Biomass-density relationships and self-thinning of shell and tissue in marine intertidal barnacles

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Abstract: Although self-thinning exponent in barnacles was assumed to be close to -3/2 widely acknowledged for space-limited plants, steeper slopes have been observed as a result of allometric growth. There is a trade-off between shell and tissue growth in barnacles and self-thinning lines for these individual parts would differ as a result of different biomass allocation. We quantified biomass-density relationships for shell and tissue in self-thinning population of *Tetraclita squamosa* in two intertidal levels to determine the corresponding scaling exponents to see whether they are close to each other and to the "-3/2 power law". The self-thinning slope for tissue in low interidal was steeper than the shell one in mid-intertidal and all slopes were higher than -3/2. In higher heights, individuals are subject to more desiccation stress and would allocate more biomass to shell than their counterparts in lower heights which allocate more biomass to tissue, thus self-thinning slope for tissue in low intertidal would be steeper. Our results suggested that self-thinning exponent for barnacle individual parts is not invariant and these different exponents would be explained by different biomass allocation to shell and tissue in response to environmental conditions.

Key-words: barnacle, biomass-density relationship, biomass allocation, self-thinning, *Tetraclita squamosa*

1. Introduction

Growth of sessile intertidal invertebrates is limited by space availability. As a result, suppression of weaker individuals due to density-dependent mortality is accompanied by an increase in biomass of survivors during growth in the so-called process of self-thinning (Yoda *et al.* 1963; Hughes & Griffiths 1988; Fréchette & Lefaivre 1995). Self-thinning can be quantified by the equation:

$$W=kN^{\alpha} \text{ or } \log W=\log k+\alpha \log N$$

Where W is mean individual biomass, N is density; k and α are intercept and exponent of the self-thinning line respectively (Yoda *et al.* 1963; Morris 2003).

Self-thinning in sessile invertebrates has been widely studied especially in the cultured mussels (Fréchette *et al.* 2010; review by Guiñez 2005). In barnacles, self-thinning has drawn less attention despite their importance in marine intertidal community dynamics (Little & Kitchings 1996) and their potential in aquaculture (Lopez *et al.* 2010). Early studies suggested that the slope (α) would be close to -3/2, the exponent that has been widely acknowledged for plants since barnacles are space-limited (Hughes & Griffiths 1988). However, steeper slopes have been found and were accounted for by allometric growth and the nature of barnacle food different from the evenly distributed light used by plants (Hogarth 1985). The difference of competition mechanisms between plants and barnacles has recently been suggested for interpreting this steeper slope (Sibomana *et al.* in press).

Although the "-3/2 power law" of self-thinning has been considered as an empirical generalization (Yoda *et al.* 1963; White & Harper 1970), the self-thinning exponent has been demonstrated to vary in plant communities (Weller 1987; Deng *et al.* 2006; Dai *et al.* 2009; Bai *et al.* 2010; Zhang *et al.* 2011). Recent results indicated that the exponent depends on species (Pretzsch 2006) or environmental conditions (Morris 2002; Deng *et al.* 2006; Bai *et al.* 2010; Zhang *et al.* 2012). Self-thinning in barnacles is still poorly understood and the generality of the scaling exponent may be questionable (Sibomana *et al.* in press), thus studies are needed for a better understanding of the self-thinning process and the underlying mechanisms in sessile barnacle populations. Moreover, previous studies have considered whole individual biomass without taking different biomass components (e.g. shell, tissue) into account (Hogarth 1985; Hughes & Griffiths 1988; Sibomana *et al.* in press).

Self-thinning of individual parts has been well studied in plant communities. Biomass-density relationship lines for roots are steeper than the shoot ones in arid nutrient-limited environments where plants allocate more biomass to belowground parts to maximize uptake of water and nutrients while in light-limited benign environments, the allometric exponent is higher for shoot since additional biomass is allocated to aboveground part in response to light competition during growth (Deng *et al.* 2006; Bai *et al.* 2010; Zhang *et al.* 2011). Likewise, there is a

trade-off between shell and tissue growth in barnacles (Lively 1986) and individuals subject to desiccation stress tend to allocate more biomass to shell while those spending longer period submerged allocate more biomass to tissue (Bertness *et al.* 1998; Lopez & Gonzalez 2003). Biomass-density relationships of barnacle shell and tissue are related to those of whole individuals by pattern of biomass allocation, therefore analyzing them is important for understanding the barnacle strategy for survival, reproduction and population dynamics.

In higher intertidal levels, barnacles are subject to higher desiccation stress, thus self-thinning lines for shell should be steeper if individuals tend to allocate more biomass to shell during growth while in low heights the corresponding lines for soft parts would be steeper if individuals allocate more biomass to tissue. In this study, we quantify biomass-density relationships of shell and tissue in self-thinning population of *Tetraclita squamosa* Bruguière, 1789 to determine the corresponding scaling exponents to see whether they are close to each other and to the "-3/2 power law". Density and tidal height effects on biomass allocation were also determined.

2. Material and Methods

The samples were collected in Zhujiajian, an island of the Zhoushan archipelago in East China (29°55'12'' North and 122°25'05'' East) from October 2011 to July 2012 during low tides. The site is a wave exposed rocky shore mainly covered by two acorn barnacle species, *Tetraclita squamosa* Bruguière, 1789 and *Tetraclita japonica* Pilsbry, 1916 and 3 seaweed species, *Ulva lactuca*, *Grateloupia filicina* and *Corallina officinalis* covering the lowest levels. *T. squamosa* is the dominant barnacle (Cai et *al.* 1991) and occupies the space between 0.4 and 2.6 m above mean lower low water where it settles twice a year (Chen *et al.* 1987). Post-recruitment mortality of barnacles due to predation and interspecific competition has been assumed not to be an important factor as compared with intraspecific density-dependent mortality since the densities of the most conspicuous mobile organisms are low in the community (Sibomana *et al.* in press). In the lowest heights, low-intertidal (LI) (0.4 m-0.7 m) and mid-intertidal (MI) (0.7 m-1.8 m), the population of *T. squamosa* undergoes self-thinning (Sibomana *et al.* in press), thus we considered this tidal heights for our investigation on self-thinning of barnacle individual parts.

Sampled barnacles were carefully scraped off the rock and transferred into airtight plastic bags. When the samples could not be taken back to the laboratory the same day, they were chilled in a refrigerator. In laboratory, shell and tissue from all the

sampled barnacles were separated before they were dried in oven at 70°C for 72 hours.

Mass-density relationships of barnacle parts

In LI and MI, 40 10 cm x 10 cm, 5 cm x 5 cm, 2.5 cm x 2.5 cm quadrats were set along 20-40 m transects parallel to the coastline randomly, according to the density and the individual size (Sibomana *et al.* in press). However, plots with empty shells or markedly heterogeneous regarding individual size were not sampled. In laboratory, individuals from each quadrat were counted and dried shell and tissue weighed to determine density and mean individual biomass for the two individual parts.

Density and tidal level effects on biomass allocation

For density and tidal level effects on biomass allocation to shell and tissue, individuals were also sampled in LI and MI. Three density levels, solitary (SOL) (with no contact with neighbors-at least 1 cm from the nearest conspecifics), low density (LD) (4-5 ind/5cm²) and high density (HD) (>5 ind/5cm²) were considered at each tidal height. 40 individuals were randomly chosen for each density level within each tidal height. We took adult barnacles into account, measuring at least 5 mm of opercular rostro-carino diameter (density-independent parameter) corresponding to 22 mm of basal rostro-carinal diameter in size for non-crowded individuals (Chan & Williams 2004). Nevertheless, only 26 solitary individuals could be found in LI and broken individuals were not considered in the analysis. Dry shell and tissue weights were determined for collected individuals and mean tissue:shell ratio estimated for each density level within the two tidal heights.

Statistical analysis

The self-thinning exponents were estimated by OLS (ordinary least square) of log-transformed data. Significant differences between exponents were tested using a permutation test in SMATR version 2.0 (Falster *et al.* 2006) and the regression lines were plotted using OriginPro 8 SR3 package for LI and MI respectively. Mean individual tissue biomass and mean individual shell biomass were used as the dependent variable and density as the independent variable.

The means of tissue:shell ratio for different density levels were compared pairwise within and between tidal levels by one-way ANOVA using SPSS statistical package.

3. Results

The results showed that self-thinning

exponent in the studied barnacle individual parts is not invariant. In fact, although mass-density scaling exponent did not significantly differ from each other within tidal levels (p>0.05), tissue thinning exponent in LI was significantly higher than the corresponding one for shell in MI (p=0.016) (fig. 1, table 1). In addition, all the barnacle components thinning lines were steeper than the theoretical "-3/2 power law" (table 1).
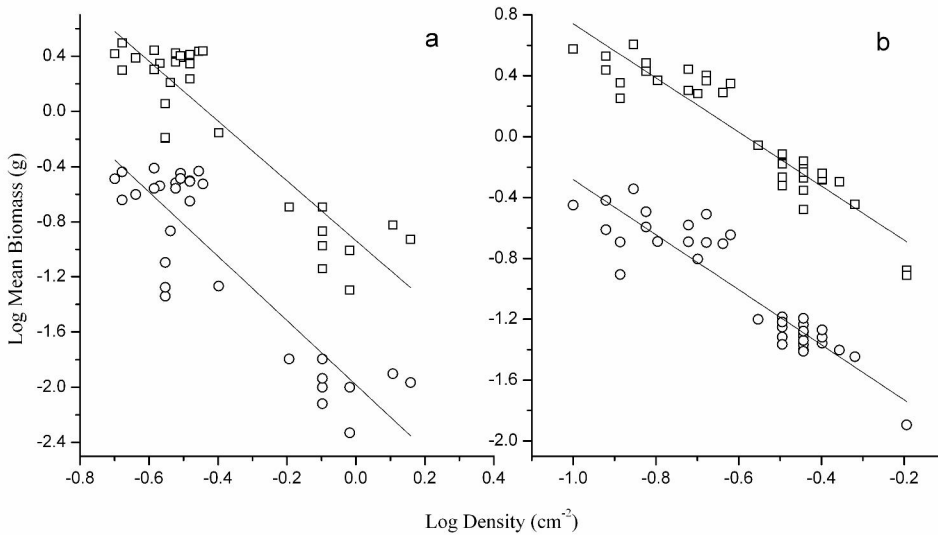

Figure 1. Shell (□) and tissue (○) mass-density relationships of *Tetraclita squamosa* in the low intertidal (a) and mid-intertidal (b).
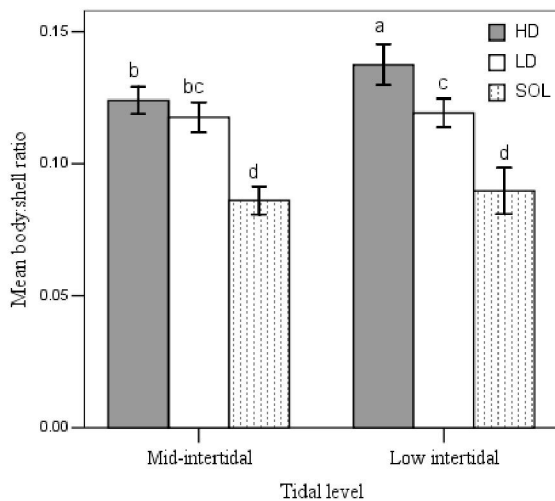

Figure 2. Comparison of tissue:shell ratio between density levels and tidal heights. Means with dissimilar letters were significantly different (ANOVA 1; p<0.05). The bars represent mean +/-2 SE of 26-40 individuals.

Biomass allocation in *T. squamosa* differed in solitary and crowded individuals. High density and low density individuals had higher tissue:shell ratio than solitary individuals (fig. 2). In addition, high density individuals in LI had a tissue:shell ratio higher than their counterparts in MI ((F=8.765, p=0.004) whereas there was no significant difference in other density levels between tidal levels (F=0.546, p=0.462 for Sol; F=0.182, p=0.671 for LD) (fig. 2).

Table 1: Slopes and intercepts of linear relationships between mean shell and tissue biomass and density in the two tidal levels.

Tidal level	Individual part	Slope (α)	(α) 95% CL	Intercept (log k)	(log k) 95% CL	R^2	n
LI	Shell	-2.166	-2.563; -1.769	-0.936	-1.120; -0.752	0.810	30
LI	Tissue	-2.332	-2.816; -1.848	-1.983	-2.397; -1.922	0.759	30
MI	Shell	-1.776	-1.995; -1.558	-1.035	-1.169; -0.901	0.880	38
MI	Tissue	-1.811	-2.058; -1.564	-2.093	-2.245; -1.941	0.856	38

4. Discussion

It is well known that crowded barnacles undergo self-thinning (Wethey 1983; Hogarth 1985; Hughes & Griffiths 1988; Lopez and Gonzalez 2003; Sibomana *et al.* in press) and barnacle population structure varies with tidal levels (Liu & Morton 1994; Bertness *et al.* 1998; Chan *et al.* 2006; Macpherson & Scrosati 2008). Although the studied *T. squamosa* shell and tissue self-thinning exponents are close to each other within tidal levels, tissue regression line in the LI is significantly steeper than the shell line in the MI (fig. 1). All the exponents are significantly higher than the classical "-3/2 power law". These results suggested that there is no common scaling exponent for barnacle individual parts, thus the data support the hypothesis of variability of the self-thinning exponent in barnacles. Different thinning exponents were also found in previous studies on barnacles (Hogarth 1985; Hughes & Griffiths 1988; Sibomana *et al.* in press). In plant communities, empirical studies reported that self-thinning of below-ground and above-ground parts varied with drought stress (Deng *et al.* 2006; Bai *et al.* 2010), nutrient availability (Morris 2002) and forest type (Zhang *et al.* 2011).

Our results indicated that the tissue biomass-density exponent in LI is significantly higher compared to the corresponding one for shell in MI (fig 1; Table 1), suggesting that individuals in the LI allocate more biomass to their soft parts than their conspecifics in higher tidal heights during the course of growth. Our results on density and tidal height effects on biomass allocation showed that crowded individuals allocate more biomass to tissue compared to solitary ones in each tidal height (fig 2). On the other hand, high density individuals in LI allocate more biomass to tissue than their counterparts in MI, thus the tendency to allocate more biomass to tissue is more pronounced in the lower heights in crowded barnacles. Therefore, the studied thinning *T. squamosa* allocate more biomass to shell in the higher intertidal heights than the specimens attached in the lower tidal levels. In crowded individuals of the acorn barnacle *Semibalanus balanoides*, it has been shown that specimens between "hummocks" and on "hummock" tops presented different biomass allocation to shell and tissue (Bertness *et al.* 1998). Our results are consistent with previous studies which indicated that more resource is allocated to shell in higher intertidal level species (Lopez & Gonzalez 2003) and specimens (Bertness *et al.* 1998).

Energy allocation to different barnacle individual parts in response to variation in tidal level may be considered an adaptive trait to maximize survivorship and enable individual growth and reproduction in the harsh intertidal environment (Bertness *et al.* 1998; Lopez & Gonzalez 2003). In the studied site, barnacles are subject to desiccation stress during low tides especially on summer days when rocky substratum temperatures can reach 45°c (personal obs.). Individuals attached in higher heights spend longer period emerged, thus need a thicker shell to enable them to lower their water loss rates (Lopez & Gonzalez 2003). As a result, the surviving barnacles in MI should allocate more biomass to shell than their counterparts in LI to minimize the desiccation stress effects whereas tissue biomass in LI increase at a faster rate than in MI in response to decreased desiccation stress. Thus, the self-thinning exponent is higher for tissue in LI.

Most studies on biomass allocation in barnacles have focused on crowded vs. solitary individuals (Wu *et al.* 1977; Wu 1980; Wethey 1984; Lopez & Gonzalez 2003); our results suggested that difference in biomass allocation in response to variation in environmental factors occurs in crowded barnacles. The present study has shown that self-thinning exponent of shell and tissue in *Tetraclita squamosa* is not invariant, confirming that a general self-thinning law in barnacles may be unwarranted. Different biomass allocation to shell and tissue in response to variation in environmental conditions would explain the difference in biomass-density exponents of these individual parts in thinning barnacles between low and higher tidal heights.

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