Global Change Biology

Global Change Biology (2012), doi: 10.1111/gcb.12061

Environmental context determines multi-trophic effects of consumer species loss

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Abstract

Loss of biodiversity and nutrient enrichment are two of the main human impacts on ecosystems globally, yet we understand very little about the interactive effects of multiple stressors on natural communities and how this relates to biodiversity and ecosystem functioning. Advancing our understanding requires the following: (1) incorporation of processes occurring within and among trophic levels in natural ecosystems and (2) tests of context-dependency of species loss effects. We examined the effects of loss of a key predator and two groups of its prey on algal assemblages at both ambient and enriched nutrient conditions in a marine benthic system and tested for interactions between the loss of functional diversity and nutrient enrichment on ecosystem functioning. We found that enrichment interacted with food web structure to alter the effects of species loss in natural communities. At ambient conditions, the loss of primary consumers led to an increase in biomass of algae, whereas predator loss caused a reduction in algal biomass (i.e. a trophic cascade). However, contrary to expectations, we found that nutrient enrichment negated the cascading effect of predators on algae. Moreover, algal assemblage structure varied in distinct ways in response to mussel loss, grazer loss, predator loss and with nutrient enrichment, with compensatory shifts in algal abundance driven by variation in responses of different algal species to different environmental conditions and the presence of different consumers. We identified and characterized several context-dependent mechanisms driving direct and indirect effects of consumers. Our findings highlight the need to consider environmental context when examining potential species redundancies in particular with regard to changing environmental conditions. Furthermore, non-trophic interactions based on empirical evidence must be incorporated into food web-based ecological models to improve understanding of community responses to global change.

Keywords: context-dependence, ecosystem functioning, eutrophication, food web, marine, multiple stressors, nutrient enrichment, species loss

Received 12 August 2012 and accepted 18 September 2012

Introduction

It has become clear that global species loss is altering key processes that sustain the existence and functioning of ecosystems (Loreau *et al*., 2002; Naeem *et al*., 2009; Cardinale *et al*., 2012) and that species loss, even at local scales, is one of the major drivers of environmental change (Hooper *et al*., 2012). Understanding the consequences of biodiversity loss in complex, natural ecosystems requires that we move beyond simple systems of competing species to incorporate processes that occur within and among trophic levels (Duffy *et al*., 2007; Stachowicz *et al*., 2007; Bruno & Cardinale, 2008). In fact, loss of diversity across trophic levels has the potential to influence ecosystem functions even more strongly than species loss within trophic levels (Cardinale *et al*., 2012). There is, however, an urgent need to test the context-dependency of effects of species loss by manipulating environmental conditions simultaneously with species diversity using robust experimental designs (Boyer *et al*., 2009; Griffin *et al*., 2009b; Crowe *et al*., 2012; O'Connor *et al*., in press). One of the main anthropogenic impacts on ecosystems globally is nutrient enrichment (Thompson *et al*., 2002; Worm & Lotze, 2006; Diaz & Rosenberg, 2008). In aquatic systems, eutrophication caused by nutrient enrichment may affect interactions between grazers and primary producers which could offset the effects of species loss (Hillebrand, 2003; Russell & Connell, 2007). However, disentangling the cumulative impacts of multiple stressors on ecosystems is complex and requires careful experimentation (Folt *et al*., 1999; Crain *et al*., 2008; Molinos & Donohue, 2010).

The majority of research into the functional consequences of species loss is based on synthetically created

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assemblages of species, which limits potential applicability of such findings for natural ecosystems, where species loss is not random (Srivastava & Vellend, 2005; Bracken *et al.*, 2008). One of the few studies that attempted to mimic realistic non-random species loss in nature found that even the rarest primary producers had disproportionally strong bottom-up impacts on the diversity and abundance of consumers (Bracken & Low, 2012). Field-based experiments that simulate the loss of species from different trophic levels are, therefore, an essential tool to further our understanding of the functional roles of all species and to reveal the mechanisms by which biodiversity affects functioning in real complex ecosystems (Diaz *et al.*, 2003; Bracken *et al.*, 2008; Stachowicz *et al.*, 2008a; Stachowicz *et al.*, 2008b; Edwards *et al.*, 2010; Bracken *et al.*, 2011; Crowe *et al.*, 2012).

The role of consumers includes both direct and indirect effects on lower trophic levels (Wootton, 1994) and recent work has yielded important insights into the direct and indirect effects of consumer species loss on ecosystem functioning and stability (O'Connor & Bruno, 2007; Griffin *et al.*, 2008; O'Connor *et al.*, 2008; O'Gorman & Emmerson, 2009). A recent field experiment by O'Connor *et al.* (in press) found that two species of marine benthic predators (the crab, *Carcinus maenas* and the whelk, *Nucella lapillus*) both enhanced macroalgal cover indirectly by altering the abundance of their prey (mussels or gastropod grazers). However, the prey species (primary consumers: mussels and gastropod grazers) determined algal assemblage composition and structure. Specifically, loss of primary consumers reduced the spatial heterogeneity of algal assemblages, with mussel loss leading to dominance in red turfing algae and loss of gastropod grazers to enhanced dominance of brown fucoid algae. The mechanisms driving the indirect effects of predators on algae included enhanced grazing pressure on some algal species and competition for space among species in different trophic levels (e.g. mussels and algae). Such mechanisms can only be observed in a field experiment of sufficient duration to include natural processes such as algal recruitment and mussel bed growth (Diaz *et al.*, 2003; Stachowicz *et al.*, 2008a). These recent empirical findings could not have been predicted based on current theoretical frameworks and highlight the need for more long-term field experiments to develop a multitrophic perspective of species loss based on realistic estimates of diversity change at local scales (Stachowicz *et al.*, 2007; Bruno & Cardinale, 2008; Stachowicz *et al.*, 2008a; Crowe *et al.*, 2012).

Here, we examine the individual and combined effects of loss of a key marine benthic predator, the whelk *Nucella lapillus*, and its prey (mussels, grazing gastropods), under both ambient and nutrient enriched conditions to test explicitly for interactions between direct and indirect effects of species loss and nutrient enrichment. We tested the hypotheses that: (i) total algal biomass will increase with the loss of grazers and decrease with the loss of whelks at both ambient and enhanced nutrient concentrations; (ii) algal assemblage structure will be determined by primary consumers at both ambient and enhanced nutrient concentrations and (iii) total algal biomass will be greater in all treatments at enhanced nutrient concentrations. Furthermore, we also examined the effects of experimental treatments on the intermediate consumers (mussels and grazers) to distinguish between direct and indirect effects of predators on algal populations and to identify the mechanisms driving species interactions.

Materials and methods

The experimental site was located at Rush, Co. Dublin, (53°31.4′N, 6°04.9′W) on the east coast of Ireland, a moderately exposed intertidal rocky reef containing a network of patches of bare rock, mussels beds and macroalgal stands, typical of rocky shores in this region (O'Connor & Crowe, 2008). Our fully factorial experimental design was balanced and had three crossed factors: 'loss of predator' (two levels: whelks present, whelks absent); 'loss of primary consumers' (three levels: all primary consumers present, gastropod grazers removed, mussels removed) and 'nutrient enrichment' (two levels: ambient conditions, nutrient enriched). The experiment ran for 14 months from June 2009 to August 2010 and each of our 12 treatments was replicated four times. We considered mussels as primary consumers in this design because they are selective filter feeders of different components of phytoplankton and macroalgal detritus (Bracken *et al.*, 2012) and ingestion of algal propagules comprises an important component of mussel diet (e.g. Santelices & Martinez, 1988). Mussels are also important ecosystem engineers modifying the physical environment on rocky shores (Jones *et al.*, 1997), potentially facilitating algal settlement by protecting propagules from desiccation and fertilizing growing thalli (Santelices & Martinez, 1988; O'Connor & Crowe, 2008). Moreover, mussels are particularly strong drivers of non-trophic interactions arising primarily from competition for space on rock surfaces (Lubchenco & Menge, 1978; O'Connor *et al.*, in press).

Experimental plots were established within the low shore. Each plot contained approximately 50% mussel cover prior to the random allocation of treatments (range 45%–55%). It was necessary to use cages to control the presence of whelks and molluscan grazers. The cages consisted of square fences measuring 35 cm × 35 cm × 12 cm made of stainless steel mesh (0.9 mm diameter, 3.33 mm aperture, 61% open area), allowing immigration and recruitment of primary producers and many epibenthic consumers (including primary consumers and small predators, e.g. amphipods, polychaetes and Nemertea). Our experimental design, therefore, caused the local extinction of key components of a larger intertidal community

(O'Connor *et al.*, in press). The local populations of each of the manipulated species are subject to multiple anthropogenic disturbances including the effects of chronic chemical pollution on whelks (Hawkins *et al.*, 2002), the harvesting of gastropod grazers (Cummins *et al.*, 2002; Martins *et al.*, 2008) and the manual removal of mussel beds to be used as spat for aquaculture (O'Connor, pers. observation, Dankers & Zuidema, 1995). To test for any experimental artefacts of the cages, we compared algal and mussel cover and grazer biomass in experimental plots without cages to the caged treatment within which all manipulated consumers were present at the end of the experiment. We found no difference in any of these variables between the caged treatments and uncaged plots (algal biomass: MS = 1.94, $F_{1,6} = 0.03$, $P = 0.86$; mussel biomass: MS = 87.58, $F_{1,6} = 0.00$, $P = 0.97$; grazer biomass: MS = 1.72, $F_{1,6} = 0.01$, $P = 0.94$).

Experimental manipulations mimicked natural patterns as closely as possible at the experimental site. For example, prior to the random allocation of treatments consumers were present at ambient densities and algal assemblages were intact, incorporating natural algal abundance patterns and variation into the design of this experiment. Mussels and molluscan grazers were removed manually from treatments to simulate loss of these species. Whelks were added to the plots if required for the treatment at a density of one individual per plot. Cages and treatments were checked regularly (approximately every 2 weeks) and maintained during the experiment. Throughout the experiment, total algal cover and algal assemblage structure were quantified approximately monthly using a 64-point double strung quadrat (25 cm × 25 cm). Destructive samples were taken at the end of the experiment and all species were identified and their biomass recorded (after drying to constant mass at 60 °C).

Nutrient concentrations were enhanced in appropriate treatments by the addition of slow release fertilizer pellets (Osmocote®) in plastic mesh cases (10 cm × 10 cm) (following Worm *et al.*, 2000; Atalha & Crowe, 2010). Empty mesh cases were added to non-enriched experimental plots to control for any experimental artefacts caused by the presence of the case rather than the nutrients. Initially, 160 g of fertilizer was added to each enriched plot. After 4 weeks, we took samples from the water column directly above each plot on an ebbing tide to test the effectiveness of this method. Water samples from experimental plots with added fertilizer had significantly (MS = 12.11, $F_{1,46} = 42.03$, $P < 0.001$) greater concentrations of dissolved inorganic nitrogen (DIN; mean (±SE) = 1.23 ± 0.14 mg L^{-1}) than treatments at ambient conditions (mean (±SE) = 0.23 ± 0.06 mg L^{-1}). Following this, fertilizer pellets were replaced every 8–12 weeks to sustain elevated concentrations of nutrients in appropriate treatments for the duration of the experiment.

Analysis of variance (ANOVA) was used to test all hypotheses involving algal, mussel and grazer biomass after first testing for homogeneity of variances with Cochran's test. Variables were transformed where necessary to homogenize variances. Total algal biomass data were log $(x + 1)$ transformed, mussel biomass data were square root transformed and grazer biomass data were not transformed prior to analyses. The Student-Newman-Keuls procedure was used to make post hoc comparisons among levels of significant terms. Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle & Anderson, 2001) was used to test hypotheses about algal assemblage structure. SIMPER (Similarity of Percentages) (Clarke & Warwick, 2001) analyses were used to identify which algal taxa contributed most to pairwise dissimilarities between treatments. Multivariate analyses were based on Bray-Curtis similarity matrices calculated from square root-transformed algal biomass data and were done with 9999 permutations of the residuals under a reduced model with PRIMER Version 6.1.10 (PRIMER-E Ltd., Plymouth, UK).

Results

Primary producers (algae)

The loss of predator and primary consumer species altered total algal biomass, which varied significantly with the combination of species removed. However, these effects were altered in turn by nutrient concentration (Fig. 1, Table 1(a)). Specifically, there were significant interactions between the loss of the predator (whelks) and nutrient enrichment and between loss of primary consumers (mussels, grazers) and predators (Table 1(a)). At ambient conditions, the mean (±SE) total algal biomass was 15.2 ± 3.7 g and the removal of grazers alone led to a dramatic increase in algal biomass (mean (±SE) algal biomass: 104.7 ± 42.9 g), while the removal of whelk alone (mean (±SE) algal biomass: 4.1 ± 2.2 g) or together with grazers (mean (±SE) algal biomass: 4.2 ± 1.9 g) led to a decrease in total algal biomass (Fig. 1). In contrast, nutrient enrichment removed those effects of species loss, resulting in no effect of loss of any of the species or functional groups removed on total algal biomass (Fig. 1). Surprisingly, nutrient enrichment did not increase total algal biomass, rather just negated the effects of loss of species (Fig. 1, Table 1(a)).

PERMANOVA results show that algal assemblage structure was affected by each treatment differently and that nutrient concentration had a direct effect on algal assemblage structure, independent of the effects of loss of whelks, mussels and grazers (Table 1(b)). Pairwise tests between all treatments with and without mussels confirmed that the loss of mussels had a significant effect on algal assemblages ($t = 2.17$, $P < 0.001$), and tests of all treatments with and without grazers also differed ($t = 2.86$, $P < 0.001$), while direct comparison of treatments without mussels compared to treatments without grazers confirmed that the loss of either primary consumer group (mussels vs. grazers) affected algal assemblage structure in different ways ($t = 4.46$, $P < 0.001$). Nutrient enriched algal assemblages had

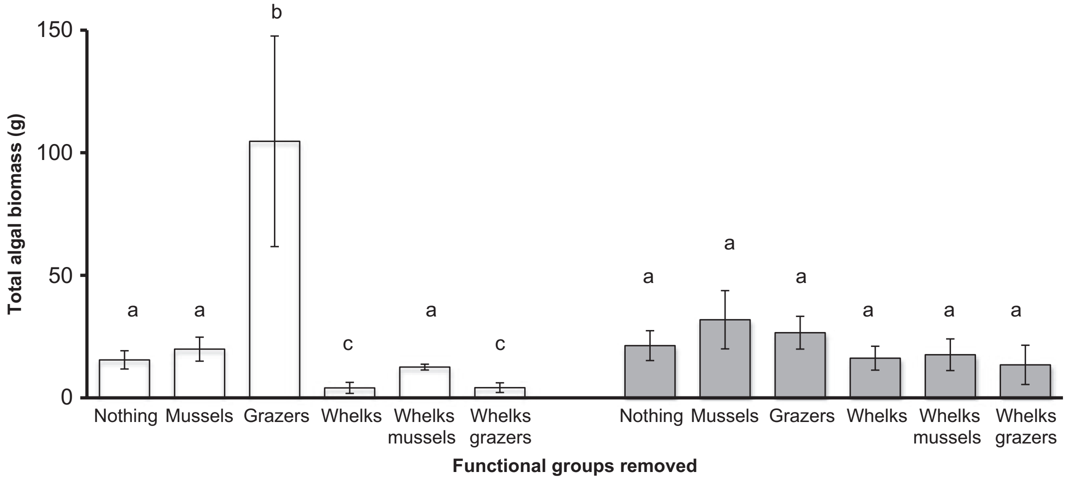

Fig. 1 Total algal biomass (mean ± SE, $n = 4$) in treatments with different combinations of consumers (mussels, grazers and whelks) removed, in ambient (open bars) and nutrient enriched conditions (grey bars) after 14 months. Letters (a, b, c) denote groups of means that are statistically indistinguishable ($P < 0.05$).

Table 1 The effects of enhanced nutrient concentrations and loss of predators and primary consumers on (a) total algal biomass (ANOVA; dependent variable was $\log[x + 1]$ transformed) and (b) algal assemblage structure (PERMANOVA; dependent variables were square-root transformed) after 14 months. Significant ($P < 0.05$) effects are highlighted in bold.

	Source of variation	DF	MS	F	P
(a)	Nutrient enrichment, N	1	0.77	1.25	0.27
	Predator, P	1	15.50	24.93	**<0.0001**
	Primary consumer, C	2	1.18	1.9	0.16
	N × P	1	2.97	4.78	**0.03**
	N × C	2	1.03	1.65	0.21
	P × C	2	2.97	4.78	**0.01**
	N × P × C	2	1.18	1.90	0.16
	Residual	36	0.62		
(b)	Nutrient enrichment, N	1	4389.9	3.00	**0.014**
	Predator, P	1	10788	7.37	**<0.0001**
	Primary consumer, C	2	13579	9.27	**<0.0001**
	N × P	1	2239.7	1.53	0.20
	N × C	2	2186.9	1.49	0.15
	P × C	2	2315.7	1.58	0.12
	N × P × C	2	2229.4	1.52	0.14
	Residual	36	1464.5		

greater dominance of species such as *Osmundea pinnatifida*, *Porphyra umbilicalis* and *Ulva lactuca* and less biomass of species such as *Fucus spiralis* and *Chondrus crispus* (possibly including some *Mastocarpus stellatus*) compared to assemblages in ambient conditions (Table 2(a)). Algal assemblages from which whelks had been removed contained greater biomass of *P. umbilicalis* and less *F. spiralis*, *C. crispus*, *O. pinnatifida* and *U. lactuca* compared to other assemblages (Table 2(b)). Assemblages from which mussels had been removed comprised greater biomass of *O. pinnatifida*, *C. crispus*, *U. lactuca* and *Ceramiun rubrum* and less *F. spiralis* and *P. umbilicalis* (Table 2(c)), while grazer loss led to increased biomass of *F. spiralis*, *P. umbilicalis*, *U. lactuca* and *Cladophora rupestris* and less biomass of *C. crispus* and *O. pinnatifida* (Table 2(d)).

Intermediate trophic level (mussels and grazers)

The removal of whelks led to an increase in total mussel biomass from a mean (±SE) mussel biomass of 193.2 ± 137.3 g when whelks were present compared to 869.5 ± 108.3 g when whelks were not present (Fig. 2(a); MS = 1268.6, $F_{1,24} = 13.63$, $P < 0.001$), while the effect of nutrient enrichment on mussel biomass was bordering on statistical significance (Fig. 2(b); MS = 353.89, $F_{1,24} = 3.8$, $P = 0.06$). There was, however, no effect of grazer loss (that may clear space for mussels by removing algae) on mussel biomass (Fig. 2(b); MS = 160.66, $F_{1,24} = 1.73$, $P = 0.2$) and there were no significant interactions among treatments.

Total grazer biomass was greater in treatments with enhanced nutrient concentrations (mean (±S.E) grazer biomass: 66.5 ± 9.2 g) compared to treatments at ambient conditions (mean (±SE) grazer biomass: 39.5 ± 7.8 g; Fig. 3(a), Table 3). We found a significant interaction between the removal of primary consumers (mussels and grazers) and the removal of whelks (Table 3) and post hoc tests showed that the loss of mussels and whelks together lead to an increase in grazer biomass regardless of nutrient conditions (Fig. 3(b); $P < 0.05$).

Table 2 SIMPER analyses identifying algal species that contributed most strongly to differences among assemblages in response to (a) nutrient enrichment (mean dissimilarity = 65.4%); (b) loss of whelks (mean dissimilarity = 67.8%); (c) loss of mussels (mean dissimilarity = 58%); (d) loss of grazers (mean dissimilarity = 71.9%) and (e) comparison of treatments without mussels and without grazers (mean dissimilarity = 76.5%).

Species	Mean biomass (g)		Contribution (%)
(a)	Ambient	Enriched	
Fucus spiralis	2.15	1.71	27.57
Chondrus crispus	1.96	1.49	20.15
Osmundea pinnatifida	1.11	1.44	18.59
Porphyra umbilicalis	0.66	0.93	15.17
Ulva lactuca	0.31	1.34	15.08
Ceramiun rubrum	0.16	0	1.97
Cladophora rupestris	0.08	0.08	1.47
(b)	Whelks present	Whelks lost	
Fucus spiralis	3.36	0.51	33.35
Chondrus crispus	2.11	1.33	18.98
Osmundea pinnatifida	1.36	1.19	17.01
Ulva lactuca	1.18	0.46	14.28
Porphyra umbilicalis	0.78	0.81	12.93
Ceramiun rubrum	0.08	0.08	1.8
Cladophora rupestris	0.16	0	1.66
(c)	Mussels present	Mussels lost	
Fucus spiralis	1.32	1.3	25.62
Osmundea pinnatifida	1.51	2	25.46
Chondrus crispus	1.36	2.53	24.22
Ulva lactuca	0.42	0.89	13.28
Porphyra umbilicalis	0.56	0.08	8.12
Ceramiun rubrum	0.07	0.17	3.3
(d)	Grazers present	Grazers lost	
Fucus spiralis	1.32	3.18	29.5
Porphyra umbilicalis	0.56	1.75	19.7
Chondrus crispus	1.36	1.28	17.49
Osmundea pinnatifida	1.51	0.31	16.5
Ulva lactuca	0.42	1.16	13.72
Cladophora rupestris	0	0.24	2.22
Ceramiun rubrum	0.07	0	0.87
(e)	Mussels lost	Grazers lost	
Fucus spiralis	1.3	3.18	25.08
Chondrus crispus	2.53	1.28	24.09
Osmundea pinnatifida	2	0.31	19.19
Porphyra umbilicalis	0.08	1.75	16.36
Ulva lactuca	0.89	1.16	11.68
Cladophora rupestris	0	0.24	1.85
Ceramiun rubrum	0.17	0	1.75

Discussion

Our findings show that nutrient enrichment can interact with food web structure to alter the effects of species loss in natural communities. At ambient conditions, the loss of certain primary consumers (grazing gastropods) led to an increase in total algal biomass and the loss of a predator (whelks) resulted in a reduction in total algal biomass as predicted. However, the positive effect of loss of grazers and the indirect negative effect of loss of a predator on total algal biomass were both negated at enriched nutrient conditions. In contrast to expectations

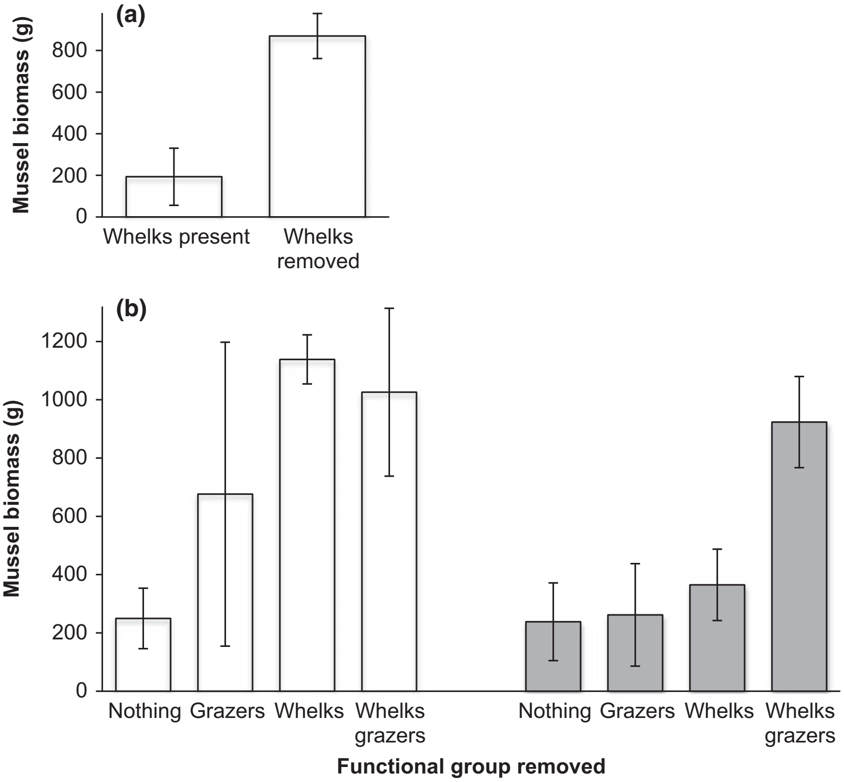

Fig. 2 Total mussel biomass (mean ± SE, $n = 4$) in (a) treatments that contained whelks compared with those that had whelks removed and (b) treatments with different combinations of consumers (grazers and whelks) removed at ambient (open bars) and nutrient enriched (grey bars) conditions.

(e.g. Leibold, 1989; Pace *et al.*, 1999; Carpenter *et al.*, 2010), we found that nutrient enrichment actually removed, rather than increased, the cascading effect of predators on algae. Mediation of these indirect effects of predators by mussels and grazers was therefore altered by nutrient concentration. Algal composition and assemblage structure varied independently in response to the loss of all species and nutrient enrichment, demonstrating that compensatory shifts in total algal abundance were driven by variation in responses of different algal species to different treatments. It is clear that the effects of species loss and the mechanisms that drive direct and indirect effects within this system were therefore strongly context-dependent, which must be considered when examining potential ecological redundancies under changing environmental conditions.

The importance of gastropod grazers in controlling total algal biomass is well known (Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983; Underwood *et al.*, 1983; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). We found that, at ambient conditions, the loss of grazers alone led to an increase in total algal biomass, whereas the loss of whelks alone or together with grazers led to a reduction in algal biomass. This indicates that the negative effect of grazers on algal biomass was dependent on the presence of whelks and shows that the positive indirect effects of whelks on algae were stronger than the negative effects of grazers because when whelks and grazers were removed together, algal biomass was reduced despite the removal of grazing pressure (probably driven by increased competition for space with mussels when their predator was not present). In contrast, there was no effect of loss of whelks, mussels or grazers on total algal biomass at enhanced nutrient conditions. This highlights the necessity to incorporate environmental conditions when attempting to predict the effects of loss of species (Boyer *et al.*, 2009; Crowe *et al.*, 2011).

Algal assemblage structure was affected by the loss of whelks, mussels, grazers and nutrient conditions all in different ways and this must be considered when interpreting the effects of loss of species on total algal biomass. It is important to examine assemblage composition within trophic level responses, especially when considering functional redundancy, because different algal taxa will perform differently in terms of primary production and secondary production owing to differences in palatability to grazers (O'Connor &

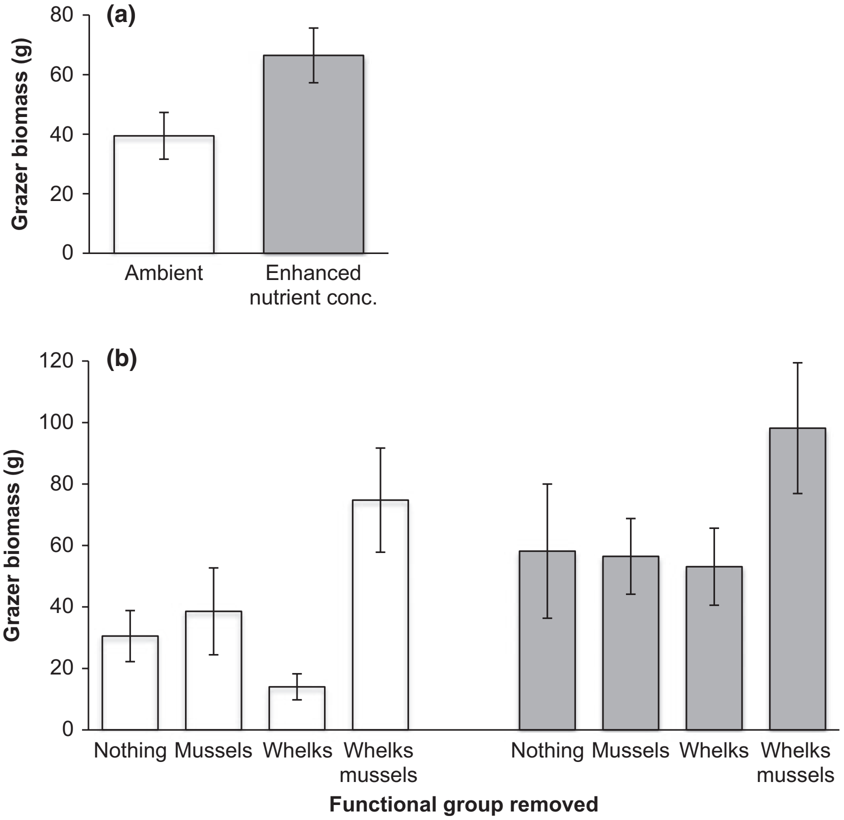

Fig. 3 Total grazer biomass (mean ± SE, $n = 4$) in (a) treatments at ambient (open bars) and nutrient enriched (grey bars) conditions and (b) treatments with different combinations of consumers (mussels and whelks) removed at ambient (open bars) and nutrient enriched (grey bars) conditions.

Table 3 ANOVA to test the effects of nutrient enrichment and loss of a predator and mussels on total grazer biomass after 14 months. Significant ($P < 0.05$) effects are highlighted in bold

Source of variation	DF	MS	*F*	*P*
Nutrient enrichment, N	1	5835.24	6.44	**0.018**
Predator, P	1	1586.23	1.75	0.2
Mussels, M	1	6289.93	6.95	**0.014**
N × P	1	143.91	0.16	0.7
N × M	1	323.09	0.36	0.56
P × M	1	4946.63	5.46	**0.028**
N × P × M	1	17.49	0.02	0.89
Residual	24	905.55		

Bruno, 2007; Bruno *et al.*, 2008; Griffin *et al.*, 2009c). Consistent with the findings of a recent experimental study (O'Connor *et al.*, in press), the loss of mussels led to an increase in dominance of red turf algae and the loss of grazers led to an increase in fucoid algae. In contrast, however, we found that the loss of whelks also led to a shift in algal assemblage structure that included greater biomass of species such as *P. umbilicalis,* which are associated commonly with mussel beds (Crowe *et al.*, 2011), suggesting that this shift was driven by an increase in mussels resulting from a reduction in predation. The predator appears to have indirectly facilitated the presence of some algal species by clearing space for them from mussels, while inhibiting other algal species that are associated with the mussels. This complex interplay of predation, competition for space between mussels and algae, and grazing pressure appears to drive the characteristic network of patches of mussels, brown and red algae on these shores.

Algal assemblage structures at enriched nutrient conditions differed significantly from those at ambient conditions and were dominated by ephemeral species. Even though there appears to have been no effect of experimental treatments on total algal biomass among the nutrient enriched plots, caution is warranted against considering these assemblages as resistant to the effects of species loss. These different algal assemblages may perform very differently in terms of ecosystem functioning (Bruno *et al.*, 2005; Stachowicz *et al.*, 2008b; Bracken *et al.*, 2011) and should not be considered as alternative states that are comparable with respect to functioning.

Several direct negative effects were identified between predators and their prey (mussels and grazers), including the direct effect of whelks on mussel biomass and the combined effects of whelks and mussels on grazer biomass. Both these effects were independent of nutrient conditions, although grazer biomass in general was greater in enriched conditions. The effect of loss of grazers on total algal biomass was probably a direct effect resulting from a reduction in grazing pressure because there was no associated increase in mussel biomass and algal assemblages shifted to dominance of the preferred species of grazing gastropods (*F. vesiculosus*, *P. umbilicalis* and *U. lactuca*; Hawkins, 1983; Hawkins *et al.*, 1992). The lack of effect of grazers on total algal biomass at enhanced nutrients could be explained by a slight compensatory shift in algal assemblage structure that maintained the total algal biomass at a similar mean biomass across treatments. However, a reduction in grazing pressure and an increase in nutrient concentration often favours similar species (e.g. *P. umbilicalis* and *U. lactuca*). This, coupled with the increased biomass of grazers observed in the enhanced nutrient treatment, indicates that when basal resources (nutrients) were increased, algae grew faster and were consumed faster. The effects of reduced grazing pressure and nutrient enrichment can interact to alter algal biomass and diversity (Lubchenco & Gaines, 1981; Worm *et al.*, 1999; Worm *et al.*, 2002; Hillebrand, 2003; Kraufvelin *et al.*, 2006; Guerry *et al.*, 2009; Atalha & Crowe, 2010), often determined by oceanic conditions (Menge *et al.*, 1999; Nielsen, 2001; Menge *et al.*, 2003; Bulleri *et al.*, 2012), and may vary among different algal functional groups (Burkepile & Hay, 2006). Nutrient additions can lead to more effective grazing (Hauxwell *et al.*, 1998) and grazers may exert some control over the effects of increasing nutrients (Bracken *et al.*, 2011), although it has been suggested that grazers can only respond to pulse elevations in nutrients and are unlikely to offer resistance to the effects of long-term eutrophication (Worm & Lotze, 2006; Russell & Connell, 2007). Our findings show clearly that at enriched nutrient levels grazers no longer controlled total algal biomass. In addition, at ambient conditions the indirect positive effect of predators on total algal biomass negated the effects of grazers. Thus, the interplay between predators and grazers plays a key role in determining algal biomass under ambient conditions, but this does not occur under eutrophic conditions.

An indirect effect of predators on total algal biomass (i.e. a trophic cascade) was identified at ambient conditions and was mediated by an increase in mussel biomass following the removal of whelks. This is evident because mussels and algae have different predatory pressures, but compete directly for space as a primary resource (Lubchenco & Menge, 1978) and algal assemblages in plots without whelks shifted towards increased dominance of species such as *O. pinnatifida*, *C. crispus*, *U. lactuca* and *P. umbilicalis*, all of which are found commonly growing epiphytically attached to mussels (O'Connor & Crowe, 2008). In addition, total algal biomass did not decrease when both whelks and mussels were removed, most likely because grazer biomass increased, which may have increased grazing pressure and compensated for the positive effect of removing their competitor for space (mussels). This increase in grazer efficiency may also explain why no trophic cascade effect was evident in nutrient enriched plots. Previous studies (e.g. Leibold, 1989; Pace *et al.*, 1999; Carpenter *et al.*, 2010) have suggested that enrichment enhances trophic cascades, whereas our findings show the opposite, highlighting the need for caution when synthesizing studies to identify general trends across ecosystems.

This study identified several direct and indirect interactions among predators (whelks), their prey (primary consumers; mussels and grazers) and primary producers (algae). Most importantly, we have shown explicitly how several direct and indirect effects of secondary and primary consumers varied with environmental context (nutrient enrichment). It is clear, therefore, that current models of the effects of species loss are inadequate to predict the multi-trophic effects of species loss under changing environmental conditions. Moreover, our study manipulated the presence of functional groups and there remains a paucity of experiments manipulating species richness gradients under different environmental conditions. It remains unclear how much trophic complexity is required to sustain ecosystem functioning and stability (O'Gorman *et al.*, 2008; Griffin *et al.*, 2009a; Cardinale *et al.*, 2012; Hines & Gessner, 2012), mainly because most empirical evidence is derived from within one trophic level and real ecosystems are much more complex (Duffy *et al.*, 2007; Hillebrand & Matthiessen, 2009; O'Gorman & Emmerson, 2009), while theoretical predictions tend to focus on simple food web typologies omitting non-trophic interactions (Arditi *et al.*, 2005; Goudard & Loreau, 2008; Kefi *et al.*, 2012). This study, together with other recent work (e.g. Hines & Gessner, 2012; Kefi *et al.*, 2012) highlights the need to incorporate traditional fields of food web ecology, and more recently ecological network modelling, with empirical evidence from the biodiversity- ecosystem functioning construct, to understand how trophic interactions determine ecosystem functioning and stability. In the case of benthic ecosystems, determining how competition for space among species interacts with predation is key to understanding the properties of ecological networks or communities (Kefi *et al.*, 2012) and, further, how they vary under anthropogenic stressors (O'Gorman *et al.*, 2012).

Acknowledgements

This research was funded by an EPA Ireland STRIVE Fellowship (2007-FS360 B-8-M5) to N. E. O'Connor and an EPA Ireland STRIVE Fellowship to I. Donohue (2008-FS-W-7-S5). We thank Queen's University Belfast Journal Club for useful comments on an earlier draft of this paper.

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