



# Modelling the effects of fishing on the North Sea fish community size composition



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## ABSTRACT

Ecosystem-based management of the North Sea demersal fish community uses the large fish indicator (LFI), defined as the proportion by weight of fish caught in the International Bottom Trawl Survey (IBTS) exceeding a length of 40 cm. Current values of the LFI are  $\sim 0.15$ , but the European Union (EU) Marine Strategy Framework Directive (MSFD) requires a value of 0.3 be reached by 2020. An LFI calculated from an eight-species subset correlated closely with the full community LFI, thereby permitting an exploration of the effects of various fishing scenarios on projected values of the LFI using an extension of a previously published multi-species length-structured model that included these key species. The model replicated historical changes in biomass and size composition of individual species, and generated an LFI that was significantly correlated with observations. A community-wide reduction in fishing mortality of  $\sim 60\%$  from 2008 values was necessary to meet the LFI target, driven mainly by changes in cod and saithe. A 70% reduction in cod fishing mortality alone, or a 75% reduction in otter trawl effort, was also sufficient to achieve the target. Reductions in fishing mortality necessary to achieve maximum sustainable harvesting rates are projected to result in the LFI over-shooting its target.

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## 1. Introduction

Many studies of exploited fish communities have demonstrated shifts towards smaller sized fish, related to increased fishing (Daan et al., 2005; Shin et al., 2005; Greenstreet and Rogers, 2006; Heath and Speirs, 2012), whilst an increase in the mean size of fish inside marine reserves is one of the most frequently observed responses following the cessation of fishing (Molloy et al., 2009). Consequently, the large fish indicator (LFI), defined as the proportion by weight of demersal fish  $>40$  cm sampled during the quarter 1 International Bottom Trawl Survey (Q1 IBTS) (Greenstreet et al., 2011), has been adopted as an OSPAR Ecological Quality Objective (EcoQO) for the North Sea fish community (Heslenfeld and Enserink, 2008) and is the principal status assessment tool for implementing an ecosystem approach to fisheries management in Europe. The LFI has also been adopted as an indicator to support implementation

of the Marine Strategy Framework Directive (MSFD), and is identified in the 2010 decision document as an indicator to monitor change in the proportion of top predators in fish components of marine food webs (European Commission, 2010). It may also fulfil the function of indicator 1.7.1, monitoring change in the relative abundance of ecosystem components, in this instance large and small fish (Modica et al., 2014).

The simplicity of the LFI belies complex processes that can influence its value. As a ratio indicator, changes towards low values can be caused by increased small fish abundance as well as by the depletion of large fish (Daan et al., 2005). Predator–prey interactions may affect the LFI, for example an increase in small fish abundance might arise from release of predation pressure, as larger piscivorous fish are removed (Christensen et al., 2003; Myers and Worm, 2003; Frank et al., 2005; Heithaus et al., 2008). In addition, the community of fish comprises species of widely varying maximum sizes, so shifts in community composition towards species with lower maximum size (e.g. in response to warming temperatures) could also cause LFI values to decline (Shephard et al., 2012; Beare et al., 2004; Simpson et al., 2011). So, use of the LFI in assessing ecosystem status and achieving particular goals for the state of the system requires a clear understanding of what has driven changes in the LFI in the past in order to predict its response in the future.

In the early 1980s the North Sea LFI had a value of  $\approx 0.3$ , before declining to  $<0.1$  in the early 2000s, followed by some recovery

*Abbreviations:* LFI, large fish indicator; IBTS, international bottom trawl survey; EU, European Union; MSFD, marine strategy framework directive; OSPAR, Oslo-Paris convention for the protection of the marine environment of the North-East Atlantic; EcoQO, ecological quality objective; PDMM, population dynamical matching model; FCSRM, fish community size-resolved model; ICES, International Council for the Exploration of the Seas; TSB, total stock biomass.

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in subsequent years (Fung et al., 2012; Greenstreet et al., 2012a). Greenstreet et al. (2011) conducted a statistical analysis of the North Sea LFI time series and, concluded that there was a 12–18 year lag in the relationship between changing demersal fish harvesting rates and the indicator response. Subsequent studies in different marine regions have demonstrated similar lagged relationships between fishing mortality and the LFI (Shephard et al., 2011). A number of size-structured models of fish communities show the anticipated inverse relationship between fishing mortality and indices of fish size (Hall et al., 2006; Pope et al., 2006; Blanchard et al., 2009; Rochet et al., 2011; Blanchard et al., 2014; Thorpe et al., 2015).

In understanding how the LFI has responded to historical changes in fishing pressure, and how it might respond to future management decisions, size-structured models are clearly important tools. However, the complexity of the factors affecting the LFI, including multispecies predator–prey interactions, has meant that attempts at modelling it have thus far been fairly few. Shephard et al. (2012) studied changes in the LFI in the Celtic Sea using two different modelling approaches. The first was based on the Population-Dynamical Matching Model developed by Rossberg et al. (2008), which uses a quasi-evolutionary process and allometric scalings to generate size-structured communities of composed of species of varying body size. The second used the Fish Community Size-Resolved Model (FCSR) of model of Hartvig et al. (2011) that involves coupled size-spectra to represent the size distributions of groups of species with similar maturation sizes. The models are contrasting in that the PDMM produces changes in the LFI only through shifts in relative species abundance, while the FCSR can do so as a result of changes in the population length distributions of groups of species. It was concluded that the changes in the Celtic Sea LFI arose mainly through changes in species abundance. Fung et al. (2013) also used the PDMM model configured for the Northeast Atlantic and predicted multi-decadal recovery times in response to reductions in community fishing pressure. Most recently, Blanchard et al. (2014) used a variant of the FCSR where individual size-spectra represented 12 individual North Sea species rather than species groups and found, by contrast, that a rapid recovery in the LFI could occur when the fishing mortality on the various species was moved to maximum sustainable yield (MSY) levels.

Here, we apply an alternative discrete-time multispecies length-structured model for the North Sea fish community developed by Speirs et al. (2010) to model the observed changes in the LFI, and then use it to explore what may happen in the future under alternative scenarios of fishing fleet activity and recruitment patterns of key species. One of the features of the model is that predator–prey interactions are specified in terms of body length ratios applicable across all species, thereby reducing the need for complex dietary parameterisation. The model also includes the key commercially exploited pelagic and invertebrate species in the North Sea, enabling the trade-offs required to restore the demersal LFI to a given state to be explored. As with Blanchard et al. (2014) individual species are explicitly represented, but the Speirs et al. (2010) model differs substantially in numerical implementation as well as a number of other key respects, including that we model individual length rather than weight, and that we represent reproduction as species-specific seasonal function of the spawning stock rather than having recruitment as an annual external driver. Since both the revised Common Fisheries Policy and the MSFD require fisheries to operate at MSY, we address the question of whether achieving this is sufficient to reach the LFI targets for North Sea fish. In contrast to earlier modelling work, we also consider the extent to which the LFI target might be achieved by changes in effort of different fishing fleets rather than changing overall fishing mortality, or species-specific mortalities.

## 2. Methods

### 2.1. The data

The North Sea First Quarter (Q1) International Bottom Trawl Survey (IBTS) is an annual survey with wide spatial coverage. Fish caught are identified to species, and numbers at length, as well as age and sexual maturity data from subsamples of selected species, are recorded (ICES, 2010). The data are publicly available from the ICES DATRAS database portal (<http://datras.ices.dk>). Individual fish weights are obtained from standard cubic-power weight-at-length relationships (Greenstreet et al., 2012b), which when applied to the survey data allowed the calculation of the LFI.

### 2.2. The model

We used the Speirs et al. (2010) discrete-time length-structured model of the North Sea fish community. The model describes a food web composed of a set of key predator and prey species together with a small number of more crudely represented alternative food sources. For the explicitly represented species the number,  $n_{i,j,t}$ , of individuals of species  $i$  in length class  $j$  at time  $t$  is updated over time step  $\Delta t$  according to

$$n_{i,j,t+\Delta t} = \begin{cases} (1 - p_i)\sigma_{i,j,t}n_{i,j,t} + h_{i,t} & j = 0 \\ (1 - p_i)\sigma_{i,j,t}n_{i,j,t} + p_i\sigma_{i,j-1,t}n_{i,j-1,t} & j > 1 \end{cases}$$

where  $0 < p_i < 1$  is a constant fraction of individuals progressing from one length class to the next over the interval  $t \rightarrow t + \Delta t$ , and  $\sigma_{i,j,t}$  and  $h_{i,t}$  are, respectively, the corresponding survivorship and hatchlings to the first length class. The length of individuals of length class  $j$  is given by

$$L_{i,j} = L_{\infty,i} - (L_{\infty,i} - L_{0,i}) \exp(-j \times \Delta q_i)$$

where  $L_{0,i}$  is the length of the smallest length class,  $L_{\infty,i}$  is the asymptotic length of species  $i$ , and  $\Delta q_i$  is a constant. In order to model growth up to a maximum length  $L_{\max,i}$  (necessarily less than  $L_{\infty,i}$ ) using  $j_{\max,i}$  length classes we set

$$\Delta q_i = -\ln \left( \frac{L_{\infty,i} - L_{\max,i}}{L_{\infty,i} - L_{0,i}} \right) / j_{\max,i}$$

As shown in Speirs et al. (2010), in our model the mean length,  $\hat{L}_{i,t}$ , of a cohort of individuals with length  $L_{0,i}$  at  $t=0$  will increase with growth rate  $\gamma_i$  according to a von Bertalanffy function

$$\hat{L}_{i,t} = L_{\infty,i} - (L_{\infty,i} - L_{0,i}) e^{-\gamma_i t}$$

provided that  $p_i = \gamma_i \Delta t / \Delta q_i$  and  $p_i \in (0, 1)$ . So, if the parameters  $L_{0,i}$ ,  $L_{\infty,i}$ , and  $\gamma_i$  are known from observations we can choose any  $j_{\max,i}$  (and hence  $\Delta q_i$ ) and  $\Delta t$  that satisfy these requirements and get the required von Bertalanffy growth. Although the choice does not impact on the mean cohort length, it does control the variability around that mean. Increasing  $\Delta q_i$  or decreasing  $\Delta t$  will have the effect of increasing the variability in length of a cohort. Biomass features in the calculation of the survival and recruitment terms, described below, so we assume that weight and length are related by  $w_{i,j} = a_i L_j^{b_i}$ , with  $a_i$  and  $b_i$  constants.

The recruitment term,  $h_{i,t}$ , is the number of eggs hatched from a distinct egg class,  $n_{e,i,t}$ . We assume that the proportion of sexually mature individuals producing eggs increases with length according to a cumulative normal distribution. So, the proportion of mature adults,  $m_{i,j}$ , in length class  $j$  is given by

$$m_{i,j} = \Phi \left( (L_{i,j} - L_{m,i}) / s_{m,i} \right)$$

where  $\Phi(\bullet)$  is the cumulative distribution function of the standard normal distribution, and the mean and standard deviation of length at maturity are  $L_{m,i}$  and  $s_{m,i}$ , respectively. Over the interval  $t \rightarrow t + \Delta t$  the rate,  $\varepsilon_{i,t}$ , at which eggs are produced and enter an egg class, depends on the total mature biomass and the time of year. If spawning occurs between days-of-the-year  $d_{0,i}$  and  $d_{1,i}$ , then measuring time in days and defining the day-of-the-year in a 365-day year at time  $t$  as  $d = t - \text{trunc}(t/365) \times 365$ , we get

$$\varepsilon_{i,t} = \begin{cases} \frac{\rho_i}{2(d_{1,i} - d_{0,i})} \sum_{j=0}^{j_{\max,i}} m_{i,j} n_{i,j,t} w_{i,j} & \text{if } d_{0,i} < d < d_{1,i} \\ 0 & \text{otherwise} \end{cases}$$

where  $\rho_i$  is the annual number of eggs produced per unit female body mass, and the factor of 1/2 assumes an equal sex ratio. If the average egg development time is  $\tau_{e,i}$  and eggs suffer a per capita background mortality  $\mu_{e,i}$ , and a constant loss rate from predation  $U_{e,i,t}/\Delta t$ , then the update rule for the egg class and hatchlings are respectively

$$n_{e,i,t+\Delta t} = \frac{\varepsilon_{i,t} - U_{e,i,t}/\Delta t}{\lambda_i} + \left( n_{e,i,t} - \frac{\varepsilon_{i,t} - U_{e,i,t}/\Delta t}{\lambda_i} \right) e^{-\lambda_i \Delta t}$$

$$h_{i,t+\Delta t} = \frac{p}{\lambda_{i,t}^2} \{ \lambda n_{e,i,t} + (\lambda n_{e,i,t} - \theta_{i,t})(1 - e^{-\lambda_{i,t} \Delta t}) \}$$

where  $\lambda_i = \mu_{e,i} + 1/\tau_{e,i}$ . The time step uptake of eggs due to predation,  $U_{e,i,t}$ , is calculated in the same way as the predation on all population length classes, as described below. Since this depends on length, we assume the length of an egg is approximated by the equivalent spherical diameter of a hatchling of mass  $w_{i,0} = a_i L_{0,i}^b$  assuming neutral buoyancy.

The survivorship of the population length classes,  $\sigma_{i,j,t}$ , can be further broken down

$$\sigma_{i,j,t} = \sigma_{i,j,t}^p \times \sigma_{i,j,t}^b \times \sigma_{i,j,t}^F$$

where  $\sigma_{i,j,t}^p$  is the survivorship from predation by modelled species,  $\sigma_{i,j,t}^b$  is the survivorship from additional biomass-dependent mortality, and  $\sigma_{i,j,t}^F$  the survivorship from fishing. Survivorship from fishing is simply  $e^{-F_{i,j,t} \Delta t}$  where  $F_{i,j,t}$  is the fishing mortality rate per unit time on length class  $j$  of species  $i$  at time  $t$ . The catch over each time step of a given species and length class is therefore  $(1 - \sigma_{i,j,t}^F) n_{i,j,t}$ . Since not all the catch are necessarily retained, we also define an effective minimum landing size  $L_{l,i}$ , such that the landed catch, or landings, is the total catch for species  $i$  of individuals of length  $L_{l,i}$  or above.

The biomass-dependent survivorship takes the same form for all individuals, but we distinguish small individuals (for demersal fish these are the planktonic individuals before settlement) from larger ones. If this transition occurs at length  $L_{s,i}$  we have

$$\sigma_{i,j,t}^b = \begin{cases} e^{-(\mu_{p,i} + \delta_{p,i} W_{p,i,t}) \Delta t} & L_{i,j} < L_{s,i} \\ e^{-(\mu_{s,i} + \delta_{s,i} W_{s,i,t}) \Delta t} & \text{otherwise} \end{cases}$$

where  $W_{p,i,t} = \sum_{j=1}^{j_{s,i}-1} w_i n_{i,t}$  and  $W_{s,i,t} = \sum_{j=j_{s,i}}^{j_{\max}} w_i n_{i,t}$  are the respective biomasses of small and large individuals, with  $j_{s,i}$  the first length class where  $L_j \geq L_{s,i}$ .

In order to calculate  $\sigma_{i,j,t}^p$  we begin by noting that all surviving individuals must have met their metabolic, growth, and reproductive costs. This means that, if  $\alpha_i$  is the assimilation efficiency, the

biomass of food (in biomass units) consumed over  $t \rightarrow t + \Delta t$  for each length class is

$$C_{i,j,t} = \frac{\sigma_{i,j,t} n_{i,j,t} (M_{i,j} + p_i G_{i,j} + R_{i,j,t})}{\alpha_i}$$

where  $M_{i,j}$ ,  $p_i G_{i,j}$ , and  $R_{i,j,t}$  are the per capita metabolic, growth, and reproductive costs in biomass units. The metabolic costs are proportional to body mass

$$M_{i,j} = \eta_i w_{i,j} \Delta t,$$

the growth cost is the difference in weight

$$G_{i,j} = w_{i,j+1} - w_{i,j}$$

and applies to the fraction,  $p_i$ , of individuals growing from one class to the next. The reproductive cost is the weight of eggs produced over the time step is therefore

$$R_{i,j,t} = \frac{s_{i,t} \rho_i m_i w_{i,0} \Delta t}{2}$$

The fraction of the total food consumption by predator class  $\{i, j\}$  that comes from prey class  $\{i', j'\}$  is the weighted proportion of the total prey biomass

$$\pi_{i,j,i',j',t} = \frac{\psi_{i,j,i',j',t} n_{i',j',t} w_{i',j'}}{\sum_{\text{all } i'} \sum_{\text{all } j'} \psi_{i,j,i',j',t} n_{i',j',t} w_{i',j'}}$$

where the weighting,  $\psi_{i,j,i',j',t}$ , is the preference of  $\{i, j\}$  for  $\{i', j'\}$  and described below. This implies that the total consumption (in units of density,  $\text{gm}^{-2}$ ) on prey class  $\{i', j'\}$  by all predators is

$$U_{i',j',t} = \sum_{\text{all } i} \sum_{\text{all } j} C_{i,j,t} \pi_{i,j,i',j',t}$$

and hence that the fraction surviving predation is

$$\sigma_{i',j',t}^p = 1 - \frac{U_{i',j',t}}{w_{i',j'} n_{i',j',t}}$$

Note that the above equation depends on the survivorship of the predators, which means that we need to define a processing order. We make the simplification that only surviving individuals get to feed, and since in our system predators are always larger than their prey we can order the calculation of the predation mortality rates accordingly. So the largest length class can never be eaten by any other class, but can predate smaller classes. Having calculated the contribution to the predation of all of its prey, the next-largest length class down (which may be a different species) can be dealt with since its mortality rate is now known, and so on in descending order of length.

We assume that the preference arises from a species-dependent term  $Z_{i,i'}$ , which is zero if a prey species is not eaten and large when a prey species is highly preferred, and a function,  $f(l/L_{i,j})$ , of the prey/predator length ratio

$$\psi_{i,j,i',j',t} = \frac{Z_{i,i'} \int_{l_{i',j'+1}}^{l_{i',j'}} f(l/L_{i,j}) dl}{\sum_{\text{all } i'} \sum_{\text{all } j'} Z_{i,i'} \int_{l_{i',j'+1}}^{l_{i',j'}} f(l/L_{i,j}) dl}$$

The function  $f(l/L_{i,j})$  peaks at a preferred prey/predator length ratio  $R_{\text{opt},i}$ , and is zero outside a range of ratios from  $R_{\text{min},i}$  to  $R_{\text{max},i}$

$$f(l/L_{i,j}) = \begin{cases} g(l/L_{i,j})^{\alpha_i-1} (1 - g(l/L_{i,j}))^{\beta_i-1} & R_{\text{min},i} < l/L_{i,j} < R_{\text{max},i} \\ 0 & \text{otherwise} \end{cases}$$

where

$$g(l/L_{i,j}) = \frac{1/L_{i,j} - R_{\min,i}}{R_{\max,i} - R_{\min,i}}$$

$$\alpha_i = 1 + (\beta_i - 1) \left( \frac{R_{\text{opt},i} - R_{\min,i}}{R_{\max,i} - R_{\min,i}} \right)$$

The parameter  $\beta_i$  sets how tightly the preference function is distributed about  $R_{\text{opt},i}$ .

For three prey types not explicitly represented on a species-by-species basis (zooplankton, benthos, and 'other fish') we model these by simple biomass spectra partitioned into length classes of equal width on a logarithmic scale. The length of the lower boundary of class  $j$  of prey type  $i$  is

$$L_{i,j} = L_{0,i} \left( \frac{L_{\max,i}}{L_{0,i}} \right)^{(i/j_{\max,i})}$$

where  $L_{0,i}$  and  $L_{\max,i}$  are the smallest and largest lengths represented for type  $i$ , and  $j_{\max,i}$  is the number of length classes used to represent the biomass spectrum. We assume that for each prey class  $\{i, j\}$  the biomass,  $B_{i,j,t}$ , follows simple chemostat dynamics

$$B_{i,j,t+\Delta t} = \left( K_i - \frac{U_{i,j,t}}{P_i \Delta t} \right) (1 - e^{-P_i j_{\max,i} t}) + B_{i,j,t} e^{-P_i j_{\max,i} t}$$

where  $K_i$  is the steady state biomass without predation,  $P_i j_{\max,i}$  is the production to biomass ratio, and  $U_{i,j,t}/\Delta t$  is rate at which the prey length class is being consumed by the explicitly modelled predators. Given an estimate of a total unexploited biomass,  $T_i$ , together with the standard result of biomass spectrum theory of equal biomass in logarithmic length classes, we set  $K_i = T_i/j_{\max,i}$ . As with the explicitly modelled species, each length class has an associated characteristic mass for individual organisms in that length class,  $w_{i,j} = a_i L_{i,j}^{b_i}$ , and the production to biomass ratio scales logarithmically with body mass

$$\log_{10}(P_{i,j}) = k_{1,i} \log_{10}(w_{i,j}) + k_{2,i}.$$

The model was configured for eight demersal species that accounted for >90% of the total demersal biomass in the North Sea (cod, haddock, whiting, saithe, Norway pout, plaice, common dab, and grey gurnard), plus two pelagic species (herring, sandeel) and *Nephrops norvegicus* (henceforth *Nephrops*). The additional food resources not modelled at the species level were zooplankton, benthos, and 'other fish'. Outputs from the model were time series of total species biomass (TSB), normalised length distributions (the sum of each species distribution equals one) at annual census dates, annual recruitment, catch and landings, for each species. By applying logistic survey catchability-at-length functions to the TSB and length distributions, we derived a model estimate of the LFI (from the eight demersal species). A summary of the parameters used to model the length-structured species is provided in Table 1, while Table 2 contains the corresponding parameter values for each of the 11 explicitly-modelled species. Table 3 gives the size-independent preference weightings used in calculating distributing the food uptake by predators among possible prey. Finally, Table 4 gives the parameters used to model the various biomass spectra used to represent alternative food resources.

### 2.3. Baseline run

We first carried out a baseline model run for the period 1960–2008. Fishing mortalities reported by ICES were used where possible (ICES, 2009a for herring, and ICES, 2009b for cod, haddock, whiting, saithe, Norway pout and sandeel). These fishing mortalities are reported as mortality-at-age, and were converted to

**Table 1**

Brief descriptions, symbols, and units, for the parameters used to model the explicitly represented species. See Table 2 for the parameter values used for each species.

Description	Symbol	Units
Number of length classes	$j_{\max}$	–
Egg development time	$\tau_e$	Days
Hatchling length	$L_0$	cm
Settlement length	$L_s$	cm
Mean maturation length	$L_m$	cm
Standard deviation of maturation length	$s_m$	cm
Maximum modelled length	$L_{\max}$	cm
Asymptotic length	$L_{\infty}$	cm
Growth rate	$\gamma$	Year <sup>-1</sup>
Fecundity	$\rho$	Eggs g <sup>-1</sup>
Spawning start date	$d_0$	Day of year
Spawning end date	$d_1$	Day of year
Effective landing size	$L_l$	cm
<i>Density-independent mortality rates</i>		
Egg	$\mu_e$	Day <sup>-1</sup>
Pre-settlement	$\mu_p$	Day <sup>-1</sup>
Post-settlement	$\mu_s$	Day <sup>-1</sup>
<i>Biomass-dependent (density-dependent) mortality</i>		
Pre-settlement	$\delta_p$	g <sup>-1</sup> m <sup>2</sup> Day <sup>-1</sup>
Post-settlement	$\delta_s$	g <sup>-1</sup> m <sup>2</sup> Day <sup>-1</sup>
Assimilation efficiency	$\alpha$	–
Metabolic cost	$\eta$	Day <sup>-1</sup>
Weight-at-length constant	$a$	g cm <sup>-b</sup>
Weight-at-length power	$b$	–
Preferred prey/predator length ratio	$R_{\text{opt}}$	–
Minimum prey/predator length ratio	$R_{\min}$	–
Maximum prey/predator ratio	$R_{\max}$	–
Predator preference function width	$\beta$	–

mortalities-at-length by inverting the von Bertalanffy age-length relationship for each species in order to obtain an approximate age,  $a_{i,j}$ , of length class  $L_{i,j}$

$$a_{i,j} = \text{trunc} \left\{ -\ln \left( \frac{L_{\infty,i} - L_{i,j}}{L_{\infty,i} - L_{0,i}} \right) \right\}$$

which allows us to use ICES stock assessments for This allows us to use We can thus get a length-dependent  $F$  from the age-class  $F$ s

$$F_{j,t} \approx F_{a_{i,j},t}$$

and so the survival from fishing is

$$\sigma_{j,t}^F = e^{-F_{j,t} \Delta t / 365}$$

where the division by 365 is necessary if  $\Delta t$  is in days, and the  $F$ s are annual rates. Stock assessments started in different years for the various species, so for years in our model run pre-dating the start of assessment we generated approximate fishing mortalities by estimating a linear scaling between fishing mortality and official recorded landings (<http://www.ices.dk/marine-data/>) and assuming that the length-dependence of the fishing mortality was the same as that of the first assessed year. This is clearly restrictive, but is a tolerable assumption when either the stock lightly exploited, or when landings are relatively constant, and only affects years prior to the LFI period. For the remaining fish species (common dab and grey gurnard) we approximated the fishing mortalities from the harvest ratio, i.e. the ratio of landings to total biomass estimated from the IBTS, with a length-dependence taken from the (single year) estimate of fishing mortality for those species (Pope et al., 2000). We estimated *Nephrops* fishing mortality using the landings and a stock biomass estimate obtained by scaling up from burrow densities obtained from underwater television surveys (Speirs et al., 2010). From 2002 onwards, larval survivorship of both herring and sandeels was lower than expected (ICES, 2009a, 2009b), probably as a result of changing environmental conditions (Payne et al., 2009). To account for this, herring and sandeel larval

**Table 2**  
Species-specific parameter values for the explicitly represented species. See Table 1 for parameter definitions and units.

Parameter	Cod	Haddock	Whiting	Norway pout	Herring	Sandeel	Common dab	Grey gurnard	Nephrops	Saithe	Plaice
$j_{max}$	140	70	65	65	80	40	45	90	50	70	60
$\tau_e$	11	15	15	1.5	7	90	7	7	1	10	24
$L_0$	0.3	0.5	0.5	0.8	0.8	0.5	0.25	0.35	0.7	0.35	0.062
											5
$L_s$	7	5	5	1	6	5	1	5	1	6.5	1
$L_m$	60	25	20	13.7	0.22	14	24.5	29	9	55	32
$s_m$	2	3	2	2	1.5	1.5	2	1	1	8	3
$L_{max}$	111	58.5	40.9	18.3	29.7	19	38	42.8	18	71	43
$L_\infty$	123	65	43	18.5	30	20	40	45	20	80	45
$\gamma$	0.164	0.292	0.402	0.986	0.529	0.87	0.584	0.291	0.16	0.3	0.35
$\rho$	500	500	880	980	400	780	1000	3000	100	750	265
$d_0$	90	75	1	60	330	1	60	150	90	1	1
$d_1$	120	105	120	120	365	30	150	240	180	120	120
$L_1$	50	34	31	10	20	10	30	35	8.5	35	27
	(45 pre-1989)	(30 pre-1989)	(29 pre-1983)								
$m_e$	0.065	0.081	0.066	0.03	0.057	0.01	0.09	0.065	0	0.13	0.05
$m_p$	0.065	0.081	0.066	0.03	0.057	0.16	0.09	0.065	0.05	0.13	0.05
$m_s$	0.0004	0.0042	0.0013	0.006	0.001	0.003	0.0085	0.002	0.002	0.0013	0.001
$\delta_p$	1.05E-04	1.75E-05	1.23E+03	1.40E-02	1.05E-05	8.77E-03	4.74E-02	2.63E-02	15.788	7.00E-5	0.6
$\delta_s$	3.51E-06	1.75E-06	8.77E-08	0	6.14E-07	0	0	8.77E-07	0	2.00E-05	5.5E-5
$\alpha$	0.06	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
$\eta$	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.1	0.1
$a$	0.00506	0.0052	0.0062	0.0068	0.006	0.0015	0.005	-0.0054	0.09045	0.01	0.009
$b$	3.1921	3.155	3.103	3	3.09	3.169	3.14	3.13	2.91	4	3.031
										2.972	
$R_{opt}$	0.3	0.1	0.3	0.03	0.03	0.3	0.1	0.3	0.03	0.3	0.1
$R_{min}$	0.04	0.005	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01
$R_{max}$	0.4	0.4	0.4	0.1	0.1	0.4	0.2	0.4	0.1	0.4	0.2
$\beta$	1.1	1.1	1.1	10	10	1.1	10	10	10	1.1	10

**Table 3**  
Length-independent diet preference weightings of post-settlement (i.e. size-classes greater than the settlement length,  $L_s$ , in Table 1) predators used in the model runs. Pre-settlement predators all feed exclusively on zooplankton. Where herring is the predator, the preferences apply solely to the pelagic eggs, larvae and pre-settlement stages of the prey species have a preference of zero). The entries marked ‘-’ indicate a value of zero.

Predator	Cod	Haddock	Whiting	Norway pout	Herring	Sandeel	Common dab	Grey gurnard	Nephrops	Saithe	Plaice
Prey											
Cod	0.199	-	0.079	-	0.317	-	-	0.129	-	-	-
Haddock	0.133	-	0.079	-	0.040	-	-	0.183	-	0.222	-
Whiting	0.199	-	0.394	-	0.040	-	-	0.322	-	-	-
Norway pout	0.066	0.533	0.039	-	0.323	-	-	0.045	-	0.112	-
Herring	0.007	0.133	0.394	-	0.040	-	-	-	-	0.222	-
Sandeel	0.013	0.133	0.008	-	0.040	-	-	0.065	-	0.222	-
Common dab	0.033	-	-	-	0.040	-	-	0.065	-	-	-
Grey Gurnard	-	-	-	-	0.040	-	-	-	-	-	-
Nephrops	0.199	-	-	-	-	-	-	-	-	-	-
Saithe	-	-	-	-	0.040	-	-	0.013	-	-	-
Plaice	-	-	-	-	0.040	-	-	-	-	-	-
Other fish	0.017	0.133	0.008	-	-	-	-	0.032	-	0.222	-
Zooplankton	-	-	-	1.00	0.040	1.000	-	-	-	-	-
Benthos	0.133	0.067	0.008	-	-	-	1.000	0.146	1.00	-	1.00

density-independent mortality rates were increased by 20% for the post-2002 period (Speirs et al., 2010). Initial runs did not replicate the high LFI values observed at the start (1983–1986) of the time series because of exceptionally high recruitment (the ‘gadoid

outburst’) associated with cooler water temperatures (Olsen et al., 2011). We therefore reduced the density independent cod larval mortality rate by 25% over the period 1973–1983 to account for this.

**Table 4**  
Parameters for the ‘unstructured’ food resources.

Description	Symbol	Units	Zooplankton	Benthos	Other fish
No. length classes	$j_{max}$	-	100	100	100
Min. length class	$L_{min}$	cm	0.01	0.1	1
Max. length class	$L_{max}$	cm	2	5	40
Weight-at-length const.	$a$	g cm <sup>b</sup>	0.5917	0.5917	0.0015
Weight-at-length power	$b$	-	3	3	3
Total biomass	$T$	g m <sup>-2</sup>	15	70	20
Log <sub>10</sub> (P) vs. log <sub>10</sub> (w) slope	$k_1$	log <sub>10</sub> (d <sup>-1</sup> )	-0.233	-0.233	-0.233
Log <sub>10</sub> (P) vs. log <sub>10</sub> (w) const.	$k_2$	log <sub>10</sub> (d <sup>-1</sup> )/log <sub>10</sub> (g)	0.92	0.1	0.1



**Table 5**  
Proportions of the total fishing mortality for each species attributed to each of six métiers. These were used in the model runs in which the fishing effort in the various métiers were changed individually.

Species	Beam trawl	Demersal otter trawl	<i>Nephrops</i> trawl	Seine trawl	Industrial fishery	Herring trawl
Common dab	0.96	0.03	0.01	0.01	0	0
<i>Nephrops</i>	0	0.16	0.84	0	0	0
Grey gurnard	0.05	0.52	0.09	0.14	0.2	0
Sandeel	0	0	0	0	1	0
Herring	0	0	0	0	0	1
Norway pout	0	0	0	0	1	0
Plaice	0.79	0.14	0.05	0.02	0	0
Whiting	0.05	0.52	0.09	0.14	0.02	0
Haddock	0	0.67	0.03	0.23	0.07	0
Cod	0.1	0.67	0.11	0.12	0	0
Saithe	0	0.99	0	0.01	0	0

#### 2.4. Forward runs

Scenarios were configured to explore the effects of variations in fishing mortality on individual species, in métiers or groups of species exploited by the same fishery, and of fishing according to maximum sustainable yield targets. In each case, a model run to 2008 was extended to 2020 under a scenario set of fishing mortalities.

First, we varied fishing mortality by various proportions of the 2008 reference year: a cessation of fishing ( $0F_{2008}$ ), a 50% reduction ( $0.5F_{2008}$ ), a continuation at the 2008 level ( $F_{2008}$ ), a 50% increase in fishing ( $1.5F_{2008}$ ), and a doubling of fishing mortality ( $2F_{2008}$ ). These scenarios were applied to all species simultaneously, and to each one of the 11 explicitly modelled species individually whilst maintaining fishing mortality for the remaining 10 species at  $F_{2008}$ .

In multi-species fisheries it is difficult to manage fishing on a purely species-by-species basis because different fleets, or métiers, catch many species (Ulrich et al., 2012). To explore this we classified fishing effort into six métiers: beam trawl, demersal otter trawl, *Nephrops* otter trawl, seine trawl, herring trawl, and the industrial fishery for sandeel, and apportioned the total fishing mortality on each species to these on the basis of landings and by-catch. Landings of cod, haddock, whiting, saithe, plaice, sole, and *Nephrops* from the North Sea for the period 1997–2004 are known for beam trawl, demersal otter trawl, *Nephrops* otter trawl, and seine trawl (Greenstreet et al., 2007). Stock assessments (ICES, 2009b) provide the by-catch of haddock and whiting in the industrial fishery. For herring we assumed that all of the catch is attributable to herring trawls, and that the by-catch of non-target species by herring trawls is negligible. For dab and grey gurnard, we assume that the proportions attributable to each métier were approximated by those of sole and whiting, respectively. The values obtained (Table 5) allowed us to explore the effects of changing the fishing effort associated with each métier. In particular, if  $p$  the proportion of that mortality attributable to a given métier, a doubling of the effort for that métier would produce a fishing mortality of  $[2p + (1 - p)]F_{2008}$ .

We next carried out runs to examine the effect of fishing at levels estimated to produce maximum sustainable yield ( $F_{MSY}$ ). Several of the species have published  $F_{MSY}$ 's; cod 0.19, haddock 0.3, saithe 0.22, plaice 0.25, and herring 0.25 (ICES, 2012). For whiting we used the EU-Norway management plan target of 0.3. For common dab and grey gurnard, which are mainly by-catch, we assumed a 15% reduction in fishing mortality as an approximation to the level that might result incidentally from targeted reductions on other species. The  $F_{MSY}$ 's were applied to the species simultaneously, and also to each species individually.

Given the critical effect of cod recruitment on the LFI in the baseline model run, six further runs were performed to simulate three fisheries management scenarios and two cod recruitment situations. We considered a continuation of current recruitment

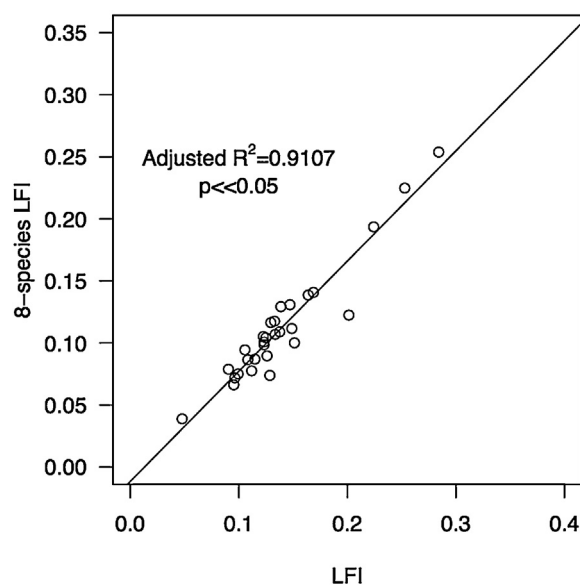
levels using the model default parameters and a situation where cod density-independent mortality is reduced by 25% to mimic high recruitment typical of the 'gadoid outburst' period (Cushing, 1984; Olsen et al., 2011). The three fisheries management scenarios were: continuation of fishing at  $F_{2008}$  for all species; fishing at  $F_{MSY}$  for all species, and a complete cessation of fishing.

Finally, we carried out a series of runs to determine more precisely the magnitude of changes in fishing mortalities required for the model to achieve the LFI EcoQO by 2020, and the impact of these on cod yield. Three management scenarios were examined: firstly, changing fishing mortality on all the model species by the same factor; secondly, changing fishing mortality on cod only while maintaining mortality at  $F_{2008}$  or all the other species; and thirdly changing fishing effort due to otter trawls cod only while maintaining effort of the other métiers at 2008 levels.

### 3. Results

#### 3.1. Relationship between the community LFI and the eight-species LFI

The empirical eight-species subset LFI was highly correlated with the LFI determined for the whole demersal fish community (Fig. 1). Therefore a model of the length-composition of these key

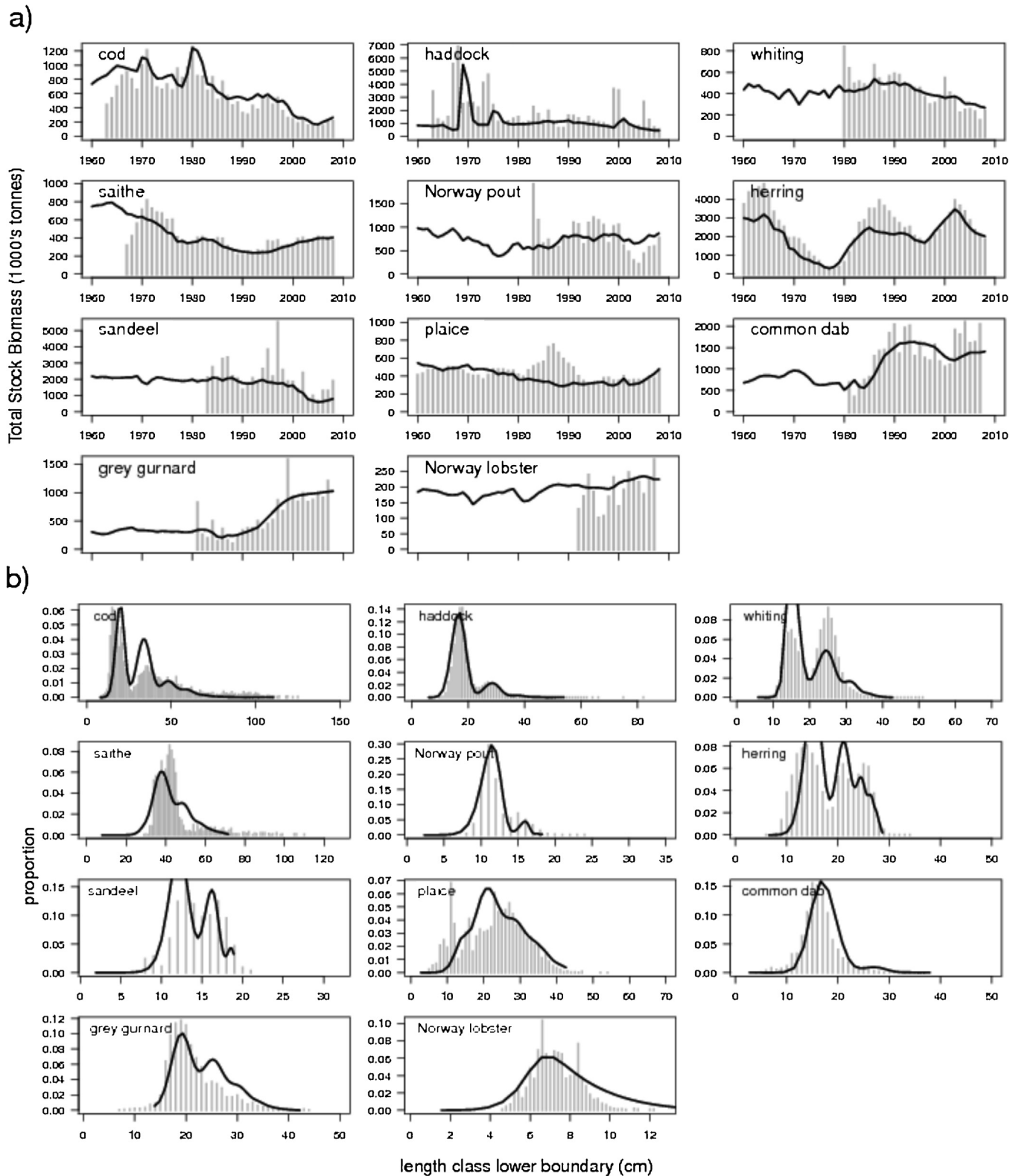


**Fig. 1.** Relationship between the full LFI determined for the whole North Sea demersal fish community and an equivalent LFI determined using biomass data for just a sub-set cadre of eight focal demersal species, which collectively contributed >90% of total demersal fish biomass in each year from 1983 to 2011.

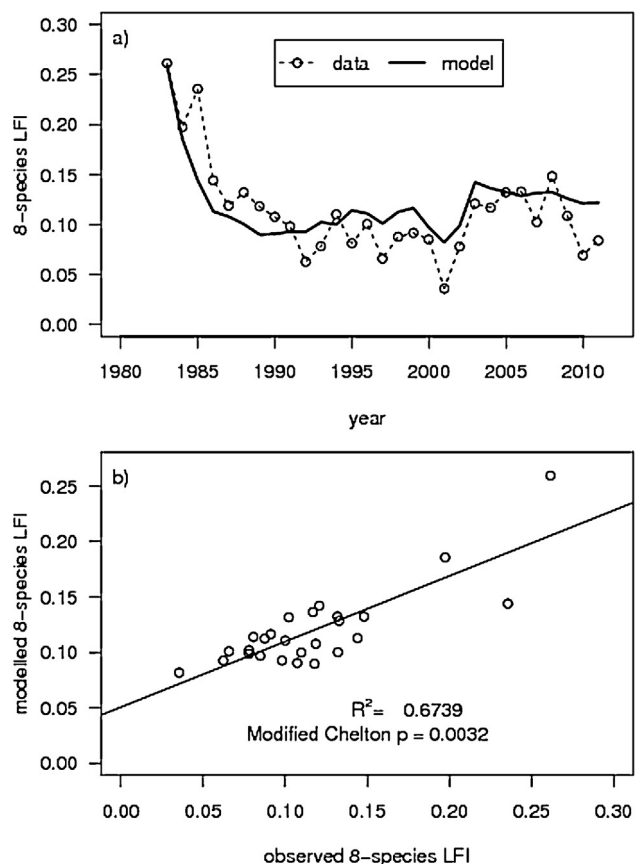
demersal species should be sufficient to capture the temporal signal in the full community LFI. The linear regression indicated that the EcoQO LFI target of 0.3 is equivalent to a value of 0.26 for the eight-species LFI (Fig. 1.), so we adopted an LFI management target of 0.26 for the model.

### 3.2. Baseline run

Following the temporal adjustments to pelagic mortality described in the methods, the model captured the species TSB trends (Fig. 2a) and length compositions (Fig. 2b). The modelled



**Fig. 2.** Model output showing: (a) time series of total species biomass (lines) and estimates from ICES stock assessments or, for the non-assessed species, derived from analysis of IBTS data (grey bars); and (b) typical species length–frequency distributions (solid lines) and observed length–frequency distributions from the quarter 1 IBTS survey (grey bars) for a sample year (1991).



**Fig. 3.** Relationship between the modelled and observed eight-species LFI a) time series b) linear regression with the p-value and correlation coefficient adjusted for time-series autocorrelation using the modified Chelton method.

LFI also closely matched observed variations in the empirical North Sea LFI (Fig. 3a). Even with a suitable reduction in the degrees of freedom to account for temporal autocorrelation (the ‘modified Chelton’ method, Pyper and Peterman, 1998) the modelled and observed LFIs were highly significantly correlated over the period from 1983 to 2008 (Fig. 3b).

### 3.3. Forward runs

Table 6 summarises the simulation results where fishing mortality is varied across all species, by species, or by métiers. A doubling of fishing pressure on the whole modelled community reduces the LFI to just above 0.04, similar to the lowest values actually observed (see Fig. 3). Conversely, reducing the community fishing mortality by around 50% produces a strong LFI recovery to a value just short of the 0.26 target. Cessation of fishing restores the eight-species LFI to a value of 0.34, well in excess of the model LFI target and corresponding to a full LFI of nearly 0.4 (see Fig. 1).

Similar results occur if the fishing pressure changes are applied only to cod while maintaining the 2008 level for the remaining species. Other than cod, saithe is the only species to cause an increase in the LFI of more than 10% when its fishing mortality is reduced by 50%. Interestingly, raising fishing mortality on some species causes small increases in the LFI. In some instances (e.g. dab, Norway pout), the species are small-bodied so that reducing their abundance raises the proportional contribution of large fish to the LFI. In other instances the effect arises through trophic interactions. For example, grey gurnard are major predators of 0-group cod (Floeter et al., 2005); reducing their abundance decreases the predation loading on juvenile cod, thereby increasing cod

**Table 6**

LFI projections for 2020 under different scenarios. ‘All species’ means that the same proportional change to the fishing mortality at length was applied to each species. The individual species labels mean that the change in fishing mortality was applied only to that species while the others were held at the fishing mortality for the reference year (2008). For the various métiers the fishing mortalities for each species were changed according to the proportion of the landings of that species attributed to the métiers. For example, if half the catch of a species comes from otter trawls and half from beam trawls, and the beam trawl fishing mortality is increased by 50%, then the fishing mortality for that species would increase by 25%. The model LFI achieved by maintaining 2008 fishing mortalities is 0.134.

Change applied over	No fishing	$F_{2008} \times 0.5$	$F_{2008} \times 1.5$	$F_{2008} \times 2$
All species	0.340	0.234	0.066	0.044
Cod	0.323	0.217	0.087	0.084
Otter trawl effort	0.285	0.205	0.077	0.051
Saithe	0.170	0.150	0.121	0.111
Seine trawl effort	0.154	0.144	0.124	0.115
<i>Nephrops</i> trawl effort	0.151	0.142	0.126	0.118
Beam trawl effort	0.148	0.140	0.127	0.121
Haddock	0.146	0.139	0.130	0.126
Whiting	0.151	0.139	0.133	0.134
Plaice	0.136	0.135	0.133	0.132
Industrial fishery effort	0.135	0.134	0.133	0.133
Sandeel	0.134	0.134	0.133	0.133
<i>Nephrops</i>	0.134	0.134	0.134	0.134
Norway pout	0.132	0.133	0.135	0.136
Herring trawl	0.129	0.132	0.135	0.136
Herring	0.129	0.132	0.135	0.136
Common dab	0.131	0.132	0.136	0.138
Grey gurnard	0.127	0.131	0.136	0.139

recruitment. Similarly, herring are predators of cod eggs and larvae, so reducing herring abundance increases cod recruitment.

Cod and saithe are primarily landed by otter trawlers (Table 5), so varying the fishing pressure exerted by this métier had a strong influence on the LFI. Reduction in otter trawl effort alone would appear to be sufficient to reach the EcoQO target (Table 6). Changing the effort in the métiers that catch few or no cod (seine trawl, *Nephrops* trawl, beam trawl, industrial sandeel fishery) have minimal impact on the LFI. Changing the effort in the herring trawl métier is the same as changing the herring fishing mortality, i.e. a small increase in the LFI with increasing effort. Overall, otter trawls are the only métier where changes in effort are capable of achieving the target LFI when everything else is held constant.

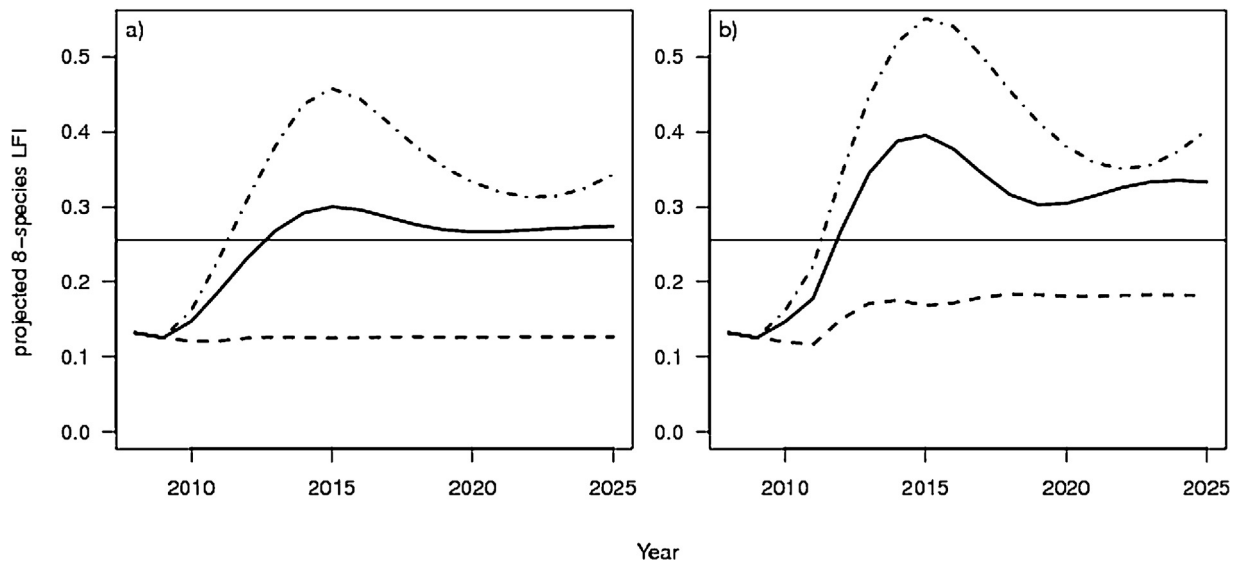
Reducing fishing mortality to  $F_{MSY}$  on all species produced a modelled 2020 LFI value that exceeded the model target of 0.26 (Table 7). Moreover, the target was still achieved when only cod is fished at  $F_{MSY}$  while the other species are fished at  $F_{2008}$ . This

**Table 7**

Percentage reduction in fishing mortality from the reference year (2008) required to achieve  $F_{MSY}$ , and the resulting modelled eight-species LFI for 2020. The percentage change in fishing mortality when the change is applied to all species is the arithmetic mean of the individual species. For species without a published  $F_{MSY}$ , or target fishing mortality we assumed either no change (*Nephrops*, sandeel Norway pout) or a 15% reduction in fishing mortality in order to reflect a reduction in by catch. The final column gives the percentage difference in the 2020 LFI under the various manipulations compared to that using 2008 fishing mortalities.

Species	% change in fishing mortality	2020 eight-species LFI	% change in LFI
All	-14.5	0.294	120.0
Cod	-75.9	0.271	102.5
Saithe	-27.4	0.159	18.6
Whiting	-36.2	0.137	2.4
Herring	5.9	0.134	0.1
<i>Nephrops</i>	0.0	0.134	0.0
Sandeel	0.0	0.134	0.0
Norway pout	-15.0	0.134	0.0
Plaice	0.0	0.134	0.0
Common dab	-15.0	0.133	-0.4
Grey gurnard	-15.0	0.133	-0.6
Haddock	19.5	0.132	-1.3





**Fig. 4.** Time-series projections of the modelled eight-species LFI under two cod recruitment scenarios a) pre-settlement model mortality parameters unaltered from the baseline, and b) a 'gadoid outbreak' with increased survival of pre-settlement cod. Each panel contains three fishing scenarios – 2008 fishing mortalities (dashed lines),  $F_{MSY}$  (solid lines), and the cessation of fishing (dot-dashed lines). The horizontal line indicates the eight-species LFI target value (0.26).

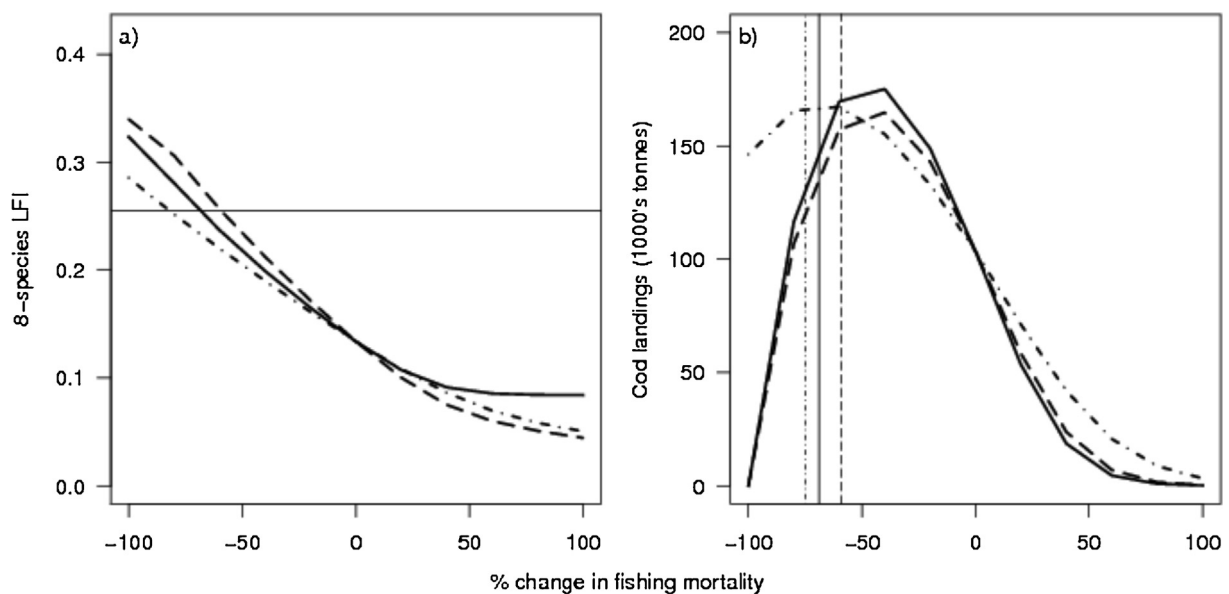
arises both because of the importance of large cod to the LFI, and because cod  $F_{MSY}$  is very much lower than  $F_{2008}$  (a reduction of 75.9%). Saithe was once again the only other species where adjusting to  $F_{MSY}$  produced a notable (18.6%) increase in the LFI, albeit one insufficient to reach the EcoQO. Whiting fishing mortality in 2008 was considerably higher than its  $F_{MSY}$ , but since whiting do not contribute greatly to the biomass above 40 cm, fishing at  $F_{MSY}$  had little impact on the modelled LFI.

Conversely, haddock  $F_{2008}$  was already substantially lower than estimated  $F_{MSY}$ , so adopting  $F_{MSY}$  for this species had minimal effect on the LFI.

Figure 4 shows LFI time-series projections under high and low cod recruitment scenarios. When default recruitment parameters were used, and fishing was at  $F_{2008}$ , the projected LFI remained

almost constant at levels close to those at the start of the projected period (Fig. 4a, dashed line). At the other extreme, immediate cessation of fishing caused rapid recovery of the LFI and the 0.26 target was reached after only four years (Fig. 4a, dot-dashed line). Fishing at  $F_{MSY}$  results in a slower response, but the target is still exceeded after seven years (Fig. 4a, solid line). Enhanced cod recruitment produced higher but qualitatively similar LFI trends under these three fishing scenarios (Fig. 4b), but the LFI target was still not met when  $F_{2008}$  was maintained (Fig. 4b, dashed line). Even were cod recruitment to improve markedly in the near future, our simulations suggest that it would still not be possible to continue fishing at 2008 levels and hope to meet the LFI EcoQO.

Fig. 5 shows 2020 modelled LFI and cod yield as fishing mortality or other trawl effort is varied continuously. As fishing mortality on



**Fig. 5.** Model projections of a) LFI and b) cod landings for the year 2020 for various level of fishing mortality and three different scenarios; changing the fishing mortality on all the species simultaneously by the same proportion (dashed lines); changing fishing mortality on cod while maintaining the fishing mortality on the other species at the 2008 levels (solid lines); changing the fishing mortality due to other trawls only (dot-dashed lines). The horizontal line in panel a) indicates the eight-species LFI target. The vertical lines in panel b) show the reduction in fishing mortality required to achieve the target.

cod alone increases the LFI declines monotonically (Fig. 5a, solid line). At a cod fishing mortality of 50% over  $F_{2008}$  the cod stock is unable to persist and the LFI response levels off (Fig. 5a, solid line) and yield falls towards zero (Fig. 5b, solid line). A 70% reduction of cod fishing mortality from  $F_{2008}$  is sufficient to achieve the 0.26 target (Fig. 5a, solid line), a value that is less than the 76% reduction required to reach  $F_{MSY}$ . When fishing mortality changes are applied to all the species the LFI response is similar, but only a 60% reduction is needed to reach the target (Fig. 5a, dashed line). By contrast, if the fishing mortality is managed only through the otter trawl métier a greater reduction (75%) is needed to achieve the same result (Fig. 5a, dot-dashed line).

In all cases reducing fishing mortality sufficiently to meet the EcoQO target resulted in cod yields between 25% and 60% higher than those obtained if fishing mortality was maintained at  $F_{2008}$  (Fig. 5b). Cod landings were maximised by a reduction in mortality on cod alone of approximately 40% (Fig. 5b, solid line) with an annual yield of just under 150 kilotonnes. However, when mortality was reduced on all species, not only was the reduction required to achieve the EcoQO less, but projected yield was about 10% higher (Fig. 5b, dashed line). When otter trawl effort is reduced sufficiently to meet the EcoQO, cod yield is close to its maximum value and is over 20 kilotonnes higher than that obtained when the target is met by changing fishing mortality on cod alone or by changing fishing mortality on all of the species simultaneously.

#### 4. Discussion

Our model replicated long-term temporal trends in both the biomass and size-composition of the explicitly modelled species, and the resulting derived LFI correlated significantly with the empirical LFI provided that an externally driven increase in the early life stage survival of cod during the 1970s was introduced. Cod recruitment is known to have been systematically higher during this period, associated with reduced temperatures and high zooplankton abundance during the so-called ‘gadoid outburst’ (Cushing, 1984; Beaugrand and Kirby, 2010; Olsen et al., 2011). The model could therefore be used to explore the effects of different fisheries management scenarios on future LFI trajectories, especially with the inclusion of high and low cod recruitment scenarios to bound the projections.

Our results confirm that the eight-species LFI primarily reflects the fortunes of cod, which is the major large bodied fish in the North Sea. The long-term decline of modelled cod abundance from the 1980s to the early 2000s was the principal driver of the corresponding decline in the LFI. By the end of this period cod abundance was similar to that of saithe, which proved to be the next most influential species. Recent low cod abundance coupled with a small increase in saithe biomass from the mid-1990s was responsible for the small partial recovery in the eight-species LFI since the early 2000s. These results match those found in the full North Sea LFI, which is approximately 66% dependent on cod and 33% dependent on saithe (Greenstreet et al., 2011, 2012a). Given the dominance of cod in the >40 cm biomass distribution the main drivers of the LFI are the fishing mortality rate on cod and the variations in its recruitment. Significantly, model results indicate that even without a return to the high recruitment of the gadoid outburst period the EcoQO LFI levels are attainable with reductions in fishing mortality equivalent to those estimated to achieve maximum sustainable yield.

The majority cod and saithe landings come from vessels using demersal otter trawls, so the effort associated with this métier is the principal driver of fishing mortality on these species and hence a major determinant of the LFI. Although the LFI was developed as an indicator of the impact of fishing in general (Greenstreet

et al., 2011), our results indicate that it is mostly a measure of otter trawl impacts and that the EcoQO LFI can be attained solely through controlling otter trawl effort. From a management perspective this is important because controlling effort by métiers is easier than attempting to control fishing mortalities on a species-by-species basis in a multi-species fishery. Moreover, although the reduction in otter trawl effort needed to achieve the EcoQO exceeds that required when the community-wide fishing effort is changed, it is considerably less than when only the cod fishing mortality is reduced. Significantly, projected cod landings are substantially higher when the EcoQO is met by reducing otter trawl effort than when it is achieved by the other measures.

Our model consistently shows a rapid approach to the steady state under constant fishing mortality. Although in most of the scenarios true equilibrium LFI values were not achieved within 15 years, approximate steady states were reached in 10 years or less. This result is at variance with those of Fung et al. (2013) who, using the PDMM approach referred to in the introduction, observed multi-decadal recovery time scales for the LFI. Two critical differences between the PDMM and our model may underpin this difference in response time scales. First, the PDMM is a community assembly model aimed at generating species-rich communities (29–189 species) without individually parameterising large numbers of equations to representing identifiable biological species. It therefore involves many more species and consequently, as suggested by Fung et al. (2013), trophic cascades take a long time to damp down. Second, although species in the PDMM are assigned a body size, different body sizes within each species are not represented. This means that the community length distribution is achieved by the relative abundances of species with different nominal body sizes, and so the only mechanism permitting the recovery of the LFI after a period of intense fishing is reproductive increase in species abundance on generational time-scales. By contrast, our model explicitly represents the length distribution within each species, and hence can produce rapid increase in the LFI as a direct consequence of individual growth when fishing mortality is reduced and a greater proportion of small fish already in the population grow to larger size.

Our results suggest that recovery of the eight-species LFI and hence the full North Sea LFI may be possible within a short timescale provided that the reduction on fishing mortality is sufficiently large. For pragmatic reasons we used 2008 as our transition point between the historical and forward runs but fishing mortality has declined for most species since 2008 (ICES, 2013). Although this means that the absolute years in our forward runs are displaced by five years, the timescales of the LFI responses are largely unaffected. By 2008 fishing mortality across the North Sea demersal fish community had dropped by around 57% from its peak in 1986. Our analysis suggests that fishing mortality needs a further reduction of 60% (when the reduction is applied to all species) from the 2008 values to permit the EcoQO LFI to be reached, or an approximate 50% reduction from 2012 values. Thus a total reduction from 1986 peak fishing levels of 83% is required. This implies that in the mid-1980s, fishing mortality was approximately five times the level that we now consider consistent with maintaining good environmental status for the broader demersal fish community of the North Sea.

#### Acknowledgements

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## References

- Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzie, M., McKenzie, E., Reid, D.G., 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Marine Ecology Progress Series* 284, 269–278.
- Beaugrand, G., Kirby, R.R., 2010. Climate, plankton and cod. *Global Change Biology* 16, 1268–1280.
- Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McClohrrie, P., Rochet, M.J., Benoit, E., 2009. How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology* 78, 270–280.
- Blanchard, J.L., Andersen, K.H., Scott, F., Hintzen, N.T., Piet, G., Jennings, S., 2014. Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *Journal of Applied Ecology* 51, 612–622.
- Christensen, V., Guénette, S., Heymans, J.J., Walters, C.J., Watson, R., Zeller, D., Pauly, D., 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* 4, 1–24.
- Cushing, D.H., 1984. The gadoid outburst in the North Sea. *Journal du Conseil International pour l'Exploration de la Mer* 41, 159–166.
- Daan, N., Gislason, H., Pope, J.G., Rice, J.C., 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science* 62, 177–188.
- European Commission, 2.9.2010. Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters. Official Journal of the European Union L232, 14–24.
- Floeter, J., Kempf, A., Vinther, M., Schrum, C., Temming, A., 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? *Canadian Journal of Fisheries and Aquatic Sciences* 62, 1853–1864.
- Frank, K.T., Petrie, B.D., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623.
- Fung, T., Farnsworth, K.D., Reid, D.G., Rossberg, A.G., 2012. Recent data suggest no further recovery in North Sea Large Fish Indicator. *ICES Journal of Marine Science* 69, 235–239.
- Fung, T., Farnsworth, K.D., Shephard, S., Reid, D.G., Rossberg, A.G., 2013. Why the size structure of marine communities can require decades to recover from fishing. *Marine Ecology Progress Series* 484, 155.
- Greenstreet, S.P.R., Fraser, H.M., Rogers, S.I., Trenkel, V.M., Simpson, S.D., Pinnegar, J.K., 2012b. Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community. *ICES Journal of Marine Science* 69, 8–22.
- Greenstreet, S.P.R., Robinson, L.A., Piet, G.J., Craeymeersch, J., Callaway, R., Reiss, H., Ehrlich, S., Kröncke, I., Fraser, H.M., Lancaster, J., Jørgensen, L., Goffin, A., 2007. The Ecological Disturbance Caused by Fishing in the North Sea. Fisheries Research Services Collaborative Report 04/07, 169.
- Greenstreet, S.P.R., Rogers, S.I., 2006. Indicators of the health of the North Sea fish community: 15 identifying reference levels for an ecosystem approach to management. *ICES Journal of Marine Science* 63, 573–593.
- Greenstreet, S.P.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E.J., Fraser, H.M., Fryer, R.J., 2011. Development of the EcoQO for the North Sea fish community. *ICES Journal of Marine Science* 68, 1–11.
- Greenstreet, S.P.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E.J., Fraser, H.M., Fryer, R.J., 2012a. A reassessment of trends in the North Sea Large Fish Indicator and a re-evaluation of earlier conclusions. *ICES Journal of Marine Science* 69, 343–345.
- Hall, S.J., Collie, J.S., Duplisea, D., Jennings, S., Bravington, M., Link, J., 2006. A length-based multispecies model for evaluating community responses to fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 1344–1359.
- Hartvig, M., Andersen, K.H., Beyer, J.E., 2011. Food web framework for size-structured populations. *Journal of Theoretical Biology* 272, 113–122.
- Heath, M.R., Speirs, D.C., 2012. Proceedings of the Royal Society Series B. Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927–2009). 279, 543–552.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23, 202–210.
- Heslenfeld, P., Enserink, E.L., 2008. OSPAR Ecological Quality Objectives: the utility of health indicators for the North Sea. *ICES Journal of Marine Science* 65, 1392–1397.
- ICES, 2009a. Report of the Herring Assessment Working Group for the Area South of 62N, 17–25 March 2009, ICES Headquarters, Copenhagen., 648.
- ICES, 2009b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak – Combined Spring and Autumn (WGNSSK), 6–12 May 2009, ICES Headquarters, Copenhagen., 10028pp.
- ICES, 2010. Manual for the International Bottom Trawl Surveys – Revision III. ICES, Copenhagen, Denmark.
- ICES, 2012. Report of the ICES Advisory Committee 2012 - ICES Advice 2012 Book 6. North Sea, 447pp.
- ICES, 2013. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 24–30 April 2013, ICES Headquarters, Copenhagen. ICES CM 2012/ACOM:13, 1346pp.
- Modica, L., Velasco, F., Preciado, I., Soto, M., Greenstreet, S.P.R., 2014. Development of the large fish indicator and associated Ecological Quality Objective for a North-East Atlantic fish community. *ICES Journal of Marine Science*, <http://dx.doi.org/10.1093/icesjms/fsu101>.
- Molloy, P.P., McLean, I.B., Cote, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. *Journal of Applied Ecology* 46, 743–751.
- Myers, R., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Olsen, E.M., Ottersen, G., Llope, M., Chand, K.-S., Beaugrand, G., Stenseth, N.C., 2011. Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proceedings of the Royal Society B* 278, 504–510.
- Payne, M.R., Hatfield, E.M.C., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Groger, J., Licandro, P., llope, M., Munk, P., Rockman, C., Schmidt, J.O., Nash, R.D.M., 2009. Recruitment in a changing environment: the 2000's North Sea herring recruitment failure. *ICES Journal of Marine Science* 66, 272–277.
- Pope, J.G., Rice, J.C., Daan, N., Jennings, S., Gislason, H., 2006. Modelling an exploited marine fish community with 15 parameters—results from a simple size-based model. *ICES Journal of Marine Science* 63, 1029–1044.
- Pope, J.G., MacDonald, D.S., Daan, N., Reynolds, J.D., Jennings, S., 2000. Gauging the impact of fishing mortality on non-target species. *ICES Journal of Marine Science* 53, 1157–1169.
- Pyper, B.J., Peterman, R.M., 1998. Comparison of methods to account for autocorrelation in correlation analysis of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2127–2140.
- Rochet, M.-J., Collie, J.S., Jennings, S., Hall, S.J., 2011. Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model. *Canadian Journal of Fisheries and Aquatic Sciences* 68, 469–486, <http://dx.doi.org/10.1139/F10-159>.
- Rossberg, A.G., Ishii, R., Amemiya, T., Itoh, K., 2008. The top-down mechanism for body-mass abundance scaling. *Ecology* 89, 567–580.
- Shephard, S., Fung, T., Houle, J.E., Farnsworth, K.D., Reid, D.G., Rossberg, A.G., 2012. Size-selective fishing drives species composition in the Celtic Sea. *ICES Journal of Marine Science* 69, 223–234.
- Shephard, S., Greenstreet, S.P.R., Reid, D.G., 2011. Interpreting the large fish indicator for the Celtic Sea. *ICES Journal of Marine Science* 68, 1963–1972.
- Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* 62, 384–396.
- Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W., Genner, M.J., 2011. Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* 21, 1565–1570.
- Speirs, D.C., Guirey, E.J., Gurney, W.S.C., Heath, M.R., 2010. A length-structured partial ecosystem model for cod in the North Sea. *Fisheries Research* 106, 474–494.
- Thorpe, R.B., Le Quesne, W.J.F., Luxoford, F., Collie, J.S., Jennings, S., 2015. Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing. *Methods in Ecology and Evolution* 6, 49–58, <http://dx.doi.org/10.1111/2041-210X.12292>.
- Ulrich, C., Wilson, D.C.K., Nielsen, J.R., Bastardie, F., Reeve, S.A., Andersen, B.S., Eigaard, O.R., 2012. Challenges and opportunities for fleet- and métier-based approaches for fisheries management under European Common Fishery Policy. *Ocean and Coastal Management* 70, 38–47.