SHORT COMMUNICATION

Allometric equations for maximum filtration rate in blue mussels *Mytilus edulis* and importance of condition index

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Abstract The relationship between body dry weight (W) and shell length (L) of blue mussels, *Mytilus edulis*, can be expressed by the condition index ($CI = W/L^3$) which varies from population to population and during the year. Here, we examine the influence of CI on the relationships between maximum filtration rate (F, $l\,h^{-1}$), W (g), and L (mm) as described by the equations: $F_W = aW^b$ and $F_L = cL^d$, respectively. This is done by using available and new experimental laboratory data on *M. edulis* obtained by members of the same research team using different methods and controlled diets of cultivated algal cells. For all data, it was found that $F_W = 6.773W^{0.678}$ and $F_L = 0.00135L^{2.088}$ which are very similar to equations for mussels with 'medium condition' ($CI = 4$–6 mg cm^{-3}): $F_W = 6.567W^{0.681}$ and $F_L = 0.00150L^{2.051}$, with b- and d-values within a few percent of the theoretically expected of 2/3 and 2, respectively. Further, based on the present data, we propose a correction factor expressed by the empirical relation $F_W/F_L = 0.3562CI^{2/3}$ which implies that F_W tends to underestimate the actual filtration rate (F_L) when CI < 4.70 and to overestimate the filtration rate when CI > 4.70.

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Introduction

Allometric equations for filtration rate of blue mussels, *Mytilus edulis*, are widely used in physiological, ecological, and modelling studies (e.g. Bayne 1976; Winter 1978; Jones et al. 1992; Riisgård 2001; Filgueira et al. 2008; Cranford et al. 2011; Larsen et al. 2013, Riisgård et al. 2013b), and therefore, it is important to understand and possibly refine these equations as more data become available. As to be expected, and also experimentally verified by Jones et al. (1992), Riisgård (2001) and Riisgård et al. (2011b), the filtration rate (F) and gill area (G) in *M. edulis* are near proportional to the square of the shell length (L) of the mussel, i.e.: $F \approx L^2$ and $G \approx L^2$. Likewise, it may be expected that the body dry weight (W) may be near proportional to L^3, or reversed: L is proportional to $W^{1/3}$, so that $F \approx (W^{1/3})^2 = W^{2/3} = W^{0.67}$. But it should be emphasized that the relationship between body dry weight and shell length as expressed by the condition index ($CI = W/L^3$) is not constant, but varies from population to population and during the year due to, e.g. spawning in spring, growth during summer, and starvation during winter. Thus, using the changes in the relationship between shell length and body dry weight in *M. edulis* reported by Dare (1976), Riisgård (2001) estimated that CI for 'standard' 55-mm–shell-length mussels was 6.6 in April, decreased due to spawning to 3.6 in June, followed by a summer recovery phase to become 7.8 in October. Because the relationship between gill area and shell length remains constant; it may be expected (see also Filgueira et al. 2008) that pronounced variations in CI

influence the weight-specific filtration rate of mussels with same shell length. Therefore, disparity of values of power-law exponents reported by different authors may, apart from varying experimental conditions, reflect differences in the mussels' CI, see also Petersen et al. (2004).

Here, we examine the influence of condition index (CI) on the relationships between filtration rate (F), dry body weight (W), and shell length (L) as described by the equations $F_W = aW^b$ and $F_L = cL^d$, respectively. This is done by using available and new experimental laboratory data on *M. edulis* measured over the years by various researchers in cooperation with the present first author using different methods that are believed to give accurate data for filtration rate of mussels stimulated by cultivated algal cells to filter at maximum speed.

Materials and methods

Earlier published data on maximum filtration rate (F, l h^{-1}) and body dry weight (W, g) of blue mussels *M. edulis* (Riisgård and Møhlenberg 1979; Møhlenberg and Riisgård 1979) were supplemented with data for shell length (L, mm) from the original research protocols in order to estimate $F_W = aW^b$, $F_L = cL^d$ and condition index $CI = W(mg)/L(cm)^3$. Further, data from more recent publications (Riisgård et al. 2011b; Pleissner et al. 2013) as well as new experimental data have been used.

Filtration experiments

F, W, and CI were obtained on *M. edulis* collected in February 2013 near the Marine Biological Research Centre, Kerteminde (Denmark). Prior to experiments, the mussels were divided into five size groups ranging from 15 to 74 mm, with five mussels in each group, and kept in separate aerated tanks (11 °C, 20 psu). Filtration rates were measured as the volume of water cleared of suspended particles per unit of time (i.e. 'clearance method'). The reduction in the number of particles as a function of time was followed by taking water samples (10 ml) at fixed time intervals from an aquarium containing a group of mussels with same shell length in well-mixed seawater, to which algal cells *Rhodomonas salina* were added, and measuring the particle concentration with an electronic particle counter (Elzone 5380). The algal cells had a diameter of about 6 μm and were therefore retained by the gills of the mussels with 100 % efficiency (Møhlenberg and Riisgård 1978). The filtration rate (F) was determined from the exponential decrease in algal concentration as a function of time using the formula (Riisgård et al. 2011a, b): $F = V \times b/n$, where V = water volume in aquarium, n = number of mussels, and b = slope of the regression line in a semi-ln plot for the reduction in algal concentration with time. A control experiment without mussels showed that sedimentation of algal cells was insignificant. After measurements of the filtration rate, the dry weight of soft parts of mussels (W, mg) was measured after drying it in an oven at 90 °C for 24 h, and the shell lengths were measured with a caliper gauge.

Comparison of feeding conditions

A common feature for the filtration-rate data in the present study is the use of micro-algae monocultures that stimulate the mussels to filter at maximum rates. Thus, *Phaeodactylum tricornutum*, *Dunaliella marina*, *Tetraselmis suesica* were used by Riisgård and Møhlenberg (1979) and Møhlenberg and Riisgård (1979), whereas *R. salina* was used by Riisgård et al. (2011b), Pleissner et al. (2013), and in the present study as feed. In all experiments, the algal concentration was kept below the threshold concentration for pseudofaeces production and incipient saturation reduction of filtration activity (i.e. <5 μg chl a l^{-1}, Clausen and Riisgård 1996; Riisgård et al. 2011a). Therefore, in spite of the various methods used, the measured filtration rates may be directly compared.

Statistical analysis

Investigation of effects of CI on F after controlling for the effects of W and L was performed using analysis of covariance (ANCOVA) in SPSS version 12 after linearization of data. Analysis of equations for estimation of F as a function of W and L was performed using one way analysis of variance (ANOVA) in SigmaPlot version 11.

Results

Table 1 shows all available data on L, W, F, and CI, along with the allometric power equations for F versus W and L from five studies on *M. edulis*. In order to evaluate the importance of CI for the allometric equations, plots of all data (Fig. 1) as well as plots for mussels with 'low condition' (CI < 4), 'medium condition' (CI = 4–6) and 'high condition' (CI > 6) have been made (Fig. 2). The choice of limits 4 and 6 is arbitrary but guided by the range of observed values. The various allometric equations are shown in Table 2, Fig. 2. It is seen that the equations for all data: $F_W = 6.773W^{0.678}$ and $F_L = 0.00135L^{2.088}$ are very similar to the 'medium condition' equations: $F_W = 6.567 W^{0.681}$ and $F_L = 0.00150L^{2.051}$, with b- and d-values statistically similar (ANOVA, $p \sim 0.9$) to the theoretically expected of 2/3 and 2, respectively. However,

Table 1 *Mytilus edulis*. Shell length (*L*), body dry weight (*W*), filtration rate (*F*), gill area (*G*), and condition index (CI) of mussels measured in various studies by means of different methods. Estimated allometric power-law equations for *F* versus *W* and *L*, and *G* versus *W* and *L* are shown

L (mm)	W (g)	F (l h^{-1})	G (cm^2)	CI (mg cm^{-3})	Equations	Reference/method/ temperature/time of mussel collection
10.8	0.006	0.18		4.49	$F_W = 7.42W^{0.72}$	Riisgård and Møhlenberg (1979)
15.2	0.018	0.37		5.21	$F_L = 0.0016L^{2.00}$	'Photoaquarium method'
23.2	0.057	1.02		4.56		15 °C
33.4	0.132	2.16		3.54		January 1978
42.8	0.283	2.46		3.61		
				4.28 ± 0.70		
16.0	0.019	0.50		4.64	$F_W = 7.29W^{0.65}$	Møhlenberg & Riisgård (1979)
27.2	0.081	1.26		4.03	$F_L = 0.0013L^{2.12}$	'Suction method'
34.5	0.131	2.52		3.19		11–13 °C
51.8	0.765	6.42		5.50		February 1978
61.5	1.345	7.80		5.78		
				4.63 ± 1.06		
16.0	0.03	0.30	3.5	7.32	$F_W = 6.38W^{0.75}$	Riisgård et al. (2011a, b)
26.1	0.08	1.80	6.3	4.50	$F_L = 0.0008L^{2.26}$	'Clearance method'
49.3	0.74	4.50	28.8	6.18	$G = 37.68W^{0.69}$	12 °C
63.8	1.88	8.70	52.6	7.24	$G = 0.01L^{2.05}$	November 2009
82.6	2.78	15.12	88.6	4.93		
				6.03 ± 1.29		
15.3	0.014	0.50		3.91	$F_W = 8.08W^{0.65}$	Pleissner et al. (2013)
30.4	0.219	2.60		7.80	$F_L = 0.0019L^{2.07}$	'FCA method'
31.8	0.279	2.90		8.68		12 °C
45.1	0.212	4.30		2.31		November 2011
				5.67 ± 3.05		
15.3	0.013	0.34		3.49	$F_W = 5.39W^{0.63}$	Present study
20.7	0.037	0.54		4.22	$F_L = 0.0016L^{2.00}$	'Clearance method'
35.0	0.095	1.65		2.21		11 °C
52.9	0.626	4.21		4.23		February 2013
73.6	1.600	6.48		4.01		
				3.63 ± 0.85		

the equations for mussels with 'low' and 'high condition' are divergent, and it is notable that the *a*-coefficient (equivalent to *F* for a 1 g mussel) takes decreasing values (9.180, 6.567, 6.380 l h^{-1}) for increasing values of condition index, from low to medium to high condition mussels, respectively, as does the *c*-coefficient (equivalent to *F* for a 'theoretical' 1-mm mussel; 0.00189, 0.00150, 0.00068 l h^{-1}, Table 2; Fig. 2).

ANCOVA revealed that there is a significant effect of CI on *F* after controlling for the effect of *W* (CI < 4 and CI > 6: $F_{(1, 7)} = 14.3$, $p < 0.05$; CI < 4 and CI = 4–6: $F_{(1, 16)} = 4.9$, $p < 0.05$). No statistical impact of CI on *F* was found between mussels with CI > 6 and CI = 4–6: $F_{(1, 12)} = 3.7$, $p = 0.08$, possibly because of the small amount of data for mussel with CI > 6. But contrarily to *W*, no impact of CI on *F* was found after controlling for the effect of *L* (CI < 4 and CI > 6: $F_{(1, 7)} = 0.3$, $p = 0.59$;

CI > 6 and CI = 4–6: $F_{(1, 16)} = 1.2$, $p = 0.29$; CI > 6 and CI = 4–6: $F_{(1, 12)} = 0.3$, $p = 0.59$).

Noting that *b*- and *d*-values for the 'medium condition' equations are close to the theoretically expected exponents (2/3 and 2), we propose an empirical *F*–*L*–CI relation for all data of the form F_W/F_L, using the theoretical exponents, yielding $F_W/F_L = (a_m/c_m)CI^{2/3}$, where a_m and c_m are mean values fitted to the 'medium condition' data as follows. For each data point, we calculate $a = F/W^{2/3}$ and $c = F/L^2$, respectively, and average these values to obtain $a_m = 6.521$ l h^{-1} g$^{-2/3}$ and $c_m = 0.00183$ l h^{-1} mm^{-2}, respectively, leading to the following 'model' equations:

$$F_W = 6.521W^{2/3}; \quad F_L = 0.00183L^2;$$
$$F_W/F_L = 0.3562CI^{2/3} \tag{1}$$

where the units are *F* (l h^{-1}), *W* (g), *L* (mm), and the constant $a_m/c_m = 3{,}562$ mm^2 g$^{-2/3} = 0.3562$ cm^2 mg$^{-2/3}$.
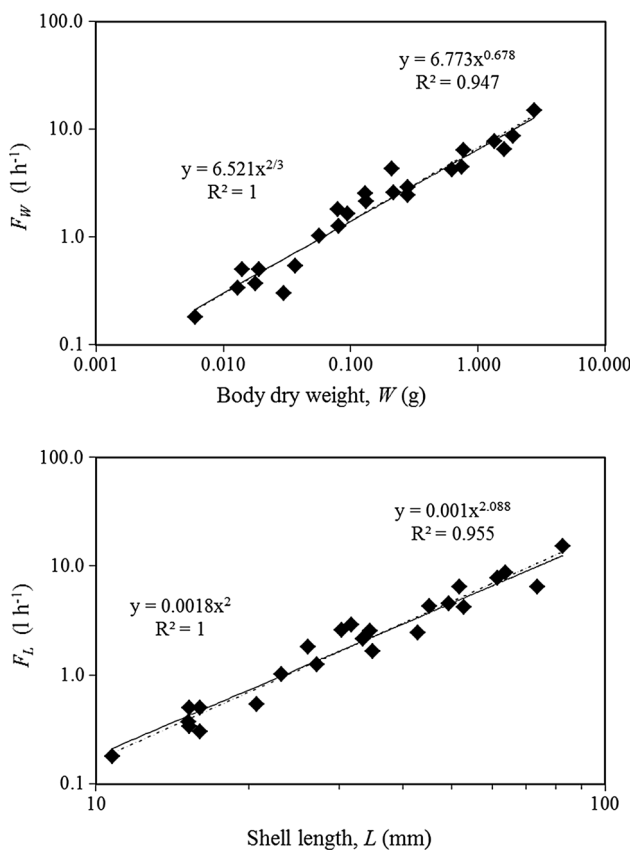
Fig. 1 *Mytilus edulis*. Filtration rate as a function of body dry weight (*W*) and shell length (*L*) based on all data in Table 1. Regression lines of data (*dash*) and of the allometric relations (*solid*) $F_W = a_m W^{2/3}$ and $F_L = c_m L^2$ based on $F_W/F_L = (a_m/c_m)CI^{2/3}$ (see text) with corresponding equations shown

Fig. 2 *Mytilus edulis*. Filtration rate as a function of body dry weight (*W*) and shell length (*L*) of mussels with low (CI < 4), high (CI > 6), and medium (CI = 4–6) condition index (CI). Regression lines (*dot, dash, solid* for low, high, medium) and corresponding equations shown

The first two relations of Eq. (1) are compared to all data in Fig. 1. The reciprocal of the third relation of Eq. (1), (F_L/F_W), is an estimate of a 'correction factor' to the estimated filtration rate based on F_W, and it appears that F_W tends to underestimate the actual filtration rate (F_L) when CI < ($0.3562^{-3/2}$ =) 4.704 and to overestimate the filtration rate when CI > 4.704 mg cm^{-3} (Fig. 3).

Discussion

Although CI for all data sets varies between 2.21 and 8.68 (Table 1), the common equation for all data $F_W = 6.76W^{0.68}$ is near identical (ANOVA, $p = 0.942$) to the 'medium condition' equation, possibly because low- and high-condition values tend to compensate each other. Due to seasonal changes in CI, the filtration rate (and gill size) is more closely related to shell length than to body weight, see also Filgueira et al. (2008) who have earlier pointed out the importance of condition index, although
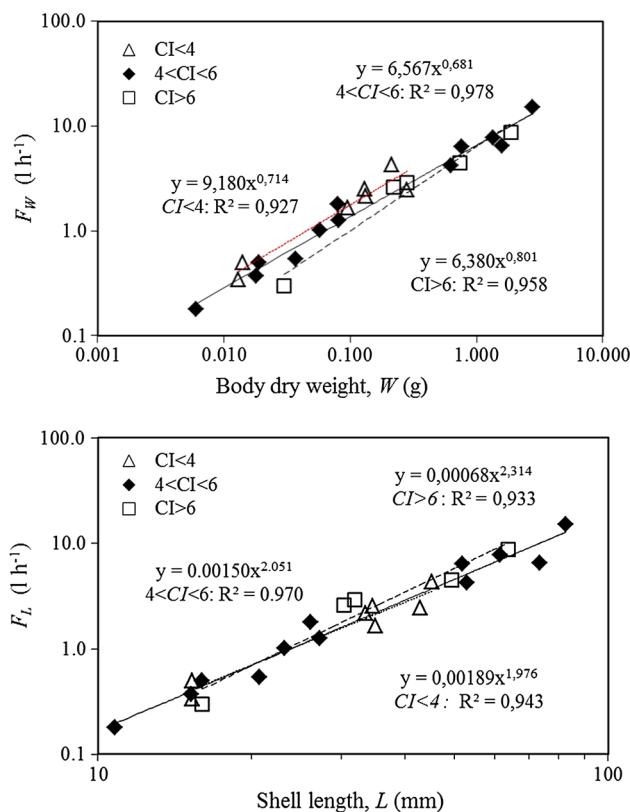
Table 2 *Mytilus edulis*. Allometric power-law equations for filtration rate (*F*, l h^{-1}) versus body dry weight (*W*, g) and shell length (*L*, mm), based on data shown in Table 1 and Fig. 2

$F_W = 6.91 \pm 1.05W^{0.68\pm0.05}$	Table 1 (all equations;
$F_L = 0.0014 \pm 0.0004L^{2.08\pm0.12}$	mean $\pm$ SD)
$F_W = 6.773W^{0.678}$	Table 1 (all data; Fig. 1)
$F_L = 0.00135L^{2.088}$	
$W = 3.48 \times 10^{-6}L^{3.08}$	
$F_W = 9.180W^{0.714}$	CI < 4 'low condition' (Fig. 2)
$F_L = 0.00189L^{1.976}$	
$F_W = 6.567W^{0.681}$	CI = 4–6 'medium condition'
$F_L = 0.00150L^{2.051}$	(Fig. 2)
$F_W = 6.380W^{0.801}$	CI > 6 'high condition' (Fig. 2)
$F_L = 0.00068L^{2.314}$	

they used another definition, i.e. CI = tissue dry weight/ shell dry weight × 100.

The present *b*- and *d*-values are within a few percent of the theoretical values of 2/3 and 2 for *F* versus *W* and *L*, respectively, and we suggest that Eq. (1) for *M. edulis*, based on maximum filtration rates measured under
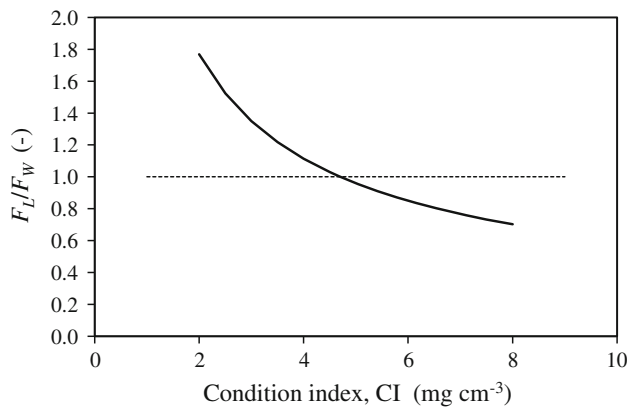
Fig. 3 Correction factor $[F_L/F_W = (0.3562CI^{2/3})^{-1}]$ to filtration rate based on $F_W = aW^b$

controlled laboratory conditions using accurate methods, may be used as 'model' reference equations in future studies. From the allometric relation of Eq. (1) and its reciprocal shown in Fig. 3, it appears that use of $F_W = 6.521W^{2/3}$ (which is close to the 'medium condition', $F_W = 6.567W^{0.681}$) may underestimate the filtration rate of *M. edulis* estimated from the shell length by 42 % at $CI = 2$ and overestimate the filtration rate by 46 % for mussels with $CI = 8$. Recent laboratory and field growth experiments with mussels have revealed a tendency of CI to initially increase during the growth period (Riisgård et al. 2012a, b, 2013a, b), and this behaviour needs to be appropriately handled in modelling studies.

The present analyses of the parameters of the allometric relationship for F versus L show that most of the b-values are close to the theoretically expected value of 2 (Tables 1, 2), which may be compared to the recent statement by Cranford et al. (2011, page 92 therein) that 'a more generally applicable b-value (for F versus L) 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)'. Nevertheless, this exponent is statistically similar to the theoretical value $b = 2$. Finally, it is noted that the present data were obtained at three different temperatures, 11, $\approx$12, and 15 °C. The sensitivity of filtration rate to change in temperature may be estimated to be $(1/F)\mathrm{d}F/\mathrm{d}t = 0.0251$ °C^{-1}, or about 2.5 % °C^{-1}, according to the data of Kittner and Riisgård (2005, Fig. 3 therein, ranging from 10.3 to 20.3 °C) implying variations from -2.5 % to $+7.5$ % about the level of the present data at 12 °C. This variation is within the scatter of data which exceeds 20 %, but a plot of the three groups of data (not shown) indicates separate regression lines that confirm the predicted trend from 10 to 12 °C but not from 12 to 15 °C.

It is clear from the present study that an additional relation is still required for models based on filtration and respiration being a function of dry weight of soft parts. This relation may involve the seasonally influenced growth period. But although changes in the mean dry weight of soft parts of mussels with a certain shell length collected from the same population generally vary with the annual cycle (Dare 1976), large individual variations in CI may be expected, dependent on living site (within or outside the tidal zone, on exposed stones, on suspended cultivation ropes, or within a dense mussel bed with strong intraspecific competition for food). Although based on controlled laboratory data, the present results may be considered as an allometric base line that would be useful for the analysis of field data that do not conform to the condition of maximum filtration rate.

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