

An Allometric Tridimensional Model of Self-Thinning for a Gregarious Tunicate Author(s): Ricardo Guiñez and Juan Carlos Castilla Source: *Ecology*, Vol. 82, No. 8 (Aug., 2001), pp. 2331-2341 Published by: Wiley on behalf of the Ecological Society of America Stable URL: http://www.jstor.org/stable/2680235 Accessed: 21-12-2017 19:43 UTC

# REFERENCES

WILEY

Linked references are available on JSTOR for this article: http://www.jstor.org/stable/2680235?seq=1&cid=pdf-reference#references\_tab\_contents You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms



Wiley, Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to Ecology

# AN ALLOMETRIC TRIDIMENSIONAL MODEL OF SELF-THINNING FOR A GREGARIOUS TUNICATE

# RICARDO GUIÑEZ AND JUAN CARLOS CASTILLA<sup>1</sup>

# Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, 6513677, Chile

Abstract. A tridimensional allometric model of self-thinning was tested in a tunicate population of Pyura praeputialis in the Antofagasta Bay, northern Chile. The theory tested follows the bidimensional allometric theory of Osawa and Allen for the self-thinning rule proposed for plants, except that in addition to mean individual mass we included three new concepts: the number of layers (an equivalent of the leaf area index, [LAI] used in plants), the effective unit area, and the density per unit effective area. We assumed constant tunicate mass per effective unit area and allometry for mean dimensions of the population. The tridimensional model can be reduced to a bidimensional one if density is expressed as the density per unit effective area, which corresponds to the number of individuals relative to the effective area occupied by individuals when they conform a monolayer. The model allows for random sampling and rules out the selection for samples or stands at maximum crowding. The self-thinning of *P. praeputialis* through a tridimensional model showed an exponent of -1.518 (95% ci, -1.635 to -1.401) for mean tunicate visceral mass, and an exponent of -1.489 (95% ci, -1.588 to -1.390) for the corrected bidimensional model. The two exponents were identical to those predicted from tridimensional allometric theory. The results of this new approach increase the variance explained in comparison to that of classical bidimensional models.

Key words: allometric theory; crowding; density per unit effective area; effective area; intraspecific competition; layering; Pyura praeputialis; tunicate; rocky shore; scaling; self-thinning rule; tridimensional model.

# INTRODUCTION

Thinning processes that occur in crowded animal and plant populations play an important role in the determination of population dynamics and community structure (e.g., Weller 1987, Fréchette et al. 1992, 1996, Bohlin et al. 1994, Marquet et al. 1995, Petraitis 1995, Guiñez 1996, Dunham and Vinyard 1997, Guo and Rundel 1998, Guiñez and Castilla 1999). As individuals grow to high population density, a negative relationship between individuals per unit area (N) and mean individual mass ( $\bar{m}$ ) or biomass per area (B) is expected (Westoby 1984). This self-thinning process can be represented by the following power equation:

$$\bar{m} = k_2 N^{\gamma_2} \tag{1}$$

where  $k_2$  and  $\gamma_2$  are constants defined as the thinning coefficient and exponent, respectively. Here, we have introduced the subscript 2 to recall that the equation represents a bidimensional model (Guiñez and Castilla 1999). The equation can be expressed in equivalent terms referred to population biomass, *B*, and density as,  $B_z = k_2 N^{\beta_2}$ , where  $\beta_z = 1 + \gamma_2$ . Eq. 1 describes a straight line of slope  $\gamma_2$  on a log-log plot.

In both theoretical and empirical studies, the defi-

Manuscript received 11 August 1999; revised 10 July 2000; accepted 31 August 2000; final version received 27 September 2000.

<sup>1</sup> Corresponding author. E-mail: jcastill@genes.bio.puc.cl

1995, Guo and Rundel 1998). A major issue has been the different concepts used for self-thinning (Sackville Hamilton et al. 1995). Osawa and Sugita (1989) argued that the original definition of self-thinning of Yoda et al. (1963) was the regression slope of the upper boundary of plant yield (or mean biomass) on a given density, nominated by Weller (1990) as the "species boundary line": a species constant defining a limit that cannot be exceeded in any environment by individuals of the given species. Weller (see also Westoby 1984) also advocated the "dynamic thinning line," which describes the time trajectory followed by a self-thinning population as it approached the boundary line. However, it will not in general converge on the species boundary line, but on the "population boundary line," a line below which a population that in a given environment can occupy any point, but cannot surpass it (White and Harper 1970, Osawa and Sugita 1989, Sackville Hamilton et al. 1995). The species and population approaches have been developed mainly in relation to plant studies. In animals, the "dynamic thinning line" approach has predominated (Hosomi 1985, Begon et al. 1986, Hughes and Griffiths 1988, Fréchette and Lefaivre 1990, 1995, Grant and Kramer 1990, Elliot 1993, Grant 1993, Latto 1994, Bohlin et al. 1994, Fréchette et al. 1996, Armstrong 1997, Guiñez and Castilla 1999); yet in salmonids Dunham and Vinyard (1997)

nition and quantification of the self-thinning process have been controversial (Sackville Hamilton et al.

combined a time and a spatial approach to self-thinning.

Even when comprehensive mathematical models have been developed to incorporate both thin and dense stands for size-density dynamics of plant populations (Hozumi 1977, 1980), it persists another major controversial issue related with the universal, but somewhat unsatisfactory, procedure of how to edit data points by examining scatter diagrams, thus selecting populations or stands undergoing natural thinning at or near the boundary condition, defined by all possible combinations of density and mean size (e.g., Osawa and Allen 1993, Guo and Rundel 1998). Ideally a curve should be fitted to all points in the data set (Sackville Hamilton et al. 1995), but serious biases in the estimation of the thinning exponent may result when sparse stands or populations are not excluded (Osawa and Sugita 1989, Lonsdale 1990, Osawa and Allen 1993). Guo and Rundel (1998) suggested that the upper boundary of data points is defined by the nature of organisms' development and competition, and that a scatter arrangement of data points below the upper thinning lines indicates the effects of environmental heterogeneity across the stands or sampling quadrats. However, Guiñez and Castilla (1999) showed that the scatter data points in bidimensional models, either in time dynamic thinning lines or population thinning lines, may be explained by a systematic bias that is produced by not considering the amount of layering in a gregarious multilayered marine mussel. They developed an allometric tridimensional self-thinning model, based on population mean allometries in which the degree of crowding (measured as the number of mussel layers, L, a positive real number), in addition to the density (N) and the mean mass  $(\bar{m})$  or total biomass per area (B) was considered, leading to the following model:,  $B = k_3 L^{1-\beta_3} N^{\beta_3}$ , where the subscript 3 is used to distinguish parameters of the tridimensional model. This equation is called the tridimensional model or the B-N-L diagram (Guiñez and Castilla 1999) in opposition to the bidimensional model or B-N diagram (Westoby 1984).

We have shown that the expected  $\beta_2$  exponent  $E(\tau)$  derived from a two-dimensional *B*–*N* diagram, applied to populations where tridimensional models are better suited, would be a biased estimate of that obtained from a *B*–*N*–*L* diagram. This is because  $E(\tau) = \beta_3(1 - b_{L-N}) + b_{L-N} = \beta_2$  (where  $b_{L-N}$  is the slope of the linear regression of log*L* on log*N*), which shows that  $\beta_2$  will always be greater than  $\beta_3$ , at least for  $\beta_3 < 1$  and  $0 < b_{L-N} < 1$  (Guiñez and Castilla 1999).

The tridimensional model can be expressed also in equivalent terms as follows:

$$\bar{m} = k_3 N^{\gamma_3} / L^{\gamma_3} \tag{2}$$

where  $\gamma_3$  and  $k_3$  are the thinning exponent and coefficient, respectively, and  $\beta_3 = 1 + \gamma_3$ . Since, if we divide

 $B = k_3 L^{1-\beta_3} N^{\beta_3}$  by *N*, then it follows that  $B/N = \bar{m} = k_3 L^{1-\beta_3} N^{\beta_3}/N = k_3 L^{1-\beta_3} N^{\beta_3-1} = k_3 N^{\gamma_3}/L^{\gamma_3}$ .

In this paper, we extend our allometric tridimensional model, to the intertidal barrel-shaped tunicate Pyura praeputialis, a gregarious noncolonial tunicate species (Castilla 1998), following our suggestion that a B-N-L approach may be used in other animal taxa where overlapping spatial configuration is present (Guiñez and Castilla 1999). We used the population boundary line approach and spatial consideration, assuming that a self-thinning line (or plane) exists below which the tunicate population can occupy any point, but cannot surpass it. The tunicate P. praeputialis (Paine and Suchanek 1983, Castilla 1998, Clarke et al. 1999) shows several morphs and has given rise to taxonomical confusion. In Chile, P. praeputialis (previously identified as P. stolonifera; see Kott 1997, 1998, Castilla et al. 2000) occurs exclusively in and around the Bay of Antofagasta, northern Chile, along  $\sim 60-70$  km of rocky shore (Castilla et al. 2000), and, according to Castilla and Guiñez (2000), was introduced from Australia. The species is a competitive dominant (Paine and Suchanek 1983) and forms tightly packed monospecific aggregations (beds or matrices) on hard substrates in the middle and low intertidal zones (and in the shallow subtidal), showing intraspecific competition associated with increased packing biomass, even under situations where the cover is <100% (Dalby 1995, Castilla et al. 2000). Therefore, the population is expected to show self-thinning.

The aims of our study were four-fold: (1) to develop a tridimensional allometric model of self-thinning for the tunicate, (2) to derive empirical coefficients and exponents of the self-thinning relationships, (3) to test the assumptions of the allometric tridimensional theory, and (4) to determine if the observed self-thinning fits the theoretical expectations of the B-N-L approach.

# THE ALLOMETRIC THEORY FOR A GREGARIOUS TUNICATE

#### Assumptions

Classical isometric and allometric models (Yoda et al. 1963, White 1981) have been developed, assuming that total surface projected to the substrate by individuals per unit of area is constant, such that the following relationship holds:

$$N\bar{S} = S_{\rm T} = \text{constant} = 1$$
 (3)

where N is the density estimated as the number of individuals per unit area,  $S_T$  is the total area projected perpendicularly to the substrate of the individuals per unit area (area per area),  $\bar{S}$  is the mean individual area projected to the substrate ( $S_T$  per individual).  $S_T$  is assumed constant and equal to one, because the individuals cover all (100% cover) the sampling area. The same assumption has been used for other sessile marine invertebrates (i.e., Hughes and Griffiths 1988, Fréch-



FIG. 1. Representation of the *Pyura praeputialis* tunicate matrix. (A) Position of a tunicate with respect to the substrate, showing tunic, viscera tissue, and maximum diameter of an individual  $(D_t, \text{ mm})$  in the direction of the siphons. (B) Case 1: Top view of tunicate matrix with 100% cover. In this case, the sampling area  $(A_s)$  is equal to the effective area  $(A_c)$ , and therefore the number of layers L = 1. (C) Case 2: Lateral view of tunicate matrix with 100% cover, but  $A_s < A_c$  and L > 1. (D) Same as (C), but the matrix is shown in a top view as expected if the individuals were laid out in a monolayer. (E) Case 3: Top view of matrix where cover <100%,  $A_s > A_c$  and L < 1.  $A_c$  is the total surface area covered by the *n* individuals in a sampling area  $(A_s)$  and was estimated as  $\sum_{i=1}^{n} (\pi/4) D_i^2$ . *L* was estimated dividing  $A_c$  by  $A_s$ . Bold arrows relate oblique view to top view.

ette and Lefaivre 1990, 1995). On the other hand, contemporary allometric theory of self-thinning for plants (see Long and Smith 1984, Osawa and Allen 1993) have been developed assuming constancy of the leaf mass per area ( $M_L$ ). This assumption is valid only when the canopy has a 100% cover and the individuals form a monolayer. An equivalent allometric model for animals, considering constancy in mean mass of some characteristic, has so far not been explored.

In gregarious sessile species such as mussels (e.g., Perumytilus purpuratus; Alvarado and Castilla 1996, Guiñez 1996) that form crowded multilayered bed aggregations, it has been shown that a new type of modeling is needed to adequately address self-thinning processes, because the classical assumption represented by Eq. 3 is violated. This leads to deviations from selfthinning expectations (Hughes and Griffiths 1988, Fréchette and Lefaivre 1990, Guiñez 1996, Guiñez and Castilla 1999). Nevertheless, consideration of the degree of overcrowding, measured as the number of layers (L) as a variable different from density (N), presents difficulties (Guiñez and Castilla 1999) for the application of bidimensional allometric self-thinning models (Eq. 1). As a solution, the modeling of Guiñez and Castilla (1999) assumes that  $N \propto L/\bar{S}$  when individuals in the matrix reach a limiting available volume, leading to the model represented by Eq. 2.

## The tunicate model

For the development of the model, we used a different concept of area: the effective unit area  $(A_e)$ , which is defined as the area occupied by individuals if they were laid out as a monolayer, and is estimated as the total area projected perpendicularly to the substrate covered by the individuals (Fig. 1). This is an important distinction, because we have demonstrated that  $A_e$  does not coincide necessarily with the sampling area  $A_s$  (Guiñez and Castilla 1999), even when the cover is 100%. This has enabled us to define the number of layers (*L*) as an index of crowding, allowing the incorporation of the overlapping spatial configuration of the individuals. *L* is estimated as the effective area divided by the sampling area:  $L = A_e/A_s$  (Guiñez 1996, Guiñez and Castilla 1999).

The model for *P. praeputialis* is developed using mean allometries instead of individual allometries and following the theory of Osawa and Allen (1993). Nevertheless, we define a new concept of density: the density per unit effective area ( $N_c$ , the corrected density): the expected density if the individual would form a

monolayer. If *n* is the number of individuals in one sampling unit of area  $A_s$ , then, as traditionally done, *N* is estimated as  $n/A_s$  (individual per area), but  $N_c$  is estimated as  $n/A_e$  (individual per effective area). Our model also contains a new assumption: that the tunicate's tunic mass per unit effective area ( $M_T$ , given in grams per area) is constant, i.e.,

$$\bar{m}_{\rm T} N_{\rm c} = M_{\rm T} = {\rm constant}$$
 (4)

where  $\bar{m}_{\rm T}$  is the mean tunicate tunic mass per individual (grams per individual). In fact, we have found evidence for this constancy in samples from *P. praeputialis* (see *Results and Discussion: Constancy in tunicate's tunic dry mass*). The model of Osawa and Allen, following Long and Smith (1984), assumes constancy of the leaf mass "per area" ( $M_{\rm L}$ ) for plants. Nevertheless, according to us constancy "per effective area" has not been demonstrated previously in animals or in plants.

So if we assume that the tunicate's tunic mass per unit area  $(M_T)$  is constant relative to the effective area occupied  $(A_e)$  (Eq. 4), it follows that

$$m_{\rm T}\left(\frac{n}{A_{\rm s}}\right)\left(\frac{1}{A_{\rm e}/A_{\rm s}}\right) = \bar{m}_{\rm T}N\frac{1}{L} = M_{\rm T} = \text{constant.}$$
 (5)

If  $\bar{m}_{\rm T}$  and  $\bar{m}_{\rm v}$  (the mean tunicate visceral mass, grams per individual) are both allometrically related to mean maximum diameter of the tunicate in the direction of the siphons ( $\bar{D}$ , length per individual), then

$$\bar{m}_{\rm T} = a\bar{D}^{\rm T} \tag{6}$$

$$\bar{m}_{\rm v} = b\bar{D}^{\rm \omega} \tag{7}$$

where a, b,  $\tau$ , and  $\omega$  are constant. Eqs. 5–7 yield the following relationship between  $\bar{m}_{\nu}$ , N and L:

$$\bar{m}_{v} = \frac{b(M_{\rm T}/a)^{\omega/\tau}L^{\omega/\tau}}{N^{\omega/\tau}}.$$
(8)

Eq. 8 is a tridimensional model that incorporates the new variable L, that is, the number of individual layers, in addition to those used in traditional bidimensional models. Comparison of Eqs. 2 and 8 indicate that  $\gamma_3$  $= -\omega/\tau$  and  $k_3 = b(M_T/a)^{\omega/\tau}$ . Therefore, the thinning exponent,  $\gamma_3$ , and the thinning coefficient,  $k_3$ , can be determined from known parameters of the population. In addition, as shown by Guiñez and Castilla (1999), when L = 1 (i.e., the number of individual layers is one and the effective area and sampling area are equal), the tridimensional model (Eq. 8) collapses to the classical bidimensional model (i.e., Osawa and Allen 1993: Eq. 7) (Fig. 1B, Case 1). The tridimensional model permits the inclusion of samples where L > 1, a situation of overcrowding (Fig. 1C, D, Case 2) (Guiñez and Castilla 1999). Here, we also extend the use of L to situations where L < 1 (Fig. 1E, Case 3), where L can be interpreted as a measure of cover. This represents a new modeling situation, whereas the individuals do compete in spite of L < 1.

If the density is expressed as the corrected density

 $(N_{\rm c})$  relative to effective area  $(A_{\rm e})$  (Eq. 4) and is estimated as

$$N_{\rm c} = n/A_e = N/L \tag{9}$$

then Eq. 5 is expressed as Eq. 4, i.e.,

$$\bar{m}_{\rm T}\left(\frac{n}{A_{\rm e}}\right) = \bar{m}_{\rm T}N_{\rm c} = M_{\rm T} = {\rm constant}$$
 (10)

and Eq. 8 changes to the following corrected bidimensional model:

$$\bar{m}_{v} = \frac{b(M_{\rm T}/a)^{\omega/\tau}}{N_{\rm c}^{\omega/\tau}}.$$
(11)

#### Methods

#### Study area

The study was conducted at three sites: Curva Lenguado (CLEN), El Way (EWAY), and Las Conchillas (LCON), on intertidal rocky platforms within the Antofagasta Bay (23°38'47.4" S, 70°23'54.8" W), in northern Chile, where *P. praeputialis* forms highly packed matrices (Paine and Suchanek 1983, Castilla 1998, Castilla et al. 2000).

# Sample measurements for observed self-thinning relationships

Individual allometries.-To estimate the parameters for individual allometries during July 1998, we sampled individuals from the middle intertidal fringe at El Way (n = 47) and at Las Conchillas (n = 47), representing the entire individual size range. The individual tunic and visceral dry masses were determined by oven drying the respective tissues at 70°C for 72 h, until stable mass was attained. Individual allometries were estimated with allometric equations by applying Reduced Major Axis (RMA) regression (Clarke 1980) on crude or log<sub>10</sub>-transformed data. In the latter case, a correction factor (CF) was applied on the allometric coefficient (Sprugel 1983, LaBarbera 1989). According to LaBarbera (1989) log-transformed data reduce the heteroscedasticity of nontransformed data. The adjusted equation of individual visceral dry mass  $(m_v, in$ grams) on tunicate maximum diameter (D<sub>t</sub>, in millimeters) was

$$m_{\rm v} = 0.0000202 D_{\rm t}^{2\,84565}.\tag{12}$$

Sample size = 94,  $R^2 = 0.94$  for log-transformed data, CF = 1.05218, and pWR, the log<sub>10</sub> of maximum-tominimum ratio of a variable (LaBarbera 1989), was 0.79 for the diameter.

For the dependence of total dry mass  $(m_d)$  on wet mass  $(m_w)$  in grams, we obtained the following linear equation:

$$m_{\rm d} = 0.00678 + 0.22908 m_{\rm w} \tag{13}$$

where sample size = 94, and  $R^2 = 0.96$ .

Self-thinning relationships.—To analyze self-thinning relationships, we used a total of 45 samples extracted from  $0.6 \times 0.4$  m quadrats taken at random in April and May 1997 (CLEN, n = 24; EWAY, n = 9; LCON, n = 12). Individuals in each sampling area were counted and the density (N) was expressed as number of individuals per square meter. Percent cover of the samples was obtained by digitizing color photograph using a video camera connected to the Optimas Software Package (Optimas Inc.). One subarea (0.06 m<sup>2</sup>) was randomly selected within each of the 45 sampling areas to measure the tunic maximum diameter  $D_{\rm t}$  (in the direction of the siphons, Fig. 1A) and the total wet mass of each individual. The diameter was measured with a caliper to the nearest 0.01 mm and wet mass was determined with a balance to the nearest 0.01 g. Mean tunicate visceral dry mass  $(\bar{m}_{v})$  (in grams) was estimated for each subarea using Eq. 12, and mean tunicate tunic dry mass  $(\bar{m}_{T})$  (in grams) using total dry mass  $(m_d)$  with Eq. 13. Then the tunicate tunic dry mass in grams was obtained by subtracting the tunicate visceral dry mass  $(m_v)$  (obtained from Eq. 12) from  $m_d$ . An estimator of the number of layers (L) was obtained as the sum of the individual area divided by the area of the corresponding subsample. The individual area was estimated as  $(\pi/4)D_t^2$  (Fig. 1). To estimate the corrected density  $(N_c)$  we followed Eq. 9, dividing the number of individuals (n) by the effective area  $(A_e)$ .

## Sample measurements for mean allometries

To obtain the parameters for the mean allometries, we took 30 independent samples during July-September 1997 at the middle intertidal fringe at El Way using a  $0.17 \times 0.17$  m sampling area, with 100% cover of P. praeputialis. We also used these data to determine the allometry between mean tunic mass and the corrected density  $(N_c)$  to test if the mean tunicate tunic mass per unit of effective area was constant. Additionally, we added 5 samples  $(0.10 \times 0.10 \text{ m})$  with 100% cover in August 1998, which included cohorts of juvenile P. praeputialis representing the smallest diameters recorded. For each individual, we measured the maximum diameter  $D_{i}$ , and the tunicate tunic and visceral dry masses by oven drying the respective tissues at 70°C for 72 h. To test the assumptions for mean allometries of the model (Eqs. 6 and 7), mean allometries from the 35 independent samples were obtained on  $\log_{10}$ -transformed data, using mean diameter (D), mean tunicate visceral dry mass  $(\bar{m}_y)$ , and mean tunicate tunic dry mass  $(\bar{m}_{\rm T})$  for each sample.

## Regression analyses

For the bidimensional corrected model, regression lines were fitted to mean tunic mass  $(\bar{m}_{\rm T})$  on corrected density (Eq. 10), and to mean visceral mass  $(\bar{m}_{\rm v})$  on corrected density (Eq. 11). We also calculated the upper boundary slope for the same data (100% cover), using the method of Blackburn et al. (1992). For that we

divided the x-axis (density) into nine segments of the same width and selected from within each segment the maximum y-variable (mean visceral dry mass). Original data were log<sub>10</sub>-transformed. We used Reduced Major Axis (RMA) regression, because (1) it is less sensitive to assumptions on the error structure in the data, (2) it is a less biased estimate of the underlying functional relationship, and (3) it appears to be a better approach than principal component analysis when the mass-density self-thinning formulation is used (La-Barbera 1989, Osawa and Allen 1993, Sackville Hamilton et al. 1995). For RMA regression for bivariate model we followed Clarke (1980), and for trivariate model we followed Kirby (1991a, b). Statistical analyses used SAS version 6 (SAS Institute 1988), and for RMA multiple regression we used the program described in the part two of Kirby (1991b).

Estimated variation in the mean individual mass for a sample and in the number of layers was little affected by density. Thus, statistical problems of spurious correlation derived from the use of mean mass values to study self-thinning (Petraitis 1995, but see LaBarbera 1989, Scrosati 1996) do not appear to be important for our data.

#### **RESULTS AND DISCUSSION**

#### Number of layers, density, and corrected density

The estimated number of layers (L) was not significantly related to the mean tunicate maximum diameter  $(R^2 = 0.004, P = 0.68)$ . This result suggests that L is independent of mean diameter  $(\overline{D})$ . This is a necessary condition for the development of the model, because we estimated L as the sum of the individual areas  $(\pi/$  $(4)D_t^2$  divided by the sampling area (Fig. 1). The log of the number of layers did show a significant relationship with the log of density (slope = 0.713,  $R^2 = 0.83$ , P < 0.001), but slopes and coefficients of determination were smaller for samples with 100% cover (slope =  $0.267, R^2 = 0.25, P = 0.023$ ) than for those with lower cover (slope = 0.617,  $R^2 = 0.77$ , P < 0.001) (Fig. 2A). According to Guiñez and Castilla (1999) the slope  $(b_{L-N})$  of the relationship between logL and logN represents changes in number of layers per individual in the population, as well as the degree in which the bidimensional estimates are biased with respect to the tridimensional ones. Our results suggest that a bias is expected from our data, either using all or segregating by cover. In the latter case, it appears that the bias is greater when the cover is <100% and justifies the need to edit the data when the bidimensional approach is applied; but still, a bias would exist for the 100% cover samples. Fig. 2A also shows that, even when a 100% cover is detected (as determined by photography), this does not necessarily imply that the individuals are effectively occupying 100% of the sampling area if they form a monolayer. For example, five samples are below the expected value of unity (shown in Fig. 2A by a



FIG. 2. Density in *Pyura praeputialis* samples in relation to (A) number of layers and (B) corrected density. Solid circles indicate samples with 100% cover; open circles indicate those with cover <100%. The dotted line in (A) shows the expected number of layers for 100% cover if the individuals form a monolayer. The continuous line in (B) shows the situation for an exact correspondence between the density and the corrected density, represented by a slope of 1. The dashed line in (B) represents the fitted reduced major axis (RMA) line for the samples.

dotted line). The number of layers of nine samples are  $\sim 10\%$  of its expected value of one (Fig. 2A), and for six samples it is >10% of the expected value. This suggests that individuals are increasing their overlapping and that the term "100% cover" in self-thinning studies may be ambiguous and require refinement. In the case of plants, Sackville Hamilton et al. (1995) suggested using the maximum or at-ceiling leaf area index (LAI<sub>c</sub>). However, because in our case the number of layers (L) (an equivalent to leaf area index LAI; Hosomi 1985) is considered a variable and not a constant, we did not follow this approach (also see Matthew et al. 1995). Instead, we followed two new criteria: (1) that represented by Eq. 8, where the number of layers is directly incorporated into a tridimensional model as a new variable, and (2) a correction factor for density as shown in Eq. 9, where density is projected to the effective area occupied by individuals (in square meters).

The corrected density for the samples of *P. praeputialis* in relation to their density is shown in Fig. 2B. The slope of the RMA line 0.730 (dimensionless; 95% CI, 0.556–0.904;  $R^2 = 0.40$ , P < 0.001, n = 45) is significantly different from unity (Fig. 2B), indicating that these two density measures are not exactly equivalent.

# Observed self-thinning relationships

Fig. 3 shows a bivariate log-log plot of mean tunicate diameter vs. density (Fig. 3A) and corrected density (Fig. 3B). According to the expectations of a bidimensional model, the samples at full density should be close to the probable boundary condition (i.e., Osawa and Allen 1993), and the RMA-adjusted regression, using only these samples, has slope of -2.033 (dimensionless; 95% CI, -2.649 to -1.416;  $R^2 = 0.63$ , P

FIG. 3. Mean tunic diameter (mm) in relation to (A) tunicate density and (B) corrected density. Solid circles indicate samples with 100% cover; open circles indicate those with cover <100\%. The RMA line (dotted) for the samples at 100% cover is shown in (A). The RMA line (continuous) for all the samples using the corrected density is shown in both graphs. Stars represent two outliers in (B), according to the Cook's distance criteria on residuals.



This content downloaded from 146.155.158.13 on Thu, 21 Dec 2017 19:43:52 UTC All use subject to http://about.jstor.org/terms

< 0.001, n = 20). The slope of -1.904 (dimensionless; 95% CI, -2.181 to -1.627;  $R^2 = 0.84$ , P < 0.001, n = 45) for all the data using the corrected density is not different from that representing the probable boundary condition (Fig. 3B). When two possible outliers (Fig. 3B) are not considered, the RMA line is exactly equal to the probable boundary condition -2.033 (95% CI, -2.267 to -1.799;  $R^2 = 0.87$ ). A negative relationships between density (N) and mean surface projected to the substrate ( $\bar{S}$ ), such that  $N \propto \bar{S}^{-1}$ , is expected in geometrical bidimensional model of self-thinning when individuals occupy the substrate as a monolayer with 100% cover of the substrate (Guiñez and Castilla 1999). If the mean surface of a tunicate projected to the substrate is isometrically related to the square of the mean diameter  $(\bar{D}^2)$ , it is expected that  $N \propto \bar{S}^{-1} \propto \bar{D}^{-2}$ . This satisfied the adjusted RMA slope for the probable boundary condition (Fig. 3B) and for the corrected density, because the slope is not significantly different from negative two. However, as shown by Guiñez and Castilla (1999), the relationship between N and  $\overline{S}$  is violated when the degree of crowding (i.e., the number of layers) or overlapping spatial configuration are incorporated in the self-thinning model. In this situation, the relationship is biased, since what is expected is that  $N \propto L/\bar{S}$ , whereas the variance explained (Fig. 3A) decreases to 0.17 (P < 0.01).

Fig. 4A shows a scatter bidimensional log-log plot of the mean tunicate visceral dry mass vs. density. The slope for the samples that had 100% cover is -1.245(95% CI, -1.608 to -0.882;  $R^2 = 0.65$ , P < 0.001, n = 20). The upper boundary slope (using the method of Blackburn et al. [1992]) of the adjusted RMA line is -1.336 (dimensionless; 95% CI, -1.898 to -0.770;  $R^2 = 0.78, P < 0.01, n = 9$  (Fig. 4A). However, the two estimates are not significantly different, nor are they different from negative one, the expected value for a competition-density effect, which could occur without density-dependent mortality (Kira et al. 1953, Osawa and Allen 1993, Fréchette and Bacher 1997, Guiñez and Castilla 1999). When the relationship is analyzed for all samples using the corrected density (two outliers are not considered, Fig. 4B) according to Eq. 11, the slope of the RMA line is -1.489 (95% CI, -1.588 to -1.390;  $R^2 = 0.96$ , P < 0.001, n = 43; correction factor, CF = 1.011). Finally, when the data are represented in a tridimensional diagram as shown in Fig. 4C, following Eq. 7, the adjusted RMA multiple regression on the log-transformed data, using mean visceral dry mass  $(\bar{m}_{y})$  as dependent variable, and density (N) and number of layers (L) as independent variables, is  $\bar{m}_{\rm v} = (23.70 \times 10^3)(L^{1.522}/N^{1.518})$  ( $R^2 = 0.96$  for the log-transformed data, P < 0.001, N = 43, CF = 1.011), with 95% CI for the exponent associated to N ranging -1.635 to -1.401). These estimates of thinning exponents, (a) -1.489 from the bidimensional approach on corrected density data, and (b) -1.518 from the tridimensional approach, do not differ significantly. As



FIG. 4. Thinning relationships (log scale) for (A) classical and (B) corrected bidimensional models, and for (C) the tridimensional model. (A) Relationship between mean visceral dry mass ( $m_v$ ) and density (N). Solid squares indicate samples with 100% cover; open squares indicate those with cover <100%. (B) Relationship between  $m_v$  and corrected density  $N_{e^*}$  (C) Relationship among  $m_v$ , N, and number of layers L.

judged by the 95% CI of the slopes of both thinning exponents, they are smaller than and significantly different from negative one, the expected value for a competition-density effect.

These results agree with the theoretical and empirical demonstrations (see Results and Discussion: Number of layers, density, and corrected density), showing that the thinning exponent obtained from a B-N diagram overestimates its value when a tridimensional diagram is considered (Guiñez 1996, Guiñez and Castilla 1999). This suggests that, for species showing multilayered packing and overlapping spatial configurations, or when consideration of the number of layers is relevant, the likelihood of detecting density dependence may be much more frequent than what has been reported so far (Guiñez and Castilla 1999). The bias implicit in the estimation of self-thinning relationships without consideration of the number of layers does not permit appropriate testing of the thinning models, and we therefore suggest that these results may not change by additional sampling, either using more data with 100% cover or looking for upper boundary slope.

The thinning coefficient for the tridimensional model  $(k_3 = b[M_T/a]^{\omega/\tau}$  (from Eq. 8) was 23.70 × 10<sup>3</sup> (95% CI, 10.21 × 10<sup>3</sup>-55.02 × 10<sup>3</sup> g·m<sup>2</sup>\gamma\_3), and for the bidimensional model, with corrected density, it was 19.94 × 10<sup>3</sup> (95% CI, 9.94 × 10<sup>3</sup>-40.04 × 10<sup>3</sup> g·m<sup>2</sup>\gamma\_2;  $\gamma_3$  and  $\gamma_2$ , which appear in the exponents of the dimensions, are the estimated values of the thinning exponent for the tri- and the bidimensional diagram, respectively, indicating the location of the self-thinning line on logarithmic coordinates (Fig. 4B, C).

Next, we test if allometric relationships could explain the observed values of the thinning exponent and coefficient. First, we test the assumptions of the model related with the constancy of the tunicate tunic mass per effective unit area occupied (Eqs. 5 and 10). Second, we test the assumption of mean population allometries (Eqs. 6 and 7), and third, we evaluate whether the theoretical and empirical thinning exponents and coefficients are or are not equal (Eqs. 8 and 11).

# Constancy in tunicate tunic dry mass

For the tridimensional model, we assumed that tunicate tunic mass per effective unit area occupied by individuals  $(M_T)$  is constant. This was tested using two independent data sets: first, data from the 30 adult independent samples were used to get the population allometric parameters (See *Results and Discussion: Sample measurements for mean allometries*). Second, the data were used to determine the observed self-thinning relationships (See section *Results and Discussion: Sample measurements for observed self-thinning relationships*). According to Eq. 4, we have  $\bar{m}_T = M_T/N_c$ , and, applying  $\log_{10}$  to both terms, it follows that  $\log \bar{m}_T = \log M_T - 1 \cdot \log N_c$ . In this way, the assumption of constancy in total tunic dry mass can be tested if the slope is negative one. In fact, the fitted RMA regression slope ( $R^2 = 0.76$ , P < 0.001, n = 30, CF = 1.01) was -1.038 (95% CI, -1.244 to -0.833) for the independent data set, and -1.187 (95% CI, -1.404 to -0.970;  $R^2 = 0.66$ , P < 0.001, n = 43, CF = 1.05, with two outliers not included) for the second data set. For both data, we were unable to reject the assumption of constant tunic mass density (slope = -1) according to the 95% CI. For the independent data set the estimated constant tunic dry mass density,  $M_{\rm T}$ , was 19 630 g/m<sup>2</sup> (95% CI, 4517–85 297 g/m<sup>2</sup>), and for the second data set it was 9380 g/m<sup>2</sup> (95% CI, 2043–43 063 g/m<sup>2</sup>). Although the former data shows higher value than the later, the estimated tunicate tunic mass per unit area effectively occupied by individuals did not differ significantly between them, according to the 95% CI.

In tunicates the tunic tissue has the function of structural skeletal support, and at Antofagasta Bay we have found that P. praeputialis tunic dry biomass can get up to 20.45 kg/m<sup>2</sup> on average, and it represents almost 95% of the total dry biomass (Castilla et al. 2000). This implies that a high proportion of the biomass is being assigned to structural skeletal support. Paine and Suchanek (1983) suggested that in this species larger body size seemed to confer competitive superiority. Furthermore, we have shown evidence that changes in body form, even at cover <100%, are determined by crowding/packing biomass competitive effects: a larger number of squat individuals at lower crowding and more thin individuals at high crowding (Castilla et al. 2000). Therefore, we propose that a constant tunic dry mass per effective unit area is expected if the tunicates are competing near their mass-carrying capacity per effective unit area.

## Mean population allometries

The other two additional assumptions of self-thinning models relate to the population allometric relationship between mean tunicate tunic dry mass ( $\bar{m}_{\rm T}$ ) and mean tunicate visceral dry mass ( $\bar{m}_{\rm v}$ ) vs. the mean tunic diameter ( $\bar{D}$ ) (Eqs. 6 and 7). Estimated values of the allometric exponents (Fig. 5) by RMA regression are  $\tau = 2.05$  (95% cI, 1.92–2.18;  $R^2 = 0.97$ ) for tunic mass and  $\omega = 2.94$  (95% cI, 2.70–3.17) ( $R^2 = 0.95$ ) for visceral mass. Values of the allometric coefficients were also estimated by RMA regression as,  $a = 662 \times 10^{-5}$  g/m<sup> $extrm{T}$ </sup> for tunic mass (95% cI, 425 × 10<sup>-5</sup>–1030 × 10<sup>-5</sup>; CF = 1.0002), and  $b = 1356 \times 10^{-8}$  g/m<sup>imes</sup> for visceral mass (95% cI, 615 × 10<sup>-8</sup>–2991 × 10<sup>-8</sup>; CF = 1.0005).

## Test of the allometric models

The mean population allometries and parameters estimated for the tridimensional self-thinning model developed in this paper lead to a predicted thinning exponent of  $= -\omega/\tau = -1.43$  (dimensionless) and to a thinning coefficient of  $b(M_T/a)^{\omega/\tau} = 24395 \text{ g/m}^{2\omega/\tau}$ . To be consistent, we have used the  $M_T$  value of 19630 g/ m<sup>2</sup> obtained from the independent sample. The empir-



FIG. 5. Allometric relationship between mean tunic mass (open circles) or mean visceral mass (solid circles) per individual and mean tunic diameter at 100% cover with fitted RMA regression lines.

ical exponent of -1.518 (95% c1, -1.635 to -1.401) and coefficient of 23.70 × 10<sup>3</sup> (95% c1, 10.21 × 10<sup>3</sup>– 55.02 × 10<sup>3</sup> g·m<sup>2</sup><sup>3</sup>), are not significantly different from their theoretical expectations, as they are within the boundaries of the empirical values. For the bidimensional diagram, using corrected density, the observed thinning exponent (-1.489, 95% c1 -1.588 to -1.390) and coefficient (19.94 × 10<sup>3</sup>, 95% c1 9.94 × 10<sup>3</sup>–40.04 × 10<sup>3</sup> g·m<sup>2</sup><sup>3</sup>) are also similar to their predicted values. Therefore, the allometric theory developed hereby for the tunicate *P. praeputialis*, considering the number of layers as a new variable, successfully explains the empirical values whether using the tridimensional model or the bidimensional corrected one.

#### Population boundary line

Assuming (1) isometric growth, (2) a constant maximum at ceiling leaf area index LAI<sub>c</sub>, and (3) that the mean leaf area per plant ( $A_1$ ) is related to the mean shoot biomass per plant ( $w_s$ , with  $w_s = k'A_1^{3/2}$  and k'indicating the mass:area ratio), Sackville Hamilton et al. (1995) proposed the following modified self-thinning equation:

$$w_{\rm s} = k' {\rm LAI_{\rm c}^{3/2}} / N^{3/2}$$
 (14)

resulting in a model with a mathematical structure analogous to our tridimensional model represented by Eq. 8, but with LAI<sub>c</sub> constant. The authors defined LAI<sub>c</sub> as the maximum leaf area index sustainable by a particular plant species in a particular environment. This led the authors to propose what is known as the "population boundary rule," which may be represented mathematically as  $w_s = k''/R$ )LAI<sub>c</sub><sup>3/2</sup>/N<sup>3/2</sup> (Matthew et al. 1995), where, k'' is the mean biomass per unit volume of shoot tissue, and R is a dimension-corrected measure of plant area:volume ratio. On the other hand, the number of layers (L) defined by Guiñez (1996) and Guiñez and Castilla (1999) for gregarious marine invertebrates could be considered analogous to the LAI in plants (Hosomi 1985). Nevertheless, in the case of P. praeputialis, L is considered a variable, while in plants' models of self-thinning (Eq. 14) LAI<sub>c</sub> is incorporated as a constant (Matthew et al. 1995). Since we have assumed that in the tunicate matrices, when a critical volume determined by space competition is reached, a dynamic compensation between N, L, and S occurs; that is  $N \propto L/\bar{S}$  (Guiñez and Castilla 1999). We also assumed constant  $M_{\rm T}$  relative to the effective area  $(A_{\rm e})$ (see Eq. 5), which was not falsified. This result is relevant, because it suggests that P. praeputialis matrices tend to maintain a maximum and constant tunic mass per effective unit of area. Thus, the characteristic of this tunicate to form extremely tightly packed matrices may explain its success as a competitively dominant species (Paine and Suchanek 1983, Castilla 1998). In fact, in the intertidal of Antofagasta Bay we have observed that Pyura intertidal matrices reaches up to 11.3 m (1 se = 0.99) wide, reaching almost 80% cover (Castilla et al. 2000). Also, the fact that the allometric tridimensional model explains successfully the empirical values, suggests that competition among P. praeputialis is driven by space. The same conclusion was reached for the mussel P. purpuratus using a tridimensional model (Guiñez 1996, Guiñez and Castilla 1999), which is expected for competitive intertidal sessile invertebrates (Paine and Suchanek 1983, Okamura 1986, Hughes and Griffiths 1988, Dalby 1995, Guiñez and Castilla 1999).

The results of this study suggest that the scatter of the data points below the upper thinning line in a B-N diagram, at least in the case of the tunicate *P. praeputialis* and the mussel *P. purpuratus* (Guiñez and Castilla 1999), can be explained as an effect of the degree of crowding and overlapping spatial configuration (i.e., number of layers). When the thinning exponent was estimated using the upper-limit concept, we were able to explain 78% of the variance; but, when *L* was incorporated following the tridimensional or the corrected density approach, the variance explained increased to 96%. Additionally, the incorporation of layering and overlapping spatial configuration permits the separation of its effects from density per se (Guiñez and Castilla 1999). In fact, we were able to evaluate the relative importance of density and layering on biomass in P. purpuratus through the properties of the model I regression with type III partial sum of squares (SS3) (PROC GLM-SAS), using as the statistical model the log version of the tridimensional model. The SS3 quantifies the percentage of variance explained by each variable not involving parameters of other effects; this is the case since it holds the effects of other variables constant and the sequence by which variables are analyzed does not affect the partial sums of squares. We showed that layering explained 50% (P < 0.001) and density only 3% (P < 0.005) of the variance in total mass. If we apply the same methodology on our data from *P. praeputialis* using the log version of Eq. 8, we find that layering explains 34% (P < 0.001) and density 63% (P < 0.001) of the variance in mean tunicate visceral mass. This suggests that the dynamics of P. purpuratus and P. praeputialis matrices differ in the degree by which they may be driven by layering effects and density per se. Although there have been several studies of layering effects and resultant consequences for the population dynamics of mussels (Hosomi 1985, Hughes and Griffiths 1988, Fréchette and Lefaivre 1990, Alvarado and Castilla 1996, Guiñez and Castilla 1999), we are not aware of approaches in tunicates that aim to estimate the effect of different overlapping spatial configurations, except for the work of Dalby (1995) showing evidence of intense intraspecific competition inside the aggregation matrices, even without physical contact among individuals.

Finally, it is noteworthy that our modeling was developed and tested including samples that were < 100%cover, where L < 1; usually, these samples are edited and deleted from the reported analyses (Westoby 1984, Osawa and Allen 1993). Instead, we obtained our samples at random, and therefore the sampling is expected to be statistically representative of the tunicate population. In our study, sampling deletion was not necessary, except in two cases considered as outliers. We suggest that in P. praeputialis matrices competition for space occurs even under conditions when L < 1, corresponding to cover <100% (e.g., Dalby 1995). In fact, for P. praeputialis at the Antofagasta Bay, we have shown evidence for the effect of intraspecific competition even under situations where the cover is <100%(L < 1) (Castilla et al. 2000). In the same vein, in Australian populations of *P. stolonifera*, Dalby (1995) has shown experimental evidence supporting intraspecific competition, even where noncontact among individuals existed (when L < 1). We suggest that this is so because P. praeputialis tends to maintain a continuous matrix structure even when cover may be reduced either by physical or biological disturbances. Finally, because of the similarity of the thinning model in this study with that of Osawa and Allen (1993) for plants, we suggest that it is possible to apply our modeling to other sessile organisms (e.g., plants), allowing for ecological comparisons not implemented to date.

## Acknowledgments

We are grateful to J. Alvarado, M. Clarke, C. Pacheco, V. Ortiz, M. Varas, M. Uribe, and I. Fuentes for their help in the field and in the laboratory. We are in debt to J. M. Kirby who estimated for us the parameters of the RMA multiple regression. We are especially grateful to P. Petraitis, F. Jaksic, J. Alvarado, and particularly to Professor A. Osawa and an anonymous referee for constructive criticisms. We acknowledge the financial support of a 1997 Presidential Chair in Science to J. C. Castilla and the Andrew Mellon Foundation.

#### LITERATURE CITED

- Alvarado, J. L., and J. C. Castilla. 1996. Tridimensional matrices of *Perumytilus purpuratus* on intertidal platforms with varying wave forces in central Chile. Marine Ecology Progress Series 133:135–141.
- Armstrong, J. D. 1997. Self-thinning in juvenile sea trout and other salmonid fishes revisited. Journal of Animal Ecology 66:519–526.
- Begon, M., L. Fairbanks, and R. Wall. 1986. Is there a selfthinning rule for animal populations? Oikos 46:122–124.
- Blackburn, T. M., J. H. Lawton, and J. N. Perry. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. Oikos 65:107–112.
- Bohlin, T., C. Delleford, U. Faremo, and A. Johlander. 1994. The energetics equivalence hypothesis and the relation between population density and body size in stream-living salmonids. American Naturalist **143**:478–493.
- Castilla, J. C. 1998. Las comunidades intermareales de la Bahía de Antofagasta: estudios de línea base y el programa ambiental de Minera Escondida Limitada en Punta Coloso. Pages 191–214 *in* D. Arcos, editor. Minería del cobre, ecología y ambiente costero: el caso de Minera Escodida Ltda. Editorial Anibal Pinto, Antofagasta, Chile.
- Castilla, J. C., and R. Guiñez. 2000. Disjoint geographical distribution of intertidal and nearshore benthic invertebrates in the Southern Hemisphere. Revista Chilena de Historia Natural 73:585–603.
- Castilla, J. C., R. Guiñez, J. A. Alvarado, C. Pacheco, and M. Varas. 2000. Distribution, population size structure, standing crop and morphological characteristics of the tunicate *Pyura stolonifera* (Heller, 1878) in the Bay of Antofagasta, Chile. Pubblicazioni della Stazione Zoologica di Napoli (PSZN) Marine Ecology 21(2):161–174.
- Clarke, M. R. B. 1980. The reduced major axis of a bivariate sample. Biometrika 67:441–446.
- Clarke, M., V. Ortiz, and J. C. Castilla. 1999. Does early development of the Chilean tunicate *Pyura praeputialis* (Heller, 1878) explain the restricted distribution of the species? Bulletin of Marine Science **65**:745–754.
- Dalby, J. E. J. 1995. Consequences of aggregated living in the tunicate *Pyura stolonifera*: evidence for non-contact intraspecific competition. Marine Freshwater Research 46: 1195–1199.
- Dunham, J. B., and G. L. Vinyard. 1997. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1025–1030.
- Elliot, J. M. 1993. The self-thinning rule applied to juvenile sea-trout, *Salmo trutta*. Journal of Animal Ecology **62**:371–379.
- Fréchette, M., A. E. Aitken, and L. Pagé. 1992. Interdependence of food and space limitation of a benthic suspension feeder: consequences for self-thinning relationships. Marine Ecology Progress Series 83:55–62.

Fréchette, M., and C. Bacher. 1997. A modeling study of

optimal stocking density of mussel populations kept in experimental tanks. Journal of Experimental Marine Biology and Ecology **219**:241–255.

- Fréchette, M., P. Bergeron, and P. Gagnon. 1996. On the use of self-thinning relationships in stocking experiments. Aquaculture 145:91–112.
- Fréchette, M., and D. Lefaivre. 1990. Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. Marine Ecology Progress Series **65**:15–23.
- Fréchette, M., and D. Lefaivre. 1995. On self-thinning in animals. Oikos **73**:425–428.
- Grant, J. W. A. 1993. Self-thinning in stream-dwelling salmonids. Pages 99–102 in R. J. Gibson and R. E. Cuting, editors. Production of juvenile Atlantic salmon, Salmo salar, in natural waters. Canadian Special Publication in Fisheries and Aquatic Sciences No. 118.
- Grant, J., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences **47**:1724–1737.
- Guiñez, R. 1996. Dinámica poblacional del chorito maico, *Perumytilus purpuratus* (Lamarck 1819) (Bivalvia: Mytilidae), en gradientes de exposición al oleaje. Ph.D. dissertation. Pontificia Universidad Católica de Chile. Santiago, Chile.
- Guiñez, R., and J. C. Castilla. 1999. A tridimensional selfthinning model for multilayered intertidal mussels. The American Naturalist 154:341–357.
- Guo, Q., and P. W. Rundel. 1998. Self-thinning in early postfire chaparral succession: mechanisms, implications, and a combined approach. Ecology 79:579–586.
- Hosomi, A. 1985. On the persistent trend of constant biomass and the constant total occupation area of the mussel *Mytilus* galloprovincialis (Lamarck). Japanese Journal of Malacology **44**:33–48.
- Hozumi, K. 1977. Ecological and mathematical considerations on self-thinning in even-aged pure stands. I. Mean plant weight-density trajectory during the course of selfthinning. Botanical Magazine Tokyo 90:165–179.
- Hozumi, K. 1980. Ecological and mathematical considerations on self-thinning in even-aged pure stands. II. Growth analysis of self-thinning. Magazine Tokyo 93:149–166.
- Hughes, R. N., and C. L. Griffiths. 1988. Self-thinning in barnacles and mussels: the geometry of packing. American Naturalist 132:484–491.
- Kira, T. H., H. Ogawa, and N. Sakazaki. 1953. Competitionyield-density interrelationship in regularly dispersed populations (Intraspecific competition among higher plants. I). Journal of the Institute of Polytechnics, Osaka City University, Series D 4:1–16.
- Kirby, J. M. 1991a. Multiple functional regression. 1. Function minimization technique. Computers and Geosciences 17:537–547.
- Kirby, J. M. 1991b. Multiple functional regression. 2. Rotation followed by classical regression technique. Computers and Geosciences 17:895–905.
- Kott, P. 1997. Tunicates (Sub-Phyllum Tunicata). Pages 1092–1255 in S. A. Shepperd and M. Davies, editors. Marine Invertebrates of South Australia, Part III. Series: handbook of the flora and fauna of South Australia. South Australian Research and Development Institute (SARDI) Aquatic Sciences, Adelaide, Australia.

- Kott, P. 1998. Tunicata. Pages 265–292 in A. Wells and W.
  W. K. Houston, editors. Zoological catalogue of Australia.
  Volume 34. Hemichordata, Tunicata, Cephalochordata.
  CSIRO, Melbourne, Australia.
- LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. Annual Review of Ecology and Systematics **20**:97–117.
- Latto, J. 1994. Evidence for a self-thinning rule in animals. Oikos **69**:531–534.
- Long, J. N., and F. W. Smith. 1984. Relation between size and density in developing stands: a description and possible mechanism. Forest Ecology and Management 7:191–206.
- Lonsdale, W. M. 1990. The self-thinning rule: dead or alive? Ecology **71**:1373–1388.
- Marquet, P. A., S. N. Navarrete, and J. C. Castilla. 1995. Body size, population density, and the energetic equivalence rule. Journal of Animal Ecology **64**:325–332.
- Matthew, C., G. Lemaire, N. R. Sackville Hamilton, and A. Hernández-Garay. 1995. A modified self-thinning equation to describe size/density relationships for defoliated swards. Annals of Botany 76:579–587.
- Okamura, B. 1986. Group living and effect of spatial position in aggregations of *Mytilus edulis*. Oecologia **69**:341–347.
- Osawa, A., and R. B. Allen. 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology **74**:1020–1032.
- Osawa, A., and S. Sugita. 1989. The self-thinning rule: another interpretation of Weller's results. Ecology **70**:279– 283.
- Paine, R. T., and T. H. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants; a tunicate-mussel comparison. Evolution 37:821-831.
- Petraitis, P. S. 1995. Use of average vs. total biomass in selfthinning relationships. Ecology **76**:656–658.
- Sackville Hamilton, N. R., C. Matthew, and G. Lemaire. 1995. In defence of the -3/2 boundary rule: a re-evaluation of self-thinning concepts and status. Annals of Botany **76**: 569–577.
- SAS Institute. 1988. SAS/STAT user's guide. Release 6.03 edition. SAS Institute, Cary, North Carolina, USA.
- Scrosati, R. 1996. Implications of the sampling procedure used to estimate mean plant biomass for the analysis of plant self-thinning. Canadian Journal of Botany 74:1543– 1544.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology **64**:209–210.
- Weller, D. E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs 57:23–43.
- Weller, D. E. 1990. Will the real self-thinning rule please stand up?—A reply to Osawa and Sugita. Ecology **71**: 1204–1207.
- Westoby, W. 1984. The self-thinning rule. Advances in Ecological Research 14:167–226.
- White, J. 1981. The allometric interpretation of the self-thinning rule. Journal of Theoretical Biology **89**:475–500.
- White, J., and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. Journal of Ecology **58**:467–485.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Selfthinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants. XI). Journal of the Institute of Polytechnics, Osaka City University, Series D 14:107–109.