Vol. 589: 129–140, 2018
https://doi.org/10.3354/meps12431

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 23[§]

Thermal and viscous effects of temperature on *Mercenaria mercenaria* suspension feeding

Jaclyn A. Specht, Heidi L. Fuchs*

Department of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ 08901, USA

ABSTRACT: Temperature can affect hard clam *Mercenaria mercenaria* growth and survival through its influence on suspension feeding. Warming raises metabolic rates and reduces dissolved oxygen in the surrounding fluid, and clams may compensate by increasing their pumping and ingestion rates. Warming also makes seawater less viscous and may affect ingestion rates through temperature-induced changes in viscous forces acting on beating gill cilia. To determine which physical property dominates suspension feeding dynamics, we conducted laboratory experiments to quantify the effects of temperature and viscosity on *M. mercenaria* clearance, ingestion and ciliary beat rates. Ingestion and clearance rates varied with temperature but not with viscosity, and unresponsiveness to viscosity was confirmed by separate ciliary beat measurements on isolated gill preparations at different viscosities. The lack of ciliary response to viscosity indicates that *M. mercenaria* ingestion rates are driven by physiological rather than biomechanical effects of temperature, a result that differs from previous findings for the mussel *Mytilus edulis*. A comparative analysis indicated that these different responses to viscosity cannot be attributed to differences in ciliary mechanics, suggesting that the 2 species differ in their ciliary control mechanisms. We also found that temperature and algal concentration are strong predictors of ingestion rate. These results have important implications for clams' ability to survive and grow in a warming ocean.

KEY WORDS: Clearance rate · Ingestion rate · Kinematic viscosity · Beat frequency · Ciliary mechanics

INTRODUCTION

Bivalves provide important economic and ecosystem services that are threatened by rising seawater temperatures. Bivalves improve water clarity, transfer organic and inorganic matter to the benthos, and alter phytoplankton community structure (Newell 2004). In addition, their value as seafood provides job opportunities and food security. However, warming temperatures may impact these economic and ecosystem services by altering bivalve growth and survival. Warming temperatures can reduce the allocation of energy for growth (Talmage & Gobler 2011, Mackenzie et al. 2014), lowering the probability of survival to reproductive age and increasing mortality. Bivalve resilience depends on the ability to acclimate to ocean warming (Widdows & Bayne 1971), but acclimation is complex and can involve a variety of responses within a single species. For example, mussels do not acclimate their heart rates but are able to acclimate their respiration rates and growth efficiencies to a finite range of temperatures (Widdows 1973). Rising temperatures impact multiple aspects of bivalve physiology, and some interactions among these effects remain poorly understood.

Bivalves' ability to gain energy is altered by temperature through its direct and indirect effects on metabolism and suspension feeding (Bayne et al. 1989). Higher temperatures reduce the concentration of dissolved oxygen in seawater (Weiss 1970) while generally raising the standard metabolic rate (Gillooly et al. 2001), making it more difficult to meet metabolic demands. Bivalves may compensate by pumping water faster to acquire more oxygen and food (Hamwi &

*Corresponding author: hfuchs@marine.rutgers.edu

[§]Corrections were made after publication. For details see www.int-res.com/abstracts/meps/v589/c_p129-140/
This corrected version: March 21, 2018

Haskin 1969, Paganini et al. 2010). At a given seston concentration, respiration and ingestion rates peak at an intermediate, optimum temperature (Hamwi 1969, Thompson & Bayne 1972, Hofmann et al. 2006). At temperature extremes, it becomes more difficult to meet metabolic demands, particularly if food concentrations are low, and bivalves may reduce pumping rates or pump discontinuously to limit their metabolic costs (Thompson & Bayne 1972, Bayne 1973). Although bivalves can acquire more oxygen and food by pumping faster, doing so may also carry higher activity costs depending on the mechanism that links temperature to pumping rate.

Bivalves draw water into their mantle cavities, both to filter food and to absorb oxygen, using gill cilia operating at a Reynolds number of $Re \ll 1$ (Jørgensen 1983). At $Re < 1$, motion is dominated by viscous rather than inertial forces (Purcell 1977), and ciliary movement is opposed by a viscous drag force proportional to kinematic viscosity, which is lower at higher temperatures. Lower viscosity often leads to greater ciliary activity (Jørgensen et al. 1990, Podolsky 1994, Riisgård & Larsen 2007, Larsen et al. 2008), either through a mechanical or physiological response. At a given seston concentration, mussels *Mytilus edulis* have higher ciliary beat rates and clearance rates in warmer seawater; altered-viscosity experiments suggest that higher temperatures reduce viscous drag on the cilia, increasing the ciliary beat rate via fluid mechanical effects (Riisgård & Larsen 2007). Alternatively, bivalves could increase their ciliary beat rate as a physiological response to the higher metabolic costs or lower dissolved oxygen concentrations associated with warmer temperatures. Either a mechanical or physiological increase in ciliary beat rate would increase food ingestion rates, but a physiological response would likely carry higher metabolic costs of ciliary activity. Thus, the mechanism controlling ciliary beat rate could affect bivalves' ability to offset the metabolic impacts of higher temperatures through increased ingestion.

Temperature and viscosity effects on suspension feeding have been examined for one bivalve species but may vary among species or habitats. The viscosity-driven suspension-feeding dynamics of *M. edulis* may not be generalizable to other bivalves because species vary in their morphology, behavior, habitat, and physiology. For example, mussels and clams differ in the structure of their gills (Atkins 1937) and in morphology of the labial palps used to sort particles (Kiørboe & Møhlenberg 1981). Cilia size can also influence suspension feeding, and bivalves with larger laterofrontal cirri have greater particle retention efficiency (Riisgård 1988). High seston concentrations negatively affect clearance rates of clams, cockles, and scallops, but not of mussels and oysters (Newell 2004). Oysters also have higher mortality than clams when exposed to high temperature and high partial pressure of CO_2 (pCO_2), possibly due to their dissimilar adaptations and physiologies (Ivanina et al. 2013). Compared to epifaunal oysters and scallops, infaunal clams are exposed to, and thus may be adapted to cope with, more acidic conditions resulting from CO_2 buildup in the sediment (Talmage & Gobler 2011). Hard clams are also less able than *M. edulis* to acclimate their feeding rate to temperature (Hibbert 1977, Widdows 1978). These differences may lead bivalve species to respond differently to changing environmental conditions.

In this study, we examined how temperature affects suspension feeding by the hard clam *Mercenaria mercenaria*, a commercially important species on the east coast of the USA, where it originated. *M. mercenaria* was abundant off the coast of New Jersey until the 1980s, when populations began to decline (Celestino 2013). Despite harvesting restrictions and clam spawner sanctuaries, hard clam populations have not fully rebounded along the New Jersey coastline. Predictions of clam population dynamics may be improved by a better understanding of how temperature affects hard clam feeding physiology and mechanics. We conducted experiments on *M. mercenaria*, altering seawater temperature and viscosity separately to identify the main mechanism — physiology or biomechanics — by which temperature affects suspension feeding. This study provides insights on how *M. mercenaria* ingestion will be affected by a warming climate.

MATERIALS AND METHODS

Clams

Small *Mercenaria mercenaria* (~2.0 cm shell length) were obtained in 2015 from a commercial hatchery in Atlantic City, NJ, where monthly-averaged seawater temperatures range from 2.7 to 27.5°C (data accessed from the NOAA National Estuarine Research Reserve System Centralized Data Management Office website: www.nerrsdata.org [accessed February 2017]). Clams were obtained in August for viscosity experiments and in August and September for temperature experiments. Clams were maintained in upweller baskets in 10 l buckets of 1 µm-filtered seawater with salinity ranging from 32 to 35 S_p (practical salinity) and held at

20°C for temperature and ciliary beat rate experiments. Clams were held at 23.5°C for viscosity experiments so that viscosity could be increased artificially to temperature equivalents of 20, 16, 12, 8.5, and 5°C. Holding buckets were aerated, but experimental chambers were not aerated to prevent aggregation of algal cells by bubbles, which could cause errors in measured algal concentrations. The clams were fed daily with preserved *Isochrysis galbana* (Reed Mariculture; 10^5 cells ml^{-1}) but were starved 2 d prior to the ingestion rate experiments to promote feeding. During experiments, clams were fed live *I. galbana* (*T-Iso*).

Feeding rates

We quantified clam suspension feeding using clearance and ingestion rates. Clearance rate is the volume of water cleared of particles per time (Coughlan 1969) and is equivalent to pumping rate when cleared particles are captured with 100% efficiency (Grizzle et al. 2001). We used algal food in the size range where *M. mercenaria* capture particles at about 100% efficiency (Riisgård 1988), so we quantified clearance rate assuming that it was equivalent to pumping rate. Ingestion rate is the number of particles ingested per time and is equivalent to filtration rate when no pseudofeces are produced (Hawkins et al. 1998, Grizzle et al. 2001). We observed little production of visible particulates, and pseudofeces production is generally low in the absence of sediment (Bricelj & Malouf 1984), so we quantified ingestion rate assuming that it was equivalent to filtration rate.

We conducted 2 series of experiments to separately estimate how *M. mercenaria* ingestion and clearance rates are affected by temperature and viscosity. Clams were exposed to 6 temperature-adjusted treatments or to 6 viscosity-adjusted treatments with viscosities equivalent to the 6 temperatures (Table 1), and each treatment was replicated 6 times. In temperature experiments, temperature treatment order was randomized to remove ordered effects associated with time in culture. For each temperature treatment, replicates were done 3 at a time concurrently with 3 control treatments held at 20°C. Only 1 temperature treatment could be conducted at a time because only 2 temperature-controlled rooms were available; one room was used for experimental treatments, and the other was used for controls. Temperature controls were used to ensure that variation in feeding was due to temperature and not to other factors such as time in culture. In viscosity experiments, all viscosity treatments were done simultaneously one replicate at a time.

Experiments were conducted in 2 l chambers of 1 µm-filtered seawater, and each treatment replicate included 3 chambers with the following conditions: (1) clams plus algae, (2) clams only, and (3) algae only. Clams (10 $chamber^{-1}$) were added 1 h before the start of each replicate, and algae (mean ± 1 SD concentration $9.8 \pm 0.24 \times 10^4$ cells ml^{-1} live *T-Iso*) was added at the start of the replicate. Although these algal concentrations are high, the associated mass concentrations (<1 mg l^{-1}) are much lower than seston concentrations in estuaries (Berg & Newell 1986). Algae was added only at the beginning of the experiment, but algal concentration varied over time due to clam feeding. On the day before each temperature treatment, clams, algae, and the 2 l chambers of seawater were separately adjusted to the appropriate temperature at a rate of 2°C h^{-1}. It is unlikely that this rate of change induced a cold shock, because the impact of temperature on clearance rate in this study was similar to its impact on pumping rate, a proxy for clearance rate, in studies where clams were temperature-acclimated for several days (Hamwi 1969). For the viscosity treatments, all chambers were maintained at 23.5°C. The viscosity was adjusted to the desired temperature equivalent (T_e) using polyvinylpyrrolidone (PVP)

Table 1. Seawater conditions in feeding and ciliary beat experiments, including temperature (T), kinematic viscosity (ν), and polyvinylpyrrolidone (PVP) concentrations. Viscosity-adjusted treatments were conducted at 23.5°C for ingestion experiments and 21°C for ciliary beat rate experiments. Viscosity was increased to temperature equivalents (T_e) using PVP

Feeding experiments					Ciliary beat rate experiments		
Temperature-adjusted		Viscosity-adjusted			Viscosity-adjusted		
T (°C)	ν ($\times 10^{-6}$ m^2 s^{-1})	T_e (°C)	ν ($\times 10^{-6}$ m^2 s^{-1})	[PVP] (g l^{-1})	T_e (°C)	ν ($\times 10^{-6}$ m^2 s^{-1})	[PVP] (g l^{-1})
23.5	0.96	23.5 ± 0.2	0.97 ± 0.00	0.00	21.2 ± 0.18	1.02 ± 0.00	0.00
20.0	1.06	19.7 ± 0.2	1.06 ± 0.00	0.50	19.2 ± 0.22	1.07 ± 0.01	0.17
16.0	1.17	15.8 ± 0.2	1.17 ± 0.00	1.15	14.5 ± 0.24	1.20 ± 0.01	0.97
12.0	1.31	12.2 ± 0.1	1.29 ± 0.00	1.90	12.2 ± 0.21	1.28 ± 0.01	1.60
8.5	1.42	8.3 ± 0.3	1.43 ± 0.01	2.60	8.6 ± 0.14	1.41 ± 0.01	2.40
5.0	1.60	5.3 ± 0.2	1.55 ± 0.01	3.35	4.1 ± 0.32	1.62 ± 0.02	3.00

(Table 1). Viscosity was not adjusted in the 23.5°C T_e treatments. PVP is commonly used for increasing viscosity in ciliary studies because mixtures are Newtonian and non-toxic (Baba & Hiramoto 1970, Podolsky & Emlet 1993). The low concentrations used here exhibit Newtonian behavior over a wide range of hydrodynamic conditions (Martinez et al. 2014). The true viscosities were determined using a calibrated Cannon Ubbelohde viscometer.

To estimate *M. mercenaria* ingestion and clearance rates in each experiment, concentrations of *T-Iso* were measured initially and then hourly for 4 h using a Multisizer 3 (Beckman Coulter). At the time of sample collection, the number of clams with siphons out was recorded. Clams produced few particulates that could contain pseudofeces, so ingestion and filtration rates should be about equivalent. Because different *T-Iso* cultures were used, the mean algal cell diameters varied (4.81 µm in temperature experiments and 5.26 µm in viscosity experiments) but were within the size range where *M. mercenaria* have a particle capture efficiency of about 100% (Riisgård 1988), so clearance and pumping rates should also be about equivalent. Overall, changing algal concentrations should accurately reflect ingestion and clearance of algal particles. Ingestion rate (I) was estimated as:

$$I = \frac{V}{n} \times \frac{A_1 - A_2}{t_2 - t_1} \quad (1)$$

where V is the water volume, n is the number of clams, and A_1 and A_2 are the algal concentrations at subsequent sampling times t_1 and t_2 (Crisp et al. 1985). Clearance rate (C) was estimated as:

$$C = \frac{V}{nt} \times \ln \frac{A_0}{A_t} \quad (2)$$

where A_0 and A_t are the algal concentrations at times 0 and t, respectively (Coughlan 1969).

Immediately after each experiment, clams were weighed and then frozen (–20°C) for later estimates of dry weights and lengths (Table 2). Shell length, width and height were measured using calipers. For dry weights (DW), clam tissue was separated from the shell, and both parts were dried in an oven at 100°C for 24 h in pre-weighed aluminum tins. Ash-free dry weights (AFDW) were measured after ashing in a furnace at 500°C for 5 h. Clam health was determined using the condition index (CI), calculated as:

$$\mathrm{CI} = \frac{W_T}{D_S} \times 100 \quad (3)$$

where W_T is the AFDW of the tissues and D_S is the DW of the shell (Table 2) (Bricelj et al. 1984).

Ciliary beat rate

To measure ciliary beat rate, live clams were weighed and measured, and then their gills were excised and placed on a microscope cover slip in viscosity-adjusted seawater at the room temperature of 21°C (Table 1). Though use of excised gills has limitations compared to observations on intact clams (Ward et al. 1991), excised-gill observations can still demonstrate the fluid-mechanical interactions between cilia and the seawater, and it is the method used previously to study viscosity responses of *M. edulis* (Riisgård & Larsen 2007). Cilia continued to beat for several hours post-dissection, so no stimulants were added to the gills (Riisgård & Larsen 2007). Lateral ciliary fields were video-recorded at 40× magnification at 250 frames s^{-1} using a Powerview HS-2000 (TSI incorporated) high-speed video camera connected to a Nikon Eclipse Ti microscope (Video S1 in the Supplement, image width = 214 µm; www.int-res.com/articles/suppl/m589p129_supp/). Six replicates were performed at each of the viscosity-adjusted temperature equivalents (Table 1). Images were later analyzed by visually tracking 3 groups of >5 cilia for 1.5 s for each replicate and calculating the time required to complete a full beat cycle. Ciliary velocities, needed for Re calculations, were calculated from beat rates in 40× videos using the assumption that the beat angle is 180° as in mussels (Aiello & Sleigh 1972). Ideally we would have repeated the ciliary beat observations at different temperatures, but we were unable to change the temperature in the laboratory containing the required equipment.

Statistical analyses

To determine whether temperature or viscosity significantly affected suspension feeding, we used a combination of multivariate analysis of variance (MANOVA), analysis of variance (ANOVA), regression analysis, and model fitting. MANOVAs were performed on ingestion rate and clearance rate for each experiment. ANOVAs were performed on wet weights for each experiment and on ciliary beat rate for the viscosity experiment. To quantify environmental effects on suspension feeding, regressions were done using the observed rates (ingestion rate, and clearance rate) as dependent variables and temperature, viscosity, or initial algal concentration as independent variables. Most regressions were done using first-order linear models, but second-order linear models were used for rates versus temperature

because ingestion rate peaks at an optimal temperature (Hamwi 1969). Clearance rate (C) appeared to saturate versus algal concentration at warm temperatures (≥16°C) and was fitted with a saturating hyperbola:

$$C = \frac{C_{max} A}{K + A} \quad (4)$$

where C_{max} is the maximum clearance rate, A is the algal concentration, and K is the algal concentration when the clearance rate is half of C_{max}. C_{max} and K were estimated by fitting Eq. (4) to the experimental data using nonlinear regression. Significance levels for regressions were adjusted using a Bonferroni correction for multiple comparisons.

We also used the experimental data to fit a model predicting ingestion rate (I) as a function of initial algal concentration A_0 and temperature T:

$$I = \beta_0 + \beta_1 A_0 + \beta_2 T + \beta_3 T^2 + \beta_4 A_0 T \quad (5)$$

We included a crossed term ($A_0 \times T$) because both temperature and initial algal concentration affect ingestion rate (Hamwi 1969, Bricelj & Malouf 1984). We did not include a squared term for algal concentration because the relationship between algal concentration and ingestion rate appeared linear. Viscosity did not influence ingestion rate and was omitted from the model. Parameters (β_i) were estimated using multiple linear regression, and an Anderson-Darling normality test was used to examine normality of residuals.

Ciliary mechanics

The Reynolds number was calculated as:

$$\mathrm{Re} = \frac{l^2 \omega}{\nu} \quad (6)$$

where l is the cilium length, ω is the ciliary angular velocity, and ν is the kinematic viscosity (Sleigh & Blake 1977). *M. mercenaria* ciliary dimensions were taken from Eble (2001). Cilia operate at a low Re, and we used the simplifying assumption that the cilium is a straight cylinder. The viscous drag force, or the resistance to forward motion due to opposing viscous forces, was calculated as:

$$D = \frac{4\pi\nu\rho u l}{\ln\left(\frac{l}{r}\right) + 0.193} \quad (7)$$

where ρ is the seawater density, u is the ciliary velocity, and r is the ciliary radius (Vogel 1994). Torque at the base of the cilium was calculated as:

$$\tau = 1.1\omega\nu\rho l^3 \quad (8)$$

(Yoneda 1962). These calculations were used to quantify how viscosity affects the magnitude of force resisting ciliary movement, which approximates the per-cilium force required to propel the ciliary beat.

RESULTS

Feeding rate experiments

All suspension feeding metrics generally increased with and were highly correlated with temperature but were unaffected by viscosity (Tables 2–4). Ingestion and clearance rates increased steadily with temperature but did not vary with viscosity (Fig. 1). Results are shown per clam and were similar when evaluated on a wet-weight basis (not shown). Algal concentration in the algae-only controls decreased by an average of 4% in temperature treatments and 1% in viscosity treatments, indicating that sedimentation was negligible relative to ingestion. Ingestion rates were the most variable among temperature treatments, with a 97.2% difference between the maximum (at 20°C) and minimum (at 5°C) over the 6 replicates (Table 2). These differences were at least partly due to apparent inhibition of feeding at cold temperatures. Clearance rates were lower in viscosity experiments than in temperature experiments, possibly because the 2 experiments were conducted at different times using different batches of clams. In all viscosity treatments and temperature treatments ≥12°C, most clams (>80%) had their siphons out simultaneously, whereas in cold (≤8.5°C) treatments, fewer clams (<60%) had their siphons out at any given time.

We also assessed how ingestion and clearance rates varied with algal concentration (Table 4, Figs. 1 & 2). During the viscosity and temperature experiments, algal concentration always decreased over time due to feeding except in some replicates at low temperatures (≤8.5°C) where feeding was inhibited. In temperature treatments, the ingestion rate was positively correlated with algal concentration at warm temperatures (16, 20, 23.5°C), was positively correlated with algal concentration but much lower at cool temperatures (5, 8.5°C), and was not significantly correlated with algal concentration at 12°C (Fig. 2C). The low ingestion rates at cool temperatures were likely due to inhibited feeding below 12°C. The clearance rate was positively correlated with algal concentration at warm temperatures (16,

Table 2. Results for temperature (T) and viscosity experiments (ν) include ingestion rate, clearance rate, clam wet, dry and ash-free dry weights, and clam lengths, given as means ± 1SE at specified temperatures or temperature equivalents (T_e) (N = 36 for rates; N = 60 for clam weights and lengths). Results for ciliary beat rate experiments include beat rate from 40× images, wet weight, and length at viscosity-adjusted temperature equivalents (N = 36 for rates; N = 36 for ciliary experiment clam weights and lengths). *Significant analysis of variance (ANOVA) and multivariate ANOVA (MANOVA) results (Table 3)

Temperature expts (T)	5°C	8.5°C	12°C	16°C	20°C	23.5°C
Ingestion rate* ($\times 10^6$ cells h^{-1} $clam^{-1}$)	0.47 ± 0.5	2.7 ± 0.7	4.2 ± 0.3	3.8 ± 0.8	5.9 ± 1	3.7 ± 1
Clearance rate* (ml h^{-1} $clam^{-1}$)	4.9 ± 5	27 ± 7	83.0 ± 8	120 ± 18	140 ± 21	120 ± 25
Wet weight (g)	2.7 ± 0.6	2.8 ± 0.7	1.2 ± 0.03	2.8 ± 0.7	2.8 ± 0.7	2.7 ± 0.6
Dry tissue weight (mg)	49.5 ± 7.2	48.4 ± 5.7	25.7 ± 1.1	47.7 ± 6.9	53.4 ± 8.0	51.1 ± 7.6
Ash-free dry weight (mg)	38.5 ± 5.5	37.8 ± 4.5	19.8 ± 1.0	36.7 ± 5.6	41.2 ± 6.4	37.8 ± 5.7
Length (mm)	19.0 ± 0.4	21.3 ± 0.4	16.6 ± 0.1	20.2 ± 0.5	20.2 ± 0.5	20.0 ± 0.4
Viscosity expts						
(ν) ($\times 10^{-6}$ m^2 s^{-1})	1.55	1.43	1.29	1.17	1.06	0.96
(T_e)	5.3°C	8.3° C	12.2° C	15.8° C	19.7° C	23.5° C
Ingestion rate ($\times 10^6$ cells h^{-1} $clam^{-1}$)	3.4 ± 0.4	3.5 ± 0.6	3.3 ± 0.5	3.5 ± 0.4	3.6 ± 0.5	3.8 ± 0.4
Clearance rate (ml h^{-1} $clam^{-1}$)	74.8 ± 8	82.0 ± 11	90.8 ± 11	83.9 ± 9	94.4 ± 9	75.6 ± 9
Wet weight (g)	2.7 ± 0.1	2.8 ± 0.1	2.8 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.7 ± 0.1
Dry weight (mg)	52.3 ± 2.1	63.8 ± 2.7	60.1 ± 2.7	48.0 ± 1.5	58.9 ± 1.8	49.3 ± 1.7
Ash-free dry weight (mg)	38.5 ± 1.3	46.4 ± 1.9	44.3 ± 2.3	37.8 ± 1.6	43.4 ± 1.8	37.3 ± 1.3
Length (mm)	20.3 ± 0.2	20.7 ± 0.2	20.7 ± 0.2	20.4 ± 0.2	20.6 ± 0.2	20.4 ± 0.2
Ciliary beat expts						
(ν) ($\times 10^{-6}$ m^2 s^{-1})	1.62	1.41	1.28	1.2	1.07	1.02
(T_e)	4.1°C	8.6°C	12.2°C	14.5°C	19.2°C	21.2°C
Ciliary beat rate (beats s^{-1})	7.2 ± 0.7	7.8 ± 0.7	7.4 ± 0.6	8.0 ± 0.9	8.8 ± 0.3	7.8 ± 0.8
Wet weight (g)	1.4 ± 0.05	1.5 ± 0.04	1.6 ± 0.1	1.5 ± 0.1	1.6 ± 0.1	1.6 ± 0.1
Length (mm)	17.0 ± 0.2	18.0 ± 0.3	17.0 ± 0.2	17.0 ± 0.4	18.0 ± 0.3	18.0 ± 0.3

Table 3. Analysis of variance (ANOVA) and multivariate ANOVA (MANOVA) results. Separate 1-way MANOVA were performed on results (ingestion and clearance) of temperature and viscosity experiments. One-way ANOVA were performed on each set of wet weights and ciliary beat rate. p-values in **bold** are significant at $\alpha = 0.05$

Altered condition	Observed rate	df	df error	Wilks' λ	F	p
MANOVA						
Temperature	Ingestion rate	5	58	0.191	11.21	**$<10^{-4}$**
	Clearance rate	5	58	0.191	8.66	**$<10^{-4}$**
Viscosity	Ingestion rate	5	58	0.684	0.20	0.96
	Clearance rate	5	58	0.684	0.72	0.30
ANOVA						
Temperature	Wet weight	5	–	–	1.12	0.37
Viscosity	Wet weight	5	–	–	0.36	0.87
	Ciliary beat rate	5	–		0.58	0.71

20, 23.5°C), was low and uncorrelated with algal concentration at cool temperatures (5, 8.5°C), and was uncorrelated with algal concentration at 12°C (Fig. 2A). At warm temperatures, the clearance rate appeared to saturate versus algal concentration, and the reduced clearance at low concentrations suggests that clams reduced their feeding effort when little food was available. Clams also fed infrequently or not at all in cool temperature treatments, where algal concentrations remained relatively constant over the course of the experiment. In viscosity treatments, ingestion rate increased significantly with algal concentration (Fig. 2D), and clearance rate decreased significantly with algal concentration (Fig. 2B). The linear decrease in clearance rate (Fig. 2B) implies that the relationship between ingestion rate and algal concentration (Fig. 2D) should be parabolic, but the parabola would peak at about the maximum concentration used in our experiments, so a linear fit is significant within the data range. The combined results indicate that as algal concentration increases clams can pump less water and still ingest more food.

Clam wet weights were not significantly different either among temperature treatments or among viscosity treatments (Tables 2 & 3). Although not signif-

Table 4. Regression results on a per clam basis. p-values in **bold** are significant at Bonferroni-corrected $\alpha = 0.006$ for temperature treatments and $\alpha = 0.01$ for viscosity treatments. For saturating curve fit, p-values are provided for individual parameters. C_{max}: maximum clearance rate; K: algal concentration when the clearance rate is half of C_{max}; b_0, b_1, b_2: regression parameters

Independent variable	Dependent variable	R^2	p	b_0	b_1	b_2
Temperature expts						
Temperature	Ingestion rate	0.52	**$<10^{-4}$**	-5.24×10^6	1.08×10^6	-1.3×10^4
	Clearance rate	0.55	**$<10^{-4}$**	−83.4	13.4	–
Algal concentration	Ingestion rate:					
	at 16, 20, 23.5°C	0.86	**$<10^{-4}$**	-8.93×10^5	1.3×10^2	–
	at 12°C	0.24	0.015	2.17×10^6	29.3	–
	at 4, 8°C	0.28	**$<10^{-3}$**	-6.48×10^6	80.2	–
	Clearance rate:					
	at 16, 20, 23.5°C		**$<10^{-4}$** (C_{max})			
	(saturating curve)	0.98	0.03 (K)	210 (C_{max})	6230 (K)	–
	at 12°C	0.47	0.31	90.9	-4.45×10^{-4}	–
	at 4, 8°C	0.13	0.012	−18.7	3.24×10^{-4}	–
Viscosity expts						
Viscosity	Ingestion rate	4.1×10^{-4}	0.91	5.29×10^6	8.6×10^3	–
	Clearance rate	1.9×10^{-5}	1.0	71.9	0.028	–
Algal concentration	Ingestion rate	0.37	**$<10^{-4}$**	6.55×10^5	49.5	–
	Clearance rate	0.18	**$<10^{-3}$**	114	-5.89×10^{-4}	–

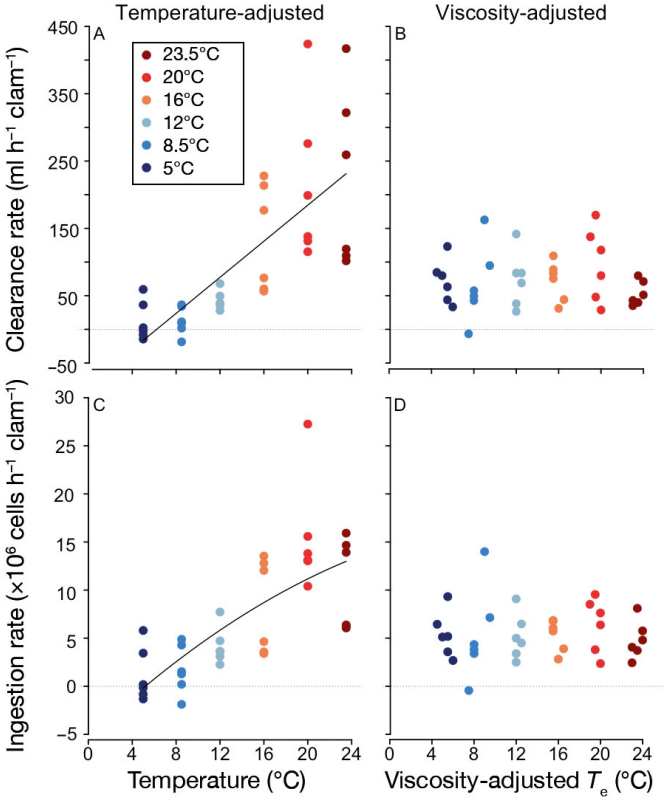

Fig. 1. *Mercenaria mercenaria* clearance and ingestion rates in the first hour, when concentrations were most similar to starting concentrations, for each of 6 replicates. Results are for (A,C) temperature-adjusted treatments and (B,D) viscosity-adjusted temperature equivalents (T_e). Black lines are regressions where significant (Table 4). Key indicates (A,C) temperatures and (B,D) viscosity-adjusted T_e

icant, the mean wet weights were ~1.6 g lower at 12°C than in other temperature treatments. The lower mean wet weights at 12°C may explain anomalous ingestion results in those treatments. However, the condition index indicated that all clams in temperature and viscosity treatments were similarly healthy, including those in the 12°C treatments. The condition indices for all experiments ranged from 1.9 to 3.4, with mean ± 1SE of 2.63 ± 0.02.

Ciliary beat rate experiments

For ciliary beat rate experiments, ANOVA results indicated that neither clam wet weights nor ciliary beat rates were significantly different among the 6 viscosity treatments (Table 3). Over all treatments, wet weights were 1.73 ± 0.11 g, lengths were 17.9 ± 0.2 mm, and ciliary beat rates were 7.8 ± 0.3 beats s^{-1} (Table 2). Beat rates were used with an assumed beat angle of 180° (Aiello & Sleigh 1972) to calculate drag forces (see 'Discussion'). Though we were unable to do controlled observations of ciliary beat rate at varying temperatures, there was one atypically cool day (18°C) when ciliary beat rates were lower than previously observed. Those data were omitted because they could not be replicated. The observations of ciliary beat provide supporting evidence that *Mercenaria mercenaria* were unresponsive to the viscous effects of temperature.

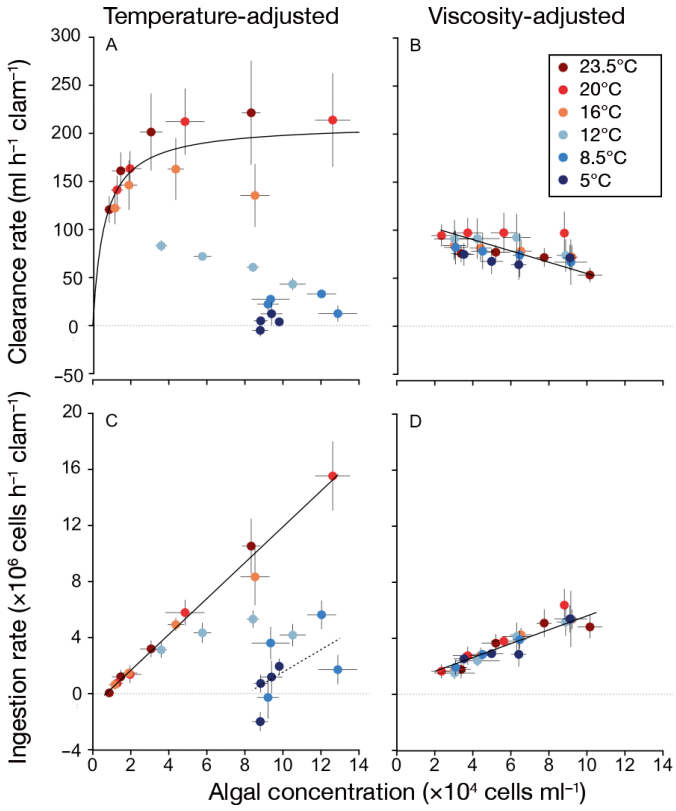

Fig. 2. *Mercenaria mercenaria* clearance and ingestion rate versus algal concentration for all samples. Rates shown as mean ± 1SE over 6 replicates per treatment at each hour of sampling. Results for (A,C) temperature-adjusted treatments and (B,D) viscosity-adjusted temperature equivalents (T_e). Warm temperatures (16, 20, 23.5°C; solid lines) and cool temperatures (5, 8.5°C; dashed line) were fitted with separate linear regressions where significant (Table 4). Key indicates (A,C) temperatures and (B,D) viscosity-adjusted T_e

Table 5. Comparison of lateral ciliary mechanics in *Mercenaria mercenaria* and *Mytilus edulis* at the given temperature equivalents (T_e). Includes cilium length and width, ciliary velocity, Reynolds number (Re), drag coefficient, drag force, and torque. Values for *M. mercenaria* calculated using Eqs. (6–8) from gill images video-recorded at 40×, with ciliary dimensions taken from Eble (2001). Values for *M. edulis* from Riisgård & Larsen (2007) and calculated using Eqs. (6–8). Ciliary beat angle of mussels taken from Aiello & Sleigh (1972) and assumed to be the same for clams

T_e	*M. mercenaria*		*M. edulis*	
	21°C	5 °C	21°C	5°C
Seawater viscosity ($\times10^{-6}$ m^2 s^{-1})	1.026	1.576	1.026	1.576
Seawater density (kg m^{-3})	1025	1028	1025	1028
Cilia length (m)	1.0×10^{-5}	1.0×10^{-5}	1.5×10^{-5}	1.5×10^{-5}
Cilia width (m)	8.2×10^{-7}	8.2×10^{-7}	2.0×10^{-7}	2.0×10^{-7}
Time per beat (s)	0.129	0.138	0.043	0.079
Velocity (m s^{-1})	4.9×10^{-4}	4.6×10^{-4}	9.2×10^{-4}	5.0×10^{-4}
Velocity (rad s^{-1})	49	46	61.2	33.0
Re	4.7×10^{-3}	2.9×10^{-3}	1.3×10^{-2}	4.7×10^{-3}
Drag (N)	1.9×10^{-11}	2.7×10^{-11}	2.6×10^{-11}	2.1×10^{-11}
Torque (Nm)	1.9×10^{-16}	2.7×10^{-16}	1.8×10^{-16}	1.5×10^{-16}

Model

Although temperature and algal concentration appeared to have complex effects on feeding, these effects were well captured by our fitted model (Fig. 3):

$$I = -3.8 + (8.8\times10^{-6})A_0 + (5.9\times10^{-1})T + (-2.0\times10^{-2})T^2 + (1.9\times10^{-6})A_0T \quad (9)$$

which explained much of the variation in ingestion rate (R^2 = 0.94, p << 10^{-4}) (Fig. 3). The Anderson-Darling normality test confirmed that the residuals of the predicted data were normally distributed (p = 0.14). This fitted model provides a predictive tool for estimating the amount of food ingested across continuous gradients of temperature and algal concentration.

DISCUSSION

In this study, we found that *Mercenaria mercenaria* feeding rates vary with temperature, but not with viscosity alone. Ingestion and clearance rates were positively correlated with temperature, corroborating previous findings for *M. mercenaria* (Hamwi 1969, Hibbert 1977, Bricelj 1984). Both rates were much lower at cool temperatures (≤8.5°C) than at high temperatures (≥16°C), probably because feeding was inhibited below 12°C. Clearance rates provide a proxy estimate of pumping rate and indicated that hard clams ingested more food at warmer temperatures by pumping and filtering more water. However, ingestion, clearance, and ciliary beat rates were uncorrelated with viscosity, indicating that the increase in pumping rate with temperature was not driven by biomechanical effects on ciliary beating. Instead, feeding responses were likely driven by the physiological effects of changing temperature. Warmer seawater induces higher metabolic rates and holds less dissolved oxygen, and hard clams could compensate for these conditions with higher pumping rates. Overall, our results suggest that feeding rates in *M. mercenaria* are not controlled by biomechanical effects of temperature, but rather by the physiological effects associated with changes in metabolism or oxygen demand.

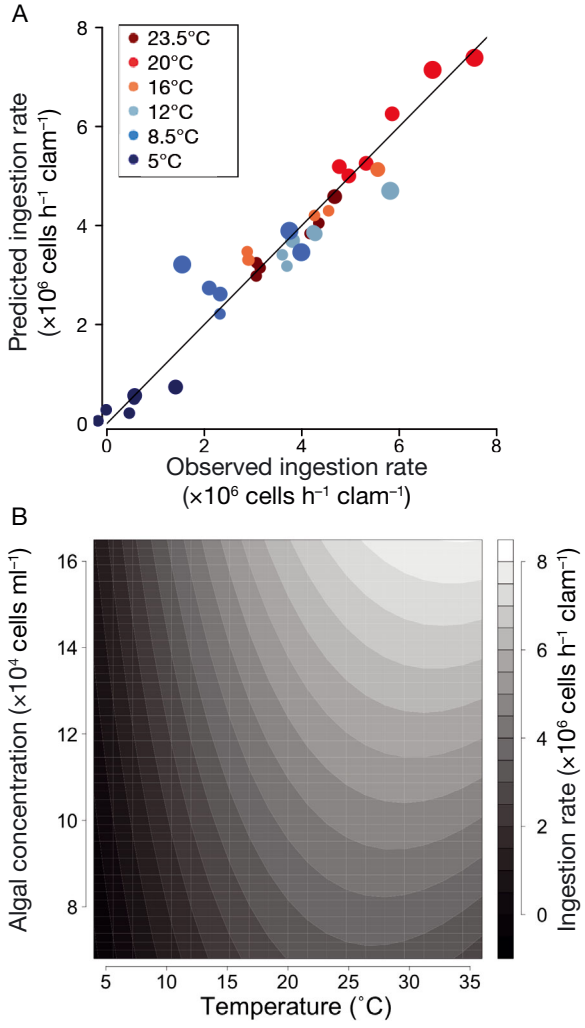

Fig. 3. Ingestion rates as a function of temperature and initial algal concentration. (A) Predicted versus observed ingestion rates, with predicted values given by fitted polynomial model (Eq. 9). Circle size is proportional to initial algal concentration. Line is linear regression ($R^2 = 0.94$, $p < 10^{-4}$). (B) Ingestion rates predicted by the fitted model (Eq. 9) across gradients of temperature and algal concentration

In addition to strong temperature effects, we found a strong link between feeding rates and algal concentration. Ingestion rates increased linearly with algal concentration, while clearance rates appeared to saturate. This effect of algal concentration differs from prior results for juvenile *M. mercenaria*, where clearance rate decreased with increasing *Pseudoisochrysis paradoxa* concentrations (Bricelj & Malouf 1984), but the difference could be explained by the use of different algal species (Coutteau et al. 1994). Saturation of the clearance rate suggests that clams use a constant pumping rate at high algal concentrations but reduce their pumping rates at low algal concentrations, possibly because there is insufficient food to meet the metabolic demand of pumping. Clams may also reduce their clearance rates at higher algal concentrations to prevent clogging of the gills (Bricelj & Malouf 1984) and reduce the fraction of particles lost to pseudofaeces, enabling them to assimilate more ingested food (Winter 1978). These compensatory effects interact with temperature effects on clearance and ingestion, and this interaction was well captured by our fitted ingestion model (Eq. 9).

Our viscosity results differ from previous findings for *Mytilus edulis*, although the methodology was generally similar between the 2 studies. *M. edulis* filtration and ciliary beat rates are driven primarily by changes in viscosity rather than by temperature itself (Riisgård & Larsen 2007). Both studies used PVP to manipulate viscosity and included observations of ciliary beating on excised gills. For *M. edulis,* gills were secured 1 cm deep in 2 cm of seawater and observed with the microscope objective submerged (Riisgård & Larsen 2007), whereas for *M. mercenaria*, the gill was secured to a slide, immersed in seawater, and observed on a standard compound microscope. *M. mercenaria* cilia beat freely in seawater, and ciliary beating was easily observed. The cilia of *M. mercenaria* beat longer (up to 12 h) after gill excision than those of *M. edulis*, and whereas 10^{-5} M serotonin was added to stimulate the ciliary beating in *M. edulis* (Riisgård & Larsen 2007), no serotonin was required in this study. Although these observational details differed, the effects of viscosity on ciliary beat were mirrored in effects of viscosity on clearance rate, confirming that *M. mercenaria* and *M. edulis* fundamentally differ in their responses to viscosity.

Results suggest that ingestion is controlled by different processes in *M. mercenaria* than in *M. edulis*, but this difference cannot be explained by mechanical forces acting on the cilia. By our estimates, the drag forces and torque on a beating cilium have similar magnitudes in *M. mercenaria* and in *M. edulis* (Table 5) (Riisgård & Larsen 2007). However, *M. mercenaria* maintains a constant ciliary beat rate, making drag and torque proportional to viscosity, whereas *M. edulis* reduces its ciliary beat rate with increasing viscosity, making drag and torque inversely proportional to viscosity (Eqs. 6 & 7, Table 5). As a result, viscosity changes cause drag and torque on the cilia to vary more in *M. mercenaria* than in *M. edulis*. If the response to viscosity were solely due to mechanical forces, we would expect *M. mercenaria* to respond to viscosity changes with an effect size similar to or greater than that observed in *M. edulis* (Riisgård & Larsen 2007). Yet *M. mercenaria*'s ciliary

beat rate did not vary with viscosity, and this lack of response is puzzling, given that changing viscosity must alter the mechanics of the ciliary beat (Larsen & Riisgård 2009, Humphries 2013).

Responses to viscosity change may reflect differences in how water flows past the gill. Although both species use metachronal beating of the lateral cilia (Aiello & Sleigh 1972, Gainey Jr. et al. 1999), they have different gill structures. *M. edulis* gills are filibranch, with filaments weakly joined by dispersed ciliary disc junctions (Sunila & Lindström 1985), whereas *M. mercenaria* gills are eulamellibranch, with filaments more tightly joined by continuous tissue junctions (Atkins 1937). These distinct gill structures result in different flow patterns (Atkins 1937) that may alter the velocity and drag on beating cilia. The interfilament canals of *M. mercenaria* are narrower than those of *M. edulis* (Jørgensen 1990, Medler & Silverman 2001), which may result in higher flow rates in *M. mercenaria* (Vogel 1994). *M. mercenaria* also can contract the interfilamental canals by 71%, as compared to 25% for *M. edulis* (Jørgensen 1990, Medler & Silverman 2001), suggesting that *M. mercenaria* can exert greater control over pumping rate without involving the cilia. These differences in gill structure create the potential for bivalves to evolve different responses to viscosity changes.

Our observations suggest that *M. mercenaria* gill cilia may operate more like some cilia in vertebrate respiratory systems, which exhibit a physiological response to maintain a constant beat frequency under variable viscosities (Spungin & Silberberg 1984, Johnson et al. 1991). The presence or absence of such a physiological response could explain why ciliary mechanics vary widely among invertebrates, such that larvae of some species exhibit strong ciliary responses to changes in viscosity (Podolsky & Emlet 1993, Bolton & Havenhand 1997), while others are relatively unresponsive over the same viscosity range (Rompolas et al. 2010). More remarkably, responses to viscosity can vary within a single species; in the protist *Parameciu*m *caudatum* viscosity changes alter the beating of locomotive cilia by 75% but of feeding cilia by only by 18% (Jung et al. 2014). This dramatic example raises the possibility that 2 bivalves, *M. edulis* and *M. mercenaria,* may have evolved cilia whose beat rate is controlled by different mechanisms.

Responses to viscosity may differ between mussels and clams due to differences in functional morphology or biochemical control of the cilia. Mussels are adapted to high seston concentrations and are equipped with enlarged palps that increase particle sorting ability (Kiørboe & Møhlenberg 1981). Efficient sorting enables mussels to maintain ingestion rates even at high algal concentration, whereas clams reduce their ingestion rates at high algal concentrations to limit clogging of the filter (Bricelj 1984). Bivalves can also alter valve gape to change their clearance rate (Frank et al. 2007, MacDonald et al. 2009), and clams and mussels may alter their valve gape differently in response to temperature. Moreover, there is evidence that ciliary beat is under different neurological control in clams and mussels. Although both clams and mussels use serotonin and dopamine to activate and deactivate the lateral cilia (Carroll & Catapane 2007), respectively, they have different chemical pathways controlling these reactions. For example, the serotonin receptor 5-hydroxytyptamine, stimulates particle transport by frontal cilia in *M. edulis* but inhibits the same activity in *M. mercenaria* (Gainey Jr. et al. 1999). Differences in pumping and filtration mechanisms, gape control, and chemical pathways could contribute to the distinct reactions to viscosity.

Regardless of the mechanism underlying the different responses of mussels and clams to viscosity, our results highlight the need for caution in generalizing suspension-feeding dynamics of one species to all species in the same taxonomic class. In particular, differences in ciliary mechanics may affect how bivalve metabolism varies with temperature. Because *M. edulis* respond to temperature primarily via a mechanical response to viscosity, they could increase their ciliary beat rate in warmer water at no added energetic cost for activity. In contrast, *M. mercenaria* shows no mechanical response to viscosity, and their apparent physiological response to temperature would require applying more force to raise the ciliary beat rate at high temperatures, likely at a higher energetic cost. This difference in active metabolism may make *M. mercenaria* more sensitive to rising temperatures, and clams may need to consume more food to compensate for their increased energy expenditure. Ingestion rate and metabolic rate are independently altered by temperature, however, and it is unclear if the food energy gained by higher pumping rates can offset the combined higher costs of resting and active metabolism at warmer temperatures. This balance of energetic gains and costs will determine the temperature range in which bivalves can survive and grow. We are currently investigating how temperature influences the complete energetic balance, in order to better understand climate change effects on clam growth and survival.

Acknowledgements. We thank O. Jensen for advice on model development and V. M. Bricelj, J. Grassle, D. Munroe, G. Saba, and 4 anonymous reviewers for helpful feedback and comments on the manuscript. B. Avery kindly provided the clams for the study. The Adams, Diez-Garias, Falkowski, and Taghon labs at Rutgers University provided space and equipment. This study was supported by the Graduate School of New Brunswick Professional Development Fund, and J.A.S. was supported by a Graduate Assistantship from the Institute of Marine and Coastal Science.

LITERATURE CITED

Aiello E, Sleigh MA (1972) The metachronal wave of lateral cilia of *Mytilus edulis.* J Cell Biol 54:493–506

Atkins D (1937) On the ciliary mechanisms and interrelationships of lamellibranchs. III. Types of lamellibranch gills and their food currents. J Cell Sci 79:375–421

Baba SA, Hiramoto Y (1970) A quantitative analysis of ciliary movement by means of high-speed microcinematography. J Exp Biol 52:675–690

Bayne BL (1973) Physiological changes in *Mytilus edulis* L. induced by temperature and nutritive stress. J Mar Biol Assoc UK 53:39–58

Bayne BL, Hawkins AJS, Navarro E, Iglesias IP (1989) Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis.* Mar Ecol Prog Ser 55:47–54

Berg JA, Newell RIE (1986) Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica.* Estuar Coast Shelf Sci 23: 375–386

Bolton TF, Havenhand JN (1997) Physiological versus viscosity-induced effects of water temperature on the swimming and sinking velocity of larvae of the serpulid polychaete *Galeolaria caespitosa*. Mar Ecol Prog Ser 159:209–218

Bricelj V (1984). Effects of suspended sediments on the feeding physiology and growth of the hard clam, *Mercenaria mercenaria* L. PhD dissertation, State University of New York at Stony Brook, Stony Brook, NY

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

Bricelj V, Malouf R, de Quillfeldt C (1984) Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. Mar Biol 84:167–173

Carroll MA, Catapane EJ (2007) The nervous system control of lateral ciliary activity of the gill of the bivalve mollusc, *Crassostrea virginica.* Comp Biochem Physiol A Mol Integr Physiol 148:445–450

Celestino MP (2013) Shellfish stock assesment of Little Egg Harbor Bay (2011) New Jersey Department of Environmental Protection, Port Republic, NJ

Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. Mar Biol 2:356–358

Coutteau P, Hadley NH, Manzi JJ, Sorgeloos P (1994) Effect of algal ration and substitution of algae by manipulated yeast diets on the growth of juvenile *Mercenaria mercenaria.* Aquaculture 120:135–150

Crisp DJ, Yule AB, White KN (1985) Feeding by oyster larvae: the functional response, energy budget and a comparison with mussel larvae. J Mar Biol Assoc UK 65: 759–783

Eble AF (2001) Anatomy and histology of *Mercenaria mercenaria*. In: Kraeuter JN, Castagna M (eds) Biology of the hard clam. Elsevier Science B.V., Amsterdam, p 117–220

Frank DM, Hamilton JF, Ward JE, Shumway S (2007) A fiber optic sensor for high resolution measurement and continuous monitoring of valve gape in bivalve molluscs. J Shellfish Res 26:575–580

Gainey LF Jr, Vining KJ, Doble KE, Waldo JM, Candelario-Martinez A, Greenberg MJ (1999) An endogenous SCP-related peptide modulates ciliary beating in the gills of a venerid clam, *Mercenaria mercenaria*. Biol Bull 197: 159–173

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248–2251

Grizzle RE, Bricelj VM, Shumway SE (2001) Physiological ecology of *Mercenaria mercenaria*. In: Kraeuter JN, Castagna M (eds) Biology of the hard clam. Elsevier Science B.V., Amsterdam, p 305–382

Hamwi A (1969) Oxygen consumption and pumping rate of the hard clam *Mercenaria mercenaria* L. PhD dissertation, Rutgers, The State University, New Brunswick, NJ

Hamwi A, Haskin HH (1969) Oxygen consumption and pumping rates in the hard clam *Mercenaria mercenaria*: A direct method. Science 163:823–824

Hawkins AJS, Bayne BL, Bougrier S, Héral M and others (1998) Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. J Exp Mar Biol Ecol 219:87–103

Hibbert CJ (1977) Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. Mar Biol 44: 77–84

Hofmann EE, Klinck JM, Kraeuter JN, Powell EN, Grizzle RE, Buckner SC, Bricelj VM (2006) A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. J Shellfish Res 25:417–444

Humphries S (2013) A physical explanation of the temperature dependence of physiological processes mediated by cilia and flagella. Proc Natl Acad Sci USA 110: 14693–14698

Ivanina AV, Dickinson GH, Matoo OB, Bagwe R, Dickinson A, Beniash E, Sokolova IM (2013) Interactive effects of elevated temperature and CO_2 levels on energy metabolism and biomineralization of marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria.* Comp Biochem Physiol A Mol Integr Physiol 166:101–111

Johnson NT, Villalón M, Royce FH, Hard R, Verdugo P (1991) Autoregulation of beat frequency in respiratory ciliated cells. Am Rev Respir Dis 144:1091–1094

Jørgensen CB (1983) Fluid mechanical aspects of suspension feeding. Mar Ecol Prog Ser 11:89–103

Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Fredensborg

Jørgensen CB, Larsen PS, Riisgård HU (1990) Effects of temperature on the mussel pump. Mar Ecol Prog Ser 64: 89–97

Jung I, Powers TR, Valles JM Jr (2014) Evidence for two extremes of ciliary motor response in a single swimming microorganism. Biophys J 106:106–113

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

Larsen PS, Riisgård HU (2009) Viscosity and not biological mechanisms often controls the effects of temperature on

ciliary activity and swimming velocity of small aquatic organisms. J Exp Mar Biol Ecol 381:67–73
Larsen PS, Madsen CV, Riisgård HU (2008) Effect of temperature and viscosity on swimming velocity of the copepod *Acartia tonsa*, brine shrimp *Artemia salina* and rotifer *Brachionus plicatilis*. Aquat Biol 4:47–54
MacDonald BA, Robinson SMC, Barrington KA (2009) Evaluating the use of exhalent siphon area in estimating feeding activity of blue mussels, *Mytilus edulis*. J Shellfish Res 28:289–297
Mackenzie CL, Ormondroyd GA, Curling SF, Ball RJ, Whiteley NM, Malham SK (2014) Ocean warming, more than acidification, reduces shell strength in a commercial shellfish species during food limitation. PLOS ONE 9: e86764
Martinez VA, Schwarz-Linek J, Reufer M, Wilson LG, Morozov AN, Poon WCK (2014) Flagellated bacterial motility in polymer solutions. Proc Natl Acad Sci USA 111: 17771–17776
Medler S, Silverman H (2001) Muscular alteration of gill geometry *in vitro*: implication for bivalve pumping processes. Biol Bull 200:77–86
Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–61
Paganini A, Kimmerer WJ, Stillman JH (2010) Metabolic responses to environmental salinity in the invasive clam *Corbula amurensis*. Aquat Biol 11:139–147
Podolsky RD (1994) Temperature and water viscosity: physiological versus mechanical effects on suspension feeding. Science 265:100–103
Podolsky RD, Emlet RB (1993) Separating the effects of temperature and viscosity on swimming and water movement by sand dollar larvae (*Dendraster excentricus*). J Exp Biol 176:207–221
Purcell EM (1977) Life at low Reynolds number. Am J Phys 45:3–11
Riisgård HU (1988) Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. Mar Ecol Prog Ser 45:217–223
Riisgård HU, Larsen PS (2007) Viscosity of seawater controls beat frequency of water-pumping cilia and filtration rate of mussels *Mytilus edulis*. Mar Ecol Prog Ser 343:141–150
Rompolas P, Patel-King RS, King SM (2010) An outer arm dynein conformational switch is required for metachronal synchrony of motile cilia in planaria. Mol Biol Cell 21: 3669–3679
Sleigh MA, Blake JR (1977) Methods of ciliary propulsion and their size limitations. In: Pedley TJ (ed) Scale effects in animal locomotion. Academic Press, London, p 243–256
Spungin B, Silberberg A (1984) Stimulation of mucus secretion, ciliary activity, and transport in frog palate epithelium. Am J Physiol 247:C299–C308
Sunila I, Lindström R (1985) The structure of the interfilamentar junction of the mussel (*Mytilus edulis* L.) gill and its uncoupling by copper and cadmium exposures. Comp Biochem Physiol 81C:267–272
Talmage SC, Gobler CJ (2011) Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of northwest Atlantic bivalves. PLOS ONE 6:e26941
Thompson RJ, Bayne BL (1972) Active metabolism associated with feeding in the mussel *Mytilus edulis* L. J Exp Mar Biol Ecol 9:111–124
Vogel S (1994). Life in moving fluids: the physical biology of flow. Princeton University Press, Princeton, NJ
Ward JE, Beninger PG, MacDonald BA, Thompson RJ (1991) Direct observations of feeding structures and mechanisms in bivalve molluscs using endoscopic examination and video image analysis. Mar Biol 111:287–291
Weiss RF (1970) The solubility of nitrogren, oxygen and argon in water and seawater. Deep-Sea Res 17:721–735
Widdows J (1973) Effect of temperature and food on the heart beat, ventilation rate and oxygen uptake of *Mytilus edulis*. Mar Biol 20:269–276
Widdows J (1978) Combined effects of body size, food concentrations and season on the physiology of *Mytilus edulis*. J Mar Biol Assoc UK 58:109–124
Widdows J, Bayne BL (1971) Temperature acclimation of *Mytilus edulis* with reference to its energy budget. J Mar Biol Assoc UK 51:827–843
Winter JE (1978) A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artifical aquaculture systems. Aquaculture 13:1–33
Yoneda M (1962) Force exerted by a single cilium of *Mytilus edulis*. J Exp Biol 39:307–317

Editorial responsibility: Emily Carrington, Friday Harbor, Washington, USA

Submitted: January 23, 2017; Accepted: November 22, 2017
Proofs received from author(s): February 7, 2018