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Self-thinning in a space-limited rocky intertidal barnacle system

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Acorn barnacles were assumed to have a self-thinning exponent close to –3/2 widely acknowledged for plant populations. However, space and food competition mechanisms would lead to a different exponent. Different recruit densities between tidal levels should result in different geometry of space occupation with adult individuals morphologically different and a different biomass–density relationship. Using *Tetraclita squamosa*, an intertidal barnacle, we investigated the biomass–density relationship along an intertidal gradient to study self-thinning. The self-thinning slope was steeper than the –3/2 power and did not differ among lower tidal levels with an intercept significantly higher in the low intertidal than in the mid-intertidal, whereas there was no significant relationship in the high intertidal. Growth in height of crowded barnacles along with the weaker effect of competition for food may retard mortality and result in a self-thinning slope steeper than –3/2. Our results suggested that self-thinning exponent in barnacles is steeper than –3/2 found for plant populations and allometric growth may not be the only factor causing this deviation from the "self-thinning law". As one progresses higher in the intertidal, self-thinning processes disappear owing to reduced competition.

Introduction

The relationship between body size and population density is an essential link between the individual- and population-level traits of species and community structure and dynamics (Woodward *et al*. 2005). Self-thinning, a particular process characterizing this relationship, is observed when a population undergoes competition-driven mortality occurring when smaller individuals are suppressed as growth of survivors continues (Yoda *et al*. 1963, Fréchette & Lefaivre 1995).

The self-thinning process has been widely and well studied in plants. Yoda *et al*. (1963) suggested that the mean individual mass of survivors (M) and population density (D) are related by the power equation $M = kD^{\alpha}$ with $\alpha = -3/2$ and k being the intercept. Their model was based on the assumption of isometric growth and space occupation, and empirical results presented for a wide variety of plants supported it (White 1981, Westoby 1984). However, there is still a debate over the generality of the "–3/2 power law" (Osawa & Sugita 1989, Dai *et al*. 2009, Zhang *et al*. 2011). Studies showed that deviations from –3/2 exponent may happen as a result of allometric growth (White 1981, Weller 1987, Norberg 1988) and recently, empirical works suggested that the self-thinning exponent depends on the species (Pretzsch 2006) or environmental factors (Morris 2002, Deng *et al*. 2006, Dai *et al*. 2009).

Studies on self-thinning in animals are more recent and remain few. For mobile animals, Begon *et al*. (1986) suggested that the relationship would be underlain by limitation by food resource instead of space and proposed the slope exponent of –4/3. Sessile barnacles were assumed to be space-limited in the manner plants are, thus α was expected to be close to –3/2 widely acknowledged for plant populations (Hughes & Griffiths 1988). However, Wethey (1983) pointed out inconsistency of barnacle functional mechanisms such as the pattern of individual variation in growth with the dominance and suppression model proposed for thinning plant populations; small individuals early in the growth season can outgrow and dominate initially larger individuals. Using natural populations of *Semibalanus balanoides*, an acorn barnacle, Hogarth (1985) suggested a thinning exponent $\alpha = -2.04$, and argued that the slope was steeper in barnacles because of their ability to grow in height when space is limited. Later on, Hughes and Griffiths (1988) proposed $\alpha = -3/2$ for barnacles. So far, there seem to be no general comparison of the self-thinning processes between the space-limited barnacle and plant populations.

Although competition for space in thinning barnacles may be regarded as driven by access to food in the water column, the same way competition in plants is driven by access to light (Bertness *et al*. 1998), the effect of competing neighbors on food availability proved to have less relative importance in barnacles (Lohse 2002). Elevation of individuals in a growing dense population may even expose them to more food (Shimeta & Jumars 1991, Bertness *et al*. 1998). On the other hand, limitation of space tends to be reduced by skeletal support from neighbors (Bertness *et al*. 1998, Lopez *et al*. 2007). As a result, these differences in barnacle- and plant-competition mechanisms may lead to different processes and consequences of self-thinning in these space-regulated systems.

The marine rocky intertidal zone is a biotope with a compressed environmental gradient with different growth rates and often different recruit densities from low to high tidal heights (Connell 1961a, Bertness 1989, Menge 2000). Different recruit densities lead to different geometry of space occupation with development of individuals morphologically different among tidal levels (Bertness *et al*. 1998, Silina & Ovsyannikova 2000). Consequently, self-thinning processes would differ between tidal levels being more intense at lower levels where densities and growth rates are higher. In the present study, we investigated the mean-mass–density relationship of *Tetraclita squamosa* populations, to test whether (1) the self-thinning exponent would be close to the "general power law" scaling exponent, and (2) the thinning exponent would change with tidal levels.

Methods

Study site

We conducted field investigations on Zhujiajian, an island of the Zhoushan archipelago. The site lies along the east coast of the island, is 400 m long, and faces the East China Sea at 29°55´12´´N and 122°25´05´´E with an average tidal range of about 2.5 m. The climate is monsoon-marine with an annual average temperature of 16 °C and a mean annual precipitation ranging from 927 to 1620 mm. Embedded boulders with a minimum diameter of 50 cm cover roughly 50% of the intertidal habitat and embedded cobbles (with a diameter < 30 cm) cover the remaining area. The dominant organisms covering almost exclusively the wave-exposed surfaces are the acorn barnacle *Tetraclita squamosa* and three seaweed species, *Ulva lactuca*, *Grateloupia filicina* and *Corallina officinalis* that are the main occupiers of the lowest heights of the intertidal zone.

Tetraclita squamosa, a subtropical barnacle (Chan & Williams 2004) covering the largest part of the studied shore (Cai *et al*. 1991), was our target species. It settles twice a year at the site (Chen *et al*. 1987) and old individuals are removed by rough weather, allowing new cohorts to settle, which leads to coverage by differently-sized cohorts. The most conspicuous mobile organisms in the community are crabs of the genus *Pachygrapsus*, gastropods *Thais*, and the chiton *Acanthochiton*. However, due to their low densities at the site, we assumed post-recruitment mortality of barnacles due to predation and interspecific competition not to be an important factor as compared with intraspecific mortality.

Field investigation

To carry out our investigation, we designated three intertidal levels: 0.4 to 1.1 m, 1.1 to 1.8 m, 1.8 and 2.6 m above the mean lower low water for the Low intertidal (LI), Mid-intertidal (MI) and High intertidal (HI), respectively. In LI, the lowest sampling limit was set above the area with significant competitive effects of seaweeds on barnacles. At each tidal height, 50 quadrats of 10 × 10 cm, 5 × 5 cm, 2.5 × 2.5 cm were randomly set along 20–40-m transects parallel to the coastline for densities of < 0.4 indiv. cm^{-2}, 0.4–1.5 indiv. cm^{-2} and > 1.5 indiv. cm^{-2}, respectively. Nevertheless, areas with empty shells or markedly heterogeneous regarding individual size were not sampled. To minimize effects of thermal stress within each level, we considered plots within a similar range of slope (±45°), aspect (facing southeast) and substrate size (individuals attached on small cobbles were not sampled) (Bertness 1989, Denny & Harley 2006, Gedan *et al*. 2011). In contrast to LI and MI where the substrate was almost totally covered by barnacles, there was a low coverage of substrate by barnacles in HI (25%, 73% and 81% for HI, MI and LI, respectively).

We conducted our survey during low tides between June and November 2010. For uncrowded plots, quadrats were photographed to get pictures that were used to assess the barnacle biomass using the basal diameter, as this measure proved to be a good index of barnacle growth (Leslie 2005). Photographs were taken with a digital camera, Canon PowerShot G10, placed above the center of a plot delimited by a plastic transparent quadrat scaled according to the density and size of barnacles. Biomass was obtained from regression of dry weight *vs*. basal diameter using the data from 100 individuals with a large body-size range (0.37–5.08 g) (dry weight = 0.000076 × $\text{diam}^{3.27}$; $r^2 = 0.80$, $n = 100$). Total biomass and number of individuals in each photographed plot were used to calculate mean individual biomass and density. However, for crowded plots, it was impossible to measure the basal diameter (Wethey 1983). Therefore, all barnacles in each quadrat were carefully scraped off the rock and transferred into airtight plastic bags (Hughes & Griffiths 1988). When the samples could not be taken back to the laboratory on the same day, they were chilled in a refrigerator. In laboratory, the samples were dried in an oven at 70 °C for 72 hours. Then, individuals from each plot were counted and weighed in aggregate to determine density and mean individual dry weight (Hogarth 1985, Hughes & Griffiths 1988).

Allometric exponents and intercepts were estimated by the OLS (ordinary least square) of log-transformed data and statistically significant differences tested using SMATR ver. 2.0 (http://bio.mq.edu.au/ecology/SMATR/; *see* also Warton *et al*. 2006). The regression lines were plotted using OriginPro 8 SR3. Mean individual biomass was used as the dependent variable and density as the independent variable for the low, mid- and high intertidal, respectively.

Results

The exponent in the equation relating mean individual biomass to density was significantly different from –3/2 in LI and MI ($p < 0.001$). The slopes in LI and MI were negative and steeper than –3/2 but did not significantly differ from each other ($p = 0.266$). However, the intercept was significantly higher in LI than MI ($p < 0.01$) (Table 1). On the other hand, there was no significant relationship between biomass and density in HI (Fig. 1 and Table 1).

Discussion

The log(mean individual biomass) in LI and MI was linearly and negatively correlated with log(population density), as found in previous

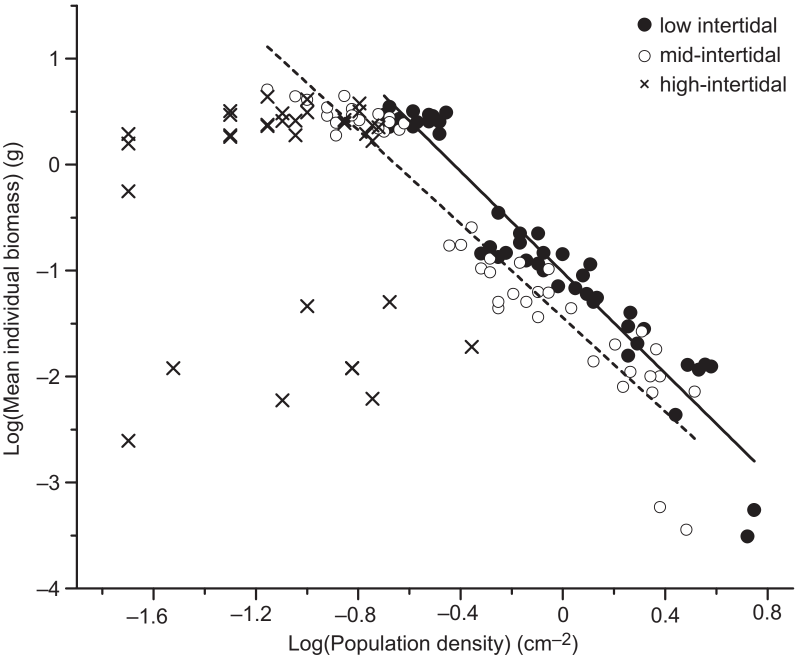

Fig. 1. Mean individual biomass and density relationships of *Tetraclita squamosa* for low intertidal (n = 46, regression significant at $p < 0.0001$), mid-Intertidal (n = 46, regression significant at $p < 0.0001$), and high intertidal (n = 33, regression insignificant p = 0.79).

studies on intraspecific biomass–density relationship in intertidal barnacles (Hogarth 1985, Hughes & Griffiths 1988). In HI, no significant relationship between population density and mean individual biomass was found (Fig. 1 and Table 1).

Unlike in HI, the populations in both the LI and MI underwent self-thinning through an increase in mean individual size and a decrease in density (Fig. 1) (Yoda 1963, Begon *et al.* 1986). Our results indicated that the self-thinning exponent α (α = –2.26 and α = –2.38 for MI and LI, respectively) was significantly different from the self-thinning exponent for plants (Yoda *et al.* 1963, White 1981, Westoby 1984). In a study on self-thinning in a rocky intertidal acorn barnacle *Semibalanus balanoides* population, Hogarth (1985) found a scaling exponent which was very close to the exponents obtained here for MI and LI. On the other hand, Hughes and Griffiths (1988) concluded that the barnacles thinning exponent may be close to –3/2. Nevertheless, like Hogarth (1985), they suggested that deviations from this exponent may occur due to allometric growth. The absence of a relationship between biomass and density in HI suggested that no self-thinning occurred in the high zone. A study on a chthamaloid barnacle got consistent results indicating that high recruit density results in self-thinning in barnacle populations (Lopez & Gonzalez 2003). Since substratum coverage in HI was very low, we think that the density might have been too low for self-thinning to occur. It was probably due to low recruitment in this area as the density remained very low throughout our field investigations. A minimum density is required for competition for food and/or space to have an effect on individual fitness (Naverrete & Menge 1997).

Table 1. Slopes and intercepts of linear relationship between individual mean mass and density for all tidal levels, as estimated by OLS.

Tidal level	Slope (α)	95%CL	Intercept	95%CL	F	r^2
High intertidal	–0.149	–1.310 to 1.011	–0.407	–1.699 to –0.885	0.069	–0.030
Mid intertidal	–2.215	–2.421 to –2.010	–1.445	–1.562 to –1.327	472.203	0.913
Low intertidal	–2.384	–2.591 to –2.176	–1.017	–1.103 to –0.931	536.363	0.922

The thinning exponent in the studied barnacles is different and higher than –3/2. This difference could be explained by the fact that growth of barnacles, especially in aggregation, is not isometric (Silina & Ovsyannikova 2000). In fact, competition for space in high-density barnacles is reduced since the contact area between each individual and the primary subtrate remain practically unchanged and independent of size as individuals grow in height (Silina & Ovsyannikova 2000, Lopez *et al*. 2007). Likewise, allometric growth in plant populations may result in deviation from the thinning "power law" (Weller 1987, Lonsdale 1990). Furthermore, while high density in plant populations, especially trees, diminish light availability with progressive canopy closure at low levels as individuals grow (Lonsdale & Watkinson 1983, Clark 1990, Osunkoya *et al*. 2007), in barnacles, crowding causes lateral compression (Connell 1961b) usually with a weaker effect on the amount of food captured by interacting individuals (Lohse 2002). Elevation of individuals due to vertical growth would enable barnacles to catch more suspended food (Shimeta & Jumars 1991, Bertness *et al*. 1998). These interactions may retard mortality in thinning barnacles and therefore result in a deviation of the self-thinning exponent which would be steeper than the exponent found for a wide variety of plants and underlain by isometric growth.

Our results failed to show a difference between the allometric exponent in LI and MI. However, the intercept in MI was significantly smaller than that in LI. Consistent with our results, shifts in the intercept have been found only with change in light intensity with a smaller intercept in moderately shaded thinning plant populations (Hutchings & Budd 1981, Lonsdale & Watkinson 1982, Dunn & Sharitz 1990). The greater intercept in LI suggests that more biomass per unit area is packed at lower tidal levels. Higher growth rates owing to higher resource availability and probably less desiccation and thermal stress would account for this difference (Bertness 1989, Bertness *et al*. 1998). Since the intercept is regarded as indicating the characteristics of morphology and growth (Norberg 1988), our results are consistent with the results which suggested that columnar growth is more pronounced at lower than at higher intertidal levels (Bertness 1989, Bertness *et al*. 1998). The slope was found to also change along water (Deng *et al*. 2006, Dai *et al*. 2009), nutrient (Morris & Myerscough 1985, 1991, Morris 2002) and light (White & Harper 1970, Lonsdale & Watkinson 1982) gradients in plant populations. Parallel thinning lines indicated that for similar densities, individual mean size in LI is larger than in MI, i.e., more crowding pressure with less substratum space available for individuals in LI. Consequently, the relative importance of vertical growth differed between LI and MI (Bertness *et al*. 1998, Silina & Ovsyannikova 2000), suggesting different growth allometries at these tidal levels. Similarity of the thinning exponents in LI and MI suggests that allometric growth would not be the only factor that accounted for the deviation of the barnacle thinning exponent from –3/2.

Our study indicates that the self-thinning exponent in barnacles is different and steeper than the "general power rule" reported for plants and does not differ between the lower intertidal heights. Our study supports the notion that the "general power law" reported for space-limited plants may not hold for the acorn barnacle, and allometric growth may not be the only factor explaining the difference between self-thinning exponents of barnacle and plant populations. Our results are consistent with the findings of Hogarth (1985) and indicate that as one progresses higher in the intertidal, self-thinning processes disappear owing to reduced competition.

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