CORA Cork Open Research Archive
Cartlann Taighde Oscailte Chorcaí

Title	The importance of interaction strength for food web dynamics and ecosystem functioning
Authors	O'Gorman, Eoin J.
Publication date	2009-09
Original Citation	O'Gorman, E.J. 2009. The importance of interaction strength for food web dynamics and ecosystem functioning. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
Link to publisher's version	http://library.ucc.ie/record=b1898015~S0
Rights	© Eoin J. O'Gorman, 2009. - http://creativecommons.org/licenses/by-nc-nd/3.0/
Download date	2026-10-10 14:53:10
Item downloaded from	https://hdl.handle.net/10468/164

UCC
University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

CHAPTER ONE

Predator diversity enhances secondary production and decreases the likelihood of trophic cascades

Eoin J. O'Gorman [1,2], Ruth A. Enright [2] and Mark C. Emmerson [1,2]

[1] *Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland.*

[2] *Department of Zoology, Ecology and Plant Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.*

The following chapter is published in the peer-reviewed journal Oecologia.

O'Gorman E.J., Enright R.A. & Emmerson M.C. (2008). Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. Oecologia, 158, 569-578.

The final publication is available at www.springerlink.com

Abstract:

We manipulated the diversity of top predators in a three trophic level marine food web. The food web included four top benthic marine fish predators (black goby, rock goby, sea scorpion, and shore rockling), an intermediate trophic level of small fish, and a lower trophic level of benthic invertebrates. We kept predator density constant and monitored the response of the lower trophic levels. As top predator diversity increased, secondary production increased. We also observed that in the presence of the manipulated fish predators, the density of small gobiid fish (intermediate consumers) was suppressed, releasing certain groups of benthic invertebrates (caprellid amphipods, copepods, nematodes, and spirorbid worms) from heavy intermediate predation pressure. We attribute the mechanism responsible for this trophic cascade to a trait mediated indirect interaction (TMII), with the small gobiid fish changing their use of space in response to altered predator diversity. In the absence of top fish predators, a full-blown trophic cascade occurs. Therefore the diversity of predators reduces the likelihood of trophic cascades occurring and hence provides insurance against the loss of an important ecosystem function (i.e. secondary production).

Keywords: BEF, TMII, multiple predator effects, species richness, risk reduction, marine, food web.

Introduction:

Food webs are immensely complex systems, with many predators and prey interacting over a range of trophic levels (Schoener 1989; Polis 1991; Martinez 1993a; Williams & Martinez 2000; Pimm 2002). Energy, nutrients and minerals are all cycled via these complex interactions (Pomeroy 1970; DeAngelis 1980). It has been shown for seven of the largest known food webs (a variety of aquatic and terrestrial) that over 95% of species are typically within three links of each other, with most species on average two links apart (Williams *et al.* 2002). This suggests that even a single species addition or deletion will propagate changes throughout an entire food web. To study the effects of a single predator or a single trophic level is to ignore the importance of this highly interconnected complexity. There is a growing appreciation that empirical studies of food web dynamics need to incorporate multiple predators and prey over more than one trophic level, reflected by the increasing number of such studies in a wide variety of ecosystems (Cardinale et al. 2003, Finke & Denno 2005 in terrestrial systems; Eklov & VanKooten 2001, Vance-Chalcraft & Soluk 2005 in freshwater systems; Bruno & O'Connor 2005, Van Son & Thiel 2006, Guidetti 2007 in marine systems; and see Duffy et al. 2007 for a comprehensive overview).

As the field of biodiversity and ecosystem functioning continues to expand, we are beginning to gain perspective on the importance of diversity, particularly at high trophic levels. A number of recent meta-analyses of studies from the published literature have all demonstrated the positive effect of diversity on ecosystem processes (Balvanera *et al.* 2006; Cardinale *et al.* 2006; Worm *et al.* 2006) and advocated caution when considering management approaches to biodiversity. Despite their low diversity and abundance when compared to basal species, high trophic level species can have disproportionately large effects on food web dynamics. Loss of just a few predators can have the same effect as large reductions in plant or algal diversity (Duffy *et al.* 2003), while cascading effects of changing top predator density or diversity on basal resources, mediated through herbivores and/or secondary consumers, are increasingly more common in the literature (Bruno & O'Connor 2005; Finke & Denno 2005; Byrnes *et al.* 2006). With 70% of extinctions in marine systems occurring in the top two trophic levels (Byrnes *et al.* 2007), it is particularly important we try to understand the importance of predator diversity for the functioning of marine ecosystems.

Benthic invertebrates also carry out a vital role in marine systems, providing a link between basal resources and the rest of the food web. Algal grazers channel energy from primary producers to higher trophic levels and decomposers recycle nutrients from detrital matter that would otherwise be lost. In this way, they facilitate the functioning of marine ecosystems and play an important role in sustaining pelagic species. An increasing number of studies recognize the importance of secondary production for ecosystem functioning (Duffy *et al.* 2003; Gamfeldt *et al.* 2005; Gascuel 2005; France & Duffy 2006); particularly in marine systems where secondary production is an important determinant of fish yield (Duffy *et al.* 2003). Hereafter, we use the term secondary production to refer to production within the benthos, irrespective of trophic position.

Multiple predators tend to have effects in mixture that cannot be predicted by summing their individual effects alone. These multiple predator effects (Sih *et al.* 1998) can lead to either risk enhancement or risk reduction for the prey. Risk enhancement can be caused by facilitative interactions between predators, which lead to higher levels of predation in mixture compared to the sum of individual predator effects (Eklov & VanKooten 2001; Nilsson *et al.* 2006). The prey can also respond to multiple predators in a manner that makes them more susceptible to predation (Soluk & Collins 1988; Losey & Denno 1998). In contrast, risk reduction can be caused by antagonistic interactions between predators, which lead to lower levels of predation in mixture (Crumrine & Crowley 2003; Siddon & Witman 2004; Preisser *et al.* 2005; Prasad & Snyder 2006), or the prey can have increased anti-predator behaviour in the presence of multiple predators (Stein & Magnuson 1976).

Here we used subtidal cages to manipulate the species richness of a benthic predator trophic level, while controlling for predator density. We examined the effects of predator species loss on ecosystem functioning by quantifying the biomass of the benthic invertebrate community as a surrogate measure of secondary production. The key focus of the study was how varying interspecific interactions with predator diversity would affect the biomass of the prey community. We chose to test for the presence of either antagonistic or facilitative interactions in our predator community and how these would affect secondary production (either positive or negative effects). To that end we test the following two-tailed hypotheses in this study:

1). *Secondary production will be highest in the absence of predation, i.e. no top predators present to lower the biomass of benthic invertebrates.*
2). *Behavioural interactions between predators will lead to a change in secondary production at high predator diversity.*
3). *As predator diversity declines, the intensity of interspecific interactions among predators will change, leading to a modification of secondary production.*

The use of *in situ* cages with a 10mm mesh size represents a balance between open and closed systems. Any effects of biofouling on environmental parameters or caging effects on the animals present was the same for all experimental treatments. The experimental communities act as model systems to test the effects of changing predator diversity. The small mesh size ensured confinement of the manipulated fish predators, whilst excluding larger predators or similarly sized competitors. The size of the mesh also allowed smaller species into the cages (intermediate consumers such as small fish, decapods and crustaceans, as well as benthic invertebrates). It is well known that body size is an excellent predictor of trophic level in marine communities (Jennings *et al.* 2001), with larger species typically feeding on smaller species (Cohen *et al.* 1993b). Therefore only lower trophic level species could assemble into the cages, i.e. the species diversity of the top trophic level in this study was fixed.

Materials and Methods:

Natural history

The chosen study site was Lough Hyne, a marine reserve in southwest Ireland (N 51˚29’52”, W 9˚17’46”). This is a highly sheltered, yet fully marine sea lough and is an ideal system in which to perform manipulative experiments. Four vertebrate predators (benthic fish species) were chosen for inclusion in the experiment, which ran for 42 days. These were the black goby, *Gobius niger*; rock goby, *Gobius paganellus*; sea scorpion, *Taurulus bubalis*; and shore rockling, *Gaidropsarus mediterraneus*. These were chosen because all four species are common in the waters within and surrounding Lough Hyne. They also have a very similar body size, which suggests that they come from the same trophic level. Gut content analysis was carried out on all remaining fish at the end of the experiment confirming that the four predators have overlapping dietary ranges (see Figure 1).

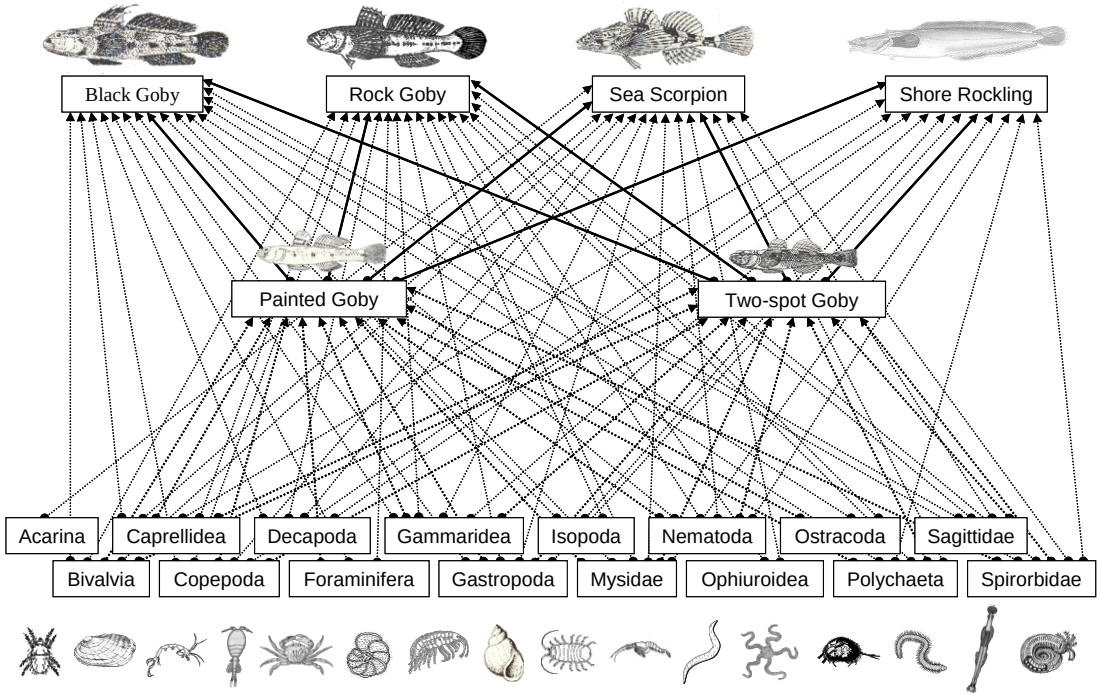

Figure 1. Food web representing the community within the experimental mesocosms, containing the four manipulated fish as top predators and all their prey recorded from the sampling procedure (intermediate consumers, as well as benthic invertebrates). The web is drawn from gut content analysis of all fish recovered from the experiment. Different grades of line thickness are used to denote the various trophic flows in the web.

Experimental design

Recent studies have advocated the use of substitutive experimental designs arguing that additive designs are fundamentally confounded because they conflate both diversity and density (e.g. Balvanera *et al.* 2006). In contrast, others (e.g. Griffen 2006; Weis *et al.* 2007), have argued that there is no single design adequate to detect the various mechanisms by which diversity might influence a process. In the current experiment, our aim was to test solely for the effects of predator diversity (not density) on the strengths of *per capita* predator-prey interactions. Consequently, we employed a modified substitutive design that maintained a constant predator density throughout the experiment, while allowing diversity to change with no more than one individual of each species present. Simply, our focus was not to quantify how intraspecific interactions were affected by predator diversity, but rather, how interspecific interactions were modified in the presence of multiple predator species.

We established a gradient of fish predator diversity within subtidal cages (10mm square mesh), which were placed in 2-3m of water (at low tide) along the south shore of Lough Hyne. Our experimental design employed 42 underwater cages: thirty cages were 30 × 30 × 10 cm (hereafter referred to as small), 6 cages were 60 × 30 × 10 cm (medium) and 6 cages were 60 × 60 × 10 cm (large) in size. The small cages contained no more than one predator species, allowing us to examine the effects of each species in isolation. We employed five treatments (each replicated six times), which consisted of: one individual black goby, one individual rock goby, one individual sea scorpion, one individual shore rockling, and empty cages (used as a predator-free treatment). The medium sized cages contained two individuals, one from each of two different species. All possible combinations of two species from the four species pool were used once, i.e. they were not replicated for identity, but there were still six replicates of the two-species treatment. The large cages contained four individuals, one from each of the four species. Again, this treatment was replicated six times.

Response variables

In the present study, we examined two different responses within the community of interest. First, we examined how changing predator diversity affected an ecosystem process of key importance in coastal ecosystems, i.e. secondary production. Secondly, we examined the effect of predator diversity on the magnitude

of *per capita* interaction strengths and hence examined how diversity is likely to affect dynamics. This approach employed common data with effects expressed in different formats so that we were able to address our different hypotheses.

Secondary Production

The effects of decreasing predator species richness on secondary production were examined using artificial habitat units. These consisted of nylon pot scourers (approx. radius = 4cm; approx. height = 2cm), which rested loosely on the substrate in the cage. The pot scourers represent a passive sampling device and were used as a settlement substrate for small benthic invertebrates. Importantly, the scourers enable us to obtain a manageable subsample of invertebrates from the stony substrate within the cages. The densities of invertebrates obtained from the pot scourers are representative of naturally occurring densities within the field and are commonly used as a settlement substrate for mobile fauna (e.g. Costello & Myers 1996; Gobin & Warwick 2006; Underwood & Chapman 2006). In the present study over 16 common taxonomic groups were identified from these substrates (see Figure 1). Biomasses for each taxonomic group were calculated as, XM, where X is the abundance of prey taxa quantified from the artificial habitat unit and M is the average body mass, obtained by calculating the dry weight (mg) of all prey, per taxonomic group, collected in the experiment ($n > 100$ for all except Decapoda ($n = 8$) and Ophiuroidea ($n = 9$), which were quite rare in the experiment).

A number of small intermediate consumers were free to assemble into the cages along with the manipulated top predators. Two vertebrate species were of particular note: the painted goby, *Pomatoschistus pictus*, is the most abundant fish in Lough Hyne with natural densities of up to 6.5 m^{-2} (Costello 1992). The two-spot goby, *Gobiusculus flavescens*, is the next most abundant with natural densities of up to 4.0 m^{-2} (Costello 1992). At the end of the experiment, both species of fish were seen swimming through the small mesh size of the cages. This unexpected result was not anticipated at the outset of the experiment and so the density of these intermediate consumers was not quantified for each cage used during the experiment. To investigate the importance of these small predators a subset of the cages were re-laid along the same stretch of shoreline at Lough Hyne. Practical constraints limited this study to three replicates of each small cage treatment, i.e. predator-free and single species treatments (containing the same four manipulated fish used above).

Surveys were carried out on all cages to estimate the density of intermediate fish consumers after 42 days (replicate 5 minute counts per cage). Natural densities occurring outside the cages were made using a 1m × 1m quadrat and counting fish over a five minute period (n = 20).

Per capita interaction strengths

The *per capita* interaction strength between the fish predators and their invertebrate prey was estimated using the dynamic index proposed by Osenberg and Mittlebach (1996) and Wootton (1997). Hereafter, we refer to the dynamic index simply as *per capita* interaction strength. The observed *per capita* interaction strength, a_{ij}, between predator j and prey i, is calculated as follows:

$$a_{ij} = \frac{\ln\left(\frac{D_i^+}{D_i^-}\right)}{D_j t}$$

where D_i^+ is the density of prey in the presence of the predator, D_i^- is the density of prey in the absence of the predator, D_j is the density of the predator and t is the duration of the experiment in days (the experiment was allowed to run for 42 days).

Data analysis

All univariate analyses were performed using SPSS 11.0 package for Windows (SPSS, Chicago, Illinois, USA). Invertebrate biomass data were $\log_{10}$ transformed to meet the assumptions of normality. A one-way analysis of variance (ANOVA) was used to examine the effects of predator diversity, from 0-4 species (the factor), on benthic invertebrate biomasses and *per capita* interaction strengths (the dependent variables). Tukey's post-hoc test was performed to assess which treatments differed significantly in multiple comparisons. Mortality of fish during the experiment meant that to investigate treatment effects on secondary production using a balanced design, only three replicates from each treatment were viable for data analysis (whilst also maintaining differences in composition of the species richness treatments). These three replicates were selected at random. By maintaining a balanced design for treatment effects we were forced to analyse for diversity effects using an unbalanced design (0 species n = 3; 1 species n = 12; 2 species n = 3; 4 species n = 3). The same issues apply to the analysis of *per capita* interaction

strengths. The predator-free cages were used in the calculation of *per capita* effects and were hence lost from that analysis. Linear regression analysis was used to examine the relationship between predator diversity (the independent variable) and Simpson's index of benthic invertebrate diversity (the dependent variable). One-way ANOVAs were used to assess for any differences in the densities of intermediate consumers (i.e. painted and two-spot gobies) among predator-free cages (n = 3), predator monocultures (n = 12), and natural densities (n = 20).

Results:

Ecosystem processes – secondary production

There were significant effects of top predator diversity on a wide range of prey taxonomic groups, intermediate consumers and net secondary production. For clarity, the results of our one-way ANOVA's are reported in the legends of Figures 2-6. There was a clear trend seen across 12 of the 16 taxonomic groups identified in this experiment. Here, benthic invertebrate biomasses were highest in the predator-free cages. There were also relatively high levels of secondary production at high predator diversity, which decreased as predator diversity declined so that the lowest levels of prey secondary production were found when predator diversity was low. This trend was shown to be significant for Bivalvia, Ostracoda, and Sagittidae (Figure 2*A*-*C*). For these three groups, the single predator diversity treatment had significantly lower prey biomasses than the predator-free treatment (Tukey, $p < 0.05$). This pattern of increased prey biomasses in predator-free cages was also shown for Acarina, Decapoda, Foraminifera, Gammaridea, Gastropoda, Isopoda, Mysidae, Ophiuroidea, and Polychaeta. Although this pattern was qualitatively the same, the difference was not significant.

There was a different trend for the remaining four benthic invertebrate groups. The Caprellidea, Copepoda, Nematoda, and Spirorbidae all had high biomasses at high predator diversity and low biomasses at low predator diversity, similar to the other 12 invertebrate groups. This trend was much stronger for these four taxonomic groups, with prey biomasses significantly higher at high fish predator diversity compared to the single species treatments (Tukey, $p < 0.05$). Interestingly, the lowest invertebrate biomasses were found in the supposed predator-free treatment. For all four invertebrate taxa, the predator-free cages had

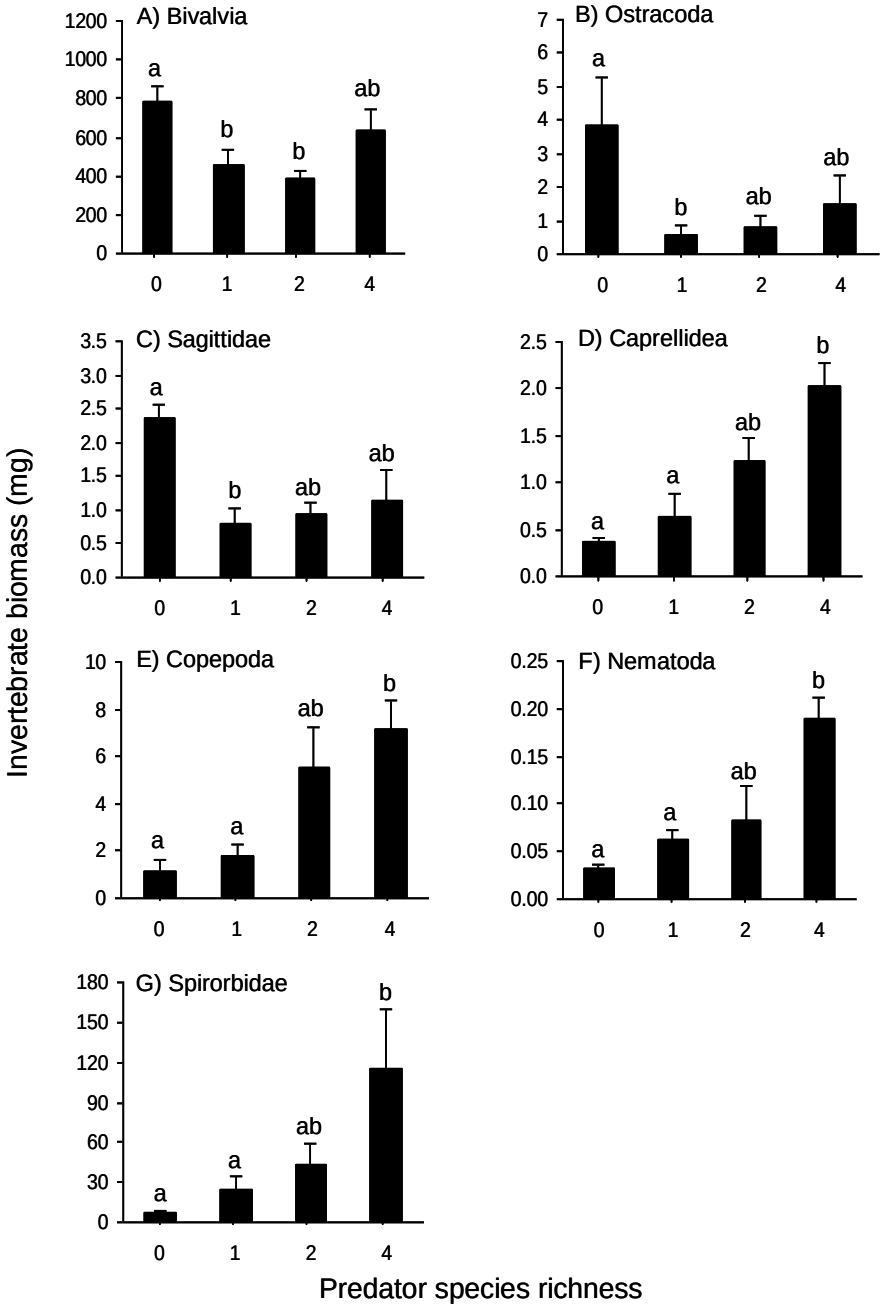

Figure 2. (*A*-*G*) Invertebrate biomasses (mean ± SE) of selected taxonomic groups, as predator richness increased from 0 to 4 species. Different letters indicate significant difference at $p = 0.05$ using the Tukey Test. (*A*) Bivalvia ($F_{3,17} = 4.890$, $p = 0.012$), (*B*) Ostracoda ($F_{3,17} = 5.764$, $p = 0.007$), (*C*) Sagittidae ($F_{3,17} = 5.562$, $p = 0.008$), (*D*) Caprellidea ($F_{3,17} = 4.308$, $p = 0.020$), (*E*) Copepoda ($F_{3,17} = 5.031$, $p = 0.011$), (*F*) Nematoda ($F_{3,17} = 4.227$, $p = 0.021$) and (*G*) Spirorbidae ($F_{3,17} = 4.068$, $p = 0.011$). Data were $\log_{10}$ transformed to meet the assumptions of parametric tests before a one-way ANOVA was carried out.

significantly lower biomasses than the four-predator species cages (Tukey, $p < 0.05$) (see Figure 2*D-G*).

Net prey secondary production in the one- and two-predator species treatments was significantly lower than in the predator-free treatment, while there was also a high level of secondary production in the four-predator species treatment (see Figure 3a). Increased predator diversity also had a dramatic effect on the diversity of the prey assemblage (see Figure 3b). There was no change in prey taxonomic richness as predator diversity increased, however, Simpson's Evenness index shows that there was a highly significant difference in the evenness of the invertebrate community among the various predator diversity treatments (ANOVA; $F_{3,17} = 7.08$, $p = 0.002$). The predator-free and one-predator species treatments had a significantly higher invertebrate evenness than the two- and four-predator species treatments (Tukey, $p < 0.05$).

By examining the identity effects in the experiment, we can see that the rock goby and the shore rockling had particularly strong effects on secondary production when they were found in monoculture. In Figure 4a, we see that the biomass of Sagittidae was significantly lower in the rock goby monocultures than in the predator-free cages, while the biomasses of Ostracoda and Sagittidae were lower in the shore rockling monocultures than in the predator-free cages. In Figure 4b, we see that the biomasses of Copepoda, Nematoda, and Spirorbidae were all significantly lower in the rock goby monocultures than in the four species treatment. The biomasses of Copepoda and Nematoda in the shore rockling monocultures were also significantly lower than in the four species treatment. Again, the low biomass of Copepoda, Nematoda, and Spirorbidae in the supposed predator-free treatment was clear here, with significantly lower biomasses than in the four species treatment.

Dynamics - Per capita interaction strength

The dynamic index was used as an estimate of *per capita* interaction strength between the fish predators and their benthic invertebrate prey. As the species richness of fish predators in the cages increased, *per capita* interaction strength became increasingly positive, i.e. negative predator-prey interactions became weaker (less negative) and weak positive interactions became stronger (more positive). For the Caprellidea, Copepoda, Nematoda, and Spirorbidae, the increase in *per capita* effect was significant (One-way ANOVA; see Figure 5). Here, the four-predator

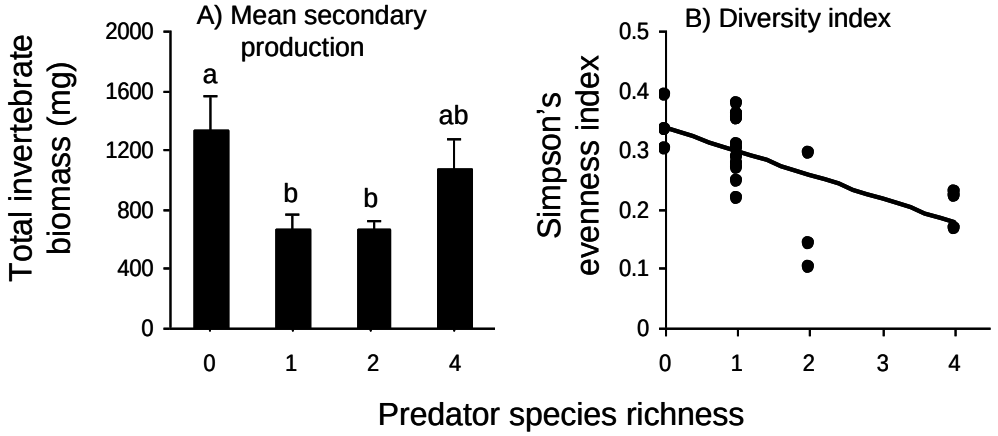

Figure 3. (*A*) Mean secondary production in the system, obtained from the mean of each treatment (± SE), showed significant differences at $p = 0.05$ using the Tukey Test ($F_{3,17} = 3.197$, $p = 0.05$). (*B*) Diversity, measured using Simpson's Evenness Index, declined with increasing predator richness at the community level of benthic invertebrates (Linear Regression; $F_{1,19} = 11.408$, $p = 0.003$, $r^2 = 0.375$).

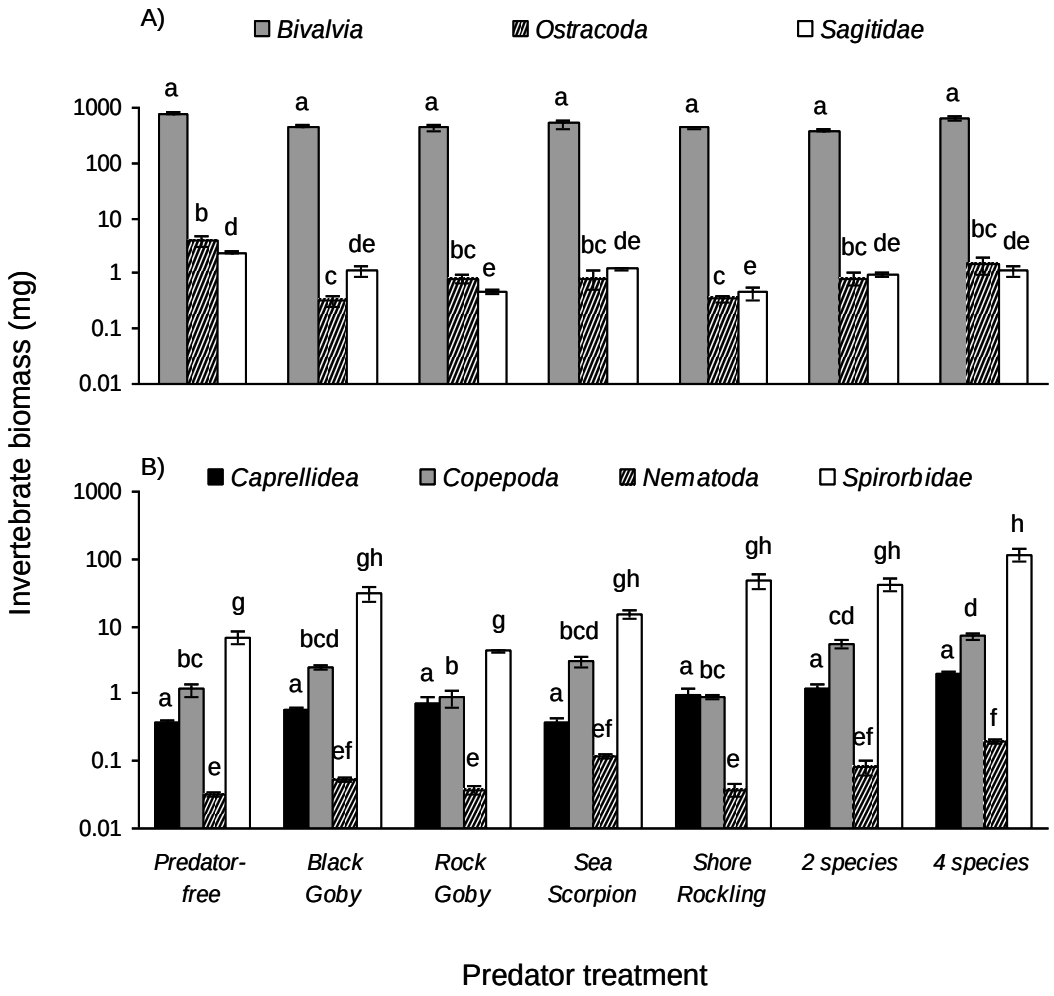

Figure 4. Invertebrate biomass for seven species of prey in predator-free treatments, monocultures of black goby, rock goby, sea scorpion and shore rockling and two- and four-predator species treatments. Two species treatments include all combinations of the four species. Four species treatments include one individual of each of the four predators. Significant differences in invertebrate biomass were found for (*A*) Ostracoda ($F_{6,14}$=3.127, p = 0.037) and Sagittidae ($F_{6,14}$=3.287, p = 0.031), but not Bivalvia ($F_{6,14}$=2.111, p = 0.117). (*B*) Copepoda ($F_{6,14}$=5.838, p = 0.003), Nematoda ($F_{6,14}$=5.625, p = 0.004) and Spirorbidae ($F_{6,14}$=5.840, p = 0.003), but not Caprellidea ($F_{6,14}$=2.585, p = 0.067). Significant differences for one-way ANOVAs are indicated by different letters above each bar, at p = 0.05 using the Tukey Test.

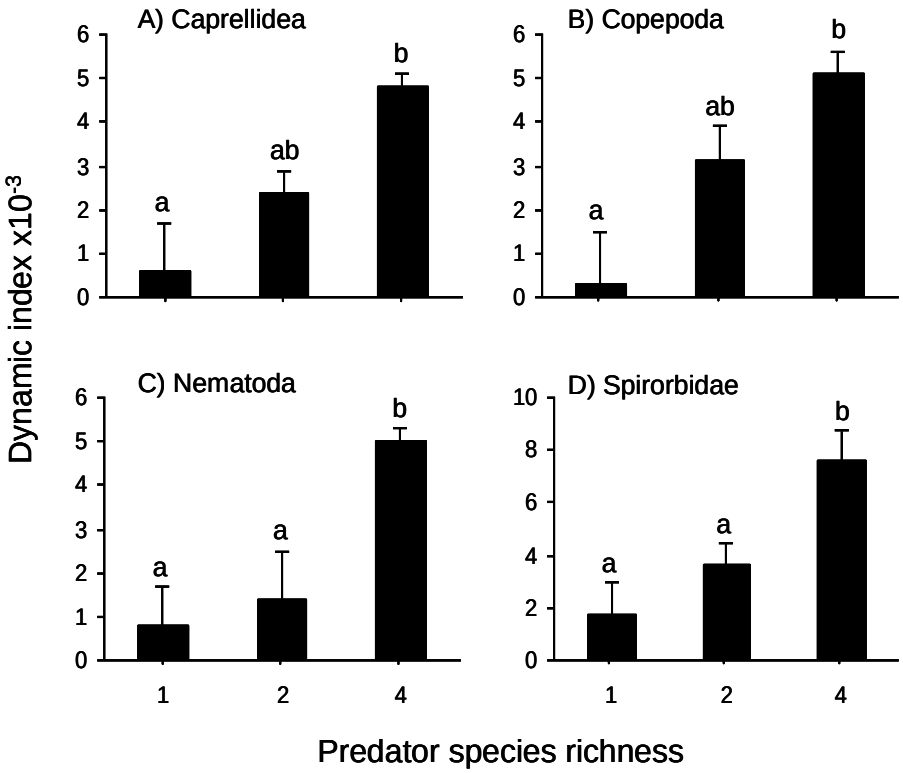

Figure 5. Mean *per capita* interaction strength (dynamic index ± SE) of fish predators on four selected invertebrate prey groups, with predator species richness of 1, 2 and 4. Significant differences between treatments are indicated by different letters above each bar, at p = 0.05 using the Tukey Test; (*A*) Caprellidea ($F_{2,15}$=8.375, p = 0.004), (*B*) Copepoda ($F_{2,15}$=9.369, p = 0.002), (*C*) Nematoda ($F_{2,15}$=9.051, p = 0.003) and (*D*) Spirorbidae ($F_{2,15}$=8.967, p = 0.003).

species treatment was significantly different from the one-predator species treatment for all four benthic invertebrate groups (Tukey, $p < 0.05$). The four-predator species treatment was also significantly different from the two-predator species treatment for Nematoda and Spirorbidae (Tukey, $p < 0.05$). In essence, there were strong positive interactions between top fish predators and all four groups of invertebrates when multiple predators were present.

Surveys to estimate the densities of the two intermediate vertebrate predators (painted goby and two-spot goby), show that there was no significant difference between natural densities (n=20) of the two gobies and densities in the single predator species treatments (see Figure 6a-b; Remember that cages were re-laid to investigate densities of these fish in our manipulated predator monocultures, i.e. 3 × 4 one species treatments (n = 12) plus 3 predator-free cages (n = 3)). In contrast, the densities of painted and two-spot gobies in the predator-free treatment were significantly higher (Painted goby: One-way ANOVA, $F_{2,32}$=5.574, p = 0.008; Two-spot goby: One-way ANOVA, $F_{2,32}$=5.031, p = 0.013) than in the one-predator species treatment and under natural conditions. These results, shown in Figure 6, indicate that the intermediate consumers aggregated in predator-free space.

Discussion:

Intuitively, it is reasonable to expect that the highest levels of net secondary production will occur in cages where there is no predation pressure on benthic invertebrate prey (from the manipulated vertebrate predators). This is particularly clear in the case of the Bivalvia, Ostracoda and Sagittidae, where biomasses in predator-free cages were significantly higher than in the single-predator species treatment (see Figure 2a-c). Such a result is in agreement with our first hypothesis: *in the absence of predation, invertebrate prey survival is maximal, leading to elevated secondary production*. Importantly, despite high levels of secondary production in the predator-free treatment, the absence of higher trophic levels means that there is little or no transfer of energy from the basal resources through the web. This is a scenario not unlike that predicted by Byrnes *et al.* (2007), where loss of diversity at top trophic levels can change the shape of the classic trophic pyramid of marine food webs into a compressed version, dominated by filter feeders and scavengers, the consequences of which are largely unknown.

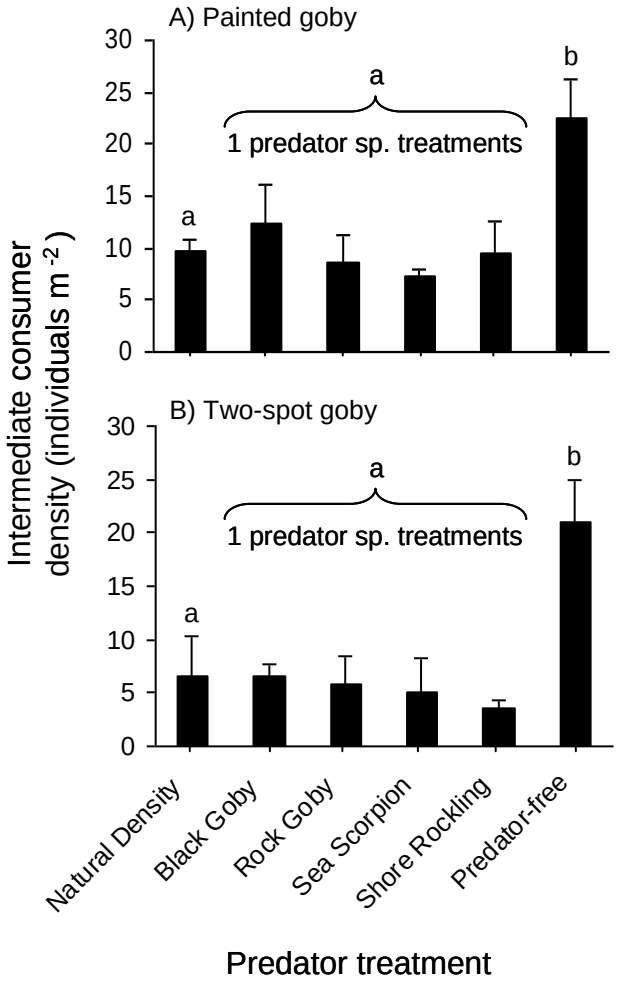

Figure 6. Density (mean ± SE) of intermediate consumers (painted and two-spot goby) along the south shoreline at Lough Hyne (natural), in cages containing one species of small fish predator, and in predator-free cages. Density data for black goby, rock goby, sea scorpion and shore rockling treatments were combined as a one-predator species treatment and compared to the predator-free treatment and natural densities. Significant differences, based on one-way ANOVA were found for p = 0.05 using the Tukey Test (painted goby $F_{2,32}$=5.574, p = 0.008; two-spot goby $F_{2,32}$=5.031, p = 0.013) and are indicated by different letters above the bars.

For all 16 taxonomic groups quantified, net secondary production increased from one to four top-predator species richness (see Figure 3a), however, this trend was only significant for the Caprellidea, Copepoda, Nematoda, and Spirorbidae. There are a number of possible mechanisms responsible for this increase. We controlled for predator density (and also intraspecific interactions), whilst the number of species present and hence the intensity of interspecific interactions was varied. Accordingly, the response of the invertebrate community (particularly clear for Caprellidea, Copepoda, Nematoda, and Spirorbidae; see Figure 2d-g) may be due to behaviourally mediated changes in the strength of trophic interactions, which underlie trait mediated indirect interactions (TMIIs). TMIIs occur when behavioural changes in a predator species either limit or enhance their ability to feed down on prey, e.g. competitive interactions (Siddon & Witman 2004), avoidance (Prasad & Snyder 2006), intimidation (Preisser *et al.* 2005), or facilitation (Eklov & VanKooten 2001). Here the TMII leads to risk reduction for the invertebrate prey as the diversity of fish predators increases, i.e. there is an emergent multiple predator effect occurring (Sih *et al.* 1998). It is important to note that we have not explicitly set out to test for TMIIs and hence using our current experimental design are unable to categorically identify the existence of a TMII (methods explained by Okuyama & Bolker 2007).

There are a number of competing hypotheses that could explain risk reduction among the benthic invertebrates in this experiment: (1) *mutual interference between the multiple fish predators, as they compete for the invertebrate prey*, e.g. Siddon & Witman (2004) showed that crab predation on sea urchins was reduced in the presence of lobsters, despite the absence of a trophic interaction between the crabs and lobsters; (2) *less time spent feeding by the fish predators as they try to avoid intraguild predation or pursue an alternate prey*, e.g. Prasad & Snyder (2006) showed that small carabid beetles consume fewer fly egg prey in the presence of large beetles (due to avoidance of possible intraguild predation) and also in the presence of a preferred prey, aphids; (3) *an increase in anti-predator behaviour by benthic invertebrates as predator species richness increases*, e.g. Stein & Magnuson (1976) showed that crayfish reduced their overall activity, including grazing on their detrital food supply, in the presence of fish predators. All three possible causes of risk reduction represent TMIIs arising from non-trophic links, i.e. behavioural

changes in predators with shared resources or vice versa (see Werner and Peacor (2003) for a review of TMIIs and the mechanisms causing them).

The increase in net secondary production cannot be due to intraguild predation between predators, as only cages with a full complement of fish predators present at the end of the experimental period were analysed (although fear of intraguild predation may still be a possibility). It is more likely that the reduction in predation pressure is due to intense interference competition or behaviourally induced changes in feeding activity through confinement to benthic cages (which might have ultimately led to mortality in discarded treatments). An increase in secondary production with an increase in predator diversity reveals the antagonistic nature of these interactions and allows us to accept our second and third hypotheses: *behavioural interactions between the predators lead to reduced feeding in high diversity treatments and therefore a significant change in secondary production*; and *reduced intensity of behavioural interactions in low predator diversity treatments leads to increased time for feeding on prey and thus a significant change in secondary production*. In particular, species such as the rock goby and shore rockling, which strongly reduced invertebrate biomasses in monoculture, had their effects dampened in the presence of other competitors (i.e. the black goby and sea scorpion).

In a recent review, Duffy *et al.* (2007) highlighted three mechanisms by which increasing consumer diversity can affect prey secondary production: 1) overexploitation of prey; 2) reduction in prey species richness and consequently reduced prey production; and 3) dominance by less competitive prey species when there is a trade–off between competitive ability and resistance to predation. Our results provide support for (3), but the mechanism was subtly different, in that increased predator diversity reduced predation pressure on benthic invertebrates via a possible TMII. Consequently, several groups of invertebrates (Caprellidea, Copepoda, Nematoda, and Spirorbidae), which may have low resistance to predation, were competitively excluded at low predator diversity, due to higher levels of predation pressure). At high predator diversity, where predation pressure was lowest, the competitive ability of these four taxonomic groups was greatest and they went on to dominate the invertebrate assemblage. This led to an overall decline in the evenness of the prey community (see Figure 3b), but led to an increase in net secondary production. Here we see an insurance type effect, which is mediated by a

diversity of predators in the system. In the absence of top fish predators, a full-blown trophic cascade occurs (see Figure 2d-g). We propose that the diversity of predators reduces the likelihood of trophic cascades occurring and hence provides insurance against the loss of secondary production, an important ecosystem function in marine systems (Duffy *et al.* 2003; Gamfeldt *et al.* 2005; Gascuel 2005; France & Duffy 2006).

Our quadrat survey of painted and two-spot goby numbers (Figure 6a-b) indicated that the two species were numerically dominant vertebrate predators on the south shoreline of Lough Hyne (painted goby: 9.7 m^{-2}; and two-spot goby: 6.6 m^{-2}). Although small, these two gobies may be extremely important predators due to their sheer numbers. Gut content analysis indicated that both species are predators of Caprellidea, Copepoda, Nematoda, and Spirorbidae, whilst black goby, rock goby, sea scorpion, and shore rockling are also known to prey on painted and two-spot gobies (see Figure 1). The results of our survey confirmed the hypothesized difference in intermediate consumer densities between the predator-free treatment and cages containing fish predators (see Figure 6). Here we have shown that intermediate predatory gobies behaviourally altered their use of space in response to the presence or absence of top fish predators, tending to aggregate in predator-free areas. This observed behavioural response led to a modification in the strength of the interaction between the intermediate consumers and their common prey, that is, a possible TMII. Here, the predator-free cages represented a refuge for these small benthic consumers, from the larger predators present in the natural environment of the Lough. Coincidentally, the small gobies were most likely intimidated and avoid the space occupied by the larger manipulated benthic fish, although a shortcoming of the present study is the lack of data describing densities of intermediate consumers in the two- and four-predator species treatments.

Trait mediated indirect effects, such as the intimidation of prey species can be as strong as direct consumption, particularly in aquatic systems (Preisser *et al.* 2005) and indeed many studies have shown trophic cascades that result from trait mediated effects rather than direct predation (see Schmitz *et al.* 2004 for a review). In our study, the benthic invertebrates may have benefitted from these effects in varying ways. Firstly, they may have been released from the intense predation pressure of the intermediate consumers that kept their numbers at low levels in the predator-free cages. Secondly, there may have been a reduced chance of being eaten

by the higher fish predators, which in turn were more likely to prey on the intermediate consumers. This is not an uncommon mechanism with Kneib (1988) and Posey & Hines (1991) both demonstrating the positive indirect effects on benthic invertebrate prey of predators controlling intermediate consumer densities.

The benefit of these responses for certain groups of invertebrates should not be underestimated. Benthic invertebrates such as Caprellidea, Copepoda, Nematoda, and Spirorbidae provide important ecosystem services and loss of biomass in these groups could adversely affect ecosystem functioning. For example, Copepoda have been shown to provide an important link between microbial and classical pelagic food webs through bacterivory (Roff *et al.* 1995), while Turner (2004) reviews the importance of their feeding ecology and their role as prey for predators at higher trophic levels in marine systems. Nematodes are considered the most abundant metazoan taxa in marine sediments with annual production of up to 60 times their biomass (Vranken *et al.* 1986). Clearly, large losses in the biomasses of these taxa, as seen at low manipulated-predator diversity in this experiment, could greatly affect the productivity of the system and the amount of energy flow to higher trophic levels. Given the importance of multi-predator assemblages in reducing overfeeding by intermediate consumers on these benthic invertebrates, high predator diversity would appear to be very beneficial for the successful functioning of this benthic marine system. Furthermore, recent meta-analyses have shown that biodiversity loss is putting increasing pressure on the productivity and stability of marine ecosystems (Worm *et al.* 2006).

There are a number of limitations to the study. Our novel experimental design allowed us to look at changing diversity with only one individual of each manipulated predator per cage, while keeping predator density constant. The drawback to this approach is that cage size is confounded with diversity. The larger the cage, the greater the number of individuals interacting with each other, which could lead to greater regulation of invertebrate populations (Shima 2001). Also, while we were only interested in examining the strength of interspecific interactions in the system, it is entirely possible that intraspecific interactions between conspecifics could be just as strong (Jolliffe 2000). It would be interesting to examine the effect of two- and four-conspecific predators on secondary production and compare this to the effect of two- and four-predator species on secondary production from this experiment.

To our knowledge experimental manipulations of vertebrate predator diversity remain rare (Duffy *et al.* 2007). Whilst, evidence to date suggests that vertebrate predators exert relatively strong top-down control on ecosystems compared with invertebrates (Borer *et al.* 2005). In the present study we suggest that predator diversity can be seen as a fundamental mechanism for maintaining a balanced structure in complex communities, by decreasing the likelihood of trophic cascades detrimental to system productivity. TMIIs such as avoidance, interference, and intimidation could be central to risk reduction for many prey species (as seen in the different effects of one- to four-predator species treatments in this experiment), limiting possible cascading effects and the time available to predators for overfeeding (as seen in the simplified predator-free and one-predator species treatments in this experiment). Negative indirect effects on important benthic invertebrates were greatest in the most simplified predator assemblages, implying that predator diversity is essential to maintain a high level of secondary production, an important ecosystem function. The increased prevalence of behavioural interactions in complex communities should then confer greater opportunity for survival of species in lower trophic levels. Although some secondary producer species may thrive in these circumstances, leading to dominance by biomass of a few species, there is likely to be an overall increase in system productivity as a result. Logistical restraints confined the scale of this experiment to just four species of small fish as "top predators". Future studies should attempt to assess the multiple predator effects of more realistic higher trophic level communities, including many of the large invertebrate predators, such as decapods and echinoderms, as well as large fish predators and mammals.

Acknowledgements:

We thank Gabriel Du Rocher, Allen Whittaker, Isobel Abbot, Aurélie Aubry, and Órla McLaughlin for their help in setting up and retrieving the cages used in the experiments. We also thank Nessa O'Connor, John Griffin, Aurélie Aubry, and Órla McLaughlin for valuable comments on early drafts of the manuscript. The work was funded by the Department of Zoology, Ecology and Plant Science at University College Cork and the Irish Research Council for Science Engineering and Technology (IRCSET). The experiments that were carried out complied with all current Irish laws.