

Macroecological patterns and niche structure in a new marine food web

Research Article

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Abstract: The integration of detailed information on feeding interactions with measures of abundance and body mass of individuals provides a powerful platform for understanding ecosystem organisation. Metabolism and, by proxy, body mass constrain the flux, turnover and storage of energy and biomass in food webs. Here, we present the first food web data for Lough Hyne, a species rich Irish Sea Lough. Through the application of individual- and size-based analysis of the abundance-body mass relationship, we tested predictions derived from the metabolic theory of ecology. We found that individual body mass constrained the flux of biomass and determined its distribution within the food web. Body mass was also an important determinant of diet width and niche overlap, and predator diets were nested hierarchically, such that diet width increased with body mass. We applied a novel measure of predator-prey biomass flux which revealed that most interactions in Lough Hyne were weak, whereas only a few were strong. Further, the patterning of interaction strength between prey sharing a common predator revealed that strong interactions were nearly always coupled with weak interactions. Our findings illustrate that important insights into the organisation, structure and stability of ecosystems can be achieved through the theoretical exploration of detailed empirical data.

Keywords: *Biomass spectra • Body size • Ecological networks • Food webs • Interaction strength • Marine ecosystems • Metabolic theory • Numerical abundance • Stability*

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1. Introduction

Ecological networks provide “road maps” of competitive, mutualistic or antagonistic species interactions within ecosystems (*sensu* Paine [1]). Here we focus on antagonistic trophic interactions documented for an assemblage of predators and prey in a previously undescribed marine food web. Food webs are essentially flow diagrams [2], with vertices (nodes) representing trophic elements (usually species, or other taxonomic units) and connecting arrows depicting fluxes (e.g. energy,

biomass, individuals) from resources to consumers. They also provide a framework for understanding how communities are structured, how they function and how they may respond to environmental change [3–6]. The architecture of trophic relations between species is inextricably linked to the stability and persistence of natural communities [7–9]. Stability can be broadly defined as the ability of a system to return to equilibrium after a perturbation [5, 10]. Understanding the behaviour of dynamical systems is now a major challenge in the context of the current biodiversity crisis. In particular,

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it is the specific structural configuration of weak and strong interactions between species which determine the stability of the community [11–14].

Since the ideas of Elton [15] and other early ecologists, one of the central questions in ecology has been: is food web structure idiosyncratic, or are general patterns evident across ecosystems? If the latter holds, this suggests that general ecological and evolutionary laws are operating in nature, as suggested by Darwin [16]. In support of this perspective, an increasing body of recent evidence alludes to remarkable similarities in the organisation of ecosystems [4–6]. One commonly observed pattern is that food webs have “small-world” properties, such that the shortest path connecting any two species is typically less than two or three links [6, 17, 18]. Recent advances in ecological theory and the proliferation of new, highly resolved, quantitative food webs have revealed other recurrent patterns, such as the allometric scaling of abundance (N) with body size (M) in “trivariate” networks [2, 19, 20]. The metabolic theory of ecology predicts such MN scaling at both macroecological and local scales within food webs and provides a mechanistic explanation: essentially, the abundance of organisms of a given size within an ecosystem is ultimately dependent on the energy available to them [21]. The availability of energy to an individual depends on its size, and decreases as we move from basal resources to predators due to the inefficiency of energy transfer across trophic links [21–26]. Ultimately, metabolism should constrain the flux, turnover and storage of energy in the food web.

To date, most studies have used the mean body mass of a species as the measure of M and this is often then used to predict its abundance (but see [25]). However, the predictions developed from metabolic theory relate to the energy available to individuals of a given body mass, not to the average body mass of a species; this latter measure ignores the many life history stages and body sizes that an individual passes through during ontogeny. The abundance of different size classes and the number of prey items available to an individual will change markedly during its life history. To overcome this problem we have used an individual- and size-based approach to analyse the abundance-body mass relationship and food web structure.

Here we present the first food web data for Lough Hyne, a species rich Irish Sea Lough that was designated Europe’s first marine nature reserve in 1981. The Lough is a relatively isolated and physically benign environment, sheltered from natural and anthropogenic disturbance. We used quantitative food web data, including measures of individual body mass, abundance and feeding interactions, to test the abundance-body

mass scaling relationship predicted by metabolic theory (*sensu* Brown *et al.* [21]). We also analysed how body size affected food web topology; in particular, how it constrained predators’ diets and trophic niche overlap. Finally, we derived an empirical measure of population level biomass flux and described how it was distributed within the food web. Specifically, we analysed the pairwise biomass flux disparity between prey that share the same predator to test whether weak interactions are coupled with strong interactions in real communities [11].

2. Experimental Procedures

2.1. Theoretical Framework

2.1.1. Relationship between body mass and abundance

We use measures of individual body mass and abundance derived from an assemblage of benthic predatory fish and their invertebrate prey in Lough Hyne (see supplementary methods) to test for allometric scaling relationships [21]. Metabolic theory predicts that, for assemblages of individuals that share a common energy source, numerical abundance per unit area typically scales with body mass as $M^{-3/4}$. Because metabolic rate, defined as the rate at which organisms uptake, transform, and allocate energy, scales with body mass as $M^{3/4}$, then the rate of energy use per unit area is invariant with respect to body size (*i.e.* M^0). This prediction has been termed the energetic equivalence hypothesis [27].

In reality, however, food webs are comprised of individuals that feed at different trophic levels and obtain their energy from different sources. In addition, aquatic food webs tend to be strongly size structured [24, 25], and size-dependent life-history omnivory and cannibalism are prevalent in both marine and freshwaters [28, 29]. Many fish increase their body mass by as much as five orders of magnitude during ontogeny, literally eating their way up the food chain [30]. In keeping with metabolic theory and several recent studies in aquatic food webs we adopt a size-based rather than species-based analysis of the abundance-body mass relationship [25, 31, 32].

Energy availability to higher trophic levels is constrained by the inefficiency of energy transfer across trophic links, often assumed to be about 10% [21, 22, 24–26]. The loss of energy between trophic levels results from both intrinsic metabolic losses at the level of the resource (*i.e.* thermodynamic losses from metabolic reactions) and inefficiencies in the conversion of resource biomass to consumer biomass. In size-structured food webs, body mass increases with trophic level, such that larger predators usually consume smaller prey

[33,34]. The reduction in available energy as body mass increases is dependent on (a) the average ecological efficiency (*i.e.* the proportion of prey production converted to predator production) across trophic links and (b) the average predator to prey body mass ratio in the food web [21,25,26]. Because the abundance of larger organisms is constrained by energy loss across trophic links, metabolic theory predicts a steeper scaling of abundance with body mass than the commonly observed $M^{-3/4}$ [21,26]. Thus, the scaling of abundance with body mass in a community in which individuals obtain energy from different sources is given by

$$N \propto M^{\left[\frac{\log(a)}{\log(b)}\right]^{-3/4}} \quad (1)$$

where a is the mean efficiency of energy transfer across trophic links and b is the average ratio of predator body mass to prey body mass (see supplementary methods for a full derivation of the theory) [25]. Because we lack sufficient empirical evidence to estimate the average efficiency of energy transfer in the Lough Hyne food web we use the classical efficiency of 10% between trophic levels reported by Lindeman [21,22,24-26]. Similarly the scaling of biomass abundance ($B = MN$) with body mass is given by

$$B \propto M^{\left[\frac{\log(a)}{\log(b)}\right]^{+1/4}} \quad (2)$$

where a and b are as described above (see supplementary methods for a full derivation of the theory) [25]. Thus, if the efficiency of energy transfer between trophic levels is 10% [22] and the mean ratio of predator : prey body mass is 10^4 , then the scaling exponent of numerical abundance with body mass will be $N \propto M^{-1}$ [21,26].

2.1.2. Predator overlap graphs

A predator overlap graph (links join predators that share at least one prey item) was constructed from the food web (see supplementary methods). Diet overlap between predators was also calculated using Pianka's Niche Overlap Index

$$o_{jk} = o_{kj} = \frac{\sum_i P_{ij} P_{ik}}{\sqrt{\sum_i P_{ij}^2 \sum_i P_{ik}^2}} \quad (3)$$

where P_{ij} and P_{ik} are the proportions of the j^{th} resource used by the j^{th} and k^{th} species, respectively [35]. A single measure of diet overlap between zero (no overlap) and one (complete overlap) was generated for each pairwise combination of predators. Diet overlap as a function of the pairwise predator-predator body mass difference (calculated as: $\log_{10 \text{ mass predator } a} - \log_{10 \text{ mass predator } b}$) was analysed to assess the potential for body size constraints on resource partitioning.

2.1.3. Prey overlap and the patterning of interaction strength

We derived an empirical measure of biomass flux between a predator and its prey to investigate the distribution of relative interaction strength within the food web and its specific configurations between pairs of prey species that share the same predator. This measure considers the effect of a population of a predator j of a given biomass on the biomass of its prey i . The measure we used is the estimated proportional biomass of prey i in the diet of predator j 's total biomass consumption (across its entire prey range) scaled to the standing population biomass of predator j .

$$a_{ij} = \frac{B_i}{\sum_{i=1}^n B_{ij}} B_j \quad (4)$$

where a_{ij} is the biomass flux between predator j and prey i , B_i is the population biomass of prey species i , $\sum B_{ij}$ is the total biomass consumption of predator j across all prey i , n is the number of prey of predator j , and B_j is the population biomass of predator j . The biomass of prey items in the diet of the predators and the estimates of total predator biomass consumption (across all prey species) were estimated from quantitative gut contents analysis (see supplementary methods) and the quantification of prey abundance and biomass (see supplementary methods).

Interaction strengths were calculated for all possible food web "modules" in which two prey share a common predator. The interaction strength disparity for each configuration was calculated as

$$ID(ij, kj) = \frac{\max(a_{ij}, a_{kj}) - \min(a_{ij}, a_{kj})}{\max(a_{ij}, a_{kj})} \quad (5)$$

where $ID(ij, kj)$ is the interaction strength disparity between prey i and k sharing predator j , and a_{ij} and a_{kj} are the interaction strengths of predator j on prey i and k respectively. The interaction strength disparity between two prey sharing a common predator gives information as to the degree of interaction strength asymmetry, an important criterion in determining the stability of food web modules [11]. We then used the following information theoretic metric [36] to assess the interaction strength disparity of the whole food web.

$$E(web) = \frac{1}{\sum_{id} P_{id}^2} \cdot \frac{1}{ID} \quad (6)$$

where $E(web)$ is a measure of the evenness of interaction strength disparity for the whole web (between 0 and 1) and provides a single informative measure of the way prey interact with shared predators, but also allows comparisons on the degree of disparity across networks. P_{id} is the proportion of all interaction strength disparities

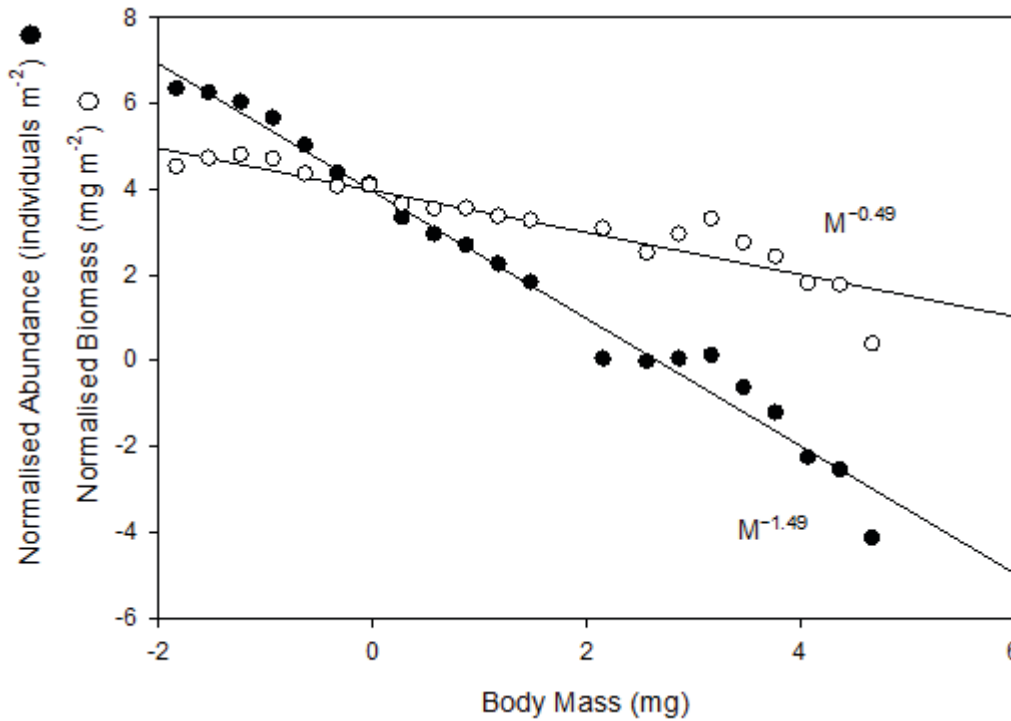


Figure 1. Normalised abundance- and biomass-body mass relationships for the Lough Hyne food web. Normalised abundance scaled with body mass as $\log(N) = 3.96 - 1.49 \log(M)$, (least squares regression of log transformed data $r^2 = 0.98$, $P < 0.01$). Normalised biomass scaled with body mass as $\log(B) = 3.97 - 0.49 \log(M)$, (least squares regression of log transformed data $r^2 = 0.87$, $P < 0.01$). Individuals have been grouped into body mass classes defined on a \log_2 integer scale. The midpoint of each interval was log transformed and used in the regression.

ID ($n = 459$) of a given magnitude. Interaction strength disparities in all sub web configurations in which two prey share a common predator were assigned to a size class (of 0.025 width; $n = 20$) for the calculation of P_{id} .

3. Results

For the predator-prey assemblage, normalised numerical abundance N^* scaled with body mass M approximately as $M^{-1.5}$ (Figure 1), and normalised biomass abundance B^* scaled as $M^{0.5}$ (Figure 1). To obtain the true relationship between numerical abundance N and biomass abundance B with M we de-normalised N^* and B^* , following the theory of size spectra outlined in [31] (see supplementary methods). After de-normalisation, N scaled allometrically with body mass M as $M^{0.5}$, and B scaled with M as $M^{0.5}$. These scalings differed significantly (t -test for difference from slope of -1, $t = 10.84$ d.f. = 19 $P < 0.01$; t -test for difference from slope of 0, $t = 10.49$ d.f. = 19 $P < 0.01$) from the expected scalings predicted from metabolic theory. If the empirically observed predator-prey body mass ratio ($M/M_i = 23,074$) and the classical ecological efficiency of 10% [22] are substituted into equation (1), we obtain the predicted scaling of $N \sim M^{-1}$, and by using them in equation (2) we get $B \sim M^0$.

Small predators generally had narrower diets, both numerically and in terms of the prey body mass spectrum exploited. As predator body mass increased, larger prey individuals and species were added to the diet sequentially (Figure 2). In addition, the degree of diet overlap between predators was determined by the magnitude of the disparity in their body masses. Figure 3 illustrates that the more similar two predators were in terms of their body mass, the more prey species they shared. Pianka's index of niche overlap was negatively correlated with pair-wise differences in predator body mass ($r = -0.59$, $P < 0.05$) (Figure 3), as previously reported in a freshwater food web [29].

Most predator-prey interactions were weak, whilst very few were strong (Figure 4), so that predators were likely to have little effect on prey population biomass. Rare, strong interactions usually occurred between predators and prey with high biomass abundance: the prey involved in these feeding links constituted the main energy source for the larger predators.

Pairs of prey species consumed by a common predator differed strongly in their relative contribution to predator total consumption. One member of the pair tended to be a strong interactor, whilst the other prey species typically interacted weakly, resulting in a high degree of interaction strength disparity (*i.e.* asymmetry)

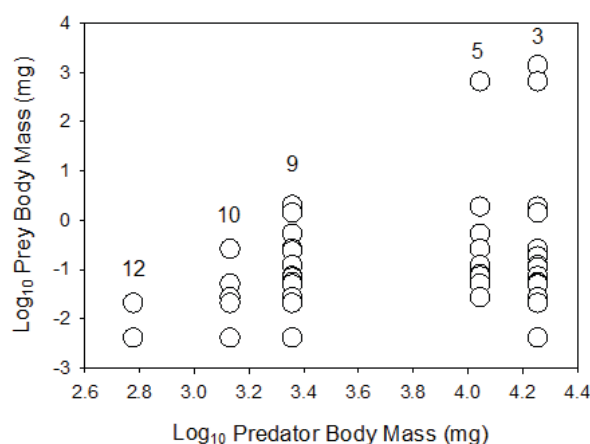


Figure 2. Relationship between predator body mass and prey body mass. Small predators tend to have narrow diets and consume smaller prey; larger predators sequentially add larger prey to their diet and thus have a wider diet width. Numbers correspond to species identification numbers see Appendix II.

within these three-species modules (Figures 5 and 6). These patterns were consistent at both the species (Figure 5 inset) and food web level (Figures 5 and 6). Most interactions were highly “asymmetric” whereas very few were symmetric, as revealed by the low evenness of interaction strength disparity within the food web as a whole ($E(web) = 0.0083$).

4. Discussion

The integration of detailed information on trophic relations among species with measures of abundance and body mass of individuals provides a potentially powerful platform for understanding ecosystem organization [2,25,26]. Metabolism, which is ultimately determined by body mass and temperature, is a promising candidate for simplifying ecosystem complexity [21,37]. Mechanistic-based theories, that build upon the first principles of metabolism and thermodynamics, and which use detailed empirical data, may provide us with a deeper understanding of the factors constraining food web architecture. To test such theories we should use the appropriate level of biological organization, and because metabolic theory is based at the individual level, predicted scalings of abundance or biomass with body size should use individual, not species-averaged data. Here we have shown how individual body mass constrains the flux of energy and the distribution of biomass within an ecosystem. Additionally, we have shown that body mass sets the boundaries of resource use at the species level, by partitioning and organising species’ niches within a food web. Finally, through the integration of empirical data with metabolic theory we

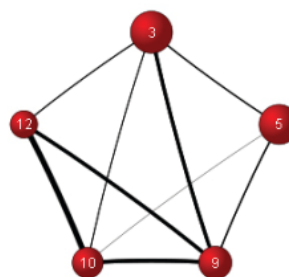


Figure 3. Predator overlap graph for the guild of benthic predators. Lines connect pairs of predators that share at least one prey species in their diets. The thickness of the lines connecting predators represents the degree of niche overlap. The diameter of the nodes is scaled by predator body mass (log scale). The diet overlap of predators of similar body mass is greater than that of predators differing in their body mass.

can estimate the distribution and patterning of biomass fluxes within the food web, which have important implications for its stability.

For the Lough Hyne assemblage described here both abundance N and biomass B scale with body mass M . These allometric scaling relationships across two trophic levels suggest that trophic interactions play a fundamental role in shaping the distribution of biomass within the food web. In the absence of predation we believe such scalings would be less pronounced. The amount of biomass available to higher trophic levels is limited by both the energy available to this particular level (bottom-up forces) and the consumption from higher trophic levels (top-down forces).

However, the allometric scalings observed for both N and B were shallower than the theoretical predictions derived from metabolic theory [21,26]. Which additional factors not considered by this theory might be responsible? Competition within a single trophic level may favour the dominance of large organisms; reducing the exponent of the allometric relationships. However, the relative role of predation *versus* competition in structuring communities is an unresolved question in ecology. In some cases, particularly benthic communities the distribution of biomass across the body mass spectrum is driven principally by competition, not predation (e.g. [38]). The Lough Hyne assemblage described in the present study constitutes a local size-density relationship (LSDR), which typically show shallow scalings of N and B with M when all population densities are measured at the same location [39]. This is because at local-scales size biases in resource acquisition driven by size based asymmetries in competition or differences in the availability of resources to organisms of different body sizes may override the importance of energy loss between trophic levels.

Body mass was an important determinant of diet width

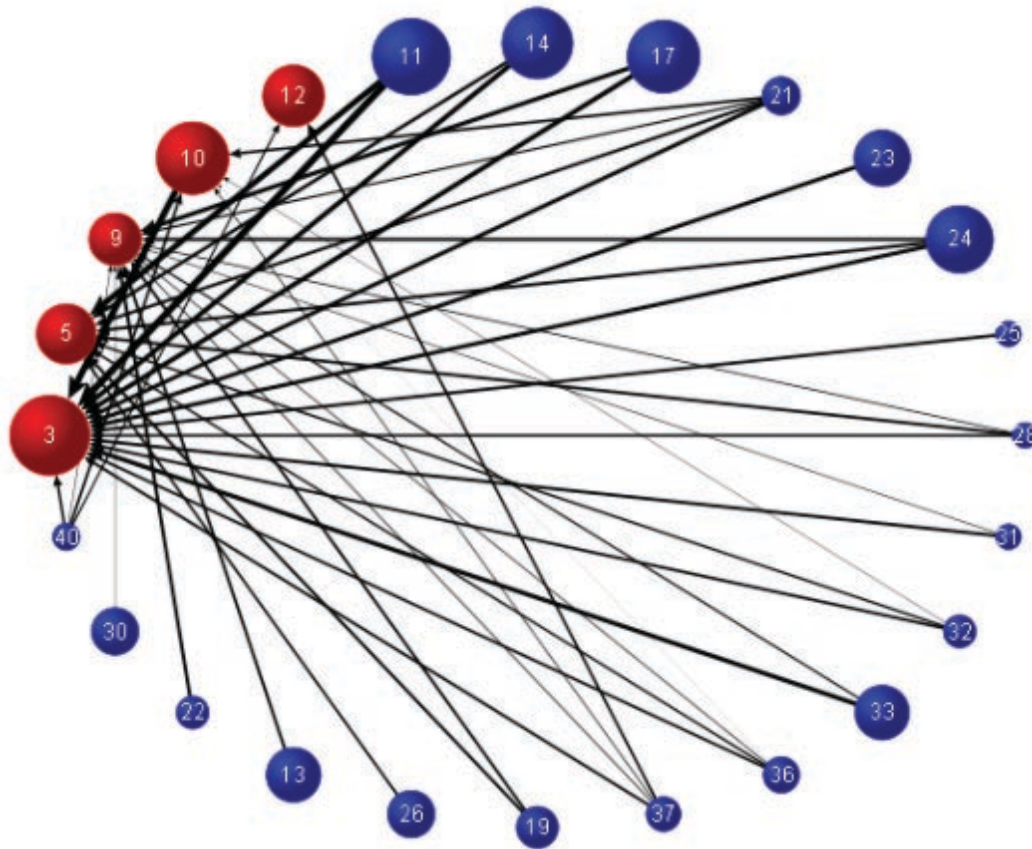


Figure 4. The quantitative food web of the sublittoral zone of Lough Hyne. Arrows join predators (red nodes) with their prey (blue nodes). The width of the arrow is determined by the strength of the interaction (see text for details). The size of the nodes are determined by the biomass abundance of the species.

and niche overlap within the guild of benthic predatory fish in Lough Hyne. The largest predator, *Gobius niger* Linnaeus, had the widest diet both in terms of the range of prey body mass consumed and the number of species taken. Conversely, the smallest predator, *Pomatoschistus pictus* Malm, had the narrowest diet. The feeding niches within this guild were organised hierarchically in relation to predator body mass, whereby the diet of the smallest species formed a subset of the next largest species, and its diet a subset of the next largest species, and so on. Nested interactions appear to be a common feature of community organisation across a wide range of ecosystems and interaction types [6,34,40]. For instance, dietary nestedness is a common feature observed in mutualistic networks of plants and pollinators and of plants and seed-dispersers [6,40], in terrestrial food webs comprising predators, pathogens, and parasitoids [41], and in freshwater food webs [29]. Within the Lough Hyne food web, asymmetries in resource use between predators that were driven by body mass meant that large predators exploited a broader size range of prey than did smaller predators

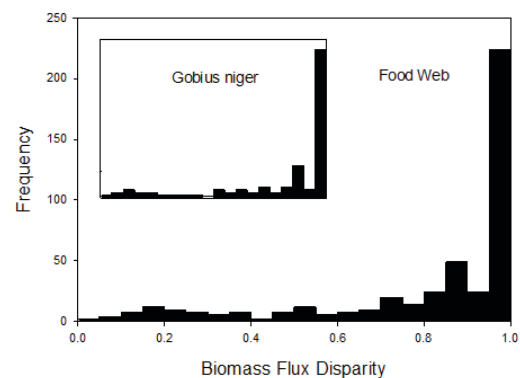


Figure 5. The distribution of interaction strength disparity between prey that share a common predator. When two prey are consumed by the same predator, one prey generally has a strong interaction whereas the other exhibits a weak interaction. Such “asymmetric” patterning on interaction strength results in a positively skewed distribution of interaction strength disparity. These patterns are robust when analysing the food web as whole and individual predators. Inset graph corresponds to predator 3, *Gobius niger*.

resulting in a hierarchical trophic structure, a pattern consistent with other aquatic systems (e.g. [29]). The differences in the prey size spectrum exploited by the

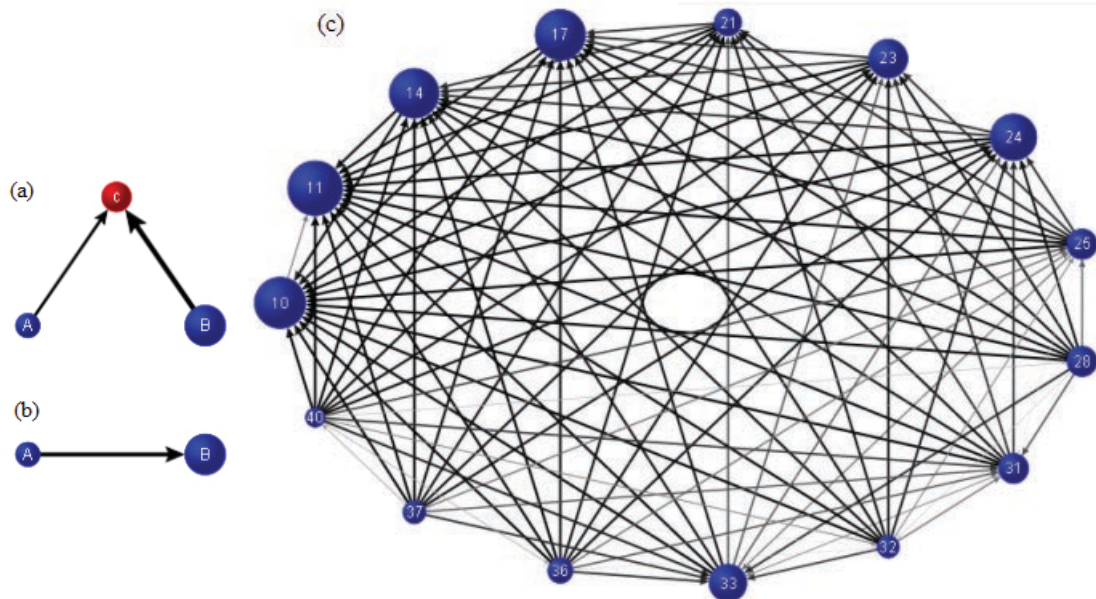


Figure 6. Quantitative prey overlap graph for *Gobius niger*. (a) shows a simple configuration taken from the food web in which prey A and B share a common predator, C. Prey B interacts strongly while A interacts weakly with predator C. This biomass flux “disparity” translates in (b) to the thickness of the line connecting A and B which are consumed by C. The direction of the arrow in (b) points towards the strongly interacting prey species, in this case B. We carried out this analysis for all prey that share a particular predator: in the case of (c) predator 3, *Gobius niger*. The thickness and darkness of the lines in (c) represent the degree of biomass flux disparity between prey consumed by predator 3. As in (b) the direction of the arrow points towards the strongly interacting prey.

predators had strong influences on dietary overlap, which was greatest between predators of similar body mass. Importantly, this suggests that resource partitioning can be collapsed into a single dimension determined by the prey body mass spectrum, as suggested by Woodward and Warren [34].

Interaction strength was influenced strongly by the biomass abundance (*NM*) of both predators and prey. The strongest interactions in the food web occurred between prey and predators of high population biomass. Prey of high biomass-abundance were likely to contribute significantly to the diet of a given predator. On the other hand, predators with a high population biomass had the potential to deplete the biomass of their prey significantly. The distribution of biomass fluxes within Lough Hyne was positively skewed, with a prevalence of weak interactions and very few strong interactions. These results are in agreement with other studies that have empirically documented interaction strengths in natural and experimental food webs [12,42–48]. Further, theoretical studies have demonstrated that a few strong interactions embedded within a network of many weak interactions can confer stability upon otherwise unstable, complex food webs [7,8,11–14,49]. This is because weak interactions help to dampen the potentially destabilising population oscillations caused by strong consumer-resource interactions [11].

To investigate this theory further we analysed the interaction strength disparity within food web modules

containing two prey species that share a predator. Within our food web all prey shared at least one predator - a product of the nested organisation of the assemblage. As such, there is considerable scope for “apparent competition” (*sensu* Holt [50]) to shape the prey assemblage. Such competition for enemy-free space might eventually lead to the local extirpation of prey species, due to the dynamical consequences of increased predator abundance in the presence of alternative prey [50]. This can induce powerful fluctuations in prey populations; *i.e.* unstable dynamics [51]. However, McCann *et al.* [11] have shown that when two prey share a common predator, if a strong predator-prey interaction is coupled with a weak interaction then apparent competition can be stabilising. This is because the predator effectively reduces the strength of the potentially oscillatory predator-prey interaction by partitioning its foraging effort to include a second prey species. In concordance with their theoretical result we found that across nearly all these three-species modules, strong interactions were paired with weak interactions (*i.e.* there is high asymmetry in interaction strengths). This phenomenon was consistent when considering each predator in isolation and also for the food web as a whole, suggesting that the coupling of weak with strong interactions might serve to stabilise each module, consequently reducing population fluctuations in the wider food web.

The simple allometric model used here to describe predator-prey biomass flux is a first approximation that does not consider many of the complex and often idiosyncratic behavioural traits of prey and predators. However, previous studies have shown that predator:prey body mass ratios explain around sixty per cent of the variation in biomass flux within a fully-quantified aquatic food web [52], supporting the use of minimal models which can be extrapolated across systems.

The documentation and quantification of the entire trophic network within the Lough is ongoing, and a study describing every representative habitat type will likely span many generations of scientists. We focused on a guild of important predatory fish and their prey in sublittoral habitats: thus the trophic interactions described here represent a subset of the wider community food web and a snapshot in time. The eventual inclusion of the pelagic food web will add further, alternative energy pathways [49] that could have important consequences for average ecological efficiency and predator-prey body mass ratios, especially as the size-structure of this portion of the community in aquatic systems often differs markedly from the benthic subsystem.

The search for, and recognition of, regularities in ecology is fundamental if we are to understand the feedbacks between environmental change, food web

architecture and ecosystem functioning at local and global scales: as the still limited catalogue of well-resolved food webs grows, we will become better placed to gain deeper insights into these questions. Systems such as Lough Hyne, with its strongly size-structured food web, represent important models for testing both established and newly-emerging ecological theories with detailed, individual-based empirical data.

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Appendix

The following supplemental information accompanies the article:

1. Supplementary Methods
2. Supplementary Data (Appendix I and Appendix II)

1. Supplementary Methods

1.1. Metabolic theory for the relationship between N and M (equation 1)

Metabolic theory predicts that whole-organism metabolic rate I (i.e. the power required to sustain an organism) is

$$I = i_0 M^{3/4} \quad (1)$$

where i_0 is a normalization constant independent of body mass M .

Brown and collaborators [21] show that in a food web, the loss of energy between trophic level 0 and 1 is characterized by the ecological efficiency a , as follows

$$a = \frac{i_1 N_1 M_1^{3/4}}{i_0 N_0 M_0^{3/4}} \quad (2)$$

where i_0 and i_1 are the normalization constants for field metabolic rate, and N_0 , N_1 , M_0 , and M_1 are the population densities and body masses at trophic levels 0 and 1, respectively. Assuming the system is in steady state and normalization constants do not differ between trophic levels, it results in

$$a = \frac{N_1 M_1^{3/4}}{N_0 M_0^{3/4}} \quad (3)$$

If we assume the mean individual body mass of species at the lowest trophic level is equal to M_0 , and b is the average ratio of predator body mass to prey body mass, then the dependence of trophic level on mass can be described by the equation

$$\tau = \log_b(M / M_0) = \frac{\log(M / M_0)}{\log(b)} \quad (4)$$

where $\tau = 0$ is the lowest trophic level for species with body mass M_0 . If we further assume that the total rate of metabolism at trophic level 0 is equal to $i_0 N_0 M_0^{3/4}$, and, for simplicity, that τ and a are constant across trophic levels, then the total rate of metabolism for organisms of mass M is

$$I_{tot} = i_0 N_0 M_0^{3/4} a^\tau \quad (5)$$

and following equation (1) the total number of individuals of given mass M is

$$N = \frac{I_{tot}}{I} = N_0 \left(\frac{M}{M_0} \right)^{\left[\frac{\log(a)}{\log(b)} \right] - 3/4} \quad (6)$$

and therefore, as N_0 and M_0 are constant, it follows that:

$$N \sim M^{\left[\frac{\log(a)}{\log(b)} \right] - 3/4} \quad (7)$$

1.2. Study Site

Lough Hyne (51°29'N, 9°18'W) is a small sea Lough in southwest Ireland, which is connected to the Atlantic Ocean by a 12 m wide channel that isolates the main water body from the exposure of the open coast. Because of the Lough's heterogeneous physical characteristics and its protected status, it is able to support a diverse suite of flora and fauna. Some of the Lough's taxa, such as the red mouthed goby *Gobius cruentatus*; Gmelin, and Couch's goby *Gobius couchii*; Miller and Eltwaill, otherwise reach their northern limits in Iberia [53]. The high biodiversity and relative isolation from natural and anthropogenic disturbance make Lough Hyne an ideal site to test ecological theory, and its entire shoreline has been divided into sectors which have been used to monitor temporal changes in community structure over many decades [53].

We focused on the sublittoral benthic food web (a subweb of the entire community food web), which is delimited within a complex three-dimensional habitat of extensive areas of coralline algal turf that cover boulder scree to a depth of approximately 3m. We characterised the trophic interactions of a guild of epibenthic fish (five common predators in the family Gobidae) upon the prey assemblage, which consisted primarily of detritivorous and scavenging amphipods, gastropods and polychaetes (Appendix II).

1.3. Quantification of macroinvertebrates

Six randomly placed Hess samples (25 cm x 25 cm quadrat; mesh aperture, 330µm; a Hess sampler is a standard sampling tool for aquatic ecosystems – it is essentially a mesh-enclosed quadrat used for taking quantitative benthic samples) were collected on 28th August 2005. Two sites were sampled to gain a representative sample of the sublittoral habitat: the southern shore (Renoufian sector S11), and a small bay adjacent to Whirlpool Cliff (Renoufian sector E15). Three replicate sample units were taken from each site at a depth of 1-2 m. Samples were returned to the on-site laboratory and preserved immediately in 4% formalin. Due to the high abundance of organisms and the large quantities of organic material, one subsample was taken from each sample-unit, by spreading the sample onto a 36 x 26 cm plastic tray and removing a sediment core with a surface area of 44.2 cm² and rescaling abundance estimates to numbers m⁻². All individuals were identified

to species where possible, counted and oven-dried to quantify body mass.

Body mass estimates for each species were derived from measurements of linear dimensions (usually body length) of 30 randomly-sampled individuals for which oven dry mass (ODM) was measured. Length-mass relationships were thus calculated for each species and subsequently length measurements were taken from all other individuals to predict ODM via linear regression (see Appendix I).

Abundance-body mass relationships were estimated from the individual perspective irrespective of species identity (after [25]) such that each individual (regardless of species) was assigned to a body mass class defined on a \log_2 integer scale, (e.g 0.015–0.03 mg; 0.03–0.06 mg; 0.06–0.12 mg) Normalised abundance (N^*) and biomass abundance (B^*) were then determined for each body mass class after [31,32,55,56]. Platt and Denman [54] proposed that a normalisation procedure was necessary to compare across abundance-body size distributions because the width of the size classes varies across the size spectrum. Abundance and biomass abundance were normalised as follows:

$$N(*) = \frac{N}{\Delta M} \quad (7)$$

where N^* is the normalised abundance or biomass N is non-normalised abundance and ΔM is the width of the body mass class.

To get the “real” regression slope of the abundance-body mass relationship to test predictions derived from metabolic theory, we needed to de-normalize abundances [31]. For the allometric relationship $N^* = aM^b$, the de-normalized abundance N must follow $N = MN^* = aM^{b+1}$

Therefore, the slope of the de-normalized NM relationship is the slope of the normalized regression plus one [31]. The same de-normalization was applied to the biomass-body mass relationship.

1.4. Quantification of the fish assemblage

Abundance estimates for the benthic fish assemblage were made via the use of ten randomly placed 1 m x 1 m quadrats in each of the two sectors sampled. Quadrats were placed at the same depths (1–2 m) as those from which the invertebrate samples were taken. The abundance of each fish species was estimated by counting the number of individuals encountered within each quadrat, using the underwater identification techniques of Wilkins and Myers [56] and Hayward and Ryland [57].

Fish were also sampled using baited fish pots, to obtain body mass estimates, measured as grams wet weight and subsequently converted to ODM assuming

ODM to be 80% of wet weight (after [58]). Each individual was then assigned to a body mass class as per Section d. The abundance (individuals m^{-2}) of each individual was then estimated from the species measure of ambient abundance.

1.5. Quantification of the food web

Lough Hyne is a protected nature reserve and to minimise our impact on the fish assemblage we restricted our study to the sampling of 10 individuals per species for gut contents analysis, in line with other food web studies [59–61]. The fish species used were: *Gobius niger*; Linnaeus, *Gobius paganellus*; Linnaeus, *Gobius couchi*; Miller and Eltwail, *Pomatoscistus pictus*; Malm, *Gobisculus flavescens*; Fabricius. Predators were collected from the two sites using baited commercial fish pots. Bait was wrapped in fine mesh bags (500 μm) to avoid contamination of gut contents. Fish pots were laid at 1–2 m depth for 12 hours, after which fish were collected, immediately killed and frozen to prevent digestion of gut contents.

The guts of all predators were dissected and analysed under high power microscopy (200 x magnification). Gut contents were identified to the highest possible taxonomic level (usually species), using reference collections obtained from the invertebrate sampling. All individual prey items observed in the guts of individual predators were counted.

2. Supplemental Data

Taxon	y	x (mm)	Equation	r ²	Source
<i>Amphipoda</i>	$\log_{10} M$ (mg)	$\log_{10} L$	$y = 2.83x - 2.99$	0.97	P
<i>Platynereis dumerilii</i>	$\log_{10} M$ (mg)	$\log_{10} L$	$y = 2.16x - 2.54$	0.92	P
<i>Amphiglena mediterranea</i>	$\log_{10} M$ (mg)	$\log_{10} L$	$y = 2.36x - 1.80$	0.63	P
<i>Asterina phylactica</i>	$\log_{10} M$ (mg)	$\log_{10} L$	$y = 2.36x - 0.89$	0.91	P
<i>Idotea</i>	$\ln M$ (mg)	$\ln L$	$y = 2.86x - 5.86$	-	H+C
<i>Mycidae</i>	$\ln M$ (mg)	$\ln L$	$y = 2.87x - 5.90$	-	H+C
<i>Palaeomon serratus</i>	$\log_{10} M$ (mg)	$\log_{10} L$	$y = 2.44x + 0.19$	0.90	E

Appendix I. Regression equations used to estimate dry mass of taxa in the Lough Hyne food web. r^2 values are given where available. M = Body mass, L = Body length. Letters correspond to sources of the regression equation. P = present study, H+C = [58], E = Mark Emmerson (unpublished data).

Spp Number	Taxa	Mean Log (M)	Mean Log (N)
1	<i>Pollachius pollachius</i>	5.44377	-1.106760
2	<i>Gobius cruentatus</i>	4.37944	-0.418032
3	<i>Gobius niger</i>	4.25641	0.176091
4	<i>Thorogobius ephippiatus</i>	4.08159	-0.225295
5	<i>Gobius paganellus</i>	4.04555	-0.698970
6	<i>Ctenolabrus rupestris</i>	3.97692	-0.070581
7	<i>Crenilabrus melops</i>	3.9653	-0.346787
8	<i>Taurulus bubalis</i>	3.92169	-0.121823
9	<i>Gobius couchi</i>	3.35928	-0.455932
10	<i>Gobisculus flavescens</i>	3.13203	0.90849
11	<i>Paleomon serratus</i>	2.80332	1.50515
12	<i>Pomatoscistus pictus</i>	2.77815	0.61816
13	Mycidae	0.296085	2.65582
14	<i>Bittium reticulatum</i>	0.264311	3.64852
15	<i>Asterina phylactica</i>	0.238685	3.00800
16	Gastropod B	0.164119	3.28421
17	<i>Rissoa parva</i>	0.137225	3.82949
18	<i>Amphithoe ramondi</i>	-0.157729	2.05376
19	Lyssianassidae	-0.284685	2.61803
20	Gammarus spp	-0.392412	2.17870
21	<i>Platyeris dumerelli</i>	-0.593408	2.73346
22	<i>Gammarus oceanicus</i>	-0.631739	2.47973
23	<i>Mytilus edulis</i>	-0.744205	3.81719
24	<i>Cingula semistriata</i>	-0.922281	4.58096
25	<i>Coriandria fulgida</i>	-0.966187	3.36903
26	<i>Ischyrocerus anguipes</i>	-1.10485	3.74982
27	<i>Amphiglena mediterranea</i>	-1.1353	3.25788
28	Tanaidacea	-1.14488	3.53088
29	Amphipod F	-1.16581	2.75273
30	<i>Parajassa pelagica</i>	-1.17504	3.78346
31	<i>Erichthonius punctatus</i>	-1.2718	3.64109
32	Idotea spp	-1.30043	3.05376
33	Gastropod A	-1.31201	4.27907
34	Amphipod E	-1.32361	3.38955
35	<i>Erichthonius brasiliensis</i>	-1.42536	2.85539
36	<i>Corophium sextonae</i>	-1.57816	3.54976
37	<i>Microdeutopus anomalus</i>	-1.69179	3.47973
38	Calanoidia	-1.79588	3.16770
39	Amphipod G	-1.97519	3.37598
40	Harpacticoidia	-2.39794	3.93266

Appendix II. Species in the benthic community of Lough Hyne. Not all species present in the list were found in the diets of the predators. Species present in the food can be identified from their id number and the food web in Figure 4. M = Mean body mass, N = Mean numerical abundance.