

# Assessing the sensitivity and specificity of fish community indicators to management action

Jennifer E. Houle, Keith D. Farnsworth, Axel G. Rossberg, and David G. Reid

**Abstract:** We assessed ten trophodynamic indicators of ecosystem status for their sensitivity and specificity to fishing management using a size-resolved multispecies fish community model. The responses of indicators to fishing depended on effort and the size selectivity (sigmoid or Gaussian) of fishing mortality. The highest specificity against sigmoid (trawl-like) size selection was seen from inverse fishing pressure and the large fish indicator, but for Gaussian size selection, the large species indicator was most specific. Biomass, mean trophic level of the community and of the catch, and fishing in balance had the lowest specificity against both size selectivities. Length-based indicators weighted by biomass, rather than abundance, were more sensitive and specific to fishing pressure. Most indicators showed a greater response to sigmoid than Gaussian size selection. Indicators were generally more sensitive at low levels of effort because of nonlinear sensitivity in trophic cascades to fishing mortality. No single indicator emerged as superior in all respects, so given available data, multiple complementary indicators are recommended for community monitoring in the ecosystem approach to fisheries management.

**Résumé :** Nous avons évalué dix indicateurs trophodynamiques de l'état des écosystèmes pour ce qui est de leur sensibilité et de leur spécificité à la gestion des pêches, en utilisant un modèle de communauté de poissons plurispécifique dont la distribution de taille est connue. Les réponses des indicateurs à la pêche dépendaient de l'effort et de la sélectivité en fonction de la taille (sigmoïde ou gaussienne) de la mortalité par pêche. La plus grande spécificité par rapport à une sélection de taille sigmoïde (semblable à celle du chalut) a été observée pour l'inverse de la pression de pêche et l'indicateur grands poissons, alors que pour la sélection de taille gaussienne, l'indicateur grandes espèces était le plus spécifique. La biomasse, le niveau trophique moyen de la communauté et de la prise et l'indice de pêche équilibrée présentaient la plus faible spécificité par rapport aux deux sélections de taille. Les indicateurs reposant sur la longueur pondérés par la biomasse plutôt que par l'abondance étaient plus sensibles et spécifiques à la pression de pêche. La plupart des indicateurs présentaient une réponse plus importante à la sélection de taille sigmoïde qu'à la sélection gaussienne. Les indicateurs étaient généralement plus sensibles à faible niveau d'effort, en raison de la sensibilité non linéaire à la mortalité par pêche dans les cascades trophiques. Aucun indicateur ne s'est avéré supérieur en tous points aux autres. Aussi, pour les données disponibles, il est recommandé d'utiliser plusieurs indicateurs complémentaires pour la surveillance des communautés dans le cadre d'une approche écosystémique à la gestion des pêches.

[Traduit par la Rédaction]

## Introduction

The aim of this work is to assess a set of trophic indicators for their sensitivity and specificity to changes in fishing management, using a standard engineering method, in support of indicator selection as recommended by Rice and Rochet (2005). Sensitivity measures how much an indicator would change if the community changed, while specificity measures the proportion of change in the indicator attributed to fishing compared with other causes. More technically, sensitivity is

defined as the marginal rate of change in indicator value with an underlying change in trophic structure of the community:  $\text{sensitivity} = dI/dc \cdot (c/I)$ , where  $I$  is the indicator value, and  $c$  is the value of an underlying community variable describing the distribution of biomass among trophic levels. Sensitivity is analogous to leverage and is termed elasticity in economics. Specificity measures the relative contribution of a fishing effort  $E$  to change in indicator value compared with all other causes:  $\text{specificity} = (\partial I / \partial E) / (dI/dc)$ . This is analogous to a regression coefficient for fishing within a multivariate nonlinear regression analysis with all causes of trophic change included among explanatory variables. A good indicator will display both high sensitivity and specificity to fishing in trophic distribution; this best ensures that changes are detected and correctly attributed to fishing.

We assess the sensitivity and specificity of indicators using a test signal approach, which seeks to isolate the performance of indicators using fundamental, simple, fishing size selection functions as inputs rather than seeking to replicate particular fishing scenarios. This is analogous to testing a complex electronic circuit with a simplified signal, for example, a sine wave, to allow the understanding of the response of the

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system to a fully understood input with known properties. Since the ecosystems approach to fisheries management (EAFM; e.g., Garcia et al. 2003) is primarily concerned with understanding how the ecosystem changes in response to fishing, it is important that indicators used for EAFM are sensitive and specific to fishing to ensure that the signals obtained from the indicators are attributable to corresponding changes in fishing. For this study we used only two fishing patterns. We acknowledge that many other possibilities exist and could be tested in the same way, but to illustrate the approach, we opted for these particular patterns.

The rise of ecosystem-based approaches for fisheries management has drawn attention to potential changes in the trophic structure of fished communities. As fisheries for larger, predatory fish become overexploited and collapse, their prey become the target; thus, the food web is effectively “eroded” (sequential removal from one end) through the removal of the largest fish and then the subsequent targeting of their prey. This erosion of the food web was memorably highlighted by the phrase “fishing down marine food webs” (Christensen 1996; Pauly et al. 1998), which referred to landings. “Fishing down” is only one of several scenarios in which fishing may affect marine community size structure, two alternatives being “fishing through” (Essington et al. 2006) and profit-maximizing species-specific (Sethi et al. 2010), against which the mean trophic level of the catch indicator has been assessed (Branch et al. 2010). More complex changes to community size distributions, which in turn affect trophic structure, have now been attributed to fishing, for example, the trophic cascades observed by Frank et al. (2005) and explained using a size-structured community model by Andersen and Pedersen (2010). Trophodynamic changes are inherently multivariate and depend on many complex relationships to be found within the marine community, which is why Greenstreet et al. (2011) called for “operational theoretical size-resolved multi-species fish community models to support management towards broader ecosystem objectives”.

Practitioners of EAFM would ideally have community-level indicators that are sensitive to a wide variety of trophic distortions caused by fishing. Empirical studies (e.g., Jennings et al. 2002; Shin et al. 2005; Blanchard et al. 2010) are able to identify some temporal trends in some relevant indicators, but these are affected by multiple unresolved drivers (not just fishing). This effectively rules out the assessment of specificity, one of the general indicator selection criteria established by Rice and Rochet (2005). Model-based studies can make a valuable contribution to indicator selection by isolating the causes of simulated community change within controlled test bed conditions.

The present work develops beyond previous, less general modelling studies of ecological indicators (e.g., Fulton et al. 2005; Pope et al. 2006; Travers et al. 2006) in two main respects. The first is by quantifying not only the sensitivity of indicators to changes in fishing pressure, but also their specificity to fisheries management. Specificity (defined earlier) indicates the confidence with which a manager may attribute a change of indicator value to catch management, rather than to natural processes. We estimate it by calculating the signal-to-noise ratio of the indicator; a change of fishing provides the signal and stochastic variation of all our community parameters provides the noise. Second, by using a freely dy-

namic size-based model of the community, we are able to capture the complex intertrophic dynamics of the community response to fishing. The model dynamics are unconstrained, and hence, free. Growth is food-dependent rather than fixed, and recruitment is density-dependent rather than fixed, which allows nonlinear effects to emerge, in contrast with the relatively constrained dynamics employed by previous models (e.g., Fulton et al. 2005; Hall et al. 2006; Pope et al. 2006).

Marine communities typically exhibit correlations between body size and trophic level (Jennings et al. 2001, 2007), so changes in their size structure are assumed to indicate distortion of food webs (Rochet and Trenkel 2003). We use a fish community model that resolves both species and individual body size to capture both the growth and mortality sides of trophic interaction. This is based on size spectrum theory, which derives the abundance of species as a function of individual size and asymptotic size using physiology and predator-prey interactions, such that there are more small organisms than large organisms, and was developed by Andersen and Beyer (2006) and operationalized by Hartvig et al. (2011). This model was recently used in the analysis of trophic responses to size-selective fishing scenarios (Andersen and Pedersen 2010) and used in a homogenous (not species resolved) form by Rochet and Benoît (2012) to demonstrate some of the complex behaviours of community size structure in response to fishing. It is one of a new generation of “mass-flow” models in which biomass flows are accounted for using the M’Kendrick–von Foerster equation (see, e.g., Benoît and Rochet 2004), such that both the marine size spectrum and trophic dynamics can be faithfully represented. This is an important development beyond previous size-structured, multi-species models (e.g., Hall et al. 2006) in which fixed growth rates and fixed recruitment meant that only the mortality side of species interactions was accounted for. That and other similar examples, such as the Atlantis model used by Fulton et al. (2005), are less suitable than the mass-flow models for testing indicators of specifically trophodynamic effects, though the Atlantis model has many useful features, such as spatial representation, not needed for the present study.

Our testing of indicators is set in the engineering framework known as system identification, which isolates the dynamic response of the system (a temperate marine fish community) to a specific input test signal (fishing pressure), measured through the ecological indicators. We take size selectivity of fishing and fishing effort as the “control levers” of fisheries management. Gaussian and sigmoid size selection (mortality) curves are used over a range of fishing efforts to create a set of systematic test signals for the indicators under inspection. It is not necessary (or even desirable) to represent complex body size – fishing mortality relations for system identification; in the engineering context, simplified test signals are found most informative. Mathematically, any real mortality profile can be constructed from a linear combination of elemental signal forms (much exploited in acoustics), but comparison among indicators requires a clear and simple test.

In the model of Hartvig et al. (2011), fish species are defined by the single trait of maturation size (the other physiological traits being correlated with this). Using this, we built a test community from model species with maturation sizes matching those of the most abundant species in the North

Sea to provide some realism. The community follows a log-normal distribution of maturation lengths, consistent with that of marine fish species (Shin and Cury 2004). The output from this size-based community model is a biomass size spectrum (Sheldon and Parsons 1967; Sheldon et al. 1972), resolved by model species and individual body size. This output shows how fishing changes the size structure of a model marine community and how this change is detected by trophodynamic indicators.

We use our test system to examine indicators, as they were originally defined, except for length-based indicators, where we also examine the effect of changing from abundance to biomass weightings. All the indicators we examine have previously been suggested for EAFM and, in the main, are expected to meet the criteria of Rice and Rochet (2005).

## Materials and methods

### The model community

The fish community size-resolved model described in Hartvig et al. (2011) was used in all our simulations, and a detailed description can be found there. Mechanistic processes that occur at the individual level, metabolism, food encounter, reproduction, and growth are dynamically represented in the model. The community is constructed from a set of modelled populations, together with an unstructured resource spectrum representing plankton as food for the smallest individuals in the community. A fish species is defined by its maturation size  $m_*$ , the body mass at which individuals of that species begin to allocate energy for reproduction. For each species  $i$ , size-structured population dynamics are described by a M'Kendrick–von Foerster partial differential equation (M'Kendrick 1926; von Foerster 1959):

$$(1) \quad \frac{\partial N_i}{\partial t} + \frac{\partial}{\partial m}(gN_i) = -\mu N_i$$

A system of these equations accounts for the dynamic balance in biomass between growth ( $g$ ) and mortality ( $\mu$ ) throughout the community, where  $N_i$  is the size spectrum describing the population structure of species  $i$ . Equations governing relationships among growth rate and feeding rate, reproductive output, and mortality rate follow Hartvig et al. (2011). Reproduction provides the lower boundary condition through a dynamically population-dependent Beverton–Holt (Beverton and Holt 1957) recruitment relation. This is more biologically justifiable than the piecewise linear recruitment function (Barrowman and Myers 2000) used by Andersen and Pedersen (2010), and it avoids discontinuity that could cause computational artefacts. Prey size selection is modelled with an asymmetric bell curve that reflects the empirical findings that (i) the selection window extends further into small sizes than large (Pinnegar et al. 2003) and (ii) the minimum prey size changes less with predator size than does the maximum prey size (Scharf et al. 2000; Floeter and Temming 2005). We set the below-peak tail of the size preference curve to be twice the width of the above-peak tail (see eq. A.1, Table A1, Appendix A).

The model was run for 100 years without fishing to ensure a steady state before the fishing treatment was applied. It was run for a further 100 years under the treatment, long enough

to ensure equilibrium in a fished state (note this does not imply that we assume fishing is constant for 100 years; it is a test signal). Indicator values were computed as the means of the indicator values from the final 20 years of the simulation (where steady state prevails). The model was discretised using the semi-implicit upwind finite difference method (Press et al. 1992), as detailed in Hartvig et al. (2011), with 202 logarithmically evenly spaced mass classes and a time step of 0.02 years. This method approximates the M'Kendrick–von Foerster equation by building up the number density size spectrum over time using a backward difference to approximate the derivative with respect to body mass.

The test community assembly was constructed with the 31 most abundant North Sea fish species by trawl survey biomass (Jennings et al. 2002), excluding the skate, ray, and shark species, for a total of 27 model species. Elasmobranchs were excluded as their life history, particularly their reproductive strategy, substantially differs from bony fish, which are the focus of the model. Average maturation lengths and allometric conversions to maturation mass were obtained from FishBase (Froese and Pauly 2010) for each of the 27 species. Species, maturation lengths, maturation masses, and allometric conversions are detailed in Appendix C, Table C1. Within the fishing model, a typical allometric conversion from length to mass (Peters 1983) was used to apply the same fishing size selectivity by body mass to all species, in keeping with the simplicity of the model.

### Models of fishing

Two fishing size selectivity types were examined: sigmoid selectivity for large fish and Gaussian selectivity for a narrow range of fish sizes. A sigmoid selectivity curve, approximating a trawl net, describes the probability of capture as a function of fish length, given contact with the gear (Millar and Fryer 1999):

$$(2) \quad f(l) = \left[ \frac{\exp(\text{SF} \cdot l - \text{MS})}{1 + \exp(\text{SF} \cdot l - \text{MS})} \right]$$

The length at 50% selectivity is  $L_{50} = \text{MS}/\text{SF}$ , where MS is the mesh size and  $1/\text{SF}$  is the selection factor (Millar and Fryer 1999; Piet et al. 2009). We represent a mesh size of 10 cm giving  $L_{50}$  of 30 cm, where  $\text{MS} = 10$  cm and  $\text{SF} = 1/3$ , which is the average  $L_{50}$  for North Sea cod, haddock, sole, and whiting (Piet et al. 2009) with typical gear.

Fishing mortality is expressed as an instantaneous rate ( $\text{year}^{-1}$ ), as follows. Let the catch of fish in length class  $dl$  be  $C(l)dl = A \cdot f(l)u(l)dl$ , where  $f(l)$  is the probability of capture by the gear,  $A$  is the area swept by the gear, and  $u(l)$  is the density of individuals in the path of the gear. Differentiating gives the catch rate by length:

$$\frac{dC(l)}{dt}dl = \frac{dA}{dt}f(l)u(l)dl$$

The instantaneous fishing mortality rate  $F$  is then

$$F = \frac{dC(l)dl}{dt} / \left( \Omega u(l)dl \right) = \frac{f(l)}{\Omega} \frac{dA}{dt}$$

where  $\Omega$  is the area occupied by the entire fish population. Fishing effort  $E$  is defined as  $\Omega^{-1}(dA/dt)$ , the cumulative proportion of sea area swept per unit time, so  $E = \frac{F}{f(l)}$ . Since

**Table 1.** Ecological indicator definitions.

Name	Symbol	Basis	Definition	Source
Large fish indicator	LFI	Survey	$\frac{\sum_m B_m(L > 50 \text{ cm})}{\sum_m B_m}$	Cury et al. 2005; Greenstreet et al. 2011
Large species indicator	LSI	Survey	$\frac{\sum_i B_i(L_{\max} > 85 \text{ cm})}{\sum_i B_i}$	Shin et al. 2010; Shephard et al. 2012
Mean trophic level (community)	$\overline{TL}$	Survey	$\sum_i TL_i \cdot \frac{B_i}{B}$	Christensen 1998
Mean trophic level (catch)	$\overline{TL}_{\text{catch}}$	Catch	$\sum_i TL_i \cdot \frac{Y_i}{Y}$	Yang 1982
Fishing in balance	FiB	Catch	$\log\left(\frac{Y_t}{TE^{TL_t}}\right) - \log\left(\frac{Y_0}{TE^{TL_0}}\right)$	Pauly et al. 2000
Mean body length	$\overline{L}$	Survey	$\sum_m L_m \cdot \frac{N_m}{N}$ or $\sum_m L_m \cdot \frac{B_m}{B}$	Rochet and Trenkel 2003
Mean body length in catches	$\overline{L}_{\text{catch}}$	Catch	$\sum_m L_m \cdot \frac{C_m}{C}$ or $\sum_m L_m \cdot \frac{Y_m}{Y}$	Rochet and Trenkel 2003
Mean maximum body length	$\overline{L}_{\max}$	Survey	$\sum_i L_{\max, i} \cdot \frac{N_i}{N}$ or $\sum_i L_{\max, i} \cdot \frac{B_i}{B}$	Jennings et al. 1999; Greenstreet and Rogers 2006
Inverse fishing pressure	InvF	Survey, Catch	$1/(Y/B)$	Shin et al. 2010
Biomass	$B$	Survey	$B$	Cury et al. 2005; Fulton et al. 2005

**Note:**  $B_m$  is biomass of individuals in a body size class centred at mass  $m$ ,  $B_i$  is biomass of individuals of species  $i$ ,  $TL_i$  is trophic level of individuals of species  $i$ ,  $B$  is the total biomass of the community,  $Y_m$  is the biomass of fish caught in size class  $m$ ,  $Y_i$  is the biomass of fish caught of species  $i$ ,  $Y$  is the total biomass of the catch,  $TE = 0.1$  is trophic efficiency,  $L_m$  is the length (cm) of an individual in size class  $m$ ,  $N_m$  is the abundance of individuals of size class  $m$ ,  $N$  is the abundance of all individuals in the community,  $C_m$  is the abundance individuals in size class  $m$  in the catch,  $C$  is the abundance of all individuals in the catch,  $L_{\max, i}$  is the maximum asymptotic length (cm) of species  $i$ ,  $N_i$  is the abundance of individuals of species  $i$ . Mean trophic level of the catch and fishing in balance are catch-based indicators but require knowledge of species' trophic levels.

these are model fish, we converted from length to mass using a simple allometry:  $m = \rho l^3$ , with  $\rho = 0.01 \text{ g}\cdot\text{cm}^{-2}$  (Peters 1983), independent of species. With these definitions, the instantaneous rate of fishing mortality for sigmoid selectivity ( $F_S$ ) as a function of body mass is expressed as

$$(3) \quad F_S(m) = E \cdot \left\{ \frac{\exp[\text{MS} + \text{SF}(\rho^{-1}m)^{1/3}]}{1 + \exp[\text{MS} + \text{SF}(\rho^{-1}m)^{1/3}]} \right\}$$

Gaussian selectivity (e.g., gill net-like) describes the probability of capture as a function of fish length, given that it contacted the gear (Millar and Fryer 1999), thus

$$(4) \quad f(l) = \exp\left[-\frac{(l - \text{LP})^2}{2\text{SD}^2}\right]$$

in which LP is the length at which the curve peaks and SD describes its width as a standard deviation. Parameter values of LP = 81 cm and SD = 11.3 cm from Revill et al. (2007) were used in this relation to represent Irish–Cornish offshore hake gill nets with a 120 mm mesh size (for a realistic example). Again, these must be transformed to an instantaneous rate of fishing mortality  $F$  to give the instantaneous rate of fishing mortality for Gaussian selectivity ( $F_G$ ) as a function of body mass:

$$(5) \quad F_G(m) = E \cdot \exp\left\{-\frac{[(\rho^{-1}m)^{1/3} - \text{LP}]^2}{2\text{SD}^2}\right\}$$

### The indicators

The indicators examined are listed in Table 1. They have all been proposed as potentially meeting the Rice and Rochet (2005) criteria for one or more particular ecosystems. These indicators relate to a range of management objectives, including conservation of biodiversity, maintaining ecosystem structure and function, and maintaining resource potential (Shin

et al. 2010). In the case of indicators conventionally weighted by abundance (mean length of fish in the community and catch; mean maximum length of fish in the community), we also calculated their values using a biomass weighting.

Trophic level per species has been calculated following the method of Levine (1980) from a diet composition matrix  $\mathbf{D}_{ij}$ , specifying the proportion of species  $i$  consumed by species  $j$ , including the proportion of diet from a “background resource spectrum” in the first column of the matrix. According to this method, the trophic level of a fish of species  $j$  is the mean trophic level of its prey plus one, so that trophic level is calculated by solving a linear algebraic system. The base of the food web,  $TL = 1$ , are autotrophs, and the model resource spectrum representing zooplankton has a trophic level of approximately 2 to 3. Trophic level was calculated separately for each fishing selectivity and effort level, since these may influence diet compositions.

### Stochastic sensitivity testing

Stochastic noise was introduced into simulations to examine indicator performance in the presence of uncertainty, whereby community state is influenced by random environmental and ecological changes (unrelated to fishing). For each scenario (community type combined with fishing gear), every level of fishing effort  $E$  was simulated with 100 stochastic replicates to build a population distribution for all the indicators examined. For each simulation, the model parameters  $\alpha$  (assimilation efficiency),  $h$  (coefficient of maximum food intake),  $n$  (exponent for maximum food intake),  $k$  (coefficient of standard metabolism),  $p$  (exponent for standard metabolism),  $\beta$  (preferred predator–prey mass ratio),  $\sigma_1$  (left width of size selection function),  $\sigma_2$  (right width of size selection function),  $\gamma$  (coefficient of volumetric search rate),  $q$  (exponent for volumetric search rate),  $\eta_*$  (size at maturation relative to asymptotic size),  $u$  (width of maturation selection function),  $\mu_0$  (coefficient of background mortality), and  $\varepsilon$  (efficiency of offspring produc-

**Table 2.** Summary of model parameters.

Symbol	Value	Unit	Parameter	Source
<b>Encounter and growth</b>				
$\alpha$	0.6	—	Assimilation efficiency	Kitchell et al. 1977
$h$	85	$\text{g}^{1-n} \cdot \text{year}^{-1}$	Coefficient of maximum food intake	Andersen and Riis-Vestergaard 2004
$n$	3/4	—	Exponent for maximum food intake	$0.6 < n < 0.8$ (Jobling 1994); 3/4 is used to match the exponent of standard metabolism $p = 3/4$
$k$	10	$\text{g}^{1-n} \cdot \text{year}^{-1}$	Coefficient of standard metabolism	Including coefficient of fish consumption (Peters 1983) and activity multiplier (Andersen and Riis-Vestergaard 2004) corrected to temperature of 10 °C (Clarke and Johnston 1999)
$p$	3/4	—	Exponent of standard metabolism	West et al. 1997
$\beta$	100	—	Preferred predator-prey mass ratio	Ursin 1973; Jennings et al. 2001
$\sigma_1$	2	—	Left width of size selection function	Scharf et al. 2000; Pinnegar et al. 2003; Floeter and Temming 2005
$\sigma_2$	1	—	Right width of size selection function	Scharf et al. 2000; Pinnegar et al. 2003; Floeter and Temming 2005
$\gamma$	40 000	$\text{m}^3 \cdot \text{g}^{-q} \cdot \text{year}^{-1}$	Coefficient of volumetric search rate	Derived, see Appendix B
$q$	0.8	—	Exponent for volumetric search rate	Ware 1978
$\eta^*$	0.25	—	Size at maturation relative to asymptotic size	Beverton 1992
$u$	10	—	Width of maturation selection function	Set so that the transition width from not reproducing to all surplus energy for reproduction (from 0 to 1) is 5 years
<b>Mortality</b>				
$\mu_0$	0.84	$\text{g}^{1-n} \cdot \text{year}^{-1}$	Coefficient of background mortality	Set so that the background mortality of a fish with a 5 kg maturation size is 0.1 year <sup>-1</sup>
<b>Resource spectrum</b>				
$\kappa_R$	0.005	$\text{g}^{1-n+q} \cdot \text{m}^{-3}$	Magnitude of the resource spectrum	Rodriguez and Mullin 1986
$r_0$	4	$\text{g}^{1-n} \cdot \text{year}^{-1}$	Coefficient of regeneration rate of resources	Savage et al. 2004; temperature 10 °C
$m_{\text{cut}}$	0.5	g	Upper mass limit of resource spectrum	The largest size preference of the smallest individual, $m_{\text{cut}} = 10^{\sigma_2} \beta m_0$
<b>Reproduction</b>				
$m_0$	0.5	mg	Offspring mass	From an egg diameter of 1 mm (Wootton 1979; Chambers 1997)
$\varepsilon$	0.1	—	Efficiency of offspring production	Calculated from the empirical gonado-somatic index (Gunderson 1997)
<b>Fishing</b>				
MS	10	cm	Sigmoid selectivity, mesh size	Piet et al. 2009
SF	1/3	—	Sigmoid selectivity, selection factor	Piet et al. 2009
LP	81	cm	Gaussian selectivity, length at curve peak	Revill et al. 2007
SD	11.3	cm	Gaussian selectivity, curve standard deviation	Revill et al. 2007

tion) were randomly varied by adding normally distributed noise with mean of zero and a standard deviation of 5% from the default parameter value (Table 2). The noise introduced was therefore proportional to each parameter. Occasional failures of simulated communities (due to implausible parameter values) were replaced. Fishing effort was varied in increments of  $\Delta E = 0.1 \text{ year}^{-1}$  from  $E = 0$  to  $1.5 \text{ year}^{-1}$  inclusive. Results for each indicator were plotted as functions of effort imposed for each fishing selectivity type.

## Results

### Effect of fishing on community size structure

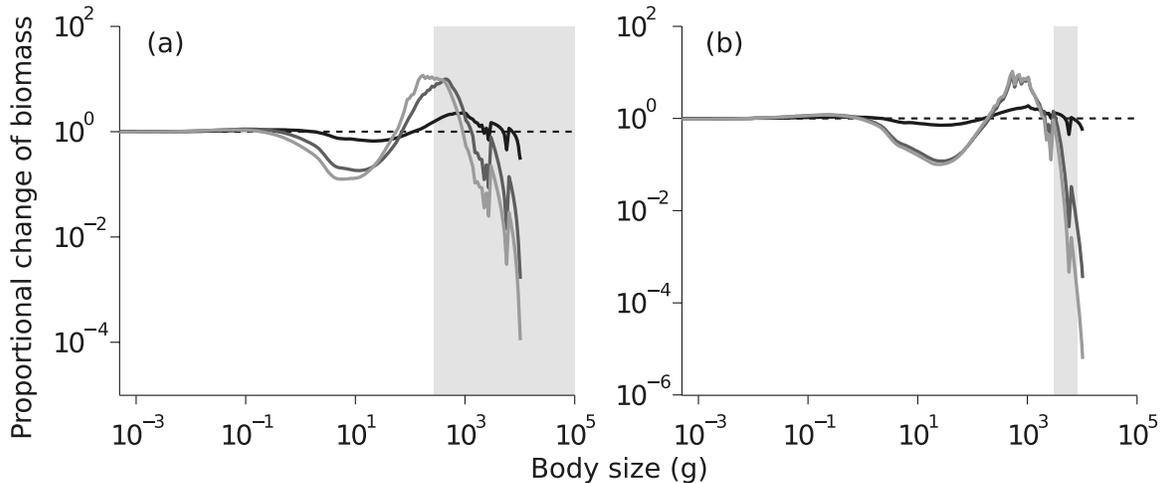
The community size structure is distorted by fishing, as shown by the relative change in biomass per size class in each scenario from the low ( $E = 0.1 \text{ year}^{-1}$ ), medium ( $E = 0.8 \text{ year}^{-1}$ ), and high ( $E = 1.5 \text{ year}^{-1}$ ) levels of effort tested (Fig. 1). Trophic cascades appear as prominent waves, apparently related to the depletion of targeted large fish. For both

sigmoid and Gaussian selectivity, the largest individuals are near-fully depleted by fishing at medium and high levels of effort. The effect of fishing on the biomass size spectrum is nonlinear in the sense that unit change in the biomass size spectrum increased as effort declined. (Note that the sawtooth structure in the curves is caused by the diminished biomass in the tails of individual species' biomass size spectra.)

### The response of ecological indicators

Qualitative comparison of indicators shows that they were generally more responsive to changes in effort  $E$  using sigmoid selectivity than using Gaussian selectivity (Fig. 2). For every indicator, increasing fishing effort increased the indicator response, though not linearly. Community biomass turned out to be resilient to fishing, implying that as an indicator it suffered high uncertainty; a trend only emerged when fishing effort fell below 0.5 (Fig. 2a). Fishing in balance (Fig. 2b) followed an asymptotic upward trend with increasing effort (an effort  $E = 0.1 \text{ year}^{-1}$  was used as a reference value) with

**Fig. 1.** Proportional change of the biomass size spectrum with sigmoid fishing size selectivity (a) and Gaussian fishing size selectivity (b) for efforts  $E = 0.1 \text{ year}^{-1}$  (black),  $E = 0.8 \text{ year}^{-1}$  (dark grey), and  $E = 1.5 \text{ year}^{-1}$  (light grey). The horizontal dashed line indicates no change from the unexploited system. Shaded areas represents fish within length at 50% selection.



sigmoid selectivity but showed no clear trend with Gaussian selectivity. This indicator, which is thought to rise with fisheries expansion, suffered the largest overall uncertainty. The large fish and large species indicators (Figs. 2c, 2d) showed clear negative trends for both sigmoid and Gaussian selectivity, with the large fish indicator giving a stronger response for sigmoid than Gaussian selectivity and the large species indicator being approximately equal for both selectivities. Inverse fishing pressure (Fig. 2e), being convex, was most sensitive to changes at low fishing efforts, displaying a clear negative trend here. Inverse fishing pressure showed a stronger response to sigmoid than Gaussian selectivity and larger uncertainty at lower levels of fishing effort. The length-based indicators (mean length and mean maximum length of fish in the community and mean length of fish in the catch) when weighted by biomass (Figs. 2f, 2g, 2h) showed convex negative responses with greater responses for sigmoid selectivity. Mean trophic level of the community and of the catch (Figs. 2i, 2j) showed negative trends for both selectivities, again with greater responses for sigmoid selectivity.

#### Indicators in the presence of extraneous ecological variation

The signal-to-noise ratio is shown for each indicator and selectivity type (Fig. 3). The signal-to-noise ratio is defined as follows:  $\{\mu[f(E)] - \mu[f(E = 0.1)]\} / \{\sigma[f(E)]\}$ , where  $\mu[f(E)]$  is the mean of the indicator–effort series  $f(E)$  at each effort point  $E$ ,  $\mu[f(E = 0.1)]$  is the mean of the indicator–effort series at effort point  $E = 0.1 \text{ year}^{-1}$ , and  $\sigma[f(E)]$  is the standard deviation of the indicator–effort series  $f(E)$  at each effort point  $E$ . The signal-to-noise ratio is expected to decline with increasing effort, as the indicator values fall as effort increases, but the noise does not. Fishing in balance is the one exception, since it is expected to rise with fisheries expansion (i.e., as effort increases). Specificity is read from the slope of a linear regression between signal-to-noise ratio and effort (since it is the rate of change due to fishing and no other cause). A stronger slope (meaning more negative for all but fishing in balance) indicates a greater specificity for an indicator. The standard error of the slope of the regression line was  $<0.07$  for all indicators.

Biomass, mean trophic level of the community and catch, and fishing in balance had the smallest specificity of all the indicators examined ( $0 \leq |\text{slope}| \leq 1$ ) for both sigmoid and Gaussian size selectivity. Inverse fishing pressure ( $|\text{slope}| = 12.4$ , not significant) and the large fish indicator ( $|\text{slope}| = 6.0$ ) had the largest specificity for sigmoid size selectivity, with the large fish indicator having only half the specificity ( $|\text{slope}| = 3.0$ ) and inverse fishing pressure only a fifth of the specificity ( $|\text{slope}| = 2.5$ ) for Gaussian size selectivity. The large species indicator had the highest specificity for Gaussian size selectivity ( $|\text{slope}| = 6.0$ ), with approximately half the specificity ( $|\text{slope}| = 3.3$ ) for sigmoid size selectivity. The length-based indicators weighted by biomass, mean length and mean maximum length of fish in the community, and mean length of fish in the catch had intermediate specificity ( $2.0 \leq |\text{slope}| \leq 5.3$ ) for both Gaussian and sigmoid size selectivity. Lower specificity for Gaussian than for sigmoid size selectivity was found for biomass, mean trophic level of the community and catch, fishing in balance, inverse fishing pressure, mean length of fish in the catch, and the large fish indicator.

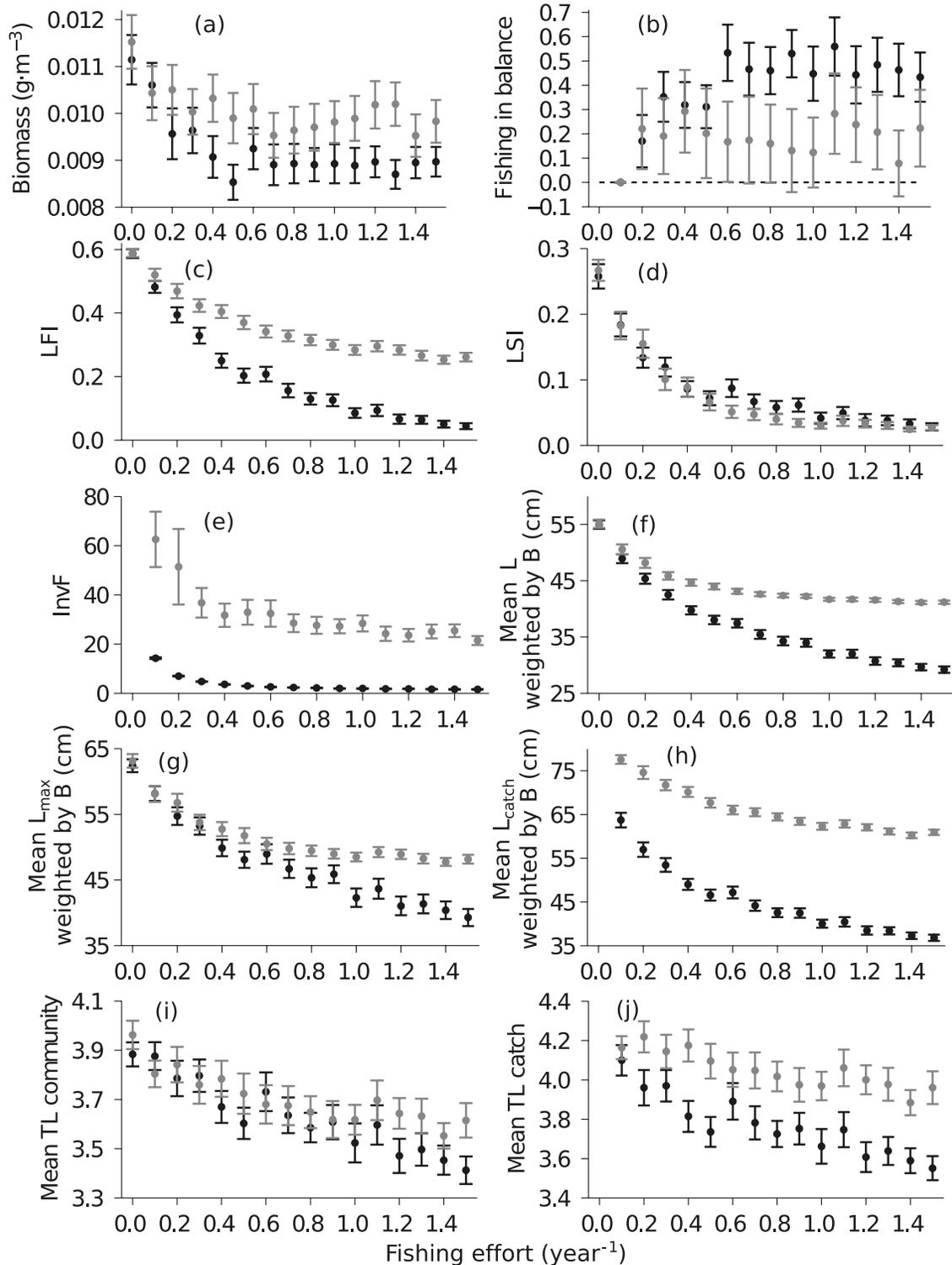
#### Weighting of length-based indicators

The response of length-based indicators (mean length and mean maximum length of fish in the community; and mean length of fish in the catch) weighted by abundance rather than biomass to changing fishing effort  $E$  is shown (Fig. 4) and the corresponding signal-to-noise ratios (Fig. 5). In the literature such abundance weighting is often used (e.g., Greenstreet and Rogers 2006; Travers et al. 2006; Shin et al. 2010), with the exception of mean length of fish in the community in Heath and Speirs (2012). Weighting by abundance rather than by biomass favours small individuals, resulting in lower indicator values. In addition, these indicators show more uncertainty and less response to changes in fishing effort than the same indicators weighted by biomass.

#### Discussion

We used system identification to study how different trophic- and size-based indicators respond to changes in fishing (repre-

**Fig. 2.** Response of indicators to fishing effort for sigmoid size selectivity (black) and Gaussian size selectivity (grey): (a) biomass; (b) fishing in balance, where the dashed line indicates the reference level; (c) large fish indicator; (d) large species indicator; (e) inverse fishing pressure =  $B/Y$ ; (f) mean length of fish in the community weighted by biomass; (g) mean maximum length of fish in the community weighted by biomass; (h) mean length of fish in the catch weighted by biomass; and mean trophic level of (i) the community and (j) the catch.

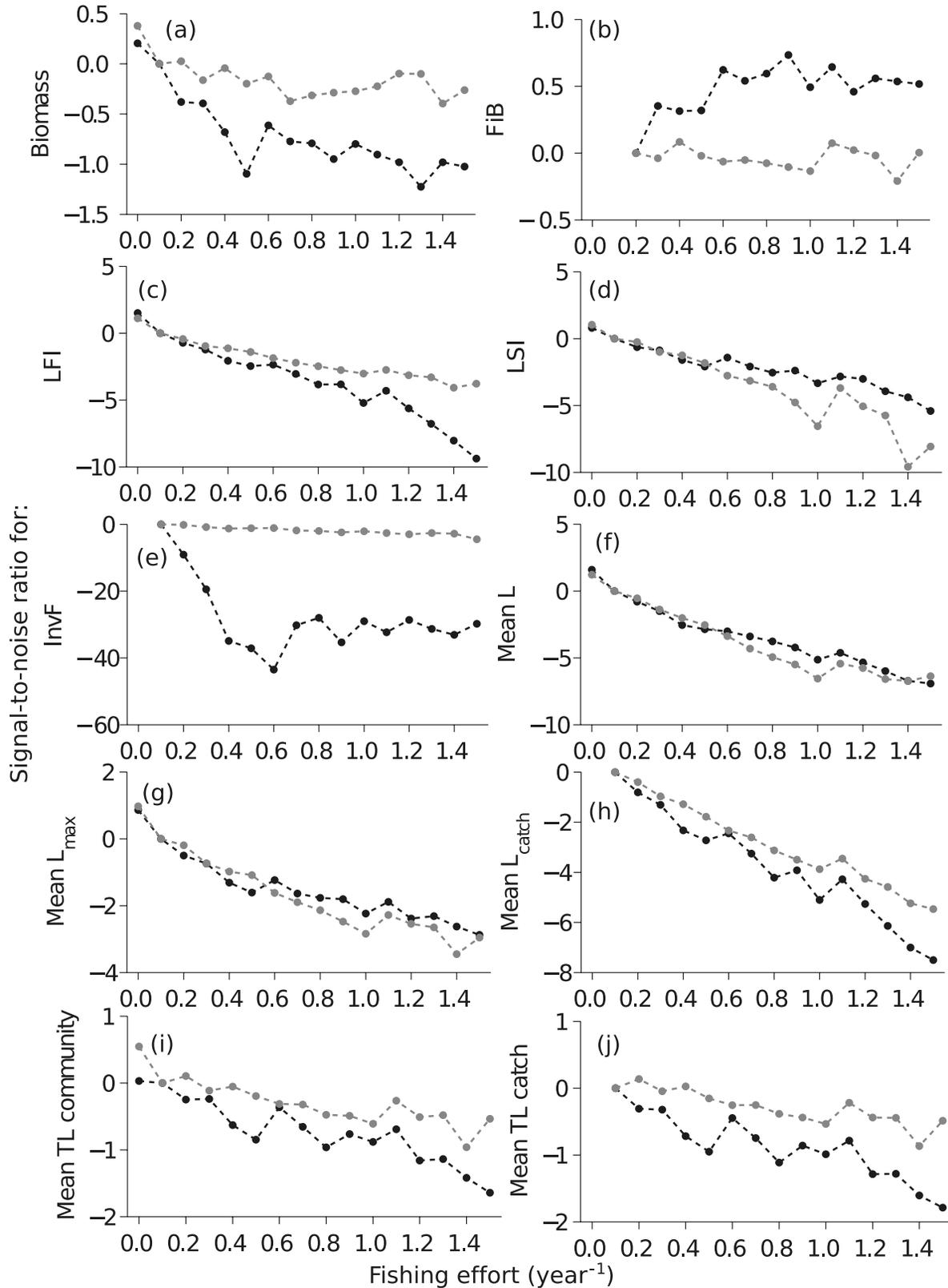


sented as size selectivity and effort), under conditions of environmental variation and uncertainty. This examination of indicators was designed as a systematic test against standard test signals to isolate their performance, not a test of them in a particular situation. The purpose was to give an unbiased account

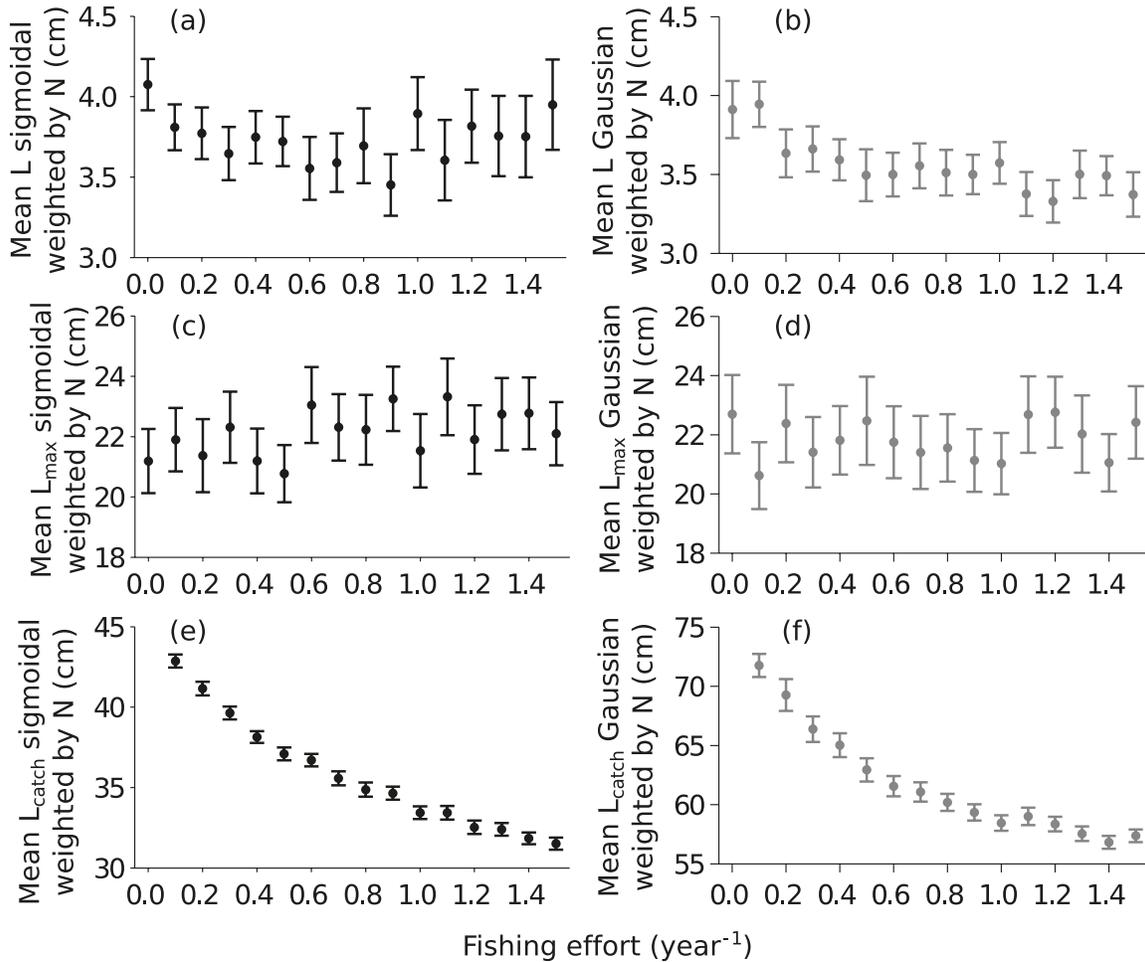
of their performance that may be transferred to any particular situation of interest. The changes to which the indicators responded manifested in the size structure of a model community, especially through (nonlinear) trophic cascade phenomena, which would be hard to quantify by earlier methods.

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**Fig. 3.** Signal-to-noise ratio,  $\{\mu[f(E)] - \mu[f(E = 0.1)]\} / \{\sigma[f(E)]\}$ , where  $\mu[f(E)]$  is the mean of the indicator–effort series  $f(E)$  at each effort point  $E$ ,  $\mu[f(E = 0.1)]$  is the mean of the indicator–effort series at effort point  $E = 0.1 \text{ year}^{-1}$ , and  $\sigma[f(E)]$  is the standard deviation of the indicator–effort series  $f(E)$  at each effort point  $E$ , for sigmoid size selectivity (black) and Gaussian size selectivity (grey): (a) biomass; (b) fishing in balance; (c) large fish indicator; (d) large species indicator; (e) inverse fishing pressure; (f) mean length of fish in the community weighted by biomass; (g) mean maximum length of fish in the community weighted by biomass; (h) mean length of fish in the catch weighted by biomass; and mean trophic level of (i) the community and (j) the catch.



**Fig. 4.** Response of length-based indicators weighted by abundance to fishing effort for sigmoid size selectivity (black) and Gaussian size selectivity (grey): (a, b) mean length of fish in the community, (c, d) mean maximum length of fish in the community, and (e, f) mean length of fish in the catch.



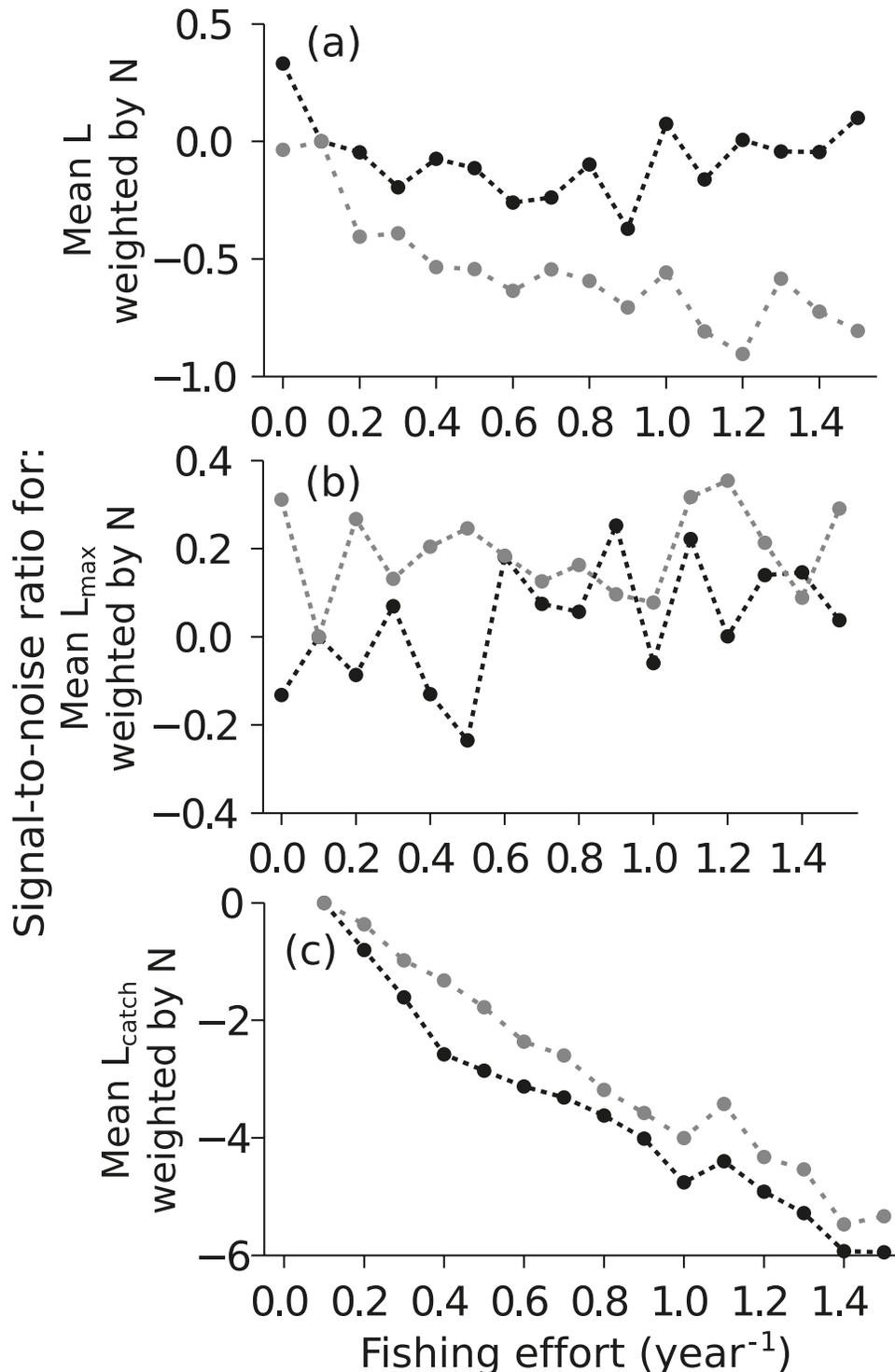
EAFM urgently needs indicators of community size structure in response to changes in fishing pressure as distinct from other causes. For that purpose indicators must meet the Rice and Rochet (2005) criteria, including that they show sensitivity and specificity to practical management measures such as effort regulation. Empirical studies comparing indicators of trophic structure by calculating signals from historic fisheries and survey records have difficulty attributing changes in indicators to particular drivers (e.g., Cury et al. 2005; Blanchard et al. 2010; Fortibuoni et al. 2010). Previous model-based studies have examined the sensitivity of certain indicators to changes in fishing pressure (Fulton et al. 2005; Hall et al. 2006; Travers et al. 2010), but were unable to account for the complex responses in size structure that arise from intertrophic dynamics. Greenstreet et al. (2011) recognized that a fully dynamic size-based model is required to support management of community size structure, and we found that of Hartvig et al. (2011) to be suitable. Faced with the substantial complexity of this model, reflecting the even greater complexity of real community dynamics, we needed to formalize the indicator testing, which we achieved using the system identification framework that has become standard practice in, for example, electrical engineering.

Nonlinear effects of fishing (in the sense that unit change

in the biomass size spectrum increased as effort declined) caused the indicator responses to fishing also to be nonlinear. Such nonlinearity may be expected in ecological systems and is a conclusion that accords with the more empirical studies of indicators (e.g., Rochet and Trenkel 2003; Trenkel and Rochet 2003). The result is a complicated picture of indicator performances.

For example, the mean length of fish in the catch (relevant in those fisheries where only catch-based data, such as landings and discards, are available) was sensitive and specific to fishing effort over all levels of effort (for both Gaussian and sigmoid selectivity), whereas fishing in balance had a low specificity and inverse fishing pressure was most sensitive at low levels of effort. Inverse fishing pressure was unusual in showing greater sensitivity to changes in fishing effort for Gaussian size selectivity than sigmoid selectivity. However, it was most sensitive and specific at lower levels of fishing effort and is only useful as a trend rather than a state indicator (Shin et al. 2010). Specificity of inverse fishing pressure depends on the fishing effort at which “noise” is measured, such that low effort (e.g.,  $E = 0.1 \text{ year}^{-1}$ ) gives higher specificity. The biomass indicator, fishing in balance, and the length-based indicators (mean length and mean maximum length of fish in the community; and mean length of fish in

**Fig. 5.** Signal-to-noise ratio,  $\{\mu[f(E)] - \mu[f(E = 0.1)]\} / \{\sigma[f(E)]\}$ , where  $\mu[f(E)]$  is the mean of the indicator–effort series  $f(E)$  at each effort point  $E$ ,  $\mu[f(E = 0.1)]$  is the mean of the indicator–effort series at effort point  $E = 0.1 \text{ year}^{-1}$ , and  $\sigma[f(E)]$  is the standard deviation of the indicator–effort series  $f(E)$  at each effort point  $E$ , for sigmoid size selectivity (black) and Gaussian size selectivity (grey) for length-based indicators weighted by abundance: (a) mean length of fish in the community, (b) mean maximum length of fish in the community, and (c) mean length of fish in the catch.



the catch) weighted by abundance had the least specificity to fishing pressure. However, weighting these length-based indicators by biomass rather than by abundance produced an important increase in their sensitivity and specificity to fishing. The remaining indicators (large fish indicator, large species

indicator, mean trophic level of fish in the community and in the catch, inverse fishing pressure, and mean length and mean maximum length of fish in the community, and mean length of fish in the catch weighted by biomass) showed a clear convex negative trend as fishing effort increased, with

a stronger response in the case of sigmoid size selectivity with the exception of inverse fishing pressure, but the large species indicator showed an equal response to both selectivity types. All the indicators tested were less sensitive at high fishing effort.

Since the indicators examined all showed different responses to variation in fishing type and effort, it would be safest to consult more than one when assessing ecosystem state (as advised by previous studies; e.g., Rochet and Trenkel 2003). Overall, though the indicators differed greatly in their sensitivity, all except inverse fishing pressure were more sensitive to sigmoid than Gaussian size selectivity of fishing mortality. Indicators also differed greatly in specificity, this variation depending to a smaller extent on the size selectivity of fishing mortality. Choice of indicator is not simple, since their performance depends on the individual circumstances of a case. We note that Fulton et al. (2005) only considered indicators informative if they observed a linear correlation with ecological attributes, precluding the findings reported here. Our results demonstrate that nonlinear responses are important because a reduction of fishing effort would not in general show a proportional change in any of the proposed indicators. The complicated dependence on individual circumstances that we found is perhaps magnified when management scenarios are broadened to include, for example, “fishing through” the food web (Essington et al. 2006). This is one of the reasons for advocating the formal method of systems identification that we adopted here. With it, complex individual scenarios can be built from the basic building blocks of Gaussian and sigmoid selection functions, meaning that our model test bed is adaptable to a broad range of practical questions.

The indicators examined here (except for mean length of fish in the catch, which was not considered by Shin et al. (2010)) were judged by Shin et al. (2010) to meet the Rice and Rochet (2005) criteria of theoretical basis, public awareness, and concreteness. The mean length of fish in the community, large species indicator, mean trophic level of the community and of the catch, inverse fishing pressure, and biomass were further judged to meet the criteria of cost, measurement, and historical data (Shin et al. 2010). The other indicators (large fish indicator, mean maximum length of fish in the community, and fishing in balance) did not meet all of these criteria, but may be applicable in some specific systems where sufficient data are available. All the indicators included in our study make similar data requirements, since they are all calculated from abundances classified by species and body size. However, they may differ in the quality and quantity of data available for their computation. For instance, the catch-based indicators (mean length of fish in the catch, inverse fishing pressure, mean trophic level of the catch, and fishing in balance) may be subject to the additional uncertainty of catch-based data, such as under-reporting or misreporting of landings or insufficient discard information, which could affect their usefulness. Other biomass-based indicators may be similarly affected by the measurement uncertainty of survey data. There may be difficulties determining maximum body length by species for the mean maximum length of fish in the community or large species indicators, necessitating the choice of either the mean length of fish in the community or in the catch or large fish

indicators instead. Similarly, it may be difficult to assign a trophic level for each species, but if biomass by size data is available, trophic level can be estimated from individual body size (Jennings et al. 2001, 2007).

Our indicator testing used Monte Carlo simulations of the size-structured community model for building statistical distributions of indicator responses to a range of fish community variables. This method greatly extends the examination of community-level indicators beyond the use of empirical data. The analysis was not entirely comprehensive, of course. It would be useful to explore additional size selectivity types, mesh sizes, and selection ogives. The mesh size used could be modified to increase or decrease the length at 50% selection for sigmoid size selectivity and length at peak selection for Gaussian size selectivity. Additional selection ogives for sigmoid size selectivity can be considered, narrowing or widening the rate at which the maximum height of the curve is reached, and additional standard deviations considered for Gaussian size selectivity. Combinations of “tuned” size selectivity functions may be used to simulate known fisheries for closer examination of particular systems, for example, those in which pelagic fisheries dominate or in hypothetical scenarios such as fishing through the food web (Essington et al. 2006). The responsiveness in time of indicators can be considered (e.g., Fung et al. 2012). If an indicator is not sensitive and specific to fishing pressure and is not practical to calculate from existing survey- and catch-based data, it is not very useful for fisheries management purposes. When using a model, we have perfect knowledge of community and catch composition by size and species. The use of imperfect catch and community composition information from survey, landing, and discard data could be simulated to examine how indicator performance may be affected by uncertain and incomplete data. Further, wherever empirical data allow, the fish communities may be refined by representing named fish species by traits in addition to maturation size, such as growth rates and fixed diets incorporating stomach data. Indeed, faced with a particular fishery to manage, parameter values may be chosen to reflect that fishery to test the indicators in the particular relevant circumstances. Our test bed provides an easily transposable decision support system for selecting indicators in each case.

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## Appendices

Appendices A, B, and C appear on the next pages.

## Appendix A. Model equations

**Table A1.** Summary of model equations.

Eq. No.	Process	Equation
<b>Food encounter</b>		
A.1	Predator size preference for prey	$s(m_p, m) = \exp\left\{-\frac{[\ln(\beta m_p/m)]^2}{2\sigma^2}\right\}$ , $\sigma = \sigma_1$ when $m_p < \beta m$ , $\sigma = \sigma_2$ when $m_p \geq \beta m$
A.2	Volumetric search rate	$v(m) = \gamma m^q$
A.3	Encountered food	$e(m) = v(m) \sum_i \int_0^m m_p N_i(m_p) c \cdot s(m_p, m) dm_p$ , where $c$ is a normalization constant such that $c \cdot \int \int_{s(\sigma=\sigma_1, \sigma_2)} [\exp(x), \exp(y)] dx dy = \int \int_{s(\sigma=\sigma_1)} [\exp(x), \exp(y)] dx dy$ , $x = \ln(m_p)$ , $y = \ln(m)$
A.4	Maximum consumption rate	$I_{\max}(m) = hm^n$
A.5	Feeding level	$f(m) = \frac{e(m)}{e(m) + I_{\max}}$
<b>Growth and reproduction</b>		
A.6	Maturation	$\Psi_i(m) = \left[1 + \left(\frac{m}{m_{*,i}}\right)^{-u}\right]^{-1} \left(\frac{\eta_* m}{m_{*,i}}\right)^{1-n}$
A.7	Somatic growth	$g_i(m) = [1 - \Psi_i(m)][\alpha f(m)hm^n - km^p]$
A.8	Recruitment (Beverton–Holt)	$R_{BH,i} = \frac{R_i}{1 + \frac{R_i}{R_{\max,i}}}$
A.9	Number of recruits	$R_i = \frac{\varepsilon}{2m_0} \int_{m_{*,i}}^{\infty} N_i(m) g_{r,i}(m) dm$
A.10	Energy available for reproduction	$g_{r,i}(m) = \Psi_i(m)[\alpha f(m)hm^n - km^p]$
A.11	Maximum no. of recruits	$R_{\max,i} = g_i(m_0)N_{0,i}$
A.12	Maximum no. of small individuals	$N_{0,i} = \left(\frac{m_{*,i}}{\eta_*}\right)^{2n-q-3+a} \Delta \frac{m_{*,i}}{\eta_*}$ , $a = \frac{f_0 h \beta^{2n-q-1} \exp\{[2n(q-1) - q^2 + 1]\sigma_1^2/2\}}{(\alpha f_0 - k)}$
<b>Mortality</b>		
A.13	Background mortality	$\mu_{b,i} = \mu_0 m_{*,i}^{n-1}$
A.14	Predation mortality	$\mu_p(m_p) = \sum_i \int_{m_0}^{\infty} s(m_p, m)[1 - f(m)] \cdot v(m)N_i(m) dm$
A.15	Fishing mortality (sigmoid selectivity)	$F_S(m) = E \cdot \left\{ \frac{\exp[MS + SF(100m)^{1/3}]}{1 + \exp[MS + SF(100m)^{1/3}]} \right\}$
A.16	Fishing mortality (Gaussian selectivity)	$F_G(m) = E \cdot \exp\left\{-\frac{[(100m)^{1/3} - LP]^2}{2SD^2}\right\}$
<b>Resource spectrum</b>		
A.17	Growth rate	$\frac{\partial N_R(m)}{\partial t} = r_0 m^{n-1} [\kappa(m) - N_R(m)] - \mu_p(m)N_R(m)$
A.18	Carrying capacity	$\kappa(m) = \kappa_R m^{-2-q+n}$ , $m_{\min} < m < m_{\text{cut}}$

## Appendix B. Volumetric search rate coefficient $\gamma$ derivation

The volumetric search rate coefficient  $\gamma$  is estimated by multiplying the swimming speed and swept reactive field area coefficients following the method detailed elsewhere (appendix E of Hartvig et al. 2011). Swimming speed  $S$  ( $\text{cm}\cdot\text{s}^{-1}$ ) is assumed to be proportional to body mass ( $\text{g}$ ) where  $S = am^b$ , and exponent  $b = 0.13$  (Ware 1978). Given a swimming speed  $S$  and body mass  $m$ , the coefficient is  $a = m^{-b}S$ . Using the relation between length and body mass  $m = xL^y$ , where  $y = 3.2$  to account for non-isometric growth and  $x = 0.01$  (Ware 1978), the coefficient  $a$  in terms of length is  $a = (xL^y)^{-b}$ .

Swept reactive field area  $A$  ( $\text{cm}^2\cdot\text{g}^{-q}$ ) is assumed to be a circle with radius  $L^c$ , the maximum citing range, proportional to body length  $L$  (in cm), where  $c = 1.1$  (Ware 1978).  $A = \pi L^{2c}$ , or in terms of mass

$$A = \pi \left(\frac{m}{x}\right)^{\frac{2c}{y}}$$

The coefficient here is  $\pi x^{-\frac{2c}{y}}$ .

Then  $\gamma$  with units of  $\text{cm}^3\cdot\text{g}^{-q}\cdot\text{s}^{-1}$  derived using body mass is  $\gamma = \pi x^{-\frac{2c}{y}} m^{-b} S$  or is  $\gamma = \pi x^{-\frac{2c}{y}} L^{-by} S$  when derived using

body length. With units of  $\text{m}^3\cdot\text{g}^{-q}\cdot\text{year}^{-1}$  as in the model,  $\gamma = 31.6\pi x^{-\frac{2c}{y}} m^{-b} S$  for body mass or  $\gamma = 31.6\pi x^{-\frac{2c}{y}} L^{-by} S$  for body length.

Using FishBase (Froese and Pauly 2010) measurements,  $\gamma \approx 40\,000 \text{ m}^3\cdot\text{g}^{-q}\cdot\text{year}^{-1}$  for a cod with length 27 cm and swimming speed  $39 \text{ cm}\cdot\text{s}^{-1}$ . Another cod measurement in FishBase, length 27 cm and swimming speed  $39 \text{ cm}\cdot\text{s}^{-1}$ , gives a  $\gamma \approx 58\,000 \text{ m}^3\cdot\text{g}^{-q}\cdot\text{year}^{-1}$ . The more conservative estimate of  $\gamma \approx 40\,000 \text{ m}^3\cdot\text{g}^{-q}\cdot\text{year}^{-1}$  is used here. This derivation assumes a well-mixed environment, with a predator that cruises for food as a feeding strategy.

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## Appendix C. Test community assembly

**Table C1.** The most abundant North Sea species by trawl survey biomass (Jennings et al. 2002), excepting shark, skate, and ray species, used to create the test community assembly.

Latin name	Common name	$L_{\text{mat}}$ (cm)	$a$	$b$	$m^*$ (g)
<i>Ammodytes marinus</i>	Lesser sandeel	16.3	0.0017	3.21	13.23
<i>Anarhichas lupus</i>	Atlantic wolffish	55.0	0.0029	3.270	1423.59
<i>Arnoglossus laterna</i>	Scaldfish	6.8	0.0055	3.1	2.09
<i>Buglossidium luteum</i>	Solenette	8.0	0.0089	3.06	5.16
<i>Callionymus lyra</i>	Dragonet	17.4	0.0224	2.46	25.23
<i>Clupea harengus</i>	Atlantic herring	16.7	0.007	3.060	37.22
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	25.0	0.0035	3.11	77.92
<i>Eutrigla gurnardus</i>	Grey gurnard	19.3	0.0065	3.09	60.99
<i>Gadus morhua</i>	Atlantic cod	41.1	0.0088	3.02	658.09
<i>Glyptocephalus cynoglossus</i>	Witch flounder	30.4	0.0013	3.44	164.07
<i>Hippoglossoides platessoides</i>	American plaice	35.0	0.0022	3.27	246.33
<i>Lepidorhombus whiffiagonis</i>	Megrim	26.6	0.0029	3.27	132.36
<i>Limanda limanda</i>	Dab	26.0	0.0061	3.15	174.78
<i>Lophius piscatorius</i>	Monkfish	55.23	0.0199	2.92	2432.23
<i>Melanogrammus aeglefinus</i>	Haddock	34.9	0.0075	3.05	380.78
<i>Merlangius merlangus</i>	Whiting	25.5	0.0062	3.08	133.21
<i>Merluccius merluccius</i>	Hake	39.6	0.0043	3.13	430.78
<i>Microstomus kitt</i>	Lemon sole	27.0	0.0116	3.03	252.05
<i>Pleuronectes platessa</i>	Plaice	30.4	0.0065	3.14	294.53
<i>Pollachius virens</i>	Saithe (pollock)	39.1	0.0094	2.99	541.67
<i>Scomber scombrus</i>	Atlantic mackerel	28.6	0.0061	3.11	206.36
<i>Sebastes viviparus</i>	Norway redfish	12.5	0.0115	3.314	49.64
<i>Solea solea</i>	Sole	30.3	0.0065	3.11	263.15
<i>Sprattus sprattus</i>	Sprat	11.6	0.0039	3.24	10.96
<i>Trachurus trachurus</i>	Horse mackerel	23.9	0.0099	2.96	119.04
<i>Trisopterus esmarki</i>	Norway pout	18.6	0.0067	3.0	43.11
<i>Trisopterus minutus</i>	Poor cod	13.0	0.0071	3.14	22.34

**Note:** Maturation length ( $L_{\text{mat}}$ , cm) and allometric conversion to maturation mass ( $m^*$ , g) ( $m^* = a \cdot L_{\text{mat}}^b$ ) obtained from FishBase (Froese and Pauly 2010).

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