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CHAPTER FOUR

Body mass-abundance relationships are robust to cascading effects in marine food webs

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Abstract:

Body mass has been shown to scale negatively with abundance in a wide range of habitats and ecosystems. It is believed that this relationship has important consequences for the distribution and maintenance of energy in natural communities. Some studies have shown that the relationship between body mass and abundance may be robust to major food web perturbations, fuelling the belief that natural processes may preserve the slope of this relationship and the associated cycling of energy and nutrients. Here, we use data from a long-term experimental food web manipulation to examine this issue. Similar benthic communities were developed in large experimental mesocosms over a six month period. Some of the mesocosms were then subjected to species removals, based on the mean strength of their trophic interactions in the communities. In treatments where the strongest interactors were removed, a community-level trophic cascade occurred. The biomass density of benthic invertebrates increased dramatically in these communities, which led to a suppression of primary production. In spite of these widespread changes in ecosystem functioning, the slope of the relationship between body mass and abundance remained unchanged. This was the case whether average species body mass and abundance or individual organism size spectra were considered. An examination of changes in species composition before and after the experimental manipulations revealed an important mechanism for maintaining the body mass-abundance relationship. The manipulated communities all had a higher species turnover than the intact communities, with the highest turnover in communities that experienced cascading effects. As some species increased in body mass and abundance, new species filled the optimal size-abundance niches that were created. This maintained the overall body mass-abundance relationship and provided a stabilising structure to the communities.

Keywords: Local size-density relationship, individual size distribution, interaction strength, predator-prey allometry, energy equivalence, marine.

Introduction:

Natural ecosystems are complex ecological networks, consisting of a range of species linked together by a myriad of interactions, e.g. predation, herbivory, parasitism, and mutualism. In spite of this complexity, ecological networks are governed and constrained by fundamental properties and structures that facilitate successful functioning (Montoya *et al.* 2006). For example, the pattern of strong and weak predator-prey interactions has been shown to confer stability to complex ecosystems (McCann *et al.* 1998; Neutel *et al.* 2007; O'Gorman & Emmerson 2009). The vast majority of species in ecological networks are closely connected (Montoya & Sole 2002; Williams *et al.* 2002), which increases network robustness (Dunne *et al.* 2002). Additionally, ecological networks are typically size structured, with large-bodied predators tending to eat more prey species and thus occurring at higher trophic levels (Cohen *et al.* 1993b; Jennings *et al.* 2001; Woodward *et al.* 2005a).

Body mass is thought to be a critical functional trait, contributing to many of the properties that confer stability to ecological networks. Body mass (M) is believed to scale with metabolic rate as $M^{3/4}$ (Kleiber 1947; Peters 1983; Elgar & Harvey 1987; Brown & Gillooly 2003), i.e. larger species have greater energy demands. It has also been shown that body mass scales with abundance on a global scale as $M^{-3/4}$ (Damuth 1981; McMahon & Bonner 1983; Brown 1995; Enquist *et al.* 1998), i.e. larger species are less abundant than smaller species. Combining these two relationships ($M^{3/4} \times M^{-3/4} = M^{0}$) produces the energy equivalence hypothesis (Damuth 1981, 1987; Brown and Gillooly 2003; but see Blackburn & Gaston 1999; Schmid *et al.* 2000), which suggests that population energy use is approximately invariant with respect to body mass. Therefore, resources should be divided equally across populations, regardless of body mass. This implies that the relationship between body mass and abundance is a key determinant of energy and nutrient cycling in ecological networks.

Many different methods exist for estimating body mass-abundance relationships (see White *et al.* 2007 for a review). These methods fall into two broad categories: (1) average body mass measured for each species, i.e. cross-species approach; and (2) individuals grouped into logarithmically defined size classes, i.e. size spectra or all-individuals approach (Jennings *et al.* 2007). The cross-species approach has been employed in a wide range of ecosystems (Damuth 1981; Marquet *et al.* 1990; Cyr *et al.* 1997; Schmid *et al.* 2000; Carbone & Gittleman 2002; Jonsson

et al. 2005), while size spectra are typically associated with aquatic communities, due to their inherent size-structuring (Jennings *et al.* 2001; Law *et al.* 2009). The two approaches have been shown to produce qualitatively different results, with size spectra thought to be a better test of the energy equivalence hypothesis (Jennings *et al.* 2007).

A limited number of studies suggest that body mass-abundance relationships may be robust to major food web perturbations. In Tuesday Lake, Michigan, the replacement of three species of planktivorous fish with one species of piscivorous fish caused widespread changes in species composition, leading to an increase in zooplankton biomass and a reduction in algal biomass (Carpenter *et al.* 1987). In spite of this perturbation, many characteristics of the Tuesday Lake food web remained relatively unchanged, including the slope of the average species body mass-abundance relationship and the shape of the individual size spectra (Jonsson *et al.* 2005). Marquet *et al.* (1990) compared the average species body mass-abundance relationships from inside and outside two marine reserves in Chile (Las Cruces and Montemar). Inside both reserves, the absence of human impacts caused an increase in the density of predatory gastropods, leading to cascading effects on the body mass and abundance of invertebrate and algal species (Castilla & Duran 1985; Castilla 1988). Again, these trophic cascades had no noticeable effect on the body mass-abundance relationships at either reserve (Marquet *et al.* 1990).

There is no definitive mechanism to explain how the slopes of the body mass-abundance relationships were maintained at Tuesday Lake, Las Cruces, and Montemar, in spite of the increases and decreases in the density and body mass of numerous species. One common characteristic after the perturbation/exclusion at all three locations was a noticeable change in species composition. This may have facilitated a process of density compensation and size shifts that maintained the body mass-abundance relationships (Marquet *et al.* 1990). Our aim was to explore these patterns in a long-term exclusion cage experiment. We established a series of replicate marine mesocosm communities and exposed some of them to a perturbation over time (targeted species removal). We tested for the presence of a community-level trophic cascade after this perturbation. We examined the average species body mass-abundance relationships and individual size spectra of the communities for changes. We also measured the species turnover of the communities to explicitly test

whether this mechanism may be responsible for the apparent robustness of these critical properties of ecological networks.

Materials and Methods:

This study utilises data from a long-term experimental food web manipulation at Lough Hyne marine reserve, southwest Ireland (see O'Gorman & Emmerson 2009). Here, 24 large mesocosms were established in the shallow subtidal of the south shoreline of Lough Hyne (1-2m deep at low spring tide). The mesocosms consisted of a cylindrical frame, made from two polypropylene rings (0.76m in diameter), connected together with six evenly spaced polypropylene struts (0.5m tall). Polyethylene netting (5mm mesh size) was attached to this structure to complete the exclusion cages, which had a benthic surface area of $0.45m^2$. Lough Hyne is a highly sheltered marine reserve, hence covering the bottom of each cage with clean stony substrate (similar to that found on the south shoreline of the Lough) was sufficient to keep them secured to the benthos for the duration of the experiment.

Ten abundant benthic species of fish, decapods and echinoderms were chosen for manipulation in the experiment. These ten species were black goby (*Gobius niger*), rock goby (*Gobius paganellus*), sea scorpion (*Taurulus bubalis*), shore rockling (*Gaidropsarus mediterraneus*), goldsinny wrasse (*Ctenolabrus rupestris*), shore crab (*Carcinus maenas*), velvet swimming crab (*Necora puber*), common prawn (*Palaemon serratus*), spiny starfish (*Marthasterias glacialis*), and purple sea urchin (*Paracentrotus lividus*). All of these species are locally common at Lough Hyne, reaching densities in the shallow subtidal during summer months that closely approximate the area of our mesocosms (Costello 1992; Crook *et al.* 2000; Verling *et al.* 2003; Yvon-Durocher *et al.* 2008). The mesh size of the cages was small enough to contain these ten species, but it was sufficiently large to allow small benthic invertebrates from lower trophic levels, such as amphipods, isopods, gastropods, and bivalves, to recruit naturally into the cages.

Two important ecosystem process rates, primary and secondary production, were monitored throughout the experiment, using sampling substrates that were attached to the inside of the cages at the start of the experiment. Primary production was measured as the square root of chlorophyll *a* (mg/m^2), which has been shown to be a good approximation for primary productivity (Friedrichs *et al.* 2009). Here,

algae were scraped from glass slides (55 × 26 mm) and chlorophyll *a* was quantified using the spectrophotometric method (Parsons *et al.* 1984). Secondary production was measured as the total biomass density (body mass (g) × numerical abundance (m^{-2})) of all benthic invertebrates in the mesocosm communities. The densities of sessile species were estimated from settlement panels (100 × 100 mm PVC squares). The densities of mobile species were estimated from nylon pot scourers (approx. radius = 40mm; approx. height = 20mm), which are ideal substrates for colonisation by mobile benthic invertebrates, and simulate the form and structure of coralline algae prevalent in the study system (Underwood & Chapman 2006; O'Gorman *et al.* 2008). We measured the length of a linear dimension for every individual benthic invertebrate identified from these sampling substrates and estimated body mass using length-weight relationships established during the study (see O'Gorman & Emmerson 2009).

The experiment was divided into two phases: (1) community assembly and (2) interaction strength manipulation. The aim of the community assembly phase was to develop similar communities in all 24 mesocosms over a six month period. Accordingly, all 24 mesocosms had the same core community at the outset of the experiment, i.e. all ten manipulated species present. Small benthic invertebrates were then free to assemble into the cages, leading to the natural development of complex communities over the coming months. The mesocosms were grouped into four blocks of six, with two blocks at a depth of 1m and two blocks at a depth of 2m (at low spring tide) in the shallow subtidal. The experiment commenced on 5th October 2006. To limit the results to a manageable number of comparisons, we present data here from the first of three sampling sessions, which was on 13th December 2006. During sampling, each cage was briefly lifted from the water and one of each sampling substrate was removed before the cage was returned to its original position on the benthos.

In the manipulation phase of the experiment, we removed some species from our core community in subsets of the cages, based on the strength of their interactions in the mesocosm communities. Here, the ten manipulated species were ranked according to their mean absolute *per capita* effect on the benthic invertebrate community (see O'Gorman & Emmerson 2009 for a detailed description of these rankings). Six treatments were then employed: (1) 10 species community (W^+S^+), i.e. an intact community; (2) two weakest interactors (*G. paganellus* and *N. puber*)

removed ($W^{-2}S^{+}$); (3) three weakest interactors (*G. paganellus*, *N. puber* and *C. maenas*) removed ($W^{-3}S^{+}$); (4) two strongest interactors (*G. mediterraneus* and *M. glacialis*) removed ($W^{+}S^{-2}$); (5) three strongest interactors (*G. mediterraneus*, *M. glacialis* and *P. serratus*) removed ($W^{+}S^{-3}$); (6) all strong and weak interactors removed ($W^{-}S^{-}$), i.e. only *G. niger*, *C. rupestris*, *T. bubalis* and *P. lividus* present. These six treatments were randomly assigned within each of the four blocks. The manipulation phase of the experiment began on 18th April 2007. Again, we present data here from the first of three sampling sessions, which was on 16th June 2007.

To test for the existence of a community-level trophic cascade as a result of the interaction strength manipulations, we compared primary and secondary production between the treatments before and after the manipulations were applied. We also explored the impact of the manipulations on the body mass-abundance relationship within each treatment. We examined the body mass-abundance relationship in two ways: (1) cross-species; and (2) all-individuals (see Jennings *et al.* 2007). For the cross-species approach, we plotted the average body mass (mg) of each species across the four replicates in a treatment against their average population density (on a log-log scale). Since these population densities are measured at a local scale within the same region, this corresponds to a local size-density relationship (LSDR) (White *et al.* 2007). For the all-individuals approach, we grouped individuals into body mass classes (irrespective of species), which were defined on a $\log_{10}$ scale (in size class intervals of 0.1). We then plotted the midpoint of these size classes against the number of individuals in each size class (which we converted to $\log_{10}$ density per m^2). This corresponds to an individual size distribution (ISD) (White *et al.* 2007). Lastly, to investigate compositional changes in the treatments before and after the interaction strength manipulations, we used Whittaker's index of beta-diversity, β_w. Here, $\beta_w = (s/\alpha)-1$, where s is the total number of species in a replicate community before and after the manipulations and α is the average species richness of the two samples.

Statistical analysis

We employed a general linear model (GLM) approach to quantify differences in primary production, secondary production and species turnover before and after the manipulations. Here, we treated the square root of chlorophyll *a*, biomass density, and β_w, respectively, as response variables, with the removal of strong and

weak interactors as explanatory variables. We carried out one GLM analysis on the December 06 data (before the interaction strength manipulations) and another on the June 07 data (after the manipulations). The secondary production (biomass density) and species turnover (β_w) data were $\log_{10}$ transformed to meet the underlying assumptions of normal linear models. We used *t*-tests (assuming unequal sample size and unequal variance) to investigate potential differences in the intercepts and slopes of the LSDR and ISD for each treatment. We compared: (1) intercepts and slopes of each treatment in December 06 to the corresponding treatment in June 07, i.e. to investigate whether the interaction strength manipulations had a significant effect; and (2) intercepts and slopes of each treatment to the intact community in June 07, i.e. to investigate whether the manipulated communities differed from an intact community during the same season. All statistical analyses were performed using *R* (version 2.7.1).

Results:

In the community assembly phase of the experiment, none of the treatments that would later have species removed from the core community had significantly different levels of primary or secondary production from the "intact community" treatment, i.e. the treatment that contained all ten manipulated species in both December 06 and June 07 ($p > 0.2$). In the interaction strength manipulation phase of the experiment, the removal of strong ($F_{2,18} = 4.587$; $p = 0.024$) and weak ($F_{2,18} = 4.258$; $p = 0.031$) interactors led to a significant increase in the secondary production of the mesocosm communities. Here, the total biomass density of benthic invertebrates in the treatments with two strong ($t = 3.217$; $p = 0.005$), three strong (t = 2.102; $p = 0.049$), and two weak ($t = 2.288$, $p = 0.034$) interactors removed was significantly higher than in the intact community (Figure 1*A*). Removal of strong interactors ($F_{2,18} = 5.394$; $p = 0.015$) also led to a significant reduction in the primary productivity of the mesocosm communities. Here, the square root of chlorophyll *a* in the treatments with two ($t = -2.755$; $p = 0.013$) and three ($t = -2.705$; $p = 0.015$) strong interactors removed was significantly lower than in the intact community (Figure 1*B*).

There were significant differences between the intercepts of the LSDR and ISD, for all experimental treatments, before and after the interaction strength manipulations (see Tables 1 and 2), i.e. when comparing the intercepts for each

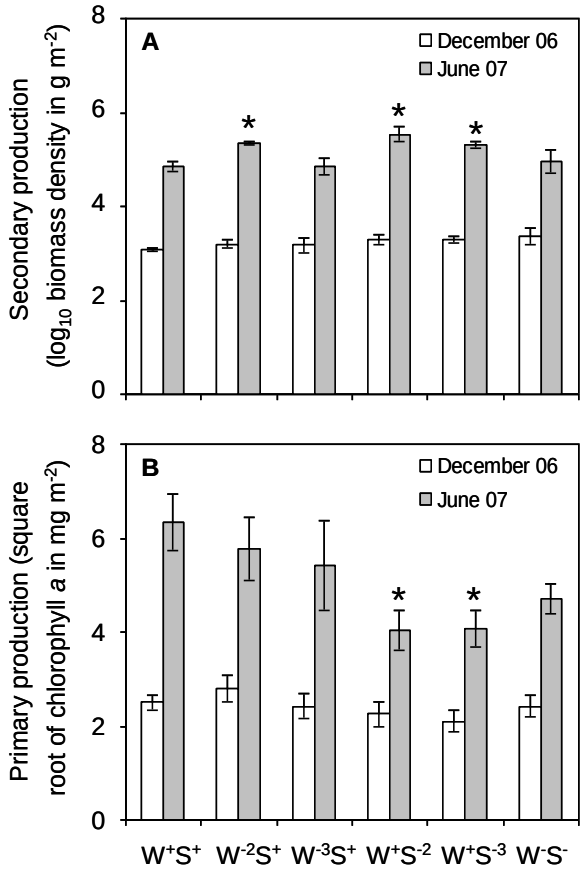

Figure 1. Level (treatment means ± 1 SE) of (*A*) secondary production and (*B*) primary production in the mesocosm communities for December 06, i.e. during the community assembly phase (white bars), and for June 07, i.e. during the interaction strength manipulation phase (grey bars). $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed. Treatments that are significantly different from the intact community are indicated by asterisks ($p < 0.05$).

Table 1. Body mass-abundance regression line intercepts and slopes for the six experimental treatments in December 06, i.e. during the community assembly phase of the experiment, and in June 07, i.e. during the interaction strength manipulation phase of the experiment. $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed. *t*1 (and *t*3) are the *t*-statistics comparing the intercept (and slope) of the body mass-abundance relationship for each treatment in December 06 to June 07. *p*1 (and *p*3) are the associated *p*-values. *t*2 (and *t*4) are the *t*-statistics comparing the intercept (and slope) of the body mass-abundance relationship for each treatment to the intact community, i.e. $W^{+}S^{+}$, in June 07. *p*2 (and *p*4) are the associated *p*-values.

	$W^{+}S^{+}$	$W^{-2}S^{+}$	$W^{-3}S^{+}$	$W^{+}S^{-2}$	$W^{+}S^{-3}$	$W^{-}S^{-}$
Dec 06 inctercept	1.69	1.75	1.73	1.71	1.74	1.77
Jun 07 intercept	1.94	1.98	2.04	1.93	2.05	2.04
***t*1 (Dec 06 v Jun 07)**	-2.619	-2.566	-3.338	-2.255	-3.214	-2.609
***p*1 (Dec 06 v Jun 07)**	**0.010**	**0.011**	**0.001**	**0.026**	**0.002**	**0.010**
***t*2 (within Jun 07)**	n/a	-0.431	-0.935	0.061	-1.044	-0.904
***p*2 (within Jun 07)**	n/a	0.667	0.351	0.952	0.298	0.368
Dec 06 slope	-0.27	-0.29	-0.26	-0.25	-0.26	-0.26
Jun 07 slope	-0.27	-0.25	-0.25	-0.22	-0.26	-0.21
***t*3 (Dec 06 v Jun 07)**	-0.046	-0.747	-0.234	-0.731	-0.037	-0.866
***p*3 (Dec 06 v Jun 07)**	0.963	0.456	0.815	0.466	0.970	0.388
***t*4 (within Jun 07)**	n/a	-0.227	-0.250	-0.881	-0.131	-0.893
***p*4 (within Jun 07)**	n/a	0.821	0.803	0.380	0.896	0.374

Table 2. Individual size distribution regression line intercepts, *a*, and slopes, *b*, for the six experimental treatments in December 06, i.e. during the community assembly phase of the experiment, and in June 07, i.e. during the interaction strength manipulation phase of the experiment. $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed. *t*1 (and *t*3) are the *t*-statistics comparing the intercept (and slope) of the individual size distribution for each treatment in December 06 to June 07. *p*1 (and *p*3) are the associated *p*-values. *t*2 (and *t*4) are the *t*-statistics comparing the intercept (and slope) of the individual size distribution for each treatment to the intact community, i.e. $W^{+}S^{+}$, in June 07. *p*2 (and *p*4) are the associated *p*-values.

	$W^{+}S^{+}$	$W^{-2}S^{+}$	$W^{-3}S^{+}$	$W^{+}S^{-2}$	$W^{+}S^{-3}$	$W^{-}S^{-}$
Dec 06 intercept	2.61	2.55	2.56	2.59	2.59	2.56
Jun 07 intercept	2.79	2.90	2.96	2.82	2.93	2.95
***t*1 (Dec 06 v Jun 07)**	-1.986	-3.590	-4.341	-2.458	-3.904	-4.196
***p*1 (Dec 06 v Jun 07)**	**0.050**	**<0.001**	**<0.001**	**0.016**	**<0.001**	**<0.001**
***t*2 (within Jun 07)**	n/a	-1.084	-1.698	-0.302	-1.410	-1.639
***p*2 (within Jun 07)**	n/a	0.281	0.092	0.763	0.161	0.104
Dec 06 slope	-0.47	-0.47	-0.46	-0.47	-0.45	-0.43
Jun 07 slope	-0.46	-0.42	-0.45	-0.43	-0.41	-0.40
***t*3 (Dec 06 v Jun 07)**	-0.249	-1.146	-0.208	-0.924	-1.001	-0.741
***p*3 (Dec 06 v Jun 07)**	0.804	0.254	0.836	0.358	0.319	0.460
***t*4 (within Jun 07)**	n/a	-0.982	-0.312	-0.810	-1.303	-1.417
***p*4 (within Jun 07)**	n/a	0.328	0.756	0.420	0.195	0.159

treatment in December 06 to those in June 07. There were no significant differences between the slopes of the LSDR and ISD, for all experimental treatments, before and after the interaction strength manipulations. There were also no significant differences between the intercepts or slopes of the LSDR and ISD for the intact community and all other experimental treatments in June 07, i.e. after the experimental manipulations were initiated (see Figure 2 for the LSDR and Figure 3 for the ISD for each treatment in December 06 and June 07).

Lastly, there were significant effects of the interaction strength manipulations on the species turnover of the mesocosm communities between December 06 and June 07. Here, the removal of two strong (t = 2.425; p = 0.026), three strong (t = 2.188; p = 0.042), and three weak (t = 2.612; p = 0.018) interactors led to significantly higher species turnover than in the intact community (Figure 4).

Discussion:

There is clear evidence for a community-level trophic cascade as a result of the interaction strength manipulations. We observed no differences in primary or secondary production between the treatments during the community assembly phase. This implies that the ecosystem functioning of the mesocosm communities that developed in this phase of the experiment were largely similar to each other. The removal of the two and three strongest interactors from this core community led to cascading effects on primary and secondary production. Here, the biomass density of benthic invertebrates increased as they were released from intensive predation pressure by the strong interactors (Figure 1*A*). Given that many of the benthic invertebrates are primary consumers (O'Gorman & Emmerson 2009), this led to a knock-on effect on primary production, as they grazed heavily on the primary producers in the community (Figure 1*B*). The removal of two weak interactors also led to a significant increase in secondary production, but with no cascading effect on the primary productivity of the corresponding mesocosm communities. We attribute this inconsistent response to the loss of weak interactors releasing different species from predation pressure. Population data indicates that the filter feeding sponge, *Clathrina coriacea*, and sea squirt, *Ascidiella aspersa*, as well as the predatory brittle star, *Ophiura ophiura*, may be driving the increased secondary production in this treatment. Such species are unlikely to impact greatly on primary production. Interestingly, *C. coriacea* and *A. aspersa* are two of the most common species found

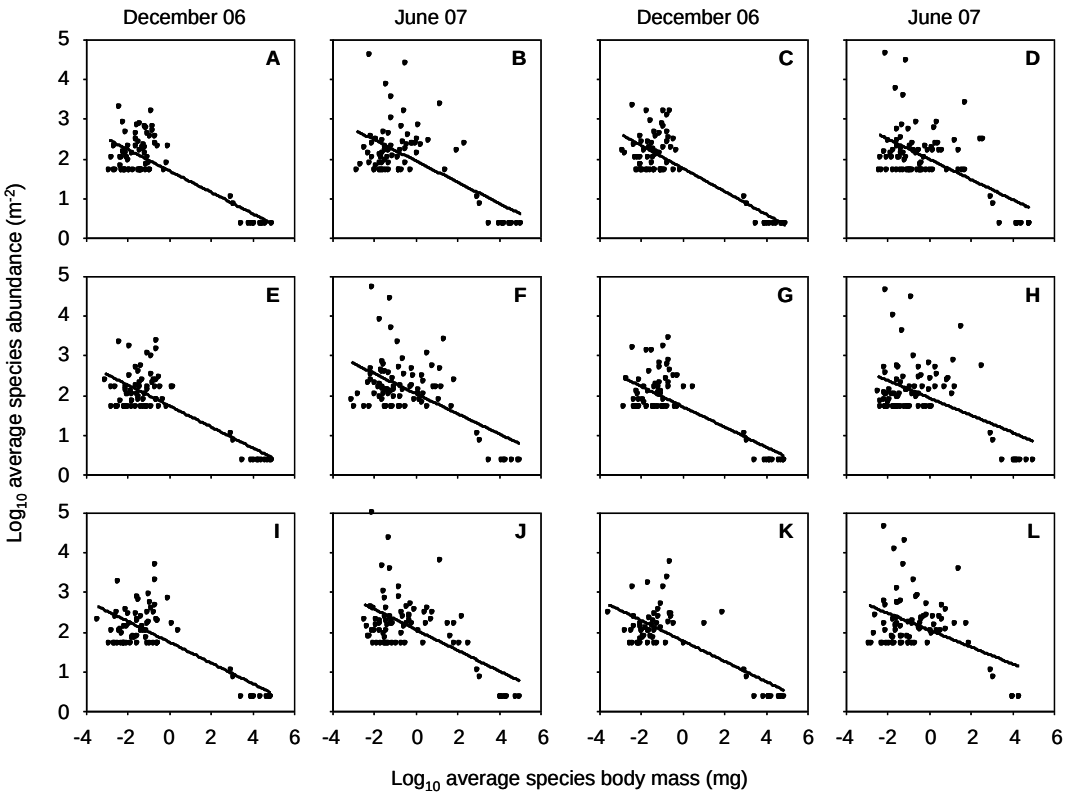

Figure 2. Comparison of average species body mass-abundance relationships between December 06 (community assembly phase of the experiment) and June 07 (manipulation phase of the experiment) for the six experimental treatments: (*A-B*) intact community, i.e. $W^{+}S^{+}$; (C-D) two weakest interactors removed, i.e. $W^{-2}S^{+}$; (*E-F*) three weakest interactors removed, i.e. $W^{-3}S^{+}$; (*G-H*) two strongest interactors removed, i.e. $W^{+}S^{-2}$; (*I-J*) three strongest interactors removed, i.e. $W^{+}S^{-3}$; (*K-L*) all strong and weak interactors removed, i.e. $W^{-}S^{-}$. Regression line slopes and intercepts can be found in Table 1.

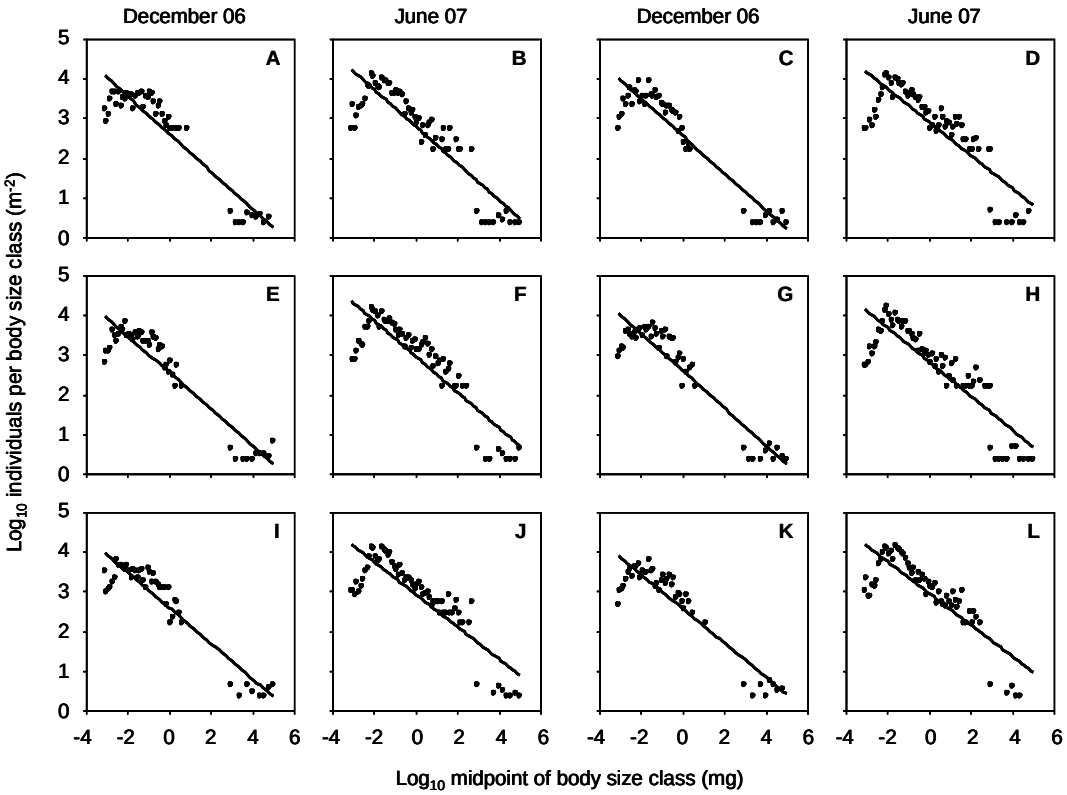

Figure 3. Comparison of individual size distributions between December 06 (community assembly phase of the experiment) and June 07 (manipulation phase of the experiment) for the six experimental treatments: (*A-B*) intact community, i.e. $W^{+}S^{+}$; (*C-D*) two weakest interactors removed, i.e. $W^{-2}S^{+}$; (*E-F*) three weakest interactors removed, i.e. $W^{-3}S^{+}$; (*G-H*) two strongest interactors removed, i.e. $W^{+}S^{-2}$; (*I-J*) three strongest interactors removed, i.e. $W^{+}S^{-3}$; (*K-L*) all strong and weak interactors removed, i.e. $W^{-}S^{-}$. Regression line slopes and intercepts can be found in Table 2.

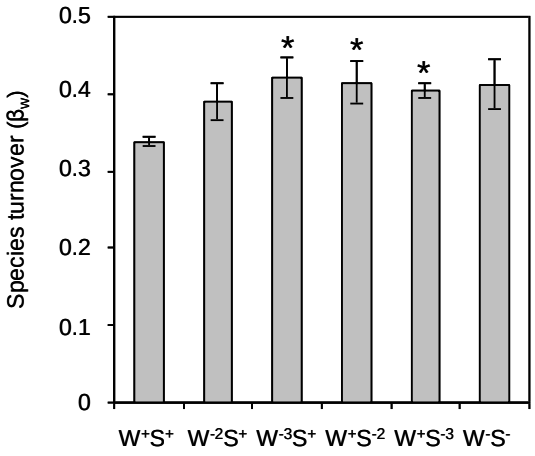

Figure 4. Species turnover (treatment means ± 1 SE) in the mesocosm communities between December 06, i.e. during the community assembly phase, and June 07, i.e. during the interaction strength manipulation phase of the experiment. Species turnover is measured using Whittaker's index of beta diversity, β_w. Treatments that are significantly different from the intact community are indicated by asterisks ($p < 0.05$).

settling on the inside mesh surface of the cages. Two of the weak interactors that were removed from these treatments, *N. puber* and *C. maenas*, are crabs that are adept at climbing the cage and removing these species. Thus, loss of these two crab species appears to make biofouling more prominent in these treatments, leading to a concurrent increase in secondary production.

The slope of the relationship between body mass and abundance appears to be extremely robust to the observed community-level trophic cascade, whether we measure the average body mass of each species, or ignore species identity and group individuals into body mass classes. We found no significant change in the slopes of the LSDR and ISD for each treatment after our targeted species removals from the core community, either by examining the same treatment before the manipulation took place (*p*3 in Tables 1 and 2), or by comparing it to the intact community treatment for the same season (*p*4 in Tables 1 and 2). Marquet *et al.* (1990) suggested that body mass-abundance slopes are maintained in the face of a perturbation by a combination of density compensation and body mass shifts. There is some evidence for this mechanism in our study, with significantly higher intercepts for both the LSDR and ISD after the manipulations in June 07, compared to the community assembly phase in December 06 (*p*1 in Tables 1 and 2). This suggests a shift towards larger body mass to compensate for any increases in benthic invertebrate density as a result of the community-level trophic cascade (Figure 1).

As we can see from the trophic cascade in Figure 1, however, the biomass density of benthic invertebrates increased across all treatments between December 06 and June 07, and not just the treatments that experienced the cascade (i.e. two and three strongest interactors removed). This implies that the shift towards larger body mass and higher density may be a seasonal characteristic, due to higher productivity in the summer months (Uehlinger 2006). This is evident from the high levels of primary production (Figure 1*B*), due to longer daylight hours and higher nutrient concentrations in the summer time (Letelier *et al.* 1993; Field *et al.* 1998), which in turn sustained an enhanced level of secondary production (Figure 1*A*). Further evidence supporting a seasonal effect of the increase in the intercepts of the LSDR and ISD can be found from the comparison between the intact community and all other treatments in June 07. Here, there were no significant differences between the intercepts of the LSDR or ISD (*p*2 in Tables 1 and 2). If the increase in the intercept was produced by the trophic cascade, we would expect the intercept of the intact

community in June 07 to be much lower than the other treatments, but this was not the case.

The examination of species turnover in the mesocosm communities between December 06 and June 07 appears to offer a more definitive explanation for how the body mass-abundance relationships are maintained in spite of the trophic cascade. There was a natural background level of species turnover from December 06 to June 07, most likely due to changes in food availability between winter and summer months (Stephens *et al.* 1967; Danovaro & Fabiano 1997) and the seasonal periodicity of the life-cycles of individual species (Allan 1976; Hull 1997). The change in species composition was lowest in the intact community (Figure 4) and most likely reflects this natural seasonal turnover of species. The removal of manipulated species from the core community of all other mesocosms led to an increase in species turnover, which was significantly higher when two or three strong interactors or three weak interactors were removed. Given that the community-level trophic cascade occurred in the absence of the two and three strongest interactors, it may be inferred that the high species turnover in these communities is a controlling mechanism, which maintains the relationship between the body mass and abundance of individuals and local populations. Here, as certain individuals or species increase in body mass and/or abundance, a niche is created for optimal energy exploitation by small-bodied organisms. This niche may then be filled from the regional pool of species (Lough Hyne marine reserve in the current study). In this manner, the composition of local communities may change, but the size structuring and density scaling should remain constant, due to the important implications of these mechanisms for the maintenance of energy within the food web (Damuth 1981, 1987; Brown & Gillooly 2003).

The slopes and intercepts of the body mass-abundance relationships vary depending on the method used to estimate them. When species identity is ignored and individuals are grouped into body mass classes (ISD), the slope of the body mass-abundance relationship is steeper (more negative) and the intercept is higher than when average species body mass and abundance (LSDR) are considered. This result is similar to that observed by Jennings *et al.* (2007) and highlights the importance of considering both approaches in studies that compare body mass-abundance relationships. It should also be noted that the slopes of the body mass-abundance relationships in this study are much shallower (LSDR = -0.21 to -0.27;

ISD = -0.28 to -0.32) than predicted by theory, i.e. -0.75 (Damuth 1981; McMahon & Bonner 1983; Brown 1995; Enquist *et al.* 1998) or -1 (Borgmann 1987; Griffiths 1992, 1998). The use of experimental mesocosms resulted in the development of local communities, with species drawn from the regional pool within the greater Lough Hyne marine reserve. Blackburn and Gaston (1997) demonstrated that body mass-abundance relationships based on data from local populations (and not global scales) had an average slope of -0.245 (± 0.050 SE). This is a close approximation of the observed mesocosm community slopes.

Since body mass clearly does not scale with abundance as $M^{-3/4}$ in the mesocosm communities, this raises a question mark over the existence of energy equivalence in this study. Blackburn and Gaston (1999) argue that the evidence for energy equivalence in nature is weak (see Blackburn & Gaston 1997; Cyr *et al.* 1997) and that the negative relationship between body mass and abundance is a consequence of the distribution of biomass. Given the link between biomass pyramids, patterns of interaction strength, and the stability of natural systems (Neutel *et al.* 2002), this may indicate that body mass-abundance patterns are inextricably connected to the persistence of communities in nature. Large, rare predators typically feed on small, abundant prey (Warren & Lawton 1987; Cohen *et al.* 1993b; Brose *et al.* 2006a) and so in theory, a consistent relationship between body mass and abundance should maintain the pattern of predator and prey body mass. This pattern has been shown to affect the arrangement of interaction strengths in real food webs (Jonsson & Ebenman 1998; Emmerson & Raffaelli 2004), which in turn determines stability (McCann *et al.* 1998; Neutel *et al.* 2002). Consequently, the robustness of the body mass-abundance relationship may maintain a stable pattern of interaction strength throughout the food web, in spite of our perturbations to interaction strength at high trophic levels.

Body mass-abundance relationships have previously been shown to be robust to major food web perturbations in marine (Marquet *et al.* 1990) and freshwater (Jonsson *et al.* 2005) systems. These studies demonstrate that the slope of the average species body mass-abundance relationship does not change as a result of the perturbation, but do not examine the slope of the ISD (although the pattern of the ISD is shown to be qualitatively unchanged in Jonsson *et al.* 2005). Here, we have demonstrated that body mass-abundance relationships are robust to cascading effects in marine food webs, whether we consider organisms at the level of individuals or

species. There is a suggestion that the intercept of these relationships may change to compensate for shifts in body mass and density, although this is most likely a seasonal effect. Longer term data are required to explicitly resolve this uncertainty. It is clear that changes in species composition observed after perturbations in other studies (Marquet *et al.* 1990; Jonsson *et al.* 2005) are consistent with the manipulated mesocosm communities. Furthermore, species turnover has been shown here to be higher than expected after a major perturbation, indicating that this is a primary mechanism for maintaining the relationship between body mass and abundance. This in turn provides a stabilising structure for the maintenance of natural communities.

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