Effects of simulated human exploitation of a key grazer, *Patella vulgata*, on rocky shore assemblages

C. D. G. Borges[1,4,*], S. J. Hawkins[1,2], C. P. Doncaster[1], T. P. Crowe[3]

[1]Centre for Biological Sciences, University of Southampton, Life Sciences Building 85, Highfield, Southampton SO17 1BJ, UK

[2]Ocean and Earth Science, National Oceanography Centre, Waterfront Campus, European Way, University of Southampton, Southampton SO14 3ZH, UK

[3]School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland

[4]*Present address:* CIIMAR- Centro Interdisciplinar de Investigação Marinha e Ambiental, Laboratório de Biodiversidade Costeira, Rua dos Bragas 289, 4050-123 Porto, Portugal

ABSTRACT: Exploitation of key consumers can have major consequences for community and ecosystem functioning. Limpets are key grazers exploited in regions such as Macaronesia, southern Africa, Chile and California. Here we describe a field experiment designed to simulate human exploitation of British limpets that are unexploited and used as model populations. Our aim was to evaluate the effects of size-selective harvesting on the composition of the rocky shore community of non-target species. Limpet populations were subjected to simulated exploitation of large size classes for 18 mo at 2 locations in the southwest of England, by systematic removal at 2 different intensities: low and high exploitation compared with unexploited plots. The exploitation of limpets led to establishment of *Fucus* spp. to differing degrees at each location, but while variation in percentage cover of *Fucus* spp. decreased over the course of the experiment in unmanipulated control plots, it increased in plots with either low or high exploitation. Multivariate analyses showed that communities at the 2 locations responded differently to the same intensity of exploitation: unmanipulated controls were similar to low-exploitation treatments at Constantine, while at Trevone low-exploitation treatments were similar to high-exploitation treatments. This was mainly due to increases in percentage cover of *F. vesiculosus* var. *evesiculosus* with exploitation, indicating that site-specific differences in assemblage structure and the size structure of the harvested populations will determine its assemblage-level responses. Therefore, reductions in density of grazers may have divergent consequences for different rocky shore communities.

KEY WORDS: Assemblage structure · Exploitation · Grazers · Key species · Rocky shore

INTRODUCTION

Exploitation of consumers has major consequences for community and ecosystem functioning in semi-natural terrestrial (Dyer & Letourneau 1999, Beschta & Ripple 2009, Teichman et al. 2013), freshwater (e.g. Power 1990, Carpenter & Kitchell 1993, Ellis et al. 2011) and marine (Estes & Palmisano 1974, Lasiak & Field 1995, Lasiak 1998, 1999, Lindberg et al. 1998, Jackson et al. 2001, Estes et al. 2004, Branch et al. 2008) systems. Overexploitation of biological resources has recently been considered the main driver of biodiversity loss as identified in the Global Bio-

diversity Outlook 4 and by the WWF Living Planet Report 2014 (Monastersky 2014). In marine intertidal habitats, reductions in density of predators and grazers due to harvesting by humans for food or bait (Moreno et al. 1984, Hockey & Bosman 1986, Eekhout et al. 1992, Brown & Wilson 1997, Kyle et al. 1997, Smith & Murray 2005) and the associated trampling and physical disturbance (Ferreira & Rosso 2009, Huff 2011, Minchinton & Fels 2013) may also have an impact on assemblages.

Harvesting at different intensities can reduce densities and size structures of populations of the target species to differing degrees (Moreno et al. 1984,

Oliva & Castilla 1986, Eekhout et al. 1992, Pombo & Escofet 1996). Variation in impact on the target species can in turn lead to variation in impact on the wider assemblage (Castilla & Durán 1985, Hockey & Bosman 1986, Durán & Castilla 1989, Lasiak & Field 1995, Lasiak 1998, 1999, Moreno 2001). Improved understanding of such variation can inform development of optimal management strategies and may reveal thresholds of exploitation that cause acceptable levels of impact on assemblages. Comparisons between areas of differing harvesting intensity cannot unequivocally reveal such variation as they may be confounded by systematic differences in assemblages in areas favoured to differing degrees by harvesters (Underwood 1991). As such, experimental work involving manipulations of target species at appropriate scales is required.

Limpets, whose grazing exerts top down control of algae in many intertidal ecosystems worldwide, are considered key species in the North Eastern Atlantic (Hawkins 1981a, Hawkins & Hartnoll 1983, Hawkins et al. 1992, Coleman et al. 2006, Crowe et al. 2011). Size-selective limpet harvesting is widespread in many parts of the world (Oliva & Castilla 1986, Lasiak 1991, Navarro et al. 2005, Espinosa et al. 2009, Fenberg & Roy 2012). Effects of harvesting have been documented for patellids in the Azores (Martins et al. 2010a) and fissurellids in Chile (reviewed by Moreno 2001). In actively harvested populations, however, it can be difficult to manipulate levels of exploitation with precision and effects of current harvesting practices can be difficult to disentangle from longer term influences (see Pauly 1995). Unlike further south in Europe and Africa (e.g. see Hockey & Bosman 1986, Lasiak 1991, Hawkins et al. 2000), limpets are not harvested for food in the United Kingdom (UK). This effectively provides an unexploited system, which can serve as a model for understanding the consequences of limpet harvesting elsewhere. Extensive research has been done on the responses of algal assemblages to complete limpet removal (Jones 1946, Hawkins 1981b), fenced exclusions (Hawkins 1981a, Hawkins & Hartnoll 1983, Coleman et al. 2006) and mass mortality of limpets following oil spill clean-up (Southward & Southward 1978, Hawkins et al. 1983, Hawkins & Southward 1992). Little has been published, however, on the consequences of reducing density of limpets experimentally and continuously at comparatively large scales.

In this study, we tested the effects on key non-target species (*Fucus* spp., *Mytilus* spp. and barnacles) of removing large limpets at 2 intensities (low and high) compared to areas from which no limpets were removed ('unmanipulated controls'). In order to address the effect of simulated exploitation of limpets and provide a realistic simulation of limpet harvesting we used 3 × 3 m unfenced plots rather than the small enclosures of reduced densities used in most experimental studies (e.g. Coleman et al. 2006, O'Connor et al. 2011). Formally the hypotheses tested were: (1) reductions in the density of limpets will influence the percentage cover of selected key taxa *Fucus* spp., *Mytilus* spp. and barnacles, and variation in harvesting intensity will cause variation in effects, indicating potential for identifying thresholds of exploitation causing limited or acceptable impact. Removal of limpets would be expected to cause increased cover of *Fucus* spp. and reduced cover of barnacles (e.g. Crowe et al. 2011) and *Mytilus* spp. (e.g. Bertness et al. 1999); (2) effects on key taxa and associated changes to the presence and/or abundance of other taxa will cause changes in multivariate assemblage structure; and (3) effects of reductions in density of limpets will vary among sites with different physical conditions and biological communities.

MATERIALS AND METHODS

Study sites and organisms

The study was carried out at Constantine (50° 31′ 52.02″ N, 5° 01′ 33.32″ W) and Trevone (50° 32′ 40.48″ N, 4° 58′ 50.08″ W) on the north coast of Cornwall, UK (Fig. 1). These 2 locations were identified as being little disturbed by people, having similar tidal range and shore profiles and where, as on much of the British coast, limpets are not major target species for human consumption. Both locations have a slate bed rock and are typical of many exposed shores on the north coast of Cornwall, with the mid shore of each being covered by a mosaic of mussels, fucoid algae and barnacles (Crowe et al. 2011). Based on the coastal topography (Fig. 1; Burrows et al. 2008), Constantine can be considered more exposed to wave and wind action than Trevone. The shore at Trevone consists mostly of gently sloping bedrock platforms with few boulders and loose rocks. Despite the exposure of this site, its shallow profile causes a reduction in wave energy up the reef. The limpet *Patella vulgata* is the dominant grazer in the mid-intertidal zone of shores in this region and is distributed across the wave exposure gradient. *Patella depressa* is also present on open rock and *Patella ulyssiponensis*

Fig. 1. Coastline of Cornwall and the 2 study locations: Constantine and Trevone (O). Inset map shows the position of the locations in Britain

occurs in depressions and rock pools, the latter being dominant on the low shore. These species feed on the microalgal film that coats the rocky intertidal shore, ingesting the early stages of algae and small invertebrates including barnacles, particularly spat (Hawkins at al. 1989, Hill & Hawkins 1991), as well as feeding on macroalgae (Davies et al. 2007). At Constantine, density (number limpets per 0.25 m^2) of *Patella* spp. was 7.8 ± 0.9 % (SE, n = 90), while at Trevone, density was about 15.1 ± 0.5 % (SE, n = 90).

At Constantine, in the experimental area, mussels (a mixture of *Mytilus edulis*, *Mytilus galloprovincialis* and hybrids) dominated the primary space, covering on average 54.0 ± 4.0 % (SE, n = 45), followed by *Fucus vesiculosus* var. *evesiculosus*, with a cover of 32.0 ± 3.0 % (SE, n = 45). At Trevone, in the experimental area, the presence of mussels was negligible (0.1 ± 0.1 % [SE, n = 45]), and the major space occupiers were barnacles (*Chthamalus stellatus*, *C. montagui* and *Semibalanus balanoides*), with 44.8 ± 7.7 % (SE, n = 45) cover, and *F. vesiculosus* var. *evesiculosus* with 8.2 ± 3.2 % (SE, n = 45).

Experimental design and procedures

The experiment was established at both locations as a block design, used to accommodate the scale of variation in physical features along the shoreline, with 3 intensities of experimental exploitation of limpets: unmanipulated control, low and high. At each of the 2 locations, 3 adjacent blocks of shore, about 20 m wide, were designated at the mean tide

level (MTL). In each block, 3 unfenced treatment plots of 3 × 3 m were randomly placed on the available rock surface, separated by at least 5 m (see diagrammatic representation in the Appendix) and treatments were randomly allocated to the experimental plots on the shore. In plots assigned to the high exploitation treatment (henceforth referred to as 'H') all limpets with a base shell length ≥25 mm were removed on each visit. At the low exploitation treatments (L), all limpets with a base shell length ≥25 mm were removed from half of the available area, by removing them from 18 alternate squares in a grid of 0.5 × 0.5 m quadrats covering the plot, starting from a randomly located quadrat. No limpets were removed from the unmanipulated control treatments (C). The exploitation simulated what happens in most exploited limpet populations, where larger individuals are preferentially removed during harvesting (e.g. Hockey et al. 1988, Fenberg & Roy 2008, Espinosa et al. 2009). No differentiation between limpet species was made during removals, but most (>95 %) large limpets were *P. vulgata*. The simulated exploitation was performed every 3 mo from March 1999 to October 2000 and the last sampling date of the assemblages was in summer, 30 August 2000.

Response of percentage cover and abundance of key species

In March 1999, data were collected prior to manipulation to provide a baseline and to check for pre-existing differences among the different treatments.

Subsequent surveys were conducted in summer 1999 and spring and summer 2000. On each occasion, percentage cover of macroalgae and of sessile invertebrates (mussels *M. galloprovincialis*, *M. edulis*, hybrids, and total barnacles *C. stellatus*, *C. montagui*, *S. balanoides*) were recorded in five 0.5 × 0.5 m quadrats placed randomly within each 3 × 3 m plot. Percentage cover was estimated using the point intersect method (49 points). Records were additionally taken of any other species that were not under an intersection point; these were given an arbitrary value of 0.5%. Whenever large algae (e.g. *Fucus* spp.) were present, sampling was stratified in different layers and canopy cover was distinguished from substrate cover. The key taxa considered were *Fucus* spp., *Mytilus* spp. and barnacles. Limpets from the genus *Patella* and other mobile invertebrates were counted. For the multivariate analysis, limpets <10 mm long were recorded as 'juvenile limpets' and we excluded limpets >10 mm since we wanted to assess changes in the non-target species, but did not want to prevent limpet recruitment from being detected.

The percentage cover of key species was compared on the last sampling date of the experiment. On the last sampling date, changes in percentage cover were also calculated as final minus first values.

Manual removals of limpets were effective in reducing the densities of 25–60 mm *P. vulgata* (target species) and hence grazing pressure at both locations. The treatments were successful in establishing differences in abundance of large 25–60 mm *P. vulgata* limpets in plots allocated to unmanipulated control, low and high exploitation treatments. Although there were significant differences in 25–60 mm *P. vulgata* abundances at both locations in spring 1999 prior to the removals (Table 1), during the following summer 1999 and spring 2000, densities of large *P. vulgata* in low and high exploitation treatments were statistically different from unmanipulated controls and distinguishable from each other (Tables 2 & 3, respectively). In summer 2000, however, densities of large *P. vulgata* in low and high exploitation treatments were different from unmanipulated controls, but not statistically distinguishable from each other (Table 4). Reductions in densities of 25–60 mm *P. vulgata* were by approximately 40% and 60% in low- and high-exploitation plots respectively at Constantine, and by 20% and 50% at Trevone.

Patella spp. density fluctuated throughout the course of the experiment. The biggest increase in density occurred at Constantine and Trevone in summer 1999, probably in response to the first removal of limpets in spring 1999, with an influx of juveniles

Table 1. Response of 25–60 mm *Patella vulgata* abundance by treatment and by location for spring 1999. A prime indicates a random factor. Orthogonal contrasts are shown partitioning the treatment SS between no exploitation (NE: unmanipulated control) and exploitation (EX: pooled low + high) and between exploitation levels (low vs. high). Orthogonal contrast main effects calculated after post hoc pooling the non-significant T × L into the Error term, giving 10 error df, *p < 0.05

Source	df	Seq SS	Seq MS	*F*
Between subjects				
Location = L′	1	13.18	13.18	11.40*
Block = B′(L′)	4	4.62	1.16	
Within subjects				
Treatment = T	2	2.83	1.42	0.66
NE vs. EX	1	0.66	0.66	0.31
Low vs. high	1	2.17	2.17	1.01
T × L′	2	2.75	1.37	0.58
{NE vs. EX} × L′	1	1.48	1.48	0.69
{Low vs. high} × L′	1	1.27	1.27	0.59
Residual error	8	18.80	2.35	

Table 2. Response of 25–60 mm *Patella vulgata* abundance by treatment and by location for summer 1999. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	*F*
Between subjects				
Location = L′	1	16.44	16.44	7.44
Block = B′(L′)	4	8.84	2.21	
Within subjects				
Treatment = T	2	32.76	16.38	10.77*
NE vs. EX	1	10.89	10.89	7.16*
Low vs. high	1	21.87	21.87	14.38*
T × L′	2	1.07	0.54	0.30
{NE vs. EX} × L′	1	0.22	0.22	0.12
{Low vs. high} × L′	1	0.85	0.85	0.56
Residual error	8	14.14	1.77	

Table 3. Response of 25–60 mm *Patella vulgata* abundance by treatment and by location for spring 2000. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	*F*
Between subjects				
Location = L′	1	0.85	0.85	0.90
Block = B′(L′)	4	3.76	0.94	
Within subjects				
Treatment = T	2	26.43	13.22	11.76*
NE vs. EX	1	19.07	19.07	16.97*
Low vs. high	1	7.36	7.36	6.55*
T × L′	2	0.37	0.19	0.14
{NE vs. EX} × L′	1	0.16	0.16	0.14
{Low vs. high} × L′	1	0.21	0.21	0.19
Residual error	8	10.86	1.36	

Table 4. Response of 25–60 mm *Patella vulgata* abundance by treatment and by location for summer 2000. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	F
Between subjects				
Location = L'	1	3.29	3.29	1.81
Block = B'(L')	4	7.30	1.82	
Within subjects				
Treatment = T	2	16.73	8.37	7.98*
NE vs. EX	1	14.56	14.56	13.89*
Low vs. high	1	2.17	2.17	2.07
T × L'	2	1.50	0.75	0.67
{NE vs. EX} × L'	1	1.48	1.48	1.41
{Low vs. high} × L'	1	0.02	0.02	0.02
Residual error	8	8.98	1.12	

Table 5. Response of *Patella* spp. abundance by treatment and by location for summer 2000. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	F
Between subjects				
Location = L'	1	206.72	206.72	2.22
Block = B'(L')	4	408.07	102.02	
Within subjects				
Treatment = T	2	6.52	3.26	0.30
NE vs. EX	1	6.25	6.25	0.57
Low vs. high	1	0.27	0.27	0.02
T × L'	2	7.90	3.95	0.31
{NE vs. EX} × L'	1	4.69	4.69	0.43
{Low vs. high} × L'	1	3.20	3.20	0.29
Residual error	8	101.53	12.69	

emerging from crevices and refuges within and near to plots. Overall densities of limpets were, therefore, balanced by influxes of juveniles to plots in exploitation treatments. No differences were detected (p > 0.05) in the total density of *Patella* spp. at the last sampling date of the experiment either by location or treatment (Table 5).

Statistical analysis

Analyses based on a 2-factor split-plot design (equivalent to models 5.6 and 6.3 iii in Doncaster & Davey 2007) were used to test the hypothesis at the end of the experiment, that selective removal through time of the largest limpets would influence responses of percentage cover of key species. This design had 3 levels of the fixed treatment factor (T_3), at each of 2 random levels of a location factor (L'_2). Three replicate random blocks (B'_3) were nested in

each level of L and responses of observations over time were taken on each block at each level of T. This design was analysed with the ANOVA model:

$$Y = T|B'(L') \qquad (1)$$

where a prime indicates a random factor, a vertical line means 'crossed with' and parentheses mean 'nested in'. The alpha level considered for each comparison is 0.05.

The use of Location as a random factor was dictated by the aim of extrapolating the final results to the coast of southwest England from which the 2 locations were selected. The residual variation ($P'(T × B'(L'))$) could not be estimated due to the absence of treatment replicates in each block. Therefore, the interaction of treatment with block [T × B'(L')] was not testable, but its mean square (MS) provided the error term for testing the treatment-by-location interaction (T × L').

Although the treatment effect was tested with only 2 error degrees of freedom, if the interaction between Location and Treatment was not detectable at α = 0.25, it was pooled with the error term to provide a more powerful test for the treatment effect with 10 error degrees of freedom (post hoc pooling, following Underwood 1997). A set of planned *a priori* contrasts were used to detect differences between Treatment effects. Treatment contrasts partitioned the sums of squares of the exploitation treatment, with a first contrast of no exploitation (NE: unmanipulated control) versus exploitation (EX: low and high pooled), and a second contrast of exploitation levels (low vs. high). When non-significant interactions of contrasts with Location were present, the interaction between Location and Treatment was pooled with the error term to provide a more powerful test for the contrasts with 10 error degrees of freedom. Prior to all ANOVAs, homogeneity of variance was assessed using Levene's test. Outcomes of all of these tests were non-significant, so no transformations were applied to the data.

Multivariate analyses were completed for each sampling date on each location to assess changes in assemblage structure using the PRIMER package. Non-metric multidimensional scaling (nMDS) was used to visualise the impact of the treatments on the overall assemblage structure (excluding limpets > 10 mm). nMDS is an ordination technique based on rank dissimilarity, in this case measured with the Bray-Curtis index on square-root transformed data (Clarke 1993). Permutational multivariate analyses of variance (PERMANOVA, McArdle & Anderson 2001, Anderson 2005) were used to test the hypothesis of

differences in assemblage structure between treatments. For each sampling time at each location, a separate analysis was conducted with 1 factor, 'treatment', which was a fixed factor with 3 levels (unmanipulated control; low; high). The analyses were based on Bray-Curtis similarities of data which had been square-root transformed to reduce the influence of the most abundant taxa such that the analysis could reveal patterns of variation in the assemblage as a whole more clearly (Clarke 1993).

RESULTS

Percentage cover and abundance of key species

The percentage cover of *Fucus* spp. increased in L and H treatment plots both at Constantine and to a greater extent at Trevone, but decreased in unmanipulated control plots (Fig. 2). At the last sampling date (summer 2000), although the main effect of treatment was not significant (Table 6: $F_{2,2} = 5.60$, p > 0.05), planned contrasts revealed that the percentage
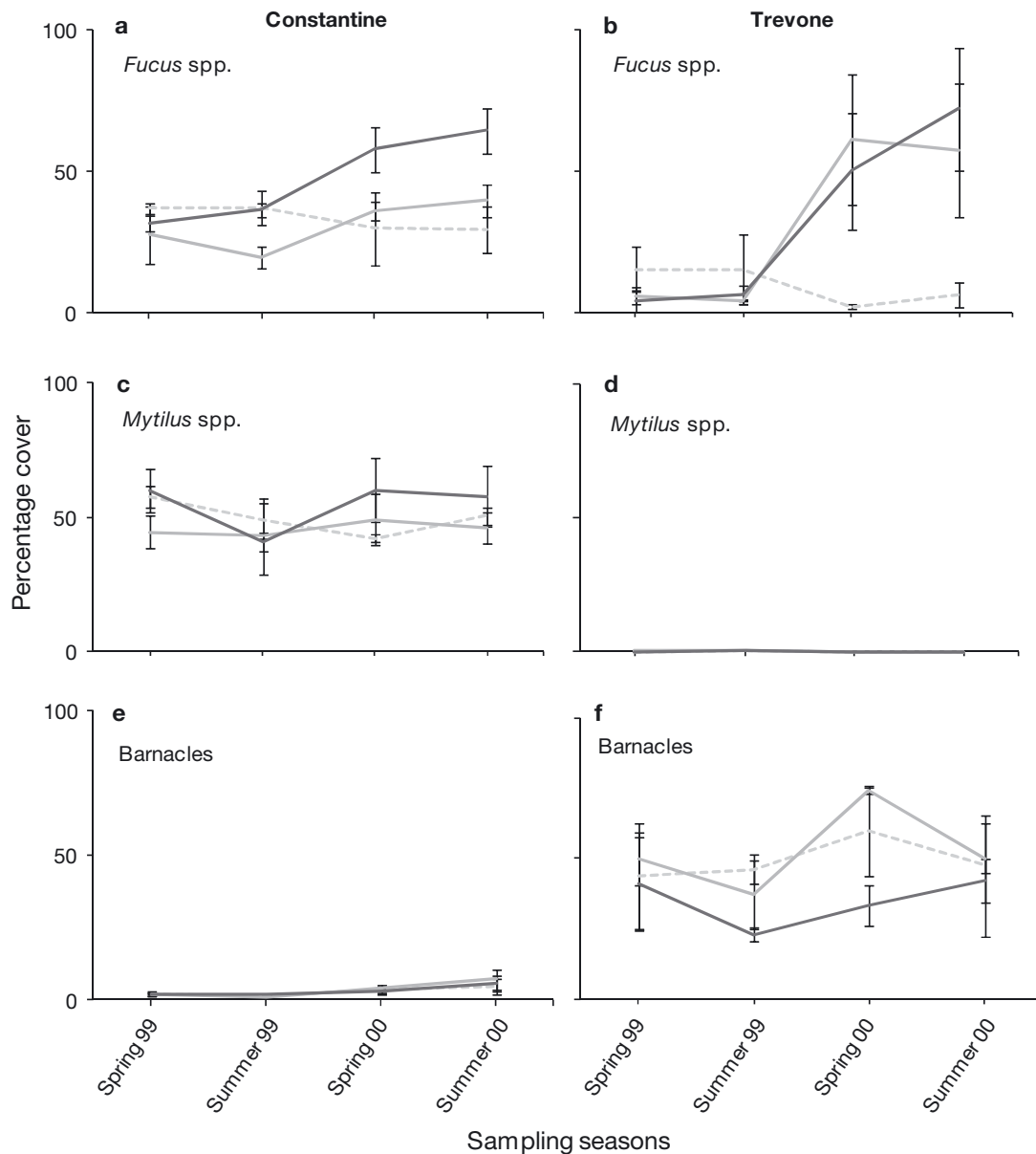

Fig. 2. Estimated mean percentage cover ± SE (n = 3 plots per sample) for (a,b) *Fucus* spp., (c,d) *Mytilus* spp. and (e,f) barnacles (*Chthamalus stellatus, C. montagui, Semibalanus balanoides*) at each sampling season for each treatment: unmanipulated control (broken line), low (light grey line) and high (dark grey line), at Constantine (left) and Trevone (right)

Table 6. Response of *Fucus* spp. percentage cover by treatment and by location in summer 2000. Contrasts as for Table 1 without pooling. *p < 0.05

Source	df	Seq SS	Seq MS	F
Between subjects				
Location = L'	1	0.80	0.80	<0.01
Block = B'(L')	4	5142.80	1285.70	
Within subjects				
Treatment = T	2	7704.20	3852.10	5.60
NE vs. EX	1	6555.60	6555.60	19.24*
Low vs. high	1	1148.60	1148.60	3.37
T × L'	2	1376.40	688.20	2.71
{NE vs. EX} × L'	1	1298.40	1298.40	5.11
{low vs. high} × L'	1	78.00	78.00	0.31
Residual error	8	2031.50	253.90	

Table 7. Response of *Mytilus* spp. percentage cover by treatment and by location in summer 2000. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	F
Between subjects				
Location = L'	1	11878.50	11878.50	116.17*
Block = B'(L')	4	409.00	102.20	
Within subjects				
Treatment = T	2	105.40	52.70	0.73
NE vs. EX	1	2.20	2.20	0.03
Low vs. high	1	103.30	103.30	1.42
T × L'	2	105.40	52.70	0.68
{NE vs. EX} × L'	1	2.20	2.20	0.03
{Low vs. high} × L'	1	103.30	103.30	1.33
Residual error	8	620.20	77.50	

Table 8. Response of barnacle (*Chthamalus stellatus*, *C. montagui*, *Semibalanus balanoides*) percentage cover by treatment and by location in summer 2000. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	F
Between subjects				
Location = L'	1	7385.20	7385.20	12.68*
Block = B'(L')	4	2329.60	582.40	
Within subjects				
Treatment = T	2	58.20	29.10	0.17
NE vs. EX	1	0.10	0.10	<0.01
Low vs. high	1	58.10	58.10	0.33
T × L'	2	36.90	18.50	0.09
{NE vs. EX} × L'	1	11.10	11.10	0.05
{Low vs. high} × L'	1	25.80	25.80	0.12
Residual error	8	1709.60	213.70	

cover of *Fucus* spp. was lower in non-exploited plots ($17.9 \pm 9.4\%$) than in exploited ones (low and high treatment pooled: $58.4 \pm 15.9\%$, Table 6: pooled $F_{1,10} = 19.24$, p < 0.05). *Mytilus* spp. were present at Constantine, where their percentage cover varied during the experiment irrespective of treatment. Cover of barnacles at Trevone varied during the experiment, but was much less variable at Constantine, where it slowly increased over time from a low level. Differences in percentage cover were only detected by location for *Mytilus* spp. and barnacles (Fig. 2, Table 7: $F_{1,4} = 116.17$, p < 0.05; Fig. 2, Table 8: $F_{1,4} = 12.68$, p < 0.05, respectively) at the last sampling date, with no differences detected between treatments.

Differences in the change of percentage cover over the course of the experiment (final minus first values) were only detected (p < 0.05) for *Fucus* spp. (Fig. 3). Planned contrasts revealed that non-exploited plots

($-9.3 \pm 7.6\%$) had experienced a greater reduction in percentage cover than exploited ones (low and high treatment pooled: $35.2 \pm 19.6\%$, Table 9: pooled $F_{1,10} = 20.12$, p < 0.05). No differences in the *Fucus* spp. change in percentage cover were detected between low- ($25.3 \pm 11.9\%$) and high-intensity exploitation plots ($30.7 \pm 14.9\%$).

Assemblage structure

Before the experiment was started in March 1999, no differences among treatments were detected at either location (see nMDS plots in Fig. 4). Shifts in assemblage structure were more pronounced from spring 2000 onwards, particularly at Trevone (Fig. 4f,h). Since the treatments only had clear effects at both locations on the last sampling date, in summer 2000, the description of results will focus primarily on that date.

At Constantine in summer 2000, the removal of all limpets ≥25 mm had significant effects on the assemblage structure (Fig. 4g). There were no discernible differences between the unmanipulated control and low-exploitation plots, but those treatments were different from the high-intensity exploitation plots (Fig. 4g, PERMANOVA analysis: 'treatment' MS = 1185.5, Pseudo-F = 2.77, p (MC) = 0.013, with df = 42 for the residual; pairwise post hoc comparisons).

On the final sampling date, unmanipulated control plots were distinct from high-exploitation plots, due principally to increases in *F. vesiculosus* var. *evesiculosus* and *Mytilus* spp. (Table 10). Those species also contributed most to the dissimilarity of low- and high-intensity exploitation plots, with higher removals raising percentage cover (Table 10). In both
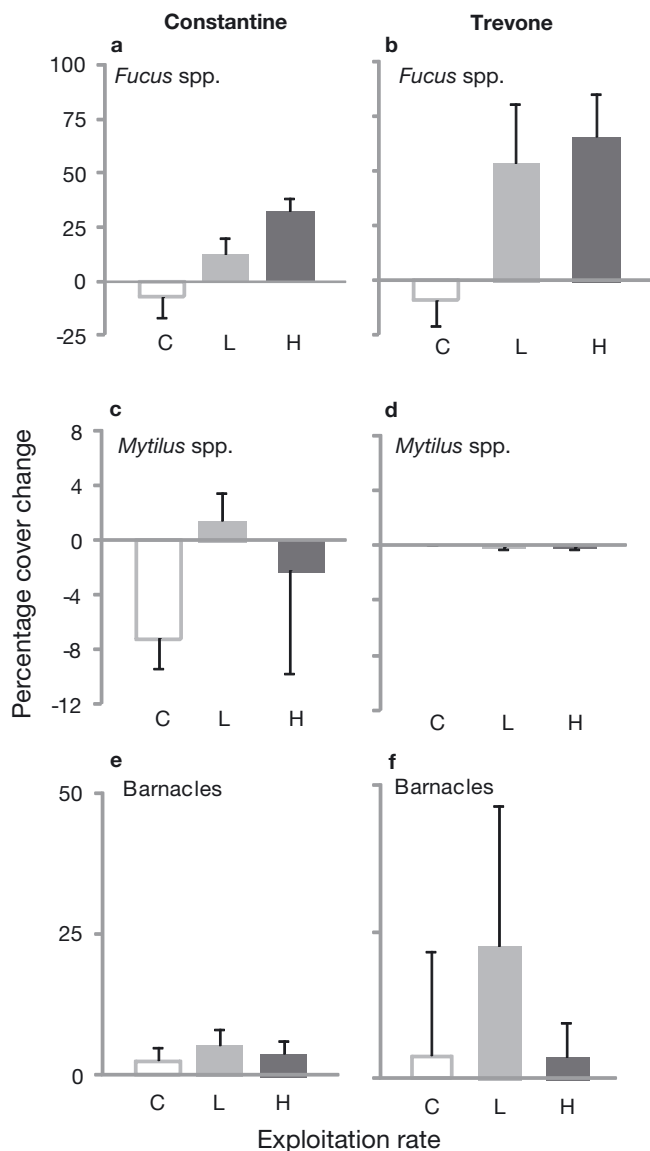
Fig. 3. Estimated mean percentage cover change (end – start values) ± SE (n = 3 plots per sample) for (a,b) *Fucus* spp., (c,d) *Mytilus* spp. and (e,f) barnacles (*Chthamalus stellatus*, *C. montagui*, *Semibalanus balanoides*) for each treatment: unmanipulated control (C), low exploitation (L), and high exploitation (H), at Constantine (left) and Trevone (right) in summer 2000 after the experiment had run for 18 mo. Note change of *y*-axis scale

Table 9. Response of *Fucus* spp. percentage cover change (end – start values) by treatment and by location. Contrasts as for Table 1. *p < 0.05

Source	df	Seq SS	Seq MS	*F*
Between subjects				
Location = L′	1	2693.80	2693.80	2.06
Block = B′(L′)	4	5231.80	1307.90	
Within subjects				
Treatment = T	2	10492.70	5246.40	10.90*
NE vs. EX	1	9689.10	9689.10	20.12*
Low vs. high	1	803.60	803.60	1.67
T × L′	2	1577.60	788.80	1.95
{NE vs. EX} × L′	1	1528.80	1528.80	3.78
{Low vs. high} × L′	1	48.80	48.80	0.12
Residual error	8	3237.20	404.60	

ences between the low- and high-intensity exploitation plots, but assemblage structure in both of those treatments was different from that in unmanipulated control plots (Fig. 4h; PERMANOVA: 'treatment' MS = 4017.1, Pseudo-*F* = 6.37, p (MC) = 0.001, with df = 42 for the residual; pairwise post hoc comparisons). As at Constantine, *F. vesiculosus* var. *evesiculosus* was important in contributing to dissimilarity among treatments and cover tended to be greater where limpets ≥25 mm had been removed (Table 11). The cyanobacteria *Rivularia bullata*, quantified with the sampling quadrats, also contributed substantially to the dissimilarity among treatments and had reduced cover where limpets ≥25 mm had been removed, probably due to competition with fucoids and other algae (Table 11). Barnacles, *G. umbilicalis* and small limpets were the other species contributing to the dissimilarity between the plots but their contribution was minor. In fact, *G. umbilicalis* density increased during the experiment, particularly in low- and high-intensity exploitation plots at Trevone (Fig. 5). This increase could be the result of the reduction of competition with limpets or due to the sheltered conditions under the fucoid canopy, which had also increased in those plots.

DISCUSSION

Limpets regulate algal recruitment by grazing the early stages of macroalgae contained within epilithic microbial films (Hawkins et al. 1989, Hill & Hawkins 1991), and in some cases by direct consumption of mature algae (Davies et al. 2007, Crowe et al. 2011). This has been demonstrated by the establishment of opportunistic and fucoid algae where limpets have

comparisons, barnacles, the encrusting algae *Lithophyllum incrustans* and the gastropod *Gibbula umbilicalis* were the other species contributing to the dissimilarity between the plots but their influence was minor.

At Trevone in summer 2000, the removal of limpets ≥25 mm also had a significant effect on assemblage structure (Fig. 4h). There were no discernible differ-
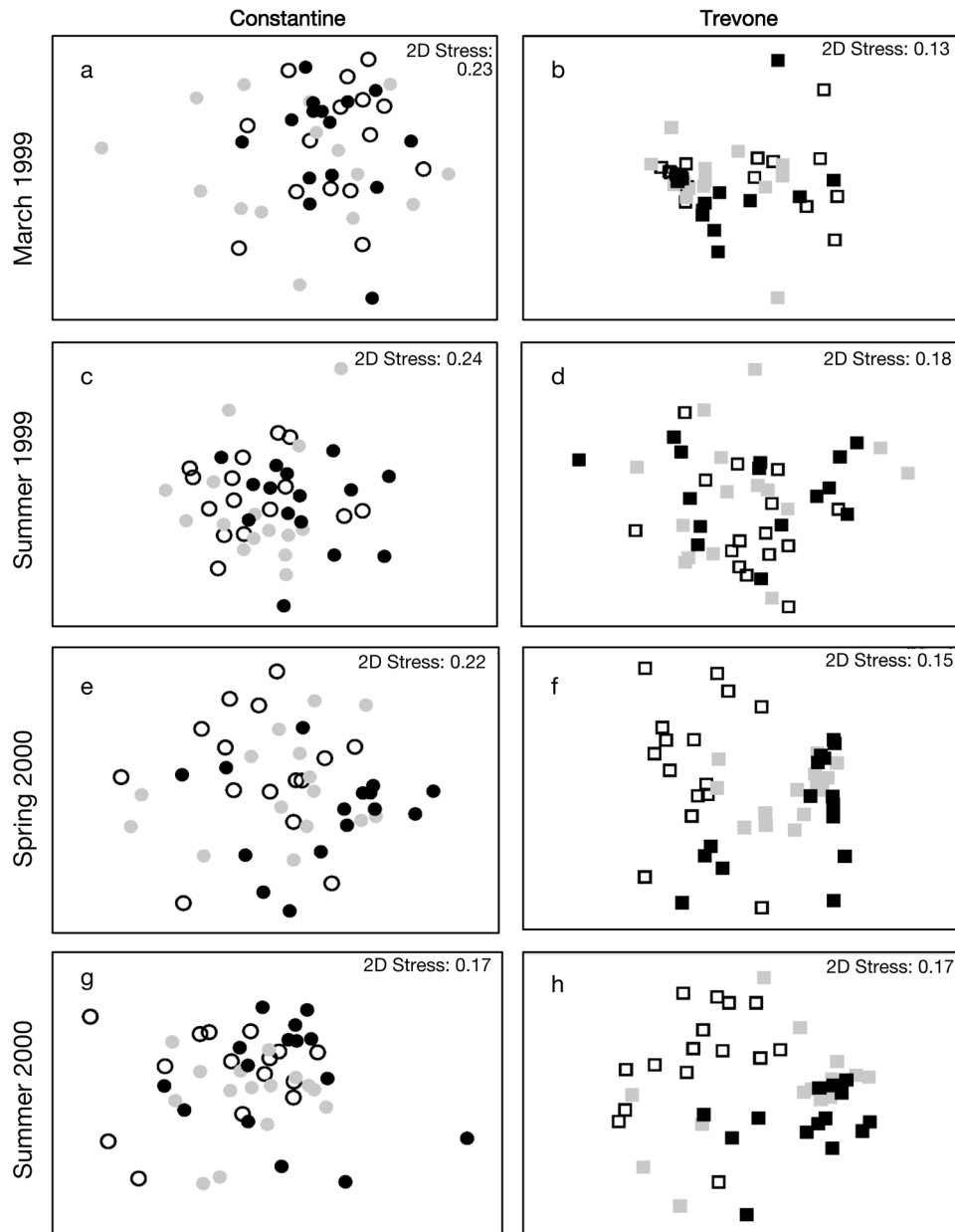
Fig. 4. Non-metric multi-dimensional scaling (nMDS) representations of community compositions in the experimental plots in (a) March 1999 at Constantine, (b) March 1999 at Trevone, (c) summer 1999 at Constantine, (d) summer 1999 at Trevone, (e) spring 2000 at Constantine, (f) spring 2000 at Trevone, (g) summer 2000 at Constantine and (h) summer 2000 at Trevone. Circles: Constantine; squares: Trevone. Unfilled symbols: unmanipulated controls; grey symbols: low plots; black symbols: high plots

been removed or excluded (e.g. Coleman et al. 2006, Jenkins et al. 2008, Crowe et al. 2011). Although other influential grazing species include littorinids, the consequences of their loss (e.g. by harvesting) has lesser effects in the north-east Atlantic (see O'Connor & Crowe 2005, Johnson et al. 2008). In mid-intertidal exposed rocky shores of central Chile, non-fissurellid molluscan grazers play a role in con-

trolling green algal cover, but they appear not to be able to compensate for the absence of large fissurel-lid limpets in controlling the abundance of late successional *Mazzaella laminarioides* (Aguilera & Navarrete 2007). In the Azores, islands where the abundance of limpets has been reduced as a conse-quence of intensive exploitation, turf-forming algae (e.g. *Gelidium* spp., *Caulacanthus ustulatus*) have

Table 10. SIMPER analyses for pairs of treatments significantly different from each other in summer 2000 at Constantine. Listed are the 5 taxa that contributed most to the dissimilarity between pairs of treatments. The SIMPER analyses presented were based on square-root transformed data. Abundance data shown were untransformed so that abundances/percentage of covers were interpretable. Avg. Abund Treat 1 and Avg. Abund Treat 2: average abundance or cover (untransformed) for the first and second treatments in the pair; Avg. Diss: average dissimilarity among pairs of samples in terms of species in question; Diss/SD: a measure of variation in the contribution of the species to dissimilarities between pairs of samples; Contrib%: percentage contribution of the species to the average overall dissimilarity between groups of treatments; Cum.%: cumulative contribution of the listed species

Species	Avg. Abund Treat 1	Avg. Abund Treat 2	Avg. Diss	Diss/SD	Contrib%	Cum.%
Unmanipulated control versus High treatment (average dissimilarity 31.29)						
Fucus vesiculosus var. *evesiculosus*	30.34	65.85	8.16	1.46	26.06	26.06
Mytilus spp.	51.43	58.91	6.09	0.99	19.47	45.53
Barnacles	5.03	5.92	4.09	1.34	13.07	58.60
Lithophyllum incrustans	2.24	1.63	2.68	0.85	8.55	67.16
Gibbula umbilicalis	1.80	1.73	2.44	1.23	7.81	74.96
Low versus High treatment (average dissimilarity 28.69)						
Mytilus spp.	46.94	58.91	5.91	1.10	20.59	20.59
Fucus vesiculosus var. *evesiculosus*	40.68	65.85	5.44	1.66	18.96	39.55
Barnacles	7.41	5.92	4.09	1.38	14.27	53.82
Lithophyllum incrustans	1.90	1.63	2.45	0.87	8.53	62.35
Gibbula umbilicalis	2.67	1.73	2.31	1.33	8.04	70.39

Table 11. SIMPER analyses for pairs of treatments significantly different from each other in summer 2000 at Trevone. Presentation as for Table 10

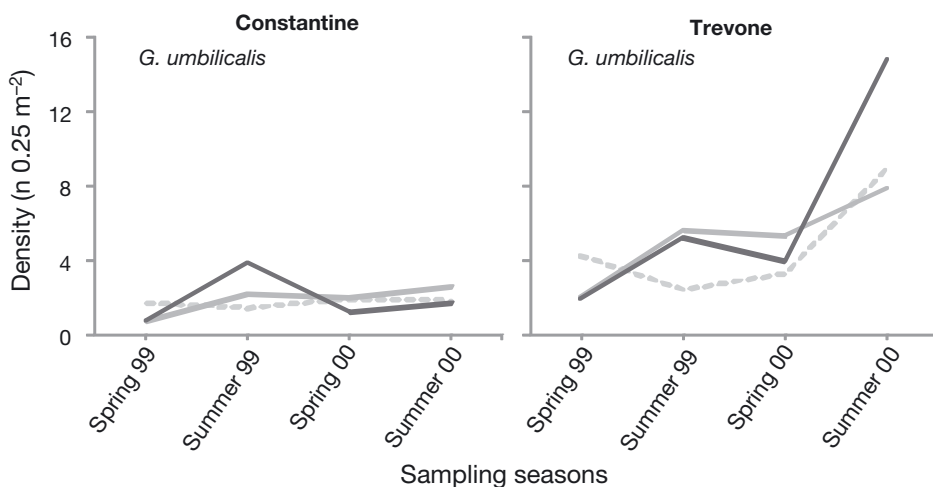| Species	Avg. Abund Treat 1	Avg. Abund Treat 2	Avg. Diss	Diss/SD	Contrib%	Cum.%
Unmanipulated control versus Low treatment (average dissimilarity 41.94)						
Fucus vesiculosus var. *evesiculosus*	6.26	58.57	13.39	1.66	31.92	31.92
Rivularia bullata	14.15	3.61	6.17	1.32	14.72	46.64
Barnacles	48.44	50.61	4.83	1.06	11.51	58.15
Gibbula umbilicalis	9.00	7.87	4.42	1.32	10.54	68.69
Juvenile limpets	8.33	8.33	3.88	1.20	9.25	77.94
Unmanipulated control versus High treatment (average dissimilarity 44.14)						
Fucus vesiculosus var. *evesiculosus*	6.26	73.33	15.91	2.11	36.04	36.04
Rivularia bullata	14.15	0.54	6.12	1.34	13.87	49.91
Barnacles	48.44	43.13	5.62	1.70	12.74	62.65
Gibbula umbilicalis	9.00	14.80	5.44	1.31	12.32	74.97
Juvenile limpets	8.33	7.87	3.10	1.25	7.01	81.98

Fig. 5. Estimated mean density (no. per 0.25 m^2; n = 3 plots per sample) of *Gibbula umbilicalis* at each sampling season for each treatment: unmanipulated control (broken line), low (light grey line) and high (dark grey line), at Constantine (left) and Trevone (right). Error bars omitted for clarity

replaced barnacles as the dominant space occupier at mid-shore levels (Martins et al. 2010a). Such dominance by algal turfs does not represent an alternative stable state, but is the result of chronic exploitation of limpets leading to the persistence of this community (Martins et al. 2010a). Several examples are documented of such cascading effects (humans-limpets-algae) in Chile (reviewed by Moreno 2001): while exclusion of humans (top predators) resulted in an increase in size and density of the limpet *Fissurella picta* and a reduction in the cover of the algae *M. laminarioides* (Moreno et al. 1984), exclusion of *F. picta* from an experimental area in a protected zone resulted in an increase in the percentage cover of *M. laminarioides* (Jara & Moreno 1984). Equivalent results were reported by Oliva & Castilla (1986), after exclusion of humans, that indicated a negative relationship between abundance of the limpets *F. crassa* and *F. limbata* and algal diversity and abundance.

Our results show that even a small reduction in density of larger limpets (at low intensity) enabled the growth of fucoids and led to increased cover. We detected no differences in percentage cover of barnacles and *Mytilus* spp. with the larger limpet removal, probably due to the sweeping effect of the dominant fucoids that would have prevented settlement (see Hawkins 1983). The observed differences by location at the last sampling date in the percentage cover of *Mytilus* spp. (more abundant at Constantine) and barnacles (more abundant at Trevone) reflect the differences in wave and wind exposure between the locations and influenced the responses of these assemblages to the limpet removal.

In the case of limpets, although they were selectively removed at 2 different effective rates, no differences in numbers were detected at the last sampling date of the experiment. This is possibly due to recruitment of juveniles from nursery grounds and refuges such as rock crevices, enhanced by the shelter provided by the fucoid canopy (Hartnoll & Hawkins 1985). Intraspecific competition between size classes of grazers is well documented (see Underwood 1976, Marshall & Keough 1994, Keough et al. 1997). Although large patellid limpets are known to be superior competitors that may modulate the abundance of small limpets on the shore (Boaventura et al. 2003), the opposite has been shown for *Cellana tramoserica*, with small limpets superior to large ones in competitive ability (Marshall & Keough 1994). This was attributed to differences in the radula mechanism that enabled small individuals to exploit food from smaller rock pits than larger individuals and survive even when no food was available to

large individuals (Keough et al. 1997). In fact, many studies have demonstrated that density-dependent processes can regulate the abundance of limpet populations (see Branch 1981, Hawkins & Hartnoll 1983, Underwood 1992 for reviews). Hence, the removal of the larger limpets perhaps enabled juvenile recruitment due to a reduction of competition, particularly at Trevone where the overall density was higher at the last sampling date. Therefore, whatever the rate of limpet exploitation applied, stock management strategies should ensure recovery of the exploited populations, allowing the recruits to attain sexual maturity. Conservative approaches should be adopted in the initial allocation of any quotas to allow sustainable harvesting (Eekhout et al. 1992). For the reasons cited above, these could include site-specific minimum (to allow reproduction of gonochoristic species) and maximum (to ensure presence of females in protandric species) size limits, effective no-take areas (Martins et al. 2011) and seasons in a rotational scheme (Eekhout et al. 1992) and modifications on the micro-topography of the shores and artificial structures (Martins et al. 2010b).

The multivariate analysis confirmed the influence of fucoids when limpets are removed. On both shores, *Fucus vesiculosus* var. *evesiculosus* was the most important species contributing to the dissimilarity between treatments. On the other hand, it is important to emphasise that even quite a small reduction in grazer densities can have a profound effect on the remaining assemblages. Nevertheless, differences in the assemblages at the 2 locations and their responses to the limpet removals were also detectable. At Constantine, plots where all limpets ≥25 mm were removed (high exploitation plots) diverged from unmanipulated control and low plots in assemblage structure. Therefore, the removal of limpets ≥25 mm from half of the plot area (low exploitation plots) had no effect on the assemblage structure. On the other hand, there was a convergence in assemblage structure between low and high exploitation treatments at Trevone. This suggests that the threshold level of exploitation of limpets causing community level impacts was lower at Trevone than at Constantine, probably due to higher initial densities and percentage reductions in density of large *Patella vulgata.* This result implies that decisions about how much exploitation can be allowed need to be site-specific, taking account of the specific nature of the community and the size structure of the target populations. In Ireland, differences in environmental conditions among particular shores of similar exposure tended to have greater importance than

exposure itself in determining the relative roles of barnacles and limpets and the interactive effects of their loss (Mrowicki et al. 2014). Such context-dependent interactive effects of the loss of key grazers and ecosystem engineers have been documented for the southwest of England (Crowe et al. 2011). Additionally, local pressures on limpet stocks, such as natural predation by birds (Lindberg et al. 1998, Coleman et al. 1999) and crabs (Silva et al. 2010), should also be considered when defining the intensity and frequency of human exploitation, since they might have a negative impact on specific limpet size classes and further reduce the sustainable level of human harvesting.

In summary, our study emphasises the value of experimentation in the management of exploitation of biological resources. We found that even light thinning of larger limpets resulted in the establishment of fucoids but that outcomes varied among locations. Effective management may need to be tailored to the specificities of the target populations and of the interactions with non-target species and assemblage-level process.

LITERATURE CITED

Aguilera MA, Navarrete SA (2007) Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. J Exp Mar Biol Ecol 349:84–98

Anderson MJ (2005) PERMANOVA: a Fortran computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland

Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80:2711–2726

Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol Conserv 142:2401–2414

Boaventura D, Cancela da Fonseca L, Hawkins SJ (2003) Size matters: competition within populations of the limpet *Patella depressa.* J Anim Ecol 72:435–446

Branch GM (1981) The biology of limpets: physical factors, energy flow and ecological interactions. Oceanogr Mar Biol Annu Rev 19:235–380

Branch GM, Thompson RC, Crowe TP, Castilla JC, Langmead O, Hawkins SJ (2008) Rocky intertidal shores: prognosis for the future. In: Polunin N (ed) Aquatic ecosystems trends and global prospects. Cambridge University Press, Cambridge, p 209–225

Brown B, Wilson WH (1997) The role of commercial digging of mudflats as an agent for change of infaunal intertidal populations. J Exp Mar Biol Ecol 218:49–61

Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. Mar Ecol Prog Ser 353:1–12

Carpenter SR, Kitchell JF (1993) The trophic cascade in lakes. Cambridge University Press, Cambridge

Castilla JC, Durán LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos 45:391–399

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Coleman RA, Goss-Custard JD, Durell SEA Le V dit, Hawkins SJ (1999) Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. Mar Ecol Prog Ser 183:253–261

Coleman RA, Underwood AJ, Benedetti-Cecchi L, Åberg P and others (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147: 556–564

Crowe TP, Frost NJ, Hawkins SJ (2011) Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. Mar Ecol Prog Ser 430:223–234

Davies AJ, Johnson MP, Maggs CA (2007) Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales. Mar Ecol Prog Ser 339:131–141

Doncaster CP, Davey AJH (2007) Analysis of variance and covariance. How to choose and construct models for the life sciences. Cambridge University Press, Cambridge

Durán LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Mar Biol 103:555–562

Dyer LA, Letourneau DK (1999) Trophic cascades in a complex terrestrial community. Proc Natl Acad Sci USA 96: 5072–5076

Eekhout S, Raubenheimer CM, Branch GM, Bosman AL, Bergh MO (1992) A holistic approach to the exploitation of intertidal stocks: limpets as a case study. S Afr J Mar Sci 12:1017–1029

Ellis BK, Stanford JA, Goodman D, Stafford CP and others (2011) Long-term effects of a trophic cascade in a large lake ecosystem. Proc Natl Acad Sci USA 108:1070–1075

Espinosa F, Rivera-Ingraham GA, Fa D, García-Gómez JC (2009) Effect of human pressure on population size structures of the endangered ferruginean limpet: toward future management measures. J Coast Res 25:857–863

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring near-shore communities. Science 185:1058–1060

Estes JA, Danner EM, Doak DF, Konar B and others (2004) Complex trophic interactions in kelp forest ecosystems. Bull Mar Sci 74:621–638

Fenberg PB, Roy K (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol Ecol 17:209–220

Fenberg PB, Roy K (2012) Anthropogenic harvesting pressure and changes in life history: insights from a rocky intertidal limpet. Am Nat 180:200–210

Ferreira MN, Rosso S (2009) Effects of human trampling on a rocky shore fauna on the São Paulo coast, southeastern Brazil. Braz J Biol 69:993–999

Hartnoll RG, Hawkins SJ (1985) Patchiness and fluctuation on moderately exposed rocky shores. Ophelia 24:53–63

Hawkins SJ (1981a) The influence of *Patella* grazing on the fucoid-barnacle mosaic on moderately exposed rocky shores. Kieler Meeresforsch 5:537−543

Hawkins SJ (1981b) The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. J Mar Biol Assoc UK 61:1−15

Hawkins SJ (1983) Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). J Exp Mar Biol Ecol 71:55−72

Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. Oceanogr Mar Biol Annu Rev 21:195−282

Hawkins SJ, Southward AJ (1992) The Torrey Canyon oil spill: recovery of rocky shore communities. In: Thayer GW (ed) Restoring the nation's marine environment. Proc NOAA Symp Habitat Restoration, Washington, DC, September 25−26, 1990, Maryland Sea Grant College, Maryland, p 583−631

Hawkins SJ, Southward AJ, Barrett RL (1983) Population structure of *Patella vulgata* during succession on rocky shores in south-west England. Oceanol Acta, Spec Vol 1983:103−107

Hawkins SJ, Watson DC, Hill AS, Harding SP, Kyriakides MA, Hutchinson S, Norton TA (1989) A comparison of feeding mechanisms in microphagous herbivorous intertidal prosobranchs in relation to resource partitioning. J Molluscan Stud 55:151−165

Hawkins SJ, Hartnoll RG, Kain JM, Norton TA (1992) Plant-animal interactions on hard substratum the North-West Atlantic. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. Clarendon Press, Oxford, p 1−32

Hawkins SJ, Corte-Real HBSM, Pannacciulli FG, Weber LC, Bishop JDD (2000) Thoughts on the ecology and evolution of the intertidal biota of the Azores and other Atlantic islands. Hydrobiologia 440:3−17

Hill AS, Hawkins SJ (1991) Seasonal and spatial variation of epilithic microalgal distribution and abundance and its ingestion by *Patella vulgata* on a moderately exposed rocky shore. J Mar Biol Assoc UK 71:403−423

Hockey PAR, Bosman AL (1986) Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. Oikos 46: 3−14

Hockey PAR, Bosman AL, Siegfried WR (1988) Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. J Appl Ecol 25:353−363

Huff TM (2011) Effects of human trampling on macro- and meiofauna communities associated with intertidal algal turfs and implications for management of protected areas on rocky shores (Southern California). Mar Ecol 32: 335−345

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629−637

Jara FH, Moreno CA (1984) Herbivory and structure in a midlittoral rocky community: a case in southern Chile. Ecology 65:28−38

Jenkins SR, Moore P, Burrows MT, Garbary DJ and others (2008) Comparative ecology of North Atlantic shores: Do differences in players matter for process? Ecology 89: S3−S23

Johnson MP, Portig A, Smyth D, Roberts D (2008) Unregulated harvesting of intertidal shellfish in Strangford

Lough. Northern Ireland Environment Agency Research and Development Series No. 09/05

Jones NS (1946) Browsing of *Patella*. Nature 158:557−558

Keough MJ, Quinn GP, Bathgate R (1997) Geographic variation in interactions between size classes of the limpet *Cellana tramoserica*. J Exp Mar Biol Ecol 215:19−34

Kyle R, Robertson WD, Birnie SL (1997) Subsistence shellfish harvesting in the Maputaland Marine Reserve in northern Kwazulu-Natal, South Africa: rocky shore organisms. Biol Conserv 82:183−192

Lasiak T (1991) The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by indigenous coastal people of Transkei, southern Africa. Biol Conserv 56: 245−264

Lasiak T (1998) Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa. Mar Ecol Prog Ser 167:15−23

Lasiak T (1999) The putative impact of exploitation on rocky infratidal macrofaunal assemblages: a multiple-area comparison. J Mar Biol Assoc UK 79:23−34

Lasiak TA, Field JG (1995) Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. J Exp Mar Biol Ecol 185: 33−53

Lindberg DR, Estes JA, Warheit K (1998) Human influences on trophic cascades along rocky shores. Ecol Appl 8: 880−890

Marshall PA, Keough MJ (1994) Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (Sowerby). J Exp Mar Biol Ecol 177:121−138

Martins GM, Thompson RC, Neto AI, Hawkins SJ, Jenkins SR (2010a) Exploitation of intertidal grazers as a driver of community divergence. J Appl Ecol 47:1282−1289

Martins GM, Thompson RC, Neto AI, Hawkins SJ, Jenkins SR (2010b) Enhancing stocks of the exploited limpet *Patella candei* d'Orbigny via modifications in coastal engineering. Biol Conserv 143:203−211

Martins GM, Jenkins SR, Hawkins SJ, Neto AI, Medeiros AR, Thompson RC (2011) Illegal harvesting affects the success of fishing closure areas. J Mar Biol Assoc UK 91: 929−937

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290−297

Minchinton TE, Fels KJ (2013) Sediment disturbance associated with trampling by humans alters species assemblages on a rocky intertidal seashore. Mar Ecol Prog Ser 472:129−140

Monastersky R (2014) Life—a status report. Nature 516: 158−161

Moreno CA (2001) Community patterns generated by human harvesting on Chilean shores: a review. Aquat Conserv Mar Freshw Ecosyst 11:19−30

Moreno CA, Sutherland JP, Jara FH (1984) Man as a predator in the intertidal zone of southern Chile. Oikos 42: 155−160

Mrowicki RJ, Maggs CA, O'Connor NE (2014) Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers? J Exp Mar Biol Ecol 461:416−424

Navarro PG, Ramírez R, Tuya F, Fernandez-Gil C, Sanchez-Jerez P, Haroun RJ (2005) Hierarchical analysis of spatial distribution patterns of patellid limpets in the Canary Islands. J Molluscan Stud 71:67−73

➤ O'Connor NE, Crowe TP (2005) Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. Ecology 86:1783–1796

➤ O'Connor NE, Donohue I, Crowe TP, Emmerson MC (2011) Importance of consumers on exposed and sheltered rocky shores. Mar Ecol Prog Ser 443:65–75

➤ Oliva D, Castilla JC (1986) The effect of human exclusion on the population-structure of key-hole limpets *Fissurella crassa* and *Fissurella limbata* on the coast of central Chile. Mar Ecol 7:201–217

➤ Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol 10:430

Pombo OA, Escofet A (1996) Effect of exploitation on the limpet *Lottia gigantea:* A field study in Baja California (Mexico) and California (USA). Pac Sci 50:393–403

➤ Power ME (1990) Effects of fish in river food webs. Science 250:811–814

➤ Silva ACF, Hawkins SJ, Clarke KR, Boaventura DM, Thompson RC (2010) Preferential feeding by the crab *Necora puber* on differing sizes of the intertidal limpet *Patella vulgata.* Mar Ecol Prog Ser 416:179–188

➤ Smith JR, Murray SN (2005) The effects of experimental bait collection and trampling on a *Mytilus californianus* mussel bed in southern California. Mar Biol 147:699–706

➤ Southward AJ, Southward EC (1978) Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. J Fish Res Board Can 35:682–706

➤ Teichman KJ, Nielsen SE, Roland J (2013) Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. J Anim Ecol 82:1288–1299

➤ Underwood AJ (1976) Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). J Exp Mar Biol Ecol 23:145–154

Underwood AJ (1991) Stupidity, myths and guess-work in the detection of marine environmental impacts: dead bird-watching for hydrographers. Second Australasian Hydrographic Symposium: The Hydrographic Society Special Publication 27:43–53

Underwood AJ (1992) Competition and marine plant–animal interactions. In: John DM, Hawkins SJ, Price JH (eds) Plant–animal interactions in the marine benthos. Clarendon Press, Oxford, p 443–475

Underwood AJ (1997) Experiments in ecology. Cambridge University Press, Cambridge

Appendix

Diagrammatic representation of the experimental design. At each site, 3 adjacent blocks of shore (~ 20 m wide) were defined at the mean tide level (MTL) facing the sea (wavy horizontal lines). Three unfenced treatment plots of 3 × 3 m were established in each block and were randomly allocated to 1 of 2 rates of exploitation: (L) low, (H) high, or (C) unmanipulated control