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A review on self-thinning in mussels

Una revisión del auto-raleo en mitílidos

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Abstract.- Marine bivalves of the family Mytilidae have achieved an impressive ability to dominate rocky shores. Mussel populations usually form highly dense, overcrowded and multilayered matrices or beds, where intraspecific competition is intense and so, self-thinning processes are expected to occur. In this work, I review the literature on self-thinning in mussels with special reference to the development of new models. I suggest that more experimental and theoretical work is needed to properly understand space- and food-driven self-thinning in overcrowded and multilayered mollusks. I conclude that the development of new kinds of 3D models that include explicitly the crowding or layering effects on self-thinning would open new theoretical and experimental avenues to explore the relationship between density and size, not only in mussels but also in gregarious animals in general.

Key words: Littoral, intraspecific competition, self-thinning, space driven, food driven, bivalves

Resumen.- Los bivalvos marinos de la familia Mytilidae, más conocidos como choritos, se destacan por su abundancia y capacidad de ser especies dominantes en las costas rocosas de todo el mundo. En general, las especies de choritos tienden a formar matrices (o mantos) altamente densas y multiestratificadas, en cuyo interior ocurre una intensa competencia intraespecífica, siendo esperable la existencia de procesos de auto-raleo. En este trabajo, reviso la literatura de auto-raleo en mitílidos, con especial referencia al desarrollo de nuevos modelos. Es evidente la necesidad de realizar más trabajo experimental y teórico para comprender apropiadamente el rol de la competencia por espacio o por explotación sobre la dinámica del auto-raleo en especies gregarias. Se concluye que el desarrollo de nuevos modelos tridimensionales, que incluyen explícitamente los efectos del modo en que se ocupa el espacio, está permitiendo abrir nuevas avenidas teóricas y experimentales para explorar la relación entre densidad, tamaño corporal y biomasa no sólo en choritos, sino que también en animales gregarios en general.

Palabras clave: Litoral, competencia intraespecífica, auto-raleo, competencia por espacio, competencia por explotación, bivalvos

Introduction

Despite recurrent criticism of its empirical and conceptual foundations, the self-thinning rule is one of the few long-lived quantitative propositions in ecology (Torres *et al.* 2001). This success lies not so much in its accurate description of self-thinning as in its capacity to attract the attention of ecologists to the relationship between size and number of individuals (Zeide 1991). The process of self-thinning (ST) occurs when individuals grow at high population density, resulting in a negative relationship between individuals per area (N) and average individual mass (m) or biomass per area (B) (Westoby 1984). Self-thinning has been observed in crowded animal and plant populations as a result of

intraspecific competition, and plays an important role in determining population dynamics and community structure (Westoby 1984, Puntieri 1993, Fréchette & Lefaiivre 1995, Marquet *et al.* 1995, Petraitis 1995, Fréchette *et al.* 1996, Guíñez & Castilla 1999, 2001, Guíñez *et al.* 2005). The aim in this paper is to review the evidence of self-thinning process as applied to mussels with special reference to the development of new self-thinning models proposed.

Mussels and crowding

Mollusks represent the second most diverse group of animals, and marine bivalves are the second most abundant mollusks after gastropods, from which

mussels (family Mytilidae) have achieved an impressive ability to dominate rocky shores, especially littoral, on all continents (Suchanek 1986). Their world-wide success as dominant space occupiers is most pronounced at exposed or semi-exposed sites in temperate habitats, especially on horizontal or gently sloping rocky substrata. Mussel species usually form highly dense and structurally complex matrices, which sometimes are overcrowded and form multilayered beds (Suchanek 1986, Alvarado & Castilla 1996, Guíñez 1996, Guíñez & Castilla 1999). For example, *Aulacomya ater* (Molina, 1872), *Mytilus galloprovincialis* (Lamarck), *Mytilus californianus* (Conrad, 1837) and *Perumytilus purpuratus* (Lamarck, 1819) form dense, multilayered beds, whereas *Choromytilus meridionalis* (Lamarck) is usually monolayered (Hosomi 1985, Suchanek 1986, Van Erkom Schurink & Griffiths 1993, Alvarado & Castilla 1996, Guíñez 1996). Also, it has been observed that multilayering varies among different sites and populations, as in the case of *P. purpuratus* and *M. californianus* (Alvarado & Castilla 1996, Connolly & Roughgarden 1998, Guíñez & Castilla 1999). Suchanek (1986) reported that the beds of *M. californianus* were often five or six layers deep; Hosomi (1985) estimated the occurrence of up to four layers in *M. galloprovincialis*; and in *P. purpuratus* beds Alvarado & Castilla (1996) reported up to three layers, and Guíñez *et al.* (2005) have estimated up to five layers in beds located in northern Chile. This mussel overcrowding leads to intense intraspecific competition (Seed 1968, Harger & Ladenberger 1971, Bertness & Grosholz 1985, Okamura 1986, Ardisson & Bourget 1991, Alvarado & Castilla 1996, Guíñez 1996, Guíñez & Castilla 1999), which has been identified as a major source of mortality (Stiven & Kuenzler 1979, Griffiths & Hockey 1987, McGrorty *et al.* 1990, Richardson & Seed 1990, Stillman *et al.* 2000). Consequently, the existence of ST processes in mussels is highly expected (Hosomi 1985, Hughes & Griffiths 1988, Fréchette & Lefavre 1990, Ardisson & Bourget 1991, Fréchette & Lefavre 1995, Petraitis 1995, Guíñez & Castilla 1999, Guíñez *et al.* 2005).

Traditional models of self-thinning and related patterns

It has been customary to describe ST as a single bidimensional self-thinning line, represented by the log transformed form of the power equation: $B = k_2 N^{\beta_2}$ (Eq. 1) or alternatively $m = k_2 N^{\gamma_2}$ (Eq. 2). Where, N is individuals per unit area, m is population mean mass, B is total biomass per area and k_2, β_2 ($\gamma_2 = \beta_2 - 1$) are constants known as the thinning coefficient and

exponent, respectively. The subscript 2 recalls that this model corresponds to a bidimensional approach (2D) (Guíñez & Castilla 1999).

Theoretical and experimental evidence of ST has been abundantly reported for plants where the classical exponent $\beta_2 = -1/2$ was suggested (Westoby 1984). The usual explanation for ST has involved competition for space (SST, space-regulated self-thinning) based on packing theory, which assumes isometric growth where shape does not change with increasing size of the growing individuals (Weller 1987). The key assumptions in SST are: (a) that the population is monolayered, (b) their cover is 100% and (c) that space is a limiting factor, in such a way that N is inversely related to S , the mean individual surface projected to the substrate ($N \propto S^{-1}$) (Westoby 1984). The exponent β_2 may take other values for SST considering different criteria of similarity, such as changes in shape with size (i.e. allometric growth, Weller 1987), or elastic characteristics (Weller 1987, Norberg 1988, 1988). Nevertheless, the value $\beta_2 = -1/2$ has been shown to hold for plants in both single and mixed-species stands and over a size range spanning 23 orders of magnitude from unicellular algae to the tallest trees (see Enquist *et al.* 1998, Midgley 2001).

For mobile animals it has been proposed that the ST process would be best described as reflecting food limitation (FST, food-regulated self-thinning) (Begon *et al.* 1986). Under the hypothesis of energetic equivalence, which states that total energy flow through a population tends to be constant, the theory of FST suggests that $\beta_2 = -1/3$ (see also Norberg 1988, Elliott 1993, Grant 1993, Bohlin *et al.* 1994, Latto 1994, Fréchette & Lefavre 1995, Armstrong 1997, Dunham & Vinyard 1997, Dunham *et al.* 2000, Keeley 2003, but see Steingrímsson & Grant 1999). The same value is predicted for plants and animals, if the rate of resource supply per unit area is constant (at equilibrium) (Enquist *et al.* 1998, Belgrano *et al.* 2002, Brown *et al.* 2004). However, Rincón & Lobón-Cerviá (2002) have shown evidence that the relationship between *per capita* resource availability and body size may be dependent on local conditions and therefore not predictable solely from scaling arguments, thus leading to a nonlinear self-thinning relationship.

Self-thinning in mussels and new models

By analogy with plants, it is expected that space-regulated self-thinning models should also apply to sessile animals such as mussels and barnacles (Hughes & Griffiths 1988). When ST models were applied to

mussels (*C. meridionalis*, *M. edulis* and *M. galloprovincialis*), it was recognized that their multilayered packing would change the ST relationship (Hosomi 1985, Hughes & Griffiths 1988, Ardisson & Bourget 1991). This was formalized in a bidimensional space-driven self-thinning model that incorporated the allometric effect of growth (α) and multilayering through their indirect effect (ε) on the relationship between density and surface, where $\beta_2 = 1 - [3(1 - \alpha) / 2(1 - \varepsilon)]$ (Fréchette & Lefaivre 1990, 1995). These propositions were experimentally tested using the intertidal mussel *P. purpuratus* (Guíñez 1996); any one of the nine mussel beds monitored during 28-mo period (in central Chile) showed the expected ST patterns, even when the experimental conditions for their occurrence were met (Guíñez & Castilla 1999). This led to a critical revision of classical bidimensional (2D) model assumptions and it was evident that the assumption that area (available resource space) was a limiting factor was not true for *P. purpuratus*, therefore, it was not expected that in this mussel $N \propto S^{-1}$; particularly for those populations forming multilayered matrices (Guíñez 1996, Guíñez & Castilla 1999). As a solution the authors developed a new kind of tridimensional models (3D), following Petraitis (1995) and Hosomi (1985), incorporating explicitly the effect of layering, which was represented by the equation: $B = k_3 L^{1-\beta_3} N^{\beta_3}$ (Eq. 3), where k_3 is a population-specific constant, L represents an index of crowding or number of layers, and β_3 is the self-thinning coefficient (Guíñez & Castilla 1999, 2001, Guíñez *et al.* 2005). A key assumption is that in mussels it holds true that $N = L \cdot S^{-1}$. The 3D model adjusted to *P. purpuratus* field data was able to: i) explain more variance than the bidimensional models, ii) show that when 3D model is better suited, the expected β_2 value is a biased estimate of the β_3 value, iii) demonstrate that for mussels, the 2D models are a particular case of 3D models; that is to say when the number of layers is strictly one (100% cover), iv) suggest that mussels matrices of *P. purpuratus* could be near their biomass carrying capacity (Guíñez & Castilla 1999). We also have been able to develop successfully a 3D model for the tunicate *Pyura praeputialis* (Guíñez & Castilla 2001) that dominate rocky intertidal platforms in the Bay of Antofagasta, northern Chile (Castilla & Guíñez 2000, Castilla *et al.* 2002, Castilla *et al.* 2004). I think that this kind of effort has opened new perspectives in the theoretical analysis of ST patterns in marine invertebrates (Guíñez & Castilla 1999, 2001, Guíñez *et al.* 2005). In particular, we have proposed a new definition of density, which results from a combination of number of individuals and size, the *effective density*, which also can be defined as the expected density if the individuals would conform as a monolayered matrix. This may be a useful definition, permitting comparison

of ST among different populations or species with different crowding strategies (Guíñez & Castilla 1999, 2001, Guíñez *et al.* 2005).

Evidence using field data for FST has been obtained partially by Fréchette & Lefaivre (1990) in *M. edulis*. The authors found that seasonally those populations could alternatively be driven by food or by space regulation. Recently, Alunno-Bruscia *et al.* (2000) studied *M. edulis* under controlled conditions with food limitation that should have induced food-driven ST but found an unexpected β_2 value greater than zero ($\beta_2 = 0.352$), suggesting the lack of evidence of ST process. Hence, they proposed that further studies are still needed to reformulate and to readdress present modeling of FST (Alunno-Bruscia *et al.* 2000). So far, I have been unable to develop a convincing 3D model for FST, despite some progress (Guíñez 1996).

Perspectives

Our efforts, jointly with a recent 3D model, developed for plants, where the third variable is productivity, not layering (Bi 2001), have for the first time attempted to define ST process as a self-thinning surface. Despite the amount of literature on self-thinning, principally in plants (Puntieri 1993), to date no attempts have been made to define the self-thinning rule as a surface (Bi 2001). I think that this would open new theoretical and experimental avenues to explore the relationship between layering, density and size with respect to space and food driven ST: Is layering or density mainly determined by space or food regulation? Another issue which has been seldom explored in animals is that of general intraspecific mass-density patterns of a given species based on 2D and 3D representation. In this regard, we have shown, on the basis of 253 samples in *P. purpuratus* from central and northern Chile, that the classical 2D approach is (as expected) biased by layering effects (Guíñez *et al.* 2005). However, the promise of the extensions of the 3D self-thinning models comes at the price of introducing one more quantity to be measured (crowding in the marine version, productivity in the plant version), thus complicating biological measurements. However, using the present classical 2D approaches with respect to mussels which are typically multi-layered (where 3D models are better suited) can lead to overestimation of the ST exponents and to an inability to detect real density-dependence patterns. I suspect that little work has been done or published in mussels because density dependence is much more frequent than hitherto indicated by bidimensional models. Finally, I think that the next great challenge with ST 3D models it is to

explicitly incorporate both space and food regulation in the modeling in the context of the metabolic theory of ecology developed recently by Brown *et al.* (2004).

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