ICES Journal of
Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2013), 70(4), 734–742. doi:10.1093/icesjms/fst071

Original Articles

Does functional redundancy stabilize fish communities?

Jake Rice[1]*, Niels Daan[2], Henrik Gislason[3], and John Pope[3]

[1]*Department of Fisheries and Oceans, 200 Kent Street, Ottawa, Ontario, K1A 0E6, Canada*
[2]*Waaldijk 39, 6621KH Dreumel, The Netherlands*
[3]*DTU Aqua, Technical University of Denmark, Charlottenlund Slot, DK–2920 Charlottenlund, Denmark*

**Corresponding Author: tel: +1 613 990 0288, fax: +1 613 991 1378, e-mail: jake.rice@dfo-mpo.gc.ca*

Rice, J., Daan, N., Gislason, H., and Pope, J. Does functional redundancy stabilize fish communities? – ICES Journal of Marine Science, 70: 734–742.

Received 12 January 2013; accepted 10 April 2013.

Functional redundancy of species sharing a feeding strategy and/or maximum size has been hypothesized to contribute to increased resilience of marine fish communities (the "portfolio effect"). A consistent time-series of survey data of fish in the North Sea was used to examine if trophic functional groups or maximum length of species (L_{max}) groups with larger numbers of species had lower coefficients of variation in abundance and biomass over time than did groupings with fewer species. Results supported this hypothesis. However, the stabilizing effect of numbers of species in a group on variation in abundance or biomass could be accounted for by the Law of Large Numbers, providing no evidence that specific ecological processes or co-adaptations are necessary to produce this effect. This implies that successful conservation policies to maintain the resilience of a marine fish community could be based on strategies to maintain the number of species in functional groups, without having to know the detailed ecological interactions between the species.

Keywords: fish community, functional group, North Sea, portfolio effect, resilience.

Introduction

One argument for why conservation of biodiversity is important for protecting ecosystem structure and function is that "redundancy" in ecosystem functions contributes to system "resilience" (Tilman, 1996; Rosenfeld, 2002; Brooks *et al.*, 2005). Although these concepts are well established in theory, the claim may be phrased differently in different sources, because "redundancy" and "resilience" are difficult to demonstrate under field conditions (O'Connor and Crowe, 2005; Giachas *et al.*, 2009; Rochet *et al.*, 2010). Nonetheless, the underlying idea is similar across papers. All suggest that having several species with the same trophic functional role helps ecosystems maintain their characteristic structure and functions (where "trophic functional roles" refer to position in the water column and diet, such as demersal benthivore, demersal piscivore, pelagic piscivore, etc.).

The linkage between functional redundancy and resilience derives from the argument that with multiple species playing each functional role, there are multiple pathways for key ecosystem processes. The multiple pathways, in turn, result in the processes being more resistant to perturbations of the abundance of individual species, because other pathways can compensate for any change in the function served by the species whose abundance initially was perturbed. This line of reasoning linking functional redundancy to resilience of a marine community implies that compensation mechanisms exist within multi-species functional groups, such that variations in the abundance of one species in a functional role can be compensated for by reciprocal variations in another species in the same functional group, thereby buffering variations in the abundance of individual species.

This relationship has been referred to as the "portfolio effect" (Figge, 2004; Schindler *et al.*, 2010), and maintenance of functional diversity itself is being promoted as a management objective to maintain ecosystem processes in an uncertain world. Because it is not possible to predict the future states of drivers (environmental and human pressures) that affect the productivities of individual species, management aimed at keeping multiple species in each functional group is needed to protect whatever ecological mechanisms are responsible for the compensation across species within a functional group. This in turn will increase the resilience of ecosystems to the uncertain future pressures.

The nature of appropriate management objectives for maintenance of functional diversity depends crucially on the nature of the compensation mechanisms that contribute to resilience within the portfolio of functionally redundant species, however. A weak interpretation of the portfolio effect would be that the stability results merely from the Law of Large Numbers. As far back as Bernoulli

(1713), the Law of Large Numbers has been well established: the average (or sum) of independent, randomly varying numbers becomes proportionately less variable as more numbers are averaged (or summed). The "compensation mechanisms" would be statistical rules, not requiring specific ecological processes.

A stronger interpretation of the portfolio effect would assume that active ecological processes underlie the compensation across species within functional groups. Building on the classical, if sometimes ill-defined (Perry *et al.*, 2002; Batchelder and Kim, 2008), interpretation of "carrying capacity" (K) as an ecosystem-determined upper limit on population size, density-dependent feedback would be a key ecological process that contributes to stabilizing individual populations. An ecologically "strong" interpretation of functional redundancy extends that idea such that the upper limit is set for a suite of species sharing a functional role rather than for each one individually. Consequently, density-dependent feedback would apply for all the species in the portfolio, such that the variations in abundance of species within a functional group would be actively *compensatory*, not just reciprocal (Hui, 2006; Shackell and Frank, 2007; Reecht *et al.*, 2009).

Commonly reported pairwise correlations of species abundances, and ordinations of correlation (or other pairwise) matrices of species' abundances would have limited power in detecting the stabilizing effect of functional groups on ecosystem structure and function. If the compensatory processes are expressed for suites of functionally redundant species, pairwise relationships of species might not show consistent patterns of covariation. Rather, more integrative analyses of patterns of variation among groups of functionally related species would be needed (c.f. Crowder *et al.*, 2008; Frank *et al.*, 2011).

With compensatory density-dependent responses to population changes potentially spread among all the species in a functional group, the concept of functional redundancy in relation to an aggregate K opens many pathways to explaining observed dynamics of marine communities. This could make it an important concept for conservation planning, in order to match scales of management measures to scales of ecosystem processes. However, it also makes the concept hard to test empirically because many different outcomes can be considered consistent with the hypothesis of compensation within large functional groups.

We indirectly evaluate the strength of active compensation processes at the scale of functional groups using a neutral model approach with the North Sea International Bottom Trawl Survey (IBTS) time-series. We first ask if larger functional groups in the survey data are indeed more stable than smaller functional groups. If they are, then it is necessary to account for the statistical effect expected from merely the Law of Large Numbers. If that statistical process, by itself, is insufficient to account for the greater stability of larger functional groups, then there is indirect evidence that active compensatory mechanisms are present within functional groups. However, if the Law of Large Numbers is sufficient to account for the greater stability of larger functional groups, then there is little basis to invoke active compensatory processes to account for the increase in stability.

Methods

The North Sea IBTS trawl survey during the first quarter (as described in Daan *et al.*, 2005) provides a consistent time-series of survey abundance (in numbers) estimates from 1977–2010 for the 83 most common fish species (or higher taxon if species identification was considered unreliable; the set includes elasmobranches; see Appendix 1) in the North Sea above ~5 cm total length. Catch weights by species have not been reported consistently by all countries, but as an approximation survey length frequencies by species and year were also transformed into biomass estimates assuming isometric growth and a constant specific gravity using the general equation $W = qL^3$ (Beverton and Holt, 1957), where q was set as 0.01, the average value observed for the condition factor of cod based on studies from all over the North Atlantic (Daan, 1974). Although species- and area-specific equations for length–weight conversions are available for some of the more common species in the data-set, a general formula was necessary for consistent treatment of observations of all 83 species across the entire survey area and time-period. Because the species differ greatly in absolute abundance and catchability by the survey gear, species abundances and biomass estimates were individually standardized to a common unit mean and variance (note that in this case the actual value of q used becomes irrelevant!). The standardization is likely to inflate the likelihood of finding evidence of compensatory variation in either data-set, by ensuring the range of variation of all species is equal, so any equivalent percent change in abundance or biomass can "compensate" fully for any other within a functional group. However, any potential scaling of abundances or biomasses across species would be arbitrary, because there is no effective basis to scale the "compensation ability" of a single individual, or the weight of any one species relative to single individuals or weights of each other species in a functional group, taking into account all the relevant sampling (catchability) and ecological (behaviour, physiology, distribution, etc.) factors that could affect compensation ability. Rather this potential directional bias is acknowledged and taken into account in the interpretation of results. In addition, the simulations were repeated using the biomass data without standardization and assuming equal catchability, *de facto* assuming a kilogram of biomass of any species of a given L_{max} group (defined by maximum length of species) and/or diet group can fully "compensate for a kilogram of biomass of another species of the same L_{max} and/or diet group. There was a very high correlation ($r = 0.85$, $p < 0.01$) of mean and variance of unstandardized biomasses across species over time, so species of high biomass would dominate this formulation, but it provides the alternative boundary condition for the scaling of compensation across species compared to the formulations using standardized abundance and biomass.

Extensive diet studies were made for North Sea fish species during the 1981 and 1991 Years of the Stomach (Daan, 1989; Hislop, 1997, respectively), and additional analyses have documented the "functional role" for most North Sea species (Greenstreet *et al.*, 1997; Jennings *et al.*, 2002; Heath, 2005; Stelzenmuller *et al.*, 2009). Using the published classifications of species into functional groups based on diets, it is possible to calculate the mean standardized abundance or biomass of each functional group for each year, and then calculate the variance in those annual values over the time-series. Previous work with these data has highlighted the extent to which size-based processes underlie community dynamics (Daan *et al.*, 2005; Pope *et al.*, 2006; Gislason *et al.*, 2008). Consequently, we also categorized each species into groups based on maximum length of the species, L_{max}, as well as for the combinations of dietary functional group by L_{max} group with at least four species; we repeated the analyses for the L_{max}–dietary group combinations. Species and their categorizations are listed in Appendix 1.

The different functional groups identified have different numbers of species, such that the aggregate abundance or biomass (annually and averaged across the time-series) of a group with many species was larger than the aggregate abundance or biomass of small groups. Consequently, the hypothesis that the greater the number of species in a functional group results in greater aggregate stability over time was tested with CVs of aggregate abundance or biomass over years, rather than directly with the variances. If the null hypothesis of equal CVs regardless of size of functional groups is rejected then the aggregate abundance or biomass of larger functional groups should be relatively more stable than the aggregate abundance or biomass of small functional groups (one sense of being more "resilient").

However, before inferring that there are compensatory ecological processes contributing to the resilience of functional groups, it is necessary to test if any of the variances differ from the expected variance if only the Law of Large Numbers was acting. To get the expected variances, we randomly sorted the species into groups of the same size (numbers of species) as observed for the functional groups in the North Sea. Sorting was done without replacement in each replication, so that all species were used once in each iteration, and all species-level patterns of variation in abundance or biomass over time were present in each replication. We then calculated the annual mean abundance or biomass in each randomly assigned "functional group" and the variance of mean abundance or biomass in each functional group over the full time-series. This was repeated 500 times to produce a frequency distribution of expected variances based solely on the Law of Large Numbers and the individual patterns of variation in each species' abundance or biomass over time (for whatever reasons it was varying). Because for each group the observed variance was compared to the variance of randomized groups of identical numbers of species, these comparisons could be done directly with the variances rather than the CVs.

The analyses were conducted for the three classifications of species presented in Table 1. For each set of randomizations we asked: was the variance of the real functional group within the distribution of variances calculated if species were assigned randomly to groups of corresponding numbers of members. If so, then the Law of Large Numbers alone is sufficient to account for the patterns of decreasing CV in abundance or biomass over time as the size of functional groups increases. If the variance of the real group consistently lies on the lower tail of the distribution of variances from random groupings of the same size, it would be evidence for additional ecological processes regulating functional groups of species relative to some group-specific carrying-capacity-like limit.

Results are presented separately for each dietary group, each L_{max} group, and the dietary–L_{max} groupings. Within each of the three classifications, probabilities were combined across the categories using Fisher's method for combining independent probabilities, to give an overall evaluation of the likelihood that the set of probabilities would have been observed under the null hypothesis of only the Law of Large Numbers being at work.

Results

For all three classification criteria, the CV is inversely correlated with the number of species in a group for both standardized abundance and biomass. The number of groups within each classification was small (Table 1), giving statistical tests of correlation low power. Nonetheless, the negative correlations were highly significant for L_{max} (abundance) and significant for the groups tested in aggregate for biomass ($p = 0.048$) and abundance ($p = 0.027$). (CVs are

Table 1. Categories according to the three classification criteria: (a) trophic group, (b) L_{max}, and (c) combined trophic–L_{max} group, used in subsequent analyses, along with numbers of species in each group (*n*) and coefficients of variation of aggregate group abundance over the time-series (CV).

	(a) Trophic functional group				**(b) L_{max} category (cm)**				
		CV					**CV**		
			Biomass					**Biomass**	
Category	***n***	**Numbers**	**Standardized**	**Unstandardized**	**Category**	***n***	**Numbers**	**Standardized**	**Unstandardized**
Demersal benthivore	35	0.0005	0.0048	0.344	<10	2	0.008	0.11	0.811
Demersal piscivore	31	0.0005	0.0005	0.240	10–20	9	0.002	0.008	0.375
Pelagic piscivore	5	0.0119	0.012	1.87	20–40	3	0.001	0.004	0.423
Pelagic planktivore	12	0.0016	0.0016	0.500	40–80	34	0.0005	0.002	0.421
					80–160	18	0.0008	0.003	0.447
					>160	7	0.004	0.019	0.441

(c) Combined functional group–L_{max}

		CV		
			Biomass	
Category	***n***	**Numbers**	**Standardized**	**Unstandardized**
Demersal benthivore 10–20	6	0.005	0.09	0.448
Demersal benthivore 20–40	8	0.003	0.09	0.869
Demersal benthivore 40–80	12	0.001	0.05	0.364
Demersal benthivore 80–160	7	0.003	0.08	1.205
Demersal piscivore 40–80	11	0.001	0.05	0.317
Demersal piscivore 80–160	13	0.002	0.07	0.333
Demersal piscivore >160	4	0.005	0.05	0.983

There are fewer total species in the combined functional L_{max} groups because several of these partitions had too few species for meaningful comparisons.

dimensionless ratios, so such a combined test is appropriate: Table 1). For the unstandardized biomass, the correlations were still significant for the L_{max}–diet grouping ($p = 0.012$) and in aggregate ($p = 0.025$), and high although not significant ($p = 0.11$) for the diet group alone. For the L_{max} group, CV was actually slightly positively correlated with numbers of species ($p = 0.55$), with relative variability stable across all the size groups. A (somewhat trivial) null hypothesis of independence between group size and relative variation in abundance or biomass over time is rejected for all but the L_{max} case with unstandardized biomasses. Large functional groups have greater relative stability in both respects.

For the more interesting tests of whether sample size alone was adequate to account for this effect, the variance of the "real" groupings of standardized data was well within the distribution of simulated variances, whether examined by diet group, by L_{max} group, or by the combined diet–L_{max} group. The frequency distributions of variances from 500 iterations of random sets of species matched in number to the observed L_{max} groups (A–F), diet groups (G–J) and combined diet–L_{max} groups (K–Q) have the observed variance for the respective group identified with an arrow for abundance (Figure 1) and biomass (Figure 2).

For abundance, there are two cases where the observed variance is on the low tail of the expected distribution from random group membership (L_{max} >160 cm, combined Demersal Piscivores 80–160 cm), and one case where the observed variance is on the high end of the expected distribution (L_{max} 20–40 cm). For standardized biomass, the only extreme observation is L_{max}20–40, which has a higher variance than expected by chance. In multiple tests of the same hypothesis such events are expected. When the tests of combined probabilities are considered, the results from all three grouping criteria are likely to be observed by chance for abundance:

$$\mathrm{L_{max}Groups}\chi^2 = 9.66 \mathrm{d.f.} = 12, p = 0.64,$$

$$\mathrm{DietGroups}\chi^2 = 6.43, \mathrm{d.f.} = 8, p = 0.60,$$

$$\mathrm{Diet} - \mathrm{L_{max}Groups}\chi^2 = 16.49, \mathrm{d.f.} = 14, p = 0.28.$$

And for biomass:

$$\mathrm{L_{maxGroups}}\chi^2 = 9.53, \mathrm{d.f.} = 12, p = 0.66,$$

$$\mathrm{DietGroups}\chi^2 = 5.83, \mathrm{d.f.} = 8, p = .67,$$

$$\mathrm{Diet} - \mathrm{L_{maxGroups}}\chi^2 = 13.60, \mathrm{d.f.} = 14, p = 0.48.$$

For the unstandardized biomass data the results are slightly less consistent (Figure 3). For the L_{max} and Diet–L_{max} groupings, the variances of the actual groupings are well within the distributions of variances of simulated groups of equal numbers of species:

$$\mathrm{L_{maxGroups}}\chi^2 = 11.66, \mathrm{d.f.} = 12.p = 0.44,$$

$$\mathrm{Diet} - \mathrm{L_{maxGroups}}\chi^2 = 17.38, \mathrm{d.f.} = 14, p = 0.22.$$

$$\mathrm{FortheDietGroups}, \chi^2 = 14.04 \mathrm{d.f.} = 8, p = 0.081,$$

suggesting that compensation may be occurring between species with similar diets. However, this marginally significant result needs to be interpreted in terms of the dominance of species of highest abundance in these simulations. Like all natural communities, the distribution of species by abundance in the North Sea is highly skewed (Daan *et al.*, 2005). In the unstandardized biomass data, 74 of the 83 species have mean biomasses under 16 000 kg per year in the IBTS biomass records, and the other nine species have mean abundances greater than 16 000 kg. Variances are similarly highly skewed with discontinuities in the distribution, as well as correlated with mean biomasses across species, with ten of the 83 species having variances $>10^8$.

Demersal Benthivores is the one diet group with an observed variance significantly ($p = 0.03$) on the low end of the distribution of variances of random groups, and is also the group with by far the most species (35 of 83). However, it has no species from the especially high biomass or high variance sets of species, both highly non-random results in their own right (Binomial tests: $P(0)$ of 35 species having biomass $>16\ 000 = 0.017$; $P(0)$ of 35 species having variances $> 10^8 = 0.011$). On the other hand, the Pelagic planktivore group is weakly overrepresented in the high biomass (three or more of 12 species are high biomass; $p = 0.24$), overrepresented in the high variance in biomass species (four or more of 12 species; $p = 0.061$), and in the 95th percentile in the distribution of variances of random groups of 12 species. Many studies of community dynamics have already concluded that at least some species of pelagic plankivores show large variance in recruitment over time, with large abundances and biomasses occasionally accumulating (ICES, 2007). Many demersal benthivores, on the other hand, lack a prey base on which to build up temporary very large abundances and biomasses, and are consequently less proportionately variable over time. This is an important ecological difference between these feeding strategies, but is explained readily by the ability of pelagic planktivores to respond rapidly to bottom-up ecological signals without invoking strong compensation in biomass among species of demersal benthivores. It also argues for some form of standardization of the biomass and abundance data, when comparing across groups of species.

Discussion

We found support in the North Sea fish community for the idea that functional redundancy does lead to greater stability of abundance and biomass over time. However, the Law of Large Numbers is sufficient to account for the observed reduction in relative variation over time. Despite a scaling of data that favoured finding evidence of compensation if it occurred, we found no need to invoke additional ecological processes acting to provide more stable abundances or biomasses of suites of North Sea fish species, whether they are functionally similar in diet, of the same L_{max} class, or a combination of the two. When the scaling was removed, demersal benthivores were found to be less variable over time than random groups of the same number of species. However, this effect could be accounted for by demersal benthivores not reaching the occasional very high abundances (and variances) observed in other groups, especially pelagic planktivores, rather than any intragroup dynamics. This does not mean that functional redundancy does not contribute to community resilience. It also does not mean that pairwise or multi-species compensation processes do not exist. More targeted studies may find evidence for such relationships as well as for reciprocal relationships between the diet or L_{max} groupings themselves, as for example in Duplisea and Blanchard (2005).

The ability to fit the patterns in functional group abundances over time with just the Law of Large Numbers does highlight that we found no evidence of special adaptations among pairs or larger groups of functionally similar species to stabilize the functional groups over time. This does have implications for conservation policy and management. We suggest that management should still

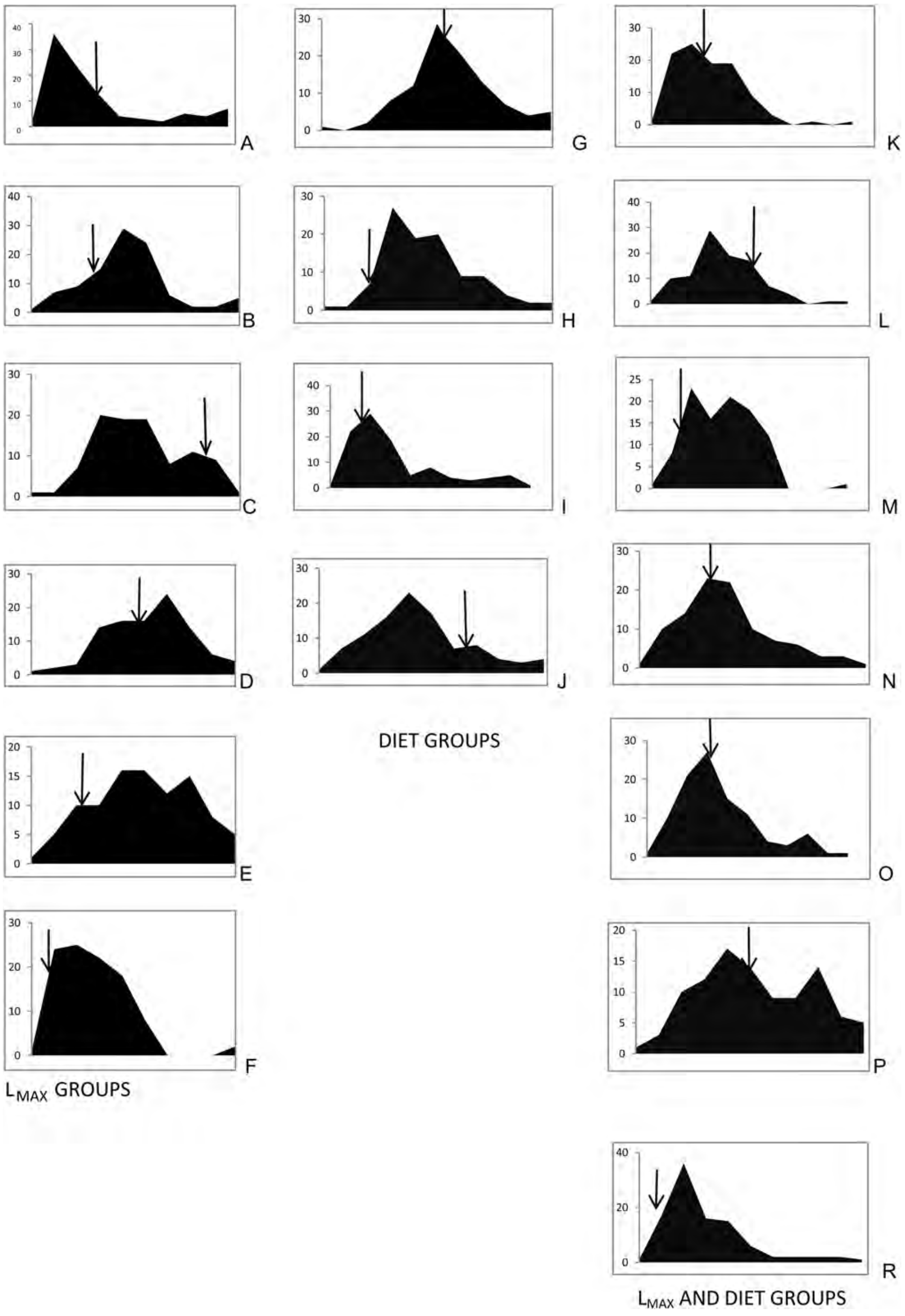

Figure 1. Frequency distributions of simulated variances of standardized abundance data for L_{max} groups (Column 1, A–F), diet groups (Column 2, G–J), and combined diet–L_{max} groups (Column 3, K–Q). The observed variances for the real data are represented by an arrow within each figure. Categories of A–F = <10, 10–20, 20–40, 40–80, 80–160 and >160 (all cm). Categories of G–H = Demersal benthivore, Demersal piscivore, Pelagic piscivore, Pelagic planktivore. Categories of K–Q = Demersal benthivore 10–20, Demersal benthivore 20–40, Demersal benthivore 40–80, Demersal benthivore 80–160, Demersal piscivore 40–80, Demersal piscivore 80–160, Demersal piscivore >160.

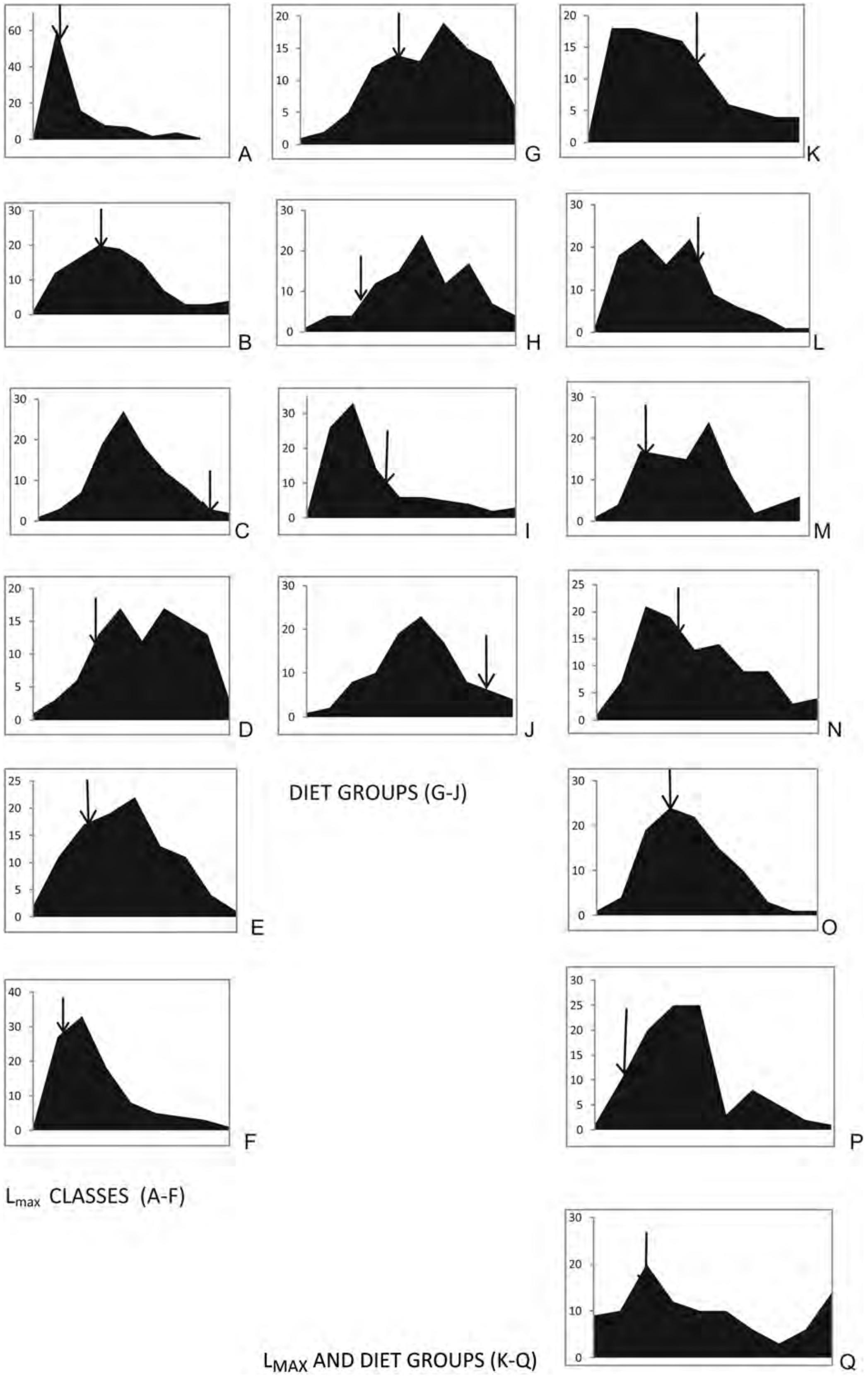

Figure 2. Frequency distributions of simulated variances of standardized biomass data for L_{max} groups (Column 1, A–F), diet groups (Column 2, G–J), and combined diet–L_{max} groups (Column 3, K–Q). See also legend to Figure 1.

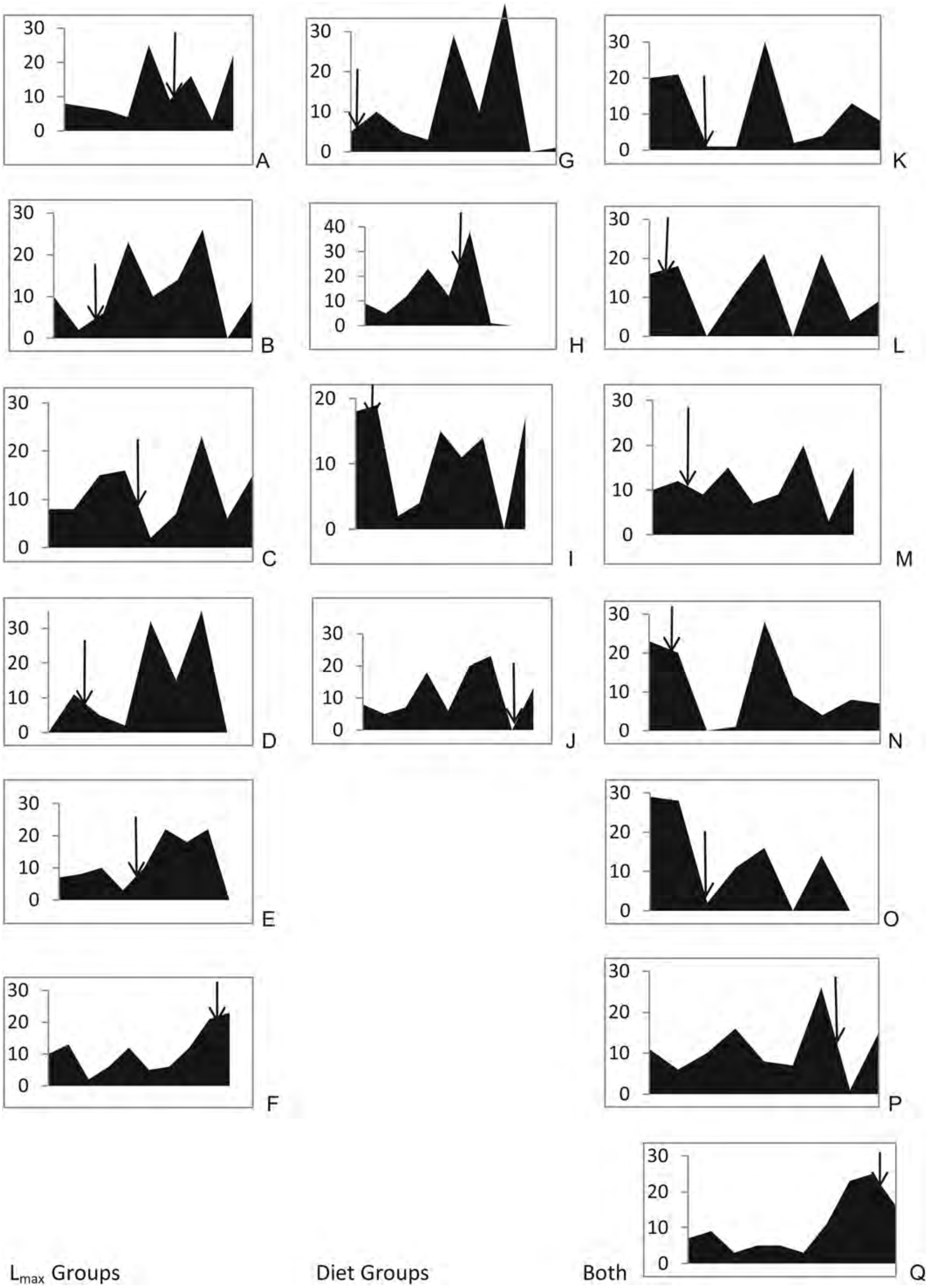

Figure 3. Frequency distributions of simulated variances of unstandardized biomass data for L_{max} groups (Column 1, A – F), diet groups (Column 2, G – J), and combined diet – L_{max} groups (Column 3, K – Q). See also legend to Figure 1.

strive to protect the diversity of species in functional and size groups to get the potential benefits of the portfolio effect, and loss of any species in a functional group should be prevented to maintain the robustness of the full system. However, robust management strategies could be formed to achieve such objectives without waiting for detailed ecological studies of the interactions between the species within the various diet or L_{max} groups.

The absence of evidence of ecological processes incremental to the expectations from the Law of Large Numbers could occur because no such structuring processes are functioning, or because the abundance of all species in the North Sea have been so extensively altered by fishing that the notion of carrying capacity is no longer relevant to its system dynamics, and the preconditions for reciprocal compensation do not exist. If the latter is the case, then density-dependent processes should have been weakened throughout the entire system. Past analyses of the North Sea fish community has found evidence of substantial changes in the distribution of abundance among fish species and size groups (Daan *et al.*, 2005; Pope *et al.*, 2006), but fish biomass overall is still large enough for the continued need for including density-dependent feedback in models of this community (Pope *et al.*, 2006). We are conducting further work with these survey data to investigate whether the lower total fish biomass over much of the time-period has increased the influence of bottom-up processes in system dynamics, or the density-dependent predation processes have remained strong but shifted to smaller size groups of fish. It is also the case that many other aspects of fish life histories covary with L_{max}, or are affected by diet choices (Pope *et al.*, 2006; Gislason *et al.*, 2008), and we are exploring their implications for the relationships observed.

Acknowledgements

The authors would like to thank two anonymous reviewers and particularly the editor for helpful suggestions on improving the presentation of this material.

References

Batchelder, H., and Kim, S. 2008. Lessons learned from the PICES/GLOBEC Climate Change and Carrying Capacity Program and Synthesis Symposium. Progress in Oceanography, 77: 83–91.

Bernoulli, J. 1713. On the law of large numbers. Translated into English by Oscar Sheynin, Berlin 2005. http://www.sheynin.de/download/bernoulli.pdf (last accessed 8 May 2013).

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery Investigations, London Series 2, 19: 1–533.

Brookes, J. D., Aldridge, K., Wallace, T., Linden, L., and Ganf, G. G. 2005. Multiple interception pathways for resource utilisation and increased ecosystem resilience. Hydrobiologia, 552: 135–146.

Crowder, L. B., Hazen, E. L., Avissar, N., Bjorkland, R., Latanich, C., and Ogburn, M. B. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. Annual Review of Ecology, Evolution, and Systematics, 39: 258–278.

Daan, N. 1974. Growth of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research, 8: 27–48.

Daan, N. (Ed.) 1989. Data base report of the stomach sampling project 1981. ICES Cooperative Research Report No. 164. ICES Copenhagen. 144 pp.

Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science, 62: 177–188.

Duplisea, D., and Blanchard, F. 2005. Relating species and community dynamics in a heavily exploited marine fish community. Ecosystems, 8: 899–910.

Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. Biological Conservation 13: 827–849.

Frank, K. T., Petrie, B., Fisher, J. A. D., and Leggett, W. D. 2011. Transient dynamics of an altered large marine ecosystem. Nature, 477: 86–89.

Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J. S., Overholtz, W., Megrey, B. A., Gjosaeter, H., *et al.* 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Progress in Oceanography, 81: 47–62.

Gislason, H., Pope, J. G., Rice, J. C., and Daan, N. 2008. Coexistence in North Sea fish communities: implications for growth and natural mortality. ICES Journal of Marine Science, 65: 514–530.

Greenstreet, S. P. R., Bryant, A. D., Broekhuizen, N., Hall, S. J., and Heath, M. R. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for foodweb dynamics. ICES Journal of Marine Science, 54: 243–266.

Heath, M. R. 2005. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES Journal of Marine Science, 62: 847–868.

Hislop, J. (Ed.) 1997. Data base report of the stomach sampling project 1991. ICES Cooperative Research Report No. 219. ICES, Copenhagen. 421 pp.

Hui, C. 2006. Carrying capacity, population equilibrium, and environment's maximal load. Ecological Modelling, 192: 317–320.

ICES. 2007. Report of the study group on recruitment variability in North Sea planktivorous fish (SGRECVAP). ICES CM 2007/LRC: 07. 65 pp.

Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K., and Warr, K. J. 2002. Long-term trends in the trophic structure of the North Sea fish community: Evidence from stable-isotope analysis, size-spectra and community metrics. Marine Biology, 141: 1085–1097.

O'Connor, N. E., and Crowe, T. P. 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. Ecology, 86: 1783–1796.

Perry, R. I., Hollowed, A. B., and Sugimoto, T. 2002. The PICES Climate Change and Carrying Capacity Program: why, how, and what next. PICES Scientific Report, 22: 87–99.

Pope, J., Rice, J. C., Daan, N., Gislason, H., and Jennings, S. L. 2006. Modelling an exploited marine fish community with 15 parameters – results from a charmingly simple size-based model. ICES Journal of Marine Science, 63: 1029–1044.

Reecht, Y., Rochet, M-J., and Trenkel, V. 2009. Direct and Indirect Effects of Fishing on Demersal Fish Trophic Groups, Defined by an Ecomorphological Approach. Ifremer, Plouzane, France. 232 pp.

Rochet, M-J., Trenkel, V. M., Carpentier, A., Coppin, F., de Sola, L. G., Leaute, J-P., Mahe, J-C., *et al.* 2010. Do changes in environmental and fishing pressures impact marine communities? An empirical assessment. Journal of Applied Ecology, 47: 741–750.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. Oikos, 98: 156–162.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., and Webster, M. S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, 465: 609–612.

Shackell, N. L., and Frank, K. T. 2007. Compensation in exploited marine fish communities on the Scotian Shelf, Canada. Marine Ecology Progress Series, 336: 235–247.

Stelzenmüller, V., Maynou, F., and Martin, P. 2009. Patterns of species and functional diversity around a coastal marine reserve: a fisheries perspective. Aquatic Conservation: Marine and Freshwater Ecosystems, 19: 554–565.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology, 77: 350–363.

Handling editor: Mikko Heino

Appendix 1. List of species used in analyses, with L_{max} and trophic functional categories. Abbreviations are the same as in Table 1.

Species	L_{max} category	Trophic functional group
Agonus cataphractus	20	Demersal benthivore
Alosa sp.	40	Pelagic planktivore
Amblyraja radiata	40	Demersal piscivore
Ammodytidae	40	Pelagic planktivore
Anarhichas lupus	80	Demersal benthivore
Argentina sp.	40	Pelagic planktivore
Arnoglossus sp.	20	Demersal benthivore
Brosme brosme	80	Demersal piscivore
Buglossidium luteum	10	Demersal benthivore
Callionymus sp.	20	Demersal benthivore
Capros aper	10	Pelagic planktivore
Chelidonichthys lucernus	40	Demersal piscivore
Chimaera monstrosa	80	Demersal piscivore
Ciliata mustela	20	Demersal piscivore
Clupea harengus	40	Pelagic planktivore
Cyclopterus lumpus	40	Demersal benthivore
Dasyatis pastinaca	80	Demersal benthivore
Dicentrarchus labrax	80	Demersal piscivore
Dipturus batis	160	Demersal benthivore
Echiichthys vipera	10	Demersal benthivore
Echiodon drummondi	20	Demersal benthivore
Engraulis encrasicolus	20	Pelagic planktivore
Entelurus aequoreus	40	Pelagic planktivore
Etmopterus spinax	40	Demersal piscivore
Eutrigla gurnardus	40	Demersal piscivore
Gadiculus argenteus	10	Pelagic planktivore
Gadus morhua	80	Demersal piscivore
Gaidropsarus sp.	40	Demersal piscivore
Galeorhinus galeus	160	Demersal piscivore
Galeus melastomus	80	Demersal piscivore
Gasterosteus aculeatus	10	Pelagic planktivore
Glyptocephalus cynoglossus	40	Demersal benthivore
Gobiidae sp.	0	Demersal benthivore
Hippoglossoides platessoides	40	Demersal benthivore
Hippoglossus hippoglossus	160	Demersal piscivore
Lepidorhombus sp.	40	Demersal piscivore
Leucoraja naevus	80	Demersal benthivore
Limanda limanda	40	Demersal benthivore
Liparis sp.	10	Demersal benthivore
Lophius piscatorius	160	Demersal piscivore
Lumpenus lampretaeformis	40	Demersal benthivore
Lycodes vahli	40	Demersal benthivore
Maurolicus muelleri	0	Pelagic planktivore
Melanogrammus aeglefinus	80	Demersal piscivore
Merlangius merlangus	40	Demersal piscivore
Merluccius merluccius	80	Demersal piscivore
Microchirus variegatus	20	Demersal benthivore
Micromesistius poutassou	40	Pelagic planktivore
Microstomus kitt	40	Demersal benthivore
Molva molva	160	Demersal piscivore
Mullus surmuletus	40	Demersal benthivore
Mustelus sp.	80	Demersal piscivore
Myoxocephalus scorpius	20	Demersal benthivore
Pholis gunnellus	20	Demersal benthivore
Platichthys flesus	40	Demersal benthivore
Pleuronectes platessa	80	Demersal benthivore
Pollachius pollachius	80	Demersal piscivore
Pollachius virens	80	Demersal piscivore
Psetta maxima	80	Demersal piscivore
Raja brachyura	80	Demersal benthivore
Raja clavata	80	Demersal benthivore
Raja montagui	80	Demersal benthivore
Raniceps raninus	20	Demersal benthivore
Rhinonemus cimbrius	40	Demersal piscivore
Sardina pilchardus	20	Pelagic planktivore
Scomber scombrus	40	Pelagic piscivore
Scophthalmus rhombus	40	Demersal piscivore
Scyliorhinus canicula	80	Demersal piscivore
Sebastes viviparus	40	Demersal piscivore
Solea vulgaris	40	Demersal benthivore
Sprattus sprattus	10	Pelagic planktivore
Squalus acanthias	80	Demersal piscivore
Syngnathus sp.	40	Pelagic planktivore
Taurulus bubalis	10	Demersal benthivore
Trachinus draco	40	Demersal benthivore
Trachurus trachurus	40	Pelagic piscivore
Triglops murrayi	10	Demersal benthivore
Trisopterus esmarkii	20	Pelagic planktivore
Trisopterus luscus	40	Demersal piscivore
Trisopterus minutus	20	Demersal piscivore
Zeugopterus sp.	10	Demersal benthivore
Zeus faber	40	Pelagic piscivore
Zoarces viviparus	40	Demersal benthivore