

STRUCTURE AND DYNAMICS OF A POPULATION OF *PALMARIA PALMATA* (RHODOPHYTA) IN NORTHERN SPAIN¹

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Palmaria palmata (Linnaeus) O. Kuntze (Rhodophyta, Palmariaceae) is a seaweed commercially harvested for human consumption. Its population density, size structure, and frond dynamics were investigated from May 1999 to May 2001 at one intertidal locality in the northern coast of Spain, which is within the southern distributional boundary of the species in the eastern Atlantic coasts. The effect of size, age, and the life-history phase (haploid vs. diploid) on frond growth and mortality were also evaluated. The study was carried out by mapping and monitoring fronds in the field. New fronds (macroscopic recruits or sprouts) appeared in spring, but subsequent mortality of these young fronds and detachment of the host plant led to lower density values in January. *Palmaria palmata* exhibited a distinctive seasonal growth cycle, with positive net growth from March to August and breakage from August to March. Interannual differences were also detected, with higher net growth in 2000 than in 1999. Net growth was apparently independent of age, reproductive status (fertile vs. reproductive), and life-history phase (haploid vs. diploid) but was dependent on size, as longer fronds showed minor growth or greater breakage than small ones. Mortality, on the other hand, was more dependent on age than on size in the period analyzed (March–May 2000). Results of the study indicate that both size and age should be included as state variables and temporal changes in transition probabilities considered in the development of demographic models of the species.

Key index words: demography; epiphyte; growth; mortality; *Palmaria palmata*; population dynamics; population structure; Rhodophyta; state variable

The vital rates of organisms (birth, growth, reproduction, and death) determine the growth or decline, persistence or extinction, fluctuation or stability of populations. Population dynamics have consequences for management strategies to protect endangered species, to harvest species of commercial interest, or to control pest species (Schemske et al. 1994) and for

analysis of life history evolution (Caswell 1982). The demographic parameters differ among individuals within populations for factors such as age, size, or other life-history stages (e.g. haploid vs. diploid). Plants exhibit indeterminate growth and can shrink and resume growth, which frequently results in equally aged individuals of different sizes. Hence, size is usually a better state variable than age as a descriptor of the fate of these organisms (Harper 1977, Chapman 1986, Caswell 2001).

In marine macroalgae, several aspects of the population ecology, such as biomass production, density, or size structure, have been widely investigated (Gunnill 1980, Bhattacharya 1985, Schiel 1990, Chopin et al. 1992, Santos 1995, Scrosati and De Wreede 1997, Scrosati and Servièrre-Zaragoza 2000). Nevertheless, estimation of vital rates in the field and the evaluation of the suitability of any state variable to describe demographic events have been seldom addressed (Chapman 1986, Dean et al. 1989, Ang 1991, Santos 1993, 1994, Scrosati 1998, Griffin et al. 1999). This is probably due to inherent methodological difficulties of such studies in seaweeds, such as recognizing the same individuals over time or finding nondestructive methods to estimate size or age. Furthermore, some species exhibit diplobiontic life cycles with isomorphic haploid and diploid free-living individuals, which are difficult to distinguish in the field. As a result, the development of demographic models that integrate both population structure and dynamics and accommodate complex life cycles have been applied to a few macroalgal species (Ang et al. 1990, Aberg 1992, Ang and De Wreede 1993, Chapman 1993, Santos 1993, Santos and Nyman 1998, Lindgren 2000, Engel et al. 2001).

Palmaria palmata (Linnaeus) O. Kuntze (Palmariales, Palmariaceae) is a red seaweed that occurs exclusively in the northern hemisphere, with its southern distributional boundary on the European shores in Portugal. The species, commonly known as Dulse, Dillisk, Dilleasc, or Creathnach (Irish), is probably the most widely known edible seaweed in the North Atlantic (Rudolph 2000) and is commercially harvested along the northeastern Atlantic for human consumption. Despite its commercial value, there have been no previous demographic studies of the species. *Palmaria palmata* is epilithic and epiphytic on brown seaweeds and appears in the low intertidal and subtidal to a depth of 20 m in both sheltered and moderately exposed areas (Irvine and Guiry 1983). The order

¹ Received 10 September 2002. Accepted 12 July 2003.

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Palmariales has a unique life cycle within red algae, due to the lack of a carposporophytic phase. Tetrasporophytes developed directly on fertilized female gametophytes (Van der Meer and Todd 1980). Female *P. palmata* gametophytes are microscopic, but male gametophytes and tetrasporophytes are macroscopic and isomorphic.

In this study, we investigated several demographic aspects of a natural population of *P. palmata* located in the northern coast of Spain over a 2-year period. In this area, the species grows epiphytically on *Cystoseira baccata* (Gmelin) Silva, *Fucus serratus* L., and *Laminaria hyperborea* (Gunnerus) Foslie, and populations are scarce and relatively isolated (personal observation). The following hypotheses were tested: 1) the density, size structure, and dynamics of the *P. palmata* population varied within and between years and 2) growth and mortality rates were dependent on size, age, and life-history phases (macroscopic male gametophytes and tetrasporophytes). This study provides valuable information for comparative studies with northern populations and for the development of stage-structured models of the species on its southern distributional boundary.

MATERIALS AND METHODS

Study site. The field study and the collection of samples were carried out at one locality in the northern coast of Spain, Estaño (43°33'N, 5°35'W), from May 1999 to May 2001. Estaño is a relatively wave-exposed area, with a gently sloping rocky platform, rocks, boulders (from 4 cm to 2 m diameter), and sand as substrata. Some of the rocky surfaces were temporally covered with sand during summer 2000. At this locality there is an abundant population of *P. palmata*, growing epiphytically on *C. baccata* and *L. hyperborea* and occupying an area of about 2500 m² of rocky platform, from approximately 0.4 m above to 4 m below the lowest astronomical tide (LAT). Population structure and dynamics were investigated at lower intertidal-shallow subtidal level, where *C. baccata* was the only host for *P. palmata*. Plants were exposed to the air only during spring tides (4–5 days a month) for a period of time that never exceeded 3 h.

Environmental variables. In the study area, rough weather and storms are frequent in autumn and winter, and breakage of fronds of both *P. palmata* and the host (i.e. *C. baccata*) usually occurs during this period due to wave action. Temperature and light are also important factors affecting the growth rate of seaweeds (Kain and Norton 1990, Lüning 1990). Because these environmental factors could influence the population structure and dynamics of *P. palmata*, they were recorded periodically throughout the study period.

Wave force values were obtained by a scalar buoy (Mod. Wave Rider, Datawell, Heerhugowaard, Netherlands) placed at 43 m depth about 7 km away from Estaño. Data were provided as maximum wave significant height (Hs), which is defined as the mean wave height of one third of the highest waves measured during 20 min every hour (8 h a day). Wave force data were corrected by multiplying Hs values by an exposure coefficient inferred for the study site. This coefficient was calculated using a wave propagation model (Oluca-MC) provided by the *Grupo de Ingeniería Oceanográfica y de Costas* from the University of Cantabria (Spain). Seawater temperature was monitored by an Optic Stow Away temperature data logger (Onset Computer Corporation, Pocasset, MA, USA) fixed next to the population. Only temperature values during high tide were considered. Temperature data from April to

July 2000 were missing because of technical problems. The Meteorological Station of Oviedo, located about 29 km away from Estaño, provided the incident solar energy values (irradiance). Theoretical surface day-length (photoperiod) was calculated as described in Kirk (1983).

General considerations. Recognition of *P. palmata* genets in the field is a very difficult task because of the common overlapping and coalescence of contiguous holdfasts along the stipe of the host plant (Maggs and Cheney 1990). For that reason, this demographic study was carried out at the frond level. In *P. palmata* it is only possible to recognize visually tetrasporophytic (diploid) and gametophytic male (haploid) fronds when they are fertile, and we followed the descriptions given in Irvine and Guiry (1983) and Guiry (1975) for this recognition. In March 2000 and 2001, we observed a clear increase of frond density, due to the appearance of macroscopic young fronds, which were easily distinguished from the rest. These young fronds were thin, membranous, smooth, and light red, whereas the rest were thick, leathery, and dark red and were usually broken and epiphytized. A sample of these young fronds was mapped in both months. Therefore, from March 2000 to March 2001 fronds were aged in two classes: young fronds of 2000 and fronds of 1999 or before (i.e. those tagged at the start of the sampling period). Similarly, from March to May 2001 fronds were aged in two classes: fronds of 2001 and fronds of 2000 or before. Hereafter we refer to these two age classes as “young” and “old.” Marginal proliferations grew from the primary blade of old fronds and were of the same color and texture as young fronds. Nevertheless, these “old” fronds were still easily recognized from “young” fronds in March because of the presence of the thick primary blade or a fragment of it.

The host *C. baccata* exhibits a seasonal growth pattern, with plants achieving full size in late summer and abscission of the entire year's growth extending over a long period from early autumn (Roberts 1967). Hence, macroscopic recruits of *P. palmata* appearing in early spring on the apical parts of *C. baccata* constitute a “transient population” that disappear every year in late summer (personal observation). This apical population (formed exclusively by recruits) was clearly discernible in the field from the “persistent population” (formed by differently aged fronds that were located on the main axis and basal parts of the branches of *C. baccata*). The apical recruits were not included in this study.

To assess individual growth in the field, a nondestructive method for estimating frond size was needed. Parameters such as length and/or width may be strongly correlated to dry mass. Maximum length and width of a sample of fronds ($n = 175$) collected in May 1999 were measured. Fronds were then dried at 60°C until constant mass (approximately 48 h). Despite the laminar morphology of *P. palmata*, the best estimator of dry mass was the maximum length, better than the combination of length and width ($r^2 = 0.874$ for the power regression line using maximum length as independent variable; $r^2 = 0.773$ for the linear regression using length \times width as the independent variable). More fronds were subsequently collected in August 1999 ($n = 193$) and January 2000 ($n = 185$) to calculate the relationship between dry mass and maximum length. May, August, and January were chosen as representative months of the life cycle of the species in the field: appearance of visible recruits (macrorecruitment) from March to May, positive net growth from May to August (see results), and reproduction in winter. The percentage of reproductive fronds, tetrasporophytes plus male gametophytes, was 85.7% in February 1999 ($n = 147$) and 0% in May 1999 ($n = 207$) (unpublished data). In March and April reproductive fronds were still present, but more than 80% had already released the tetraspores/spermatia (unpublished data).

Population structure and density. To guarantee a sufficient number of *P. palmata* fronds to study the population structure,

5–18 epiphytized *C. baccata* plants (some were barely epiphytized) were collected by detaching the holdfast with a scraper in January, May, and August (May 1999 to May 2001), taken to the laboratory, and frozen until examined. Length of the main axis and total length of *C. baccata* plants were measured. All *P. palmata* fronds (an average of 150) growing on the main axis and lateral branches of the host plant were measured. From May 2000 onward they were also classified as young or old using the variables of texture and color that were monitored on mapped fronds in the field (see below). The distance of every *P. palmata* frond from the holdfast of the host plant was measured, so it was possible to divide the main axis of the latter in 10-cm segments and count the number of fronds growing on each segment, to assess the distribution of *P. palmata* upon the host.

To estimate the density of *P. palmata* per unit area, 20–30 plots (0.3 × 0.3 m) were randomly chosen on the shore in January and May 2000 and 2001. All *C. baccata* individuals within each plot were counted and classified depending on their load of *P. palmata* (without fronds, five or less fronds, or more than five fronds). Each month, densities of *P. palmata* were estimated by multiplying the number of *C. baccata* having an epiphytic load of the red alga per plot by the mean number of fronds per host. Monthly average values were then calculated. Individuals of *C. baccata* with five or less fronds of *P. palmata* were included in the calculation assuming they had five fronds.

Age, size, and stage-dependent growth and mortality. Growth and mortality, as well as losses due to breakage of the host, were quantified by monitoring fronds in the field. The fronds were selected to cover all the size range in the study site, except those measuring less than 0.5 cm long, which were excluded from the field survey. Tags were fastened around *C. baccata* stipes, next to the attaching disk. These tags were made of numbered plastic labels threaded onto small nylon electrical ties.

On each host, some *P. palmata* fronds were mapped, starting with a total of 144 fronds in May 1999. Mortality and loss of fronds were compensated by mapping new ones at each sampling event until May 2001, rendering a total of 668. Considering the whole study period, there was an average of 37 ± 2.7 (mean \pm SE) *C. baccata* stipes tagged at the start of each sampling event, with an average of 3 ± 0.3 *P. palmata* fronds mapped on each *C. baccata*. Fronds were measured monthly, except in winter 2000–2001, due to bad weather conditions and rough seas, when sampling was carried out every 2 or 3 months. On each visit, the maximum length of fronds was measured *in situ* to the nearest 1 mm. In December 1999 and January 2000, many of the fronds in the population were fertile, so it was possible to map male gametophytes and tetrasporophytes to estimate the vital rates of vegetative and fertile (both life-history phases) fronds. During March 2000 young fronds were mapped and monitored until the end of the study. Therefore, vital rates were estimated for fronds of two different ages (young and old) from March 2000 to May 2001 (see above).

Growth was measured as elongation and specific growth rate. Elongation rate ($\text{cm} \cdot \text{d}^{-1}$).

$$E = \frac{L_f - L_i}{t}$$

was calculated as

$$E = \frac{L_f - L_i}{t} \quad (1)$$

where L_i and L_f are the initial and final maximum lengths (in cm) at each sampling event and t is the duration (in days) of the measurement period.

Specific growth rate ($\% \cdot \text{d}^{-1}$) was calculated using the following equation (see Hunt 1990):

$$\text{Specific growth rate} = \frac{\ln\left(\frac{L_f}{L_i}\right)}{t} \times 100 \quad (2)$$

where t is the duration (in days) of the measurement period and L_i and L_f are the initial and final maximum lengths (in cm) at each sampling event. Any interpretation of specific growth rate data should be cautious because of the manifold problems engendered by ratios to scale data for variations in body size (Packard and Boardman 1999). In the present study, specific growth rate of *P. palmata* is calculated and its temporal variation presented graphically only for comparative purposes with specific growth rate given in previous studies.

Mortality rate ($\% \cdot \text{d}^{-1}$) was calculated as

$$M = \frac{\left(\frac{d}{n_i}\right)}{t} \times 100 \quad (3)$$

where d is the number of lost fronds at each sampling period, n_i is the initial number of fronds at the beginning of the sampling period, and t is the duration (in days) of each period. Fronds doubtfully identified or localized in the following sampling event were not included in the mortality calculations.

Statistical analysis. Temporal differences in the density of *P. palmata* and the mean length of *C. baccata* were analyzed by two-way analysis of variance (ANOVA), with year and month as orthogonal and fixed factors. Before analysis, the assumption of variance homogeneity was tested using Cochran's test (Winer et al. 1991). *A posteriori* multiple comparison of means was made with the Student-Newman-Keuls procedure (Underwood 1981).

The structure of the population of *P. palmata* was characterized by two size-structure descriptors, which are common measures of inequality: coefficient of variation and Gini coefficient (Bendel et al. 1989). Pearson chi-square analysis (2×2 contingency table) was used to assess the differences in proportion of fronds less than 1 cm long and fronds at least 1 cm long between January and May in 2000 and 2001.

The relationship between environmental variables and frond length of *P. palmata* was determined with Pearson correlation coefficients of the monthly means. Data transformations were necessary due to the autocorrelative nature of the original time series. First-differenced time series of the logarithm of raw data were used (Scrosati 2001). Moreover, due to the lack of independence, the significance of the correlation coefficients were determined by randomization tests making 5000 random permutations (Bjornstad et al. 1999, Scrosati 2001). The method of cross-correlation was used to identify the time lag that maximized the correlation between the variables (Legendre and Legendre 1998). The relation between initial length and elongation at each sampling period was analyzed graphically, using the linear or polynomial regression that best fit the data only as a way to create a smooth curve showing the general trend (Motulsky 1999).

Analyses of covariance (ANCOVAs), with initial length as covariate, were used to analyze, respectively, the effect of age and reproductive stage (including both life-history phases) on elongation. Before the ANCOVA, the homogeneity of slopes was tested. When there was no significant relationship between initial length and elongation, one-way ANOVA was performed. ANCOVAs with initial length as covariate were also used to study temporal variation of growth.

Differences in initial length between live and missing fronds were tested by one-way ANOVA. Differences in proportion of old and young fronds among live and missing fronds were analyzed with a chi-square analysis (2×2 contingency table), and log-linear analysis was used to evaluate the relative

contribution of age and size to predicting frond mortality (Caswell 2001).

RESULTS

Frond biomass/length allometry. In all the studied months, the relationship between maximum length and dry mass fitted the following potential regressions:

- May 1999: $W = 0.38 \times L^{2.28}$, $r^2 = 0.874$, $n = 175$
- August 1999: $W = 0.48 \times L^{2.20}$, $r^2 = 0.904$, $n = 193$
- January 2000: $W = 0.54 \times L^{2.28}$, $r^2 = 0.888$, $n = 185$

where, W is the dry mass in mg and L is the maximum length in cm; only fronds at least 0.5 cm were included.

The slopes of the linear regressions between dry mass and length of fronds (log-transformed data) were not significantly different in the three studied periods (ANCOVA, interaction length \times month, $F_{2,547} = 0.635$, $P = 0.530$). However, the intercept values differed between months (ANCOVA, effect of month, $F_{2,549} = 13.037$, $P < 0.001$). The intercept for the January regression was significantly higher than those of May and August (Student's t -tests and Bonferroni corrections for post-hoc comparison on adjusted means, January 2000 > August 1999 \approx May 1999). Therefore, fronds of the same average length were slightly heavier in January than in May and August. Length can be considered a good estimator of dry mass ($r^2 > 88\%$ in all the cases), although elongation and change in biomass are not exactly equivalent over the year.

*Population density and distribution of *Palmaria palmata* on the host.* There was a trend for density of *P. palmata* to increase from 2000 to 2001 in the area of study, but this variation was not significant (Fig. 1, Table 1). Density did change significantly within years (Fig. 1, Table 1). It was about four to five times higher in May than in January, although this difference slightly decreased when *P. palmata* fronds less than 0.5 cm (excluded in the field monitoring) were not considered (Fig. 1). The density of the host plant, *C. baccata*, and the percentage of these plants epiphytized with *P. palmata* were also higher in May than in January in both years (Fig. 1).

On the host plant, most of the fronds of *P. palmata* were located near the holdfast, as the two first 10-cm

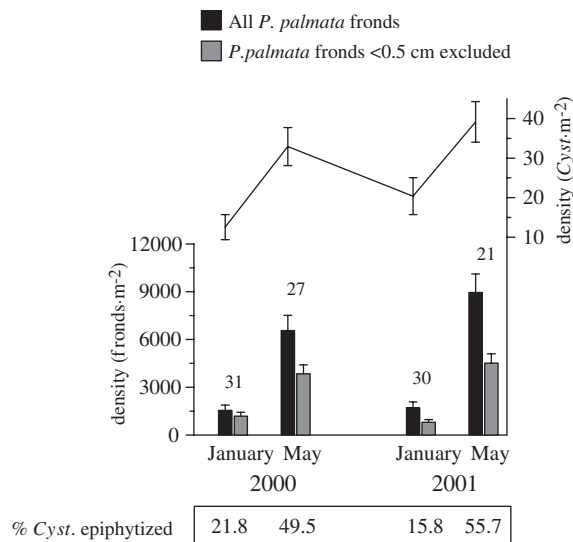


FIG. 1. Temporal variation of *Palmaria palmata* density (means \pm SE) and density and percentage of epiphytized *C. baccata* in the studied area. Numbers above the bars indicate the number of plots (30 \times 30 cm) sampled at each period.

segments of the axis (between 0 and 20 cm from the *C. baccata* holdfast) were the most frequently (although not always the most densely) colonized (e.g. in January 2000, Fig. 2). There were differences in the total length of *C. baccata* plants between years 2000 and 2001, with plants in 2001 shorter than in 2000 (Fig. 2, Table 2).

Population structure and dynamics: size structure. Size distributions were highly skewed, with many small fronds throughout the year (Fig. 3). There was not a conspicuous seasonal pattern of change in the size-structure descriptors, with an average value of 0.59 ± 0.01 for the Gini coefficient (mean \pm SE, $n = 7$) and 1.40 ± 0.06 for the coefficient of variation. Nevertheless, a chi-square test detected a significant increase in the number of fronds less than 1 cm long from January to May 2000 ($P < 0.001$) but not in 2001. It is important to note that a higher percentage of the fronds in the smaller size classes (<4 cm) were old (see Materials and Methods) in January (43% in 2000 and 27% in 2001), in contrast with May and August (5% and 6% in May and August 2000, respectively, and 3% in May 2001). In the studied

TABLE 1. Two-way ANOVA for differences between years (2000 and 2001) and months (January and May) on mean densities of fronds of *Palmaria palmata*.

Source of variation	df	All fronds			<0.5 cm excluded		
		MS	F	P	MS	F	P
Year	1	2351.348	2.907	0.080	85.706	0.189	0.728
Month	1	63005.746	77.908	0.000	30487.210	67.580	0.000
Y \times M	1	1457.416	1.802	0.121	970.543	2.151	0.185
Error	105	808.719			451.124		

Unbalanced data ($n = 21$ – 31 per month, see Fig. 1).

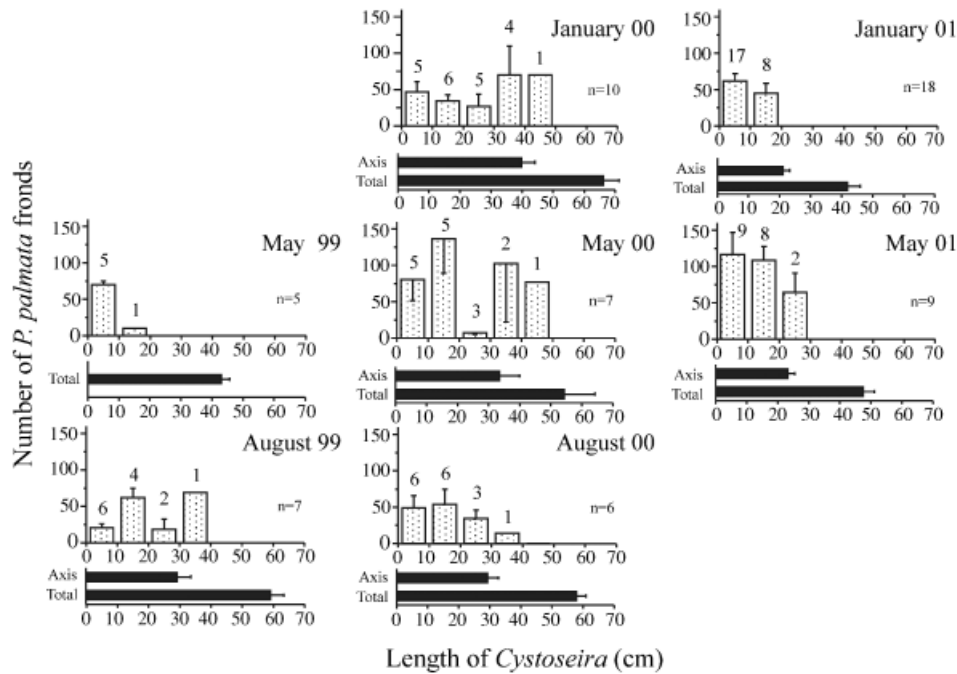


FIG. 2. Spatial distribution of *Palmaria palmata* on the main axis of the host *Cystoseira baccata*. For each sampled month, the upper graph shows the number of *P. palmata* fronds (means \pm SE; fronds < 0.5 cm included) growing on 10-cm segments of the main axis of *C. baccata*. Numbers above the bars indicate number of segments covered with *P. palmata*. The lower graph shows the length of the main axis and total length (means \pm SE) of *C. baccata* collected per month. n = number of *C. baccata*.

population, fronds longer than 20 cm were only found in August (Fig. 3).

Growth rates: general pattern. The growth cycle of *P. palmata* in the studied population can be divided into two distinct phases: a period of positive net growth, from March to August, and a period of predominance of frond breakage, from August to March (Fig. 4A). Growth rates were higher during spring, with a maximum in May–July in 1999 and 2000, whereas frond shrinkage was maximum during fall (Fig. 4A).

Elongation of fronds for the whole period of May to August 1999 and May to August 2000 (periods of positive net growth, Fig. 4A) differed significantly (one-way ANOVA, $F_{1,74} = 9.65$, $P = 0.003$), with higher growth in 2000 than in 1999. On the other hand, although fronds apparently suffered more breakage in August 2000–March 2001 than in the same period in 1999–2000 (Fig. 4A), interannual differences were not

detected if we compared fronds of the same average length (ANCOVA, $F_{1,32} = 1.031$, $P = 0.318$).

Seasonal environmental conditions on the shore were those typical of temperate zones. Higher values of temperature, irradiance, and day length were recorded in summer (Fig. 4, B and C). Wave force was stronger in winter (Fig. 4D), matching up with the period of predominance of frond breakage (Fig. 4A). Monthly means of frond length were positively correlated with temperature ($r = 0.16$, $n = 24$), and cross-correlation showed this was the maximum correlation. On the other hand, the correlation with irradiance was maximum and significant if irradiance data were taken from 1 month before length measurements ($r = 0.52$) and with a photoperiod from 2 months before ($r = 0.73$).

Size, age, and stage-dependent growth. The two distinct phases in the growth cycle of *P. palmata*, a phase of predominance of positive net growth from

TABLE 2. Two-way ANOVA for differences between years and months on mean total length of *Cystoseira baccata* plants.

Source of variation	May and August 1999 and 2000				January and May 2000 and 2001			
	df	MS	F	P	df	MS	F	P
Year	1	156.956	0.616	0.441	1	2146.988	6.799	0.014
Month	1	585.715	2.299	0.144	1	29.319	0.092	0.762
Y \times M	1	237.685	0.933	0.345	1	711.221	2.252	0.143
Error	21	254.679			30	315.764		

Unbalanced data ($n = 5$ –9 per month).

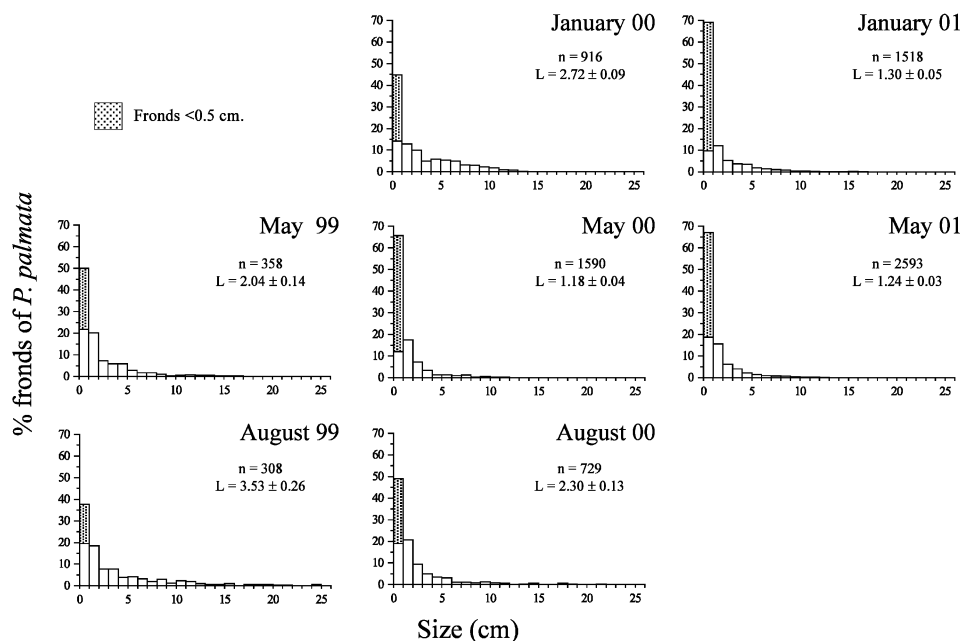


FIG. 3. Size (length) frequency histograms of *Palmaria palmata* population from Estaño, over a 2-year period. *n*, number of fronds measured; *L*, mean length of fronds (cm; means \pm SE).

March to August and another with predominance of frond breakage (negative elongation values) from August to March, are also patent in Figure 5. However, growth seemed to be dependent on size: in August–November 1999 and August 2000–March 2001, when breakage predominated, longer fronds suffered greater breakage than small ones (Fig. 5). Even in periods when net positive growth prevailed, longer fronds had apparently minor growth or suffered greater breakage than small ones (e.g. July–August 1999, March–May 2000, June–July 2000, March–May 2001, Fig. 5).

Longer fronds were always old, but smaller fronds were either young or old (Fig. 5, from March 2000 onward). In the range of the smaller sizes net growth was similar for fronds of different age (Table 3). From December 1999 to May 2000, breakage (the predominant event) of vegetative, male gametophytic (haploid), and tetrasporophytic (diploid) fronds were similar (Table 4). From May to June 2000, when the three stages had positive net growth, there was not a difference between them (Table 4).

Mortality. Because *P. palmata* grows epiphytically on *C. baccata*, mortality had two origins: disappearance of fronds from the *C. baccata* axis or host breakage (Fig. 6). There was not a clear seasonal trend in mortality of fronds, only values from May to November 1999 were apparently higher in comparison with the rest of the sampling period (Fig. 6). It is important to notice that a high percentage of *P. palmata* mortality was due to breakage of the host plant and sand burial, these two factors accounting for more than 50% of the total mortality in some periods (Fig. 6).

When comparing initial length of live (present) and missing fronds (i.e. lost from the *C. baccata* stipe), there was a general trend toward live fronds being longer than missing ones, which was significant in three periods (Fig. 7). From March 2000 onward, age of fronds was known (see Materials and Methods), but only in the period March–May 2000 were there enough fronds to assess the effect of age on mortality. In this period, 73% of live fronds (longer) but only 25% of missing fronds (smaller) were old (chi-square test, $P < 0.05$). Results of the log-linear analysis in this period indicated that the effect of age and/or size on mortality was significant and also the effect of age on mortality, given the contribution of size (Table 5). Nevertheless, when the contribution of age was known, size had no effect on mortality (Table 5). The effect of reproductive stage (vegetative, male gametophyte, and tetrasporophyte) on mortality could not be assessed because the number of missing fertile fronds was too low to make statistical analyses (less than five fronds in all periods).

DISCUSSION

Temporal variation in population density, population structure, and vital rates. Seasonal density variation, as a logical consequence of the population dynamics, has been observed in many seaweeds from cold and temperate waters (e.g. members of the family Gigartiniaceae, Scrosati 1998). In this study, the increase in the density of fronds of *P. palmata* observed from January to May could be the consequence of recruitment from spores as well as vegetative growth. This is in accordance with the fact that fronds were fertile

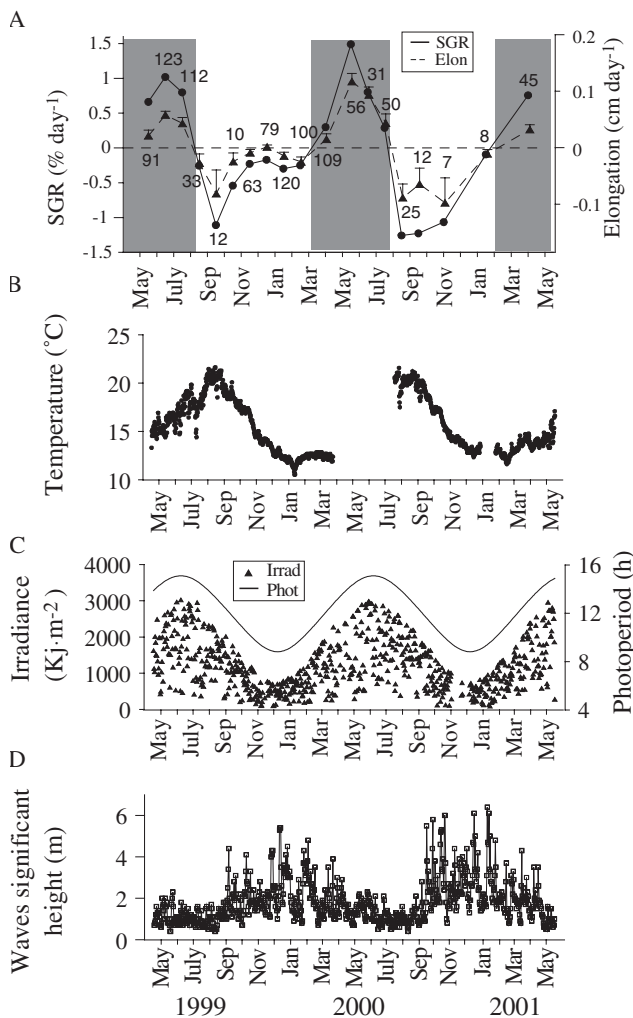


FIG. 4. Temporal variation of the specific growth rates (SGR, %·d⁻¹) and elongation (cm·d⁻¹; means±SE) of *Palmaria palmata* (A) and environmental variables: daily seawater temperature (B), daily incident solar energy (irradiance) and photoperiod (C), and daily wave height (D) in the studied area from May 1999 to May 2001. Numbers in A indicate the number of fronds measured in each period, and shaded rectangles indicate periods of positive net growth.

in this population only during winter and growth started in spring. The increase in the percentage of *C. baccata* plants epiphytized with *P. palmata* fronds during the same period, from January to May, indicated that recruitment from spores did occur to some extent, although the importance of sexual reproduction versus vegetative regeneration could not be evaluated in this study.

Surprisingly, the subsequent decline of frond density from May to January was not reflected in higher mortality rates obtained from the field survey. In fact, we did not observe any distinct seasonal pattern of mortality, in contrast to what has been reported for many seaweed species, where mortality was often greater in winter as a result of storms (Kain and

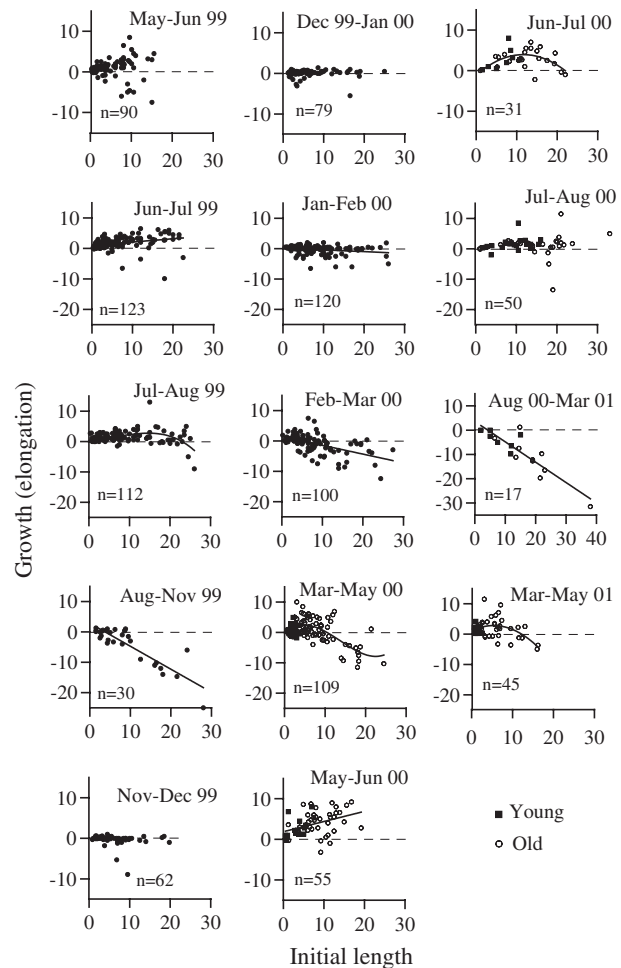


FIG. 5. Relationship between initial length (in cm) and growth (elongation) for *Palmaria palmata* fronds at each period studied. The significant linear or polynomial regressions that best fit the data are represented to show the general trends. n = number of fronds measured. From March 2000 onward, “young” and “old” fronds are indicated (see Materials and Methods for specific ages).

Norton 1990). This seeming contradiction between the estimations of population density and mortality rates may be explained by the fact that all the size categories were represented in similar proportions in the field survey, whereas the smaller fronds were predominant in the natural population. From May to August most of these small fronds were young and the youngest fronds suffered higher mortality rates.

Density exhibited a clear variation within years, but there were not significant changes between years. Although the length of the host plant decreased from 2000 to 2001, the density of *P. palmata* did not decrease. In fact, there was a trend, though not significant, to increase. The shrinkage of the host plant would feasibly affect the “transient” population (not studied here) formed exclusively by recruits that settled on the very apical part of the host plant in early spring. Previous studies (D’Antonio 1985, Arrontes 1990) found

TABLE 3. ANCOVA and one-way ANOVA for differences between growth (elongation) of *Palmaria palmata* fronds of different ages from March 2000 to May 2001.

Type of analysis	Period	Source of variation	df	MS	F	p	Size range (cm)
ANOVA	March–May 2000	Age	1	9.036	1.5956	0.169	≤4
		Error	42	4.620			
ANCOVA	May–June 2000	Age	1	0.006	0.002	0.968	≤8
		Initial length	1	65.252	16.480	0.000	
		Error	32	3.960			
ANOVA	June–July 2000	Age	1	0.361	0.086	0.773	≤12
		Error	16	4.200			
ANOVA	July–August 2000	Age	1	0.896	0.322	0.574	≤16
		Error	33	2.784			
ANCOVA	August 2000–March 2001	Age	1	49.923	2.342	0.154	≤20
		Error	11	21.320			
ANOVA	March–May 2001	Age	1	14.581	2.350	0.141	≤4
		Error	20	6.204			

The covariate was the initial length in each period. Slopes in ANCOVA and ANOVA were homogeneous in all cases.

differential location of epiphytes on the host plant and showed that the most persistent epiphytes tended to be those that grew on basal parts of the host plant.

The size structure observed in the *P. palmata* population under study, with predominance of the smallest fronds, has been frequently documented in natural and experimental populations of terrestrial plants and seaweeds (Harper 1977, Weiner 1985, Dean et al. 1989, Santos 1995, Creed et al. 1996, Arenas and Fernandez 2000). However, the origin of the small fronds was different in January, May, and August. Most of the small fronds (<4 cm) in May and August were young (i.e. recruits of the year), coinciding with increases in population density, whereas in January a high percentage of the small fronds were old (i.e. recruits of the precedent year or before), which most probably were broken in the previous months.

Maximum frond lengths were measured in August, concurring with the end of the positive net growth phase. Nonetheless, fronds longer than 25 cm were rarely found throughout the study site, although they were more abundant in other subtidal populations of

the northern coast of Spain (personal observation). In Britain and Ireland, length of subtidal *P. palmata* fronds is about 50 cm, although in some areas, plants up to 1 m in length may be found (Irvine and Guiry 1983). Kain (1986) and Browne (2001) commonly observed subtidal *P. palmata* fronds longer than 25 cm off the Isle of Man and Northern Ireland, respectively. The reduced maximum size of the studied versus northern populations could be due to its position within the distributional boundary of the species, because mean size of individuals in peripheral populations tend to be smaller (Carter and Prince 1988, Bengtsson 1993). However, specific growth rates measured in this study fell in the range of other red seaweeds growing under controlled conditions or in the field (Kain and Norton 1990) and were similar to specific growth rates of *P. palmata* fronds from Northern Ireland (specific growth rate from June to July 2000 = $0.89 \pm 0.22\% \cdot d^{-1}$, $n = 33$, unpublished data). Very probably, the intertidal character of the studied population and the greater wave pressure at the intertidal level also imposed restrictions on the size of fronds (Denny et al.

TABLE 4. ANCOVA and one-way ANOVA for differences between growth (elongation) of *Palmaria palmata* vegetative and fertile (gametophytes and tetrasporophytes) fronds from December 1999 to June 2000.

Type of analysis	Period	Source of Variation	df	MS	F	P
ANOVA	December 1999–January 2000	Stage	2	0.658	0.717	0.492
		Error	76	0.918		
ANCOVA	January–February 2000	Stage	2	0.978	0.225	0.799
		Initial length	1	33.477	7.699	0.006
		Error	115	4.348		
ANCOVA	February–March 2000	Stage	2	3.994	0.547	0.580
		Initial length	1	164.317	22.516	0.000
		Error	95	7.298		
ANCOVA	March–May 2000	Stage	2	2.710	0.223	0.800
		Initial length	1	440.705	36.327	0.000
		Error	74	12.131		
ANOVA	May–June 2000	Stage	2	3.687	0.299	0.743
		Error	36	12.332		

All fronds considered are “old” (see Materials and Methods). The covariate was the initial length in each period. Slopes in ANCOVA and ANOVA were homogeneous in all cases.

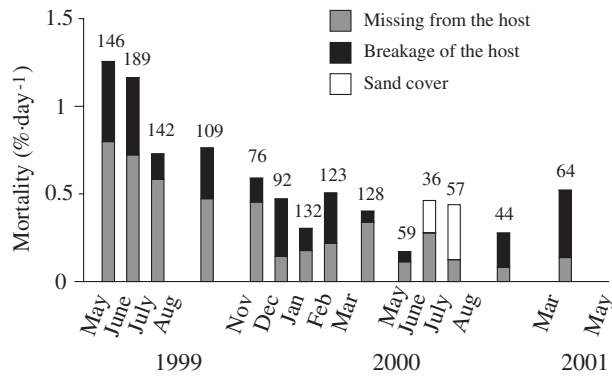


FIG. 6. Temporal variation in mortality rate of *Palmaria palmata* from May 1999 to May 2001. Numbers above the bars indicate the number of initial fronds at each sampling period.

1985, Carrington 1990, Gaylord et al. 1994, Blanchette 1997).

Palmaria palmata exhibited a distinctive seasonal growth cycle, coinciding with the seasonal cycles of environmental factors, as other *Palmaria* species (Hawkes 1985) and many seaweeds from cold and temperate regions (Lüning 1990, Molenaar 1996, Scrosati 1998). Maximum frond lengths were observed in August, which was the period of highest seawater temperature. Maximum growth rates were observed 1 or 2 months before, when irradiance and photoperiod were at their highest. Although the existence of a significant correlation does not imply a causal relationship, it seems that irradiance and photoperiod are important signals regulating the growth cycle of the species. Another factor that may play a key role is the annual cycle of nutrients (Lüning 1993). Martínez and Rico (2002) measured N and P seawater concentration and nutrient storage in *P. palmata* in the same population. These authors indicated that N and P were stored in autumn and winter, coinciding with the highest nutrient seawater concentrations. These reserves could be diverted into growth in late spring–summer, when nutrient supply was low.

At the end of the growing season, fronds showed signs of senescence, specially the apical parts, and they either died or suffered subsequent breakage due to wave action. High summer temperatures and low

TABLE 5. Results of log linear analysis for the effect of size vs. age on mortality of *Palmaria palmata* fronds in the period March–May 2000.

Model	df	G	P
Size × age × mortality	3	11.3262	0.0101
Size × mortality	2	8.3948	0.0166
Age × mortality	1	13.1969	<0.001
Size × mortality/age	2	2.1731	0.3581
Age × mortality/size	1	6.9753	0.006

Size classes: ≤ 3 cm; > 3 cm and ≤ 7 cm; > 7 cm. Age classes: “young” (fronds of 2000) or “old” (fronds of 1999 or before).

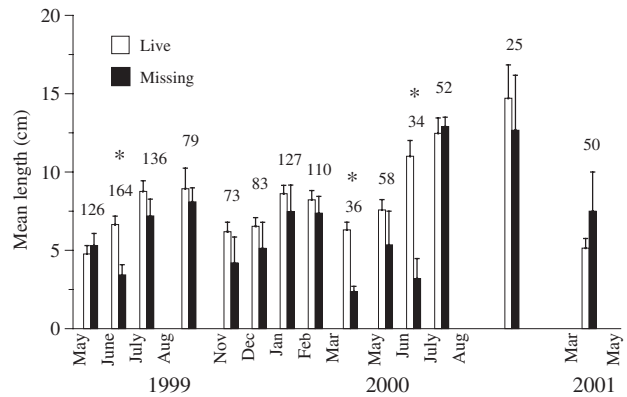


FIG. 7. Mean initial length of *Palmaria palmata* fronds (\pm SE) from May 1999 to May 2001. The number above the bars indicate the number of fronds per period. Asterisks indicate periods with significant difference in the mean length of live and missing fronds (one-way ANOVA, $P < 0.05$).

external nutrient concentration contribute to frond damage (Davison and Pearson 1996, Martínez and Rico 2002) and may facilitate subsequent breakage. Grazing by small invertebrates (isopods, amphipods, and gastropods) that are typically most abundant in spring and summer (Arrontes and Anadón 1990, Viejo 1999) could weaken fronds and also make them more susceptible to breakage. Previous studies have proved the high nutritional value and preferential consumption of *P. palmata* by herbivores (Shacklock and Doyle 1983, Mai et al. 1996). We frequently observed grazing marks in *P. palmata* fronds in the field, and grazers such as gammarid amphipods and the gastropod *Helcion pellucidum* (L.) actively fed on the alga in laboratory trials.

The growth rate of *P. palmata* also varied between years in the studied population, with values higher in 2000 than in 1999. In the present study, we can only hypothesize about the causes of this pattern. Desiccation stress could have been lower during spring 2000 than in 1999, as a consequence of shorter exposure to air during spring tides (the mean \pm SE of spring tide height was 0.218 ± 0.028 m above LAT from March to June 1999, 0.342 ± 0.011 from March to June 2000, $n = 8$). Tolerance to desiccation was measured in the *P. palmata* population under study, and most of the fronds exposed to the air over a period of about 4 h did not recuperate their normal photosynthetic activity when submerged (Álvarez and Rico 1999). Although fronds were never exposed for so long at our study site, annual differences in exposure times during spring tides could have caused some photosynthetic damage and reduced growth.

Size, age, and stage-dependent growth and mortality. Results of this study suggested that growth was dependent on size, because larger fronds had minor growth or suffered greater breakage than smaller ones. The higher susceptibility of larger fronds to breakage has already been observed in other seaweeds, such as the

red species *Gelidium sesquipedale* (Clem.) Born. et Thur. (Santos 1994) and the brown algae *Ascophyllum nodosum* (L.) Le Jol. (Viejo and Åberg 2001) and *Fucus gardneri* Silva (Blanchette 1997). Ang (1991) also observed degeneration (negative growth) of terminal branches among older and larger *F. gardneri* plants (as *F. distichus*). Longer fronds are exposed for a longer time to epiphytism, endophytism, or grazing and are more vulnerable to wave action (Gaylord et al. 1994).

When the growth rate of fronds with the same average length was compared, no differences were found between different ages. This result indicates that size is more important than age in predicting growth of *P. palmata* fronds. Previous studies in higher plants, colonial animals (Harper 1977, Caswell 2001), and seaweeds (Ang 1991) also showed a weaker dependence of growth on age than on size.

Ecological differences among isomorphic life-history phases have rarely been investigated in red seaweeds (May 1986, Luxoro and Santelices 1989, Dyck and DeWreede 1995) and, so far, have not been investigated in *P. palmata*. In this study we did not find differences in the net growth of old haploid (male gametophyte) and diploid (tetrasporophyte) fronds, either in periods of positive growth or when breakage events predominated. Therefore, if ecological differences existed between male gametophytes and tetrasporophytes, they should affect other demographic rates, as reproductive output, growth, and survival of young fronds or perennation of phases. In the studied population tetrasporophytes predominated amply over male gametophytes (tetrasporophytes = 70.7%, gametophytes = 15.1%, vegetative fronds = 14.3%, $n = 147$ in February 1999; tetrasporophytes = 62.6%, gametophytes = 21.7%, vegetative fronds = 15.6%, $n = 115$ in February 2000, unpublished data). The dominance of tetrasporophytes is also evident at subtidal levels (January 2002: tetrasporophytes = 48.6% and gametophytes = 11.3% at low intertidal levels, tetrasporophytes = 53.2%, gametophytes = 11.8% at subtidal levels, 2–5 m below LAT, unpublished data). In *P. palmata* equal numbers of male and female individuals will develop from the released tetraspores (C. Maggs, personal communication). The macroscopic thalli are either diploid tetrasporophytes, which have developed directly on microscopic fertilized females, or haploid males (van der Meer and Todd 1980). The clear predominance of tetrasporophytes over male gametophytes suggests either the presence of ecological differences between sexes (in favor of microscopic females) or between phases (in favor of tetrasporophytes). Nevertheless, empirical and modeling studies are necessary to confirm this hypothesis, because it was demonstrated that the stable ratio between ecologically similar phases may differ from 1:1 (Scrosati and De Wreede 1999).

Reproduction may reduce future survival, growth, and/or reproduction of individuals in both terrestrial plants and marine seaweeds (Tuomi et al. 1983, Bell and Koufopanou 1986, Pfister 1992). Survival of fertile

and vegetative *P. palmata* fronds could not be investigated in the present study, but both had similar growth rates, which points to the nonexistence of a cost of reproduction. Reproductive cost in algae may be reduced by increasing resource uptake, supported by nutrient reserves or compensated by the photosynthetic capacity of reproductive structures (De Wreede and Klinger 1988). The population studied could use the former process, because fronds were fertile in winter, when seawater nutrient concentration was at the highest (Martínez and Rico 2002).

Both age and size had a significant effect on frond mortality, but the results of the log linear analysis indicated that age was a better predictor of mortality than size, at least in the period analyzed (March–May 2000). This pattern is in contrast with the results of Ang (1991) and Dean et al. (1989), who found that size was a better predictor of mortality than age in *F. gardneri* (as *F. distichus*) and *Macrocystis pyrifera* (L.) C. Agardh, respectively. Chapman (1986), however, found that mortality was unrelated to size and only partially related to age. Our results indicate that mortality is more age than size dependent in *P. palmata*.

Non-mutually exclusive processes could result in a higher mortality of young *P. palmata* fronds (recruits or sprouts) in comparison with the old ones. First, density-dependent mortality could affect young fronds, due to the increase in their density during spring (Black 1974, Schiel 1985, Schmitt et al. 1987, Santos 1994). Moreover, herbivory and wave impact are important mortality factors affecting juvenile stages (Vadas et al. 1992). Detachment of recruits may be facilitated by small attachment strength of their less-developed holdfast, which caused adhesive failure (Norton et al. 1982, Dudgeon and Johnson 1992, Milligan and De Wreede 2000). In our field survey some mapped young fronds were easily detached when measured in contrast with old fronds of similar sizes. Additionally, young fronds may be more susceptible to grazing pressure because of their soft texture (Padilla 1985) or their greater palatability than older fronds (Lobban and Harrison 1997).

We describe the temporal changes in density, size structure, and the growth cycle of a *P. palmata* population, as well as the dependence on size, age, and the life-history phase of its vital rates (growth and mortality). Growth varied between years and was apparently more dependent on size than on age, but mortality was more age dependent. The results indicated that both size and age should be included as state variables in a demographic model of the species, as well as temporal changes in the transition probabilities between stages. Macroscopic male gametophytes and tetrasporophytes did not differ in their growth rates in the studied population, but we hypothesized that other ecological differences may exist between phases. This information is necessary for the development of stage-structured models of *P. palmata* in the relatively isolated populations of the northern coast of Spain.

We thank D. Alvarez, F. Arenas, C. Fernández, R. Díez, B. Martínez, A. Menéndez, and J. Oliveros for their invaluable field and laboratory help and support. We thank F. J. Méndez and I. Losada for kindly providing the wave data and the propagation program and R. Scrosati for help with statistics. Critical comments from C. Fernández, J. M. Rico, R. Scrosati, and an anonymous reviewer greatly improved earlier drafts of the manuscript. This research was partially funded by the Commission of European Communities, Agriculture and Fisheries (FAIR) specific RTD programme, project CT97-3828. Vanesa A. Faes held a predoctoral fellowship from the Spanish Ministry of Education and Culture and Rosa M. Viejo held a postdoctoral contract from the Spanish Ministry of Science and Technology.

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