A Tridimensional Self-Thinning Model for Multilayered Intertidal Mussels

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abstract: Intertidal mussels usually form complex multilayered matrices with density-dependent effects on survival and growth, and self-thinning scaling between biomass (B) and density (N) is expected. This article develops a tridimensional model of space-driven self-thinning that in addition to B-N explicitly includes the degree of packing of the mussels, measured as the number of layers (L). The structure of our model (B-N-L) encompasses previous bidimensional models (B-N) of self-thinning as special cases and enables comparisons between mono- and multilayered populations. We contrast the predictions of the bi- and tridimensional models using data obtained from Perumytilus purpuratus mussel beds on the rocky shores of central Chile monitored during a 28-mo period. The tridimensional model suggests that density dependence is much more frequent than hitherto indicated by bidimensional models. We propose that our space-driven tridimensional model may be applied not only to mussels but also to other species where spatial overlapping configurations occur.

Keywords: self-thinning, mussel, scaling, rocky shore, food driven, space driven, intraspecific competition.

Thinning processes that occur in crowded animal and plant populations play an important role in determining population dynamics and community structure (Westoby 1984; Weller 1987*a*; Marquet et al. 1990, 1995; Bohlin et al. 1994; Fréchette and Lefaivre 1995; Petraitis 1995*a*; Fréchette et al. 1996). As individuals grow at high population density, negative relationships between individuals per area (N) and average individual mass (m) or biomass per area (B) are expected (Westoby 1984). This self-thinning process can be represented by the power equation

$$B = k_2 N^{\beta_2}, \tag{1}$$

or equivalently by $m = k_2 N^{\beta_2 - 1}$, where $B = N \times m$.

Theoretical and experimental evidence of self-thinning has been reported mostly for plants (Fréchette and Lefaivre 1995), where the classical exponent $\beta_2 = -1/2$ has been suggested (Westoby 1984). The usual explanation for selfthinning involves competition for space (space-regulated self-thinning) based on packing theory, which assumes isometric growth where shape does not change with increasing size of the growing individuals (Weller 1987b). The exponent (β_2) may take other values considering different criteria of similarity, such as changes in shape with size (i.e., allometric growth; Weller 1987b) and/or elastic characteristics (Weller 1987b; Norberg 1988a, 1988b). Begon et al. (1986) proposed that the self-thinning process would be best described as reflecting food limitations for mobile animals (food-regulated self-thinning) and suggested $\beta_2 = -1/3$ (see also Norberg 1988*a*; Elliot 1993; Bohlin et al. 1994; Latto 1994; Armstrong 1997; Dunham and Vinyard 1997). Furthermore, Fréchette and Lefaivre (1990) suggested that both space and food regulate selfthinning (see also Dunham and Vinyard 1997).

By analogy with plants, it is expected that space-regulated self-thinning models should also apply to sessile animals such as mussels and barnacles (Hughes and Griffiths 1988). Mussel populations, however, usually form highly dense multilayered beds. For example, Suchanek (1986) reported that the beds of Mytilus californianus were often five or six layers deep; Hosomi (1985) estimated the occurrence of up to four strata in *Mytilus galloprovincialis*; and Alvarado and Castilla (1996) counted up to three layers in Perumytilus purpuratus beds. Multilayering affects the self-thinning in mussel beds (Hosomi 1985; Hughes and Griffiths 1988; Fréchette and Lefaivre 1990; Ardisson and Bourget 1991). Hughes and Griffiths (1988) suggested that multilayered packing changes the relationships between density and the area (or surface) occupied per individual in Choromytilus meridionalis, and Fréchette and Lefaivre (1990) formalized this proposition in a spacedriven self-thinning model that incorporated multilayering

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through the indirect effect of density and surface, but they did not explicitly address multilayering packing.

The mussel *P. purpuratus* is a dominant species that inhabits rocky intertidal hard substrata along the southeastern Pacific coast of South America (Castilla 1981). It forms multilayered matrices (beds) and shows strong intraspecific competition with increased packing (Alvarado and Castilla 1996; Guiñez 1996). Therefore, these populations are expected to show self-thinning.

In this article, we present a tridimensional model that incorporates the number of P. purpuratus layers (L), assuming that the thinning relationships arise from the geometry of space filling (spatial or geometric constraints), with space as the regulating factor (Hughes and Griffiths 1988; Norberg 1988a; Fréchette and Lefaivre 1990). We explore its consequences for the B-N scaling in beds of this mussel and compare the self-thinning exponent following two approaches: the classical bidimensional B-N diagram model proposed for multilayered populations (Fréchette and Lefaivre 1990) and the tridimensional model (B-N-L diagram) developed below. We show that the *B*-*N*-*L* approach explains more variance and that the B-N diagram tends to overestimate the self-thinning exponent when applied to multilayered populations. Departures of empirical estimations from theoretical expectations under space restrictions are discussed.

Tridimensional Model

Basic Assumptions

Population Mean Allometry. We develop a model based on population mean allometry rather than on individual allometry. This distinction is relevant to maintain appropriate dimensions in the models. Consider, for example, that the individual mass (m_i) is allometrically related to the individual length (l_i) by an exponent θ_i and coefficient q_i , such that $m_i = q_i l_i^{\theta_i}$ (the individual allometry), and let θ and q represent exponent and coefficient, respectively, of the population mean mass (m) versus population mean length (l), such that $m = q l^{\theta}$ (the population mean allometry). Mean mass (m) is expressed as

$$m = q_{i} \int_{l_{\min}}^{l_{\max}} l^{\theta_{i}} \phi(l) dl, \qquad (2)$$

where I_{\min} and I_{\max} are minimum and maximum length of individuals within the population, and $\phi(I)$ is the probability density function for the distribution of individual length in a population. Then $\theta_i = \theta$ and $q_i = q$ if all the individuals in a population have the same length; otherwise, they are not necessarily the same (Osawa and Allen 1993).

Multilayered Populations. Bidimensional models, initially developed for plant populations and applied to sessile animals (Hughes and Griffiths 1988; Fréchette and Lefaivre 1990), assume that density (N) is inversely proportional to the average area projected onto the substrate (S), given that organisms occupy the substrate as a monolayer. However, in modeling self-thinning for multilayered populations, this assumption is violated (see appendix). The assumption that $N \propto S^{-1}$ (eq. [A1]) is only correct if the individuals are strictly monolayered and occupy 100% of the substrate. If we define *L* as the number of layers, then L represents the height of the mussel bed. We assume that mussel beds show tight geometrical packing (Hughes and Griffiths 1988) and that there is a critical or maximum volume determined by space competition. In Perumytilus purpuratus, packing geometry consists of a more or less regular pattern of mussels within the matrix (Alvarado and Castilla 1996), usually with the anterior-posterior axes of individuals positioned perpendicular to the substrate (fig. 1). If the mussels in the matrix reach the critical volume determined by space competition, discussed above, we expect that $N \propto LS^{-1}$ (eq. [A7]). This means that density (N) is inversely proportional to the average area projected onto the substrate (S) and directly proportional to the number of layers (L). Observe that when L = 1, the situation for monolayered populations, then equation (A7) equals equation (A1). We use equation (A7) as a formal approach to modeling self-thinning in the multilayered mussel P. purpuratus.

Number of Layers. Two approaches have been used to measure the degree of packing in mussels (Hosomi 1985; Alvarado and Castilla 1996). We follow Hosomi (1985) and estimate the number of layers as a stratum index, in which the total area (*T*) that would be occupied by individuals if they formed a monolayer is divided by the sampling area (A_s): $L = T \times A_s^{-1}$. This definition is similar to the leaf area index used in plant ecology (Hosomi 1985), and as such, the index does not take into account the differential interlayer structure of the bed (e.g., size distribution). The number of layers (*L*) reflects an increase in the layer packing of individuals and enables us to incorporate explicitly the number of layers into the derivation of a model of self-thinning (see appendix), accounting for multilayering with spatial constraints.

Space-Driven Self-Thinning Model

If self-thinning in a mussel bed is determined by the geometry of packing and allometric growth (Hughes and



Figure 1: Representation of the disposition of the mussels in the beds with respect to the substrate. If it is assumed that maximum length (I) is perpendicular to the substrate, then the area projected onto the substrates is estimated by multiplying the maximum width (W) by maximum height (H). The parallelepiped represents the exclusive individual space occupied per mussel, and p is the proportion occupied with mass (appendix).

Griffiths 1988), and assuming that the volume of the space occupied per mussel is a rectangular parallelepiped (fig. 1), then the self-thinning dynamics may be described by the following equation in a tridimensional model (appendix):

$$B = k_3 L^{1-\beta_3} N^{\beta_3}.$$
 (3)

The subscript 3 is used to distinguish the parameters of the tridimensional model from the parameters of bidimensional models with subscript 2 (eq. [1]). Our model is based on the assumptions that mussels are packed with geometrical regularity into the bed and that the relationships among density, average area projected onto substrate, and the number of layers are determined by competitive restrictions according to equation (A7). For the spacedriven model (eqq. [3] and [A13]), the geometrical tridimensional model represents the population mean allometry of growth only through its effects on the exponent β_3 . The constant k_3 changes with the proportion (*p*) of the average volume (*v*) that is filled with biomass, the intercepts of the mean surface-length ratio, and the population mean allometry of surface growth (see appendix). It follows that only changes in mussel mean shape affect the exponent β_3 , while the constant k_3 is affected by both shape and size (Somers 1986).

A log transformation of the bidimensional model (eq. [1]) predicts a linear function according to

$$\log B = \log k_2 + \beta_2 \log N, \tag{4}$$

and a log transformation of the tridimensional model (eq. [3]) predicts a plane according to

$$\log B = \log k_3 + (1 - \beta_3) \log L + \beta_3 \log N.$$
 (5)

Observe that when L = 1 (monolayered population), equation (1) is equal to equation (3) and equation (4) is equal to equation (5), showing that the bidimensional model is a special case of the tridimensional one. Another relationship can be demonstrated between both models using the log version of the tridimensional model (eq. [5]) expressed as $\log B = \log k + \gamma \log L + \lambda \log N$, where $\lambda = \beta_3$ and $\gamma = 1 - \beta_3$. Suppose that the tridimensional model can be represented in a bidimensional B-N diagram as $\log B = \log k_o + \tau \log N$, then the expectation of τ is $E(\tau) = \lambda + \gamma \times b_{L-N}$, where b_{L-N} is the slope of the linear regression of log L on log N (Snedecor and Cochran 1980), representing the changes in number of layers per individual in the population. Therefore, the expected adjusted equation for the bidimensional model derived from the tridimensional one is $\log B = \log k_0 + (\lambda + \gamma \times$ b_{L-N} log N, and because $\lambda = \beta_3$ and $\gamma = 1 - \beta_3$, the expectation of τ becomes

$$E(\tau) = \beta_3 (1 - b_{L-N}) + b_{L-N} = \beta_2.$$
 (6)

This means that for nonzero values of b_{L-N} , the expected β_2 exponent derived from a two-dimensional *B*-*N* diagram applied to a multilayered population will be a biased estimate of the value that would be obtained from a *B*-*N*-*L* diagram. According to equation (6), with multilayering β_2 will be always greater than β_3 , at least for $\beta_3 < 1$ and $0 < b_{L-N} < 1$.

Material and Methods

From May 1992 to September 1994 we monitored mussel beds of *Perumytilus purpuratus* located on rocky platforms from the middle-upper intertidal fringe (Castilla 1981) at three sites at Punta de Tralca, Chile (33°26'S, 71°43'W). The three sites were along a gradient of wave exposure, ranging from 3.0 to 5.7 m/s of maximum wave velocity (Guiñez 1996). At each site, three mussel matrices were randomly selected. The matrices were numbered M1–M3 at the exposed site, M4–M6 at the semiexposed site, and M7–M9 at the sheltered site. Two of the nine matrices initially selected for this study went extinct during the period of sampling. One went extinct after the first sampling (May 1992) and was replaced by another matrix (M1) in September 1992, and the other (M4) went extinct before February 1994 and was not replaced.

Two mussel samples per matrix were taken in May 1992. September 1992, February 1993, February 1994, and September 1994. Each sample was taken by removing all the individuals from an area of 10×10 cm, chosen where the rock surface was homogeneous and without crevices. Before sampling, the outer mussel layer was painted so that we would be able to recognize the individuals belonging to the first layer (Alvarado and Castilla 1996). Samples were frozen at -20° C until processed, and no attempt was made to measure the physiological status of the individuals. Dead mussels recognized by empty shells were present in low percentages in the samples and were discarded from analyses. Individuals <1.5 mm were assumed to be recruits and were discarded from the analyses because observational and experimental data suggested they do not experience the effects of intraspecific competition (Alvarado and Castilla 1996; Guiñez 1996). All the collected mussels were counted, and those >1.5 mm were measured by recording the total length using a digital caliper (± 0.005 mm). Total dry weight (± 0.05 mg) for each sample was estimated after drying at 70°C for 24 h. Density (N) and biomass (B) per sample were expressed as the number of individuals and the total dry weight (g) per unit area (m²) for individuals >1.5 mm. Additional samples of P. pur*puratus* were taken in February (n = 12) and September 1994 (n = 12) at the same three sites at Punta de Tralca for estimating individual and population allometries.

Analyses of regression (model 1), covariance (ANCOVA), and variance (ANOVA) were run using PROC GLM and PROC REG (SAS Institute 1988); PROC NLIN was used for nonlinear regressions by maximum likelihood least square methods. For functional regressions (model 2), we used reduced major axis (RMA) regression, following LaBarbera (1989). For comparison of model 2 regressions, we used a *T*-test (after Clarke 1980) or the 95% confidence intervals (CIs) of slopes. For individual or population mean allometric relationships, variables were logarithmically transformed before application of the regression analyses, with correction for log transformation (LaBarbera 1989). Model 2 and nonlinear regressions were applied when estimation of scaling exponents and constants were needed, and model 1 was used when the goal

was to describe the data set or to enable prediction of expected values, as suggested by LaBarbera (1989).

The projected area to the substrate was determined from length measures using regression equations of individual area on length obtained from a subsample of the additional 1994 data. It was assumed that density does not affect the individual area/length allometry. Total area occupied (*T*) by a sample was estimated as the sum of the individual area of all mussels collected >1.5 mm. Finally, the number of layers (*L*) of each sample was determined by dividing *T* by the sampling area ($A_s = 100 \text{ cm}^2$). Hence, the number of layers may be interpreted as the expected number of layers if all the mussels followed a perfect geometric arrangement, as illustrated in figure 1.

Density (N), biomass per unit of area (B), and the number of layers (L) were used to assess observed self-thinning relationships, considering that they were parent (random) variables rather than derived variables (Scrosati 1996). Spurious correlation arises when a derived ratio (derived from two random variables) is plotted against its own denominator as a common term, as could be the case if we were using mean mass (biomass divided by density) instead of biomass per area, or the number of layers estimated as the mean area projected to the substrate multiplied by density instead of summing the areas for all the individuals (for discussion, see Scrosati 1996 and Petraitis 1995*b*).

The proposition that for multilayered populations a plane in a log *B*-*N*-*L* diagram (eq. [5]) is a better representation of the scaling than a line in a *B*-*N* diagram (eq. [4]) was tested applying linear regressions to the log transformation of *B*, *N*, and *L*, using log *B* as the dependent variable in both equations. Two validation criteria were used to select the best model: the adjusted determination coefficient (R^2) and the value of *F* (Sokal and Rohlf 1989). The space-driven tridimensional model (eq. [3]) predicts that the parameter β_3 determines the exponent of both *L* and *N*, being $1 - \beta_3$ and β_3 , respectively. This cannot be accomplished with the linear regression used above but requires a nonlinear regression protocol. So, we use equation (3) as the model in the nonlinear regression for fitting the data and to determine the value of β_3 .

The expected (β_2 and β_3) theoretical exponents were obtained from population allometries using data from the separate samples obtained in February and September 1994 and applying RMA regression. The β_2 exponent for the bidimensional model according to space constraints and growth allometry models was estimated following equation (A3), where the allometric index (α) was obtained from the mean mass on mean length regression and the allometric effect of multilayering (ε) from the mean size-density relationships. For the tridimensional model, the expected β_3 exponent was obtained following equation (A14) but using the following relationship:

$$m = c_z \times (c_y \times p)^{z/y} \times S^{z/y}, \qquad (7)$$

derived from equations (A5) and (A6), given that m = pv (appendix). The exponent z/y was obtained from RMA regression applied on log transformation of m and S, and β_3 was estimated as 1 - z/y. The observed exponents (β_2 and β_3) and the expected values according to the bi- and tridimensional models were compared to test whether the observed exponents agreed with the predictions of the space-driven models.

Results

A total of 17,287 *Perumytilus purpuratus* individuals were sampled, of which 57.2% were larvae, postlarvae, or juveniles <1.5 mm. The frequency distribution of mussel maximum length for the five collection dates had two modes: one corresponding to juveniles under 1.5 mm and the other to adults from 21.5 to 27.5 mm, confirming previous results (Alvarado and Castilla 1996).

The slopes of the fitted regression of (log) individual projected area (S_i) on (log) individual length (I_i) between dates (February 1994 vs. September 1994) within sites were not significantly different (P > .21) and not affected by density (F = 0.09, df = 1, 23, P = .77). The predictive regression equations fitted for the relationship S_i versus l_i , when dates were pooled within sites, were $S_i = 0.350 \times$ $l_{i}^{1.972}$ ($R^{2} = 0.990$, P < .001, n = 334) for the exposed site, $S_i = 0.298 \times I_i^{2.015}$ ($R^2 = 0.989$, P < .001, n = 276) for the semiexposed site, $S_i = 0.301 \times I_i^{2.012}$ ($R^2 = 0.990$, P < .001, n = 308) for the protected site, and $S_i = 0.318 \times I_i^{1.997}$ $(R^2 = 0.995, P < .001, n = 918)$ for the pooled data. The slopes among sites were significantly different (ANCOVA, F = 4.23, df = 2, 912, P = .015). Slopes of the sheltered and semiexposed sites were not statistically different (t =0.05, P = .96), but these two were significantly steeper than that at the exposed site (P < .001). The frequency distribution of the estimated number of layers (L) for all samples had a mean of 1.4 and ranged from 0.6 to 2.2, with a normal distribution (P = .48, Kolmogorov-Smirnov test). Only four samples out of 84 had an estimated number of layers <1, which implies that if they adopted the assumed geometrical arrangement, the mussels could not have covered all the area sampled. Biomass, density, and the number of layers showed statistically significant temporal changes, but there were no significant variations associated with sites and their interaction with dates (table 1; fig. 2). The maximum ranges of variables expressed as pWR, the log of the ratio of maximum to minimum values

 Table 1: Three-way ANOVA: sites, matrix, and date of sampling on biomass, density, and number of layers

1 0 5		5		
Source of variation	df	Sum of squares	F	Р
Biomass:				
Site	2	.00032	.03	.973
Matrix within site	6	.03488	.75	.615
Date	4	.14576	4.68	.003
Interaction date × site	8	.04494	.72	.671
Error	42	.32690		
Density:				
Site	2	.23053	2.24	.187
Matrix within site	6	.30822	6.91	<.001
Date	4	.56731	19.07	<.001
Interaction date × site	8	.07329	1.23	.305
Error	42	.31241		
Number of layers:				
Site	2	.03523	2.06	.209
Matrix within site	6	.05137	1.47	.210
Date	4	.16239	6.99	<.001
Interaction date \times site	8	.05305	1.14	.356
Error	42	.24381		

Note: Sites and dates were considered fixed factors, and matrix was considered a random factor nested within sites. The error term for sites was the effect of matrix within site.

(LaBarbera 1989), were 0.57 for density, 0.32 for biomass, and 0.31 for the number of layers.

Comparisons of Self-Thinning Models Predictions

B-N versus B-N-L Representations. Figure 3 shows the data and the adjusted regressions for the bi- and tridimensional model representations (*A* and *B*, respectively). The adjusted determination coefficients between the bi- and tridimensional models were significantly different ($F_s =$ 162.9, P < .001). The tridimensional model (fig. 3*B*) explains more variance with correspondingly larger *F* values (F = 140.5) than the bidimensional model (F = 24.9; fig. 3*A*), using either all the data pooled or the samples averaged by mussel bed and date. The residuals of the tridimensional model were normally distributed (fig. 3*C*), and they do not show heterogeneity of variance.

Table 2 (columns in pt. A) shows the slopes obtained from adjusted regressions for the bidimensional model (B-N diagram) of the nine matrices, pooled data, and sites, wherein the number of layers (L) was not considered. All the slopes for each matrix, pooled data, and sites were positives except for matrix M4, whose lower confidence interval was negative. The average slope across the nine matrices (average slope = 0.72, SE = 0.07) was not significantly different from the value obtained from pooled data (P > .5).

The regressions for the nine matrices using the B-N-L



Figure 2: Means (+1 SE) of the log of mussel biomass (log *B*), density (log *N*), and number of layers (log *L*) among the three sites and five dates of sampling at Punta de Tralca. The sites were located in a gradient of wave exposure: E = exposed, SE = semiexposed, and S = sheltered.



Figure 3: Comparison of the graphical representation of the data between (*A*) the bidimensional model and (*B*, *C*) the tridimensional model. *A*, Graph of log *B* on log *N* for the data with replicated samples averaged. The continuous line represents the adjusted regression (model 2), but the statistics (R^e and *P*) are from model 1. *B*, Tridimensional graph (log-log) representing the self-thinning relationships among mussel biomass (log *B*), density (log *N*), and number of layers (log *L*) for the data with replicated samples averages. The plane represents the linear regression adjusted (model 1). *C*, Residuals versus number of layers (log *L*) for the adjusted regression from the tridimensional model. The residuals were normally distributed (P > .5, Kolmogorov-Smirnov test).

	A. $B = k_2 N^{\beta_2}$			B. $B = kN^{C}L^{D}$			C. $B = k_3 N^{\beta_3} L^{1-\beta_3}$		
Matrix	n	β_2	[95% CI]	R^2	С	D	R^2	eta_3	[95% CI]
M1	10	.66	[.16, 1.17]	.14	26	1.36	1.00	26	[36,16]
M2	10	.76	[.22, 1.30]	.14	08	1.18	.91	09	[31, .13]
M3	10	1.25	[.70, 1.80]	.71	06	1.11	.99	11	[29, .08]
M4	6	.71	[02, 1.43]	.46	12	1.18	.94	08	[44, .22]
M5	10	.69	[.33, 1.06]	.59	02	.99	.98	03	[14, .09]
M6	10	.70	[.31, 1.09]	.94	08	1.11	.86	.03	[31, .36]
M7	10	.61	[.27, .95]	.53	13	1.14	.93	10	[29, .10]
M8	10	.46	[.08, .84]	.00	18	1.17	.98	18	[25,12]
M9	8	.61	[.23, .98]	.62	01	1.05	.96	.01	[16, .19]
Site:									
Exposed	30	.87	[.58, 1.17]	.34	16	1.21	.97	17	[26,09]
Semiexposed	26	.66	[.46, .85]	.52	09	1.08	.92	07	[19, .05]
Sheltered	28	.50	[.34, .66]	.41	15	1.14	.94	15	[21,08]
Pooled data	84	.62	[.50, .73]	.35	18	1.17	.92	16	[21,11]

 Table 2: Summary of observed exponents for each mussel matrix, pooled data for sites, and all data pooled (95% confidence limits in brackets) fitted by regression for bi- and tridimensional models

Note: A: Bidimensional model fitted by functional regression. B: Tridimensional model fitted by linear regression on log transformed data. C: Tridimensional model fitted by nonlinear regression.

representation (table 2, columns in pts. B and C) were all statistically significant (P < .02), β_3 ranged from +0.03 to -0.26, with a mean across matrices of -0.09 (SE = 0.03), not significantly different from the slope obtained from pooled data (P > .1). The explained variance ranged from 86% to 100%. In addition, the *B*-*N*-*L* representation showed no statistical differences in the slopes of log *N* and log *L* among sites with different wave exposure (table 2, columns in pt. B; table 3). Nevertheless, when we corrected for differences in log *N* and log *L*, using multiple ANCOVA, the exposed site showed the smaller adjusted biomass (table 3).

Nonlinear Regression Fits. The regressions fitted for the tridimensional model using nonlinear methods were $B = 2,192.8 \times L^{1.088}N^{-0.088}$ for the samples averaged by bed and date ($\beta_3 = -0.088$), and $B = 2,192.8 \times L^{1.160}N^{-0.160}$ when all samples were included ($\beta_3 = -0.16$; table 2, columns in pt. C). Table 2 (columns in pt. C) includes the β_3 values fitted for all the matrices and the three sites. The comparisons of the intercepts and exponents from these regressions and those estimated through linear regression (table 2, columns in pt. B; fig. 3*B*), showed no statistical differences (P > .1).

Biased Estimations. Comparisons of the fitted observed β_2 exponents (using model 1 linear regression) and the expected values $E(\tau)$ from equation (6) were accomplished to test the prediction that β_2 is a biased estimator of β_3 . The b_{L-N} regression coefficient was estimated for each of the nine mussel beds studied; values ranged from 0.1 to >1.0 (fig. 4*A*). The higher the regression coefficient, the

larger was the overestimation. Figure 4*B* shows that equation (6) can be used to predict the observed β_2 exponent (*B*-*N* diagram) from the β_3 exponent (*B*-*N*-*L* diagram).

Mean Mussel Allometries. All the allometric estimations that follow were obtained from the separate 1994 data samples, where dates (February and September) were pooled within sites because we did not find significant differences (P > .5) in the exponents between both dates within sites for all the comparisons. The estimated values of the allometric exponents by RMA of $\log m$ on $\log l$ (fig. 5A) were 2.31 with 95% CI (1.89, 2.72; $R^2 = 0.84$) for the pooled data; 2.74 with 95% CI (0.24, 5.25; $R^2 =$ 0.17) for the exposed site; 2.53 with 95% CI (1.46, 3.59; $R^2 = 0.82$) for the semiexposed site; and 1.95 with 95% CI (1.50, 2.40; $R^2 = 0.95$) for the sheltered site. There were not significant differences between sites, as shown by the overlap of the confidence intervals of the allometric exponents. The allometric index (α) for the pooled data was 0.23, and it increases as the exposure of the sites decreases: 0.09, 0.16, and 0.35, for the exposed, semiexposed, and sheltered sites, respectively.

The estimated values of the allometric exponents by RMA of log *N* on log *l* (fig. 5*B*) were: -2.51 with 95% CI (-3.74, -1.28; $R^2 = 0.23$) for the pooled data; -3.88 with 95% CI (-8.34, 0.59; $R^2 = 0.10$) for the exposed site; 1.88 with 95% CI (0.02, 3.73; $R^2 = 0.31$) for the semiexposed site; and -1.70 with 95% CI (-3.24, -0.16; $R^2 = 0.18$) for the sheltered site. The exponents between the exposed and the sheltered sites are negatives and do not differ significantly, but both differ significantly with the positive value estimated for the semiexposed site. The al-

Source of variation	df	Sum of squares	F	Р
Model	8	.7081	175.01	<.001
Error	75	.0379		
Corrected total	83	.7461		
Equality of slopes:				
C	2	.0006	.56	.573
D	2	.0009	.91	.405
ANCOVA:				
Sites	2	.0193	19.56	.001
Error	79	.0391		
	Exposed	Semiexposed	Sheltered	
Adjusted mean log biomass	4.1021	4.1387	4.1308	

 Table 3: Test for equality of slopes and ANCOVA of the biomass at three sites

 with different wave exposure

Note: (Site = exposed, semiexposed, and sheltered). The covariates are log *N* and log *L*, to control for differences in log biomass at different densities and number of layers. Italicized values are adjusted means that are not significantly different (Tukey-HSD, P > .05). (*C* and *D* as in the regression equation: $\log B = \log K + C \log N + D \log L$).

lometric effect of multilayering (ε) was -0.26 for the pooled data and ranged from -0.94 to 1.94 to 0.15 for the exposed, semiexposed, and the sheltered site, respectively.

The estimated values of the allometric exponents by RMA of log *m* on log *S* (eq. [7]; fig. 5*C*) were 1.30 with 95% CI (1.14, 1.46; $R^2 = 0.92$) for the pooled data; 1.52 with 95% CI (0.46, 2.58; $R^2 = 0.52$) for the exposed site; 1.30 with 95% CI (0.93, 1.68; $R^2 = 0.92$) for the semiexposed site; and 1.19 with 95% CI (1.05, 1.32; $R^2 = 0.99$) for the sheltered site. The confidence intervals overlap between the sites, showing that the exponents are not significantly different between sites.

Space-Driven Self-Thinning Model

Bidimensional Model. The theoretical expectation of the β_2 self-thinning exponent according to the bidimensional model was estimated from the exponents of the *m* versus *I* and the *N* versus *I* relationships, dividing the first by the second, which gave values of 0.08 for the pooled data and 0.29, 2.35, and -0.15 for the exposed, semiexposed, and sheltered sites, respectively. For pooled data and all sites, the differences between expected and observed values were significant (table 2, columns in pt. A). With the exceptions of two matrices (M1 and M2), the exponents of the matrices were significantly different from the expected values.

Tridimensional Model. The theoretical expectation of the β_3 self-thinning exponents obtained as 1 – the slope from the regression of log *m* on log *S* (eq. [7]; fig. 5*C*) gave values of -0.30 for the pooled data and -52, -30, and

-19 for the exposed, semiexposed, and sheltered sites, respectively. Only the observed value for the sheltered site overlapped with the confidence interval of the expected value for that site. The observed values for the other sites and for the pooled data were greater than the corresponding expected values. The confidence intervals of the observed values for four matrices (M4, M6, M7, and M8) overlapped with the expected value for their corresponding site, and the others differed from the expected values.

Discussion

B-N and B-N-L Representations

Variance Explained. When comparing the data fitted with the B-N and B-N-L models, we showed that more of the variation, 86%–99%, of log *B* can be explained with the tridimensional B-N-L model. The small variance explained by the bidimensional model could be attributed to the lack of resolution of our empirical measurements of density and biomass, which at most cover half an order of magnitude measured by the pWR statistic. In this case, it is expected that there would be a high probability that the scaling exponents and coefficients could be distorted by sampling error (LaBarbera 1989). But this consideration also would be valid for the tridimensional model, where the problem was not seen. However, in the tridimensional model the increase in the variance explained could also be due to statistical artifacts produced by the nonindependence of the variables. Lack of independence could result from violation of the assumption that density does not affect the individual allometry when estimating L from the area/length allometry; nevertheless, density did not



Figure 4: *Perumytilus purpuratus* observed and predicted values for β_2 . *A*, Using a *B*-*N* diagram, β_2 overestimates the values of β_3 ; thus, the larger the regression coefficient (b_{L-N}) of log *L* on log *N*, the larger the overestimation. The line represents the adjusted regression (model 1). *B*, Relationship between the expected value of β_2 according to equation (6) and the observed β_2 in a *B*-*N* diagram. The slope is not different from 1 (*P* = .155), indicating that the observed β_2 exponent in a *B*-*N* diagram can be predicted from the β_3 estimation obtained from the *B*-*N*-*L* regression.

significantly affect allometry (F = 0.09, df = 1, 23, P = .77). Spurious correlations might also be produced if L were estimated as the mean area projected to the substrate (*S*) multiplied by density, but this is not the case (see "Material and Methods").

Although there have been several studies of layering effects and their consequences for the population dynamics of mussels (Hosomi 1985, 1987; Hughes and Griffiths 1988; Fréchette and Lefaivre 1990; Alvarado and Castilla 1996; Guiñez 1996), we are not aware of approaches in bivalves aiming to separate the effect of both density and layering. For example, consider two experimental treatments with equal density and all other conditions equal, but in one case the mussels are configured in one layer while in the other they are in two or more layers. If differences (e.g., growth rate or mortality) between both treatments were observed, the results might be explained by the layering but not by the density effects. Differences of mussel size structure or other traits between layers might suggest evidences for layering effects. To test this, we reanalyzed our data of maximum mussel length at Punta de Tralca and found significant differences between layers (F = 167.1, df = 1, 6, P < .001, using the interaction termlayer × matrix within sites as the error term). The mussels from the upper layer were larger (mean length = 19.44mm, SD = 8.86) than those from the lower layer (mean length = 13.55 mm, SD = 8.10). This result supports the findings of Hosomi (1987) and Alvarado and Castilla (1996) regarding the existence of different mussel size structure between layers. In addition, Hosomi (1987) suggested growth rate differences between mussel layers. The evidence suggests that an increase in the number of layers



Figure 5: Allometric relationships for the separate mussel samples from 1994, with fitted functional regression lines when the slopes for the different sites (exposed, semiexposed, and sheltered) were not statistically significant (P > .05). *A*, Between mean mass (log *m*) and mean maximum length (log *h*). *B*, Between density (log *N*) and mean maximum length (log *h*). *C*, Between mean mass (log *m*) and mean area projected to the substrate (log *S*).

in mussel beds means not only an increase in substrate heterogeneity (as the mussels are substrate for others, including recruits) but also an increase in the level of intraspecific competition, whether by physical interference and/or food limitation. The degree of the competitive effects are likely differential according to the position of the individuals within the matrix; the mussels in the lower strata will be more affected than those at the upper layer. But an increase in the layering will also be associated with an increase in the average effects of the competition on all the mussels. So it is not unexpected that multilayered packing (measured as the number of layers) can improve the fit in B-N relationships in mussels.

Our theoretical effort has been oriented to explore the possible differential consequences for the mussel population dynamics of both density and layering. The tridimensional model permits us to separate both components, the former representing the effects of changes in mussel number on the biomass and the latter the packing configuration. For example, in our data we can evaluate the relative importance of density and layering on biomass through the properties of the model 1 regression with Type III partial sum of squares (SS3) (PROC GLM-SAS), using as the statistical model the log version of the tridimensional model (eq. [5]). The SS3 quantifies the percentage of variance explained by each variable not involving parameters of other effects because it holds the effects of the other variables constant and the sequence by which variables are analyzed does not affect the partial sums of squares. Consequently, the resulting sums of squares reflect the relative correlation of density and number of layers with biomass. Layering explained 50% (P < .001) and density only 3% (P < .005) of the variance in biomass. This suggests that the dynamics of *Perumytilus purpuratus* matrices may be driven by overcrowding effects and layering effects rather than by density per se. We conclude that in mussel matrices showing multilayering packing, the inclusion of the number of layers improves significantly the fit in relationships between biomass and population density.

Biases. It was shown, theoretically and empirically, that the self-thinning exponent (β_2) obtained from a *B*-*N* diagram overestimates the value for the self-thinning exponent (β_3) of the B-N-L diagram. So, when inferences are obtained from multilayered populations using the bidimensional approach, the self-thinning exponent is overestimated. This suggests caution when inference is used as a criterion to provide evidence regarding the nature of the limiting factor. For example, in our case almost all the values of the exponents are positive, which does not suggest selfthinning scaling at all. This could be used to conclude that there is no evidence for density dependence. Nevertheless, we propose that for species showing multilayering packing the occurrence of density dependence is likely to be much more frequent than reported. Accordingly, because of this bias it would not be unexpected that the theoretical thinning exponent (β_2) was statistically different from empirical exponents obtained from *P. purpuratus*.

We suggest that the B-N-L approach developed here enables comparisons among mussel populations not only of β_3 exponents but also of density and the added effect of the degree of packing both intra- and interspecifically. Consequently, when interpreting *B*-*N* scaling or self-thinning, we recommend consideration of the degree of packing in addition to density. The B-N-L approach may be used in other animal taxa where overlapping spatial configuration (i.e., home range) is present, such as in salmonids (Mason and Chapman 1965; Puckett and Dill 1985; Grant and Kramer 1990; Grant 1993), herbivorous mammals (Damuth 1981), and Hemiptera (Latto 1994, as suggested by Fréchette and Lefaivre [1995]). In salmonids with overlapping territories, the percent habitat saturation (Grant and Kramer 1990) may be considered as an equivalent to the number of layers (L) in mussels.

Assumptions

As model expectations disagree with some empirical relationships, it is possible that there may be a violation of key assumptions related to (1) inappropriate use of population parameters or (2) invasion of exclusive space by neighbors. We address these points.

1. Population Parameters. First, we have consistently used population means as one of the principal assumptions for

the theoretical and empirical approach. This is not only to maintain appropriate dimensions of variables but also because the individual allometries and the population mean allometries are not necessarily the same (see eq. [2]). This implies that individual allometries could not be used to test the self-thinning theory (Osawa and Allen 1993). Second, population mean allometries must be obtained using independent data from those used for the empirical data of self-thinning relationships (but see Weller 1987b; Osawa and Allen 1993). In our study, the allometries of population parameters were obtained from separate samples at the same sites of study but coetaneous with only two dates (February and September 1994). Population changes observed between 1992 and 1994 (fig. 2), where variations occurred with biomass, density, and number of layers, may explain the differences between observed and expected values.

2. Invasion of Exclusive Space. The significantly smaller adjusted biomass observed (i.e., k_3 , the *B*-intercept at the exposed site; table 3) could be explained by changes in the degree of overlap as a consequence of the invasion of the exclusive space by neighbors, which could be associated with site characteristics (e.g., wave exposure). Also, it is possible that beds may be near to the saturation packing level (i.e., the maximum biomass per layer; eq. [A16]) since the results indicated that the observed β_3 values for some matrices are near 0 (table 2, columns in pt. C). The extent of multilayer packing could be determined by the degree of overlap between neighboring individuals that the mussels can tolerate, probably a species-specific characteristic. For example, Choromytilus meridionalis is usually monolayered, whereas Aulacomya ater, Mytilus galloprovincialis, Mytilus californianus, and P. purpuratus form dense, multilayered beds (Hosomi 1985; Suchanek 1986; Van Erkom Schurink and Griffiths 1993; Alvarado and Castilla 1996; Guiñez 1996). Also, it has been observed that multilavering varies among different sites and populations in P. purpuratus and in M. californianus (Alvarado and Castilla 1996; Guiñez 1996; Connolly and Roughgarden 1998).

Geometrical Constraints

Our tridimensional model was developed under the assumption that space drives the competition in multilayered populations because it is expected that mechanical interference among individuals within the matrix will increase as the crowding increases (Bertness and Grosholz 1985; Fréchette and Lefaivre 1990). We have observed that, in *P. purpuratus*, increases in the number of layers are associated with an increase in the exponent of the dry tissue weight/length allometry equation (Guiñez 1996, and unpublished results); this is expected in the case of interference-driven competition affecting the growth rate asymmetrically with respect to the size of the individuals (Fréchette et al. 1992). However, in our data only the observed exponent (β_3) at the sheltered site agrees with the theoretical expectations, and when all matrices are considered, only four of nine agree with the expectations (see above). Therefore, the tridimensional allometric model at most can explain the empirical relationships at local scales. The lack of generality of the allometric model may be

The lack of generality of the allometric model may be related to the existence of other competition-driven forces such as consumption or trophic regulation, but how physiological constraints affect the *B-N-L* self-thinning relationships for multilayered populations remains a problem to be solved. Alternatively, it is possible that physical and biological perturbations may be affecting our study system. In fact, in our sampling design we used natural beds located in a gradient of wave velocity and did not attempt to exclude predators, such as crabs, muricid gastropods, or sea stars (Castilla and Durán 1985; Paine et al. 1985; Navarrete and Castilla 1988; Castilla et al. 1989, 1994). Therefore, we may not offer any assurance that competition is the only cause of mortality.

Thinning may be dictated by a compromise between perturbation (biological and physical) and competition. With monolayered populations, biological and physical perturbations can generate open patches that increase mortality and relax intraspecific competition. But with multilayered populations, only intense and persistent perturbations could open up patches (Paine and Levin 1981; Castilla and Durán 1985; Guiñez 1996). These effects may explain the extinction of two of our matrices. But under less intense and/or persistent perturbations, the mussel biomass, density, and the number of layers could be affected without losses in ground-projected cover. Intraspecific competition could eventually be relaxed, allowing for the arrival of recruits, and thus their faster growth could ameliorate the effects of predation or physical disturbance on the bed and bring it back to the previous level of intraspecific competition (see Petraitis 1995a for a similar proposition in monolayer populations). The simultaneous decreases and increases of both density and biomass in our matrices (fig. 2) may represent the effect of mortality, recruitment, and growth resulting from the compromise between disturbance and intraspecific competition. This could explain the fact that the mussel matrices are maintained in a plane according to a self-thinning tridimensional diagram and ensuing expectations. More theoretical and experimental work is needed to improve our understanding of population regulation in multilayered species.

Conclusions

Our tridimensional self-thinning model is a general one that incorporates previous bidimensional models devel-

oped for sessile organisms as special cases (Hughes and Griffiths 1988; Fréchette and Lefaivre 1990, 1995). The tridimensional space-driven self-thinning model developed may be further improved by incorporating competitive constraints, such as consumption or food. The model may be used to compare scaling processes both intra- and interspecifically and for different crowding and packing strategies, whether the target population is monolayered or multilayered. The B-N-L approach may be used in other animal taxa where tridimensional spatial configuration is found. Self-thinning models, including those of Hughes and Griffiths (1988), Fréchette and Lefaivre (1990, 1995), Fréchette et al. (1992), and the one discussed in this article. are the first steps leading to the development of a theory of space occupation as a function of size for multilayered organisms.

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APPENDIX

Derivation of the Space-Driven Self-Thinning Models with Allometric Growth and Geometrical Constraints

Bidimensional Model

Models of geometrical similarity have been developed for individuals arranged on a surface in a monolayer with 100% cover of the substrate. In this condition it is expected that the density (N) should be inversely proportional to the average area occupied by individuals or average surface area projected to the substrate (S), implying that

$$N \propto S^{-1}$$
. (A1)

If individuals grow isometrically (sensu Weller 1987*b*), and mean mass (*m*) and *S* are proportional to the cube and the square of a linear dimension (*I*), respectively, then it follows that $m = k_2 N^{-3/2}$. Furthermore, since the total biomass *B* per area is equal to $N \times m$, this leads to B =

Variable	Definition	Dimensions
1	Mean (maximum) length	Length/individual
Η	Mean (maximum) height	Length/individual
W	Mean (maximum) width	Length/individual
S	Mean area projected to the substrate	Area
$A_{\rm s}$	Sampling area	Area
Т	Total area projected to the substrate occupied by the <i>n</i> individuals in a sample $(T = \sum_{i=1}^{n} S_i)$	Area
L	Number of layers or T/A_s	
N	Density (individuals per unit area)	Individuals/area
m	Mean mass	Mass/individual
В	Biomass per unit area = $N \times m$	Mass/area
V	Mean spatial volume	Volume/individual
р	Proportion of mean mussel spatial volume occu- pied with biomass	
h	Exponent for height/length relationships	
C_h	Coefficient for height/length relationships	Length/[individuals \times (length \times individuals ⁻¹) ^h]
W	Exponent for width/length relationships	
C_w	Coefficient for width/length relationships	Length/[individuals \times (length \times individuals ⁻¹) ^w]
у	Exponent for surface/length relationships	
c_y	Coefficient for surface/length relationships	Area/[individuals × (length × individuals ^{-1}) ^y]
Ζ	Exponent for spatial volume/length relationships	
C_z	Coefficient for spatial volume/length relationships	Volume/[individuals × (length × individuals ^{-1}) ^{z}]
β_2	Self-thinning exponent for a <i>B</i> - <i>N</i> diagram	
k_2	Self-thinning coefficient for a <i>B</i> - <i>N</i> diagram	Mass/[area × (individuals × area ⁻¹) ^{β_2}]
β_3	Self-thinning exponent for a <i>B</i> - <i>N</i> - <i>L</i> diagram	
k_3	Self-thinning coefficient for a <i>B</i> - <i>N</i> - <i>L</i>	Mass/[area × (individuals × area ⁻¹) β_3]
α	Allometric index for weight/length relationships such as $z = 3(1 - \alpha)$ ($\alpha = 0$ for isometric growth)	
ω	Allometric index for surface/length relationships such as $y = 2(1 - \omega)$ ($\omega = 0$ for isometric growth).	
ε	Allometric effect of multilayering on density/ length relationships ($\varepsilon = 0$ for monolayering; $\varepsilon > 0$ for multilayering)	
k_1	Coefficient for the density/length relationships	$(Individuals/area)^{-1} \times (length/individual)^{-2(1-\varepsilon)}$
k '' ₃	Maximum biomass per layer	Mass/area

 $N \times m = k_2 N^{1-3/2} = k_2 N^{-1/2}$. However, because growth is generally allometric (sensu Weller 1987*b*), the population length-mass relationship may be rewritten as $m = k_2 l^{3(1-\alpha)}$; here $\alpha \neq 0$ is used as an index for measuring the deviation from isometry due to allometric effect, and k_2 is a constant (Fréchette and Lefaivre 1995). This equation may be also expressed as: $l = k_2 m^{1/[3(1-\alpha)]}$; and, because $N^{-1} \propto S \propto l^2$, this leads to $m = k_2 N^{-[3(1-\alpha)]/2}$ or, expressed in the *B*-*N* diagram representation,

$$B = k_2 N^{1 - [3(1 - \alpha)/2]}.$$
 (A2)

Then the self-thinning exponent is $\beta_2 = 1 - 3(1 - \alpha)/2$.

This implies that allometric growth may produce different β_2 exponents in relation to those expected under isometry ($\alpha = 0$).

Hughes and Griffiths (1988) suggested that multilayer packing in mussels resulted in density increases with respect to average surface area at a faster rate than expected under allometric growth. The suggestion was formalized by Fréchette and Lefaivre (1990) as $N^{-1} \propto S^{(1-\varepsilon)} \propto (l^2)^{(1-\varepsilon)} = k_1 l^{2(1-\varepsilon)}$, with $0 \le \varepsilon \le 1$, where the parameter ε would take values proportional to the multilayered packing.

Then, according to the reasoning used for growth allometry (eq. [A2]) and further incorporating the effect of multilayered packing (Fréchette and Lefaivre 1990, 1995), the following scaling relationship is obtained: $m = k_2 N^{3(1-\alpha)/2(1-e)}$ or, in terms of the *B*-*N* representation,

$$B = k_2 N^{1 - \frac{3(1 - \alpha)}{2(1 - \varepsilon)}},$$
 (A3)

implying that in this case the self-thinning exponent is

$$\beta_2 = 1 - \frac{3(1-\alpha)}{2(1-\varepsilon)}.$$
 (A4)

For simplicity, we do not consider the effect of substrate roughness here, as incorporated by Fréchette and Lefaivre (1990).

Tridimensional Model

We assume the mean spatial volume of mussels could be described as a rectangular parallelepiped, assuming an arrangement as in figure 1. The mean width (*W*) and height (*H*) are related to mean (maximum) length (*I*), as $W = c_w l^w$ and $H = c_h l^h$. The average area projected to the substrate (*S*) is

$$S = WH = c_w c_h l^w l^h = c_v l^y, \tag{A5}$$

and the mean spatial volume occupied by mussel is

$$V = l \times S = l \times c_v l^y = c_z l^z.$$
(A6)

When a critical total volume becomes limited by competitive constraints, and if L represents the number of layers, the following relationship is expected:

$$N = L \times S^{-1}.$$
 (A7)

Replacing S from (A5) into (A7) gives

$$N = L \times (c_v l^y)^{-1} = c_v^{-1} \times L \times l^{-y}.$$
 (A8)

Rearranging for *l*, we obtain

$$l = c_v^{-1/y} \times L^{1/y} \times N^{-1/y}.$$
 (A9)

Replacing *l* into (A6) leads to

$$V = c_z \times c_y^{-z/y} \times L^{z/y} \times N^{-z/y}.$$
 (A10)

Following Norberg (1988*a*), if *p* is the proportion of the spatial volume of the parallelepiped (*v*) that is occupied with biomass, then the volume of the individual biomass, estimated as the mean weight (*m*), is $m = p \times v$. Substituting *v* from (A10) gives

with

$$k_3 = p \times c_z \times c_v^{-z/y}.$$
 (A12)

(A11)

The population mean allometries of growth on weight and surface area projected to the substrate (represented by the exponents *z* and *y*, respectively) are expressed as $z = 3(1 - \alpha)$ with $\alpha \neq 0$ and $y = 2(1 - \omega)$ with $\omega \neq 0$. Then (A11) may be rewritten as: $m = k_3 L^{3(1-\alpha)/2(1-\omega)} N^{-3(1-\alpha)/2(1-\omega)}$. In the *B*-*N*-*L* notation,

 $m = k_3 L^{z/y} \times N^{-z/y},$

$$B = k_3 L_{2(1-\omega)}^{3(1-\alpha)} N^{1-\frac{3(1-\alpha)}{2(1-\omega)}}.$$
 (A13)

Then, for space-driven self-thinning in multilayered populations, β_3 is given by

$$\beta_3 = 1 - \frac{3(1 - \alpha)}{2(1 - \omega)},$$
 (A14)

so the scaling equation can be expressed by the following geometrically trivariate model:

$$B = k_3 L^{1-\beta_3} N^{\beta_3}.$$
 (A15)

Under a high degree of packing in mussel beds, it is expected that the individuals will invade the exclusive space (1 - p) of neighbors (fig. 1), increasing the overlapping between neighbors and permitting more shared space, but the average volume (v) and proportion occupied with mass (p) will remain the same. The average area occupied per mussel will decrease and more individuals will be allowed, increasing the density (N) and/or the number of layers (L). Displacement of the plane by changing the intercept k_3 is expected, even though the mussels maintain the same average form, structure, and volume. If the increase in the overlap between neighbors affects the allometry for growth, it is expected that both the self-thinning coefficient (k_3) and the exponent (β_3) will change (eq. [3]).

When all of the shared space is filled with individuals and the maximum mechanical packing per layer is achieved (an extreme situation of overlapping between neighbors), the biomass per layer is saturated. The variation of B will be determined only by the variation in L, no matter how many individuals by layer are present. Accordingly, the model (eq. [A15]) becomes

$$B = k_3'' L^1 N^0, (A16)$$

where k_3'' is the maximum biomass per layer (i.e., the saturation packing biomass by layer is not amenable to description with a bidimensional model).

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