Biodiversity of North Sea fish: why do the politicians care but marine scientists appear oblivious to this issue?

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Political drivers underpinning the development of an Ecosystem Approach to Marine Management (EAMM) focus on conserving and restoring biodiversity. However, the Element of Ecological Quality for Fish Communities that emerged from the 2002 Bergen North Sea Ministerial Conference relates to "Changes in the proportion of large fish and hence the average weight and average maximum length of the fish community". How did this apparent change in direction arise? Responding to advice requests from OSPAR, ICES established seven criteria for identifying "state" indicators capable of supporting indicator-based management. Application of these criteria underlined the merits of indicators of fish size, whereas diversity indices performed poorly against four of the criteria. These difficulties are examined here. Far from being oblivious to the issue of biodiversity, marine scientists recognized that they were not in a position to recommend Ecological Quality Objectives (EcoQOs) for fish biodiversity that would have relied on the use of biodiversity indicators. The use of indicators of size structure, for which the theoretical foundation was better developed, allowed the continued development of an EAMM in the short term. However, if the issue of biodiversity is to be addressed in the longer term, then shortcomings associated with the use of biodiversity indicators need to be addressed.

Keywords: biodiversity, ecosystem approach to marine management, indicators, selection criteria.

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Biodiversity: evidence of political concern

The Convention on Biological Diversity (CBD), signed by 150 nations at the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in June 1992, provides one of the earliest indications that politicians care about the preservation and restoration of biodiversity. Article 1 of the CBD explicitly states conservation of biological diversity as one of the convention's principal objectives, whereas Article 8 declares the need to restore biodiversity in degraded ecosystems. Agenda 21, another document delivered at UNCED, stipulates the "action plan" for the 21st century, which is designed to meet the CBD's objectives. Chapter 17 of that document considers marine ecosystems and the need to mitigate the detrimental impacts of fishing activities on them. Therefore, ministers attending the 1997 Intermediate Ministerial Meeting (IMM) on Integration of Fisheries and Environmental Issues in Bergen recognized the "need to develop an ecosystem approach" to management in the North Sea, a primary objective of which should be "to ensure sustainable, sound and healthy ecosystems in the North Sea, thereby restoring, and/or maintaining their characteristic structure and functioning, productivity and biological diversity" (Heslenfeld and Enserink, 2008). At the Bergen IMM, ministers recognized OSPAR (the combined Oslo/Paris Commissions) as the authority competent to identify issues that an ecosystem approach to management would need to address. Reflecting this, in 1998, a fifth annex on the "Protection and Conservation of the Ecosystems and Biological Diversity of the Maritime Area" was added to the Convention for the Protection of the Marine Environment of the Northeast Atlantic (see also Heslenfeld and Enserink, 2008; Johnson, 2008). This annex again highlights the need to "take the necessary measures to protect and conserve the ecosystems and biological diversity of the maritime area, and to restore, where practicable, marine areas which have been adversely affected".

More recently, the proposal for a European Union Marine Strategy Directive (MSD) emphasized "the ultimate aim of providing biologically diverse and dynamic oceans and seas that are safe, clean, healthy, and productive". In its current form, the proposal reaffirms the EU's intentions, in respect to the CBD, of "halting biodiversity loss" and "ensuring the conservational and sustainable use of marine biodiversity". Ambitious time-scales for meeting these objectives are also proposed, the intention being to "achieve good environmental status of the EU marine waters by 2020". To meet these objectives, individual member states have introduced their own initiatives. For example, documents such as "Charting Progress" and "Seas the Opportunity" indicate the UK government's intention of achieving "clean, healthy, safe, productive, and biologically diverse oceans and seas". The continuing political focus on biodiversity is clear.

Biodiversity: the scientific community's response

At the last North Sea Ministerial Conference in 2002, the establishment of Ecological Quality Objectives (EcoQOs) for the ten critical components of the North Sea ecosystem identified by OSPAR was high on the agenda. "Fish Communities" was one of these components, and although no specific EcoQOs were identified, the element of ecological quality for the North Sea fish community was established as "Changes in the proportion of large fish and hence the average weight and average maximum length of the fish community" (Heslenfeld and Enserink, 2008). Against a backdrop of published evidence of declining species diversity within the demersal fish community in the northern North Sea (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999), which was later linked to fishing activity (Greenstreet and Rogers, 2006), how did the focus of attention become redirected towards the size structure of the North Sea fish community?

In 2001, OSPAR approached ICES for advice on identifying the most appropriate indicators of state on which to base an EcoQO for the North Sea fish community (Heslenfeld and Enserink, 2008). Aware that such indicators would be used to mitigate the adverse impacts of anthropogenic activity on the North Sea fish community, and therefore would have to be operational, ICES (2001a) established seven criteria by which to judge the effectiveness of candidate indicators when used within management frameworks such as the pressure-state-response (PSR) framework. These criteria were applied to indices of North Sea fish species diversity. Against two criteria, species diversity indices scored well, against a third, some concerns were noted, but against the remaining four criteria, species-diversity indices scored poorly (Table 1). In frameworks such as the PSR, understanding the linkage between indicators is critical. Species-diversity indices scored particularly poorly against criteria related to singular cause–effect relationships (ICES, 2001b).

Problems with species-diversity indices as indicators of "state"

Sensitivity to a manageable activity

Although fishing-induced declines in fish species diversity have been demonstrated (see above), other North Sea studies have demonstrated little or no long-term trend in species diversity (Piet and Jennings, 2005). Such inconsistencies led ICES (2001b) to conclude that species-diversity indicators, when applied to the North Sea fish community, were not always sensitive or responsive to changes in fishing regime.

Species-diversity indices are influenced by sample size (Magurran, 1988; Colwell *et al.*, 2004). Assessment of the sampling effort required to produce index values that adequately characterize the state of the community is therefore a necessary precursor to any study of species diversity (Soetaert and Heip, 1990; Boulinier *et al.*, 1998). Aggregation of at least 20 half-hour trawl samples may be required before estimates of species diversity stabilize and represent actual community diversity (Greenstreet and Piet, in press). Studies that demonstrated long-term, fishery-linked trends in demersal fish species diversity have generally followed such an approach (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Greenstreet and Rogers, 2006). Conversely, studies where such trends have not been observed have generally ignored the sample-size dependence of these indices, for example, reporting trends in the mean diversity of single trawl samples (Piet and Jennings, 2005).

With appropriate aggregation of samples, species-diversity indices are sensitive to changes in the fish community caused by fishing. However, the analytical complexities involved open diversity indices up to the criticism that they are not easily measured and may be inaccurate or error prone; one of the criteria that ICES (2001b) already identified as causing difficulty for these metrics (Table 1). Sample aggregation may also introduce additional problems. To answer temporal questions, samples collected across space will be aggregated. This could cause estimates of α (local point) diversity to become inflated through the inclusion of elements of β (habitat gradient) diversity (Whittaker, 1972; Lande, 1996; Kiflawi and Spencer, 2004). Analysis of North Sea International Bottom Trawl Survey (IBTS) data suggests that this becomes critical when the "search radius" for sample aggregation exceeds 50 km (Greenstreet and Piet, in press). Similar problems arise when addressing spatial issues and aggregating samples in time: estimates of "time-point" diversity may become inflated through the inclusion of elements of "time-trend" diversity (e.g. through species turnover; Hadley and Maurer, 2001; Adler and Lauenroth, 2003; Adler *et al.*, 2005; White *et al.*, 2006; Magurran, 2007; Shurin, 2007).

Tightly linked to a human activity

Fish landings from the North Sea almost tripled over the course of the 20th century (Daan *et al.*, 1990), but both positive and negative long-term trends in groundfish species diversity have been reported. Such inconsistency led ICES (2001b) to question whether changes in fish species diversity were actually linked to the increase in fishing pressure on the marine ecosystem. However, such disparities are predicted by community ecology theory. Huston's (1994) Dynamic Equilibrium Model (DEM) suggests that species diversity might be positively related with disturbance in regions of high productivity, whereas negative relationships should occur in areas of low productivity. Primary productivity is higher in the southern North Sea than in the northern North Sea (Reid *et al.*, 1990). Long-term increases in groundfish species diversity have tended to be recorded in the more productive southern North Sea (Rogers and Ellis, 2000; Piet and Jennings, 2005), whereas in the less productive northern North Sea, species diversity has generally declined (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Greenstreet and Rogers, 2006). At least qualitatively, these apparently disparate trends in fish diversity are therefore consistent with expectations from Huston's DEM.

Accepting this explanation, however, might require a reconsideration of what is involved in restoring biodiversity. Degraded communities in marine ecosystems subject to excessive anthropogenic activity may have both lower and higher species-diversity

Table 1. ICES criteria for a good Ecological Quality metric (after ICES, 2001a) and the scores achieved by indices of species diversity with respect to each criterion (ICES, 2001b).

Criterion	Score
Relatively easy to understand by non-scientists and those who will decide on their use	Moderate
Sensitive to a manageable human activity	Poor
Relatively tightly linked in time to that activity	Poor
Easily and accurately measured, with a low error rate	Poor
Responsive primarily to a human activity, with low responsiveness to other causes of change	Poor
Measurable over a large proportion of the area to which the EcoQO metric is to apply	Good
Based on an existing body or time-series of data to allow a realistic setting of objectives	Good

index values than would have been observed if the ecosystem were in a more natural state. Under certain circumstances, therefore, this may mean that remedial action intended to restore community biodiversity may actually result in a decline in species-diversity indices calculated at the community level.

Primarily responsive to a human activity

Most of the North Sea fish diversity studies cited so far are essentially correlative in nature, comparing temporal trends in species diversity with temporal trends in fishing activity. However, it is a well-known statistical axiom that correlation does not confirm a cause-and-effect relationship between pairs of variables. Because of this, and because the precise theoretical processes by which fishing disturbance might bring about changes in species diversity have yet to be elucidated, little evidence was available to ICES to suggest that species diversity in fish communities was primarily responsive to changes in fishing activity (ICES, 2001b). Other factors could equally well have been responsible for the observed trends in groundfish species diversity.

Although shedding no light on the mechanisms involved, a recent study by Greenstreet and Rogers (2006) addressed this issue through a combination of spatial and temporal analysis. They grouped 75 ICES rectangles in the northwestern North Sea, where otter trawling was the principal anthropogenic activity likely to influence the structure and composition of the fish community, into three fishing effort "treatments": high ($>$20 000 h year^{-1}), medium (5000–19 999 h year^{-1}), and low ($<$5000 h year^{-1}). Various diversity trends might be predicted for the three effort treatments, depending on whether groundfish species diversity was responsive primarily to fishing activity, to environmental influences, to both, or to neither. Analysis of Scottish August Groundfish Survey (SAGFS) data revealed that declines in groundfish species diversity in the northwestern North Sea were primarily a response to increased fishing pressure in the region (Greenstreet and Rogers, 2006).

Easily and accurately measured

Diversity indices are calculated on species abundance data, and such data are the main product of groundfish surveys. Such surveys have been carried out annually for decades, covering the entire North Sea as well as other ICES Areas. When assessing the suitability of diversity indices as indicators of state for the fish community, ICES's main concern with respect to this criterion focused on methodological issues. Over time, taxonomic skills have varied, resulting in variation in the extent to which rare species were identified, or variation in the taxonomic level to which difficult groups, such as gobies, were identified. Other factors, such as variation in trawl speed, trawl duration, or the extent to which particularly large samples were worked through, can affect resulting indices of species diversity.

But a further problem exists. All trawl gears are subject to catchability issues: catching different proportions of each species and, within species, catching different proportions of each size class of fish (Harley and Myers, 2001; Fraser *et al.*, 2007). Estimates of species diversity depend heavily on the fishing gear used. This has been demonstrated within a spatial context, comparing spatial patterns of groundfish species diversity derived from survey data obtained using different types of trawl gear (Fraser *et al.*, 2008). Therefore, major changes in survey fishing gear within a groundfish survey time-series could affect the interpretation of diversity trends profoundly. In 1997, the SAGFS essentially came to an end when, in the following year, the "48-ft Aberdeen trawl", which had been in use since the mid-1920s, was replaced by the "Grande Ouverture Verticale" (GOV) trawl, the standard IBTS gear.

Recently, catchability coefficients have been derived for every size class of each species sampled by the GOV between 1998 and 2004 (Fraser *et al.*, 2007). Application of these coefficients profoundly affected the resulting spatial patterns of groundfish species diversity (Fraser *et al.*, 2008), again illustrating the extent to which catchability can influence estimates of species diversity. In supporting management towards species-diversity-based EcoQOs for the fish community, could time-series of species-diversity indices based on "raw" groundfish survey data still provide reliable biodiversity indicators? There is an urgent need to address this question. If species composition does not change substantially, the answer could be yes. However, long-term changes in average life-history characteristics within the community have been demonstrated in the northern North Sea (Jennings *et al.*, 1999), suggesting that species composition in this region has changed as a result of fishing activity. This casts doubt on whether species-diversity indices can be used as operational indicators within an EcoQO management context, unless catchability can be taken into account.

Discussion

First, to answer the question posed by the title, it is obvious that European marine fishery scientists have not been oblivious to the issue of biodiversity. On the contrary, many studies examining species-diversity trends in the North Sea have been undertaken, and in many of these, the possible impacts of fishing have been considered. Only after full consideration of the information available at the time did ICES (2001a, b) conclude that species-diversity indicators could not be recommended as operational indicators to support an EcoQO-based EAMM.

At the time, the processes by which fishing influenced variation in the size structure of the fish community were better understood. Generally, large fish in the community suffer fishing mortality (Beverton and Holt, 1957), and declines in the abundance of large fish, which are frequently piscivorous (Hislop, 1997; Greenstreet *et al.*, 1998), result in reduced predation mortality among smaller fish (Kerr and Dickie, 2001). Population models used in the individual stock assessments, the foundation on which traditional, single-species fishery management is based, clearly illustrate the relationship between fishing mortality and age structure (and hence size structure) within each stock. The effects of fishing mortality on species with different life-history characteristics had also been clarified (Jennings *et al.*, 1998), so that observed reductions in populations of species characterized by large ultimate body length and concomitant expansions of small-bodied species (Jennings *et al.*, 1999) were entirely predictable. Finally, many studies had already demonstrated the anticipated long-term trends in the size structure of fish communities towards a community consisting of more small fish and fewer large fish (Rice and Gislason, 1996; Bianchi *et al.*, 2000; Zwanenburg, 2000). Consequently, ICES concluded that size-based metrics could provide reliable operational state indicators for the fish community (ICES, 2001a), and advice to this effect explains the Element of Ecological Quality that emerged from the 2002 North Sea Ministerial Conference.

Since then, however, the situation has changed. Compliance of size-based indicators with the seven ICES criteria is no longer quite so clear-cut (Shin *et al.*, 2005). Environmental and density-dependent effects on growth and recruitment may also affect metrics of fish size, regardless of the level of fishing activity (Ricker, 1995; Ottersen and Loeng, 2000; Lekve *et al.*, 2002). Poor recruitment, at least initially, may cause the average size of fish in a community to increase as populations become progressively dominated by older fish (Wilderbuer *et al.*, 2002). Conversely, increased rates of recruitment may cause the mean size of fish to decline or remain constant, even in the absence of overexploitation (Badalamenti *et al.*, 2002). Furthermore, in a more recent study, the criteria for the selection of state indicators have also been re-examined, placing much stronger emphasis on aspects of the ecosystem that have stimulated political concern (Rice and Rochet, 2005), once again raising the profile of biodiversity. But has the situation changed sufficiently that this issue might be addressed directly through the use of biodiversity state indicators?

Application of the original ICES (2001a) criteria to species-diversity indices allowed identification of the specific problems associated with these particular metrics. It is to be hoped that this paper demonstrates that, to some extent, these problems have been or can be addressed. Methodology needs to be standardized to ensure that the indices derived are indeed sensitive to anthropogenic drivers of change. However, in assessing the necessary levels of sample aggregation, problems associated with confounding different types of diversity will need to be resolved. It is clear that the issue of catchability in survey trawl gears can influence species-diversity analyses of groundfish survey data. How critical this is to time-series analysis has yet to be determined. However, catchability correction factors for some survey gears are starting to be produced, and experimental work investigating catchability in survey trawls is in progress. Therefore, soon, the extent of the problems caused by catchability can be thoroughly investigated. Although the biological processes underlying the relationship were not identified, the study by Greenstreet and Rogers (2006) provided the strongest evidence that, at least in the northwestern North Sea, fishing activity had been the principal factor driving change in demersal fish species diversity. However, exactly how fishing disturbance brings about changes in groundfish species diversity remains unclear; the precise mechanisms involved have yet to be identified. The brief consideration of community theory presented here suggests that the relationship between the two variables may well be complex. More than any other factor, this gap in our theoretical knowledge presents the largest obstacle to using species-diversity indices as operational state indicators. However, several multispecies, size-based simulation models have been published recently (Hall *et al.*, 2006; Pope *et al.*, 2006), and research along these lines provides the best opportunity to address this shortcoming.

To conclude, although the need for operational state indicators for biodiversity remains as strong as ever, the original conclusion of ICES (2001a, b) remains the correct one: we are still not in a position to use species-diversity indices as operational state indicators for the North Sea fish community. The ICES (2001a) approach of applying their seven criteria to candidate metrics provided the ideal mechanism by which to identify specific issues of concern. We have gone some way towards addressing these issues with respect to diversity indices, but finishing the job remains a priority for marine scientists.

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References

Adler, P. B., and Lauenroth, W. K. 2003. The power of time: spatio-temporal scaling of species diversity. Ecology Letters, 6: 749–756.

Adler, P. B., White, E. P., Lauenroth, W. K., Kauffman, D. M., Rassweiller, A., and Rusak, J. A. 2005. Evidence for a general species–time–area relationship. Ecology, 86: 2032–2039.

Badalamenti, G., Anna, G. D., Pinnegar, J. K., and Polunin, N. V. C. 2002. Size-related trophodynamic changes in three target fish species recovering from intensive trawling. Marine Biology, 141: 561–570.

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

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., *et al.* 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science, 57: 558–571.

Boulinier, T., Nichols, J. D., Sauer, J. R., Hines, J. E., and Pollock, K. H. 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology, 79: 1018–1028.

Colwell, R. K., Mao, C. X., and Chank, J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology, 85: 2717–2727.

Daan, N., Bromley, P. J., Hislop, J. R. G., and Nielsen, N. A. 1990. Ecology of North Sea fish. Netherlands Journal of Sea Research, 26: 343–386.

Fraser, H. M., Greenstreet, S. P. R., Fryer, R. J., and Piet, G. J. 2008. Mapping spatial variation in demersal fish species diversity and composition in the North Sea: accounting for species- and size-related catchability in survey trawls. ICES Journal of Marine Science, 65: 531–538.

Fraser, H. M., Greenstreet, S. P. R., and Piet, G. J. 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. ICES Journal of Marine Science, 64: 1800–1819.

Greenstreet, S. P. R., and Hall, S. J. 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. Journal of Animal Ecology, 65: 577–598.

Greenstreet, S. P. R., McMillan, J. A., and Armstrong, F. 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? ICES Journal of Marine Science, 55: 121–133.

Greenstreet, S. P. R., and Piet, G. J. Assessing the sampling effort required to estimate alpha species diversity in the groundfish assemblage of the North Sea. Marine Ecology Progress Series, in press.

Greenstreet, S. P. R., and Rogers, S. I. 2006. Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. ICES Journal of Marine Science, 63: 573–593.

Greenstreet, S. P. R., Spence, F. E., and McMillan, J. A. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish assemblage between 1925 and 1996. Fisheries Research, 40: 153–183.

Hadley, E. A., and Maurer, B. A. 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. Evolutionary Ecology Research, 3: 477–486.

Hall, S. J., Collie, J. S., Duplisea, D. E., Jennings, S., Bravington, M., and Link, J. 2006. A length-based multispecies model for evaluating community responses to fishing. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1344–1359.

Harley, S. J., and Myers, R. A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1569–1584.

Heslenfeld, P., and Enserink, E. L. 2008. OSPAR Ecological Quality Objectives: the utility of health indicators for the North Sea. ICES Journal of Marine Science, 65: 1392–1397.

Hislop, J. R. G. (Ed). 1997. Database report of the stomach sampling project 1991. ICES Cooperative Research Report, 219. 422 pp.

Huston, M. A. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press. 701 pp.

ICES. 2001a. Report of the ICES Advisory Committee on Ecosystems. ICES Cooperative Research Report, 249. 75 pp.

ICES. 2001b. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES CM 2001/ACME: 09. 102 pp.

Jennings, S., Greenstreet, S. P. R., and Reynolds, J. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68: 617–627.

Jennings, S., Reynolds, J. D., and Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London, Series B, 265: 1–7.

Johnson, D. 2008. Environmental indicators: their utility in meeting the OSPAR convention's regulatory needs. ICES Journal of Marine Science, 65: 1387–1391.

Kerr, S. R., and Dickie, L. M. 2001. The Biomass Spectrum: A Predator–Prey Theory of Aquatic Production. Columbia University Press. 352 pp.

Kiflawi, M., and Spencer, M. 2004. Confidence intervals and hypothesis testing for beta diversity. Ecology, 85: 2895–2900.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos, 76: 5–13.

Lekve, K., Ottersen, G., Stenseth, N. C., and Gjosaeter, J. 2002. Length dynamics in juvenile coastal Skagerrak cod: effects of biotic and abiotic factors. Ecology, 86: 1676–1688.

Magurran, A. E. 2007. Species abundance distributions over time. Ecology Letters, 10: 347–354.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Chapman and Hall, London. 192 pp.

Ottersen, G., and Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES Journal of Marine Science, 57: 339–348.

Piet, G. J., and Jennings, S. 2005. Response of potential fish community indicators to fishing. ICES Journal of Marine Science, 62: 214–225.

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

Reid, P. C., Lancelot, C., Gieskes, W. W. C., Hagmeier, E., and Weichart, G. 1990. Phytoplankton of the North Sea and its dynamics: a review. Netherlands Journal of Sea Research, 26: 295–331.

Rice, J., and Gislason, H. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES Journal of Marine Science, 53: 1214–1225.

Rice, J. C., and Rochet, J. 2005. A framework for selecting a suite of indicators for fisheries management. ICES Journal of Marine Science, 62: 516–527.

Ricker, W. E. 1995. Trends in the average size of Pacific salmon in Canadian catches. *In* Climate Change and Northern Fish Populations, pp. 593–602. Ed. by R. J. Beamish. Canadian Special Publication of Fisheries and Aquatic Sciences, 121. 739 pp.

Rogers, S. I., and Ellis, J. R. 2000. Changes in the demersal fish assemblages of British coastal waters during the 20th century. ICES Journal of Marine Science, 57: 866–881.

Shin, Y-J., Rochet, M-J., Jennings, S., Field, J. G., and Gislason, H. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science, 62: 384–396.

Shurin, J. B. 2007. How is diversity related to species turnover through time? Oikos, 116: 957–965.

Soetaert, K., and Heip, C. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Marine Ecology Progress Series, 59: 305–307.

White, E. P., Adler, P. B., Lauenroth, W. K., Gill, R. A., Greenberg, D., Kaufman, D. M., Rassweiler, A., *et al.* 2006. A comparison of the species–time relationship across ecosystems and taxonomic groups. Oikos, 112: 185–195.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon, 21: 213–251.

Wilderbuer, T. K., Hollowed, A. B., Ingraham, W. J., Spencer, P. D., Connors, M. E., Bond, N. A., and Walters, G. E. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Progress in Oceanography, 55: 235–247.

Zwanenburg, K. C. T. 2000. The effects of fishing on demersal fish communities of the Scotian Shelf. ICES Journal of Marine Science, 57: 503–509.

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