Ecology of *Fucus vesiculosus* (Phaeophyceae) at its southern distributional limit:

growth and production of early developmental stages

Inés G. Viana[1*], Antonio Bode[1] & Consolación Fernández[2]

[1] Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo. 130,

E15080- A Coruña. Spain.

[2] Universidad de Oviedo. Departamento de Biología de Organismos y Sistemas. C/

Catedrático Rodrigo Uría, s/n, E33071-Oviedo, Spain.

* Correspondence to: Inés G. Viana. E-mail: inesgviana@gmail.com

Running title: Ecology of *Fucus vesiculosus*

24   **Abstract**

25   Growth and survival of two populations of *Fucus vesiculosus* were studied at its

26   southern limit of distribution on the eastern Atlantic coast. Experimentally denuded

27   areas at an estuarine and a semi-exposed site in an upwelling area (NW Spain) were

28   followed for 17 months. Three different cohorts were detected during the sampling

29   period. Differences among the three cohorts in terms of growth, reproduction and

30   survival were detected; these differences may be due to the different time of appearance

31   of the different cohorts or the presence of the previously established individuals when

32   the second and third cohorts were recruited. Although the growth of the cohorts

33   recruiting in autumn was higher than for the later cohorts, the individual growth was

34   represented in all cases by a logistic function, as the fastest rates of increase in length

35   occurred during the first six months of life, and maximum length was attained after the

36   thallus reached one year in age. In the same way, production was maximum for the first

37   cohort, recruiting in autumn, even when it had the lowest survival rate, because of the

38   rapid growth of survivors during spring and summer. For both populations, reproduction

39   was continuous through the year but it was maximal during spring and summer.

40   Protection from waves might have favoured higher production and standing stock

41   biomass values at the estuarine site than at the semi-exposed site, while turnover rates of

42   biomass were higher at the latter. Contrary to these expectations, most of the nutrients

43   available for the studied populations were not related to upwelling. Despite the fast

44   initial growth of new recruits, both populations appeared to be very sensitive to

45   denudation.

46   **Keywords:** macroalga, demography, growth, reproduction, production, upwelling

Introduction

The shifting of environmental variables in the course of ongoing global warming is expected to impact the performance and distribution of numerous species in marine coastal systems (Wahl *et al.*, 2011). Recent studies have predicted a potential northward shift of intertidal canopy-forming macroalgae along temperate North Atlantic rocky shores, especially in the warm-temperate eastern Atlantic region from Portugal to Brittany (Jueterbock *et al.*, 2013). As temperature profoundly influences the survival, recruitment, growth and reproduction of seaweeds (Breeman, 1988), the study of the response of populations living on the edge could be very important in terms of changes in species' distribution.

Fucoids are the most representative species covering intertidal rocky shores along the European Atlantic coasts from Iceland to Portugal. At their southern limit, the NW Iberian Peninsula, these brown seaweeds show a discontinuous distribution, reappearing in isolated patches associated with cold water from spring–summer upwelling (Lüning, 1990). These marginal populations have often been shown to be smaller and more fragmented than central populations. As these populations are considered to live under suboptimal conditions, small variations in their environment could be critical. An increase in seawater temperature, a decrease in the upwelling intensity and other factors like biological interactions or physiological tolerances (Lamela-Silvarrey *et al.*, 2012; NiCastro *et al.*, 2013; Araújo *et al.*, 2014) can affect the performance of the individuals and increase the risk of disappearance of local populations (Jueterbock *et al.*, 2013).

Fucus vesiculosus Linnaeus is one of the most common fucoids and it is usually dominant in the mid intertidal rocky shores on both sides of the North Atlantic Ocean.

70   *F. vesiculosus* is found in a wide range of wave exposures, from sheltered to moderately

71   exposed areas (Bárbara *et al.*, 1995) and tolerates a range of salinities (Kautsky *et al.*,

72   1992). This species has been widely studied but most investigations were restricted to

73   central populations (Keser & Larson, 1984; Carlson, 1991; Chapman, 1995; Lehvo *et*

74   *al.*, 2001; Lamote & Johnson, 2008; Wahl *et al.*, 2011). In marginal areas, previous

75   studies of *Fucus* species were mainly focused on community structure and dynamics

76   (Niell, 1977; Fernández & Niell, 1982; Bárbara *et al.*, 1995; Lamela-Silvarrey *et al.*,

77   2012) or on the morphological plasticity of the species (Seoane-Camba, 1966; Cairrão

78   *et al.*, 2009; Araújo *et al.*, 2011). However, few studies focusing on growth, production

79   or recruitment have been made in these environments (Niell, 1977; Fuentes, 1986;

80   Lamela-Silvarrey *et al.*, 2012; Araújo *et al.*, 2014).

81   Recent studies of genetic variability in *F. vesiculosus* at its southern limit of

82   distribution suggest that populations differ in their phenological responses based on

83   adaptation to changing habitats and stress tolerance (Billard *et al.*, 2010; Zardi *et al.*,

84   2013; Jueterbock *et al.*, 2014). The objective of the present study is to quantify growth

85   rates, survivorship, reproduction and production of *F. vesiculosus* at an estuarine and at

86   a semi-exposed site at Ría de A Coruña (Galicia, NW Spain). These sites are in an

87   upwelling area at the southern distributional limit of of this species.

88   **Material and Methods**

89   *Study sites*

90   The coast of Galicia (NW Spain) is characterized by the presence of rias (tidal inlets)

91   sustaining high levels of biological production due to seasonal upwelling (Arístegui *et*

92   *al.*, 2006). The dominance of *F. vesiculosus* in mid intertidal levels suggests that this

93   species is also one of the main contributors to primary productivity at local scales

94   (Niell, 1977).

95   The Ría de A Coruña is 6 km long and 3 km wide and can be divided in a large bay

96   and a small estuarine zone (Cabanas *et al.*, 1987). The bay has a large oceanic influence

97   and has a mean depth of 25 m. The estuarine zone (Ría do Burgo) has a mean depth of

98   10 m and a sharp salinity gradient due to the discharge of the river Mero, with a mean

99   flow of 204 hm^3 yr^{-1}. The eastern margin of the ria and the estuarine zone are heavily

100   populated (ca. 250,000 inhabitants) while the northern and western margins are

101   characterized by mostly rural landscapes. *F. vesiculosus* is well distributed in the rocky

102   intertidal areas of this ria from semi-exposed to wave protected areas (Bárbara *et al.*,

103   1995).

104   The study was conducted at two sites representative of the range of habitats of *F.*

105   *vesiculosus* in the region. Mera (43º 22'N, 8º 20'W) is a rocky semi-exposed shore near

106   the outer limit of the bay where *F. vesiculosus* is the dominant macroalga from the mid

107   to the lower intertidal, although the population shows a patchy distribution. Individuals

108   in this area typically lack of air bladders and have been described as *F. vesiculosus* var.

109   *evesiculosus* (Bárbara *et al.*, 1995). The site at Ría do Burgo (43º 20'N, 8º 22'W) is

110   located at the sheltered part of the ria where a dense *F. vesiculosus* belt is restricted by

111   the presence of a dense population of *Ascophyllum nodosum* in the upper intertidal zone

112   and by the absence of rocky substrata in the lower zone.

113   The study period lasted 26 months, starting in November 2010 until December 2012.

114   During a 15 month-period (November 2010-January 2012), monthly or bimonthly visits

115   to both sites were made to record the growth, density, biomass and reproduction of *F.*

116 *vesiculosus*, along with some seawater variables. After the first period, bimonthly visits

117 were made just to record the growth of selected individuals.

118   At each visit, salinity ($\pm$ 0.1, Practical Salinity Scale) and temperature ($\pm$ 0.1 °C) of

119 surface water were measured *in situ* with a portable conductivity meter (YSI Model 30).

120 Samples of surface water were also collected for further determination of dissolved

121 nutrients ($NO_3^- + NO_2^-$, NH_4^+ and PO_4^{3-}) in the laboratory following Grashoff *et al*.

122 (1983).

123   Intensity of upwelling in the study area was represented by an upwelling index

124 (Lavín *et al*., 1991) that estimates the Ekman transport of surface water in m^3 s^{-1} by km

125 of coastline computed from geostrophic winds. We used monthly means of the values of

126 the upwelling index data obtained from the Instituto Español de Oceanografía

127 (http://www.indicedeafloramiento.ieo.es) in a grid of 1°•1° centred at 43° N, 9° W.

128 Positive values of this index indicate upwelling of deep waters near the coast while

129 negative values indicate accumulation of shelf surface waters towards the coast

130 (downwelling).

131 *Size distributions, growth and reproduction*

132 At each sampling site, three 50x50 cm experimental quadrats were randomly set up in

133 the *F. vesiculosus* dominant zone. The position of the experimental quadrats relative to

134 the Lowest Astronomic Tide (LAT) was between 1.62 and 2.30 m at Ría do Burgo, and

135 between 1.25 and 1.56 m at Mera. The experimental quadrats were denuded in

136 October 2010. All macroalgae constituting the initial undisturbed population inside the

137 quadrats were removed as close to the ground as possible and the substrate was cleaned

138 with a metal brush to ensure no small individuals or the holdfast of any adult individual

139   could remain attached. The material obtained was transported to the laboratory in plastic

140   bags and used for the description of the initial undisturbed population. Observations of

141   the accompanying flora along the studied period were also recorded. All removed

142   individuals were measured, and fronds from the same holdfast were considered as an

143   individual. The total biomass of *F. vesiculosus* and accompanying flora was determined

144   as wet and dry weight (± 1 g).

145   During a 15 month-period (November 2010 to January 2012) all individuals within

146   each experimental quadrat were measured monthly, excepting in February and

147   December 2011. All individuals inside the quadrats were mapped and measured to the

148   nearest mm from the base of the holdfast to the tip of the longest frond. During summer

149   sampling surveys, when the abundance in some of the experimental areas was high,

150   individuals shorter than 0.5 cm were counted and 90 of these individuals were measured

151   to determine their mean length. All individuals were classified in size classes 5-mm

152   wide, from < 0.5 to > 30.5 cm. Five months after the beginning of the experiment

153   (March 2011), 10 randomly selected individuals within experimental quadrats of each

154   site, and that had been already mapped and measured during the previous period, were

155   labelled. Their growth in length was monitored every month until January 2012, and

156   every 2-3 months until December 2012. Density estimations were made by combining

157   all the results obtained in the three experimental quadrats.

158   At each site, monthly frequency distributions of size classes were calculated from the

159   number of individuals in each size class. Individuals that were first detected in each

160   experimental quadrat were considered as new recruits, and each set of new recruits was

161   monitored as a new cohort. Cohorts were assumed to have normal or log-normal

162   frequency distributions and selection of cohort size ranges was made from the

163   comparison of frequency distributions of consecutive dates.

164   The growth was monitored by monthly changes of the modal length of each cohort

165   fitted to a logistic equation (Niell, 1979):

166    $$L_t = \frac{L_{max}}{1 + e^{a1 + a2\ Age}}$$

167   where L_t is the modal length at time t, L_{max} is the asymptotic length, and a1 and a2 are

168   constants. GraphPad Prism 4 software was used to estimate the fitted curves.

169   To estimate the age of maturity and reproductive periods of *F. vesiculosus* in the

170   area, the presence of reproductive tips in individuals of the different cohorts within the

171   experimental quadrats was also recorded during the first 15 months of the sampling

172   period (November 2010-January 2012).

173   *Demography and production*

174   The fate of individuals in the quadrats was monitored based on the monthly maps. New

175   recruits were considered when they were first detected and any individual that

176   disappeared from the experimental quadrats was considered dead. The survivorship (S)

177   of each cohort was estimated from the date when the maximum abundance (maximum

178   recruitment) was detected. Survivorship was calculated as the fraction of individuals

179   remaining from the cohort maximum recruitment and fitted to an exponential decay

180   function with age:

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

182   where S_0 is the density when the cohort was detected (maximum recruitment) and m is

183   the mortality rate.

184   The dry weight biomass of each individual (w, g) was determined using a length-

185   weight relationship computed from individuals of different lengths (L, cm) and without

186   receptacles sampled at both sites (L = 15.460 w $^{0.407}$, r^2 = 0.938, P < 0.001, n = 60).

187   Cohort biomass was computed as the sum of the biomass of the individuals recorded in

188   all experimental quadrats and reported as g m^{-2}.

189   The production of each cohort was calculated by the Allen-curve method (Niell,

190   1979; Cousens, 1984). This is a graphical method that relates the number of individuals

191   of a cohort (N) with their mean individual weight (w) at different times. After the

192   maximum of abundance is reached (maximum recruitment), only mortality (a decline in

193   density) and individual growth (an increase in mass) occur through the rest of the life

194   cycle of each cohort. The standing stock biomass (B) of each cohort at a given time is

195   defined by N x w under the curve, while the production (P) of the cohort can be

196   computed as the integral under the curve. Standing stock, production and production to

197   biomass ratio (P:B) were computed for each cohort and for the total population for

198   different time intervals.

199   **Results**

200   *Environmental variability*

201   The upwelling dynamics in the study area were characterized by a period of positive

202   values between March and August and negative values in autumn and winter months,

203   except for December 2010 when the mean value was also positive (Fig. 1). Contrary to

204   expectations, the average upwelling conditions had no effect on the properties of surface

205 seawater when grouped by upwelling and downwelling periods (Table 1). Besides, there

206 were no significant differences between locations for any of the measured variables, and

207 there were only significant differences in temperature and $NO_3^- + NO_2^-$ between

208 upwelling and downwelling periods (two way ANOVA for the effect of location and

209 period, as fixed factors, and their interaction, $P > 0.05$ for location and for the

210 interaction for all variables in Table 1). However, these differences are the opposite of

211 those expected from the effect of upwelling, as average values of both temperature and

212 $NO_3^- + NO_2^-$ during upwelling conditions were lower than during downwelling

213 conditions, suggesting a major role of continental water inputs at both locations.

214 *Description of the macroalgal assemblages*

215 The mean (±se) biomass of the initial undisturbed population was higher at Mera

216 (643±514 g m^{-2}) than at Ría do Burgo site (415±97 g m^{-2}). Accordingly, size class

217 distributions of the initial population showed a higher number of individuals at Mera,

218 with a predominance of individuals longer than 30.5 cm (top left, Figs. 2 and 3). The

219 mean (±se) biomass of all accompanying flora summed up to 54±47 and 45±21 g m^{-2} at

220 Ría do Burgo and Mera respectively. *Ulva* sp. was quite abundant at both sites at the

221 denudation time (October 2010). In Ría do Burgo, some individuals of *A. nodosum* were

222 also present at the experimental quadrats, contributing to ca. 10% of total biomass.

223 During the sampling period, the accompanying flora reached maximum abundance in

224 June 2011. Mera showed the highest species diversity, with *Corallina elongata*,

225 *Osmundea pinatifida*, *Chondracanthus acicularis*, *Gelidium pusillum*, *Cladostephus*

226 *spongiosus*, *Leathesia difformis*, and some species in the order Ceramiales and *Ulva*

227 species, especially *U. compressa* that were abundant from May until July. In contrast,

228   only *G. pusillum*, *Caulacanthus ustulatus* and *Chaetomorpha aerea* were recorded at

229   Ría do Burgo.

230   *Size distributions*

231   After the initial denudation of the experimental quadrats, three cohorts were identified

232   during the sampling period at each site (Figs 2 and 3). However, the progress of the size

233   class distributions of these cohorts was different at both sites. Ría do Burgo was

234   characterized by its fast recovery after scrapping, while recovery at Mera was slower.

235   The cohorts appeared in November 2010, and in March and June 2011 in Ría do Burgo,

236   although new recruits had progressively joined up the population in previous months

237   (Fig. 2). In Mera, the cohorts appeared in November 2010 and January and July 2011

238   (Fig. 3). Total and cohort abundance were always higher at Ría do Burgo than at Mera.

239   The lowest recruitment was observed for the first cohort (November 2010) at

240   Ría do Burgo and for the second cohort (January 2011) at Mera, while the highest

241   recruitment was recorded for the third cohort in June and July 2011 at both sites

242   respectively.

243   In January 2012 (15 months after the denudation), the size distribution of

244   Ría do Burgo was the most similar one to the initial undisturbed population (Fig. 2). On

245   the contrary by the same time, the size distribution of the population in Mera was

246   skewed towards individuals < 5 cm, very different from the initial undisturbed

247   population (Fig. 3).

248   *Growth*

249   Individuals from the first cohort showed the fastest growth and maximum length, and

250   individuals from the third cohort the lowest growth (Fig. 4), but in Mera, the growth

251 was slower than at Ría do Burgo. At both sites, however, there was a relatively large

252 variation in individual growth rates during the first year of life.

253 *Reproductive structures*

254 Some of the individuals, but particularly those of cohort 1 originated in November,

255 showed reproductive tips after 6 months of life (Fig. 5). At that time, individuals with

256 receptacles ranged from 8.5 to 25.5 cm long in Ría do Burgo, and from 9.5 to 15 cm

257 long in Mera. The smallest individuals with receptacles were 7 cm (in September 2011,

258 Ría do Burgo) and 6 cm long (in June 2011, Mera).

259 The highest proportion of reproductive individuals from the first cohort was observed

260 in January 2012 and October 2011 at Ría do Burgo and Mera respectively (Fig. 5).

261 However, only a few individuals of the second cohort showed receptacles at both sites,

262 especially at Ría do Burgo, where they were absent until September 2011. In Mera, the

263 highest percentage of reproductive individuals of the second cohort was observed in

264 July 2011. No reproductive individuals from the third cohort were observed at Ría do

265 Burgo while in Mera they did not appear until January 2012.

266 *Survivorship and production*

267 The population from Ría do Burgo displayed a pattern of increasing mortality rates and

268 recruitment from the first (highest values) to the third cohort (lowest values), while the

269 population from Mera showed similar mortality values for all cohorts and only

270 relatively high recruitment for the third cohort (Fig. 6). In all cases, recruitment was

271 higher at Ría do Burgo.

272 Despite the low recruitment, the first cohort of both populations was always the most

273 productive because of their relatively high survival rates and their faster growth, as

274   shown by the Allen-curves (Fig. 7). The net production values estimated from the areas

275   under the curves were particularly high at Ría do Burgo, where accumulated production

276   of cohort 1 exceeded 16 times that of cohort 3 and ca. 3 times the production of cohort 2

277   for the first 3 years of life (Table 2). At Ría do Burgo, the highest values of biomass and

278   production were reached by all cohorts during the first year of life of the population.

279   While in Mera, only the first cohort showed the same pattern, and cohorts 2 and 3

280   showed the highest biomass and production values during their second year of life. For

281   both populations, most cohorts showed a turnover rate > 1 during the first two years of

282   life, except cohort 1 at Ría do Burgo that during the second year only produced an

283   equivalent amount to the standing stock (P:B = 1). Production would be minimal during

284   the third year for all cohorts, even if some standing stock biomass is still present

285   (Table 2).

Discussion

287   The genotypic differentiation observed in Fucoid species at their southern marginal

288   limits of distribution suggest population´s different responses in their phenology due to

289   changes in environmental variables (Billard *et al.*, 2010; Zardi *et al.*, 2013; Jueterbock

290   *et al.*, 2014). In this study, populations of *F. vesiculosus* showed lower growth,

291   recruitment and mortality rates compared to central populations. The low production

292   rates measured imply that populations studied are very sensitive to habitat disturbances.

293   *Growth rates and recruitment*

294   Previous studies have highlighted the multiple factors influencing *Fucus* growth, i.e.

295   temperature, nutrient concentration or wave exposure (Knight & Parke, 1950;

296   Mathieson *et al*., 1976; Chapman, 1995; Bonsdorff & Nelson, 1996), resulting in a

297 variability that makes comparisons between sites and studies difficult. Even at the same

298 site, there are differences among individual´s growth rates, as it was observed in this

299 study (Fig. 4). Variability among sampling sites has been attributed to external factors

300 as temperature, salinity, or nutrient concentration (Steen & Rueness, 2004) but also to

301 intrinsic factors of the macroalga (Fuentes, 1986; Ang, 1991*a*, *b*). While external factors

302 have been widely studied little is known about intrinsic factors affecting the growth of

303 *F. vesiculosus*.

304 The growth in length of the studied populations followed a logistic pattern, as it was

305 described for other Fucales (e.g. Niell, 1979) but never before for this species. The

306 growth rate reached a maximum when individuals were between 6 months and 1 year

307 old, but stabilized thereafter. The length of old individuals can even decrease due to

308 breakages after gamete release or apical damage and it has been observed that

309 individuals of *F. vesiculosus* can easily regenerate new fronds from the holdfast after

310 destructive events (Åberg, 1989; Malm & Kautsky, 2004). These results agree with the

311 reports of significant differences in growth rates between size classes of *F. vesiculosus*

312 (Fuentes, 1986) and other *Fucus* species (Ang, 1991*b*), with maximum rates in the

313 smaller sizes.

314 However, the direct comparison of growth rates from different studies is difficult

315 because only maximum or average increases in length per unit of time, but without

316 reference to the age or initial length of the individuals are reported (Knight & Parke,

317 1950; Fuentes, 1986; Bonsdorff & Nelson, 1996). From our results, the growth in length

318 expressed as a function of age is markedly nonlinear, implying that growth rates vary

319 continuously from quasi exponential increases during the first months of colonization to

320 almost no increase after the first year. Still, some comparisons can be made by

321   assuming that maximum growth rates reported in other studies are similar to the

322   exponential growth increases averaged over the first year of life in this study. We found

323   increases of up to 2 cm mo^{-1} that are close to those reported in other locations in Galicia

324   (Fuentes, 1986) while values of up to 3 cm month^{-1} were reported for French (Lemoine,

325   1913) and British Isles populations (Knight & Parke, 1950).

326   Differences among cohorts were also clear in terms of growth rates at both sites.

327   Maximum growth rates were observed for the first cohort (1.8 and 1.3 cm mo^{-1} at Ría

328   do Burgo and Mera respectively) while individuals from the third cohort were the ones

329   with the lowest growth rates (0.6 cm mo^{-1} at both sites, Fig. 4). Based on previous

330   studies, several factors might influence these differences. The time when the different

331   cohorts initially grew vary. Individuals from the first cohort started their exponential

332   growth at spring time, one of the periods of maximum growth of this species at this

333   latitude (Fuentes, 1986; Lamela-Silvarrey *et al.*, 2012). On the contrary, individuals

334   from the third cohort started their exponential growth phase in autumn, when conditions

335   for growth are suboptimal. Besides, the presence of a denser and longer canopy of

336   individuals from the previously settled cohorts would have reduced the availability of

337   nutrients and light for smaller individuals of the second and third cohort due to

338   intraspecific competition. This is supported by the absence of any new cohort after the

339   first 9 months of the study, when the three cohorts were observed. In contrast to what it

340   was observed with germlings, the presence of a canopy from the previously settled

341   cohorts seemed to be a good environment soon after settlement, as maximum

342   recruitment was observed in the third cohort at both sites (Figs. 2 and 3). In this case,

343   the presence of longer individuals might be beneficial for zygote implantation, as this

344   coverage protects the individuals from desiccation, grazers or sedimentation, the major

345 factors that influence survivorship during this first stage (Vadas *et al.*, 1992). The

346 absence of this initial coverage might also be related with the high mortality observed in

347 the cohort 1 at Ría do Burgo (Fig. 6).

348   Differences between sites in terms of recruitment and growth rates were also found

349 for all cohorts in our study, although results may be taken with caution due to all factors

350 influencing both sites, apart from the ones considered. As seawater conditions were not

351 very different among sites (Table 1), other reasons as the differential wave exposure or

352 the spatial distribution of the populations may be partly responsible of the differences

353 between sites. The population in the scraped area at the semi-exposed conditions of

354 Mera was not protected by other macroalgal species due to the patchy distribution of

355 this species in this location; and individuals from the first cohort were barely 5 cm long

356 when the second appeared (Fig. 3). In contrast, the protected conditions at Ría do Burgo

357 would facilitate the implantation and growth of new recruits as the experimental

358 quadrats were surrounded by a dense population of *Fucus* but also by other large

359 macroalgae (e.g. *A. nodosum*). This hypothesis might be supported by the differences

360 found in growth rates related to the degree of wave exposure in other studies, with the

361 result of maximum growth rates and sizes in estuaries, and minimum rates at open

362 ocean locations (Knight & Parke, 1950; Kalvas & Kautsky, 1993; Bonsdorff & Nelson,

363 1996). However, this is just a hypothesis as other authors have observed that individuals

364 at oceanic influenced sites were longer than individuals at estuarine locations sampled

365 in the same ria although no mention is made to the growth rates or exposure conditions

366 in these studies (Pazó & Romarís, 1979).

367 *Life span and reproduction*

368   A large number of individuals of *F. vesiculosus* were able to survive through the 15

369   months of the present study and healthy populations remained in the experimental

370   quadrats (Figs. 2 and 3). These results agree with the life span of 2-3 yr reported in

371   many studies for most *Fucus* species, including *F. distichus* (Sideman & Mathieson,

372   1983), *F. vesiculosus* (Knight & Parke, 1950), *F. spiralis* (Niemeck & Mathieson, 1976)

373   and *F. serratus* (Knight & Parke, 1950).

374   The studied adult populations might have a large reproductive potential (i.e. zygote

375   production, Ang, 1991*a*) as recruitment of the denudated surfaces occurred only one

376   month after removal of adult plants. The identification of different cohorts through the

377   year suggests continuous release of gametes, or at least that this release lasts for a long

378   period of time, as observed in other *Fucus* populations (Knight & Parke, 1950; Keser &

379   Larson, 1984).

380   The reproduction of individuals growing within the experimental quadrats also

381   appeared as a continuous process, as individuals with receptacles were always observed

382   and its proportion in the populations increased through the period of observation (Ría do

383   Burgo) or at least until the first autumn (Mera). In contrast, marked bimodal patterns,

384   i.e. two distinct reproductive peaks, along the year were described for *F. vesiculosus*

385   from other locations (Knight & Parke, 1950; Niemeck & Mathieson, 1976; Carlson,

386   1991; Berger *et al.*, 2001). Indeed, a population studied in the years 1983-1984, located

387   only 10 km from Mera in the nearby Ría de Ares, was reported to produce receptacles

388   between autumn and early spring and to release most gametes in early summer

389   (Fuentes, 1986). Nevertheless, the presence of fertile individuals, as the ones with

390   receptacles recorded within the quadrats, would not necessarily imply that those

391   receptacles are mature (Berger *et al.*, 2001). Moreover, receptacles could appear in the

392   same individual but in different tips, giving the impression of continuous reproduction

393   at the level of the whole plant (Ang, 1992).

394   For most *Fucus* species, receptacles were first observed in individuals from 4.5 to up

395   to 20 cm long or from 7 months to up to 2 years old (Knight & Parke, 1950; Niemeck &

396   Mathieson, 1976; Ang 1991*b*). Such a large variability might be due to differences

397   among growth rates in different sites, but cannot be directly related to the age of the

398   individuals. Fuentes (1986) observed than the mean length of fertile individuals in the

399   nearby Ría de Ares was 11 cm, although he also found receptacles in individuals 7 cm

400   long, as in the present study.

401   The results provided by our study could suggest that either local factors (like nutrient

402   availability and wave exposure) or decadal fluctuations in the regional oceanography

403   influenced the length of the reproductive period of this species. Even when the annual

404   range of water temperature values reported in both Fuentes (1986) and our study are

405   coincident (13-21 ^{o}C) the intensity of the Galician upwelling has decreased significantly

406   since early 1980s (Bode *et al.*, 2011). A decrease in upwelling implies a decrease in the

407   supply of new nutrients to the surface, but the concentrations of most nutrients near

408   A Coruña have not shown any significant trend in the last two decades (Bode *et al.*,

409   2011), suggesting a compensation of the loss of upwelling nutrients with an enhanced

410   input of terrestrial (mostly anthropogenic) nutrients. Besides, the variables measured in

411   the surface water do not support a major role of upwelling dynamics in the present

412   study. Runoff is maximum during autumn and winter, as indicated by the low salinity

413   values in Table 1, and may introduce significant amounts of nutrients from terrestrial

414   sources. Therefore the long period of reproduction found in this study cannot be

415   attributed to a general increase in nutrients, at least at a regional scale.

416   Ladah *et al*. (2003) reported that protection from waves neither explains reproductive

417   success nor influence in fertilization. Therefore the low impact of waves is not the

418   reason for the persistence of receptacles in the studied population through the year in

419   contrast with the findings of Fuentes (1986) in a more exposed population.

420   *Production*

421   As expected from growth and recruitment results, the rank in production of the cohorts

422   was led by the first cohort at both studied sites while the third cohort was generally the

423   less productive for all time periods considered (Table 2). Early implantation in autumn

424   allowed the increase of the standing stock of the first cohort with rapid individual

425   growth in the spring despite the low recruitment. In contrast, a relatively high

426   recruitment in summer did not warrant high production because of the reduced growth

427   rates and high mortality observed during winter for the second and third cohorts.

428   Estimated total production reached its maximum when the cohort was from 0.5 to 2

429   years old, depending on the site considered (Table 2). At this age, the increment in

430   biomass depends only on the growth of survivors, and the presence of other *Fucus*

431   individuals results in a competition due to the limitation for light and nutrients.

432   In all cases, but particularly for the first and second cohort, the values of production

433   estimated for Ría do Burgo largely exceeded those for Mera, supporting the hypothesis

434   that growth and survivorship are higher in wave protected, estuarine sites than at

435   exposed, oceanic sites (Knight & Parke, 1950). However, another study in Ría de

436   Arousa (Galicia) reported lower production for estuarine sites than for oceanic sites

437   (Fuentes, 1986), suggesting that additional factors other than exposure and nutrients are

438   also influencing local production.

All cohorts of the population studied at Ría do Burgo showed a lower turnover rate than those at Mera (Table 2). A larger turnover of biomass at exposed sites than at estuarine sites was also reported for other populations of *F. vesiculosus* in Galicia (Fuentes, 1986) and was related to the enhanced energy flow in the former, favouring the access to nutrients and light in turbulent environments. For both sites, the production during the first year was almost equivalent to the standing stock biomass (P:B $\approx$ 1) indicating low renovation rates.

Mean annual production of the three cohorts in our study was much lower than that reported for *Fucus* species in other nearby sites but some decades ago (Table 3). The same reduction pattern in the production of fucoid species (including *F. vesiculosus*) was observed in the Cantabrian coast over the last 30 years (Lamela-Silvarrey *et al*., 2012). Although no direct causal mechanisms can be inferred to this fact, the general trend of increasing temperature due to climate change could be responsible (Lamela-Silvarrey *et al*., 2012). Still, comparisons of data from this study might be done with caution as methodological variations may in part explain this discrepancy. Previous production studies only consider average changes in biomass between consecutive sampling periods (generally 1 month apart) and our estimation is based on conservative modal values for growth and demographic parameters. Cousens (1984) has shown that differences in the assumptions when computing production using Allen curves in macroalga may produce estimates varying by a factor of 2, and even larger differences may result when considering only part of the annual cycle in the computations (Niell, 1977). Besides, in the present study the production was computed for a newly developed population after denudation, while in other studies the production is estimated for mature populations.

463   The low production rates estimated imply that the studied populations will recover

464   slowly after denudation even when there were old plants remaining in the vicinity,

465   particularly at the wave exposed site where the distribution of *F. vesiculosus* was

466   patchy. Therefore these populations are sensitive to mechanical damage causing a loss

467   in biomass and production not only in the dominant macroalgal cover but also in the

468   accompanying flora and fauna.

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Table 1. Mean and standard error (se) values of temperature (t, $^{\circ}$C), salinity (S), total nitrate ($NO_3^- + NO_2^-$, μM), ammonium (NH_4^+, μM), and phosphate (PO_4^{3-}, μM) measured at each site and grouped for periods of upwelling (n = 7) and downwelling (n = 6) following the mean values in Fig. 1. P: significance of differences between periods (two way ANOVA, *: P < 0.05).

| Variable | period | Ría do Burgo | | Mera | | |
		mean	se	mean	se	P
t	upwelling	15.0	1.3	17.3	1.1	*
	downwelling	14.3	1.0	18.2	0.8	
S	upwelling	32.7	0.5	34.1	0.8	n.s.
	downwelling	28.0	3.9	33.7	1.5	
$NO_3^-+NO_2^-$	upwelling	18.24	5.63	7.74	2.43	*
	downwelling	38.98	13.08	14.85	2.74	
NH_4^+	upwelling	11.52	3.16	8.90	2.75	n.s.
	downwelling	21.22	4.70	19.47	3.02	
PO_4^{3-}	upwelling	1.74	0.27	1.92	0.26	n.s.
	downwelling	2.18	0.62	2.16	0.42	

n.s., not significant

Table 2. Standing stock biomass (B, g dry weight m^{-2}), production (P, g dry weight m^{-2} period^{-1}), and P:B ratio (period^{-1}) computed for the three cohorts observed at each site for different age periods (years).

	Ría do Burgo								
	Cohort 1			Cohort 2			Cohort 3		
Age	B	P	P:B	B	P	P:B	B	P	P:B
(yr)	(g m^{-2})	(g m^{-2})		(g m^{-2})	(g m^{-2})		(g m^{-2})	(g m^{-2})	
0.0-0.5	37.64	39.93	1.06	8.49	10.06	1.19	4.05	5.59	1.38
0.5-1.0	211.27	204.73	0.97	52.84	62.82	1.19	8.12	11.81	1.45
1.0-2.0	179.87	76.28	0.42	32.63	46.64	1.43	1.30	2.29	1.76
2.0-3.0	109.46	0.54	0.01	9.07	0.49	0.05	0.15	0.01	0.03
0.0-3.0	-----	321.49	-----	-----	120.01	-----	-----	19.69	-----
	Mera								
	Cohort 1			Cohort 2			Cohort 3		
Age	B	P	P:B	B	P	P:B	B	P	P:B
0.0-0.5	1.57	1.88	1.19	0.52	0.59	1.14	0.32	0.40	1.26
0.5-1.0	8.36	10.56	1.26	4.77	5.35	1.12	2.17	2.56	1.18
1.0-2.0	3.19	4.21	1.32	4.99	6.46	1.29	4.63	8.65	1.87
2.0-3.0	0.72	0.02	0.02	1.89	0.12	0.06	1.42	0.77	0.54
0.0-3.0	-----	16.66	-----	-----	12.62	-----	-----	12.37	-----

Table 3. Production (g dry weight m^{-2} yr^{-1}) of *Fucus spiralis* and *F. vesiculosus* in the literature and in this study.

Species	Production	Reference
F. spiralis	922.8	Niell, 1977
F. vesiculosus	979.9 - 1828.5	Fuentes, 1986
	1431.8 - 2255.01	Lamela-Silvarrey *et al*., 2012
	41.65	Mera, this study
	461.79	Ría do Burgo, this study

Figure legends

Fig. 1. Monthly means (± se) of the upwelling index (m^3 s^{-1} km^{-1}) computed in a grid of 1°x 1° centred at 43° N, 9° W from November 2010 to January 2012. Does a negative value mean downwelling?
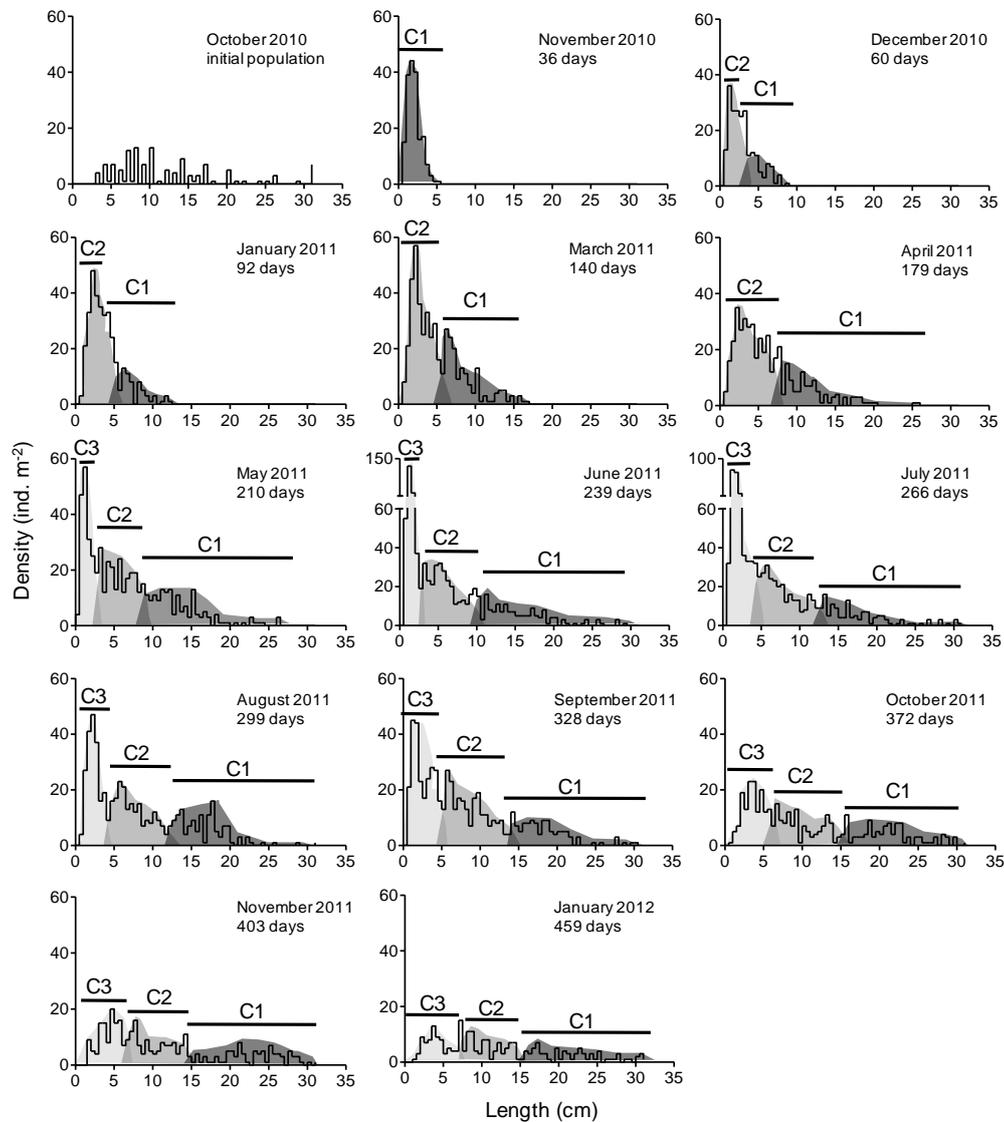
Figure 2. Temporal variation of the size-class frequency distributions of *F. vesiculosus* at Ría do Burgo. Three cohorts (C1, C2 and C3) are identified. The number of days since the denudation date (October 2010) is specified on each histogram. The upper left histogram shows the size distribution of the scraped individuals in the experimental quadrats in October 2010.

Figure 3. Temporal variation of the size-class frequency distributions of *F. vesiculosus* at Mera. Three cohorts (C1, C2 and C3) are identified. The number of days since the denudation date (October 2010) is specified on each histogram. The upper left histogram shows the size distribution of the scraped individuals in the experimental quadrats in October 2010.

Figure 4. Variability of individual growth of selected *F. vesiculosus* specimens at Ría do Burgo (top graph) compared with the modal growth curves of cohort 1 (black line, $L=22.6/(1+e^{(2.8-4.7\ Age)})$), cohort 2 (grey line, $L=15.1/(1+e^{(3.0-3.9\ Age)})$) and cohort 3 (dashed line, $L=7.85/(1+e^{(2.5-4.3\ Age)})$) and at Mera, compared with the modal growth curves of cohort 1 (black line, $L=15.6/(1+e^{(3.1-4.5\ Age)})$), cohort 2 (grey line, $L=14.3/(1+e^{(3.2-3.8\ Age)})$) and cohort 3 (dashed line, $L=11.7/(1+e^{(3.3-2.8\ Age)})$). For each site, sets of points of the same symbol represent the observed growth of one individual (n= 10 individuals at each site).

Figure 5. Percentage of individuals with receptacles of each cohort at each sampling site from November 2010 to January 2012. No fertile plants were found for cohort 3 at Ría do Burgo.

Figure 6. Survivorship curves of the three different cohorts at the two sampling sites. The corresponding exponential equations ($r^2 > 0.9$) are shown.

Figure 7. Allen curves computed for each cohort at the sampling sites. Density of the individuals at each time was calculated using the survivorship equation in Fig. 6 and the individual weight at age (g) obtained from growth equations in Fig. 4 and the length-weight relationship. The age (years) corresponding to each weight was represented in a supplementary X-axis. Notice the different density scales for each site and the different weight scales for each cohort.

Figure 1. Monthly means (± se) of the upwelling index (m^3 s^{-1} km^{-1}) computed in a grid of 1°•1° centred at 43° N, 9° W from November 2010 to January 2012.
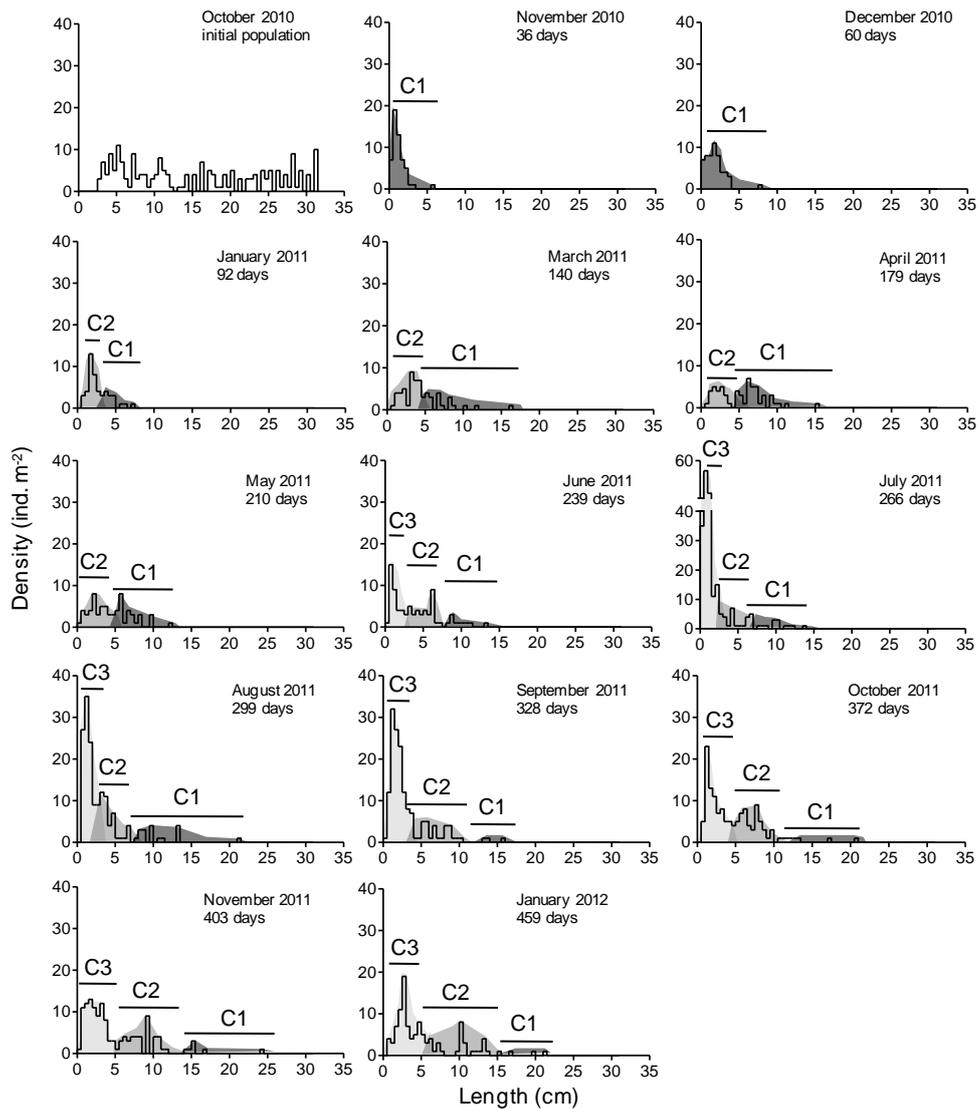
Figure 2. Temporal variation of the size-class frequency distributions of *F. vesiculosus* population at Ría do Burgo. Three cohorts (C1, C2 and C3) are identified. The number of days since the denudation date (October 2010) is specified on each histogram. The upper left histogram shows the size distribution of the scrapped individuals in the experimental quadrats in October 2010.
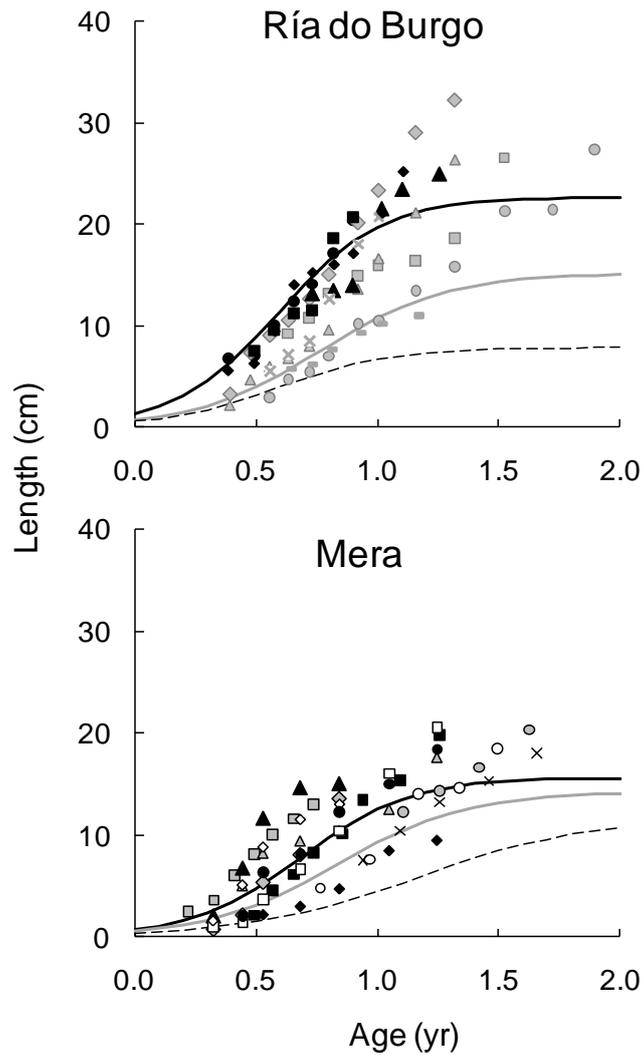
Figure 3. Temporal variation of the size-class frequency distributions of *F. vesiculosus* population at Mera. Three cohorts (C1, C2 and C3) are identified. The number of days since the denudation date (October 2010) is specified on each histogram. The upper left histogram shows the size distribution of the scrapped individuals in the experimental quadrats in October 2010.

Figure 4. Variability of individual growth of selected *F. vesiculosus* specimens at Ría do

Burgo (top graph) compared with the modal growth curves of cohort 1 (black line,

L=22.6/(1+e$^{(2.8-4.7\ Age)}$)), cohort 2 (grey line, L=15.1/(1+e$^{(3.0-3.9\ Age)}$)) and cohort 3

(dashed line, L=7.85/(1+e$^{(2.5-4.3\ Age)}$)) and at Mera, compared with the modal growth

curves of cohort 1 (black line, L=15.6/(1+e$^{(3.1-4.5\ Age)}$), cohort 2 (grey line,

L=14.3/(1+e$^{(3.2-3.8\ Age)}$) and cohort 3 (dashed line, L=11.7/(1+e$^{(3.3-2.8\ Age)}$). For each site,

sets of points of the same symbol represent the observed growth of one individual (n=

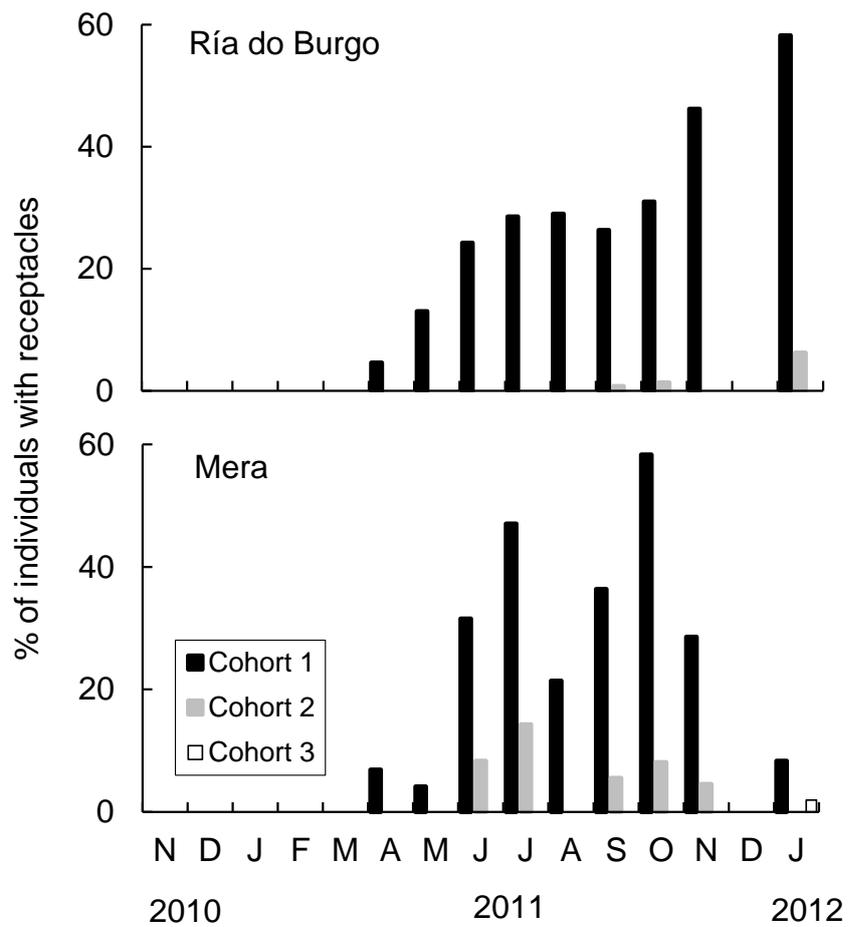10 individuals at each site).

Figure 5. Percentage of individuals with receptacles of each cohort at each sampling site from November 2010 to January 2012. No fertile plants were found for cohort 3 at Ría do Burgo.
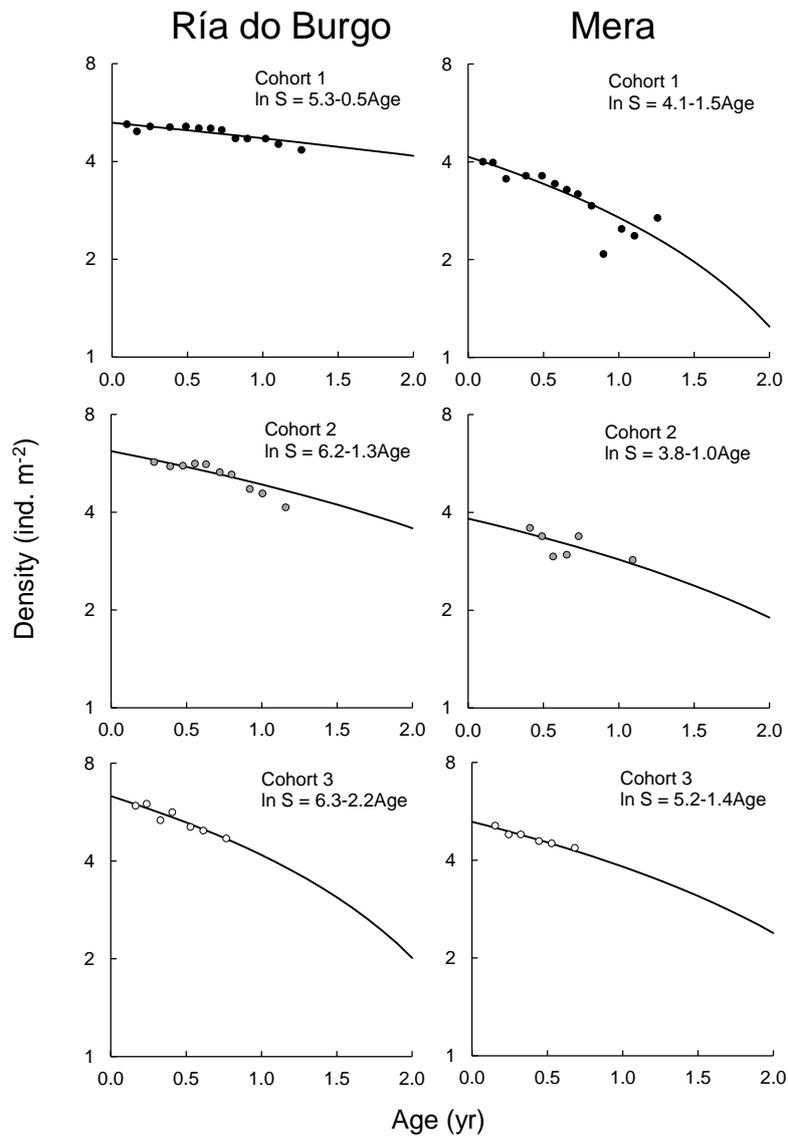
Figure 6. Survivorship curves of the three different cohorts at the two sampling sites.

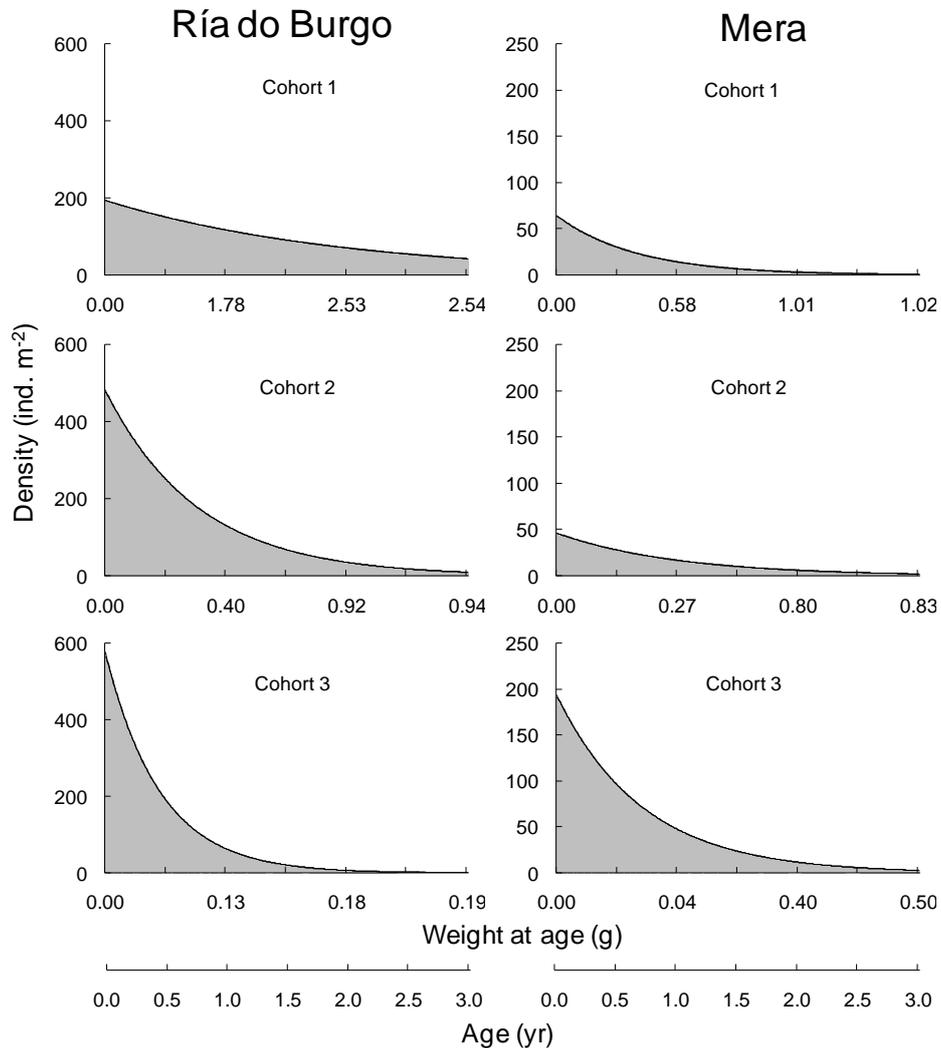The corresponding exponential equations ($r^2 > 0.9$) are shown.

Figure 7. Allen-curves computed for each cohort at the sampling sites. Density of the individuals at each time was calculated using the survivorship equation in Fig. 6 and the individual weight at age (g) obtained from growth equations in Fig. 4 and the length-weight relationship. The age (years) corresponding to each weight was represented in a supplementary X-axis. Notice the different density scales for each site and the different weight scales for each cohort.