2016-11-05

Factors limiting the establishment of canopy-forming algae on artificial structures

Cacabelos, E

<http://hdl.handle.net/10026.1/9610>

10.1016/j.ecss.2016.08.036

ESTUARINE COASTAL AND SHELF SCIENCE

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Disclaimer:

This is a pre-publication version. Readers are advised to refer to the final published version.

Year 2017, Estuarine and Coastal Shelf Science 181, 277-283

Factors limiting the establishment of canopy-forming algae on artificial structures

Eva Cacabelos^{a*}, Gustavo M. Martins^{a,b}, Richard Thompson^c, Afonso C. L. Prestes^a,

José Manuel N. Azevedo^a, Ana I. Neto^a

^a cE3c - Centre for Ecology, Evolution and Environmental Changes / Azorean Biodiversity Group, and Universidade dos Açores, Departamento de Biologia, 9501-801 Ponta Delgada, São Miguel, Azores, Portugal.

^b CIIMAR-Centro Interdisciplinar de Investigação Marinha e Ambiental, Rua dos Bragas 289, Porto, Portugal

^c Marine Biology and Ecology Research Centre, Plymouth University, Plymouth PL4 8AA, Devon, UK

* Corresponding author: e-mail: evacacabelos@yahoo.es

Abstract

Macroalgal canopies are important ecosystem engineers, contributing to coastal productivity and supporting a rich assemblage of associated flora and fauna. Yet, they are often absent from infrastructures such as coastal defences and there has been a worldwide decline in their distribution in urbanised coastal areas. The macroalga *Fucus spiralis* is the only high-shore canopy forming species present in the Azores. It is widely distributed in the archipelago but is never found on coastal infrastructures. Here we

evaluate factors that may potentially limit its establishment on artificial structures. A number of observational and manipulative experiments were used to test the hypotheses that: (i) limited-dispersal ability limits the colonisation of new plants onto artificial structures, (ii) vertical substratum slope negatively influences the survivorship of recruits, and (iii) vertical substratum slope also negatively influences the survivorship and fitness of adults. Results showed that the limited dispersal from adult plants may be a more important factor than slope in limiting the species ability to colonise coastal infrastructures, since the vertical substratum slope does not affect its fitness or survivorship.

Keywords: coastal defences; intertidal; rocky shores; macroalgae; benthic communities; coastal urbanization

1. Introduction

Canopy-forming algae are key species on intertidal rocky shores (Jonsson et al., 2006) as they can provide shelter from environmental stressors (e.g. desiccation or ultraviolet radiation) for a diverse range of flora and fauna. By doing this, they play an important role in regulating community structure, nutrient cycling and primary production and therefore their conservation should be considered a priority (Bertocci et al., 2011; Perkol-Finkel and Airoldi, 2010; Perkol-Finkel et al., 2012). Despite their importance, marine canopy-forming algae have declined over the past decades (Perkol-Finkel and Airoldi, 2010; Strain et al., 2015), with major implications for the biodiversity and rocky reefs ecosystem goods and services (Airoldi and Beck, 2007; Smale et al., 2013; Voerman et al., 2013). There is thus a clear need to understand the drivers underlying their loss (Perkol-Finkel and Airoldi, 2010), the mechanisms that confer them stress tolerance (but see Martínez et al., 2012), and how the relative balance of physical (e.g. wave action) and biological factors (e.g.

grazing) control their establishment and persistence (Davison and Pearson, 1996; Jonsson et al., 2006). Evidence worldwide has demonstrated that stressors such as climate change, eutrophication or urbanisation strongly affect marine canopies (e.g. Mangialajo et al., 2008). However, both direct and indirect human-induced modifications on physical habitat, acting as drivers for the decline of canopy-forming algae, have been usually overlooked (Perkol-Finkel and Airoidi, 2010).

Many coasts are becoming increasingly urbanised worldwide. This coastal urbanisation can result in extensive modification of natural shores, altering habitat heterogeneity, complexity, slope and available area for benthic biota. This affects natural processes e.g. recruitment, colonization, survival, population densities and connectivity, fecundity or/and species interaction (Bulleri et al., 2004; Bulleri, 2005; Chapman and Bulleri, 2003; Moreira et al., 2006; Perkol-Finkel and Airoidi, 2010). Several studies have investigated the patterns of distribution of benthic communities supported by artificial coastal defence structures and showed they are generally poor surrogates for the habitats they replace (e.g. Moschella et al., 2005). Although a variety of factors differ between artificial structures and the adjacent rocky shores, substratum slope is often fundamentally different. This modified slope has been shown to be a major determinant influencing the structure of intertidal assemblages (Bulleri and Chapman, 2004; Glasby and Connell, 2001). The differences in assemblages generated and maintained by a combination of differential recruitment and post-recruitment processes (Vaselli et al., 2008), result in considerable changes to coastal ecology. Canopy-forming algae are strongly affected by urbanisation (Airoidi and Beck, 2007; Benedetti-Cecchi et al., 2001), and little is known about the consequences of changes in the habitat related characteristics of the shore for their functional properties, like productivity and resilience (i.e. the ability of organisms to recover after events of disturbance, Grimm and Wissel, 1997). Changes have already been

showed in demographic parameters such as growth or mortality of populations submitted to disturbance (Araújo et al., 2011), or in morphological parameters such as thalli thickness against desiccation stress or thalli size against wave exposure (Blanchette, 1997; Jorve, 2008). The steep slope of artificial structures could alter the physical stress to which plants are submitted, e.g. different desiccation regimes, and therefore change life-history traits, namely differentiation of populations via phenotypic plasticity (Blanchette, 1997). Moreover, although dispersal via drifting algal rafts has been cited as a mechanism to increase its gene flow (Coleman and Brawley, 2005), gamete dispersal is limited in fucoids (Coyer et al., 2011). This can limit its ability to colonise the “newer” habitats.

Understanding the processes that maintain differences in canopy-forming algae recruitment, growth and survival among different substrata, and identifying the factors that promote the loss of canopy-forming species, is thus of great importance in order to evaluate the consequences of coastal urbanisation worldwide and effectively manage and preserve marine coastlines (Coleman et al., 2008; Perkol-Finkel et al., 2012). But although potential explanations have been suggested, experimental tests of causal effects are not common and have usually focused on artificial substrata (Glasby, 2000).

In the Northeast Atlantic midshore there is generally a dynamic balance between fucoids, barnacles and limpets on the shore (Hawkins and Hartnoll, 1983; Hawkins et al., 1992; Thompson et al., 1996), although fucoids become less predominant at lower latitudes (Ballantine, 1961). The upper eulittoral in the Azores oceanic archipelago (located between 37-40°N and 25-31°W) is often dominated by two perennial macroalgae species, the Ochrophyta *Fucus spiralis* Linnaeus and the Rodophyta *Gelidium microdon* Kützinger, 1849. The desiccation-resistant *F. spiralis* is the unique species of the genus found in Azores, where it forms scattered populations. It appears on exposed shores, in areas that are partially sheltered and not directly exposed to the full force of the incoming waves

(Neto, 2000), and although it can appear on a variety of slopes, their abundance generally increase with decreasing slope (pers. observ). In Azorean coasts, formed by steep cliffs and volcanic rubbles, most artificial structures are used to protect nearby towns from high sea levels during winter storms. Coastal defences are mostly built by deploying piles of locally quarried rock or concrete boulders upon natural rocky shores, resulting in artificial structures with steeper inclination than natural shores. Although epibenthic assemblage composition differ (Cacabelos et al., in press), qualitative similarities were found on both natural habitats and coastal defences. However, *F. spiralis* is conspicuously absent from these coastal defences, even though it can occur in the adjacent rocky intertidal.

Here we investigate factors that could potentially limit the ability of *F. spiralis* from establishing onto artificial structures. Specifically, we investigate the effects of substratum slope (vertical vs horizontal) on the growth and the level of desiccation of adult *F. spiralis*, and on the survival of recruits. In addition, we measured recruitment at several distances from the nearest source of propagules (clumps of *F. spiralis*) to investigate the species ability to disperse and colonise new areas.

2. Material and Methods

We tested the hypothesis that *F. spiralis* is absent from artificial structures because adult plants do not survive on vertical or nearly vertical slopes. Adult individuals were collected in the field from horizontal substrates and plants. They were weighed (fully hydrated wet weight, WW) and the fronds length (L) and maximum circumference (perimeter, P) measured. Dichotomies and receptacles were counted. Plants were then attached to nets that were subsequently attached to the substratum using stainless screws. Experimental plants were placed following the same procedure in interspersed areas with nearly horizontal and nearly vertical surfaces in the natural shore. Plants transplanted to horizontal surfaces were used to control the effects of manipulation (procedural control).

The entire procedure was accomplished *in situ* and as quickly as possible to minimize the disturbance effect of the manipulation. Unmanipulated individuals (on horizontal surfaces) were randomly selected and marked to be measured as above and used as controls ($n = 6$). For these, WW was estimated indirectly using WW-LC² regressions (Åberg, 1990). The experiment was initiated at the end of July 2014 and replicated on two natural shores of similar wave exposure (site 1, Farol; site 2, Vulcanológico). After 3 months plants were re-measured and re-weighed, and linear growth, variations in biomass and number of dichotomies and receptacles were calculated by subtracting the initial values to the final ones.

The effect of slope on desiccation was investigated by comparing loss of water from plants ($n = 6$) deployed on horizontal and vertical surfaces in mesocosm. Tissue weight (Wt) was recorded for each plant every hour for a period of 5 hours, and finally, plants were dried at 60°C for 48h to estimate the dry weight (DW). The relative water content (RWC) of each plant was calculated according to the formula $RWC = (Wt - DW) / (WW - DW)$ (DW, dry weight; Shafer et al. 2007). RWC of each plant was plotted against elapsed time, and exponential curves were fitted to each plot by using the formula $I_t = I_0 e^{-kt}$ (I_t , RWC at time t ; I_0 , RWC at initial time; k , desiccation coefficient; Tanaka and Nakaoka, 2004).

To test the hypothesis that surface slope affects the early survivorship of recently recruited plants, fertile receptacles of *F. spiralis* were collected from the field early April 2015 to be used as source of zygotes. Receptacles were taken to the laboratory inside plastic bags in an ice-chest and kept in darkness. Receptacles were then washed in cold seawater, wiped with paper towels and placed on dry tissue paper at room temperature for zygotes release, following the protocol of McLachlan et al. (1971). The partially dehydrated receptacles were then placed inside dry grass covered Petri dishes and kept inside a culture chamber at 8°C in the dark overnight. When zygotes started to release, receptacles were covered

with cold sterile seawater until zygotes complete release and sunk to the bottom of the dish. Zygotes were then isolated from conspicuous mucilage, translated to aquaria with sterile seawater where the bottom was covered with recruitment plates (6 x 6 cm), and allowed to settle. Plates were incubated at room temperature, changing half of the water every 3 days. After 10 days, the initial concentration of recruits in plates was counted in 6 fixed sub-quadrats 1.5 x 1.5 cm under binocular lens. Plates were then transported to the field and randomly attached onto horizontal and vertical surfaces ($n = 8$) using stainless screws. After a period of 24 h, plates were retrieved, carefully brought to the laboratory where recruits density was estimated as described above. Percentage survivorship of recruits was calculated as $N_f / N_0 * 100$, where N_f is the average number of surviving settlers per plate at 24h, and N_0 is the number of settled recruits at the initial moment.

We further investigated if substratum slope influences local hydrodynamic conditions by deploying pre-weighted plaster discs attached to the substratum in horizontal and vertical areas of the shore ($n = 5$ per treatment). Discs were retrieved 48 h and one week later, dried until constant weight was obtained and re-weighted to calculate weigh loss.

To test the hypothesis that the absence of *F. spiralis* on artificial structures is due to a limitation of a source of propagules for colonisation we investigated recruitment rates at increasing distances from clumps of mature plants. Recruitment plates ($n = 5$) 6 x 6 cm were deployed in the field at three increasing distances from adults: 0 cm (i.e., under the frond), 10 cm and > 0.5 m. After 75 days, plates were collected and carefully brought to the laboratory where the number of recruits was counted on each plate under binocular lens in four sub-quadrats (3.25 cm²) per plate.

2.1. Data analysis

A two-way mixed model analysis of variance (ANOVA) was used to compare linear growth, variations in biomass, numbers of dichotomies and receptacles among sites (Si, random factor, 2 levels) and treatments (Tr, fixed factor, 3 levels: Horizontal (procedural control), Vertical, Control). Student-Newman-tests (SNK) were used to compare means within significant terms. In order to examine initial differences among plants assigned to each treatment, linear length, biomass, and numbers of dichotomies and receptacles measured before manipulations were compared using ANOVA, with the same model described above. A one-way ANOVA was used to compare the desiccation coefficients of adult plants, recruit survivorship and weight loss of plaster discs between slopes (Or, fixed factor, 2 levels: Horizontal, Vertical). A two-way ANOVA was also used to compare the recruitment rates among plates (Pl, random factor) at increasing distances (Dist, fixed factor, 3 levels: 0 cm, 10 cm, > 0.5 m). Prior to analyses, Cochran's tests were used to detect heterogeneity of variances and data were transformed where appropriate (Underwood, 1997). When homogeneity of data was not achieved after transformation, analyses were run on the untransformed data but using a more conservative significance level ($\alpha < 0.01$) (Underwood, 1997).

3. Results

Comparisons among plants before experimental manipulations

ANOVA did not detect any significant differences among the measures of the plants allocated to each treatment at the beginning of the study (Table 1).

Effect of substratum slope.

Significant variation was found in the length and number of dichotomies of *Fucus spiralis* between treatments (Table 2). SNK tests showed that the length of *F. spiralis* transplanted to vertical surfaces differed significantly from both plants transplanted to horizontal

surfaces and unmanipulated controls, while no significant difference was found between the last two treatments (Table 2). *F. spiralis* transplanted to vertical surfaces suffered a reduction in length (Fig. 1, mean $\pm$ SE; site 1: -1.2 ± 1.1 cm, site 2: -3.7 ± 0.9 cm), whilst plants transplanted to horizontal surfaces as well as controls grew similar lengths (site 1: 2.3 ± 0.3 , site 2: 0.0 ± 0.9 cm). Similarly, the number of dichotomies was also significantly lower, and showed on average a 6.8 ± 3.3 reduction compared to original numbers) in plants transplanted to vertical surfaces, whereas similar numbers of dichotomies were found in plants transplanted to horizontal surfaces and controls and there were on average 11.0 ± 3.7 more dichotomies since the start of the experiment (Fig. 1, Table 2). Even though *F. spiralis* wet weight and number of receptacles tended to increase in both controls and plants transplanted to horizontal surfaces (especially on site 1), there was no significant difference among treatments (Fig. 1, Table 2) as there was large variability among individuals. There were also no differences on desiccation coefficients of adult plants deployed on horizontal and vertical surfaces (Fig. 2, Table 3).

After 24 h, the survivorship of recruits deployed on horizontal and vertical surfaces was similar, as was the mean weight loss of plaster discs across time (Fig. 3, Table 3).

Ability of Fucus spiralis to disperse away from source plants. Mean density of recruits on plates deployed at different distances from source clumps of *F. spiralis* differed markedly. While mean densities of up to 18 ind. cm² were observed under the canopy, few recruitments were observed at 10 cm and 0.5 m away from *F. spiralis* clumps (Fig. 4, Table 4).

4. Discussion

There were negative effects of vertical slope on the development of adult *Fucus spiralis*. Lower linear growth and increment in number of dichotomies on adults were observed on

vertical surfaces, suggesting that the different conditions were determinant for *F. spiralis* populations. We expected differences would rely on hydrodynamic forces or desiccation regimes to which plants are submitted. In fact, several studies concluded that wave force was the dominant controlling factor affecting *Fucus* spp. and other canopy-forming algae (Jonsson et al., 2006; Moschella et al., 2005; Perkol-Finkel et al., 2012), limiting their survival through mechanical abrasion, dislodging or pruning. However, no differences were found in the hydrodynamic regime among vertical and horizontal slopes (plaster discs), nor on desiccation levels. This suggests that other physical and/or biological factors could be involved in shaping *F. spiralis* populations, as mentioned by Thompson et al. (2004) for algal biofilm. For example, grazers such as amphipods, limpets, periwinkle *T. striatus*, or fishes such as *Salpa salpa*, usually present in the studied intertidal level, were not excluded in our experimental study, and their effect on macroalgae may be among possible relevant causes for obtained patterns. Previous studies showed grazing was sufficient to prevent the establishment of macroalgae, being important determinants for either adult or post-settler stages (Chapman, 1989; Creese, 1988; Jenkins et al., 2005 and references therein). Besides variations in grazing and predation activity, changes in geomorphology or whiplash by seaweed itself (see Chappuis et al. 2014), together with wave exposure, barnacle presence or microtopography have been cited as other important factors in determining the abundance of *Fucus* spp. at either juvenile or adult stages (Chapman, 1989; Lamote and Jonhnson, 2008; Moschella et al., 2005). Findings for other canopy-forming algae, *Cystoseira*, suggested that both the availability and the stability of substrata, as well as biotic disturbances (both consumptive and non-consumptive interactions), proved to be key determinants in limiting their abundance (Ferrario et al., 2015; Perkol-Finkel and Airoldi, 2010). Therefore, these and other potential physical and/or biological factors should be evaluated in further studies to determine their role in

245 shaping *F. spiralis* populations, e.g. when managing assemblages on newly built man-
246 made structures.

247 Our results on the recruitment patterns strongly contrast with those of Chapman (1989),
248 who found the intraspecific suppression of *F. spiralis* recruits by adult canopy. In our case,
249 the analysis of natural recruitment patterns on bedrocks showed that the most important
250 regulator of recruitment density was the presence of a canopy of conspecific adults,
251 whereas transplanted recruits did not show different survival patterns related to substratum
252 slope. Contrastingly, negative effect of increased slope (i.e. vertical) was evident from
253 transplantation experiments of adults. Reduced density of canopy-forming algae has been
254 already observed in urbanised coasts (e.g. in the Mediterranean, Benedetti-Cecchi et al.,
255 2001; in Sydney, Coleman et al., 2008). Responses obtained in this study, together with
256 the lack of surrounding adult fronds on Azorean artificial structures, and the fact that
257 distance from canopy greatly reduced juvenile recruitment, is sufficient to explain the
258 absence of canopies on these coastal defences. This knowledge could aid programmes of
259 restoration or rehabilitation of damaged habitats and contribute to the ecological criteria
260 that should be considered in the design and management of artificial structures.

261 Conservation, planning and policy targets for biodiversity enhancement could be
262 supported by establishment and recovery of canopy-forming species on rocks and
263 engineered structures (Coombes et al., 2013). Understanding how characteristics of
264 shores alter the structure and functioning of canopy-forming algae should be relevant
265 information to be used for conservation purposes, namely in definition of criteria to be
266 integrated into the design and construction of future urban structures (Coombes et al.,
267 2013; Perkol-Finkel et al., 2012). This information would minimise ecological impacts on
268 artificial structures, allowing targeted management of diversity and natural living resources.
269 Many habitat restoration efforts are concentrated on preservation of biodiversity, as well as

of the critical socioeconomic resources provided by many natural habitats, such as canopies (Perkol-Finkel and Airoidi, 2010). Increase the supply of canopy-forming propagules to artificial structures, turfs removal for extending the area over which canopies can maintain free substratum for recruitment, or active canopy transplantation has been proposed as means of aiding the restoration of forested landscapes and facilitating the recovery of large gaps (Emmerson and Collings, 1998; Gorman and Connell, 2009; Irving and Connell, 2006; Mangialajo et al., 2008). Although potential recovery measures have been globally suggested in the literature, management requires approaches that focus on local scales (Strain et al., 2015). Therefore understanding how local characteristics modulate the structure and functioning of canopies should be information to be considered for conservation purposes. Our study reinforces the notion that a greater proportion of vertical surfaces compared to natural habitats, consequence of urbanisation, could strongly affect Azorean canopy-forming algae. Assisted introductions for other canopy-forming algae have been suggested as potential strategies for management of coastal defences (Perkol-Finkel et al., 2012). Although we observed a high recruitment rate under adult plants and successful survival rates for transplanted recruits, the negative effects observed on adult growth do not insure assisted introductions as a promising measure to facilitate the colonization of coastal defences. Climate-driven threats (e.g. increased storminess, adding instability) could also play an important role in regulating the loss of marine canopies, limiting their adaptive capacity to future scenarios (Perkol-Finkel and Airoidi, 2010). These could have important effects on Azorean coasts, where *F. spiralis* is the only leathery canopy-forming algae at upper intertidal level (Neto, 2000) ameliorating the otherwise harsh conditions during low tides (Watt and Scrosati, 2014).

Acknowledgements

Authors are grateful to Virginie Leyendecker, Mónica Martínez, Rubén Mosquera, Enrique Almira, Eduardo García and Ane Laborda for field and laboratory assistance. This research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE – Operational Competitiveness Programme and national funds through FCT – Foundation for Science and Technology, under the project “PEst-C/MAR/LA0015/2013, by the Strategic Funding UID/Multi/04423/2013 through national funds provided by FCT and European Regional Development Fund (ERDF) in the framework of the programme PT2020, and by cE3c funding (Ref: UID/BIA/00329/2013). GMM was supported by a postdoctoral grant awarded by FCT (SFRH/BDP/63040/2009). ACLP was funded by a FRCT research grant M3.1.5/F/098/2012. Support was also provided by CIRN/UAc (Centre of Natural Resources of University of the Azores).

References

- Åberg, P., 1990. Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. Mar. Ecol. Prog. Ser. 63, 281–287.
- Airoidi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. Annu. Rev. 45: 345–405.
- Araújo, R., Serrão, E., Sousa-Pinto, I., Åberg, P., 2011. Phenotypic differentiation at southern limit borders: the case study of two fucoid macroalgal species with different life-history traits. J. Phycol. 47, 451–462.
- Ballantine, W.J., 1961. A biologically defined exposure scale for the comparative description of rocky shores. Field Stud 1, 1–19.

- 317 Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Aioldi, L., Relini, G.,
318 Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale
319 effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137-150.
- 320 Bertocci, I., Araújo, R., Vaselli, S., Sousa-Pinto, I., 2011. Marginal populations under
321 pressure: spatial and temporal heterogeneity of *Ascophyllum nodosum* and associated
322 assemblages affected by human trampling in Portugal. *Mar. Ecol. Prog. Ser.*, 439: 73-82.
- 323 Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action: A
324 case study with *Fucus gardneri*. *Ecology* 78(5), 1563-1578.
- 325 Bulleri, F., 2005. Role of recruitment in causing differences between intertidal
326 assemblages on seawalls and rocky shores. *Mar. Ecol. Prog. Ser.* 287, 53-65.
- 327 Bulleri, F., Chapman, M.G., 2004. Intertidal assemblages on artificial and natural habitats
328 in marinas on the north-west coast of Italy. *Mar. Biol.* 145, 381–391.
- 329 Bulleri, F., Chapman, M.G., Underwood, A.J., 2004. Patterns of movement of the limpet
330 *Cellana tramoserica* on rocky shores and retaining seawalls. *Mar. Ecol. Prog. Ser.* 281,
331 121-129.
- 332 Cacabelos, E., Martins, G.M., Thompson, R.C., Prestes, A.C.L., Azevedo, J.M.N., Neto,
333 A.I. (in press) Material type and roughness influence structure of intertidal communities on
334 coastal defences. *Mar. Ecol.*
- 335 Chapman, A.R.O., 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high
336 eulittoral zone: effects of grazers, canopy and substratum type. *Mar. Biol.* 102, 565-572.
- 337 Chapman, M.G., Bulleri, F., 2003. Intertidal seawalls-new features of landscape in
338 intertidal environments. *Landscape Urban Plann.* 62(3), 159-172.

- 339 Chappuis, E., Terradas, M., Cefali, M.E., Marinai, S., Ballesteros, E., 2014. Vertical
340 zonation is the main distribution pattern of littoral assemblages on rocky shores at a
341 regional scale. *Estuar., Coast. Shelf Sci.* 147, 113-122.
- 342 Coleman, M.A., Kelaher, B.P., Steinberg, P.D., Millar, A.J.K., 2008. Absence of a large
343 brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for
344 historical decline. *J. Phycol.* 44(4), 897-901.
- 345 Coleman, M.A., Brawley, S.H., 2005. Are life history characteristics good predictors of
346 genetic diversity and structure? A case study of the intertidal alga *Fucus spiralis*
347 (Heterokontophyta; Phaeophyceae). *J. Phycol.* 41, 753–762.
- 348 Coombes, M.A., Naylor, L.A., Viles, H.A., Thompson, R.C., 2013. Bioprotection and
349 disturbance: seaweed, microclimatic stability and conditions for mechanical weathering in
350 the intertidal zone. *Geomorphology* 202, 4-14.
- 351 Coyer, J.A., Hoarau, G., Costa, J.F., Hogerdijk, B., Serrão, E.A., Billard, E., Valero, M.,
352 Pearson, G.A., Olsen, J.L., 2011. Evolution and diversification within the intertidal brown
353 macroalgae *Fucus spiralis*/*F. vesiculosus* species complex in the North Atlantic. *Mol.*
354 *Phylogenet. Evol.* 58(2), 283-296.
- 355 Creese, R.G., 1988. Ecology of molluscan grazers and their interactions with marine algae
356 in north-eastern New Zealand: a review. *N. Z. J. Mar Freshwater Res.* 22, 427-444.
- 357 Davison, I.R., Pearson, G.A., 1996. Stress tolerance in intertidal seaweeds. *J. Phycol.* 32,
358 197-211.
- 359 Emmerson, L.M., Collings, G.J., 1998. Macroalgal recruitment in artificially disturbed areas:
360 interactive effects of temporal and spatial scale. *Mar. Freshwater Res.* 49, 541–546.

- 361 Ferrario, F., Iveša, L., Jaklin, A., Perkol-Finkel, S., Airoldi, L., 2015. The overlooked role of
362 biotic factors in controlling the ecological performance of artificial marine habitats. *J. Appl.*
363 *Ecol.* DOI: 10.1111/1365-2664.12533.
- 364 Glasby, T.M., 2000. Surface composition and orientation inter-act to affect subtidal
365 epibiota. *J. Exp. Mar. Biol. Ecol.* 248, 177–190.
- 366 Glasby, T.M., Connell, S.D., 2001. Orientation and position of substrata have large effects
367 on epibiotic assemblages. *Mar. Ecol. Prog. Ser.* 214, 127–135.
- 368 Gorman, D., Connell, S.D., 2009. Recovering subtidal forests in human-dominated
369 landscapes. *J. Appl. Ecol.* 46, 1258-1265.
- 370 Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory
371 and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334.
- 372 Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates.
373 *Oceanogr. Mar. Biol. Annu. Rev.* 21, 195–282.
- 374 Hawkins, S.J., Hartnoll, R.G., Kain, J.M., Norton, T.A., 1992. Plant animal interactions on
375 hard substrata in the North-east Atlantic, in: John DM, Hawkins SJ , Price JH (Eds) *Plant*
376 *animal interactions in the marine benthos. Systematics Association Spec Vol 46.*
377 *Clarendon Press, Oxford*, pp. 1–32.
- 378 Irving, A.D., Connell, S.D., 2006. Predicting understorey structure from the presence and
379 composition of canopies: an assembly rule for marine algae. *Oecologia* 148, 491–502.
- 380 Jenkins, S.R., Coleman, R.A., Della Santina, P., Hawkins, S.J., Burrows, M.T., Hartnoll,
381 R.G., 2005. Regional scale differences in the determinism of grazing effects in the rocky
382 intertidal. *Mar. Ecol. Prog. Ser.* 287, 77–86.

- 383 Jonsson PR, Granhag L, Moschella PS, Aberg P, Hawkins SJ, Thompson RC., 2006.
384 Interactions between wave action and grazing control the distribution of intertidal
385 macroalgae. *Ecology* 87(5), 1169–1178.
- 386 Jorve, J.P., 2008. Ecological consequences of morphological variability in a habitat-
387 forming alga. Master's Theses. San Jose State University, California, 133 pp.
- 388 Lamote, M., Johnson, L.E., 2008. Temporal and spatial variation in the early recruitment of
389 furoid algae: the role of microhabitats and temporal scales. *Mar. Ecol. Prog. Ser.* 368, 93–
390 102.
- 391 Mangialajo, L., Chiantore, M., Cattaneo-Vietti, R., 2008. Loss of furoid algae along a
392 gradient of urbanisation, and structure of benthic assemblages. *Mar. Ecol. Prog. Ser.* 358,
393 63–74.
- 394 Martinez, B., Viejo, R.M., Carreño, F., Aranda, S.C., 2012. Habitat distribution models for
395 intertidal seaweeds: responses to climatic and non-climatic drivers. *J. Biogeogr.* 39, 1877–
396 1890.
- 397 McLachlan, J., Chen, L.C.-M., Edelstein, T., 1971. The culture of four species of *Fucus*
398 under laboratory conditions. *Can. J. Bot.* 49, 1463–9.
- 399 Moreira J., Chapman M.G., Underwood A.J., 2006. Seawalls do not sustain viable
400 populations of limpets. *Mar. Ecol. Prog. Ser.* 322, 179–188.
- 401 Moschella P.S., Abbiati M., Aberg P., Airoidi L., Anderson J.M., Bacchiocchi F., Bulleri F.,
402 Dinesen G.E., Frost M., Gacia E., Granhag L., Johnson P.R., Satta M.P., Sundelöf A.,
403 Thompson R.C., Hawkins S.J., 2005. Low-crested coastal defence structures as artificial
404 habitats for marine life: using ecological criteria in design. *Coastal Eng.* 52, 1053–1071.

- 405 Neto, A.I., 2000. Ecology and dynamics of two intertidal algal communities on the littoral of
406 the island of São Miguel (Azores). *Hydrobiologia* 432, 135–147.
- 407 Perkol-Finkel, S., Airoidi, L., 2010. Loss and recovery potential of marine habitats: an
408 experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic
409 Sea. *PLoS ONE* 5(5): e10791. doi:10.1371/journal.pone.0010791
- 410 Perkol-Finkel, S., Ferrario, F., Nicotera V., Airoidi, L., 2012. Conservation challenges in
411 urban seascapes: promoting the growth of threatened species on coastal infrastructures. *J.*
412 *Appl. Ecol.* 49, 1457–1466.
- 413 Shafer, D.J., Sherman, T.D., Wyllie-Echeverria, S. 2007. Do desiccation tolerances control
414 the vertical distribution of intertidal seagrasses?. *Aquat. Bot.* 87, 161-166.
- 415 Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and
416 knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic
417 perspective. *Ecol. Evol.* 3(11), 4016–4038.
- 418 Strain, E.M.A., van Belzen, J., van Dalen, J., Bouma, T.J., Airoidi, L., 2015. Management
419 of local stressors can improve the resilience of marine canopy algae to global stressors.
420 *PLoS ONE* 10(3): e0120837. doi:10.1371/journal.pone.0120837
- 421 Tanaka, Y., Nakaoka, M., 2004. Emergence stress and morphological constraints affect
422 the species distribution and growth of subtropical intertidal seagrasses. *Mar. Ecol. Prog.*
423 *Ser.* 284, 117–131.
- 424 Thompson R.C., Wilson B.J., Tobin M.L., Hill A.S., Hawkins S.J., 1996. Biologically
425 generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial
426 scales. *J. Exp. Mar. Biol. Ecol.* 202, 73–84.

427 Thompson, R.C., Norton, T.A., Hawkins, S.J., 2004. Physical stress and biological control
428 regulate the producer-consumer balance in intertidal biofilms. *Ecology* 85, 1372–1382.

429 Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation*
430 *using analysis of variance*. Cambridge University Press, Cambridge.

431 Vaselli, S., Bertocci, I., Maggi, E., Benedetti-Cecchi, L., 2008. Assessing the
432 consequences of sea level rise: effects of changes in the slope of the substratum on
433 sessile assemblages of rocky seashores. *Mar. Ecol. Prog. Ser.* 368, 9–22.

434 Voerman, S.E., Llera, E., Rico, J.M., 2013. Climate driven changes in subtidal kelp forest
435 communities in NW Spain. *Mar. Environ. Res.* 90, 119–127.

436 Watt, C.A., Scrosati, R.A., 2014. Experimental and mensurative data on the abundance of
437 primary producers and consumers from intertidal habitats in Canada. *Ecology* 95, 1429–
438 1429.

439

440

441

442

443

444

445

446

447

448 **Tables**

449 Table 1. ANOVA testing for differences on *F. spiralis* linear length and numbers of
 450 dichotomies and receptacles and in wet weight at different sites and treatments (H
 451 Horizontal, V Vertical, C Control) (n = 6). * $P < 0.05$, ^{ns} no significant.

Source	df	Linear length		N dichotomies		N receptacles		WW	
		MS	F	MS	F	MS	F	MS	F
Site (=Si)	1	9.56	3.41 ^{ns}	11.11	0.14 ^{ns}	17.36	5.06*	0.29	0.93 ^{ns}
Treatment (=Tr)	2	3.92	1.40 ^{ns}	6.08	0.08 ^{ns}	1.36	0.40 ^{ns}	0.10	0.32 ^{ns}
Si x Tr	2	1.80	0.64 ^{ns}	37.53	0.49 ^{ns}	1.36	0.40 ^{ns}	0.04	0.12 ^{ns}
Res	30	2.81		76.99		3.42		0.31	
Total	35								
SNK									
Cochran's test		0.2411 ^{ns}		0.2812 ^{ns}		0.6110**		0.3636 ^{ns}	
Transformation		None		None		None		None	

452

453

454

455

456

457

458 Table 2. ANOVA testing for the effects of site and treatment (H Horizontal, V Vertical, C
 459 Control) on *F. spiralis* linear growth and variation numbers of dichotomies and receptacles
 460 and in wet weight (n = 6). ** $P < 0.01$, * $P < 0.05$, ^{ns} no significant.

Source	df	Linear growth		N dichotomies		N receptacles		WW	
		MS	F	MS	F	MS	F	MS	F
Site (=Si)	1	41.11	6.90*	448.03	1.75 ^{ns}	462.25	6.45*	8.64	0.60 ^{ns}
Treatment (=Tr)	2	50.66	8.50**	1384.02	5.42**	103.86	1.45 ^{ns}	45.01	3.15 ^{ns}
Si x Tr	2	3.59	0.60 ^{ns}	105.86	0.41 ^{ns}	18.58	0.26 ^{ns}	12.36	0.87 ^{ns}
Res	30	5.96		255.33		71.68		14.29	
Total	35								
		H diff V**		H diff V*					
SNK		V diff C**		V diff C**					
		C = H		C = H					
Cochran's test		0.5071*		0.4543*		0.8070**		0.4718*	
Transformation		None		None		None		None	

461

462

463

464

465

466

Table 3. ANOVA testing for the effects of slope on desiccation coefficient of *F. spiralis* adults (n = 6), and on survivorship of recruits (n = 8), and weight loss (WL) of plaster discs (n = 5) after different time periods. ** $P < 0.01$, * $P < 0.05$, ^{ns} no significant

	Desiccation			Survivorship			WL(48h)			WL(1week)		
	coefficient			(24h)								
Source	df	MS	F	df	MS	F	df	MS	F	MS	F	
Slope	1	0.0021	3.21 ^{ns}	1	507.38	1.05 ^{ns}	1	651.73	2.50 ^{ns}	627.74	3.23 ^{ns}	
Res	10	0.0007		14	482.97		8	260.34		194.59		
Total	11			15			9					
Cochran's test		0.8105 ^{ns}			0.5193 ^{ns}			0.9114*			0.9407*	
Transformation		X^3			None			None			None	

480 Table 4. ANOVA testing for the effects of distance (0 cm, 10 cm, > 0.5m) and plate on *F.*
 481 *spiralis* recruitment (n = 4). ** $P < 0.01$.

Source	Recruitment		
	df	MS	F
Distance (D)	2	19910.8	9.21**
Plate (=PI)	4	2160.9	1.56 ^{ns}
Dist x PI	8	2160.9	1.56 ^{ns}
Res	45	1381.1	
Total	59		
Cochran's test	0.6764, $P < 0.01$		
Transformation	None		

Figure captions

Fig. 1. Linear growth (A) and variation in wet weight (B) and number of dichotomies (C) and receptacles (D) (mean number $\pm$ SE, $n = 6$) associated with Horizontal (=procedural controls), Vertical and Control treatments.

Fig. 2. Relative water content (RWC) of adult plants associated with horizontal and vertical slope across time. Each line represents an individual.

Fig. 3. (A) Survivorship (Mean $\pm$ SE, $n = 8$) of *F. spiralis* germlings associated with horizontal and vertical slopes; (B) Weight loss (Mean $\pm$ SE, $n = 5$) of plaster discs with horizontal and vertical slopes across time.

Fig. 4. Number of recruits (Mean $\pm$ SE, $n = 5$) of *F. spiralis* found at increased distances from adults.

Fig. 1. Cacabelos et al.

506

507

508

Fig. 2. Cacabelos *et al.*

Fig. 3. Cacabelos et al.

Fig. 4. Cacabelos *et al.*

523