Distinguishing between direct and indirect effects of predators in complex ecosystems

Nessa E. O’Connor¹,² *, Mark C. Emmerson¹,², Tasman P. Crowe³ and Ian Donohue⁴,⁵

¹School of Biological Sciences, Queen’s University Belfast, Northern Ireland, BT9 7BL, UK; ²Environmental Research Institute, University College Cork, Cork, Ireland; ³School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland; ⁴School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland; and ⁵Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland

Summary

1. Global declines in biodiversity have stimulated much research into the consequences of species loss for ecosystems and the goods and services they provide. Species at higher trophic levels are at greater risk of human-induced extinction yet remarkably little is known about the effects of consumer species loss across multiple trophic levels in natural complex ecosystems. Previous studies have been criticized for lacking experimental realism and appropriate temporal scale, running for short periods that are not sufficient to detect many of the mechanisms operating in the field.

2. We manipulated the presence of two predator species and two groups of their prey (primary consumers) and measured their independent and interactive effects on primary producers in a natural marine benthic system. The presence of predators and their prey was manipulated in the field for 14 months to distinguish clearly the direct and indirect effects of predators on primary producers and to identify mechanisms driving responses.

3. We found that the loss of either predator species had indirect negative effects on species diversity and total cover of primary producers. These cascading effects of predator species loss were mediated by the presence of intermediate consumers. Moreover, the presence of different intermediate consumers, irrespective of the presence or absence of their predators, determined primary producer assemblage structure. We identified direct negative effects of predators on their prey and several indirect effects of predators on primary producers but not all interactions could have been predicted based on trophic level.

4. Our findings demonstrate the importance of trophic cascade effects coupled with non-trophic interactions when predicting the effects of loss of predator species on primary producers and consequently for ecosystem functioning. There is a pressing need for improved understanding of the effects of loss of consumers, based on realistic scenarios of diversity loss, to test conceptual frameworks linking predator diversity to variation in ecosystem functioning and for the protection of biodiversity, ecosystem functioning and related services.

Key-words: Algae, assemblage structure, biodiversity, crabs, ecosystem functioning, field experiment, grazers, mussels, trophic cascade, whelks

Introduction

Given accelerating rates of species extinctions globally (Pimm et al. 1995; Regan et al. 2001), predicting the consequences of species loss from ecosystems remains an elusive goal of critical importance (Loreau et al. 2001; Hooper et al. 2005; Burkepile & Hay 2008; O’Gorman & Emmerson 2009). Understanding the consequences of loss of species in complex, natural ecosystems requires that we move beyond simple systems of competing species to incorporate processes that occur across trophic levels (Duffy et al. 2007; Stachowicz, Bruno & Duffy 2007). Species at higher trophic levels are more at risk of human-induced extinction (Duffy 2003; Estes et al. 2011) yet relatively few studies have examined the effects of loss of consumer diversity across multiple trophic levels in natural ecosystems (Worm et al. 2002; Duffy, Richardson &
France 2005; Byrnes, Reynolds & Stachowicz 2007; Duffy et al. 2007; Bruno & Cardinale 2008; Burkepile & Hay 2008). The magnitude and direction of the effects of loss of consumers are highly variable, probably determined by the unique natural history of each species and may also vary in different environmental contexts (Boyer, Kertesz & Bruno 2009; O’Connor & Bruno 2009). The effects of consumer species are difficult to predict because they depend on many indirect, non-additive and behavioral interactions (Sih, Englund & Wooster 1998; Byrnes, Reynolds & Stachowicz 2007; Bruno & Cardinale 2008). Whilst many studies have examined the relationship between biodiversity and ecosystem functioning (Hooper et al. 2005; Stachowicz, Bruno & Duffy 2007), few have done so at appropriate experimental scales to capture a realism that would enable current knowledge about the functional roles of consumers to be incorporated into ecosystem management (Bracken et al. 2008; Bruno & Cardinale 2008; Naem 2008a).

A growing number of studies have examined the inter-trophic level effects of loss of species (Menge & Lubchenco 1981; O’Connor & Crowe 2005; Navarrete & Berlow 2006; Duffy et al. 2007; Stachowicz, Bruno & Duffy 2007; Bruno & Cardinale 2008; Griffin et al. 2008). Few, however, have been designed to test for interactive effects of loss of diversity within and among trophic levels (Bracken et al. 2008; Bruno & Cardinale 2008; Naem 2008a; Mooney et al. 2010). Most factorial manipulations of diversity at adjacent trophic levels to date were based on plant-pollinators (Fontaine et al. 2006), laboratory-based microbial systems (Naem, Hahn & Schuurman 2000; Fox 2004; Gamfeldt, Hillebrand & Jonsson 2005) or artificial experimental marine systems (Bruno & O’Connor 2005; Duffy, Richardson & France 2005; O’Connor & Bruno 2007; Douglass, Duffy & Bruno 2008). Moreover, the majority of this research is from short-term mesocosm experiments which can only detect a subset of possible mechanisms, lack sufficient environmental heterogeneity to allow expression of niche differences and are of insufficient duration to capture population-level processes, such as recruitment (Diaz et al. 2003; Srivastava & Vellend 2005; Stachowicz, Bruno & Duffy 2007; Bracken et al. 2008; Bruno & Cardinale 2008; Stachowicz et al. 2008a, b). Experiments performed in spatially homogenous mesocosms also risk underestimating the value of species richness because spatial heterogeneity of the physical environment plays a key role mediating the effects of species diversity on ecosystem processes (Stachowicz et al. 2008a,b; Griffin et al. 2009a; Crowe, Bracken & O’Connor 2012).

Longer-term field experiments are accumulating and have shown that the duration of a species loss experiment is important in determining its outcome (O’Connor & Crowe 2005; Navarrete & Berlow 2006; Stachowicz et al. 2008a). Experimental removals have shown that consumers can have dramatic direct effects on lower trophic levels (Paine 1976, 2002; Hawkins & Hartnett 1983; O’Connor & Crowe 2005; O’Connor et al. 2008; Edwards et al. 2010) even when interaction strengths are variable (Navarrete & Berlow 2006). However, the indirect effects of the loss of predators remain poorly understood (Stachowicz, Bruno & Duffy 2007; Bruno & Cardinale 2008; Duffy 2009). Predators may affect primary producers indirectly by suppressing the activity of primary consumers through density-dependent processes, such as consumption (Silliman & Bertness 2002) or through trait-mediated effects on primary consumers (Trussell et al. 2004), or directly by omnivory (Bruno & O’Connor 2005). Changes in consumer abundance or behaviour can also alter competitive interactions among species at different trophic levels for other shared resources such as space (Benedetti-Cecchi 2000). The direct and indirect (cascading) effects of loss of predators on lower trophic levels are complex (Woottton 1994; Bruno & Cardinale 2008; O’Gorman, Enright & Emmerson 2008) and experimental manipulation is required to separate direct from indirect effects. Field-based species removal experiments are an additional tool that can be used to simulate the loss of species from different trophic levels to further our understanding of the functional roles of consumers in ecosystems and to reveal the mechanisms by which biodiversity affects ecosystem functioning in nature (Bracken et al. 2008; Stachowicz et al. 2008a,b; Edwards et al. 2010; Crowe, Bracken & O’Connor 2012).

We tested for effects of loss of species of predators and their prey, both separately and together, on the diversity and functioning of primary producers (macroalgae) on a moderately exposed rocky shore. We manipulated two common predatory species, whelks (Nucella lapillus) and crabs (Carcinus maenas), and two groups of their primary prey, mussels (Mytilus edulis) and grazing gastropods (comprising primarily Patella vulgata, Littorina littorea and Gibbula umbilicalis) (Fig. 1a), to identify and characterize the indirect effects of loss of predator species on intertidal algal assemblages over 14 months. Only by manipulating both predators and their prey separately can we test clearly whether predators affect primary producers directly (e.g. omnivory) or indirectly (e.g. mediated by intermediate consumers) and investigate the mechanisms involved (O’Connor & Bruno 2007; Mooney et al. 2010). A crossed design of nine treatments (Fig. 1b) allowed us to identify independent and interactive effects of predator species and functional groups of their prey on total algal cover and algal assemblage structure and diversity. To help identify mechanisms driving the indirect effects of predators on algae, we also examined interactions between predator species (biomass) and their prey species (mussel % cover, grazer biomass). Comparison of the two predator species would also highlight the occurrence of intraguild predation (Polis & Holt 1992). We examined whether (i) the loss of predators or their prey affected the structure or functioning of algal assemblages (measured as total algal cover, diversity and assemblage structure [i.e. a multivariate measure incorporating both species...
Fig. 1. (a) Simplified trophic interaction network of a moderately exposed rocky shore (adapted from Little, Williams & Trowbridge 2009), with the components whose presence we manipulated and highlighted in red. While mussels may not interact tropically with benthic macroalgae consistently, they can comprise important consumers of algal propagules (Santelices & Martinez 1988) and can also have strong non-trophic interactions with macroalgae arising primarily from competition for space on the shore (Lubchenco & Menge 1978), which may also interact with the presence of grazers (Crowe, Frost & Hawkins 2011). Such strong non-trophic interactions are largely absent from food web-based theoretical frameworks yet play a key role in determining the structure of algal assemblages. While crabs have been found to feed on whelks (e.g. Hughes & Elner 1979), no predation by crabs upon whelks was observed during our experiment. (b) Experimental design comprising nine treatments, involving the removal of two species of predator and two groups of their prey, to measure the independent and interactive effects of predators on primary producers and test for direct and indirect effects across trophic levels. 

composition and abundance) and (ii) any effects were species identity-dependent or could be predicted based solely upon trophic level (i.e. whether both predators had similar effects).

Materials and methods

EXPERIMENTAL DESIGN

Our experimental site was located at Rush, Co. Dublin (53°31.4′ N, 6°04.9′ W) on the east coast of Ireland on a moderately exposed flat rocky reef containing networks of patches of bare rock, mussels, barnacles and macroalgal stands typical of rocky shores in the region (Appendix S1; O’Connor & Crowe 2008). Our experimental design (Fig. 1b) was balanced with two fixed factors: (i) ‘loss of predators’ (three levels: no predators removed, whelks removed and crabs removed) and (ii) ‘loss of their prey (primary consumers)’ (three levels: no primary consumers removed, grazers removed and mussels removed). Whelks and crabs are both highly susceptible to human impacts (Hawkins et al. 2002; Sheehan et al. 2010), making them extremely pertinent for species loss experiments. Moreover, recent work has indicated that the roles of mobile predators structuring European rocky shore communities have not been fully recognized (Silva et al. 2008). We incorporated the removal of mussels in our experimental design because, although mussels were regarded as basal species in some classic food web studies (e.g. Pimm 1980), in fact algal propagules can comprise an important component of mussel diet (Santelices & Martinez 1988), which may affect macroalgal settlement. Moreover, mussels are autogenic ecosystem engineers (Jones, Lawton & Shachak 1997) and can drive strong non-trophic interactions on rocky shores, potentially arising from competition for space on rock surfaces (Lubchenco & Menge 1978). Mussels have also been shown to facilitate the presence of certain algal species, and this may interact with grazing activity (Crowe, Frost & Hawkins 2011). Thus, mussels are a source of both strong trophic and non-trophic interactions, which should be included in rocky shore interaction webs (Fig. 1a). For analyses of mussel cover and grazer biomass, there were only two levels of the factor ‘loss of primary consumers’ across the six treatments in which they themselves were not manipulated. Similarly, there were two levels of the factor ‘loss of predators’ for analyses of whelk biomass and crab biomass. Each treatment was replicated four times.

Experimental plots were established within the mid- to low shore. Each 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 mobile predators and molluscan grazers. The cages consisted of square fences measuring 35 × 35 × 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, tested for effects of the local extinction of key components of a larger intertidal food web, in an open experimental system without removing entire trophic levels (Fig. 1a). 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. We found no difference in any of these variables between the caged and uncaged treatments (Appendix S2).

Experimental manipulations mimicked as closely as possible natural patterns at the field site. Mussels and molluscan grazers were removed manually from the treatments to simulate loss of these species. Predators were added to the plots if required for the treatment at a density of one individual per plot. In treatments where species were removed, there was no experimental compensation for the loss of species, or artificial increase in biomass of remaining species, similar to an additive design (Byrnes & Stachowicz 2009). Crabs found on the shore and used in the experiment had a carapace width of 3–6 cm. This size range is thought to feed mainly on mussels and small gastropods (Rangeley & Thomas 1987), including limpets (Silva et al. 2008). Although larger crabs may feed on whelks (Hughes & Elner 1979), no predation by crabs upon whelks was observed during our experiment. Cages and treatments were checked regularly (approximately every 2 weeks) and maintained during the experiment. Juveniles of species that were being excluded were removed from the appropriate treatments as they became visible while settlement and recruitment of all other species was left intact. As the experimental plots form part of a long-term study, we did not take destructive samples to quantify the biomass of algae or mussels and instead quantified their percentage cover (O’Connor & Crowe 2005; Martins et al. 2010). Algal cover and assemblage...
Distinguishing between direct and indirect effects of predators in complex ecosystems

Results

When all consumer species were present in an experimental plot, the mean total algal cover was 78.5% (SE ±24) (Fig. 2a). Effects of predator species loss on algal cover (Fig. 2a), taxon richness (Fig. 2b) and evenness (Fig. 2c) were mediated by the presence or absence of intermediate species, shown by significant interactions between loss of predators and loss of primary consumers (algal cover: MS = 3704.08, F_{4,27} = 3.02, P = 0.035; taxon richness: MS = 7.53, F_{4,27} = 3.78, P = 0.014; evenness: MS = 0.13, F_{4,27} = 4.56, P = 0.006). The removal of either species of predator alone (crabs or whelks) reduced total algal cover and both measures of algal diversity (P < 0.05 in all cases), whereas there was no distinguishable effect of any of the other treatments (Fig. 2). Further, the loss of crabs in isolation reduced algal taxon evenness more than when only whelks were lost (P < 0.05; Fig. 2c). Both predators had significant negative indirect effects on total algal cover and diversity of algal assemblages, but only when primary consumers were present. Surprisingly, the loss of primary consumers either alone or in combination with the loss of a predator had no effect on total algal cover, taxon richness or evenness of algal assemblages (Fig. 2). In terms of interaction strengths, both grazers (−1.31 ± 0.07; mean ± SE, n = 4) and mussels (−1.42 ± 0.09) had similar total interaction strengths with their algal prey, as did whelks (1 ± 0.8) and crabs (1.39 ± 0.76).

The multivariate structure of algal assemblages was not affected by the loss of predators (MS = 2105.20, pseudo-F_{2,27} = 1.15, P = 0.30), but rather was altered significantly following the loss of primary consumers (MS = 19510, pseudo-F_{2,27} = 10.8, P ≤ 0.0001; Fig. 3). Pairwise tests showed that the loss of grazers (grazers present versus grazers removed: pseudo-t = 1.98, P < 0.001) and the loss of mussels (mussels present versus mussels removed: pseudo-t = 2.97, P ≤ 0.0001) both altered algal assemblage structure, although in significantly different ways (grazers removed versus mussels removed: pseudo-t = 6.31, P ≤ 0.0001). The removal of mussels resulted in a shift in dominance towards red algae such as crustose algae ‘Lithothamnium’ spp., Osmundea spp., Chondrus crispus (possibly incorporating some Mastocarpus stellatus) and Corallina officinalis, while assemblages without grazing gastropods were dominated by brown and ephemeral algae such as Fucus serratus, Porphyra umbilicalis and Ulva spp. (Appendix S3).

The local extinction of whelks resulted in a significant increase in the biomass of crabs (MS = 49.88, F_{1,18} = 5.17, P = 0.036; Fig. 4a), whereas the loss of either group of primary consumers had no effect on crab biomass (MS = 15.5, F_{2,18} = 1.61, P = 0.23). In contrast, we did not detect any difference in whelk biomass in any of the treatments involving removal either of their prey or crabs (Appendix S4; Fig. 4b). There was, however, a significant interaction between the loss of predators and the loss of grazers on mussel cover (MS = 1938.54, F_{2,18} = 10.02, P = 0.001). The removal of whelks or crabs in isolation led to increased mussel cover, whereas the loss of grazers, either in isolation or in combination with the

structure were quantified using a 64-point double-strung quadrat (25 x 25 cm), which was placed in each plot, and all taxa under each intersection point were recorded. Species within the quadrat that did not match any intersection point were also recorded and assigned a value of 1% cover. On these shores, it is not uncommon for total mean algal cover to be in excess of 100% owing to the layered nature of benthic algae (encrusting, turfing, canopy and epiphytic morphologies were all included). We calculated taxon richness (number of taxa) and evenness (Simpson’s 1 − λ) as measures of algal diversity as recommended for diversity manipulation experiments (Kirwan et al. 2007; Hillebrand, Bennett & Cadotte 2008).

We quantified total interaction strengths between the manipulated consumers and algae over the duration of the experiment based on the dynamic index (Laska & Wooton 1998) as:

\[
\ln \left( \frac{X_i^{t+1}}{X_i^t} \right)
\]

where \( X \) represents density of either prey (algal) species \( j \) (expressed here in terms of percent cover) or consumer \( j \) density set equal to one. Prey species densities were quantified in the presence, \( +j \) (calculated from the experimental treatment with no species losses), or absence, \( -j \), of consumer species \( j \), whilst \( t \) represents time. We quantified interaction strengths only in experimental plots belonging to treatments from which the manipulated consumers were removed in isolation. The experimental design employed here did not permit the calculation of direct per capita effects. Rather, we used the resulting values to provide an estimate of the net effect of consumer \( j \) on algal per cent cover in the treatments over the duration of the experiment (O’Gorman et al. 2010). The effects detailed here for predators therefore represent indirect effects of the predators on algal per cent cover mediated by their impact on intermediate consumers.

Statistical Analyses

Data were examined for normality, and analysis of variance (ANOVA) was used to test hypotheses involving algal and mussel cover and grazer, crab and whelk biomass after first testing for homogeneity of variances with Cochran’s test. Variables were transformed where necessary to homogenise variances. 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. Non-metric multidimensional scaling (MDS) was used to produce two-dimensional ordinations to compare algal assemblages among different treatments (Field, Clarke & Warwick 1982; Clarke 1993). SIMPER (Similarity of Percentages; Clarke & Warwick 2001) analyses were used to identify which algal taxa contributed most to pairwise dissimilarities between treatments. All multivariate analyses were based on Bray-Curtis similarity matrices calculated from log (\( x + 1 \))-transformed per cent cover data and were performed with 9999 permutations of the residuals under a reduced model with PRIMER Version 6.1.10 (PRIMER-E Ltd., Plymouth, UK).

Results

When all consumer species were present in an experimental plot, the mean total algal cover was 78.5% (SE ±24)
Fig. 2. (a) Total cover, (b) taxon richness (number of taxa) and (c) taxon evenness (Simpson’s $1 - \lambda$) of algae in each experimental treatment. Values are untransformed means (±SE, $n = 4$). Letters (a–c) indicate groups that are statistically indistinguishable from each other ($P > 0.05$).
loss of either predator species, reduced mussel cover significantly ($P < 0.01$; Fig. 4c). There was also a significant interaction between the loss of predators and loss of mussels on grazer biomass (MS = 14.81, $F_{2,18} = 22.1$, $P \leq 0.0001$; data were square-root transformed). The loss of either predator species, in combination with the loss of mussels, led to an increase in grazer biomass ($P < 0.01$; Fig. 4d).

**Discussion**

Our results demonstrate clearly that species at intermediate trophic levels regulate the cascading effects of predators on primary producers and highlight the importance of indirect effects in natural ecosystems. Loss of either of the two common predators we manipulated had negative indirect effects on the total cover and diversity of benthic primary producers. However, these effects were mediated by the presence of species in an intermediate trophic level and, moreover, different functional groups of these intermediate species determined different assemblages of primary producers. Specifically, the loss of whelks or crabs led to a reduction in total algal cover and diversity (both

---

**Fig. 3.** Non-metric multidimensional scaling (MDS) ordination of algal assemblages in each experimental treatment based on a Bray–Curtis similarity matrix calculated from log ($X + 1$)-transformed algal cover data (stress = 0.18). Open symbols represent plots with all primary consumers present, grey symbols represent plots that had grazing gastropods removed, and filled symbols represent plots that had mussels removed.

**Fig. 4.** (a) Crab biomass, (b) whelk biomass, (c) mussel cover and (d) grazer biomass in the experimental treatments containing these consumers. Inset in (a) shows the overall main effect of whelk removal on crab biomass. Values are untransformed means ($\pm$SE, $n = 4$). Letters (a–c) indicate groups that are statistically indistinguishable from each other ($P > 0.05$).

taxon richness and evenness), but only when intermediate trophic levels (their prey) were intact. In addition, the loss of one group of their prey, mussels, led to a shift towards dominance of red algae, whereas the loss of another group of their prey, grazing gastropods, led to the dominance of brown and ephemeral algae. We have, therefore, identified several cascading effects of predators on primary producers. Not all of these could have been predicted based on trophic level alone because the different groups of their prey had different effects on primary producers that may or may not be related to trophic interactions (e.g. mussels may compete with some algal species for space or facilitate the establishment of other algal species (Lubchenco & Menge 1978; Crowe, Frost & Hawkins 2011). Our results demonstrate the importance of cascading effects of predators coupled with knowledge of the functional roles of intermediate species when predicting the indirect effects of loss of predators on ecosystem processes such as primary production.

Previous studies of marine benthic predators concluded that predator effects were probably non-additive, antagonistic interactions or emergent predator effects that operate at larger spatial or temporal scales than included in most short duration experiments (Leroux & Loreau 2009; O’Connor & Bruno 2009). We found that the loss of either predator species affected their prey positively (mussels directly; grazers when combined with the loss of mussels), even though an alternative predator was always present. Therefore, neither species appears to compensate for the loss of the other, suggesting that their combined effects on their prey may be additive. However, further manipulations of predator diversity are required to test this explicitly (Sih, Englund & Wooster 1998). Interestingly, whelks were not affected by the loss of crabs or either prey group. However, the loss of whelks led to an increase in crab biomass, indicative of inter-specific competition between whelks and crabs and suggesting that whelks may outcompete crabs for their shared prey. This was a surprising result, considering that crabs have been shown to prey on whelks (Kitching, Muntz & Ebling 1966; Hughes & Elander 1979). However, we found no evidence of this during the experiment.

Further complications can be expected to occur when the effects of loss of predators are density dependent, vary with the presence of other species at different trophic levels, or vary with evenness of the consumer species (Griffin et al. 2008; O’Connor et al. 2008). Previous work on predatory crabs has shown that some species can compensate for the removal of key predators, but these effects were density dependent (O’Connor et al. 2008). Our results show that it is necessary to consider the role of the species present across trophic levels to predict the effects of loss of predators. For example, the loss of either crabs or whelks led to a dramatic reduction in total algal cover, indicating that both species play a similar role in terms of their indirect effects on algae, consistent with their interaction strengths. However, the mediation of this indirect effect varied significantly with the presence of different intermediate consumers. When either predator was removed in isolation, mussel cover increased, and this appears to have been facilitated by the presence of grazers as indicated by the decrease in mussel cover when grazers were removed, probably caused by grazers removing algal propagules that ultimately compete with the mussels for space. This positive interaction, or facilitation, between grazers and mussels is important for the continued existence of mussels and negated any negative effect of crabs or whelks on mussel cover. In contrast, only the combined removal of either predator with mussels led to an increase in grazer biomass, possibly because the combination of reduced predation pressure and increased availability of space following removal of mussels allowed for greater algal production providing optimal feeding conditions for grazers.

Despite decades of research, the key processes determining community structure on rocky shores are not understood fully and our findings draw together two paradigms. In Europe, strong grazer control of algal communities has long been known (Jones 1948; Hawkins 1981; Jenkins et al. 2005; O’Connor & Crowe 2005; Coleman et al. 2006; Jonsson et al. 2006), whereas on the east coast of North America where patellids are absent, competitive interactions among key space holders mediated by predation are considered key to understanding how the system functions (Jenkins et al. 2008). Here we show that a combination of cascading predation effects, competitive interactions and direct consumption regulate algal assemblages, but the exact mechanism determining species presence and abundance varies among algal species.

Although the cumulative effects of consumers have been shown to affect prey populations (e.g. Lubchenco & Menge 1978; Menge & Lubchenco 1981; Rilov & Schiel 2006; O’Connor et al. 2011), separating the effects of different species and types of consumers has proven difficult (Edwards, Conover & Sutter 1982; Menge 1982). It is widely accepted that N. lapillus has a strong regulatory role on the abundance of filter feeders such as mussels and barnacles (Connell 1961; Menge 1976; Petraitis 1987) and that C. maenas is an opportunistic scavenger, preying on mussels (Kitching, Sloane & Ebling 1959; Bertness et al. 2004), barnacles (Burrows, Kawai & Hughes 1999), littorinids (Janke 1990), limpets (Griffin et al. 2008; Silva et al. 2008, 2010) and whelks (Kitching, Muntz & Ebling 1966). The generality of the indirect effects of these predators on algae were, however, previously unclear. On American Atlantic shores, it has been argued that C. maenas (where it is an invasive non-native species) has a positive indirect effect on the abundance of algae by suppressing herbivore (mainly L. littorea) and whelk populations (Lubchenco & Menge 1978; Lubchenco 1983). Although there is some controversy surrounding the evolution of L. littorea, it now seems most probable that it is also non-native on west Atlantic shores (Reid 1996; Wares et al. 2002; Chapman et al. 2007; Cunningham 2008;
Brawley et al. 2009). Further, studies have shown that the presence of *C. maenas* affects the behaviour of littorinids and whelks leading to a trait-mediated indirect effect on algal populations (Trussell, Ewanchuk & Bertness 2002, 2003). In contrast, in Europe, the effects of predation on the dominant grazers, limpets, have only been demonstrated recently (Griffin et al. 2008; Silva et al. 2008, 2010) and, until now, there was extremely limited evidence of indirect effects of predators on algal assemblages. This led to suggestions that *C. maenas* may have a much reduced role in indirect control of algal populations than in the western Atlantic owing to differences in vulnerability of dominant grazers (Jenkins et al. 2008; Silva et al. 2010). Our results suggest the opposite because, although the cages we used also excluded other potentially important predators, such as other crabs and birds (Coleman et al. 1999; Silva et al. 2010), the fact that algal and mussel cover and grazer biomass in (uncaged) control plots did not differ from that of plots that had cages and both predators present, indicating that both *N. lapillus* and *C. maenas* are key predators driving direct and indirect effects in this system.

Our study demonstrates clearly that the loss of a predator (*C. maenas* or *N. lapillus*) has indirect positive effects on total algal cover. However, this effect was mediated via different mechanisms than predicted for American shores. This may be due to the dominance of patellid limpets, rather than littorinids, as key grazers in Europe (Jones 1948; Hawkins 1981; Jenkins et al. 2005; O’Connor & Crowe 2005; Coleman et al. 2006; Jonsson et al. 2006) or because algal populations on North American shores are dominated by *C. crispus* (Lubchenco & Menge 1978) and *M. stellatus*, whereas European shores comprise of mixtures of algal taxa that include *F. serratus* (barely present on western Atlantic), as well as *Osmundea* spp., *C. crispus* and *M. stellatus* (Jenkins et al. 2008; Brawley et al. 2009). We show that the network of patches of mussels, fucoid and red algal stands, typical of moderately exposed rocky shores in this region, results from the direct effects of predators on grazers, which determine the fucoid dominance, and on mussels, which determine red algal dominance. Thus, it is necessary to understand the interactions among mussels, grazers and algae to predict the effects of loss of predators on ecosystem functioning.

We found that predator removals led to increases in their prey and subsequent shifts in algal composition. These different algal assemblages have important implications for the functioning and stability of the system because different algal taxa may perform differently in terms of primary and secondary productivity (Bruno et al. 2008). For example, trade-offs exist so that rates of net primary productivity may vary depending on the palatability of the primary producer (Bruno et al. 2005; Griffin et al. 2009b).

Recent studies have challenged the presumption that predator species cause qualitatively similar kinds of indirect effects in ecosystems (Chapin et al. 1997; Loreau et al. 2001; Schmitz 2008). Schmitz (2008) showed that two predator spider species with different hunting modes (actively hunting versus sit-and-wait) had different indirect effects on primary producers (diversity and functioning) mediated by an intermediate prey species (grasshopper). These species-specific identity effects emerged as predators altered plant assemblage composition and showed that trait-based functions, such as hunting modes, could be used to predict the effects of predators. Our experiment expanded this approach by testing for effects of two phylogenetically, morphologically and behaviourally different predator species (with very different hunting modes) on their prey, while simultaneously testing for interactions between the predators across trophic levels and including whole prey assemblages (intermediate species and primary producers). In contrast, our results show that although we found evidence of some intra-guild predator interactions (whelks had a negative effect on crab biomass), both predators had similar direct effects on their prey (grazers and mussels) and indirect effects on algae, suggesting that neither predator functional traits nor species identity were required to predict the effects of loss of benthic predators in this system. However, the identity of intermediate consumers determined algal assemblage structure; therefore, more empirical research examining the multi-trophic effects of loss of consumers is required to undertake phylogenetic and trait-based forecasting of biodiversity effects for ecosystem functioning (Naeem 2008b; Schmitz 2009).

**GENERAL METHODOLOGICAL CAVEATS**

There are several complicating factors to consider when attempting to identify and characterise the direct and indirect effects of predator species loss. It is also important to consider that there are several approaches to investigating the effects of loss of consumers, each employing different experimental designs that may pre-determine the likelihood of detecting certain interactions (Byrnes & Stachowicz 2009). We have chosen to mimic the local extinction of several species of consumer at different trophic levels so that we could test for interactions across trophic levels and identify potential species-specific effects within trophic levels. An important next step would be to test whether such interactions are density dependent which could be addressed using a substitutive design (e.g. O’Gorman, Enright & Emmerson 2008; Griffin et al. 2010) or a combination of additive and substitutive designs to test explicitly for compensation effects of remaining species (e.g. O’Connor & Crowe 2005; O’Connor et al. 2008). Another useful, albeit logistically challenging, advancement would be to test whether other species not considered explicitly as part of this study could provide a level of biological insurance and whether these remaining species are likely to increase in response to the loss of species. The use of cages will nearly always introduce certain caveats. For example, the density of...
enclosed species may not be completely representative of how they would respond in an entirely open system following species loss. However, careful controls can limit this (Underwood 1980; Benedetti-Cecchi & Cinelli 1997; Miller & Gaylord 2007). Finally, the duration of this study was considerably longer than most marine biodiversity–ecosystem functioning experiments (Crowe, Bracken & O’Connor 2012). However, more studies over even longer periods are required to assess the degree to which species are ecologically redundant (Stachowicz, Bruno & Duffy 2007).

CONCLUSION

Our findings demonstrate that, in order to advance an understanding of the role of predators in ecosystems, we must simultaneously consider non-additive and non-trophic interactions of consumers in addition to their direct effects through local prey consumption and their indirect effects on lower trophic levels (Leroux & Loreau 2009). It is essential that future empirical studies are conducted over longer periods than many previous biodiversity experiments, are open to processes such as dispersal and recruitment, include naturally heterogeneous substrates and environmental conditions and are based on realistic estimates of diversity change (Srivastava & Vellend 2005; Stachowicz, Bruno & Duffy 2007; Bracken et al. 2008; Stachowicz et al. 2008a; Crowe, Bracken & O’Connor 2012). There are extremely few studies, such as the experiment described here, that have attempted to mimic the removal of several species from different trophic levels simultaneously in the field. We argue that the next step is to test the context-dependency of these results preferably under different environmental conditions aligned with predicted global change scenarios. Such studies are essential to test conceptual frameworks linking predator diversity to species loss and variation in ecosystem functioning (Bruno & Cardinale 2008; Schmitz 2009), an essential step to making realistic predictions of effects of species loss that may be tested across ecosystems (Naem 2008a,b).

Acknowledgments

This work was funded by an Irish Research Council for Science, Engineering and Technology (IRCSET) Embark Postdoctoral Fellowship and an EPA Ireland STRIVE Fellowship (2007-FS-B-RMS) to N. E. O’Connor and an EPA Ireland STRIVE grant to I. Donohue (2008-FS-W-7-S5).

References


Distinguishing between direct and indirect effects of predators in complex ecosystems


Received 14 March 2012; accepted 1 September 2012
Handling Editor: Guy Woodward

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Description of the experimental site.

Appendix S2. ANOVA tests for experimental artefacts of the cages used to simulate the local extinction of target consumers.

Appendix S3. Results of SIMPER analyses identifying the taxa contributing most strongly to differences in algal assemblage structure following the loss of primary consumers.

Appendix S4. ANOVA test for effects loss of crabs, grazers and mussels, both separately and together, on whalek biomass.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.