

Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland

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There is currently a global call for more use of an ecosystem approach to fisheries management (EAFM), and ecosystem models such as Ecopath with Ecosim (EwE) are being used to provide a holistic view of ecosystem–fisheries interactions. Although these can be useful for an EAFM, the relative paucity of data available for deep-sea ecosystems raises concerns whether we can effectively apply an EAFM to the deep sea. The deep-sea ecosystem off the west coast of Scotland has been studied for longer and in more detail than most. This study assimilates the significant published and unpublished information available on this ecosystem into an EwE model. The results suggest that there are sufficient data available to construct an ecosystem model, but the quality of the data varies and serious potential sources of error are present in biomass and discard estimates. The assumptions needed to produce a model are varied and must be considered when interpreting the outputs of the model. Ecosystem modelling provides a unique view of the deep-water ecosystem and facilitates hypothesis development concerning predator–prey and inter-fishery interactions. Sharks are used to illustrate the benefits of using an ecosystem model to describe changes in their biomass and their prey species. The results show that both fishing for sharks and fishing for their prey affect the biomass of sharks.

Keywords: deep-water fisheries, deep-water sharks, Ecopath, ecosystem-based assessment, Rockall Trough.

Introduction

The Common Fisheries Policy (Lutchman *et al.*, 2009), United Nations Fisheries and Agriculture Organization (FAO, 2008), and the Northeast Atlantic Fisheries Commission (NEAFC, 2006) all call for the application of the “ecosystem approach” to fisheries management. Ecosystem-based fisheries management in the deep sea, however, is hampered by a lack of information, which is why models of the deep sea are limited to those constructed of the well-studied seamounts (Bulman *et al.*, 2002; Morato *et al.*, 2009). It is now widely accepted that many deep-water fish stocks cannot sustain high levels of exploitation and that different management systems are required (Clarke *et al.*, 2003). Some deep-water species are slow-growing, mature late, and have low fecundity (Clarke *et al.*, 2003; Camhi *et al.*, 2009), which makes them very susceptible to overfishing. To compound the problem, deep-water species are data-deficient (Clarke *et al.*, 2003).

This paper looks at one of the most studied deep-sea fisheries ecosystems to evaluate critically whether the ecosystem approach can be applied to this system and, by inference, to other deep-sea ecosystems around the world. It uses a trophic foodweb

model as a tool to assess the quality and quantity of data available in this system. In the production of the model, we aimed to discover whether this dataset could be used to predict or replicate observed changes over the last 40 years and, therefore, to deliver the ecosystem approach to fisheries management (EAFM).

Deep-water fishing in the Rockall Trough

The deep sea off the west coast of Scotland has been exploited since the early 1970s, as reviewed by Gordon (2001) and Gordon *et al.* (2003). There is a long-established longline fishery for ling (*Molva molva*), tusk (*Brosme brosme*) and, to a lesser extent, blue ling (*Molva dypterygia*) along the continental margin to the west of Scotland (Bergstad and Hareide, 1996). Spawning aggregations of blue ling were discovered by the German trawl surveys (see description below) in the northern Rockall Trough, which led to a brief exploitation by the German fleet. French trawlers from a fleet traditionally targeting saithe (*Pollachius virens*) took over in the mid-1970s. Since the mid-1980s, the Rockall Trough has become the major deep-water bottom-trawl fishing area in the northern Northeast Atlantic. The present fishery derives from the development of markets for the previously discarded species such as

roundnose grenadier (*Coryphaenoides rupestris*), black scabbardfish (*Aphanopus carbo*), and deep-water sharks in the late 1980s. The mixed shelf-edge fishery by Scottish and French vessels target megrim and monkfish on the continental slope, and has a bycatch of sharks, etc. (Anon, 2007). Aggregations of orange roughy (*Hoplostethus atlanticus*) were discovered in 1990 but these stocks were depleted after a few years (Lack et al., 2003).

There are also two semi-pelagic trawl fisheries in the Rockall Trough, for blue whiting (*Micromesistius poutassou*) and argentine (*Argentina silus*). Blue whiting aggregates for spawning along the upper slope of the Trough. The commercial fishery began in the early 1970s and increased rapidly, especially from the 1990s. The stock is managed as a single Northeast Atlantic unit and part of it is in international waters. The catch in recent years has significantly exceeded the recommended quota set by ICES (2007a). Argentine are targeted by some fleets, notably by the Netherlands since 1989, and sometimes opportunistically when encountered along with blue whiting. The landings of these species are significantly higher than those of the more demersal deep-water species.

Management of the deep-water fishery

Large et al. (2003) found that most of the deep-water fisheries in the Northeast Atlantic were being harvested outside safe biological limits. An outline of the assessment and management of the deep-water fisheries since the establishment of the ICES Study Group on the Biology and Assessment of Deep-sea Fisheries Resources (now a Working Group) to the implementation of quotas in 2003 is given in Gordon (2003). The management of the deep-sea fisheries off the west coast of Scotland is mainly by a total allowable catch (TAC), with quotas being introduced in 2003. The area of this system (including the Rockall Trough) is situated mostly in European Union (EU) waters, so management measures are set by the EU, TACs being allocated between Member States based on previous track record of reported landings (Anon, 2007). Some TACs are set based on the precautionary principle, with no assessment of the status of their stock (Anon, 2007). In setting TACs, the EU usually includes catches taken in international waters, but obviously fishing vessels of non-Member States are not bound by EU rules in these waters (Anon, 2007), where regulations introduced by the Northeast Atlantic Fisheries Commission (NEAFC) apply. In 2008, the EU introduced phased reductions to zero tonnes for the orange roughy and deep-water shark TACs, and the TACs for other species were reduced by 15% for 2009–2010 (Council Regulation (EC) No. 1359/2008 of 28 November 2008).

Scientific research on fish populations in the Rockall Trough

The deep sea off the west coast of Scotland has more information on the biology of the fish and invertebrate species of the system than any other deep-sea system in the world (Gordon, 1999, 2003; Gage, 2001; Gordon et al., 2003). Studies of the fish populations of this region began when a series of deep-water research vessel fishery surveys (Tiefenfischerei = TIFI) were carried out during the 1970s and 1980s in the northeastern Atlantic by the Federal Research Centre for Fisheries of Germany (hereafter referred to as the German trawl surveys). The investigations focused initially on the technology of fishing in the deep water of the continental slope and seamounts. They concentrated mostly on selected

species of potential interest for exploitation. The results of most of these surveys were described in more detail by Ehrich (1983) and Rätz (1984). In 1973, the Scottish Marine Biological Association (now Scottish Association for Marine Science) began a multidisciplinary study of the biology and oceanography of the Rockall Trough (Mauchline, 1986). The demersal fish studies (hereafter referred to as SAMS surveys) began in 1975 and were centred on an area of the slope known as the Hebridean Terrace (approximately 56–57°N and 9–11°W). Unlike the German fisheries surveys, these were aimed at providing biological information with an emphasis on seasonality. Different trawls were used to sample the total depth range which also provided information on catchability (Gordon and Duncan, 1985; Gordon and Bergstad, 1992). Detailed dietary studies were made for >70 fish species. The surveys ran until 1990.

Since 1998, Fisheries Research Services, Aberdeen (now Marine Scotland—Science), have conducted twice-yearly and now annual deep-water surveys (hereafter referred to as FRS surveys) in the Rockall Trough (ICES, 2008a). These three sources collectively provide a unique dataset, spanning >30 years, allowing us to study long-term trends in the fish populations of the Rockall Trough and the impact of fishing from an ecosystem perspective.

The ecosystem approach

One method of investigating the ecosystem impact of fisheries is to use an ecosystem model, which can be used to examine the ecological, economic, and social trade-offs in an integrated manner (Christensen et al., 2009). Although various models are available (Plagányi, 2007), many have high data demands and are therefore not suitable for use in a system such as the deep sea, for which data are sparse. The Ecopath with Ecosim modelling approach has been described as “excellent” by the FAO in its ability to conduct assessment and policy exploration and is capable of addressing the widest range of topical EAFM research questions (Plagányi, 2007).

Ecopath is conceptually simple and ecologically sensible. It takes a trophic perspective and treats fisheries as the ultimate predator. Ecosim converts the simple trophic flows into dynamic time-dependent predictions (Plagányi, 2007). It makes similar assumptions to most other ecosystem or even single-species models and can handle less than perfect data (Christensen and Walters, 2005; Christensen et al., 2009). It is therefore an appropriate ecosystem modelling tool to apply to deep-water fisheries for which there are limited data.

The data requirements of the Ecopath with Ecosim model are minimal. With only basic biomass, production, and consumption values needed, and the relatively rich dataset available for this region of the deep sea, is it possible to apply the ecosystem approach to deep-water fisheries? The aim of this paper is to assess critically whether we can apply the ecosystem approach to deep-water fisheries by attempting to construct an Ecopath with Ecosim model of the deep-water fisheries off the west coast of Scotland. The following questions are addressed:

- Are the data available sufficient to allow the ecosystem approach to deep-water fisheries?
- What assumptions have to be made to produce a working model?
- What can we hope to learn from such models that we cannot get from single-species models?

Material and methods

Ecopath methodology

Ecopath with Ecosim (EwE version 5.1; Christensen and Walters, 2004) is a tool used to analyse exploited aquatic ecosystems. It combines software for ecosystem trophic mass balance analysis (Ecopath) with a dynamic modelling capability (Ecosim) to explore past and future impacts of fishing and the environment (Christensen *et al.*, 2005).

For Ecopath, the algorithm requires that three of the following four data points for each group be entered into the model:

- Biomass (B , t km⁻²) for the year under consideration
- Production/biomass ratio (P/B , year⁻¹);
- Consumption/biomass ratio (Q/B , year⁻¹);
- Ecotrophic efficiency (proportion): this parameter indicates the unexplained mortality for each group and is often set to 95% when estimating the biomass, except for migratory species or long-lived species that have very little explained mortality in the system.

In addition, for each group, the diet composition is required as a contribution of the prey items by mass and for each fishery the group-specific landings (t km⁻² year⁻¹) and discards (t km⁻² year⁻¹) are required. To run the dynamic simulations in Ecosim, yearly estimates of biomass, fishing mortality, and catch by species and/or gear are required to drive the model.

Ecopath uses two equations to parameterize models: one for the energy balance of each group [Equation (2)] and one to describe the production [Equation (4); Christensen *et al.*, 2005]. Energy balance of each group is ensured using the equation (Christensen *et al.*, 2005)

$$\begin{aligned} \text{Consumption} = & \text{catch} + \text{predation mortality} \\ & + \text{net migration} + \text{biomass accumulation} \\ & + \text{other mortality} + \text{respiration} \\ & + \text{unassimilated food,} \end{aligned} \quad (1)$$

or, more formally,

$$P_i = Y_i + B_i \times M2_i + E_i + BA_i + P_i \times (1 - EE_i), \quad (2)$$

where P_i is the total production of group i , Y_i is the total fishery catch rate of i , $M2_i$ is the instantaneous predation rate for group i , E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for i , and $P_i \times (1 - EE_i)$ is the “other mortality” rate for i (Christensen *et al.*, 2005). Equation (2) can be rewritten as

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i - \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0, \quad (3)$$

where P/B_i is the production/biomass ratio for i and under most conditions corresponds to the total mortality rate, Z , commonly estimated as part of fishery stock assessments. EE_i is the ecotrophic efficiency of group i , describing the proportion of the production that is utilized in the system, Q/B_j is the consumption/biomass ratio of j and DC_{ji} is the fraction of prey i in the average diet of predator j (Christensen *et al.*, 2005).

Ecosim is the dynamic expression of the ecosystem over time and is defined by a series of differential equations:

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

which is the growth rate during time t of group i in terms of its biomass B_i ; g_i is the net growth efficiency of group i ; M_i is the non-predation “other” mortality rate; F_i is the fishing mortality rate; e_i is the emigration rate; and I_i is immigration rate (Christensen *et al.*, 2005). $\sum_j Q_{ji}$ is the total consumption by group j and is calculated based on the foraging arena concept, where values of B_j are divided into vulnerable and invulnerable components (Walters *et al.*, 1997). The vulnerability (v_{ij}) is the maximum predation mortality divided by the baseline predation mortality in the Ecopath model (Christensen *et al.*, 2008). $\sum_j Q_{ij}$ is the predation by all predators of group i (Christensen *et al.*, 2005). For each predator–prey interaction, consumption rates are calculated from:

$$C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij}/D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot P_j \cdot S_{ij} \cdot T_j/D_j}, \quad (5)$$

where a_{ij} is the effective search rate for predator i feeding on a prey j , v_{ij} is the base vulnerability expressing the rate with which prey move between being vulnerable and not-vulnerable, B_i is prey biomass, P_j is predator abundance, T_i represents prey relative feeding time, T_j is predator relative feeding time, S_{ij} is user-defined seasonal or long-term forcing effects, M_{ij} is mediation forcing effects, and D_j represents handling time as a limit to consumption rate (Christensen *et al.*, 2005).

The area modelled

The area modelled off the west coast of Scotland comprises the part of ICES Division VIa between the 400 (on some occasions as shallow as 376 m) and 2000 m depth contours. This includes the Rockall Trough and its seamounts (Anton Dohrn, Rosemary Bank, and the Hebridean Terrace) but excludes the small area of Division VIa that is north of the Wyville-Thomson Ridge, which is strongly influenced by Arctic water and represents a different ecosystem (Gordon, 2001). The investigated area was 75 539 km² (Figure 1). A model was constructed in 1974, which was the first year that biomass estimates were available for most species, and importantly predates most of the deep-water fishery.

Model groups

The model consists of 34 functional groups, including one marine mammal group, four elasmobranch groups, 19 fish groups, eight invertebrate groups (cephalopods, prawns and shrimps, gelatinous zooplankton, large zooplankton, small zooplankton, polychaetes, echinoderms, and other benthic invertebrates), phytoplankton, and detritus. All the commercially important fish species were, in general, defined as individual groups. For most of the other species, there were insufficient data, so species were aggregated into trophic groups based on similar depth distributions and general trends in biomass.

The elasmobranchs were combined into “shallow sharks” (*Etmopterus spinax*, *Galeus melastomus*), “deep sharks” (*Centroscyllium fabricii*, *Etmopterus princeps*), “skates and rays” (*Dipturus batis*, *D. oxyrinchus*, *D. nidarosiensis*, *Raja clavata*, *Leucoraja naevus*, *Leucoraja circularis*, *Rajella fyllae*, *R. bathyphila*,

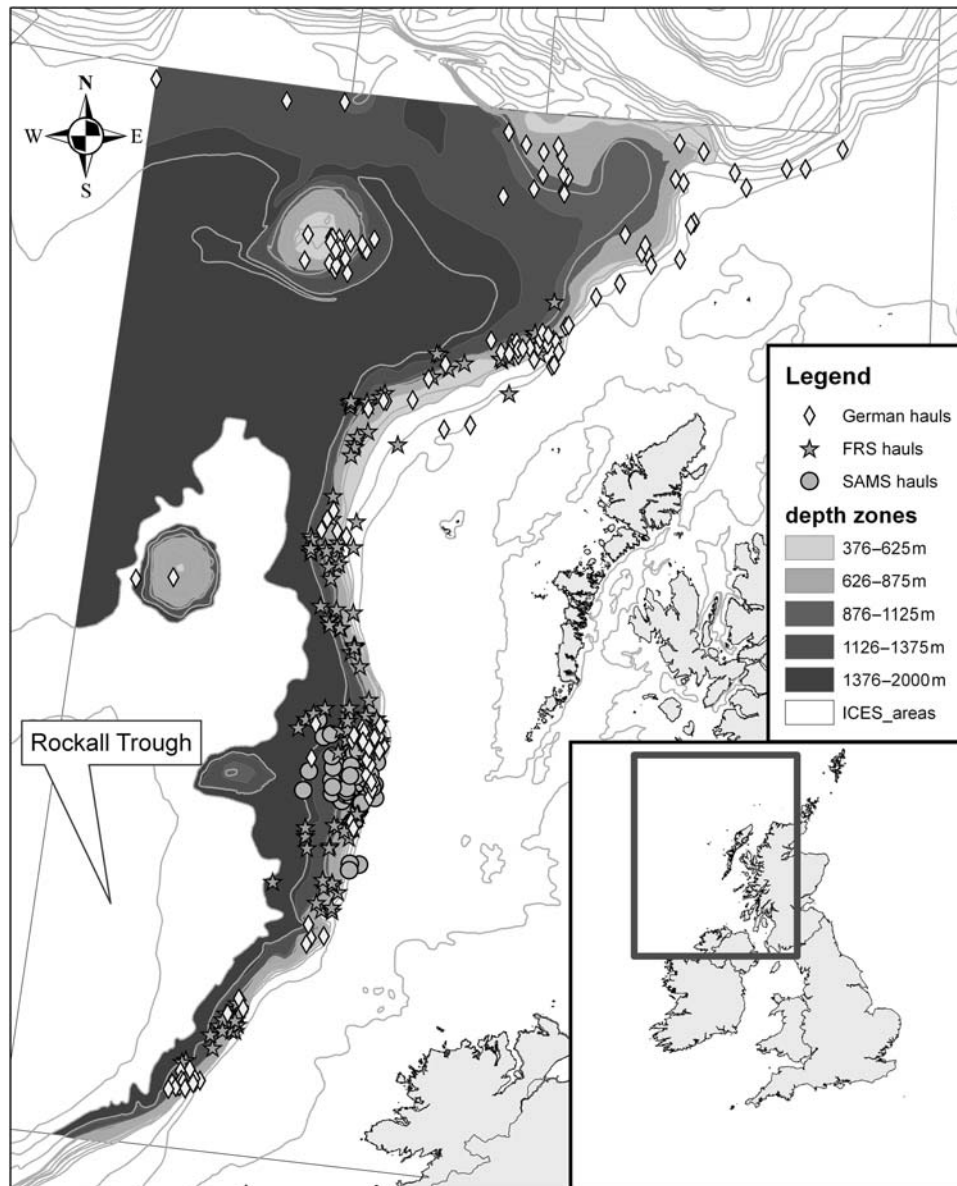


Figure 1. West coast of Scotland study area showing the depth strata from 376 to 2000 m and the position of all trawls used for biomass estimates.

R. bigelowi, *Neoraja caerulea*, *Bathyraja pallida*, *B. richardsoni*), and “intermediate sharks”. The intermediate sharks include two species that are targeted extensively (*Centroscyrnus coelolepis*, *Centrophorus squamosus*), and other species that are discarded (*Deania calcea*, *Centroscyrnus crepidater*, *Apristurus laurussonii*, and other *Apristurus* spp.). Large demersal species such as tusk (*Brosme brosme*) and European hake (*Merluccius merluccius*) were grouped. Other combined fish groups include mesopelagic fish (*Cyclothone braueri*, *C. microdon*, *Maurollicus muelleri*, *Argyropelecus hemigymnus*, *Bathylagus euryops*, *Benthosema glaciale*, *Lampanyctus macdonaldi*, *Gadiculus argenteus thori*), benthopelagic fish (*Helicolenus dactylopterus*, *Coryphaenoides mediterraneus*, *Caelorinchus caelorhincus*, *C. labiatus*, *Coryphaenoides guentheri*, *Halargyreus johnsonii*, *Lepidion eques*, *Mora moro*, *Nezumia aequalis*, *Trachyrhynchus murrayi*, and all *Sebastes* spp.), benthic teleosts (*Notacanthus bonaparte*, *Polyacanthonotus*

rissoanus, *Antimora rostrata*), and chimaeras (*Chimaera monstrosa*, *Hydrolagus mirabilis*).

The commercially important fish species include roundnose grenadier (*Coryphaenoides rupestris*), which was divided into two linked, multistanza groups (large, i.e. >21.5 cm, and small, i.e. ≤21.5 cm, month 24) based on differences in diet (Mauchline and Gordon, 1984). The weight at maturity to weight at infinity ratio of 0.03 and K estimates of 0.1 needed for the multistanza group division in Ecopath were obtained from Fishbase (Froese and Pauly, 2000). Other commercially important species include monkfish (*Lophius piscatorius*), orange roughy (*Hoplostethus atlanticus*), argentine (*Argentina silus*), blue whiting (*Micromesistius poutassou*), black scabbardfish (*Aphanopus carbo*), blue ling (*Molva dypterygia*), ling (*Molva molva*), greater forkbeard (*Phycis blennoides*), deepwater cardinal fish (*Epigonus telescopus*), and megrim (*Lepidorhombus wiffiagonis*). The

abundant Baird's smoothhead (*Alepecephalus bairdii*) and Kaup's arrowtooth eel (*Synaphobranchus kaupii*) were included as single-species groups.

Biomass estimates

Estimates of phytoplankton biomass were calculated from monthly means for phytoplankton colour index (PCI) for 1974 within the study area, provided by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) from continuous plankton recorder (CPR) data (see description in Howell *et al.*, 2009), and the primary productivity was assumed to be similar to that of the North Sea (Mackinson, 2001). The biomass of gelatinous, large and small zooplankton was estimated by the model, and that of prawns and shrimps, cephalopods, polychaetes, echinoderms, and other benthic invertebrates was assumed to be similar to that of the Porcupine Seabight (Lampitt *et al.*, 1986). Finally, the biomass of marine mammals was assumed to be similar to that obtained for the shallower waters of the west coast of Scotland (Haggan and Pitcher, 2005).

For fish species, the initial biomass estimate and time-series data were obtained from the three key survey datasets available for the region (German trawl, SAMS, and FRS). Total catch data from the German trawl fisheries surveys were used to provide estimates of the pre-fishery biomasses and specifically estimates for the steady-state Ecopath model of 1974. A subset of 374 hauls, consisting of those that were fished within the model area, were used in this study.

Biomass time-series estimates required by Ecosim were obtained from German surveys (1974–1986), SAMS (1975–1990), and FRS (2002–2007). All three surveys used different gears. The German trawl surveys used commercial 140- and 200-foot bottom trawls with a fine mesh codend. The SAMS surveys used a Granton trawl and a semi-balloon otter trawl (OTSB) fished on paired and single warps. The details of German and SAMS trawl gears, as well as a comparison of the catchability of the Granton trawls used by SAMS and two German trawls, are given in Merrett *et al.* (1991). Gordon and Bergstad (1992) compared the catches of the Granton trawl and the OTSB at different depths in the Rockall Trough. For the purpose of this study, only the catch of the Granton trawl and an OTSB fished on paired warps in the SAMS surveys were used because these were most comparable with the German trawls. The FRS surveys used a Jackson trawl with a headline length of 41.5 m, groundrope length of 53.4 m, a headline height of approx. 5 m, and a codend of 100 mm + 20 mm blinder. For the purposes of calculating the swept area in this project, the wing end spread was estimated as 23.5 m. This gear was comparable with that used in the German trawl surveys.

The spatial distribution of the hauls within Division VIa also varied considerably between the three key datasets and between the years for the German trawl surveys (see figures in Howell *et al.*, 2009). The German trawl surveys were, in general, focused at depths shallower than 1300 m and were distributed along the continental margin within VIa, with sampling of Rosemary Bank Seamount in some years. The SAMS surveys were centred on an area of the continental slope known as the Hebridean Terrace (approx. 56–57°N and 9–11°W) and incorporated sampling in the full range of depth strata. The FRS surveys were distributed along the continental margin within Division VIa with depth stratification principally at 500, 1000, 1500, and 1800 m (ICES, 2008a). From 2005, the survey began to expand its geographic

scope to the eastern flank of Rockall Bank and to the Anton Dohrn Seamount and Rosemary Bank. See Howell *et al.* (2009) for a full description of biomass estimates used in the 1974 Ecopath model and the time-series used in the fitting of the model.

Production and consumption estimates

As most fish species were not caught in 1974, the P/B ratio was assumed to be similar to natural mortality, which was preferentially taken from published data from the region or estimated using empirical equations of Pauly (1980) in Fishbase (Froese and Pauly, 2000). Similarly, the Q/B ratios were mostly estimated based on the empirical equations of Palomares and Pauly (1998) in Fishbase (Froese and Pauly, 2000). Where needed, these estimates were adapted and compared with ratios for the same species in similar habitats and adapted accordingly. See Howell *et al.* (2009) for an in-depth description of the calculation of P/B and Q/B ratios.

P/B and Q/B estimates for marine mammals were assumed to be similar to those obtained for the shallower waters of the west coast of Scotland (Haggan and Pitcher, 2005). The P/B and Q/B ratios for large zooplankton were assumed to be similar to those for the Bay of Biscay (Ainsworth *et al.*, 2001), and the ratios for large zooplankton and gelatinous zooplankton were assumed to be similar to those for the North Sea (Mackinson and Daskalov, 2007). For prawns and shrimps, cephalopods, polychaetes, echinoderms, and other benthic invertebrates, the P/B and Q/B ratios and diets were obtained from the Bay of Biscay (Ainsworth *et al.*, 2001) and Faroe Islands (Zeller and Reinert, 2004).

Trophic data

For most fish species, diets were obtained from the extensive dataset held by SAMS as a result of their multidisciplinary study of the biology and oceanography of the Rockall Trough, in which detailed dietary studies were made for >70 fish species. Many of these data are published in the peer-reviewed literature. The dataset held by SAMS is in the form of prey numbers, and these had to be converted to biomass for input to the model. Prey numbers were converted to biomass using conversion factors developed by the project following dissection of 151 individuals from 12 species (K. L. Howell, unpublished data). Dietary data available from SAMS were supplemented by published peer-reviewed dietary data from the nearest region/closest related species. For the deep-water sharks *Centroscymnus crepidater*, *Etmopterus princeps*, and *Deania calcea*, SAMS data were supplemented with new data obtained from stomach dissections of 172, 55, and 19 individuals, respectively (K. L. Howell, unpublished data). For cetaceans and invertebrate groups, diet data were principally taken from appropriate published EwE models such as that of the west coast of Scotland (Haggan and Pitcher, 2005), the Bay of Biscay (Ainsworth *et al.*, 2001), the North Sea (Mackinson and Daskalov, 2007), or the Faroe Islands (Zeller and Reinert, 2004).

Landings

The fisheries in the defined model area included a mixed demersal trawl fishery, longliners, pelagic trawlers, orange roughy trawlers, monkfish gillnetters, and red crab potters. Landings data for these fisheries were obtained from various sources. The landings data as adopted by ICES working groups for assessment purposes were considered more reliable than the national officially reported (STATLANT) landings data collated by ICES and accessible

through Fishstat Plus (Shatz, 2007). However, for some species, only STATLANT data were available and therefore were used.

Estimates for large demersals, orange roughy, Baird's smoothhead, roundnose grenadier, black scabbardfish, blue ling, chimaeras, and benthic invertebrates were taken from the Report of the Working Groups on the Biology and Assessment of Deep-sea Fisheries Resources (ICES, 2008c). For some species, landings data were aggregated to Subarea VI. Estimates for monkfish and megrim were taken from the Report of the ICES Working Group on the Assessment of Southern Shelf Stocks of hake, monk, and megrim (ICES, 2008b). Estimates for shallow sharks, intermediate sharks, deep sharks, and skates and rays were taken from Reports of the ICES Working Group on Elasmobranch Fishes (ICES, 2005a, 2007b). For all other fish groups, landing estimates for ICES Division VIa were obtained from ICES catch data (STATLANT) accessed through Fishstat Plus (Shatz, 2007). Where data were not available for VIa, landings for Subarea VI were used.

Estimates for the French fleet were provided by P. Lorance (IFREMER, pers. comm.) for roundnose grenadier, orange roughy, argentine, blue whiting, greater forkbeard, Baird's smoothhead, black cardinalfish, and benthopelagic fish. Landings by other countries, which were generally smaller, were added. Where these were reported as Subarea VI, the landings by countries with no fishing rights in Division VIa were excluded. Length frequency data of roundnose grenadier catches in the French fishery showed that no small individuals were landed (Allain et al., 2003), so all landings were assigned to adults. For species that occur both above and below 400 m (specifically large demersals and blue whiting), catch rates by depth were used to calculate the landings below 400 m (ICES, 2005b, 2008b, c), which was part of this model. Monkfish estimates were reduced for the French (down to a third) and Scottish fleets (down to 5%), and landings by other countries were removed to account for fishing carried out in deep water only.

Discards

Discards were calculated separately for each fishery using the published data available. For the mixed demersal trawl fishery, the biomass and composition of discards were calculated for 1995 using the ratio of discarded fish to grenadier landings calculated from Allain et al. (2003), then multiplied by the 1995 grenadier landings for Division VIa. The calculated biomass of *C. rupestris* discarded in 1995 was then used to calculate the biomass of species discarded from the French vessels landing in Scotland in 1995 using the percentage by weight values of discards per trip given in Blasdale and Newton (1998). For each species identified by Allain et al. (2003) as a discard species, the total biomass discarded in Division VIa in 1995 was calculated by averaging the values calculated for each species using both Allain et al. (2003) and Blasdale and Newton (1998). Where a species was not present in Blasdale and Newton (1998), only the values from Allain et al. (2003) were used (i.e. not the average). For each species, the ratio of tonnes discarded per tonne of roundnose grenadier landed was calculated and these ratios used to calculate the discard biomass by species for the years 1974 to present.

Connolly and Kelly (1996) provide data from experimental longlines in 1995 on the mean weight, in kilogrammes, of species landed and discarded per longline set. Tusk landings for 1995 in Division VIa, as given in the WGDEEP 2008 report (ICES, 2008c), have been used to calculate the number of longlines set in 1995 in Division VIa by dividing the weight of tusk caught in

tonnes per set, by the total landings for Division VIa. We have then used the calculated total number of sets to calculate landings and discards of each species in Division VIa in 1995, based on the mean weight in kilogrammes of species landed and discarded per longline set given in Connolly and Kelly (1996). For each species, the ratio of tonnes discarded per tonne of tusk landed has then been calculated for 1995. This ratio has been used to calculate the discard weights for each species from 1974 to present based on tusk landings for Division VIa as given in the WGDEEP report (ICES, 2008c) over this period.

Discards from the blue whiting pelagic trawl fishery were assumed to lie somewhere between 3% by numbers and 13% by weight as given in the Report of the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (ICES, 2007a). Here, an average value of 8% by weight of catch of blue whiting as discards is used. Discarding from the directed orange roughy fishery was assumed to be zero, because spawning aggregations were targeted (Anderson et al., 2001; ICES, 2008c). No discard data were available for the deep gillnet fishery, so discards for this fishery were not included in the model.

The description of the species encapsulated in the model and the estimates of all parameters are given in detail in Howell et al. (2009), and the input data are given in Supplementary Material, Tables S1, S2, and S3.

Results

The estimates of landings and discards used in the construction of the Ecopath model for 1974, and subsequently to drive the model from 1974 to 2007 are given in Figure 2. For some species, most of the catch consisted of discards, with shallow sharks, Kaup's arrowtooth eel, mesopelagics, benthic fish, Baird's smoothhead, benthopelagic fish, and chimaeras being mainly discarded (Figure 2). Most groups are mainly fished by one fishing gear, with only invertebrates, ling, and blue ling being exploited by two different fisheries.

The estimates of biomass used in the construction of the Ecopath model and for fitting the Ecosim model and the fitted and non-fitted biomasses estimated by the model are given in Figure 3. It is clear from Figure 3 that there is often not very good agreement between the SAMS and German survey data, and there are often no clear trends in the data. Similarly, for species such as argentine and mesopelagics, which are not well sampled by the FRS trawl surveys, the estimates were quite scattered (Figure 3). In addition, the fitting procedure changed the estimates of biomass for some species to increase the fit of the model to the data; specifically, for large *Coryphaenoides* the fit of the model to the FRS data was improved by the fitting procedure.

The time-series of catch and biomass were used to estimate a mortality rate (F) which was used to drive the 1974 model forwards. As most of the biomass and catch time-series do not overlap in time, however, this was only possible from 2002 to 2007. Before 2002, the catch in each year was removed from the ecosystem similar to a stock-reduction model and therefore not available for consumption by predators. This is called a forced catch. The forced catches and fishing mortalities used to drive the model as well as the fitted and non-fitted estimates of catch for each species are given in Figure 4. For those species not represented in Figure 4, the total catch in Figure 2 was used to force the model, because there were not enough biomass data to drive the model with a fishing mortality. The fit of the estimated catch to the catch data was improved for intermediate sharks

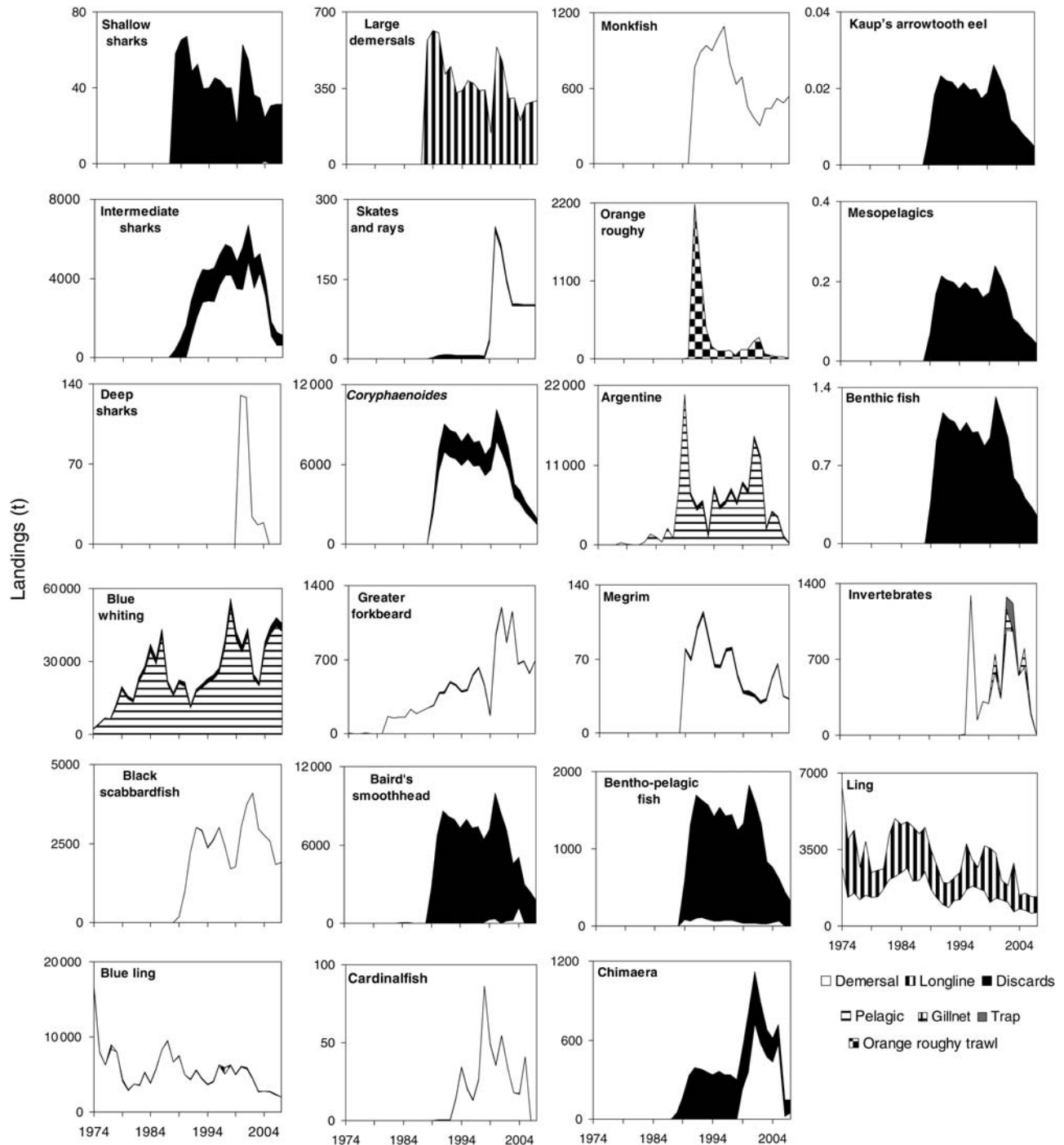


Figure 2. Landings by fishing gear and discards for all the main fish groups (t). See text for a description of the different gear types.

and large demersals by the fitting procedure, but for benthopelagic fish the catches were overestimated (Figure 4).

Ecosim includes a sum of squares (SS) minimization procedure based on a Marquardt non-linear search algorithm with trust region modification of the Marquardt steps (Christensen and Walters, 2004). The model was fitted to the data by changing the predator-prey vulnerability parameters, v_{ij} in Equation (5), for the most sensitive predator-prey interactions. The default vulnerability is set at 2, which indicates mixed control (i.e. not top-down or bottom-up control). However, 20 interactions were changed

(Table 1), with some interactions being bottom-up controlled (1) and some being top-down controlled (100). Fitting the model to data reduced the sum of squares of difference between the predicted and observed biomass and catch estimates by 27%.

Figure 5 shows the biomass, catch, and fishing mortality estimates given in Figures 3 and 4 for the intermediate sharks group as well as the biomass estimates of the main prey species of that group, the change in the proportion of main prey species in their diet and the total prey consumed by intermediate sharks. It shows that although the biomass estimated for mesopelagics

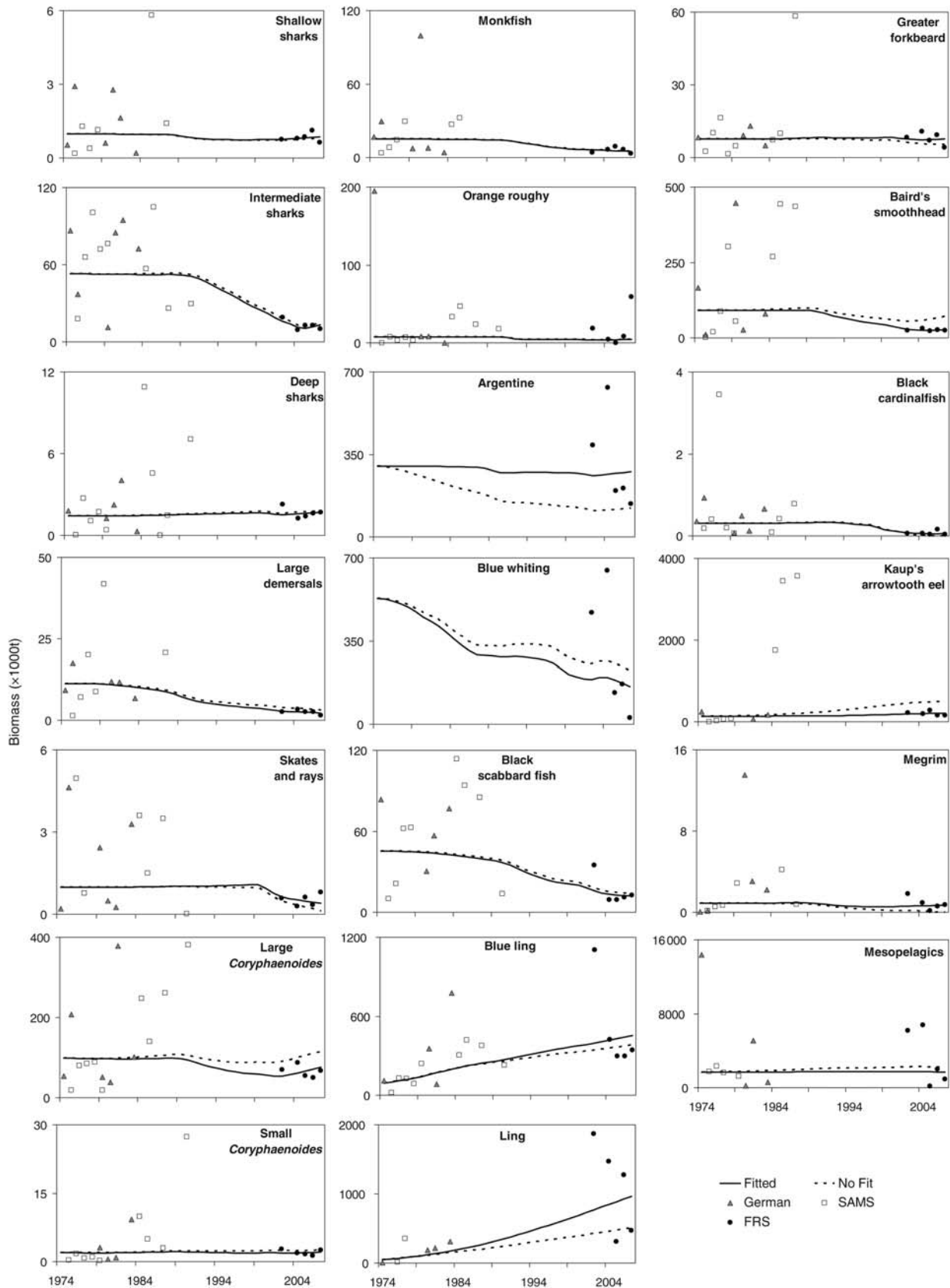


Figure 3. Biomass estimates ($\times 1000 t$) used for construction and fitting of the Ecosim model, obtained from the German, SAMS, and FRS trawl surveys, and outputs of the model when it was fitted (solid line) and not fitted (dashed line) to the data.

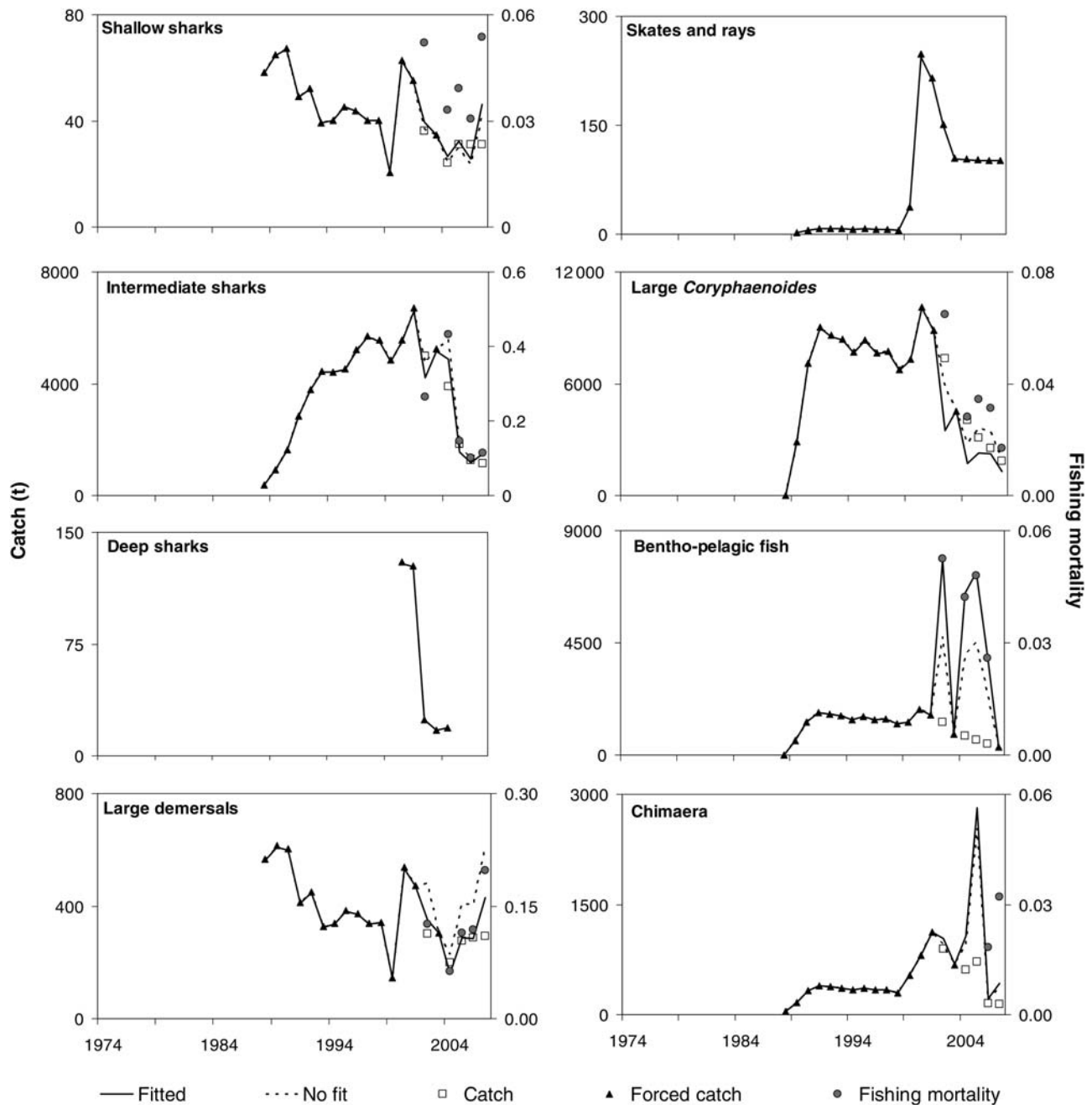


Figure 4. Catch estimates (t), forced catch (t), and fishing mortalities (right y-axis) used to fit the model and estimates of modelled catches with and without fitting for those species where fishing mortalities were used to fit the model.

increased substantially, their proportion in the diet of intermediate sharks did not increase. Instead, the proportion of cephalopods increased as they were the main prey species of this group, although the total tonnage of prey consumed decreased substantially with the reduction in the biomass of intermediate sharks (Figure 5).

Discussion

Ecosystem-based management is a challenge that is not easily met. Arguably, very few top-down managed, single-species fisheries have been sustainable (Pauly *et al.*, 1998; Pauly, 2000; Myers and Worm, 2003), and traditional fisheries management using

maximum sustainable yield and employment as objectives has led to heavily exploited stocks (Hilborn, 2007a). What constitutes sustainability is controversial and depends on the definition and objectives that were used (Hilborn, 2007b). However, adaptive management (Walters, 1986), one of the most widely advocated approaches for natural resource management, requires the manager to learn from the many fisheries around the world and emulate the most successful ones (Hilborn, 2007b). These competing views on the state of fisheries and their ecosystems still requires lower fishing pressure, higher fish abundances, and less impacted ecosystems, with the challenge of finding tools that best achieve these outcomes (Hilborn, 2007c).

Table 1. Changes in vulnerability settings for the fitted model, with only the changed settings shown.

Prey	Predator							
	Argentine	Blue whiting	Blue ling	Ling	Black cardinalfish	Megrim	Prawns and shrimp	Echinoderms
Argentine			1					
Blue whiting			5					
Megrim				1				
Mesopelagic fish	1.1							
Bentho-pelagic fish				1		1		
Benthic teleosts						1		
Chimaeras						1		
Prawns and shrimp		100		7.3	1	100		
Large zooplankton		1.1				1		
Echinoderms				100				
Other benthic inverts						100		100
Phytoplankton							1	
Detritus							100	

All other interactions were left at the default (2) setting.

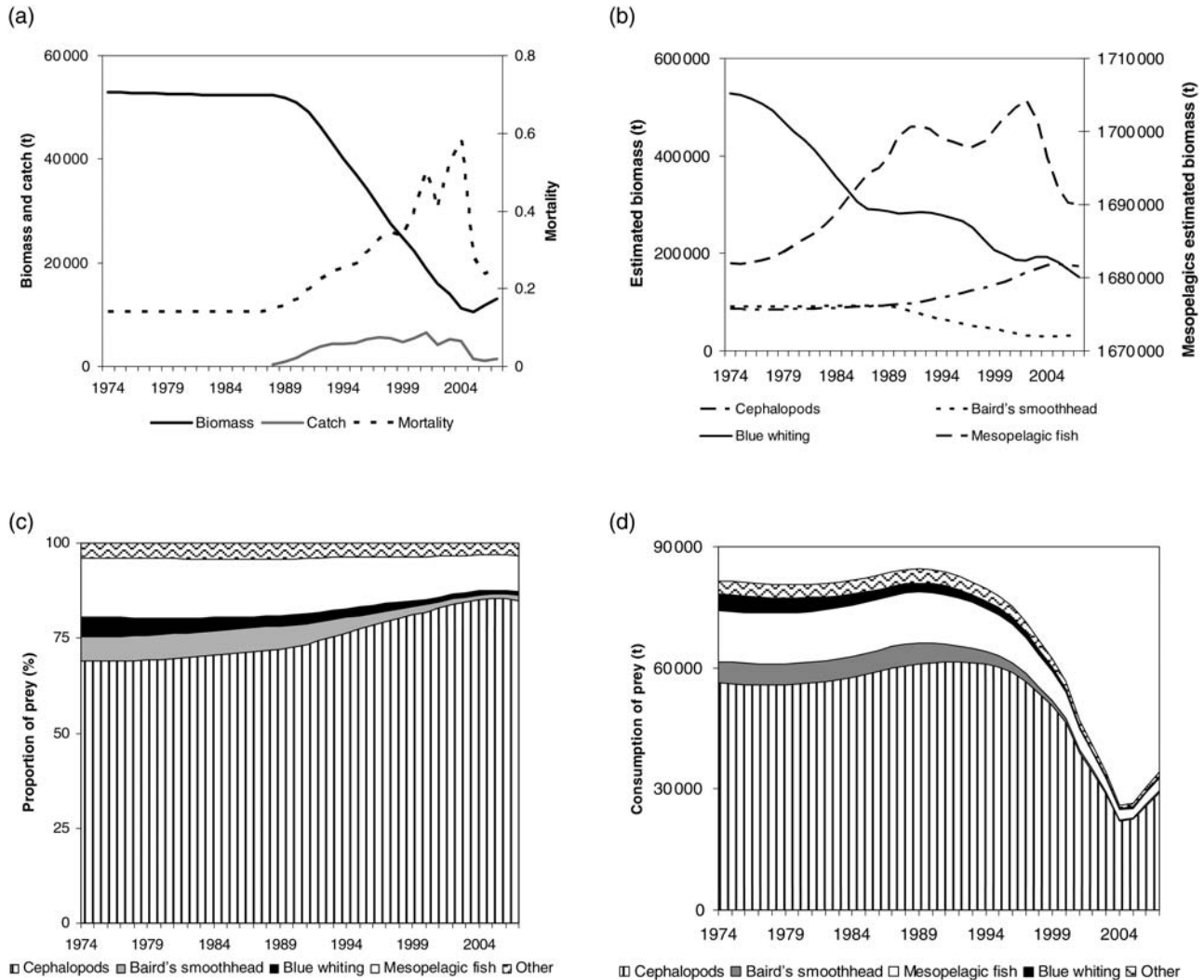


Figure 5. (a) The changes in intermediate shark biomass (t), catch (t), and mortality over time. (b) Estimated biomass (t) of intermediate shark prey species. Note that the biomass of mesopelagics is given on the right y-axis and does not cross the x-axis at zero. (c) Changes in the proportion of the main prey species in the diet of intermediate sharks. (d) Prey consumption by intermediate sharks (t).

The deep sea of the west coast of Scotland has one of the most extensive databases on both species distribution and diets of deep-sea systems in the world, but there will never be perfect information to construct any ecosystem model. Here we consider each of the data requirements of the EwE model.

Biomass data

Differences in catchability between the different gears used as well as differences in the spatial and bathymetric distribution of samples taken between the three key datasets (German, SAMS, and FRS) resulted in serious challenges in obtaining reliable and comparable biomass estimates for fish species. The estimates obtained from German trawl surveys and FRS surveys were comparable, but those obtained from SAMS surveys were vastly different. For this reason, when fitting the models, only German and FRS data were used in the statistical procedures, and SAMS data were only shown for comparison (Figure 3). The differences in the biomass estimates between the 1970–1980s and 2000s led to the model providing an interpolation between the German surveys (1974–1986) and the FRS surveys (2001–2007). The large changes between the biomass estimates by the German trawl surveys and FRS for groups such as intermediate sharks, Baird's smoothhead, skates and rays, black scabbardfish, *Coryphaenoides*, ling, and blue ling could therefore be either perceived (as a result of differences in gear catchability) or real (owing to fishing or trophic changes).

One way to address these differences is to look at other estimates of biomass, such as the catch per unit effort (cpue) for ling, blue ling, orange roughy, *Coryphaenoides*, scabbardfish, and forkbeard given in the WGDEEP report (ICES, 2008c) or the spawning-stock biomass for blue whiting from the ICES assessments (ICES, 2007a). The cpue of ling in Division VIa (ICES, 2008c) and the spawning-stock biomass of blue whiting (ICES, 2007a) show opposite trends from what is predicted in Figure 3. The model predicts an increase in ling biomass because of the reduction in ling catches (Figure 2), and in fitting the model the biomass increased as a result of the increase in biomass in the FRS surveys (Figure 3). Similarly, the model predicts a decline in blue whiting caused by the increase in blue whiting catches (Figure 2). It might be more useful to use the cpue trend for ling in Division VIa to fit future models and to use the fishing mortality estimated for blue whiting by the ICES survey (ICES, 2007a). However, this might disregard any changes in their distribution, because both the cpue trend and the fishing mortality trends are for larger areas than the area modelled here—Division VIa, and restricted to depths between 400 and 2000 m.

Blue ling, orange roughy, greater forkbeard, and *Coryphaenoides* cpue trends in the WGDEEP report cover the period 1990–2007, with both the cpue trends and the biomass estimates for the 2001–2007 period being relatively stable for all four species, similar to that seen in Figure 3. However, the *Coryphaenoides* biomass estimates for Divisions Vb, VI, and VII combined showed a much more marked decline from 1996 to 2007, while our model predicts a decline from 1996 to 2002 then an increase from 2002 to 2003. As the biomass estimates in the WGDEEP report (ICES, 2008c) include a larger area, it is not possible to distinguish whether this difference is real or the model predictions are wrong. Finally, the reduction in scabbardfish cpue seen from 2001 to 2007 in the WGDEEP report is also reproduced by the FRS data and, to some degree, by the model (Figure 3).

For some species, the biomass estimates calculated from the trawl survey estimates that we used here were much lower than the reported landings, and subsequently the estimated catches, because the catchability coefficients were not available for all species. As studies of catchability and comparisons between gear types had been made, the biomass estimates produced from the German trawl survey estimates could be adapted for catchability using informed judgement, such as personal observations on the reaction of deep-sea fish to submersibles by one of the authors (JDMG), in fitting the model. Adjustments had to be made for large demersals (hake and tusk), skates and rays, ling, greater forkbeard, Kaup's arrowtooth eel, and megrim, all of which were not well sampled by the German trawls.

Issues concerning catchability were compounded for aggregating species where the biomass estimates varied substantially over time. The biomass estimated for orange roughy in 1974 was significantly higher than the previous estimates made of virgin stock biomass (Basson *et al.*, 2002) and orders of magnitude larger than any other year (Figure 3), and was therefore considered unreliable. Similarly, the biomass estimates for blue whiting varied quite substantially in the FRS estimates, probably because of their seasonal schooling behaviour and low efficiency of capture by bottom trawls (Figure 3). The biomass of blue ling estimated from German trawl data was also very low, and even previous estimates of virgin stock biomass for this species (Basson *et al.*, 2002) were too low to fit the model. For aggregating species such as orange roughy, Argentine, blue ling, and blue whiting, it was necessary to allow Ecopath to estimate their biomass.

Variation in the spatial distribution of samples both within and between datasets also resulted in spurious estimates of biomass for some species. For example, the estimates obtained for Baird's smoothhead from German trawl data for 1974 and 1975 varied between ~209 000 t and 15 000 t, respectively. These values are unlikely to reflect true variation in species biomass, so cast doubt on the reliability of biomass estimates for this species. In such cases, assumptions had to be made, again using informed judgement, as to what the true biomass was. For other species, no such judgement could be made and Ecopath was allowed to estimate the initial biomass based on all other data in the mass-balanced equation. This was the case for mesopelagic fish, benthopelagic fish, benthic fish, and chimaeras.

It was necessary to attempt to compensate for the difference in spatial distribution and depth stratification between the three key surveys and between years within the German trawl dataset. The 1981 German trawl survey had the broadest coverage along the VIa continental margin but critically also incorporated two deep hauls (<1300 m), allowing comparison with SAMS and FRS datasets. It was used as the reference for apportioning biomass to unsampled depth zones in other years.

An additional consideration arose from the area contained within the constructed model. The model contained the area within VIa between 400 and 2000 m depth. Many species occur and are fished both above and below 400 m. Examples of such species are blue whiting, monkfish, and tusk. Assumptions needed to be made as to the proportion of the biomass of these species (and landings taken) within the model area.

It is not possible for an ecosystem model to reproduce the trends in a stock that is much larger than the area modelled. To fit the model, the algorithm minimizes the sum of squares difference between the model estimates and the data in each time-step by

looking at all the different time-series, including biomass and catches for all species, and will therefore not be biased by large fluctuations in one species only. Ecopath with Ecosim works best when there is a long time-series of fishing mortality to drive the model, and a long time-series of catch and biomass to fit the model too. Unfortunately, neither of these two factors is present for pelagic species such as argentine and blue whiting. If the dynamics of blue whiting and argentine were the main focus of this study, a more pelagic-orientated model would have been constructed.

Production and consumption estimates

For production estimates, it was relatively easy to use natural mortality rates as proxies. These data were available for most species. Estimates of production and consumption made using the empirical relationships of Pauly (1980) and Palomares and Pauly (1998) for fish given in Fishbase (Froese and Pauly, 2000) may be unreliable because these empirical relationships have not been demonstrated for deep-sea fish, which can have very different body morphologies and biochemical compositions. For many of the invertebrate species, assumptions had to be made based on published production and consumption estimates for similar species in similar ecosystems. This is unfortunately often the case in the production of EwE models and not a unique problem to the deep sea. Usually, these estimates were vetted when the model was fitted to time-series data because it was often not possible for the model to fit the data with insufficient primary producers or an overabundance of secondary producers.

Trophic data

Dietary data available for the species modelled in this region were fairly extensive. The collection of stomach contents by SAMS was opportunistic, however, and may not always be representative of the size range in the catch. This inevitably will lead to error in representing the trophic relationships between species, which is a problem for all trophic models and not restricted to the deep-sea ecosystem. Error may also have arisen from the conversion of prey numbers to biomass, but again this is not a problem restricted to the deep-sea ecosystem. For many of the top predatory species (cetaceans, monkfish, sharks, blue ling), it was necessary to assume trophic links with other top predators resulting from consumption of juveniles. The validity of these assumptions must be considered when interpreting outputs from model scenarios.

Landings

Landings estimates in both deep-water and other fisheries are often uncertain as a result of misreporting, non-reporting, etc. In this model, landings have been underestimated because no information on the landings of the deep-sea gillnet fishery is available. Underestimated landings (and discards) will lead to underestimated starting biomasses in the instances where Ecopath was required to calculate a biomass, such as for argentine, blue ling, ling, etc. (Supplementary Material, Table S1).

For species that occur both above and below 400 m (specifically large demersals and blue whiting), catch rates by depth were used to calculate the landings below 400 m (ICES, 2005b, 2008b, c).

Discards

With very few published data available on discards from deep-water fisheries, this area of the model perhaps required the most assumptions to be made and as a result may be a substantial source of error in the model. Rates of discarding and the species

composition of discards vary with depth. Allain *et al.* (2003) found that the mean total discarding rate for grenadier rose significantly from 25.1% in the 800 m depth stratum to 55.4% in the 1000 m stratum and non-significantly to 60.9% in the 1200 m stratum. However, Lorance *et al.* (2008) found no evidence of increased discarding with depth and no depth effects on size distribution of discards in later discard surveys. Observations of the number of species discarded in the deep-water trawl fishery ranges from 25 to 85 (Connolly and Kelly, 1996; Blasdale and Newton, 1998; Dupouy *et al.*, 1998). This variation is again likely to be related to changes in the depth of fishing. No variation in the rate of discarding by depth band was incorporated into the model. It is highly likely that temporal changes in rates of discarding and species composition of discards have also occurred over the life of the fishery and thus the Ecosim model. For example, fishing activity changes relative to factors such as seasonal abundance of the target species and the long-term requirements of the market. This will affect the fishing depth and hence the patterns of discarding. In addition, the impact of fishing activity on fish populations over time will have resulted in changes in catch composition and subsequently discarding. With no information available on the direction and magnitude of temporal changes, the species composition of discards was assumed to be constant, as was the relationship between biomass of discards and biomass of the target species landed (e.g. roundnose grenadier or tusk).

It is likely that rates of discarding have increased over time, given that the fishery has expanded into deeper water and target species stocks have declined (Basson *et al.*, 2002). The ratio of landed target species biomass to discard biomass was calculated for 1995, and this ratio was used to estimate discards from 1974 to present. Discard estimates are therefore at best likely to be an overestimate for the first 20 years of the Ecosim model, and possibly an underestimate for the final 11 years.

The absence in the model of estimates of discards (and landings) from the deep gillnet fishery is also a potentially serious source of error. Discard rates from this fishery are thought to be high as a result of the long soak times (Hareide *et al.*, 2005). Data from the Norwegian Coastguard suggest that between 54 and 71% (average 65%) of the monkfish catch per deployment (average length of gillnet per deployment is 19 km) is discarded (Hareide *et al.*, 2005). Rihan *et al.* (2005) suggested monkfish discard rates of 50%. However, a recent UK Government report (DEFRA, 2007), based on observer trips in the western gillnet fishery for monkfish, found that discard rates across the four grounds examined (Rosemary Bank, Lousy Bank, northwest and west Rockall Bank) were generally very low (except Rosemary Bank), accounting for <1% of the total catches of this species at each ground. Unpublished data from the Institute of Marine Research, Norway, suggest discard rates of between 20 and 70% in the ling fishery with gillnets on the Norwegian slope (Hareide *et al.*, 2005). Discards of blue ling in the western gillnet fishery for monkfish (DEFRA, 2007) were also generally high (12–60% of blue ling catch by numbers) because of the catch of this species being in poor condition on hauling. The deep gillnet fishery primarily developed in the 1990s (Hareide *et al.*, 2005). Its exclusion from the model increases the likelihood that the estimates of discards used for the last 11 years of the model 1995–2007 are an underestimate.

General comments

Ecosystem-based management is called for in all ecosystems and using the best available information in different modelling

techniques is the best chance there is to achieve it. Unfortunately, all techniques, whether single-species modelling or any other ecosystem-based technique, will also have many of the same problems with uncertainty based on the available data. Alternative techniques available for ecosystem-based assessments include minimal realistic models, such as multispecies virtual population analysis (MSVPA), which is useful for systems where the age structure of fish is well known (such as the North Sea) and where discards, uncertainty, environmental effects, and policy assessment can be included (Plagányi, 2007). Similarly, Object-oriented Simulator of Marine ecOSystem Exploitation (OSMOSE) is a spatial individual-based model that uses simple individual predation rules to model trophic interactions and includes environmental effects, non-target fish species and the policy assessments needed for ecosystem-based management (Plagányi, 2007). Another approach, Invitro, includes age and size structure, bycatch discards, and uncertainty testing for target species (Plagányi, 2007). Atlantis, a physical transport–biogeochemical process model that is coupled with efforts to evaluate potential methods and tools for ecosystem-based management, also incorporates bycatch, discards, non-target species, environmental effects, habitat-related process, migration, and policy exploration (Plagányi, 2007). Most of these techniques, however, have data requirements that are at least similar to or greater than EwE, given that most are age- or spatially explicit. In addition, MSVPA includes only a few species and excludes non-target species; OSMOSE does not include uncertainty, non-target species that are not fish, habitat-related process, and migratory species; Invitro does not handle non-target species well; and Atlantis is the most data-intensive-modelling approach, with data requirements including both physical processes and biogeochemical information (Plagányi, 2007). The increased data requirements make these techniques difficult to implement in a data-poor system such as the deep-sea system off the west coast of Scotland.

Ecopath with Ecosim does not necessarily have all the answers. The inability of Ecosim to deal elegantly with migratory species and the impact that biogeochemical process might have on the ecosystem needs to be studied further using other modelling techniques. In addition, the impact of environmental drivers and habitat on the ecosystem can be included in Ecosim and Ecospace, respectively, but needs more information on the ecosystem that is not currently available. Information on the impact that sea temperature might have on primary and secondary production can be included in Ecosim as an environmental driver, but without explicit empirical information of these interactions it was not included in this study. Similarly, migration is dealt with in more detail in Ecospace, but this technique requires information on habitat preferences, dispersal rates, and feeding rates in different habitats for each functional group in the model (Christensen *et al.*, 2008), which makes Ecospace as difficult to implement as the techniques mentioned above. However, Ecopath with Ecosim gives one way to constrain the possible biomass calculations by taking foodweb interactions into consideration, thereby constraining the possible biomass estimates of predators. Sufficient information is available to create an ecosystem model of the west coast of Scotland, provided the limitations of the dataset, and thus the model outputs, are fully understood. The model is plagued by the lack of information that most ecosystem models face, but the long time-series of biomass data decrease uncertainty in the possible results.

At various stages in the model construction, various assumptions had to be made, specifically concerning biomass estimates and dietary relationships of some fish species and most benthic

and pelagic invertebrates. This is often the case with ecosystem models based on fisheries data. However, it is a problem compounded for deep-sea systems where even less information is available. One of the biggest assumptions required in model construction was related to estimates of discards and reflects the near total lack of published information on discarding rates from deep-water fisheries.

Given the challenges surrounding data availability and the number of often quite critical assumptions that need to be made, it is prudent to ask what the benefit of using an ecosystem model is, such as Ecopath with Ecosim, to apply the ecosystem approach to these fisheries. The benefit is quite simply that they consider the ecosystem as a whole and highlight not only the direct effect of fishing on a target species (as in single-species models), but also the indirect effects of fishing on non-target species and on other fisheries. They also allow the development of hypotheses concerning predator–prey relationships that might not be obvious from single-species approaches.

Deep-water sharks provide a good illustration of the view that modelling approaches such as EwE can provide on the deep-sea ecosystem that single-species models cannot. The cpue of deep-water squalid sharks declined significantly in the French fishery in Subarea VI between 1991 and 1996 (Lorance and Dupouy, 2001). Surveys show that intermediate sharks have declined in abundance by an order of magnitude (Jones *et al.*, 2005), from 45 000 t in 1974 to 4400 t in 2004 (Figure 5a). The reason for this decline could be that the unregulated fishery has increased from 360 t in 1988 to a peak of 6500 t in 2001. During that time, however, the model predicted that the main prey species of intermediate sharks (cephalopods, Baird's smoothhead, blue whiting, and mesopelagic fish) have also changed in abundance. This is confirmed, to some degree, by the decline in biomass estimates of Baird's smoothhead and blue whiting (Figure 3). In most marine ecosystems, it is assumed that predators change their diet with the abundance of their prey, so in order for the model to fit the data given, the diet of most species changes with the changes in the proportion of their prey species. In Ecosim, the predators do not necessarily switch prey, but they do adapt their predation pressure to the most available prey. A prey-switching parameter has been instituted in Ecosim (Christensen *et al.*, 2008), but it can only be used if there is some empirical proof of it happening in the ecosystem.

The modelled abundance of the prey species of intermediate sharks changed substantially over the 30 years (Figure 5b), and the proportion of these species in their diet changed (Figure 5c). The total consumption of intermediate sharks, however, has declined because of the reduction in their biomass (Figure 5d). From the model it therefore seems that both targeted and non-targeted shark fishing has had an impact on the biomass of intermediate sharks. This is confirmed by many literature sources (Basson *et al.*, 2002; Jones *et al.*, 2005; Dulyv *et al.*, 2008; Gibson *et al.*, 2008, among others). The mixed bottom-trawl fishery impacts significantly on all shark species, including the targeted *Centroscygnus coelolepis* and *Centrophorus squamosus*, but also other species that are taken as bycatch then discarded. As these species live in waters deeper than 400 m, the mortality of discards is likely to be high (Gordon, 2001). In addition, longlining can be very selective and in some cases sharks are specifically targeted. The increase in shark extractions from this ecosystem, either by catches of targeted shark species (*Centroscygnus coelolepis* and *Centrophorus squamosus*) or by discarding of other intermediate-depth species such as *Deania calcea*, *Centroscygnus crepidater*, and *Apristurus* spp., have increased

their total mortality from their natural mortality rate of 0.14 year^{-1} to a rate of 0.58 year^{-1} (Figure 5a), which indicates a fishing mortality rate of 0.4 year^{-1} (Figure 4). This is way beyond the $0.15\text{--}0.25 \text{ year}^{-1}$ suggested for fishing mortality by García *et al.* (2008) for oceanic or deep-sea sharks and even higher than the 0.37 year^{-1} suggested as a fishing mortality that leads to extinction in continental shelf species (García *et al.*, 2008). The extinction risk of a species depends on the life history traits of the species, and as sharks are slow-growing, reach sexual maturity late, and have low fecundity (Dulvy *et al.*, 2008; García *et al.*, 2008), they will be especially vulnerable.

The survival of sharks, however, also depends on them having enough food to eat, which is why it is useful to look at the changes in the predation mortality estimated by the model. Based on the model, the diet of intermediate sharks may have changed over the past 35 years, with two of their main prey species, Baird's smoothhead (*Alepocephalus bairdii*) and blue whiting (*Micromesistius poutassou*), having declined over that time. These two species were also impacted extensively by fishing over that time (Figure 2). Specifically, the large blue whiting fishery that was in operation before the start of this study has decreased the biomass of this species from an estimated 500 000 t in 1974 to around 150 000 t (Figure 3) in the model (although the last year estimated by FRS was only around 20 000 t). Baird's smoothhead was never really targeted, but they are often caught when fishing for roundnose grenadier (*Coryphaenoides rupestris*), and there have therefore been significant discards since the late 1980s, which have decreased the biomass estimated for this species from around 90 000 t in 1974 to 32 000 t in 2007 (both estimated by the model and given by FRS, Figure 3).

According to the model there was probably some change in the prey composition of intermediate sharks during the period, with cephalopods becoming more important in their diet (Figure 5c). It is noticeable that although there are significantly more mesopelagic fish estimated by the model than cephalopods (Figure 5b), the model does not necessarily predict that the diet of intermediate sharks would include more mesopelagics, because cephalopods comprised the largest proportion of their diet at the start of the simulation (Figure 5c). Therefore, the model predicts that the intermediate sharks would preferentially take cephalopods, although there is a much higher biomass of mesopelagic fish. Our lack of knowledge of mesopelagic and cephalopod abundance in the deep sea, however, makes this result quite uncertain and unsubstantiated. If a switch from cephalopods to mesopelagics in the diet of sharks had been observed in nature it would have been possible to include this in the model with the prey-switching parameter. What is more certain, however, is that the two other main prey species of intermediate sharks, viz. blue whiting and Baird's smoothhead, have declined as a result of fishing and discarding, so intermediate sharks may have been forced to switch from these preferred prey to another group, either cephalopods or mesopelagic fish. This hypothesis can be tested by looking at stomach content analyses of intermediate sharks over time.

When a species runs out of food in its usual range, it might be possible for it to expand its range. The distribution of sharks in the deep sea is limited, however, by their physiology, with pelagic species being restricted to about 1500 m depth and most sharks being absent from areas deeper than 3000 m (Priede *et al.*, 2006). Therefore, sharks cannot move deeper to find food if their prey declines in the upper water column. Moving higher in the water column to find food would also be difficult, because

these species are often limited by preferential low temperature. Continued improvements in fishing gear and boat efficiency also mean that even if sharks were moving to below the 2000 m depth we have modelled here, these species would not be safe for long. Fishing at depths below 2000 m has its own problems, however, not least of which is the cost.

At present, there is a zero TAC for deep-water sharks on the west coast of Scotland. The main fishery in this area, however, is a mixed trawl fishery and it is not possible for deep-sea trawlers to target roundnose grenadier, monkfish, or black scabbardfish without taking some sharks as bycatch. The combined effect of the discards and reduction in the prey species of deep-water sharks may result in further decrease in abundance for bycatch species and more species on the IUCN Red List in future.

Conclusions

Ecopath with Ecosim is one of the tools available for ecosystem-based assessments of deep-sea fisheries and resources, and may form the basis for ecosystem management, including adaptive approaches. This technique is useful because it uses data similar to those used for most single-species stock assessments, but it combines these data with estimates of trophic information. It must be emphasized, however, that the modelling techniques need to be used appropriately. Ecopath with Ecosim has been misused in the past, by using the steady-state Ecopath model without fitting it to time-series, by using default settings for all parameters in Ecosim, and by using the model as a "black box" without understanding the model parameters. These practices should be avoided, so this study has used the best available data fitted extensively to time-series data. One of the main advantages of using Ecopath with Ecosim is that it points to the data gaps and collates information needed for other modelling techniques, such as Ecospace, OSMOSE, Invitro, and Atlantis, which can be used in future to answer questions that cannot be answered using Ecopath with Ecosim. In answer to the question "can we do ecosystem-based assessments and create a basis for ecosystem management?", the answer is yes, but there are still some gaps in the data.

This exercise has pointed to gaps in our knowledge of the west coast of Scotland deep-sea fishery, specifically on the catches made by gillnets, discarding practices, changes in diets, and good estimates of biomass over time. In addition, there is uncertainty in the vulnerability parameters estimated by the models, although these would probably be more believable if we had better data on biomass, catch, discards, and diets to which to fit the model. This exercise has shown the impact that fishing for both targeted and non-targeted shark species has had; this has increased the fishing mortality for sharks above the values suggested by García *et al.* (2008). In addition, the increased fishing mortality of both the sharks and their prey species have caused changes in the ecosystem that cannot at present be assessed with simpler approaches such as single-species models.

In conclusion, this model provides outputs that are relevant to the questions being asked of fisheries managers and gives indications of long-term effects of fishing that should be tested further through empirical studies. Future work should include the inclusion of environmental drivers on primary and secondary production, sensitivity analysis using the Monte-Carlo routine in Ecosim (for instance), and data gathering on age structure, spatial structure, habitat preferences, dispersal rates which can be used to parameterize an Ecospace, Invitro, OSMOSE, or Atlantis model.

Supplementary material

Supplementary material is available at *ICESJMS* online: Tables S1–S3.

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