



**QUEEN'S
UNIVERSITY
BELFAST**

Consistent effects of consumer species loss across different habitats

Mrowicki, R. J., Maggs, C. A., & O'Connor, N. E. (2015). Consistent effects of consumer species loss across different habitats. *Oikos*, 124(12), 1555-1563. <https://doi.org/10.1111/oik.02138>

Published in:
Oikos

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights
Copyright 2015 The Authors. Oikos Copyright 2015 Nordic Society Oikos

This is the accepted version of the following article: Mrowicki, R. J., Maggs, C. A. and O'Connor, N. E. (2015), Consistent effects of consumer species loss across different habitats. *Oikos*. doi: 10.1111/oik.02138, which has been published in final form at <http://onlinelibrary.wiley.com/doi/10.1111/oik.02138/abstract>

General rights
Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access
This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

| | |
|-------------------------------|--|
| Journal: | <i>Oikos</i> |
| Manuscript ID: | OIK-02138.R1 |
| Wiley - Manuscript type: | Research |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | Mrowicki, Robert; Queen's University Belfast, School of Biological Sciences Maggs, Christine; Queen's University Belfast, School of Biological Sciences; Queen's University Belfast, School of Biological Sciences O'Connor, Nessa; Queens University Belfast, Biological Sciences |
| Keywords: | species loss, algae-grazer interactions, benthic |
| Abstract: | <p>Our knowledge of the effects of consumer species loss on ecosystem functioning is limited by a paucity of manipulative field studies, particularly those that incorporate inter-trophic effects. Further, given the ongoing transformation of natural habitats by anthropogenic activities, studies should assess the relative importance of biodiversity for ecosystem processes across different environmental contexts by including multiple habitat types. We tested the context-dependency of the effects of consumer species loss by conducting a 15-month field experiment in two habitats (mussel beds and rock pools) on a temperate rocky shore, focussing on the responses of algal assemblages following the single and combined removals of key gastropod grazers (<i>Patella vulgata</i>, <i>P. ulyssiponensis</i>, <i>Littorina littorea</i> and <i>Gibbula umbilicalis</i>). In both habitats, the removal of limpets resulted in a larger increase in macroalgal richness than that of either <i>L. littorea</i> or <i>G. umbilicalis</i>. Further, by the end of the study, macroalgal cover and richness were greater following the removal of multiple grazer species compared to single species removals. Despite substantial differences in physical properties and the structure of benthic assemblages between mussel beds and rock pools, the effects of grazer loss on macroalgal cover, richness, evenness and assemblage structure were remarkably consistent across both habitats. There was, however, a transient habitat-dependent effect of grazer removal on macroalgal assemblage structure that emerged after three months, which was replaced by non-interactive effects of grazer removal and habitat after 15 months. This study shows that the effects of the loss of key consumers may transcend large abiotic and biotic differences between habitats in rocky intertidal systems. While it is clear that consumer diversity is a primary driver of ecosystem functioning, determining its relative importance across multiple contexts is necessary to understand the consequences of consumer species loss against a background of environmental change.</p> |



SCHOLARONE™
Manuscripts

For Review Only

1 **CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS**
2 **ACROSS DIFFERENT HABITATS**

3
4 ROBERT J. MROWICKI, CHRISTINE A. MAGGS AND NESSA E. O'CONNOR

5 School of Biological Sciences, Queen's University Belfast, UK
6

7 **Type of paper:** Research paper

8
9 **Corresponding author:** Robert J. Mrowicki

10 **Address:** School of Biological Sciences, Queen's University Belfast,
11 Medical Biology Centre, 97 Lisburn Road, Belfast, BT9 7BL,
12 Northern Ireland, UK

13 **Email:** rmrowicki01@qub.ac.uk

14 **Telephone:** +44 (0)28 9097 2030

15 **Fax:** +44 (0)28 9097 5877

16 **Abstract:**

17

18 Our knowledge of the effects of consumer species loss on ecosystem functioning is limited by
19 a paucity of manipulative field studies, particularly those that incorporate inter-trophic effects.

20 Further, given the ongoing transformation of natural habitats by anthropogenic activities,

21 studies should assess the relative importance of biodiversity for ecosystem processes across

22 different environmental contexts by including multiple habitat types. We tested the context-

23 dependency of the effects of consumer species loss by conducting a 15-month field

24 experiment in two habitats (mussel beds and rock pools) on a temperate rocky shore,

25 focussing on the responses of algal assemblages following the single and combined removals

26 of key gastropod grazers (*Patella vulgata*, *P. ulysiponensis*, *Littorina littorea* and *Gibbula*

27 *umbilicalis*). In both habitats, the removal of limpets resulted in a larger increase in

28 macroalgal richness than that of either *L. littorea* or *G. umbilicalis*. Further, by the end of the

29 study, macroalgal cover and richness were greater following the removal of multiple grazer

30 species compared to single species removals. Despite substantial differences in physical

31 properties and the structure of benthic assemblages between mussel beds and rock pools, the

32 effects of grazer loss on macroalgal cover, richness, evenness and assemblage structure were

33 remarkably consistent across both habitats. There was, however, a transient habitat-dependent

34 effect of grazer removal on macroalgal assemblage structure that emerged after three months,

35 which was replaced by non-interactive effects of grazer removal and habitat after 15 months.

36 This study shows that the effects of the loss of key consumers may transcend large abiotic and

37 biotic differences between habitats in rocky intertidal systems. While it is clear that consumer

38 diversity is a primary driver of ecosystem functioning, determining its relative importance

39 across multiple contexts is necessary to understand the consequences of consumer species loss

40 against a background of environmental change.

41 **Introduction**

42

43 Global biodiversity loss continues to threaten the provision of ecosystem services and
44 ultimately human wellbeing (Naeem et al. 2009, Hooper et al. 2012). Following more than
45 two decades of intensive research, it is now accepted widely that declining biodiversity affects
46 rates of ecosystem processes, such as resource capture and biomass production (Loreau et al.
47 2001, Cardinale et al. 2012, Gamfeldt et al. in press). In recognition of the complexity of
48 biotic interactions within natural communities, an increasing number of biodiversity–
49 ecosystem functioning studies have incorporated inter-trophic effects (Duffy et al. 2007).
50 Despite this important move towards a multi-trophic perspective, our knowledge of the
51 influence of consumer diversity loss on lower trophic levels is relatively incomplete (Duffy et
52 al. 2007, Griffin et al. 2013). This is of particular concern, given that consumers generally
53 have impacts that are disproportionate to their abundance and face a higher risk of extinction
54 compared to producers (Duffy 2002).

55

56 Long-term field removal experiments are an effective means of characterising the effects of
57 species loss within diverse natural assemblages (Díaz et al. 2003) and complement laboratory
58 studies by revealing mechanisms that may not be manifested in smaller scale experiments
59 conducted under more homogeneous conditions (Stachowicz et al. 2008). Further, as the
60 ecological effects of biodiversity change are influenced by environmental context (Boyer et
61 al. 2009, Crowe et al. 2011, Mrowicki and O'Connor in press), empirical studies that examine
62 consumer diversity effects under a range of abiotic and biotic conditions (Griffin et al. 2009,
63 O'Connor and Donohue 2013) will improve our ability to predict the consequences of species
64 loss in the face of global environmental change involving multiple anthropogenic stressors
65 (Harley et al. 2006).

66

67 Coastal ecosystems are exposed to a range of anthropogenic impacts, which can result in
68 rapid declines in biodiversity and dramatic transformation or loss of habitat (Airoldi and Beck
69 2007). For example, on temperate rocky shores, overexploitation and pollution, coupled with
70 the physiological and phenological responses of organisms to climate change, may lead to
71 reduced densities or extinctions of key grazer species in certain localities (Thompson et al.
72 2002, Mieszkowska et al. 2005). Additionally, intertidal biogenic habitats, such as macroalgal
73 and mussel beds on rocky substrata, have decreased in extent and structural complexity in
74 many regions in response to various factors including physical disturbance and compromised
75 water quality (Airoldi and Beck 2007). Changes in habitat complexity and heterogeneity alter
76 interspecific interactions and the degree of resource partitioning among consumers, and can
77 thus modify consumer diversity effects on resources (Hughes and Grabowski 2006, Griffin et
78 al. 2009). In combination, these processes have the potential to shift the dynamic balance
79 between producers and consumers and alter the functioning of coastal marine ecosystems
80 (Hawkins et al. 2009).

81

82 The aim of this study was to determine whether the ecological consequences of consumer
83 species loss vary with environmental context, in light of ongoing reductions in biodiversity
84 and habitat homogenisation in coastal ecosystems. We quantified changes in macroalgal
85 assemblages in response to individual and combined removals of common gastropod grazers,
86 *Patella vulgata*, *P. ulyssiponensis*, *Littorina littorea* and *Gibbula umbilicalis*, in two different
87 habitats on an exposed north-east Atlantic rocky shore. Patellid limpets are key grazers in
88 European rocky intertidal habitats, and although their presence or absence often dominates the
89 effects of grazer assemblages on algal communities on emergent rock and in rock pools
90 (Hawkins and Hartnoll 1983, O'Connor and Crowe 2005, Coleman et al. 2006, Griffin et al.

91 2010), the extent of their influence in other habitats, such as mussel beds, is less well known
92 (O'Connor and Crowe 2008). Further, the relative roles of these grazer species may vary
93 across different conditions, and the importance of changes in the richness versus identity of
94 these species is likely to increase with environmental heterogeneity (Griffin et al. 2009). To
95 examine the context-dependency of the roles of these key consumers, we performed
96 simultaneous grazer removals in mussel beds (on emergent rock) and in rock pools. These
97 two distinct habitats differ greatly with respect to the intensity and variability of a range of
98 abiotic stressors such as desiccation potential, temperature and wave disturbance.
99 Specifically, emergent rock habitats experience relatively greater fluctuations in abiotic
100 variables, but conditions can be more spatially variable among rock pools (Metaxas and
101 Scheibling 1993). At the same time, the physical structure afforded by either mussels or turf
102 algae (e.g. *Corallina officinalis*) enables diverse, yet divergent, biotic assemblages to persist
103 (Seed 1996, Kelaher 2002). Thus, owing to contrasting patterns of physical and biological
104 heterogeneity in mussel beds versus rock pools, the relative effects of grazer removal may
105 differ between these two habitats. Focussing on changes in macroalgal abundance, diversity
106 and assemblage structure, we hypothesised that: (1) there are species-specific consumer
107 identity effects, dominated by the influence of *Patella* spp. in both mussel beds and rock
108 pools; (2) the effects of the combined removal of multiple grazer species will exceed the
109 effects of removals of single species; and (3) these effects of grazer species loss will differ
110 between rock pools and mussel beds and vary according to experimental duration.

111

112 **Materials and methods**

113

114 *Study site*

115

116 The experiment was conducted on an exposed rocky shore in Glashagh Bay, Fanad, Co.
117 Donegal, Ireland (55.265°N, 7.675°W). The shore was characterised by a large, gently sloping
118 granitic platform, covered by a mosaic of patches of barnacles and macroalgae, typical of
119 exposed shores in the region (O'Connor and Crowe 2008, Mrowicki et al. 2014). Beds of
120 mussels (*Mytilus* spp.) were distributed patchily along the shore above mid-tidal level (2.0–
121 2.5 m above Chart Datum). Numerous discrete rock pools of varying area and depth were
122 present throughout the intertidal zone. Macroalgal assemblages associated with mussels
123 consisted of extensive epibiotic turfs of coarse red algae (mostly *Gelidium* spp.) interspersed
124 with ephemeral red (e.g. *Porphyra umbilicalis*) and green (e.g. *Ulva intestinalis*) algae. Small
125 clumps of brown algae (e.g. *Fucus spiralis* and *F. serratus*) were also found in and around the
126 mussel beds. The rock pools were dominated by turfs of upright calcareous algae (*Corallina*
127 *officinalis*), which supported an array of macroalgal species including fine (e.g. *Polysiphonia*
128 *elongata* and *Ceramium rubrum*) and coarse (e.g. *Osmundea hybrida* and *Gelidium* spp.)
129 branched red algae, ephemeral (e.g. *U. compressa*) and perennial (e.g. *Codium tomentosum*)
130 green algae and brown canopy algae (e.g. *F. vesiculosus* and *Halidrys siliquosa*). Encrusting
131 coralline algae (*Lithothamnia* spp.) covered most of the remaining substratum. Thus, on this
132 shore, in addition to there being large differences in algal assemblage structure between the
133 two habitats, the diversity of algae was greater in rock pools compared to mussel beds (see
134 *Results*).

135

136 Grazing gastropods were common and widespread across the shore. The most conspicuous
137 species, which occurred in both mussel beds and rock pools, were the common and China
138 limpets (*Patella vulgata* and *P. ulyssiponensis*, respectively), common periwinkle (*Littorina*
139 *littorea*) and flat top shell (*Gibbula umbilicalis*). Although the two limpet species co-occurred
140 in both habitat types, particularly as newly settled juveniles in rock pools, *P. ulyssiponensis*

141 adults were dominant in rock pools (Firth and Crowe 2008), whereas *P. vulgata*, which tends
142 to disperse out onto emergent rock, constituted the majority of limpets in mussel beds. Other
143 gastropod species, including *L. saxatilis*, *L. obtusata* and *G. cineraria*, were also present in
144 both habitats. Non-gastropod grazers such as chitons (e.g. *Acanthochitona crinita*) and
145 amphipods (e.g. *Echinogammarus marinus*) were found on the shore at lower densities.

146

147 *Experimental design*

148

149 Our experiment involved the single and combined removal of three genera of gastropod
150 grazer within each of the two habitat types (mussel beds and rock pools). We employed a
151 ‘subtractive’ approach with no compensation for the reduction in biomass of particular
152 species by increasing that of the remaining species. Unlike a substitutive design, whereby
153 total grazer density would be equalised across treatments, such an approach avoids
154 confounding changes in intraspecific interactions with changes in interspecific interactions
155 among grazers (Byrnes and Stachowicz 2009). Further, instead of standardising species
156 densities across habitat types, we opted to mimic actual densities specific to mussel beds and
157 rock pools. Thus, we did not elicit potentially unsustainable experimental densities by
158 exceeding natural densities in either habitat (Harley 2006) and we minimised transplant-
159 induced stress or mortality of grazers, particularly limpets (Firth and Crowe 2010).
160 Importantly, although our design did not allow the effects of grazer removal and habitat type
161 to be separated from those of grazer density, incorporating (rather than eliminating) natural
162 variability in species densities was intended to enhance the realism of our study (Diaz et al.
163 2003) with respect to this particular system.

164

165 Within each of the two habitats, 20 plots (35 × 35 cm) were located haphazardly around mid-
166 tidal level across approximately 100 m of shoreline, with a minimum separation between any
167 two plots of 1 m. Mussel bed plots were positioned on well-drained, approximately
168 horizontal, substratum and incorporated 50.8 ± 2.2% (mean ± SE) mussel cover. Rock pool
169 plots were situated in separate pools of relatively similar area (range 0.5–5.0 m²) and depth (<
170 15 cm) and included 46.5 ± 4.2% cover of *Corallina officinalis*. By incorporating, rather than
171 controlling for, environmental heterogeneity such as inherent differences in habitat size (i.e.
172 mussel patch extent and rock pool volume), we aimed to enhance the relevance of this study
173 to variable natural systems.

174

175 Five grazer removal treatments were assigned randomly among the plots in each habitat type
176 ($n = 4$): one ‘non-removal’ treatment requiring the removal of no species; three ‘single-
177 removal’ treatments involving the removal of either *Patella* spp. (*P. vulgata* and *P.*
178 *ulyssiponensis*; hereafter *Patella*), *Littorina littorea* (hereafter *Littorina*) or *Gibbula*
179 *umbilicalis* (hereafter *Gibbula*); and one ‘multi-removal’ treatment, in which all three grazer
180 genera were removed. Owing to difficulties in the identification of *P. vulgata* and *P.*
181 *ulyssiponensis*, particularly juveniles and small adults, without causing substantial
182 disturbance, it was not possible to discriminate between limpet species. On rocky shores in
183 Ireland, adults of these two species tend to be segregated so that *P. vulgata* is more common
184 on emergent substrata than *P. ulyssiponensis*, which is more common in rock pools (Firth and
185 Crowe 2010). Further, there is the potential for contrasting functional roles of different limpet
186 species within the same habitat (Moore et al. 2007). Therefore, it is not possible here to
187 separate the effects of *P. vulgata* and *P. ulyssiponensis* across mussel beds and rock pools.
188 Instead, as both species are considered key grazers within their respective primary habitats
189 (Hawkins and Hartnoll 1983, O’Connor and Crowe 2005), the removal of *Patella* should be

190 interpreted as the combined loss of putative strongly-interacting consumers in the case of both
191 mussel beds and rock pools. While it is possible here to make inferences regarding the
192 specific roles of *Littorina* and *Gibbula*, caution must be exercised when attributing the effects
193 of *Patella* removal, and their context-dependency, to particular species.

194

195 Experimental grazer abundances were derived from natural densities in mussel beds (*Patella*,
196 $27.5 \pm 6.2 \text{ m}^{-2}$ [mean \pm SE; $n = 25$]; *Littorina*, $40.3 \pm 14.3 \text{ m}^{-2}$) and rock pools (*Patella*, 201.6
197 $\pm 26.8 \text{ m}^{-2}$; *Littorina*, $90.2 \pm 13.9 \text{ m}^{-2}$; *Gibbula*, $9.6 \pm 2.9 \text{ m}^{-2}$), adjusted to account for the high
198 proportion (~50%) of *Patella* juveniles (< 15 mm) encountered in both habitat types.

199 Although not encountered within the area sampled by preliminary surveys, *Gibbula* was
200 present in mussel beds at low overall density, often in small aggregations adjacent to mussel
201 patches (R. J. Mrowicki, pers. obs.). Thus, experimental abundances were as follows: 3
202 *Patella*, 5 *Littorina* and 2 *Gibbula* in mussel bed plots; and 12 *Patella*, 11 *Littorina* and 2
203 *Gibbula* in rock pool plots. In a few cases, *Littorina* and *Gibbula* populations were
204 supplemented with additional individuals to meet target densities, although this was not
205 necessary for *Patella*. Treatments were maintained using stainless steel mesh cages (35 \times
206 35 cm area, 12 cm high) fixed to the substratum with stainless steel screws and washers. This
207 method was found to be most effective means of manipulating densities of mobile grazers
208 over extended time periods on this particular shore. The mesh size (0.9 mm wire diameter,
209 4.17 mm aperture, 67% open area) of cages restricted the movement of the target grazer
210 species while allowing access to smaller mobile consumers and leaving plots open to
211 propagule supply.

212

213 To enable the detection of cage effects on experimental assemblages, an additional four plots
214 were established within each habitat and marked at opposite corners with stainless steel

215 screws, thus remaining open to ambient densities of mobile organisms. Although there is the
216 potential for experimental artefacts to vary among treatments (Peterson and Black 1994,
217 Benedetti-Cecchi and Cinelli 1997), testing for interactions between cage effects and grazer
218 removal treatments would require the manipulation of grazer densities independently of the
219 use of cages, which is not feasible. Therefore, these uncaged control plots were designed to
220 test for the direct (e.g. shading and disruption of water flow) and indirect (e.g. altered grazer
221 behaviour) effects of cages on algal assemblages in the presence of ambient grazer densities
222 only, by comparing controls with non-removal caged plots. This approach follows previous
223 studies that have demonstrated no consequences of identical cages on the structure of
224 macroalgal assemblages in mussel beds and rock pools on similar shores (O'Connor and
225 Crowe 2005, O'Connor and Donohue 2013).

226

227 The experiment ran for 15 months starting in July 2011 and plots were surveyed at the
228 beginning of the experiment, after three months (October 2011) and after 15 months (October
229 2012). At each census, percent cover of macroalgal and sessile invertebrate species in each
230 plot was recorded by identifying species under 64 intersections of a 25×25 cm quadrat.

231 Species present within the quadrat but not located under an intersection were recorded and
232 assigned a value of 1% each. The quadrat was positioned centrally within plots to avoid edge
233 effects. Total percent cover values often exceeded 100% owing to the multi-layered nature of
234 macroalgal communities. The numbers of grazer species within each plot were also recorded.
235 Treatments were maintained during monthly visits, at which times cages were also cleaned of
236 fouling species or debris to minimise cage effects on assemblages.

237

238 To determine whether percent cover served as a reliable proxy for macroalgal biomass, on the
239 final sampling date, a destructive sample of the central 25×25 cm area in each experimental

240 plot was taken to estimate biomass of each macroalgal species (excluding crustose corallines)
241 following drying to constant mass at 60°C. Dry biomass values for *Corallina officinalis* were
242 multiplied by 0.2 to convert them to calcium carbonate-free estimates (Griffin et al. 2010).
243 There was a significant linear relationship between total dry biomass and total cover of
244 macroalgae (excluding crustose corallines), which differed between mussel beds and rock
245 pools (mussel beds: biomass [g m^{-2}] = $-2.07 + 4.42 \times \text{cover} [\%]$, $R^2 = 0.929$, $P < 0.001$; rock
246 pools: biomass = $-31.98 + 1.74 \times \text{cover}$, $R^2 = 0.808$, $P < 0.001$).

247

248 *Data analysis*

249

250 For each sampling date separately, differences in macroalgal total cover, taxon richness (S)
251 and evenness (Simpson's $1-\lambda$) were tested using two-way factorial ANOVA involving habitat
252 (fixed, 2 levels) and grazer removal treatment (fixed, 5 levels). Richness and evenness are
253 complementary measures that are recommended for use in studies examining the
254 consequences of biodiversity change (Altieri et al. 2009). Total algal cover was found to
255 differ among grazer removal treatments across both habitats at the start of the experiment,
256 although it was not possible to resolve these differences fully (Supplementary material
257 Appendix 1 Table A1). Therefore, algal cover data were converted into the overall change in
258 total cover to simplify interpretation. We used a priori planned contrasts to test for differences
259 between the single-removal treatments and the multi-removal treatment but, given the
260 limitations on making inferences regarding limpet identity, the variance explained by grazer
261 removal was not partitioned further to isolate grazer 'identity' effects explicitly (Duffy et al.
262 2005). To test for cage effects, comparisons between caged non-removal plots and uncaged
263 control plots were made for all variables. Prior to ANOVA, Shapiro-Wilk and Cochran's tests
264 were used to check normality and homoscedasticity of data, respectively. In the case of total

265 cover data for three months, transformation was unable to stabilise heterogeneous variances,
266 therefore results were interpreted with caution by reducing the limit for statistical significance
267 ($\alpha = 0.01$). Student-Newman-Keuls (SNK) tests were used to make post hoc comparisons
268 between levels of significant effects. Although SNK tests have the potential for excessive
269 Type I error rates when treatments fall into groups spaced widely apart (Day and Quinn
270 1989), which was generally not the case in the current study, a greater problem is the loss of
271 power resulting from the use of alternative procedures where SNK tests would otherwise be
272 suitable (Underwood 1997). Therefore, in this study, SNK tests were an appropriate means of
273 examining alternatives following the rejection of null hypotheses.

274

275 Permutational multivariate analysis of variance (PERMANOVA; McArdle and Anderson
276 2001, Anderson 2001) was used to test for effects of grazer treatments on macroalgal
277 assemblage structure in mussel beds and rock pools, separately for each sampling date, based
278 on the same model structure as the ANOVAs. Analyses were performed on zero-adjusted
279 Bray-Curtis dissimilarity matrices, i.e. via the addition of a dummy species with 1% cover to
280 all plots (Clarke et al. 2006), to deal with instances where no algae were recorded within
281 plots. Tests involved 9,999 permutations of residuals under the reduced model (Anderson and
282 ter Braak 2003). Differences among levels of significant factors were examined with post hoc
283 pairwise permutational *t*-tests. Where significant differences were found, similarity of
284 percentages analysis (SIMPER; Clarke 1993) was used to identify the algal taxa responsible
285 for differences in assemblage structure between treatment levels. To visualise differences in
286 macroalgal assemblage structure among treatment groups, nonmetric multidimensional
287 scaling (MDS) plots were produced. For all multivariate analyses, percent cover data were
288 $\log_{10}(x+1)$ -transformed to reduce the influence of dominant algal species (Clarke and
289 Warwick 2001). All analyses were conducted in R (v3.0.1; R Development Core Team 2013),

290 except for the PERMANOVAs, which were performed using the PERMANOVA+ add-on
291 (v1.0.3) in PRIMER (v6.1.13; PRIMER-E Ltd., Plymouth, UK).

292

293 **Results**

294

295 At the start of the experiment, macroalgal total cover, richness and evenness were greater in
296 rock pools than in mussel beds, and macroalgal assemblage structure differed between the two
297 habitats (Appendix 1 Table A1). After three months, there were still differences in algal
298 richness, evenness and assemblage structure between habitats (Fig. 1c,e; Table 1b–d).

299 Additionally, richness and evenness differed among grazer removal treatments, independently
300 of habitat (Fig. 1c,e; Table 1b,c). Across both mussel beds and rock pools, algal richness was
301 greater in the multi-removal treatment than in any other treatment (Fig. 1c). Although post
302 hoc tests were unable to resolve differences among the non-removal and single-removal
303 treatments fully, the removal of *Patella* appeared to result in an increase in algal richness
304 relative to the non-removal treatment across both habitats (Fig. 1c). Further, algal richness
305 was greater in the multi-removal treatment compared to the single-removal treatments (Table
306 1b). There also appeared to be an increase in algal evenness in the multi-removal treatment
307 compared to both the non-removal treatment and the *Littorina* single-removal treatment, but
308 post hoc tests were unable to resolve treatment differences fully (Fig. 1e).

309

310 After 15 months, the overall decline in total macroalgal cover was greater in rock pools than
311 in mussel beds (Fig. 1b; Table 1a). Again, macroalgal richness and evenness were found to be
312 greater in rock pools compared to mussel beds (Fig. 1d,f; Table 1b,c) and assemblage
313 structure differed between the two habitats (Table 1d). In addition to algal richness, total
314 cover change and assemblage structure were affected by grazer removal independently of

315 habitat (Fig. 1b,d; Table 1a,b,d). The removal of *Patella* led to an increase in algal richness
316 relative to the non-removal treatment and the other two single-removal treatments (Fig. 1d).
317 Further, the multi-removal of all three grazers resulted in greater algal richness than any other
318 treatment (Fig. 1d) in addition to the mean of the single-removal treatments (Table 1b). The
319 multi-removal treatment led to an overall increase in total algal cover, which appeared to
320 differ significantly from the overall declines exhibited by the non-removal and the *Patella* and
321 *Gibbula* single-removal treatments, but post hoc tests were unable to resolve differences
322 among all treatments fully (Fig. 1b). In terms of algal evenness, there was no longer any
323 effect of grazer removal (Fig. 1f; Table 1c). The presence of cages reduced macroalgal
324 richness at three months (ANOVA; $F_{1,12} = 5.83$, $P = 0.033$; Fig. 1c) and evenness at 15
325 months ($F_{1,12} = 5.23$, $P = 0.041$; Fig. 1f; Appendix 2 Table A2)

326
327 There was a significant interaction between habitat and grazer removal treatments affecting
328 algal assemblage structure after three months, indicating that the responses of algal
329 assemblages to grazer removal differed between mussel beds and rock pools (Fig. 2a,c; Table
330 1d). Although post hoc tests were unable to resolve differences among treatments fully, they
331 suggested tentatively that, in mussel beds, the *Patella* single-removal and multi-removal
332 treatments resulted in a shift in algal assemblage structure relative to the *Littorina* and
333 *Gibbula* single-removal treatments (Fig. 2a; Appendix 3 Table A3). In contrast, in rock pools,
334 algal assemblage structure appeared to differ only between the non-removal and multi-
335 removal treatments (Fig. 2c; Appendix 3 Table A3). Algal assemblage structure also differed
336 between caged non-removal and uncaged control plots (Appendix 2 Table A2). After 15
337 months, there was no longer any interactive effect of habitat and grazer removal on algal
338 assemblage structure, indicating that the effects of grazer species loss were consistent between
339 mussel beds and rock pools (Fig. 2b,d; Table 1d). Across both habitats, there was a shift in

340 algal assemblage structure in the *Patella* single-removal and multi-removal treatments relative
341 to all other treatments (Appendix 3 Table A3). This shift was driven consistently (i.e.
342 $\bar{\delta}_i/SD(\delta_i) > 1$) by a relative increase in *Fucus vesiculosus* ($\bar{\delta}_i = 13.3\%$) and by relative
343 decreases in calcareous encrusting algae and *Corallina officinalis*, both of which were
344 primarily constituents of rock pool assemblages (Table 2). These changes were accompanied
345 by an increase in *Cladophora rupestris* and fucoid germlings across both habitats (Table 2).

346

347 **Discussion**

348

349 To advance our understanding of the consequences of species loss in the face of changing
350 environmental conditions, we must assess the relative contribution of biodiversity to
351 ecosystem processes across a range of contexts, while incorporating the complexity that
352 characterises natural ecosystems (Duffy et al. 2007, Cardinale et al. 2012). We performed
353 single and multiple removals of common grazer species, or groups of species, simultaneously
354 in mussel beds and rock pools, which represent two contrasting ecological contexts against a
355 background of natural environmental variability. The most striking aspect of our findings is
356 the overall consistency of responses to consumer loss across habitats over the duration of the
357 study, demonstrated by a general lack of interactions between habitat and grazer removal
358 treatments. While the effects of limpet removal cannot be attributed to individual species, the
359 loss of this group of putative key grazers, versus that of other grazer species, resulted in
360 similar relative changes to algal assemblages in mussel beds and rock pools. The fact that this
361 pattern emerged despite obvious differences in grazer densities and relative abundances
362 between habitats, in addition to initial differences in algal assemblages and environmental
363 conditions, suggests that consumer diversity (i.e. both identity and richness) is a major driver
364 of ecological processes in this system. In addition, the changes in the patterns of algal

365 abundance and diversity over the course of the experiment and the transient habitat-dependent
366 response of algal assemblage structure emphasise that experimental duration is critical to the
367 interpretation of studies examining the effects of species loss across environmental contexts
368 (Cardinale et al. 2004, O'Connor and Crowe 2005, Stachowicz et al. 2008).

369

370 In both mussel beds and rock pools, algal total cover, species richness and evenness
371 underwent significant changes in response to grazer removal. In particular, the removal of
372 limpets led to a greater increase in algal richness than the removal of either *Littorina littorea*
373 or *Gibbula umbilicalis*. The key ecological role of patellid limpets, relative to other grazer
374 species, regulating the establishment of algae on emergent substrata and in tide pools on
375 European rocky shores is well known (Hawkins and Hartnoll 1983, O'Connor and Crowe
376 2005, Coleman et al. 2006, Griffin et al. 2010). The extent of their influence on algal
377 community dynamics in mussel beds, however, is perhaps less well appreciated (O'Connor
378 and Crowe 2008, Crowe et al. 2011). Our findings suggest that the relative functional roles of
379 limpets collectively, whether represented predominantly by *Patella ulyssiponensis* or by *P.*
380 *vulgata*, may be of similar importance in mussel beds compared to other habitats on rocky
381 shores, in spite of natural differences in total abundance.

382

383 Further, the differences among single-removal treatments suggest that other common grazer
384 species, even those present at higher natural densities, appear to be limited in their capacity to
385 compensate for the loss of limpets in mussel beds as well as rock pools (O'Connor and Crowe
386 2005, Griffin et al. 2010). Although our experiment allowed only for behavioural rather than
387 numerical compensation, previous research has demonstrated that even corresponding
388 increases in the abundance of *L. littorea* and *G. umbilicalis* are insufficient to compensate for
389 limpet removal in this system over similar timescales (O'Connor and Crowe 2005). While we

390 cannot separate the effects of different limpet species, our results imply some degree of
391 functional complementarity between *P. ulyssiponensis* and *P. vulgata* at the scale of this study
392 owing to their spatial segregation between mussel beds and rock pools (Firth and Crowe
393 2010). Nonetheless, further experimentation is required to determine precisely how the
394 relative roles of these key species vary across habitats in which they coexist, particularly
395 because other closely related limpet species are known to have idiosyncratic effects on rocky
396 shore communities in this region (Moore et al. 2007).

397

398 A key finding of our study was that the removal of multiple grazer species led to a greater
399 increase in algal richness than did the removal of limpets alone, even though the single
400 removal of either *Littorina littorea* or *Gibbula umbilicalis* had no effect. This effect was
401 accompanied by a shift in algal assemblage structure in the limpet single-removal and multi-
402 removal treatments compared to all other treatments, which was driven largely by the
403 increased establishment and growth of furoid macroalgae at the apparent expense of other
404 species. While consumer identity can be of overarching importance for the functioning of
405 marine ecosystems (O'Connor and Crowe 2005, Stachowicz et al. 2007), declines in
406 consumer diversity per se may lead to reduced top-down control owing to trait differentiation
407 among consumer species in terms of, for example, feeding preferences (Duffy 2002, Griffin et
408 al. 2009).

409

410 Alternatively, these patterns may have resulted from the reduction in grazer abundance
411 associated with the multi-removal treatment in our 'subtractive' experimental design, rather
412 than a reduction in grazer species richness. For example, the establishment of furoid
413 macroalgae on rocky shores may occur only when grazer density falls below a certain
414 threshold (Jonsson et al. 2006). Indeed, the effects of grazer removal observed here may have

415 been driven, at least in part, by differences in density among experimental treatments as
416 opposed to grazer identity or richness. Previous research has emphasised the importance of
417 density-dependent effects in regulating biodiversity–ecosystem functioning relationships (e.g.
418 Benedetti-Cecchi 2004, Maggi et al. 2009). To improve our understanding of complex, non-
419 linear effects of consumer species loss, future studies should aim to separate the importance
420 of consumer density from that of identity and richness, such as by incorporating density
421 explicitly as an additional treatment (Benedetti-Cecchi 2004, Byrnes and Stachowicz 2009).
422 While there were logistical constraints on the maximum number of treatments and replicates
423 in our study, incorporating (rather than eliminating) differences in grazer density between
424 treatments helped to maintain the relevance of our findings to species loss from natural
425 habitats in this system, at least for comparable spatial and temporal scales. Importantly, even
426 though the mechanisms underlying differences between the single-removal and multi-removal
427 treatments are unclear, our results suggest that, in both mussel beds and rock pools, the roles
428 of grazer species, or groups of species, depend on the presence or absence of other grazers
429 and, therefore, cannot be deduced from the effects of their removal in isolation.

430

431 Initially, grazer-driven changes in algal assemblage structure varied according to habitat.
432 Although the mechanisms driving this context-dependency remain unclear, there was some
433 indication of a greater overall response of algal assemblages, at least in terms of the number
434 of differences between treatment groups, in mussel beds compared to rock pools.
435 Nonetheless, the suggestion of a transient effect of habitat on community responses highlights
436 the importance of experimental duration in assessing the consequences of species loss from
437 complex ecosystems (O'Connor and Crowe 2005, Stachowicz et al. 2008). It is perhaps
438 surprising that habitat-dependent effects of grazer removal were not more common in our
439 study, given the contrasting patterns of environmental heterogeneity (Metaxas and Scheibling

440 1993) and inherent differences in the abundance and structure of grazer and algal assemblages
441 between habitats (e.g. the difference in limpet densities between mussel beds and rock pools).
442 Instead, for the majority of responses measured in our study, the effects of grazer removal on
443 algal assemblages were remarkably consistent across habitats. Although this may mean that
444 the effects of consumer loss on algal communities were not mediated strongly by local-scale
445 variability between habitats on the same shore, other processes such as variation in
446 recruitment or disturbance regimes may play a greater role over larger scales (Jenkins et al.
447 2005, Mrowicki et al. 2014). For example, divergent effects of grazer removal may emerge
448 even in similar habitats on different rocky shores separated by kilometres (Crowe et al. 2011).
449 While the consequences of changing diversity are expected to be more apparent over larger
450 spatial and temporal scales (Cardinale et al. 2004, Stachowicz et al. 2008), it is less clear how
451 the importance of abiotic factors in determining the effects of species loss varies across
452 multiple scales.

453

454 There are some caveats that should be considered when attempting to extend our findings to
455 rocky intertidal systems in general. First, the presence of experimental cages appeared to
456 influence the structure of algal assemblages, either directly, via shading or hydrodynamic
457 disruption, or indirectly, by altering the movement of grazers or providing habitat for other
458 consumers. Owing to the nature of the study system, cages were the most suitable means of
459 manipulating grazer populations over the timescale of the experiment, and it was not possible
460 to test whether cage effects interacted with grazer removal treatment. The fact that clear
461 differences emerged among caged treatments despite substantial environmental variability
462 within and between habitats, however, suggests that the observed effects of grazer species
463 loss may indeed be representative of unmanipulated, 'real world' communities within this
464 system. Second, it was found that total algal cover was not equivalent across treatments at the

465 start of the experiment, which may have influenced the responses of algal assemblages to
466 grazer removal. The initial pattern of algal cover, however, did not correspond with that
467 observed later in the experiment, in addition to the differences (or lack thereof) in richness
468 and evenness between treatments. Again, this suggests that grazer removal was the most
469 important force driving changes in algal assemblages over the course of the experiment.
470 While it is important to exercise caution in relating the results of manipulative studies to real
471 world scenarios, field-based removal experiments are useful for understanding how complex
472 ecosystems respond to species loss, serving as much-needed tests of fundamental ecological
473 theory (Díaz et al. 2003, Stachowicz et al. 2008, Gamfeldt et al. in press).

474

475 In conclusion, our results demonstrate that the relative effects of the loss of key groups of
476 consumers can transcend different physical and biological conditions between habitats.
477 Specifically, limpets, which comprised predominantly *Patella vulgata* in mussel beds and *P.*
478 *ulyssiponensis* in rock pools, were of comparable importance, in relation to *Littorina littorea*
479 and *Gibbula umbilicalis*, in the maintenance of the abundance, diversity and structure of algal
480 assemblages. We found clear effects of grazer removal despite inherent environmental
481 heterogeneity both between and within habitats, which provides compelling evidence of the
482 overarching importance of these grazer species across the contexts examined in this study. On
483 European rocky shores, community processes and energy transfer are driven by the spatial
484 and temporal dynamics of algae, which in turn are regulated largely by the activities of such
485 mobile grazers (Hawkins and Hartnoll 1983). Therefore, although the applicability of our
486 findings to other rocky shore habitats remains to be tested, shifts in the dynamics of algal
487 communities resulting from changing compositions and densities of consumer populations
488 may have important consequences across multiple environmental contexts in coastal
489 ecosystems. Overall, while it is clear that biodiversity plays a fundamental role in driving

490 ecosystem functioning, our ability to predict the ecological consequences of species loss will
491 be enhanced by determining the range of relevant contexts and scales over which it has the
492 greatest influence, particularly against the current background of global environmental change
493 (Hooper et al. 2012).

494

495 **Acknowledgements**

496

497 We thank S. J. Hawkins, J. D. R. Houghton and four anonymous reviewers for useful
498 comments that improved this manuscript substantially. We are grateful to M. Alexander, R.
499 Burgundy, N. Carey, C. Magill, E. Nolan, C. Reddin, E. Strain, R. Thomson and S. Vye for
500 assistance in the field. This study was completed as part of a PhD funded by the Department
501 for Employment and Learning Northern Ireland.

502

503 **References**

504

505 Airoldi, L. and Beck, M. W. 2007. Loss, status and trends for coastal marine habitats of
506 Europe. - *Oceanogr. Mar. Biol. Annu. Rev.* 45: 345–405.

507 Altieri, A. H. et al. 2009. Consumers control diversity and functioning of a natural marine
508 ecosystem. - *PLoS One* 4: e5291.

509 Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. -
510 *Austral Ecol.* 26: 32–46.

511 Anderson, M. J. and ter Braak, C. J. F. 2003. Permutation tests for multi-factorial analysis of
512 variance. - *J. Stat. Comput. Sim.* 73: 85–113.

513 Benedetti-Cecchi, L. 2004. Increasing accuracy of causal inference in experimental analyses
514 of biodiversity. - *Func. Ecol.* 18: 761–768.

- 515 Benedetti-Cecchi, L. and Cinelli, F. 1997. Confounding in field experiments: direct and
516 indirect effects of artifacts due to the manipulation of limpets and macroalgae. - *J. Exp.*
517 *Mar. Biol. Ecol.* 209: 171–184.
- 518 Boyer, K. E. et al. 2009. Biodiversity effects on productivity and stability of marine
519 macroalgal communities: the role of environmental context. - *Oikos* 118: 1062–1072.
- 520 Byrnes, J. E. and Stachowicz, J. J. 2009. The consequences of consumer diversity loss:
521 different answers from different experimental designs. - *Ecology* 90: 2879–2888.
- 522 Cardinale, B. J. et al. 2004. Effects of species diversity on the primary productivity of
523 ecosystems: extending our spatial and temporal scales of inference. - *Oikos* 104: 437–
524 450.
- 525 Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. - *Nature* 486: 59–
526 67.
- 527 Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure.
528 - *Aust. J. Ecol.* 18: 117–143.
- 529 Clarke, K. R. and Warwick, R. 2001. Change in marine communities: an approach to
530 statistical analysis and interpretation, 2nd edition. - PRIMER-E Ltd., Plymouth, UK.
- 531 Clarke, K. R. et al. 2006. On resemblance measures for ecological studies, including
532 taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded
533 assemblages. - *J. Exp. Mar. Biol. Ecol.* 330: 55–80.
- 534 Coleman, R. A. et al. 2006. A continental scale evaluation of the role of limpet grazing on
535 rocky shores. - *Oecologia* 147: 556–564.
- 536 Crowe, T. P. et al. 2011. Interactive effects of losing key grazers and ecosystem engineers
537 vary with environmental context. - *Mar. Ecol. Prog. Ser.* 430: 223–234.
- 538 Day, R. W. and Quinn, G. P. 1989. Comparisons of treatments after an analysis of variance in
539 ecology. - *Ecol. Monogr.* 59: 433–463.

- 540 Díaz, S. et al. 2003. Functional diversity revealed by removal experiments. - Trends Ecol.
541 Evol. 18: 140–146.
- 542 Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. - Oikos 99:
543 201–219.
- 544 Duffy, J. E. et al. 2005. Ecosystem consequences of diversity depend on food chain length in
545 estuarine vegetation. - Ecol. Lett. 8: 301–309.
- 546 Duffy, J. E. et al. 2007. The functional role of biodiversity in ecosystems: incorporating
547 trophic complexity. - Ecol. Lett. 10: 522–538.
- 548 Firth, L. B. and Crowe, T. P. 2008. Large-scale coexistence and small-scale segregation of
549 key species on rocky shores. - Hydrobiologia 614: 233–241.
- 550 Firth, L. B. and Crowe, T. P. 2010. Competition and habitat suitability: small-scale
551 segregation underpins large-scale coexistence of key species on temperate rocky shores. -
552 Oecologia 162: 163–174.
- 553 Gamfeldt, L. et al. In press. Marine biodiversity and ecosystem functioning: what's known
554 and what's next? - Oikos. DOI: 10.1111/oik.01549
- 555 Griffin, J. N. et al. 2009. Spatial heterogeneity increases the importance of species richness
556 for an ecosystem process. - Oikos 118: 1335–1342.
- 557 Griffin, J. N. et al. 2010. Consumer effects on ecosystem functioning in rock pools: roles of
558 species richness and composition. - Mar. Ecol. Prog. Ser. 420: 45–56.
- 559 Griffin, J. N. et al. 2013. Effects of predator richness on prey suppression: a meta-analysis. -
560 Ecology 94: 2180–2187.
- 561 Harley, C. D. G. 2006. Effects of physical ecosystem engineering and herbivory on intertidal
562 community structure. - Mar. Ecol. Prog. Ser. 317: 29–39.
- 563 Harley, C. D. G. et al. 2006. The impacts of climate change in coastal marine systems. - Ecol.
564 Lett. 9: 228–241.

- 565 Hawkins, S. J. and Hartnoll, R. G. 1983. Grazing of intertidal algae by marine invertebrates. -
566 *Oceanogr. Mar. Biol. Annu. Rev.* 21: 195–282.
- 567 Hawkins, S. J. et al. 2009. Consequences of climate-driven biodiversity changes for
568 ecosystem functioning of North European rocky shores. - *Mar. Ecol. Prog. Ser.* 396: 245–
569 259.
- 570 Hooper, D. U. et al. 2012. A global synthesis reveals biodiversity loss as a major driver of
571 ecosystem change. - *Nature* 486: 105–108.
- 572 Hughes, A. R. and Grabowski, J. H. 2006. Habitat context influences predator interference
573 interactions and the strength of resource partitioning. - *Oecologia* 149: 256–264.
- 574 Jenkins, S. R. et al. 2005. Regional scale differences in the determinism of grazing effects in
575 the rocky intertidal. - *Mar. Ecol. Prog. Ser.* 287: 77–86.
- 576 Jonsson, P. R. et al. 2006. Interactions between wave action and grazing control the
577 distribution of intertidal macroalgae. - *Ecology* 87: 1169–1178.
- 578 Kelaher, B. P. 2002. Influence of physical characteristics of coralline turf on associated
579 macrofaunal assemblages. - *Mar. Ecol. Prog. Ser.* 232: 141–148.
- 580 Loreau, M. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future
581 challenges. - *Science* 294: 804–808.
- 582 Maggi, E. et al. 2009. Effects of changes in number, identity and abundance of habitat-
583 forming species on assemblages of rocky seashores. - *Mar. Ecol. Prog. Ser.* 381: 39–49.
- 584 McArdle, B. H. and Anderson, M. J. 2001. Fitting multivariate models to community data: a
585 comment on distance-based redundancy analysis. - *Ecology* 82: 290–297.
- 586 Metaxas, A. and Scheibling, R. E. 1993. Community structure and organization of tidepools. -
587 *Mar. Ecol. Prog. Ser.* 98: 187–198.

- 588 Mieszkowska, N. et al. 2005. Marine biodiversity and climate change: assessing and
589 predicting the influence of climatic change using intertidal rocky shore biota. Scottish
590 Natural Heritage Commissioned Report No. 202 (ROAME No. F01AA402).
- 591 Moore, P. et al. 2007. Effects of grazer identity on the probability of escapes by a canopy-
592 forming macroalga. - *J. Exp. Mar. Biol. Ecol.* 344: 170–180.
- 593 Mrowicki, R. J. and O'Connor, N. E. In press. Wave action modifies the effects of consumer
594 diversity and warming on algal assemblages. - *Ecology*. DOI: 10.1890/14-0577.1
- 595 Mrowicki, R. J. et al. 2014. Does wave exposure determine the interactive effects of losing
596 key grazers and ecosystem engineers? - *J. Exp. Mar. Biol. Ecol.* 461: 416–424.
- 597 Naeem, S. et al. 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing: An
598 Ecological and Economic Perspective. - Oxford Univ. Press.
- 599 O'Connor, N. E. and Crowe, T. P. 2005. Biodiversity loss and ecosystem functioning:
600 distinguishing between number and identity of species. - *Ecology* 86: 1783–1796.
- 601 O'Connor, N. E. and Crowe, T. P. 2008. Do mussel patches provide a refuge for algae from
602 grazing gastropods? - *J. Mollus. Stud.* 74: 75–78.
- 603 O'Connor, N. E. and Donohue, I. 2013. Environmental context determines multi-trophic
604 effects of consumer species loss. - *Glob. Change Biol.* 19: 431–440.
- 605 Peterson, C. H. and Black, R. 1994. An experimentalist's challenge: when artifacts of
606 intervention interact with treatments. - *Mar. Ecol. Prog. Ser.* 111: 289–297.
- 607 R Development Core Team 2013. R: A language and environment for statistical computing.
608 in press. R Foundation for Statistical Computing, Vienna, Austria.
- 609 Seed, R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel
610 patches on rocky shores. - *J. Mar. Biol. Assoc. UK* 76: 203–210.
- 611 Stachowicz, J. J. et al. 2007. Understanding the effects of marine biodiversity on communities
612 and ecosystems. - *Annu. Rev. Ecol. Evol. Syst.* 38: 739–766.

- 613 Stachowicz, J. J. et al. 2008. Complementarity in marine biodiversity manipulations:
614 reconciling divergent evidence from field and mesocosm experiments. - P. Natl. Acad.
615 Sci. USA 105: 18842–18847.
- 616 Thompson, R. C. et al. 2002. Rocky intertidal communities: past environmental changes,
617 present status and predictions for the next 25 years. - Environ. Conserv. 29: 168–191.
- 618 Underwood, A. J. 1997. Experiments in Ecology: Their Logical Design and Interpretation
619 Using Analysis of Variance. - Cambridge Univ. Press.
- 620
- 621 Supplementary material (Appendix oik.XXXX at
622 <www.oikosjournal.org/readers/appendix>). Appendix 1–3.

623 **Tables**

624 **Table 1.** ANOVAs and PERMANOVA testing effects of habitat (mussel beds versus rock pools) and grazer removal treatments (non-removal;
 625 single-removals of *Patella*, *Littorina* and *Gibbula*; multi-removal of all three grazers) on macroalgal (a) total cover change, (b) taxonomic
 626 richness, (c) Simpson's evenness ($1-\lambda$) and (d) assemblage structure, after three and 15 months. Initial total algal cover and grazer density are
 627 included as covariates. Significant *P*-values are highlighted in bold.

| Source of variation | DF | (a) Total cover change [†] | | | (b) Richness | | | (c) Evenness | | | (d) Assemblage structure | | |
|----------------------|----|-------------------------------------|----------|------------------|--------------|----------|------------------|--------------|----------|--------------|--------------------------|------------------|------------------|
| | | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | Pseudo- <i>F</i> | <i>P</i> |
| <u>Three months:</u> | | | | | | | | | | | | | |
| Habitat, H | 1 | 23.93 | 0.07 | 0.789 | 455.62 | 236.69 | <0.001 | 0.62 | 13.13 | 0.001 | 64400.00 | 93.74 | <0.001 |
| Grazer removal, Gr | 4 | 479.77 | 1.46 | 0.240 | 19.29 | 10.02 | <0.001 | 0.16 | 3.41 | 0.021 | 2155.10 | 3.14 | <0.001 |
| Single vs. multi | 1 | 802.15 | 2.43 | 0.129 | 37.50 | 19.48 | <0.001 | 0.18 | 3.78 | 0.061 | 3086.90 | 3.91 | 0.006 |
| H × Gr | 4 | 62.87 | 0.19 | 0.941 | 3.81 | 1.98 | 0.123 | 0.06 | 1.29 | 0.295 | 1771.70 | 2.58 | <0.001 |
| Residual | 30 | 329.59 | | | 1.92 | | | 0.05 | | | 686.99 | | |
| <u>15 months:</u> | | | | | | | | | | | | | |
| H | 1 | 1329.00 | 6.13 | 0.019 | 250.00 | 100.00 | <0.001 | 0.20 | 5.45 | 0.026 | 56223.00 | 75.95 | <0.001 |
| Gr | 4 | 1510.80 | 6.96 | <0.001 | 37.96 | 15.19 | <0.001 | 0.09 | 2.60 | 0.056 | 3770.90 | 5.09 | <0.001 |
| Single vs. multi | 1 | 3711.80 | 17.11 | <0.001 | 82.51 | 33.00 | <0.001 | 0.12 | 3.42 | 0.074 | 7052.70 | 7.74 | <0.001 |
| H × Gr | 4 | 199.60 | 0.92 | 0.465 | 0.69 | 0.28 | 0.892 | 0.02 | 0.63 | 0.644 | 1090.10 | 1.47 | 0.089 |
| Residual | 30 | 216.90 | | | 2.50 | | | 0.04 | | | 740.24 | | |

628 [†]Transformation of data for three months was unable to stabilise heterogeneous variances.

629 **Table 2.** SIMPER analysis of algal assemblage structure across both habitats (mussel beds
 630 and rock pools) after 15 months, comparing the treatments involving the removal of *Patella*
 631 (the *Patella* single-removal treatment and the multi-removal treatment) to all other grazer
 632 removal treatments collectively (the non-removal treatment and the *Littorina* and *Gibbula*
 633 single-removal treatments). $\bar{\delta}_i/SD(\delta_i)$ = average species contribution to group dissimilarity
 634 divided by standard deviation of contributions; $\bar{\delta}_i\%$ = percent contribution of species to
 635 overall between-group dissimilarity. Calculations are based on $\log_{10}(x+1)$ -transformed species
 636 abundances. Only the most important species ($\bar{\delta}_i > 3\%$) are shown.

| Species | Mean cover (%) | | $\bar{\delta}_i/SD(\delta_i)$ | $\bar{\delta}_i\%$ |
|--|-----------------------------|-----------------------------|-------------------------------|--------------------|
| | <i>Patella</i> and | | | |
| | multi-removal treatments | Other removal treatments | | |
| <i>Fucus vesiculosus</i> | 11.91 | 0.50 | 1.50 | 13.32 |
| <i>Lithothamnia</i> spp. | 18.62 | 27.60 | 1.04 | 12.69 |
| <i>Corallina officinalis</i> [†] | 30.66 | 19.79 | 1.08 | 12.59 |
| <i>F. spiralis</i> | 6.15 | 0.07 | 0.87 | 8.82 |
| <i>Ceramium shuttleworthianum</i> [‡] | 1.37 | 2.17 | 0.86 | 6.97 |
| <i>Gelidium pusillum</i> | 2.37 | 1.44 | 0.98 | 5.44 |
| <i>Cladophora rupestris</i> | 2.37 | 1.58 | 1.15 | 5.18 |
| <i>Fucus</i> sp. (juvenile) | 0.95 | 0.04 | 1.05 | 4.51 |
| <i>Asparagopsis armata</i> [†] | 0.58 | 1.84 | 0.90 | 3.73 |
| <i>Ulva intestinalis</i> [‡] | 0.88 | 0.13 | 0.55 | 3.39 |
| <i>Polysiphonia fucoides</i> [†] | 0.94 | 1.45 | 0.86 | 3.30 |

637 [†]Recorded in rock pools only; [‡]Recorded in mussel beds only.

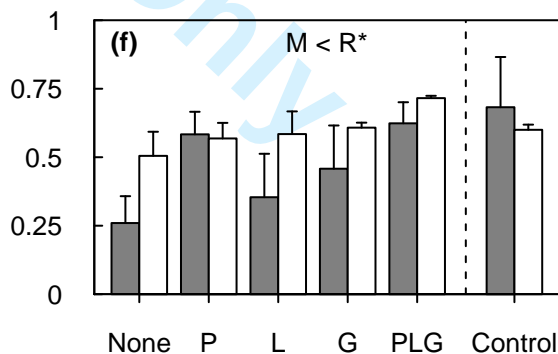
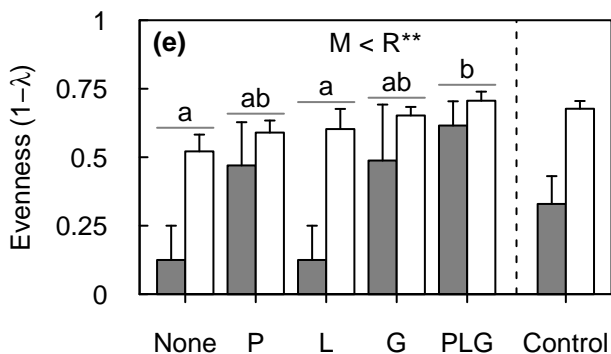
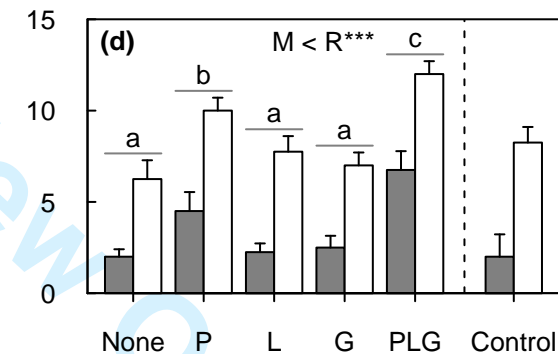
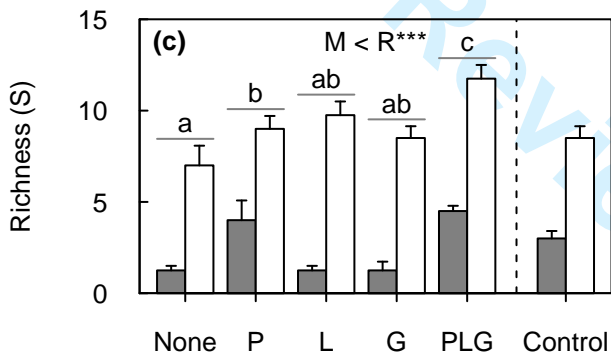
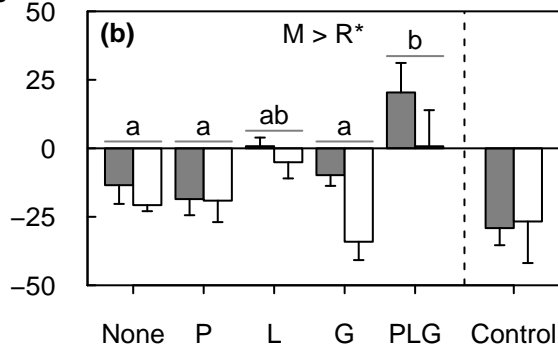
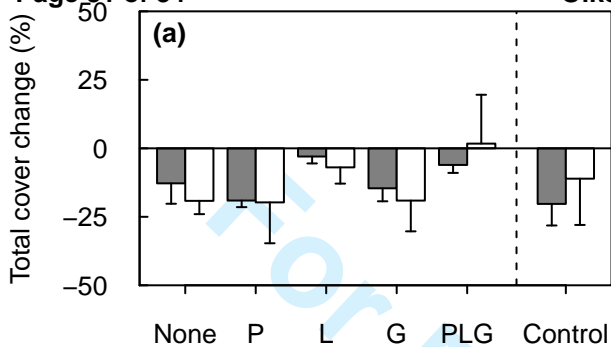
638 **Figure legends**

639

640 **Figure 1.** Mean (+ or – SE) macroalgal (a,b) total cover change, (c,d) species richness and
641 (e,f) evenness for different grazer removal treatments (None = non-removal; P, L and G =
642 single-removal of *Patella*, *Littorina* and *Gibbula*, respectively; PLG = multi-removal of all
643 three grazers) in mussel beds (shaded bars, M) and rock pools (open bars, R), after (a,c,e)
644 three and (b,d,f) 15 months. ‘M \neq R’ indicates a significant difference between habitats ($*P$
645 < 0.05 , $**P < 0.01$, $***P < 0.001$), based on ANOVA results. Letters denote grazer removal
646 groups (i.e. across both levels of habitat) that are not significantly different ($P \geq 0.05$), based
647 on post hoc SNK tests, to illustrate significant main effects of grazer removal independently
648 of habitat.

649

650 **Figure 2.** Non-metric MDS ordinations of macroalgal assemblages for different grazer
651 removal treatments (None = non-removal; P, L and G = single-removal of *Patella*, *Littorina*
652 and *Gibbula*, respectively; PLG = multi-removal of all three grazers) in (a,b) mussel beds and
653 (c,d) rock pools after (a,c) three and (b,d) 15 months, based on $\log_{10}(x+1)$ -transformed species
654 abundances. Care should be taken when interpreting plots for which stress > 0.2 (Clarke
655 1993).



Grazers removed

Grazers removed

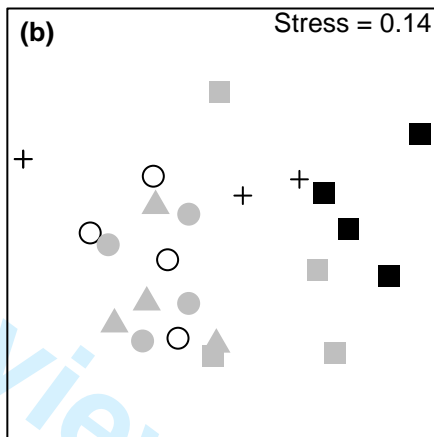
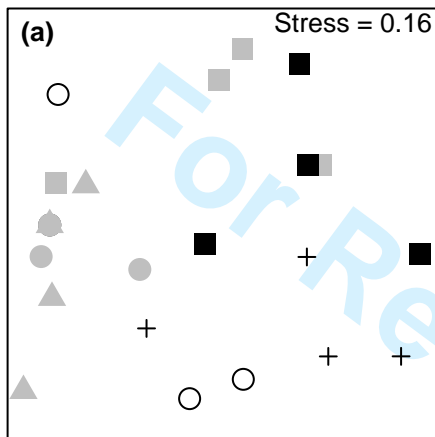
Three months

Oikos

15 months

Page 32 of 34

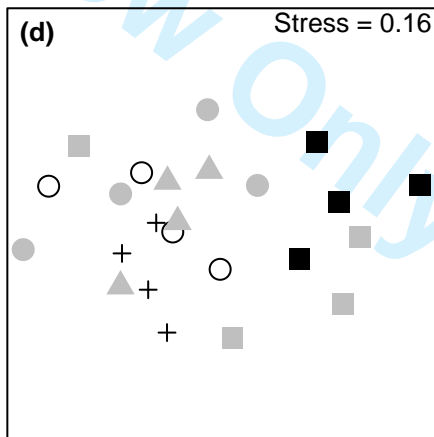
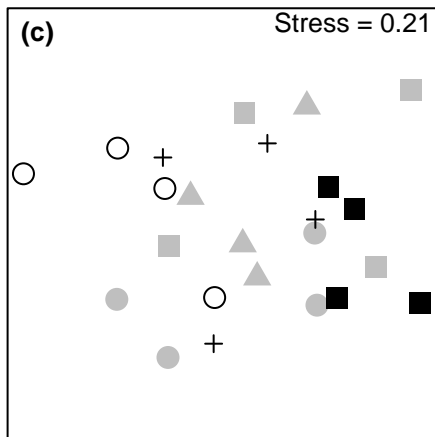
Mussel beds



Species removed

- None
- P
- L
- ▲ G
- PLG
- + Control

Rock pools



CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

ROBERT J. MROWICKI, CHRISTINE A. MAGGS & NESSA E. O'CONNOR

Appendix 1. Results of tests for differences in algal assemblages among treatments at the start of the experiment.

Table A1. ANOVAs and PERMANOVA testing effects of habitat (mussel beds versus rock pools) and grazer removal treatments (non-removal; single-removals of *Patella*, *Littorina* and *Gibbula*; multi-removal of all three grazers) on macroalgal (a) total cover, (b) taxonomic richness, (c) Simpson's evenness ($1-\lambda$) and (d) assemblage structure at the start of the experiment in July 2011. Significant *P*-values are highlighted in bold.

| Source of variation | DF | (a) Total cover | | | (b) Richness | | | (c) Evenness [†] | | | (d) Assemblage structure | | |
|---------------------|----|-----------------|----------|--------------------------|--------------|----------|------------------|---------------------------|----------|------------------|--------------------------|------------------|------------------|
| | | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | Pseudo- <i>F</i> | <i>P</i> |
| Habitat, H | 1 | 156622.00 | 615.84 | <0.001 | 161.33 | 80.67 | <0.001 | 0.60 | 20.38 | <0.001 | 69095.00 | 76.70 | <0.001 |
| Grazer removal, Gr | 5 | 816.00 | 3.21 | 0.017[‡] | 4.88 | 2.44 | 0.053 | 0.05 | 1.54 | 0.201 | 1407.00 | 1.56 | 0.073 |
| H × Gr | 5 | 294.00 | 1.16 | 0.350 | 2.43 | 1.22 | 0.321 | 0.02 | 0.70 | 0.630 | 1307.30 | 1.45 | 0.114 |
| Residual | 36 | 254.00 | | | 2.00 | | | 0.03 | | | 900.85 | | |

[†]Data were squared to improve normality and stabilise heterogeneous variances; [‡]Student-Newman-Keuls post hoc tests were unable to resolve differences fully among grazer removal treatments.

CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

ROBERT J. MROWICKI, CHRISTINE A. MAGGS & NESSA E. O'CONNOR

Appendix 2. Results of tests for the effects of experimental cages on algal assemblages.

Table A2. ANOVAs and PERMANOVA testing the effects of habitat (mussel beds versus rock pools) and the presence of cages (caged non-removal treatment versus uncaged control treatment) on macroalgal (a) total cover change, (b) taxonomic richness, (c) Simpson's evenness ($1-\lambda$) and (d) assemblage structure, after three (October 2011) and 15 (October 2012) months. Significant *P*-values are highlighted in bold.

| Source of variation | DF | (a) Total cover change [†] | | | (b) Richness | | | (c) Evenness [‡] | | | (d) Assemblage structure | | |
|----------------------|----|-------------------------------------|--------------------|----------|--------------|----------|------------------|---------------------------|----------|--------------|--------------------------|------------------|------------------|
| | | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | <i>F</i> | <i>P</i> | MS | Pseudo- <i>F</i> | <i>P</i> |
| <u>Three months:</u> | | | | | | | | | | | | | |
| Habitat, H | 1 | 7.91 | 0.02 | 0.894 | 126.56 | 69.83 | <0.001 | 0.29 | 18.57 | 0.001 | 26479.00 | 30.47 | <0.001 |
| Cage, C | 1 | 0.35 | 0.00 | 0.978 | 10.56 | 5.83 | 0.033 | 0.06 | 4.10 | 0.066 | 2541.60 | 2.92 | 0.029 |
| H × C | 1 | 243.17 | 0.57 | 0.465 | 0.06 | 0.03 | 0.856 | 0.01 | 0.64 | 0.439 | 1807.90 | 2.08 | 0.096 |
| Residual | 12 | 426.59 | | | 1.81 | | | 0.02 | | | 869.07 | | |
| <u>15 months:</u> | | | | | | | | | | | | | |
| H | 1 | 2×10^{-4} | 3×10^{-3} | 0.959 | 110.25 | 31.88 | <0.001 | 0.03 | 0.52 | 0.486 | 25273.00 | 28.18 | <0.001 |
| C | 1 | 0.05 | 0.74 | 0.408 | 4.00 | 1.16 | 0.303 | 0.27 | 5.23 | 0.041 | 1046.60 | 1.17 | 0.310 |
| H × C | 1 | 0.08 | 1.21 | 0.292 | 4.00 | 1.16 | 0.303 | 0.11 | 2.09 | 0.174 | 1183.70 | 1.32 | 0.254 |
| Residual | 12 | 0.07 | | | 3.46 | | | 0.05 | | | 896.76 | | |

[†]Data for 15 months were squared to stabilise heterogeneous variances; [‡]Data for three months were squared to improve non-normality.

CONSISTENT EFFECTS OF CONSUMER SPECIES LOSS ACROSS DIFFERENT HABITATS

ROBERT J. MROWICKI, CHRISTINE A. MAGGS & NESSA E. O'CONNOR

Appendix 3. Results of post hoc tests for differences in algal assemblage structure among experimental treatments.

Table A3. PERMANOVA post hoc pairwise tests of differences in algal assemblage structure among grazer removal treatments (None = non-removal; P, L and G = single-removal of *Patella*, *Littorina* and *Gibbula*, respectively; PLG = multi-removal of all three grazers), (a) after three months, for mussel beds and rock pools separately, and (b) 15 months, across both habitats. Significant *P*-values are highlighted in bold.

| Comparison | (a) Three months [†] | | | | (b) 15 months | |
|--------------|-------------------------------|--------------|------------|--------------|---------------|------------------|
| | Mussel beds | | Rock pools | | Both habitats | |
| | <i>t</i> | <i>P</i> | <i>t</i> | <i>P</i> | <i>t</i> | <i>P</i> |
| None vs. P | 1.38 | 0.161 | 1.31 | 0.178 | 1.88 | 0.012 |
| None vs. L | 1.07 | 0.339 | 1.48 | 0.100 | 1.14 | 0.280 |
| None vs. G | 1.08 | 0.337 | 1.36 | 0.152 | 0.88 | 0.555 |
| None vs. PLG | 1.59 | 0.099 | 2.44 | 0.011 | 3.38 | <0.001 |
| P vs. L | 2.47 | 0.016 | 1.31 | 0.180 | 2.27 | 0.003 |
| P vs. G | 2.14 | 0.022 | 0.97 | 0.443 | 2.00 | 0.009 |
| P vs. PLG | 1.18 | 0.272 | 1.31 | 0.176 | 1.49 | 0.054 |
| L vs. G | 0.68 | 0.686 | 1.21 | 0.233 | 1.03 | 0.407 |
| L vs. PLG | 2.98 | 0.007 | 1.17 | 0.273 | 3.37 | <0.001 |
| G vs. PLG | 2.34 | 0.012 | 1.54 | 0.078 | 3.41 | 0.001 |

[†]Owing to the low number of possible permutations (≤ 35), Monte Carlo asymptotic *P*-values, rather than standard permutational *P*-values, are presented.