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ORIGINAL PAPER

Feeding physiology of the Argentine mussel *Mytilus edulis platensis* (d'Orbigny, 1846): does it feed faster in suspended culture systems?

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Abstract The feeding behavior of *Mytilus edulis platensis*, one of the most important aquaculture resources on the East Coast of southern South America, was studied by analyzing clearance rate (CR) and ingestion rate (IR) to test the hypothesis that cultivated mussels can attain higher clearance and ingestion rates than their wild counterparts. A number of morphometric relationships between cultivated and wild mussels were also compared. Gill surface (GS) growth relative to length (L) is isometric in *M. e. platensis*, with no significant differences between wild and cultivated mussels. At low food concentrations (<15 *Chaetoceros gracilis* cells μl^{-1}), the CR is maximum and similar in both cultivated and wild mussels, decreasing when the concentration of experimental food surpasses a threshold level. This concentration threshold is higher in cultivated mussels than in wild ones. While culture conditions do not affect either GS growth or potential CR, they do affect CR regulation patterns in response to fluctuations in food concentration, allowing the attainment of higher maximum IR.

Keywords Bivalve · Clearance rate · Culture · Feeding physiology · Growth · *Mytilus edulis platensis*

Abbreviations

ANOVA	Analysis of variance
CR	Clearance rate
GS	Gill surface

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IR	Ingestion rate
LRT	Likelihood ratio test

Introduction

The Argentine mussel *Mytilus edulis platensis* (d'Orbigny, 1846) is distributed throughout a latitudinal range of more than 20° along the Atlantic Coast of South América, from Rio Grande do Sul (southern Brazil) to Santa Cruz Province (southern Argentina) (Fig. 1). In the southern limit of its latitudinal distribution, the species is sympatric with *Mytilus chilensis* (Hupe, 1854). Several aspects of the taxonomy (Castellanos 1957), ecology (Penchaszadeh 1974; Trancart 1978; Bala 1996), fisheries (Lasta et al. 1984) and aquaculture (Ruzzante and Toyos de Guerrero 1984; Bertolotti et al. 1987; Zaixso and Bala 1988; Bala 1996; Pascual and Zampatti 1999; Elvira et al. 2000) have been studied so far. In recent years, commercial activities related to the suspended culture of *M. e. platensis* have increased (FAO 2006). The results of a number of studies indicate that *M. e. platensis* shows enhanced growth under suspended culture conditions (Table 1); however, to date, the possible physiological causes of this differential growth have not been evaluated.

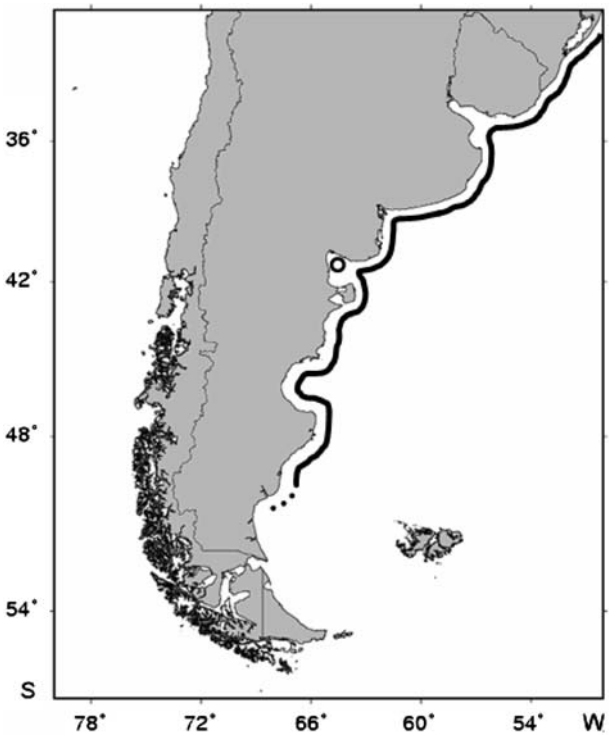

Fig. 1 Latitudinal distribution of *Mytilus edulis platensis*. *Continuous line* documented distribution of the species, *dotted line* undetermined southern limit of the species distribution, *open circle* study area

Table 1 Growth measurements of *Mytilus edulis platensis* as reported by several authors (*n/m* not mentioned)

Site	Growing environment	L_∞ (mm)[a]	k[a]	one year size (mm)	CMY (%)[b]	WMY (%)[b]	Author
Querandí Lighthouse	Natural bed	91	0.380	26–30	n/m	n/m	Penchaszadeh (1974)
San José Gulf	Natural bed	103	0.254	34	n/m	45.0	Trancart (1978)
San José Gulf	Natural bed	105.6	0.451	n/m	n/m	n/m	Bala (1996)
San José Gulf	Suspended culture	n/m	n/m	58	n/m	52.15	Trancart (1978)
Nuevo Gulf	Suspended culture	n/m	n/m	59.8[c]	n/m	n/m	Zaixso and Bala (1988)
San Matías Gulf	Suspended culture	83.27	1.961	Approx. 65	25.65	51.7	Elvira et al. (2000)
San Matías Gulf	Suspended culture	n/m	n/m	Approx. 55	n/m	40	Bertolotti et al. (1987)
San Matías Gulf	Suspended culture	n/m	n/m	39.7[d]	n/m	47.8	Dellatorre and Barón (unpublished data)

[a] L_∞ and k, Parameters of Von Bertalanffy growth equation

[b] CMY and WMY, Cooked meat yield and wet meat yield, respectively

[c] Mussels seeded with a length of 30 mm

[d] Length attained 9.5 months after settlement

Mussels tolerate a wide range of environmental conditions by adjusting their physiological responses to achieve maximum rates of growth (Labarta et al. 1997). These adjustments may take place in (1) pre-ingestive processes involving pumping rate, retention efficiency and selective rejection rate (parameters that determine organic ingestion rate) (Navarro and Winter 1982; Velasco and Navarro 2002) or in (2) digestive processes such as gut-passage time, gut content, quali-quantitative enzyme production and absorption efficiency (Hawkins et al. 1990, 1998). It is well known that in order to maintain a constant IR, the feeding rate increases with increasing body size and decreases with an increase in food concentration once a critical concentration threshold has been surpassed (Winter 1978; Navarro and Winter 1982). Furthermore, long-term adaptations to high-quality seston can involve increments in gut capacity and digestive enzyme activity (Ibarrola 1996; Labarta et al.1997).

In the study reported here we have tested the hypothesis that cultivated mussels can attain higher clearance and ingestion rates (CR and IR respectively) than wild ones by analyzing these physiological parameters from wild and cultivated specimens of *M. e. platensis* over a range of microalgae concentrations and mussel sizes. We also compared a number of morphometric relationships between wild and cultivated mussels to explore the influences of suspended culture conditions on the shape of the specimens.

Materials and methods

Mussel sampling

Mussels were collected in April 2002 at Piedras Coloradas (San Matías Gulf, Patagonia, Argentina; 40°53′S, 65°04′W) (Fig. 1) from a long-line system (cultivated mussels) and a

natural bed (wild mussels) located in the nearby area on a sandy bottom at a depth of 15 m. Mussels on the culture lines came from natural settlement on artificial substrate at the same site. After collection, the mussels were brushed to detach epibionts and placed in tanks filled with filtered seawater (1-μm filters).

Physiological measurements

Each mussel was placed in an 8-l beaker containing a gently aerated suspension of microalgae of a known concentration. *Chaetoceros gracilis* Schutt, obtained from a monospecific culture in f/2 medium (Guillard 1975) (20–21°C, continuous light and aeration), was used as food in all of the experiments. The mean length of the three axis of *C. gracilis* were 6.07 μm (SD = 0.95), 5.59 μm (SD = 1.00) and 4.05 μm (SD = 0.63). The mean dry weight (DW) and volume of *C. gracilis* cells were 19.57×10^{-9} mg (SD = 4.52, $n = 3$) and 111.28 μm^3 (SD = 43.16), respectively. For this characterization, 17 cells were measured on their three normal axis under 600× magnification, and mean volume was calculated under the assumption that the cells had an oval-prism shape. The mean dry weight of a cell was calculated by filtrating a known number of cells (0.45-μm Millipore filter), rinsing them with ammonium formate and weighing them oven-dried (80°C, 48 h).

The experiments lasted between 60 min and 120 min, or until the remaining concentration of food fell below 75% of the initial concentration. The concentration of the cells was monitored with a particle counter (Coulter counter, model TA, fitted with a 140-μm pore-opening tube) in 30-ml samples taken from each beaker every 15 min. A beaker with no specimens was used as a control to calculate the microalgae's settling rate. Couglan's (1969) method was used to estimate CR (''filtering rate'' in Coughlan 1969), and IR was estimated as the product between CR and the initial experimental concentration.

Experiments with a fixed concentration of microalgae and variable mussel sizes

To compare the feeding rates of wild and cultivated mussels over a given size range, CR and IR were measured on samples of 49 wild (length: 30–84.5 mm) and 51 cultivated (length: 16–73 mm) mussels that showed similar size frequency distributions (Kolmogorov-Smirnov test, $P > 0.05$). All mussels were fed at 30 cells μl^{-1} (0.59 mg dry matter l^{-1}) of initial food concentration (16°C, 33‰ salinity). At the beginning of the experiments, the mussels were maintained for 48 h in 1-μm filtered and aerated seawater and then acclimated in a 30 ± 5 cells μl^{-1} suspension for 24 h before the measurements were started. After completing CR and IR determinations, the morphology of the specimens was characterized by measuring maximum distances between the umbo and posterior margin (length, L), between the dorsal and ventral margins (height, H) and between the external surface between opposite valves (width, W) with a Vernier caliper to the nearest 0.5 mm. In addition, total gill surface (GS) was estimated on 31 cultivated and 43 wild mussels. To do this, animals were dissected, submerged in seawater and photographed with a digital camera, sagittal plane facing up. The surface of the projection of the inner lamella of one hemibranch was then measured on the photographs with Scion Image software (Beta 4.0.2), and GS was computed by multiplying it by four. The soft body of each mussel was oven-dried during 48 h at 110°C, and weighed to the nearest 1 mg to obtain the DW.

Experiments with fixed mussel size and variable microalgae concentrations

To evaluate the food concentration effect on feeding rates, we measured CR and IR on similarly sized mussels fed at several different microalgae concentrations. A preliminary experiment was performed using 12 cultivated mussels that were 30.15 ± 0.745 mm ($\bar{L} \pm SD$). After sampling, the mussels were starved for 10 days in 1-µm-filtered seawater, and thereafter acclimated during 1 h before CR determinations, with experimental diets of 5, 10, 20, 30 and 60 cells μl^{-1} (0.1, 0.2, 0.39, 0.59 and 1.17 mg dry matter l^{-1}) of initial microalgae concentration, at 16.5°C (±0.5°C) and 33‰ salinity.

To compare the regulation patterns of CR and IR as a function of food concentration between wild and cultivated mussels, ten specimens from each group, 67 ± 0.75 mm and 66.93 ± 0.61 mm ($\bar{L} \pm SD$) for cultivated and wild mussels, respectively, were fed on experimental rations of 4, 9, 15, 20 and 40 cells μl^{-1} (0.08, 0.18, 0.29, 0.39 and 0.78 mg dry matter L^{-1}), at 12.5°C (±0.5°C) and 35‰ salinity, following the same maintenance and acclimation protocol as in the preliminary experiment.

Statistical analysis

Morphometric variables were ln-transformed, and relationships between them were evaluated by regression analysis after testing normality and homogeneity of variances by means of a graphical method (Zar 1984). For each regression, the null hypothesis of isometry was tested following the methodology used by Voight (1991) and Barón and Ré (2002). A likelihood ratio test (LRT) (Hilborn and Mangel 1997; Anderson et al. 2000) was used to compare regression lines between wild and cultivated mussels. Residual's variance of ln W and ln H on ln L, and ln W on ln H regressions were compared between wild and cultivated mussels using a Bartlett's test (Sokal and Rohlf 1969) to detect shell-shape variability differences.

Regression lines of ln L, ln GS and ln DW on ln CR were calculated and subsequently compared between cultivated and wild mussels using LRT. Given that IR = $\alpha \times$ CR, where α is the experimental concentration, regression analysis of ln IR on ln GS, ln L and ln DW would yield the same results as those obtained for ln CR on these variables. The food concentration effect was analyzed by comparing $\overline{CR}$ and $\overline{IR}$ of wild and cultivated mussels at different food concentrations. $\overline{CR}$ was analyzed using two-way ANOVA and SNK multiple comparisons (Sokal and Rohlf 1969), and one-way ANOVA in the preliminary experiment. Since $\overline{IR}$ variances from different concentrations were significantly different (Bartlett's test, $P < 0.05$), food-concentration effect on $\overline{IR}$ was analyzed using Friedman two-way ANOVA by ranks and multiple comparisons (Daniel 1990), and Student's *t*-tests for comparison between wild and cultivated mussels at each experimental food concentration.

Results

In the present study, the growth of GS was isometric relative to L and that of H relative to L was positively allometric in both wild and cultivated mussels. DW growth relative to L was positively allometric in cultivated mussels and negatively allometric in wild ones. GS growth relative to DW was negatively allometric in cultivated mussels and isometric in wild ones (Table 2).

Table 2 Parameters of morphometric and physiological linear regression equations for wild and cultivated mussels

Parameters[a]	Wild mussels[b]					Cultivated mussels[b]					a_{pop}[c]	b_{pop}[d]
	n	*a*	*b*	R^2	al	*n*	*a*	*b*	R^2	al		
Morphometric												
ln H on ln L	49	−0.174	0.882	0.954	–	51	−0.397	0.936	0.984	–	ns	ns
ln W on ln L	49	−0.995	1.023	0.908	0	51	−1.173	1.053	0.965	0	ns	**
ln H on ln W	49	0.868	0.802	0.909	–	51	0.722	0.861	0.958	–	ns	*
ln DW on ln L	49	−10.48	2.610	0.828	–	51	−13.16	3.302	0.965	+	**	**
ln GS on ln L	41	−5.021	1.957	0.971	0	28	−4.864	1.900	0.947	0	ns	ns
ln GS on ln DW	41	2.838	0.653	0.869	0	28	2.694	0.505	0.846	–	*	*
Physiological												
ln CR on ln GS	41	1.478	0.923	0.626		28	2.391	0.802	0.786		**	ns
ln CR on ln L	49	−2.702	1.715	0.681		51	−3.290	1.973	0.887		ns	**
ln CR on ln DW	49	4.174	0.558	0.593		51	4.561	0.579	0.862		**	ns

*$P < 0.05$; **$P < 0.01$; ns, $P > 0.05$

[a] CR, Clearance rate (ml min^{-1}); DW, dry weight (mg); GS, gill surface (cm^2); H, height (mm); L, length (mm); W, width (mm)

[b] *n,* Sample size; *a*, intercept; *b*, slope; R^2, regression coefficient; al, allometry (+, −, 0: positive allometry, negative allometry and isometry, respectively)

[c] a_{pop}, Significance of intercepts differences

[d] b_{pop}, Significance of slope differences

Differences in ln GS on ln L and ln H on ln L regression parameters were not statistically significant, while both parameters (slope and intercept) of ln DW on ln L and ln GS on ln DW were significantly different between cultivated and wild mussels. The slope of ln W on ln L and ln H on ln W regression lines were significantly different between wild and cultivated mussels (Table 2). Variances of the residuals of ln H on ln W, ln H on ln L and ln W on ln L regressions were significantly higher in wild than in cultivated mussels (Table 3).

Regressions of ln CR on ln GS, ln L and ln DW (Fig. 2) were all significant for both wild and cultivated mussels. The regression slopes of ln CR on ln L and on ln GS, and the regression intercept of ln CR on ln DW were significantly different between cultivated and wild mussels (Table 2).

In both wild and cultivated mussels, CR and IR showed pronounced differences in response to changes in food concentration (Fig. 3). These differences were statistically significant (ANOVA, $P < 0.0001$ for CR; Friedman test, $P < 0.0001$ for IR) in all of the experiments. Multiple comparison results are shown in Fig. 3. Wild and cultivated mussels showed differences in $\overline{CR}$ (ANOVA: $P = 0.047$; Fig. 3). Nevertheless, a posteriori comparisons did not detect significant differences between wild and cultivated mussels for any specific experimental food concentration. Maximum $\overline{CR}$ and $\overline{IR}$ were 6.7 and 31% higher in cultivated mussels than in wild ones. Cultivated mussels showed a significantly higher $\overline{IR}$ compared to wild ones at the experimental concentration of 20 cells μl^{-1} (Studenťs *t*-test, $P = 0.03$). This difference persisted at the concentration of 40 cells μl^{-1} but was not statistically significant (Student's *t*-test, $P = 0.22$).

Table 3 Morphometric variability of wild and cultivated mussels

Regressions	Residual variance		*P*
	Wild mussels	Cultivated mussels	
ln W on ln L	3.42	1.36	0.0015
ln H on ln L	2.93	1.03	0.0004
ln W on ln H	4.36	1.92	0.0048

Bartlett's test results. H, height (mm); L, length (mm); W, width (mm)

Discussion and conclusions

Food availability and mussel density exert a large effect on the morphometry and L–DW relationship of *Mytilus edulis* (Alunno-Bruscia et al. 2001). A higher DW, lower W relative to L and decreased shape variability in cultivated mussels compared to wild mussels probably result from the availability of three-dimensional space for growth in the water column experienced by the former as compared to the bottom two-dimensional space availability experienced by wild specimens.

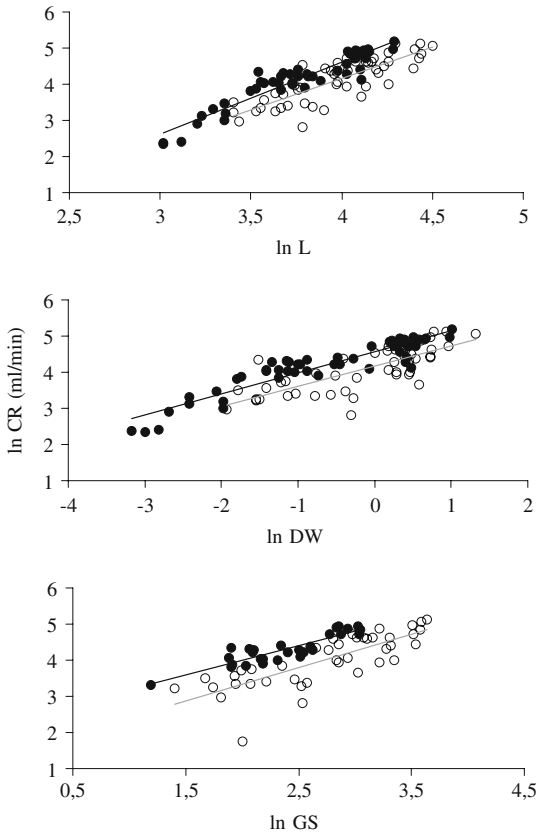

Fig. 2 Relationship between the size of *Mytilus edulis platensis*, as measured by shell length (*L*, mm), dry weight (*DW*, g) and gill surface (*GS*, cm^2), to the clearance rate of algae. *Filled circles* CR estimates from cultivated mussels, *open circles* CR estimates from wild mussels, *black and grey lines* regression lines fitted to cultivated and wild mussel data, respectively

It is an accepted fact that the gill area of bivalves is proportional to the potential CR (Honkoop et al. 2003). It has also been shown that GS can experience space and time variability in response to environmental conditions (Honkoop et al. 2003). In this work, we did not find differences in the GS on the L relationship between cultivated and wild *M. e. platensis*. This result allowed us to use L as the standard dimension to relate IR and CR to the size of mussels and suggests that the feeding mechanism of *M. e. platensis* adapts to different environmental conditions by responses other than changes in GS.

The short-term regulation patterns of CR and IR as a function of food concentration observed in all of our experiments are similar to those proposed by Winter (1978), who suggested that CR is at a maximum and constant at low food concentration, decreasing when this concentration surpasses a threshold level. As a result, IR is maintained at a constant rate and is at a maximum level when food concentration is high (Winter 1978). In this study, while the microalgae concentration threshold at which CR started to decrease was between 9 and 15 cells μl^{-1} (0.18–0.3 mg dry matter l^{-1}) for wild mussels, this threshold was between 20 and 40 cells μl^{-1} (0.4–0.8 mg dry matter l^{-1}) for cultivated ones. Our results agree with those reported by Navarro and Winter (1982), who found that in cultivated *M. chilensis* this threshold is about 0.54 mg dry matter l^{-1}. Nevertheless, in *M. chilensis*, reported weight-specific maximum IR was found to be about fourfold lower than that in *M e. platensis* under similar experimental conditions (Navarro and Winter 1982).

The abrupt increase in $\overline{CR}$ observed when the microalgae concentration increased from 4 to 9 cells μl^{-1} was not an expected behavior if compared with the regulation pattern observed in our preliminary experiment and that reported by Navarro and Winter (1982). One possible cause of this difference could be that since acclimation period was brief (1 h after 10 days of starvation), mussels may have been adjusting inter-filamentary spaces or

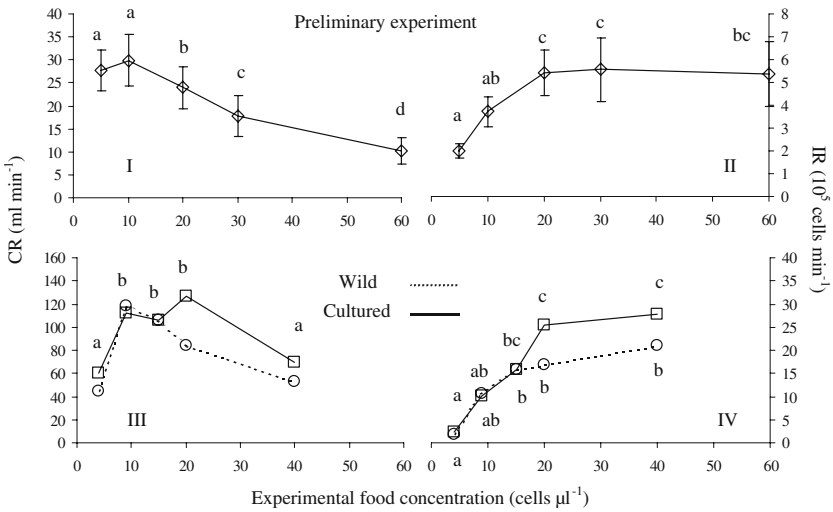

Fig. 3 Comparison of clearance rate (*CR*, ml min^{-1}) and ingestion rate (*IR*, 10^5 cells min^{-1}) of cultured and wild *M. e. platensis* at different food concentrations. *Solid lines* Cultivated mussels, *dashed lines* wild mussels, *vertical bars* standard deviations. *Different letters* represent differences in multiple comparisons. In plot IV, the *upper letters* represent multiple comparisons of cultivated mussels and the *lower letters* those of wild ones

mucus secretion to experimental conditions and, consequently, filtering at lower pumping rates or efficiencies (Ward et al. 1998).

For cultivated *M. chilensis*, Navarro and Winter (1982) found that the regulation pattern of CR is independent of mussel size (Fig. 3 in their study). The combined results of our experiments (Figs. 2, 3) show that for experimental concentrations higher than 20 cell/µl (Fig. 3), CR is higher in cultivated mussels than in wild ones independently of mussel size.

CR and IR regulation patterns in bivalves can be interpreted to be the combined results of genetic differences and adaptive responses to the environment (Iglesias et al. 1996). In the present work, cultivated mussels were obtained from seed settled on artificial collectors in the same zone inhabited by wild ones. Therefore, although the possibility cannot be discarded, genetic differences would seem to be unlikely.

Based on our results, we conclude that *M. e. platensis* do not change GS or maximum CR in response to suspended culture conditions. Instead, cultivated mussels clear the water at maximum rates up to higher microalgae concentrations than wild ones, reaching a higher maximum IR at this condition. Therefore, it can be stated that *M. e. platensis* can feed faster in suspended systems. This response could be related to a higher digestive capacity (gut capacity or gut-passage time; Hawkins et al 1990) in cultivated mussels, which could explain the higher growth rates of *M. e. platensis* in suspended culture conditions.

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