Aquatic
Living
Resources

Body size, population density and factors regulating suspension-cultured blue mussel (*Mytilus* spp.) populations

Marcel Fréchette[1,a], Myriam Lachance-Bernard[1] and Gaétan Daigle[2]

[1] Institut Maurice-Lamontagne, Ministère des Pêches et des Océans, CP 1000, Mont-Joli, Québec, Canada G5H 3Z4
[2] Département de Mathématiques et de Statistique, Faculté des sciences et de génie, Pavillon Alexandre-Vachon, Université Laval, Québec, QC, G1V 0A6, Canada

Abstract – We sampled 27 month-old mussel populations grown on collector ropes in Cascapédia Bay, Quebec, to test whether density-dependent growth was present concomitantly to self-thinning, a process which was previously shown to occur in this system and thought to be driven by spatial constraints. Biomass-density curves of raw samples were curvilinear, suggesting density-dependent growth. However, at least two cohorts were present. Fractionating the samples on the basis of age yielded a linear relationship for the main, 2 year-old cohort. This implies density-independent growth and rules out food regulation in these populations. Therefore, our results are consistent with inferences drawn previously from the values of the self-thinning exponent, that is, space-regulated self-thinning. Our results suggest that curvilinearity of the raw biomass-density curves resulted from a bias caused by including the 1 year-old cohort and spat of the year in the analysis. This conclusion is supported by a model showing that samples with mixed cohorts can yield linear, concave or convex biomass-density curves without density-dependent growth. The shape of the curves depends on the scaling relationships between cohort abundances. It appears that the shape of biomass-density curves may be a useful complementary criterion – in addition to the value of self-thinning exponents – for the identification of food or space as factors regulating cultured populations.

Key words: Mussel culture / Population regulation / Mussel density / Self-thinning

Résumé – Le processus d'autoréduction (mortalité par compétition, "self-thinning") observé chez les populations de moules élevées sur collecteurs de naissain dans la baie de Cascapédia (Québec) a été attribué à la compétition pour l'espace. Dans le but de déterminer si la compétition affecte également la croissance individuelle, nous avons étudié la courbe biomasse-densité d'échantillons en culture depuis 27 mois. Nous observons des courbes concaves, ce qui à première vue correspond à un processus dépendant de la densité. Toutefois, les échantillons comptaient au moins deux cohortes. L'analyse des moules de la cohorte principale, âgée de 2 ans, indique une relation linéaire. La croissance est donc indépendante de la densité, ce qui exclut toute forme de compétition pour la nourriture et confirme les conclusions des travaux antérieurs, fondées sur la valeur de l'exposant de la fonction d'autoréduction. L'analyse suggère que la concavité des courbes biomasse-densité brutes s'explique par un biais causé par l'inclusion des moules âgées d'un an et du naissain dans l'analyse. Cette conclusion est appuyée par un modèle de l'effet du mélange des cohortes. Ce modèle indique qu'en absence de compétition, les courbes biomasse-densité peuvent être linéaires, convexes ou concaves, la forme de la relation dépendant de la relation entre les effectifs des cohortes. Il semble que la courbe biomasse-densité soit un outil diagnostique utile – s'ajoutant à l'exposant de la fonction d'autoréduction – pour la mise en évidence du facteur régulant les populations en élevage.

1 Introduction

Self-thinning (ST) has been reported in sessile animals such as barnacles (Hughes and Griffiths 1988), tunicates (Guiñez and Castilla 2001) and mussels (reviewed by Guiñez 2005) and probably occurs also in scallop spat collector bags (Fréchette et al. 2000). Although ST appears an undesirable situation in routine culture operations because it implies density-dependent mortality, the ST function may reveal useful management information. For instance, it shows the upper limit to production (Westoby 1984). This property has been put to use to assess whether profitability of growing mussels on spat collectors was limited by intrinsic constraints to biological production or by economic constraints (Bilodeau et al. 2008). ST has also been used to assess the relative magnitude of

---

density-dependent and density-independent mortality on mussel sleeves (Fréchette et al. 1996).

ST curves typically fit the power equation $m = kN^\gamma$, where m is the mean mass of the survivors, N the population density and γ is the self-thinning exponent. ST may also be expressed as $B = kN^\beta$, where B is population biomass and $\beta = \gamma+1$ (Westoby 1984). The value of k may vary in different locations, for example depending (in plants) on the level of light or available nutrients (White 1981; Westoby 1984; Weller 1987b; Bi 2004). It was originally thought that the value of γ is constant, irrespective of species and environments (Yoda et al. 1963). ST exponents, however, may vary with allometry (e.g., Weller 1987a,b; see also Lonsdale 1990) or packing configuration (Norberg 1988) and is dependent on initial conditions (Reynolds and Ford 2005).

It has been proposed that the exponent of ST curves may also vary according to the nature of factors regulating populations. In cases where population regulation is driven by bioenergetic constrains (e.g. food-regulated self-thinning, FST), the predicted value of the exponent is $\beta = -0.33$ (Norberg 1988; Fréchette and Lefaivre 1990; Enquist et al. 1998), while in space-regulated situations (SST), ignoring allometry, the predicted value is $\beta = -0.5$ (Yoda et al. 1963; Weller 1987a,b; Norberg 1988). The implications for modelling population production are significant. With SST only and no density-dependent effect on growth, one may model growth as $g(m, t)$, for instance. In contrast, with food regulation acting, one gets a more complex model with $h(m, N, t)$. However, attempts to discriminate between FST and SST based on the value of the ST exponent have been inconclusive. FST and SST exponents of mussel populations grown on intertidal stakes were not significantly different (Fréchette and Lefaivre 1990). In a study of juvenile steelhead trout, the ST exponent was consistent with FST but not significantly different from the expected value under the hypothesis of SST (Keeley 2003). A further source of uncertainty is the ability of gregarious sessile animals such as mussels to form multi-layered beds. This clearly biases bidimensional SST models (Guiñez and Castilla 1999). Consequently, Guiñez and Castilla (1999) proposed a tridimensional model, $B = kL^{1-\beta}N^\beta$, where L is the number of mussel layers.

Two methods have been developed to take multi-layering into account in ST models, the effective-density method (Guiñez and Castilla 2001) and the multi-layer method (Guiñez and Castilla 1999). The effective-density method is based on a projection of the population as a single-layered matrix of individuals. Based on an extensive data set, Filgueira et al. (2008) estimated the ST exponent of suspension-grown mussels in the Ría de Ares-Betanzos, using the effective-density approach. They found $\beta = -0.32$, which they ascribed to food regulation. This result raises some concern, however, because the method assumes that ST is driven by spatial constraints. It appears that the effective-density method is not well suited for suspension-grown mussels. The multi-layer approach was used by Lachance-Bernard et al. (2010) in a study of blue mussels (*Mytilus* spp.) growing in suspension on spat collectors. The number of layers was estimated as $L = \ell/R$, where ℓ is mean shell length and R is the average radius of the sample on the ropes. They found $\beta = [-0.557, -0.423]$, suggesting that ST was driven by competition for

space. Lauzon-Guay et al. (2006), using a population model of growth and survival of mussels cultured on long lines in two estuaries of Prince Edward Island, Canada, also concluded that mussel population density was regulated by spatial constraints. Although these studies were based on different numerical methods, all involved similar mussel species grown in suspension (*Mytilus edulis*, *M. galloprovincialis* and *M. trossulus*). Therefore one might have expected that the factor identified as regulating the populations would have been the same in all cases.

The present study was made to examine whether the multi-layer method leads to inferences consistent with its assumptions in suspension-grown mussels. It is based on the assumption that in the absence of metabolic constraints, individual size is density-independent and *B-N* curves are linear. On the other hand, if food regulation is operating, individual growth is affected (this may also occur in space-regulated situations) and *B-N* curves are curvilinear because growth slows down with increasing population density, as in Alunno-Bruscia et al. (2000, see their Fig. 3). A further assumption of this analysis is that only one cohort is present. Therefore we made this study to test whether in a situation where the ST exponent suggested regulation by spatial constraints (Lachance-Bernard et al. 2010), *B-N* curves would concomitantly indicate the absence of metabolic constraints on individual growth. We also examined the consequences of the violation of the single cohort assumption.

2 Materials and methods

2.1 Sampling procedure

We studied mussels cultured in Baie de Cascapédia, an open body of water within Baie des Chaleurs, Quebec. Wild mussel populations in the vicinity are made of roughly 75% *Mytilus edulis* and 25% *Mytilus trossulus* (Moreau et al. 2005). We assume that mussels cultured in Baie de Cascapédia follow the same frequencies. These mussels were cultured on longlines moored at farm 2 in Lachance-Bernard et al. (2008). Sampling was made on 9 and 11 September 2008. We sampled collectors from a single longline deployed 27 months earlier. Therefore, mussels were nominally 2^+ year old. At this age, ST is under way on collectors at this site (Lachance-Bernard 2008). On both occasions we sampled 6 collectors at the rate of 2-4 samples per collector. Each collector was pulled out of the water complete. Sleeves were placed underwater around the samples to prevent mussel fall-off. Nominal length of samples was 30.5 cm. The actual length of samples varied somewhat and data were corrected to a standard 30.5 cm length. All samples from one collector were discarded because the sleeves had moved along the collector and piled up at its bottom end, thus preventing reliable measurement of actual sample length.

For each sample, we first declumped the mussels, cleaned them with seawater and removed byssal filaments. Samples were passed through a 0.2 cm sieve, which retains mussels $\geqslant$ 0.5 cm shell length (ℓ). No age determination was made on 9 September mussels. However, age was determined from annual shell rings on mussels sampled on 11 September as preliminary analysis suggested that the presence of more

than a single year class might have biased the B-N curve on 9 September Two age classes were defined (2 year old and 1 year old and less, hereafter cohort 2 and cohort 1, respectively). All mussels were counted and weighted in bulk for each age group separately.

2.2 Criterion for density-dependent growth

With density-independent growth, mean size at time t is constant with respect to population density (N). Therefore, $\partial m/\partial N = 0$ and $m = m_0$, where m_0 is density-independent mean mass of the mussels. Multiplying both sides of the equation by N to get biomass yields

$$B = m_0 N. \tag{1}$$

To provide an efficient model of density-dependent growth, we assume that mussel mass at time t decreases proportionally to mussel density. This is reflected by parameter k ($k > 0$) in the equation of mussel mass, $\partial m/\partial N = -k$. Integration leads to $m = -kN + C$. With $N = 0$, $C = m_0$, the density-independent mussel mass. Multiplying both sides of the equation by N to get biomass yields

$$B = m_0 N - kN^2. \tag{2}$$

Equation (2) is appropriate for populations made of a single cohort. The ropes we sampled, however, were 27 month old. Therefore, individuals in our samples may be from more than one cohort. Experiments (Brichette et al. 2001) and computer simulations (Fréchette et al. 2005) suggest that intraspecific competition for food in mussels has symmetric and asymmetric components with respect to individual size. The symmetric component of competition implies that growth of cohort 2 is negatively impacted by cohort 1 when competition is present. Consequently, a model of the effect of food-regulated competition on cohort 2 mussels must include the potential effect both cohorts, such that we have

$$\partial m_2/\partial N_2 = -k_2 - k_1 B_1 \tag{3}$$

where the subscripts 1 and 2 stand for cohorts 1 and 2, respectively, B_1 is biomass of cohort 1 and constants k_1 and k_2 are positive. Integrating and multiplying both sides by population density of cohort 2 yields

$$B_2 = m_0 N_2 - (k_2 + k_1 B_1)N_2^2 \tag{4}$$

where B_2 is biomass of cohort 2 and m_0 is density-independent individual mass of mussels as before.

In addition to the case depicted by Eq. (4), a third situation may prevail, where cohort 1 alone impacts growth of cohort 2 mussels. This could occur in cases where animals of cohort 2 were prevented from accessing sufficient food resources independently of their own abundance. Mussel beds have complex surface rugosity patterns (Commito and Rusignuolo 2000). The presence of such rugosity itself increases mussel recruitment on artificial substrates (Petraitis 1990). Recruitment in sown mussel beds is enhanced by the presence of older conspecifics (McGrorty et al. 1990;

McGrorty and Goss-Custard 1993). Therefore, one may speculate that numerous cohort 1 mussels packed between cohort 2 mussels may physically prevent them from opening properly, with ensuing negative effects on their clearance rate and food consumption (Jørgensen et al. 1988; Dolmer 2000; Newell et al. 2001; Riisgård et al. 2006, but see Fréchette and Despland 1999). In this case the effect of cohort 1 mussels on individual mass of cohort 2 mussels may be modelled as

$$\partial m_2/\partial N_2 = -k_1 B_1. \tag{5}$$

Integrating and multiplying both sides of Eq. (5) by population density of cohort 2 leads to

$$B_2 = m_0 N_2 - k_1 B_1 N_2^2. \tag{6}$$

Equations (1), (4) and (6) provide models of B-N curves which we fitted to the data in order to infer the nature of processes controlling individual growth on the ropes. The data were analysed using SAS (PROC NLIN) and model selection was based on Akaike's Information Criterion (AIC; the AIC differences Δ_i, and Akaike weights w_i; see Mazerolle 2006).

2.3 Curvilinearity of B-N curves without density-dependent growth

The situations depicted by Eqs. (2)-(6) assume that curvilinearity in B-N curves is caused by density-dependent interactions. With more than one cohort present, however, it is likely that this assumption be violated. Curvilinearity in B-N curves may arise simply because smaller individuals from young cohorts would contribute less to biomass, but equally to population density, than those from older ones. This effect would occur even in density-independent situations and therefore is a source of bias in the models depicted above.

To study the potential effect of pooling individuals from different cohorts, we developed a model of B-N curves with 2 cohorts and examined the effect of various mixing scenarios on the second derivative of B-N curves. In the model, mean individual mass of each cohort is constant and individuals of cohort 2 are larger than those of cohort 1. Therefore we write $m_2 = k_3 m_1$, with $k_3 > 1$. The relationship between population density of cohort 1 (N_1) and cohort 2 (N_2) is $N_1 = k_4 N_2^x$, with $k_4 > 0$. Depending on the value of x, the relationship is either linear ($x = 1$), concave (downward concavity; $0 < x < 1$ as in Fig. 2, broken line) or convex ($x > 1$). Total population density (N) is given by $N = N_1 + N_2$ and total biomass (B) is given by $B = N_1 m_1 + N_2 m_2$. The derivative of N_1 with respect to N_2 is

$$\partial N_1/\partial N_2 = xk_4 N_2^{x-1} = \frac{xk_2 N_2^x}{N_2} = \frac{xN_1}{N_2} \tag{7}$$

Next, we write

$$B' = \partial B/\partial N = \frac{\partial B/\partial N_2}{\partial N/\partial N_2} \tag{8}$$

which is

$$B' = \frac{\frac{m_1 x N_1}{N_2} + m_2}{\frac{x N_1}{N_2} + 1} = \frac{m_1 x N_1 + m_2 N_2}{x N_1 + N_2}. \tag{9}$$

The second derivative of B with respect to N is then

$$\partial^2 B / \partial N^2 = \partial B' / \partial N = \frac{\partial B' / \partial N_2}{\partial N / \partial N_2}. \qquad (10)$$

The numerator of Eq. (10), however, is

$$\partial B' / \partial N_2 = \frac{x N_1 (m_2 - m_1)(1 - x)}{(x N_1 + N_2)^2} \qquad (11)$$

and its denominator is

$$\partial N / \partial N_2 = x \frac{N_1}{N_2} + 1 = \frac{x N_1 + N_2}{N_2}. \qquad (12)$$

Dividing (11) by (12), we get

$$\partial^2 B / \partial N^2 = \frac{x N_1 N_2 (m_2 - m_1)(1 - x)}{(x N_1 + N_2)^3} \qquad (13)$$

Since $m_2 > m_1$, we get

$$\partial^2 B / \partial N^2 \begin{cases} > 0 \ \ \text{if} \ \ 0 < x < 1 \\ = 0 \ \ \text{if} \ \ x = 0 \ \ \text{or if} \ \ x = 1 \\ < 0 \ \ \text{if} \ \ x > 1 \end{cases} \qquad (14)$$

Therefore, in density-independent situations, the shape of B-N curves may vary if more than one cohort is present and cohorts are pooled during sample analysis. The resulting B-N curve may be either linear (if $x = 0$ or if $x = 1$), convex (if $0 < x < 1$) or concave (if $x > 1$), depending on the scaling relationships between population densities of the cohorts.

3 Results

We sampled 24 and 17 rope segments on 9 Sept. and 11 Sept., respectively. The ropes supported very little macrobenthic organisms other than mussels. We found only two medium-sized sea stars, and sparse populations of bryozoans apparently associated to lower mussel biomass, on the twelve collectors sampled. Predation appeared negligible and for all practical purposes we sampled monospecific mussel assemblages. This is consistent with spatial dominance of natural mussel beds being maintained by individual growth while the population as a whole undergoes self-thinning (Petraitis 1995).

Population density ranged roughly between 100 ind./30.5 cm and 1400 ind./30.5 cm of rope (Fig. 1). The similarity of the raw B-N curves (Fig. 1) was obvious, and supported by statistical analysis of log-log relationships (Model II regression slopes; $t = 1.95$: $df = 14$; $0.05 < p < 0.10$; Clarke 1980). This suggests that similar processes were operating on samples of both dates. The two B-N curves (all cohorts included) apparently followed a concave pattern. Linear (Eq. (1)) and curvilinear (Eq. (2)) models provided very good fit to the data (Table 1). On both dates, however, the AIC values were lower for the curvilinear model than for the linear model. AIC weights supported a curvilinear model on both dates. Age determination of the mussels of the 11 Sept. samples, however, showed that at least two age classes were present, cohort 2 (settled in 2006) and cohort 1 (settled in 2007; cohort 1 presumably included 0^+ individuals if larger
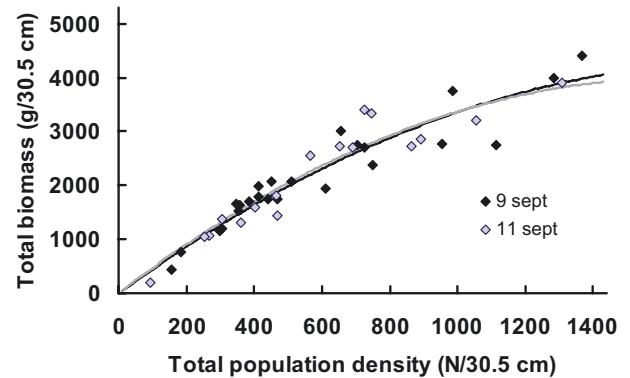

Fig. 1. Relationship between mussel biomass and population density in Cascapédia Bay, Baie des Chaleurs, Québec. Raw data. All cohorts included. Black symbols: 9 Sept. 2008. Grey symbols: 11 Sept. 2008.
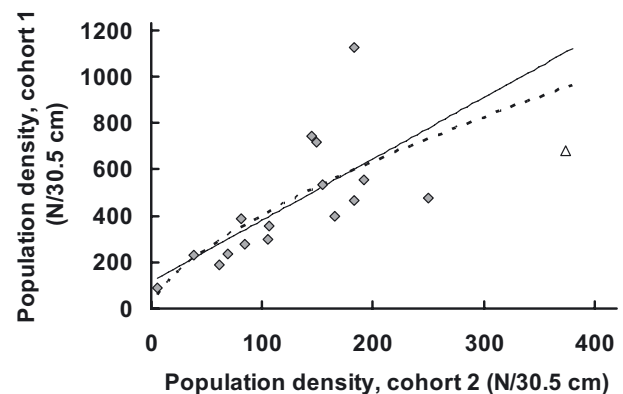

Fig. 2. Relationship between population density of cohort 1 and population density of cohort 2: 11 Sept. 2008. Solid line depicts the linear relationship $N_1 = 116.60 + 2.64 N_2$. Broken line depicts the power function $N_1 = 19.92 \cdot N_2^{0.65 \pm 0.55}$. Data point shown by a triangle was not included in the calculations.

than 0.5 cm shell length). The presence of cohorts younger than cohort 2 raises the possibility that the B-N curves (in Fig. 1) be biased (see Sect. 2.3). To assess this possibility, we examined the abundances of cohort 1 and cohort 2 for the Sept. 11 samples (Fig. 2, Table 2). The general pattern between the cohorts was significant (Kendall's $\tau_b = 0.6444$, $n = 16$, $p = 0.0005$) and cohort 1 was about three times as abundant as cohort 2. This indicates that cohort mixing occurred in Sept. 11 samples. We fitted two models to these abundance data, a linear model $N_1 = a + b N_2$ and the power function $N_1 = a N_2^x$, where a, b and x are parameters. The AIC value was lower with the power function ($\Delta = 0.62$ for the linear model; Table 2; $N_1 = 19.92 N_2^{0.65}$), suggesting that it might be more appropriate. With $w = 0.5769$, however, the situation is not clear cut and both models appear equivalent (AIC differences smaller than 2 units are thought to be negligible; Burnham and Anderson 2002). Assuming a power function between cohort abundances, the expected change in B-N curves attributable to cohort mixing would be toward increased convexity (Eq. (14)).

The effect of cohort mixing was assessed by examining the B-N curves of each cohort separately (Fig. 3). The data point shown by a triangle was from cohort 2 and clearly is an outlier.

Table 1. Relationship between mussel biomass and population density with all cohorts pooled. Based on the assumptions of density-independent and density-dependent growth, respectively, the data were fitted linear (Eq. (1)) and curvilinear (Eq. (2)) model. AIC is Akaike's Information Criterion, Δ_i is the difference in AIC value between the ith model and the model with the lowest AIC value and w_i is the Akaike weight for the ith model. On both days the best model was the curvilinear model, as shown by high Akaike weigths.

Date	Model	Parameter values		n	p	R^2	AIC	Δ_i	w_i
		m_0	k						
9 Sept.	$B = m_0N$	3.42	—	22	< 0.001	0.8051	268.13	10.71	0.0047
	$B = m_0N - kN^2$	4.55	0.00119	22	< 0.001	0.8906	257.42	0	0.9953
11 Sept.	$B = m_0N$	3.63	—	16	< 0.001	0.8326	194.55	7.24	0.0261
	$B = m_0N - kN^2$	4.78	0.00136	16	< 0.001	0.9060	187.31	0	0.9739

Table 2. Relationship between the abundances of cohort 1 and cohort 2 for 11 Sept. samples. The data were fitted two models, a linear model and a power function. AIC, Δ_i and w_i as in Table 1.

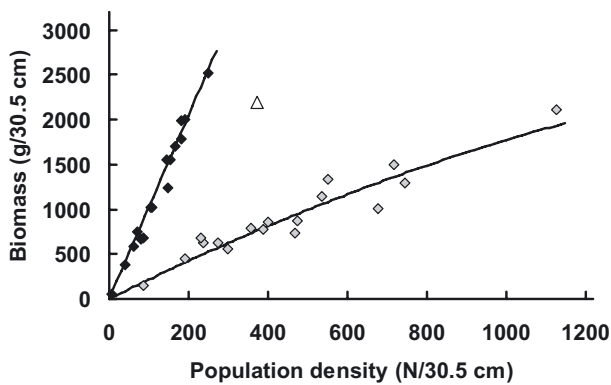| Model	Parameter values			n	p	R^2	AIC	Δ_i	w_i
	a	b	x						
$N_1 = a + bN_2$	116.6	2.64	—	16	< 0.0047	0.4454	171.17	0.62	0.4231
$N_1 = aN_2^x$	19.92	—	0.65	16	< 0.0001	0.4667	170.55	0	0.5769

Fig. 3. Relationship between population density and biomass of cohorts 1 and 2: 11 Sept. 2008. Grey symbols, cohort 1. Black symbols, cohort 2. Data point shown by a triangle was not included in the calculations.

It was excluded from the analyses. The *B-N* curve of cohort 2 appeared quite linear. A linear model (Eq. (1), AIC = 149.79) apparently provided a better fit than the other models tested (Eq. (4), AIC = 150.61; Eq. (6), AIC = 151.77; Table 3, although the difference between the AIC values for Eq. (1) and Eq. (4) was small ($\Delta = 0.82$). The Akaike weights were quite similar for Eq. (1) ($w = 0.4913$) and Eq. (4) ($w = 0.3261$) but lower for Eq. (6) ($w = 0.1826$). It is noteworthy that the value of parameter k_2 was negative, indicating that if anything, the relationship was convex, not concave, which is not consistent with density-dependent growth. The *B-N* curve of cohort 1 was described better by a curvilinear model (Eq. (2), AIC = 155.77) than by a linear model (Eq. (1), AIC = 157.20).

4 Discussion

The *B-N* curves (Fig. 1 and 3) followed well-defined patterns which allow making inferences about the process(es) governing individual growth, provided that the single-cohort assumption is not violated. The raw *B-N* curves (Fig. 1) were curvilinear, which suggests that individual growth was density-dependent, as inferred from Eq. (2). It must be considered, however, that the raw samples were made of at least two cohorts (Fig. 2). In such instances, the assumption underlying Eq. (2) does not hold. As a matter of fact, considering each cohort separately led to radically different conclusions. There was no evidence for rejecting a linear model for the *B-N* curve of cohort 2 (Fig. 3, Table 3). Therefore, we adopt a parsimonious view and conclude that there was no evidence for density-dependent growth in cohort 2. This rules out food regulation (or other metabolic constraints such as chemical competition) in mussel populations grown on ropes in Cascapédia Bay. ST is under way on these ropes at 27 months (Lachance-Bernard et al. 2010). The present study implies that the process is driven by spatial constraints. Therefore, our results directly support the inference based on the exponent of 3-D ST curves (Lachance-Bernard et al. 2010).

Mussel populations form multi-layered matrices, which has consequences for the estimation of SST exponents (Guiñez and Castilla 1999). The appropriate representation of ST requires that multilayering be taken into account. Two methods are presently available to this end. The multilayer method was developed for the analysis of intertidal mussels (Guiñez and Castilla 1999). The effective-density method was developed for the analysis of an intertidal tunicate (Guiñez and Castilla 2001). The multilayer method was applied to suspension-grown mussels (Lachance-Bernard et al. 2010) and provided estimates of the 3-D ST exponent which are consistent with the present study i.e., that ST in suspension-grown mussels is driven by spatial constraints (see also Lauzon-Guay et al. 2006). This conclusion clearly diverges from that of Filgueira et al. (2008), who reported FST in suspension-grown mussels using the effective-density method. Therefore, the effective-density method led to inferences that are not consistent with its assumptions. We conclude that the effective-density method is not appropriate for the study of ST in suspension-grown mussels, while the multilayer method is.

No evidence of density-dependent growth was found in this study (see also Fuentes et al. 2000), although it has been found in suspension-cultured mussels in a number of instances.

Table 3. Relationship between mussel biomass and population density for cohort 2 mussels, 11 Sept. samples. The data were fitted linear and curvilinear models under the hypotheses of density-independent growth (Eq. (1)), density-dependent growth (Eq. (4)) and asymmetric density-dependent growth (Eq. (6)). AIC, Δ_i and w_i as in Table 1.

Eq.	model	Parameter values			n	p	R^2	AIC	Δ_i	w_i
		m_0	k_1	k_2						
1	$B_2 = m_0 N_2$	9.9877	—	—	16	< 0.0001	0.9766	149.79	0	0.4913
4	$B_2 = m_0 N_2 - (k_2 + k_1 B_1) N_2^2$	9.0781	1.93×10^{-6}	-0.00739	16	< 0.0001	0.9808	150.61	0.82	0.3261
6	$B_2 = m_0 N_2 - k_1 B_1 N_2^2$	9.9327	-2.8×10^{-7}	—	16	< 0.0001	0.9767	151.77	1.98	0.1826

The evidence has been either direct, based on the analysis of the effect of population density manipulation on meat weight (Mallet and Carver 1991, but see Lauzon-Guay et al. 2005 for a transient effect of seeding density) or indirect, as assessed experimentally from the effect of spacing out sleeves on long lines (Drapeau et al. 2006) or from rafts (Navarro et al. 1991; Mueller 1996; Heasman et al. 1998). Modeling phytoplankton uptake by mussels cultured in low current speed situations (5 cm s^{-1}) predicted density-dependent food uptake (Smith et al. 2006). Sleeves on rafts are arranged densely and cause water flow retardation and seston depletion (Boyd and Heasman 1998; Heasman et al. 1998). In other instances, presumably with higher water flow than in the aforementioned studies, little evidence has been found that individual growth was affected by intraspecific (Fréchette et al. 1996; Sénéchal et al. 2008) or interspecific competition (Lesser et al. 1992) in mussel suspension culture. Current speed near our study site was measured for one month in 2005 (Weise et al. 2009). Nominal height of the collectors is about 1 to 5 m above the bottom (Lachance-Bernard 2008). At 4 m above the bottom, mean current speed was 10.3 ± 6.6 cm s^{-1} (SD; A. Weise, IML, pers. comm.). Presumably at this level current speed is too high for phytoplankton to be depleted and cause growth to be density-dependent at the scale of individual ropes.

The raw B-N curves (Fig. 1) were based on samples in which cohorts 1 and 2 co-occurred. Sorting the mussels on the basis of age removed the bias for cohort 2 but not for cohort 1 (Fig. 3). This may be caused by the presence of spat among cohort 1 mussels. Mussel beds have complex surface rugosity patterns (Commito and Rusignuolo 2000). The presence of such rugosity itself increases mussel recruitment on artificial substrates (Petraitis 1990). Therefore, rugosity provided by mussels at the surface of the collector ropes presumably contributed to increasing spat recruitment. Spat abundance has been found to increase with adult density because spat settle in the byssus threads of adults and because post-settlement survivorship increases with adult density (McGrorty et al. 1990; McGrorty and Goss-Custard 1993). Adult mussels and shell debris in mussel beds increase structural complexity of the bottom and this also has been related to increased post-settlement survivorship in mussel beds (Frandsen and Dolmer 2002; Dolmer and Stenalt 2010). Therefore, we may speculate that the situation with cohort 1 was analogous to that of raw samples and that cohort 1 was made of 1 year old animals (hereafter cohort 1$^+$) and spat of the year (hereafter cohort 0$^+$), both growing without density-dependence. Based on our model of the effect of cohort mixing, and given the concave relationship between cohort 2 and (the mixed) cohort 1

abundances, the raw B-N curves should have been convex (see Eq. (14)). Unexpectedly, however, they were not. Furthermore, we infer that with two cohorts present (cohort 0$^+$ and cohort 1$^+$), the concave pattern of the cohort 1 B-N curve implies that the abundance of cohort 0$^+$ increased faster than that of cohort 1$^+$ (i.e., $x > 1$ in Eq. (14)) and perhaps also faster than that of cohort 2. Because of the larger size difference between cohort 0$^+$ and 2 year old mussels than between cohort 1$^+$ and cohort 2 (Eq. (14)), it appears that the effect of cohort 0$^+$ prevailed over the effect of cohort 1$^+$ on the raw B-N curves. This conclusion remains unchanged if a linear relationship is assumed instead of a power function in Figure 2.

A basic assumption of the analysis of biomass-density relationships is that individuals are even-aged (Westoby 1984; Weller 1987a). This assumption is somewhat relaxed by Eqs. (3–6) and by our model of the effect of cohort mixing. We were able to use B-N curves in presence of more than one cohort to test hypotheses about processes controlling growth dynamics. This requires, however, that the age of individuals be known. Furthermore, in the particular cases where cohort abundances are not related or scale linearly with one another, our model predicts the absence of bias in the shape of B-N curves.

Therefore, we conclude that there was no evidence for density-dependent growth in 27-month old collector ropes in Baie de Cascapédia. Density-dependent effects are found in survivorship only. Our results support the conclusion based on the exponent of the tridimensional ST curve that these mussel populations are regulated by competition for space (Lachance-Bernard et al. 2010). The combination of density-independent growth (present study) with density-dependent mortality (Lachance-Bernard et al. 2010) indicates that mussel populations on these ropes traveled along the self-thinning line at the junction between the maximum mean mass boundary and the maximum crowding index boundary depicted by Guiñez et al. (see their Fig. 3; 2005). Although mussel age was not determined in the 9 Sept. samples, the similarity between the raw B-N curves found for both sampling days suggests that processes acting on the ropes sampled on both occasions were similar.

References

Alunno-Bruscia M., Petraitis P.S., Bourget E., Fréchette M., 2000, Body size-density relationships for *Mytilus edulis* in an experimental food-regulated situation. Oikos 90, 28-42.

Bi H., 2004, Stochastic frontier analysis of a classic self-thinning experiment. Aust. Ecol. 29, 408-417.

Bilodeau F., Lachance-Bernard M., Wilson J.R., Fréchette M., 2008, Étude de la rentabilité de la production de moules sur collecteur autogéré à Carleton, Québec. Report No. 282

Boyd A.J., Heasman K.G., 1998, Shellfish mariculture in the Benguela system: Water flow patterns within a mussel farm in Saldanha Bay, South Africa. J. Shellfish Res. 17, 25-32.

Brichette I., Reyero M.I., Garcia C., 2001, A genetic analysis of intraspecific competition for growth in mussel cultures. Aquaculture 192, 155-169.

Burnham K.P., Anderson D.R., 2002, Model selection and multimodel inference: a practical information-theoretic approach, Vol. Springer-Verlag, New York.

Clarke M.R.B., 1980, The reduced major axis of a bivariate sample. Biometrika 67, 441-446.

Commito J.A., Rusignuolo B.R., 2000, Structural complexity in mussel beds: the fractal geometry of surface topography. J. Exp. Mar. Biol. Ecol. 255, 133-152.

Dolmer P., 2000, Feeding activity of mussels *Mytilus edulis* related to near-bed currents and phytoplankton biomass. J. Sea Res. 44, 221-231.

Dolmer P., Stenalt E., 2010, The impact of adult blue mussel (*Mytilus edulis*) population on settling of conspecific larvae. Aquac. Internat. 18, 3-17.

Drapeau A., Comeau L.A., Landry T., Stryhn H., Davidson J., 2006, Association between long-line design and mussel productivity in Prince Edward Island, Canada. Aquaculture 261, 879-889.

Enquist B.J., Brown J.H., West G.B., 1998, Allometric scaling of plant energetics and population density. Nature 395, 163-165.

Filgueira R., Peteiro L.G., Labarta U., Fernández-Reiriz M.J., 2008, The self-thinning rule applied to cultured populations in aggregate growth matrices. J. Molluscan Stud. 74, 415-418.

Frandsen R.P., Dolmer P., 2002, Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. Mar. Biol. 141, 253-262.

Fréchette M., Alunno-Bruscia M., Dumais J.-F., Daigle G., Sirois R., 2005, Incompleteness and statistical uncertainty in competition/stocking experiments. Aquaculture 246, 209-225.

Fréchette M., Bergeron P., Gagnon P., 1996, On the use of self-thinning relationships in stocking experiments. Aquaculture 145, 91-112.

Fréchette M., Despland E., 1999, Impaired shell gaping and food depletion as mechanisms of asymmetric competition in mussels. Écoscience 6, 1-11.

Fréchette M., Gaudet M., Vigneau S., 2000, Estimating optimal population density for intermediate culture of scallops in spat collector bags. Aquaculture 183, 105-124.

Fréchette M., Lefaivre D., 1990, Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. Mar. Ecol. Prog. Ser. 65, 15-23.

Fuentes J., Gregorio V., Giráldez R., Molares J., 2000, Within-raft variability of the growth rate of mussels, *Mytilus galloprovincialis*, cultivated in the Ría de Arousa (NW Spain). Aquaculture 189, 39-52.

Guiñez R., 2005, A review of self-thinning in mussels. Rev. Biol. Mar. Oceanogr. 40, 1-6.

Guiñez R., Castilla J.C., 1999, A tridimensional self-thinning model for multilayered intertidal mussels. Am. Nat. 154, 341-357.

Guiñez R., Castilla J.C., 2001, An allometric tridimensional model of self-thinning for a gregarious tunicate. Ecology 82, 2331-2341.

Guiñez R., Petraitis P.S., Castilla J.C., 2005, Layering, the effective density of mussels and mass-density boundary curves. Oikos 110, 186-190.

Heasman K.G., Pitcher G.C., McQuaid C.D., Hecht T., 1998, Shellfish mariculture in the Benguela system: raft culture of *Mytilus galloprovincialis* and the effect of rope spacing on food extraction, growth rate, production, and condition of mussels. J. Shellfish Res. 17, 33-39.

Hughes R.N., Griffiths C.L., 1988, Self-thinning in barnacles and mussels: the geometry of packing. Am. Nat. 132, 484-491.

Jørgensen C.B., Larsen P.S., Møhlenberg F., Riisgård H.U., 1988, The mussel pump: properties and modelling. Mar. Ecol. Prog. Ser. 45, 205-216.

Keeley E.R., 2003, An experimental analysis of self-thinning in juvenile steelhead trout. Oikos 102, 543-550.

Lachance-Bernard M., 2008, Relation biomasse-densité et phénomène d'autoréduction chez la moule bleue (*Mytilus edulis*) élevée sur collecteur autogéré. M.Sc., Université Laval.

Lachance-Bernard M., Himmelman J.H., Daigle G., Fréchette M., 2010, Biomass-density relationships and self-thinning of blue mussels (*Mytilus* spp.) reared on self-regulated long lines. Aquaculture 308, 34-43.

Lauzon-Guay J.-S., Barbeau M., Watmough J., Hamilton D.J., 2006, A model for growth and survival of mussels, *Mytilus edulis*, reared in Prince Edward Island, Canada. Mar. Ecol. Prog. Ser. 171-182.

Lauzon-Guay J.-S., Dionne M., Barbeau M., Hamilton D.J., 2005, Effects of seed size and density on growth, tissue-to-shell ratio and survival of cultivated mussels (*Mytilus edulis*) in Prince Edward Island, Canada. Aquaculture 250, 652-665.

Lesser M.P., Shumway S.E., Cucci T., Smith J., 1992, Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates. J. Exp. Mar. Biol. Ecol. 165, 91-102.

Lonsdale W.M., 1990, The self-thinning rule: dead or alive? Ecology 71, 1373-1388.

Mallet A.L., Carver C.E., 1991, An assessment of strategies for growing mussels in suspended culture. J. Shellfish Res. 10, 471-477.

Mazerolle M.J., 2006, Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphibia-Reptilia 27, 169-180.

McGrorty S., Clarke R.T., Reading C.J., Goss-Custard J.D., 1990, Population dynamics of the mussel *Mytilus edulis*: density changes and regulation of the population in the Exe estuary, Devon. Mar. Ecol. Prog. Ser. 67, 157-169.

McGrorty S., Goss-Custard J.D., 1993, Population dynamics of the mussel *Mytilus edulis* along environmental gradients: spatial variations in density-dependent mortalities. J. Anim. Ecol. 62, 415-427.

Moreau V., Tremblay R., Bourget E., 2005, Distribution of *Mytilus edulis* and *M. trossulus* on the Gaspé coast in relation to spatial scale. J. Shellfish Res. 24, 545-551.

Mueller K.W., 1996, A preliminary study of the spatial variation in growth of raft-cultured blue mussels *Mytilus trossulus* in Northern Puget Sound, Washington. J. World Aquac. Soc. 27, 240-246.

Navarro E., Iglesias J.I.P., Pérez Camacho A., Labarta U., Beiras R., 1991, The physiological energetics of mussels (*Mytilus galloprovincialis* Lmk) from different cultivation rafts in the Ria de Arosa (Galicia, N.W. Spain). Aquaculture 94, 197-212.

Newell C.R., Wildish D.J., MacDonald B., 2001, The effect of velocity and seston concentration on the exhalent siphon area, valve gape and filtration rate of the mussel *Mytilus edulis*. J. Exp. Mar. Biol. Ecol. 262, 91-111.

Norberg R.Å. 1988, Self-thinning of plant populations dictated by packing density and individual growth geometry and relationships between animal population density and body mass governed by metabolic rate. In: Ebenman B., Persson L. (Eds.) Size-structured populations. Ecology and Evolution. Springer-Verlag, Berlin, Heidelberg, pp. 259-279.

Petraitis P.S., 1990, Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. Oecologia 83, 405-413.

Petraitis P.S., 1995, The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). Ecology 76, 1337-1346.

Reynolds J.H., Ford E.D., 2005, Improving competition representation in theoretical models of self-thinning: a critical review. J. Ecol. 93, 362-372.

Riisgård H.U., Lassen J., Kittner C., 2006, Valve-gape response times in mussels (*Mytilus edulis*)—Effects of laboratory preceding-feeding conditions and *in situ* tidally induced variation in phytoplankton biomass. J. Shellfish Res. 25, 901-911.

Sénéchal J., Grant J., Archambault M.-C., 2008, Experimental manipulation of suspended culture socks: Growth and behavior of juvenile mussels (*Mytilus* spp.). J. Shellfish Res. 27, 811-826.

Smith A., Nikora V., Ross A., Wake G., 2006, A lattice-Boltzmann-based model of plankton-flow interaction around a mussel cluster. Ecol. Model. 192, 645-657.

Weise A.M., Cromey C.J., Callier M.D., Archambault P., Chamberlain J., McKindsey C.W., 2009, Shellfish-DEPOMOD: Modelling the biodeposition from suspended shellfish aquaculture and assessing benthic effects. Aquaculture 288, 239-253.

Weller D.E., 1987a, A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57, 23-43.

Weller D.E., 1987b, Self-thinning exponent correlated with allometric measures of plant geometry. Ecology 68, 813-821.

Westoby M., 1984, The self-thinning rule. Adv. Ecol. Res. 14, 167-225.

White J., 1981, The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89, 475-500.

Yoda K., Kira T., Ogawa H., Hozumi K., 1963, Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). J. Biol. Osaka City Univ. 14, 107-129.