

Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain

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ABSTRACT: The distribution of *Fucus serratus* has a sharp boundary in northern Spain. *F. serratus* dominates the mid-intertidal region west of Novellana, Asturias, but is absent further east. In a short transition zone, *F. serratus* is abundant within patches. The causes underlying this pattern were investigated by experimental transplants of *F. serratus* to locations in the transition zone and outside its normal range. Plants moved outside the normal range had similar growth and reproductive rates to those transplanted to the transition zone and within the zone of abundance. *F. serratus* recruited at sites outside the normal boundary, apparently from transplanted thalli. Temperature affected the growth rate of embryos of *F. serratus* in laboratory experiments. Though high summer temperatures may be responsible for the lack of *F. serratus* in the inner part of the Bay of Biscay, temperature alone cannot explain the observed limit of distribution. Other factors such as limited dispersal ability and inter-specific competition with other macroalgae might also be important in setting the boundary for *F. serratus* in northern Spain.

INTRODUCTION

The geographical distribution of marine algae has frequently been related to the influence of physical factors (e.g. Dring 1982, van den Hoek 1982, Lüning 1990). The limits of distribution are often set by the effect of critical temperatures on survival, reproduction and growth of plants (van den Hoek 1982). Much experimental work has shown the relationship between distribution and tolerance to temperature in algae (e.g. Norton 1977a, Yarish et al. 1987, Breeman 1988, Cambridge et al. 1990). In addition to temperature, photoperiod (Breeman 1988), longitudinal barriers (van den Hoek 1975, 1987) and salinity (Bird & McLachlan 1986, Russell 1987) have been invoked to explain patterns of distribution.

In addition to physical factors, biological factors are recognized as acting on the distribution of macroalgae at small scales. Their role has been much less frequently studied, though herbivory can be important in explaining the patterns of algal abundance in different geographical areas (Lubchenco 1980, Hay 1981, Gaines & Lubchenco 1982).

A conspicuous change in the composition of marine algae has been described along the shores of northern

Spain. Important differences exist in the species composition between northwestern Spain (facing the open Atlantic waters) and the Basque coast (in the inner part of the Bay of Biscay) (e.g. Fischer-Piette 1957, Anadón & Niell 1981, Anadón 1983, Lüning 1990). In his study on phytogeographic provinces, van den Hoek (1975) grouped the flora of NW Spain with the floras of NW Brittany and Clare Island, and the flora of the Basque coast with the flora of Morocco. Several species of large brown algae reach their limit of distribution in a middle zone in north Spain (including *Fucus serratus*, *Laminaria ochroleuca*, *Himantalia elongata* and others) (Anadón & Niell 1981, Anadón 1983, Lüning 1990). Their pattern of distribution has been frequently explained by the lack of rocky substratum from the Loire to the Basque coast and locally high temperature during summer in the inner part of the bay (Lüning 1990). Summer upwelling conditions would produce temperature ranges suitable for these macroalgae, permitting their reappearance on the west shore of northern Spain. Although the distributional boundaries are not exactly coincident for all these species, they lie in approximately the same part of the shore. Past evidence suggests, however, that the limits of distribution of these species have moved considerably during this century (Fischer-Piette 1957).

Among the species displaying an unequal distribution along the shore of N Spain, *Fucus serratus* exhibits a sharp decline in abundance from west to east. It is abundant in NW Spain, where it often dominates the space in mid and lower tidal levels, but is absent from the Basque coast. *F. serratus* is a species widely distributed on the Atlantic shores of Europe and is locally abundant in Nova Scotia (Canada). Its southern distributional boundary on the European shores lies in northern Portugal (Pazó & Niell 1977, Lüning 1990). If its distribution is primarily determined by temperature, then it can be assumed that high temperatures are important in setting the distribution boundary on the shore of N Spain (see Breeman 1988).

Several oceanographic features with potential influence on the dispersal, growth and survival of macroalgae have been described for the Spanish shore of the bay of Biscay. Coastal currents are W–E during winter but inverse, E–W, during summer. During summer, surface waters are warmer towards the inner part of the bay (US Naval Oceanographic Office 1967, Maillard 1986). The difference in temperature between the inner and outer part can be as large as 3 °C. This difference can be temporarily increased in some zones due to upwelling conditions near the shore during summer. Underwater currents, driven by northeasterly winds, are responsible for the elevation of cold water (Botas et al. 1990). Upwelling conditions are more persistent and intense towards the western part of the Spanish north shore of the bay. During winter, minimum seawater temperature is between 10 and 11 °C. Maximum temperature in summer is 19 to 20 °C for most of the shore and 21 and occasionally 22 °C in the inner part of the bay. In the littoral zone of those parts of the shore under upwelling conditions, temperature is expected to be lower and concentration of inorganic nutrients (e.g. nitrate, phosphate) to be higher than those in oceanic waters or in adjacent, non-upwelled coastal waters. During winter, oceanographic conditions are the same for the entire coast (Maillard 1986, SATMER 1990a).

In this paper, I explore the factors with putative influence on the distribution of *Fucus serratus* in northern Spain. Specifically, I investigate the ability of transplanted thalli of *F. serratus* to grow and develop reproductive structures in localities outside its range of distribution. It was hypothesized that the environment of the places where the species is

absent negatively influences growth and/or reproduction and so prevents the spread of *F. serratus*. In addition to the transplant experiment, I present information on the growth and reproduction of the species in its natural environment and a laboratory experiment on the effect of temperature on the growth of *F. serratus* embryos.

MATERIAL AND METHODS

A survey, between 6° and 7° W, was made along the coast of Spain to detect the exact location of the distributional boundary of *Fucus serratus*. Field experiments were made at 3 localities, Oleiros (43° 34' N, 6° 12' W), Campiello (43° 33' N, 6° 24' W) and Torbas (43° 33' N, 6° 47' W) (Fig. 1). All 3 stations are rock platforms under steep cliffs exposed to moderate wave action. The substratum is formed by quartzite and slate. Oleiros is outside the normal range of distribution of *Fucus serratus*, Campiello is in a transition zone, where *F. serratus* occurs in patches, while at Torbas *F. serratus* is abundant. Intertidal zonation was studied at Torbas and Oleiros by making a transect perpendicular to the shoreline from 0.5 m to 2.5 m above the lowest tidal level. At regular intervals (2 m at Oleiros, 3 m at Torbas), percentage cover of macroalgae was estimated in 3 replicate 1 m² quadrats with 100 regularly spaced points.

At the 3 localities, temperature and concentration of nitrate and nitrite were measured at monthly or fortnightly intervals, coinciding with spring tides, from January 1990 to January 1991. At each locality, 4 replicate samples of seawater were collected at each of 4 randomly chosen sites. Nitrate and nitrite were analysed using an Autoanalyser Technicon AAIL. Chemical analysis were made using the methods

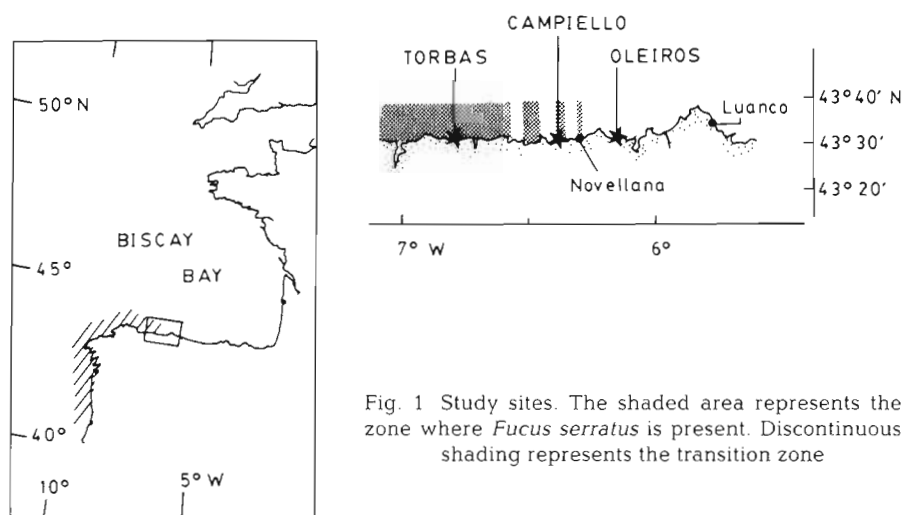


Fig. 1 Study sites. The shaded area represents the zone where *Fucus serratus* is present. Discontinuous shading represents the transition zone

described in Grashoff (1983). No other nutrients were analysed since they are considered less important for the primary production of macroalgae (DeBoer 1981, Lobban et al. 1985).

To study the seasonal variation in biomass and reproductive status of *Fucus serratus* at Torbas and Campiello, 5 canopy-forming plants were collected at random from 4 sites at monthly intervals. Reproductive allocation of each plant was calculated as percentage of dry weight represented by receptacles. Differences in size between canopy plants of *F. serratus* in Torbas and Campiello were estimated from 2 random samples of 65 plants taken at each locality in May 1990 (5 sites \times 13 plants site⁻¹).

Growth of *Fucus serratus* under natural conditions was investigated at 3 sites at Torbas and Campiello. Plants of 2 size categories were chosen, individuals less than 20 cm long (which did not form part of the canopy) and large, canopy-forming, specimens. Fifteen plants of each size group were individually marked at each site by tying fishing line with coloured beads to their stipes. Length of the plants was recorded at monthly intervals from May to November 1990.

Vegetative thalli 15 to 22 cm long were chosen for the transplantation experiment. Pieces of rocks with attached algae were chipped off with a chisel and transported to the laboratory where they were individually marked (as above) and measured. At the destination locality, stones with the *Fucus serratus* plants attached were cemented to the rock substratum in groups of 5 plants, within an approximate area of 30 \times 30 cm. Three groups were set at each of 3 randomly chosen sites.

The experimental design consisted of reverse transplants between Torbas and Campiello (within abundance and transition zones) and from Torbas to Oleiros (outside the zone). I predicted that plants moved outside their normal range of distribution would suffer higher mortality and slower growth rates than those moved within their normal range. To control for the effects of the transplanting process per se, 45 plants collected at Torbas and 45 collected at Campiello were moved to different sites at Torbas and Campiello respectively. Length of thalli was measured at monthly or fortnightly intervals and the number of receptacles per plant recorded. As an estimate of bushiness, the number of tips per plant was counted at 3 different times. Although the experiment was designed to run for 6 mo, from April to October 1990, additional measurements were made in November 1990 and January, May and September–October 1991.

The ability of *Fucus serratus* to recruit in zones where it was not naturally present was investigated in the 3 localities by scraping clean quadrats of 60 \times 60 cm

size. Three sites were chosen at Torbas and Oleiros and 4 at Campiello. At each site, 4 replicated quadrats were scraped at each of 2 tidal levels. At Oleiros, the quadrats were cleared in the zones dominated by *Fucus vesiculosus* (high tidal level) and *Bifurcaria bifurcata* (low tidal level). At Campiello, in 2 sites the quadrats were scraped in the zones dominated by *F. vesiculosus* and *B. bifurcata*, while in the remaining 2 the experimental surfaces were in zones of *F. vesiculosus* (high level) and *F. serratus* (low level). At Torbas, the quadrats were in the zones dominated by *F. vesiculosus* and *F. serratus*. The experimental surfaces were left to recover for 6 mo. Then, abundance of algae in each was estimated as percent cover of the algae in two 20 \times 20 cm quadrats with 100 regularly placed points.

The effect of temperature on the growth rate of embryos was tested in the laboratory. Mature receptacles were excised from plants collected at Torbas. Release of gametes and fertilization was induced following the procedure described in McLachlan et al. (1971). Between 25 and 40 zygotes were placed in 55 \times 15 mm disposable petri dishes with 15 ml of medium. Culture medium consisted of half-strength Provasoli medium (PES) (McLachlan 1973). The medium was changed weekly. The embryos were incubated at 12, 15, 18 and 21 °C, with a light:dark cycle of 12:12 h. Photon flux density was 60 $\mu\text{E m}^{-2} \text{s}^{-1}$. Four replicate dishes were incubated at each temperature. Twenty-six days after fertilization, length of 5 randomly chosen embryos was measured in each dish. Only the pigmented part of the embryos was measured.

RESULTS

The disappearance of *Fucus serratus* occurs in a short stretch of the coast of about 30 km. The survey of the coast indicated that *F. serratus* is patchily distributed within the transition zone; although absent from many locations, it monopolizes the substratum at others. It is the size of the patches and not the density of *F. serratus* which defines the abundance of the alga in the localities of the transition zone. In localities at the limits of distribution, only a few small patches were found. Although plants were smaller in these patches (see below), the density and appearance of the plants did not differ greatly from stands found within the zone of abundance. East of Novellana (in Luanco), an isolated population of *F. serratus* was found which consisted of a conspicuous single patch of 4 \times 8 m size (see Fig. 1 for localities).

Zonation profiles of abundant species of algae at Torbas and Oleiros are shown in Fig. 2. The obvious

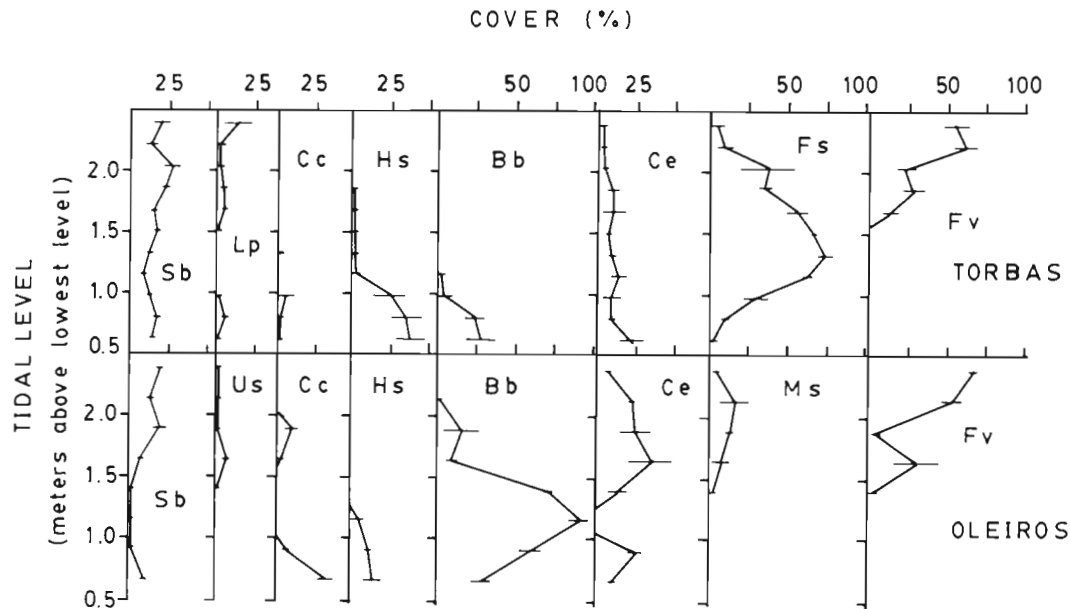


Fig. 2. Zonation profiles of Torbas and Oleiros. Means \pm SE. Fv = *Fucus vesiculosus*, Fs = *Fucus serratus*, Ms = *Mastocarpus stellatus*, Ce = *Corallina elongata*, Bb = *Bifurcaria bifurcata*, Hs = *Halopteris scoparia*, Cc = *Chondrus crispus*, Lp = *Laurencia pinnatifida*, Us = *Ulva* sp., Sb = substratum

difference between them is the absence of *Fucus serratus* in Oleiros. At this locality, the tidal level occupied in Torbas by *F. serratus* is occupied by *F. vesiculosus*, *Corallina elongata*, *Bifurcaria bifurcata* and *Mastocarpus stellatus*. Patterns of zonation at Campiello (not presented here) vary, depending on whether *F. serratus* is present. Where *F. serratus* is present, zonation is similar to that of Torbas, and where it is absent, the shore looks like that at Oleiros.

Temperatures were similar at all 3 localities studied (Fig. 3). They had a minimum temperature of 12 °C. The maximum summer temperature was 18.5 °C at Torbas and Campiello and 19 °C at Oleiros (Fig. 3).

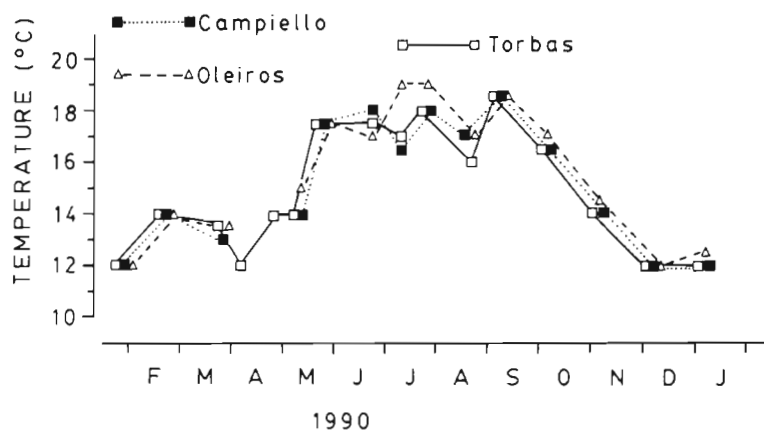


Fig. 3. Temperature of seawater at the study sites

The concentration of nitrate and nitrite in the seawater at the sampling localities followed a seasonal cycle (Fig. 4). At all 3 localities, concentration was highest in January 1991 (5 to 6 $\mu\text{mol l}^{-1}$) and lowest from May to September. Although the concentration of nitrate during summer was below 0.5 $\mu\text{mol l}^{-1}$ at the 3 localities, Torbas consistently showed significantly higher concentrations than those found at either Oleiros or Campiello (Table 1). However, the concentration did not only vary among the localities, but also among sites within each locality and date (Table 1).

The biomass of individual *Fucus serratus* thalli varied with the seasons at Torbas and Campiello (Fig. 5A). Biomass was highest during summer, from June to September, and was lowest in January–February (Fig. 5A). Biomass of plants was consistently greater at Torbas than at Campiello. In May, canopy plants at Torbas were larger than those measured at Campiello (Torbas; mean = 45.15 cm, SE = 1.62; Campiello; mean = 29.81 cm, SE = 1.72) (Table 2).

Although fertile *Fucus serratus* were found throughout the year, seasonal variations in the percentage of biomass devoted to reproduction existed (Fig. 5B). Maximum weight of receptacles per plant was reached in summer (28 % at Torbas and 26 % in Campiello). From February to August 1990 the percentage of biomass

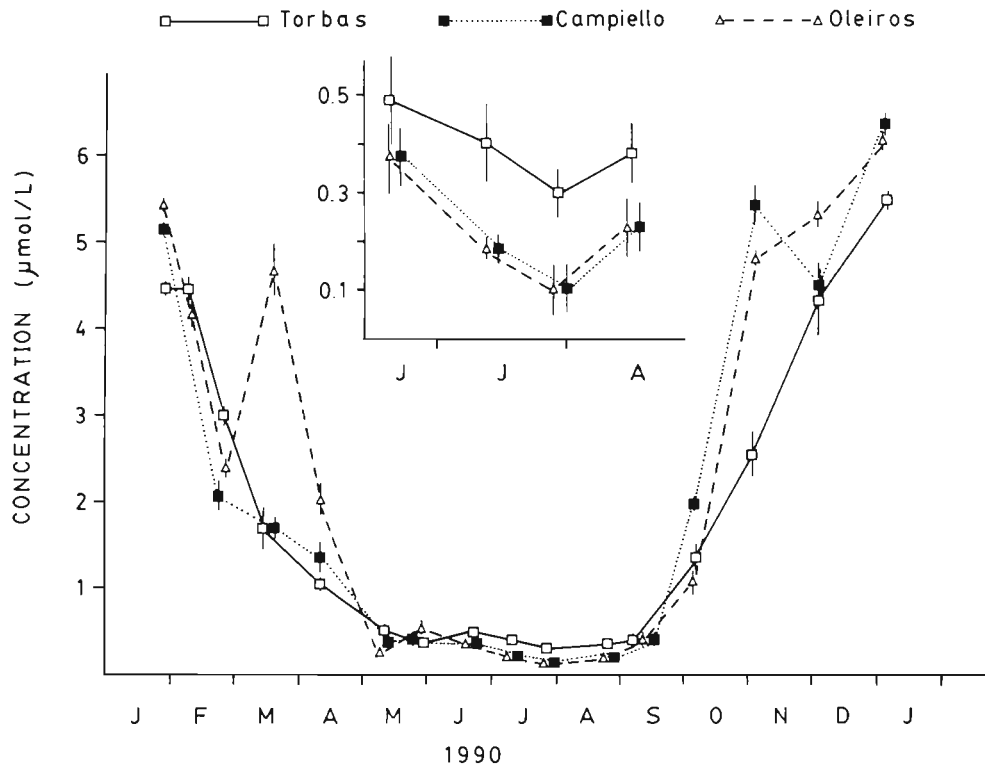


Fig. 4. Concentration of dissolved nitrate and nitrite during the study period at the 3 study localities. Inset: rescaled concentrations during summer. Means \pm SE

devoted to reproduction was larger at Torbas than at Campiello; however, these differences were not apparent from August 1990 to January 1991.

The growth rate of small plants was similar at all sites at Campiello and Torbas (Fig. 6A). There were no significant differences among localities as calculated from the difference between final and initial size (Table 2). There was, however, evidence of significant variation in growth rate among sites (Table 2). Plants grew continuously from late July to December. No loss

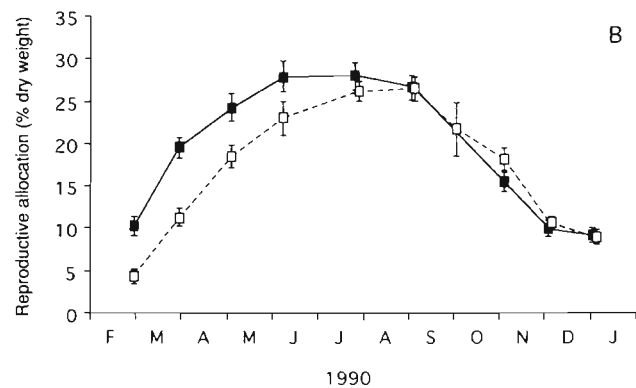
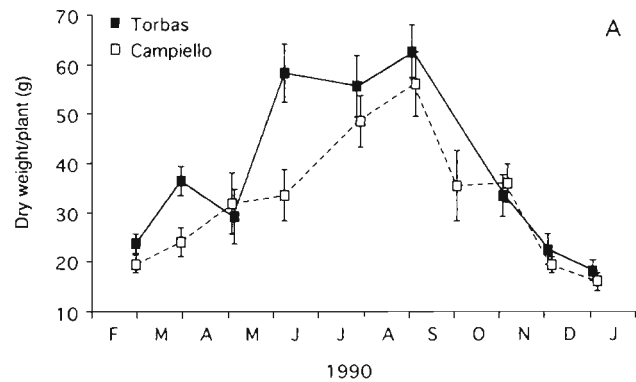


Table 1. Analyses of mean values of nitrate and nitrite concentration at the 3 localities studied during summer. Some samples were contaminated. Therefore 3 replicate samples (instead of 4) were chosen at random from each site and location. Variances were homogeneous (Cochran's test, $p > 0.05$). Data are in Fig. 4

| ANOVA | | | |
|---------------------|----|-------|---------|
| Source of variation | df | MS | F-ratio |
| Date | 3 | 0.353 | 5.67** |
| Location | 2 | 0.452 | 7.27** |
| D \times L | 6 | 0.034 | 0.54 ns |
| Site (D \times L) | 36 | 0.062 | 1.94* |
| Residual | 96 | 0.032 | |

SNK test for differences among locations (= denotes not significantly different, $p < 0.05$):
 Torbas > Campiello = Oleiros
 * $p < 0.05$, ** $p < 0.01$; ns: non-significant

Fig. 5. *Fucus serratus*. (A) Seasonal variation in weight of individual plants collected at Torbas and Campiello. (B) Seasonal variation in the proportion of biomass devoted to reproduction plants at Torbas and Campiello. Means \pm SE

Table 2. *Fucus serratus*. Analyses of (a) mean size of canopy plants and (b) mean increase in size of small plants, in Campiello and Torbas. Variances were homogeneous (Cochran's test, $p > 0.05$). See text

| Source of variation | (a) Size | | | (b) Growth | | |
|---------------------|----------|---------|---------|------------|-------|---------|
| | df | MS | F | df | MS | F |
| Location | 1 | 7646.22 | 12.29** | 1 | 4.02 | 0.11 ns |
| Site (L) | 8 | 621.97 | 4.05*** | 4 | 37.05 | 2.83* |
| Residual | 120 | 153.49 | | 36 | 13.08 | |

* $p < 0.05$, ** $p < 0.01$; *** $p < 0.001$; ns: non-significant

of biomass was detected. In contrast, 2 distinct periods of growth and loss of biomass existed in canopy plants (38 to 44 cm long; Fig. 6B). Plants grew from May (date of marking) to early October. Loss of biomass occurred between October and December (end of the experiment). Plants longer than 50 cm at Torbas showed no net increase in size over the period of the experiment (Fig. 6B).

At the end of the experiment (October 1990) and 1 yr later (October 1991), significant differences between transplants existed in the number of remaining plants (Fig. 7) ($\chi^2_4 = 9.51$, $p < 0.05$ and $\chi^2_4 = 14.68$, $p < 0.01$, respectively). The greatest number of plants was lost at Oleiros, and the smallest in the 'autotransplant' at Torbas. No significant differences in growth existed between plants of the different transplants (Fig. 8, Table 3). Even after 17 mo from the beginning of the experiment, no differences existed. Growth was fast from April (at the start of the experiment) to early September. There was no evidence of artifactual effects of moving plants. The sizes of plants collected at Torbas or Campiello and moved to Campiello and Torbas, respectively, were not significantly different to those of plants transplanted within the same locality (Fig. 8). Similarly, there were no significant differences

in bushiness of plants among these treatments (Fig. 9A, Table 4). Differences existed, however, at the smaller scale, as the effect of site was found to be significant.

In all 5 transplants, individuals became fertile, and gametes were apparently viable, though no fertilization experiments were carried out (antherozoids were mobile and oogonia had a spherical 'healthy' aspect). There were, however, significant differences in the number of reproductive

structures per plant (Table 4a, Fig. 9B). Plants moved to Oleiros from Torbas developed the largest number of reproductive tips. No differences existed between specimens of all other transplants (Table 4b). The effect of site was, again, significant. Recruitment of young *Fucus serratus* has been observed among the transplanted specimens in those sites where *F. serratus* was absent (Oleiros and some sites at Campiello). At Oleiros, in October 1991, more than 100 small *F. serratus* were found around the transplanted specimens (mean size = 13.8 cm, SE = 0.97, $n = 24$). Some of the new plants have subsequently developed receptacles (pers. obs.). Exhaustive exploration of the rock platform at Oleiros failed to reveal newly recruited *F. serratus* other than those close to the transplants.

Six months after clearing, *Fucus serratus* recolonized the scraped areas in the *F. serratus* zone. No *F. serratus* grew in quadrats cleared in the areas dominated by *F. vesiculosus* or *Bifurcaria bifurcata*. Differences existed in the rate of recolonization in scraped quadrats high on the shore, in the *F. vesiculosus* area. It was slower at Oleiros than at Campiello or Torbas. Almost no plants of *B. bifurcata* grew in the scraped quadrats in the area dominated by this alga. Most of the algae colonizing the *Bifurcaria* quadrats were ephemerals.

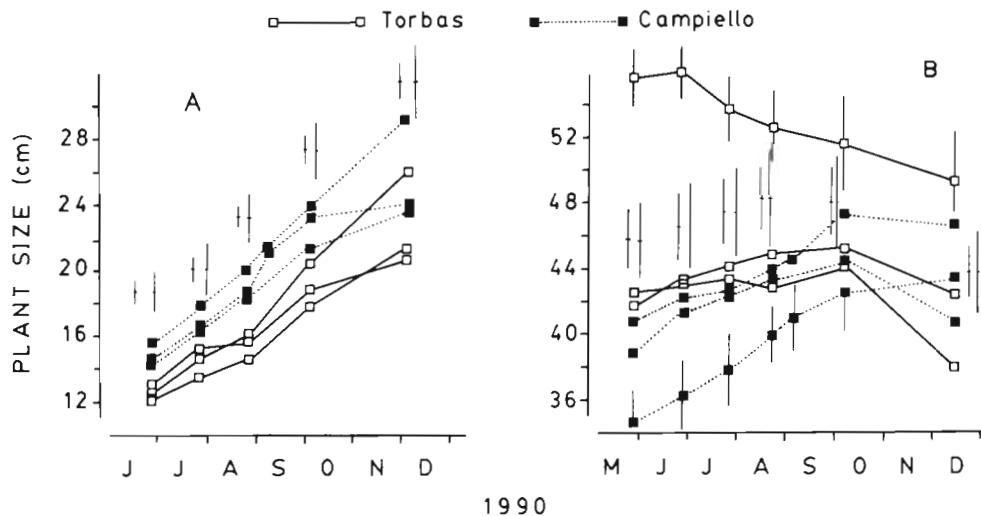


Fig. 6. *Fucus serratus*. Variation in size specimens marked at Torbas and Campiello. (A) Small plants. (B) Canopy-forming specimens. Means \pm SE. Smallest and largest SE bars are shown where no clear graphical presentation was possible

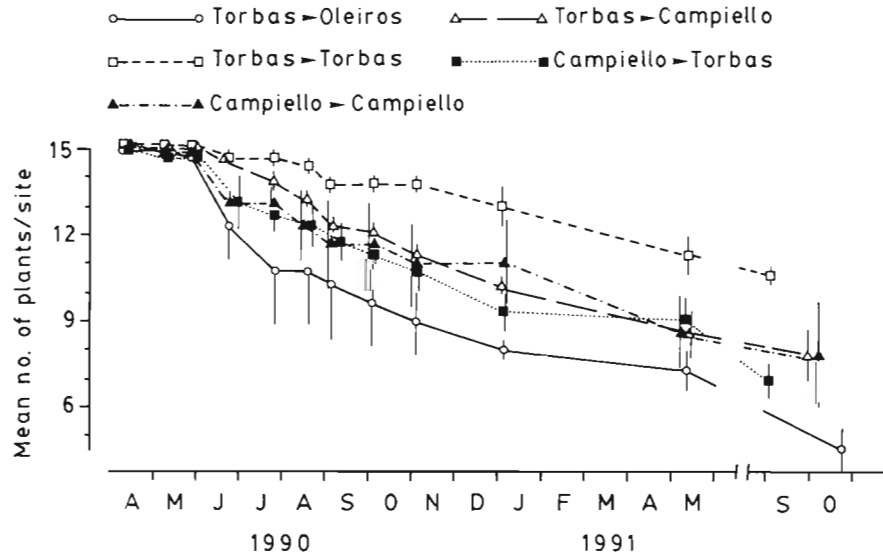


Fig. 7. *Fucus serratus*. Number of remaining transplanted specimens. Means \pm SE

Temperature had a measurable effect on the growth of *Fucus serratus* embryos (Fig. 10, Table 5). Maximum growth was recorded at 18 °C. Growth of embryos incubated at 21 °C was identical to that of embryos at 12 °C.

DISCUSSION

Thalli of *Fucus serratus* transplanted outside the normal range of the species grew and reproduced at similar rates to those transplanted within the distributional limit. New plants, apparently recruited from fertile, transplanted individuals, were found and these too developed reproductive structures. This result suggests that, at least in average years, physical factors alone cannot be invoked to explain the nature of the boundary itself, its location and why the transition zone is so small.

The southern boundaries of many macroalgae in Europe are set by temperatures that are too high in winter and/or summer. High temperatures during winter usually inhibit completion of the life history while high temperatures in summer have often lethal effects (see Breeman 1988 for examples). In the case of the north coast of Spain, marked differences in temperature exist during summer from west to east, but not during winter (US Naval Oceanographic Office 1967, Maillard 1986, SATMER 1990a, b). If temperature is a factor controlling the distribution of *Fucus serratus*, its influence is most likely to occur during summer. Temperature can be invoked to explain the absence of *F. serratus* in the inner part of the Bay of Biscay, where it commonly reaches 21 °C or more during summer. The results of the laboratory experiment reported here are consistent with

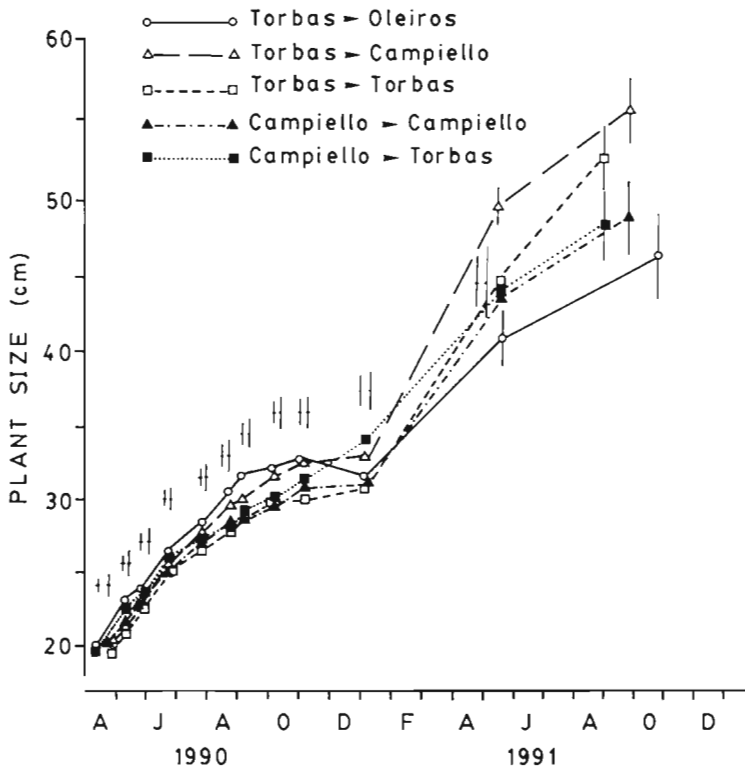


Fig. 8. *Fucus serratus*. Variation in size of transplanted specimens. Means \pm SE. Error bars as in Fig. 6

Table 3. *Fucus serratus*. Analyses of mean size of transplanted specimens in (a) October 1990 and (b) September 1991, after 6 and 17 mo, respectively, from the beginning of the experiment. (a) Some experimental plants were lost in some transplants, therefore 10 plants were chosen at random from each transplant and site. The sizes of 2 additional missing plants in 2 sites were estimated from the mean of those sites and transplants, and 2 degrees of freedom subtracted from the residual. (b) Five replicated plants were chosen at random. The sizes of 3 missing replicated plants were estimated as above and 3 df subtracted from the residual. In both cases, variances were homogeneous (Cochran's test, $p > 0.05$). Data are in Fig. 8

| Source of variation | (a) October 1990 | | | (b) September 1991 | | |
|---------------------|------------------|-------|---------|--------------------|--------|---------|
| | df | MS | F | df | MS | F |
| Transplant | 4 | 25.69 | 0.75 ns | 4 | 176.05 | 1.06 ns |
| Site (T) | 10 | 34.28 | 1.66 ns | 10 | 166.20 | 1.36 ns |
| Residual | 133 | 20.66 | | 57 | 135.13 | |

ns: non-significant

this explanation. At 21 °C, the growth rate of embryos of *F. serratus* was significantly lower than that at 18 and 15 °C. Considering that development of reproductive structures shows a maximum in summer, the effect of temperature on the growth rate of the embryos may be important in explaining the distribution of *F. serratus* on the coast of northern Spain at a large scale. However, differences in maximum temperature among the 3 localities are too small (0.5 °C) to explain the lack of *F. serratus* at the easternmost locality.

The effect of small differences in the concentration of dissolved nitrate and nitrite among the 3 localities during summer is probably irrelevant for large mature plants. Macroalgae can mobilize nitrogen reserves during summer when the availability of nitrogen salts in the seawater is significantly reduced (Chapman &

Craigie 1977, DeBoer 1981, Lobban et al. 1985). Such differences, however, might be important for germlings as their nitrogen supply probably relies exclusively on dissolved nitrogen. In some species, juvenile plants do not appear to store nitrogen (Wheeler & North 1980).

There is evidence that the conditions in the intertidal zone are far from homogeneous for *Fucus serratus*. First, the factor 'site' was found to be significant in most of the analyses. This suggests that small-scale events may be important in explaining the distribution of *F. serratus*. Second, in the transition zone, *F. serratus* usually appears in conspicuous patches. Plants forming these patches, though smaller in length, exhibit a cycle of abundance and reproduction

and a growth rate similar to those of plants growing within the normal range of distribution. Few or no plants are found outside the patches. In these localities it is suggested, therefore, that *F. serratus* exists within a mosaic of suitable and unfavourable locations. Such heterogeneity in the local environment may be responsible for the larger number of transplants lost at Oleiros. Plants moved to unfavourable sites would have been lost, while those moved to adequate sites remained and did not grow at different rates to those fixed at Torbas or Campiello.

If *Fucus serratus* can grow and reproduce beyond its distributional boundary, then the nature of this boundary must be different from mere physiological incompetence. Two non-exclusive alternate explanations may be: limited dispersal ability; and competition with other macroalgae.

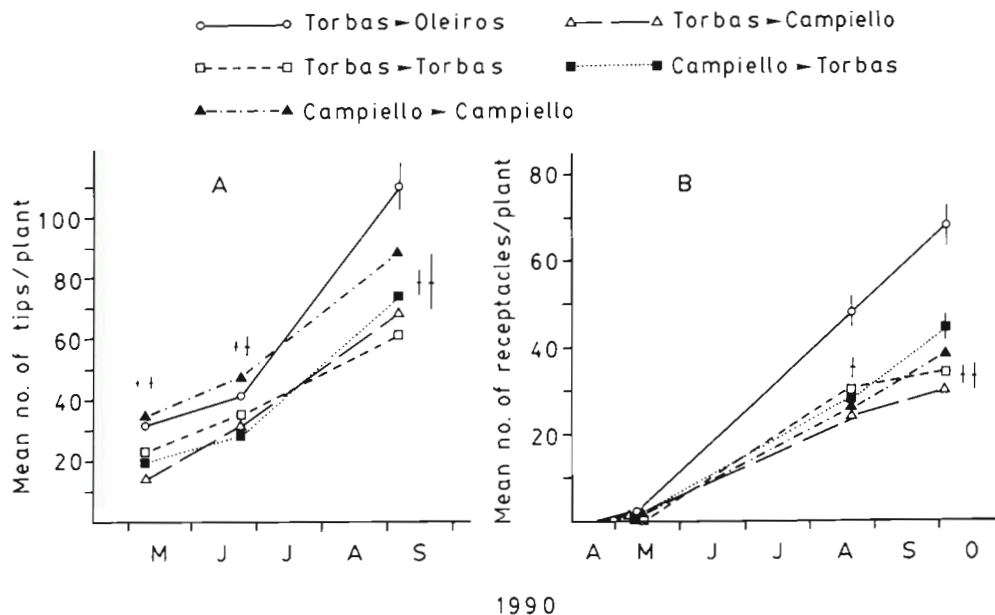


Fig. 9. *Fucus serratus*. (a) Growth in bulk of transplanted specimens, expressed as mean number of tips per plant. (b) Development of reproductive structures in transplanted thalli. Means \pm SE. Error bars as in Fig. 6

Table 4. *Fucus serratus*. Analysis of (i) mean number of tips and (ii) mean number of reproductive tips per plant in transplanted specimens. Number of replicated plants used in analysis and df of the residual as in Table 3. Variances were homogeneous (Cochran's test, $p > 0.05$). Data are in Fig. 9

| (a) ANOVA | | | | | |
|---------------------|-----|-----------------|---------|-------------------|-------|
| Source of variation | df | (i) No. of tips | | (ii) Reproductive | |
| | | MS | F | MS | F |
| Transplant | 4 | 11033.86 | 3.28 ns | 6329.16 | 4.67* |
| Site (T) | 10 | 3361.70 | 2.38* | 1355.77 | 2.42* |
| Residual | 133 | 1415.49 | | 559.33 | |

(b) SNK tests for differences among transplants in the number of reproductive tips (= denotes not significantly different, $p < 0.05$):
 Torba → Oleiros > Torbas → Torbas = Torbas → Campiello = Campiello → Torbas = Campiello → Campiello
 * $p < 0.05$; ns: non-significant

A low dispersal ability of *Fucus serratus* was found in this work: (1) *F. serratus* only recruited on those experimental surfaces which were surrounded by *F. serratus* (i.e. in which the removed algae were *F. serratus*); (2) new plants found at Oleiros were all within 2.5 m from the parental plants. In addition, *F. serratus* is a dioecious species and thus, for efficient dispersal, it is necessary that 2 propagules (zygotes) of different sex arrive at the same suitable site and become fertile at the same time, and, of course, that the 2 plants are close enough to allow fertilization.

Considerable evidence exists regarding the limited dispersal of propagules of several macroalgae (Anderson & North 1966, Dayton 1973, Paine 1979, Chapman 1986, see Santelices 1990 for review). In some cases dispersal is limited to a few meters around the parental plants. Even in the case of some large macroalgae, such

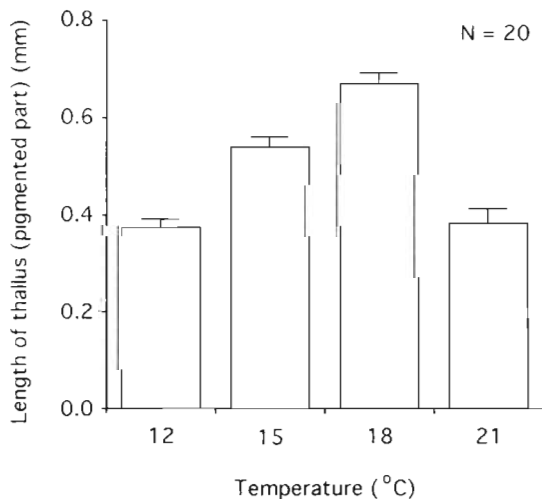


Fig. 10. *Fucus serratus*. Final size of embryos cultivated in the laboratory at 4 different temperatures. Only the pigmented part of the embryos was measured

as *Macrocystis pyrilera*, in which dispersal can be initially thought to be effective, recruitment occurs within a mere 4 m radius from isolated parental plants (Anderson & North 1966, Reed et al. 1988), although episodic, long-range dispersal also occurs in this species (Reed et al. 1988). More efficient dispersal occurs in mature floating algae, among others, this has been reported for *Fucus vesiculosus*, *F. spiralis*, *Cystoseira* spp., *Halidrys siliquosa* and *Himantalia elongata* [Stegenga & Mol 1983 (cited in van den Hoek 1987)]. A striking example is *Sargassum muticum*. While the dispersal ability of attached algae is limited, usually within 5 m from parentals (Deysher & Norton 1982), mature floating specimens

can disperse seedlings over enormous distances (Norton 1977b, Deysher & Norton 1982). *F. serratus*, however, cannot float and this was invoked to explain the absence of the species from shores where it was expected to occur, such as the Faeroe Is. [Borgesen 1908 (cited in van den Hoek 1987)].

Competition with *Fucus vesiculosus* and perhaps *Bifurcaria bifurcata* and *Mastocarpus stellatus* may be occurring in the transition zone and beyond the distributional boundary. Within the normal range of distribution of *F. serratus*, *F. vesiculosus* and *B. bifurcata* occur above and below, respectively, the tidal level occupied by *F. serratus*, while *M. stellatus* is almost absent. At Oleiros, where *F. serratus* is absent, *F. vesiculosus* occurs lower on the shore, *B. bifurcata* higher, and *M. stellatus* appears at mid-tidal levels. Collectively they replace *F. serratus* on this shore. The outcome of competition might be different depending on the nature of the environment. In those zones where the physical environment is favourable for *F. serratus*, this alga would be the superior competitor, while in unfavourable locations it would be outcompeted by other

Table 5. *Fucus serratus*. Analyses of mean size of embryos after 26 d of incubation at 12, 15, 18 and 21 °C. Variances were homogeneous (Cochran's test, $p > 0.05$). Data are in Fig. 10. The analysis was made on the untransformed arbitrary measurement units of the microscope eyepiece

| ANOVA | | | |
|---------------------|----|-----------|----------|
| Source of variation | df | MS | F |
| Temperature | 3 | 397583.12 | 48.28*** |
| Dish (T) | 12 | 8590.62 | 1.94* |
| Residual | 64 | 4425.36 | |

SNK tests (= denotes not significantly different, $p > 0.05$):
 18 °C > 15 °C > 12 °C = 21 °C
 * $p < 0.05$, *** $p < 0.001$

macroalgae. Competition between *F. serratus* and *F. vesiculosus* is important in determining the distribution of both algae in the tidal range (Schonbeck & Norton 1980). Based on phytosociological associations, competition with *F. edentatus* has been invoked to limit the spread of *F. serratus* in Nova Scotia (Dale 1982). Pazó & Niell (1977) concluded from observational studies that the distribution of *F. serratus* on the Atlantic coast of northwestern Spain is influenced by competition with *F. vesiculosus*. To my knowledge, however, no experiments have been done investigating the role of competition in setting the geographic limits of distribution of macroalgae.

There is evidence that the location of the boundary for some species has changed during this century. For instance, Sauvageau (1897) (cited in Fischer-Piette 1957) reported the presence of *Fucus serratus* in San Vicente, some 250 km east of Torbas. Later, Miranda (1931) indicated the presence of this species and other 'northern species' in Gijón (about 125 km east of Torbas). Fischer-Piette (1957) located the boundary in the region of Torbas. More recently, Anadón & Niell (1981) and Anadón (1983) did not find *F. serratus* 25 km east of Torbas, while in this paper, the presence of *F. serratus* is reported in Novellana (50 km east of Torbas) and Luanco (115 km east of Torbas), in the latter as a small isolated population. In Luanco *F. serratus* was absent 10 yr ago (pers. obs.). The most feasible explanation for this is that the patterns of distribution are influenced by medium-term variations of climate or by fluctuating intensity of the upwelling events. Upwelling conditions depend upon the continuity of northeasterly winds during summer (Botas et al. 1990). Thus, important variations can be observed in temperature, even on a weekly basis (SATMER 1990b, c). Variations in the wind regime also occur on a yearly basis (Gijón Weather Station unpubl. data). Changes in the environmental conditions (weather or oceanographic features) could, in turn, influence the outcome of interspecific relationships (e.g. competition). In benign or average years, *F. serratus* might survive and reproduce beyond its distributional boundary and colonize new localities. The boundary would displace to the east. Massive mortality of *Fucus serratus* plants should be expected in marginal localities in extreme years (e.g. exceptionally hot summers), thus limiting the spread of the species. In this case the boundary would move to the west.

In conclusion, the evidence presented here suggests that while temperature may be important in setting the large-scale distributional limits of *Fucus serratus* and can be used to explain the absence from the inner part of the Bay of Biscay, it cannot, alone, explain the present limit of distribution. When transplanted beyond that boundary, plants survive and reproduce success-

fully. However, data for longer periods of time are necessary to assess the importance of extremely adverse years in the survival of *F. serratus* populations in marginal localities. Variation in the environmental conditions, low dispersal range and competition with other macroalgae probably act in conjunction with physical factors in shaping the present boundaries of *F. serratus*.

Acknowledgements. I am very grateful to R. M. Viejo, L. Gutiérrez, R. Anadón, A. Bode and L. Díaz for help in the field. I thank Prof. B. Santelices for advice in the design of the experiments. Comments and corrections from Dr N. L. Andrew considerably improved the manuscript. Comments by Prof. C. van den Hoek are greatly appreciated. Corrections of 2 anonymous referees are acknowledged. The work was done under the tenure of a PFPI postdoctoral fellowship.

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This article was submitted to the editor

Manuscript first received: June 1, 1992

Revised version accepted: November 16, 1992