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LONG-TERM MODIFICATIONS OF COASTAL DEFENCES ENHANCE MARINE BIODIVERSITY

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SUMMARY

34 Realisation that hard coastal infrastructures support lower biodiversity than
natural habitats has prompted a wealth of research seeking to identify design
36 enhancements offering ecological benefits. Some studies showed that
artificial structures could be modified to increase levels of diversity. Most
38 studies, however, only considered the short-term ecological effects of such
modifications even though reliance on results from short-term studies may
40 lead to serious misjudgements in conservation. In this study, we conducted a
7-year experiment to examine how the addition of small pits to otherwise
42 featureless seawalls could enhance the stocks of a highly exploited limpet.
Modified areas of the seawall supported enhanced stocks of limpets 7 years
44 after the addition of pits. Modified areas of the seawall also supported a
community that differed in the abundance of littorinids, barnacles and
46 macroalgae compared to the controls. Responses to different treatments
(numbers and size of pits) were species-specific and while some species
48 responded directly to differences among treatments, others might have
responded indirectly via changes in the distribution of competing species. This
50 type of habitat enhancement can have positive long-lasting effects on the
ecology of urban seascapes. Understanding of species interactions could be
52 used to develop a rule-based approach to enhance biodiversity.

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

56

INTRODUCTION

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

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

78 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
80 such artificial habitats.

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

96 A common feature of these studies, however, is that their duration is typically
< 1 year (e.g. Martins *et al.* 2010; Browne & Chapman 2014) and little is
98 known about how modifications made to coastal defence structures continue
to influence community structure in the longer term, yet results from short-
100 term experiments may not mirror those in the longer-term (e.g. O'Connor &
Crowe 2005) and this may influence feasible management actions (Callahan
102 1984; Magnuson 1990).

Patella candei d'Orbigny is endemic to Macaronesia where it is extensively exploited for human consumption. In the Canary Islands, for instance, *P. candei* is virtually extinct, presumably due to over-exploitation (Côrte-Real *et al.* 1996; Navarro *et al.* 2005). In the Azores, *P. candei* stocks collapsed in the mid-1980s (Hawkins *et al.* 2000) and may constitute the largest anthropogenic impact on Azorean coastal ecosystems, being correlated with archipelago-wide changes in the balance between consumers and producers (Martins *et al.* 2008). In 1993, legislation established fishing protected zones (where the collection of limpets is fully prohibited), seasonal fishing closures and minimum catch sizes but these have proved largely unsuccessful due to lack of enforcement and the limpets still show signs of over-exploitation (Martins *et al.* 2011).

In 2006, experimental habitat enhancements, consisting of the addition of pits differing in size drilled into seawalls at different densities, showed that over the short-term (4 months) the abundance of limpets increased in enhanced areas of the seawall (in comparison to unmanipulated controls) as a result of both animal immigration and new recruitment (Martins *et al.* 2010). 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 of the larger size, whereas small limpets were limited by the density of pits of whatever size. Here we re-surveyed the experiment to evaluate effects of experimental habitat enhancement on the abundances of the limpet *P. candei* after seven years. We also examined the wider community level impacts of changes in

128 patellid limpet populations, because patellid limpets play a key community
structuring role on European shores (e.g. Hawkins & Hartnoll 1983; Jenkins *et*
130 *al.* 2005; Coleman *et al.* 2006), suggesting that variation in the distribution of
limpets as a response to different habitat enhancements may have led to
132 community-wide effects. Moreover, different species of grazing gastropods
have distinct influences on the community (e.g. Hawkins *et al.* 1989;
134 O'Connor & Crowe 2005; Griffin *et al.* 2010).

136 **METHODS**

Study sites and community

138 The study area was São Roque (São Miguel Island, Azores), which has a
gentle sloping basaltic rocky shore with many rock pools, that has been
140 largely replaced by the construction of a 4-5 km long seawall for shoreline
protection . Our experimental habitat enhancement was applied to a seawall
142 made of 2 m wide natural basaltic blocks; these had smooth surfaces and
lacked the micro-topographic rugosity characteristic of adjacent natural shores
144 (Martins *et al.* 2010). The experimental treatments were applied at mid-shore
level just above the algal-dominated lower shore in areas where the barnacle
146 *Chthamalus stellatus* is the dominant space occupier and the limpet *Patella*
candei reaches its largest abundance. Other patellid limpets (*P. aspera*)
148 present on Azorean shores are not common at this tidal height. At this height,
macroalgae are generally restricted to ephemeral species (e.g. *Ulva* spp.,
150 *Chaetomorpha* spp.) and a few perennial turf-forming algae (e.g.
Caulacanthus ustulatus). Other grazing gastropods, including the littorinids
152 *Tectarius striatus* and *Melarhaphe neritoides*, can also be locally abundant.

At each of two sites 200 m apart, 25 areas of 25 × 25 cm were marked and randomly assigned to 5 treatments. Five replicate areas were assigned to unmanipulated controls. The remaining 20 areas were randomly assigned to a 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 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 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 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 established between November and December 2006.

Sampling design

Experimental areas were resurveyed in November 2013 (84 months after establishment) and March 2014 (87 months after establishment). During the period of time between the start of the experiment and the initial sampling to determine short-term effects of habitat enhancements (see Martins *et al.* 2010) and the resurveys in 2013 and 2014, the experimental areas were left untouched and no sampling occurred. In November 2013, experimentally enhanced plots were re-located and assessed to ensure that pits within experimental treatments were still evident and not masked by natural erosion. At this time, the abundance of mobile gastropods (*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) within each area (25 x 25 cm) was

counted. Control areas were not evaluated and sampled at this time. In March 2014, we resurveyed the experiment and recounted all gastropods including those in control areas. In addition, we estimated the percentage cover of sessile species (macroalgae and barnacles). For this purpose, we used a 25 × 25 cm sampling quadrat divided 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 obtained by summing the scores of the 25 subquadrats (see Dethier *et al.* 1993 for further details). Mobile animals (limpets and littorinids) were counted as described above, and limpets were measured (shell maximum length) using a Vernier calliper. We were able to find all areas except 3 control locations (marks were gone). We replaced these missing controls with 3 randomly selected areas scattered among experimental areas. No attempt was made to sample communities surrounding the experimental areas (25 x 25 cm) since the strongest interacting species in this system, *P. candei*, exhibits a homing behaviour (Cacabelos unpublished data) and was thus unlikely to influence assemblage structures a few centimetres away from the experimental areas.

Data analysis

A mixed model asymmetrical analysis of variance (ANOVA) was used to test for differences in the abundance of taxa among experimental treatments using the factors 'site' (random) and 'among all' (fixed and orthogonal to site). The latter was partitioned into 'control vs treatments', to compare the abundance of taxa in control areas to the average of the enhanced areas, and 'among treatments'. In addition, the factor 'among treatments' was further

decomposed and restructured to allow testing the effects of pit 'size' (fixed)

and 'density' (fixed and orthogonal to 'size'). These are effectively two separate analyses, which can subsequently be built together into a single ANOVA table. Residuals were also decomposed to match changes in the numbers of replicates for both analyses.

Prior to analysis, data were checked for heterogeneity of variances and transformations were applied where necessary (Underwood 1997). Student-Newman-Keuls (SNK) tests were used a posteriori to examine for differences within significant terms.

The variables analysed were the abundance of the gastropods (*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) and the percentage cover of the barnacle *Chthamalus stellatus* and macroalgae. Prior to analysis, macroalgae were grouped into two morpho-functional groups (Steneck & Dethier 1994) uncorticated ephemeral algae including both filamentous (*Chladophora* spp.) and foliose (*Ulva* spp.) species (hereafter referred to as ephemerals alone) and corticated perennial turfs such as *Caulacanthus ustulatus* (hereafter referred to as corticated turfs alone). Encrusting algae 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 March 2014 as no controls were sampled during November 2013. A simple 3-way ANOVA with 'site' 'pit density' and 'pit size' was used to analyse November 2013. Results were similar between these two dates and we only

present data from March 2014 for simplicity (analysis of November 2013 in
Appendix S2).

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

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

RESULTS

Enhanced vs control areas

Analysis of the gastropod assemblages showed that all the three species
(*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) were on
average, more abundant in enhanced areas of the seawall compared to
unmanipulated controls (Fig. 1 A-C). This result was significant in the cases of
P. candei and *T. striatus* (Table S1 - Appendix S1), which were around 5 and
11 times 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 seawall (Fig. 1C), no significant effect of seawall
modification was found (Table S1). The mean limpet biomass per plot (dry
body weight estimated for each individual from an established length-mass

relationship, see Martins et al., 2008) of *P. candeï* was also approximately 5 times greater (mean limpet 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 assemblage (all species together), there was on average a significantly greater number of grazers in enhanced areas of the seawall than in unmanipulated controls (Fig. 1D, Table S1).

Using SNK tests to examine for differences within the factor 'among all' (and not only the control to the average of enhanced areas) showed that, in comparison to controls, the numbers of limpets were effectively and significantly greater in all of the enhanced treatments but one (small and low pit density)(Table S2 – Appendix S1). In the case of *T. striatus*, and despite the significant effect detected between controls and the average of enhanced areas, SNK tests failed to find significant differences between control and all the four enhanced treatments but one (small and low pit density)(Table S2).

Among the remainder of the assemblage, a significant difference was also found between controls and the average of enhanced areas in the abundance of barnacles and corticated turfs (Table S1). These were nearly twice and 11 times more abundant in enhanced areas than in controls respectively (Fig. 2A,B). In contrast, the abundance of ephemerals was highly variable and did not respond consistently to treatments (Fig. 2C, Table S1)

Using SNK tests to examine for differences within the factor 'among all' (and not only the control to the average of enhanced areas) showed that, in

comparison to controls, the abundance of barnacles was significantly greater
in treatments with large pits, independently of their density (Table S2). For
corticated turfs, results were spatially variable; at one site no difference was
found, whilst on the other site there were significant differences only between
controls and areas with large and high density of pits (Table S2).

Effects of pit size and density

Species making up the gastropod assemblage had variable responses to the
different treatments. The limpet *P. candei* responded positively to both the
density and size of pits (Fig. 1A), being significantly more abundant in
enhanced areas with a higher density of pits and in areas with larger pits
(Table S1). In contrast, the littorinids *T. striatus* and *M. neritoides* did not
respond to pit density, but were significantly more abundant in areas of the
seawall enhanced with small pits (Fig. 1B-C, Table S1). For *M. neritoides* this
result was only detected at one of the sites examined.

Overall, the null hypothesis of no association between the gastropod
assemblage and the experimental treatments was rejected (Table 1). This
result suggests that each enhancement treatment supports a structurally
divergent assemblage of grazers (Fig. 1D). This was especially evident in
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
contribution of each treatment (Table 1). All the above patterns were also
present and similar 4 months earlier in November 2013 (Appendix S2)
suggesting that this pattern was temporally consistent.

302

When considering the remainder of the assemblage, the abundance of
304 barnacles was significantly greater in areas with large pits (Fig. 2A, Table S1).
A significant interaction between site, pit density and pit size was detected in
306 the case of corticated turfs (Table S1). Inspection of Figure 2B suggests that
these tended to increase in abundance with increasing pit area although
308 results were spatially variable (see SNK tests in Table S2).

The abundance of ephemerals also varied among enhancement treatments
310 (Fig. 2C). A significant interaction was found between site and pit density, and
to lesser extent ($\alpha = 0.10$) between site and pit size (Table S1). SNK tests
312 showed that the abundance of ephemerals was greater in areas with lower pit
density (Fig. 2C), although this was only significant at site 1 (Table S2).

314

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

324 DISCUSSION

Long-term effects on the target species

Our results suggest that those areas of the seawall that were experimentally modified to enhance the abundance of the highly exploited limpet *Patella candei*, have had a long-term impact. Although no sampling was done in between the two periods, our resurvey has shown that the short-term enhancement of *P. candei*, observed by Martins et al (2010) has been 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 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 areas of the seawall.

As with results from the short-term experiment (Martins *et al.* 2010), limpets responded differently to the different habitat enhancement treatments. Observations after 7 years indicate that limpet abundance as a whole (not differentiating among different size classes; see Martins *et al.* 2010) was positively influenced by the abundance and size of pits, suggesting that particularly the availability of large pits is potentially a limiting factor. This information can thus 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 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 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 animal size (Martins *et al.* 2010). Such larger

individuals are, however, uncommon on Azorean shores due to over-exploitation (Martins *et al.* 2008).

Community-wide effects

Even though the modifications made to the seawall were initially designed considering one specific species (*P. candei*), a longer-time perspective allows examination of the influence on the structure of the entire assemblage, including littorinids, barnacles and macroalgae (see Fig. 2). When considering 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 by the availability of large pits, littorinids were more abundant in the smaller pits. Their abundance also did not appear to be limited by the 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. 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 inhabiting pits alone. This different behaviour between limpets and littornids likely reflects differences in the relative strength of intraspecific competition among these gastropods (Underwood 1978).

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

many organisms (e.g. Crisp 1955; Harlin & Lindbergh 1977; Raimondi 1988).

376 There is, however, an alternative explanation: that changes in the abundance
of barnacles and macroalgae are an indirect effect of treatments through
378 changes in the structure of the grazer assemblage (e.g. Hartnoll & Hawkins
1985; Lubchenco 1983; Farrell 1988; Johnson *et al.* 1998; Jenkins *et al.*
380 2005). For instance, the abundance of ephemeral algae, in contrast with that
of limpets, tended to decrease with increasing pit area. Although in such
382 areas there were also increased densities of littorinids, there was little
difference in the community structure between these areas and the smooth
384 unmanipulated control areas of the seawall. This result suggests that
littorinids have little influence on the overall structure of the community - as
386 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
388 contrast, areas of the seawall enhanced by the addition of large pits
supported the most distinct community structure with a comparatively higher
390 abundance of limpets, corticated turfs and barnacles, and a lower abundance
of ephemeral algae (Fig. 3). Unlike ephemeral algae, a positive correlation
392 was found between barnacles and corticated turfs and the abundance of
limpets suggesting that the latter may facilitate their establishment. As is
394 widely known, intertidal limpets generally have a large negative effect on the
abundance of ephemeral algae (Hawkins 1983; Van Tamelen 1987).
396 Ephemeral algae, in turn, can have an inhibitory effect of the establishment of
perennial algae (e.g. Sousa 1979; Hawkins 1981; Viejo *et al.* 2008, Jenkins &
398 Martins 2010). Selective removal of ephemerals by high density of limpets in
areas of the seawall enhanced with large pits may have thus indirectly

facilitated the establishment of barnacles and corticated perennial turfs (Hawkins & Hartnoll 1983; Van Tamelen 1987; Benedetti-Cecchi 2000) (Fig. 4). Overall, these results appear to suggest that the changes seen in the community structure in areas of the seawall enhanced with the addition of large pits may be a result of modifications to the network of interactions among intertidal species (as schematically represented in Figure 3).

Conclusion

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

Supplementary material

For supplementary material accompanying this paper, visit

426 <http://www.journals.cambridge.org/ENC>

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438

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Table 1. Results of χ^2 tests of independence comparing the mean abundance
 600 of grazers among treatments (χ^2 global = 30.26, d.f. = 4, $P < 0.001$)

	Species of grazers			
602	Treatment	<i>P. candei</i>	<i>T. striatus</i>	<i>M. neritoides</i>
	Large, High			
604	Observed	19.6	2.3	6.0
	Expected	10.07	5.89	11.94
606	χ^2 contribution	9.03	2.19	2.96
	Large, Low			
608	Observed	8.3	1.9	8.5
	Expected	6.74	3.95	8.00
610	χ^2 contribution	0.36	1.06	0.03
	Small, High			
612	Observed	8.5	6.9	16.7
	Expected	11.58	6.78	13.74
614	χ^2 contribution	0.82	<0.01	0.64
	Small, Low			
616	Observed	1.2	10.9	13.4
	Expected	9.20	5.38	10.91
618	χ^2 contribution	6.96	5.65	0.57

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

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

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648 Figure caption

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, in unmanipulated controls and habitat-enhanced areas of the seawall in November 2014. C – control, SL – small and low pit density, LL – large and low pit density, SH – small and high pit density, LH – large and high pit density. In (d) bar length corresponds to the mean abundance of *Patella candei* (black), *Tectarius striatus* (grey) and *Melarhaphe neritoides* (white). Data from the two sites was pooled together for clarity as there was no significant variation between sites (Table S1).

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Fig. 2. Mean (+SE) percentage cover of (a) barnacles, (b) corticated turfs and (c) ephemerals in November 2014. See legend on Figure 1.

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Fig. 3. Conceptual representation of the possible network of interactions as result of habitat enhancement treatments. Continuous arrow – direct effect, dashed arrow – indirect effect. Arrow thickness indicates the relative strength of effect; $\pm$ indicates whether effects are negative or positive.

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674 Fig. 1

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688 Fig. 2

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692 Fig. 3