the study of each group. In fact, it may be

Table 4.4 Summary statistics on average ($\pm 2SE$) standardized (1 g dry tissue weight and 60 mm shell length or height) clearance rate values reported in papers listed in Tables 4.2 and 4.3 and after restandardization using average b -values (n = number of mean values applicable).

	Mussel	Scallop	Oyster	Cockle
Dry tissue weight as reported ($Lg^{-1}h^{-1}$)				
n	401	123	123	111
Median	2.32	2.63	3.00	3.37
Mean $\pm 2SE$	2.98 ± 0.23	3.63 ± 0.59	3.47 ± 0.49	3.53 ± 0.44
Shell length (or height) as reported ($Lind^{-1}h^{-1}$)				
n	72	—	—	—
Median	3.18	—	—	—
Mean $\pm 2SE$	3.23 ± 0.34	—	—	—
Dry tissue weight using $b = 0.58$ ($Lg^{-1}h^{-1}$)				
n	357	172	68	90
Median	2.46	3.21	2.05	3.57
Mean $\pm 2SE$	3.24 ± 0.26	5.10 ± 0.76	2.54 ± 0.48	3.58 ± 0.38
Seston-based diet mean $\pm 2SE$ (n)	2.43 ± 0.28 (161)	3.49 ± 0.86 (79)	4.78 ± 0.56 (10)	2.81 ± 0.66 (50)
Algae-based diet mean $\pm 2SE$ (n)	4.18 ± 0.41 (178)	6.66 ± 1.27 (79)	2.15 ± 0.49 (58)	4.12 ± 0.54 (61)
60 mm shell length (height) using $b = 1.8$ ($Lind^{-1}h^{-1}$)				
n	361	130	49	67
Median	3.26	5.18	1.09	5.30
Mean $\pm 2SE$	3.82 ± 0.28	7.89 ± 1.37	1.39 ± 0.28	6.03 ± 0.81

expected that mussels would have a higher feeding rate than cockles based on the observation of Hawkins et al. (1990) that the gill area of *Mytilus edulis* was more than four times greater per unit tissue mass than *Cerastoderma edule*. However, it is important to note that this morphological characteristic can be population specific, with the gill area-to-dry tissue mass ratio varying considerably within a species. For example, *Mytilus edulis* from Denmark and Spain exhibited gill area-to-dry weight ratios of $2458 \text{ mm}^2 \text{ g}^{-1}$ (Møhlenberg and Riisgård 1979) and $4322 \text{ mm}^2 \text{ g}^{-1}$ (Hawkins et al. 1990), respectively. Morphology by itself does not fully explain inter- and intraspecific

variations in clearance rate. The tropical oyster *Pinctada margaritifera* consistently exhibited the highest clearance rates of any bivalve studied (averaged $21.3 Lg^{-1}h^{-1}$; Pouvreau et al. 1999, 2000; Yukihiro et al. 1998) and had an intermediate gill area of $3502 \text{ mm}^2 \text{ g}^{-1}$ (Pouvreau et al. 1999). This was the only species omitted from the meta-analysis owing to the large outlier effect on calculations of the mean clearance rate response.

The average clearance rates reported in Table 4.4 for different bivalve species are useful for the first-order approximation of population and community clearance values. However, because of the very wide range of

clearance rates and b -values reported for individual bivalve populations, we stress the importance of measuring actual clearance rates at the study site during the time(s) of year that is (are) pertinent to the specific application of the data. The effect of the allometric exponent employed can be seen in the difference between the reported mean and the restandardized mean clearance rate (Fig. 4.4 and Table 4.4). In addition, a sensitivity analysis of a scallop (*Chlamys farreri*) growth model showed that a 10% change in the weight exponent caused a 13% change in tissue growth predictions (Hawkins et al. 2002). This effect is relatively small owing to the small size of the scallops studied. The magnitude of the growth effect will increase with the size of the animal, such that the difference in b -values (e.g., 0.76 in Eq. 4.2 vs. 0.58 calculated from data in Table 4.1) would have a substantial impact on population food removal and aquaculture production predictions.

Precision and accuracy of clearance rate measurements

The usual consequence of a high degree of intraindividual variability in feeding activity (see above) is that a large number of replicate measurements are required to obtain sufficient precision (i.e., the degree of agreement between replicated measurements) to protect the analyst from reaching erroneous conclusions when conducting statistical hypothesis tests. Although seldom reported, zero clearance rate values are often discarded prior to statistical analysis. This is a subjective practice that will increase the precision of the mean response, but which will cause overestimation when extrapolating mean individual rates to the population level. The periodic cessation of feeding activity is a normal occurrence (Fig. 4.2) that should not be ignored. Analysis of clearance rate data collected by Strohmeier et al. (2009), who collected 18 replicate measurements to ensure maximum precision, indi-

cate that the highest precision obtainable was ~10% (SE/mean) and that achieving this level required a minimum of 12 replicate measurements. The studies listed in Table 4.2 (mytilid species) were examined and 30 studies provided sufficient data to calculate a precision of 15% for 254 average clearance rate estimates (average sample size was 11.6 replicates). The following illustrates the importance of this degree of intraindividual variability for studies attempting to detect significant differences in average clearance rate responses using inferential statistics. Power analysis was conducted for a paired t -test and one-way analysis of variance (ANOVA) (Power and Precision Ver. 2 software) based on the typical error variance observed across these clearance rate studies at $n = 10$. To achieve an acceptable statistical power of 80% at $\alpha = 0.05$, the minimum “effect size” (the standardized mean difference in clearance rate between experimental treatments) that can be detected is 50%. This is a relatively large effect size for biological measurements, making it difficult to detect differences in average clearance rates between experimental treatments. When measuring clearance rate, the following quote by Nakagawa and Cuthill (2007) is particularly relevant: “. . . all biologists should be ultimately interested in biological importance, which may be assessed using the magnitude of an effect, but not its statistical significance.”

Other relevant statistical considerations that require more attention include the use of regression analysis in cases where both the dependent and independent variables are based on the same data (e.g., clearance rate vs. seston organic content) and the need to use repeated-measures designs when clearance rate values are not independent (MacDonald and Ward 2009). Time series measures on the same individuals cannot be avoided in some cases (e.g., *in situ* observations of shell gape and biodeposition) so the independence assumption needs to be tested prior to the use inferential statistics. Strohmeier et al. (2009)

employed autocorrelation analysis to show that mussel and scallop clearance rates were independent when repeated measurements were taken at time intervals greater than 1 day.

Although clearance rate measurements of individual animals dominate the literature, an alternative approach is to measure population responses. Population responses tend to require fewer measurements to achieve a higher level of precision due to the “built-in” averaging of interindividual variations (Cranford et al. 1998; Iglesias et al. 1998). Individual and population measures do not necessarily provide comparable information, and it should not be assumed that average weight-standardized individual estimates are equal to similarly standardized population estimates. Interactions between individuals (e.g., disturbance, crowding, flow alteration, refiltration of water) may influence some population-based methodologies if they are not controlled.

In an attempt to justify the general application of maximum clearance rate measurements in nature and related theories on shellfish feeding nonresponsiveness to environmental forcing, Riisgård (2001a; see also Jørgensen 1996) concluded that “. . . conflicting data on filtration [clearance] rates seem partially due to the incorrect use of methods, and partly to be caused by differences in experimental conditions.” Bayne (2001) has already provided sufficient rationale why this conclusion is unacceptable, but statements such as this continue to impede the objective discussion of the extrinsic factors that affect shellfish feeding behavior (e.g., Cranford 2001; Widdows 2001; Filgueira et al. 2006) and severely affect the peer review process. There is a need for accuracy in any biological measurement and this need is particularly critical when the intent is to extrapolate the responses of a few animals to predict the biofiltration capacity of extremely dense populations. Any significant errors in estimating the individual response will be magnified immensely at the population level. Consequently, an assessment of the accuracy

of clearance rate measurements continually requires attention, including discussion of the validity of assumptions inherent with available clearance rate methodologies, assumptions regarding the true feeding rate, and the intercalibration of clearance rate methodologies.

A wide range of indirect clearance rate methodologies exist and can be classified based on the measurement of bivalve particle removal (depletion) or egestion (biodeposition). Particle removal methodologies include open (flow-through chambers, *in situ* tunnels, and suction methods) and closed (chambers, aquaria, and mesocosms) systems. Examples of the closed method include the “static method” and the so-called “clearance method” described by Riisgård (2001a). Both determine clearance rate from the exponential decline in particle concentration as a function of time (Coughlan 1969), but the latter may be differentiated by the use of a bivalve population, an optimal algal cell diet, and an algal dosing pump to somewhat maintain the algal concentration. The flow-through chamber method has been the most commonly employed method and clearance rate is calculated using either of the following two equations:

$$\text{Flow-through equation: } C = U ((F_{\text{in}} - F_{\text{out}})/F_{\text{in}}) \quad (4.5)$$

$$\text{Steady-state equation: } C = U ((F_{\text{in}} - F_{\text{out}})/F_{\text{out}}), \quad (4.6)$$

where U is the flow through the chamber (Lh^{-1}), and F_{in} and F_{out} are food particle concentrations in the inflow and outflow of the chamber, respectively. The “flow-through” equation applies to systems where all the particles in the inflow are available to the animals and recirculation of filtered water is absent. The “steady-state” equation represents an alternative for systems with low flow and water recirculation. The importance of ensuring that the flow rate is adequate to meet assumptions inherent with using the

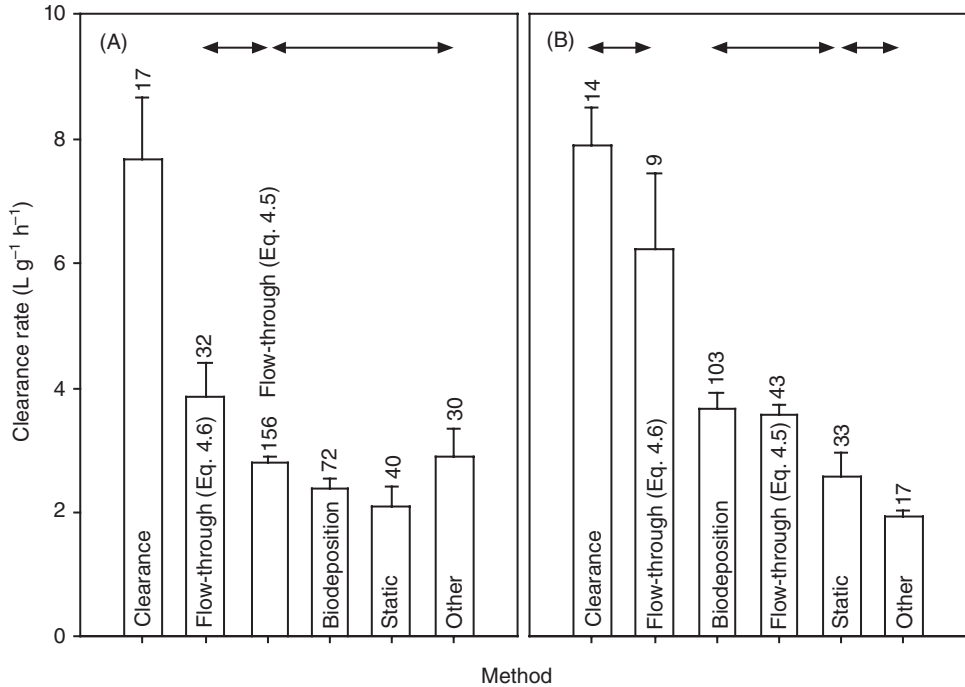


Figure 4.5 Average (+standard error [SE], with sample size shown) weight-standardized clearance rates estimated for mytilid species by the displayed methods. Data are from studies listed in Table 4.2. Plot A summarizes reported standardized rates and plot B includes restandardized rates assuming $b = 0.58$. Arrows on the top of each plot connect methods that provided statistically equivalent results (ANOVA, $P < 0.05$).

flow-through equation has long been recognized (e.g., Riisgård 1977; Bayne et al. 1985) and can be demonstrated simply by measuring no change in clearance rate with increasing flow rate (U). Riisgård (2001a) stated, however, that “the prerequisites for using the method have often been disregarded” resulting in underestimated rates. Filgueira et al. (2006) and Pascoe et al. (2009) critically examined two different flow-through feeding chamber designs and the application of Equation 4.5 and concluded that the method complies with all theoretical requirements provided that the percentage of particles cleared from the flow is less than 25–30% (achieved at $U > 150 \text{ mL min}^{-1}$). This maximum percentage of particles cleared will vary somewhat with the geometry of different feeding chambers and is not a substitute for examining the relationship between clearance values and flow

rates; however, most published studies have reported less than 30% reduction of particles. Although several of the reviewed studies on mytilid species (Table 4.2) report levels of food depletion up to 40%, it is particularly important to note that *even at 40% particle depletion, the potential underestimation of true clearance values resulting from insufficient chamber flow is relatively small compared with the large difference between the median and maximal clearance rates* shown in Figure 4.4 (see figs. 4.4 and 4.5 in Filgueira et al. 2006). The steady-state equation (Eq. 4.6) was employed to estimate clearance rate in 10% of the studies listed in Table 4.2. However, Filgueira et al. (2006) and Pascoe et al. (2009) showed that this equation resulted in reduced precision and overestimation of clearance rate and concluded that Equation 4.5 provided a more accurate representation of true clearance

rate. Petersen et al. (2004) reported similar results, but nonetheless promoted the general application of the steady-state equation.

Feeding rate methodologies based on a combination of shellfish biodeposit production and suspended particle measurements have become increasingly prominent (Table 4.2) since the development of the pseudofeces/feces biodeposition method (Navarro et al. 1991) and the related *in situ* biodeposition method (Cranford and Hargrave 1994). Both methods are similar except that the former approach permits measurements to be made at higher food concentrations where pseudofeces production becomes a significant fraction of filtration rate. As with all other methods, there is a need to ensure that certain assumptions are met for the proper application of these techniques. These assumptions include the need for accurate characterization of suspended particles retained by the gill (a common assumption for all indirect methods) and quantitative biodeposit collection. Assessment of these assumptions has become routine with the application of the *in situ* biodeposition method (Cranford and Hargrave 1994; Cranford et al. 1998), and a sensitivity analysis has shown that potential errors in seston diet characterization using standard water filtration methods could only result in underestimating feeding rates by less than 12% (Cranford and Hill 1999).

A fundamental difference between biodeposition and particle depletion methodologies for measuring clearance rate is that they provide temporally integrated and near-instantaneous responses, respectively. In addition, the biodeposition method often provides an integrated response for several animals. Short-lived extreme clearance rate responses (maximum and zero) that may be of little ecological relevance can greatly influence the short-term mean response, but have little effect on integrated clearance rates obtained with the biodeposition method. As a result, the direct comparison of results obtained with these fun-

damentally different methodologies is not strictly justified, but such comparisons have been made and the results deserve some discussion. A number of studies have shown that clearance rate values obtained with the biodeposition and flow-through chamber methods provide statistically equivalent clearance rate estimates (Urrutia et al. 1996; Iglesias et al. 1998; Cranford and Hill 1999; Bayne 2004; Newell et al. 2005). Comparison of rates obtained with the biodeposition and indirect methods also gave similar results for both *Mytilus edulis* and *Mulinia edulis* (Navarro and Velasco 2003). Conversely, Petersen et al. (2004) concluded that the biodeposition method resulted in significantly lower clearance rate estimates relative to other methods tested. This intercalibration study and the results reported have been questioned based on (1) the failure to sample biodeposits quantitatively (Bayne 2004), (2) the lack of any validation that the experimental conditions actually conform with the basic requirements of the deposition method (Riisgård 2004), and (3) the erroneously high rates that can be obtained when using Equation 4.6 in conjunction with the flow-through method (Filgueira et al. 2006; Pascoe et al. 2009).

Average weight-standardized clearance rate data summarized in Figure 4.4 (Table 4.2) were further analyzed to examine possible effects of different methodologies on mean clearance rates of mytilid species. Reported (Fig. 4.4A) and restandardized clearance rates (Fig. 4.4C) were analyzed separately by means of one-way ANOVAs, which indicated a significant difference in mean results obtained by the different methods (degree of freedom [d.f.] = 341 and 213, respectively; $P < 0.001$). Tukey post hoc comparisons of reported rates showed that most methods provided similar results. The exception was the clearance method, which provided an overall mean rate that was significantly higher by about a factor of two (Fig. 4.5A). When reported results were restandardized, the flow-through method

(Eq. 4.5) gave similar results as the biodeposition and static chamber methods (Fig. 4.5B), but the clearance and steady-state flow-through method (Eq. 4.6) provided significantly ($P < 0.05$) higher clearance rates (Fig. 4.5). Data from these two methods are largely responsible for the second smaller peak in the frequency distribution (Fig. 4.4C).

The majority of published comparisons of indirect clearance rate methodologies, as well as the results of our meta-analysis, shows that similar mean clearance rate results are obtained with most methods when they are employed properly under the same range of experimental conditions. An exception is that the application of Equation 4.6 with the flow-through method can cause overestimated values, particularly when chamber flow rates are relatively low (Pascoe et al. 2009). The clearance method has only been employed under a narrow range of conditions (optimal algal cell rations) and the anomalously high clearance rates that have been obtained reflect these conditions as opposed to any methodological error. This method is not compatible with the use of more complex diets (i.e., natural seston) and a direct comparison is not possible.

Questions regarding the accuracy of clearance rate measurements have generated a rather fruitless debate in the literature because we cannot arbitrarily assume that any rate is more accurate than another. Accuracy may best be assessed by determining the ability of reported clearance values to predict measured tissue growth or the magnitude of phytoplankton depletion resulting from the feeding activity of a given bivalve population. Assessing feeding rates by examining tissue growth over time requires numerous assumptions regarding measurement accuracy for all the physiological components of growth as well as for any applicable energy conversion factors. Further complicating such an approach are the possible effects of resource limitation (selection of energy, carbon or nitrogen budget approaches) and problems comparing a time-integrated

measure (growth) with instantaneous physiological and dietary measures. This approach, however, has been used on several occasions. For example, Fréchette and Bacher (1998) used published data on seston clearance rates and tuned the parameters of the allometric relationship until a growth model provided estimates that matched the observed growth of mussels. The clearance relationship that yielded accurate growth predictions ($2.12W^{0.408}$) was similar to the equation taken from the literature (Thompson 1984; $1.72W^{0.413}$). In this case, a relatively low clearance rate appeared to provide accurate predictions. Cranford and Hill (1999) showed that the growth of *Mytilus edulis* and *Placopecten magellanicus* was similar to predictions based on seasonal clearance rates measured using the *in situ* biodeposition method. Clausen and Riisgård (1996) attempted the only validation of the application of maximum clearance rates (C_{\max}) to a natural population of bivalves and concluded that *Mytilus edulis* must fully exploit their clearance capacity to explain the growth observed in nature. These authors, however, assumed that phytoplankton were the sole food resource. If the other available detrital and living food resources had been included in these growth calculations, a lower clearance rate would also calculate the observed growth.

A somewhat more direct approach to assessing clearance measurement accuracy (i.e., fewer assumptions) is to back-calculate individual clearance rates required to explain the measured population effects on particle sedimentation or depletion in the surrounding water. Doering and Oviatt (1986) showed that clearance rates of *Mercenaria mercenaria* measured using a natural diet and the flow-through method gave estimates of gross sedimentation that agreed well with observations of gross sedimentation in a mesocosm. They noted that the use of maximum clearance rates (Eq. 4.2) would overestimate sedimentation by up to an order of magnitude. Results of a

high-resolution spatial model of seston depletion in dense *Mytilus edulis* culture (Grant et al. 2008), which assumed an average clearance rate of $2.4 \text{ L g}^{-1} \text{ h}^{-1}$ (similar to median values reported herein), predicted bay-scale phytoplankton depletion levels that correspond well with measurements obtained using rapid, high-resolution phytoplankton mapping surveys with a towed sensor vehicle. Petersen et al. (2008) utilized an advection depletion model to determine particle depletion rates for a raft-culture unit containing 40-mm shell length mussels. They concluded that the measured depletion rates could be estimated using clearance rates between 0.6 and $0.9 \text{ L ind.}^{-1} \text{ h}^{-1}$. This is lower than would be predicted using clearance rates reported in Table 4.4, but this is expected given water refiltration under such dense culture conditions. Assumptions regarding the above back-calculation approach to assessing clearance rate accuracy include: No refiltration of water by bivalves located down-current, and no feedback effect on clearance rate from changing food concentration (depletion). Although both assumptions can compromise the validity of this approach, the general similarity of measurements and predictions across these studies tends to validate the high accuracy of most clearance rate methodologies when they are conducted under ecologically relevant conditions.

Controls on bivalve clearance rate

Accurate descriptors of shellfish feeding behavior, which are needed to predict growth and environmental interactions, have to incorporate responses to the major endogenous and exogenous factors and must reflect the net response to multiple, simultaneous forcing parameters. Temperature is one factor that is known to limit the maximum feeding response in shellfish (e.g., Kittner and Riisgård 2005; see above). However, temperature has not been identified as an important control on

feeding behavior under more natural conditions for several mytilid and pectinid species (Widdows and Bayne 1971; Widdows 1973, 1976, 1978; Widdows et al. 1979; Thompson 1984; Thompson and Newell 1985; Prins et al. 1994; Smaal et al. 1997; Cranford and Hill 1999; Cranford et al. 2005; Strohmeier et al. 2009). For example, a time series of *in situ* sea scallop (*Placopecten magellanicus*) clearance rates measured at 3°C showed that feeding activity was variable and that the maximum clearance rate can be achieved even at this low temperature (Cranford et al. 2005). *In situ* measurements of mussel (*Mytilus edulis*) clearance rates at different times of the year also revealed little dependence of feeding on temperature (Fig. 4.6; Ward and MacDonald, unpublished data).

An important consideration when exploring the effect of temperature on bivalve feeding is the need to distinguish between the well-documented effects of temperature on the maximum clearance rates of fully open bivalves and the potential effects on animals that feed at submaximal rates. Animals stimulated to exhibit the maximum clearance response are essentially physiological slaves to the constraints that limit bivalve feeding capacity

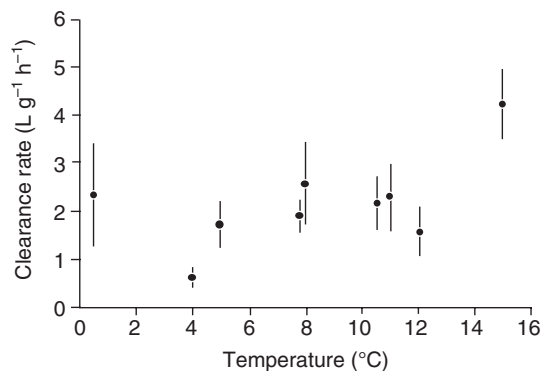


Figure 4.6 Average (\pm SD) standardized clearance rates of *Mytilus edulis* measured in the field over a wide range of water temperatures using the flow-through chamber method (J.E. Ward and B.A. MacDonald, unpublished data obtained in Newfoundland, Canada).

(body size, fluid dynamics, and related temperature effects). Although no physiological mechanisms can override these fundamental constraints on clearance rate, a number of studies have nonetheless employed optimal laboratory conditions as a basis for concluding that evidence for the regulation of feeding performance is lacking in shellfish (Jørgensen 1996; Riisgård 2001b; Kittner and Riisgård 2005). Geometric and physical factors only constrain the upper limits of filtration activity and do not rule out flexibility in feeding performance at reduced rates. Riisgård (2001b) concluded that it is important that future research on bivalve compensatory responses to variations in the environment be made under optimal conditions that result in maximum feeding activity. This would perpetuate an expected result that could only be extrapolated to cultured or wild shellfish populations if bivalves in nature always exhibited maximal feeding rates such as those stimulated by a controlled, artificial diet. The above discussion on feeding variability and range of mean responses clearly shows that it is unacceptable to limit observations to an artificial condition that does not exist in nature.

Seston concentration has a strong influence on bivalve clearance rate and explains a large fraction of the variance in clearance rate measurements (Table 4.4). Although the shape of the relationship varies within and between species, clearance eventually declines as seston concentration increases over a narrow to broad range (e.g., Hawkins et al. 2001; James et al. 2001; Wong and Cheung 2001b; Hewitt and Pilditch 2004; Velasco and Navarro 2003). Numerous studies have shown that clearance rates exhibit an initial peak at relatively low concentrations, followed by a slow decline (Hawkins et al. 1999; James et al. 2001; Hewitt and Pilditch 2004). The example illustrated in Figure 4.7A from Hawkins et al. (1999) shows that variations in clearance rate of *Perna canaliculus* exposed to a wide turbidity range could largely be explained by a com-

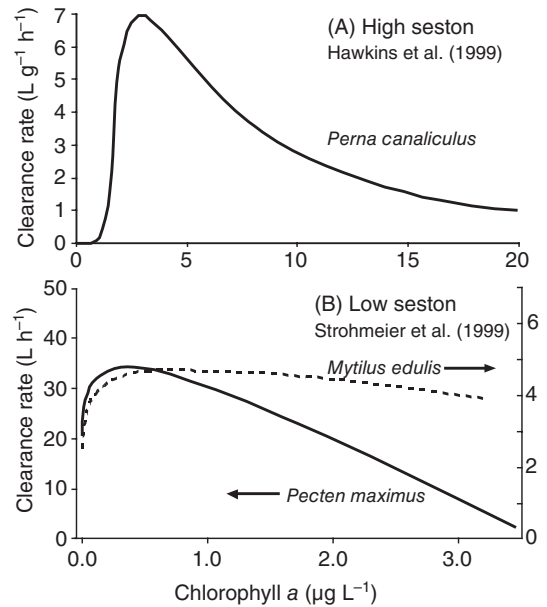


Figure 4.7 Clearance rate in relation to food concentration (chlorophyll a; $\mu\text{g L}^{-1}$) from studies on bivalve species from high (A) and low (B) seston environments. The curves are described by regression equations given in Table 4.4.

bination of Chl and total particulate matter (TPM) concentrations. Rates peaked around $2\mu\text{g Chl L}^{-1}$ and declined at lower and higher concentrations (Fig. 4.7A). James et al. (2001) showed a similar result for this species, except that clearance rates of a population acclimated to low food availability peaked at a considerably lower concentration ($\sim 0.4\mu\text{g Chl L}^{-1}$). This unimodal response to food concentration maximizes food intake during periods of low food availability (Bayne et al. 1987) and can benefit energy intake at higher concentrations by preventing saturation of preingestive particle sorting mechanisms on the ctenidia and labial palps (Iglesias et al. 1992).

The majority of bivalve feeding measurements have been conducted in regions where seston concentrations exceed $1\mu\text{g Chl L}^{-1}$ for most of the year, and the general consensus from these studies is that feeding ceases at Chl concentrations between 0.5 and $1\mu\text{g L}^{-1}$

(Riisgård and Randløv 1981; Newell et al. 2001; Riisgård et al. 2003). The cessation of feeding at low Chl concentrations ($<0.86 \mu\text{gL}^{-1}$) resulted in tissue loss (Hawkins et al. 1999). A study of *Pecten maximus* and *Mytilus edulis* from an area with naturally low seston levels (Norwegian coast), however, showed that both species did not cease feeding even when Chl was as low as $0.01 \mu\text{gL}^{-1}$ (Strohmeier et al. 2009; Fig. 4.7B). This indicates that some bivalve species can functionally adapt to prolonged exposure to low-seston conditions such that their biogeographical distribution is not constrained simply by their ability to clear dilute particles from suspension. Studies on bivalves residing in oligotrophic waters have reported some of the highest feeding rates for the given species measured under natural dietary conditions (Essink et al. 1989; Hawkins et al. 1998; Yukihira et al. 1998; Loret et al. 2000; Pouvreau et al. 1999, 2000; Maire et al. 2007; Strohmeier et al. 2009). This is apparently a necessary adaptation for growth and survival in low seston conditions (Pouvreau et al. 1999).

Controlled laboratory experiments provide valuable insights into the responses of molluscan shellfish to specific conditions but have a limited capacity to duplicate the natural environment where food quantity and quality, and the ambient flow regime, can vary dramatically over different timescales. Although observations under laboratory conditions are needed to isolate specific responses, the knowledge required to predict temporal changes in food acquisition by bivalves must also come from field studies where feeding behavior may be affected by multiple variables. An example of the importance of obtaining clearance rate estimates under strictly *in situ* conditions is illustrated by the results shown in Figure 4.2D. Simultaneous time series of the feeding activity (siphon area) of mussels were markedly different for animals in feeding chambers compared with those in a natural benthic setting (Newell et al. 2005). Mussels in the chambers fed at a

consistent and relatively high rate, while the animals on the bottom exhibited large tidal variations in feeding activity. This may have resulted from location-specific differences in the food supply, exposure to flow conditions in the chambers that were unrepresentative of ambient conditions, and/or a response of the animals to experimental manipulation.

In a review that highlighted the high plasticity of bivalve physiological processes, Bayne (1998) postulated “. . . the *a priori* expectation (and the hypotheses that flow from it) is that flexibility will lead to some measurable level of compensation in feeding behaviour, where compensation is defined as a change in a physiological process, in response to a change in feeding conditions, which results in an increase in nutritional uptake over the rate that would apply if no compensatory change occurred.” An endogenous factor potentially influencing clearance rate in nature, therefore, is the instinctive feeding strategy of a given bivalve species. There appears to exist a continuum of strategies ranging from species that primarily regulate clearance rate (e.g., *Venerupis pullastra*, *Mercenaria mercenaria*, *Mya arenaria*, and *Pinctada margaritifera*; Foster-Smith 1975; Bricelj and Malouf 1984; Bacon et al. 1998; Hawkins et al. 1998), to those that mainly regulate the production of pseudofeces (e.g., *Mytilus edulis* and *Cardium edule*; Foster-Smith 1975; Bayne 1993; Navarro et al. 1994; Hawkins et al. 1996), to others that employ both mechanisms to varying degrees (e.g., *Atrina zelandica*, *Cerastoderma edule*, *Crassostrea gigas*, *Mulinia edulis*, *Mytilus chilensis*, *Placopecten magellanicus*, and *Perna viridis*; Cranford and Gordon 1992; Navarro et al. 1992; Soletchnik et al. 1996; Urrutia et al. 1996; Barillé et al. 1997; Iglesias et al. 1996; Bacon et al. 1998; Hawkins et al. 1998; Velasco and Navarro 2002; Hewitt and Pilditch 2004). The strategy employed also appears to vary between geographic locations for the same species (e.g., *Crassostrea gigas*; Ren et al. 2000). In areas where the nutritional

quality of the seston is generally high, there is little bioenergetic benefit to regulating particle selection (pseudofeces production), so the regulation of clearance rate with changing food abundance is the more effective strategy. Bivalves residing in more turbid regions with variable seston conditions benefit from regulating pseudofeces production, but those species that are best suited to high turbidity also regulate clearance rate to maximize energy intake (see Velasco and Navarro 2002).

The so-called “bivalve functional response” to diet variability also depends on qualitative aspects of the available seston, which make it difficult to categorize the feeding strategy of many species from the available literature when only a limited range of seston qualities and quantities have been employed. A good indication of the important effect of diet quality on clearance rate can be seen in the difference between average rates measured using algal cell- and seston-based diets. For mussels, scallops, and cockles, laboratory measurements using algal cell cultures resulted in average clearance rates that are 60% higher than rates obtained using seston-based diets (Table 4.4). Feeding behavior is highly stimulated by specific nutritive compounds present in the diet (Navarro et al. 2000) owing, at least in part, to the capacity for chemoreception (Ward et al. 1992). Statistical descriptions of clearance rate responses to natural dietary conditions have been developed for several bivalve species and are summarized in Table 4.5. These models indicate that diet quality, which is generally expressed as seston organic content, is an important factor. However, clearance rate tends to be better explained by changes in quantitative rather than qualitative aspects of the diet (see also Hewitt and Pilditch 2004 and cited papers).

Despite an abundance of knowledge on the responses of bivalves to a range of environmental forcing functions, no clear relationships are apparent between seasonal variations in feeding activity and these variables (e.g.,

Deslous-Paoli et al. 1987; Smaal et al. 1997; Cranford and Hill 1999; Hewitt and Pilditch 2004; Strohmeier et al. 2009). Additionally, bivalves residing in adjacent areas with apparently similar conditions can show marked differences in their feeding behavior (Hewitt and Pilditch 2004). The general lack of correlation between clearance rate and ambient environmental conditions may stem from a number of factors including

1. the limited ability of the statistical methods employed to quantify complex interactions between multivariate forcing functions, many of which may cause a nonlinear response;
2. the measurement of bulk seston variables that inadequately characterize food quantity and quality and the stimulatory/inhibitory properties of seston components on feeding behavior;
3. the inability to continuously measure many potentially important environmental parameters, particularly diet quality;
4. the presence of time-averaged behavior in which the bivalves do not compensate for relatively short-term environmental variations but remain adapted to longer-term conditions;
5. feedback from the regulation of digestive processes that effect feeding behavior; and
6. the additional influence of seasonally variable endogenous nutrient demands on the animal’s energy balance and compensatory feeding responses. The high energy costs of gametogenesis are an obvious, albeit poorly understood, seasonally variable factor potentially forcing the need for compensatory feeding adjustments (Deslous-Paoli et al. 1987; Cranford and Hill 1999).

Whereas the majority of bivalve feeding studies have been concerned primarily with determining instantaneous responses to environmental change, the role of past feeding history (e.g., the persistence of feeding behavior in the face

Table 4.5 Significant ($P < 0.05$) regressions between bivalve clearance rate (C) and the total particulate matter concentration (TPM) and organic content (OC; proportion) of TPM.

Species and source	Equation	Applicable range	r^2
<i>Atrina zelandica</i>			
Hewitt and Pilditch (2004) (Four determinations)	$C \text{ (mL g}^{-1} \text{ h}^{-1}) = 337 \times e^{-0.5(\log(\text{TPM}-100)/1.1) \times 2}$	50–580 mg TPML ⁻¹	0.81
	$C \text{ (mL g}^{-1} \text{ h}^{-1}) = 193 \times e^{-0.5(\log(\text{TPM}-86)/0.81) \times 2}$	18–550 mg TPML ⁻¹	0.88
	$C \text{ (mL g}^{-1} \text{ h}^{-1}) = 428 \times e^{-0.5(\log(\text{TPM}-1.06)/160) \times 2}$	70–600 mg TPML ⁻¹	0.85
	$C \text{ (mL g}^{-1} \text{ h}^{-1}) = 360 \times e^{-0.5(\log(\text{TPM}-1.3)/93) \times 2}$	50–580 mg TPML ⁻¹	0.65
<i>Argopecten irradians</i>			
Palmer (1980)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = -0.649(\text{TPM}) + 6.364$	0–10 mg algae L ⁻¹	0.80
<i>Cerastoderma edule</i>			
Iglesias et al. (1996)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = e^{(0.3968 - 0.2118(\text{TPM}) \times \text{OC})}$	5–22 mg TPML ⁻¹	0.50
Navarro et al. (1992)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = e^{(-0.0409 \times \text{Vol} + 0.560)}$	3–30 mg TPML ⁻¹	0.66
<i>Chlamys farreri</i>			
Hawkins et al. (2001)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = [91 \times (\text{Vol} + 1)^{1.2} \times (\text{Chl} + 1)^{2.1} \times e^{(-1.7 \times (\text{Vol} + 1) + (-1.4 \times (\text{Chl} + 1)) + (0.21 \times (\text{Vol} + 1) \times (\text{Chl} + 1))}] - 1$	3.2–105 mg TPML ⁻¹	0.58
<i>Crassostrea gigas</i>			
Ren et al. (2000)	$C \text{ (L h}^{-1} \text{ cm}^{-1}) = 0.17 \times (\text{TPM}/(\text{TPM} + 0.39)) \times e^{(-0.00378 \times \text{TPM})}$	~1–650 mg TPML ⁻¹	0.79
<i>Mulinia edulis</i>			
Velasco and Navarro (2002)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 10^{(2.95 - 0.59 \times \log \text{TPM} - 1.53 \times \log \text{OC})}$	2–203 mg TPML ⁻¹	0.82
Velasco and Navarro (2003)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 2.3841 \times e^{(-0.0054 \times \text{TPM})}$	3–200 mg TPML ⁻¹	0.85
<i>Mytilus edulis</i>			
Hawkins et al. (1996)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 0.60 + 0.039(\text{TPM})$	5–120 mg TPML ⁻¹	0.54
Strohmeier et al. (2009)	$C \text{ (L h}^{-1}) = 5.35 - 0.67(\text{Chl}) + 0.56(\ln \text{Chl}) + 0.001/(\text{Chl})$	0–3 µg Chl L ⁻¹	0.34
<i>Mytilus chilensis</i>			
Velasco and Navarro (2002)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 10^{(2.94 - 0.61 \times \log \text{TPM} - 1.33 \times \log \text{OC})}$	2–203 mg TPML ⁻¹	0.83
Velasco and Navarro (2003)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 1.2423 \times e^{(-0.0064 \times \text{TPM})}$	3–200 mg TPML ⁻¹	0.92
<i>Perna canaliculus</i>			
Hawkins et al. (1999)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 6.81 \times (\ln \text{Chl}/1.1)^{2.71} \times e^{(-2.71 \times ((\ln \text{Chl}/1.1) - 1))} \times e^{(-0.19 \times \ln \text{TPM})}$	2–3790 mg TPML ⁻¹	0.53
James et al. (2001)*	$C \text{ (L h}^{-1}) = (a \times (e^{(b \times \text{Chl})})) / (1 + (\text{Chl}/c)^d)$	0.3–0.51 µg Chl L ⁻¹	0.83
<i>Perna viridis</i>			
Hawkins et al. (1998)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 12.2 \times \text{POM}^{-0.90}$	2–17 mg POM L ⁻¹	0.33
Wong and Cheung (2001b)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 4.351 \times \text{TPM}^{-1.140}$	1–18 mg TPML ⁻¹	0.68
Wong and Cheung (2001b)	$C \text{ (L g}^{-1} \text{ h}^{-1}) = 3.114 \times \text{TPM}^{-1.462}$	1–18 mg TPML ⁻¹	0.64
<i>Pecten maximus</i>			
Strohmeier et al. (2009)	$C \text{ (L h}^{-1}) = 44.12 - 13.96(\text{Chl}) + 5.02(\ln \text{Chl}) + 0.018/(\text{Chl})$	0–3 µg Chl L ⁻¹	0.44

Seston abundance was measured as chlorophyll a (Chl; µg L⁻¹), total particulate matter (TPM; mg L⁻¹), particle volume (Vol; mm³ L⁻¹), and/or particulate organic matter (POM; mg L⁻¹).

*Equation constants not reported.

of further change) and time-dependent physiological acclimation processes in defining food acquisition processes has seldom been addressed (Bayne 1993). It has been suggested that at least some bivalves do not regulate food utilization over the short term, but utilize time-averaged optimization behavior (Hawkins et al. 1985). For example, if food availability fluctuates rapidly over short-time scales, the animal may waste valuable internal resources responding to every change. Although clearing particles requires minimal energetic cost, the higher costs of digestion and the need to make continuous digestive enzyme adjustments may make continuous adaptation an overly wasteful strategy. The time-averaged optimization strategy was supported by time series data on sea scallop feeding responses to storm-induced dietary changes (Cranford et al. 1998).

Emerging knowledge on ecosystem interactions with the bivalve biofilter

Research on ecosystem-level interactions with the feeding activity of bivalve populations has focused on the potential control of phytoplankton assemblages and seston via particle depletion, and the consequences of excreted and egested waste products to energy flow and nutrient cycling. Two emerging research topics are briefly summarized here that emphasize the need for consideration of additional effects of biofiltration on coastal ecosystems. These effects further contribute to the characterization of some bivalve molluscs as “ecosystem engineers.”

Transparent exopolymer particle (TEP) production

The feeding processes of bivalves can directly affect the water column through removal of suspended particulate matter, that is, biofiltra-

tion. Suspension feeding, however, might have indirect effects on suspended particles as well, further contributing to benthic-pelagic coupling. Studies by Ward and coworkers demonstrate that bivalves and other suspension-feeders can produce significant quantities of TEPs; Mckee et al. 2005; Heinonen et al. 2007; Li et al. 2007). TEPs are discrete, gel-like particles that can be found in both marine and freshwater systems (Alldredge et al. 1998; Passow et al. 2001; Passow 2002). They are composed of high-molecular-weight mucopolysaccharides that are released into the water column by a variety of microorganisms including phytoplankton and bacteria (Decho 1990; Kiørboe and Hansen 1993; Passow and Alldredge 1994; Alldredge et al. 1998). The presence of TEPs can have a substantial impact on coagulation efficiency and flocculation of suspended matter into marine snow (Alldredge et al. 1993; Passow 2002). TEPs can act as a glue that binds together small organic and inorganic material, resulting in the formation of larger aggregates that sink rapidly to the benthos (Alldredge and Silver 1988; Alldredge et al. 1993; Kiørboe et al. 1994; Passow and Alldredge 1995).

The abundance and distribution of TEPs in the marine environment has been measured in numerous studies (measured as gum xanthan [GX] equivalents). In general, mean TEP concentrations are lower in open-ocean waters (e.g., 29–512 $\mu\text{g GXL}^{-1}$, Engel 2004; Wurl and Holmes 2008) and higher in coastal waters (e.g., 100–3500 $\mu\text{g GXL}^{-1}$; Passow 2002; Wetz et al. 2009). Peak concentrations are associated with phytoplankton blooms, and high concentrations have been measured in near-shore waters inhabited by dense assemblages of corals, macroalgae, mangroves, seagrasses, and suspension-feeders (e.g., 290–>8000 $\mu\text{g GXL}^{-1}$, Ramaiah et al. 2001, Fabriciusa et al. 2003; Mckee et al. 2005; Wurl and Holmes 2008; Wetz et al. 2009). The concentration of TEPs at any specific location, however, can vary widely depending on

local physical and biological conditions. One potentially significant source of TEPs in near-shore waters is assemblages of suspension-feeding bivalves. In laboratory studies, biomass-specific production rates of TEPs from suspension-feeders fall within the range of 0.8–6.7 $\mu\text{g GX g}^{-1} \text{h}^{-1}$ (Mckee et al. 2005; Heinonen et al. 2007; Li et al. 2007), but can vary due to differences in water pumping activity of the animals. Species-specific TEP production rates under natural conditions, however, may be higher. For example, in a field study using benthic chambers, Mckee et al. (2005) measured a production rate for eastern oysters of 34 $\mu\text{g GX g}^{-1} \text{h}^{-1}$. Using this field production rate, an oyster with a dry tissue mass of 1 g could produce about 816 μg of TEPs in 24 h. Although the fate and turnover time of TEPs is not entirely known (hours to months; Passow 2002), some of this material is likely transported both vertically and horizontally away from shellfish beds. Bivalve-derived TEPs are known to enhance the aggregation of suspended particulate matter (Li et al. 2007). Therefore, such processes could increase deposition of particulate matter, and enhance benthic-pelagic coupling, in areas devoid of suspension-feeders.

Size-dependent particle retention

Grazing of phytoplankton by dense assemblages of bivalves not only has the potential to change phytoplankton biomass but may also affect community composition (Prins et al. 1998; Norén et al. 1999). Bivalves effectively retain particles larger than ~2–8 μm , depending on the species, and therefore some nanoplankton and all picoplankton (both photoautotrophic and heterotrophic) are not effectively captured and consumed. Picoplankton cells essentially exist within a size range that represents refugia from capture by bivalves and where they may benefit from bivalves depleting

their major competitors and predators (ciliates and flagellates), the increased light availability that accompanies bivalve-mediated seston depletion, and the excretion of ammonia directly into nutrient-depleted summer surface waters by the suspended culture. Picoplankton may become available to the bivalves, however, through particle aggregation processes (Cranford et al. 2005; Kach and Ward 2008), or through linkage to higher trophic levels via the microzooplankton (Loret et al. 2000).

Mesocosm studies show that mussel grazing can change phytoplankton species composition, shifting the community to one dominated by picoplankton (Olsson et al. 1992; Prins et al. 1997). Size-selective feeding by extensive bivalve culture is thought to be an important reason why picoplankton cells constitute the most abundant component of the phytoplankton community in the Thau Lagoon in France (Courties et al. 1994; Vaquer et al. 1996; Souchu et al. 2001), and in Tracadie Bay, Canada (Cranford et al. 2008). Picoplankton species have also been shown to dominate the phytoplankton biomass in several embayments supporting extensive suspended mussel culture in Prince Edward Island (50–80% of total Chl), but not in an adjacent unfarmed bay where the microphytoplankton dominate (Cranford et al. 2008). That study showed a close relationship between the average bay-wide picophytoplankton contribution and an index of bay-scale seston depletion by mussel culture. Future research is needed to assess the ecosystem consequences of this top-down destabilization of the food chain, including possible changes in predator–prey relationships and competitive interactions that could result in trophic regime shifts. A shift from microphytoplankton to picophytoplankton biomass could affect particle transport dynamics via reduced settling velocity and altered flocculation processes. The latter is dependent on the production of sticky exopolymers that can be produced in large quantities by diatoms

(see also previous section). These potential ecological effects of shellfish culture need to be better understood and considered in the determination of carrying capacity predictions and when considering implementing schemes that use bivalve farms for combating eutrophication (Lindahl et al. 2005).

Conclusions

Forty years ago, Brian Morton wrote: “The view that bivalve molluscs are ideally adapted to fulfilling a mode of life in which the processes of feeding and digestion are continuous has long been accepted by most zoologists. An increasing amount of evidence, however, is being put forward to suggest that the opposite is true, that is, that bivalves are discontinuous in their feeding and digestive habits” (Morton 1970). This evidence has since increased dramatically and, with few exceptions, reveals a remarkable capacity of bivalve suspension-feeders to finely adjust clearance rate as opposed to simply switching between feeding and nonfeeding states (see Fig. 4.8). The above meta-analysis of the contemporary literature demonstrates that accurate and comparable estimates of clearance rate can easily be obtained using many direct and indirect methodologies using familiar precautions. A major methodological pitfall stems from the application of artificial dietary conditions that stimulate a predetermined (e.g., maximal) feeding response as a basis for developing theories on bivalve feeding behavior in nature. This approach represents an experimental bias that defies basic scientific principles, but has been a prerequisite for all studies that continue to support the autonomous view of bivalve feeding. Whether or not the exhibited high flexibility in clearance rates constitutes a homeostatic strategy to maximize the individuals net energy balance is outside the scope of this review. However, the preponderance of

the literature demonstrates that the opposing theory of autonomous feeding is obsolete.

Bivalve feeding behavior has important implications for aquaculture, including the optimization of farm location and layout, the forecasting of bivalve growth and carrying capacity, and the determination of potential ecological services and impacts. An abundance of information is available on the clearance rate responses of bivalves in nature that can support these applications. Clearance rates are highly variable across short to long temporal scales and large near- and far-field differences in feeding behavior occur within the same species. Predicting wild and farmed bivalve population responses to environmental variability over different scales is a major challenge. For clearance rate measurements to be relevant to addressing aquaculture issues, they need to address scales of variation that are relevant to the specific question being addressed. Incorporating additional elements of environmentally induced physiological regulation into bivalve growth models is challenging as it is difficult for the models to deal with fine-scale temporal variations in the seston (Grant 1996). Despite this shortcoming, the current modeling capacity appears sufficient for accurately replicating observed seasonal growth responses of bivalves (Chapter 6 in this book), and also appears acceptable for accurately predicting effects of feeding on ambient food supplies (see above). Nonetheless, site- and time-specific measurements of clearance rate are encouraged whenever possible to help improve or to test model applications. These measurements will increase confidence among aquaculture stakeholders on the practical and regulatory applications of population-level clearance calculations. They will also improve ecophysiological and ecosystem model predictions and will increase capacity to address more specific questions related to fine-scale changes in feeding behavior. For example, greater spatial resolution within models would



Figure 4.8 Blue mussels, *Mytilus edulis*, actively filtering seawater. (Courtesy of Tore Strohmeier and Øivind Strand.)

permit more quantitative assessments of optimal farm site location/layout and multi-farm interactions, whereas increased temporal resolution will aid in predicting seasonally variable bivalve controls on the phytoplankton. Additional work is needed across a wide range of biogeographical settings, timescales, and species to further resolve details on the interactions between bivalves and their environment, and the way in which feeding responds to quantitative and qualitative dietary stimuli.

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