COMMENT

GROWTH PATTERN, REPRODUCTION AND SELF-THINNING IN SEAWEEDS: A RE-EVALUATION IN REPLY TO SCROSATI

Antonio Flores-Moya, José A. Fernández
Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos s/n, E-29071 Málaga, Spain
and
F. Xavier Niell
Departamento de Ecología, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos s/n, E-29071 Málaga, Spain

Our previous analysis of the relationships between the logarithm of individual mean weight (measured as g dry weight-plant−1) and the logarithm of density (d, expressed as number of shoots-m−1) for two species of seaweed from the Strait of Gibraltar (Flores-Moya et al. 1996) has been reviewed and criticized by Scrosati. We showed that density and mean weight are related by the −5/2 power law (Yoda et al. 1963) in the deep-water kelp Phyllospora purpurascens (C. Agardh) Henry et South. The self-thinning analysis for the red alga Asparagopsis armata Harvey presented two different components: a slope of −2.1, more negative than proposed by the −3/2 power law, at densities >500 shoots-m−2, and no dependence between density and mean weight at densities <500 shoots-m−2. It was argued that the diapause of growth produced by reproduction (cystocarp and carpospore production) was responsible for the lack of dependence between density and mean weight in A. armata. We will now re-evaluate our previous conclusions by considering Scrosati’s criticisms of our paper.

According to Weller (1987) and Scrosati (1996), to study self-thinning in plants, it is necessary to relate density and stand biomass rather than density and mean weight. This is because mean plant weight is usually obtained by dividing the total biomass of the sample surface area by the number of shoots per sample surface area. Thus, a spurious correlation arises when mean biomass is plotted against plant density because the number of plants is present in both axes (Scrosati 1996). This was indeed our method and Scrosati’s criticism is valid, so in this re-evaluation we will use as variables stand biomass and plant density.

Data were log-transformed and fit by the reduced major axis (RMA) procedure (Sokal and Rohlf 1995). This is one of the appropriate techniques that can be used when the model I regression cannot be applied, as in this case, because the measurements of both variables is subject to error that is not experimentally controlled (Weller 1987, Sokal and Rohlf 1995). Other alternative techniques for model II regression may be used, but a clear strategy to select the appropriate statistical procedure is still an open question (Sokal and Rohlf 1995:543–9).

Scrosati followed the proposal of Weller (1987) and suggested principal component analysis (PCA) as an appropriate technique to study the biomass–density relationship. The equivalence of PCA with correlation is well known (Pielou 1977) but two-dimensional PCA is not appropriate because it consists of a double transformation of rotation and translation in order to varimax the PCA in the cloud of data.

In our previous paper (Flores-Moya et al. 1996), we included both active and nonactive growth periods of the two seaweed species in the self-thinning analysis. However, nonactive growth must be dropped in the self-thinning study, as pointed out by Scrosati. According to Flores-Moya et al. (1993; see figs. 4, 5), active growth of P. purpurascens occurred between April and September, and only this time period was restudied. To study self-thinning in A. armata, we selected densities >2000 shoots-m−2 (Fig. 1) because a clear negative biomass–density relationship occurs.

The temporal variation of the relationship between biomass and density was also calculated for each cohort of A. armata during the period with active growth. The Pearson correlation coefficient was calculated in every case. The 95% confidence limits (Sokal and Rohlf 1995) on slopes were calculated to establish significant correlation between biomass and density.

A significant correlation (Fig. 1, Table 1) between biomass and density was obtained for the single cohort of P. purpurascens growing at 30 m depth, indicating the existence of self-thinning in this population. That is to say, intraspecific competition among P. purpurascens occurs. Flores-Moya (1997) showed that photon irradiance beneath a single layer of P. purpurascens in this same population was lower than the photosynthetic compensation point and that the population was over-dispersed on the sea bottom. Thus, light competition among sporophytes may be responsible for self-thinning in P. purpurascens.

1 Received 5 August 1997. Accepted 15 September 1997.
2 Author for reprint requests: e-mail flores@uma.es.
Fig. 1. Relationship between \(\log_{10}\) (stand biomass) (g m\(^{-2}\)) and \(\log_{10}\) (shoot density) (no m\(^{-2}\)) for *Phyllosporos purpurascens* (filled circles) and *Asparagopsis armata* (open symbols, each one corresponding to a different seasonally separated cohort).

The relationship between stand biomass and density in *A. armata* showed three different components (Fig. 1). Active growth occurs from recruitment of the cohorts until the time when plants become fertile in the second month of the cohort’s life span, which is coincident with \(d \approx 2000 \text{ shoots m}^{-2}\). During this stage, strong self-thinning among young plants occurs (Fig. 1). The self-thinning slopes for data from the four cohorts are not significantly different throughout the seasons (Table 1). As soon as reproduction began, coincident with \(500 < d < 2000 \text{ shoots} \text{ m}^{-2}\), the relationship between the two variables was not significant \((r = 0.293, n = 24, P < 0.01)\), and there was no increment in stand biomass as density decreased. This can be explained by the diapause of growth produced by the production of cystocarps and carpospores (Aranda et al. 1984). In conclusion, the effect of reproduction cannot be argued as a factor modifying self-thinning, as we pointed out in our previous paper (Flores-Moya et al. 1996), because reproduction occurred after growth ceased, and active growth is a requirement for self-thinning analysis (Weller 1987). After reproduction, the number of shoots per unit surface area decreased. Because no new shoots were recruited and the old plants did not grow, the disappearance of shoots (principally by senescence and drag effect by waves) was linearly correlated with the diminution of stand biomass.

A significant self-thinning slope of \(-\frac{1}{2}\) was computed for the four combined cohorts of *A. armata*, as was proposed by Weller (1987). A similar result was obtained in three of the cohort when computed separately. However, the correlation for the second cohort reflects a nonsignificant rather than a false relationship between stand biomass and density because of the low number of samples \((n = 3)\). Moreover, the differences among the four slope values were not significant. Summarizing, self-thinning takes place in *A. armata* at densities >2000 shoots m\(^{-2}\), but no seasonal differences were detected between the self-thinning patterns. The possible spatial and seasonal effects on self-thinning remain to be studied in depth in seaweeds.

### Table 1: Self-thinning slope for the four cohorts of *Asparagopsis armata* (density >2000 shoots m\(^{-2}\)) and for the single cohort of *Phyllosporos purpurascens* from April to September: 95% confidence limits for the slopes, and Pearson correlation coefficient. The slopes were calculated by linear fit of stand biomass and shoot density by the reduced major axis procedure (Sokal and Rohlf 1995).

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>95% Confidence limits</th>
<th>(r)</th>
<th>(n)</th>
</tr>
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<tr>
<td><em>Asparagopsis armata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvey</td>
<td>-0.525</td>
<td>[-0.627, -0.424]</td>
<td>-0.842</td>
<td>7*</td>
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<tr>
<td>Cohort II</td>
<td>-0.436</td>
<td>[-0.502, -0.399]</td>
<td>-0.995</td>
<td>3 ns</td>
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<tr>
<td>Cohort III</td>
<td>-0.466</td>
<td>[-0.539, -0.394]</td>
<td>-0.912</td>
<td>5*</td>
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<tr>
<td>Cohort IV</td>
<td>-0.529</td>
<td>[-0.670, -0.387]</td>
<td>-0.902</td>
<td>6*</td>
</tr>
<tr>
<td>All together</td>
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<td>[-0.756, -0.454]</td>
<td>-0.483</td>
<td>21*</td>
</tr>
<tr>
<td><em>Phyllosporos purpurascens</em> (C. Agardh)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Henry et South</td>
<td>-0.196</td>
<td>[-0.484, 0.297]</td>
<td>-0.931</td>
<td>6*</td>
</tr>
</tbody>
</table>

* *: Significant at \(P < 0.05\); ns, nonsignificant.

Dr. Eric C. Henry kindly revised the style and English grammar.


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