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Using size-based indicators to evaluate the ecosystem effects of fishing

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The usefulness and relevance of size-based indicators (SBIs) to an ecosystem approach to fisheries (EAF) are assessed through a review of empirical and modelling studies. SBIs are tabulated along with their definitions, data requirements, potential biases, availability of time-series, and expected directions of change in response to fishing pressure. They include mean length in a population, mean length in a community, mean maximum length in a community, and the slope and intercept of size spectra. Most SBIs can be derived from fairly standard survey data on length frequencies, without the need for elaborate models. Possible fishing- and environment-induced effects are analysed to distinguish between the two causes, and hypothetical cases of reference directions of change are tabulated. We conclude that no single SBI can serve as an effective overall indicator of heavy fishing pressure. Rather, suites of SBI should be selected, and reference directions may be more useful than reference points. Further modelling and worldwide comparative studies are needed to provide better understanding of SBIs and the factors affecting them. The slow response to fishing pressure reflects the complexity of community interactions and ecosystem responses, and prohibits their application in the context of short-term (annual) tactical fisheries management. However, movement towards longer-term (5−10 years) strategic management in EAF should facilitate their use.

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Introduction

Size of organisms is a central factor to key ecological processes, and changes in size distributions may have many causes, including environment-induced or genetic variability in life history characteristics, predator−prey relationships, or competitive interactions. More important, fishing is always size-selective. Targeting large fish, which are more valuable, modifies the size structure and functioning of fish assemblages, with consequences for productivity and resilience of some stocks. Therefore, size-based indicators (SBI: statistics summarizing the size distribution of fish assemblages and populations) may provide a relevant integration of the effects of fisheries on community structure and processes.

SBIs are typically used to describe the response of communities or individual populations to exploitation, and may contribute to the development of an ecosystem approach to fisheries (EAF; Garcia *et al.*, 2003) by considering a range of fisheries impacts greater than those on target species alone. Building up time-series of size-abundance data allows one to trace the history of fished assemblages, and to do so in a cost-effective manner, because size data are collected routinely in surveys and are often recorded for commercial catch returns. A variety of indicators can be developed from this single source of data

by calling on different theoretical considerations and different postulated mechanisms regarding fishing effects.

The usefulness and relevance of SBIs are assessed through a review of empirical and modelling studies. First, theoretical and empirical bases are presented. Then, their measurability (sampling constraints, availability of size data, potential biases), sensitivity to fishing effects, responsiveness (time of response), and specificity (discrimination of fishing and environmental effects) are evaluated and documented. Finally, some pragmatic propositions are made to improve the use and interpretation of SBIs in an EAF perspective.

Theoretical basis

Size and ecosystem functioning

The individual body mass of animals in marine communities spans 20 orders of magnitude, from bacteria supporting the microbial loop to whales filtering several tonnes of krill every day. Despite their variation in size, all organisms obey remarkably simple and consistent scaling laws that dictate how biological features change with size (Brown and West, 2000).

Most life history traits are correlated with size, which acts as a constraint on metabolic rates and energy assimilation, so influencing the entire lives of animals, including their growth, reproduction, and survival (Reiss, 1989). Species with smaller adult body mass are generally characterized by faster growth rates (Brey, 1999), higher natural mortality (Beverton and Holt, 1959; Pauly, 1980), greater reproductive output (Gunderson and Dygert, 1988; Charnov, 1993), recruitment, and production per spawning adult (Fenchel, 1974; Denney *et al.*, 2002). Consequently, production to biomass ratios (P:B) are inversely related to size (Banse and Mosher, 1980). Size differences within species also account for differences in growth, production, and mortality, smaller individuals growing faster and realizing more production per unit body mass, while suffering higher natural mortality (Jennings *et al.*, 2002b).

Foodweb processes in marine ecosystems are strongly related to size. The principal primary producers are small unicellular algae, and these support size-structured food chains, in which most predators are larger than their prey (Pope *et al.*, 1994). Trophic level is therefore expected to increase with increasing size. Recent studies using nitrogen stable isotope (δ^{15}N) as an index of trophic level have shown that δ^{15}N increases with the size of fish (Badalamenti *et al.*, 2002; Jennings *et al.*, 2002a, b), and of marine organisms in general (Fry and Quinones, 1994; France *et al.*, 1998). These results are consistent with the view that predator–prey relationships lead to powerful size-based trophic structuring. This may be seen even within the lifespan of individual fish, because body mass may increase by five or more orders of magnitude (Cushing, 1975), and a species may begin life as prey, only to become the main

predator on those species that it suffered from within its first year of life (Boyle and Boletzky, 1996).

Given the dominant role of size in marine ecosystems, there are compelling reasons to adopt size-based analyses to complement species-based analyses of marine foodwebs. Cannibalism, cross-predation, and transient predator–prey relationships (i.e. the consequences of opportunistic, size-based predation) are common features, but they are difficult to analyse and model on a species-by-species basis. Because size provides a proxy for trophic level, SBIs may be used to describe changes in trophic structure of communities.

Fishing leads to substantial modifications in the size structure of exploited communities. These changes may be captured by different SBIs (Table 1), reflecting both direct and indirect effects of fishing (Figure 1). The only data required are the size distributions of organisms. There are many ways of combining this simple information into an SBI for different processes at different levels of organization (individual, population, community).

Direct effects of fishing

There are several reasons why SBIs theoretically allow tracking of direct fishing effects on fish communities: (i) high-value, generally larger species are targeted through spatio-temporal fishing strategies; (ii) fishing gears are size-selective and often designed to remove larger fish and allow smaller ones to escape; (iii) older (and larger) fish in a population become fewer, because cohorts accumulate the effects of fishing mortality through time; and (iv) large-sized species are more vulnerable because they have lower potential rates of increase, and will be less able to withstand a given rate of mortality (Jennings *et al.*, 1998, 1999).

At a population level, the removal of larger fish may be reflected in changes in mean length or weight of population i in surveys ($\overline{L}_i$, $\overline{W}_i$), and in some index of maximum length $L_{max,i}$. (Because maximum observed length is highly dependent on sample size, upper quartiles such as $L_{90\%}$ or $L_{95\%}$ may be more robust.) Traditional single-species assessment models account for the reduction in mean size caused by increasing exploitation rate (Beverton and Holt, 1957). Stock indices, such as proportional stock density (PSD) or relative stock density (RSD), which are widely used in freshwater ecosystems, may also account for larger fish forming a smaller proportion of a population. Their calculation is based on reference lengths (Table 1), which have variously been defined as approximate length at maturity, minimum length effectively sampled by traditional fishing gears, or the minimum length of fish having recreational value (Willis *et al.*, 1993). The definition of reference lengths has been set almost exclusively from a recreational point of view, and their use would therefore have to be rigorously expanded in the context of commercial fisheries for stock indices to be useful for EAF.

At the level of a community, the simplest SBI accounting for fish removals is mean length or weight of all individuals

Table 1. Definition of size-based indicators, objectives, and reference directions of change (RD) under fishing pressure, based on theory and empirical evidence (B, total biomass; N, abundance; i, population index; L, length; W, weight). Empirical evidence refers also to models fitted to observations.

| Indicator/Notation	Description	Units	Objective	RD	Theoretical basis	Empirical evidence
Mean L (W) in community/$\overline{L}\left(\overline{W}\right)$	$\overline{L} = \sum_N L/N$, $\overline{W} = B/N$	cm, mm, (g)	Quantifies relative abundances of large and small individuals (including species composition)	↘	Rochet and Trenkel (2003)	Bellail et al. (2003); Dulvy et al. (2004); Nicholson and Jennings (2004)
Mean L (W) in population/$\overline{L}_i\left(\overline{W}_i\right)$	$\overline{L}_i = \sum_{N_i} L/N_i$, $\overline{W}_i = B_i/N_i$	cm, mm, (g)	Quantifies relative abundance of large and small individuals (recruitment)	↘	Beverton and Holt (1957)	Haedrich and Barnes (1997); Babcock et al. (1999); Bellail et al. (2003)
Mean length-at-age a in population i/$\overline{L}_{i,a}$	$\overline{L}_{i,a} = \sum_{N_{i,a}} L/N_{i,a}$	cm, mm	Reflects size and age structure of population, as well as differential growth rates caused by density-dependent effects and environmental conditions	↗	Beverton and Holt (1957); Parma and Deriso (1990); Walters and Post (1993)	Ross and Almeida (1986); Bowering (1989); Overholtz (1989); Overholtz et al. (1991); Rijnsdorp and van Leeuwen (1996); Shin and Rochet (1998)
Mean maximum length in community/$\overline{L}_{max}$	$\overline{L}_{max} = \sum_i N_i \overline{L_{max,i}}/N$ ($\overline{L}_{max,i}$, or alternatively $L_{inf,i}$, is fixed.)	cm, mm	Quantifies relative abundances of large and small species	↘		Jennings et al. (1999); Nicholson and Jennings (2004)
Maximum length in population i/$L_{max,i}$	Maximum observed length, or alternatively $L_{95\%}$	cm, mm	Quantifies depletion of large fish within a population	↘		
Mean L-at-maturity in population i/$\overline{L}_{mat,i}$	Length at which 50% of the population has attained maturity	cm, mm	Reflects differential growth rates caused by genetic variability, density-dependent effects, and environmental conditions	↗ ↘	Hutchings (1993); Reznick (1993)	De Veen (1976); Beacham (1983); Rochet (1998); Hempel (1978); Beacham (1983); Bowering (1989); Rijnsdorp (1993); Rowell (1993); Olsen et al. (2004)
Fulton's condition index in population i/K_i	$K = (W/L^3) \times 100$	10^2 g cm^{-3}	Reflects overall habitat quality for growth and reproduction	↗		Winters and Wheeler (1994)
Slope and intercept of length spectra (ls)/slope$_{ls}$, int$_{ls}$	Represented in log scales, ls are approximated by decreasing linear functions		Quantifies relative abundances of small and large fish and overall productivity of system	↘ ↗	Gislason and Rice (1998); Shin and Cury (2004)	Rice and Gislason (1996); Gislason and Rice (1998); Bianchi et al. (2000); Dulvy et al. (2004)
Slope and intercept of weight spectra (ws)/slope$_{ws}$, int$_{ws}$	Represented in log scales, ws are approximated by decreasing linear functions		Quantifies relative abundances of small and large fish and overall productivity of system	↘ ↗		Pope and Knights (1982); Pope et al. (1988); Murawski and Idoine (1992); Duplisea et al. (1997); Jennings et al. (2002a)
Slope and intercept of size diversity spectra (DS)/slope$_{ds}$, int$_{ds}$	Distribution of diversity (e.g. Shannon index) against fish size		Reflects species diversity along energy flow	?		Hall and Greenstreet (1996); Rice and Gislason (1996)
Proportional and relative stock density/PSD, RSD	$PSD = (Ni_{L \ge quality\ length})/$ $(Ni_{L \ge stock\ length}) \times 100$ $RSD = (Ni_{L \ge specified\ length})/$ $(Ni_{L \ge stock\ length}) \times 100$		Quantifies proportion of large fish in population	↘	Willis et al. (1993)	
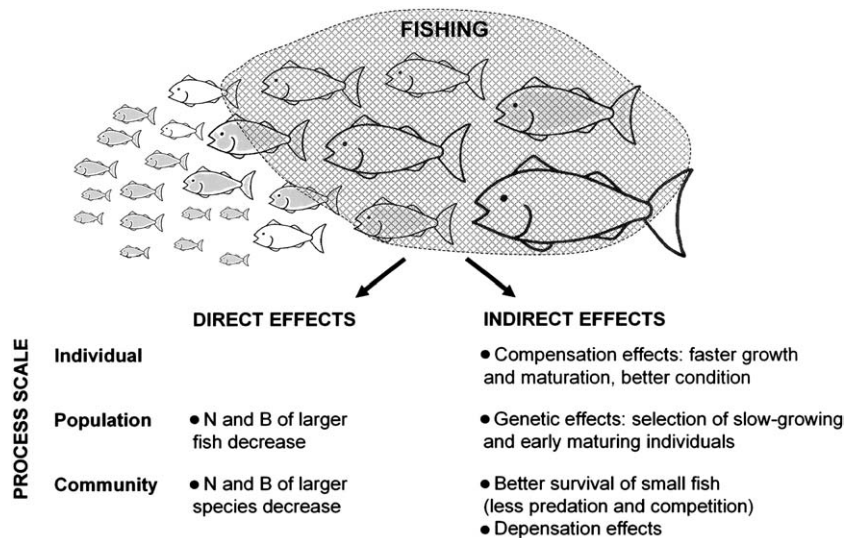
Figure 1. Theoretical direct and indirect effects of fishing on fish populations and communities (N: abundance, B: biomass).

therein. It aims at quantifying the combined changes in mean size within each population, and in the relative abundance of small- and large-bodied species. Mean length must be calculated on the basis of the total size distribution, in order to estimate the variance. In contrast, changes in $\overline{L}_{max}$ are used to quantify the relative abundance of small and large species, using a fixed maximum length of each species (Jennings *et al.*, 1999), rather than to reflect changes of intra-specific maximum size. For convenience, maximum size is sometimes expressed using the L_{inf} parameter of the von Bertalanffy growth equation (Jennings *et al.*, 2001). Other reported community SBIs refer to mean age and size at maturity (Jennings *et al.*, 1999). However, while these are based upon fixed life history parameters by species, they are not more informative than $\overline{L}_{max}$, because they do not account for phenotypic plasticity, but only for changes in the relative abundance of species with different life history parameters.

Among community SBIs, size spectra have attracted most empirical and theoretical work. However, their definition needs clarification because various representations are used. Where necessary, we will distinguish between length spectra, based on the distribution of log abundance against log median length by size class, and weight spectra, based on the distribution of log biomass against log median weight. The width of the size class used represents a compromise between the precision of available measurements, sample size, and the number of classes required to fit a suitable function. Spectra may be normalized by dividing abundance by size-class width, and Rochet and Trenkel (2003) recommend subtracting average length from length measures prior to performing a linear regression, to avoid correlations between parameter estimates.

In many instances, the shape of size spectra remains remarkably stable despite variable species compositions in

fish communities (Murawski and Idoine, 1992; Duplisea *et al.*, 1997; Bianchi *et al.*, 2000). This relative stability suggests that size-based interactions play a major role in regulating the dynamics of marine fish communities. The length-based spectrum, documented for many fish communities from different parts of the world's oceans (Rice and Gislason, 1996; Bianchi *et al.*, 2000), is usually described by a decreasing linear function. However, irregularities may occur, particularly among the smaller sizes, causing a curvature in the spectrum (Duplisea *et al.*, 1997; Bianchi *et al.*, 2000). Such curvatures are also observed in freshwater communities (Boudreau *et al.*, 1991; Sprules and Goyke, 1994), and their significance has been supported by modelling studies (Thiebaux and Dickie, 1992; Shin and Cury, 2004). Whether deviations from a linear spectrum result only from sampling bias or reflect higher predation mortality among small fish (or a combination of the two) remains an open question. However, when smaller sizes are excluded, size spectra generally have been considered as linear functions that can be characterized by their slopes and intercepts.

Several size-structured models have been explored in order to quantify the effects of fishing on emergent size spectra. The theoretical simulations of Gislason and Rice (1998), applying the length-based method of Sparre and Venema (1992) to 11 North Sea stocks, and basing the parameterization on Multispecies Virtual Population Analysis, suggest a linear relationship between fishing mortality (F) and both slope and intercept of the size spectrum. Expanding the model of Silvert and Platt (1978), which formalizes the flux of matter in a pelagic plankton community as a function of time and individual weight, and assuming that respiration and growth are allometric processes and (fishing and predation) mortality is a function of size, Benoît and Rochet (2004) suggest that fishing

effects may be better captured by the curvature of the size spectrum than by its slope. Based on simulations with an individual-based model in which predation is a size-based opportunistic process, and key processes of the life cycle (growth, reproduction, mortality) depend on food intake, Shin and Cury (2004) showed that slope and curvature of the size spectrum decrease quasi-linearly as a function of F.

By adding taxonomic information to the size spectra, diversity size spectra (DS) can be established, theoretically accounting for the removal of large species by fishing. The term DS has been applied to various measures. Rice and Gislason (1996) analysed trends in species diversity (expressed as Shannon's H′) against length classes. The observed DS were not linear, but those authors still chose to describe them in a simple way by their slope and intercept. Hall and Greenstreet (1996) found a simple power−law relationship between species richness (S) and the number of individuals within a size class (I). Plotting log S against log I gives a straight line that can be described by a slope and intercept. There is no consensus on how best to represent DS, because other totally different concepts have been formulated. For example, Ruiz (1994) calculated a Shannon diversity index over the size spectrum, considering each size class as the equivalent of a "species", and called it a DS. For a constant number of size classes, a lower index would indicate a lower "evenness" of the distribution of individuals among size classes.

Indirect effects of fishing

By removing large fish, fishing may also act indirectly on small fish by releasing predation pressure, so enhancing their survival (Figure 1). This indirect effect may be accounted for by a decrease in $\overline{L}$ and by an increased intercept and steeper slope of the size spectrum, whereas $\overline{L}_{max}$ would quantify the relative decrease in the abundance of "large" species. Such a response must be seen in the light of the "cultivation effects" theory stating that large species may be successful in unexploited communities, partly because the adults crop small forage species that represent potential competitors/predators of their own offspring (Walters and Kitchell, 2001). When fishing exerts a top-down effect by reducing the abundance of large species, subsequent increases in forage species may lessen juvenile survival of large species, thus inhibiting the rebuilding of depleted predator stocks. Such depensatory effects may accentuate the response of size-based indicators to fishing.

Compensatory responses at the level of individuals and populations are expected under fishing pressure (Figure 1). Exploitation is supposed to partly release stocks from intra-specific competition, and increase food availability. Life history parameters are remarkably plastic and change in response to the environment and food supply (Reznick, 1993). Short-term density-dependent responses, such as faster growth (increase in length-at-age) and improved condition, may be expected. Typically, morphometric and physiological (hepatosomatic and gonadosomatic) condition factors provide indices of well-being. Traditionally, Fulton's morphometric condition factor K has often been applied (Anderson and Neumann, 1996), which assumes isometric growth. However, concerns have been expressed about the use of condition factors for making comparisons within and among fish populations (Cone, 1989). Murphy *et al.* (1991) promoted the use of a relative (morphometric) weight index for inter-population comparisons, reflecting the average condition of a species over its entire geographical range. However, its calculation relies on standard values that have been estimated mainly for freshwater fish species (Blackwell *et al.*, 2000).

Fishing is also suspected of being selective with respect to heritable life history traits, causing exploited populations to evolve in response to harvesting (Law, 2000). Such selection may lead to reduction in the mean size of individuals and mean size or age at maturity, because slow growth is favoured if small and early maturing individuals have a higher probability of reproducing before being caught (Trippel, 1995). Recently, decreases in length at maturity have been reported that could be ascribed partly to fishery-induced genetic selection (Grift *et al.*, 2003; Engelhard and Heino, 2004; Olsen *et al.*, 2004).

Empirical evidence of sensitivity to fishing

Changes in the size composition of populations and communities are well documented using different SBIs. Spatial comparisons between areas subject to different fishing intensities, and temporal comparison within areas where fishing effort has increased over time, show responses that are generally consistent with theory. This allows assignment of reference directions of change to indicators (Table 1).

At a population level, mean size has been the subject of many empirical studies (Table 1 has a selection). In an analysis of survey data (1978−1993) in Newfoundland waters, the mean size of 31 of 34 (both target and non-target) species dropped drastically in the 1990s compared with the early 1980s (Haedrich and Barnes, 1997). Babcock *et al.* (1999) found substantial contrasts in $\overline{L}$ inside no-take reserves in New Zealand compared with fished areas.

Because interest in the mean size of fish communities is quite recent, empirical studies reporting historical temporal and spatial trends are few, although calculation of this index using existing data sets would be straightforward and informative. Other community indicators may account for a decrease in abundance of fish growing potentially to a large size. Jennings *et al.* (1999), examining long-term trends in 23 North Sea demersal species (1925−1996), showed a decrease in the average L_{inf} that can be attributed largely to a decline in the relative abundance of large species, such as cod (*Gadus morhua*; Cook *et al.*, 1997).

Several empirical studies have tracked community-level fishing effects on size spectra. Pope and Knights (1982) and Pope et al. (1988), using size spectra to contrast different ecosystems, suggested that the steeper slope observed in the North Sea was caused by higher exploitation than at the Faroe Bank and Georges Bank. Size spectra also allow detection of the effects of temporal changes in fishing intensity. Rice and Gislason (1996) suggested that the steepening of the spectrum slope for the North Sea fish community during the years 1973−1993 was related to increasing fishing pressure. Similar observations were made in an extensive study encompassing tropical to arctic ecosystems (Bianchi et al., 2000). Cross-system comparison suggested that slopes are less sensitive to fishing pressure in tropical regions (Bianchi et al., 2000), where growth rates are fast (Pauly, 1980). More explicitly than in the above-cited studies, Dulvy et al. (2004) found that spectrum slope for Fijian islands coral-reef fish communities was a linear decreasing function of an index of fishing intensity.

In contrast to the relatively clear patterns identified in size spectra, diversity spectra (DS) do not exhibit consistent responses to fishing intensity. In their study of the North Sea fish assemblage, Rice and Gislason (1996) expected changes in DS because larger, slow-growing species with a higher age at maturity should have been more vulnerable to fishing than smaller, faster-growing species. However, no overall trend could be detected for either slopes or intercepts. Using species richness as a measure of diversity, Hall and Greenstreet (1996) demonstrated a significant decline in the intercept between the periods 1929−1956 and 1981−1993, without an associated change in slope. Those authors concluded that the observed change reflected an overall, size-independent reduction in species richness.

Finally, a wealth of information demonstrates density-dependent changes in growth and maturation in major commercial fish stocks over time, in response to increased fishing (Trippel, 1995; Rochet, 1998; Law, 2000). Shin and Rochet (1998) suggest that changes in mean length-at-age of North Sea herring were mainly caused by fishing-induced changes in abundance. However, the observations on $\overline{L}_{mat,i}$ do not lead to a consensus view (Table 1). In a large comparative study across 77 fish stocks, Rochet (1998) showed that short-term fishing effects resulted in increased $\overline{L}_{mat,i}$, consistent with theory. However, many empirical single-stock studies indicate that $\overline{L}_{mat,i}$ decreases or remains stable under fishing pressure (Table 1; Rochet, 1998). These apparently conflicting results may be due to the confounding effects of phenotypic plasticity (of growth and maturation) and genetic selection for earlier maturing fish (Trippel, 1995; Rochet, 1998).

Measurement problems

Even indicators that are highly sensitive to fishing may be useful only if they can be measured easily and reliably.

Size-abundance (or -biomass) data are usually obtained from scientific surveys. This section (see also Table 2) examines how well SBIs may be estimated, based on criteria developed by Rice and Rochet (2005).

The main requirement is consistency of measurement. When dealing with diverse morphologies such as among invertebrates, weighing organisms may be more appropriate than measuring lengths, but when most organisms have similar morphologies, such as among fish, and assuming a well-defined and consistently applied protocol, lengths may be preferred to minimize measurement error and to avoid some of the seasonal variability (animals may temporarily lose weight, but rarely become smaller). At sea, measuring fish is often more accurate and less time-consuming than weighing them (Gutreuter and Krzoska, 1994; Anderson and Neumann, 1996), although equipment for the latter has improved considerably over the years.

The main problem is that information on size distribution of fish communities is almost universally derived from (trawl) catches, and that fishing gears are both species- and size-selective. The size composition of trawl catches depends not only on mesh size, but also on rigging, vessel speed, sediment type, light conditions, and any factor interacting with the behaviour and swimming ability of individual fish (Engas, 1994). Consequently, SBIs are sensitive to gear and rigging. For example, the size spectrum slope proved sensitive to survey design in a comparison of surveys carried out by different countries in the Celtic Sea deploying similar gear (Trenkel et al., 2004).

Although the variance in SBIs can be estimated easily, interpretation is not always straightforward because of the underlying assumptions. Variance in average size is a direct measure of dispersion, whereas variance in spectrum slope and intercept incorporates the adequacy of the model used. If exploitation increases the curvature of the size spectrum (Benoît and Rochet, 2004; Shin and Cury, 2004), the use of the slope as a descriptor is questionable. Owing to non-linearity, estimates of slope and intercept depend on the size range included in the analysis. Bias may occur if numbers of specific sizes are systematically over- or under-estimated. This is a direct and unavoidable consequence of gear selectivity (Willis et al., 1993). More generally, therefore, any SBI applies specifically to the fish assemblage sampled by the gear as employed in a specific survey design.

SBIs exhibit seasonal variability in response to variations in reproduction, recruitment, and growth (Willis et al., 1993; Blackwell et al., 2000). Because the underlying processes are influenced by environmental variability, however, lack of synchronization between annual surveys and seasonal events may cause interannual variability in SBI.

Size distributions of populations/communities may also be structured spatially (Willis et al., 1993; Greenstreet and Hall, 1996; Macpherson and Gordoa, 1996), so SBIs are representative of the area sampled, and consistent spatial

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Table 2. Data requirements, availability, and potential bias for different size-based indicators (SSG, sensitive to size and/or species selectivity of the gear).

Indicator	Data required	Availability	Potential sampling bias
Mean length in population	Survey time-series data	Usually; survey design often not consistent	SSG
Mean weight in population	ditto	ditto	SSG; if fish not weighted individually, no variance estimates
Stock density indices (PSD or RSD)	ditto	ditto	Probably SSG
Mean length in community	Survey time-series data; gear not too species-specific	Usually; survey design often not consistent	SSG
Mean weight in community	ditto	ditto	SSG; if fish not weighed individually, no variance estimates
Maximum length in population	Survey time-series data	ditto	Estimates depend on sample size
Fulton's condition index (population)	Individual weight and length in survey time-series data	Usually not measured or only for selected species	Bias towards commercial species
Mean maximum length in community	Catch time-series data, or survey time-series data	Usually; especially for commercial species	ditto
Mean length at maturity in community	ditto	Uncommon; relatively expensive	ditto
Size diversity	Survey time-series data; gear not too species-specific	Usually; survey design often not consistent	SSG; no distinction between changes towards smaller or larger sizes
Slope and intercept of length spectra	ditto	ditto	ditto
Slope and intercept of weight spectra	ditto	Requires conversion from length spectra by length/weight relationships	SSG; slope and intercept correlated

coverage is crucial when trying to establish temporal trends. This poses the important and universal problem of the identity of ecological units, which applies to all indicators used in ecosystem assessment (Grimm, 1998; Jax *et al.*, 1998): to appraise change in a system, the units to be examined have to be defined first. Whereas the appropriate unit is obvious for populations, for higher levels of organization, it is much less clear.

In summary, SBIs are easy to measure, but very dependent on the gear used, time, and location (Table 2). This restricts their interpretation to consistently collected time-series data, and across-system comparisons are often problematic. In specific cases, some progress may be expected for assessing gear selectivity by means of new visual methods for measuring animals underwater (van Rooij and Videler, 1996; Harvey *et al.*, 2002). Size spectrum slope and intercept pose a specific problem owing to the variance component relating to potential model misspecification. Other descriptors of size spectra, such as modal weight or shape, might be further examined (Duplisea and Kerr, 1995; Duplisea *et al.*, 1997).

Responsiveness and specificity

Ideally, the effects of management measures should be measurable within a time horizon of a few years. Therefore,

one desired feature of ecosystem indicators is great responsiveness (Garcia and Staples, 2000; Rochet and Trenkel, 2003). Changes in fishing mortality cannot be expected, however, to result in instant changes in SBI. Single-species models suggest that the direct effects of fishing may take at least one generation to become fully manifest in the size composition of a population, whereas indirect effects caused by intra- and inter-specific interactions may well take much longer to settle.

With a view to establishing a rigorous framework for the evaluation of responsiveness, Nicholson and Jennings (2004) tested the statistical power of a large-scale North Sea annual trawl survey to detect trends in some common SBIs. While such analyses provide useful information on historical changes in community structure, the power to detect meaningful trends within 10 years of monitoring was generally too low to provide effective support for short-term ecosystem-based management decisions. Similarly, Trenkel and Rochet (2003) tested the performance of a set of indicators for the Celtic Sea groundfish community during 4 years on the basis of the achieved precision of each estimate. Among population indicators, the estimated mean length of the catch was the most precise, and the corresponding tests had consistently large powers. At a community level, no significant trend was detected within 4 years, but spectrum slope appeared to be more sensitive to

changes in abundance of larger fish than mean size, possibly because each size class is given equal weight in estimating the slope (Jennings et al., 2002a).

SBIs may be expected to respond also to factors other than fishing. For example, temperature influences growth rates (Jones, 1976), and is correlated with weight-at-age among cod stocks (Brander, 1995). Some studies suggest, however, that in the short term, temperature is less influential than fishing-induced density-dependence (Tanasichuk, 1997; Shin and Rochet, 1998; Law, 2000). At a community level, Gislason and Rice (1998) suggest that temperature may theoretically change the spectrum slope. Based on simple simulations, they showed that when growth rates increase, the sensitivity of the slope to fishing decreases. Temperature variations, however, are expected to have differential growth effects on species exhibiting different temperature optima (Jobling, 1981). To disentangle environmental and fishing effects properly, it is necessary to evaluate their respective contributions systematically, both by the use of statistics and by the development of size-based models that integrate both types of effects.

Assuming bottom-up control (Cury et al., 2003), environmental factors also may affect fish communities indirectly by influencing primary productivity. Boudreau and Dickie (1992) and Kerr and Dickie (2001) suggest that intercepts of size spectra reflect the productivity of aquatic ecosystems. Some empirical studies support this idea. In an analysis of a worldwide set of 24 lakes and reservoirs, Cyr and Peters (1996) found a positive relationship between the intercepts of biomass size spectra of plankton communities and phytoplankton productivity. Using a cross-system comparison, Bianchi et al. (2000) showed that the most productive systems (northern Benguela, Angola, Eastern central Pacific) exhibit higher intercept values than the least productive systems (off East Africa, western Arabian Sea). In addition, simulations by Shin and Cury (2004) show that, on theoretical grounds, an increase in carrying capacity leads to a higher intercept, while the slope remains relatively stable.

Reference points

So far, few reference points (RPs) have been defined for SBIs, either as limits to be avoided or as targets for management. Rochet and Trenkel (2003) suggest that the average length of a species in the commercial catch may be used as an operational indicator because its meaning is clear, its response to fishing is well understood, and an appropriate RP might be set. Caddy and Mahon (1995) suggested that the RP be set higher than mean length at maturity, to ensure that at least half the individuals of a cohort caught have had a chance to spawn at least once. Because commercial catch data exclude discards, Trenkel and Rochet (2003) stress that species mean length may be more accurately measured from surveys.

RPs characterizing unfished situations would be useful for assessing fishing impacts, because the shifting baseline syndrome (Pauly, 1995) could be avoided. However, such RPs have little value as management targets, as long as resource use is deemed acceptable. Empirical studies of unexploited communities report values for the slope of weight spectra in the range from -0.2 to -1 (Platt and Denman, 1978; Banse and Mosher, 1980; Quinones et al., 2003). Assuming that weight is related to length cubed and that slopes are consistent over the entire ecosystem (Thiebaux and Dickie, 1992), this range should correspond to a slope between -4 and -6 for fish length spectra. Observed slopes for weakly to heavily exploited fish communities range from -4 to -10 (Rice and Gislason, 1996; Bianchi et al., 2000). Jennings et al. (2002c) and Jennings and Mackinson (2003) proposed a method to appraise the slope in unfished situations, based on the assumption that the rate at which available energy decreases with increasing weight depends on the mean predator:prey body mass ratio (estimated on the basis of diet or nitrogen stable isotope analysis; Jennings et al., 2002c), and the trophic transfer efficiency. Predictions of the slope of the unexploited size spectrum then can be compared with contemporary slope estimates to assess changes caused by fishing.

While RPs may not easily be agreed upon, empirical and corroborating modelling studies generally indicate in which direction SBI should move to reflect a less impacted system. Therefore, reference directions (RDs) may provide more useful medium-term management targets (Rochet and Trenkel, 2003; Jennings and Dulvy, 2005). Possible ways to use RDs in scientific advice are provided in comprehensive studies by Link et al. (2002) and Bellail et al. (2003). Link et al. (2002) promoted the concept of RDs as an ecosystem-level analogue to single-species RPs. The message is that we know whether heavy fishing leads to an increase or decrease of the different SBIs, and hence the direction to be avoided (Jennings and Dulvy, 2005).

Because SBIs integrate diverse, multi-fleet impacts, and are expected to exhibit time lags in their response to changes in exploitation, they would be best used for surveillance, rather than to support short-term management decisions. Trends counter to RDs should trigger analyses to identify their causes and to institute relevant management action.

Discussion

Like many other ecosystem indicators, SBIs are sensitive but not specific to fishing impacts. Although RDs can be established for most SBIs, changes in their values may have different interpretations. For example, a decrease in mean size at a population level may either point to overexploitation or to enhanced recruitment. Superimposed on the interplay between small and large fish is the

influence of the environment on growth rate. Such confounding effects may mislead the interpretation of observed change in indicator value. In assessing the effects of a 9-year trawl ban in the Gulf of Castellammare, mean length increased in only one species out of three investigated (Badalamenti *et al.*, 2002). Those authors suggested that the lack of the expected response in the other two species was due to increased recruitment.

To make interpretations less speculative, complementary information provided by different SBIs and by other indicators may be used. If an observed decrease in mean length in the population were caused by adverse environmental conditions, there should be a concomitant decrease in mean length-at-age and in condition factor (Figure 2). The difference between the latter two is that K_i reflects recent conditions whereas $\overline{L}_{i,a}$ integrates past conditions, at least for older age classes. Their use for discriminating between environmental and fishing effects, however, must be subject to caution, because the processes involved may be complex. Consider for example inter-specific competition. A reduction in population size in response to fishing pressure would influence growth rate only if food availability increases. However, another species sharing the same diet may have become more abundant (Law, 2000). In addition, according to the school-trap hypothesis, there may be detrimental effects on food availability if the reduction in biomass is too drastic (Bakun and Cury, 1999). Evaluating $\overline{L}_{i,a}$ and K_i is therefore advocated for highlighting possible causes of changes in $\overline{L}_i$, but a diagnosis of population state is not straightforward. Rather, we recommend investigating whether there has been a change in the proportion of large and small fish. If the abundance of large fish has decreased, $L_{max,i}$ is expected to decrease

concomitantly (Figure 2). To complement the analysis, it would be useful to evaluate trends in recruitment by means of an abundance index (e.g. survey cpue; Haedrich and Barnes, 1997; Bellail *et al.*, 2003). The simultaneous analysis of trends in $\overline{L}_i$, $L_{max,i}$, and abundance should facilitate proper diagnosis of population state. The potential outcome of such a trend comparison is summarized in Figure 3. The six realistically possible combinations have been coded according to three states: improving, uncertain, and deteriorating. Two cases show that looking at $\overline{L}_i$ alone can be misleading. In case 3, the abundance of large fish declined and that of small fish decreased even more steeply, suggesting growth- and recruitment-overfishing, a situation clearly to be avoided. Case 4 represents the opposite situation, where available evidence points to increased abundance of large fish and good recruitment, suggesting a population in good condition.

Similar reasoning applies when interpreting decreasing mean length at a community level. A decline would not necessarily indicate harmful effects of fishing if it was associated with a more-or-less stable $\overline{L}_{max}$, with no population in a critical state, and few with decreasing $L_{max,i}$.

Although RDs can be defined for most SBIs, they reflect many processes and therefore must be used cautiously, in a domain of validity constrained by the type of assemblage considered, by fishing configuration, and by environmental conditions. The main problem is to disentangle the different sources of variation. According to Bellail *et al.* (2003), the complexity of ecosystem or community processes has to be reflected in a multiplicity of indicators. Selecting a suite of complementary indicators and developing a rational framework for interpretation, to move towards an EAF, is challenging. Several SBIs are serious candidate indicators,

Figure 2. Possible causes leading to a decrease in mean length of population i ($\overline{L}_i$), and in mean length of the community ($\overline{L}$), as confirmed by complementary indicators (see text).

Figure 3. Six cases showing different reference directions for mean length ($\overline{L}_i$), maximum length ($L_{max,i}$), and an index of abundance of population i leading to different interpretations of population state (white, state improving; light grey, state uncertain; dark grey, state deteriorating; see also text).

because they meet essential prerequisites (Rice and Rochet, 2005):

  (i) Their definition and meaning are consensual within the scientific community, and the underlying processes can be understood intuitively by non-scientists.

  (ii) Because many ecological and fishing processes are strongly size-dependent, SBIs integrate much information on the state and functioning of exploited ecosystems.

  (iii) Using SBIs is cost-effective and straightforward. All can be calculated from roughly the same sources, yet still provide information at different levels of organization. Complex models are not required.

  (iv) The variety of size-based models developed to predict fishing effects on SBIs provides a unique opportunity to initiate cross-comparison of their output. As no single model can represent the complexity of natural ecosystems, and as multispecies and ecosystem models, whether size-based or not, cannot really be validated (Oreskes, 1998), applied ecology increasingly relies on the simultaneous use of independent models (Bouleau, 2002; Shin *et al.*, 2004). If they provide similar answers, SBI-based advice will gain confidence. If results diverge, comparison may help to identify gaps in knowledge, as well as to determine the range of possible trajectories of system dynamics.

  (v) SBIs are sensitive to variations in fishing intensity. Reference directions of change can be established on the basis of theoretical, empirical, and modelling studies. In some cases, response time may be improved by suitable selection of the most informative size classes, and by improving survey design (increased standardization and replication within strata). Although a slow response to changes in exploitation limits their use in the context of short-term, tactical fisheries management, the failure of conventional management systems to sustain fisheries has led to a strong movement towards strategic (5–10 year) approaches to managing fisheries (Butterworth and Punt, 1999; Geromont *et al.*, 1999; Smith *et al.*, 1999). In this context, SBIs score high for inclusion in the suite of indicators required for an EAF.

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