

Size structure and inequality in a commercial stand of the seaweed *Gelidium sesquipedale*

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ABSTRACT: The temporal dynamics of the frequency distributions of 2 measures of *Gelidium sesquipedale* frond size, length and weight, was investigated in a subtidal stand under commercial exploitation. Frond weight/length allometry was highly variable, both seasonally and between years, showing that in this species weight and length cannot be used interchangeably as a measure of frond size. Physical disturbances played a fundamental role in allometric variability. The loss of branches due to commercial harvest and storms reduced the slope of the log weight/log length relationship. During spring the slope increased, indicating the production and growth of lateral branches. Size differences among individuals in the population (inequality) were quantified by 3 statistics: the skewness coefficient (g_1), the coefficient of variation (CV), and the Gini coefficient (G). Highly significant changes in frond length inequality, but not weight, were shown. These correspond to periods when *G. sesquipedale* length structure varied due to the combined effects of the demographic parameters that regulate the population (frond recruitment, survival, breakage and growth). Graphical analysis of significantly different length structures revealed that a recruitment peak of vegetatively developed fronds occurred during winter, following periods of high frond mortality and breakage caused by both human (summer harvesting) and natural (late fall storms) disturbances. During late spring and summer, the density of smaller fronds decreased due to mortality and growth into higher size classes. To assess density-dependent regulation processes, such as suppressed growth of smaller fronds and self-thinning, the time variation of both relationships, inequality/mean frond weight and biomass/density, was analysed. Inequality/mean frond weight and biomass/density values decreased from summer to winter and increased to the following summer. The increase of inequality while mean frond weight is increasing is consistent with the asymmetric competition theory on the development of crowded plant stands, and supports the hypothesis that the slower growth of smaller fronds during this period (Santos 1994; Mar. Ecol. Prog. Ser. 107: 295–305) is due to intraspecific competition. The time trajectory of the biomass/density relationship is perpendicular to and lies above the theoretical self-thinning line. Evidence for self-thinning was thus not detected. A conceptual model for the functioning of this population is proposed. Thinning and frond breakage caused by disturbances might be keeping intraspecific competition in these *G. sesquipedale* crowded stands (up to 18 000 fronds m⁻²) at low levels.

KEY WORDS: Size structure · Size hierarchy · Inequality · Gini coefficient · Skewness · *Gelidium sesquipedale* · Population dynamics · Self-thinning

INTRODUCTION

To assess the structure and functioning of populations, plant ecologists have studied the temporal dynamics of frequency distributions of some measure of an individual's size such as plant length, plant mass, stem diameter or leaf area. Changes of these size structures through time reflect the combined effect of the demographic parameters growth, survival and recruitment.

Variation in size structure within and among populations has been studied graphically (Mack & Harper 1977) or mathematically by considering some statistical measure of distributions such as mean, variance, skewness and kurtosis (Hara 1988). Research has focused on the skewness of size structures because most plant populations consist of many small individuals and relatively few large ones (Koyama & Kira 1956, Rabinowitz 1979, Higgins et al. 1984, Schiel 1985, Higgins & Mack 1987). The coefficient of varia-

tion ($CV = \text{standard deviation}/\text{mean}$) has been used as a statistical measure of the variability among members in a population (Kira et al. 1953, Edmeades & Daynard 1979, Mack & Pyke 1983).

Weiner & Solbrig (1984) recently proposed the use of the Gini coefficient to define how individuals of a plant population are ranked in size classes. The Gini coefficient measures the mean size differences among individuals in a population (inequality). There have been several applications of the Gini coefficient to study size variability in higher plant populations (Weiner 1985, Schmitt et al. 1986, 1987, Weiner & Thomas 1986, Bonan 1988, Geber 1989, Thomas & Weiner 1989). Populations of seaweeds have seldom been described in such a way (Martinez & Santelices 1992).

During the development of crowded monospecific stands, weight inequality generally increases over time until the onset of self-thinning due to differential growth rates between larger and smaller 'suppressed' plants. Then, inequality decreases as self-thinning progresses due to higher mortality rates of smaller plants (Weiner & Thomas 1986, Bonan 1988, Weiner & Whigham 1988, Geber 1989). This trend is interpreted as being consistent with the asymmetric competition hypothesis of dominance and suppression of smaller individuals by larger ones (Begon 1984, Hara 1988).

Self-thinning has also been studied in terms of concurrent changes in mean plant mass (or total biomass) and density. In crowded plant stands under self-thinning, the relationship between biomass and density forms a thinning line of slope $-3/2$ with an intercept of 4.3, when mean plant weight and density are plotted on a log scale; an equivalent line of slope $-1/2$ and with the same intercept is defined when the logarithm of stand biomass is plotted in place of average plant weight (see review in Westoby 1984). This relationship was defined as a general 'law' governing any even-aged plant population, the self-thinning rule, or the $-3/2$ power law (Yoda et al. 1963), and is supported by a wide variety of data from both artificial and natural stands of land plants (White & Harper 1970, White 1980, Westoby 1984), and seaweeds (Cousens & Hutchings 1983). Weller (1987) has since shown that the slopes and intercepts of thinning lines are more variable than previously thought. Even within the same species, different stands might have different 'dynamic self-thinning lines' (Weller 1990).

Gelidium sesquipedale (Clem.) Bornet et Thuret (Rhodophyta, Gelidiales) is a clonal alga that grows in the subtidal zone off the northeast Atlantic coast. Upright fronds are produced from a small, prostrate system of axes (Dixon 1958, Fan 1961). Dense monospecific stands of clumped fronds develop on exposed shores along the Portuguese coast, covering wide areas of the bottom. The populations are subjected

every summer and fall to commercial harvesting by divers, who hand-pluck the seaweed for its agar (Santos & Duarte 1991).

In a previous tagging study of the dynamics of frond number in *Gelidium sesquipedale* (Santos 1994), it was found that during the favourable growth season (spring/early summer), growth and survival of smaller fronds were lower than those of longer fronds. Intraspecific competition may be determining the survival and growth of small fronds within *G. sesquipedale*'s dense stands. Natural wave-induced physical stresses also play an important role in *G. sesquipedale* demographics (Santos 1994).

This study assesses *Gelidium sesquipedale* population dynamics through an analysis of its size distribution variability. As size is not a unified concept in plant species showing plasticity in growth form (Weiner & Thomas 1992), 2 size measures, frond weight and frond length, are used, and their allometric variability through time is followed. Three statistics are used to quantify size variability, and to detect significant changes of size structures through time: the skewness coefficient (g_1), the coefficient of variation (CV), and the Gini coefficient (G). Graphical analysis of the significantly different size structures reveals the underlying demographic events (recruitment, survivorship and growth) that regulate those changes.

Seasonal changes of population level parameters such as total biomass and density per unit area, and mean frond weight and length, are also investigated. The temporal variation of the empirical relationships biomass/density and inequality/mean frond weight is followed to assess density-dependent processes of growth suppression and self-thinning. Based on the information gathered, a conceptual model for the functioning of the population is proposed.

METHODS

The field study was conducted in one of the most important *Gelidium sesquipedale* commercial beds, off Cape Espichel, Portugal (Santos & Duarte 1991). Santos (1993a) described the main abiotic and biotic interactions in the bed. Additional information on the species size-dependent demographic rates in a dense stand of this bed is available in Santos (1994). In this study, the same stand was sampled monthly from July 1989 to September 1990, except for November and December 1989 and February 1990, when sea storms prevented diving. Both frond morphology and size structure appeared to be different in the upper and lower portions of the inclined strata upon which the population develops (Santos pers. obs.). Sampling was thus restricted to the middle zone of the strata, at a

constant depth of 9 m. Quadrat samples were spread through an area where *G. sesquipedale* is most abundant (transect 2; see Santos 1993a), and thus most likely to be harvested. Samples represent a mixture of harvested and nonharvested plants, reflecting the harvest efficiency of commercial divers. Sampling in July was just prior to the harvest season, which starts mid-July and extends through the summer and fall (Santos & Duarte 1991).

It is difficult to match upright fronds with their prostrate system of axes within *Gelidium sesquipedale*'s dense stands, and thus to distinguish fronds that originated from different spores (different genets *sensu* Harper 1977). Therefore, *G. sesquipedale* population dynamics was studied at the frond level. A sample size of five 40 × 40 cm quadrats was selected, following a study of the variation of biomass sample precision (Riddle 1989) for different quadrat sizes (15, 25, 40 and 50 cm) and a fixed diving time (Santos unpubl. data). All fronds inside the quadrats were removed by carefully scraping the substrate; the fronds were placed in a mesh bag. The resultant frond-length frequency distribution was similar to that obtained when fronds were scraped and collected with a compressed-air device (Santos unpubl. data).

All plant material was preserved by freezing. *Gelidium sesquipedale* mean frond weight and length were estimated for each monthly quadrat sample by measuring all fronds to the nearest mg and mm, respectively, in 3 randomly selected subsamples. Prior to measuring, the frozen fronds were thawed and surplus water was removed by blotting with paper towels. Allometric relationships between log weight and log length were analyzed by regression for all monthly samples.

Quantifying size structure variability. All data analyses were computed using Systat 5.1 for Macintosh (Wilkinson 1989), except the Gini coefficient calculations, which were done using a BASIC program. The skewness coefficient (g_1), the coefficient of variation (CV) and the Gini coefficient (G), (Kendall & Stuart 1969, Sokal & Rohlf 1969), were computed for all quadrats, to assess the shape and inequality levels of both frond length and weight distributions. Skewness is a shape parameter quantifying deviations from a normal distribution; positive values indicate a long right tail (more small fronds and fewer large fronds) and vice versa for negative values. In contrast, CV and G are measures of relative precision that reflect the ratio of a measure of dispersion (respectively the standard deviation and the coefficient of mean difference,

$\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j| / n$; from Gini 1912 in Weiner & Solbrig 1984) to the mean. Unbiased Gini coefficients, G' (Weiner & Solbrig 1984), were calculated as:

$$G' = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2 \bar{x} n(n-1)}$$

where x_i and x_j are the measures of all possible pairs of individuals. If all observations are the same, representing a minimum inequality, then $G = 0$. In an infinite population where all observations are zero except one, then G is maximum and has a value of 1.

Variability of size-structure coefficients through time was analyzed using a 1-way ANOVA. May 1990 values were not included in the statistical analysis, because only 2 quadrats were sampled. Data were log transformed, when necessary, to fulfil the condition of heteroscedasticity (Sokal & Rohlf 1969). Post hoc multiple contrasts analysis was done following Rodger (1974, 1975), to detect significant transitions between contiguous time periods. The critical values for rejecting null contrasts were taken from the F -value tables provided in Rodger (1975).

Density-dependent empirical relationships. To assess density-dependent processes, the temporal variation of the relationship between the logs of stand biomass and density were analyzed, rather than the more common approach of plotting log mean frond weight and log density (Yoda et al. 1963, White & Harper 1970, Westoby 1981, 1984, White 1981). Weller (1987) showed that use of average plant weight is statistically incorrect. The time trajectory of the relationship between weight inequality, given by the Gini coefficient, and mean frond weight were also analyzed (Weiner & Thomas 1986, Bonan 1988, Geber 1989).

RESULTS

Temporal variation of population parameters

There were significant differences among sampling dates (1-way ANOVA, $p \leq 0.001$) for mean frond weight, mean frond length, biomass and density in *Gelidium sesquipedale*. Post hoc multiple contrast analyses revealed 3 significant ($p < 0.05$) seasonal transitions of mean frond weight (Fig. 1A) and total biomass m^{-2} (Fig. 1C). High summer preharvest conditions in July 1989 were followed by lower levels, coincident with the start of harvesting. Unlike biomass, July 1989 mean frond weight was not significantly different ($p < 0.01$) from summer/early fall. Both parameters troughed in winter, after a period of severe sea conditions (November/December 1989), when waves up to 7 m high hit the coast of Cape Espichel (Santos 1994). In the seasonal transition from winter to spring/summer, mean frond weight and biomass increased, but never recovered to the levels of July 1989 (Fig. 1A & C).

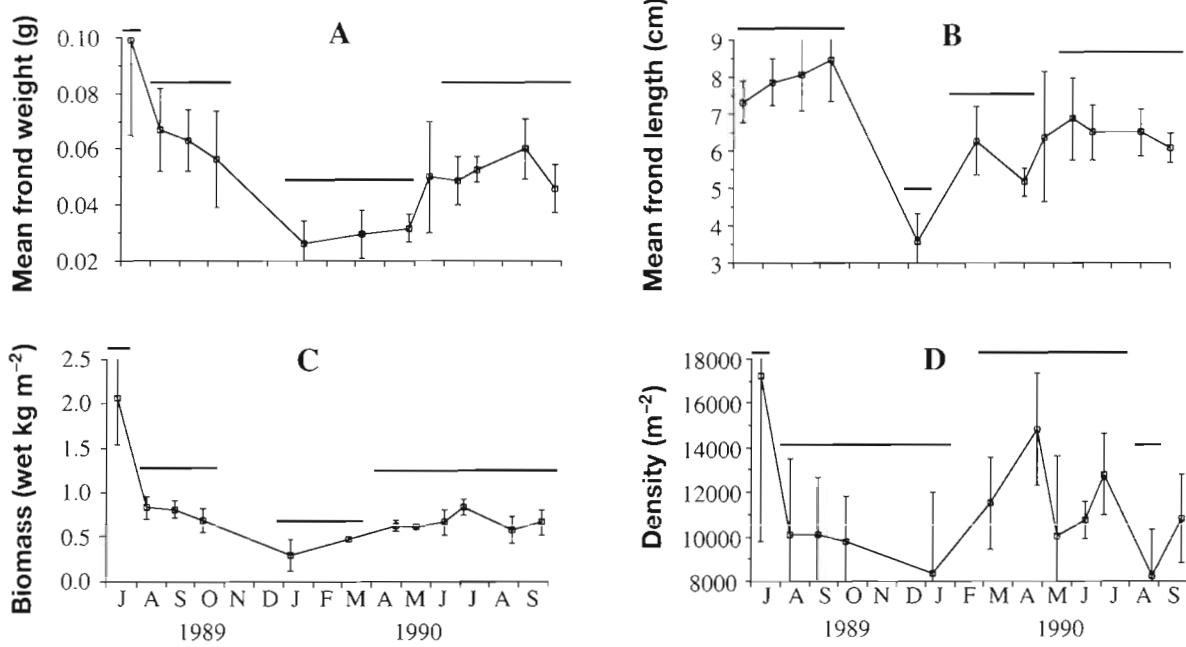


Fig. 1. *Gelidium sesquipedale*. Temporal variation in (A) mean frond weight, (B) mean frond length, (C) biomass m^{-2} and (D) density m^{-2} . Error bars indicate 1 SD from the mean ($n = 5$). Sample means under horizontal bars are not significantly different ($p < 0.05$). Horizontal bars at the same level are not significantly different. The May sample ($n = 2$) was not included in statistical analysis

Gelidium sesquipedale mean frond length showed a similar seasonal pattern to mean frond weight and total biomass: a low in winter and incomplete recovery to postharvest levels of 1989. However, mean frond length did not decrease during harvest seasons (Fig. 1B). Frond length increase, observed after the lowest level (January 1990), was faster than frond weight (Fig. 1B), indicating that during this period fronds elongate rather than branch. Branching was more intense after April 1990, based on the rapid increase in mean frond weight (Fig. 1A).

Seasonal variation of *Gelidium sesquipedale* frond density was not as great as the other variables, and in fact seasonal periods could not be detected at a significance level of $p = 0.01$. Four seasonal periods are separated at $p < 0.05$ (Fig. 1D). Density decreased from July 1989 to August 1989, and troughed during fall and early winter. In spring/early summer, frond density recovered to July 1989 levels, decreasing again in August 1990. This was the only significant drop in population parameters during the 1990 harvest season (Fig. 1D), but it is likely not related to harvest since the rest of the population parameters did not decrease during this period (Fig. 1A to C). September 1990 density was not significantly different from August 1990, but when the 2 months were lumped, density was not significantly different ($p > 0.05$) from July.

Frond weight/length allometry

Linear and second-order regressions between log frond weight and log frond length are highly significant for all months ($p < 0.001$), and varied significantly through time (Slope \pm SE; Table 1). The coefficients of determination of linear regressions, r^2 , are generally

Table 1 *Gelidium sesquipedale*. Allometric relationships between log frond weight and log frond length. n: no. of observations; r^2 : coefficient of determination of linear model; SE: slope standard error; Increase in r^2 : fraction of sample variation that is explained by second-order term, i.e. r^2 2nd-order – r^2 linear

Date	n	r^2	Slope \pm SE	Increase in r^2
4 Jul 1989	462	0.67	1.86 ± 0.062	0.07
2 Aug 1989	706	0.69	1.49 ± 0.038	0.06
6 Sep 1989	494	0.66	1.43 ± 0.046	0.11
4 Oct 1989	556	0.72	1.38 ± 0.037	0.08
8 Jan 1990	1970	0.63	1.10 ± 0.019	0.06
9 Mar 1990	1186	0.62	1.00 ± 0.023	0.14
24 Apr 1990	1113	0.77	1.37 ± 0.023	0.02
18 May 1990	357	0.84	1.56 ± 0.036	0.00
16 Jun 1990	825	0.84	1.52 ± 0.023	0.01
10 Jul 1990	865	0.80	1.53 ± 0.026	0.02
29 Aug 1990	789	0.83	1.52 ± 0.024	0.02
25 Sep 1990	910	0.77	1.55 ± 0.029	0.03

high, particularly from April 1990 to September 1990 when allometric relationships were almost linear (Increase in r^2 ; Table 1). Although the second-order terms were significant for all months ($p < 0.001$), they only slightly improved the models' performances. Exceptions are September 1989 and March 1990, when the increase in r^2 was 11 and 14%, respectively (Table 1). The slope of *Gelidium sesquipedale* log weight / log length relationship decreased from a maximum in July 1989 to a minimum in March 1990, suggesting the loss of branches due to harvest and storms. It increased during spring 1990, indicating the production and growth of lateral branches, and stabilized during summer 1990.

Temporal variation of population structure

Gelidium sesquipedale weight distributions had high inequality values (Fig. 2), and were highly skewed. All coefficients showed a general decreasing trend through time, but the statistical significance was low (p -values; Table 2). Seasonal patterns were not detected. Temporal variation of CV and g_1 (Fig. 2B & C), at significance levels of $p = 0.06$ and $p = 0.05$, were due to the reduction of *G. sesquipedale* fronds in the small

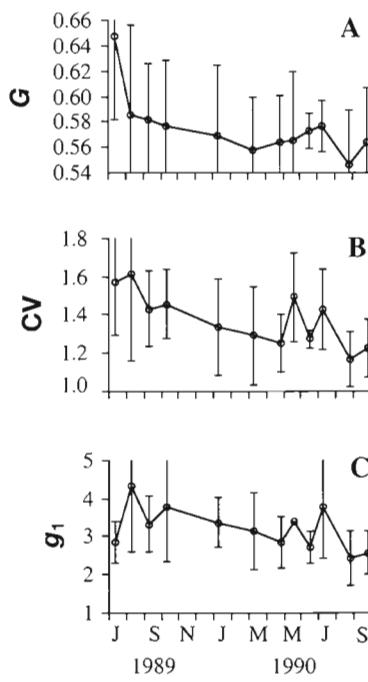


Fig. 2. *Gelidium sesquipedale*. Annual variation of weight distribution inequalities, measured by (A) the Gini coefficient (G), (B) the coefficient of variation (CV) and (C) the skewness coefficient (g_1). Error bars indicate 1 SD from the mean ($n = 5$). The May sample ($n = 2$) was not included in statistical analysis

Table 2. *Gelidium sesquipedale*. ANOVA summary statistics for time variance of weight and length distribution inequality. G : Gini coefficient; CV: coefficient of variation; g_1 : skewness coefficient

Size measure	Coefficient	SS:		F	p
		between groups	within groups		
		(df = 10)	(df = 44)		
Weight	G	0.034	0.097	1.532	0.160
	Log CV	0.491	1.074	2.014	0.055
	Log g_1	1.454	3.074	2.081	0.047
Length	G	0.075	0.025	13.409	0.000
	Log CV	0.745	0.283	11.562	0.000
	g_1	3.219	3.405	4.159	0.000

and large weight classes (Fig. 3) between August 1989 and August 1990. This caused both a decrease in the variation of frond weights in relation to the mean (CV) and a flattening of the shape of the distribution, reducing the skewness coefficient value (g_1).

In contrast, length inequality and skewness have lower values and their time variation is highly significant ($p < 0.001$; Table 2). Length inequality and skewness increase to winter and decrease to summer. Three significant seasonal transitions were detected by post hoc multiple contrast analysis ($p < 0.05$), when using G and CV statistics (horizontal lines in Fig. 4A, B). The 2 periods, August–October 1989 and June–September 1990, are not significantly different from each other. When analyzing the length distributions with the skewness coefficient (g_1), only 2 significant transitions are revealed (Fig. 4C). Length distribution skewness in July 1989 was not significantly different from that of August/September 1990.

Significant transitions in size distribution inequalities represent periods when the combined effect of frond growth, breakage and mortality, and recruitment of new fronds was significant. To investigate these, all

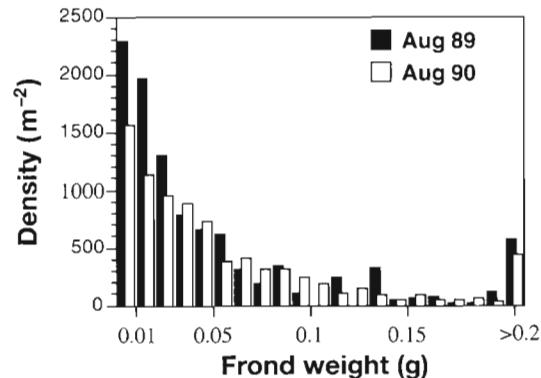


Fig. 3. *Gelidium sesquipedale*. Changes in weight distributions from August 1989 to August 1990

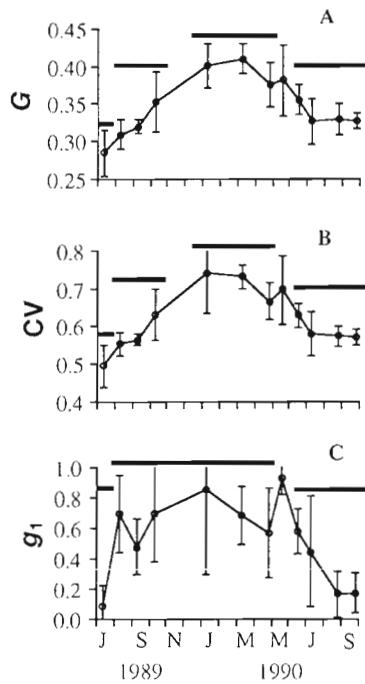


Fig. 4. *Gelidium sesquipedale*. Annual variation of length distribution inequalities, measured by (A) the Gini coefficient (G), (B) the coefficient of variation (CV) and (C) the skewness coefficient (g_1). Error bars indicate 1 SD from the mean ($n = 5$). Horizontal lines show significant $p < 0.05$) seasonal transitions. The May sample ($n = 2$) was not included in statistical analysis

length data in each time period were pooled and frequency distributions plotted (1 cm size class density m^{-2} ; Fig. 5). There was a general reduction in frond density between July 1989 and the period August–October 1989 (Fig. 5A), due to harvesting. Also, the right tail of the distribution increased, reflecting elongation of shorter fronds and determining the increase of length inequality and skewness (Fig. 4).

The next significant inequality increase was between August–October 1989 and January–April 1990, characterized by a pulse of fronds $< 4 \text{ cm}$, and a decrease in density of fronds $> 6 \text{ cm}$ (Fig. 5B). During the last seasonal transition, to the period June–September 1990, a reverse pattern was observed (Fig. 5C). Length inequality decreased due to the decrease in density of smaller fronds, and growth into higher size classes.

Density-dependent empirical relationships

Additional data from 7 quadrat samples obtained at the same site in July 1988 were included in the analysis of both relationships, inequality-mean frond weight (Fig. 6A) and biomass-density (Fig. 6B). *Gelidium sesquipedale* weight inequality was positively correlated

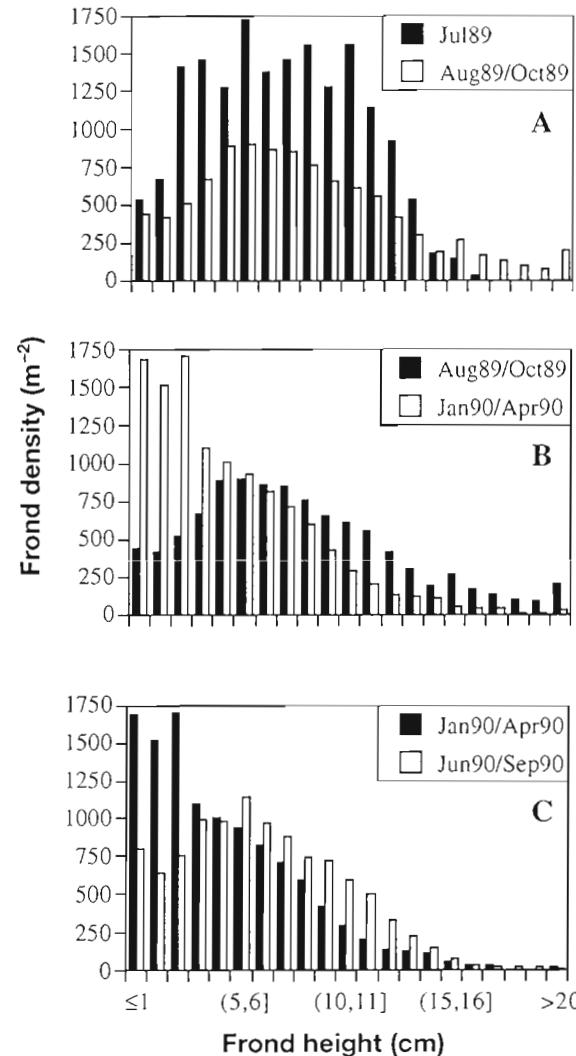


Fig. 5. *Gelidium sesquipedale*. Comparison of the 3 significant changes on the inequality of length distributions; from (A) July 1989 to August–October 1989, (B) August–October 1989 to January–April 1990 and from (C) January–April 1990 to June–September 1990

with mean frond weight ($r^2 = 0.45$, $p < 0.001$). The highest values were in July 1988 and July 1989, while the lowest values occurred the following winter (January 1990–March 1990; Fig. 6A). The temporal variation of the relationship swings between summer high values and winter low values, along the line $y = 0.88 + 0.23x$ (Fig. 6A).

Data points of the biomass/density relationship (Fig. 6B) lie mostly above the theoretical boundary line for self-thinning populations shown in the graph, $\log_{10}B = 4.3 - 1/2 \log_{10}N$, where B is stand biomass (m^{-2}) and N is frond density (m^{-2}) (Fig. 6B). The time trajectory of this relationship shows a similar pattern to the inequality/mean weight relationship (Fig. 6A); it increased from winter to summer, decreasing after-

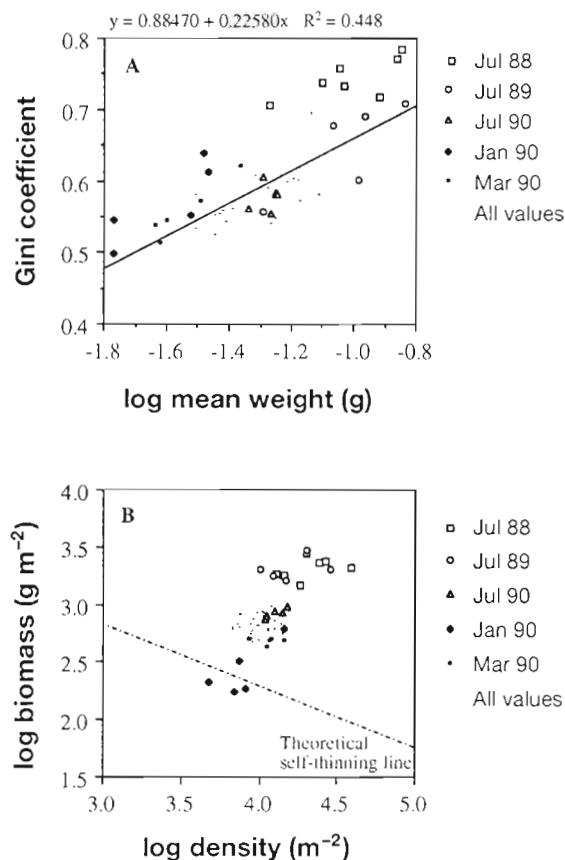


Fig. 6. *Gelidium sesquipedale*. Time trajectory of the relationships between (A) frond weight inequality (Gini coefficient) and log mean frond weight and (B) log biomass (m^{-2}) and log density (m^{-2}). Line in (B) is the theoretical self-thinning line, $\log \text{biomass} = 4.3 - 1/2 \log \text{density}$ (see text). Regression between the Gini coefficient and log mean weight includes July 1988 values

wards. Biomass/density values during 1990 peaked in July, but did not reach the values of July 1988 and 1989.

DISCUSSION

Population dynamics

Gelidium sesquipedale population parameter variability (Fig. 1) was related to both environmental and human-induced disturbances (storms and harvest). The sharp drop in all population parameters (except mean frond length after July 1989) reflected in the first significant transition of frond length distribution (Fig. 5A) is coincident with the start of the harvest season. During this season, 12 boats carrying an average of 4 divers collected about 1700 t of wet seaweed (J. Oliveira pers. comm.). That mean frond length did not decrease

with the 1989 harvest suggests that some fronds may have lost their branches while their main axis remained intact, or that heavier fronds (more branched with more surface) are more likely to be detached than longer, less-branched fronds. A similar situation was observed in *Chondrus crispus* commercial beds off Prince Edward Island, Canada, where the drag-rake method of harvesting appears to select for the branched fronds (Pringle & Semple 1988).

Winter low values for the measured population parameters followed a period of unusually strong storms. The dynamics of frond survival and growth during this period, derived from the analysis of the seasonal transitions of length structures (Fig. 5), are supported by Santos' (1994) tagging study of *Gelidium sesquipedale* frond dynamics. Summer to winter transitions are caused by the longer fronds' higher mortality during harvest and higher frond breakage during storms.

The pulse of short fronds (≤ 4 cm) observed in winter/early spring (Fig. 5B) reflects recruitment of new fronds rather than breakage of longer fronds, because density increased during this period (Fig. 1D). Santos (1993b) showed that the number of size class 1 fronds (4 to 10 cm) is high even after discounting both frond breakage and growth, respectively, into and out of the class. The pulse of size class 1 fronds was detected in March/April, indicating that new fronds developed some months earlier, probably in reaction to the reduction of the canopy due to late fall storms.

Frond recruitment appears to originate by vegetative growth of the prostrate system (Dixon 1958, Fan 1961), rather than through the development of new fronds from spores. Vegetative growth is the most important process for the recovery of populations of *Gelidium* species (Santelices 1988). This was supported by the low frond recruitment of *G. sesquipedale* on ceramic tiles placed in the study site (Santos unpubl. data). A similar dynamic has been suggested for the highly disturbed commercial stands of *Chondrus crispus* off Prince Edward Island, which have higher densities of small fronds than do nonharvested beds (Chopin et al. 1992).

Gelidium sesquipedale fronds recruited in winter grew to longer size classes during spring/summer 1990 (Fig. 5C). Yet, the stand did not recover to the maximum values of July 1989. Frond length distribution changes from summer 1989 (Fig. 5A) to 1990 (Fig. 5C) reflect this. The same trend is shown in demographic simulations of the population and was supported by the large decrease in harvest landings between 1989 and 1990 (Santos 1993b). The effects of harvesting on the *G. sesquipedale* population parameters were not detected in 1990, likely due to reduced effort.

Size distribution coefficients

The behaviour of the 3 statistics used to quantify the temporal variability of the size distributions of *Gelidium sesquipedale* generally agrees with those reported in the literature (Weiner & Thomas 1986, Bendel et al. 1989). The Gini coefficient and the coefficient of variation had similar performances, whereas skewness was more related to the latter. G and CV were highly correlated to one another for both weight and length ($r = 0.84$ and $r = 0.98$, respectively), while g_1 was, in both cases, more correlated to CV ($r = 0.78$ and $r = 0.68$, respectively) than to G ($r = 0.36$ and $r = 0.57$, respectively). G is a more robust inequality measure than CV and g_1 ; it has lower values of sum of squares within groups (Table 2), because it is less sensitive to variation in the distribution tails (Bendel et al. 1989).

Contrary to length, the dynamics of weight structures did not reveal clear seasonal variations (Fig. 2), because the statistics are sensitive to variations of the right tail of these highly skewed distributions. The presence of sporadic heavy fronds has a great effect on weight statistics.

Allometric relationships

Gelidium sesquipedale frond weight/length allometry was highly variable, both seasonally and between years, indicating great plasticity in the species form. Inferences from one size measure to another in *G. sesquipedale* must take into account the temporal variability of weight/length allometry. Plant allometric changes can be explained in terms of intraspecific competition and size-dependent growth after the onset of competition (White 1981, Weller 1987, Weiner & Thomas 1992). Yet, in natural populations of *G. sesquipedale*, physical disturbances are likely to play a fundamental role in allometry variability. The loss of branches due to commercial harvest and storms reduced the slope from summer 1989 to winter 1990. The same was not observed during the summer of 1990, due to the reduced harvest effort in this season.

Gelidium sesquipedale weight/length allometry shows that frond branching was high in the spring. Branching was also evident from the increase in mean frond weight from April to May/June, after a period when weight was constant despite the increase of frond mean length (Fig. 1A, B). Higher branching during spring and summer is typical of *Gelidium* species (Seoane-Camba 1969, Barilotti & Silverthorne 1972, Reguera et al. 1978, Carter & Anderson 1986). Higher irradiance during this season may be the environmental factor determining this response. Culture studies of *Gelidium latifolium* showed that the number of

branches and branch initials increased markedly with irradiance, rather than temperature (Fredriksen & Rueness 1989).

Density-dependent empirical relationships

The time trajectory of the *Gelidium sesquipedale* inequality/mean frond weight relationship (Fig. 6A) is consistent with the asymmetric competition theory (Begon 1984, Hara 1988), where, in crowded stands, weight inequality is predicted to increase with increased mean plant weight until the onset of self-thinning. At this point, inequality decreases as mortality of smaller plants progresses (Weiner & Thomas 1986). The *G. sesquipedale* population studied here never reached a self-thinning situation.

The *Gelidium sesquipedale* weight inequality/mean frond weight relationship increased from a low in winter to a maximum in summer (Fig. 6A), suggesting a differential biomass increase between heavier and lighter fronds during this period. A similar pattern was also observed for frond elongation rate (Santelices 1994). Differential growth may be due to density-dependent suppression of smaller fronds by larger ones or by a density-independent difference in growth patterns. Although a *G. sesquipedale* axis elongates by division of 1 apical cell (Rodriguez & Santelices 1987), the rate of elongation of subsequent cells may be higher in larger fronds, independent of crowding. Further studies are needed to clarify this point.

Both inequality/mean frond weight and biomass/density relationships in *Gelidium sesquipedale* showed no evidence of self-thinning. Thomas & Weiner (1989) noted that the ability of small, suppressed plants of the annual *Impatiens pallida* Nutt. to survive was critical in determining the relationship between mean plant weight and size inequality. They report a slope of 0.41 before the onset of self-thinning, which is similar to the slope of 0.45 found for *G. sesquipedale* (Fig. 6A). In plant populations where self-thinning is important, slopes of -0.20 and -0.10 were reported, respectively, for 2 conifer species (Weiner & Thomas 1986) and for the annual wild-rice *Zizania aquatica* (Weiner & Whigham 1988).

The onset of natural self-thinning in *Gelidium sesquipedale* populations is perhaps precluded by the thinning and frond breakage caused by harvest during early summer. *Gelidium* spp. generally occur in habitats exposed to strong wave surge (Santelices 1988), hence they likely rarely reach a self-thinning situation. Following summer production peaks, large biomass losses occur during fall/winter storms. Tossed *Gelidium* spp. are harvested along the shores in different parts of the world and constitute the basis of important

agar industries (Michanek 1975, Santelices 1988, Santos 1993c).

A general trend towards increasing weight inequality with increased mean plant weight through time has been observed in greenhouse studies (see review by Weiner & Thomas 1986) and in natural land plant stands (Schmitt et al. 1987, Thomas & Weiner 1989). In seaweeds, there are insufficient data to determine whether density-dependent thinning is common. Possibly the only published work analyzing this relationship is that of Martinez & Santelices (1992), who found no significant relationship between G and mean frond weight in a Chilean population of the red alga *Iridaea laminarioides*. The authors suggest this might be common in seaweed species, resulting from a lack of self-thinning, as Pitelka (1984) reported for physiologically integrated clonal ramets. However, Martinez & Santelices (1992) studied this relationship at only 1 point in time. It is thus not possible to understand the time trajectory of the relationship. Ang & De Wreede (1992) observed a general increase in size inequality in the development of seeded blocks and cleared plots of *Fucus distichus* (L.) Powell from winter to spring, probably due to a greater mortality of smaller plants (Ang & De Wreede 1992). This trend became less distinct in summer due to increased mortality of larger plants.

In seaweeds, the more appropriate competition model might be the 1-sided as opposed to 2-sided model, in which resource depletion will have an effect proportional to the size of the plant (see review of plant competition models in Weiner & Thomas 1986). The 1-sided competition model predicts that small plants will be more suppressed than bigger ones when resources are not evenly distributed, i.e. when larger plants can have more resources than the smaller ones, because of size. This is the generally accepted model in higher plants when competition is for light, but, when it is for nutrients, the 2-sided model may be more appropriate. In subtidal seaweeds, not only is light more readily available for larger plants, but so are nutrients due to the fluid mechanics of this environment. Under the canopy, water movement is reduced and the boundary layers of small fronds can be more easily nutrient depleted (Koehl 1986, Denny 1988). Larger plants are more exposed to both light and water movement, at least in the upper parts of the thallus. This might be particularly important in species such as *Gelidium* spp. in which growth is apical.

Conceptual model of population

This work shows the importance of disturbances, both natural (storms) and human (harvesting) on the regulation of *Gelidium sesquipedale* population size

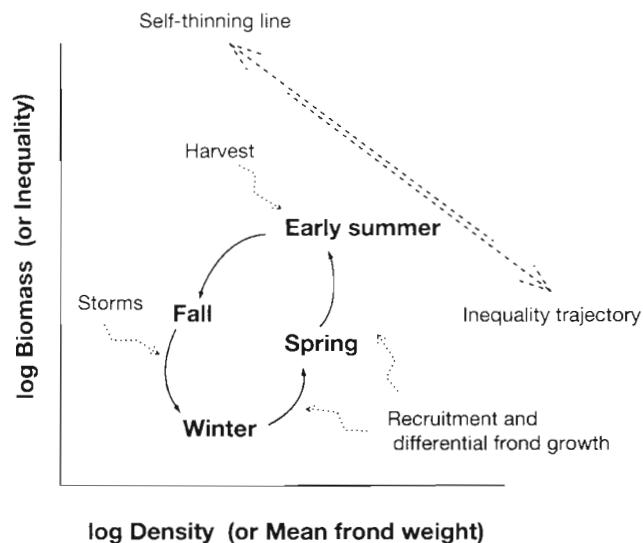


Fig. 7. *Gelidium sesquipedale*. Conceptual model of population dynamics. Relationships between both log biomass and log density and between inequality (Gini coefficient) and log mean frond weight increased from winter to summer. This was due to the suppressed growth of smaller fronds during this period of high elongation rates. The population studied did not attain a self-thinning condition, when the time trajectory of the relationships should bend along opposite directions (dashed arrows). Physical disturbances (harvest and storms; dotted lines) caused high mortality and breakage, particularly of larger fronds, reducing intraspecific competition pressure to low levels where self-thinning does not occur. Both relationships decreased during this period to a low in winter

structure. The following conceptual model of the species population dynamics is suggested (Fig. 7). Both the relationships, biomass/density and inequality/mean frond weight, decrease from summer to winter (Fig. 6) due to physical disturbances. Disturbances cause high mortality and breakage of larger fronds during summer and fall (Santos 1994), keeping intraspecific competition at low levels. During such periods, smaller frond elongation rate is high and their mortality is low (Santos 1994). The recruitment peak of vegetatively developed fronds follows these disturbances (Fig. 5B), and is probably induced by biomass loss. During spring and early summer, the opposite pattern was observed (Fig. 7) due to faster growth and lower mortality of larger fronds (Santos 1994). The *G. sesquipedale* stand studied never reached the level where extensive self-thinning caused the time trajectory of these relationships to bend in opposite directions (Fig. 7), as Weiner & Thomas (1986) and Weller (1987, 1990) reported for higher plants. The dynamic/thinning line (Weller 1990) of this *G. sesquipedale* stand may be well above the interspecific self-thinning line (Yoda et al. 1963, Weller 1987).

Acknowledgements. P. Duarte and A. Morais provided invaluable field and laboratory support. The comments of J. Pringle, G. Sharp, S. Walde, P. Ang, R. De Wreede, C. Hudon, J. Weiner and B. Husband greatly improved the manuscript. This research was funded by Laboratório Nacional de Engenharia e Tecnologia Industrial through Dr C. Peneda's grant, to whom I am particularly grateful. Grants from Junta Nacional de Investigação Científica e Tecnológica, scholarship (BIC no. 402), Government of Canada Awards, and Lett Bursary, Dalhousie University, supported my stay in Canada. The Halifax Fisheries Research Laboratory provided the conditions as well as an excellent working environment for data analyses and writing.

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This article was submitted to the editor

Manuscript first received: May 6, 1994

Revised version accepted: November 26, 1994