ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2015), 72(2), 436–449. doi:10.1093/icesjms/fsu149

Original Article

Investigating the recent decline in gadoid stocks in the west of Scotland shelf ecosystem using a foodweb model

Karen A. Alexander[1]*, Johanna J. Heymans[1], Shona Magill[1], Maciej T. Tomczak[2], Steven J. Holmes[3,4], and Thomas A. Wilding[1]

[1]*Scottish Association for Marine Science, Oban, Argyll PA37 1QA, UK*
[2]*Baltic Sea Centre, Stockholm University, S-106 91 Stockholm, Sweden*
[3]*Marine Scotland Science, 375 Victoria Road, Aberdeen AB11 9DB, UK*
[4]*Joint Research Centre, TP 051, Via Enrico Fermi 2749, I-21027 Ispra (VA), Italy*

**Corresponding author: tel: +44 1631 559444; fax: +44 1631 559001; e-mail: karen.alexander@sams.ac.uk*

Alexander, K. A., Heymans, J. J., Magill, S., Tomczak, M. T., Holmes, S. J., and Wilding, T. A. Investigating the recent decline in gadoid stocks in the west of Scotland shelf ecosystem using a foodweb model. – ICES Journal of Marine Science, 72: 436–449.

Received 24 March 2014; revised 10 July 2014; accepted 6 August 2014; advance access publication 5 September 2014.

Abundance and biomass of cod, haddock, and whiting in the waters off of the west coast of Scotland (wcoS) have undergone large changes in recent years, most notably a recent decline. These three species contribute a considerable part of Scottish demersal landings from this area and as such it is important to understand why these stocks are behaving the way they are. A number of explanations for the decline have been proposed, including: seal predation, pressure from Nephrops trawls, and fishing pressure more generally. We used an ecosystem model of the wcoS continental shelf (<200 m depth) to investigate whether these proposed explanations for declining gadoid stocks are feasible. Results suggest that the rise in the grey seal population over recent years has not led to the decline in gadoid stocks; there is insufficient bycatch by the Nephrops fleet to have a large impact on gadoid stocks; however, fishing, as a key driver of the west of Scotland shelf ecosystem, has impacted stocks and by decreasing fishing levels to maximum sustainable yield cod biomass may increase slightly though not returning to previous levels. Although this means we are little further forward in understanding the cause of recent gadoid declines in the area, the development of this model has enabled us to further our knowledge and understanding of aspects of trophic structure and the impacts of fishing on the wcoS.

Keywords: cod, Ecopath with Ecosim, haddock, seals, shelf ecosystem model, whiting.

Introduction

Humans depend on ocean ecosystems for important and valuable goods and services. However, anthropogenic and environmental disturbances have altered the seas directly and indirectly, thus affecting natural resource availability (Lotze *et al.*, 2006). The waters off of the West Coast of Scotland (wcoS) are extremely important to the Scottish fishing industry with a number of finfish and shellfish species being caught including: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), monkfish (*Lophius piscatorius* and *Lophius budegassa*), saithe (*Pollachius pollachius* and *Pollachius virens*), whiting (*Merlangius merlangus*), edible crab (*Cancer pagurus*), European lobster (*Homarus gammarus*), nephrops (*Nephrops norvegicus*), scallops (*Pecten maximus* and *Aequipecten opercularis*), and velvet crab (*Necora puber*). Limited information is available for the wcoS (in relation to survey data); however, Scottish groundfish surveys between 1997 and 2008 revealed declines in most commercial finfish stocks (ICES, 2008).

Cod, haddock, and whiting contribute considerably to the value of Scottish demersal landings from this area. For all three species, spawning-stock biomass remains low compared with historical estimates and recruitment for cod has been so low over the last decade it is considered impaired (ICES, 2013b). Stock assessments indicate that the biomass of cod shows a steady downward trend since 1987, haddock since 2000, and whiting, after a huge increase in biomass at the beginning of the 1990s shows a steady decrease thereafter (Bailey *et al.*, 2011). One possible explanation for the decline in these stocks is increased predation from grey seals (ICES Advice 2013, Book 5) which have been increasing in number substantially since the 1960s (Sea Mammal Research Unit, 2004). Seal predation suppressing cod abundance has been suggested to occur in Newfoundland (Lilley *et al.*, 2008). A second reason may be that the Nephrops fishery has become increasingly important on the wcoS, and bycatch of gadoid species may be accounting for the decline, particularly in whiting (ICES Advice 2013, Book 5). Nephrops trawlers catch and discard some of these juvenile fish, particularly juvenile whiting and haddock (Kelleher, 2005) and this pressure may be enough to suppress the population as a whole.

Alternatively, these stocks may just be unable to sustain the fishing pressure applied to them (Myers *et al.*, 1996). Fisheries management plans are in place for these species using measures such as total allowable catch (TAC) with a zero TAC for cod, bycatch restrictions (introduced through EU emergency measures in 2009), and technical measures such as larger mesh sizes. For cod, spawning area closures and effort restrictions have also been implemented as part of a cod recovery plan employed in Scotland since 2008 (Marine Scotland Science, undated). These measures are also expected to affect whiting and haddock (ICES, 2013b). However, results for the wcoS are disappointing with little evidence so far of a reduction in cod fishing mortality and discard rates remaining high (Marine Scotland Science, undated; ICES, 2013b).

Despite the economic importance of these fisheries, gadoid stocks (and the wcoS ecosystem in general) are not as well studied on the wcoS as in the North Sea. Empirical exploration of interactions within the ecosystem that could lead to these stock trends is very difficult. Instead, we have used a model (a representation of an ecosystem) of the wcoS marine environment to provide indications of how the ecosystem is likely to change in response to changing human activities and how this will subsequently affect the fishing industry. Most ecosystems are complex, making them difficult to manage comprehensively, which implies that creating a suitable model is challenging. If a credible model can be developed, model parameters can then be changed to explore scenarios (a range of possible futures).

Ecosystem models have been used for a variety of purposes, for example: to understand ecosystem functioning and the impacts of fishing in the North Sea (Allen and Clarke, 2007; Mackinson *et al.*, 2009b), South Catalan Sea (Coll *et al.*, 2006), the Northern and Central Adriatic Sea (Coll *et al.*, 2007), and the Eastern Scotian Shelf (Bundy, 2005; for a review of 75 models, see Heymans *et al.*, 2011); and to investigate the impacts of ocean productivity (Morato *et al.*, 2009; Piroddi *et al.*, 2010) and climate change (Travers *et al.*, 2007; Ainsworth *et al.*, 2011) upon foodwebs. There are several ecosystem models in use (e.g. Baretta *et al.*, 1995; Shin and Cury, 2001; Fulton *et al.*, 2004); however, the most used and tested ecosystem modelling tool for investigating how ecosystems respond to changes in fishing (and other pressures) is Ecopath with Ecosim (EwE; Christensen, 2009). EwE is a dynamic foodweb modelling suite which describes ecosystem resources and their interactions (Christensen and Walters, 2004). This model was previously used to characterize the wcoS ecosystem by Bailey *et al.* (2011).

Here, we describe further development of the model of the wcoS ecosystem described by Bailey *et al.* (2011), explore the trophic interactions and external drivers needed to reasonably simulate the observed dynamics of the ecosystem between 1985 and 2008, and present the results of re-running forward simulations (as in Bailey *et al.*, 2011) to address the issue of decreasing gadoid stocks on the wcoS. Three key research questions were identified: (i) Is increased seal predation such that gadoid stocks are unable to grow? (ii) Is the Nephrops fishery catching too many juvenile fish? (iii). Is it simply fishing that has caused the decline and would fishing at F_{MSY} benefit gadoid stocks?

Material and methods

Area of study

The study area consists of the continental shelf, defined as all sea area above the 200 m contour, within ICES Division VIa (Figure 1). The study area covers ~110 000 km^2 of sea surface, and includes the waters around the Outer Hebrides, Skye, the Small Isles, Mull, Islay, and the Firth of Lorn and Firth of Clyde island groups.

Temperature and salinity studies have shown that the area is influenced by water masses from the Irish Sea and the Atlantic Ocean as well as freshwater run-off from the Scottish mainland (Gillibrand *et al.*, 2003). Climate variability which drives temperature and salinity in the area [and indirectly primary production (PP)] is thought to be influenced by the North Atlantic Oscillation (NAO; Hurrell *et al.*, 2001).

Commercial fisheries operating in the study area include demersal trawls, pelagic trawls, dredges, gillnets, longlines, creels, and shell fishing by hand with 2177 fishers operating 975 vessels on the west coast as of 2010 (Scottish Government, 2011). Most fishers on the wcoS occupy the "10 m and under" section of the Scottish fleet, and focus upon demersal (mainly cod, haddock, and whiting) and shellfish (mainly Nephrops and scallops) fishing (Scottish Government, 2011).

Ecopath: mass balance model

Ecopath was created by Polovina (1984) and subsequently updated by Christensen and Pauly (1992) and Walters *et al.* (1997). In Ecopath, a static mass balance model of an ecosystem is created; a snapshot of the ecosystem for a given year (in this case, 1985). The energy and/or mass input and output of all living groups must be balanced. This mass balance constraint is implemented through two master equations. The first equation describes how production (the rate of biomass generation) for each functional group can be split in components:

$$\begin{aligned}\text{Production} = {} & \text{catches} + \text{predation mortality}\\ & + \text{biomass accumulation}\\ & + \text{net migration} + \text{other mortality}.\end{aligned} \tag{1}$$

Or, more formally:

$$\begin{aligned}\left(\frac{P}{B}\right)_i \times B_i = {} & Y_i + B_j \times \left(\frac{Q}{B}\right)_j \times (DC)_{ji} + E_i + \left(\frac{B}{A}\right)_i\\ & + \left(\frac{P}{B}\right)_i \times (B_i)_i(1 - EE_i),\end{aligned} \tag{2}$$

where $(P/B)_i$ is the production to biomass ratio for a certain functional group (i), B_i the biomass of group (i), Y_i the total fishery catch rate of group (i), $(Q/B)_j$ the consumption to biomass ratio for the predator j, DC_{ji} the proportion of group (i) in the diet of predator (j), E_i the net migration rate (emigration−immigration), BA_i the biomass accumulation rate for group (i), EE_i the ecotrophic efficiency (the proportion of the production that is utilized in the system), and $(1-EE_i)$ represents mortality other than predation and fishing.

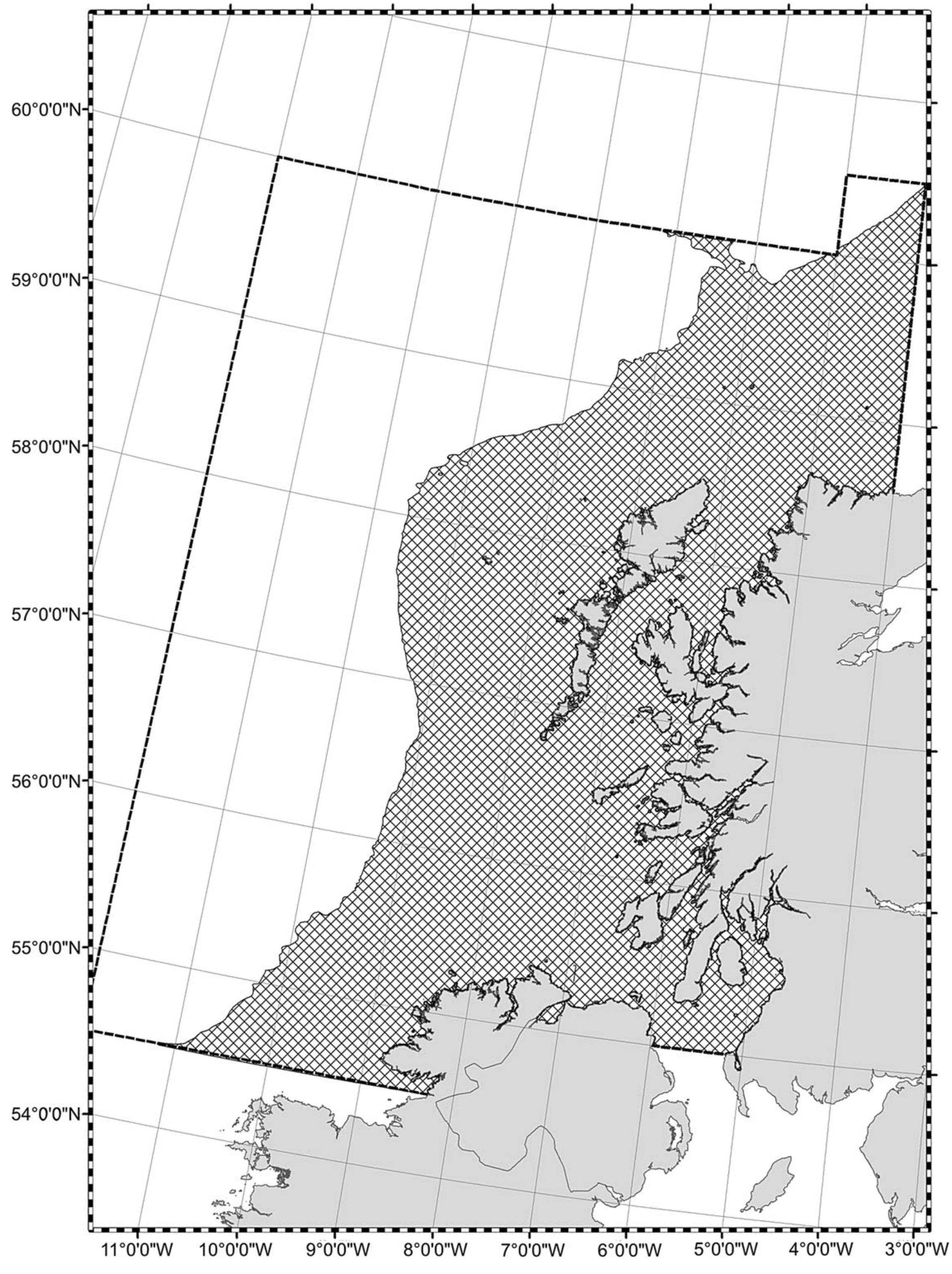

Figure 1. Map of Scotland showing the model extent (cross-hatched area). The dashed outline represents the ICES VIa fishing area.

The second master equation describes consumption (the intake of food over a period) for each functional group:

$$\text{Consumption} = \text{production} + \text{respiation} + \text{unassimilated food}. \quad (3)$$

There are six key data requirements for parameterizing an Ecopath model: Biomass (B), production/biomass (P/B), consumption/biomass (Q/B), other mortality, diets, and catches. Several supplementary parameters can be included such as discards, landings values, and fishing costs. Ecopath is both well known and well described; see Christensen and Walters (2004) and Pauly *et al.* (2000) for a more detailed description.

Ecopath input parameters and model structure improvement

To further develop the initial wcoS model, shellfish species of commercial importance, including European lobster, edible crab, velvet swimming crab, and scallops, were added as groups (Bailey *et al.*, 2011). Overall, a total of 41 functional groups were considered in the model including marine mammals (3), seabirds (1), fish (23, six of which were composed of adult and juvenile stages for cod, haddock and whiting), invertebrates (5), cephalopods (1), zooplankton (2), benthos (3), primary producers (2), and detritus (1).

In the Bailey model, data for the six key Ecopath parameters were obtained from a number of sources. P/B values were derived from an equation by Pauly (1980) based on an empirical relationship between natural mortality, temperature, and von Bertalanffy growth parameters. Q/B values were obtained largely from Fishbase.org, although values from an earlier version of the west coast model (Haggan and Pitcher, 2005) or the Irish sea model (Lees and Mackinson, 2007) were also used. Diet data were obtained from a combination of sources including the previous version of the west coast model and the literature. For species added during this study, the P/B and Q/B ratios were calculated using empirical equations (Cammen, 1980; Brey, 2001) or were taken from the literature and expressed as annual rates. Data sources for these parameters (and those from the Bailey model) can be viewed in Supplementary Table S1. Biomass for all the additional groups was estimated by the model. A diet matrix was constructed for the additional species, and the diet of existing model species updated (accounting for new species) using data obtained from the literature (Supplementary Table S2).

In Ecopath, fisheries are defined by fleet structure, costs of fishing, landings, discards, and off-vessel prices (landings values). Five fleets were defined: demersal trawl, nephrops trawl, other trawl, potting and diving, and pelagic trawl. Catch data (Supplementary Table S3) was procured from a number of sources including STATLANT (an international database of landings data from the Northeast Atlantic www.nafo.int/data/frames/stats.html) and the ICES Working Group Reports: for cod, haddock, mackerel, and herring, catch was estimated by stock assessment models (provided by the ICES Working Group for the Celtic Seas Ecoregion WGCSE 2009 report; ICES, 2010b). These estimates are more accurate than reported catch which does not take into account misreporting. For mackerel, the data were scaled to the shelf area using Scottish landings data resolved to ICES statistical rectangle level. Whiting catch was calculated based upon SURBA [a model which uses catch per unit effort (cpue) survey data from research vessel surveys] and scaled to absolute abundance estimated by the 2004 stock assessment. For the "pollock" group which also includes saithe, as well as other groups such as monkfish, flatfish, rays, sharks, gurnards (*Eutrigla gurnardus* and *Aspitrigla cuculus*), other demersals, other small fish, Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*), sprat (*Sprattus sprattus*), sandeels (*Hyperoplus* sp. and *Ammodytes* sp.), horse mackerel (*Trachurus trachurus*), and nephrops, data were obtained from STATLANT and scaled to the shelf. Based on a lack of other available information, only 50% of the blue whiting catch was assumed to be from the shelf. Data for lobster, brown crab, velvet crab, other crustaceans, scallops, and other epifauna were obtained from the Eurostat ICES database (http://ecosystemdata.ices.dk/inventory/index.aspx?).

Discard data were obtained from the Scottish Multi-species Discards database, or from the ICES Working Group for the Celtic Seas Ecoregion 2009 report, and was available for all species except for pollock, flatfish, sharks, gurnards, Norway pout, sprat, sandeels, horse mackerel, and nephrops (Supplementary Table S4).

PREBAL

"PREBAL" or prebalancing analysis (Link, 2010) assesses whether data are coherent to the system level by respecting some basic laws, rules, and principles of ecosystem ecology. It is argued that by using PREBAL diagnostics, problems in initial model balancing can be headed off before progressing to dynamic simulations. A number of diagnostics were used in this study, after the initial Ecopath model was created, including: assessing biomass across taxa/trophic levels (where biomass should span 5–7 orders of magnitude and slope on log scale should be ~5–10% decline); biomass ratios (where predators biomass should be less than that of 1 relative to their prey); and vital rates across taxa/trophic levels (should be a general decline with increasing trophic level).

Ecosim: temporal simulations

A critical step in the development of a credible ecosystem model is calibration, which is done by showing that the model can reproduce observed historical trends. Ecosim can incorporate time-series data, allowing the model to be "fitted" to the data (by tuning parameter estimates so as to show which values could explain the observed historical patterns). A goodness-of-fit is calculated as the weighted sum of squared differences (SS) between the log "observed" and log "predicted" data (Christensen *et al.*, 2001).

Ecosim expresses biomass dynamics based upon the initial parameters of the Ecopath master equation [Equation (1)] using a series of coupled differential equations which take the form:

$$\frac{dB_i}{dt} = g_i \sum_J Q_{ji} - \sum_J Q_{ij} + I_i - (M_i + F_i + e_i)B_i, \quad (4)$$

where dB_i/dt is the biomass growth rate of group (i) during the interval dt, g_i the net growth efficiency (production/consumption ratio), I_i the immigration rate, M_i and F_i the natural and fishing mortality rates of group (i), and e_i the emigration rate. The consumption rates Q_{ji} are calculated based on the "foraging arena" concept (animals optimize the way they spend their time, balancing predation risk with foraging) where B_i's are divided into vulnerable and invulnerable components (Christensen *et al.*, 2001).

An important aspect of Ecosim is its ability to describe the interactions between predators and prey by attributing a "vulnerability" term for each of these interactions, indicating how the biomass of different groups in the ecosystem is controlled (Christensen *et al.*, 2001). The vulnerability term controls the effect on a prey group for a given increase in predator biomass (Ahrens *et al.*, 2012). Low vulnerability (close to 1) means that an increase in predator biomass will not cause any noticeable increase in the predation mortality the predator may cause on the given prey. A high vulnerability (e.g. 100) indicates that the predator biomass is low compared with its carrying capacity (Guénette *et al.*, 2008) and so the predator will be capable of inflicting greater mortality, increasing its consumption and recovering more quickly (Araujo *et al.*, 2008). The default value is 2 (indicating neither a top-down nor bottom-up control of a predator–prey interaction). Ecosim uses a "fit to time series" search interface to allow users to undertake "fitting" procedures, namely: to search for vulnerability estimates which give better "fits" of the model to time-series data; and to search for time-series values of annual relative primary productivity which may represent how productivity has impacted biomass throughout the ecosystem.

Ecosim input parameters

Biomass time-series data (Supplementary Table S5) from the previous wcoS model (Bailey *et al.*, 2011) were used, with relative biomass time-series based upon absolute biomass data when available (although coded in Ecosim as relative) and cpue data otherwise (Table 1). Catch data (Supplementary Table S6) was calculated in the same way as described in the Ecopath input parameters and model structure improvement section. Fishing mortality was calculated as catch/biomass (Christensen *et al.*, 2001) and used to drive the model.

Ecosim fitting procedure

Similar to the methodology suggested by Mackinson *et al.* (2009a) and used by Tomczak *et al.* (2012), the following procedure was used to "fit" the wcoS model to the observed time-series. Eight alternative hypotheses (or models) were parameterized and compared (each alternative hypothesis starts from a point where all "fitting factors"—vulnerabilities and PP anomaly—are reset):

(i) Baseline model: no environmental or fishery data were used to drive the model. All vulnerabilities were set to 2.

(ii) Baseline and trophic effects: no environmental or fishery data were used to drive the model. The optimal numbers of vulnerabilities (for predator–prey interactions) were identified using the "sensitivity to vulnerabilities" subroutine of the "fit to time series" algorithm. This algorithm incremented one vulnerability value slightly in each run, so as to calculate the "Jacobian matrix" of sensitivities of each of the predicted time-series observations to each of the parameters. After $N + 1$ checks (N is the number of parameters with non-zero variances), the Jacobian matrix is used to estimate an initial best step change for each parameter (Christensen *et al.*, 2001).

(iii) Baseline and environmentally driven changes in PP: no environmental or fishery data were used to drive the model. The "PP anomaly" procedure was used to search for time-series values of annual relative primary productivity that may represent historical productivity trends impacting biomasses. The same procedure as that for identifying the optimal vulnerabilities is used, but in this instance, the annual PP value is changed slightly in each run until a best fit to the time-series data is achieved. These time-series values can then be compared with known environmental variables such as the NAO.

(iv) Baseline and trophic effects and environmentally driven changes in PP: no environmental or fishery data were used to drive the model. Vulnerabilities and a PP anomaly were estimated using the "fit to time series" algorithm.

Table 1. Sources of time-series data used in Ecosim.

Species	Source of biomass time-series data	Source of catch time-series data
Grey seals	Model outputs based on pup counts (SCOS)	–
Harbour seals	Calculation based on 5-yearly surveys	–
Cod (m)	Stock assessment output	Stock assessment output
Cod (i)	Stock assessment output	Stock assessment output
Haddock (m)	Stock assessment output	Stock assessment output
Haddock (i)	Stock assessment output	Stock assessment output
Whiting (m)	Stock assessment output (to 2007)	Stock assessment output
Whiting (i)	Stock assessment output (to 2007)	Stock assessment output
Pollock	Stock assessment output	STATLANT
Gurnards	Cpue	STATLANT
Monkfish	Stock assessment output	STATLANT
Flatfish	Cpue	STATLANT
Rays	Cpue	STATLANT
Sharks	Cpue	STATLANT
Large demersals	Cpue	STATLANT
Other small fish	Cpue	STATLANT
Mackerel	Stock assessment output (from Northeast Atlantic population)	Stock assessment output (from Northeast Atlantic population)
Horse mackerel	Stock assessment output (from Western Stock assessment)	Reported international landings
Blue whiting	Stock assessment output (from Western Stock assessment and scaled to shelf)	STATLANT (and scaled to shelf)
Herring	Stock assessment output	–
Norway pout	Cpue	STATLANT
Poor cod	Cpue	–
Sandeel	Stock assessment output (to 1996)	STATLANT
Sprat	Q1 Sco. Via IBTS data	STATLANT
Nephrops	Stock assessment output	STATLANT

(v) Fishing: fishing was included as a model driver (fishing mortality).

(vi) Fishing and trophic effects: catch, biomass, and fishing mortality were included in the model. The optimal vulnerabilities were identified.

(vii) Fishing and environmentally driven changes in PP: catch, biomass, and fishing mortality were included in the model. A PP anomaly was estimated using the "fit to time series" algorithm.

(viii) Fishing, trophic effects, and environmentally driven changes in PP: catch, biomass, and fishing mortality were included in the model. Vulnerabilities and a PP anomaly were estimated using the "fit to time series" algorithm.

There are less data available for the wcoS than for other more intensively studied systems such as the North Sea. In addition, little is understood about environmental drivers on the system. Therefore, time-series forcing on egg production and predator/prey interactions was not taken into consideration. At each step, the goodness-of-fit (SS) of the model was assessed, and Akaike's information criterion (AIC), a tool for model selection which takes into account the predictive accuracy (SS) and complexity (number of parameters), was applied as proposed by Mackinson *et al.* (2009a).

PP anomaly and environmental time-series data

The PP anomaly (with and without smoothing) identified in the model was tested against a number of environmental time-series data using the Spearman's rank-order correlation test (for non-normal distributed data). The environmental time-series data included sea surface temperature (British Oceanographic Data Centre, 2012), salinity (British Oceanographic Data Centre, 2012), the NAO index, winter and annual mean (NOAA Climate Prediction Centre, 2012d), the Arctic Oscillation index (NOAA Climate Prediction Centre, 2012a), the Atlantic Multi-decadal Oscillation (NOAA Climate Prediction Centre, 2012b), and the Multivariate ENSO Index (NOAA Climate Prediction Centre, 2012c).

Ecosim simulations

Four Ecosim simulations were run to address the research question. The question of seal predation upon gadoid stocks was addressed by two separate simulations: first, mortality was imposed upon the grey seal population to prevent population biomass rising above the 1985 value for the duration of the simulation (to 2008; Figure 2a); second, a high mortality was imposed to remove all predation by grey seals (Figure 2b). To investigate the impacts of the nephrops trawl, landings and discards of all species except nephrops were removed to simulate a clean nephrops fishery (from 1985 to 2008). Finally, to investigate the effects of fishing at maximum sustainable yield, catch rates were calculated from stock assessment values and reduced to 0.17 (cod) and 0.25 (haddock and whiting; ICES, 2010a) from 2009 for a period of 15 years while fishing mortality was held at the 2008 level for all other species. The model results were then compared with actual ICES stock assessment values to 2014.

Results

The updated version of the model balanced on the first attempt. The model was evaluated against PREBAL diagnostic checks. Biomass was found to span 5 orders of magnitude and to decline with increasing trophic level with a few taxa (cetaceans, seabirds, and lobster) notably below the slope line; vital rates were largely found to decline with increasing trophic level with a few taxa (cetaceans, seabirds, epifauna, and infauna) notably above the slope line; consumption of each taxa was less than production by said taxa and consumption by each taxa was more than production by said taxa; and finally, total human removals were less than total production, suggesting that general ecological and fishery principles were met, thus no further modifications would be undertaken. The resulting mass balance foodweb model for the wcoS ecosystem is presented in Figure 3, and the model parameters in Table 2.

Model fitting and choice of best model

The most statistically significant results from fitting the model were obtained when forced fishing, trophic effects, and a PP anomaly search were included together in the model (Model 7, last row in Table 3).

The final model improved the fit by 63.6% over the baseline model. The largest improvement to model fit (AIC reduction) was obtained by adding known fishing mortality (AICc reduced by 43.3%). The addition of customized trophic interactions for 25 interactions provided the second largest advance in the fit of the model (AICc reduced by a further 14.6%), with the additional

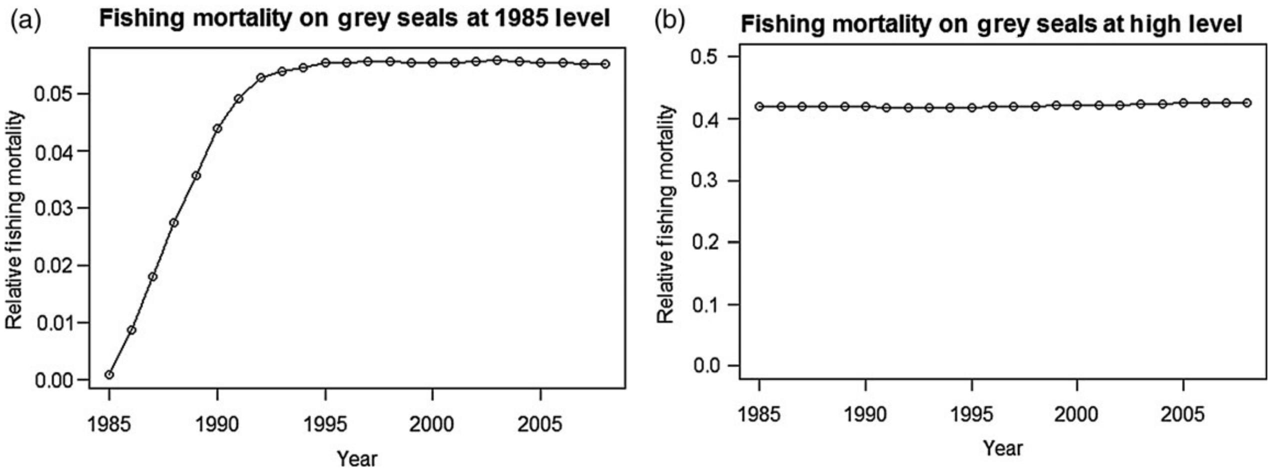

Figure 2. Mortality limits imposed upon grey seal population in Ecosim scenarios: (a) mortality intended to keep seal population at 1985 levels; (b) mortality intended to reduce seal population to a nominal level. (Note: this shows the mortality imposed, not the grey seal biomass.)

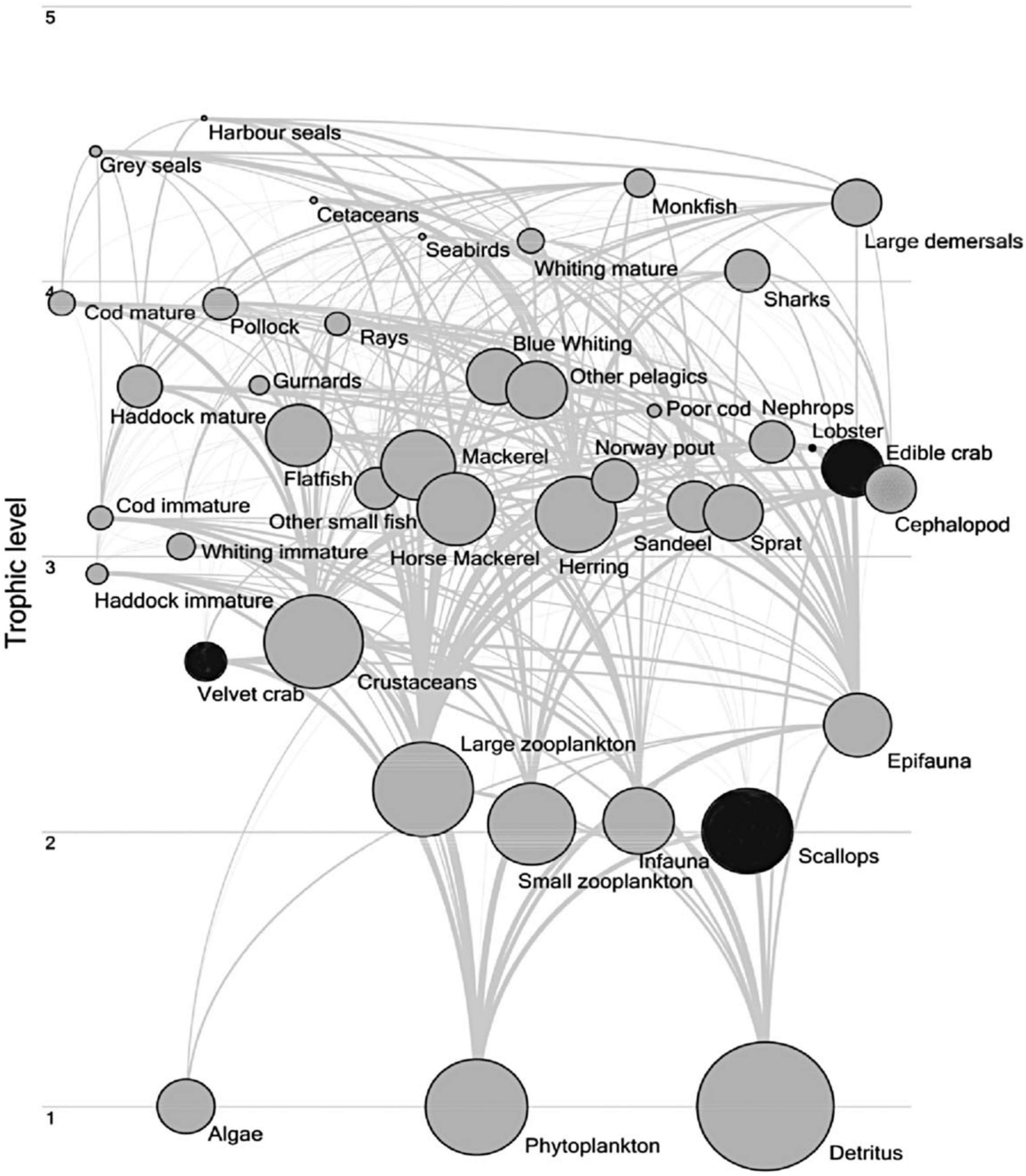

Figure 3. Energy flow and biomass diagram for the wcoS ecosystem. Nodes represent organisms within the ecosystem; the size of the node is proportional to the biomass it represents. Flows enter a node from the bottom and exit a node from the top and are scaled to flow proportion. The *y*-axis denotes the trophic level of the species.

inclusion of a PP anomaly providing the smallest improvement in fit (AICc reduced by a further 5.7%).

Using the "best-fit" model (the model with the lowest AICc), the Ecosim estimations emulated the biomass trends well for adult cod (although the peak between 1985 and 1990 is not matched), adult haddock, adult whiting, juvenile whiting, blue whiting, nephrops, monkfish, flatfish, skates and rays, large demersals, and Norway pout (Supplementary Figure S1). Biomasses were overestimated for juvenile cod, juvenile haddock, herring, gurnard and sharks, and even more so for sprat. The model did not represent the trend well for harbour seals, horse mackerel, mackerel, other small fish, poor cod,

Table 2. Balanced parameter estimates for all functional groups in the balanced model (parameters estimated by model in bold).

Group name	Trophic level	Biomass $t\ \mathrm{km}^{-2}\ \mathrm{year}^{-1}$	Production/biomass (Z) (year^{-1})	Consumption/ biomass (year^{-1})	Ecotrophic efficiency	Production/ consumption
Grey seals	4.471	0.056	**0.114**	11.388	**0**	0.01
Harbour seals	4.592	0.012	**0.101**	10.124	**0**	0.01
Cetaceans	4.296	**0.014**	0.02	14	0.1	**0.001**
Seabirds	4.164	0.025	0.4	83.051	**0.294**	**0.005**
Cod (m)	3.922	0.254	1.17	3.500	**0.499**	**0.334**
Cod (i)	3.138	0.229	2.21	9.078	**0.973**	**0.243**
Haddock (m)	3.615	0.836	0.72	4.96	**0.681**	**0.145**
Haddock (i)	2.939	0.163	1.67	15.115	**0.444**	**0.110**
Whiting (m)	4.148	0.265	1.3	4.500	**0.540**	**0.289**
Whiting (i)	3.039	0.287	1.73	9.242	**0.754**	**0.187**
Pollock	3.922	0.44	**0.937**	4.686	**0.897**	0.2
Gurnards	3.623	**0.153**	**0.824**	4.122	**0.95**	0.2
Monkfish	4.358	**0.306**	**0.480**	1.714	0.95	0.28
Flatfish	3.440	**2.536**	**0.754**	3.768	**0.95**	0.2
Rays	3.843	**0.228**	**0.449**	2.243	**0.95**	0.2
Sharks	4.036	0.792	**0.682**	3.410	**0.433**	0.2
Large demersals	4.288	**1.087**	**0.488**	2.442	0.95	0.2
Other small fish	3.245	**0.850**	**1.581**	5.27	0.95	0.3
Mackerel	3.335	4.19	0.767	4.4	**0.640**	**0.174**
Horse Mackerel	3.170	4.73	**0.74**	3.7	**0.645**	0.2
Blue Whiting	3.654	1.783	1.5	**6**	**0.637**	0.25
Other pelagics	3.609	**2.096**	**1.8**	6	**0.95**	0.3
Herring	3.156	5.952	1.5	10.1	**0.824**	**0.149**
Norway pout	3.276	**0.875**	**1.68**	5.6	0.95	0.3
Poor cod	3.530	**0.071**	**1.17**	3.9	0.95	0.3
Sandeel	3.184	**1.368**	**1.826**	6.085	**0.95**	0.3
Sprat	3.159	**1.799**	**1.584**	5.28	**0.95**	0.3
Nephrops	3.415	**0.803**	0.73	4.876	**0.95**	**0.150**
Lobster	*3.395*	***0.020***	*0.338*	*3.65*	***0.95***	***0.093***
Edible crab	*3.329*	***2.029***	*0.354*	**2.36**	***0.95***	*0.15*
Velvet crab	*2.622*	***0.648***	*0.646*	*12.775*	*0.95*	***0.051***
Crustaceans	2.691	**14.313**	0.871	5.807	**0.95**	**0.150**
Cephalopod	3.248	**1.146**	1.981	15	0.95	**0.132**
Large zooplankton	2.158	**15.116**	10	35	**0.95**	**0.286**
Small zooplankton	2.031	**8.156**	18	72	**0.95**	**0.25**
Infauna	2.037	**3.285**	20	80	**0.95**	**0.25**
Scallops	2	**9.746**	*0.445*	*14.333*	***0.95***	***0.031***
Epifauna	2.391	**2.994**	20	80	**0.95**	**0.25**
Algae	1	**1.684**	15		**0.95**	
Phytoplankton	1	**17.302**	70		0.95	
Detritus	1	100			**0.867**	

(m) means mature, (i) means immature. Species added to the previous version of the model are show in italics.

Table 3. Comparison of model fits.

Model	Description	N	minSS (from Ecosim)	K	AICc	% improved fit
0	Baseline model	1248	590.1	0	−406.0	
1	Baseline and trophic effects (5v)	1248	590.1	5	−395.9	−2.4
2	Baseline and PP anomaly (5PP)	1248	558.5	5	−425.8	4.9
3	Baseline and trophic effects and PP anomaly (5v, 5PP)	1248	556.5	10	−417.6	2.9
4	Forced fishing	1248	426.6	0	−581.8	43.3
5	Forced fishing and trophic effects (30v)	1248	341.3	30	−641.3	57.9
6	Forced fishing and PP anomaly (5PP)	1248	408.1	5	−595.8	46.7
7	Forced fishing and trophic effects and PP anomaly (25v, 5PP)	1248	327	30	−664.5	63.6

AICc is Akaike information criterion with a second-order correction for small sample sizes. ($\mathrm{AICc} = \mathrm{AIC} + 2\ K(K-1)/n - K - 1$, where n is the number of observations and K the number of parameters). V is the number of vulnerability parameters, PP the number of primary production spline points (for smoothing).

Pollock, or sharks. Additionally, often, the amplitude in variation was not as high as observed in the stock assessments. A good reproduction of the yield time-series data was shown for most species (Supplementary Figure S2). Adult cod, pollock, and blue whiting catches were slightly overestimated, while sprat was slightly underestimated.

Table 4. Most sensitive predator/prey interactions (estimated vulnerability values for pollock/Norway pout and other small fish/large zooplankton were not included as they were very close to the default value of 2).

Prey/predator	Whiting (i)	Pollock	Monkfish	Rays	Large demersal	Other small fish	Blue whiting	Norway pout
Cod (i)	–	100	1	–	–	–	–	–
Whiting (i)	–	–	1	–	–	–	–	–
Flatfish	–	–	1	–	–	–	–	–
Rays	–	–	–	–	1	–	–	–
Other small fish	–	–	100	–	1	–	–	–
Horse mackerel	–	1	–	–	–	–	–	–
Herring	–	100	1	–	100	–	–	–
Norway pout	–	–	1	–	–	–	–	–
Sandeel	–	–	100	–	–	–	–	–
Sprat	–	1	–	–	–	–	–	–
Crustaceans	–	1	–	100	–	–	–	–
Cephalopod	–	–	1	–	–	–	–	–
Large zooplankton	100	1	–	–	–	–	100	100
Epifauna	–	–	–	100	–	–	–	–

(i) means immature.

Table 5. Spearman's rank-order correlations.

Variables	Valid n	Spearman R	$T\ (N-2)$	p-value
Anomaly and temperature	21	-0.070130	-0.30644	0.762600
Anomaly and salinity	21	-0.077922	-0.34069	0.737075
Anomaly and NAO	24	0.084348	0.39704	0.695163
Anomaly and AO	24	-0.213913	-1.02712	0.315527
Anomaly and AMO	24	0.100870	0.47555	0.639086
Anomaly and MEI	24	0.091304	0.43005	0.671341
Anomaly and PNA	24	-0.106957	-0.50456	0.618881
Anomaly (no spine points) and temperature	21	-0.58442	-0.25518	0.801328
Anomaly (no spine points) and salinity	21	-0.094805	-0.41512	0.682707
Anomaly (no spine points) and NAO	24	-0.037391	-0.17550	0.862289
Anomaly (no spine points) and AO	24	-0.236522	-1.14178	0.265820
Anomaly (no spine points) and AMO	24	-0.044348	-0.20821	0.836977
Anomaly (no spine points) and MEI	24	0.309565	1.52700	0.141011
Anomaly (no spine points) and PNA	24	-0.213913	-1.02712	0.315527

The vulnerability search indicated a top-down control (high vulnerability, 100) by juvenile whiting, blue whiting, and Norway pout upon large zooplankton, pollock upon juvenile cod and herring, monkfish upon other small fish and sandeel, rays upon crustaceans and epifauna, and large demersals upon herring (Table 4). The model identified bottom-up controls (with a low vulnerability close to 1) by pollock on horse mackerel, sprat, crustaceans, and large zooplankton, monkfish upon juvenile cod, juvenile whiting, flatfish, herring, Norway pout, and cephalopods, and large demersals upon rays and other small fish. Two main species held the majority of low and high vulnerabilities: pollock and monkfish. Large zooplankton (such as jellyfish, amphipods, mysids, and euphausiids) was identified as a prey species most likely to be affected by increases in the biomass of its predators.

The PP anomaly also improved the model fit to biomass data. However, on checking for a correlation with available environmental time-series, no meaningful correlation was found (Table 5).

Scenario simulation results

Grey seal population control

Where mortality was imposed to prevent the grey seal population rising above the 1985 value, there was no impact upon cod, haddock, or whiting (Figure 4b–d). This is likely because the population control ensures that the grey seal biomass stays constant (Figure 4a). Where a high fishing mortality was imposed to remove grey seals and thus prevent predation by them, an impact upon cod, whiting, and haddock can be seen. All showed slightly higher biomass trajectories, most notably for cod. However, even when predation from grey seals was removed entirely, the model still predicted a decline of cod biomass.

Nephrops trawl selectivity measures

The removal of landings by wcoS nephrops trawlers caused little change in adult or juvenile cod biomass (Table 6). The model further predicted that adult and juvenile haddock biomass and adult and juvenile whiting would, in fact, be reduced with a "clean" nephrops fishery. Even larger decreases in some other species were also shown by the model: flatfish, large demersals, monkfish, and skates and rays.

Fishing at maximum sustainable yield

When running the model forward for 10 years (2009–2018), cod biomass was predicted to increase (Figure 5a). However, when fishing at F_{MSY} was implemented, the biomass recovery was both slightly quicker and to a higher level than the equilibrium model. Within 2 years, a plateau had been reached, but the biomass did not return to the previous maximum level observed in 1996. For haddock, fishing at F_{MSY} produced little change in haddock biomass (Figure 5b), likely due to there being little difference between the F_{MSY} and the non-F_{MSY} catch rates. For whiting (Figure 5c), fishing at F_{MSY} produced a slight reduction in catch and consequently a slight increase in biomass. This would suggest that of the three gadoid species investigated here, cod would be the species most likely to benefit from a move to fishing at F_{MSY}.

Discussion

Model assumptions and limitations

When interpreting modelled outputs from this study, several assumptions and limitations of EwE and indeed ecosystem models

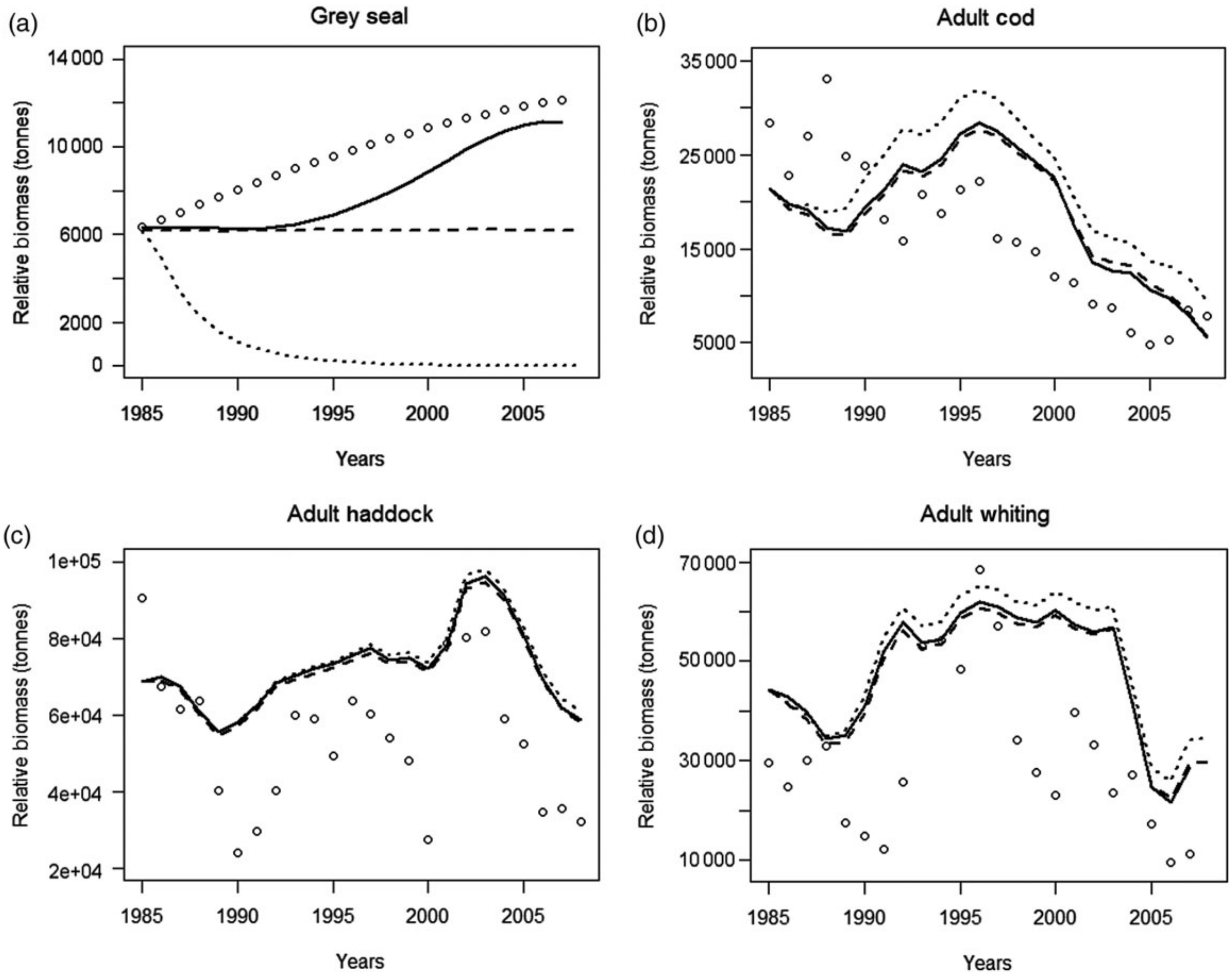

Figure 4. The results of applying grey seal population controls: (a) on the grey seal population; (b) on the adult cod population; (c) on the adult haddock population; and (d) on the adult whiting population. The dots are data points, the continuous black line is the original fitted model, the long dash is the 1985 control level, and the short dash is the high control level.

Table 6. Percentage changes to species biomass due to applying a clean Nephrops trawl fishery.

Species	% change (range)	% change (average)
Adult cod	+6.8 to −3.3	−0.25
Juvenile cod	+8.8 to −4.5	−0.24
Adult haddock	−0.8 to −7.6	−5.5
Juvenile haddock	−4.5 to −4.7	−6.6
Flatfish	−2.9 to −4	−3.3
Large demersals	−15.1 to −17.9	−16.5
Monkfish	−18.8 to −8.6	−12
Skates and rays	−12 to −15.2	−13.3

in general must be considered. First, Ecopath models are a "snapshot" representation of an ecosystem. This study provides a snapshot of the wcoS in 1985 and our knowledge of the ecosystem in 1985 is limited by a lack of data. Further pitfalls include: that the omission of prey rarely found in the diet of a predator may lead to inaccuracies in the modelled effects of the predator on these prey and vice-versa; that trophic mediation effects, where the behaviour or presence of a third group affects predator/prey interaction, may be overlooked as we do not have any knowledge of mediation in this ecosystem (Christensen and Walters, 2004). Also, temporal variations in species-specific habitat factors, e.g. a loss of spawning sites, cannot be addressed in Ecosim, but needs a spatial model (Christensen and Walters, 2004).

There are also limitations to this specific EwE model. First, due to a lack of specific knowledge, several functional groups have been aggregated, e.g. flatfish and sharks, and this may mask important species interactions. Temporal changes in diet that might have occurred were also not addressed. The major limitation, however, was the poor quality of data used for parameterization. The main reasons for this are a lack of biomass and diet data (over time) from the study site, particularly for invertebrates; the large number of parameter values taken from the North Sea (Mackinson and Daskalov, 2007) and Irish Sea models (Lees and Mackinson, 2007); and the large number of parameters that have been estimated by the model.

Despite these limitations, EwE remains the most suitable ecosystem modelling routine for investigating the wcoS ecosystem as it can characterize a data-poor system and include all necessary functional groups and fishing activities. Although a few time-series trends were not well emulated, this amended version of the wcoS model reproduced many time-series trends well; as such, it should be viewed as the best available approximation of the wcoS ecosystem.

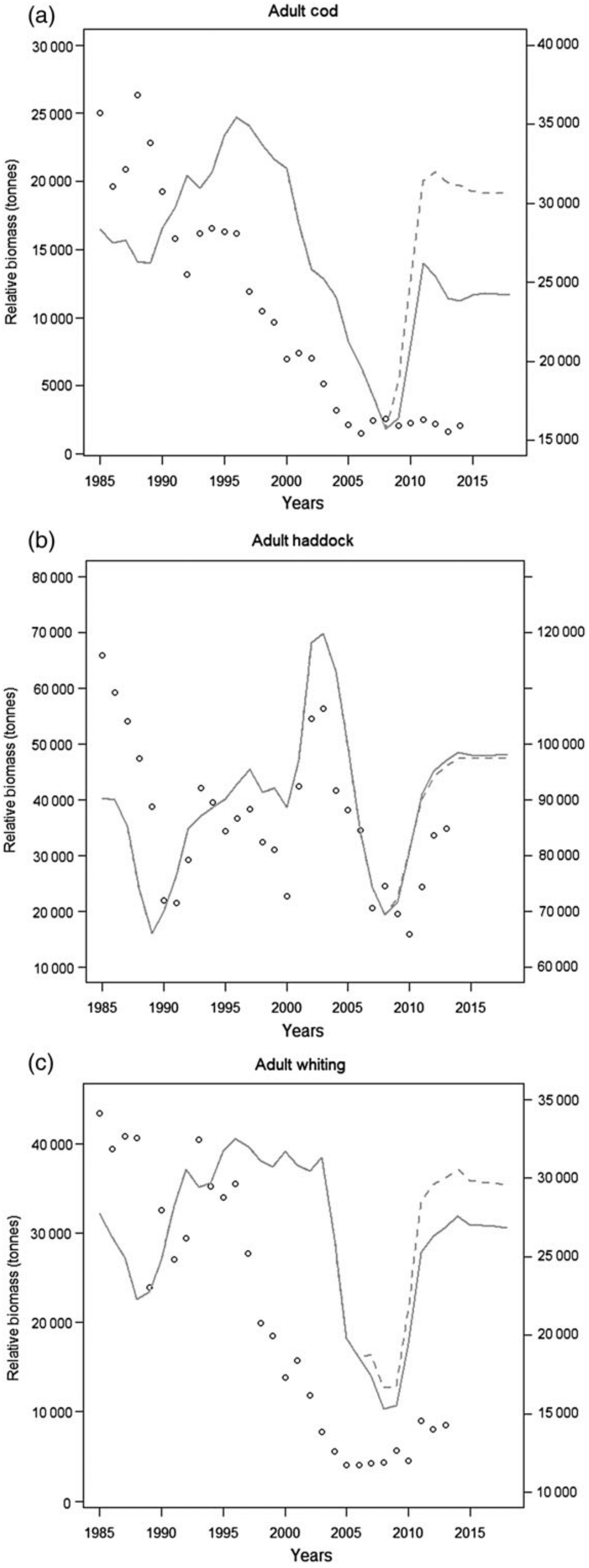

Figure 5. The results of applying fishing at maximum sustainable yield: (a) on the adult cod population; (b) on the adult haddock population; and (c) on the adult whiting population. The dots are data points, the continuous black line is the results of fishing at the status quo for an additional 10 year run, the long dash is the result of fishing at F_{MSY} for the species identified.

Drivers and trophic interactions

Fishing pressure (top-down drivers) as well as climatic drivers of PP (bottom-up drivers) may independently affect the functioning of marine ecosystems. However, ecosystems are often not driven entirely by only one control or the other, but by a combination of the two (Cury *et al.*, 2003). In this instance, fishing pressure had the largest impact on the fit of the model, suggesting that it is the strongest driver upon the wcoS ecosystem. Fisheries affect fish stocks and through foodweb interactions may also affect other trophic levels. This was most clearly indicated for grey and harbour seals. A reduction in fishing for certain species may mean that fishing pressure was replaced (although perhaps not to the same extent) by a top predator. For example, a decrease in fishing for large demersals occurred concurrently with an increase in large demersals as a prey item for grey and harbour seals. That top predators, such as seals, occupy the niche vacated by a fishery was also found in the Gulf of St Lawrence (Morissette *et al.*, 2009).

Each species exists in many interactions with other species, thus natural ecosystems exhibit a mixture of low and high vulnerabilities (Pinnegar and Polunin, 2004), and this appears the case in the wcoS ecosystem. Of the 25 interactions most sensitive to changes in vulnerabilities, two main species held the majority of low and high vulnerabilities: pollock and monkfish, suggesting that they are sensitive to changes in predator/prey interactions and dependent on the abundances of their predators and prey. However, it may be that the lack of data on diets may lead to a perception of sensitivities which is not accurate. Therefore, in any future modelling of the wcoS ecosystem, a focus must be on collecting biological data to ensure that the model parameters, particularly diet, are correct for these two species.

Bottom-up forcing of the wcoS ecosystem from predicted changes in phytoplankton biomass resulted in a small improvement in the fit of the model, indicating that the ecosystem was not largely driven by environmental drivers over the modelled period 1985–2008. There is some variability between studies with respect to how much a PP anomaly improved the fit of the model. PP forcing improved the overall fit for several models, including the Irish Sea, East China Sea, and Catalan Sea, although it worsened the fit of the North Sea model (Mackinson *et al.*, 2009a). In the Southern Benguela model, however, a similar small improvement was made by including a PP anomaly (Shannon *et al.*, 2004).

Environmental factors are recognized as a determinant of recruitment success; it is suggested that interannual variability in physical processes can, by influencing primary productivity, affect the recruitment level of fish (Runge, 1988), but the simulated PP trajectory was compared with several environmental driver datasets and no significant correlation found. Given that the inclusion of the PP anomaly in the model led to only a small improvement in the fit of the model, it may be that the upper trophic levels of the wcoS foodweb are not tightly coupled with PP and the anomaly does not well represent the PP dynamics within the ecosystem which is dependent not on a single environmental factor but rather a stochastic interplay between a number of factors. Or it may be that the impact that the environment has on the ecosystem is not manifested through PP but rather through an impact on egg production or mortality of an important secondary producer. Without any further information to that effect, we cannot test it in this model. The PP anomaly identified by the model may also in fact be due to interactions between different types of primary producers, or through the microbial loop, which are not explicitly accounted for in this model, although it is encompassed in the detritus of the ecosystem. This should be explored further in future research.

The decline in cod, haddock, and whiting stocks

Running scenarios in Ecosim to investigate the factors influencing the decline of gadoid stocks on the wcoS have provided some interesting results.

Seals are abundant marine predators and predation by this species has been suggested to play a role in declining stocks of commercially valuable fish species (Chouinard *et al.*, 2005; Trzcinski *et al.*, 2006; Lilley *et al.*, 2008). The results of this study would suggest that grey seals are not a major factor in declining gadoid stocks on the wcoS. This has also been found in other studies on the eastern Scotian Shelf and the Baltic Sea which used model simulations (Mohn and Bowen, 1996; MacKenzie *et al.*, 2011). In these instances, it was suggested that a lack of understanding of the functional responses (the intake rate of a consumer as a function of food density; Holling, 1959) of predators to prey abundances and of prey switching (switching away from prey that are declining in abundance) may have important implications for prey dynamics. With a type I or II functional response, seals could push cod populations to extinction, but with a type III functional response, this may not be possible (MacKenzie *et al.*, 2011). This point should be borne in mind here; Ecosim uses a "multispecies disc equation" to calculate the feeding rates of predators which is a generalization of Holling's type II functional response model (although the software can produce the other responses). This may be caused by incomplete data leading to a bias in vulnerability estimations. It is more likely that the level of mortality inflicted by seals upon gadoid stocks is not large to begin with.

The results suggested that moving to a clean Nephrops trawl would have very little impact on the cod stocks and would result in a decrease for haddock and whiting stocks. This contradicts the hypothesis that Nephrops trawl pressure on juvenile whiting and haddock may be enough to suppress the population as a whole. The findings are also in disagreement with another modelling study which found that eliminating discarding in the Nephrops fishery in the North Sea would cause cod stocks to increase by 2%, haddock by 1%, and whiting by 13% (Catchpole *et al.*, 2007). In the Ecopath model, discards are apportioned to detritus and by removing catches by the nephrops fishery, there may be less food for those species which eat detritus, such as zooplankton, infauna, and epifauna, and therefore, less prey availability and this can propagate through the foodweb. Future research could investigate the impact of changing discard scenarios upon diets throughout the foodweb.

A goal of the reformed Common Fisheries Policy is to operate all fisheries by fishing at maximum sustainable yield by 2016 (European Union, 2011) and the final scenario involved predicting biomass and catch trajectories based on fishing gadoid stocks at F_{MSY}. The construction of this scenario did involve certain assumptions including that F_{MSY} can be achieved in the context of a mixed fishery, and that F remained constant over the 10-year period which is unlikely to be the case. Of the three species, cod was predicted to have the largest response to F_{MSY}. Although it may appear surprising that cod would increase to such an extent in response to F_{MSY}, this has been seen to happen in the Barents Sea and Norwegian Sea ICES region (ICES, 2013a). Cod can have a high growth rate (and in the model a high P/B); therefore, given low mortality rates and increased recruitment, this is possible. None of the species showed a biomass decrease which would indicates that fishing at maximum sustainable yield would be a good management practice which may benefit some species. However, at the same time, fishing at maximum sustainable yield would likely lead to a reduction in catches for some sectors of the fishing industry, which may have financial implications. It should be noted that the model predictions for cod and whiting did not match the actual stock assessment trend from 2008 to 2014, although the trend appears similar for haddock. For cod, this is likely to be because fishing at maximum sustainable yield is not occurring, and in fact recently, there has been an increase in fishing effort (ICES, 2014a). For whiting, an additional problem has been reduced reproductive capacity (ICES, 2014b).

It may be that it is a combination of two or more of these factors which are influencing gadoid stocks, as was demonstrated in the Baltic Sea (Eero *et al.*, 2011), and this should be further investigated in future work. It may also be for other reasons, not investigated here, that gadoid stocks have been declining on the wcoS. In the North Sea, the suppression of the cod stock has been linked to herring preying on their eggs (Segers *et al.*, 2007). To investigate whether this is the case on the west coast, it would be necessary to resolve the egg and larval stages of this species, and this should be considered in future research. It may also be useful in future research to consider further splitting out zooplankton groups as species survival may be affected by a mismatch with the type of zooplankton food available. Bottom-up controls could also affect abundance and there are mechanisms which could link climate change and associated changes in ocean currents and nutrient levels to the performance of these stocks (Cook and Heath, 2005; Drinkwater, 2005; Brunel and Boucher, 2007). As noted in the previous section, the model predicts that phytoplankton biomass is (to a small extent) driving this ecosystem, but it has not, to date, been possible to determine which environmental factors, or combination of such, are influencing PP on the west coast.

Conclusions

This research attempted to gain insight into the direct and indirect processes that govern the inshore west of Scotland ecosystem. This is important if we are to understand the effects of environmental and human-induced change upon this ecosystem and upon those who rely on it. The study has shown that we can reproduce the trends in most of the important fish stocks but that we are still not able to reproduce the absolute changes. This indicates that we still do not have a good handle on the diet and predator–prey dynamics of even the most important gadoid species on the wcoS.

In summary, we found that fishing was the most important driver of modelled ecosystem dynamics on the wcoS during the 24 years from 1985 to 2008 (inclusive). Implementing a reduction in catch by fishing at maximum sustainable yield was predicted to benefit cod stocks particularly. However, the impact of grey seal predation and nephrops trawling pressure on gadoid stocks does not appear to be major factors. Indeed, we are little further forward in understanding the key causes behind the decline in gadoid stocks on the wcoS. What is driving PP in the wcoS ecosystem model needs to be identified. Also incorporating egg stages of gadoids to better understand recruitment processes would be a logical next step in the EwE approach to understanding this ecosystem.

The development of an ecosystem model for the wcoS is an important effort to integrate the available biological data from the area into a coherent format. It has enabled us to further our knowledge and understanding of aspects of trophic structure and the impacts of fishing. While this approach alone may not provide direct tactical management advice, it is certainly useful for strategic thinking.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

The authors would like to thank Marine Scotland Science, especially Graham Tyldesley, and Marine Scotland Statistics for their assistance in this study. The authors would also like to thank the European Research Development Fund and Highlands and Islands Enterprise for funding this research.

References

Ahrens, R. N. M., Walters, C. J., and Christensen, V. 2012. Foraging arena theory. Fish and Fisheries, 13: 41–59.

Ainsworth, C. H., Samhouri, J. F., Busch, D. S., Cheung, W. W. L., Dunne, J., and Okey, T. A. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. ICES Journal of Marine Science, 68: 1217–1229.

Allen, J. I., and Clarke, K. R. 2007. Effects of demersal trawling on ecosystem functioning in the North Sea: a modelling study. Marine Ecology Progress Series, 336: 63–75.

Araujo, J. N., Mackinson, S., Stanford, R. J., and Hart, P. J. B. 2008. Exploring fisheries strategies for the western English Channel using an ecosystem model. Ecological Modelling, 210: 465–477.

Bailey, N., Bailey, D., Bellini, L., Fernandes, P., Fox, C., Heymans, S., Holmes, S., *et al.* 2011. The West of Scotland Marine Ecosystem: a Review of Scientific Knowledge.

Baretta, J. W., Ebenhöh, W., and Ruardij, P. 1995. The European regional seas ecosystem model, a complex marine ecosystem model. Netherlands Journal of Sea Research, 33: 233–246.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.thomas-brey.de/science/virtualhandbook.

British Oceanographic Data Centre. 2012. National Oceanographic Database. https://www.bodc.ac.uk/data/online_delivery/nodb/search/?xmlSupplied=true.

Brunel, T., and Boucher, J. 2007. Long-term trends in fish recruitment in the north-east Atlantic related to climate change. Fisheries Oceanography, 16: 336–349.

Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1453–1473.

Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia, 44: 303–310.

Catchpole, T. L., Tidd, A. N., Kell, L. T., Revill, A. S., and Dunlin, G. 2007. The potential for new Nephrops trawl designs to positively effect North Sea stocks of cod, haddock and whiting. Fisheries Research, 86: 262–267.

Chouinard, G. A., Swain, D. P., Hammill, M. O., and Poirier, G. A. 2005. Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1991–2000.

Christensen, V. 2009. Ecopath with Ecosim: linking fisheries and ecology. *In* Handbook of Ecological Modelling and Informatics. Ed. by S. E. Jørgensen, T. S. Chon, and F. A. Recknagel. WIT Press, Southampton.

Christensen, V., and Pauly, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Walters, C. J., and Pauly, D. 2001. Ecopath with Ecosim: a User's Guide.

Coll, M., Palomera, I., Sergi, T., and Sarda, F. 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. Journal of Marine Systems, 59: 63–96.

Coll, M., Santojanni, A., Palomera, I., Tudela, S., and Arneri, E. 2007. An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. Journal of Marine Systems, 67: 119–154.

Cook, R. M., and Heath, M. R. 2005. The implications of warming climate for the management of North Sea demersal fisheries. ICES Journal of Marine Science, 62: 1322–1326.

Cury, P., Shannon, L., and Shin, Y. J. 2003. The functioning of marine ecosystems: a fisheries perspective. *In* Responsible Fisheries in the Marine Ecosystem, pp. 103–123. Ed. by M. Sinclair, and G. Valdimarsson. CAB International, Wallingford.

Drinkwater, K. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES Journal of Marine Science, 62: 1327–1337.

Eero, M., MacKenzie, B. R., Koster, F. W., and Gislason, H. 2011. Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. Ecological Applications, 21: 214–226.

European Union. 2011. Proposal for a regulation of the European Parliament and of the Council on the Common Fisheries Policy. Brussels.

Fulton, E. A., Fuller, M., Smith, A. D. M., and Punt, A. 2004. Ecological Indicators of the Ecosystem Effects of Fishing: Final Report.

Gillibrand, P. A., Sammes, P. J., Slesser, G., and Adams, R. D. 2003. Seasonal water column characteristics in the Little and North Minches and the Sea of the Hebrides. I. Physical and chemical parameters. Fisheries Research Services Internal Report No. 08/03.

Guénette, S., Christensen, V., and Pauly, D. 2008. Trophic modelling of the Peruvian upwelling ecosystem: towards reconciliation of multiple datasets. Progress in Oceanography, 79: 326–335.

Haggan, N., and Pitcher, T. 2005. Ecosystem simulation models of Scotland's West Coast and Sea Lochs. Fisheries Centre Research Reports, 13 (4).

Heymans, J. J., Coll, M., Libralato, S., and Christensen, V. 2011. 9.06—Ecopath theory, modeling, and application to coastal ecosystems. *In* Treatise on Estuarine and Coastal Science, pp. 93–113. Ed. by W. Eric, and M. Donald. Academic Press, Waltham.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist, 91: 385–398.

Hurrell, J. W., Kushnir, Y., and Visbeck, M. 2001. The North Atlantic oscillation. Science, 291: 603–605.

ICES. 2008. Report of the ICES Advisory Committee 2008: Book 5 Celtic Sea and West of Scotland. 267 pp.

ICES. 2010a. Report of the ICES Advisory Committee.

ICES. 2010b. Report of the Working Group on the Celtic Seas Ecoregion (WGCSE). ICES Document ICES CM 2009/ACOM: 09. 1430 pp.

ICES. 2013a. Barents Sea and Norwegian Sea. Cod in Subareas I and II (Northeast Arctic Cod). Advice for 2014.

ICES. 2013b. ICES Advice 2013 Book 5.

ICES. 2014a. Celtic Sea and West of Scotland. Cod in Division VIa (West of Scotland) Advice for 2015.

ICES. 2014b. Celtic Sea and West of Scotland. Whiting in Division VIa (West of Scotland) Advice for 2015.

Kelleher, K. 2005. Discards in the worlds marine fisheries: an update.

Lees, K., and Mackinson, S. 2007. An Ecopath model of the Irish Sea: ecosystems properties and sensitivity analysis. ICES Document 138. 40 pp.

Lilley, G. R., Wieland, K., Rothschild, B. J., Sundby, S., Drinkwater, K. F., Brander, K., Ottersen, G., *et al.* 2008. Decline and recovery of Atlantic Cod (*Gadus morhua*) stocks throughout the North Atlantic. *In* Resiliency of Gadid Stocks to Fishing and Climate Change. Alaska Sea Grant College Programme.

Link, J. S. 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecological Modelling, 221: 1580–1591.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., *et al.* 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science, 312: 1806–1809.

MacKenzie, B. R., Eero, M., and Ojaveer, H. 2011. Could seals prevent cod recovery in the Baltic Sea? PLoS ONE, 6: e18998.

Mackinson, S., and Daskalov, G. 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. ICES Document 142. 196 pp.

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., Jiang, H., *et al.* 2009a. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. Ecological Modelling, 220: 2972–2987.

Mackinson, S., Deas, B., Beveridge, D., and Casey, J. 2009b. Mixed-fishery or ecosystem conundrum? Multispecies considerations inform thinking on long-term management of North Sea demersal stocks. Canadian Journal of Fisheries and Aquatic Sciences, 66: 1107–1129.

Marine Scotland Science. undated. Data Provision and evaluation of measures employed in Scotland under the management plan for cod stocks Article 13 provision during 2012. http://stecf.jrc.ec.europa.eu/documents/43805/595773/Evaluation+Measures+employed+in+Scotland+under+Cod+Recovery+plan+Article+13+provision+during+2012.pdf.

Mohn, R., and Bowen, W. D. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2722–2738.

Morato, T., Bulman, C., and Pitcher, T. J. 2009. Modelled effects of primary and secondary production enhancement by seamounts on local fish stocks. Deep Sea Research Part II: Topical Studies in Oceanography, 56: 2713–2719.

Morissette, L., Castonguay, M., Savenkoff, C., Swain, D. P., Chabot, D., Bourdages, H., Hammill, M. O., *et al.* 2009. Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. Deep Sea Research Part II: Topical Studies in Oceanography, 56: 2117–2131.

Myers, R., Hutchings, J., and Barrowman, N. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series, 138: 293–308.

NOAA Climate Prediction Centre. 2012a. Arctic Oscillation Dataset. http://www.esrl.noaa.gov/psd/data/correlation/ao.data.

NOAA Climate Prediction Centre. 2012b. Atlantic Multi-decadal Oscillation Dataset. http://www.esrl.noaa.gov/psd/data/correlation/amon.us.data.

NOAA Climate Prediction Centre. 2012c. Multivariate ENSO Index Dataset. http://www.esrl.noaa.gov/psd/data/correlation/mei.data.

NOAA Climate Prediction Centre. 2012d. North Atlantic Oscillation Dataset. http://www.esrl.noaa.gov/psd/data/correlation/nao.data.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil, 39: 175–192.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57: 697–706.

Pinnegar, J. K., and Polunin, N. V. C. 2004. Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecological Modelling, 172: 249–267.

Piroddi, C., Giovanni, B., and Villy, C. 2010. Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. Ecological Modelling, 221: 1526–1544.

Polovina, J. J. 1984. Model of a coral reef ecosystem. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs, 3: 1–11.

Runge, J. A. 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia, 167–168: 61–71.

Scottish Government. 2011. Scottish Sea Fisheries Statistics 2010. Marine Scotland, Edinburgh.

Sea Mammal Research Unit. 2004. Sea Mammal Research Unit Scientific Report.

Segers, F., Dicky-Collas, M., and Rijnsdorp, A. 2007. Prey selection by North Sea herring (*Clupea harengus*) with special reference to fish eggs. ICES Journal of Marine Science, 64: 60–68.

Shannon, L. J., Christensen, V., and Walters, C. J. 2004. Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. African Journal of Marine Science, 26: 179–196.

Shin, Y-J., and Cury, P. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquatic Living Resources, 14: 65–80.

Tomczak, M. T., Niiranen, S., Hjerne, O., and Blenckner, T. 2012. Ecosystem flow dynamics in the Baltic Proper—using a multi-trophic dataset as a basis for food-web modelling. Ecological Modelling, 230: 123–147.

Travers, M., Shin, Y. J., Jennings, S., and Cury, P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Progress in Oceanography, 75: 751–770.

Trzcinski, M. K., Mohn, R., and Bowen, W. D. 2006. Continued decline of an Atlantic Cod population: how important is gray seal predation? Ecological Applications, 16: 2276–2292.

Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139–172.

Handling editor: Marta Coll