1 **DYNAMIC SELF-THINNING MODEL FOR SESSILE ANIMAL**
2 **POPULATIONS WITH MULTILAYERED DISTRIBUTION**

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Abstract

The main drawback of the traditional self-thinning model is how time is handled. Self-thinning (ST) has been formally recognized as a dynamic process, while the current ST models have not included the temporal effect. This restricts the analysis to the average competitive behavior of the population and produces a biased estimation of the self-thinning parameters. In this study we extend the dynamic ST model introduced by Roderick and Barnes (2004) to the analysis of multilayered sessile animal populations. For this purpose, we incorporate the number of layers and the density per layer into the dynamical approach. The performance of the dynamic model was checked and compared with the classical ST model through the analysis of mussel populations grown at different density treatments. Unlike the traditional model, the dynamical approach detected the effect of culture density on the competitive behavior of individuals and allowed to analyze the temporal evolution of intraspecific competition by estimating the ST exponent trajectory. Moreover, this approach provided an ecological interpretation of any possible value of the ST exponent. Thus, our results support the use of the dynamic model in the analysis of self-thinning in sessile animal multilayered populations. The estimation of the ST exponent trajectory reflects the dynamic nature of the ST process, providing a more realistic description of population dynamics than the traditional model.

Keywords: dynamic approach, intraspecific competition, multilayered population, population density, population dynamics.

Introduction

The self-thinning process (ST) describes the inverse relationship between body size of individuals and population density when intraspecific competition causes mortality during growth (Westoby 1984). This mechanism, observed in plants and animals at high population densities, plays an important role in determining population dynamics and community structure (Westoby 1984, Weller 1987, Puntieri 1993, Fréchette and Lefavre 1995, Marquet et al. 1995, Petraitis 1995, Fréchette et al. 1996, Guíñez and Castilla 1999, 2001, Guíñez et al. 2005).

Self-thinning has been analyzed by sequential sampling of even-aged populations growing at different densities (Fig. 1 in Alunno-Bruscia et al. 2000). This allows plotting individual mass-density (m-N) trajectories through time. In sessile animals with multilayered distribution, self-thinning has been modeled by the allometric relationship (Guíñez and Castilla 1999):

$$\bar{m} = K \left(n / SL \right)^{\beta} = K \left(N / L \right)^{\beta} = K N_e^{\beta} \quad (1)$$

where $\bar{m}$ is mean individual mass, n is number of individuals, S is total surface area occupied, N is density, L is number of layers, $N_e = N / L$ is the density per layer or effective density and (K, β) are the model parameters. For a given population, these parameters are estimated from sequential measurements of individual mass and effective density.

ST has been extensively studied in plant populations, where competition is attributed to space limitations (spatial self-thinning, SST) and the theoretical exponent $\beta_{SST} = -3/2$ is proposed (Westoby 1984). On the other hand, Begon et al. (1986) stated that in mobile

animal populations the ST process would be regulated by food limitations (food self-thinning, FST) and suggested the exponent $\beta_{\text{FST}} = -4/3$. Both exponents were proposed under assumptions not always fulfilled under natural conditions; therefore these theoretical exponents should be calculated for each population under study (Lobón-Cervia and Mortensen 2006). As sessile animal populations can be constrained by space or food limitations, most studies have focused on determining the competition factor by comparing the estimated with the theoretical ST exponents (Fréchette and Lefavre 1990, Filgueira et al. 2008, Lachance-Bernard et al. 2010).

The main drawback of the traditional self-thinning model (eqn 1) is how time is handled. While time is present implicitly due to (K, β) are estimated from sequential samplings, the time effect is not explicitly included. This gives rise to two sources of error in the estimation of the ST parameters. First, β and K are assumed to be constant across the entire study period, while the self-thinning is a dynamic process and the ST exponent (β) would vary over time (White 1981, Westoby 1984, Norberg 1988). Therefore, we are estimating a mean value when we should estimate a temporal trend. On the other hand, the regression methods currently used for its study (reviewed by Zhang et al. 2005) assume that observations are independent, overlooking their temporal autocorrelation and resulting in a biased estimation of the self-thinning parameters.

Thus, while self-thinning has been formally recognized as a dynamic process, the current analysis procedures have not been dynamic, failing to include the time effect. Cubillo et al. (2012b) partially overcame this problem fitting the traditional ST model by frontier analysis, which provides a dynamic interpretation of the ST process through the temporal evolution of site occupancy. On the other hand, Roderick and Barnes (2004) proposed a new formulation of self-thinning as a dynamic problem. The main

assumption of this approach is that β can vary over time, but converges to -1 when total biomass is constant, given that:

$$\bar{m} = \frac{\sum m}{n} = \frac{\sum m}{SL} \frac{SL}{n} = \frac{\sum m}{SL} \left(\frac{n}{SL} \right)^{-1} = \frac{\sum m}{SL} N_e^{-1} = K N_e^{-1}$$

This study extends the dynamic self-thinning model proposed by Roderick and Barnes (2004) for plants to the study of multilayered sessile animal populations. For this purpose we include the effective density (N_e) in the original model. Then, we give insight into the dynamic interpretation of the different values of the ST exponent. Finally, we compare the dynamic ST model with the classical model through the analysis of mussel (*Mytilus galloprovincialis* Lmk.) populations grown in suspended culture.

Materials and methods

Experimental design

This work analyzes the dataset from Cubillo et al. (2012b) that studied the population dynamics of *Mytilus galloprovincialis* grown in suspended culture. Data were obtained by sequential sampling of seven initial densities (220, 370, 500, 570, 750, 800 and 1150 individuals per meter of rope, ind/m) randomly distributed over a commercial raft. Seven monthly samplings were performed from thinning-out to harvest (May-November 2008). In each sampling, a section of known length was taken from 4 ropes of each density (28 ropes per sampling date). Each sample was weighed to obtain the population biomass (B; g). Density was calculated as number of mussels per meter of

rope (N_0 ; ind/m) and standardized to number of individuals per square meter of rope (N ; ind/m²). Mean individual fresh mass ($\bar{m}$; g) was obtained dividing the weight of subsamples containing 250-300 mussels by the number of individuals. To account for multilayering, we need the effective surface area occupied (S_e), that is, the surface occupied if individuals were arranged in a single layer (Guiñez et al. 2005). The effective surface area (S_e) was obtained by image analysis techniques (Filgueira et al. 2008). The effective density or mean number of individuals per layer ($N_e = N_0/S_e$) and number of layers ($L = N/N_e$) were calculated according to Guiñez and Castilla (2001).

Dynamic self-thinning model

We extended the dynamic model proposed by Roderick and Barnes (2004) for the analysis of self-thinning in plants to the study of multilayered sessile animal populations. For this purpose, we substituted the density or number of individuals per unit area (N) by the effective density (N_e) defined in the self-thinning model (Guiñez and Castilla 1999, Cubillo et al. 2012b).

Assuming that the allometric relationship expressed in eqn 1 is an identity, the unknown parameters (K , β) are uniquely determined by the effective density and mean individual mass observed in two instants of time. If $(\bar{m}_1, N_{e1})$ and $(\bar{m}_2, N_{e2})$ are the values observed at successive instants of time t_1 and t_2 , substituting these values in the logarithmic transformation of eqn 1 yields:

$$\begin{aligned} \ln \bar{m}_1 &= \log K + \beta \ln N_{e1} \\ \ln \bar{m}_2 &= \log K + \beta \ln N_{e2} \end{aligned} \quad (2)$$

121 Solving eqn 2 by elimination:

$$122 \quad \beta = \frac{\ln(\bar{m}_2/\bar{m}_1)}{\ln(N_{e2}/N_{e1})} \quad (3)$$

123 and

$$124 \quad \ln K = \ln \bar{m}_1 - \beta \ln N_{e1} \quad (4)$$

125 Thus, the estimated values of K and β belong to the same time interval as the
 126 measurements used to estimate them. This procedure is repeated for each pair of
 127 consecutive samplings to estimate the parameters corresponding to each time interval.

128 The procedure above would be used when observations are made for a finite number of
 129 points in time. However, from a theoretical viewpoint it is useful to extend the analysis
 130 to infinitesimal time intervals which allows an analytical treatment of self-thinning
 131 (Roderick and Barnes 2004). For this purpose, we should note that:

$$132 \quad \begin{aligned} \bar{m}_2 &= \bar{m}_1 + \delta \bar{m} \\ N_{e2} &= N_{e1} + \delta N_e \end{aligned} \quad (5)$$

133 where δ denotes a finite difference. Using eqn 5, we can rewrite eqn 3 as:

$$134 \quad \beta = \frac{\ln(1 + \delta \bar{m}/\bar{m}_1)}{\ln(1 + \delta N_e/N_{e1})} \quad (6)$$

135 For infinitesimal time increments, $\delta \bar{m} \rightarrow d\bar{m}$ and $\delta N_e \rightarrow dN_e$, as $\ln(1+x) \rightarrow x$ for small
 136 values of x:

$$137 \quad \beta = \frac{d\bar{m}}{\bar{m}} \frac{N_e}{dN_e} \quad (7)$$

Eqn 7 defines the self-thinning exponent (β) as the quotient between the rates of change of individual mean mass and density, which is very useful in interpreting the dynamic model.

In order to link the dynamic model with the self-thinning process we should note that, for a set of n individuals in a given area at time t , the total biomass of the area is:

$$B = m_1 + \dots + m_n = n\bar{m} \quad (8)$$

Thus if N_e is the effective density, that is, the number of individuals per unit of area in each layer, the biomass per layer is:

$$B_L = \frac{n\bar{m}}{SL} = N_e \bar{m} \quad (9)$$

The biomass rate of change is then:

$$\frac{dB_L}{dt} = \bar{m} \frac{dN_e}{dt} + N_e \frac{d\bar{m}}{dt} \quad (10)$$

and when the biomass remains constant, $dB_L/dt = 0$, we have:

$$\bar{m} \frac{dN_e}{dt} = -N_e \frac{d\bar{m}}{dt} \quad (11)$$

Thus, since $\bar{m}$ and N_e are always positive, dN_e and $d\bar{m}$ must have opposite signs, that is, an increase in mass implies a decrease in density, which can be due to mortality as well as reorganization of the individuals into new layers (migration), and viceversa.

Comparing eqn 7 and 10, we see that β is the ratio of the terms on the right side of eqn 10. Thus, when biomass remains constant, $\beta \approx -1$ (eqn 11). This can reflect two situations: (i) dN_e/dt and dm/dt are bounded away from 0, and the rates of change of

individual mass and effective density are equivalent, or (ii) $dN_e/dt \approx 0$ and $dm/dt \approx 0$, thus competition ameliorates and the system is stabilized. Generalizing, when $dN_e/dt < 0$, such as with mortality and/or migration, then $\beta < -1$ (e.g. $-3/2$, $-4/3$) if $dB_L/dt > 0$, that is, the growth rate is greater than the mortality rate; and $\beta > -1$ if $dB_L/dt < 0$, that is, the growth rate is lower than the mortality rate. The opposite holds for $dN_e/dt > 0$. When the effective density remains constant, $dN_e/dt = 0$, β tend to (either positive or negative) infinity (see Table 1).

Statistical analysis

We tested the validity of the dynamic self-thinning model and compared this approach with the traditional ST model through the analysis of multilayered mussel populations grown in suspended culture. Firstly, for each density treatment, the traditional ST model (eqn 1) was fitted by the regression methods applied in Cubillo et al. (2012b). We tested whether the traditional model can detect different competition patterns among densities. The estimated exponents were also compared with the theoretical food self thinning (FST) exponent ($\beta_{FST}=-1.33$) and the space self-thinning (SST) exponent obtained by image analysis techniques ($\beta_{SST}=-1.23$; Cubillo et al. 2012b), to discriminate the competition limiting factor.

In order to fit the dynamic model, $M=1000$ replicates of effective density (N_e) and mean individual mass ($\bar{m}$) were obtained by Monte Carlo simulations for each time and density treatment. Then, the self-thinning exponent and its 95% confidence interval were estimated for each sampling interval (eqn 7). Tukey tests were applied to determine whether $\beta = -1$, that is, whether the biomass remained constant between samplings.

The statistical analysis was performed with the help of the statistical package R 2.12.2 (R Development Core Team, 2011).

Results

Fig. 1 shows the temporal evolution of density (N), effective density (N_e), biomass (B), biomass per layer (B_L), number of layers (L) and mean individual fresh mass ($\bar{m}$) for each density treatment (Tables A.1-A.7). While density, number of layers, and biomass depended on the initial density; mean individual mass, effective density and biomass per layer were homogeneous over the density gradient. We observe a trade-off between the exponential decrease in effective density and the increase in individual fresh mass, for all treatments. The density plot shows that mortality occurred only at high initial densities ($N > 500$ ind/m). Thus, for low-density populations the decrease in N_e would respond only to reorganization of individuals into new layers (migration), while for higher densities this would also include mortality. At lower densities the number of layers increased steadily throughout the experimental period, while at higher densities the reorganization of growing individuals caused a continuous readjustment between the number of layers and the effective density. Mean individual mass, biomass, and biomass per layer increased in the first months and remained constant in the last three months.

Table 2 shows the fits of the classical self-thinning model (eqn 1) for each density treatment. Since the different regression methods applied provide equivalent estimates, only the linear regression (ordinary least squares, OLS) fit is shown. Although we obtained a good fit for m - N_e relationships ($R^2 > 0.94$), no significant effect of density treatment on the estimated exponents was observed (see CIs for β in Table 2). Comparison of the estimated exponents with the theoretical space ($\beta_{SST} = -1.23$; Cubillo

et al. 2012b) and food ($\beta_{\text{FST}}=-1.33$) ST exponents, concluded that competition for food and space dominated at 220, 500, 700 and 800 ind/m with competition for food dominating at 370, 570 and 1150 ind/m (Table 2). These results point out the inefficiency of the classical model to discriminate the competition limiting factor.

Table 3 shows the estimated self-thinning exponents obtained with the dynamic model, and Figures 2-8 show the plots of the traditional and dynamic fits for each density treatment. The high variability observed for β in certain months responded to small changes in effective density ($dN_e/dt \approx 0$).

During the first three months, mussels grown at lower initial densities (220, 370 and 500 ind/m) presented higher growth than migration rates, giving rise to a progressive increase in biomass per layer and to a ST exponent $\beta < -1$ (Figs 2-4). As $dL/dt \geq 0$, population biomass also increased. In the last three months (from September onwards) both rates were fairly equivalent and tended to 0, thus $\beta \approx -1$.

Mussels grown at 570 ind/m (Fig. 5) showed a different behavior. In June, the decrease in effective density - which from this treatment is attributable to both mortality and reorganization into new layers (migration) (Fig. 1) - was lower than the growth rate, and $\beta < -1$. In July, the rate of growth and decrease in effective density were similar and $\beta = -1$; as $dL/dt \approx 0$, population biomass remained constant. In August, the growth rate rose leading to an increase in biomass and $\beta \ll -1$. From August onwards growth and density decrease rates were similar and $\beta = -1$.

The 700 and 800 ind/m density treatments (Figs 6 and 7) showed a similar pattern. During the first months (up to September and August, respectively) the growth rate was higher than the decrease in effective density, leading to a progressive increase in both

biomass per layer and population biomass ($\beta < -1$). Afterwards, both rates tended to 0 and $\beta = -1$, with the exception of November for 700 ind/m, where the growth rate was higher than 0 and $\beta < -1$.

Mussels grown at 1150 ind/m (Fig. 8) followed a different pattern than the other density treatments. In June, the mortality-migration rate was higher than the growth rate ($\beta > -1$) indicating stronger intraspecific competition than at lower densities. After the readjustment in density, this trend was reversed in the next two months and led to $\beta < -1$, being particularly low in July as $dN_e/dt \rightarrow 0$. In September, the growth and N_e decrease rates were equivalent ($\beta = -1$) and the biomass per layer remained constant. From October $\beta < -1$, but the change in sign of dN_e/dt between samplings reflected different behaviors and caused discontinuities in the ST trajectory. In October the effective density rose - due to a reduction in the number of layers (Fig. 1) - at a lower rate than individual mass decreased. In November, $dN_e/dt < 0$ again, and the decrease in effective density was lower than the rate of growth. Thus, on contrast to the other density treatments, at 1150 ind/m effective density did not stabilize at the end of the experimental period.

Discussion

In this study we extend the dynamic self-thinning model proposed by Roderick and Barnes (2004) to the analysis of multilayered sessile animal populations. Comparison of this model against the classical self-thinning model shows that the dynamic approach outperforms the traditional model in several points.

The estimation of the ST exponent trajectory reflects the dynamic nature of the ST process (White 1981; Westoby 1984), while the traditional model assumes constant ST

parameters, and restricts the analysis to the average competitive behavior of the population. The “dynamic thinning line” had already been defined as the temporal evolution of the mass-density relationship in a population (Xue and Hagihara 1998; Begon et al. 2006; Nash et al. 2007; Chen et al. 2008). However, its study was limited to the linear asymptote of this relationship (Fig. 6 in Chen et al. 2008), overlooking the time effect. From the methodological viewpoint, the assumption of independence for sequential autocorrelated data by the classical model leads to underestimate the error (overestimate the goodness of fit) and produces a biased estimation of the self-thinning parameters. The dynamic model, which analyzes each sampling interval separately, overcomes this error.

Unlike the classical self-thinning model, the dynamical approach detected the effect of density treatment on the competitive behavior of individuals and population dynamics. Particularly, the exponent trajectory of the highest density (1150 ind/m) differed from the other density treatments, which showed similar trends. However, it should be noted that similar exponent trends could reflect different dynamics. Thus, at initial densities lower than 570 ind/m, the decrease in effective density was exclusively due to reorganization into new layers (migration), while at higher densities (570 - 1150 ind/m) it also included mortality. At the beginning of our study, mussel growth exceeded mussel migration-mortality rate, except for the 1150 ind/m treatment. This indicates a greater intraspecific competition at high density levels and suggests that the carrying capacity of the system was reached. After the initial fall in N_e , the availability for limiting resources increased and in the next two months, as for the lower densities, the individuals were able to grow at a greater rate than density decreased. In populations with initial densities below 1150 ind/m, from September onwards the biomass remained

constant and both density decrease and individual growth tended to 0, probably because the growth curve asymptote had been reached (Cubillo et al. 2012a). Therefore, intraspecific competition was no longer observed for these densities, while at higher density levels (1150 ind/m) population kept regulating at the end of the experiment and need longer to reach asymptotic growth (Fig. 1).

The classical ST model is based on allometric relationships depending on a series of assumptions (Fréchette and Lefavre 1990) that do not always hold in the natural field. Conversely, the dynamic model is based on a mathematical axiom (eqn 8) and its validity does not depend on the environmental conditions. The dynamic model is a generalization of the former but, as it is not based on the same allometric relationships, the estimated exponents are not comparable to the theoretical exponents of the classical model. Rather than discriminating the limiting factor, which has been one of the main goals in the ST analysis, the dynamic model focuses on analyzing the evolution of intraspecific competition over time (Table 1). Therefore, this new approach provides a more realistic description of population dynamics. Moreover, the dynamic model allows the ecological interpretation of any possible value of β , while the traditional model cannot explain any exponent different from the theoretical ones. Finally, our results confirm the difficulty of the classic model to achieve its main objective of distinguishing the competition limiting factor, as observed in Cubillo et al. (2012b).

In the application of the dynamic self-thinning approach two aspects should be noted. First, changes of sign in dN_e/dt introduce a discontinuity in the trajectory of the ST exponent. This should be considered when describing the ST process, since similar exponents can actually reflect opposite behaviors (Table 1), as observed for the 1150 ind/m density in the last two months (Fig. 8, Table 2). In addition, for a proper

ecological interpretation of self-thinning we should analyze simultaneously the estimated exponent (β) and the variables involved in the process (density, total biomass and individual mass, as well as effective density, number of layers and biomass per layer for multilayered populations). This highlights the difficulty of interpreting an intricate process as self-thinning through a single parameter (β).

In summary, this study demonstrates the applicability of the self-thinning dynamic model proposed by Roderick and Barnes (2004) to the analysis of multilayered sessile animal populations. Moreover, in contraposition with the classical self-thinning model, the dynamical approach allows studying the effect of population density on the competitive behavior of individuals and gives insight into the temporal evolution of intraspecific competition, providing a more realistic description of population dynamics. Therefore this approach would lead to an improvement in the ecological and economic management of gregarious sessile animal populations.

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APPENDIX 1: Descriptive analysis of the variables involved in the self-thinning process for each density treatment.

Table A.1. Mean and SD of density (N ; ind/m²), effective density (N_e ; ind/m²L), number of layers (L), mean individual fresh mass (m ; g), total biomass (B ; kg) and biomass per layer (B_L ; kg) over the experimental period for 220 ind/m.

	220	N	N_e	L	m	B	B_L
May	Mean	2759.50	2622.40	1.05	12.99	33.90	32.25
	SD	289.20	74.73	0.11	0.90	3.06	1.24
June	Mean	2799.77	2011.78	1.40	18.74	49.83	35.48
	SD	121.82	124.16	0.15	2.02	7.44	1.67
July	Mean	2835.44	1707.40	1.66	23.07	61.83	37.24
	SD	383.80	33.84	0.25	1.44	9.15	2.04
August	Mean	2218.35	1463.75	1.52	28.61	60.05	39.65
	SD	195.11	59.32	0.11	0.99	4.85	1.69
September	Mean	2493.67	1283.57	1.93	32.28	75.05	38.99
	SD	613.28	87.43	0.34	2.94	11.40	1.08
October	Mean	2550.63	1194.06	2.14	35.42	91.05	42.34
	SD	402.62	53.49	0.32	2.50	20.58	3.10
November	Mean	2591.77	1159.85	2.23	37.16	90.18	40.42
	SD	140.34	28.73	0.11	1.79	3.42	1.17

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412 **Table A.2.** Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L),
 413 number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and
 414 biomass per layer (B_L; kg) over the experimental period for 370 ind/m.

370		N	N _e	L	m	B	B _L
May	Mean	4689.88	2559.75	1.83	12.26	56.15	30.90
	SD	669.97	92.89	0.21	0.86	4.05	2.62
June	Mean	4778.48	2114.39	2.25	16.45	75.18	33.30
	SD	822.26	94.65	0.31	1.45	12.62	1.79
July	Mean	4643.99	1784.59	2.61	20.67	94.23	35.97
	SD	800.32	74.40	0.48	0.68	19.94	1.07
August	Mean	4219.62	1520.97	2.77	26.94	105.23	37.97
	SD	285.48	53.70	0.09	0.98	5.74	0.88
September	Mean	3817.72	1248.79	3.06	32.26	127.20	41.64
	SD	213.27	32.70	0.16	1.42	10.94	4.14
October	Mean	4351.27	1228.51	3.54	33.36	143.55	40.59
	SD	796.19	28.11	0.64	1.57	25.23	1.06
November	Mean	3517.18	1181.08	2.99	39.95	130.45	44.25
	SD	455.92	58.66	0.49	3.84	8.07	5.80

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Table A.3. Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L), number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and biomass per layer (B_L; kg) over the experimental period for 500 ind/m.

500		N	N _e	L	m	B	B _L
May	Mean	6342.70	2759.13	2.30	11.73	82.95	36.52
	SD	750.91	111.82	0.22	0.94	5.80	5.87
June	Mean	5750.00	2041.44	2.82	17.06	96.30	33.91
	SD	911.18	24.84	0.45	1.46	21.60	3.14
July	Mean	6144.62	1762.92	3.52	21.14	123.85	35.04
	SD	814.83	128.43	0.67	2.42	27.50	1.59
August	Mean	5991.46	1501.06	3.99	26.13	146.58	36.74
	SD	594.01	14.25	0.38	0.63	13.80	0.20
September	Mean	6334.50	1346.27	4.71	29.63	174.43	37.13
	SD	581.04	59.31	0.36	2.31	8.93	1.08
October	Mean	5142.09	1230.78	4.17	33.26	160.23	38.44
	SD	503.83	40.78	0.33	1.87	10.20	0.73
November	Mean	5664.56	1234.90	4.59	33.00	174.25	38.02
	SD	363.17	17.44	0.25	0.57	7.54	0.57

Table A.4. Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L), number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and biomass per layer (B_L; kg) over the experimental period for 570 ind/m.

	570	N	N _e	L	m	B	B _L
May	Mean	7192.60	2660.65	2.71	11.57	83.35	30.77
	SD	514.96	136.99	0.29	0.15	8.23	1.29
June	Mean	7626.27	2022.27	3.78	17.67	120.90	31.95
	SD	373.49	102.35	0.33	1.39	23.58	5.30
July	Mean	7272.15	1793.32	4.08	19.49	137.08	33.57
	SD	465.61	111.37	0.47	1.84	19.48	1.34
August	Mean	6487.34	1628.62	3.99	25.12	174.70	43.96
	SD	513.19	64.97	0.38	2.38	18.51	4.70
September	Mean	6281.65	1385.94	4.54	28.86	173.45	38.21
	SD	738.80	28.98	0.58	0.72	23.07	0.94
October	Mean	6246.84	1368.73	4.58	30.30	175.60	38.43
	SD	363.58	52.19	0.43	0.96	12.34	1.09
November	Mean	5113.93	1214.18	4.21	33.52	160.30	38.12
	SD	573.22	29.61	0.36	1.95	13.64	1.49

Table A.5. Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L), number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and biomass per layer (B_L; kg) over the experimental period for 700 ind/m.

700		N	N _e	L	m	B	B _L
May	Mean	8936.70	2630.53	3.41	12.63	110.50	32.42
	SD	109.39	149.70	0.18	0.83	10.54	1.79
June	Mean	7694.30	2048.47	3.78	16.72	131.90	34.92
	SD	669.19	148.59	0.56	1.84	18.51	1.47
July	Mean	6621.84	1664.80	3.98	23.17	145.48	36.45
	SD	995.50	47.66	0.59	1.14	26.31	2.01
August	Mean	6898.74	1461.62	4.71	27.58	175.88	37.42
	SD	1237.58	45.95	0.71	3.53	24.17	1.61
September	Mean	7055.38	1296.67	5.45	30.94	208.83	38.32
	SD	1074.40	23.54	0.91	1.64	34.92	1.27
October	Mean	6934.18	1246.34	5.57	32.98	164.75	29.59
	SD	366.46	75.80	0.26	2.02	46.98	8.18
November	Mean	6929.21	1169.08	5.93	35.86	260.10	43.87
	SD	366.28	43.29	0.19	2.84	45.55	7.56

Table A.6. Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L), number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and biomass per layer (B_L; kg) over the experimental period for 800 ind/m.

800		N	N _e	L	m	B	B _L
May	Mean	10126.60	2667.28	3.80	11.61	113.38	29.82
	SD	576.59	64.30	0.27	1.46	9.91	1.01
June	Mean	9603.48	2166.36	4.44	15.53	138.17	31.00
	SD	121.12	136.69	0.24	1.45	24.26	4.47
July	Mean	9224.68	1800.66	5.13	19.73	177.70	34.49
	SD	1179.69	41.57	0.69	0.73	31.38	1.53
August	Mean	8821.20	1508.45	5.85	25.45	212.95	36.45
	SD	775.75	24.50	0.46	1.28	16.60	1.27
September	Mean	7531.65	1406.15	5.36	27.01	225.70	42.64
	SD	896.57	31.23	0.70	1.20	5.89	5.64
October	Mean	7372.15	1284.94	5.74	30.74	166.60	29.40
	SD	546.22	32.36	0.48	3.41	37.43	8.28
November	Mean	8268.99	1219.98	6.77	33.86	249.38	36.78
	SD	744.01	51.11	0.45	4.69	52.37	6.65

Table A.7. Mean and SD of density (N; ind/m²), effective density (N_e; ind/m²L), number of layers (L), mean individual fresh mass (m; g), total biomass (B; kg) and biomass per layer (B_L; kg) over the experimental period for 1150 ind/m.

1150		N	N _e	L	m	B	B _L
May	Mean	14588.63	3007.03	4.87	10.13	160.78	33.18
	SD	323.78	182.61	0.32	0.96	19.18	4.84
June	Mean	14373.42	2149.96	6.71	13.70	214.38	31.93
	SD	645.57	113.28	0.56	2.92	29.67	2.80
July	Mean	12286.39	2042.59	6.05	17.28	215.05	35.48
	SD	974.49	113.84	0.79	0.58	33.70	1.51
August	Mean	9683.23	1491.20	6.49	27.05	243.75	37.52
	SD	1076.51	45.10	0.67	1.59	29.26	1.39
September	Mean	10056.01	1338.80	7.52	29.62	315.43	42.02
	SD	403.61	42.42	0.49	1.72	62.80	8.78
October	Mean	9061.08	1530.06	5.96	25.31	266.93	46.04
	SD	782.88	106.10	0.79	2.74	33.20	13.00
November	Mean	8452.88	1221.20	6.93	33.57	292.00	42.26
	SD	925.28	47.87	0.77	1.50	53.44	7.22

Figure legends.

Fig. 1. Temporal evolution of density (N), effective density (N_e), biomass (B), biomass per layer (B_L), number of layers (L) and mean individual mass ($\bar{m}$) for each density treatment. 1: May, 2: June, 3: July, 4: August, 5: September, 6: October and 7: November.

Fig. 2. Left: classical self thinning model. Right: dynamic self-thinning model, exponents (solid line) and 95% confidence band (dashed line) for 220 ind/m. 1: June, 2: July, 3: August, 4: September, 5: October and 6: November.

Fig. 3. Left: classical self thinning model. Right: dynamic self-thinning model, exponents (solid line) and 95% confidence band (dashed line) for 370 ind/m. 1: June, 2: July, 3: August, 4: September, 5: October and 6: November.

Fig. 4. Left: classical self thinning model. Right: dynamic self-thinning model, exponents (solid line) and 95% confidence band (dashed line) for 500 ind/m. 1: June, 2: July, 3: August, 4: September, 5: October and 6: November.

Fig. 5. Left: classical self thinning model. Right: dynamic self-thinning model, exponents (solid line) and 95% confidence band (dashed line) for 570 ind/m. 1: June, 2: July, 3: August, 4: September, 5: October and 6: November.

Fig. 6. Left: classical self thinning model. Right: dynamic self-thinning model, exponents (solid line) and 95% confidence band (dashed line) for 700 ind/m. 1: June, 2: July, 3: August, 4: September, 5: October and 6: November.

463 **Fig 7.** Left: classical self thinning model. Right: dynamic self-thinning model,
464 exponents (solid line) and 95% confidence band (dashed line) for 800 ind/m. 1: June, 2:
465 July, 3: August, 4: September, 5: October and 6: November.

466 **Fig. 8.** Left: classical self thinning model. Right: dynamic self-thinning model,
467 exponents (solid line) and 95% confidence band (dashed line) for 1150 ind/m. 1: June,
468 2: July, 3: August, 4: September, 5: October and 6: November.

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470 **Table 1.** Ecological interpretation of self-thinning exponents (β).

Biomass		Effective density	β	Interpretation
$dB_I/dt=0$	$\frac{dN_e}{N_e} = -\frac{d\bar{m}}{\bar{m}}$		$\beta = -1$	Total biomass remains constant.
$dB_I/dt>0$	$\frac{dN_e}{N_e} > -\frac{d\bar{m}}{\bar{m}}$	$dN_e/dt < 0$	$\beta < -1$	$dm/dt > 0$, growth rate is greater than mortality-migration rate.
		$dN_e/dt > 0$	$\beta > -1$	If $dm/dt < 0$, individual mass loss is lower than density increase ($-1 < \beta < 0$). If $dm/dt > 0$, both density and mass increase, no competition is observed ($\beta > 0$).
		$dN_e/dt = 0$	$\beta \rightarrow +\infty$	$dm/dt > 0$
$dB_I/dt<0$	$\frac{dN_e}{N_e} < -\frac{d\bar{m}}{\bar{m}}$	$dN_e/dt < 0$	$\beta > -1$	If $dm/dt > 0$, growth rate is lower than mortality/migration rate ($-1 < \beta < 0$). If $dm/dt < 0$, both density and mass decrease ($\beta > 0$).
		$dN_e/dt > 0$	$\beta < -1$	$dm/dt < 0$, i.e. individual mass loss is greater than the rate of density increase.
		$dN_e/dt = 0$	$\beta \rightarrow -\infty$	$dm/dt < 0$

473 **Table 2.** OLS fit for the tridimensional model ($\bar{m} = KN_e^\beta$), estimated parameters and
 474 95% confidence intervals for each density treatment.

Ind/m	log(K)	CI	β	CI	R^2
220	12.402	[11.539, 13.265]	-1.2461	[-1.363, -1.129]	0.9464
370	13.488	[12.639, 14.336]	-1.3970	[-1.512, -1.282]	0.9585
500	12.640	[11.878, 13.401]	-1.2844	[-1.387, -1.182]	0.9606
570	13.300	[12.558, 14.043]	-1.3730	[-1.473, -1.273]	0.9672
700	12.684	[11.876, 13.491]	-1.2895	[-1.399, -1.180]	0.9558
800	13.011	[12.137, 13.886]	-1.3381	[-1.456, -1.220]	0.9527
1150	13.433	[12.413, 14.454]	-1.3944	[-1.531, -1.258]	0.9421

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Table 3. Estimated self-thinning exponents for the dynamical approach, 95% confidence intervals and p-values of Tukey test for $H_0: \beta = -1$.

		June	July	August	September	October	November
220	β	-1.370	-1.356	-1.495	-1.030	-1.863	-0.303
	2.5%	-1.403	-1.410	-1.536	-1.099	-2.352	-1.496
	97.5%	-1.338	-1.301	-1.453	-0.961	-1.375	0.892
	p	<0.0001	<0.0001	<0.0001	0.3964	0.0005	0.2525
370	β	-1.579	-1.415	-1.747	-0.940	-0.179	-2.649
	2.5%	-1.620	-1.457	-1.781	-0.963	-1.160	-4.553
	97.5%	-1.538	-1.373	-1.712	-0.918	0.802	-0.745
	p	<0.0001	<0.0001	<0.0001	<0.0001	0.1008	0.0895
500	β	-1.243	-1.503	-1.452	-1.483	-1.343	-0.271
	2.5%	-1.267	-1.574	-1.509	-1.875	-1.962	-0.954
	97.5%	-1.218	-1.433	-1.394	-1.091	-0.723	0.413
	p	<0.0001	<0.0001	<0.0001	0.0157	0.2781	0.0365
570	β	-1.539	-0.997	-3.021	-0.963	-0.814	-1.123
	2.5%	-1.561	-1.099	-3.247	-1.010	-1.578	-1.376
	97.5%	-1.517	-0.895	-2.795	-0.915	-0.050	-0.871
	p	<0.0001	0.954	<0.0001	0.1255	0.6327	0.3382
700	β	-1.148	-1.618	-1.412	-1.183	-1.464	-2.357
	2.5%	-1.181	-1.659	-1.501	-1.281	-2.383	-3.334
	97.5%	-1.115	-1.576	-1.323	-1.085	-0.545	-1.380
	p	<0.0001	<0.0001	<0.0001	0.0003	0.3220	0.0065
800	β	-1.484	-1.333	-1.502	-1.139	-1.177	-1.751
	2.5%	-1.536	-1.371	-1.533	-1.394	-1.734	-3.458
	97.5%	-1.432	-1.295	-1.470	-0.883	-0.619	-0.045
	p	<0.0001	<0.0001	<0.0001	0.2882	0.5341	0.3878
1150	β	-0.842	-5.690	-1.438	-0.975	-1.280	-1.249
	2.5%	-0.889	-7.834	-1.454	-1.066	-1.413	-1.285
	97.5%	-0.796	-3.545	-1.421	-0.885	-1.146	-1.214
	p	<0.0001	<0.0001	<0.0001	0.5946	<0.0001	<0.0001

Fig. 1.

Fig. 2.

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486 **Fig. 3.**

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Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.