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Growth and production of new recruits and adult individuals of *Ascophyllum nodosum* in a non-harvested population at its southern limit (Galicia, NW Spain)

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Abstract

Populations near the geographic distribution limits of the species are considered to live under suboptimal conditions, and hence slight environmental changes can be critical for their survival. The potential sensitivity to disturbances of the long living macroalga *Ascophyllum nodosum* was analyzed by the determination of growth, recruitment, mortality, and production of biomass in a population near its southern distribution limit. Recruitment, survival and growth rates of <2 yr old individuals were determined in a new population growing in experimentally denudated squares. Demographic data for >2 yr old individuals were obtained from individuals in the original population after estimating their age from the number of gas bladders in the thallus. Growth and survival were described as continuous non-linear functions of age applied to the population and were further used to make demography-based production estimates. Recruitment of *A. nodosum* in denudated substrates required a previous cover of other macroalgae (as *Fucus vesiculosus*) but subsequent settlement of new recruits was not observed, as only one cohort was detected during the 26 month-period of the study. The low production estimates (2,033 g m⁻² for a 10 yr period) and poor recruitment indicates high sensitivity of this population to denudation. However, the large variability observed in the growth curves of different populations along this southern distribution area suggest a large potential for adaptation to local conditions that may overcome environmental changes at regional scales.

Introduction

In the last years an increasing attention has been focused on studying biogeographic differences among macroalgal populations along their distribution limits (Svensson et al. 2009; Araújo et al. 2014). Such studies have addressed that populations living near marginal areas of distribution are presumably constrained in their capacities, and that more variable and lower vital and growth rates would be expected in edge populations compared to central populations (Angert 2009).

Consequently, changes at large spatial scales, like those associated with climate change, may have particularly high impact on these populations, and lower recovery capacities from disturbances are predicted to occur. Recent studies suggest that significant changes in brown seaweed populations are already occurring in temperate environments (Lima et al. 2007; Fernández 2011; Lamela-Silvarrey et al. 2012; NiCastro et al. 2013) supporting the importance of understanding the ecology of single species (Viana et al. under review). Large perennial fucoids are important habitat-forming species in temperate intertidal rocky shores, contributing to the biodiversity in these regions (Riera et al. 2009). Therefore, we need to investigate how sensitive these species are to disturbances, since their population dynamics influence also the dynamics of associated species (Svensson et al. 2009).

Ascophyllum nodosum (Linnaeus) Le Jolis is a dominant intertidal brown seaweed species, with its global distribution restricted to the North Atlantic Ocean. In the East coast, it is widely distributed from Northern Norway and The White Sea to the North of Portugal (Sharp 1987; Araújo et al. 2009, 2014). Present from sheltered to moderately exposed areas (Cousens 1982), it usually occupies the mesolittoral zone. Populations of *A. nodosum* generally occupy moderately dense areas where long fronds grow from a

common holdfast covering a large proportion of the rocky shore (Åberg 1992). This species can reach up to 2 m long as, even though they show slow growth rates, it is one of the most long-lived macroalgae. Populations older than 15 years old have been described worldwide (David 1943; Niell 1979; Keser et al. 1981). Fronds have large egg shaped gas bladders at intervals along the shoot that enable them to float during high tides. It presents apical growth (Moss 1970) and gas bladders are formed at the tip previously to the dichotomously branching that generally occurs once a year (MacFarlane 1932; Moss 1970). Receptacles are formed in lateral branches that could also be vegetative.

The main differences between central and marginal populations are due to the density of the populations and the continuity of their distribution along the coast. In areas above 50°N the distribution is almost continuous along the estuaries, with high densities that support a significant economic activity related to harvesting (Sharp 1987). These populations are also subject to sharp changes in environmental conditions, as ice covering, resulting in characteristic autoecological patterns (Strömberg 1986; Åberg 1992).

In areas below 50°N the distribution is discontinuous, and the populations appear in isolated patches along the coast. These local populations are related with the seasonal inputs of cold water, as those caused by the spring-summer upwelling along the coast of NW Spain and N Portugal (Anadón and Niell 1981; Lüning 1990). Increasing sea surface temperature (SST) during the last decade has been related to changes in the distribution of several fucoid species (Lima et al. 2007; NiCastro et al. 2013), and although distributional shifts in *A. nodosum* southern limit were not observed (Lima et al. 2007), it appears that some populations have retreated in the Bay of Biscay (Alcock 2003).

A. nodosum populations show poor sexual reproduction success. Zygotes disperse short distances and suffer high mortality before and after settlement (Chapman 1995; Dudgeon et al. 2001). Thus, recruitment can be highly variable between years and established populations often consist on large, old individuals and relatively few recruits (Dudgeon and Petraitis 2005). Therefore, knowledge about the ecology of their early life stages and recruitment is important to estimate the possibilities of recuperation of these populations following a disturbance, as well as the conditions of mature populations. The sensitivity of *A. nodosum* populations to small and large-scale disturbances has been studied experimentally (Dudgeon and Petraitis 2001; Cervin et al. 2004; Araújo et al. 2009), but there is scarce information about the demography of populations under environmental stress (Araújo et al. 2014).

The objective of the present study is to quantify growth rates, recruitment, survivorship and production of a population of *A. nodosum* near the southern limit of distribution of this species to infer its sensitivity to disturbances. The study site is located at the Ría do Burgo (Galicia, NW Spain), included in a region under the influence of coastal upwelling. Individual growth in length is also estimated for other populations along the Galician coast as an indicator of the variability in the responses of this species at local scale.

Material and Methods

Study site

The coast of Galicia (NW Spain) is characterized by the presence of rias (tidal inlets) sustaining high levels of biological production due to seasonal upwelling (Aristegui et al. 2006). *A. nodosum* occurrence is restricted to the inner part of the rias in this area (Niell 1977). Besides the inflow of marine waters, the rias receive water and nutrient

inputs from small rivers that drain into them (Bode et al. 2011). This area is within the southern distribution limit of *A. nodosum* in the East Atlantic coast.

The study was conducted at Ría do Burgo (43° 20'N, 8° 22'W) (Fig. 1), the inner part of the Ría de A Coruña, which opens to the sea by a bay of 15.7 km². The Ría do Burgo has a mean depth of 10 m and a short salinity gradient with estuarine characteristics. It is in the mouth of the river Mero, a small river with a small drainage basin (385 km²) and a mean annual flow of 6.6 m s⁻¹ (Varela et al. 1994). *A. nodosum* forms here a dense population at the mid-upper intertidal zone of the littoral and constitutes the dominant species of this range (Bárbara et al. 1995). *Fucus spiralis* and *F. vesiculosus* are the dominant species at the upper and mid-lower intertidal zone respectively, although other Fucaceae, as *F. serratus* or *Pelvetia canaliculata*, are also present in the area. The littoral at this site follows the typical zonation described for rias in this area (Niell 1977).

During the first sampling year, salinity (± 0.1 , Practical Salinity Scale) and temperature (± 0.1 °C) of surface water were measured *in situ* with a portable conductivity meter (YSI Model 30, YSI Inc. Yellow-Springs, Ohio, USA). Samples of surface water were also collected for further determination of dissolved nutrients (NO₃⁻ + NO₂⁻, NH₄⁺ and PO₄³⁻) in the laboratory following Grashoff et al. (1983).

Size distributions and abundance of new recruits from experimentally denudated squares

In the *A. nodosum* dominant zone at Ría do Burgo (Fig. 1), three 50x50 cm experimental squares were randomly set up at 2-2.92 m relative to the lowest sea level during spring tide (tidal height). The size of each quadrat represents the minimum sampling area required for biomass and demographic studies in this region (Niell 1977,

1979). The experimental squares were completely denuded in October 2010. All macroalgae individuals constituting the original population inside the squares were removed as close to the ground as possible and the substrate was also cleaned with a metal brush to ensure no small individuals or the holdfast of any adult individual could remain attached. No further treatment was applied to the substrate to preserve as much as possible the integrity of the existing microflora. The material obtained from the scraping was transported to the laboratory in plastic bags. All removed individuals were measured and the total biomass of *A. nodosum* and accompanying flora was determined as wet and dry weight (± 0.01 g). Dry weight was determined after drying in an oven (50 °C) until constant weight. All fronds from the same holdfast were considered as an individual.

During a 26 month-period (November 2010 to December 2012) all macroalgal individuals within each experimental square were counted and measured. From November 2010 to January 2012 the samplings were made every month, except in February and December 2011; and since January 2012 until December 2012 individuals were measured bimonthly. To report individual growth, all individuals longer than 0.3 cm were mapped inside each square and measured (± 0.2 cm) from the base of the holdfast to the tip. During early summer sampling surveys, when the abundance in some of the experimental squares was high, individuals shorter than 1.5 cm were counted and 90 of these individuals were measured to determine their mean length. All individuals recorded were classified in size classes, each size class corresponding to a 0.5 cm interval. Density estimations were made by combining all the results obtained in the three experimental quadrats.

Monthly mean frequency distributions of size classes were calculated from the number of individuals in each size class. Cohorts, or individuals that share a particular

event during a life span, i.e. a year class (Crisp 1971), were identified from the modes of the size frequency distributions, assuming normal or log-normal distributions. Because recruitment (i.e. the number of new individuals appearing in the experimental squares) can occur during several months, we defined as age 0 of a cohort the first month that the mode of the distribution reached a distinguishing maximum density peak.

Growth and appearance of the annual gas bladders in new recruits and adult individuals

Due to the slow growth of this species, the growth was recorded following two approaches: first as the growth of new recruits within the experimental denudated areas and second as the growth of adult individuals from the original population.

Within the experimental squares, the growth was monitored by monthly changes of the size-class distributions. The changing position of the mode between consecutive sampling dates affords an approximate measure of the changing mean size (growth) of that cohort (Crisp 1971). The modal length of cohorts can be fitted to a logistic equation (Niell 1979):

$$L_t = \frac{L_{max}}{1 + e^{a_1 + a_2 Age}}$$

where L_t is the length of the individual at time t , L_{max} is the asymptotic length, and a_1 and a_2 constants. The regression parameters were estimated by iteration after an initial estimation of their value and subsequent minimization of the sum of squares by the Marquardt method. GraphPad Prism 4 software was used to estimate the fitted curves.

The second approach was based on the determination of the minimum age of adult *A. nodosum* individuals by assuming the annual production of one gas bladder (Baardseth 1955), and by establishing the appearance of the first gas bladder in the year class 2 (Niell 1979; Cousens 1982). A growth curve can be back estimated if the length and

number of gas bladders of different individuals in a population are recorded at one moment in time. Following this method, the growth of *A. nodosum* was estimated from the original population sampled at Ría do Burgo in October 2010. Temporal and geographic variability in growth was analyzed after estimating growth curves from samples collected at Ría do Burgo in 2006 and at other sites along the coast of Galicia (Fig. 1). These curves were also compared with the curves determined for Cies Islands and San Simón by Niell (1979).

To test that the formerly assumptions were correct, the appearance of the annual gas bladder in new recruits and labeled adult individuals was checked. Two approaches were made, i) the percentage of new recruits within the experimental squares with the first gas bladder was recorded; and ii) seven adult individuals close to the experimental squares were labeled to follow the appearance of the annual gas bladder.

Demography and production of new recruits from the experimentally denudated squares

The fate of individuals within the experimental squares was monitored based on the monthly records of their position on each experimental square. New recruits were considered when they were first detected. Any individual that disappeared from the experimental squares was considered dead. Survivorship (*S*) was calculated as the fraction of individuals remaining from the cohort maximum recruitment and fitted to an exponential decay function with age:

$$S = S_0 e^{-(m \text{ Age})}$$

where *S*₀ is the density when the cohort showed maximum recruitment and *m* the mortality rate.

The dry weight biomass of each individual (w) was determined using a length-weight relationship computed from a set of individuals of different lengths (L) and without receptacles collected at Ría do Burgo ($L=21.962 w^{0.418}$, $r^2=0.962$, $P<0.001$, $n=42$). The total biomass of the population was computed as the sum of the biomass of the individuals recorded in all experimental quadrats and reported as $g\ m^{-2}$.

The production was calculated by the Allen-curve method (Niell 1979; Cousens 1984). Production estimates using this technique can be obtained graphically by relating the number of living individuals of a cohort (N) and the mean weight of those survivors (w) at corresponding times (Crisp 1971). After the maximum of abundance is reached (maximum recruitment), only mortality (a decline in density) and individual growth (an increase in biomass) occurs through the rest of the life cycle of the cohort. The standing stock biomass (B) of each cohort during a period of time is given by the square defined by $N \cdot w$ under the curve, while the production (P) of the cohort can be computed as the integral under the curve. Standing stock, production and production to biomass ratios ($P:B$) were computed for different time intervals.

Results

Environmental settings and characteristics of the experimental squares

The site showed large ranges of variation in both temperature and salinity (Fig. 2). Temperature reached a maximum of ca. 23 °C by the end of summer while minimum values in winter reached 10 °C. Low salinity values were recorded during autumn and winter. Nutrient concentrations also varied during the sampling period (Fig. 2). Nitrate plus nitrite and phosphate were maximum during winter months, while values in early summer were below 5 μM . The fact that the lowest values were found during upwelling

months (spring and summer) and the inverse variation of salinity vs. nitrate plus nitrite suggest a major role of river nutrient inputs in this location.

The mean ($\pm$ SE) dry biomass of *A. nodosum* individuals removed from the original population within experimental squares was $3,456 \pm 1,241 \text{ g m}^{-2}$. Among the possible accompanying species, only *F. vesiculosus* was present within all the experimental squares in the original macroalgal assemblage, averaging $108 \pm 144 \text{ g m}^{-2}$. During the first months after denudation several specimens of *F. vesiculosus* appeared in the experimental squares, reaching higher densities than *A. nodosum* (Fig. 3). Nevertheless, other seasonal macroalgae were recorded during the sampling months, with the maximum number of species detected in June 2011. From May until July, when water temperature was high, *Chaetomorpha aerea* was present, and among Rhodophyceae, only *Gelidium pusillum* and *Caulacanthus ustulatus* were recorded.

Size distributions of new recruits from the experimentally denudated squares

After the denudation, and during the period of study (~ 2 yr), new recruits were observed during almost all months, but a marked peak was identified in May 2011 based on the annual variation of the size-distributions. This peak was identified as the start of a cohort, the only cohort detected during the study (Fig. 4). Although the denudation was made in October 2010, during the first months the recruitment of *A. nodosum* in the experimental squares was minimum, and only up to 50 individuals m^{-2} were mapped until April 2011 (Figs. 3 and 4). In spring, when the number of *F. vesiculosus* individuals started to increase, the number of individuals of *A. nodosum* also started to rise, although at slower rates than *Fucus* (Fig. 3). Since June 2012 a few individuals longer than 12.5 cm were observed, but their abundance was very low comparing to smaller size classes, reaching approximately 60 individuals m^{-2} by the end

of the sampling period. The longest individual recorded at the end of the survey was 26 cm long. In December 2012, 26 months after the denudation, the size-class distribution was still different from the original population; individuals longer than 26 cm were absent while in the original population most individuals were longer than 60 cm (Fig. 4).

Growth and appearance of the annual gas bladders in new recruits and adult individuals

The first gas bladder in the new recruits within the experimental squares appeared in March 2012 (Fig. 5). All individuals that showed a gas bladder were between 7 and 18 cm long and were not more than 17 months old, the time since the denudation was done. But during the 26 months of the study not all longer recruits had a gas bladder.

Among adult labeled individuals, the annual gas bladder was present at the tip of all individuals in the spring of both recorded years. During the first spring (2011) the bladder was developed earlier (between April and May) than in the second year (January-March). The month after a new gas bladder was observed for the first time, it was not at the tip of the individual anymore, and in some individuals a bifurcation was already present following the formation of the gas bladder. This last feature was not conspicuous to all the individuals, as some of them showed 2 vesicles in a row or even a bifurcation on the vesicle.

Although there were some individuals within the experimental squares exceeding 12 cm at the end of the study, the modal length of the new recruits was much lower (Fig. 4). To complete the growth curve of Ría do Burgo, data from the individuals of the original populations within the experimental squares were combined along with data from the new recruits (Fig. 6a). The growth curve obtained showed slow growth during the first years of life and an exponential growth until the individuals were 95 cm long

(Table 1). As individuals got older a relatively large variation in individual growth rate was observed, probably due to the breakages the individuals can suffer.

The populations from other localities showed growth curves similar to those obtained at Ría do Burgo (Fig. 7a). The growth curve of Cíes Islands showed the slowest growth rate (Fig. 7a). There were no differences between the growth curves of Ría do Burgo at different sampling years; and for both years, the oldest individuals observed were 9 years old (Fig. 7b).

Survivorship and production of the new recruits within experimental squares

The survivorship was estimated from the date the maximum abundance of the cohort was detected. The new population displayed high recruitment ($\sim 2,500$ individuals m^{-2}) but also high mortality among individuals younger than 2 years old (Fig. 6b). The survivorship curve was completed with density values of the older individuals (≥ 4 years) of the original population. The mortality among individuals older than 3 years old was estimated to be much lower.

Despite the lower recruitment, individuals between 2 and 6 years old were the most productive (Table 2). This is due to the higher standing stock biomass of the individuals at these ages because of the higher growth rates (Fig. 6a). Individuals between 8 and 10 years old may suffer several breakages, diminishing the standing stock biomass of the aged population, and in consequence reducing its production. The P:B ratio also supports that the biomass produced annually is over the standing stock ($P:B > 1$) until the population is between 6 and 8 years old.

Discussion

The studied population of *A. nodosum* showed low recruitment, growth, survival and productivity rates. These results are consistent with low recovery capacity associated to environmental stress at the southern limit of the distribution of this species (Araújo et al. 2014). However, the local variability observed in individual growth suggests the existence of different life history traits that may enhance the survival of this species under stress.

Recruitment

The slow recovery of *A. nodosum* following natural or experimental denudation was previously reported in natural and harvested areas (Knight and Parke 1950; Baardseth 1970; Vadas et al. 1990; Jenkins et al. 1999; Cervin et al. 2005; Ingólfsson and Hawkins 2008). At the experimental squares of Ría do Burgo, new *A. nodosum* individuals were almost absent during the first six months of the study (Figs. 3 and 4) when most individuals outside the squares did not have receptacles (pers. obs.). The start of the cohort was established in May 2011, when the first peak (mode) was observed, in agreement with the presence of mature receptacles in March that were reabsorbed in April after releasing the gametes. Nevertheless, a continuous recruitment was observed in the subsequent months after the cohort was established. The existence of a bank of gametes that gradually developed could have originated the subsequent increase in density of the cohort months later it was established. However, recruitment may not be simply related with the reproduction of adult individuals. For instance, a peak in recruitment was not observed in spring 2012 (Fig. 4), likely because the already high density of plants within the experimental squares. They may have prevented the settlement of significant numbers of zygotes or at least their survival until they were first detected.

Within the experimental squares, the rock was initially colonized by *F. vesiculosus* individuals, even though the biomass of the latter species was 32 times lower than *A. nodosum* biomass in the original population. The initial appearance of *Fucus* spp. individuals in denudated areas was also observed in northern areas (Keser and Larson 1984; Jenkins et al. 1999; Dudgeon and Petraitis 2001; Cervin et al. 2005). Soon after settlement, a dense canopy seems to be a good environment that enhances survivorship of germlings (Cervin et al. 2005; Choi and Norton 2005; Sánchez and Fernández 2006), although later on, high densities may derive in a inhibition of growth rates due to the competition for nutrients, light, space, wave action or due to sweeping by large individuals (Vadas et al. 1992; Creed et al. 1996; Viejo et al. 1999; Steen and Rueness 2004; Cervin et al. 2005; Choi and Norton 2005).

Densities of new recruits observed in the present study (up to 2,500 indiv. m⁻²) were much lower than those reported for other localities above 50°N, where they can reach up to 700,000 indiv. m⁻² (Dudgeon and Petraitis 2001). The density of the original population (160 indiv. m⁻²) was equivalent to densities recorded at similar latitudes in the West Atlantic coast (up to 91 indiv. m⁻², Peckol et al. 1988). However, these values are also low when compared to those found in regions above 50°N, where densities can reach up to 521 indiv. m⁻² (Keser et al. 1981). This suggests that environmental conditions in the populations near its southern limit can be suboptimal for recruitment, as supported by the lower reproductive value of *A. nodosum* populations in Portugal compared to populations in France (Araújo et al. 2014).

Growth of young and adult individuals

Most of the reported growth rates of *A. nodosum* were obtained from adult individuals (Vadas and Keser 1972; Mathieson et al. 1976; Stengel and Dring 1997)

while studies recording the growth of young individuals are scarce (Vadas and Keser 1972; Schonbeck and Norton 1980). In this study, growth rates varied between 0.2-0.6 cm month⁻¹ during the first 1.5 yr since the start of the cohort (Fig. 6a). These rates were slightly lower than the average value of 0.8 cm month⁻¹ reported for young individuals at populations growing above 50°N (Vadas and Keser 1972; Cervin et al. 2005). For adults, growth increased exponentially after the second year of life, with maximum growth rates of 18.7 cm yr⁻¹ for individuals between 5 and 7 years old (Fig. 6a). The maximum growth rates estimated in this study for other populations in Galicia varied between 5.5 to 21.3 cm yr⁻¹ (Fig. 7a). In general, these values agree with reported growth rates in other regions (Vadas and Keser 1972; Mathieson et al. 1976; Peckol et al. 1988; Stengel and Dring 1997).

The studied population at Ría do Burgo showed a similar timing in the appearance of the first gas bladder to other populations (Baarsdeth 1955; Keser and Larson 1984). This further supports the use of the number of gas bladders to calculate the approximate age of an individual of this species, although with a maximum error of ± 2 yr (Niell 1979; Cousens 1984). Because the appearance of the first gas bladder occurs sometime between the first and second year, the growth curve estimated only from gas bladders data had a large uncertainty in the estimation of growth for individuals < 2 yr old. To our knowledge, the present study is the first providing a growth curve based on direct measurements through all the life time of *A. nodosum*, from newly implanted to old individuals. The length-at-age results of the direct length measurements for individuals younger than 2 yr old fitted along with those estimated for older individuals using gas bladders. This estimation provides a continuous function of individual growth for this species with reduced uncertainty at young ages.

Net growth in length for mature individuals is reduced, particularly for those >5 yr old, because of breakages of the thallus, even leading to shortening in maximum length (Keser et al. 1981; Araújo et al. 2014). This effect is represented in the logistic growth curve by the plateau or maximum length ($L_{\max}$) which is characteristic of each population and indicative of the local environmental conditions for sustaining a healthy adult population. Large values of $L_{\max}$ can result from the combination of high growth rates (i.e. enough nutrients and light) and small losses of biomass (e.g. by breakages), and are generally associated to eutrophic areas with low wave and current velocities (Niell 1977). Thus, the analysis of the logistic growth curve parameters of different populations can be used for estimating life history traits and adaptation to local conditions. For instance, the variety of local growth curves found in Galicia (Table 1, Fig. 7) is consistent with the large susceptibility to changes in individual length reported for southern populations of this species (Araújo et al. 2014). Populations with fast growth of young individuals (high a_1) and reduced breakage with age (high a_2) will reach high asymptotic length ($L_{\max}$), as observed at Foz (Table 1). These populations will be less sensitive to extinction than those with low growth rates and high risk of breakage (e.g. San Simón, Table 1).

Production

The estimated produced biomass of one cohort at Ría do Burgo after a 10 year-period (2,033 g m⁻², Table 2) was close to the range of variation of the biomass of the original population (2,215-4,697 g m⁻²). This suggests that this value is not severely biased by the inclusion of a new starting population after denudation in the calculations. However, the overall productivity estimated in this study was below the values estimated for the same species at other sites in Galicia using only demographic data estimated from natural and mature populations. For instance, Niell (1979) estimated accumulated

production values of 5,000 g m⁻² for a 10 year-period at Cíes and almost the same value only for a 7 year-period at San Simón, but the populations at these localities had larger densities and lower mortality rates than the studied population at Ría do Burgo. Reported values of standing stock biomass in areas above 50°N reach up to 11.3 kg m⁻² (Cousens 1984; Åberg 1992) but only up to 5 kg m⁻² in other sites at the same latitude as the present study (Niell and Soneira 1976; Cremades et al. 2004; Lamela-Silvarrey et al. 2012). In all cases, the maximum production is observed for individuals of more than 4 years of life (Niell 1979; Cousens 1984), and in our study when the individuals are 4-6 years old (maximum P:B value in Table 2).

As found for recruitment and mortality, the low productivity estimated for the studied population at Ría do Burgo implies a high risk of failure when recovering from disturbances. However, the large range of productivity of this species in Galicia, and the local differences in growth suggest that the persistence of *A. nodosum* in the southern distribution limit would be mainly determined by the adaptation of populations to local conditions, while changes in regional climate would be of secondary importance. This conclusion is also supported by demographic studies showing higher adaptability of populations in Portugal compared to those in France (Araújo et al. 2014). Future studies of *A. nodosum* populations will benefit from determining key demographic parameters (as individual growth and Allen curves in this study) as indicators of local adaptation and sensitivity to disturbances.

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Table 1 Parameters of the logistic equations describing growth in length (cm) of *A. nodosum* computed for different sites along the Galician coast (see Figs. 1 and 7). The equation is in the form: $\text{Length} = L_{\max} / (1 + e^{[a_1 + a_2 \cdot \text{Age}]})$, where $L_{\max}$ is the asymptotic length (cm) and age is measured in years. a_1 and a_2 are constants; n : number of data; r^2 : determination coefficient

	Sampling	Latitude	Longitude					
	year	N	W	$L_{\max}$	a_1	a_2	n	r^2
Foz	2010	43.56468	-7.24599	135.90	3.61	-0.55	42	0.88
Cabanas	2010	43.41146	-8.17255	113.50	3.21	-0.58	46	0.79
Ría do Burgo	2010	43.32777	-8.07357	95.09	3.70	-0.80	133	0.77
Ría do Burgo	2006	43.32777	-8.07357	101.40	3.21	-0.61	37	0.80
Camariñas	2007	43.13694	-9.177050	97.07	3.40	-0.90	25	0.86
San Simón *	1978	42.30645	-8.62840	100.00	2.27	-0.43	-	0.82
Cíes Islands *	1976	42.22461	-8.90689	105.65	2.40	-0.18	-	0.90

* from Niell (1979)

Table 2 Standing stock biomass (B, g m⁻²), production (P, g m⁻² period⁻¹) and P:B ratio (period⁻¹) estimated for the population of *A. nodosum* at Ría do Burgo using the Allen method for different time periods (yr)

Age	B	P	P:B
(yr)	(g m ⁻²)	(g m ⁻² period ⁻¹)	(period ⁻¹)
0-1	33.52	46.95	1.40
1-2	96.42	104.16	1.08
2-4	455.99	708.66	1.55
4-6	568.68	925.00	1.63
6-8	231.04	229.75	0.99
8-10	62.19	18.43	0.30
0-10		2032.96	

Figure legends

Fig. 1 Location of study sites

Fig. 2 Variations in water temperature (a, °C), salinity (b), nitrate+nitrite and ammonium (c, µM, continuous and dashed lines respectively), and phosphate (d, µM) at Ría do Burgo site during the first 15 months of the study period

Fig. 3 Variations in density (individuals m⁻²) of the new recruits of *A. nodosum* and *F. vesiculosus* in the experimental squares at Ría do Burgo during the first 15 months of the study period

Fig. 4 Variations in density (individuals m⁻²) of *A. nodosum* by size-classes in the experimental squares at Ría do Burgo during the study period. The size distribution of the original population before denudation is shown in the upper left panel. The time after denudation (days) along with the date of observation is also indicated on each histogram. Distributions shown are from April 2011 just before first density peak was detected. Note the different scales of the y- axis

Fig. 5 Record of the appearance of the annual gas bladders in new recruits longer than 7 cm and percentage of those new recruits with or without a gas bladder within the experimental squares at Ría do Burgo during the sampling period. *: No data

Fig. 6 Growth in length (a, cm), log survivorship (b, individuals m⁻²) and Allen diagram (c) of *A. nodosum* population at Ría do Burgo. The open dots in panel **a** indicate adult individuals measured in the original population dated using the number of gas bladders and length. The parameters of the growth curve in panel **a** are listed in Table 1. The open dots in panel **b** indicate density estimations not used in the computation of the

598 survivorship curve and the gray dots represent adult individuals from the original
599 population

600 **Fig. 7** Growth in length (cm) of *A. nodosum* at several locations in Galicia (a) and at Ría
601 do Burgo for years 2006 and 2010 (b). The parameters of the logistic equations are
602 given in Table 1. The curves of San Simón and Cíes Islands are from Niell (1979)

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