

Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model

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Summary

1. Marine environmental management policies seek to ensure that fishing impacts on fished populations and other components of the ecosystem are sustainable, to simultaneously meet objectives for fisheries and conservation. For example, in Europe, targets for (i) biodiversity, (ii) food web structure as indicated by the proportion of large fish and (iii) fishing mortality rates for exploited species that lead to maximum sustainable yield, F_{MSY} , are being proposed to support implementation of the Marine Strategy Framework Directive. Efforts to reconcile any trade-offs among objectives need to be informed by knowledge on the consequences of alternate management actions.

2. We develop, calibrate and apply a multispecies size spectrum model of the North Sea fish community to assess the response of populations and the community to fishing. The model predicts species' size distributions, abundance, productivity and interactions and therefore provides a single framework for evaluating trade-offs between population status, community and food web structure, biodiversity and fisheries yield.

3. We show that the model can replicate realistic fish population and community structure and past responses to fishing. We assess whether meeting management targets for exploited North Sea populations (fishing species at F_{MSY}) will be sufficient to meet proposed targets for biodiversity and food web indicators under two management scenarios (status quo and F_{MSY}).

4. The recovery in biodiversity indicators is 60% greater when fishing populations at F_{MSY} than if status quo (2010) fishing rates are maintained. The probability of achieving a food web target was 60% under both scenarios in spite of major community restructuring revealed by other indicators of community size structure.

5. *Synthesis and applications.* Our model can be applied to evaluate indicator targets and trade-offs among fisheries and conservation objectives. There is a significant probability that reductions in fishing mortality below F_{MSY} would be needed in Europe if managers make a binding commitment to a proposed large fish indicator target, with concomitant reductions in fisheries yield.

Key-words: community ecology, ecosystem-based management, fisheries ecology, maximum sustainable yield, trophic interactions

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Introduction

One tenet of an 'ecosystem approach to fisheries' is to ensure that fishing impacts on fished populations and other components of the ecosystem are sustainable (FAO 2003; CBD 2011) consistent with policy commitments for fisheries, biodiversity and the environment (Rice & Ridgeway 2010). In many management regions, fished populations are below target abundance, and managers are working to rebuild them in a variety of ways including the reduction in fishing mortality rates (Worm *et al.* 2009). Managers' actions are expected to lead to concomitant reductions in the ecosystem impacts of fishing, but it is rarely known whether the reductions are sufficient to meet explicit targets for biodiversity and the environment.

In Europe, there is a pressing need to take account of the relationship between fisheries management actions and progress towards meeting biodiversity and environmental targets, owing to the adoption of the Marine Strategy Framework Directive (MSFD; EC 2008). This policy seeks to set targets for commercially exploited fish and shellfish as well as aspects of biodiversity and food webs that are impacted by fishing and other human pressures. In terms of fishing pressure, the management target for each commercially fished population that has been set is the fishing mortality rate (F) predicted to lead to maximum sustainable yield (F_{MSY}). Management actions to control F will be taken using the Common Fisheries Policy (CFP) (EC 2008). Management targets for biodiversity and food webs are also currently being developed and proposed. If necessary, management actions to meet these targets will also be taken using the CFP (EC 2008).

The size structure of fish communities responds to fishing in fairly predictable ways (e.g. Rice & Gislason 1996; Shin *et al.* 2005). For this reason, size-based indicators have been proposed as 'food web' and 'biodiversity' indicators for the MSFD (EC 2010), building on their development and application by the Oslo and Paris Commission (OSPAR) and the European Commission. Scientists have proposed targets for some of these size-based indicators, for example, in the case of the 'large fish indicator' (LFI; the proportion of total catch weight in defined surveys comprising 'large' fishes). Greenstreet *et al.* (2010) proposed that fishes >40 cm total length should account for >30% of total catch weight during the North Sea Quarter 1 ground fish survey (ICES 2012). For the Celtic Sea, Shephard, Reid & Greenstreet (2011) proposed that fishes >50 cm total length should account for >40% of total catch weight for a defined set of species in the now discontinued Celtic Sea Portuguese High-Headline Trawl Survey.

The perceived legitimacy, credibility and relevance of proposed targets for the 'food web' or 'biodiversity' are crucial for the development of indicator frameworks in management. Whether indicators legitimately reflect a state of the environment that is seen to provide benefit or avoid harm to society, whether they are technically

achievable through management and whether the costs of meeting the targets are considered affordable will need to be demonstrated. Thus, the debate about target setting needs to be informed by an understanding of the trade-offs among ecological, social and economic objectives. Further, if targets are agreed, managers need to know the options for management actions, in addition to those for exploited populations, that are needed to meet them.

Size-based food web models are ideal for understanding the impacts of fishing on populations and communities. This is because they capture the main processes and inter-relationships between population and community dynamics, as supported by theoretical (Andersen & Beyer 2006) and empirical analysis (Blanchard *et al.* 2005; Daan *et al.* 2005). Size-based multispecies models have been developed for fisheries applications to provide abundance and catch predictions for target populations as well as community properties such as size composition, mean maximum length and trophic level (Pope *et al.* 2006; Hall *et al.* 2006; Speirs *et al.* 2010). These size-based food web models assume that growth approximates a von Bertalanffy growth equation, but growth can be influenced by many factors (including food availability and environmental conditions).

Another class of size-based models, size spectrum models, has long been used to elucidate food web and ecosystem properties from the dynamics of predator-prey interactions without accounting for the identity of component species (Silvert & Platt 1978; Benoît & Rochet 2004; Law *et al.* 2009). More recently, species' identity has been incorporated into these models with a 'trait-based' approach where 'species' are defined by their asymptotic mass (or maturation mass) (Andersen & Pedersen 2010; Hartvig, Andersen & Beyer 2011). Growth and foraging behaviour are food-dependent in this modelling framework, and every bit of individual growth, respiration and reproduction is balanced by a corresponding mortality on prey organisms.

Size spectrum models have yet to be applied to realistic communities, but the potential for full accounting of species' size distributions, abundance and interactions suggests that they can usefully be applied to assess the effects of fishing on population and community properties. Here, we develop and calibrate a multispecies size spectrum model of the North Sea fish community and then apply it to assess the response of populations and the community to fishing and to assess whether meeting management targets for exploited North Sea populations will be sufficient to meet proposed targets for biodiversity and food web functioning.

Materials and methods

PUTTING SPECIES INTO A SIZE SPECTRUM MODEL

We developed a dynamic multispecies size spectrum model comprising 12 interacting fish species and a background resource

community (see Table S1, Supporting Information for full details). The model is based on the equations of Hartvig, Andersen & Beyer (2011) and Andersen & Pedersen (2010), but with an explicit representation of species-specific traits. The model provides a means of scaling from individual processes (growth and mortality rates) to population structure (size distribution of each species) and community structure (sum of size distributions of all species). The R package 'mizer' implements the multispecies size spectrum model and also contains documentation on the model equations and processes (Scott, Blanchard & Andersen 2013).

We focused on common and commercially important species since the aspects of biodiversity we are interested in relate to population dynamics in a size-structured and multispecies food web (rather than species richness or rarity). The 12 species accounted for nearly 90% of the total biomass of all species sampled by research trawl surveys in the North Sea. Each species is characterized by a set of parameters detailing its physiological, life-history and foraging traits. Species-specific parameters (Table S2) were estimated from a statistical analysis of biological sampling data and stock assessment inputs and outputs publicly available from ICES. The biological sampling data included survey relative abundance (numbers per hour towed) at length as well as individual lengths, weights, maturation stages and ages (www.ices.dk/datas; Table S3, Supporting Information) and predator-prey sizes (CEFAS, Dapstom database; <http://www.cefass.defra.gov.uk/our-science/fisheries-information/fish-stomach-records.aspx>).

Assuming all species interact with each other equally in the model is equivalent to assuming that all species occur homogeneously across the whole of the North Sea. Interactions between each species pair were based on spatial co-occurrence averaged across two separate life stages (above and below size at maturation; Table S4, Supporting Information). Spatial overlap for each predator and prey pair was estimated using Schoener's (1970) overlap index (Kempf *et al.* 2010) using the International Bottom Trawl Survey (IBTS) relative abundance data that were averaged over 1985–1995.

Foraging is size-dependent so interactions occur between species and size classes. Preferred predator-prey size ratio is given by a log-normal size selectivity function which takes as parameters a mean and a standard deviation (Table S1, Supporting Information). The mean and standard deviation of the predator-prey mass ratios (PPMR) were estimated from individual predator and prey sizes obtained from a published data base of predators and their prey (Pinnegar & Platts 2011). The predator-prey size mass ratio was then adjusted to account for available prey abundance and size selection under 'average' conditions, to approximate their preferred values (Hartvig, Andersen & Beyer 2011).

Fishing mortality is a size- and species-specific component of the mortality function in the community model, which can remain constant throughout the projection or can vary at each time step. A standard fixed logistic selectivity function was used to describe the ability of the fishery to catch each species. The maximum fishing mortality rates and selectivity functions for each species were obtained from the estimated weight-at-age and *F*-at-age given by single-species stock assessments (www.ices.dk; Supporting Information) to calculate the fishing mortality rate at full selectivity, *F*.

Some parameters were non-species-specific and were assumed to be the same for all species (Table S5). The 13 least known model parameters, the maximum recruitment for each species, $R_{\max,i}$, and the constant κ_r for the resource carrying capacity

were estimated. These parameters are important for setting the relative abundance of each species and basal resources in the system.

CALIBRATION

We aimed to resolve realistic equilibrium patterns of the size-structured community across a time period (1985–1995) when the fishing exploitation pattern was fairly stable (Fig. S1, Supporting Information). We fit the modelled output of each species catches and spawner biomass to time-averaged landings data and spawner biomass estimates from stock assessments (www.ices.dk). We estimated the vector of values for the 13 parameters by minimizing the sum of squared errors between log-transformed observed and modelled catches and spawner biomass using the quasi-Newton method with box constraints 'L-BFGS-B' (Byrd *et al.* 1995) in the R package 'optim'. The dynamical model was run to equilibrium as part of the estimation procedure. The average *F* for each species over the period 1985–1995 was used as model input (Table S2, Supporting Information). The calibrated model produced strong correlations between log predicted versus log observed catches and spawner biomass (Fig. S2, Supporting Information, $r = 0.97$ and 0.98 , respectively, both with $P < 0.001$) with overall proportion of bias of 0.38 (catches) and 0.16 (spawner biomass). The calibrated model was used as a base model for further model validation and fishing simulations.

VALIDATION

We compared the modelled species size distributions with fisheries independent trawl survey data (that were not used to calibrate the model) collected during the North Sea Quarter 1 International Bottom Trawl Survey from 1983 to 2010 (ICES 2012) as an independent validation of the model under time-averaged conditions. All fishes in the trawl catches are sorted to species, and all individuals or subsamples of species groups are measured to produce raised length-frequency distributions for all species. Lengths were converted to weight using weight-length relationships based on measurements from subsamples. Survey size distributions were converted to density estimates and were corrected for selectivity and availability by species, using the corrections of Fraser, Greenstreet & Piet (2007) to compare the survey estimates with model predictions of density at size at the scale of the whole North Sea. The species- and size-specific catchability corrections are based on ratios between the IBTS data, stock assessments and other surveys. Statistical metrics to evaluate goodness-of-fit were Pearson's correlation coefficient (r) and the proportion of bias between predictions and observations (Allen, Somerfield & Gilbert 2007). A correlation closer to 1 and proportion of bias (pb) closer to 0 represent better fits.

MODEL HINDCASTS AND SCENARIO PROJECTIONS

The ability of the model to reproduce observed dynamics with only fishing mortality inputs changing through time was evaluated by simulating changes over the period 1967–2010. The model was forced with the full multispecies time series of fishing mortality rates (see Fig. S1, Supporting Information) and then projected to 2050 under two scenarios. These were: (i) 'status

quo' scenario where fishing mortality rates were held constant at 2010 levels and (ii) a 'target' scenario where fishing mortality rates increased linearly over the 2010–2015 period and then were held constant at the ICES F_{MSY} estimates given in Table 1.

We added a stochastic term to recruitment in the calibrated deterministic model (as in Andersen & Pedersen 2010, Table S1, Supporting Information) to simulate dynamical changes under time-varying fishing. The standard deviation from standardized detrended time series of recruitment estimates (www.ices.dk) for all available species was calculated and applied using a log-normal noise function with a spread independently for each species and with a value which is renewed each year. Recruitment time series were not available for dab, gurnard and sprat. Standard deviations for these species were set to 0.9, 0.5 and 0.5, respectively. A burn-in period of 300 years with stochastic recruitment and with fishing mortality held constant at 1967 rates preceded the dynamical time-series simulation.

We consider the observed time series as a single stochastic realization and computed the percentage of observed points contained within the 95% quantiles (pci) of the model predictions to evaluate this aspect of model skill. Correlation and bias metrics were also used to assess the goodness-of-fit between the median of the model output and the observations but these metrics are likely to be overly stringent measures given that we do not: (i) expect the median of the model results to resolve annual fluctuations in the observed time series and (ii) we have not fit the model to time-series data.

Table 1. Species included in the model and their asymptotic weights (W) along with single-species fishing mortality rate F (year^{-1}) estimates used in projection scenarios. The ICES single-species F values estimated to achieve maximum sustainable yield (F_{MSY}) were only available for six species (from www.ices.dk), and a value of 0.2 was assumed for missing species (in brackets). $F_{status-quo}$ values were based on estimates from 2010 where available. Values in brackets were inferred from landings and relationships with targeted species

Species	Name	W (g)	ICES	
			F_{MSY} (year^{-1})	$F_{status-quo}$ (year^{-1})
<i>Sprattus sprattus</i>	Sprat	33	(0.2)	(0.31)
<i>Ammodytes marinus</i>	Sandeel	36	(0.2)	0.36
<i>Trisopterus esmarkii</i>	Norway pout	100	(0.2)	0.42
<i>Clupea harengus</i>	Herring	334	0.25	0.12
<i>Limanda limanda</i>	Dab	324	(0.2)	(0.14)
<i>Merlangius merlangus</i>	Whiting	1192	(0.2)	0.27
<i>Solea solea</i>	Sole	866	0.22	0.34
<i>Eutrigla gurnardus</i>	Gurnard	668	(0.2)	(0.10)
<i>Pleuronectes platessa</i>	Plaice	2976	0.25	0.24
<i>Melanogrammus aeglefinus</i>	Haddock	3485	0.3	0.23
<i>Gadus morhua</i>	Cod	40 044	0.19	0.68
<i>Pollachius virens</i>	Saithe	16 856	0.3	0.38

POPULATION AND COMMUNITY-LEVEL INDICATORS AND BASELINES

The performance of simple single-species management strategies in relation to proposed population and community-level targets of the MSFD were described with indicators, their associated unexploited baselines and targets for the abundance of target species, fish catches and community structure.

Each species' spawner biomass was calculated from the model output along with four fish community indicators. These were: (i) slope of the community size spectrum, calculated as the slope obtained from a linear regression of log (total abundance of individuals) versus log (body mass); (ii) mean weight of all individuals in the community; (iii) mean maximum weight calculated as: $\bar{W} = \sum_i (W_i b_i / b)$, where W_i is the maximum weight of species i (estimated as the asymptotic weight), b_i is the total biomass of species i and b is the total biomass of all individuals; and (iv) the proportion of 'large fish', LFI, calculated as: $P_{>40\text{ cm}} = b_{>40\text{ cm}} / b$, where $b_{>40\text{ cm}}$ is the total biomass of all individuals $>40\text{ cm}$ in length and b is the total biomass of all fish in the sample.

Only sizes between 10 g and 100 kg were used in the calculation of the indicators for consistency with empirical indicators. Indicators were calculated based on bottom-dwelling (demersal) species only, as these are the species most effectively sampled by the survey trawl and to which selectivity and availability corrections might reasonably be applied (Fraser, Greenstreet & Piet 2007; ICES 2012). Total biomass and the total catches were also calculated from the model output. The community-level indicators calculated here are based on a subset of the full demersal assemblage typically used for the calculation of survey-based community indicators to support the MSFD (Fung *et al.* 2012). However, the empirical large fish indicator based on the 12 species subset was strongly and positively correlated with the indicator when it comprised many more species ($r = 0.80$, $P < 0.001$ for all species given in Fraser, Greenstreet & Piet 2007).

Baselines for unexploited species spawner biomass and the community indicators were derived by running the calibrated model with zero fishing mortality rates for all species. The biodiversity target was based on 'all species at or above safe limits', where the reference point was $0.1B_{i,F=0}$ (Rochet *et al.* 2011). The community target was based on achieving a high (0.8) proportion of the unexploited value of the large fish indicator, which corresponds to a value of 0.32. We adopted the unexploited value as a target for this indicator, which corresponded to -2.1 based on normalized density size spectra and -1.1 based on log abundance vs. log weight since the size spectrum is supposed to be a conservative feature of communities.

Results

VALIDATION

A comparison of the modelled and observed species' size distributions averaged over the 1985–1995 time period revealed significant positive correlations ($r > 0.6$, $P < 0.05$) with the data for all species except for gurnard and saithe (Fig. 1). Although the survey data were corrected for availability and catchability, high levels of bias in the species size distributions were found for sole, gurnard, plaice and saithe ($pb > 1$). The survey only sporadically catches sandeel and

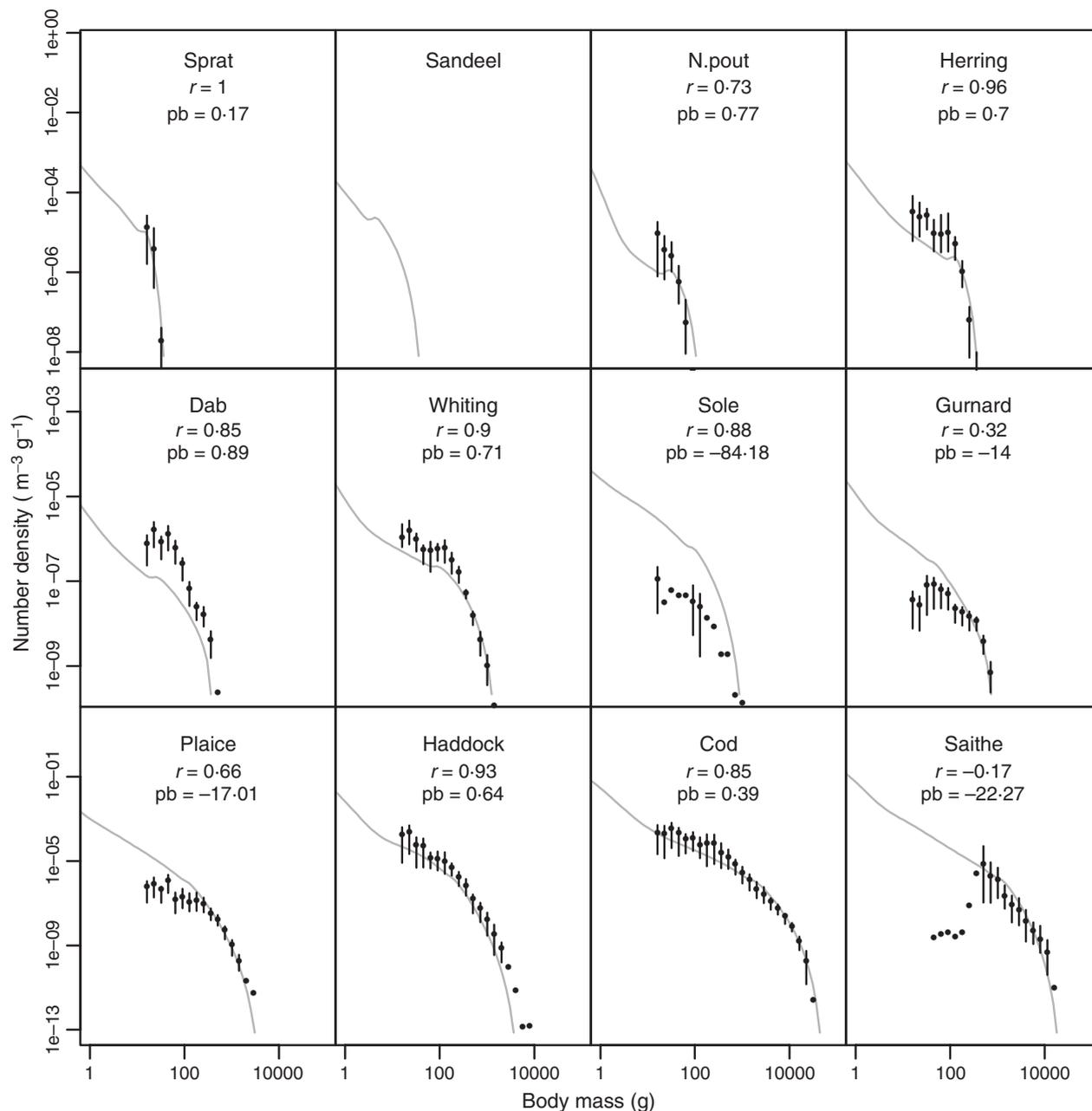


Fig. 1. Modelled and observed populations size distributions, under time-averaged conditions, 1985–1995. Goodness-of-fit metrics were Pearson's correlation coefficient (r) and the proportion of bias (pb) between predictions and observations.

therefore these data were omitted from the analysis. The calibrated model produced growth curves that passed through individual weight-at-age data showing that the model can also capture observed growth (Fig. S3, Supporting Information).

CONFRONTING SIMULATED POPULATION AND COMMUNITY DYNAMICS WITH DATA

Forcing the model with historical estimates of changes in fishing mortality resulted in the vast majority ($pci > 84\%$) of data points contained within the simulation envelope for spawner biomass of all species except for cod

($pci = 57\%$). Significant positive correlations between predicted and ICES stock assessment estimates of population spawner biomass were also found for 6 of the 10 species for which estimates were available (Fig. 2). The exceptions were whiting, sandeel, Norway pout and haddock although visually parts of time series for these species were closely matched. Proportion of bias was < 0.55 for all species with higher values showing larger misfits during the earlier part of the time series.

The model did not replicate the time series of reported catches as well as spawner biomass. For some species (dab, whiting, gurnard and plaice), the envelope of model predictions contained $< 50\%$ of the reported catches,

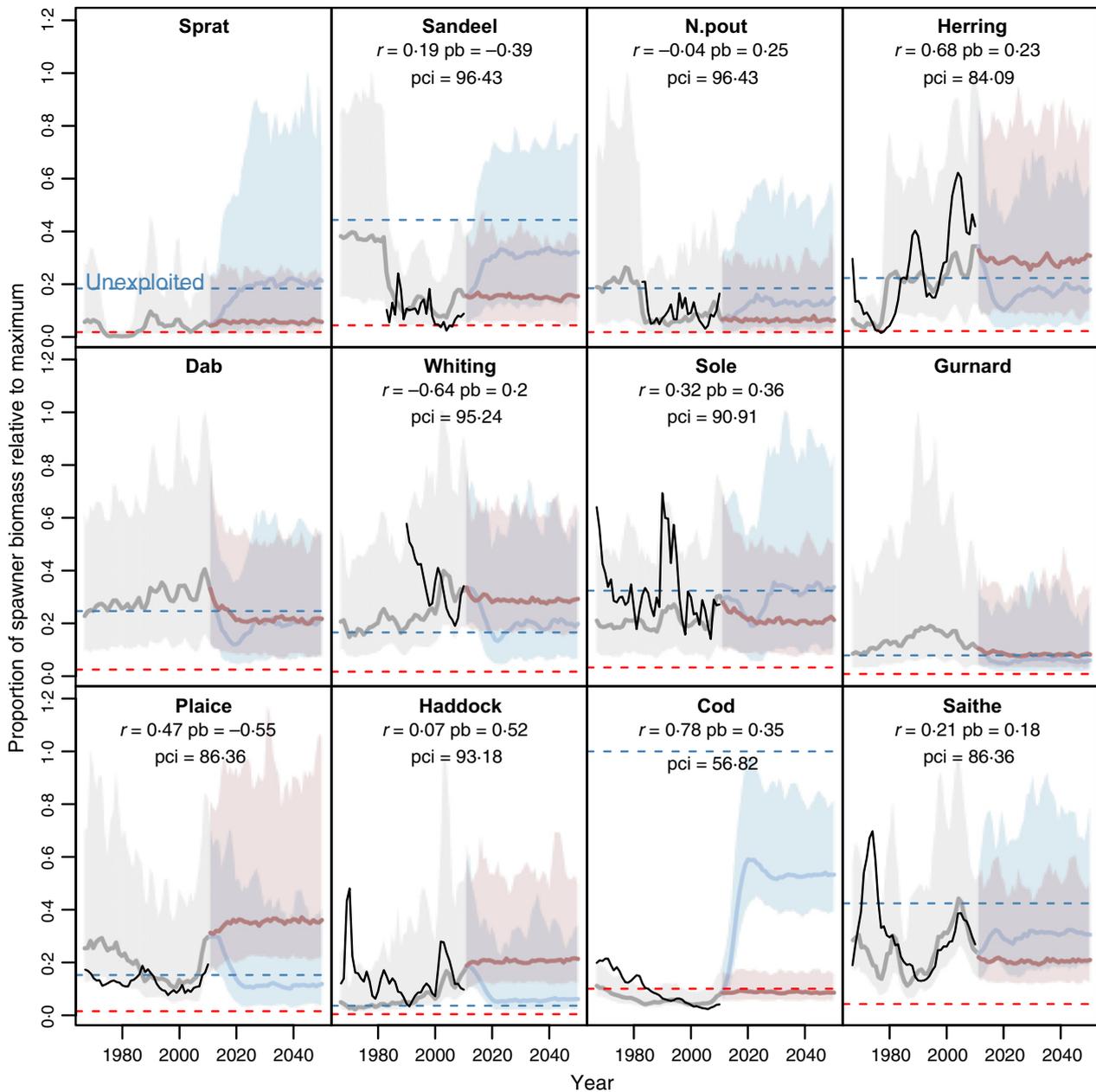


Fig. 2. Population time series of spawner biomass expressed relative to maximum values under time-varying fishing. Black lines are spawner biomass estimates from ICES stock assessments. Grey areas show quantiles of stochastic simulations with dark grey line equal to the median. Blue dashed lines show the unexploited spawner biomass, and red lines show the threshold at 10% of unexploited spawner biomass. Scenario projections are shown for ‘status quo’ in red and the ICES F_{MSY} ‘targets’ in blue. Pearson’s correlation coefficient (r), the proportion of bias (pb) between predictions and observations and the percentage of observed points contained within the 95% confidence intervals of the model (pci) capture different aspects of model skill.

whereas for others the pci was high (Fig. 3). However, strong significant positive correlations between the time series of predicted catches and reported landings were found for 7 out of the 12 species ($r > 0.47$, $P < 0.05$; Fig. 3). Exceptions were sprat, dab, sole, haddock and saithe. A high proportion of bias (>0.6) was evident for sprat, dab, whiting, gurnard and plaice.

A higher percentage of the mean weight and the size spectrum slope time series were contained within the

simulation envelopes compared with mean maximum weight and LFI, which were both lower than the model (Fig. 4). This is not surprising given that the latter two indicators will be more influenced by the higher abundance of saithe and sole. Trends were much more consistent in the later part of the time series (particularly after 1986 for Quarter 1 and for full Quarter 3 IBTS). There was very low bias in the size spectrum slope compared with other indicators.

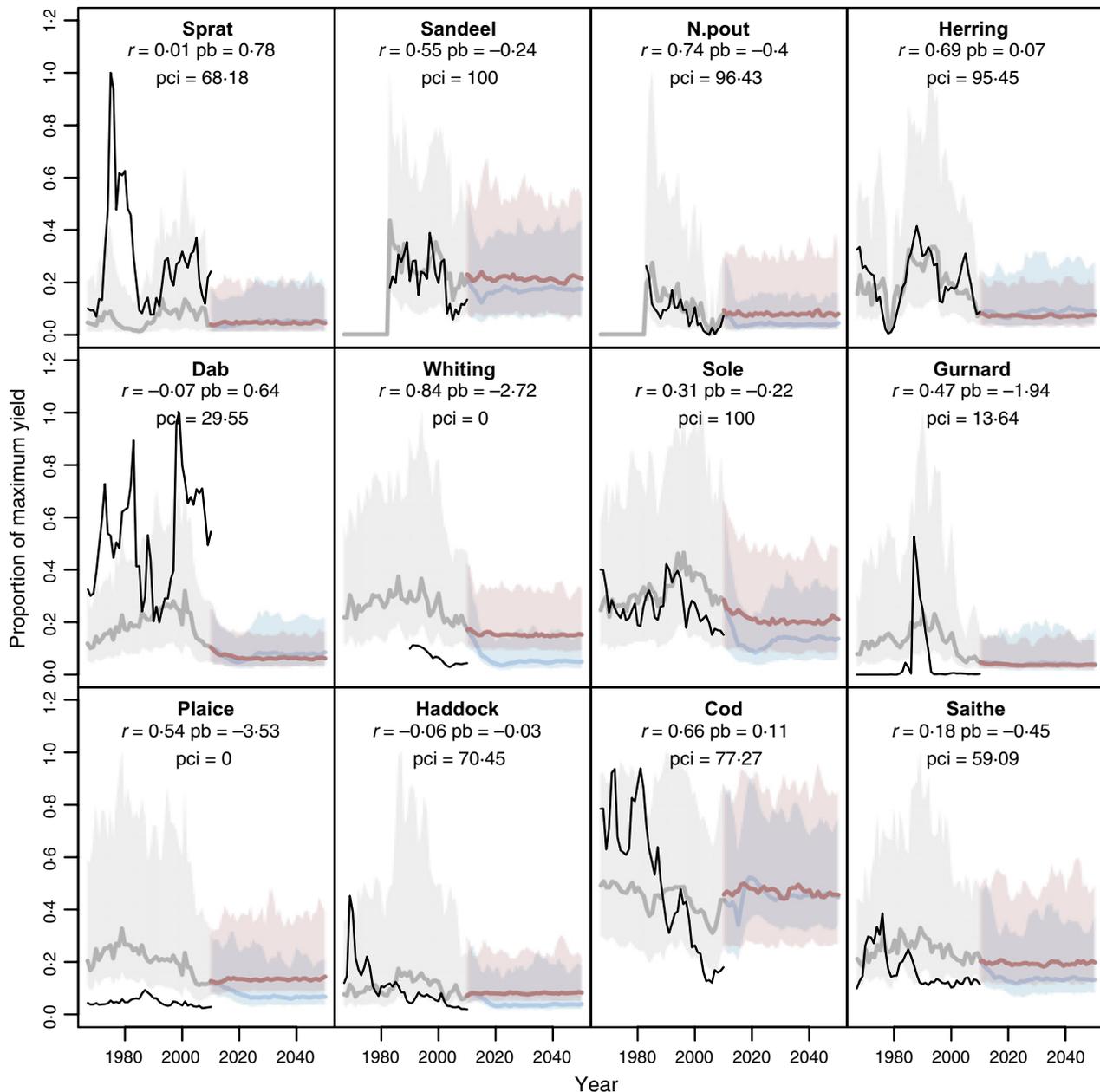


Fig. 3. Time series of yields expressed relative to maximum values under time-varying fishing. All other features are explained in Fig. 2 caption.

RECONSTRUCTING RELATIVE STATUS FROM A MULTISPECIES SIZE SPECTRUM PERSPECTIVE

The calibrated deterministic model was used to establish the baseline values of indicators in the absence of exploitation. The model predicted that cod were below the $0.1B_{i,F=0}$ conservation threshold throughout most of the past three decades. Similarly, small forage fish (sprat and herring) were predicted to be below the threshold during the 1980s, consistent with past single-species assessments (Dickey-Collas *et al.* 2014). The model predicted superabundance of some species (notably plaice, haddock, gurnard and whiting) during the period of decline in cod spawner biomass.

The community-level indicators allowed for a complementary exploration of ecological status (Fig. 4). Past

levels of fishing mortality revealed patterns of reduced community size structure relative to unexploited baselines as measured by the four indicators. A recent recovery due to the increase in large demersal fish species was reflected in increases in mean maximum weight and the shallower slope of the size spectrum.

FUTURE SCENARIO PROJECTIONS: CAN MULTIPLE MANAGEMENT OBJECTIVES BE ACHIEVED SIMULTANEOUSLY?

In the projection period, the ICES F_{MSY} 'targets' scenario resulted in a recovery of cod accompanied by declines in plaice, haddock and whiting and increases in smaller fish (sprat, sandeel, Norway pout). Cod do not recover under

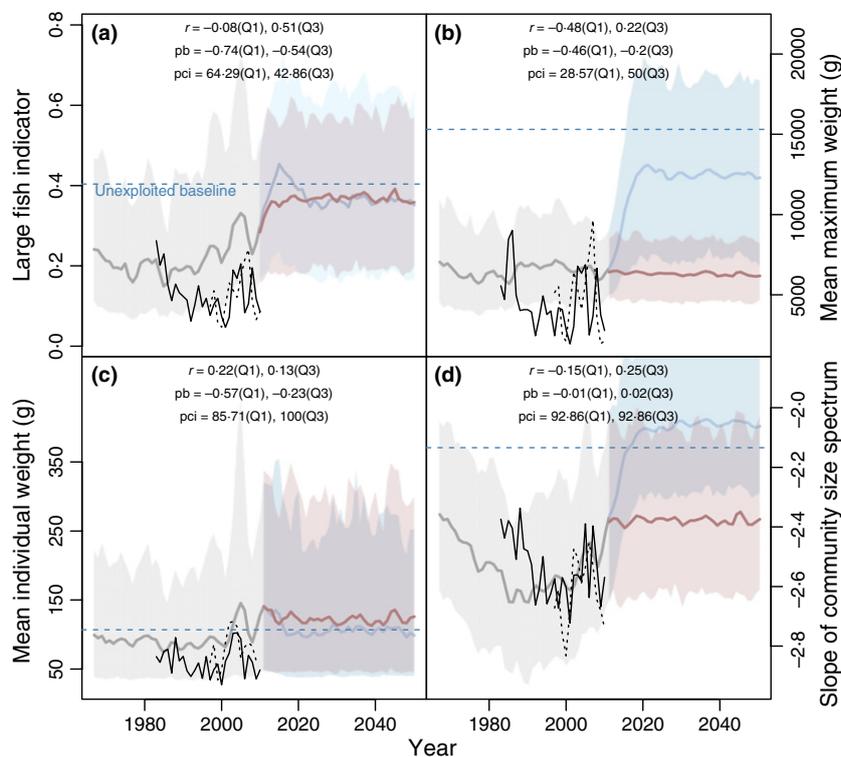


Fig. 4. Community indicator time series (a) large fish indicator, (b) mean maximum weight, (c) mean individual weight, (d) slope of community size spectrum. Black lines are empirically derived indicators from international bottom trawl survey data (Q1, solid, Q3 dotted). Blue dashed lines show the value of the modelled community indicator obtained from an unexploited community. All other features are described in Fig. 2 caption.

the ‘status quo’ scenario. At the community level, recovery was most notable under the ICES F_{MSY} ‘targets’ scenario for the mean maximum weight and the size spectrum slope (Fig. 4). There was very little difference between scenarios for the mean weight and large fish indicator (Fig. 4), in spite of major restructuring of species composition (Fig. 2) and size structure.

Overall projections under the ICES F_{MSY} ‘targets’ scenario show that there was a high probability (0.9) of achieving the biodiversity target ($0.1B_{i,F=0}$) (Fig. 5). However, the probability was only 0.6 for the food web target of an LFI of $0.8LFI_{F=0}$, and importantly, it did not differ substantially from the probability estimated for the ‘status quo’ scenario in which biodiversity targets were not met. Using an alternative food web target of the unexploited community size spectrum slope (-2.1) revealed recovery in size structure under the ‘targets’ scenario relative to the ‘status quo’. In terms of trade-offs, under the ‘targets’ scenario, the yield declined to 75% of the 2010 yield. Total biomass was stable in both scenarios, although it was slightly higher and gradually increasing in the ‘targets’ scenario.

Discussion

We have shown how a dynamical multispecies size spectrum model can be applied to a real community. The model replicated many aspects of population and community size structure including some past trends even though it was not fitted to time-series data. The model has the advantage that it accounts for species’ size distributions, abundance and interactions and has therefore allowed us

to examine directly, and in the same framework, the trade-offs between population status, community and food web structure, biodiversity and fisheries yield. Model simulations suggest that there is a high probability that achieving the accepted F_{MSY} management targets for exploited North Sea populations will lead to recovery in food webs and biodiversity in the North Sea ecosystem. The observed recovery is greater when fishing populations at F_{MSY} than if the status quo (2010) fishing rates are maintained. This recovery comes with 25% loss in total yield relative to the status quo scenario.

Ultimately, it is a societal decision whether to adopt different targets or to forego yield to meet the existing targets, but access to outputs from models such as this will increase the likelihood that those contributing to the debate are informed about the consequences of alternate decisions. For the large fish indicator, a target of 0.3 has been proposed in the North Sea (Greenstreet *et al.* 2010), but the simulations suggest that meeting F_{MSY} management targets will only lead to a 60% probability of achieving the LFI target of 0.32 we considered here. This means that further reductions in fishing mortality are likely to be needed to meet a 0.3 target, with concomitant reductions in fisheries yield.

The probability of achieving the LFI target did not differ substantially between the ‘targets’ and ‘status quo’ scenario, whilst the community size spectrum showed greater recovery in size structure under the ‘targets’ scenario. This implies that the community size spectrum slope is potentially more discriminatory in terms of community status, a property that is recognized as desirable for indicators that are intended to track the consequences

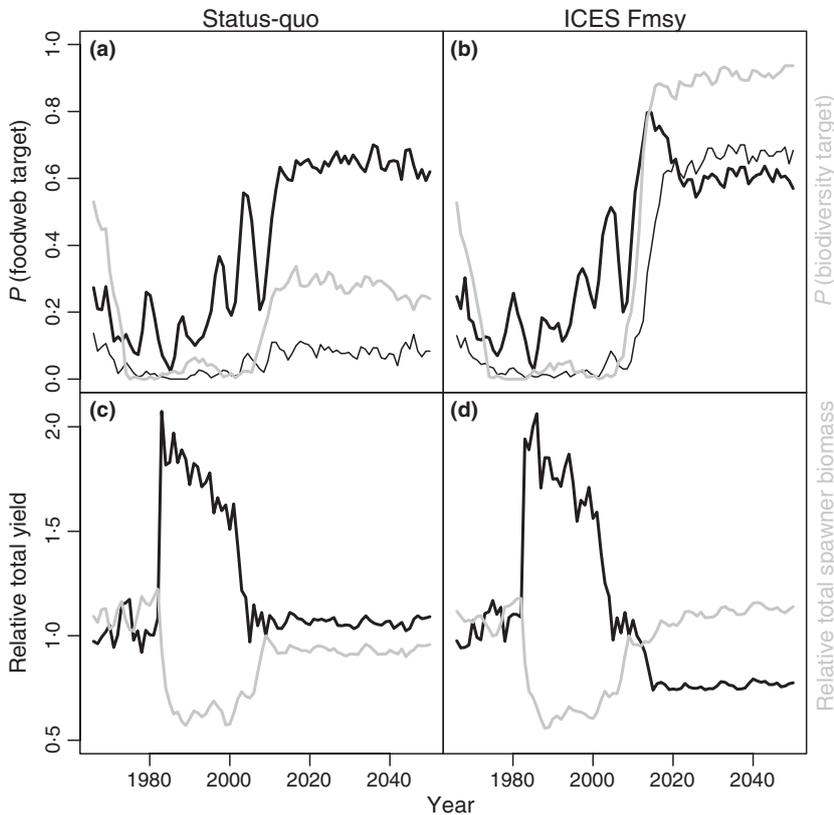


Fig. 5. Probability of achieving hypothetical targets for (a,b) food webs and biodiversity under the status quo (a,c) and ICES F_{MSY} (b,d) fishing scenarios. Probability was assessed as the proportion of stochastic scenarios where targets for food webs (value of large fish indicator $\geq 0.8LFI_{F=0} = 0.32$, thick black line; \geq size spectrum slope $_{F=0}$, thin black line) and for biodiversity (spawner biomass of all species $\geq 0.1B_{i,F=0}$, grey line) were achieved through time. (c,d) Related changes in total yield (black lines) and total community spawner biomass (grey lines) both relative to values in 2010.

of changing human impacts on the environment (Rice & Rochet 2005). For this reason, the selection of the LFI as the most appropriate choice of food web or community indicator may be premature. Improved understanding of the sensitivity and performance of these and other indicator frameworks is needed (Fulton, Smith & Punt 2005; Houle *et al.* 2012).

The North Sea has undergone large-scale historical changes in the relative abundance of species and overall community size structure and has been fished for many centuries (Alward 1932). We used the model to establish baselines in the absence of fishing at both population and community levels. These baselines differ substantially from a single-species perspective and show increases in some populations when others are heavily impacted. The results shown here are consistent with trophic cascades and the release of meso-predators (Heath, Speirs & Steele 2014; Myers *et al.* 2007). Returning to a more 'balanced' state in the context of community size structure would involve some population declines from current abundance.

One of the limitations of this study is that we considered only fishing effects driving change. Environmental change is acting on abundance and body size distributions of species and communities (Genner *et al.* 2010; Simpson *et al.* 2011). For simplicity, we calibrated the model to a single period to estimate the unknown parameters that relate to carrying capacity of the background resource and fish recruitment. Misfits between indicators and data were evident earlier in the time series, and this may be due to environmental changes that affect carrying capacity. Recent

advances linking size spectrum models to changes in oceanographic variables and size distributions of plankton and invertebrates could be used to explore whether targets would be met under changing resource carrying capacity and environmental conditions (Blanchard *et al.* 2009, 2012; Woodworth-Jefcoats *et al.* 2013).

Cross-validation with independent data and quantification of model skill is rarely carried out for multispecies and ecosystem models in fisheries. Cross-validation showed that the model captured most species size distributions with a couple of exceptions. Abundance of saithe and sole predicted by the model was higher than that derived from survey data. For saithe, it is well-established that young fish are found predominantly in inshore rocky areas that are unsuitable for trawling and are rarely caught in the North Sea International Bottom Trawl Survey that samples predominantly soft-bottomed areas further offshore (Knijn *et al.* 1993). Further, data and model abundance predictions were similar for saithe >300 g. As such, the model does not necessarily misrepresent the abundance or dynamics of saithe in the North Sea as a whole. For sole, the distribution is restricted to the southern North Sea and sole, as a species that often burrows in seabed sediments, is not efficiently caught by the International Bottom Trawl Survey trawl (Fraser, Greenstreet & Piet 2007). One explanation for the discrepancy in the abundance estimates is that the catchability estimate from Fraser, Greenstreet & Piet (2007) was overestimated because the 8-m beam trawl survey used to correct the IBTS catchability still underestimates the true abundance.

The current model is appropriate for strategic rather than tactical use in management. It has sufficient flexibility for testing alternative assumptions as well as integration with different data sources using this modelling framework. These aspects make it a good candidate for use in management strategy evaluation alongside other models (Plagányi *et al.* 2014). Moving into the tactical space for use alongside single-species stock assessment methods would require higher standards for model skill as well as more careful consideration of parameter and model uncertainty. A key challenge is identifying and choosing which data are suitable for use in model fitting as estimated parameters are sensitive to these decisions (Mackinson 2014). We also assumed that the main source of uncertainty in our projections was due to environmental stochasticity (e.g. process error in the model). The quality of the data also matters and fisheries data can be rife with uncertainty and bias as a result of misreporting. Data assimilation and Bayesian inference methods would enable formal quantification of parameter and model uncertainty, sensitivity and greater integration of various data types as part of the model framework (Dowd 2007). Such methods have not yet been used for size spectrum models, and challenges include the presence of oscillations under particular parameter combinations (Law *et al.* 2009). These issues may be overcome through integration with more robust and newer statistical methods (Sunnaker *et al.* 2013).

Our model outputs suggest that expected reductions in fishing mortality rates to reach F_{MSY} will lead to concomitant reductions in the impacts of fishing on food webs and biodiversity. In itself, this will help to reconcile the aspirations of conservationists and fisheries managers. Targets for Marine Strategy Framework Directive indicators are still being agreed, but the LFI target we considered implies that reductions in fishing mortality to F_{MSY} may not be sufficient to achieve the target and that having more large fishes in the community may require further reductions in fishing mortality and yield. Given that there may be political and economic costs associated with not achieving a binding target, society will need to decide whether potential reductions in yield are an appropriate price to pay for a community structure more comparable with the unexploited baseline.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Multispecies size spectrum model equations

Table S2. Species-specific input parameters

Table S3. Sample sizes for species individual-level biological data

Table S4. Species' interaction matrix from spatial overlap

Table S5. Fixed input parameters

Fig. S1. Historic time series of fishing mortality rates used in simulations over for the 1967–2010 period.

Fig. S2. Model calibration results: predicted versus observed species time-averaged catches and spawner biomass.

Fig. S3. Predicted and observed individual weights standardized by asymptotic size W for each species versus age.

Data S1. Contains further details on the multispecies model and data sources for parameterization.