

SIZE STRUCTURE AND DYNAMICS IN A POPULATION OF *SARGASSUM MUTICUM* (PHAEOPHYCEAE)¹

Francisco Arenas and Consolación Fernández²

Unidad de Ecología, Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, E-33071 Oviedo, Spain

***Sargassum muticum* (Yendo) Fensholt is an introduced brown seaweed with a very distinctive seasonal growth cycle on European shores. The present study links the dynamics of a population of *S. muticum* with the seasonal growth cycle of the species and the density-dependent processes operating throughout this cycle. Results indicate that both growth cycle and intraspecific competition influenced the structure and population dynamics. Size inequality increased during the slow growth phase (autumn–winter) of the 2-year study. Mechanisms generating inequality of size could be the existence of asymmetric competition and the inherent differences in growth rates between old (regenerated) and new thalli (recruits). Inequality of size distributions decreased progressively during the last months of the growth phase (spring–summer) and could be related to a process of self-thinning. There was a negative biomass–density relationship (as a measure of biomass accumulation-driven mortality) that confirms the importance of self-thinning as a major demographic factor in the *S. muticum* population.**

Key index words: Gini coefficient; intraspecific competition; population dynamics; *Sargassum muticum*; self-thinning; size structure

Since the pioneering studies by Yoda et al. (1963), increasing attention has been dedicated to the role of population density on the dynamics of plant populations. Two important relationships that link the mean and range in plant size with population density have emerged from such investigations (Watkinson 1985, Firbank and Watkinson 1990). The first is the existence of positive relationships between size inequality and population density during the development of plant stands in crowded conditions (Weiner and Solbrig 1984, Weiner 1985, Weiner and Thomas 1986). Size distributions with few large individuals and numerous smaller ones have been frequently reported in plant populations (Harper 1977, Turner and Rabinowitz 1983, Weiner 1985, Schmitt et al. 1987, Knox et al. 1989, Thomas and Weiner 1989). These size distributions, usually called size hierarchies (Weiner and Solbrig 1984), are a consequence of differences in the individual growth rates, mainly caused by a process of asymmetric competition, also called one-side competition (Weiner

and Thomas 1986). Asymmetric competition involves a nonproportional sharing of resources between the individuals of the population, with larger plants growing “at the expense” of smaller individuals (Harper 1977, Weiner and Thomas 1986). Thus, the dynamics of size inequality as a function of plant density and size are important to understand not only the population structure, but also the interaction between individuals (Hara 1986).

The second density-related process is the negative linear relationship found between biomass and density, both variables in logarithmic scale (White 1981, Westoby 1984, Lonsdale 1990). This relationship is called the self-thinning line (Weller 1987) and was formerly known as the self-thinning rule or $-3/2$ rule (for reviews, see Weller 1987, Lonsdale 1990, Sackville Hamilton et al. 1995). Underlying self-thinning is a mechanism of density-dependent mortality, implying plant growth at the expense of death of other plants (Harper 1977).

Intraspecific effects in macroalgal populations traditionally have been ignored (Paine 1990). However, increasing attention has been focused on the study of size distributions in seaweed populations (Dean et al. 1989, Ang 1991, Martínez and Santelices 1992, Creed et al. 1996a, b, Creed et al. 1998, Scrosati and DeWreede 1997), and to the relationship between mean plant size or total biomass and density in nonclonal (Schiel and Choat 1980, Cousens and Hutchings 1983, Robertson 1987, Creed 1995, Flores-Moya et al. 1996, 1997) and clonal (Martínez and Santelices 1992, Santos 1995, Scrosati 1996b, Scrosati and DeWreede 1997, Flores-Moya et al. 1996, 1997) species. In general, results from nonclonal species of algae agree with predictions from theories for nonclonal terrestrial plants, and intraspecific competition is regarded as a major determinant of the dynamics of seaweed populations. In clonal algae, most studies published to date do not show evidence of self-thinning among ramets (i.e. fronds), which is in agreement with findings in clonal terrestrial plants (e.g. Room and Julien 1994).

Manipulative experiments on natural or laboratory populations of seaweeds (e.g., Reed 1990, Creed et al. 1998) have confirmed the importance of density as a major regulator in macroalgal populations. However, few studies have directed their attention to the seasonal variation of the size-structure and the dynamic of biomass–density relationships in natural populations of seaweeds, particularly in nonclonal species. Thus, the evidence that the suggested mechanisms are actually occurring and have major consequences in the natural populations is limited. Moreover, knowl-

¹Received 30 December 1999. Accepted 26 September 2000.

²Author for correspondence: e-mail chely@sci.cpd.uniovi.es.

edge of intraspecific effects is essential because it provides the baseline against which interspecific relations are calibrated (Paine 1990). This is particularly important in the case of invasive species like *Sargassum muticum*, whose impact in the local communities has been barely analyzed (Walker and Kendrick 1998, but see also De Wreede 1983, De Wreede and Vandermeulen 1988, Viejo 1997).

The present study was undertaken on a natural population of *S. muticum*, a nonclonal pseudoperennial invasive brown seaweed. A few years after its first appearance on the northern coast of Spain (Fernández et al. 1990), the species developed dense populations on some sheltered shores, where it dominates the community at the low intertidal levels. We analyzed the dynamics of size structure in a natural population of *S. muticum* and examined the patterns of change in the size structure in the context of the growth cycle of the species and the intraspecific interactions. Second, we assessed the importance of self-thinning in the population dynamics by investigating the temporal variation of biomass–density relationships.

MATERIALS AND METHODS

The growth form of *S. muticum* closely approaches the structural complexity of higher plants (Chamberlain et al. 1979). Following the nomenclature by Yoshida (1983), thalli consist of a perennial holdfast attached to the substratum that arises from a solitary stem. One to several main branches issue annually from the terminal part of the stem. Main branches produce numerous lateral branches that hold leaflike structures, air vesicles, and receptacles during the fertile season. Genetic individuals of this species are easily distinguishable. Although the holdfasts of two different individuals sometimes coalesce, each individual retains its own stem and branching system. Genetic individuals and thalli are considered as synonymous throughout this article.

The field study was conducted at the El Truhán Inlet (43°36'41"N, 5°46'29"W), west coast of Cape Peñas (Asturias, Spain). El Truhán Inlet is a small sheltered area (approximately 150 × 300 m) with a substratum of boulders and stones overlaid by sand. The population of *S. muticum* covered nearly 500 m².

A destructive sampling program was designed to assess the dynamic of the *S. muticum* population. The choice of a destructive sampling program instead of a nondestructive one was due the low tidal level of the population (ca. 0.5–0.2 m above Lowest Astronomical Tide) and the difficulties in targeting the numerous small thalli of the population.

Samples were collected monthly from November 1991 to October 1993 (except in February 1993). Three 50 × 50 cm quadrats were randomly placed, and all thalli inside the quadrats were carefully removed, bagged, and carried to the laboratory. Care was taken to ensure that samples were scattered throughout the population and to avoid repeated sampling of the same area.

Once in the laboratory, thalli were cleaned of epiphytes and rinsed with fresh water. All the thalli were measured in length (from the holdfast to the apex), grouped in nine size classes, and weighed after drying during 24 h at 60° C. The size classes used were in 25 cm intervals, but the smallest class was separated in three (0–5, 5–10, and 10–25 cm).

Structure and dynamics of the population. The structure and dynamics of the population of *S. muticum* were characterized by monthly changes in standing crop (g dry biomass·m⁻²) and density (thalli·m⁻²) and size-structure descriptors. Three statistics have been frequently used as size-structure descriptors: 1)

skewness coefficient (g_1), 2) coefficient of variation, and 3) Gini coefficient (G'). As Bendel et al. (1989) noted, these descriptors are highly correlated (in our population, Pearson's correlation coefficients were all significant [$P < 0.05$], with the highest coefficient between the coefficient of variation and G' [$r = 0.90$] and the lowest between the g_1 and G' [$r = 0.54$]). The unbiased Gini coefficient was selected for the study because it is the statistic that reflects more accurately the size hierarchy in the population (Weiner and Solbrig 1984).

Although size structure is frequently reported from the biomass of the individuals of the population, in our work we used the length as the size descriptor. Light is the primary resource for algae, and taller thalli intercept more light (Carpenter 1990). Thus, length is probably crucial in the survival and reproduction of the individuals (i.e. in their final fitness), and the length structure of the population accurately reflects the size hierarchy of the population. Moreover, thalli of *S. muticum* show an inclination to a monopodial growth form when growing in high densities (Andrew and Viejo 1998); thus, length and biomass were highly correlated (Arenas and Fernández, unpublished data).

Our temporal sampling procedure ensured independence of the data, and therefore a factorial analysis of variance with a nested factor was used to examine the existence of interannual and seasonal differences in the population descriptors (Underwood 1997).

Year was considered a fixed factor. Seasons were selected using biological criteria and considered also as a fixed factor. Seasonality of *S. muticum* on the north coast of Spain has been shown in previous works (Arenas et al. 1995, Rico and Fernández 1997, Fernández 1999). Arenas et al. (1995) identified an autumn–winter slow growth phase, a faster spring growth phase, an early summer reproductive phase, and a late summer senescence phase in the seasonal growth cycle of *S. muticum*.

For each phase two different sampling times (random factor nested within the interaction year × growth-cycle phase) were chosen: December and January for the slow-growth period, March and April for the fast-growth period, May and June for the reproductive phase, and August and September for the senescence phase.

To achieve homogeneity of variances, total biomass and density were log transformed. *A posteriori* Student-Newman-Keuls (SNK) multiple comparisons were performed for biomass, density, and G' assess the differences between the growth-cycle phases. Following Underwood's (1997) suggestions for multiple comparisons in the case of nested analysis, care was taken to construct standard error in the SNK procedure. The Ryan method to adjust the probability of type I error was used to preserve the test against excessive type I error (Day and Quinn 1989).

Finally, to verify predictions by Weiner and Thomas (1986) concerning the increase and posterior decrease of the population asymmetry during the growth phase as a result of a dominance–suppression process, we plotted temporal patterns of change in inequality (G') versus mean biomass of thalli.

Biomass–density relationship. Biomass–density relationships traditionally have been analyzed using graphical models that plot average plant biomass (w) versus density (d) in bilogarithmic scale (Yoda et al. 1963). Westoby (1984) and particularly Weller (1987) recommended replacing mean plant biomass (w) with total biomass (B) to avoid both misleading interpretations of the relationship and undesirably autocorrelative effects. Macroalgal studies of biomass–density relationships used both methods (see Martínez and Santelices 1992, Scrosati 1996a, b). Following recommendations by Scrosati (1997), in this study we use the B - d model. Therefore, the equation for the self-thinning line would be (Westoby 1984):

$$\log B = k - b \log N$$

where B is total biomass, N is density, k is the intercept point (usually between 3.5 and 5), and b is the slope.

The choice of a correct regression algorithm to fit the relationship is another important premise in biomass–density relationship studies. The ordinary least square (OLS) regression is

recognized as inappropriate by several authors (Weller 1987, Sackville Hamilton et al. 1995), and other procedures have been recommended, such as principal component analysis (Weller 1987, Lonsdale 1990, Scrosati 1996b, 1997) or reduced major axis (RMA), also known as model II regression (Osawa and Allen 1993, Flores-Moya et al. 1997).

In this study we used the RMA algorithm to define the biomass–density relationships. An assumption of RMA is that error variances of variables are proportional to their true variances (McArdle 1988). Moreover, the RMA model is directly calculated from OLS computations (Ricker 1984). Confidence intervals of the slopes were calculated using the formulae given in Jolicoeur and Misimann (1968, cited in McArdle 1988). The statistical tests proposed by Clarke (1980) were used to verify the equality of slopes for the two annual RMA regressions.

Because the self-thinning relationship has been described for the active growth period of plant populations, it is important to include only samples from this period, when the dominance–suppression is taking place (Scrosati 1997). In our study we used the samples from December to June 1992 and December to July 1993, when substantial increases in the population biomass were recorded (see Results, Fig. 1A). A second selection of scattered samples was also made to avoid the effect of individual samples in the equation that probably were not suffering crowding-dependent processes (Weller 1987). Finally, the temporal trajectory of density–biomass relationship was graphically examined.

RESULTS

Temporal variations in the structure of the population of Sargassum muticum. Table 1 shows the results of the nested analysis of variance for the standing crop, density, and G' . There were significant differences in the population parameters between the seasonal growth-cycle phases that were consistent in the 2 years of study (neither year nor year \times growth-cycle phase interaction were significant). Hence, in the case of the standing crop and density, significant values were found for time. A graphical summary of the results of the SNK multiple comparisons test is shown in Figure 1.

The beginning of the autumn coincided in the population with the start of the slow-growth phase and the emergence of the first new recruits (Fig. 1, A and B). Thallus density increased during this season until the annual peak in December (974 and 986 thalli·m⁻² in 1992 and 1993, respectively, Fig. 1B). Meanwhile, and despite the increase in density, standing crop of the population did not show a significant increase (Fig. 1A). Throughout the slow-growth phase (autumn and winter), thallus size inequality progressively increased (Fig. 1C), although small thalli (length <25 cm) dominated the population (Fig. 2).

During the second phase of growth (fast-growth phase), standing crop of the population increased significantly while density decreased (Fig. 1, A and B). Thalli were progressively shifting to bigger size classes, but as in the earlier phase, thalli of the first class were dominant (Fig. 2). As a consequence of these changes, the population reached the maximum inequality ($G' = 0.7 - 0.75$) between March and April of both years (Fig. 1C).

At the beginning of the reproductive phase, late spring–summer, the population reached the maximum standing crop (≈ 500 g·m⁻² for both years) (Fig. 1A). Meanwhile, density and size inequality decreased (Fig. 1B).

From July onward, senescence provoked the shedding of branches and the subsequent reduction in population biomass. Moreover, and as a result of senescence, the thalli from the larger size classes shifted to smaller size classes and the lowest values in the Gini coefficient were recorded ($G' = 0.32$ in September 1992 and $G' = 0.38$ in August 1993) (Fig. 1C). Minimum annual densities were recorded in the reproductive and senescence phases (81 and 28 plants·m⁻² in August 1992 and June 1993, respectively, Fig. 1B).

The dynamic relationship between the Gini coefficient and thallus size for the samples of the 2 years studied are shown in Figure 3. Size inequality of the thalli increased during the winter growth period, that is, thallus size and G' showed a positive relationship ($F_{1,34} = 7.159$, $P < 0.05$ for the period November–March). Once the peak in the Gini coefficient was reached in the early spring, the inequality was progressively decreasing. During the spring season, thallus size and the Gini coefficient showed a negative relationship ($F_{1,22} = 22.296$, $P < 0.05$ for the period March–June). Thereafter, the onset in the summer of the reproductive season and the later senescence reduced thallus size and also the size inequality in the population.

Biomass–density relationship. The temporal variations of the density–biomass relationship are shown in Figure 4A. Although use of data from nonpermanent plots may complicate the interpretation, two general temporal trajectories can be described according to the growth-cycle phases:

1. A descending trajectory from July to November, including senescence and the end of reproduction. During this period and as a result of senescence and recruitment, density increased from its annual minimum in July–August, whereas biomass decreased.

2. An ascending trajectory from December to June, including the growth phases and the beginning of reproduction. During this period, density decreased whereas biomass increased until the summer peak.

Figure 4B shows the total biomass–density relationship through the growth period (December–June in 1992 and December–July in 1993). Only black and white dots were used for the analysis, because the remaining data (crosses) were not representative of a crowded situation and did not affect the slope of the final line.

The resulting annual RMA parameters plot biomass (B) versus density (d) were as follows:

1992

$$\text{Log } B = 4.315 - 0.815 \log d$$

OLS $r^2 = 0.307$; $n = 21$; $F_{(1,19)} = 8.441$; $P < 0.01$; 95% confidence intervals of slope: -1.203 , -0.552 (Jolicoeur and Mosimann estimator).

1993

$$\text{Log } B = 3.636 - 0.567 \log d$$

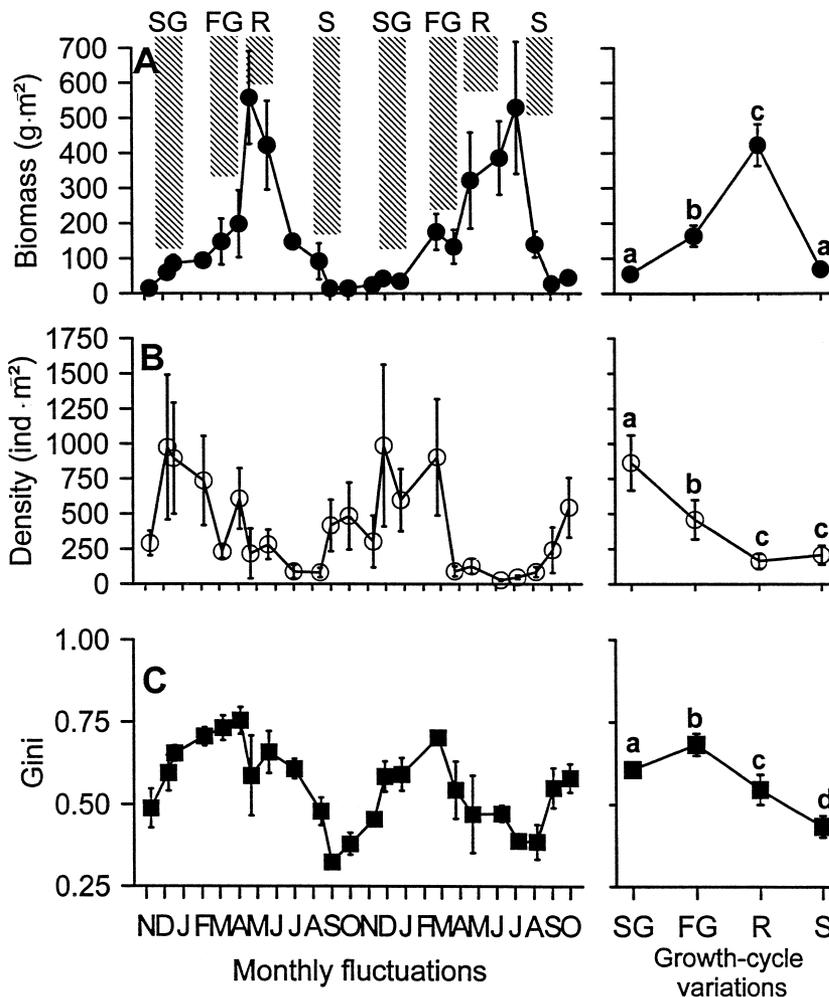


FIG. 1. Monthly fluctuations and growth-cycle phase variations of (A) stand biomass ($\text{g}\cdot\text{m}^{-2}$, mean \pm standard error, $n = 3$), (B) plant density ($\text{ind}\cdot\text{m}^{-2}$, mean \pm standard error, $n = 3$), and (C) Gini coefficient (mean \pm standard error, $n = 3$) of the *Sargassum muticum* population from El Truhán. SG, slow-growth period; FG, fast-growth period; R, reproductive period; S, senescence. Shaded bars indicate the selected months for the analysis of variance. Letters indicate the different group means on the SNK test at $P < 0.05$.

OLS $r^2 = 0.405$; $n = 13$; $F_{(1,11)} = 7.496$; $P < 0.05$; 95% confidence intervals of slope: -0.928 , -0.347 (Jolicoeur and Mosimann estimator).

Clarke's T test (Clarke 1980) did not show significant differences between the slope of the two regressions (Clarke $t_{0.05,(17)} = 1.813$, $P > 0.05$). Therefore, a new regression was calculated by pooling all data, as follows:

1992–1993

$$\text{Log } B = 3.924 - 0.6771 \log d$$

OLS $r^2 = 0.387$; $n = 34$; $F_{(1,32)} = 20.21$; $P < 0.001$; 95% confidence intervals of slope: -0.895 , -0.513 (Jolicoeur and Mosimann estimator).

Confidence intervals of slope of this relationship showed that the fitted line was slightly steeper than -0.5 . However the test for the slope proposed by Clarke (1980) did not show differences (Clarke's test, $T 0.306$, $P > 0.05$).

DISCUSSION

Dynamic of population parameters. Despite some remarkable differences in phenology (Fletcher and Fletcher 1975, Jephson and Gray 1977, Hales and Fletcher 1989,

Givernaud et al. 1991, Arenas et al. 1995, Fernández 1999), *S. muticum* on European coasts exhibits a very characteristic annual growth cycle.

The growth period, initiated in autumn and extending through the next summer, exhibited two distinct phases (Arenas et al. 1995): An autumn–winter moderate growth phase, with small increases in biomass, and a faster spring growth period extending until early summer, when the population reached its maximum biomass. During both growth phases, the population of *S. muticum* showed a size distribution dominated by the smallest thalli. This size hierarchy, with few large individuals and numerous smaller ones (Harper 1977), has been documented in natural and experimental populations of several seaweeds, such as *Macrocystis pyrifera* (Linnaeus) C. Agardh (Dean et al. 1989), *Fucus distichus* Linnaeus (Ang 1991), *Sargassum thunbergii* (Mertens ex Roth) Kuntze (Koh et al. 1993), and *Fucus serratus* Linnaeus (Creed et al. 1996b). Analogous size distributions have also been found in the fronds of some clonal algae, for example, *Mazzaella laminarioides* (Bory) Fredericq (Martínez and Santelices 1992) and *Gelidium sesquipedale* (Clem.) Bornet et Thuret (Santos 1995).

Despite numerical dominance of small thalli through

TABLE 1. Analysis of variance for interannual, growth-cycle phase, and dates differences on standing crop (g dry biomass·m⁻²), density (plants·m⁻²), and Gini coefficient of the population of *Sargassum muticum* in El Truhán.

Source	df	Standing crop ^a			Density ^a			Gini		
		MS	F	P	MS	F	P	MS	F	P
Year	1	0.0265	0.1149	0.743	0.6668	1.6522	0.234	0.0444	2.7764	0.134
Growth-cycle phase	3	2.4500	10.605	0.003**	1.8831	4.6655	0.036*	0.1318	8.2267	0.007**
Year × growth cycle	3	0.1807	0.7825	0.536	0.0902	0.2234	0.877	0.0287	1.7960	0.225
Time (Year × Lf)	8	0.2310	2.2526	0.049*	0.4036	2.7108	0.021*	0.0160	1.4087	0.230
Residual	32	0.1025			0.1488			0.0113		

^aLog transformed data. Cochran test for homogeneity, $P > 0.05$.

* $P < 0.05$, ** $P < 0.01$.

the growth phases, the dynamics of the size inequality in the population showed opposite patterns during the slow and the fast growth phases. During the first months of the growth period, the inequality of the population increased; however, once the spring peak was achieved, the trend reverted and the inequality progressively attenuated. Similar patterns of increase and decrease in inequality have been recorded in experimental populations of *F. serratus* and *Laminaria digitata* (Hudson) J.V. Lamouroux (Creed et al. 1998).

In our population the increase of inequality during autumn and winter could be caused by two synergistic processes. The first process is the existence of differences in plant growth rates (Turner and Rabinowitz 1983, Bonan 1988). Because of the deciduous nature of *S. muticum*, thalli develop a new lateral branching system each year and hence all branches in the population are evenly aged. However, in other species of *Sargassum* (Ang 1985), the growth of lateral branches in the regenerated thalli is faster than in the recruits (Arenas and Fernández, personal observation), and differences in sizes become larger as the growth period advances, increasing the size inequality of the population. Second, asymmetric competition might be an additional factor promoting the size inequality of the population. As larger plants suppress the growth of smaller plants (Weiner and Thomas 1986), one-side competition will probably intensify the differences in growth rates between regenerated thalli and recruits. Positive relationships between asymmetry and competition have been described in seaweed populations. Reed (1990) in *Pterygophora californica* Ruprecht and Creed et al. (1996a) in *F. serratus* proved that higher density populations became more positively skewed. Thus, these two processes (differences in growth rates and asymmetric competition) would occur simultaneously and might explain the high size inequalities ($G' = 0.7$) reached by our population in early spring.

As mentioned previously, the inequality of size distributions in the studied population was progressively decreasing during the last months of the growth period. The simultaneous reduction in the density and size inequality might be related to self-thinning: As a result of size-dependent mortality, small suppressed thalli would die, which would reduce the variability in thallus size (Watkinson et al. 1983, Weiner 1985, Weiner

and Thomas 1986, Schmitt et al. 1987). It is remarkable from our results that the beginning of the decrease in the size inequality concurred with the greatest accumulation of biomass in the population as a consequence of the high spring growth rates. This suggests that increased crowding rather than density itself could be the cause of self-thinning in our population, as Chapman and Goudey (1983) indicated for *Leathesia difformis* (Linnaeus) J.E. Areschoug.

Moreover, from midspring and during early summer other processes could explain the inequality reduction. As in many other seaweeds, the onset of reproduction in *S. muticum* occurs at the end of the growth period. Because maturation is not simultaneous, at the beginning of the reproductive period the first mature thalli have completed their growth, whereas some smaller nonreproductive thalli could still grow for some time (Norton 1977, Hales and Fletcher 1989, Arenas and Fernández 1998), which would result in a size inequality reduction.

Biomass–density relationship. Although the self-thinning was once considered a universal process in plant populations, an increasing amount of evidence has shown that not all plant species undergo self-thinning in crowded conditions (Pitelka 1984, Room and Julien 1994). Thus, in those populations where dynamic density–biomass relationships follow a negative trajectory (i.e. self-thinning occurs), departures from the previously accepted $-1/2$ thinning line have been widely reported and the relationship is now considered population and site dependent (see Weller 1987, Lonsdale 1990, Sackville Hamilton et al. 1995).

Studies of the dynamic of the biomass–density relationship in populations of seaweeds are not abundant in the literature, and the results differ depending on the growth form of the thallus (clonal or nonclonal). Santos (1995), Scrosati and DeWreede (1997), and Scrosati and Servièrre-Zaragoza (2000) found positive trajectories of the biomass–density relationship in natural populations of the red clonal algae *Gelidium sesquipedale*, *Mazzaella cornucopiae* (Postels and Ruprecht) Hommersand, and *Pterocladia capillacea* (Gmelin) Santelices et Hommersand, respectively, and concluded that these species do not suffer self-thinning in crowded conditions. In nonclonal species of algae, Creed et al. (1998) investigated the self-thinning trajectory in experi-

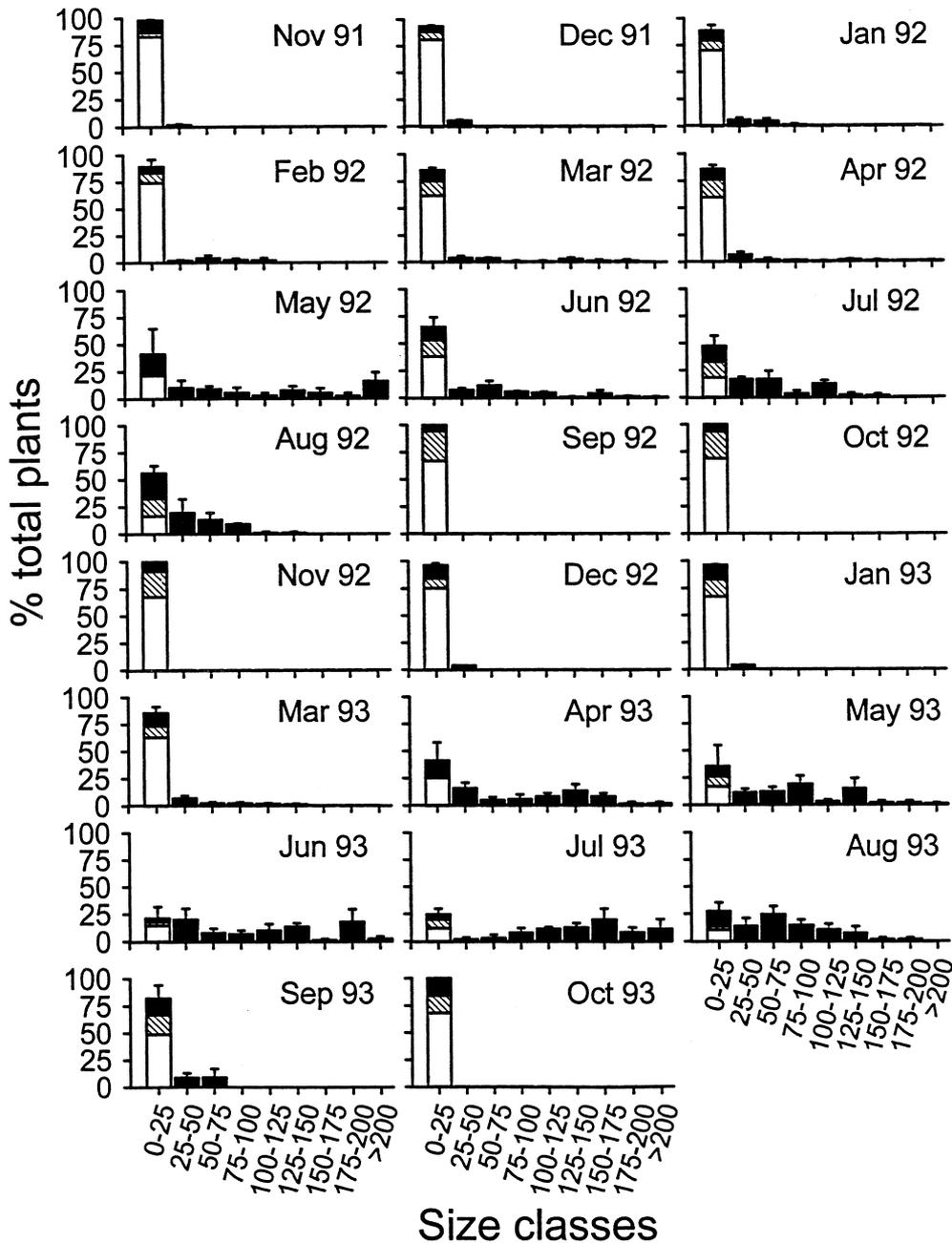


FIG. 2. Plant length–frequency distributions of the *Sargassum muticum* population from El Truhán. First length–class bars include three subclasses: white bar, 0- to 5-cm plants; gray bar, 5- to 10-cm plants; and black bar, 10- to 25-cm plants.

mental populations of *F. serratus* and *L. digitata* and recorded negative trajectories whose slopes (-0.574 and -0.59 , respectively) were not significantly different from the slope recorded in our population (-0.67). Studies focused on nonclonal or clonal species use different units to evaluate the intraspecific interactions: fronds (i.e. ramets) in clonal studies and whole thalli (i.e. genets) in nonclonal studies. Thus, these contradictory results in clonal and nonclonal species of algae have been attributed to the physiological integration of the fronds, which may reduce the mortality of

smaller fronds, preventing the occurrence of self-thinning. Other studies have analyzed static biomass–density combinations (i.e. all the samples were collected at a single date) and found evidence supporting the differences suggested above. Negative biomass–density is common in nonclonal species (i.e. *Fucus spiralis* Linnaeus, Robertson [1987]; *Himanthalia elongata* [Linnaeus] S. F. Gray, Creed [1995]; *Sargassum* spp., Kendrick [1994]). On the contrary, Martínez and Santelices (1992) did not find a significant relationship between mean biomass and density of fronds in a pop-

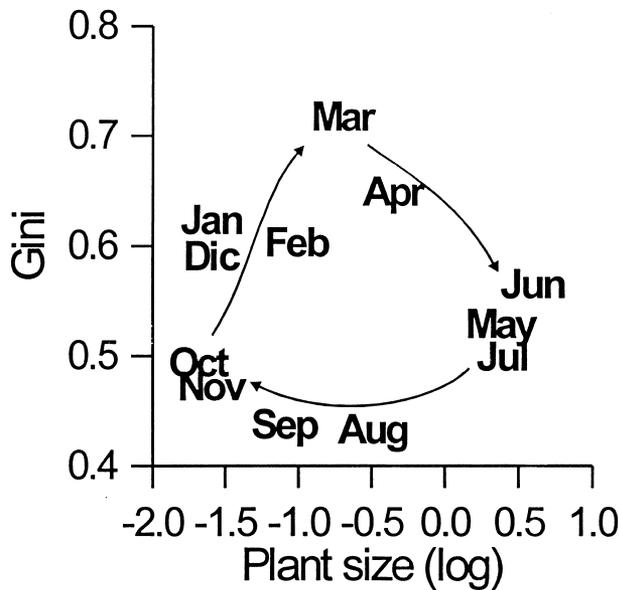


FIG. 3. Temporal dynamics of the relationship between mean size and the Gini coefficient in the population of *Sargassum muticum* for the two analyzed cycles.

ulation of the clonal seaweed *Mazzaella laminarioides*. However, not all clonal species seem to have the same behavior. Flores-Moya et al. (1996) found a negative biomass–density relationship among the fronds of the clonal red algae *Asparagopsis armata* Harvey similar to those predicted by Pitelka (1984) for clonal species with low physiological integration level. Unlike the clonal species mentioned above, whose fronds develop from a holdfast, *A. armata* has a stoloniferous growth form and presumably a lower physiological integration among the fronds.

The slope of the biomass–density relationship found in our study was slightly steeper than -0.5 . According to White (1981), self-thinning lines with slope -0.5 are expected when the plants have the same density of biomass (i.e. the same grade of biomass packing) across the range of densities of the relationship. Thus, trajectories with slopes steeper than 0.5 would indicate that as the plants grow, the efficiency of occupation of volume increase. *Sargassum muticum* has a high phenotypic plasticity, and in crowded conditions the species shows a clear tendency to a monopodial growth form (Andrew and Viejo 1998), which could change the packing density of the thalli during the period of growth. However, many other factors have been claimed as determinant in the slope of the self-thinning relationship. Environmental factors (like seasonal increase of light intensity) could gradually shift the position on the line upward, increasing the steepness of the relationship (Lonsdale 1990), or the fact that in natural conditions plants die not only as a result of density-dependent processes (Sackville Hamilton et al. 1995) might play a major role in the self-thinning relationship. Further experiments are needed to determine the importance

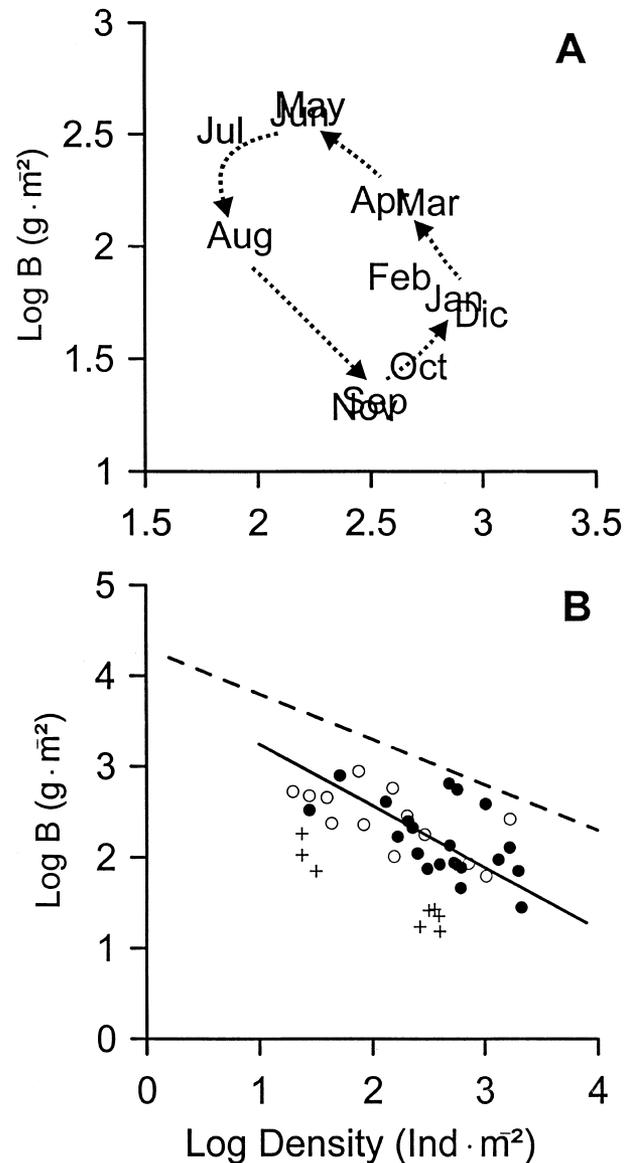


FIG. 4. (A) Temporal dynamics of the density–biomass in the population of *Sargassum muticum* for the two analyzed cycles. (B) Density and biomass (bilogarithmic scale) relationship in the population of *Sargassum muticum* from El Truhán. Dotted line, population boundary rule (see Discussion); bold line, calculated relationship; ●, 1992 samples; ○, 1993 samples; +, rejected samples.

of all these factors, and probably others, on the self-thinning line.

Osawa and Sugita (1989) defined the thinning rule as the upper possible boundary for all the biomass–density combinations in one species. This definition is in some way related to the interspecific size–density relationship established by Weller (1987) in terrestrial plants, which was tested in seaweeds by Cousens and Hutchings (1983). Considering this interpretation, none of the samples of our study falls above the proposed rule (slope $b = -0.5$, y intercept $k = 4.3$; White 1981), and the so-called population boundary rule

(Osawa and Sugita 1989) is thus pertinent for the studied population because the samples showed a “tangential” conformity to the rule (see Fig. 4B). Similar results were found by Creed (1995) in *Himanthalia elongata* (Linnaeus) S.F. Gray and by Kendrick (1994) in three species of the genus *Sargassum*; however, as expected, the boundary is not applicable to clonal species of algae (see Martínez and Santelices 1992, Santos 1995, Scrosati and DeWreede 1997), although a recent study by Scrosati (2000) showed that stand biomass of the clonal red seaweeds *Mazzaella cornucopiae* and *Pterocladia capillacea* laid below the ultimate biomass–density line.

In summary, the results of this study confirm the similarities between the mechanisms structuring terrestrial plants and some seaweed populations under crowded conditions. Asymmetric competition seemed to be a crucial factor in the population of *S. muticum*. Moreover, self-thinning determined the biomass–density relationships in the predicted trend for nonclonal plants.

We thank Dr. R. Viejo, Dr. J. M. Rico, and Dr. R. Scrosati for their helpful comments and suggestions. We also acknowledge the expert assistance of Dr. R. Santos and Dr. J. Arrontes. Comments from two anonymous reviewers improved an early draft of the manuscript. Supported by CICYT (project MAR90-0170). Dr. F. Arenas received additional support from the MAST III project EUROROCK (MAS3-CT95-0012).

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