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INFLUENCE OF A BREAKWATER ON NEARBY ROCKY INTERTIDAL**2 COMMUNITY STRUCTURE**

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26 ABSTRACT

1
2 It is widely recognised that coastal defence structures generally affect the structure of
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4
5 28 the assemblages they support, yet their impact on adjacent systems has been largely
6
7 ignored. Breakwaters modify the nearby physical environment (e.g. wave-action)
8
9
10 30 suggesting a local impact on biological parameters. In the present study, an ACI (After-
11
12 Control-Impact) design was used to test the general hypothesis that the artificial
13
14 32 sheltering of an exposed coast has a strong effect on the structure and functioning of
15
16 adjacent systems. The effects of a reduction in hydrodynamics were clear for a number
17
18 of taxa and included the replacement of barnacles, limpets and frondose algae by an
19
20 34 increasing cover of ephemeral algae. These effects were evident both at early and late
21
22 successional stages. Results suggest that the artificial sheltering of naturally exposed
23
24 36 coasts can have a strong impact promoting a shift from consumer- to producer-
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26 dominated communities, which has important ecological and energetic consequences
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28 38 for the ecosystem.

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Keywords: sea defence structure, environmental impact, benthic assemblages, wave-
exposure, recruitment, ACI (After-Control-Impact) design.

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1. Introduction

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2 52 Since the 1960's there has been an unprecedented rate of habitat loss,
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4 modification or degradation with some European countries reporting reductions over
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6
7 54 50% of the original coastal habitat (Airoldi and Beck, 2007). Coastal urbanisation
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9 including the replacement of natural substrata by artificial ones or the deployment of
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12 56 artificial structures to protect the flooding of low-lying lands and to prevent coastal
13
14 erosion is likely to increase in the next decades due to sea-level rise or increased storm
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17 58 frequency (Thompson et al., 2002). There is an increasing awareness that coastal
18
19 urbanisation leads to important changes in the structure and functioning of marine
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22 60 ecosystems including the loss of keystone taxa and associated reductions of local
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24 diversity (e.g. Benedetti-Cecchi et al., 2001; Mangialajo et al., 2008). Although
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26
27 62 similarities exist between assemblages on natural and built reefs, patterns of species
28
29 distribution are generally modified in the latter (Bulleri et al., 2004; Bulleri and
30
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32 64 Chapman, 2004) and the assemblages are characterised by a reduced subset of species
33
34 that commonly occur on natural shores (e.g. Chapman, 2003; Chapman and Bulleri,
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37 66 2003). Patterns of species recruitment to seawalls also tend to differ from that on natural
38
39 shores (Bulleri, 2005). In addition, artificial structures can also facilitate the
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42 68 colonisation and spread of non-indigenous species (Bulleri and Airoldi, 2005; Glasby et
43
44 al., 2007), acting as stepping-stones. Thus, sea defence structures seem to act as
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47 70 functional different habitats.

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49 The above mentioned studies have generally compared the assemblage structure
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52 72 on artificial and natural shores while little is known on how these structures affect the
53
54 structure of adjacent rocky intertidal communities (but see Goodsell et al., 2007). Work
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57 74 done on other systems including mangrove forests (Kelaher et al., 1998), fish
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59 assemblages (Clynick et al., 2008) and soft-sediment habitats (see Bertasi et al., 2007
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76 and references therein) has shown that the influence of artificial structures can extend
1 well beyond the very communities they support.
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78 Breakwaters are deployed for reducing wave action and preventing coastal
erosion. Breakwaters also modify near-shore water circulation (Zyserman et al., 2005)
4 and sediment transport (Thomalla and Vincent, 2003; Cuadrado et al., 2005). Changes
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80 and sediment transport (Thomalla and Vincent, 2003; Cuadrado et al., 2005). Changes
in the physical environment produced by the deployment of breakwaters will likely
82 affect the structure of assemblages under their influence. For instance, wave-action
conditions have recurrently been shown to affect the distribution and abundance of
84 intertidal organisms (e.g. Underwood and Jernakoff, 1984), organism settlement (e.g.
Abelson and Denny, 1997), mortality (e.g. McQuaid and Lindsay, 2000), and biological
86 interactions (e.g. Jonsson et al., 2006). Sedimentation has also been shown to influence
rocky intertidal community structure of intertidal assemblages (reviewed by Airoidi,
88 2003). Specifically, sedimentation increases disturbance leading to a reduction in the
vertical structure of algal assemblages and thus the replacement of frondose by turf-
90 forming algae (Airoidi, 1998). In addition, sedimentation interferes with grazing
gastropod activities and thus reducing their abundance (Airoidi and Hawkins, 2007).

92 In the present study we compared the rocky intertidal structure of assemblages
sheltered by an existing breakwater to that of control areas. Specific hypothesis were
94 that the increased sediment deposition in the area sheltered by the breakwater will lead
to a reduction in the abundance of frondose algae promoting the proliferation of turf-
96 forming species lower on the shore and a reduction in the abundance of grazing
gastropods upper on the shore. *Chthamalus stellatus*, a barnacle which dominates on
98 wave-exposed shores (Jenkins, 2005) is predicted to decrease in cover in response to the
reduction in wave-action and to abrasion by the increased sedimentation in the sheltered
100 area. In addition, changes in the water-circulation caused by the presence of the

breakwater are hypothesised to affect macroalgae and/or invertebrate recruitment

102 (Abelson and Denny, 1997). However, and except for the recruitment of *Chthamalus*
104 *stellatus*, there is no directional hypothesis as to how early successional assemblages
will differ between the impacted and control locations.

106 **2. Materials and methods**

108 2.1. Study site and community

108 The present study was done on a moderate to highly exposed rocky platform on
the south coast of Pico, Azores (Fig. 1). Unlike most shores on the remainder of the
110 Azores archipelago, Lajes do Pico is a large and gentle sloping reef with a variety of
habitats (Morton et al., 1998) that support a diverse community of plants and animals
112 (for details on the composition and community structure of this reef see Morton et al.,
1998; Ávila et al., 2005; Martins et al., 2008). The uniqueness of this area has
114 contributed to its classification as SCI (*site of community interest*) and SAC (*special*
area of conservation). The main economic activity of the small village of Lajes do Pico
116 is agriculture and, to a smaller extent, fishing and tourism (whale-watching). Extractive
activities on the coastal area include angling, crabbing and harvesting of octopus and
118 limpets. The rocky platform is divided in two by a small lagoon in which the inner part
is used as an anchorage point harbouring small fishing and recreational boats. Due to
120 high wave action in winter, an already existing, but small, breakwater was extended
~100 m offshore towards the north in order to protect the entrance of the lagoon. The
122 breakwater runs parallel to the northern rock platform at approximately 50 m away from
the shore and is made of large, regularly sized concrete blocks that rise approximately 4
124 m above seawater level. The construction resulted in the artificial sheltering of the
northern area of the rocky platform, locally denominated as Lajido, previously exposed

126 to open swell. Besides the presence of the breakwater, there are no apparent differences
127 (e.g. geomorphology) between the northern and southern rock platforms and the impact
128 of the small harbour is expected to be small. The study began one year following the
129 completion of the breakwater. During the course of study, occasional construction work
130 was done in the inner part of the lagoon close to the harbour. Although the harbour is
131 ~200 m away this may have led to pulse increases in sediment load. The southern
132 platform is protected from such disturbances due to the ground elevation separating the
133 two areas.

134

2.2. Sampling design

136 In order to examine the effects of the breakwater on the adjacent algal and
137 animal assemblages, a beyond-BACI design (see Underwood, 1991, 1992, 1993 and
138 1994 for revision) was not possible due to the lack of *a priori* data. However, beyond-
139 BACI designs can be modified and applied to situations where no before data exist and
140 have been widely used (e.g. Chapman et al., 1995; Terlizzi et al., 2005). These designs
141 allow the determination of consistent differences between the disturbed and several
142 control locations although it is generally not possible to attribute causation to a
143 particular event (see Terlizzi et al., 2005, Glasby, 1997 for discussion).

144 In the present study, we used an asymmetrical ACI design to compare the
145 abundance of conspicuous eulittoral taxa in a putatively disturbed location (a rocky
146 platform artificially sheltered by a breakwater) and three control locations. All locations
147 (the disturbed and controls) are on the same rocky platform and at least 150 m apart
148 from each other. The disturbed location is located in the northern part of this platform
149 whereas all control locations were located south to this. Although the non-interspersion
150 of control locations introduces an issue of spatial confounding which may affect the

1 interpretation of results (Underwood, 1994), this situation was compulsory as north of
2 152 the disturbed location the rocky platform gives rise to a vertical wall falling directly into
3
4 the water. As mentioned above, this specific rocky platform is unique on the Azorean
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6 154 shores, which are characterised by steep slopes. Since the slope of the shore can
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8 significantly affect the processes structuring intertidal communities (Knott et al., 2004)
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10 these were not considered appropriate controls to the disturbed location (see Underwood
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12 156 (1994) for the desirable characteristics that control locations must have). Analyses of
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14 spatial correlation (data not shown) showed that the abundance of organisms was only
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16 158 weekly correlated with the location of controls and hence suggesting that no discernible
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18 horizontal gradients were operating along this platform, which could interfere with the
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20 interpretation of results.
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26 162 At each location (disturbed and controls), sampling of mature assemblages was
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28 done by means of 10 random quadrats (25 x 25 cm) located at least 1 m apart at the
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30 164 lower algal dominated shore (~0.6 m above Chart Datum) and upper animal dominated
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32 shore (~1.8 m above CD). Sampling was done at 4 different times of the year (July '06,
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34 October '06, January '07, March '07) to provide an estimate of temporal variability in
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36 166 the abundance of organisms. Quadrats were not permanent and were randomly selected
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38 on each sampling occasion so as to guarantee independence of data. The percentage
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40 168 cover of algal species was estimated from 36 uniformly distributed points and expressed
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42 as percentage cover. An arbitrary value of 0.5 percentage cover was given to species
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44 170 whose position did not match any of the intersections. Barnacle cover was estimated by
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46 giving a score from 0 (absent) to 4 (100% cover) in each of the 25 sub-quadrats (Dethier
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48 et al., 1993), while mobile animals (limpets and littorinids) were counted and expressed
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50 172 as density per quadrat. Other animals present (e.g. chitons, whelks) were rare in the
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52 sampled areas and, although their presence was recorded, they were not further
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176 analysed. Sampling of algae was done at the highest taxonomic resolution achievable in
1 the field. This included the identification of several organisms to species level, although
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5 178 others were identified to genera. Algae were later grouped into distinct
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7 morphological/functional groups which included: leathery and corticated erect algae
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10 180 (e.g. Fucooids, *Stypocaulon scoparium*; hereafter referred to as frondose algae), coarsely
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12 branched algae (e.g. *Osmundea* spp., articulated coralline algae; hereafter referred to as
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14 182 turf-forming algae), filamentous algae (e.g. *Ceramium* spp.), ephemeral algae (e.g.
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16 *Enteromorpha (Ulva)* spp., *Rivularia* sp.) and crustose algae (e.g. *Nemoderma* sp.,
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19 184 encrusting coralline algae).

21
22 The influence of the breakwater on organism recruitment was examined by
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24 186 means of 10 x 10 cm recruitment plates (n = 5 per combination of location and tidal
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26 height). The selected locations and shore height were as described above. Plates were
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29 188 preferred over experimental clearings since these constitute suitable colonisation
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31 substrates for a variety of organisms (at least in the short-term) and eliminate the
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34 190 influence of non-evident processes that could affect the interpretation of results between
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36 the impacted and control locations (Chapman and Underwood, 2008). Hence, if
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39 192 recruitment in the impacted location differs from that of control locations, this is most
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41 likely due to the presence of the breakwater and consequent changes in the local
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44 194 physical environment (e.g. water circulation). The plates were made of basaltic rock, the
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46 natural substratum in the area, perforated in the centre and screwed to the shore with
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49 196 stainless steel screws at least 1 m apart. In order to provide temporal replication, after
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51 first deployment in July '07, plates were retrieved and replaced every three months. A
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54 198 total of three sets of plates were thus available for analysis corresponding to the periods
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56 of colonisation of July '06 – October '06, October '06 - January '07 and January '07 –
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59 200 April '07. The percentage cover of algae on recruitment plates was done under a

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202 dissecting microscope by overlaying a translucent sheet with 50 uniformly-spaced
points and recording the species underneath. A space of 1 cm was left between the
edges of the plate and the beginning of the quantification points as well as to the central
204 hole (used to attach the plate to the shore) to reduce edge effects. Barnacles were
counted and expressed as density per 100 cm². Four sub-samples of 1 cm² were used
206 where these were too abundant to be counted and the mean of the 4 sub-samples
standardized to 100 cm². Other animals present were either too rare to be analysed (e.g.
208 bryozoans) or were mobile (limpets and littorinids) and thus it was not possible to be
sure in ascribing their presence on plates to recruitment.

210 Plaster discs were used to examine the effect of the breakwater on the
hydrodynamics of the adjacent reef. This was done by screwing three replicate plaster
212 discs (~5 m apart) of known weight per site to mid-shore tidal heights. The loss of mass
(dry weight) after one high tide was used as a surrogate for water motion or wave action
214 (e.g. Lindegarth and Gamfeldt, 2005). Wave action was estimated three times during the
study - in July '06, October '06 and April '07. Although the typical large small-scale
216 variation in water-motion suggests that the number of plaster discs used is small, the
small size of error bars (see Fig. 6) indicates replication was enough to provide a precise
218 estimate of this variable. We also aimed at quantifying the level of sedimentation by
deploying sediment traps in July '07 (Airoldi, 2003) but this methodology proved rather
220 unfruitful in the intertidal since the majority of the sediment traps were lost after 5 days,
probably due to the high resistance of the containers to wave action. As an alternative,
222 the abundance of sediment was estimated as percentage cover while sampling for
mature assemblages in subsequent sampling events.

224 2.3. Data analysis

226 To test for differences in the abundance of the different taxa between the
23 disturbed and control locations, data were analysed using 2-way asymmetrical
24 ANOVAs with time and location as random factors and orthogonal to each other. A
25 general model of the analysis as well as the calculation of the expected mean squares
26 and the consequent determination of denominators for each test was adapted from
27 Terlizzi et al., (2005) and is presented in Table 1. Generally, the factor location was
28 partitioned into two components: one contrasting the impacted and control locations (*I*
29 vs. *C*'s) and the other contrasting control locations among each other (*C*'s). This was
30 also true for the time x location interaction and for the residuals associated with
31 variability among quadrats respectively within *I* and *C*'s (see Terlizzi et al., 2005 for a
32 detailed description of these procedures). Prior to analysis, Cochran's test was used to
33 check for problems of heteroscedascity and data were transformed where appropriate
34 (Underwood, 1997). Where heterogeneity of variances persisted, data were analysed
35 untransformed but a more conservative *P*-value was used (Underwood, 1997, Blockley
36 and Chapman, 2006).

242 3. Results

3.1. Mature assemblages

244 Patterns of distribution in the disturbed and control locations were variable among the
245 different taxa examined. As expected, on the lower shore algal dominated assemblage
246 (Fig. 2, Table 2) the cover of frondose algae was lower in the disturbed location and this
247 was consistent in time despite variability among control locations. Crustose algae also
248 occurred at lower abundances in the disturbed location although this was temporally
249 variable. The space released by the reduction in cover of frondose and crustose algae in
250 the disturbed location was occupied by ephemeral algae, which increased in cover

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252 although its cover varied with time. Turf-forming and filamentous algae showed no clear variation being similarly distributed across the rocky platform.

On the upper animal dominated shore (Fig. 3, Table 3), both the cover of barnacles and the number of limpets were consistently lower in the disturbed location. Again, ephemerals seemed to take advantage from the release in competition and were consistently more abundant in the upper shore of the disturbed location. Although the abundance of littorinids in the disturbed locations tended to be lower than the mean abundance among control locations, this was not statistically significant.

260 3.2. Early successional assemblages

Recruitment of organisms to lower shore settlement plates was also variable and depended on taxa (Fig. 4, Table 4). Recruitment to panels was dominated by ephemeral species and this was similar in the disturbed and control locations. The colonisation of turf-forming algae was temporally variable among control locations although no clear difference was detected between the disturbed and its overall mean abundance in control locations. In contrast, the abundance of filamentous algae was consistently lower in the disturbed location. The abundance of crustose algae also differed between the disturbed and control locations, but this was variable in time. The barnacle *Chthamalus stellatus* also recruited to lower shore plates, albeit at lower abundances compared to that recorded on upper shore plates. However, although recruitment tended to be lower in the disturbed location, this was not statistically significant.

On the upper shore recruitment plates (Fig. 5, Table 5), the only discernible algal recruitment was that of ephemeral species, which were present at larger abundances in the disturbed location during most of the study period. Filamentous and crustose algae were sporadically recorded but were too rare to be analysed. In contrast, barnacle

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5 276 recruitment was virtually null in the disturbed location, whilst reaching a mean number
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10 of 146 ± 33 (mean ± 1SE) recruits per plate among control locations during the peak of
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15 278 recruitment.

10 280 3.3. Physical environment

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12 As expected, plaster dissolution was 2-fold greater in control sites than in the
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14 282 area sheltered by the breakwater (Fig. 6, Table 6) and this was consistent in time
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16 revealing that the breakwater exerts a putative impact on this part of the rocky platform.
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18
19 284 Accumulation of sediment occurred lower on the shore in the impacted location trapped
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21 inside mats of turf-forming algae although this was temporally variable. A peak of
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24 286 sediment accumulation was recorded in October '06 with a mean percentage cover of
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26 19.7 ± 4.4 (mean ± SE), whilst lower abundances were recorded in January '07 (3.9% ±
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28 288 1.6) and April '07 (6.7% ± 3.7). No sedimentation was recorded on the lower shore of
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30 control sites, or on the upper shores of either the disturbed or control locations.
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36 4. Discussion

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39 292 Generally, the area sheltered by the breakwater supported a structurally and
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41 functionally different assemblage than that recorded in control locations and this was
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44 294 especially evident in the upper eulittoral. At this tidal height, ephemeral algae replaced
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46 the dominant space occupier, the barnacle *Chthamalus stellatus*, in the disturbed area
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49 296 and persisted throughout the year. The shift between animal dominated and algal
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51 dominated assemblages along a decreasing gradient of wave action is common to
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54 298 temperate regions worldwide even though the processes that structure these
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56 communities can differ among locations (see Jenkins et al., 2008 and references
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58 300 therein). In European coasts, much experimental work has convincingly shown that
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1 grazing by patellid limpets limits the growth of macroalgae in wave-beaten shores and
2 302 that their removal leads to a change in dominance between barnacles and mussels, and
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4 macroalgae (e.g. Hawkins, 1981; Jenkins et al., 2005; Arrontes et al., 2004; Coleman et
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7 304 al., 2006). Similarly, the reduced abundance of patellid limpet in the sheltered area
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9 probably led to the divergence in structure of assemblages found between the disturbed
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12 306 and control locations. Such shift in dominance at the upper eulittoral zone has important
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14 ecological and energetic consequences by altering a net consumer ecosystem into one
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17 308 dominated by producers.

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19 At the lower algal dominated shore, important differences in the assemblage
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22 310 structure were also clear with ephemeral algae similarly replacing frondose algae in the
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24 disturbed location. The hydrodynamic forces generated by the breaking of waves in the
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27 312 intertidal are known to limit the size and survival of larger plants so that these generally
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29 become restricted to more sheltered conditions (Blanchette, 1997). However, this was
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32 314 not the case. While our attempts to estimate the intensity of sedimentation were not
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34 particularly successful, they do suggest that sediment tended to accumulate in the
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37 316 disturbed area and this is known to negatively affect the colonisation of space by erect
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39 algae, while having no discernible effect on the spatial dominance of algal turfs
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42 318 (Airoldi, 1998).

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44 Significant differences between the disturbed and control locations were also
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47 320 evident during the early successional stages of assemblage development. During the
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49 peak of barnacle settlement, these recruited in abundance on upper shore plates in the
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52 322 control locations but not in the sheltered area, where ephemeral algae composed the
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54 bulk of the early successional assemblage. In the lower shore, recruitment of
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57 324 filamentous algae was also lower in the disturbed location than on the adjacent exposed
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59 controls. As for adult populations, exposure to wave-action is known to influence the
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5 328 *Ascophyllum nodosum*, and thus explaining its inability to colonise exposed locations
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7 (Vadas et al., 1990). Although populations of the barnacle *Chthamalus stellatus*
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10 330 predominate on wave-exposed shores (e.g. Jenkins, 2005), their ability to colonise
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12 sheltered shores does not seem limited by the abundance of larvae, which actually tend
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14 332 to concentrate on sheltered bays (Jenkins and Hawkins, 2003), but by post-settlement
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16 processes that limit the ability of barnacles to settle (Jenkins and Hawkins, 2003) or
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19 334 cause the mortality of recently settled animals (e.g. the sweeping of frondose algae,
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21 Jenkins et al., 1999). In the present study, barnacle settlement on plates in the sheltered
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24 336 location was probably limited by competition for space with ephemeral algae.
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26 Alternatively, both the recruitment of barnacles and filamentous algae in the sheltered
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29 338 areas may have been driven by the breakwater-induced variations in water-motion,
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31 which likely influence the dispersion of propagules and nutrients (Mullineaux and
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34 340 Butman, 1991; Abelson and Denny, 1997).

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39 342 Although the non-interspersion of controls and the disturbed location is a
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41 potential confounding factor (Underwood, 1994), the range of responses of individual
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43 taxa, or the assemblage as a whole, to the sheltering by the breakwater could easily be
44
45 344 interpreted in light of the vast literature examining the influence of wave-action as a
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47 structuring process. In addition, the lack of spatial correlation in the abundance of the
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49 346 various taxa among control locations, indicating that no major gradients are affecting
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51 the horizontal distribution of organisms on this rocky platform, suggests that results
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54 348 have not been affected by the segregation of controls in relation to the impacted
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56 location.

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2 352 the artificial sheltering is similar to that of sheltered shores in warmer-temperate regions
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5 (Airoldi, 2001; Boaventura et al., 2002). However, caution is needed as there is
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7 354 evidence that the impacts of natural and artificial rocky reefs on the structure of marine
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9 assemblages can differ, while being similar in the way they may affect the environment
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11 356 (e.g. wave exposure) (Barros et al., 2001; Knott et al., 2004; Vaselli et al., 2008).
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16 358 **5. Conclusion**

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19 The present study has shown that the construction of breakwaters can have a
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21 360 strong effect on the structure and functioning of adjacent rocky intertidal communities.
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23 The artificial sheltering of naturally exposed shores is itself a strong impact and here
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25 362 resulted in the development of a structurally and functionally divergent assemblage.
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28 This study adds to the existing literature by showing that anthropogenic activities such
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30 364 as the construction of artificial structures can have important ecological as well as
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32 energetic consequences for the functioning of the local ecosystem.
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37 38 39 **Acknowledgements**

40
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51 372 supported by Secretaria Regional do Ambiente e do Mar.
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57 58 **References**

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Fig. 1. Azores archipelago; Pico island; and the study area showing the built breakwater

546 and the impacted (I) and control (C) locations used.

548 Fig. 2. Mean (+ SE) % cover of lower shore conspicuous taxa in the impacted and
control locations.

550

Fig. 3. Mean (+ SE) % cover of upper shore conspicuous taxa or number of limpets and
552 littorinids per quadrat (625 cm²) in the impacted and control locations .

554 Fig. 4. Mean (+ SE) % cover of lower shore conspicuous taxa on recruitment plates in
the impacted and control locations.

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Fig. 5 Mean (+ SE) % cover of upper shore conspicuous taxa on recruitment plates in
558 the impacted and control locations.

560 Fig. 6. Mean (+ SE) plaster dissolution in g (dry weight) in the impacted and control
locations.

Figure 1

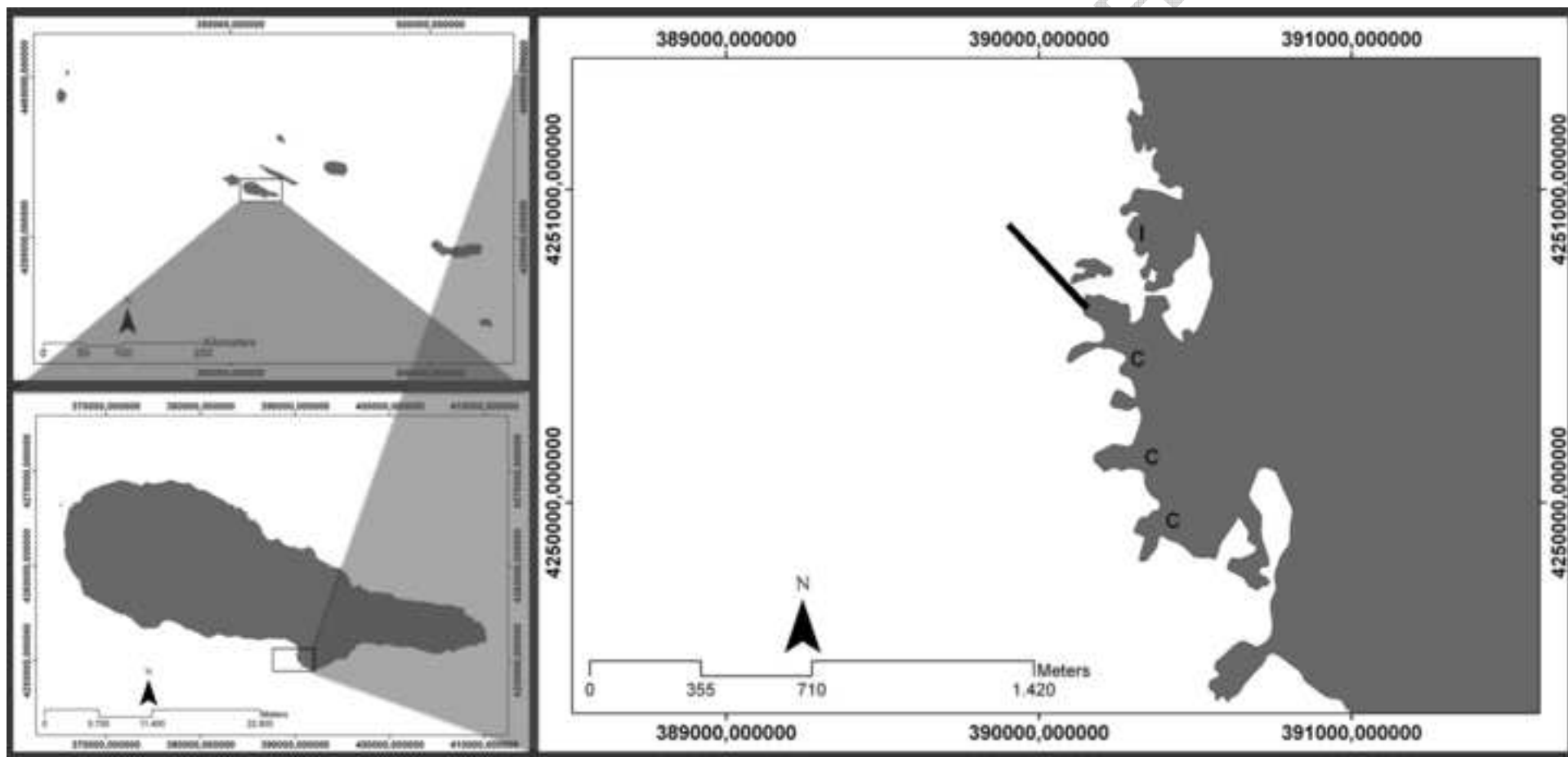


Figure 2

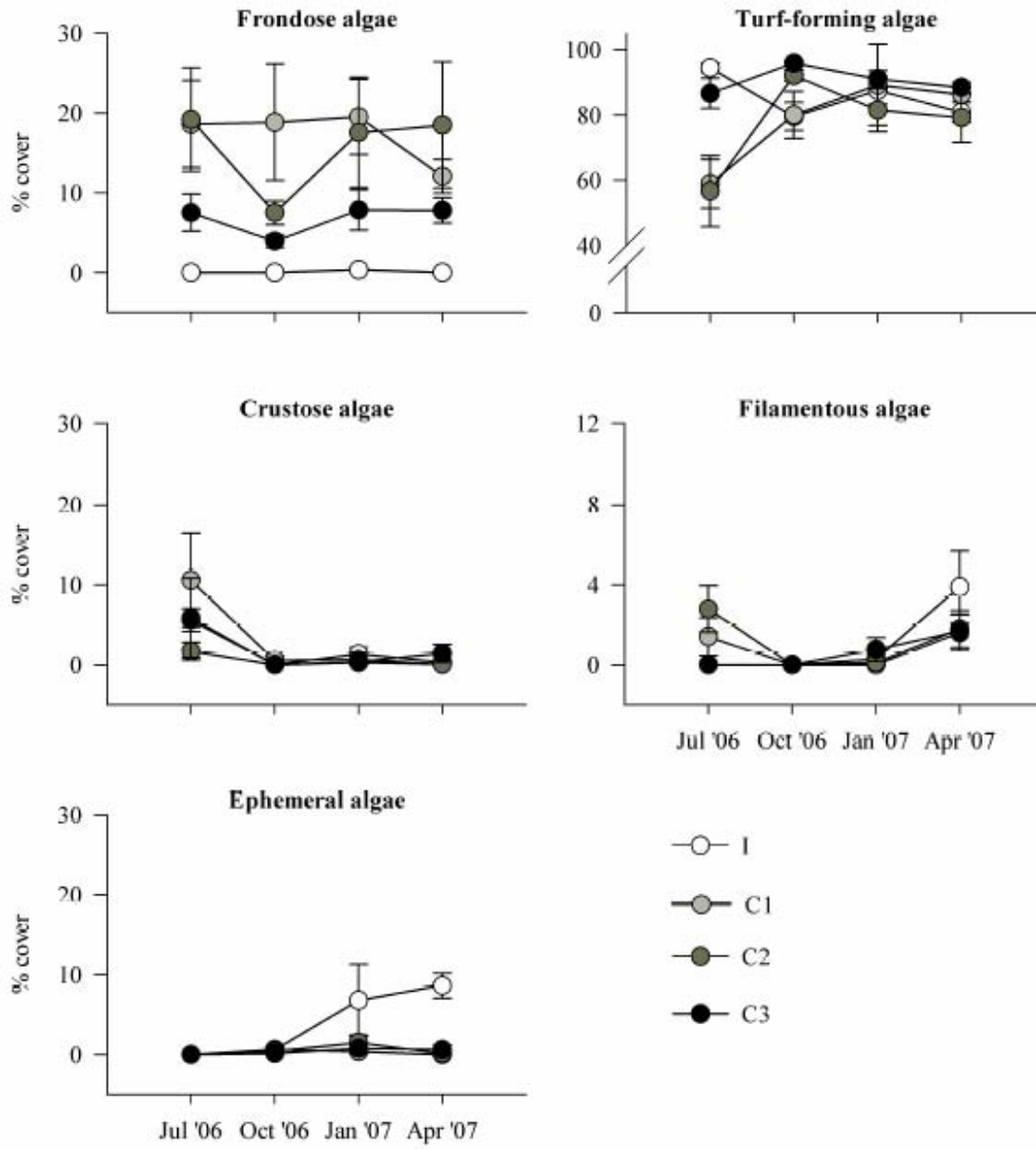
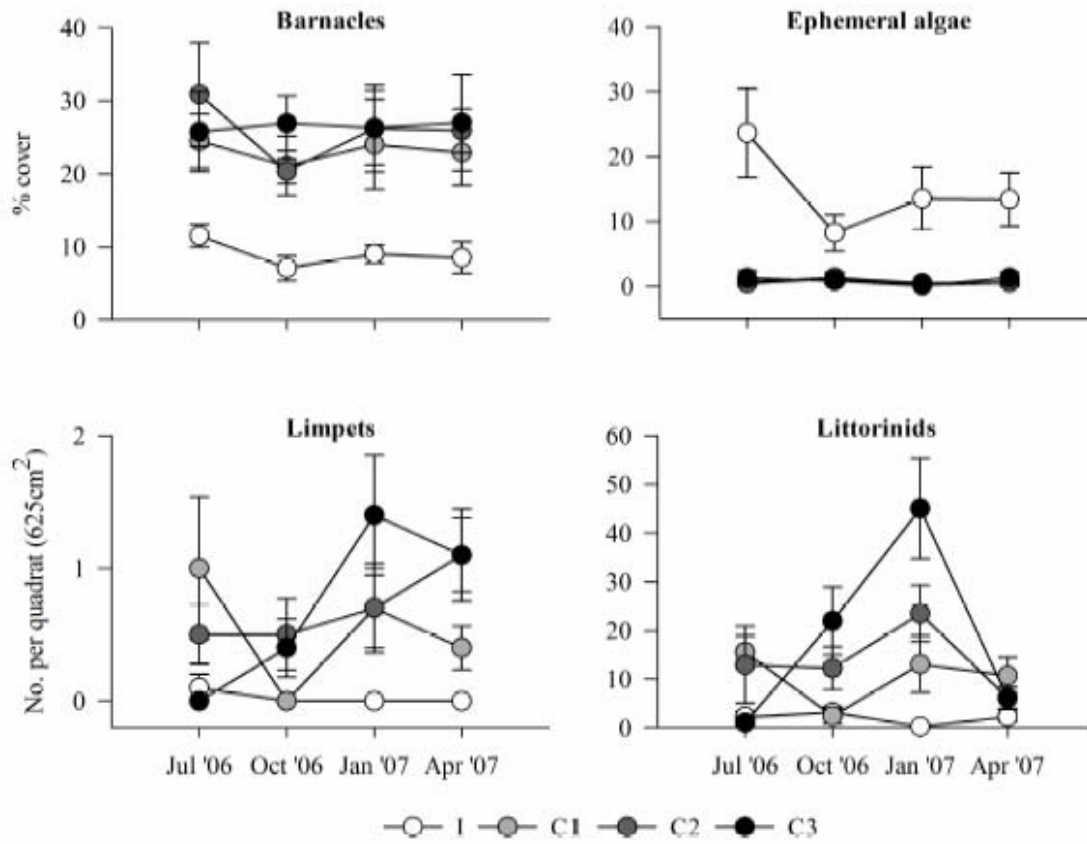


Fig.3



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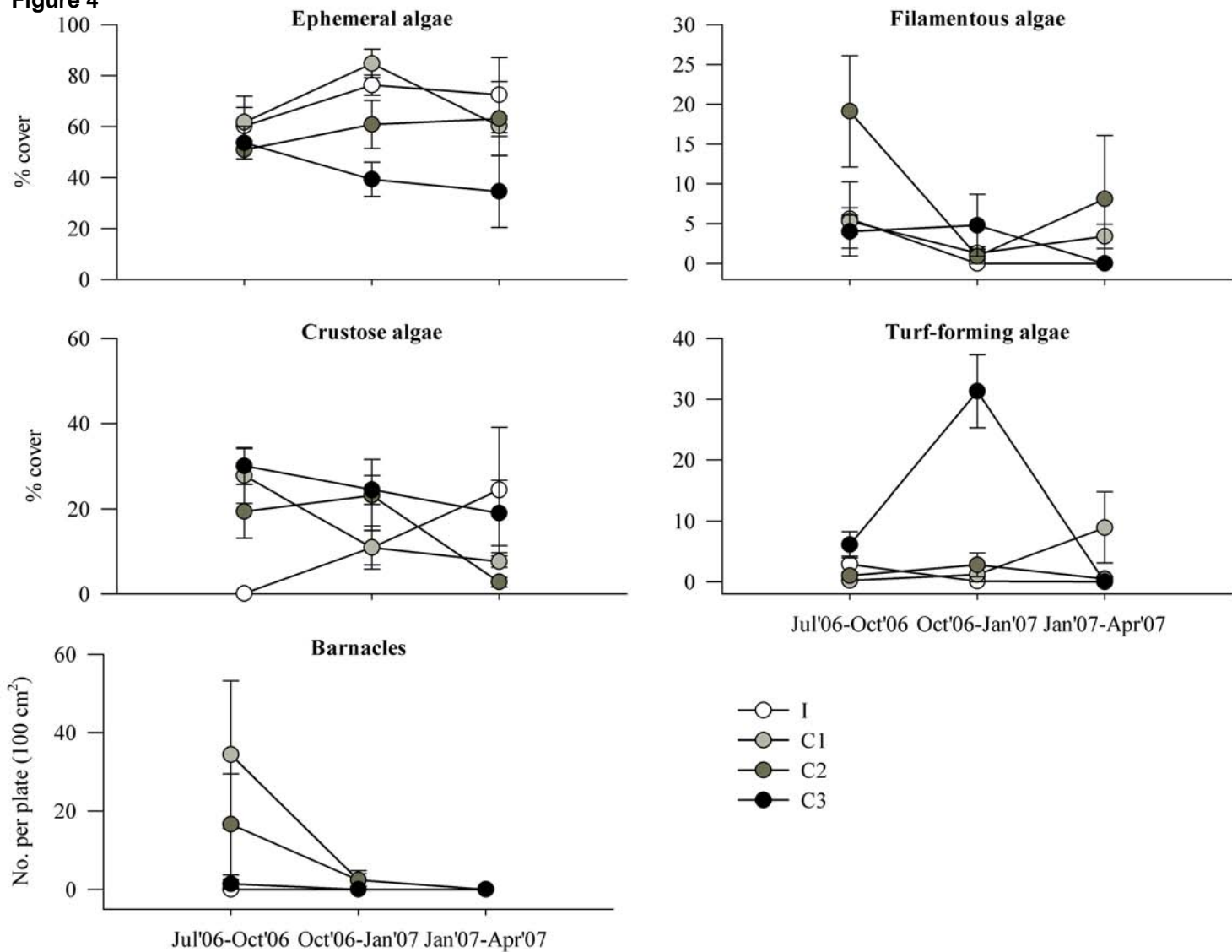
Figure 4

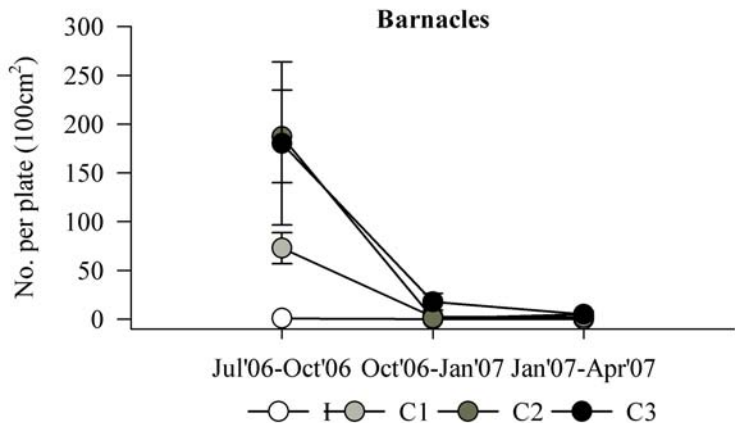
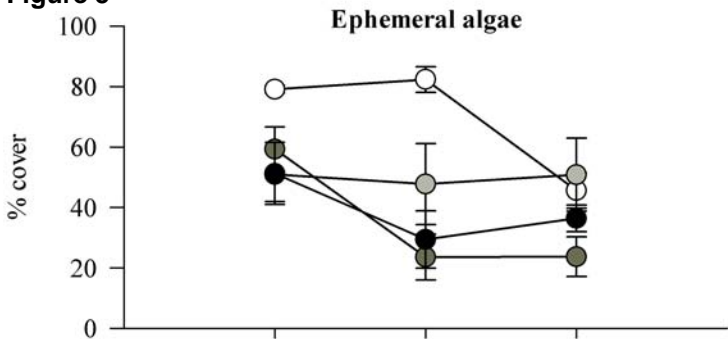
Figure 5

Figure 6

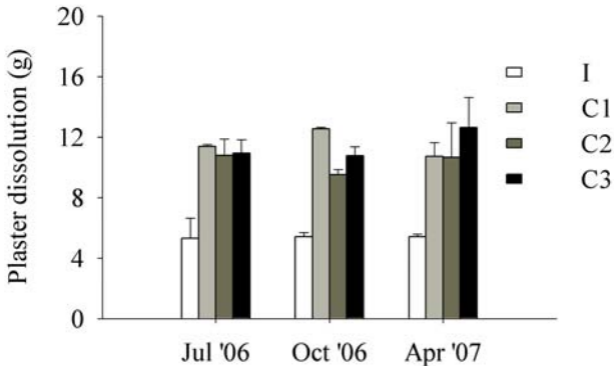


Table 1. Asymmetrical analysis of variance comparing the disturbed (*I*) and control (*C*'s) locations, where: *a* = times of sampling, *b* = all locations (the disturbed and 3 controls), *n* = number of replicates. Both time and location are random and orthogonal with each other.

Source of variation	df	Expected mean square
Time = T	<i>a</i> -1	$\sigma_e^2 + n\sigma_{TxL}^2 + bn\sigma_T^2$
Location = L	<i>b</i> -1	$\sigma_e^2 + n\sigma_{TxL}^2 + an\sigma_L^2$
^e <i>I</i> vs. <i>C</i> 's	1	$\sigma_{e-I}^2 + n\sigma_{TxIvs.C's}^2 + an\sigma_L^2 + an\beta_{Ivs.C's}^2$
^d <i>C</i> 's	<i>b</i> -2	$\sigma_{e-C's}^2 + n\sigma_{TxC's}^2 + an\sigma_{C's}^2$
^c T x L	(<i>a</i> -1)(<i>b</i> -1)	$\sigma_e^2 + n\sigma_{TxL}^2$
^b T x <i>I</i> vs. <i>C</i> 's	(<i>a</i> -1)	$\sigma_{e-I}^2 + n\sigma_{TxL}^2 + n\sigma_{TxIvs.C's}^2$
^a T x <i>C</i> 's	(<i>a</i> -1)(<i>b</i> -2)	$\sigma_{e-C's}^2 + n\sigma_{TxC's}^2$
Residual	<i>ab</i> (<i>n</i> -1)	σ_e^2
Res <i>I</i>	<i>a</i> (<i>n</i> -1)	σ_{e-I}^2
Res <i>C</i> 's	<i>a</i> (<i>b</i> -1)(<i>n</i> -1)	$\sigma_{e-C's}^2$

^a tested over Res *C*'s

^b tested over the Residual if T x *C*'s can be eliminated from the model (not significant at $\alpha = 0.25$, Underwood, 1997); tested over T x *C*'s otherwise. These tests assume equivalence among σ_{TxL}^2 and $\sigma_{TxC's}^2$ (see Glasby, 1997).

^c tested over the Residual

^d tested over T x *C*'s

^e tested over the Residual if T x L and *C*'s can be eliminated from the model; tested over T x L if *C*'s can be eliminated but not T x L; tested over *C*'s if this term cannot be eliminated from the model. These tests assume equivalence among $\sigma_{TxIvs.C's}^2$, $\sigma_{TxC's}^2$ and σ_{TxL}^2 , and among σ_L^2 and $\sigma_{C's}^2$.

Adapted from Terlizzi et al., (2005)

Table 2. Asymmetrical analysis of variance comparing the abundance of conspicuous lower shore taxa in the disturbed (*I*) and control (*C*'s) locations.

Source	df	Frondose algae		Turf-forming algae		Crustose algae		Filamentous algae		Ephemeral algae	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
T	3	0.17		1.49E ³		1.72		2.00		2.13	
L	3	45.97		153E ³		0.66		0.12		2.49	
<i>I</i> vs. <i>C</i> 's	1	126.77	22.76*	3.55E ²	0.17	1.64		0.11	0.43	7.16	
<i>C</i> 's	2	5.57	9.24*	2.11E ³	3.41	0.17	1.76	0.13	0.46	0.15	2.13
T x L	9	0.44	0.45	1.07E ³	3.01***	0.32	1.80	0.24	1.53	0.45	2.98**
T x <i>I</i> vs. <i>C</i> 's	3	0.12	0.13	1.98E ³	3.20	0.78	4.32**	0.15	0.51	1.22	8.01***
T x <i>C</i> 's	6	0.60	0.46	6.20E ²	1.42	0.10	0.52	0.29	1.68	0.07	0.44
Residual	144	0.99		3.57E ²		0.18		0.16		0.15	
Res <i>I</i>	36	0.05		1.19E ²		0.17		0.12		0.13	
Res <i>C</i> 's	108	1.30		4.36E ²		0.02		0.17		0.16	
Transformation		Ln (<i>x</i> + 1)				<i>x</i> ^{0.1}		<i>x</i> ^{0.1}		<i>x</i> ^{0.1}	
Cochran's test		<i>C</i> = 0.17		<i>C</i> = 0.27**		<i>C</i> = 0.17		<i>C</i> = 0.15		<i>C</i> = 0.13	

Significant terms in bold: * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001

E = x10

Table 3. Asymmetrical analysis of variance comparing the abundance of conspicuous upper shore taxa in the disturbed (*I*) and control (*C*'s) locations.

Source	df	Barnacles		Limpets		Littorinids		Ephemeral algae	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
T	3	1.25E ²		0.60		16.99		0.14	
L	3	2.69E ³		1.30		31.93		6.78	
<i>I</i> vs. <i>C</i> 's	1	7.80E ³	61.01*	3.54	9.27*	87.94	4.58	19.97	68.73***
<i>C</i> 's	2	1.28E ²	2.17	0.18	0.40	3.93		0.18	0.67
T x L	9	4.01E ¹	0.21	0.38	2.24*	19.21	7.58***	0.29	1.41
T x <i>I</i> vs. <i>C</i> 's	3	2.67E ⁰	0.01	0.25	0.57	18.58	0.95	0.31	1.53
T x <i>C</i> 's	6	5.88E ¹	0.24	0.45	1.99	19.52	6.10***	0.28	1.15
Residual	144	1.94E ²		0.17		2.53		0.21	
Res <i>I</i>	36	2.83E ¹		0.01		0.54		0.10	
Res <i>C</i> 's	108	2.50E ²		0.22		3.20		0.24	
Transformation				Ln (<i>x</i> + 1)		Sq-rt		<i>x</i> ^{0.1}	
Cochran's		C = 0.16		C = 0.16		C = 0.15		C = 0.09	

Significant terms in bold: p-values as in Table 2.

Table 4. Asymmetrical analysis of variance comparing the abundance of conspicuous lower shore taxa on recruitment plates in the disturbed (*I*) and control (*C*'s) locations.

Source	df	Ephemeral algae		Filamentous algae		Crustose algae		Turf-forming algae		Barnacles	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
T	2	4.50E ²		8.44		1.77E ²		2.10		1.05E ³	
L	3	2.41E ³		2.69		4.42E ²		5.40		5.00E ²	
<i>I</i> vs. <i>C</i> 's	1	1.92E ³	0.73	5.83	6.09*	4.80E ²		4.49	0.74	4.54E ²	1.13
<i>C</i> 's	2	2.65E ³	3.99	1.13	0.62	4.23E ²	2.37	5.86	0.75	5.22E ²	1.22
T x L	6	5.15E ²	1.19	1.23	1.28	6.28E ²	3.02*	6.07	14.08***	4.00E ²	1.81
T x <i>I</i> vs. <i>C</i> 's	2	2.18E ²	0.33	0.06	0.03	1.53E ³	7.34**	2.67	0.34	3.50E ²	0.82
T x <i>C</i> 's	4	6.64E ²	1.59	1.81	1.73	1.79E ²	1.21	7.76	16.04***	4.26E ²	1.44
Residual	48	4.31E ²		0.96		2.08E ²		0.43		2.21E ²	
Res <i>I</i> 's	12	4.74E ²		0.69		3.88E ²		0.27		0	
Res <i>C</i> 's	36	4.17E ²		1.05		1.48E ²		0.48		2.95e ²	
Transformation				Ln (<i>x</i> + 1)				Ln (<i>x</i> + 1)			
Cochran's		C = 0.21		C = 0.23		C = 0.43**		C = 0.25		C = 0.67**	

Significant terms in bold: p-values as in Table 2.

Table 5. Asymmetrical analysis of variance comparing the abundance of conspicuous upper shore taxa on recruitment plates in the disturbed (*I*) and control (*C*'s) locations.

Source	df	Ephemeral algae		Barnacles	
		MS	<i>F</i>	MS	<i>F</i>
T	2	2.31E ³		52.13	
L	3	3.40E ³		20.24	
<i>I vs. C's</i>	1	8.54E ³		55.14	
<i>C's</i>	2	8.30E ²	1.67	2.80	1.48
T x L	6	8.38E ²	2.43*	5.80	7.81***
T x <i>I vs. C's</i>	2	1.52E ³	4.41*	13.61	7.17*
T x <i>C's</i>	4	4.97E ²	1.15	1.90	2.03
Residual	48	3.45E ²		0.74	
Res <i>I</i>	12	9.04E ¹		0.17	
Res <i>C's</i>	36	4.30E ²		0.93	
Transformation				Ln (<i>x</i> + 1)	
Cochran's		<i>C</i> = 0.22		<i>C</i> = 0.26	

Significant terms in bold: p-values as in Table 2.

Table 6. Asymmetrical analysis of variance comparing plaster dissolution (g of dry weight) in the disturbed (*I*) and control (*C*'s) locations.

Source	df	MS	<i>F</i>
T	2	0.30	
L	3	76.89	
I vs. C's	1	222.17	61.17***
C's	2	4.26	1.26
T x L	6	2.28	0.63
T x I vs. C's	2	0.09	0.02
T x C's	4	3.38	0.54
Residual	24	3.63	
Res I	6	1.92	
Res C's	12	6.31	
Transformation			
Cochran's		<i>C</i> = 0.36	

Significant terms in bold: p-values as in Table 2.