



Long-term modifications of coastal defences enhance marine biodiversity

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LONG-TERM MODIFICATIONS OF COASTAL DEFENCES ENHANCES
DIVERSITY BY MODIFYING NETWORKS OF INTERACTIONS

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4

GUSTAVO M. MARTINS^{1,2*}, STUART R. JENKINS³, ANA I. NETO^{1,2},
STEPHEN J. HAWKINS^{4,5}, RICHARD C. THOMPSON⁶

6

8

1 CIIMAR/CIMAR - Interdisciplinary Centre of Marine and Environmental
Research, University of Porto, Rua dos Bragas 289, 4050-123 Porto, Portugal

10

2 CIRN & Grupo de Biologia Marinha, Departamento de Biologia,
Universidade dos Açores, 9501-801 Ponta Delgada, Azores, Portugal

12

3 School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey
LL59 5AB, UK

14

4 Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth
PL1 2PB, UK

16

5 Ocean and Earth Science, National Oceanography Centre Southampton,
University of Southampton, Waterfront Campus, Southampton SO14 3ZH, UK

18

6 Marine Biology and Ecology Research Centre, Marine Institute, Plymouth
University, Plymouth PL4 8AA, UK

20

* EMAIL: gmartins@uac.pt

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26 SUMMARY

Realisation that hard coastal defence structures support lower biodiversity
28 than natural habitats prompted a wealth of research seeking to identify design
enhancements that offer ecological benefits. Some studies showed that
30 artificial structures could be modified to increase levels of diversity. The
majority of studies, however, have only considered the short-term effects of
32 such modifications even though reliance on results from short-term studies
may lead to serious misjudgements in conservation ecology. In this study, we
34 planned a long-term 7-year experiment to examine how the addition of small
pits to otherwise featureless seawalls could enhance the stocks of a highly
36 exploited limpet (*Patella candei*). Modified areas of the seawall supported
enhanced stocks of limpets 7 years after the addition of pits. Modified areas of
38 the seawall also supported a community that differed in the distribution of
littorinids, barnacles and macroalgae compared to the controls. Responses to
40 the different treatments (varying in the numbers and size of experimental pits)
were species-specific and there was evidence that some species responded
42 directly to differences among treatments, whereas others responded indirectly
via changes in the distribution of competing species. This type of habitat
44 enhancements is easily done and can have positive long-lasting effects on the
ecology of urban seascapes. Understanding the interactions between species
46 can lead to a rule-based approach to interventions to enhance biodiversity.

48 Keywords: Azores, coastal urbanisation, community structure, conservation,
habitat enhancement, long-term, *Patella*

50

INTRODUCTION

52 The replacement of natural shores by hard coastal defence structures (e.g.
seawalls, breakwaters, revetments, groynes) is increasing as a response to
54 the growing need to defend the coast from sea level rise and stormier seas
(e.g. Airoldi *et al.* 2005; Moschella *et al.* 2005; Chapman 2006). Realisation
56 that these structures generally support lower biodiversity than natural habitats
(e.g. Chapman 2003; Chapman 2006; Chapman & Bulleri 2003; Moschella *et*
58 *al.* 2005; Vaselli, Bulleri & Benedetti-Cecchi 2008; Firth *et al.* 2013a; Browne
& Chapman 2014) has focused attention on designing structures that help
60 facilitate specific ecological outcomes (Firth *et al.* 2014).

62 In cases where natural shores are completely replaced by artificial habitats
there will be an obvious loss of habitat and the species therein. However,
64 even when species colonise such artificial structures, they can hardly be
considered as surrogates for the natural shores they replace (see review by
66 Chapman & Underwood 2011). For instance, there is now documented
evidence that on such hard coastal defence structures (e.g. seawalls) there
68 can be changes in the composition of species assemblages (Bulleri *et al.*
2005; Moschella *et al.* 2005), abundances (Chapman 2003), size-structure
70 and reproductive output of populations (Moreira *et al.* 2006) and competitive
interactions (Jackson *et al.* 2008; Iveša *et al.* 2010). Moreover, less obvious
72 changes in community structure can also be found on natural shores
surrounded (Goodsell *et al.* 2007) or in the vicinity (e.g. Martins *et al.* 2009) of
74 such artificial habitats.

76 Lack of habitat heterogeneity has been put forward as the main cause of the
lower level of biodiversity generally observed on sea defence structures
78 (Chapman & Underwood 2011). There is now mounting evidence that
experimentally increasing the complexity and heterogeneity of otherwise
80 topographically simple surfaces, for example by including water-retaining
features, pits and crevices, can substantially increase the biodiversity of the
82 structure (Chapman & Blockley 2009; Firth *et al.* 2013b; Browne & Chapman
2014; Firth *et al.* 2014). Modifications can also be tailored to increase the
84 abundances of species of economic interest (Martins *et al.* 2010). These
studies generally support the idea that hard coastal defence structures can be
86 modified to support an increasing level of diversity and thus contribute toward
the conservation and management of urbanised coastlines whilst providing
88 effective protection from sea level rise and stormier seas.

90 A common feature of these studies, however, is that they are relatively short-
term (typically < 1 year, e.g. Martins *et al.* 2010; Browne & Chapman 2014)
92 and little is known about how modifications made to coastal defence
structures continue to influence community structure in the longer term. This
94 is important as there is evidence that results from short-term experiments do
not always mirror those in the longer-term (e.g. O'Connor & Crowe 2005) and
96 that this may have important implications when considering management
actions (Callahan 1984; Magnuson 1990).

98

Patella candei d'Orbigny is an endemic species to the Macaronesia where it is
100 extensively exploited for human consumption. In the Canary Islands, for

instance, *P. candei* is virtually extinct, presumably to due to over-exploitation
102 (Côte-Real *et al.* 1996; Navarro *et al.* 2005). In the Azores, *P. candei* has
also been historically collected with an important input to the local economy
104 until the collapse of the stocks in the mid 1980s (Hawkins *et al.* 2000). The
decline in limpet abundances is arguably the largest anthropogenic impact on
106 Azorean coastal ecosystems and has been correlated with archipelago-wide
ecological impacts including changes in the balance between consumers and
108 producers (Martins *et al.* 2008). In 1993, legislation has been passed
establishing fishing protected zones (where the collection of limpets is fully
110 prohibited), seasonal fishing closures and minimum legal catch sizes. Such
measures, however, have proved largely unsuccessful due to lack of
112 enforcement and populations of limpets are currently still showing clear signs
of over-exploitation (Martins *et al.* 2011).

114

In 2006, experimental habitat enhancements, consisting of the addition of pits
116 differing in size drilled into seawalls at different densities, showed that over
the short-term (4 months) the abundance of limpets increased in enhanced
118 areas of the seawall (in comparison to unmanipulated controls) as a result of
both animal immigration and new recruitment (Martins *et al.* 2010). Results
120 showed that the overall effects of pit density and size varied with limpet size
class with the numbers of large limpets being limited by the availability of pits
122 of the larger size, whereas small limpets were limited by the density of pits (of
whatever size). In this study we re-surveyed the experiment after 7 years to
124 evaluate the long-term effects of experimental habitat enhancement on the
abundances of the limpet *P. candei*.

126

As well as their economic value in some parts of the world, patellid limpets
128 also play a key community structuring role on European shores (e.g. Hawkins
& Hartnoll 1983; Jenkins *et al.* 2005; Coleman *et al.* 2006), suggesting that
130 variation in the distribution of limpets as a response to different habitat
enhancements may have led to community-wide cascading effects. Moreover,
132 different species of grazing gastropods have distinct influences on the
community (e.g. Hawkins *et al.* 1989; O'Connor & Crowe 2005; Griffin *et al.*
134 2010). A 7-year period was judged long enough to allow the full influence of
changes in habitats on the establishment of networks of interactions (e.g.
136 competition, facilitation, predation).

138 **METHODS**

Study sites and community

140 The study was done at São Roque on the island of São Miguel, Azores. São
Roque was a gentle sloping basaltic rocky shore with a large number of rock
142 pools that has been largely replaced by the construction of a 4-5 km long
seawall for protection of the shoreline. Our experimental habitat enhancement
144 was applied to a seawall made of 2 m wide natural basaltic blocks; these had
smooth surfaces and lacked the micro-topographic rugosity characteristic of
146 adjacent natural shores (Martins *et al.* 2010). The experimental treatments
were applied at mid shore level just above the algal dominated lower shore in
148 areas where the barnacle *Chthamalus stellatus* is the dominant space
occupier and the limpet *Patella candei* reaches its largest abundance. Other
150 patellid limpets (*P. aspera*) present on Azorean shores are not common at this

tidal height. At this height, macroalgae are generally restricted to ephemeral
152 species (e.g. *Ulva* spp., *Chaetomorpha* spp.) and a few perennial turf-forming
algae (e.g. *Caulacanthus ustulatus*). Other grazing gastropods, including the
154 littorinids *Tectarius striatus* and *Melarhaphe neritoides*, can also be locally
abundant.

156

At each of two sites 200 m apart, 25 areas of 25 × 25 cm were marked and
158 randomly assigned to 5 treatments. Five replicate areas were assigned to
unmanipulated controls. The remaining 20 areas were randomly assigned to a
160 2-way orthogonal design including the factors pit size (small and large) and pit
density (high and low) with five replicates per treatment. Small and large pits
162 were 12 and 24 mm in diameter (both with a depth of 10 mm). Lesser and
greater density treatments corresponded to 8 and 16 pits drilled within each
164 area. Pits were drilled using an electrical power drill and were evenly spaced
within the experimental areas. The sizes and densities of pits used are within
166 the range of sizes and densities of pits observed on natural shores (for further
details see Martins *et al.* 2010). The experimental habitat enhancement was
168 established between November and December 2006.

170 **Sampling design**

Experimental areas were resurveyed in November 2013 (84 months after
172 establishment) and March 2014 (87 months after establishment). During the
period of time between the start of the experiment and the initial sampling to
174 determine short-term effects of habitat enhancements (see Martins *et al.*
2010) and the resurveys in 2013 and 2014, the experimental areas were left

176 untouched and no sampling occurred. In November 2013, experimentally
enhanced plots were re-located and assessed for signs of deterioration (e.g.
178 experimental treatments, i.e. number and size of pits, were still evident and
not masked by natural erosion). At this time, the abundance of mobile
180 gastropods (*Patella candei*, *Tectarius striatus* and *Melarhappe neritoides*)
within each area (25 x 25 cm) was counted. Control areas were not evaluated
182 and sampled at this time. In March 2014, we resurveyed the experiment and
recounted all gastropods including those in control areas. In addition, we
184 estimated the percentage cover of sessile species (macroalgae and
barnacles). For this purpose, we used a 25 × 25 cm sampling quadrat divided
186 in 25 sub-quadrats. Within each sub-quadrat, a score between 0 (absent) and
4 (full cover) was attributed to all species present. Total percentage cover was
188 obtained by summing the scores of the 25 subquadrats (see Dethier *et al.*
1993 for further details). Mobile animals (limpets and littorinids) were counted
190 as described above, and limpets were measured (shell maximum length)
using a Vernier calliper. We were able to find all areas except 3 control
192 locations (marks were gone). We replaced these missing controls with 3
randomly selected areas scattered among experimental areas. No attempt
194 was done to sample communities surrounding the experimental areas (25 x
25 cm) since the strongest interacting species in this system, *P. candei*,
196 exhibits a homing behaviour (Cacabelos unplished data) and was thus
unlikely to influence assemblage structures a few centimetres away from the
198 experimental areas.

200 **Data analysis**

Enhanced vs control areas

202 To test the hypothesis that experimentally enhanced areas (no matter the
treatment) support a greater abundance of limpets and a community structure
204 that differs from unmanipulated controls, we used a 2-way mixed model
PERMANOVA (a permutational-based analysis of variance, Anderson 2001)
206 with the following factors: site (2 levels, random) and treatment (2 levels:
enhanced treatments vs controls, fixed). We used the contrast function, which
208 makes a partition of the variance and allows the comparison of the variable of
interest among controls and the experimentally enhanced areas as a whole (a
210 similar approach to that used in an asymmetrical analysis). The variables
analysed were the abundance of the gastropods (*Patella candei*, *Tectarius*
212 *striatus* and *Melarhappe neritoides*) and the percentage cover of the barnacle
Chthamalus stellatus and macroalgae. Prior to analysis, macroalgae were
214 grouped into two morpho-functional groups: uncorticated ephemeral algae
including both filamentous (*Chladophora* spp.) and foliose (*Ulva* spp.) species;
216 hereafter referred to as ephemerals alone) and corticated perennial turfs (e.g.
Caulacanthus ustulatus; hereafter referred to as turfs alone). Encrusting algae
218 were also present in some areas, but their overall abundance was very low (<
1%) and was not analysed. This analysis was applied to data sampled on
220 March 2014 as no controls were sampled during November 2013.

222 *Comparison among habitat enhancement treatments*

To test the hypothesis that different enhancement treatments (variation in pit
224 density and size) influence the distribution of limpets leading to community-
wide differences we used a 3-way PERMANOVA design with the following

226 factors: site (2 levels, random), pit size (2 levels, fixed) and pit density (2
levels, fixed). The analyses were run to test for differences in the abundance
228 of all three gastropods species in November 2013 and March 2014. Results
were similar between these two dates and we only present data from March
230 2014 for simplicity (analysis of November 2013 in supplementary online
material 2). These analyses were also run to test for differences in percentage
232 cover of barnacles and macroalgae (turfs and ephemerals).

234 All the univariate analyses were run using the routine PERMANOVA
(Anderson 2001) available on PRIMER V6 (Clarke & Gorley 2006) based on
236 Euclidean distances and using 999 permutations of residuals under a reduced
model (similar to traditional ANOVA). Prior to analyses, data were checked for
238 heterogeneity of variances using the PERMDISP (Anderson 2004) function
and transformations were applied where necessary (Underwood 1997). Pair-
240 wise comparisons were done to test for differences among means within
significant terms.

242

The chi-squared test of independence (or association) was used to test the
244 null hypothesis of no association between the frequency of the three species
of grazing gastropods and the experimental treatments. The mean number of
246 each species in each of the four treatments was used as observed
frequencies, respectively.

248

We used Pearson's product-moment correlation to highlight potential
250 relationships emerging from changes in the abundance of grazers on the
sessile taxa.

252

RESULTS

254 **Enhanced vs control areas**

Analysis of the gastropod assemblages showed that all the three species
256 (*Patella candei*, *Tectarius striatus* and *Melarhappe neritoides*) tended to be
more abundant in enhanced areas of the seawall compared to unmanipulated
258 controls (Fig. 1 A-C). This result was significant in the cases of *P. candei* and
T. striatus (Table S1 - Appendix ST1), which were around 5 and 11 times
260 more abundant in enhanced areas of the seawall, respectively. Although the
abundance of *M. neritoides* was over 2 times greater in enhanced areas of the
262 seawall (Fig. 1C), no significant effect of seawall modification was found
(Table S1). The mean limpet biomass per plot (dry body weight estimated for
264 each individual from an established length-mass relationship, see Martins et
al., 2008) of *P. candei* was also approximately 5 times greater (mean limpet
266 biomass in mg \pm SE, control: 38.2 ± 17.2 , enhanced areas: 182.9 ± 30.4) in
enhanced areas of the seawall. When considering the entire grazing
268 assemblage (all species together), there was a significantly greater number of
grazers in enhanced areas of the seawall than in unmanipulated controls (Fig.
270 1D, Table S1 - Appendix ST1).

272 The abundance of barnacles and turfs was greater in enhanced areas of the
seawall (Fig. 2A,C), although this was only statistically significant in the case

274 of barnacles (Table S2 - Appendix ST1). The abundance of ephemerals was
highly variable among areas and there were no differences observed in the
276 comparison between enhanced and control areas (Fig. 2E, Table S2 -
Appendix ST1).

278

Comparison among habitat enhancement treatments

280 Species making up the gastropod assemblage had variable responses to the
different treatments. The limpet *P. candei* responded positively to both the
282 density and size of pits (Fig. 3A), being significantly more abundant in
enhanced areas with a higher density of pits and in areas with larger pits
284 (Table S3 - Appendix ST1). In contrast, the littorinids *T. striatus* and *M.*
neritoides did not respond to pit density, but were significantly more abundant
286 in areas of the seawall enhanced with small pits (Fig. 3 B-C, Table S3 -
Appendix ST1). For *M. neritoides* this result was only detected at one of the
288 sites examined.

290 Overall, the null hypothesis of no association between the gastropod
assemblage and the experimental treatments was rejected (Table 1). This
292 result suggests that each enhancement treatment supports a structurally
divergent assemblage of grazers (Figure 3D). This was especially evident in
294 those treatments that differed the most (small pit size and low density vs large
pit size and high density) - as indicated by the relative chi-squared
296 contribution of each treatment (Table 1). All the above patterns were also
present and similar 4 months earlier in November 2013 (Appendix S2)
298 suggesting that this pattern was temporally consistent.

300 When considering the remainder of the assemblage, the abundance of
barnacles tended to be greater in areas with large pits (Fig. 2B), although this
302 was not statistically significant (Table S4 - Appendix ST1). A significant
interaction between site, pit density and pit size was detected in the case of
304 turfs (Table S4 - Appendix ST1). Pair-wise comparisons showed that the
abundance of turfs was similar among areas with small and large pits, but was
306 significantly greater in areas with higher pit density (Fig. 2D), at site 1 (Table
S4 - Appendix ST1). The abundance of ephemerals also varied among
308 enhancement treatments (Fig. 2F). A significant interaction was found
between site and pit density (Table S4 - Appendix ST1). The abundance of
310 ephemerals was greater in areas with lower pit density (Fig. 2F), although this
was only significant at site 1 (see pair-wise comparisons in Table S4 -
312 Appendix ST1).

314 Strong correlations were found between the abundance of barnacles, turfs
and ephemerals and *P. candei* (Table 2). The correlation was positive for
316 barnacles and turfs, but negative between ephemerals and limpets. The
abundance of barnacles and ephemerals was also weakly positively
318 correlated with *T. striatus* but there was a strong and negative correlation
between the later and the abundance of turfs (Table 2). All the sessile taxa
320 (barnacles, turfs and ephemerals) showed a negative correlation with the
abundance of *M. neritoides* (Table 2).

322

DISCUSSION

324 **Long-term effects on the target species**

Our results suggest that those areas of the seawall that were experimentally
326 modified to enhance the abundance of the highly exploited limpet *Patella*
candei, have had a long-term impact. Although no sampling was done in
328 between the two periods, our resurvey has shown that the short-term
enhancement of *P. candei*, observed by Martins et al (2010) has been
330 maintained over a 7 year period. Thus the simple approach of drilling pits in
the rock is highly effective in promoting the abundance and biomass of this
332 exploited species over many years; the abundance and biomass of *P. candei*
7 years on was at least 5 times greater in enhanced compared to control
334 areas of the seawall.

336 As with results from the short-term experiment (Martins *et al.* 2010), limpets
responded differently to the different habitat enhancement treatments.
338 Observations after 7 years indicate that limpet abundance as a whole (not
differentiating among different size classes; see Martins *et al.* 2010) was
340 positively influenced by the abundance of larger pits, suggesting that the
availability of large pits is potentially a limiting factor. This information can thus
342 be used when designing new infrastructure; in order to enhance limpet stocks,
emphasis should be placed on designing structures that offer a high density of
344 pits of the larger size. It should be noted that the larger individuals in this
study were all able to fit within the larger pits. It is unclear what happens to
346 animals larger than those that fit into pits. Such larger animals may eventually
seek other areas of the seawall as reliance on pits decreases with increasing

348 animal size (Martins *et al.* 2010). Such larger individuals are, however,
uncommon on Azorean shores due to over-exploitation (Martins *et al.* 2008).

350

Community-wide effects

352 Even though the modifications made to the seawall were initially designed
considering one specific species (*P. candei*), a longer-time perspective allows
354 examination of the influence on the structure of the entire assemblage,
including littorinids, barnacles and macroalgae (see Fig. 4). When considering
356 littorinids, it is interesting to note that their response to the distinct treatments
differed from that observed for limpets. While limpets appeared to be limited
358 by the availability of large pits, littorinids were more abundant in the smaller
pits (see Fig. 4a). Their abundance also did not appear to be limited by the
360 density of pits in contrast to that found for limpets. This might reflect the
gregarious nature of littorinids as several individuals of both *T. striatus* and *M.*
362 *neritoides* were often found sharing a single pit, as was also noted by Skov *et*
al. (2011). This was uncommon among limpets that were generally found
364 inhabiting pits alone. This different behaviour between limpets and littornids
likely reflects differences in the relative strength of intraspecific competition
366 among these gastropods (Underwood 1978).

368 Substantial variation in abundance of the other taxa (barnacles and
macroalgae) was also observed among experimental treatments, especially in
370 relation to pit size (see Fig. 4a). This suggests that the modifications made to
the seawall may have also influenced species other than prosobranch
372 gastropods. This is not surprising as surface topography is known to affect the

settlement by many organisms (e.g. Crisp 1955; Harlin & Lindbergh 1977;
374 Raimondi 1988). There is, however, an alternative explanation: that changes
in the abundance of barnacles and macroalgae are an indirect effect of
376 treatments through changes in the structure of the grazer assemblage (e.g.
Hartnoll & Hawkins 1985; Lubchenco 1983; Farrell 1988; Johnson *et al.* 1998;
378 Jenkins *et al.* 2005). For instance, ephemeral algae were generally more
abundant in areas of the seawall enhanced with small pits. Although in such
380 areas there were also increased densities of littorinids, there was little
difference in the community structure between these areas and the smooth
382 unmanipulated control areas of the seawall. This result suggests that
littorinids have little influence on the overall structure of the community - as
384 noted also by O'Connor & Crowe (2005) and Griffin *et al.* (2010) - even
though their abundance was enhanced by the addition of small pits. In
386 contrast, areas of the seawall enhanced by the addition of large pits
supported the most distinct community structure with a comparatively higher
388 abundance of limpets, turfs and barnacles, and a lower abundance of
ephemeral algae (Fig. 4a). Unlike ephemeral algae, a positive correlation was
390 found between barnacles and turfs and the abundance of limpets suggesting
that the latter may facilitate their establishment. As is widely known, intertidal
392 limpets generally have a large negative effect on the abundance of ephemeral
algae (Hawkins 1983; Van Tamelen 1987). Ephemeral algae, in turn, can
394 have an inhibitory effect of the establishment of perennial algae (e.g. Sousa
1979; Hawkins 1981; Viejo *et al.* 2008, Jenkins & Martins 2010). Selective
396 removal of ephemerals by high density of limpets in areas of the seawall
enhanced with large pits may have thus indirectly facilitated the establishment

398 of barnacles and turfs (Hawkins & Hartnoll 1983; Van Tamelen 1987;
Benedetti-Cecchi 2000) (Fig. 4b). Overall, these results appear to suggest
400 that the changes seen in the community structure in areas of the seawall
enhanced with the addition of large pits are a result of modifications to the
402 network of interactions among intertidal species (as schematically
represented in Figure 4b).

404

Conclusion

406 Our results suggest that the experimental modifications made to coastal
engineering can have long-lasting effects. This result is important from a
408 conservation perspective and reinforces the concept that simple modifications
made to coastal defence structures, that are unlikely to affect structural
410 integrity of the building blocks, can be used as a lasting and effective tool for
the conservation of species, provided that a solid understanding of the
412 ecology of the focal species is known. While the enhancement of unprotected
coastal infrastructures may be pointless, many infrastructures actually have
414 regulated access. In these cases, coastal infrastructures may positively
influence stocks of important species but also impact nearby areas via spill-
416 over effects. Our results, however, also suggest that the modifications to the
seawalls can influence non-targeted species both directly, by affecting the
418 spatial distribution of the organisms, and indirectly, by affecting the spatial
distribution of competitors and predators. Understanding the interactions
420 between species can lead to a rule-based approach to interventions to
enhance biodiversity.

422

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618 Table 1. χ^2 test of independence comparing the mean abundance of grazers
 among treatments. χ^2 global = 30.26, d.f. = 4, $P < 0.001$

		Species of grazers		
Treatment		<i>P. candei</i>	<i>T. striatus</i>	<i>M. neritoides</i>
622	Large, High			
	Observed	19.6	2.3	6.0
624	Expected	10.07	5.89	11.94
	χ^2 contribution	9.03	2.19	2.96
626	Large, Low			
	Observed	8.3	1.9	8.5
628	Expected	6.74	3.95	8.00
	χ^2 contribution	0.36	1.06	0.03
630	Small, High			
	Observed	8.5	6.9	16.7
632	Expected	11.58	6.78	13.74
	χ^2 contribution	0.82	<0.01	0.64
634	Small, Low			
	Observed	1.2	10.9	13.4
636	Expected	9.20	5.38	10.91
	χ^2 contribution	6.96	5.65	0.57

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642 Table 2. Pearson's product-moment correlation coefficients between the
abundance of grazers and the sessile taxa in experimental enhanced areas of
644 the seawall.

	Barnacles	Turfs	Ephemerals
646 <i>P. candei</i>	+0.36	+0.36	-0.31
<i>T. striatus</i>	-0.03	-0.27	+0.08
648 <i>M. neritodes</i>	-0.16	-0.32	-0.20

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Figure caption

668 Fig.1. Mean (+SE) abundance each of the prosobranch gastropod species (a)
P. candei, (b) *T. striatus*, (c) *M. neritoides* and (d) their combined abundance,
670 in unmanipulated controls and habitat-enhanced areas of the seawall in
November 2014. Abundance of enhanced areas of the seawall is averaged
672 among all the four enhancement treatments. Data from the two sites was
pooled together for clarity as there was no significant variation between sites
674 (Table S1).

676 Fig.2. Mean (+SE) percentage cover of (a,b) barnacles, (c,d) corticated turfs
and (e,f) ephemerals in November 2014. Comparison between unmanipulated
678 controls and habitat enhanced areas of the seawall on the left (see legend on
Fig. 1 for further details); comparison among different habitat enhancement
680 treatments on the right. LH – Large pit size and High density, LL – Large pit
size and Low density, SH – Small pit size and High density, SL – Small pit
682 size and Low density. Data from the two sites was pooled together for clarity
as there was no significant variation between sites in such most cases (Table
684 S3).

686 Fig.3. Mean (+SE) each of the prosobranch gastropod species (a) *P. candei*,
(b) *T. striatus*, (c) *M. neritoides* in each of the enhancement treatments in
688 November 2014. The last panel (d) is a duplication of data from previous
panels (without error bars for clarity) to show the relative differences in the
690 abundance of all species in each treatment. As such, bar length corresponds

to the mean abundance of *Patella candei* (black), *Tectarius striatus* (grey) and
692 *Melarhappe neritoides* (white). Legend as in Figure 2.

694 Fig. 4. a) Graphical representation of the community-wide effects of as a
result of habitat enhancement treatments related to pit size as of November
696 2014. For each of the five taxa data were standardised as the mean/maximum
abundance to represent magnitude of differences and to put abundance of the
698 different taxa at equal scale levels; continuous line – unmanipulated controls,
small-dotted line – areas enhanced with small pits; long-dotted line – areas
700 enhanced with large pits. b) Conceptual representation of the possible
network of interactions as result of habitat enhancement treatments (b1, b2
702 and b3). Continuous arrow – direct effect, dashed arrow – indirect effect.
Arrow thickness indicates the relative strength of effect; \pm indicates whether
704 effects are negative or positive.

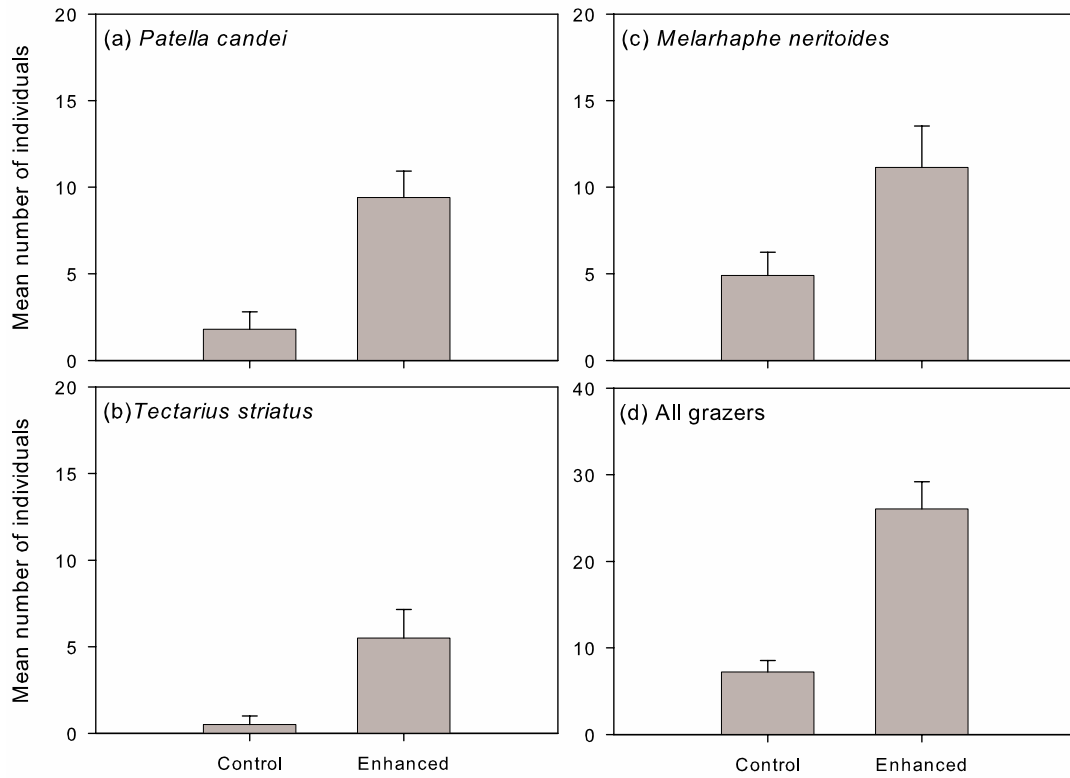
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Figure 1

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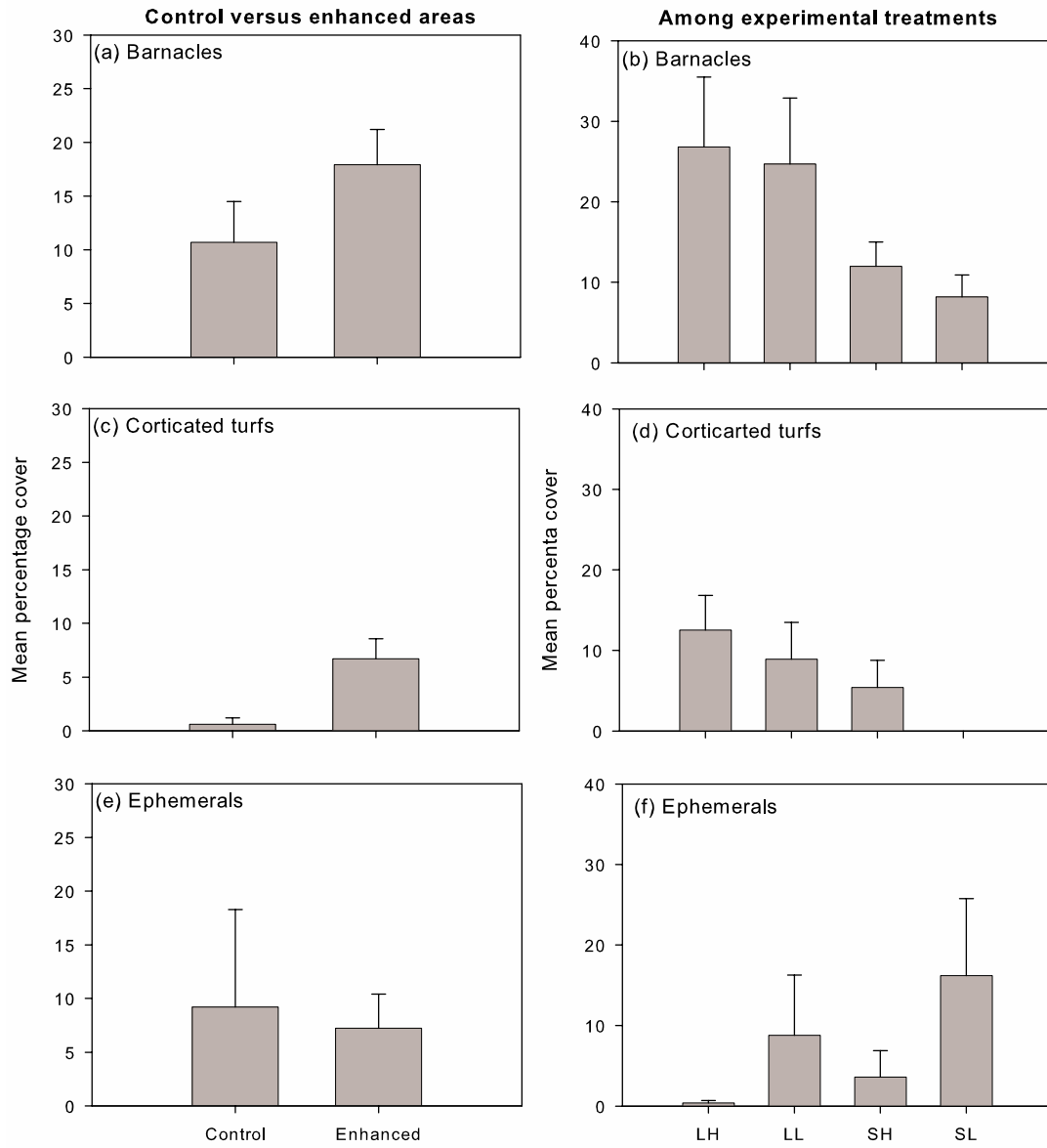
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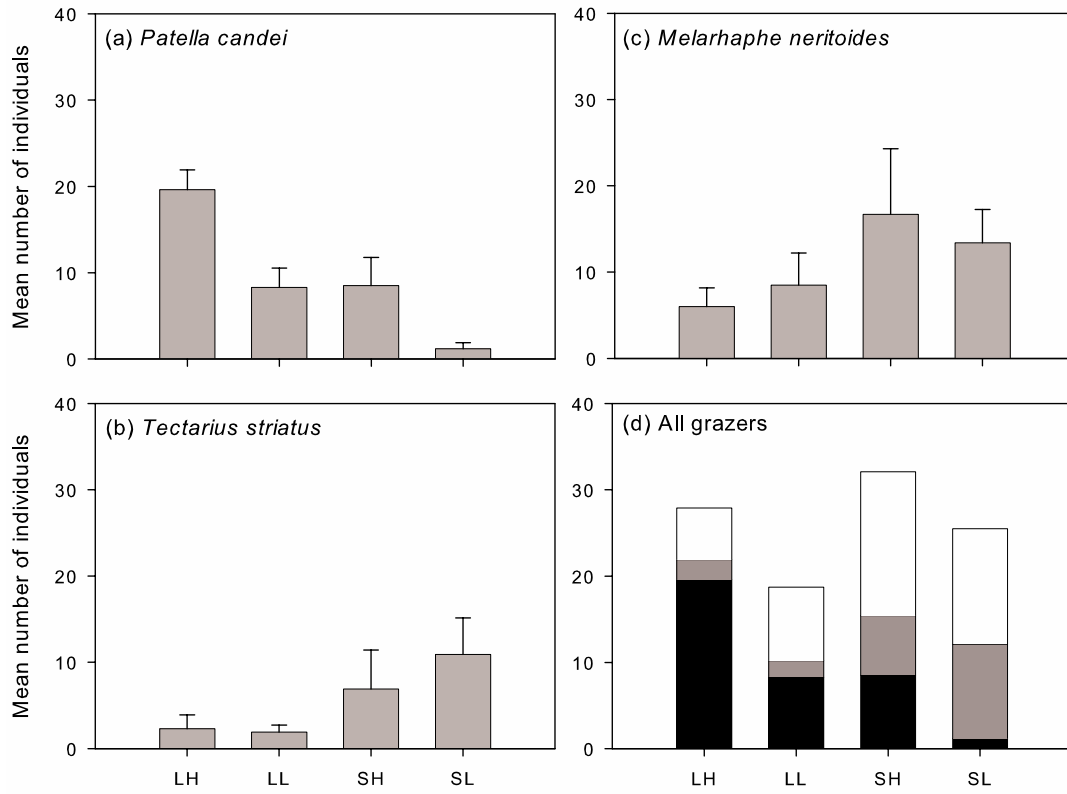


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Figure 3

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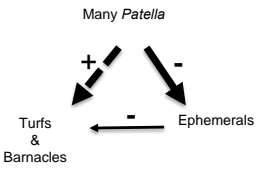
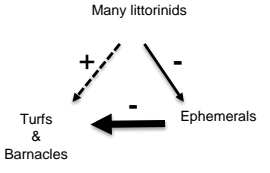
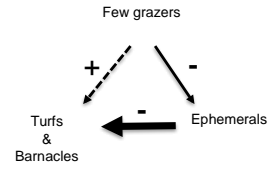
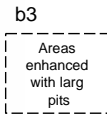
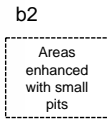
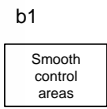
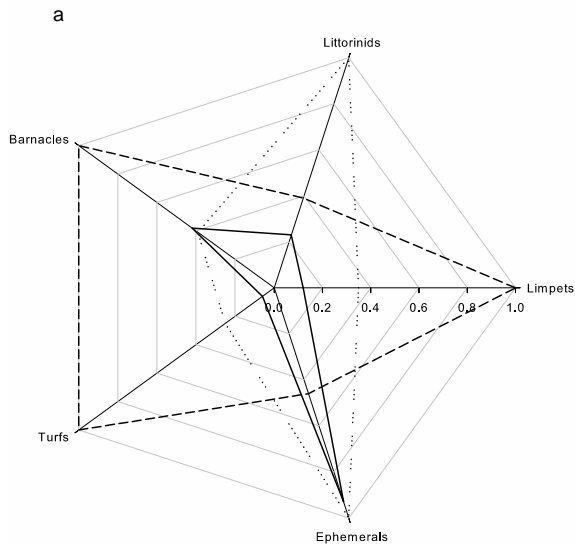
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Figure 4