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Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs

Fisheries Centre, University of British Columbia, Canada

ECOSYSTEM SIMULATION MODELS OF SCOTLAND'S WEST COAST AND SEA LOCHS

Edited by
Nigel Haggan and Tony J. Pitcher

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DIRECTOR'S FOREWORD

Modelling marine ecosystems is not that difficult and it certainly is useful. This document, devoted to a model of the west coast of Scotland, illustrates this very well. Here, the usefulness of the model is based on two features:

1. It demonstrates that one can not only account for the feeding relationships of all groups within such a complex system, but also account for the distribution in space of these same group, i.e., their habitat preferences;

2. It helps identify data gaps and researchable topics which would lead to a better understanding of the waters of western Scotland.

This model is the result of a very productive collaboration between the UBC Fisheries Centre and the Scottish Association for Marine Science.

The 'Next Steps' identified on pages 55-57 will hopefully lead to a continuation of this collaboration and further insights into the structure and function of the marine ecosystem of the west coast of Scotland.

Dr Daniel Pauly

Director, UBC Fisheries Centre
July 25, 2005.

ABSTRACT

Trophic flows of the west coast of Scotland (WCS) ecosystem (ICES zone VIa) for the period 1995 to 2000 were reconstructed using *Ecopath*. The *Ecopath* model is divided into 37 functional groups or trophic compartments ranging from phytoplankton and detritus to marine mammals and seabirds, and including harvested species of pelagic, demersal, and benthic environments. We present here details of the input data (biomass, production, consumption, catch, and diet composition) for each compartment used for modelling. This work represents the first ecosystem model for the west coast of Scotland and is the result of an important assemblage of data on the biological characteristics of species occurring in the zone VIa.

Fisheries data for 1995-2000 for all commercial species was collated from annual statistics provided by the appropriate fishing country. All fisheries combined are estimated to collect 1.36 tons of marine organisms per square kilometre per year, approximately 70% of what might be expected from ICES data for area VIa. Preliminary estimates of discards total 0.51 t•km^{-2} for a total extraction of 1.87 t•km^{-2}, although the discard figure is thought to be low. The catches were divided into 8 gear types: demersal trawl, beam trawl, midwater trawl, dredge, purse seine, lines (handline and longline), creels and pots and miscellaneous gear types (Table 4).

Simple tests suggest that the *Ecosim* model for the west coast of Scotland is behaving in a reasonable manner under dynamic simulations. We assign the critical prey-predator vulnerability parameters using a short-cut method which has been validated by previous work, and use three procedures to test the model's dynamic performance. 1.) An equilibrium analysis determines for each commercial functional group the long-term catch rate and biomass level that would result under varying degrees of fishing mortality. 2.) Pulse fishing simulations reveal how quickly the ecosystem can recover from disturbance. 3.) All fishing pressure is removed from the dynamic simulation to show the recuperative potential of commercial groups and secondary trophic effects throughout the ecosystem. Much more can be done to improve the dynamic behaviour of *Ecosim*, but the model appears to be robust and free from instabilities.

Preliminary spatial simulations were set up by mapping the 31,085 km^{-2} model area into 450 cells of 69.1 km^{-2} each (nominally square, with 8.3 km sides). An approximate coastline was sketched in on the map, avoiding isolated bays at the edge of the model area, with 335 marine cells. Four habitats were allocated using depth zones 0-10 m (representing 19% of total model area); 10-100 m (46%); 100-200 m (28%); and 200–1000 m (2%). Primary production levels were allocated for each model square from the Sea Around Us database. The 37 functional groups and 8 fisheries in the model were allocated to their preferred habitats in suitable combinations of the 4 habitat categories. All of these allocations were performed in a preliminary fashion, and need to be validated with local data in future refinements to the model. Likewise, for each model group in its preferred and non-preferred habitats, using information from similar *Ecospace* models elsewhere, we adjusted default dispersal rates in km•year^{-1}, the relative dispersal rate in bad habitats, the relative vulnerability to predation in bad habitats, and the relative feeding rate in bad habitats. Fishery management zones, termed "MPAs" in the software, were set up as examples; results may also be obtained in separate designated zones. The section concludes with a demonstration 50-year spatial simulation of the west coast of Scotland under default assumption of no changes to the existing fishing effort. Before attempting to analyse realistic spatial management scenarios, the present *Ecospace* model of the west coast of Scotland should be used in a diagnostic mode by running trial scenarios with large no-take zones, under progressive annual increases and decreases in fishing power, in order to refine the habitat-related dispersal parameters and the underlying *Ecosim* and *Ecopath* model structure.

The preliminary *Ecopath*, *Ecosim* and *Ecospace* models will benefit from more input from local experts. Workshops with scientific and lay experts on individual species fisheries and other areas would be highly recommended. The resulting models would then lend themselves to a number of research priorities identified in the course of the project, some of which are identified at the end of the report.

PREFACE

Scotland's coastal waters (Figure 1) comprise a wide range of habitats from deepwater corals to coastal seagrass beds and serpulid reefs in the sheltered waters of long fjords or sea lochs. Increasing pressure from fisheries, oil and gas, aquaculture and other use require an ecosystem approach that can evaluate the cumulative effects of environmental change and anthropogenic pressure over time. This pressure is reflected in a EU proposal to set up 'Regional Advisory Councils' to implement and oversee 'sustainable management of fish stocks' in an overall approach based on 'ecosystems and the precautionary principle': www.europa.eu.int/comm/fisheries/doc_et_publ/factsheets/legal_texts/docscom/en/com_03_607_en.pdf

Intensive marine fisheries in what is now the UK appear to have started around AD 1000 (Barrett *et al.* 2004). Concern about overfishing has grown in recent years, with some disquieting information about loss of genetic diversity (North Sea cod, Hutchinson *et al.* 2002), the number of effective breeders in a population *vs* total number of females (Hauser *et al.* 2002) and new insights into the importance of age as well as size in determining larval survival (Berkeley *et al.* 2004). These findings and concern about impacts of fishing on marine ecosystems in the UK the prompted the Royal Society to call for sharp reductions in fishing pressure (Blundell 2004).

The *Ecopath* approach to whole ecosystem modelling is gaining wide acceptance with ~1,250 users in 100 countries (www.ecopath.org). The first *Ecopath* model of the French Frigate Shoals in Hawaii was constructed by Polovina (1985). The approach was further developed at ICLARM (Christensen and Pauly 1992) and later, dynamic and spatial models (*Ecosim*, Walters *et al.* 1997 and *Ecospace*, Walters *et al.* 1998) were developed at UBC Fisheries Centre enabling the posing of 'what if?' questions and assessment of the effects of area closures, artificial reefs (Pitcher *et al.* 2002a and b and 2000), the effect of climate shifts in relation to fishing (Stanford and Pitcher 2004) and other spatial interventions.

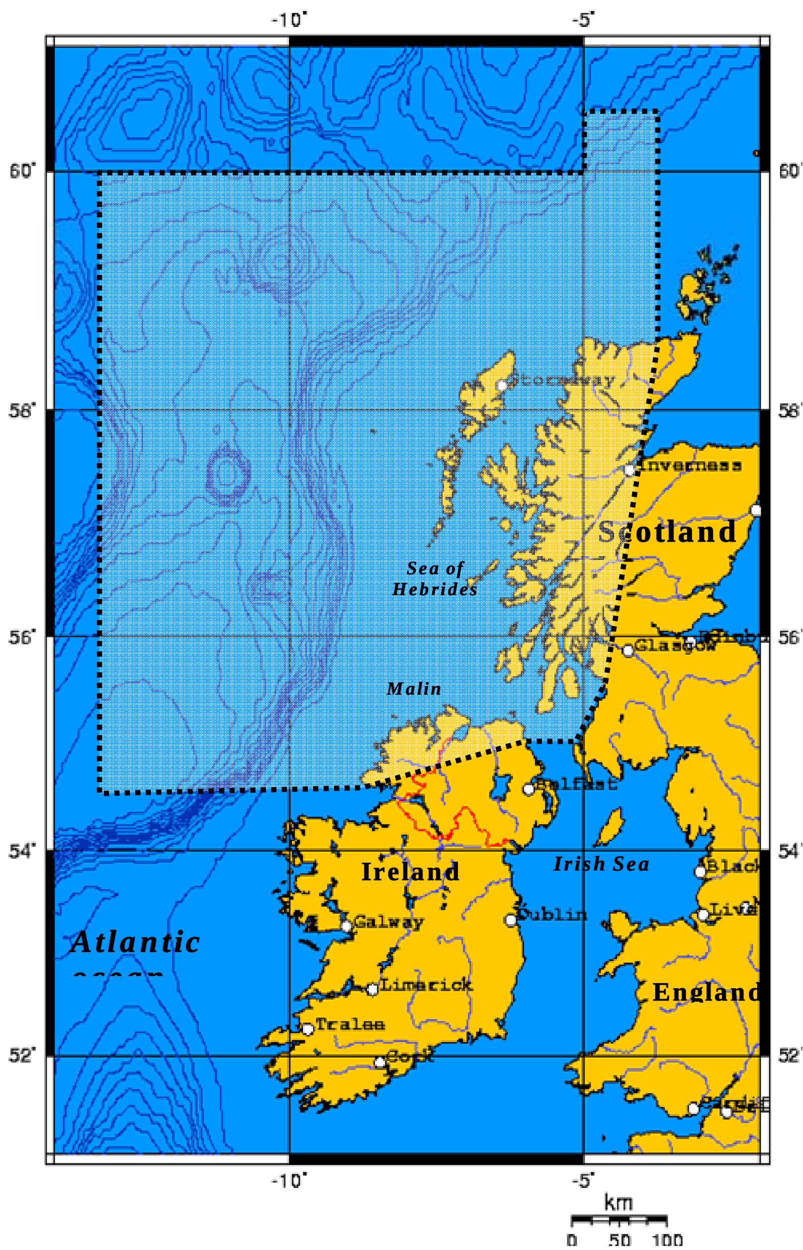

Figure 1. The Scottish West Coast with delimitation of ICES zone VIa; The approximate area of Via is 236,153 km-2.

In one of the most advanced uses to date, *Ecopath with Ecosim* (EwE) has been used to analyse the interplay of killer whale predation, competition for food, fisheries and long term environmental interactions and provide a convincing explanation for the decline in abundance of Steller sea lions in the Aleutian Islands and for their parallel increase in SE Alaska (Sylvie Guénette, Research Associate UBC Fisheries Centre, pers. comm.).

The previous examples represent the results of a substantial investment in methodology development and, in the case of the sea lion example, two full years of research by two Research Associates. Although less sophisticated, the preliminary Scottish EwE models are early charts of the west coast of Scotland (WCS) ecosystem. Like their mediaeval counterparts, they have large white areas representing the unknown. Where there are signs saying 'Here be Dragons', we have tried to give a rough idea of the size and species of dragon and how, in time, local heroes might contrive to slay them.

This report is organized as follows:

The report opens with a ***Model Structure and Balancing*** section that describes the study area, major oceanographic influences and reason for choice of model period. Data sources are discussed. Major commercial species and functional groups in the ecosystem are described in terms of biology, distribution, biomass, production, and consumption ratios and diet composition. Model parameters for mass-balance are presented.

The ***Fisheries in the Model*** section identifies eight main fleets/gear types. The total estimated annual catch of 1.36 t•km^{-2} is reasonably close to the average from ICES area VIa, that includes the west coast of Scotland. Catch is broken down by sector, with preliminary discard estimates, where available, of about 0.5 t•km^{-2}.

A ***Model Characteristics and Performance*** section discusses the west coast of Scotland model relative to related models in terms of treatment of main species and their prey, estimates and causes of mortality and the reliability of the source data. The section concludes with a discussion of uncertainty and a comparison with an English Channel model (Stanford and Pitcher 2004).

A ***Dynamic Simulations with Ecosim*** section presents 50-year diagnostic simulations that test biomass response. Vulnerability settings are evaluated under 'standard' fishing rates and under more precautionary fishing values used in 'Back to the Future' simulations. A ***Spatial Simulations using Ecospace*** section presents a preliminary spatial model that links biomass changes to primary production and habitat by depth zone and fisheries.

Concluding ***Discussion and Conclusions*** and ***Next steps*** sections identify priority areas for model improvement, ground truthing and application to particular research questions. A major Back to the Future project to assess productive potential based on 1920s data and future conditions is outlined.

MODEL STRUCTURE AND BALANCING

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Abstract

Trophic flows through the entire west coast of Scotland ecosystem (ICES zone VIa) were reconstructed using the *Ecopath* approach. The ecosystem model is divided into 37 functional groups or trophic compartments ranging from phytoplankton and detritus to marine mammals and seabirds, and including harvested species of pelagic, demersal, and benthic environments. We present here details of the input data (biomass, production, consumption, catch, and diet composition) for each compartment used for modelling. This work represents the first ecosystem model for the west coast of Scotland and is the result of an important assemblage of data on the biological characteristics of species occurring in zone VIa.

Introduction

Scotland's west coast waters (Figures 1, 2 and 3) form part of International Council for the Exploration of the Sea (ICES) area VIa and include the Sea of Hebrides and part of the Malin Shelf (McKinley *et al.* 1981). The main hydrographical influence is the Slope Current (SC) that flows along the continental slope bringing warm North Atlantic water onto the shelf. Water also flows in from the Irish Sea and from the Clyde Sea through the North Channel, forming the Coastal Current (CC). Water generally moves northwards in both currents. In summer, a pronounced front to the west of Islay, named the Islay Front, represents the boundary between water from the coastal current and shelf water. Residual currents of 20 cm•s^{-1} have been recorded parallel to this front. This region shows a significant increase in phytoplankton density, likely associated with an increase in nutrient availability (Simpson *et al.* 1979).

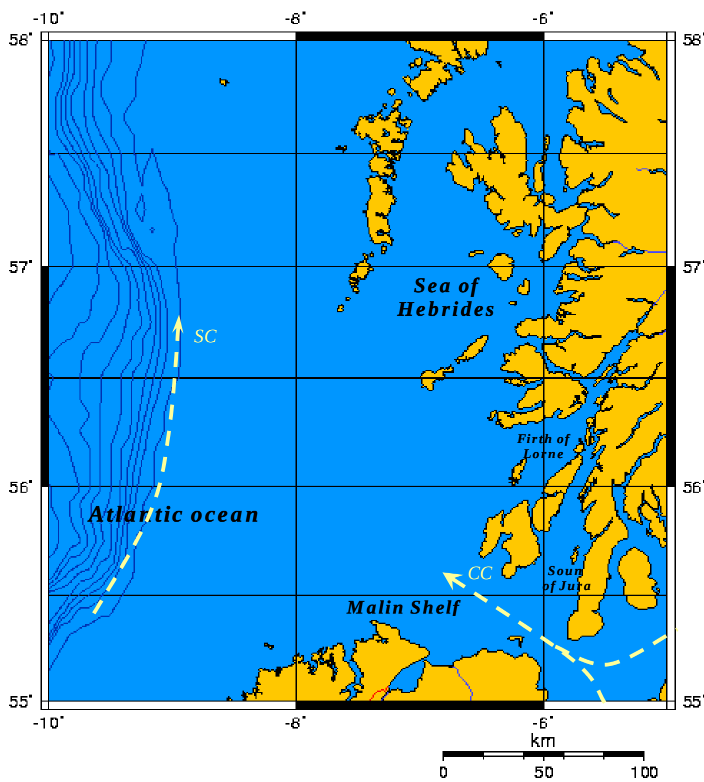

Figure 2. Major currents and sea lochs in the west of Scotland. CC = Coastal current; SC = Slope current.

Because of the complex fjordic nature of the west coast of Scotland there is also a substantial freshwater input from the numerous sealochs, notably the Firth of Lorne sealoch system (McKinley *et al.* 1981). Temperature and salinity vary across the region depending on the influence of each of the water sources. Average minimum temperature recorded at a shallow inshore site in the Firth of Lorne between 1995 and 2001 was 6.0°C (late February to early March) with an average summer (August - September) maximum of 14.4°C (Magill and Sayer 2004). Inshore shallow subtidal sites are particularly influenced by freshwater input with salinities as low as 12‰ recorded in the Firth of Lorne (Sayer *et al.* 1993). Offshore, the north Atlantic influence is greater with a winter minimum of 7.5°C and a summer maximum of 13°C. Shelf water is generally more saline than the coastal water, particularly at

Morissette, L. and Pitcher, T.J. 2005. Model Structure and Balancing. *In*: Haggan, N. and Pitcher, T.J. (eds) Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs, pp 5-24. UBC Fisheries Centre Research Reports 13(4), 67pp.

Figure 3. Highlighted area of map shows the region of western Scotland included in the ecosystem model: the marine area shown is approximately 31085 km^2.

depth, with salinities of approximately 35‰ (Ellet 1979).

The bathymetry is complex, largely because of scouring of many of the channels and sealochs by ice (JNCC 1997). Away from the coastal and island area, the seabed is generally between 40-80 m deep, with a number of exceptions, such as the Sound of Jura and Loch Linnhe where depths can reach over 200 m (JNCC 1997). Moving westward from the inshore waters of the mainland and islands, the depth then increases to 200-500 m towards the shelf edge.

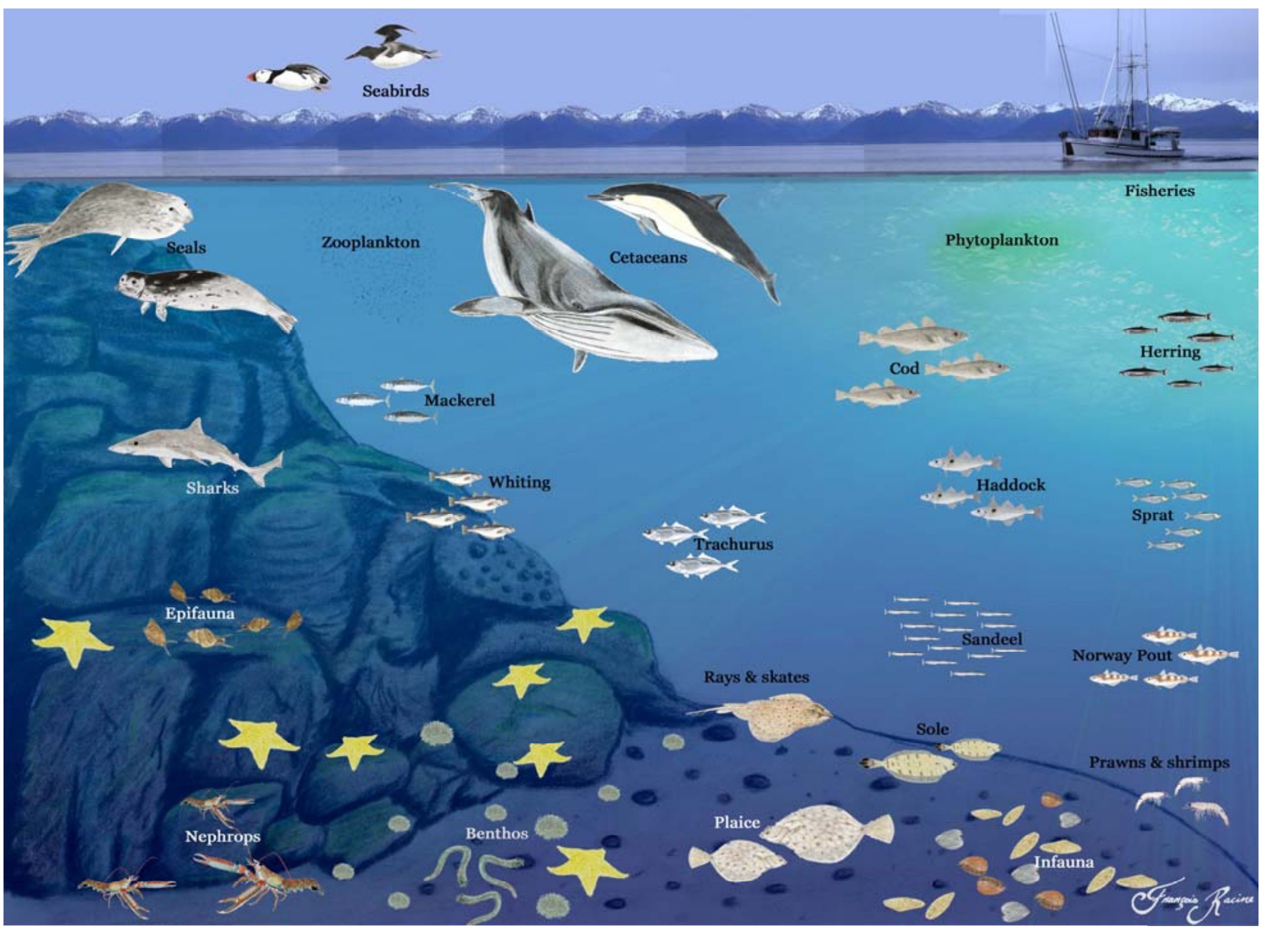

Figure 4. West coast of Scotland ecosystem drawn by François Racine and designed by Lyne Morissette.

The west coast waters of Scotland support a wide range of habitats, plant and animal communities from shallow water sea grass beds to deep coldwater corals (Lophelia pertusa). In particular, the physical environment within the sea lochs gives rise to a number of important marine habitats (Serpulid reefs for instance). The coastal waters support a number of rare and scarce marine species (JNCC 1997). Cetaceans are particularly abundant in offshore waters compared to other regions of the UK with a total of 23 species recorded (Shrimpton and Parsons 2000), eight of which are observed regularly (JNCC 1997). This is likely caused by the close proximity to the continental shelf edge where larger cetaceans are more abundant.

Table 1. Functional groups in the *Ecopath* model of western Scotland, and main species *per* group. Groups that may be split by diet type in later models are noted.

Group Name	Main species
Seals	*Halichoerus grypus, Phoca vitulina*
Cetaceans	*Balaenoptera acutorostrata, Orcinus orca, Globicephala melaena, Phocoena phocoena, Lagenorhynchus albirostris, Grampus griseus, Delphinus delphis, Tursiops truncates* (To be later split by diet type)
Seabirds	*Uria aalge, Fratercula arctica* (To be later split by diet type)
Halibut/turbot/brill	*Hippoglossus hippoglossus, Reinhardtius hippoglossoides, Psetta maxima, Scophthalmus rhombus*
Whiting	*Merlangius merlangus*
Other demersals	*Hippoglossoides platessoides, Glyptocephalus cynoglossus, Platichthys flesus, Pollachius pollachius, Trisopterus minutus, Merluccius merluccius, Molva molva, Lophius* sp.
Sharks	*Scyliorhinus caniculus, Scyliorhinus stellaris, Galeorhinus galeus, Mustelus mustelus, Squalus acanthias, Cetorhinus maximus* (To be later split by diet type and size)
Rays/Skates	*Raja batis, Raja clavata, Raja naevus*
Cod	*Gadus morhua*
Saithe	*Pollachius virens*
Other pelagics	*Micromesistius poutassou*
Crabs/lobsters	*Cancer pagurus, Necora puber, Homarus gamarus, Munida rugosa*
Gurnards	*Chelidonichthys lucernus, Aspitrigla cuculus, Chelidonichthys gurnardus*
Haddock	*Melanogrammus aeglefinus*
Inshore fish	*Labridae* sp. and all the juvenile gadoids and flatfish (To be later split)
Salmo	*Salmo salar, Salmo trutta trutta*
Mackerel	*Scomber scombrus*
Trachurus	*Trachurus trachurus*
Plaice	*Pleuronectes platessa* L.
Sole	*Solea solea, Solea lascaris, Buglossidium luteum, Microchirus variegatus*
Nephrops	*Nephrops norvegicus*
Norway pout	*Trisopterus esmarkii*
Cephalopods	Sepiolidae, Architheutidae (To be later split by diet type)
Sandeel	*Ammodytes tobianus, Ammodytes marinus, Hyperoplus lanceolatus*
Sprat	*Sprattus sprattus*
Herring	*Clupea herangus*
Echinoderms	Sea stars, urchins and crinoids
Other benthic inverts	*Pecten maximus, Aequipecten opercularis*
Prawns/shrimps	*Crangon crangon, Crangon allmanni, Palaemon elegans, Palaemon serratus, Pandulus montagui*
Euphausiids	Local krill species
Large zooplankton	Chaetognaths, hyperiid amphipods, Jellyfish (cnidarians and ctenophores), mysids, tunicates >5 mm and ichtyoplankton.
Polychaetes	Local ragworms
Small zooplankton	*Calanus finmarchicus, Oithona similes,* meroplankton and tunicates < 5 mm (To be later split by diet type)
Epifauna	*Bittium reticulatum, Gibbula cineraria, Porcellana longicornis, Rissoa parva, Idotea* spp.*, Tricolia pullus, Xantho* spp.*, Musculus discors*
Infauna	*Golfingia sp., Mysella bidentata, Lucinoma borealis, Hiatella arctica*
Phytoplankton	Mixture of autotrophic and mixotrophic organisms including: cryptophytes, diatoms, dinoflagellates, prasinophytes, and Spirotrichea

Diversity within fish species in the region is not as high as the rest of the UK. However, the abundance of many species increases during the summer months (Magill and Sayer 2002). This is, in part, caused by the inshore movement of juvenile gadoids (Magill and Sayer 2004), flatfish (Zijlstra 1972) ands other species, which utilise shallow inshore environments as nursery areas. In summer, migratory fish such as mackerel (Scomber scombrus) and horse mackerel (Trachurus trachurus) head northwards along the shelf waters.

The *Ecopath* model

An *Ecopath* model divides the system into a number of individual species and 'functional groups' (Table 1.). Species of high importance (e.g., commercial or sport fishery, keystone, charismatic, cultural) are usually assigned to an individual group. Individual groups can, in turn, be split into adult and juvenile groups where there are important differences in ecology and diet. Figure 4 represents the west coast of Scotland ecosystem.

Model period and data sources

The model period is 2000-2004, a time of relatively constant biomass for major commercial species (Fisheries Research Service, 2003) and the time when the greatest amount of fish diet data were available. To the extent possible, input data were obtained from local experts. However, information on several groups was sparse or hard to find for the area and period studied. These values were thus taken from the literature or from other models.

Species description

Functional groups were based on individual species of commercial significance as predator or prey or groupings of ecologically or taxonomically related species. Some groups such as large pelagic feeders and large demersal feeders are aggregated on the basis of similar size and ecological role (Table 1). Groups may be split and revised in later versions of the model as noted. Each functional group of the ecosystem is described in the following section. For each group, biomass, P/B, Q/B and ecotrophic efficiency (EE) are presented, either as estimated by mass-balance in the model or as input parameters, in Table 2 which also shows the estimated (non-integer) trophic levels. The complete diet matrix for the model, after adjustment during balancing, is detailed in Appendix Table 1.

Table 2. Parameters of the balanced *Ecopath* model of the west coast of Scotland. Values in shaded cells were estimated by the mass-balance procedure; other values are inputs described in the next section.

Group name	Trophic level	B ($t \cdot km^{-2}$)	P/B ($/year^{-1}$)	Q/B ($/year^{-1}$)	Ecotrophic efficiency	P/Q
Seals	4.99	0.185	0.070	12.000	0.800	0.006
Cetaceans	4.42	0.027	0.090	6.775	0.008	0.013
Seabirds	4.07	0.005	0.800	53.500	0.800	0.015
Halibut/turbot/brill	4.25	0.269	0.350	1.800	0.800	0.194
Whiting	4.36	2.556	0.700	2.400	0.883	0.292
Other demersals	4.16	3.979	0.770	2.567	0.933	0.300
Sharks	4.14	0.682	0.160	3.000	0.926	0.053
Rays/Skates	3.86	1.400	0.480	1.450	0.798	0.331
Cod	3.94	2.309	0.750	3.797	0.851	0.198
Saithe	3.97	0.249	0.870	4.023	0.915	0.216
Other pelagics	3.8	4.326	0.869	2.895	0.923	0.300
Crabs/lobsters	3.8	0.239	4.500	30.000	0.900	0.150
Gurnards	3.72	0.150	1.400	4.667	0.723	0.300
Haddock	3.71	0.716	1.000	4.000	0.800	0.250
Inshore fish	3.6	0.207	5.000	16.667	0.900	0.300
Salmo	3.57	0.039	0.800	3.570	0.800	0.224
Mackerel	3.37	0.835	1.021	3.950	0.950	0.259
Trachurus	3.24	1.873	0.700	2.900	0.805	0.241
Plaice	3.45	1.637	0.975	3.420	0.792	0.285
Sole	3.38	0.456	0.800	2.700	0.869	0.296
Nephrops	3.32	2.200	3.000	10.000	0.497	0.300
Norway pout	3.23	0.395	2.000	7.000	0.900	0.286
Cephalopods	3.19	0.386	3.000	10.000	0.835	0.300
Sandeel	3.23	0.876	3.000	10.250	0.800	0.293
Sprat	3.15	1.435	1.900	8.500	0.800	0.224
Herring	3.15	3.609	1.800	7.000	0.818	0.257
Echinoderms	3.00	3.945	4.000	16.000	0.920	0.250
Other benthic inverts	2.67	7.306	6.000	24.000	0.950	0.250
Prawns/shrimps	2.47	16.312	3.000	12.000	0.917	0.250
Euphausiids	2.26	2.317	9.000	36.000	0.862	0.250
Large zooplankton	2.05	6.288	10.000	35.000	0.879	0.286
Polychaetes	2.04	10.000	5.000	16.667	0.430	0.300
Small zooplankton	2.03	7.809	18.000	72.000	0.800	0.250
Epifauna	2.00	10.584	20.000	80.000	0.384	0.250
Infauna	2.00	1.561	20.000	80.000	0.731	0.250
Phytoplankton	1	80.000	70.000	-	0.182	-
Detritus	1	100.000	-	-	0.205	-

Seals

Background

Two species of pinniped occur on the west coast of Scotland. The grey seal (*Halichoerus grypus*) is the larger of the two, and is found in the Baltic Sea and across the north Atlantic Ocean (Thompson *et al.* 1996). Grey seals come ashore on remote islands and coastlines to give birth to their pups in the autumn, to moult in spring, and at other times of the year to haul out between trips to forage for food at sea. Female grey seals give birth to a single white-coated pup, which moults and is abandoned by its mother following a lactation period of about 3 weeks. According to the Special Committee on Seals (SCOS), about 39% of the global grey seal population is found in Britain, over 90% breed in Scotland, the majority in the Hebrides and in Orkney (SCOS 2003).

Common or harbour seals, (*Phoca vitulina*) in the UK represent approximately 40% of the world population of the European sub-species (SCOS 2003). Common seals are ubiquitous on the west coast of Scotland and throughout the Hebrides and Northern Isles. The total British population cannot be estimated accurately, as some animals are not seen during surveys. Common seals come ashore in sheltered waters typically on sandbanks and in estuaries but also in rocky areas. They give birth to their pups in June and July and moult in August. At other times of the year, common seals haul out in a pattern that is often related to the tidal cycle (SCOS 2003).

There is no hunt for any seal species in the Scottish waters.

Biomass

Information on seal abundance was available in the SCOS (2003) report from the Sea Mammal Research Unit of St. Andrews University in Scotland. Grey seal abundance was estimated at 45,500 individuals, and common seals at 15,575. Abundance was then multiplied by average weight to obtain the biomasses of the two populations. Grey seal weights were based on average male weight of 233 kg and female's weight of 155kg (both averaged for a final species weight, assuming a sex-ratio of 1:1. For common seals, the SCOS report gives a weight of 80-100kg (male or female), so an average value of 90kg was used in the model.

As much as 40% of the population may be in the water at any one time; the SCOS report cautions that abundances are absolute minima. Therefore, the biomass estimate is also a minimum value. To compensate for this, biomass was estimated by the model by using an ecotrophic efficiency (*EE*) of 0.8 (Morissette *et al.* 2003). This gave a biomass of 0.185 t•km^{-2} (Table 2), similar to what was found in the northwest Atlantic for grey and harbour seals (Morissette *et al.* 2003).

Production and Consumption

The *P/B* ratio was assumed to be equivalent to that estimated for Gulf of St. Lawrence populations (Morissette *et al.* 2003). In that model, *P/B* was estimated by dividing the pup biomass by the population biomass. The P/B ratios were 0.079 year^{-1} for grey seals and 0.071 year^{-1} for harbour seals. The average of both species (0.075 year^{-1}) was modified to 0.070 year^{-1} to balance for diet (Table 2). Based on an average of grey and harbour seals in the northern Gulf of St. Lawrence (Morissette *et al.* 2003), a *Q/B* value of 5.647 year^{-1} was obtained, assuming that seals do not live in the same area year round. However, according to SCOS (2003), a *Q/B* value of 16.22 year^{-1} was obtained for harbour seals and 10.34 year^{-1} for grey seals, resulting in an average of 13.29 year^{-1}. In order to obtain balance, a value of 12 was used in this preliminary model (Table 2).

Diet composition

Seal diet data were collected from local literature, adjusted to balance the model (Appendix Table 1). Diet composition was based mainly on Pierce and Santos (2003) for the Inner Hebrides. The main prey items were whiting, herring and other demersal fish (accounting for 87% of the diet). Sandeel was described as a dominant prey fish in the literature but their proportion was reduced in the model to obtain mass balance and to allow efficient *Ecosim* scenarios (Ainsworth, this vol.).

Cetaceans

Background

23 species of cetacean have been reported in the Hebridean waters (Shrimpton and Parsons 2000). The main whale species are minke whales (*Balaenoptera acutorostrata*), killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melaena*). Dolphins and other odontocetes are also present, the

most common being the harbour porpoise (*Phocoena phocoena*), white-beaked dolphin (*Lagenorhynchus albirostris*), Risso's dolphin (*Grampus griseus*), common dolphin (*Delphinus delphis*) and bottlenose dolphin (*Tursiops truncates*) (Shrimpton and Parsons 2000).

Although there is no reported whaling in that area of the British Isles, there are reports of cetacean by-catch in the west coast of Scotland fisheries. As these reports have yet to be accurately quantified, the model assumes that there is no fishing mortality.

Biomass

Cetacean biomass was taken from northern Gulf of St. Lawrence model densities (Morissette *et al.* 2003), then updated with data from the Hebridean Whale and Dolphin Trust (Shrimpton and Parsons 2000), resulting in a total biomass of 0.027 t•km^{-2} in the study area (Table 2).

Production and Consumption

No information was available on total mortality for cetaceans in the model area. Therefore, production is assumed to be equivalent to the biomass multiplied by natural mortality plus catch. Natural mortality for a combination of cetaceans of the northwest Atlantic (Morissette *et al.* 2003) was estimated to range between 0.074 (Tanaka 1990) and 0.075 (Ohsumi 1979), and mean annual catch used was 92 tons in the northern Gulf of St. Lawrence (Fontaine *et al.* 1994). This resulted in a total P/B of 0.077 year^{-1}. This value was later modified to allow the model to balance (Table 2). The daily consumption by species was calculated using:

$$R = 0.1W^{0.8} \tag{1}$$

where R is the daily ration for an individual in kg and W is the mean body weight in kg (Trites *et al.* 1997). Information on weight was taken from the Hebridean Whale and Dolphin Trust (Shrimpton and Parsons 2000). The resulting daily ration was then multiplied by 365 to obtain the annual rate of consumption for whales. This value was then divided by the biomass calculated above, giving a mean annual consumption of 6.78 t•km^{-2} (Table 2). This value is similar to that found in other models (Mackinson 2001; Morissette *et al.* 2003).

Diet composition

Diet for locally-present whale species was mainly based on a diets for whale and dolphin species in the northwest Atlantic (Morissette *et al.* 2003), and for the North Sea (Santos *et al.* 1999; 2001; 2002). As there are fewer sperm whales off the west coast of Scotland, cephalopods and mackerel are less important in the diet. These species were thus lowered in the diet of that group. The diet was also broadened to represent species or groups particular to Scottish waters. Therefore, the west coast of Scotland model shows that cetaceans mainly consume pelagic fish and large zooplankton (Appendix Table 1).

Seabirds

Background

The Joint Nature Conservancy Committee (JNCC); rates the west coast of Scotland of global importance for several seabird populations (JNCC 1997). Seabird populations and their breeding success around the British and Irish coasts are monitored on an annual basis, jointly by JNCC and the Royal Society for the Protection of Birds (RSPB). In 2002, the ICES Working Group on Seabird Ecology reported seabird population estimates within all ICES areas. For ICES Area VIa west of Scotland (within which our modelled area lies) a total of 1.2 million pairs of breeding seabirds were reported. Auks, predominantly the common guillemot (*Uria aalge*), razorbill (*Alca torda*) and the Atlantic puffin (*Fratercula arctica*) accounted for 51% of the total, while petrels (including fulmar, *Fulmarus glacialis*; storm petrel, *Hydrobates pelagicus*; and Manx shearwater, (*Puffinus puffinus*) accounted for 29% (ICES 2002). There are also many cormorants, shags and sea ducks. Breeding birds, gannets, gulls and terns also forage extensively in the area. There is no reported catch or anthropogenic mortality (by–catch in fishing gear or oil pollution) reported for the area. Consequently, no catch value is entered for that group in the model.

Biomass

The number of seabird breeding pairs in ICES Area VIa is taken from ICES (2002). The estimates reported were taken from the results of the Seabird 2000 survey of the UK coastline (http://www.rspb.org.uk/birds/sotukb/seabird2000.asp). This survey does not include estimates of nonbreeding birds, which are obviously an important part of the population. Two approaches were used to estimate the number of non-breeders. The first method (option 1 figures in Table 2) was to assume that non-breeders present at colonies represent 20% of the breeding pairs (Furness 1990). The second method (option 2 figures in Table 2) uses conversion factors from Tasker and Furness (1996). Option 1 resulted in a biomass density of 0.01334 t•km^{-2}, with option 2 resulting in a biomass density of 0.01261 t•km^{-2}. The latter biomass was too low to reach mass-balance in the *Ecopath* model, thus, we decided to let the model estimate the most plausible biomass by using an *EE* of 0.8 as in Morissette *et al.* (2003). The biomass calculated by the model was 0.05 t•km^{-2} (Table 2), which is between that found in the Gulf of St. Lawrence (0.001 t•km^{-2}; Morissette *et al.* 2003) and the North Sea (0.1 t•km^{-2}, Mackinson 2001).

<u>Production and Consumption</u>

Nestling estimates were derived from the 'Seabird Numbers and Breeding Success in Britain and Ireland' reports from 1997-1999 (Thompson *et al.* 1998; 1999; Upton *et al.* 2000). An average of fledgling rates from 1997, 1998 and 1999 was calculated for each species. Production for all seabird species in the region was estimated at 679.32 t giving an annual production rate of 0.0028 t•km^{-2} and a P/B ratio of 0.212 year^{-1}. As this value was too low to balance the model, a 'guesstimate' of 0.80 year^{-1} was used (Table 2). In the absence of appropriate consumption data for seabirds, the *Q/B* ratio was estimated. In other models, *Q/B* values of about 120 year^{-1} are used. However, this is was too much for the seabird group in the model, so a value of 53.5 year^{-1} was entered (Table 2).

<u>Diet composition</u>

Seabird diet was based on the North Sea model (Mackinson 2001), where it was based on a detailed quantitative analysis of stomach content of both shags and cormorants based on the number of stomachs containing each prey item (Rae 1969). These were used to represent the proportion of each item in the stomach of birds by constructing a composite 'bird' diet from an average of both species. The diet information was then updated with data from Morissette *et al.* (2003) representing the diet of 14 seabird species of the northwest Atlantic (Appendix Table 1).

Halibut, Greenland halibut, turbot and brill

<u>Background</u>

This group is composed of four flatfish species commonly caught as bycatch in the Scottish fishery (Fisheries Research Services, 2003). The halibut (*Hippoglossus hippoglossus*) is a bottom dwelling fish, found at depth between 100-1500 m, but predominantly in deeper water on a wide range of habitats, from rock and gravel to sand. To the west of Scotland halibut spawn along the edge of the continental shelf. After spawning, the adults may migrate to shallow water feeding grounds. Unlike many flatfish the halibut makes feeding forays into mid-water where it preys on a variety of fish. Juvenile halibut feed on crustaceans, cephalopods and small fish (Wheeler 1978).

The Greenland halibut (*Reinhardtius hippoglossoides*) is distributed throughout the north Atlantic, to a depth of 2,000 m. Off Scotland, Greenland halibut are found in the Faroe-Shetland Channel at depths of around 600 m (Gundersen *et al.* 1997). This species should not really be included in this group as it lives in much deeper water on the European side of the Atlantic.

UK waters represent almost the northerly limit of the turbot (*Psetta maxima*). Turbot thus become scarcer north of the Irish Sea and southern North Sea (Whitehead *et al.* 1986). Turbot prefer sandy bottoms, gravel or shell gravel from about 20 m to a depth of 80 m but occur occasionally on muddy bottoms or areas of mixed sand and rock (Tyler-Walters 2004).

The brill, (*Scophthalmus rhombus*) is the smallest species in this functional group. Like the turbot, brill are almost at their northern limit of their distribution in UK coastal waters (Wheeler 1978). Brill prefer sandy bottoms but are also found on gravel and mud (Wheeler 1978).

<u>Biomass</u>

In the absence of local data for these 3 species, biomass was estimated by the model at 0.27 t•km^{-2}, using an *EE* of 0.8 (Morissette *et al.* 2003) (Table 2).

Production and Consumption

The P/B estimate of 0.27 year^{-1} was taken from the North Sea model (Mackinson 2001), but later modified to 0.35 year^{-1} (Table 2) to balance the model properly. The Q/B value was averaged from the Q/B of halibut, turbot and brill in Fishbase (Froese and Pauly 2004), with the following biological criteria for all species: maximal weight of 8kg, water temperature of 10°C and type 4 tails for each fish (S. Magill, Scottish Association for Marine Science, pers. comm.). This gave a Q/B of 1.8 year^{-1} for this group (Table 2).

Diet composition

The diet composition of this group was taken from the North Sea model (Mackinson 2001), which, in turn, is based on McIntyeare (1952), and on the assumption that these species have stronger piscivory than other flatfish, although, especially as juveniles, they also eat polychaetes, macrobenthos, echinoderms, crustaceans and other invertebrates. The diet was then roughly adjusted for the west coast of Scotland model in order to represent the functional groups found in the system (Appendix Table 1).

Whiting

Background

Traditionally, whiting (*Merlangius merlangus*) has been an important component of west coast demersal fish landings. Whiting contribute to both inshore and offshore fisheries and are mainly caught by light trawlers. Approximately half the total whiting catch by weight is discarded because it is uneconomic to land. This species is widely distributed throughout the west coast of Scotland and high numbers of immature fish can be found in most sea lochs and inshore areas (Fisheries Research Services 2003).

Biomass

In the absence of whiting biomass data for the study area, the model was allowed to estimate biomass, using an EE of 0.8 (Morissette *et al.* 2003). The resulting biomass was 2.56 t•km^{-2} (Table 2).

Production and Consumption

In the absence of information for production of west coast Scottish whiting, the P/B of whiting from the North Sea model (Mackinson 2001), was used in model construction. This value of 0.9 year^{-1} proved too high to reach mass balance, so a lower value (0.7 year^{-1}) was used (Table 2). The Q/B used for whiting was calculated by Fishbase with the following characteristics: water temperature of 10°C and max weight of 3.1kg (S.Magill, pers. comm). This results in a Q/B of 2.4 year^{-1} for whiting (Table 2).

Diet composition

The diet composition of whiting in Scotland was based on a study by DuBuit (1991) on that same area. Herring, sprat, and other demersal and pelagic fish were the major prey (Appendix Table 1).

Other demersal fish

Background

This group represents an aggregation of different fish species that live in the lower part of the water column, mostly associated with the seabed. Aggregation was done on the basis of similarity of ecological niche, diet composition, and biological characteristics. Hence, flatfish such as dab (*Limanda limanda*), long rough dab (*Hippoglossoides platessoides*), witch flounder (*Glyptocephalus cynoglossus*) and flounder (*Platichthys flesus*), and gadoid species such as pollock (*Pollachius pollachius*), poor cod (*Trisopterus minutus*), hake (*Merluccius merluccius*) and ling (*Molva molva*), being the most commercially important. Also represented in this group are the monkfish (*Lophius* sp.) an increasingly valuable species, particularly in the waters approaching the shelf slope (Fisheries Research Services 2004).

Biomass

In the absence of local biomass data for any demersal species in this group, biomass was estimated by the model using an EE of 0.92 (Morissette *et al.* 2003). The demersal fish biomass calculated by the model was 3.98 t•km^{-2} (Table 2).

Production and Consumption

The P/B ratio for demersal fish was assumed to equal that of a similar 'other predatory fish' group in the North Sea model (Mackinson 2001), for which the value of 0.77 year^{-1} was used (Table 2). No information was available for Q/B representing the whole range of species aggregated in the demersal fish group.

Thus, this parameter was estimated by the model by entering the *P/B* (as mentioned above) and by assuming a *P/Q* of 0.3 (Christensen and Pauly 1992). The *Q/B* calculated by *Ecopath* was 2.57 year^{-1} (Table 2).

Diet composition
Diet composition for the aggregated 'demersal fish' group was adapted from the Gulf of St. Lawrence model (Morissette *et al.* 2003). However, the original diet was modified to reduce the amount of pelagic fish in the diet of demersal predators and to include hake diet from Guichet (1995) (Appendix Table 1).

Sharks

Background
At least 21 species of shark have been recorded in British coastal waters (Vas 1991). The most common species represented in the model are lesser spotted dogfish (*Scyliorhinus caniculus*), nursehound (*Scyliorhinus stellaris*), tope (*Galeorhinus galeus*), smooth hound (*Mustelus mustelus*) and spur dog (*Squalus acanthias*). These species are relatively small, with the largest species, tope, up to two metres long. These five species have strong associations with the seabed and their diet consists largely of benthic invertebrates and fish (Dipper 1987). The largest shark occurring off the west coast of Scotland is the basking shark (*Cetorhinus maximus*). During the late summer months this planktivorous shark can be seen feeding at, or close to the surface. The capture fishery for sharks is mainly for the smaller species, particularly spur dog, taken mainly by Scottish demersal trawlers (Scottish Sea Fisheries Statistics 2000).

Biomass
No information on biomass is available for sharks in the Scottish waters. Thus, biomass was estimated by the model at 0.68 t•km^{-2} (Table 2) using an *EE* of 0.93 (Morissette *et al.* 2003).

Production and Consumption
The *P/B* of sharks in Scottish waters was assumed to be similar to that of the North Sea. The *P/B* of sharks in the North Sea is based on estimates of natural mortality and Allen's (1971) demonstration that, under equilibrium, *P/B* = Z. The average *P/B* value for juvenile and adult sharks was taken and a P/B value of 0.16 year^{-1} was obtained (Table 2). The Q/B ratio was assumed to be similar to the North Sea. The average *Q/B* for juvenile and adult sharks of the North Sea was calculated at 3.0 year^{-1} (Table 2).

Diet composition
The diet composition of shark species was taken from Mackinson's North Sea model (2001), which based its diet on dogfish (Appendix Table 1). Diet was predominantly pelagic (herring being the main prey with sand eels and mackerel), although semi-pelagic species were present (whiting and Norway pout). Crustaceans and molluscs were eaten fairly commonly, while tunicates, annelids, coelenterates and ctenophores were also consumed, albeit less frequently (Mackinson 2001, after Rae 1967).

Rays and skates

Background
Skates and rays (Family Rajidae) are relatively large-bodied elasmobranch fishes, with 15 species recorded from UK waters. Three species occur commonly; skate, *Raja batis*, thornback ray, *Raja clavata*, and cuckoo ray, *Raja naevus*. All are bottom dwelling species, often found on softer sediments, and can be found in shallow water down to 200-300 m (although the skate can be found as deep as 600 m) (Gibson *et al.* 2001). The diet mainly consists of bottom living invertebrates and fish. Rays and skates are taken as part of the west coast mixed demersal trawl fishery (Scottish Sea Fisheries Statistics 2000).

Biomass
In the absence of local biomass data for any species of ray or skate, biomass was estimated by the model at 1.40 t•km^{-2} (Table 2), using an *EE* of 0.80 (Morissette *et al.* 2003).

Production and Consumption
A P/B ratio of 0.48 year^{-1} was used for a similar 'Rays and skates' group in the North Sea. A value of 0.299 year-1 was calculated for rays in the northwest Atlantic (Morissette *et al.* 2003). In the absence of local data, an intermediate value of 0.4 year-1 (Table 2) was used to make the model balance. The Q/B ratio of 1.45 year^{-1} for rays and skates was calculated by Christensen 1995 and used in the North Sea model (Mackinson 2001). In the absence of local data, this same value was used in the present model (Table 2).

Diet composition
Diet composition for rays and skates was taken directly from the North Sea model (Mackinson 2001). This was incorporated into a composite group diet based on diets given for skate (Smith 1890). The main prey items were prawns and shrimps, N*ephrops* and herring (Appendix Table 1).

Cod

Background
Cod (*Gadus Morhua*) are distributed throughout the west coast Scotland from inshore to depths in excess of 200 m. Like many other gadoid species, juveniles are abundant in shallow inshore habitats from approximately four months old (Magill and Sayer 2004). They may then spend the first winter in shallow inshore waters before moving into deeper offshore waters. Adult fish are generally concentrated in the northern and more offshore regions of the North Sea and west coast (Fisheries Research Service 2003).

Biomass
In the absence of good local biomass estimates, an *EE* of 0.85 (Morissette *et al.* 2003) was used to let the model estimate biomass at 2.31 t•km^{-2} (Table 2).

Production and Consumption
In the absence of local information for cod, the value of 0.75 year^{-1} (Table 2) was used, based on Mackinson (2001). Consumption values for cod in the northeast Atlantic range between 1.41 year^{-1} (Norway) to 4.55 year^{-1} (UK), (Pauly 1989; Froese and Pauly 2004). The value 3.80 year^{-1} used in the model represents the average of Q/B calculated for UK (3.41; 3.43; 4.55) as given in Fishbase (Table 2).

Diet composition
According to a quantitative analysis, cod off the coast of Scotland feed primarily on prawns and shrimps, pelagic fish and herring (DuBuit, 1989) (Appendix Table 1).

Saithe

Background
Saithe (*Pollachius virens*) are active, gregarious fish inhabiting inshore and offshore waters. Saithe usually enter coastal waters in spring and over winter around the 200 m depth contour (Frimodt 1995). In late summer and autumn, young saithe are found in large numbers within Scottish and Norwegian coastal waters, usually on grounds which are unsuitable for commercial fishing. Adults can form dense shoals which move around the water column and are often caught hundreds of metres above the seabed (Fisheries Research Services, 2003).

Biomass
The biomass of saithe was calculated by the model using an *EE* of 0.92 year^{-1} (Mackinson 2001) resulting in 0.25 t•km^{-2} (Table 2).

Production and Consumption
P/B was estimated from the North Sea model (Mackinson 2001). This was based on demonstration that *P/B* = *Z* (Allen 1971) g a value of 0.87 year^{-1} for the west coast of Scotland (Table 2). A value of 4.76 year^{-1} has been reported for USA populations (Pauly 1989) and 3.286 year^{-1} for the North Sea (Mackinson 2001). An average value of 4.023 year^{-1} (Table 2) was used for the west coast of Scotland model.

Diet composition
The diet of saithe was based on the North Sea adult diet and MSVPA diet data (V. Christensen, Fisheries Centre, UBC, cited as pers. comm. in Mackinson's (2001)). The main prey items come from the euphausiid, herring, and prawns and shrimps functional groups (Appendix Table 1).

Other pelagic fish

Background
Pelagic feeders are an important part of the ecosystem, and some species are also exploited commercially. This group is composed mainly of blue whiting (*Micromesistius poutassou*), a pelagic fish found over the continental slope and shelf to more than 1,000 m, but more common at 300-400 m (Cohen *et al.* 1990). This group also includes juveniles and larvae of other pelagic fish.

Biomass
Biomass was estimated by *Ecopath* at 4.33 t•km^{-2} (Table 2), using an *EE* = 0.92 year^{-1} (Mackinson 2001).

Production and Consumption
No information was available for pelagic fish production in the study area. Thus, a *P/Q* ratio of 0.3 (Christensen and Pauly 1992) was used to determine *P/B*, resulting in a value of 0.87 year^{-1} (Table 2). The consumption value for pelagic fish comes from an estimate for a similar group in the North Sea model. The value used in the west coast of Scotland model is thus 2.90 year^{-1} (Table 2).

Diet composition
The diet of blue whiting is variable; however, meso-pelagic crustaceans feature prominently. In the absence of relevant quantitative diet information for species in the 'other pelagic fish' group, information was taken from the North Sea model (Mackinson 2001). The main prey items in the aggregated group diet were benthic invertebrates and *nephrops* (Appendix Table 1).

Crabs and lobsters

Background
The main crustaceans found in the west coast of Scotland were edible crab (*Cancer pagurus*), velvet crab (*Necora puber*), green shore crabs (*Carcinus maenas*), lobster (*Homarus gammarus*) and squat lobsters (*Munida rugosa*). This group of shellfish fisheries forms an important aspect of the Scottish fishing industry, with recent annual values of over £90 million (Fisheries Research Services 2003).

Biomass
Biomass was estimated by the model at 0.24 t•km^{-2} (Table 2), using a *EE* = 0.9 year^{-1} (Mackinson 2001).

Production and Consumption
In the absence of local information for production or consumption of crabs and lobsters, the mortality rate of 2.5 year^{-1} for Dungeness crab, *Cancer magister,* reported by Guénette (1996) was used as a substitute for *P/B*, as in the North Sea (Mackinson 2001) (Table 2). Using the *P/B* estimated above, and a gross efficiency (*P/Q*) of 0.15 (Christensen 1995), gives a consumption (*Q/B*) of 30 year^{-1} (Table 2).

Diet composition
This group of macro-crustaceans feed predominantly in the benthic environment. Some qualitative information on shrimp diet composition indicates that echinoderms, other benthic invertebrates, and prawns and shrimps groups were the main prey items (Ansell *et al.* 1999) (Appendix Table 1).

Gurnards

Three species of gurnard occur in Scottish waters: tub gurnard (*Chelidonichthys lucernus*), red gurnard (*Aspitrigla cuculus*), and grey gurnard (*Chelidonichthys gurnardus*). These species occasionally form schools, and are found over sand and gravel and rocks in the continental shelf (Blanc and Hureau 1979).

Biomass
No information was available for gurnards in the study area; thus the model was allowed to calculate biomass with a resulting value of 0.15 t•km^{-2} (Table 2)

Production and Consumption
In the North Sea model, Mackinson (2001) estimate a *P/B* at 1.4 year^{-1} (Table 2), by setting it to half the r_{max} (see FishBase). Using the *P/B* estimated above, and a gross efficiency (*P/Q*) of 0.30 (Christensen and Pauly 1992), results in a consumption (*Q/B*) of 4.67 year^{-1} (Table 2) for gurnards.

Diet composition
Diet composition was based on Smith (1890) and an MSVPA diet for gurnard after Mackinson (2001), resulting in a predominance of large zooplankton, prawns and shrimps and sandeels (Appendix Table 1).

Haddock

Background
Haddock (*Melanogrammus aeglefinus*), is one of the most valuable food fishes of Europe, particularly in

Scotland where it's famous as *finnan haddie*, a traditional recipe where haddock is served smoked. Haddock are common round the British and Irish coasts and generally distributed along the shores of the North Sea, extending across the Atlantic to the coast of North America. Haddock are rarely found in waters over 300 m deep. Juveniles overwinter in the northern North Sea, in summer; the area of highest density is off the northeast coast of Scotland (Frimodt 1995).

Biomass

Since no biomass was available for haddock, an *EE* of 0.8 $year^{-1}$ was used, resulting in a biomass of 0.72 $t{\bullet}km^{-2}$ for the study area (Table 2).

Production and Consumption

The annual production and consumption to biomass ratio for haddock was taken from the North Sea model (Mackinson 2001) and is thus assumed to be 1.0 $year^{-1}$ (Table 2). Haddock consumption values in Fishbase (Froese and Pauly 2004) ranged from 3.00 $year^{-1}$ in the USA to 12.76 $year^{-1}$ in the UK (Pauly 1989) and 5.69 in Iceland (Pauly 1989). The UK value was used initially, but proved too high to achieve mass balance and an intermediate value of 4.0 was used (Table 2).

Diet composition

Haddock diet was taken from Ritchie (1937; 1938), Jones (1954), and Smith (1890). These data sources were adapted to the North Sea by Mackinson (2001). The resulting diet was mainly composed of prawns, shrimps, and benthic invertebrates (Appendix Table 1).

Inshore fish

Background

This group includes all the juvenile gadoids and flatfish that inhabit the shallow inshore waters of west coast Scotland to the northeast Atlantic open ocean. Other species such as wrasse (Family Labridae) are largely dependent on subtidal rocky reefs (Sayer *et al.* 1996)

Biomass

The biomass was estimated by the model using an *EE* of 0.90, for a total biomass of 0.21 $t{\bullet}km^{-2}$ (Table 2).

Production and consumption

In the absence of local information, the *P/Q* was assumed to be 5.0 (Table 2), which was high, but conceivable given the higher annual growth rate of juvenile fish in inshore waters. However, this represents a bias for wrasse species which are long-lived and slow-growing. Based on the *P/B* estimated above, a *P/Q* ratio of 0.3 (Christensen and Pauly 1992) was used in order to obtain a *Q/B* value of 16.67 $year^{-1}$ for inshore fish (Table 2).

Diet composition

This group includes a wide range of species. In the absence of readily available quantitative diet information, it was assumed that they feed on benthic invertebrates, as it is known that these species are highly associated with benthos. The diet was thus approximated to include the most important species of benthic invertebrates of the ecosystem, echinoderms, shrimps prawns, polychaetes, infauna (bivalves), epifauna (gastropods) and other benthic invertebrates (Appendix Table 1).

Salmon

Background

The many lochs along the west coast of Scotland are a preferred habitat for Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta trutta*), both important economic fisheries on the west coast of Scotland. Atlantic salmon is considered the key species in this aggregated group.

Biomass

The biomass was estimated by the model with an *EE* of 0.8 $year^{-1}$, resulting in an annual biomass of 0.04 $t{\bullet}km^{-2}$ for salmon in the study area (Table 2).

Production and Consumption

Specific growth rate for Atlantic salmon (% body weight·day^{-1}) varied from 0.3 to 1.0 for mature individuals (Stead *et al.* 1999). This value, averaged and transformed into *P/B*, represented 0.8 $year^{-1}$ for salmon (Table 2). This was assumed to be representative of both species. The food consumption of Atlantic salmon was also calculated by Stead *et al.* (1999). Calculations were done in weight-specific food conversion ratio ($mg \cdot g^{-1}$). This, transformed in *Q/B*, gave us a value of 3.57 $year^{-1}$ for the model (Table 2). This was again assumed to represent both species in the group.

Diet composition

Juvenile diet was based on a study by Winfield *et al.* (2002) on Arctic charr from the freshwater Loch Ness, where diets were dominated by chironomid larvae, with chironomid pupae, *Bythotrephes longimanus*, *Bosmina coregoni* and *Daphnia hyalina* also frequently taken. In the model, large zooplankton (including euphausiids) were thus given the highest proportion, and the diet was then completed with other prey that are common in adult diet, such as herring, prawns and shrimps (Morissette *et al.* 2003) (Appendix Table 1).

Mackerel

Background

Atlantic Mackerel (*Scomber scombrus*) are one of the most commercially-important species of the west coast of Scotland (ICES 2003). Two main stocks exist in the north-east Atlantic (Fisheries Research Services 2004). The North Sea stock is predominantly confined to the eponymous waters. The western mackerel population forms a complex stock concentrated along the surface waters of the continental shelf off north west Europe from the Gulf of Cadiz in the South to the Norwegian Sea in the north (Fisheries Research Services 2004). The stock spawns from March to July, predominantly to the south and west of the UK. After spawning, the stock migrates northwards to feeding grounds along the continental shelf. This migration crosses a number of different ICES management zones (ICES 2003). In recent decades there has been evidence to suggest that the southern migratory patterns have altered (Fisheries Research Services 2004). Because of the complex nature of mackerel stocks, and the vast area of distribution, management is primarily based on annual egg surveys.

Biomass

The biomass was calculated by *Ecopath* with an assumed *EE* of 0.95 $year^{-1}$, resulting in a total biomass of 0.83 $t \cdot km^{-2}$ for mackerel in the west coast of Scotland (Table 2).

Production and Consumption

P/B was assumed to be equivalent to that calculated for North Sea mackerel by Mackinson (2001, after Christensen 1995). The value was initially set to 0.9 $year^{-1}$, but was then increased to 1.02 $year^{-1}$ to reach a balanced solution (Table 2). The *Q/B* of USA mackerel is given in FishBase as 4.4 $year^{-1}$ (Pauly 1989). Closer to the study area, the North Sea model (Mackinson 2001) gives a value of 3.5 $year^{-1}$. The average of these two values, 3.95 $year^{-1}$, was used in the west coast of Scotland model, (Table 2).

Diet composition

Diet was based on the North Sea model (Mackinson 2001), which, in turn, was based on MSVPA data and another model (Christensen 1995). According to these different sources, mackerel feed mainly on zooplankton (mostly euphausiids), prawns and shrimps (Appendix Table 1).

Horse mackerel

Background

Horse mackerel, *Trachurus trachurus*, support a highly valuable fishery in the west of Ireland and the UK, particularly for the Irish fleet. Horse mackerel form large pelagic schools in coastal areas with sandy substrate (Froese and Pauly 2004) and are caught predominantly in pelagic nets (Hammer and Zimmermann 2001). There are two stocks in the north east Atlantic (Soriano and Sanjuan 1997). The North Sea stock is confined largely within eponymous waters. The western stock is complex and primarily distributed along the continental shelf margin to the west of Europe (Fisheries Research Services 2004). This stock undertakes a significant migration between spawning, feeding and overwintering grounds across a number of ICES management zones (ICES 2003). Following early spring spawnings in the south westerly part of the range, horse mackerel migrate northwards towards the Norwegian Sea (Fishbase). The species is found primarily in the waters west of Scotland during summer months (Fisheries Research Services 2004).

Biomass
The biomass calculated by the model was 1.86 t•km^{-2}, based on an *EE* of 0.81 year^{-1} (Table 2).

Production and Consumption
The *P/B* of horse mackerel was taken from the North Sea model (Mackinson 2001). Since those data were able to balance the model in the North Sea, we assumed that it could be ecologically pertinent in the west coast of Scotland. Thus, the value of 0.7 year^{-1} was used in our model (Table 2). The consumption rate of horse mackerel was calculated with FishBase (Froese and Pauly 2004) with a water temperature of 10.0 °C degrees (S. Magill, pers. comm.), resulting in a *Q/B* of 2.9 year^{-1} (Table 2), very comparable to the 0.3 year^{-1} used by Mackinson (2001) for horse mackerel in the North Sea.

Diet composition
Horse mackerel are similar in foraging habits to the mackerel (Mackinson 2001). Diet composition was taken from the North Sea model and divided among euphausiids, copepods and other crustaceans (Mackinson 2001) (Appendix Table 1).

Plaice

Background
The European plaice (*Pleuronectes platessa* L.) is an important flatfish for Scottish fisheries (Hoarau *et al.* 2004). Distribution covers shallow European waters (<100 m) from the western Mediterranean to Iceland and the White Sea (Wimpenny 1953). Plaice are found offshore during the winter reproductive period and in shallow costal waters at early-maturity (Zijlstra 1972). The egg and larval stages are pelagic but at three to four months the young plaice take up demersal nursery habitats (Harding *et al.* 1978). Plaice undergo seasonal migration patterns from spawning to feeding grounds (de Veen 1978)

Biomass
Biomass was estimated by *Ecopath* at of 1.64 t•km^{-2} (Table 2), based on an *EE* of 0.79 similar to the North Sea model (Mackinson 2001).

Production and Consumption
The *P/B* ratio for flatfish in the Gulf of St. Lawrence ranged from 0.245 to 0.427 year^{-1} (Morissette *et al.* 2003). Similarly, the *P/B* for plaice in the North Sea model was 0.65 year^{-1}. As these values were too low to allow the current model to balance, a value of 0.975 year^{-1} was used (Table 2). According to a study by Palomares and Pauly (1989) in FishBase (Froese and Pauly 2004), the *Q/B* of plaice varies from 2.1 to 3.42 year^{-1}. In order to reach a *P/B* lower than 30% (Christensen and Pauly 1992), the maximum value was used for plaice in the west coast of Scotland (Table 2).

Diet composition
Diet was based on the percentage frequency occurrence of prey items from Smith (1890). The main prey items were polychaetes, benthic invertebrates, prawns and shrimps, and echinoderms (Appendix Table 1).

Sole

Background
The soles (Family Soleidae) are a group of flatfish with eyes on the right side of the compressed body (Wheeler 1978). Four species are found in northern European waters. Sole or Dover sole (*Solea solea*) is the most common, and is another important species for Scottish commercial fishery. Soles are all benthic fish, preferring mostly soft muddy habitats. Like most flatfish they have planktonic eggs and young that settle close inshore (van den Broek 1980; Henderson 1989). Also included in this group are the sand sole (*Solea lascaris*) the solenette, (*Buglossidium luteum*) and the thickblack sole, (*Microchirus variegates*); however, these three species are less common than *S. solea*.

Biomass
Biomass was estimated by *Ecopath* at 0.46 t•km^{-2} (Table 2), based with an *EE* of 0.87 for sole in the North Sea model (Mackinson 2001).

Production and Consumption
P/B for sole was 0.93 year^{-1} in the North Sea model (Mackinson 2001). However, this value was too high to balance the west coast of Scotland. Thus, the value was lowered to 0.8 year^{-1} in order to reach

equilibrium (Table 2). The *Q/B* of sole was reported in FishBase (Froese and Pauly 2004) with a maximum weight of 3000 g, a water temp of 10°C (S. Magill, pers. comm.) and a type-4 tail. This resulted in a *Q/B* of 2.7 $year^{-1}$ (Table 2). This is comparable to 3.36 $year^{-1}$ for sole in the North Sea) Mackinson (2001).

<u>Diet composition</u>
The diet composition for sole on the west coast of Scotland was taken from the lemon sole and witch diets in the North Sea model (Mackinson 2001). These species mainly prey on the prawns and shrimps functional group but also the polychaetes and euphausiids groups (Appendix Table 1).

Norway lobster

<u>Background</u>

The Norway lobster (*Nephrops norvegicus*), is a small lobster that grows to a maximum total length of 25 cm (including the tail, carapace and clawed legs), although individuals are normally between 18-20 cm (Sardà 1995). *Nephrops* is one of most important fisheries in Scotland and benthic trawls or pots/creels are the two methods of fishing employed (Dyer *et al.* 1982). *Nephrops* burrow into soft muddy bottoms and emerge to hunt during the hours of darkness. Males generally dominate catches mostly because the females remain in the burrow while carrying eggs (Fisheries Research Services 2004).

<u>Biomass</u>
Biomass information for Norway lobster was taken from Tuck *et al.* (2000). These authors calculated the density for the area; this was multiplied by the average weight of about 40 g (Howard 1989), resulting in a total biomass of 2.20 t•km^{-2} (Table 2).

<u>Production and Consumption</u>
The *P/B* for Norway lobster was assumed to be similar to the production rate of American lobster (*Homarus americanus*) as reported in the model of Bundy *et al.* (2000). A value of 3.0 $year^{-1}$ (Table 2) was therefore used for Norway lobster of the Scottish coast.

<u>Consumption</u>
In the absence of local information on the consumption of Norway lobsters, generic information on crabs and lobsters from the North Sea (Mackinson 2001) was assumed to represent the consumption of Norway lobster from the west coast of Scotland. As a result, the *Q/B* used in our model was 10.0 $year^{-1}$ (Table 2).

<u>Diet composition</u>
Many studies were available on *Nephrops* diet in the Scottish waters. Both juvenile and adult *Nephrops* feed on molluscs, annelid worms, crustaceans, echinoderms and small fish (Cristo 1998; Rotllant *et al.* 2001) and microscopic organisms such as foraminifera (Howard 1989). Information from all studies was merged into one global diet for *Nephrops*. The main prey items were zooplankton (including euphausiids) and benthic invertebrates (mainly echinoderms and polychaetes) (Appendix Table 1).

Norway pout

<u>Background</u>
The Norway pout (*Trisopterus esmarkii*) is a benthopelagic to pelagic fish that lives over muddy bottoms, mostly between 100 and 200 m (Cohen *et al.* 1990). Bergstad (1990) identified Norway pout as the numerically dominant species in several of the upper and mid-slope assemblages of the Norwegian Deep. Elsewhere, as in the North Sea, the Norway pout stock is estimated to be within safe biological limits. However, there is no current information on which to evaluate the west of Scotland stock (ICES 2002).

<u>Biomass</u>
The biomass was estimated to 0.395 t•km^{-2} in the study area, assuming that the *EE* is 0.9 $year^{-1}$ (Table 2).

<u>Production and Consumption</u>
P/B was assumed to be similar to Norway pout in the North Sea (Mackinson 2001, after Christensen 1995). Thus, a *P/B* value of 2.0 $year^{-1}$ was used in the west coast of Scotland model (Table 2). The *Q/B* rate for Norway pout was calculated from FishBase (Froese and Pauly 2004), with water temperature of 10°C (S. Magill, pers. comm.), resulting in a *Q/B* of 5.0 $year^{-1}$. The North Sea model used a value of 9.6

year^{-1}. Consequently, an intermediate value of 7.0 year^{-1} (Table 2) was used for west coast of Scotland waters.

Diet composition

Norway pout feed mainly on crustaceans (Scott 1902, 1903; Gokhale 1953). This was also used as the base for diet composition in the North Sea model (Mackinson 2001). The resulting diet of Norway pout on the west coast of Scotland was dominated by large zooplankton, euphausiids, and prawns and shrimps (Appendix Table 1).

Cephalopods

Background

Cephalopods are short-lived molluscs, characterised by rapid growth rates, and are important predators and prey in oceanic and neritic environments. They can range in size from 1.5 cm in pygmy squid (Sepiolidae) to 20 m in giant squid (Architheutidae) (Stowasser *et al.* 2004). Cephalopods are very important for many predators, especially whales (e.g. Clarke 1996, Croxall and Prince 1996, Smale, 1996, Santos *et al.* 2001a). Many species make important feeding and spawning migrations, thus influencing prey and predator communities strongly on a seasonal and regional basis (Stowasser *et al.* 2004). Cephalopods also interact with commercial finfish fisheries (Caddy and Rodhouse 1998). Their commercial significance to world fisheries is of relatively recent, but growing, importance (Boyle and Pierce 1994).

Biomass

The biomass was calculated from the *Ecopath* model with a *EE* of 0.83 year^{-1} (Mackinson 2001), resulting in a biomass of 0.388 t•km^{-2} (Table 2).

Production and Consumption

P/B was assumed to be similar to cephalopods in the North Sea model (Mackinson 2001) which, in turn, used values from an Alaska Gyeare model (Pauly *et al.* 1996). The resulting *P/B* was 3.0 year^{-1} (Table 2). In the absence of local information, the *P/Q* ratio of 0.3 from Christensen and Pauly (1992) was used. Using the *P/B* calculated above, this resulted in a *Q/B* of 10.0 year^{-1} (Table 2).

Diet composition

Cephalopods feed mainly on zooplankton, but also consume the larvae of many species. Diet composition information was adapted from Mackinson (2001) who used indices of relative importance in prey composition of *Loligo opalescens* published in Karpov and Cailliet (1978) (Appendix Table 1).

Sandeel

Background

Sandeels, (*Ammodytes* spp.) are widely distributed in the north Atlantic and can be extremely abundant over shallow sandy bays and beaches (Wheeler 1978; Lythgoe and Lythgoe 1992), including the intertidal zone and estuaries; rarely offshore. Included in this group are *Ammodytes tobianus*, *A. marinus* and *Hyperoplus lanceolatus* (greater sandeel). Sandeels can alternate between lying buried in the sandy substrate and swimming in schools in the water mass (Froese and Pauly 2004). They are important forage fish for many larger commercially important species (Lythgoe and Lythgoe 1992)

Biomass

In the absence of sandeel data, the model was allowed to estimate biomass using an *EE* of 0.80 (Mackinson 2001). This resulted in a total annual biomass of 0.88 t•km^{-2} for the study area (Table 2).

Production and Consumption

As the only available source of information, the *P/B* value used in the North Sea (Mackinson 2001) was adapted to balance the west coast of Scotland model. A value of 3.9 year^{-1} was decreased to about 3.0 year^{-1} (Table 2), because of the much lower P/B of 1.1 year^{-1} for sandeels in the northwest Atlantic (Morissette *et al.* 2003). The *Q/B* was calculated from FishBase (Froese and Pauly 2004), with a water temperature of 10 ^{o}C (S. Magill, pers. comm.), resulting in a ratio of 8.3 year^{-1}. However, this value was too low to reach mass balance for the studied ecosystem, thus the value in the North Sea model (10.25 year^{-1}, Table 2) was used (Mackinson 2001).

Diet composition
No quantitative information was available for sandeel diet of the west coast of Scotland. However, it is commonly known that this species feeds on zooplankton and some large diatoms (Bauchot 1987). The diet was thus divided into large zooplankton and prawns and shrimps, with smaller proportions for euphausiids, polychaetes and small zooplankton (Appendix Table 1).

Sprat

Background
Sprat, (*Sprattus sprattus*) are small inshore pelagic fish that are fished commercially in Scotland. Sprats sometimes enter estuaries (especially the juveniles), tolerating salinities as low as 4‰ (Whitehead 1985).

Biomass
Biomass was calculated by *Ecopath* with an *EE* of 0.80 year^{-1}, resulting in a balanced biomass of 1.44 year^{-1} (Table 2) for sprat on the west coast of Scotland.

Production and Consumption
The *P/B* was based on the value of 1.4 year^{-1} used in the North Sea model (Mackinson 2001), but was increased to 1.9 year^{-1} (Table 2), a value closer to that of herring which have a similar life history. According to FishBase (Froese and Pauly 2004), the *Q/B* of sprat can be calculated to 8.5 year^{-1} (Table 2) using a water temperature of 10°C (S. Magill, pers. comm.). This is similar to the value of 8.1 year^{-1} used in the North Sea model (Mackinson 2001).

Diet composition
Diet was based on data for herring, a similar species occupying approximately the same ecological niche. Sprat were classed as planktivores preying predominantly on large zooplankton (copepods), small crustaceans (shrimp and prawns) and euphausiids (Appendix Table 1).

Herring

Background
Herring are widely distributed throughout the north-east Atlantic, ranging from the Arctic Ocean in the north to the English Channel in the south. On the west of Scotland, the herring stock is composed of two groups of fish: one spawning in spring and the other in autumn. The majority of the population is made up of the latter group (Fisheries Research Services 2003).

Biomass
Biomass of herring was estimated by *Ecopath* to be 3.6 t•km^{-2} based on an *EE* of 0.8 year^{-1} (Table 2).

Production and Consumption
The value of *P/B* used in the present model was based on Christensen's (1995) estimate for the North Sea, giving a P/B of 1.8 year^{-1} for herring in west coast of Scotland (Table 2). According to Fishbase (Froese and Pauly 2004), the *Q/B* of herring for the UK was 10.1 year^{-1} (based on Pauly 1989). However, another Q/B value for herring on the north west Atlantic region was much lower at 4.59 year^{-1} (Pauly 1989). Consequently, an intermediate value of 7.0 year^{-1} was used for herring of the west coast of Scotland (Table 2).

Diet composition
Herring feed mainly on crustaceans (shrimps and copepods) and young sandeels (Froese and Pauly 2004). The diet composition for the present model was based on Mackinson (2001), where, in addition to the species described above, it was likely that they also took pelagic larvae of other fishes and some phytoplankton. The main prey items were thus large zooplankton, euphausiids, and small crustaceans (prawns and shrimps) (Appendix Table 1).

Benthic invertebrates

Background
The benthic invertebrates were divided into five groups: echinoderms, epifauna (gastropods), infauna (bivalves), polychaetes and other benthic invertebrates. This last group consisted of miscellaneous crustaceans, nematodes, and other meiofauna. These groupings parallel the structure of a Grand Banks

model (Morissette *et al.* 2003). However, the benthic data for the west coast of Scotland is very poor. Consequently, in many cases, it was assumed that benthic biomass, consumption and diet composition were similar to the North Sea and Gulf of St. Lawrence (Mackinson 2001; Morissette *et al.* 2003).

Biomass

The biomass for three of the five benthic invertebrates groups was calculated by *Ecopath*, using *EE* values for similar species from the North Sea (Mackinson 2001):

- Echinoderms: 0.92 $year^{-1}$ (Mackinson 2001);
- Infauna (bivalves): 0.73 $year^{-1}$ (Morissette *et al.* 2003);
- Other benthic invertebrates (OBI): 0.95 $year^{-1}$ (Morissette *et al.* 2003).

This resulted in respective biomasses of 3.95 $t{\bullet}km^{-2}$ for echinoderms, 1.56 $t{\bullet}km^{-2}$ for infauna and 7.31 $t{\bullet}km^{-2}$ for OBI (Table 2).

Polychaete biomass was set to 10 $t{\bullet}km^{-2}$ to support the high level of predation and to achieve a balanced solution. Epifaunal biomass was derived from the information presented in Feder and Pearson (1988) for Loch Linnhe and Loch Eil (Table 2).

Production and Consumption

P/B for the five benthic invertebrates groups was derived from other studies on similar species groups. *P/B* ratios (summarised in Table 2) were thus:

- Echinoderms: 4.0 $year^{-1}$ (Mackinson 2001);
- Epifauna: 20.0 $year^{-1}$ (Mackinson 2001);
- Infauna: 20.0 $year^{-1}$ (Morissette *et al.* 2003);
- Polychaetes: 5.0 $year^{-1}$ (increased from 4.0 in Morissette *et al.* (2003) to reach mass balance);
- Other benthic invertebrates: 6.0 $year^{-1}$ (Mackinson 2001).

No information was found for *Q/B* ratios of benthic invertebrates. Consequently, the *P/Q* ratios were used with the *P/B* described above to derive consumption rates for each group. The *P/Q* ratios were assumed to be equal to 0.25 $year^{-1}$ for all groups except polychaetes where *P/Q* was 0.30 $year^{-1}$ (Morissette *et al.* 2003). This resulted in *Q/B* estimates of:

- Echinoderms: 16.0 $year^{-1}$
- Epifauna: 80.0 $year^{-1}$
- Infauna: 80.0 $year^{-1}$
- Polychaetes: 16.7 $year^{-1}$
- Other benthic invertebrates (OBI): 24.0 $year^{-1}$

These estimates are also summarised in Table 2.

Diet composition

Mackinson (2001) assumed that echinoderms feed mainly on phytoplankton and detritus. This differs from the Gulf of St. Lawrence (Morissette *et al.* 2003) where their only food source is detritus with a small proportion of filtered phytoplankton (Appendix Table 1). Polychaetes mainly feed on phytoplankton and detritus (Mackinson (2001) (Appendix Table 1). The 'Other benthic invertebrates' group also feeds mainly on detritus, but also on epifauna and infauna (Mackinson (2001) (Appendix Table 1).

Prawns and shrimps

Background

This group consists of several species of *penaeid* and *caridean* shrimp. *Crangon crangon*, the brown shrimp, is found principally in the shallow sublittoral usually on fine sand and mud. *Crangon allmanni* is a similar shrimp, but mostly found in deeper water. *Palaemon elegans* and *Palaemon serratus* are both common in the intertidal and lower shore on the west coast of the UK. The larger pink shrimp, *Pandulus montagui*, is principally found from the sublittoral down to approximately 230 m (Gibson *et al.* 2001). This species is fished commercially mostly by benthic trawls.

Biomass

For shrimps and prawns, an *EE* of 0.95 $year^{-1}$ was used to calculate the biomass with *Ecopath*. The resulting biomass was 16.3 $t{\bullet}km^{-2}$ (Table 2).

Production and Consumption

A *P/B* ratio of 3 $year^{-1}$ was used as an estimate for this group (Table 2), as for the North Sea model (Mackinson 2001). A gross food conversion efficiency of 15% was assumed. Given the *P/B* calculated above, this resulted in a *Q/B* of 12.0 $year^{-1}$ for prawns and shrimps of the west coast of Scotland (Table 2).

Diet composition

Diet information for prawns and shrimps was taken from Ansell *et al.* (1999) in a study of a Scottish sandy beach. The resulting diet composition is composed mainly of detritus, phytoplankton and small zooplankton (Appendix Table 1).

Zooplankton

Background

Three trophic groups are part of the zooplankton in the west coast of Scotland ecosystem: euphausiids, large zooplankton and small zooplankton. Large zooplankton are defined as those >5 mm and include chaetognaths, hyperiid amphipods, jellyfish (cnidarians and ctenophores), mysids, tunicates >5 mm and ichthyoplankton. This group is comprised mostly of omnivorous (hyperiid amphipods, mysids and large tunicates) and carnivorous (chaetognaths and jellyfish) species (Morissette *et al.* 2003). Euphausiids were also part of the large zooplankton but were considered separately in the west coast of Scotland model. Most species of euphausiids are omnivorous, but some are herbivorous.

Small zooplankton (i.e., less than or equal to 5 mm in length) include copepods, of which *Calanus finmarchicus*, and *Oithona similis* are the most numerous. Other small plankton include meroplankton and tunicates < 5 mm, which are generally underestimated by sampling gear (Morissette *et al.* 2003).

Biomass

The biomasses of all three groups of zooplankton were estimated by *Ecopath*. Large zooplankton and euphausiids were given an *EE* of 0.86 $year^{-1}$, while a value of 0.80 $year^{-1}$ was given for small zooplankton. The resulting biomasses were 6.29, 2.31, 7.83 $t{\bullet}km^{-2}$ for large zooplankton, euphausiids, and small zooplankton, respectively (Table 2).

Production and Consumption

The *P/B* of large zooplankton was about 4.0 $year^{-1}$ in the northwest Atlantic (Morissette *et al.* 2003), and was higher (27.0 $year^{-1}$) in the North Sea (Mackinson 2001). An intermediate value of 10.0 $year^{-1}$ for the west coast of Scotland was used to make the model balance (Table 2). In the absence of local euphausiid data, the north Atlantic annual production of up to 10 $mgC{\cdot}m^{-3}$ (Lindley 1980; 1982), was used, resulting in a *P/B* of 9.0 year-1 (Mackinson 2001) (Table 2).

P/B for small zooplankton was derived from values used in the northwest Atlantic and the North Sea (Morissette *et al.* 2003; Mackinson 2001). The value was then adjusted to a higher value of 18 $year^{-1}$ to balance the model (Table 2). The *Q/B* of large zooplankton was taken from (Mackinson 2001). In the present model, the production was derived from Fransz *et al.* (1991), resulting in a west coast of Scotland value of 35.0 $year^{-1}$ for large zooplankton (Table 2).

The *P/Q* value of 0.25 for both groups (Christensen and Pauly 1992) was used in order to estimate the *Q/B* for euphausiids and small zooplankton. This resulted in a *Q/B* of 36 $year^{-1}$ and 72 $year^{-1}$ for euphausiids and small zooplankton, respectively (Table 2).

Diet composition

The diet of large zooplankton was taken from the North Sea model (Mackinson 2001) with a high dominance of phytoplankton, followed by detritus and small zooplankton (Appendix Table 1). Euphausiid diet was based on Morissette *et al.* (2003) and Lass *et al.* (2001). Species in that group fed mainly on phytoplankton but also on copepods (small zooplankton) and detritus (Appendix Table 1). Small zooplankton also fed mainly on phytoplankton, with some detritus and cannibalism included in lower proportions. The small plankton diet was based on Morissette *et al.* (2003) (Appendix Table 1).

Phytoplankton

Background

The species composition of the phytoplankton group was assumed to include a mixture of autotrophic and mixotrophic organisms including: cryptophytes, diatoms, dinoflagellates, prasinophytes, and spirotrichea as in Morissette *et al.* (2003).

Biomass

Biomass information for primary production was taken from the average annual values for the UK in the *Sea Around Us* database (Lai 2004), and was reduced to about 3/4 to cover this area and to make the model balance. Consequently, the biomass of phytoplankton in the model was 80 $t \cdot km^{-2}$ (Table 2).

Production

The primary productivity used in the west coast of Scotland model was assumed to be similar to the North Sea (Mackinson 2001). Thus, a *P/B* value of 70 $year^{-1}$ was used for phytoplankton in the study area (Table 2).

Detritus

Biomass

Information is very sparse about the biomass of detritus in the west coast of Scotland. As a result, an arbitrary total biomass of 100 $t \cdot km^{-2}$ (Table 2) was used for this trophic component, similar to the value used for the North Sea model (Mackinson 2001).

MODELLING SCOTLAND'S WEST COAST FISHERIES

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Abstract

Fishing fleets operating off the west coast of Scotland modeled by *Ecopath* were grouped into 8 gear types: demersal trawl, beam trawl, midwater trawl, dredge, purse seine, lines (handline and longline), creels and pots and miscellaneous gear types. In future work the *Nephrops* trawl fishery should be separated. Average annual catch in tonnes per square kilometre in 2000 was calculated by gear type for all commercial species using catch statistics for region VIa provided by the appropriate ministry in each of the fishing nations. Unreported catch should be estimated in future work.

Introduction

Fishing fleets from Scotland, England, Wales, Northern Ireland, Ireland, Belgium, France, Germany, Netherlands, Spain, and the Isle of Man, are active in the west coast of Scotland area. The lucrative mackerel and horse mackerel fishery are concentrated along the continental shelf edge. This fishery is seasonal as it is dependent on the migrations of both species. There are also substantial fisheries for herring that have a high commercial value. Most of the catch is landed at Scottish and some at other UK ports, but some catches are landed in France and Ireland outside of the area. Total reported catch amounts to about 1.36 t•km^{-2} in the model area, representing about 70% of what might be expected from ICES data for the whole of area VIa, which includes some large offshore fisheries outside the modelled region. Discarded organisms and amounts were approximated using reports from trawl fisheries in nearby Scottish regions, making total extractions about 1.87 t•km^{-2}; in future, local data on discards should be obtained for all gear types and covering all marine organisms.

Fleets and data sources

Fisheries data for 1995-2000 for all commercial species were collated from annual statistics provided by the appropriate ministry in each of the nations where VIa fish are landed. When scaled approximately to the area covered by the *Ecopath* with *Ecosim* (EwE) model, all fisheries combined are estimated to land 1.36 t•km^{-2} (Table 3). This figure represents about 70% of what might be expected as an average over the entire ICES area VIa (1.95 t•km^{-2}; R. Watson, pers. comm.) It is therefore a reasonable preliminary approximation given that the large ICES area VIa fisheries lie somewhat offshore and to the north of the modelled area. Fishery catches were divided into 8 gear types: demersal trawl, beam trawl, midwater trawl, dredge, purse seine, lines (handline and longline), creels and pots and miscellaneous gear types (Table 3). Discard data were added where possible (Table 4).

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Table 3. Total catch per modeled fleet, in tonnes per km^{-2}, in the west coast of Scotland area and landed in France, Ireland, England, Wales and Scotland for the period 1995-2000.

Model group	DTrawl	BTrawl	Mid Trawl	Dredge	Purse	Line	Creel/Pot	Misc.	TOTAL
Seals									0
Cetaceans									0
Seabirds									0
Halibut/turbot/brill	0.004	0			0				0.004
Whiting	0.022	0	0.063		0.003			0	0.088
Other demersals	0.118	0.001	0.001	0	0.001	0.001			0.121
Sharks	0.011	0	0		0.002	0.002	0		0.015
Rays/Skates	0.007	0	0		0.001	0			0.009
Cod	0.022	0	0		0.003	0			0.026
Saithe	0.015	0	0		0.002	0			0.017
Other pelagics	0.079	0	0.009		0.001			0.001	0.089
Crabs/lobsters	0			0	0		0.044	0	0.045
Gurnards	0	0			0				0
Haddock	0.036	0	0		0.008				0.044
Inshore fish	0.021	0	0		0	0	0	0.003	0.024
Salmo					0	0			0
Mackerel	0.012		0.207		0.145	0		0	0.364
Trachurus	0.005		0.228		0.001	0			0.235
Plaice	0.004	0.001			0.001			0	0.006
Sole	0.001	0			0				0.001
Nephrops	0.044			0	0		0.005		0.049
Norway pout	0		0						0
Cephalopods	0								0
Sandeel	0.023		0.002						0.025
Sprat	0		0.025		0		0		0.025
Herring	0.003		0.065		0.045				0.114
Echinoderms									0
Other benthic inves	0.001		0	0.036	0		0.005	0.019	0.061
Prawns/shrimps	0								0
Euphausiids									0
Large zooplankton									0
Polychaetes									0
Small zooplankton									0
Epifauna									0
Infauna									0
Phytoplankton									0
Detritus									0
TOTAL	0.43	0.002	0.599	0.036	0.213	0.003	0.054	0.022	1.36

Demersal trawl fishery

Demersal trawls target mainly bottom-living species. Demersal trawlers range from small inshore vessels to large factory ships in excess of 60 m. The boat (or pair of boats) tows a funnel-shaped net with a weighted ground rope and buoyant headline along the seabed. Forward placed 'otter boards', serve to keep the mouth of the net open. Gadoids such as cod, whiting and haddock, together with monkfish (*Lophius piscatorius*) are the most important demersal species, accounting for 60% of landings (Table 4). In recent years ICES have expressed concerns that both cod and whiting stocks in the west coast of Scotland are outside safe biological limits with spawning stock biomass below precautionary levels (ICES 2004). This is largely caused by increased fishing pressures while recruitment and stock biomass in both species has been declining (Fisheries Research Services 2004). The current ICES management advice for cod is for zero catch in the west coast of Scotland (ICES 2004). Demersal fisheries can target individual species, or assemblages but demersal species are often caught in a mixed demersal fishery.

One of the most valuable targeted fisheries is for Norway lobster (*Nephrops;* known locally as prawns, Dublin Bay prawns, or scampi; Table 3) which is principally fished for in soft muddy habitats by specialized *Nephrops* demersal trawls. Indeed much of the inshore trawl fleet, mostly smaller vessels, relies on this fishery with south west Scotland landing 20.7% of the UK *Nephrops* total (JNCC 1997). In subsequent versions of the model, it would be useful to make the targetted *Nephrops* demersal trawl a separate gear type.

Table 4. Estimated approximate discards, in tonnes per km^{-2}, per modelled fishing fleet for the west coast of Scotland ecosystem. These values could be considerably improved: for method please see text.

Model group	DTrawl	BTrawl	Mid Trawl	Dredge	Purse	Line	Creel/ Pot	Misc	TOTAL
Seals									0
Cetaceans									0
Seabirds									0
Halibut/turbot/brill	2.84691E-02	1.18769E-06							2.84703E-02
Whiting	2.25380E-02	9.40253E-07	2.47558E-02						4.72948E-02
Other demersals	1.38391E-02	5.77348E-07							1.38397E-02
Sharks	1.97702E-03	8.24783E-08							1.97710E-03
Rays/Skates	1.42345E-02	5.93844E-07							1.42351E-02
Cod	4.50760E-03	1.88051E-07	6.18895E-03						1.06967E-02
Saithe	1.97702E-03	8.24783E-08							1.97710E-03
Other pelagics	1.97702E-03	8.24783E-08							1.97710E-03
Crabs/lobsters	3.95404E-02	1.64957E-06							3.95420E-02
Gurnards	1.42345E-02	5.93844E-07							1.42351E-02
Haddock	1.80304E-02	7.52202E-07	3.09447E-02						4.89759E-02
Inshore fish	1.42345E-02	5.93844E-07							1.42351E-02
Salmo									0
Mackerel			2.17427E-02						2.17427E-02
Trachurus			3.42688E-02						3.42688E-02
Plaice	1.42345E-02	5.93844E-07							1.42351E-02
Sole	1.42345E-02	5.93844E-07							1.42351E-02
Nephrops	7.11727E-02	2.96922E-06							7.11757E-02
Norway pout	3.95404E-04	1.64957E-08							3.95420E-04
Cephalopods									0
Sandeel									0
Sprat	3.95404E-04								3.95404E-04
Herring	3.95404E-04	1.64957E-08	6.79686E-03						7.19228E-03
Echinoderms	3.16323E-02	1.31965E-06							3.16336E-02
Other benthic inverts	4.74485E-02	1.97948E-06							4.74504E-02
Prawns/shrimps	3.95404E-02	1.64957E-06							3.95420E-02
Euphausiids									0
Large zooplankton									0
Polychaetes									0
Small zooplankton									0
Epifauna									0
Infauna									0
Phytoplankton									0
TOTAL	0.395008	0.000016	0.124698	0	0	0	0	0	0.51972

Stratoudakis *et al.* (1999) present discard data for the general west Scotland demersal fleet, and Bergmann *et al.* (2002) and Stratoudakis *et al.* (2001) discuss discard composition for *Nephrops* trawls in the Firth of Clyde area. Where possible, the published figures were converted to percentage of total retained catch to obtain approximate discard values. These percentage rates were then extrapolated to the west coast of Scotland model area. Where reported discards included non-commercial species, such as echinoderms, we based the discard percentage on an approximately similar benthic animal. Gear and discard practices will likely differ somewhat in the model area from the Firth of Clyde and so our discard values here very much represent a first approximation. More precise values should be easily obtainable with the help of experts on the local fisheries.

Beam trawl fishery

Beam trawlers or 'Beamers' use a metal beam up to 12m in length to hold the mouth of the trawl open. 'Tickler' chains in front of the beam raise fish from the seabed to ensure they are taken up by the net (Fisheries Research Services 2004). Beamers primarily catch flatfish from a number of functional groups in the model - 'halibut, turbot and brill', 'plaice', and 'other demersal species' (Table 4). This fleet also generates some discards, mainly of *Nephrops,* benthic invertebrates, prawns, shrimps, crabs and lobsters. Assuming the same discard rule as for the demersal trawl and total catch of 0.0224 t•km^{-2}, beam trawlers would generate discards of about 0.0002 t•km^{-2} (Table 4). More precise values should be easily obtainable with the help of experts on the local fisheries.

Midwater trawl fishery

The midwater trawl fishery is the most important pelagic fishery on the west coast of Scotland. Vessels or pairs of vessels between 15 and 50 m tow large midwater trawls at target depth for mackerel, horse mackerel, herring and blue whiting. This fleet collects about 0.599 t•km^{-2} (Table 3). Using the same sources as above, we estimated that it also discards a total of 0.125 t•km^{-2} of other species per year (mainly haddock, horse mackerel and whiting) (Table 4).

Scallop dredge

Dredging is primarily used to capture king scallops (*Pecten maximus*), which are assigned to the 'other benthic invertebrates' group in the model. This is the second most valuable shellfish species on the west coast of Scotland. Queen scallops (*Aequipecten opercularis*) are also caught by this method. A dredge consists of bed of steel rings attached to a toothed bar. The toothed bar rakes the scallops from the seabed that are then carried along to a net bag at the back of the dredge (Fisheries Research Services 2004). Dredgers, commonly called 'clammers' in Scotland, range in size from small boats towing two or three dredges to large vessels capable of towing more than 20 at a time (Fisheries Research Services 2004). The approximate estimate in Table 3 suggests that this fleet takes 0.36 t•km^{-2} of organisms per year in the study area. We have no information on discards.

Purse seine

Purse seines are used to capture dense shoals of pelagic fish found near the surface. The shoal is surrounded by a curtain of net, which is then pursed under the shoal. This fishery mainly targets mackerel and herring but industrial fish species, such as horse mackerel and blue whiting, are also caught (Fisheries Research Services 2004). No discards are reported for this fleet in the west coast of Scotland. The total catch of the purse seine fleet is estimated at 0.21 t•km^{-2}•year^{-1} (Table 3).

Longliners

Scotland has a small longline fleet. Longlines consist of a main line set to fish just above the seabed, with many short lines with baited hooks attached. Most longline boats are less than 10 m although there has been a recent increase in the technique with a small number of larger boats using this system (Fisheries Research Services 2004). It is estimated that this gear type lands a total of 0.003 t•km^{-2}•year^{-1}. The main groups caught by this fleet are sharks, predominantly dogfish, and other demersal fish (Table 3). The SW Scotland longline catch of dogfish, *Scyliorhinus canicula*, accounts for 4% of the UK total (JNCC 1997). We have no information on discards.

Creels and pots

The creel and pot fishery is important for many west coast communities. Most vessels are small, often operated by one person. Vessels deploy lines of small baited traps along the sea bed, which are later retrieved. It is estimated that this gear types lands a total of 0.05 t•km^{-2}•year^{-1}. Much of the fleet targets *Nephrops*, which can fetch premium prices compared with trawled individuals. Squat lobsters are often caught as by-catch in *Nephrops* creels. Creels and pots are also used to catch edible crabs, swimming crabs, lobsters and crawfish (*Palinurus vulgaris*). Again these tend to be small but valuable operations, particularly in small fragile coastal communities (JNCC 1997). Most of the catch for this gear type was assigned to the *Nephrops* and crabs and lobsters functional groups (Table 3). No discards are reported for this fishery. We have no information on discards or ghost fishing by discarded pots.

Miscellaneous gear types

Miscellaneous gear types include fishing by hand, such as for scallops and razorfish (*Ensis* spp) which are collected by divers. On the west coast of Scotland scallops fished by this method have a high commercial value. Cockles and periwinkles are also hand picked low in the intertidal zone during low tides. The fishery mainly targets the 'other benthic invertebrates' group, as well as the inshore fish group, for a total of 0.02 $t \cdot km^{-2} \cdot year^{-1}$ for the west coast of Scotland (Table 3). No discard information is available for these fisheries. However, given the techniques employed it is likely that discard would be minimal.

MODEL CHARACTERISTICS AND PERFORMANCE

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Abstract

An *Ecopath* model was constructed to describe and analyse the west coast of Scotland ecosystem. As opposed to traditional approaches, this type of model considers the whole ecosystem rather than its separate components. *Ecopath* models generate a 'snapshot' of the system at one moment in time and use mass-balance principles to estimate flows of organic matter or energy among components. Ecosystem structure indices were used to evaluate the structure of the whole food web, while specific indices such as mortalities, predation, and consumption rates were used to analyse the importance of each species within the foodweb. The ecosystem represents more than 75 species totalling a biomass of 277 t•km^{-2}. The effort made to put all the biological information on the west coast of Scotland species together also allowed us to focus attention on uncertainties in our knowledge on the ecosystem's structure and to identify where research efforts should be directed in order to gain a better understanding of this ecosystem.

Introduction

Food Web

The model represents more than 75 species aggregated in 37 functional groups. The total biomass of the system is 277 t•km^{-2} or 177 t•km^{-2} if we exclude detritus. 2,590 tons of marine organisms per km^{-2} are consumed annually (Table 5). Figure 5 shows the main linkages in the west coast of Scotland food web, plotted against trophic level. Important commercial species are modelled reasonably thoroughly but the key role of shrimps, krill, small zooplankton, epifauna and polychaetes in trophic levels 2 to 3 is evident. If this model is to be adapted for use in sea lochs or for human-made reefs, additional benthic organisms, such as crabs, encrusting colonial animals, benthic algae, ascidians crinoids and sponges will likely have to be modelled more explicitly. Note also the omission of explicit model groups for jellyfish, comb-jellies and sea gooseberries, pelagic sea squirts and other jellies, chaetognaths and the microbial loop organisms.

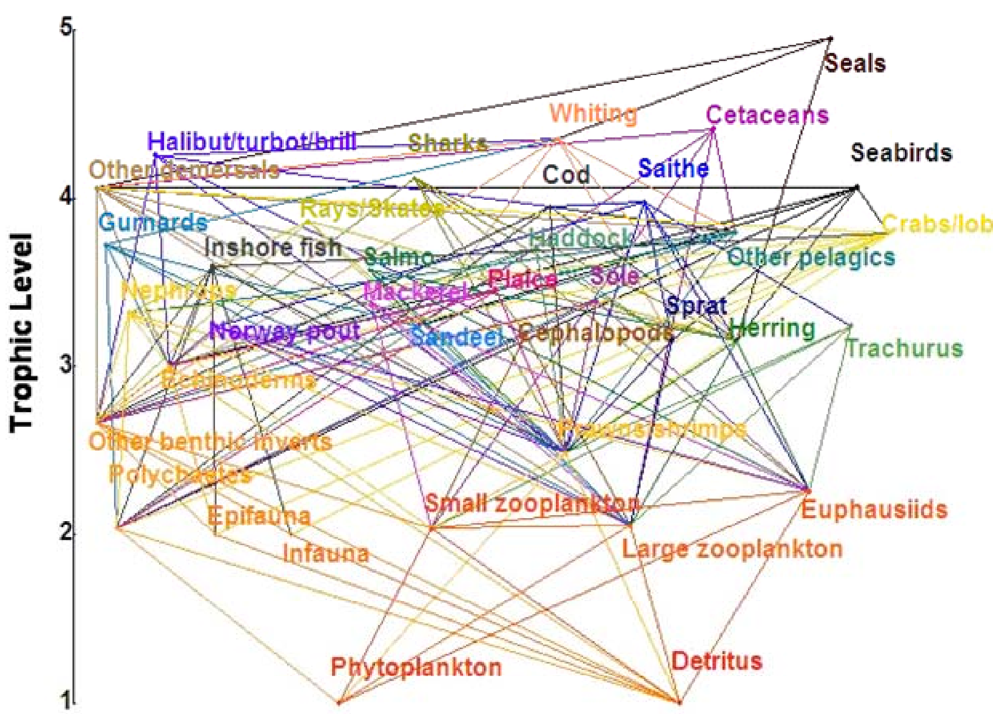

Figure 5. Diagram of the food web simulated by the West Scotland ecosystem model.

Morissette, L. and Pitcher, T.J. 2005. Model Characteristics and Performance. *In*: Haggan, N. and Pitcher, T.J. (eds) Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs, pp. 30-41. UBC Fisheries centre Research Reports 13(4), 67pp.

Table 5. System flows from *Ecopath*.

Sum of all consumption	2590.069	t•km^{-2}•year^{-1}
Sum of all exports	4358.54	t•km^{-2}•year^{-1}
Sum of all respiratory flows	1241.974	t•km^{-2}•year^{-1}
Sum of all flows into detritus	5481.891	t•km^{-2}•year^{-1}
Total system throughput	13672	t•km^{-2}•year^{-1}
Sum of all production	6267	t•km^{-2}•year^{-1}
Mean trophic level of the catch	3.5	
Gross efficiency (catch/net p.p.)	0.000335	
Calculated total net primary production	5600	t•km^{-2}•year^{-1}
Total primary production/total respiration	4.509	
Net system production	4358.026	t•km^{-2}•year^{-1}
Total primary production/total biomass	31.608	
Total biomass/total throughput	0.013	
Total biomass (excluding detritus)	177.168	t•km^{-2}
Total catches	1.874	t•km^{-2}•year^{-1}
Connectance Index	0.288	
System Omnivory Index	0.175	
Throughput cycled (including detritus)	61.74	t•km^{-2}•year^{-1}
Finn's cycling index	0.54	% of total throughput
Finn's mean path length	2.05758	
Finn's straight-through path length	1.35502	without detritus
Finn's straight-through path length	2.04655	with detritus
Throughput cycled (inc. detritus)	61.74	t•km^{-2}•year^{-1}
Finn's cycling index	0.54	% of total throughput
Finn's mean path length	2.05758	

System Flows

The sum of all flows into an ecosystem, i.e., imports, exports of usable materials or energy (e.g., fishery catches, or emigration), respiration and flows between boxes is termed the total system throughput (Christensen *et al.* 2000). In the west coast of Scotland model, this represents 13,672 t•km^{-2} (Table 5).

Total production in the system reaches 6267 t•km^{-2}, and 90% of that energy is produced *via* primary producers (5600 t•km^{-2}). The gross efficiency (the percentage of the primary production collected by fisheries) is 0.03%. All of the modelled fisheries combined extract (including estimated discards) a total of 1.87 t•km^{-2} per year, at an average trophic level of 3.5, which is relatively high (Pauly and Christensen 1997; Pauly *et al.* 1998) (Table 5) compared with other depleted marine areas where extensive invertebrate fisheries reduce the TL of catches.

Main species, main prey

Today's west coast of Scotland ecosystem appears to be dominated largely by invertebrates (other than microbial organisms, which have not been modelled explicitly in this preliminary model). The most important commercially exploited species are shrimp and prawns. This group has the largest biomass in the ecosystem after detritus and phytoplankton (16 t•km^{-2}) (Figure 6), followed by epifauna with about 11 t•km^{-2}.

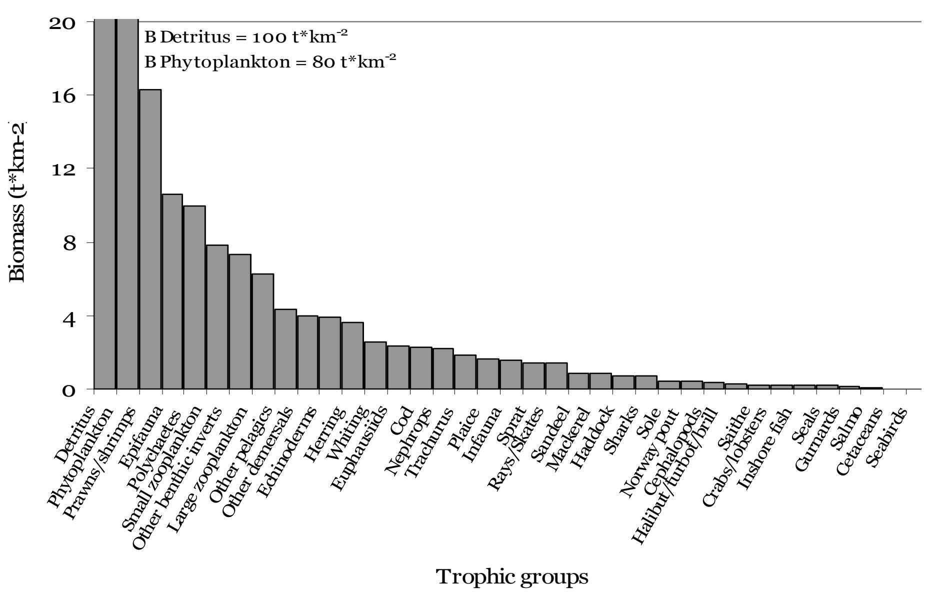

Figure 6. Biomass (t•km^{-2}) of all the trophic groups modelled for the Scottish West Coast ecosystem. The total biomass of the ecosystem was 277 t•km^{-2}.

The most abundant fish groups are 'other pelagic fish', mainly blue whiting (*Micromesistius poutassou*), and 'other demersal fish' (mainly flatfish and gadoid spp.) with about 4 t•km^{-2} of biomass each

Prawns and shrimps, other pelagics and other demersals account for over 50% of the total biomass of commercially-exploited species. Other species like herring, whiting, cod and Norway lobster are also important in terms of biomass (Figure 7).

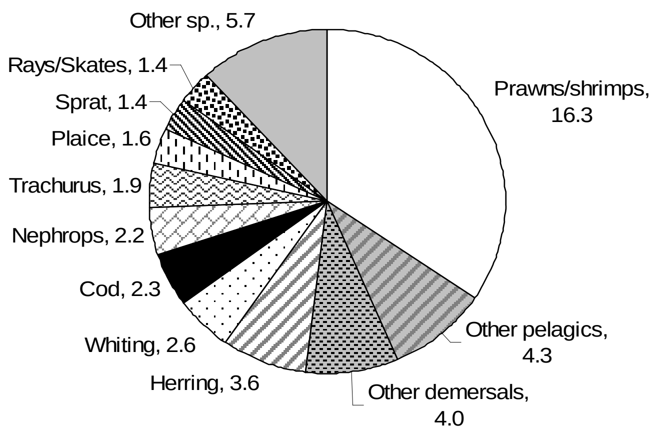

Figure 7. Main commercial species (t•km^{-2}) in the west coast of Scotland ecosystem.

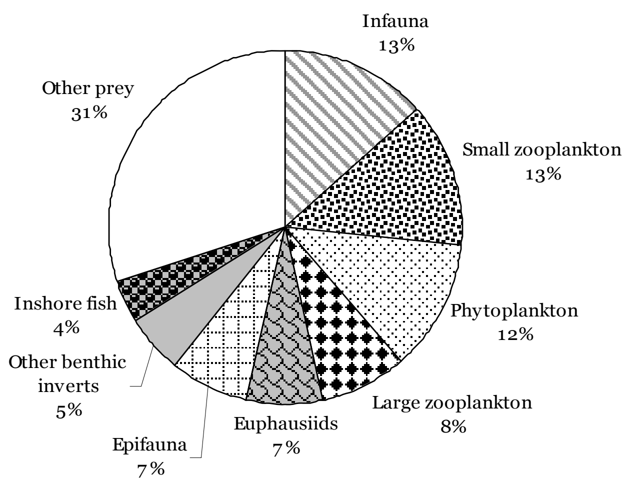

Figure 8. Main prey species in the west coast of Scotland ecosystem.

In the west coast of Scotland model, more than 50% of the consumption involves only five trophic groups: infauna, zooplankton (large and small), phytoplankton and euphausiids (Figure 8).

This predation on lower trophic level prey is mainly because the ecosystem appears to be dominated by invertebrates and small species of fish.

Predation and other mortality

Under equilibrium, each trophic group can be represented by three sources of instantaneous mortality: predation (M2), catch (F) and other, or unexplained, mortality (M0). The total mortality (Z) should be compensated by the production of each group.

The highest values of total mortality, Z, (in absolute terms) are found in the lower part of the food chain: phytoplankton, epifauna, infauna and small zooplankton (Table 6).

Among commercial species, the inshore fish and crab and lobster groups had the highest total mortality, while sharks, halibut, turbot and brill, had the lowest.

Fishing mortality, F, has its greatest impact on mackerel, crabs and lobsters, and inshore fish, which are also groups with high predation mortality. Nephrops, sandeels and inshore fish were the commercial species groups with the greatest unexplained mortality (Table 6).

Five groups: benthic invertebrates, prawns and shrimps, demersal fish, small zooplankton and echinoderms accounted for more than 50% of predation mortality in the WCS model (Figure 9; Table 6), while other demersals, cod, whiting and other pelagics account for more than 60% of predation mortality on fish (Figure 10). Fishing comes after these four predators as the fifth source of "predation" mortality on fish groups.

While fish predation appears to have a greater impact on smaller fish groups in the model, fishing mortality evidently has a greater impact on big fish (Figure 11).

As usual, fractional trophic levels were estimated by *Ecopath* from the weighted average of prey trophic levels. They vary from 1 by definition for phytoplankton and detritus to 4.6 for upper trophic level predators such as seals and cetaceans (Table 6). The 37 functional groups were aggregated into a simple food web with ten discrete trophic levels following Christensen *et al.* (2000). Most fisheries on these fractional trophic levels occur at trophic level III and IV (Figure 12). The fishery also targets higher trophic levels, showing that this ecosystem is heavily exploited.

Table 6. Distribution of the different annual causes of mortality and trophic level (TL) estimation for the west coast of Scotland trophic groups. Z = Total instantaneous annual mortality rate; F = Annual fishing mortality rate; M2 = Annual predation mortality rate; M0 = Other annual mortality.

Model Group	Z	F	M2	M0	TL
Seals	0.07	0.00	0.06	0.01	4.99
Cetaceans	0.09	0.00	0.00	0.09	4.42
Seabirds	0.80	0.00	0.64	0.16	4.07
Halibut/turbot/brill	0.35	0.12	0.16	0.07	4.25
Whiting	0.70	0.05	0.56	0.08	4.36
Other demersals	0.77	0.03	0.68	0.05	4.16
Sharks	0.16	0.02	0.12	0.01	4.14
Rays/Skates	0.48	0.02	0.37	0.10	3.86
Cod	0.75	0.02	0.62	0.11	3.94
Saithe	0.87	0.07	0.72	0.07	3.98
Other pelagics	0.87	0.02	0.78	0.07	3.80
Crabs/lobsters	4.50	0.35	3.70	0.45	3.80
Gurnards	1.40	0.10	0.92	0.39	3.72
Haddock	1.00	0.13	0.67	0.20	3.71
Inshore fish	5.00	0.19	4.31	0.50	3.60
Salmon	0.80	0.01	0.63	0.16	3.57
Mackerel	1.02	0.46	0.51	0.05	3.37
Trachurus	0.70	0.14	0.42	0.14	3.24
Plaice	0.98	0.01	0.76	0.20	3.45
Sole	0.80	0.03	0.66	0.10	3.38
Nephrops	3.00	0.05	1.44	1.51	3.32
Norway pout	2.00	0.00	1.80	0.20	3.23
Cephalopods	3.00	0.00	2.50	0.50	3.19
Sandeel	3.00	0.03	2.37	0.60	3.23
Sprat	1.90	0.02	1.50	0.38	3.15
Herring	1.80	0.03	1.44	0.33	3.15
Echinoderms	4.00	0.01	3.67	0.32	3.00
Other benthic invertebrates	6.00	0.01	5.69	0.30	2.67
Prawns/shrimps	3.00	0.00	2.75	0.25	2.47
Euphausiids	9.00	0.00	7.76	1.24	2.26
Large zooplankton	10.00	0.00	8.79	1.21	2.05
Polychaetes	5.00	0.00	2.15	2.85	2.04
Small zooplankton	18.00	0.00	14.40	3.60	2.03
Epifauna	20.00	0.00	7.68	12.32	2.00
Infauna	20.00	0.00	14.62	5.38	2.00
Phytoplankton	70.00	0.00	12.79	57.21	1.00

Mixed trophic impacts

The *Ecopath* Mixed Trophic Impact (MTI) routine assesses direct and indirect interactions between species. It indicates the effect that a small biomass change in one group would have on the biomass of other groups (Christensen *et al.* 2000). The MTI tool was used to demonstrate the positive or negative impacts of major predators on other trophic groups in the model, as well as the magnitude of these direct and indirect impacts.

Predators usually have a negative impact on their prey. This was the case for other demersals, cod and whiting, the main predators of fish prey in the ecosystem (Figure 10). Their biggest impacts were on whiting, rays and skates, and saithe (Figure 13). On the other hand, these predators had some slight positive impacts on some species such as gurnards and inshore fish.

Although other demersal species have a huge negative effect on whiting, the presence of seals and individuals of their own species was beneficial for them (Figure 13). Because of their size and their behaviour, seals are generally important predators in north temperate marine ecosystems (e.g., Morissette *et al.* submitted). In the west coast of Scotland ecosystem, their biggest negative impact was on whiting, while they also had a slight positive impact on the sprat and ray and skates groups.

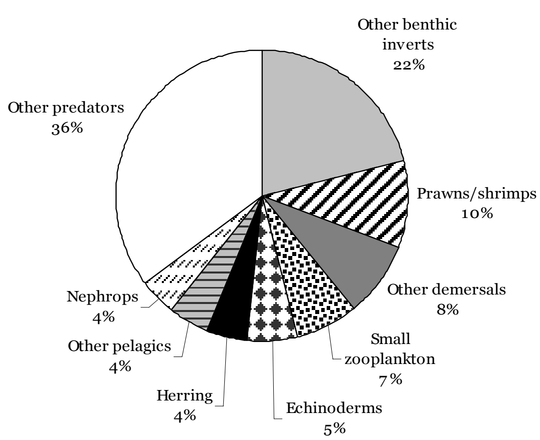

Figure 9. Main predators on all prey in the west coast of Scotland ecosystem model.

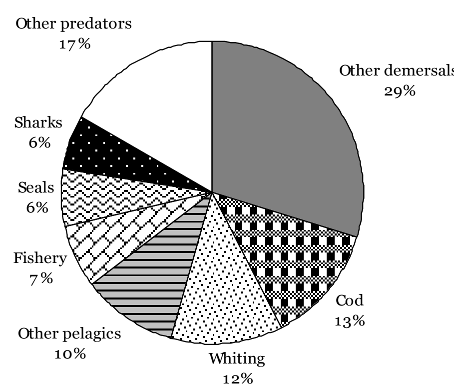

Figure 10. Main predators on fish prey in the west coast of Scotland ecosystem model.

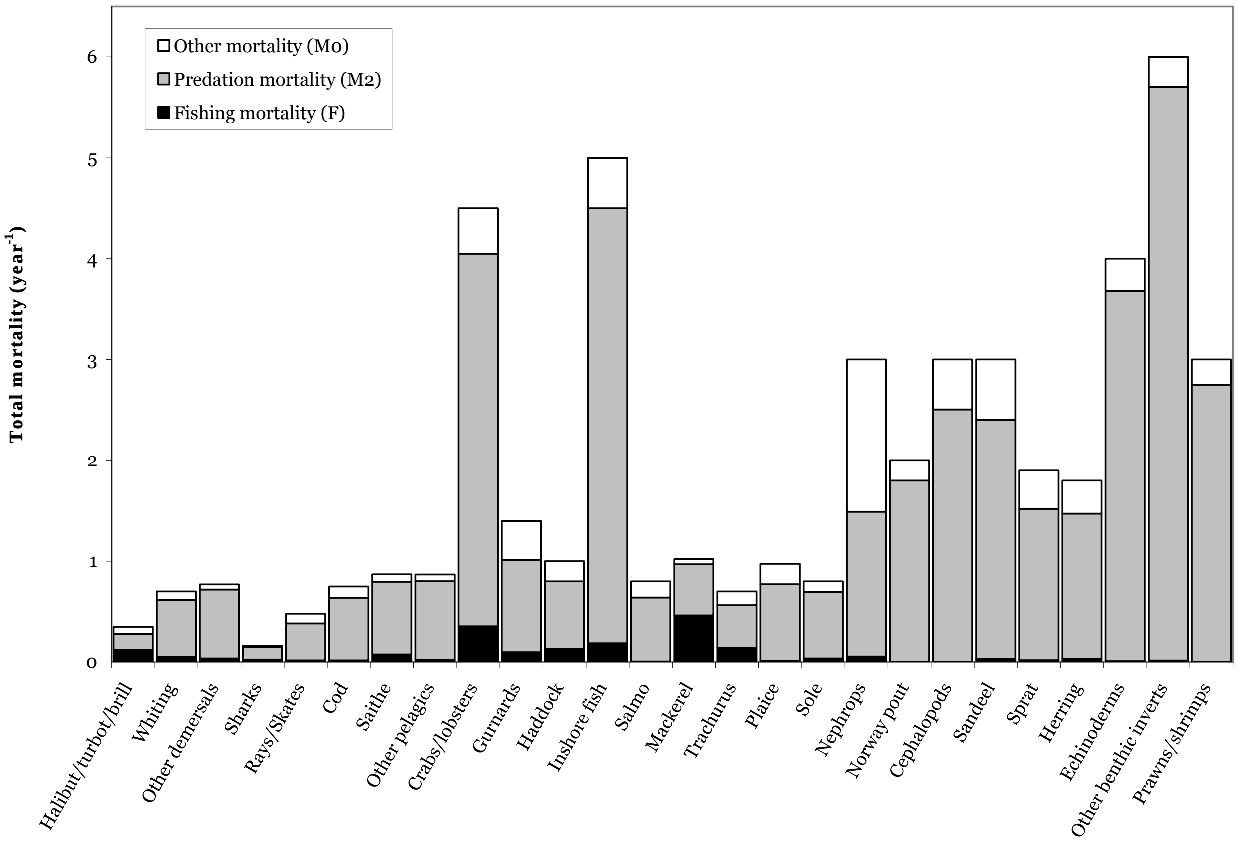

Figure 11. Breakdown of total annual mortality (Z) into fishing (F), predation (M2) and unexplained (M0) mortalities for commercial species of the west coast of Scotland.

The overall positive impact of some predators on their prey resulted from predators targeting more than one kind of organism. For example, a predator on species X, may also feed on species that compete with X for the same resources or on species that are also predators of that species X. Sometimes, this effect is even greater than the predation itself, leading to an overall positive impact of the predator to its prey.

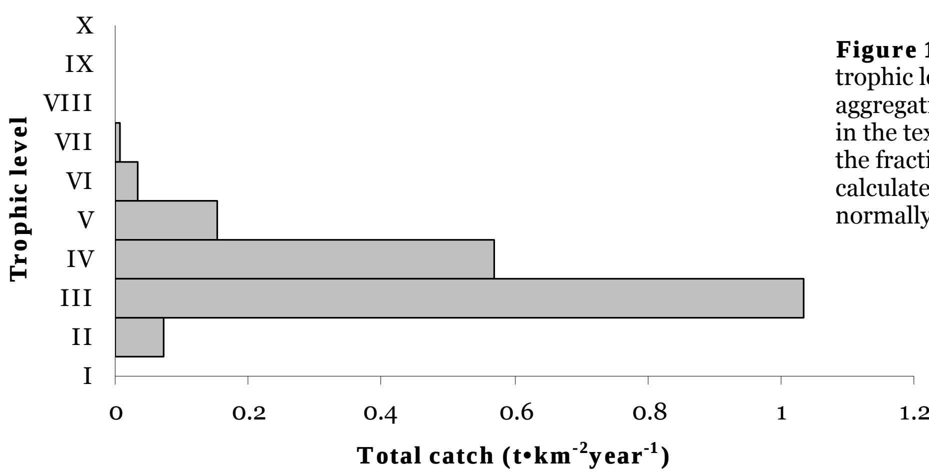

Figure 12. Catch per discrete trophic level provided by the aggregation process described in the text. (Note these are not the fractional trophic levels calculated from diet as normally quoted.

The same routine was then repeated for the different fisheries present in the west coast of Scotland model. In the majority of cases, fisheries had a negative impact on the trophic groups of the ecosystem. The midwater trawl fishery had the greatest impact on seals, seabirds, whiting and salmon (Figure 14). This negative impact represents competition for the same resources. This fishery doesn't target seals or seabirds, but many of the species they feed on. Compared with trawlers, fisheries such as longlines, dredges or miscellaneous techniques had a minor effect on trophic groups in the WCS model.

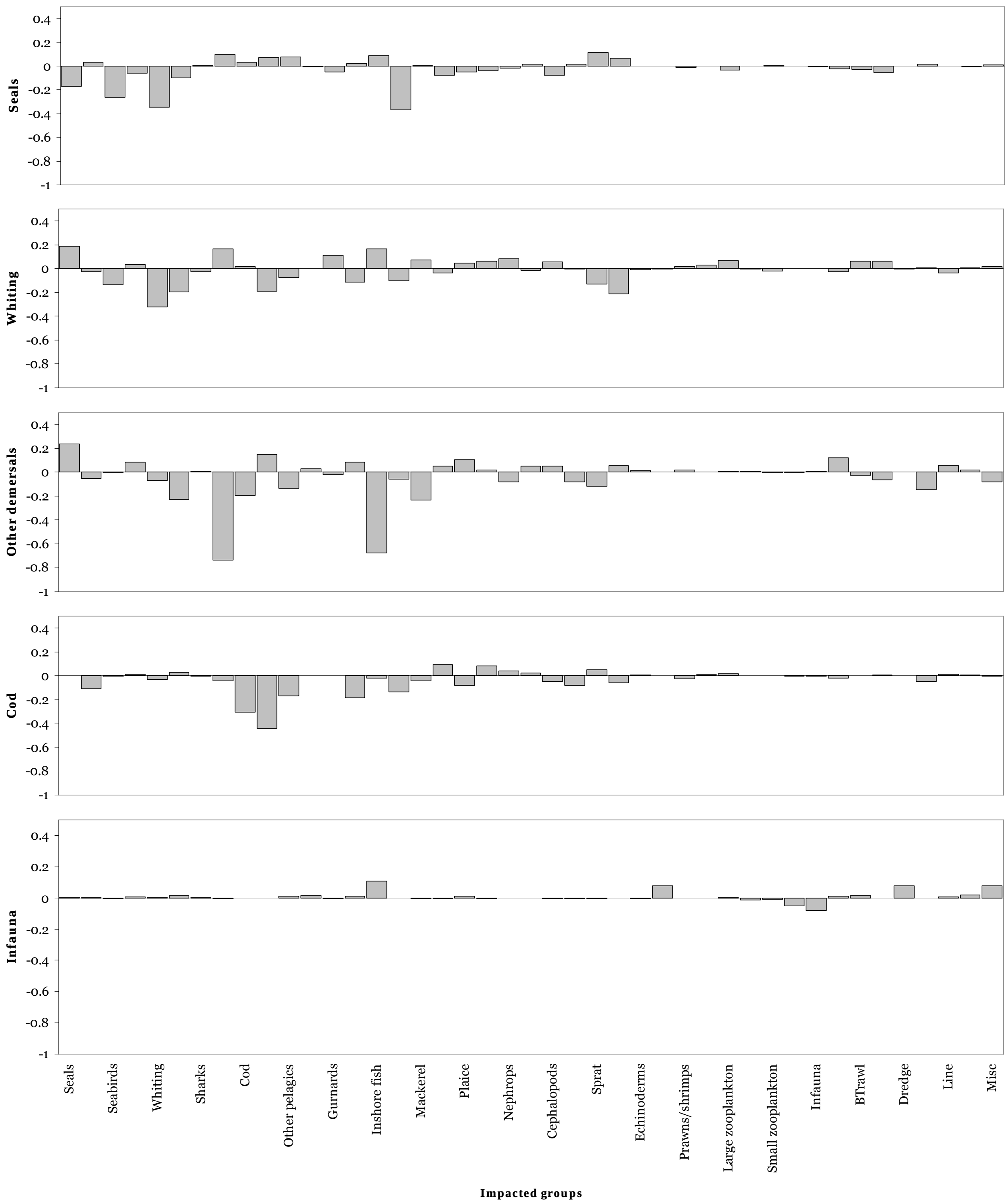

Figure 13. Mixed trophic impact plots for the main groups in the west coast of Scotland ecosystem model.

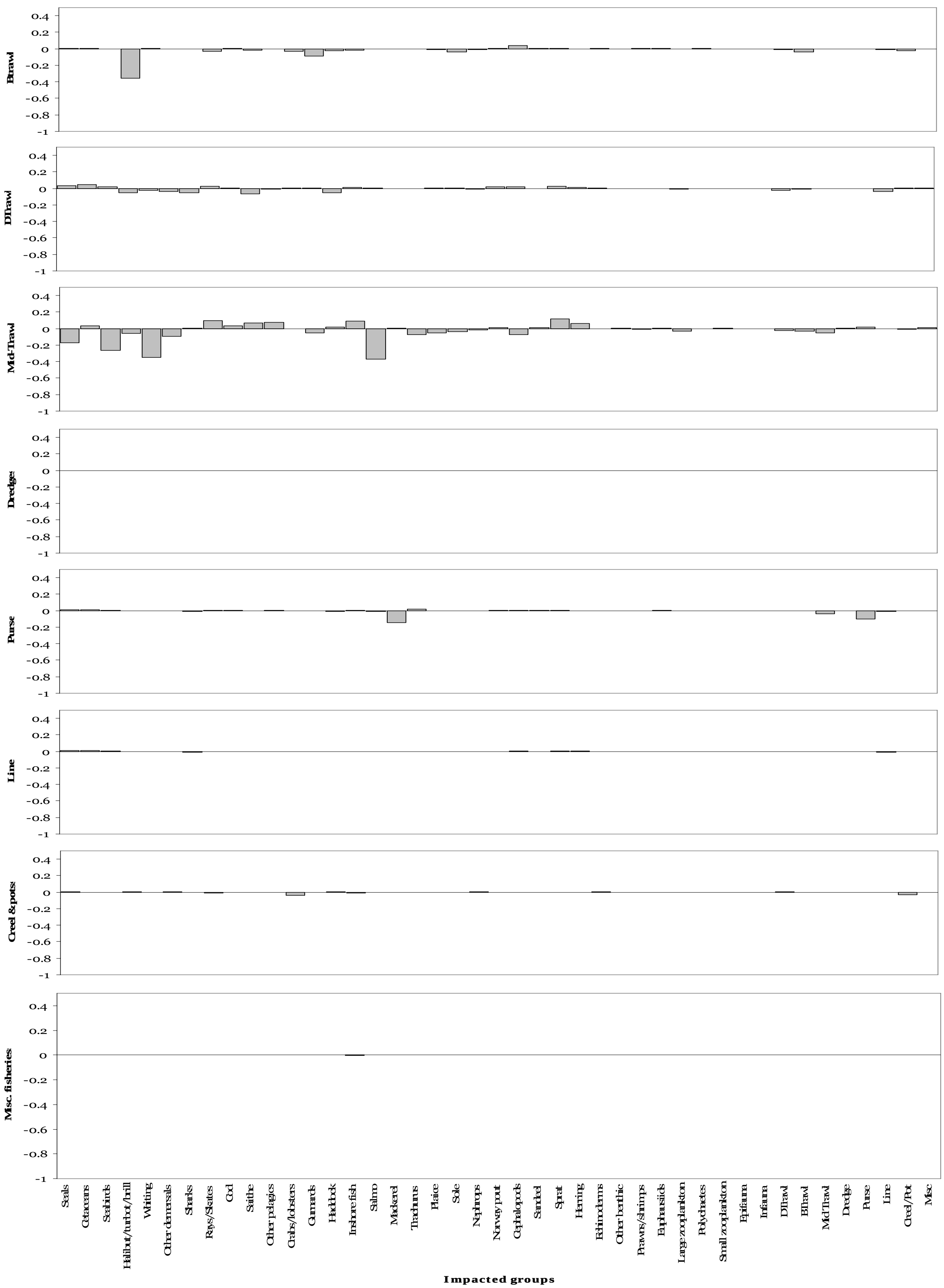

Figure 14. Mixed trophic impact plots for the 8 different fisheries in the west coast of Scotland ecosystem model.

Biomass pyramid

The overall distribution of biomass between fractional trophic levels of the west coast of Scotland provides a a simple way to compare it with other ecosystems. Biomass pyramids are drawn such that the volume of each compartment representing a fractional trophic level is proportional to the total biomass of that level.

Two systems could have the same total biomass but have completely different distributions within the foodweb. The WCS biomass pyramid (Figure 15) is relatively sharp-pointed, indicating that the overall TE is high and that many predation and trophic levels could be supported by the primary producers.

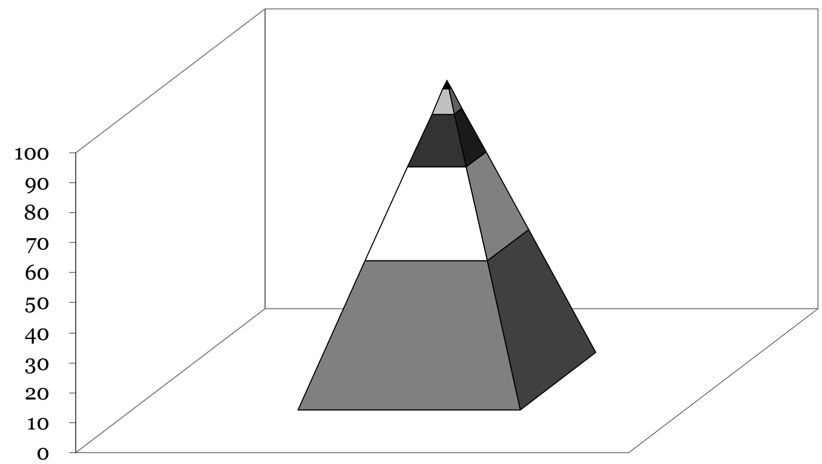

Figure 15. Trophic pyramid of the total biomass in the west coast of Scotland marine ecosystem, separated into five discrete trophic levels; maximum tropic level is 4.2. Vertical axis is percent of total biomass in model.

Comparison with the English Channel model

We compared the west coast of Scotland model with an English Channel model (Stanford and Pitcher 2004) to evaluate similarities between the two ecosystems and the reliability of values used in the current model.

Total biomass for both systems was fairly similar (277 vs 228 t•km^{-2}); however, there were huge differences in terms of species density in the two models. The west coast of Scotland model has a lot more seals, cetaceans, seabirds, whiting, demersal fish, sharks, cod and plaice than the English Channel (EC). However, the latter showed a predominance of crabs and lobsters, gurnards, mackerel, and echinoderms.

These differences are difficult to explain or justify, because each ecosystem is unique and shows a species composition of its own. However, some points require attention:

- The density of detritus was set to 1 in the EC model and another group of detritus (discarded catch) was included. In the WCS model, the detritus density comes from a gross estimate for the North Sea (Mackinson 2001);
- Cetaceans biomasses for both models come from aerial survey, so we can assume a real density difference between both systems;
- Seal and seabird biomasses come from a marine mammal research centre and a bird census in the EC, while they are estimated from *EE* in the WCS model and may estimate more seals than there really are. However, the seal and seabirds biomasses in the WCS model are similar to what we find in the north Atlantic models;
- The only local biomass in the WCS model is for gurnards. All other biomasses are calculated by the model. Consequently, it is likely that the estimates are overestimated (if we compare with the results presented in the EC model) in the case of crab, lobsters, and mackerel and low for whiting, demersal fish, sharks, cod, and plaice.

P/B ratios

Stanford and Pitcher (2004) report a P/B of 0.04 year^{-1} for seals, seabirds and cetaceans. This appears to be a textual error, as the value they used in their *Ecopath* model was 0.4. This is very different from the WCS model values, which are much closer to the 0.04 reported in the publication (Stanford and Pitcher 2004). This mistake creates a huge discrepancy between EC and WCS models. In other ecosystems, such as the northern Gulf of St. Lawrence, P/B estimates are much closer to the 0.04 used in the WCS model, which gives us reasons to believe this estimate makes sense. The P/B ratios for the crab and lobster and echinoderm groups come from assumptions or other models.

Q/B ratios

The difference in cetacean Q/B between the WCS and EC models comes from the difference in the biomasses. The Q/B estimates are both estimated from the individual ration in body weight per day estimated by Innes *et al.* (1987).

The Q/B for crabs and lobsters appear to be overestimated in the WCS model. The value of 30 $year^{-1}$ is estimated by the P/Q ratio and is thus less accurate. We should base our estimates on comparisons with other models (North Sea [Mackinson 2001], northern Gulf of St. Lawrence [Morissette *et al.* 2003], and EC [Stanford and Pitcher 2004]) for a more accurate estimation.

The Scottish mackerel and sole estimates come from Fishbase, while the source of information is missing for the EC. We can assume our values are correct, even if they are lower than those used to balance the EC model.

Diet compositions

Seals
Seal diet in the EC model came from the North Sea and Hebrides regions. 63% of seal diet is composed of cod, pollack, sandeels and other large bottom fish and flatfish. In the WCS model, data for seals came from local literature, adjusted for balancing the model. Whiting, herring and other demersal fish account for 87% of seal diet. Sandeel was described as a dominant fish in the literature but their proportion in the diet for the WCS model was reduced to obtain mass balance and to allow efficient *Ecosim* scenarios.

Cetaceans
In the EC model, cetaceans' diet is mainly composed of cephalopods and mackerel, followed by sprat (*Sprattus sprattus*), pilchard (*Sardinops sagax*) and scad (*Trachurus trachurus*). This is very different than what is seen in the WCS model, where cephalopods and mackerel are insignificant. Cetaceans mainly consume pelagic fish and large zooplankton in this model. The data used in the EC model come from approximate diet estimation for many cetaceans of the world, while data in the WCS model was based on stomach contents analyses from the northwest Atlantic.

Seabirds
In the EC model, seabirds fed mainly on sandeels, sprat and mackerel (61% of the diet), while they feed mainly on herring, polychaetes, echinoderms, sprat and sandeel in the WCS model (79% of their diet). This is quite analogous, even if the data sources were different for both models.

Whiting
Whiting diet in the EC ecosystem was composed of sandeels, small gadoids and zooplankton, while the one used in the WCS model was composed of herring, sprat, and other demersal and pelagic fish. EC diet for whiting was adjusted from information in the North Sea, the WCS diet came from local information. Apart from the fact that zooplankton seems low in the WCS whiting diet, there is a strong case for using local data for diet information.

Other demersals
This group had a diet composed of benthic invertebrates, pelagic fish and prawns/shrimps in WCS while the same group in the EC model fed on small demersals and gadoids. In the description of data sources for the EC model (before the diet was adjusted for balancing the model), the diet composition was similar to what used in the WCS model (benthic invertebrates, whiting and other finfish). The difference is because the diets had to be changed in order to reach mass balance.

Sharks
Sharks in both models fed mainly on cephalopods. However, the diet of sharks is much more diverse in the WCS than in the EC model, where they fed only on 5 different groups. In the WCS model, they fed on most groups but mainly on cephalopods, benthic invertebrates and prawn/shrimp. In the EC model the diet information came from the coast of France, where sharks feed almost exclusively on cephalopods. In the WCS model, we opted for a diet based on Mackinson (2001).

Cod
In the EC model, cod fed mainly on crab, shrimp, juvenile plaice, small gadoids (cannibalism) and deposit feeders. This was similar to what we have in the WCS model, where cod consume prawns/shrimps, pelagic fish, and herring. Cannibalism was also important for that group in the WCS (about 7.7%, compared to 13.2% in EC).

Crab/lobsters
This group fed mainly on detritus (for crabs) and echinoderms (for lobster) in the EC model, while they fed on a variety of benthic invertebrates and some demersal feeders in the WCS. The major difference between the two diet compositions was that this group doesn't seem to consume detritus in the WCS. Part of this difference may be because the group is an aggregation of many different species in the WCS and it's mainly crabs that are known to feed on detritus. This particularity is probably lost in the aggregation as the trophic group represents too many different species.

Gurnards
In the EC model, gurnard diet was mostly composed of deposit feeders, zooplankton and shrimps. In the WCS model, this group fed essentially on shrimp with some zooplankton. Diets for both models were therefore similar.

Mackerel
Mackerel diet in the EC comes from the mid-north Atlantic (Warzocha, 1988), while it's based on the North Sea (Mackinson 2001) in the WCS model. Mackerel in both models fed mainly on zooplankton, as would be expected.

Plaice
Plaice fed mainly on benthic invertebrates in both models. The only difference wss that 22% of plaice diet in the EC was allocated to imports.

Sole
Here again, benthic species were the major source of food for both models. Diet information is therefore similar, even though the data sources are different, (Belgium, North Sea and Spain for EC and only North Sea for WCS).

Herring
While herring fed mainly on large zooplankton, prawns/shrimps and other benthic invertebrates in the WCS model, they fed mainly on zooplankton and on small demersal fish in the EC model. However, the diet fractions in the EC model do not sum to 1.000 (see Table 2.27 in Stanford and Pitcher 2004), so it is hard to see if this diet information really was comparable. The diet information for herring came from a study in the Irish Sea for the EC model (Rice 1963), and from Mackinson (2001) in the present model.

Echinoderms
Echinoderms had a wider diet composition in the WCS model, feeding mainly on detritus and benthic invertebrates (24% each) but also on epifauna and polychaetes. In the EC model, echinoderms fed mainly on detritus (73%) but also on different benthic invertebrates and primary production. The data came from northwest Atlantic in the EC model and from the North Sea in the WCS model.

Prawns/shrimps
Prawns and shrimps fed mainly on detritus but also on zooplankton. This was true for both models, where diet composition was very similar.

Model 'Pedigree'

The 'pedigree' of an *Ecopath* input is a coded statement categorizing the origin and quality of the source data. See Table 1 in Christensen *et al.* (2000) for an example of the available choices for the quality of Biomass input. The routine combines these individual inputs to derive an overall 'pedigree' or index of model 'quality'. A model is of high quality when it is constructed mainly using parameters based on data from the system represented. The pedigree index values scale from 0 for a model that is not rooted in local data up to 1 for a model that is fully rooted in local data.

Table 7. Pedigree of biomass (B), production (P/B), consumption (Q/B), diet and catch inputs for the trophic groups of the west coast of Scotland *Ecopath* model. The overall pedigree of this model was 0.29. The different numbers refer to confidence limits (+/- %) as follows: 1=10; 2=20; 3=30; 4=40; 5=50; 6=60; 7=70; 8=80. "*x*" indicates that the parameter was estimated by the model, while "-" indicates that no data were calculated.

	B	P/B	Q/B	Diet	Catch
Seals	4	7	4	4	-
Cetaceans	6	7	5	5	-
Seabirds	*x*	8	8	5	-
Halibut/turbot/brill	*x*	7	5	5	5
Whiting	*x*	8	5	4	5
Other demersals	*x*	7	*x*	5	5
Sharks	*x*	4	7	7	5
Rays/Skates	*x*	4	7	7	5
Cod	*x*	7	5	4	5
Saithe	*x*	5	5	5	5
Other pelagics	*x*	*x*	4	7	5
Crabs/lobsters	*x*	7	*x*	5	5
Gurnards	1	7	*x*	7	5
Haddock	*x*	7	5	7	5
Inshore fish	*x*	8	*x*	7	5
Salmo	*x*	2	2	4	5
Mackerel	*x*	7	5	7	5
Trachurus	*x*	7	5	7	5
Plaice	*x*	7	5	5	5
Sole	*x*	8	5	7	5
Nephrops	1	7	7	3	5
Norway pout	*x*	7	5	4	5
Cephalopods	*x*	7	*x*	7	5
Sandeel	*x*	8	5	7	5
Sprat	*x*	8	5	7	5
Herring	*x*	7	5	5	5
Echinoderms	*x*	7	*x*	7	5
Other benthic inverts	*x*	7	*x*	7	5
Prawns/shrimps	*x*	8	*x*	4	5
Euphausiids	*x*	7	*x*	7	-
Large zooplankton	*x*	8	7	7	-
Polychaetes	*x*	8	*x*	7	-
Small zooplankton	*x*	7	*x*	7	-
Epifauna	4	7	*x*	7	-
Infauna	7	7	*x*	7	-
Phytoplankton	1	7	-	-	-

For the west coast of Scotland, after qualifying all the input data used in the model (Table 7), an overall pedigree of 0.29 was obtained, with a fit of 1.74. Compared to a few other pedigreed models, this is an average value (Figure 16) (L. Morissette, unpublished PhD data).

Uncertainty in the model

The major sources of uncertainty in the data used for model construction lie in the biomass and the production of all groups, especially fish. It is common to have models with sparse information on benthos or fish species that are not commercially targeted. However, more information is usually available for commercially important species, on which more research and census are normally carried out (Morissette 2005).

No local biomass data were available for most of the species in the model. Almost all groups had their biomass estimated using ecotrophic efficiencies taken from other models. This method is very uncertain and so does not reliably represent the real density of each species modelled. As a result, the prediction of biomass change through time is not backed up by accurate biomass information. To improve predictive ability, the estimated biomass of each group should be verified by experts on each of the different species.

Very little diet information was found specific to the study area, but all species for which a diet or consumption study was available were included in the model's database. Where no local diet information was available, the extensive diet composition literature reviews in Morissette *et al.* (2003) and Mackinson (2001) were used. Knowing that most fish species undergo important migrations, the similarity for diet composition can easily be assumed (this is particularly true for species of the North Sea, an ecosystem that has some similarities to the west coast of Scotland).

The relatively low pedigree could have been avoided by reducing the number of groups in the model, so reducing the amount of information that had to be taken from other models where no WCS data were available. This would, at best, postpone the task of creating additional groups and splitting existing groups, as indicated in Table 1. Hence pedigree comparisons among models with different numbers of groups can be misleading.

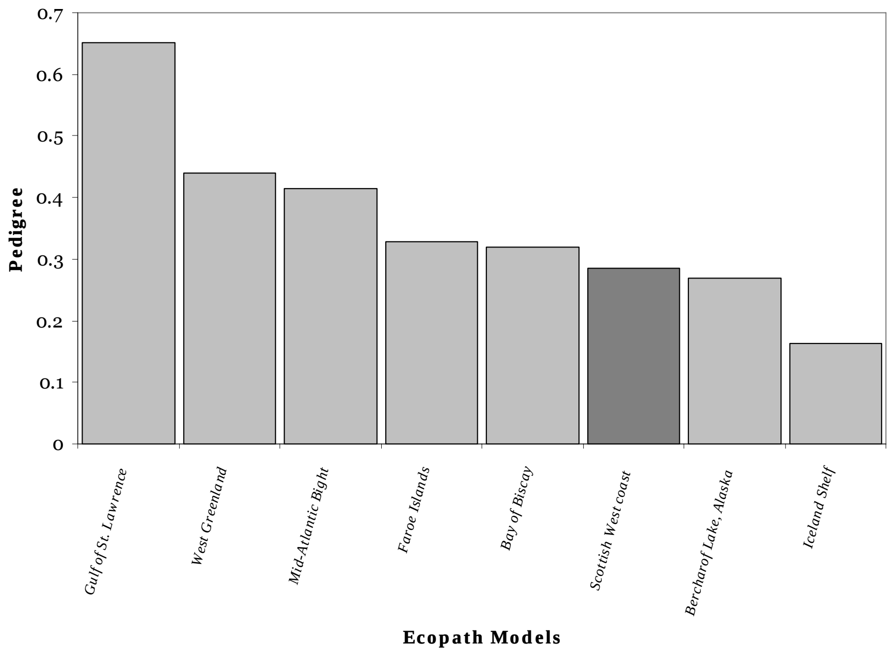

Figure 16. Pedigree values for some different *Ecopath* models.

This lack of information creates an important uncertainty on the different predictions simulated by the model with *Ecosim*. Given the high degree of uncertainty associated with dynamic predictions, we should continue to modify and advance the models as new data becomes available. Of particular importance is time series information, with which we can compare predicted results to improve the EwE initialization. A sensitivity analysis would also help determine which data elements are most critical to dynamic functioning, and allow us to explore the effect of alternate estimates for key parameters. Although much more can be done to improve this *Ecosim* model preliminary testing does suggest a reasonable representation of broad-scale ecosystem dynamics. This reliability, unusual for a new model, has likely been inherited from the existing (tested) models that inform its basic structure.

DYNAMIC SIMULATIONS WITH *ECOSIM*

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Abstract

Simple tests suggest that the *Ecosim* model for the west coast of Scotland is behaving in a reasonable manner under dynamic simulations. We assign the critical prey-predator vulnerability parameters using a short-cut method which has been validated by previous work and use three procedures to test the model's dynamic performance: 1.) An equilibrium analysis to determine for each commercial functional group the long-term catch rate and biomass level that would result under varying degrees of fishing mortality; 2.) Pulse fishing simulations to reveal how quickly the ecosystem can recover from disturbance; 3.) All fishing pressure removed from the dynamic simulation to show the recuperative potential of commercial groups and secondary trophic effects throughout the ecosystem. Much more can be done to improve the dynamic behaviour of *Ecosim* but the model appears to be robust and free from instabilities.

Introduction

Where the previous section evaluates the static *Ecopath* model of the west coast of Scotland, here we conduct rudimentary tests to demonstrate the dynamic behaviour of the *Ecosim* model. The equilibrium analysis routine is used in *Ecosim* to determine the long-term catch rates and biomass that result under varying degrees of fishing mortality, and determine the maximum sustainable yield of fished stocks. These values should be validated by expert opinion or compared with the output of other models such as the kind used in management. Tests using pulse fishing determine the resilience of the ecosystem, or its ability to recover from disturbance. The dynamic response of the ecosystem will depend greatly on the predator-prey vulnerability matrix in use. Two sets of vulnerability parameters are compared, the default assumption (global value of 2) and an alternate method which has proven reliable in other systems (scaling vulnerabilities in proportion to prey trophic level). Ideally, the vulnerabilities should be individually adjusted through a standard fitting procedure so that dynamic predictions agree with time series biomass information. This next step will require the assembly of time series information in the format of the modelled functional groups, and modification of the current model to resemble a point in the recent past for which time series is available. As another test of dynamic behaviour, all fishing is removed to analyze the recovery potential of fished populations. Other default *Ecosim* parameters for dynamic whole-ecosystem simulations were adjusted according to the following guidelines.

Feeding Time Adjustment

This parameter adjusts feeding time as food density changes to keep ration rate constant. *Ecosim* solves this numerically. The value should probably be close to 1, but this but causes instability and makes predators have Type II functional response which can cause cycles. Type II responses are strongly destabilizing because they cause depensation. Setting this parameter higher is necessary to create Beverton-Holt type recruitment. The parameter should be set close to zero for organisms that do not adjust their feeding rates (e.g. jellyfish, corals). Close to zero is probably a safer default for most things except the smallest juveniles in split groups.

Density Dependent Catchability

This parameter is used to build in range collapse (See EwE Help file), where F increases exponentially as stock is depleted and q increases. Around 10 is recommended for highly aggregating schooling species (Carl Walters, UBC Fisheries Centre, pers. comm.), but in practice most users find values this large destabilising. Values up to 1.5 appear to be sufficient to capture the range-collapse catchability effect.

Ainsworth, C. and Pitcher, T.J. 2005. Dynamic Simulations with *Ecosim*. *In*: Haggan, N. and Pitcher, T.J. (eds) Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs, pp. 42-46. UBC Fisheries centre Research Reports 13(4), 67pp.

Handling time adjustment

This adjustment is set lower to represent Type II functional response, mainly for marine mammals.

The *Ecosim* parameter values adopted for the preliminary west coast of Scotland model are listed in Table 8; these values represent approximations that could be improved in later versions of the model.

Equilibrium analysis

By increasing fishing mortality stepwise from zero to several times the baseline value, the automated equilibrium routine in *Ecosim* calculates the equilibrium biomass established for the subject functional group under that level of fishing mortality (Christensen *et al.* 2004). The analysis for the west coast of Scotland model is presented in Figure 17 and effectively provides *Ecosim* with output per fishery and target species/group equivalent to a series of single species surplus production assessment models but using the whole-ecosystem dynamics of *Ecosim*.

For this example, we hold biomass of other functional groups constant to remove confounding effects of trophic interactions. At their left-most extent, the biomass equilibrium curves tell us what biomass level the group assumes under zero fishing mortality (B_0). The catch equilibrium curves are essentially single-species surplus production curves; the maximum height of the curve shows the maximum sustainable yield (MSY) of the stock and the fishing mortality at which that occurs, the F_{MSY}. The dotted vertical line shows the baseline (current) level of fishing mortality. In a properly parameterized model, the baseline fishing mortality of underexploited groups should generally fall to the left of F_{MSY}, and to the right for overexploited stocks.

Table 8. Adjusted *Ecosim* parameters for the West Scotland model.

	Feeding time adjustment	Density-dependent catchability	Handling time adjustment
Seals	0.8	1	500
Cetaceans	0.8	1	500
Seabirds	0.8	1	500
Halibut/turbot/brill	0.8	1	1000
Whiting	0.5	1	1000
Other demersals	0.5	1	1000
Sharks	0.6	1	1000
Rays/Skates	0.5	1	1000
Cod	0.6	1	1000
Saithe	0.6	1	1000
Other pelagics	0.5	1	1000
Crabs/lobsters	0.2	1	1000
Gurnards	0.5	1	1000
Haddock	0.6	1	1000
Inshore fish	0.5	1	1000
Salmo	0.8	1	1000
Mackerel	0.5	1.3	1000
Trachurus	0.5	1.1	1000
Plaice	0.5	1	1000
Sole	0.5	1	1000
Nephrops	0.5	1	1000
Norway pout	0.5	1	1000
Cephalopods	0.5	1	1000
Sandeel	0.5	1.1	1000
Sprat	0.5	1.2	1000
Herring	0.5	1.2	1000
Echinoderms	0.1	1	1000
Other benthic inverts	0.1	1	1000
Prawns/shrimps	0.1	1	1000
Euphausiids	0.1	1	1000
Large zooplankton	0.1	1	1000
Polychaetes	0.1	1	1000
Small zooplankton	0.1	1	1000
Epifauna	0.1	1	1000
Infauna	0.1	1	1000

In the Figure 17 graphs, mackerel, whiting, halibut/turbot/brill and horse mackerel appear to be overexploited, while other demersals, crabs, haddock, inshore fish and gurnards are fully exploited. Herring, sprat, cod, rays, sharks, skates and salmon appear to be underexploited according to the parameters in this preliminary model, For many of these groups this is far from the case and so, clearly, we need a reality check with these groups.

The behaviour of each functional group under dynamic simulation will be greatly influenced by the initial relative level of exploitation represented in the basic *Ecopath* model. Review of these equilibrium graphs in Figure 17 by fisheries experts in the west coast of Scotland area should help us to gauge whether production and mortality parameters are assigned properly in the basic *Ecopath* model.

Testing biomass dynamics

The predator-prey vulnerability settings, entered as a matrix in *Ecosim*, are the main parameters governing ecosystem behaviour in temporal simulations. Each predator-prey trophic interaction is assigned a vulnerability coefficient, from one to infinity. The figure is unitless and it describes the maximum increase in predation mortality allowable on that feeding interaction. By assigning a low value, we imply a donor-driven density-dependant interaction. With regard to foraging arena theory (Walters and Martell 2004), the prey can remain hidden or defended during periods of high predator abundance. By assigning a high value we imply a predator driven density-independent interaction, in which predation mortality is proportional to the product of prey and predator abundance (Lotka-Volterra).

As time series data on biomass and fishing mortality is collected from surveys and Virtual Population Analyses (VPAs) for the west coast of Scotland model (e.g. biomass, fishing mortality, catch), it will become possible to tune the vulnerability matrix and improve the dynamic behaviour of *Ecosim*.

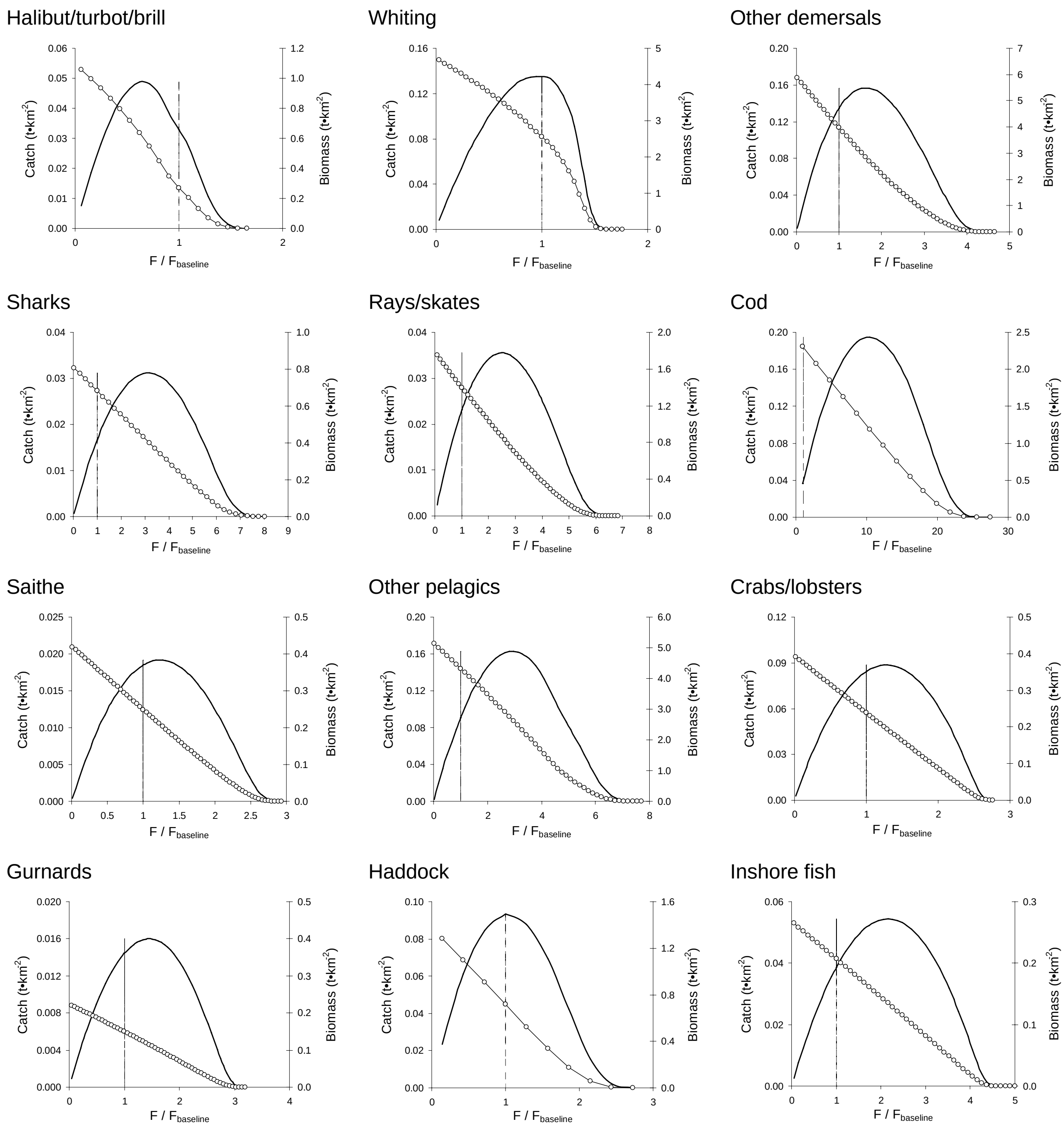

Figure 17 (part 1). Equilibrium catch (solid line) and biomass (open circles) resulting after 50 years of harvest at various levels of fishing mortality. Broken vertical line shows baseline fishing mortality.

For now, we have used a short-cut method to assign vulnerabilities, scaling them in proportion to prey trophic level, with upper and lower bounds determined by convention (*viz* Ainsworth and Pitcher 2004a and b). Ainsworth (2002) and Ainsworth and Pitcher (in prep.) compared this and other short-cut methods, and found that it provides a reasonable description of dynamics for depleted ecosystems. Vulnerability parameters used in this report are presented in Appendix Table 2.

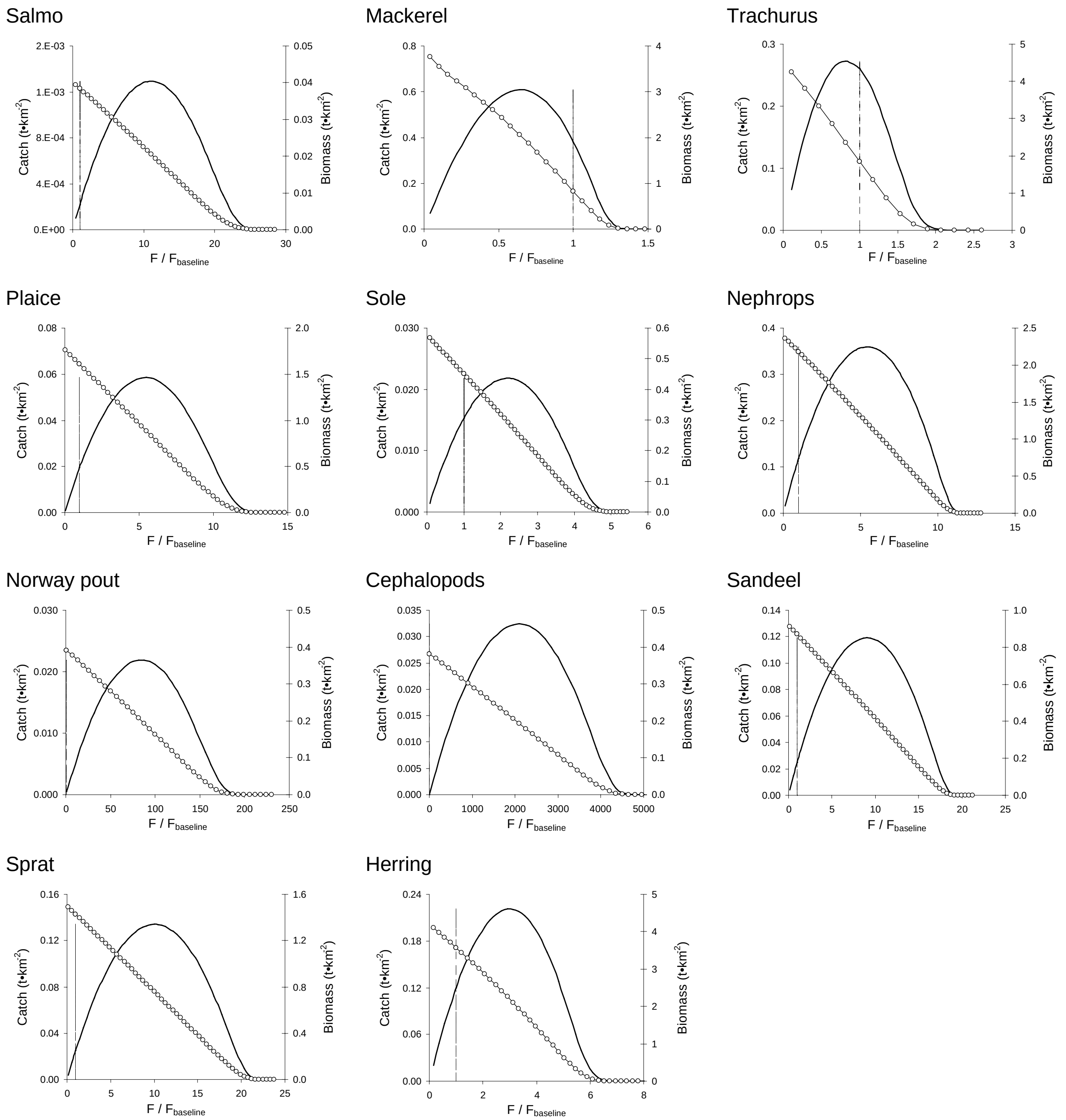

Figure 17 (part 2). Equilibrium catch (solid line) and biomass (open circles) resulting after 50 years of harvest at various levels of fishing mortality. Broken vertical line shows baseline fishing mortality. See text for discussion.

Figure 18 provides an illustrative comparison of ecosystem dynamics under pulse fishing using default *Ecosim* vulnerability parameters (global setting of 2) and scaling by trophic level. The TL-scaled parameters provide more conservative ecosystem dynamics and avoid a near extinction of mackerel upon cessation of fishing. There is much more that can be done to improve the dynamics of the Scotland model pending development of time series information.

Figure 19 offers another example of a model test using *Ecosim* predictions. All fishing is removed from the model for 50 years. Functional groups that have a high level of baseline fishing mortality will tend to increase in biomass despite the presence of any secondary trophic effects. Such effects are evident in the biomass change of unfished functional groups such as cetaceans, seals and seabirds. In combination with the equilibrium plots, simple tests like this can help to flesh out basic *Ecopath* parameters for fishing mortality, production, and biomass accumulation. Highly commercial groups that suffer a large loss in biomass upon cessation of fishing should be reviewed, particularly if current fishing effort is shown to be conservative by the surplus production graphs (Figure 17).

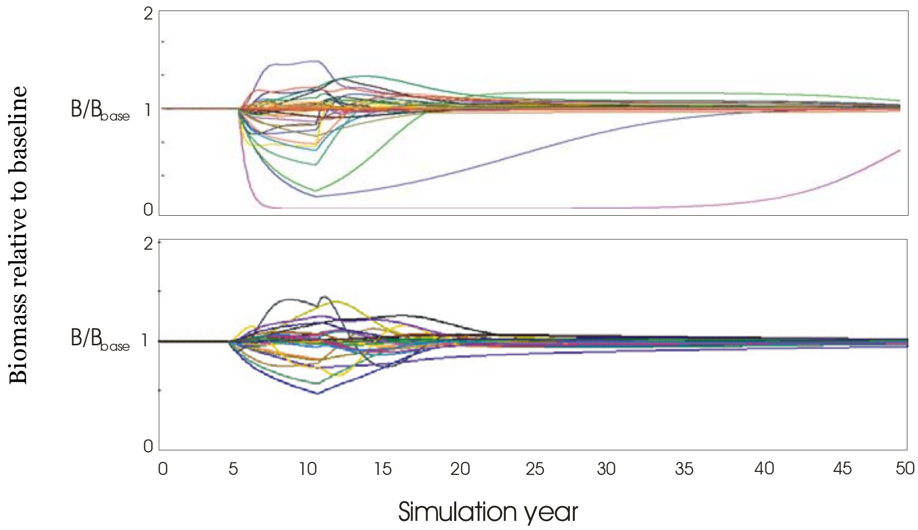

Figure 18. Trial *Ecosim* runs showing ecosystem recovery after pulse fishing. Fishing mortality increased by 5-fold for all fished functional groups in simulations years 5 to 10. Top panel shows result with default *Ecosim* vulnerabilities; lower panel with vulnerabilities scaled by trophic level.

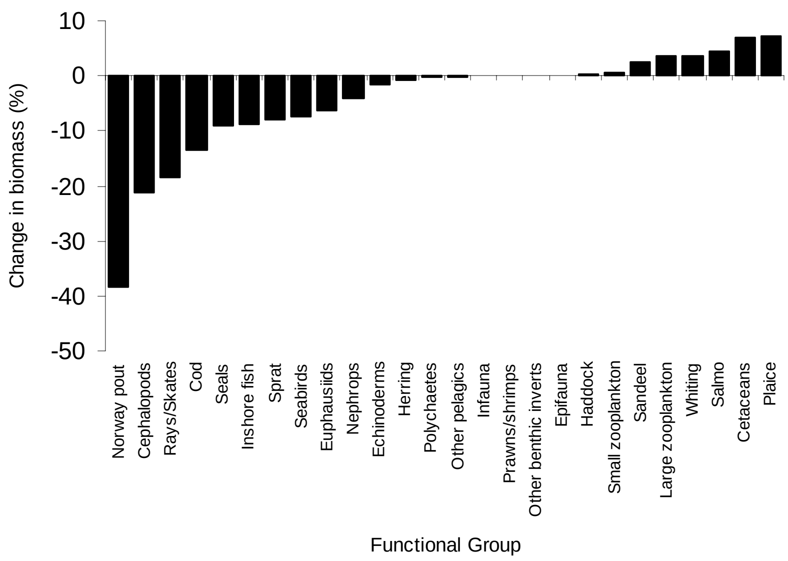

Figure 19. Model *Ecosim* run showing ecosystem effects of shutting off all fishing for 50 years. Functional groups which are subject to a high level of baseline fishing mortality tend to increase in biomass.

Spatial Simulations with *Ecospace*

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Abstract

The west coast of Scotland ecosystem model was set up for preliminary spatial simulations by mapping the 31,085 km^{-2} model area into 450 cells of 69.1 km^{-2} each (nominally square, with 8.3 km sides). An approximate coastline was sketched in on the map, avoiding isolated bays at the edge of the model area, with 335 marine cells. Four habitats were allocated using depth zones 0-10 m (representing 19% of total model area); 10 m-100 m (46%); 100-200 m (28%); and 200–1000 m (2%). Primary production levels were allocated for each model square from the Sea Around Us database. The 37 functional groups and 8 fisheries in the model were allocated to their preferred habitats in suitable combinations of the 4 habitat categories. All of these allocations were performed in a preliminary fashion and need to be validated with local data in future refinements to the model. Likewise, for each model group in its preferred and non-preferred habitats, using information from similar *Ecospace* models elsewhere, we adjusted default dispersal rates in km•$year^{-1}$, the relative dispersal rate in bad habitats, the relative vulnerability to predation in bad habitats and the relative feeding rate in bad habitats. Fishery management zones, termed "MPAs" in the software, were set up as examples; results may also be obtained in separate designated zones. The section concludes with a demonstration 50-year spatial simulation of the west coast of Scotland under default assumption of no changes to the existing fishing effort. Before attempting to analyse realistic spatial management scenarios, the present *Ecospace* model of west coast of Scotland should be used in a diagnostic mode by running trial scenarios with large no-take zones, under progressive annual increases and decreases in fishing power, in order to refine the habitat-related dispersal parameters and the underlying *Ecosim* and *Ecopath* model structure.

Introduction

Ecospace is a spatial version of *Ecosim* that dynamically allocates biomass across a grid map (Walters *et al.* 1998). *Ecospace* assumes symmetrical movements from a cell to its four adjacent cells, modified by whether a cell is defined as 'preferred habitat' or not; with user defined increased predation risk and reduced feeding rate in non-preferred habitats; and a level of fishing effort that is proportional to the overall profitability of fishing in that cell. Using *Ecospace* will often identify problems with a preliminary *Ecopath* model. Predators assigned to a given habitat type must be able to encounter sufficient prey in that habitat and prey have refuges from predation. *Ecospace* allows users to explore the potential role of Marine Protected Areas (MPAs) as a tool to mitigate and reverse various ecosystem effects of fishing. Trophic cascades within small MPAs, set up as a result of lower mortality and higher biomass of predators therein may increase fisheries catches operating near their perimeter as fish leave to seek food. Large MPAs, with a short outer perimeter relative to their surface area, are protected from this effect. *Ecospace* has been used to simulate human-made ("artificial") reefs in Hong Kong (Pitcher *et al.* 2000, 2002a, 2002b).

Habitats

'Habitats', in *Ecospace*, are sets of (water) cells sharing certain features affecting the movements, feeding rate, and survival of the *Ecopath* model components occurring therein. Typically, the features defining habitats are distance from the coast (inshore, offshore…), or depth (shallow, intermediate, deep…) and/or bottom type (rocky, sandy, muddy…). Habitats are, thus, as easy to define as it is to obtain rough bathymetric maps or maps indicating bottom types.

Pitcher, T.J. 2005. Spatial Simulations with *Ecospace In*: Haggan, N. and Pitcher, T.J. (eds) Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs, pp. 47-53. UBC Fisheries Centre Research Reports 13(4), 67pp

Table 9. Allocation of ecosystem model functional groups to four depth habitats for preliminary west coast of Scotland *Ecospace* model.

Group \ Habitat #	All habitats	inshore <10 m	11-100 m	100-200 m	200-1000 m	*Ecospace* area
Seals		+	+			0.6918
Cetaceans			+	+	+	0.8050
Seabirds	+					1
Halibut/turbot/brill				+	+	0.3082
Whiting			+	+	+	0.8050
Other demersals				+	+	0.3082
Sharks				+	+	0.3082
Rays/Skates	+					1
Cod			+	+	+	0.8050
Saithe				+	+	0.3082
Other pelagics	+					1
Crabs/lobsters		+	+			0.6918
Gurnards		+				0.19250
Haddock				+	+	0.3082
Inshore fish		+				0.1950
Salmo		+				0.1950
Mackerel			+	+	+	0.8050
Trachurus				+	+	0.3082
Plaice		+	+			0.6918
Sole		+	+			0.6918
Nephrops			+	+		0.7830
Norway pout			+	+	+	0.8050
Cephalopods	+					1
Sandeel			+	+		0.7830
Sprat		+	+			0.6918
Herring			+	+		0.7830
Echinoderms	+					1
Other benthic inverts	+					1
Prawns/shrimps		+	+			0.6918
Euphausiids	+					1
Large zooplankton			+	+	+	0.8050
Polychaetes	+					1
Small zooplankton	+					1
Epifauna	+					1
Infauna	+					1
Phytoplankton	+					1
Detritus	+					1
Habitat area	1	0.1950	0.4969	0.2862	0.0220	

The habitats defined in *Ecospace* should correspond to 'subwebs', i.e., to sets of primary producers, herbivorous and other consumers occurring only over that habitat, defined through the diet composition matrix of the *Ecopath* file. Subwebs may be linked, through higher trophic levels groups, with other subwebs in the same system. Higher trophic level groups, through their ability to feed in different habitats, integrate the different subsystem into a whole. Such subwebs should be implicit in the *Ecopath* file underlying an *Ecospace* analysis. This has not yet been done explicitly in the preliminary west coast of Scotland model.

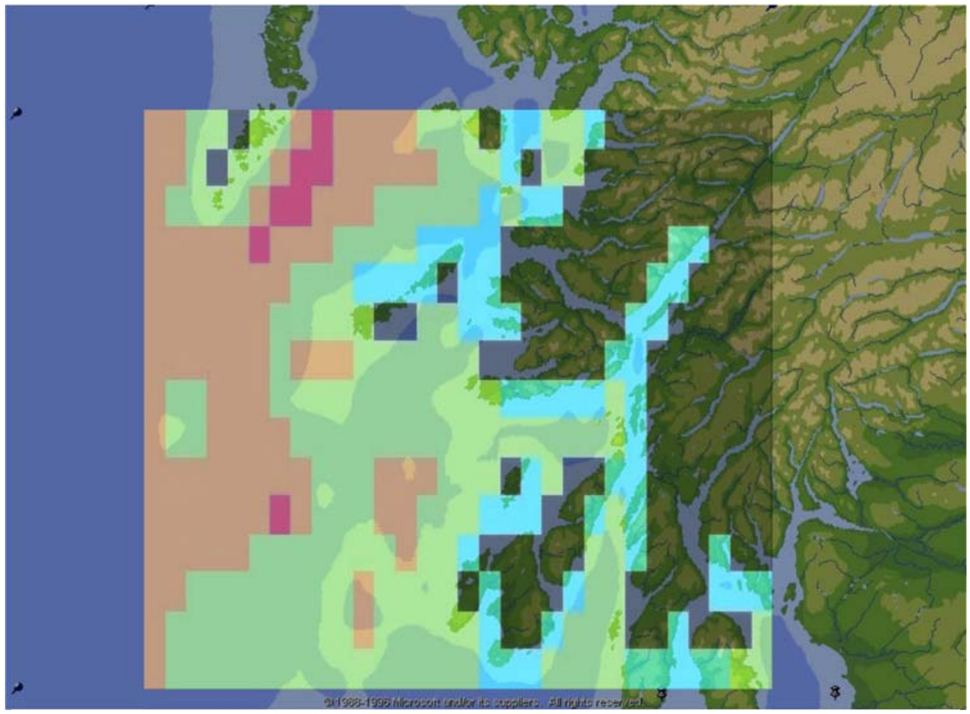


Figure 20. West Scotland ecosystem model map: dark shaded overlay shows the coastline used in the Ecospace model, with habitats taken from depth zones supplied by the Sea Around Us world database. The model area is divided into 450 cells of 69.1 km^{-2} (nominally 8.3 km sides), of which 335 cells represent the marine area, (See Figure 3).

Depth-zone habitats, along with the approximate coastline (Figure 3, were roughly positioned on the 335, 8.3 by 8.3 km marine cells of the basemap using an overlay of the true depths obtained from the Sea Around Us database (Figure 20). Depths from this source are very convenient to apply as they read directly into the software but do not appear to exactly match depths from other maps, so that we recommend that locally constructed habitats be used in any revisions to this preliminary model.

In *Ecospace*, narrow, crooked channels must be simplified, as movements on the *Ecospace* map can only resemble those of rooks on chessboards but not those of bishops. Also, basemap cells defined as 'land' consume memory and computing time; thus, their number should be kept as small as possible, e.g. by orienting the basemap sideways where appropriate. The basemap may include open borders, i.e., water areas not bounded by land. In such cases, the flow of organisms out of a border cell is compensated for by an equal flow of organisms into the cell, i.e., the system will not 'leak'. Hence, to the south of the modelled area, the Mull of Kintyeare was truncated to avoid having an enclosed bay and several small islands, bays and promontories which cannot be well represented in the relatively coarse map resulting from this cell size. A better model of the area might use cells half of this size, with approx 4 km sides, but, given uncertainties in the model, it is not recommended to reduce the cell size below about 2 km side.

Model groups of organisms are assigned to their 'preferred' habitat in Table 9. 'Preferred' here means that the group in question will be adapted such that its feeding rate, and hence its growth rate as well is higher in that habitat than in others; its survival rate is higher in that habitat (because the predation rate is higher in non-preferred habitat); and its movement rate is higher outside than within good habitat. Assignments to habitats here were somewhat arbitrary and, again, we recommend careful revision using literature on field studies in future improvements to the model. It should be noted that the definition of habitat in *Ecospace* includes the entire water column, from the surface to the bottom.

For human-made reefs, the present *Ecospace* representation is unsatisfactory because it does not allow for the surface to change over time as the community of encrusting organisms matures, changing its attractiveness for foraging and its efficacy as a refuge from predators. Similarly, *Ecospace* cannot presently capture change in bottom structure due to intensive trawling or the change in size of natural coral reefs due to growth or other dynamic changes due to grazing, erosion, storm damage and bleaching. As a result, we have to assume that human-made reefs are already mature at the start of any simulation. However, the ability to simulate these changes could be added to the software (Villy Christensen, pers. comm.).

Spatial parameters for the model organisms and fisheries

Primary Production

Spatially allocated average annual primary production rates were obtained from the Sea Around Us database and mapped onto the *Ecospace* grid (Figure 21, left panel). In further improvements to the west coast of Scotland ecosystem model, local data may be available to improve upon this.

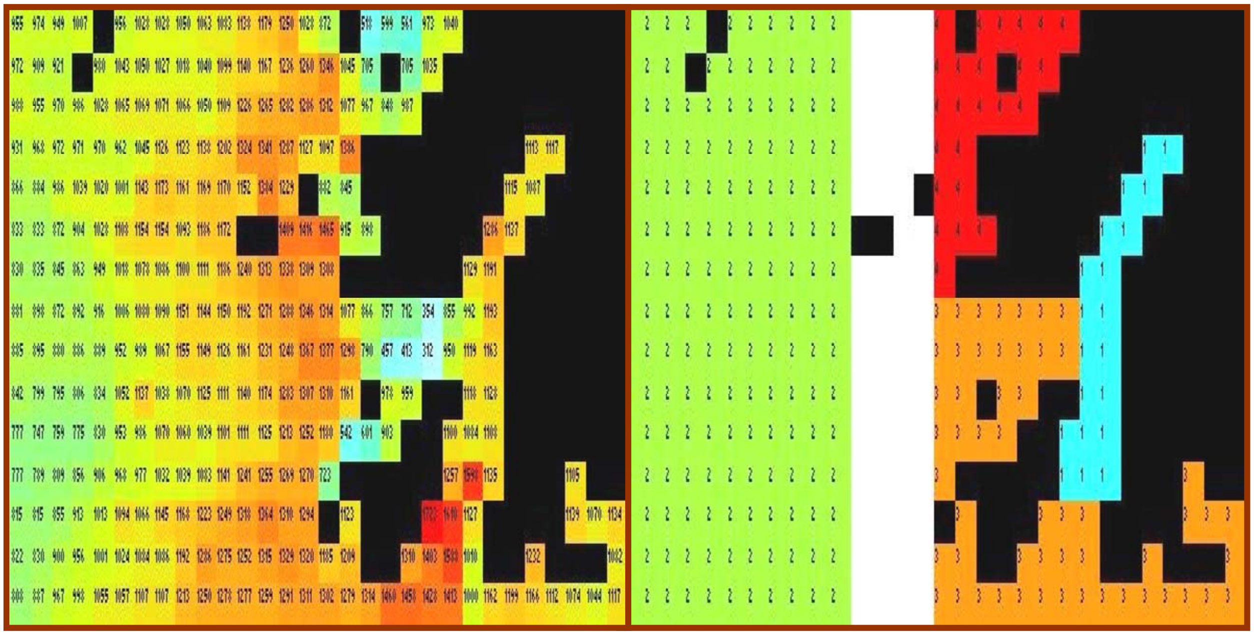


Figure 21. Map cell attributes used in spatial modelling with *Ecospace*. Left panel shows relative primary production imported to the model from the Sea Around Us global database (hotter colours represent higher production). Right panel shows five example management zones set up for spatial modelling of the fisheries: offshore (green); islands (white); north inshore (red); south inshore(orange); Oban area (blue).

Dispersal rates

The organisms (i) in an *Ecopath* model have an aggregated biomass (Bi), and are not assumed to move within the area covered by that *Ecopath* model. But in *Ecospace*, a fraction (B'i) of the biomass of each cell is always on the move, wherein

B'i = m • Bi

with m having the dimension of length / time (i.e., km•year^{-1}) i.e., a velocity or 'speed'; m is not a rate of directed migration but the rate (in km•year^{-1}) the organisms of a given ecosystem would disperse as a result of random movements: a default value of 300 km•year^{-1} for all groups apart from detritus groups (where we use a default of 10 km•year^{-1}). Rates assigned to the 37 groups in the preliminary west coast of Scotland ecosystem model are listed in Table 10.

Relative dispersal in non-preferred habitats

Rates are assumed to differ between preferred and non-preferred habitats, with higher values of 'm' within non-preferred habitats than in preferred habitats. This assumption is realistic as it implies that organisms in non-preferred habitats will strive to leave them and attempt to return as rapidly as possible to preferred habitats. The default value for the multiplier of m is 5.0, which is accepted for all the 38 groups in this preliminary west coast of Scotland ecosystem model as listed in Table 10.

Ecospace simulations are initiated by distributing all organisms evenly onto the basemap, at the density (t•km^{-2}) defined by the underlying *Ecopath* model. Then all biomass pools start moving, as a function of their value of m, out of their cell and into adjacent cells where they both consume food and are themselves consumed.

Table 10. Spatial dispersal, feeding and predation parameters for preliminary west coast of Scotland *Ecospace* model.

Group	Base dispersal rate km•year^{-1}	relative dispersal in bad habitat	relative vulnerability to predation in bad habitat	relative feeding rate in bad habitat
Seals	1000	5	1	0.5
Cetaceans	2000	5	1	0.5
Seabirds	1000	5	1	0.5
Halibut/turbot/brill	300	5	2	0.5
Whiting	300	5	2	0.5
Other demersals	300	5	2	0.5
Sharks	1000	5	2	0.5
Rays/Skates	300	5	2	0.5
Cod	600	5	2	0.5
Saithe	1500	5	2	0.5
Other pelagics	300	5	2	0.5
Crabs/lobsters	50	5	10	0.1
Gurnards	100	5	2	0.5
Haddock	600	5	2	0.5
Inshore fish	50	5	10	0.1
Salmo	300	5	2	0.5
Mackerel	1000	5	2	0.5
Trachurus	1000	5	2	0.5
Plaice	100	5	2	0.5
Sole	100	5	2	0.5
Nephrops	50	5	10	0.1
Norway pout	300	5	2	0.5
Cephalopods	1000	5	2	0.5
Sandeel	100	5	2	0.5
Sprat	600	5	2	0.5
Herring	1200	5	2	0.5
Echinoderms	25	5	10	0.1
Other benthic inverts	25	5	10	0.1
Prawns/shrimps	50	5	5	0.5
Euphausiids	1000	5	2	0.5
Large zooplankton	1000	5	2	0.5
Polychaetes	25	5	5	0.2
Small zooplankton	1000	5	2	0.5
Epifauna	10	5	10	0.1
Infauna	10	5	10	0.1
Phytoplankton	300	5	2	0.5
Detritus	300	5	2	0.5

Vulnerability to predation in bad habitats

The increased vulnerability to predation (or grazing) of various organisms outside their 'preferred' habitat can be changed using a multiplier. The default value of the multiplier is 2.0. Rates assigned to the 37 groups in the preliminary west coast of Scotland ecosystem model are listed in Table 10.

Relative feeding rates in bad habitats

Organisms outside their preferred habitat may be less likely to consume as much appropriate food as within the preferred habitat, due to the unavailability of such food, or the danger associated with foraging. To simulate this, *Ecospace* users can reduce the feeding rate of ecosystem components down to 0.01 times

Table 11. Allocation of fisheries to *Ecospace* habitats and fishery mamagement zones.

Fleet \ Habitat	All habitats	inshore <10 m	11-100 m	100-200 m	200-1000 m	MPA1
DTrawl				+	+	
BTrawl		+	+	+		
Mid Trawl			+	+	+	
Dredge		+	+			
Purse	+					
Line		+				
Creel/Pot		+				
Misc		+	+			

the *Ecopath* baseline (i.e., the Q/B value). The default is 0.5 and rates assigned to the 37 groups in the preliminary west coast of Scotland ecosystem model are listed in Table 10.

Fitness-driven dispersal behaviour

The default assumption in *Ecospace* is that dispersal and migration rates for each biomass pool are stable over space and time, except for "hardwired" seasonal migration patterns. This default setting ignores the possibility that movement rates (and possibly directions) are dependent on local "fitness" conditions, as measured by food intake rates and predation risk. For some species, at least, dispersal (emigration) rates may well depend on local resource conditions and/or predation, with creatures having higher probabilities of leaving areas where fitness is lower. Such behaviors could have major implications for design of marine protected areas, since food resource densities (for predators) are likely to be lower in protected areas, while predation risks (for smaller species) are likely to be higher. Thus for a variety of creatures, emigration rates from protected areas might be considerably higher than base rates measured under relatively low (pre-protection) conditions.

Ecospace allows users to explore two alternative hypotheses about fitness-driven dispersal rates: (1) total emigration rates are inversely proportional to fitness in each spatial cell, without these rates being spatially oriented or biased toward more favourable cells ("Type 1" fitness response); (2) emigration rates are proportional to the difference in fitness between each source cell and each cell around it, i.e., dispersal rates are higher across cell faces representing directions of higher fitness and are lower in directions toward cells or areas of lower fitness ("Type 2" fitness response). This option is not set up in this preliminary west coast of Scotland model.

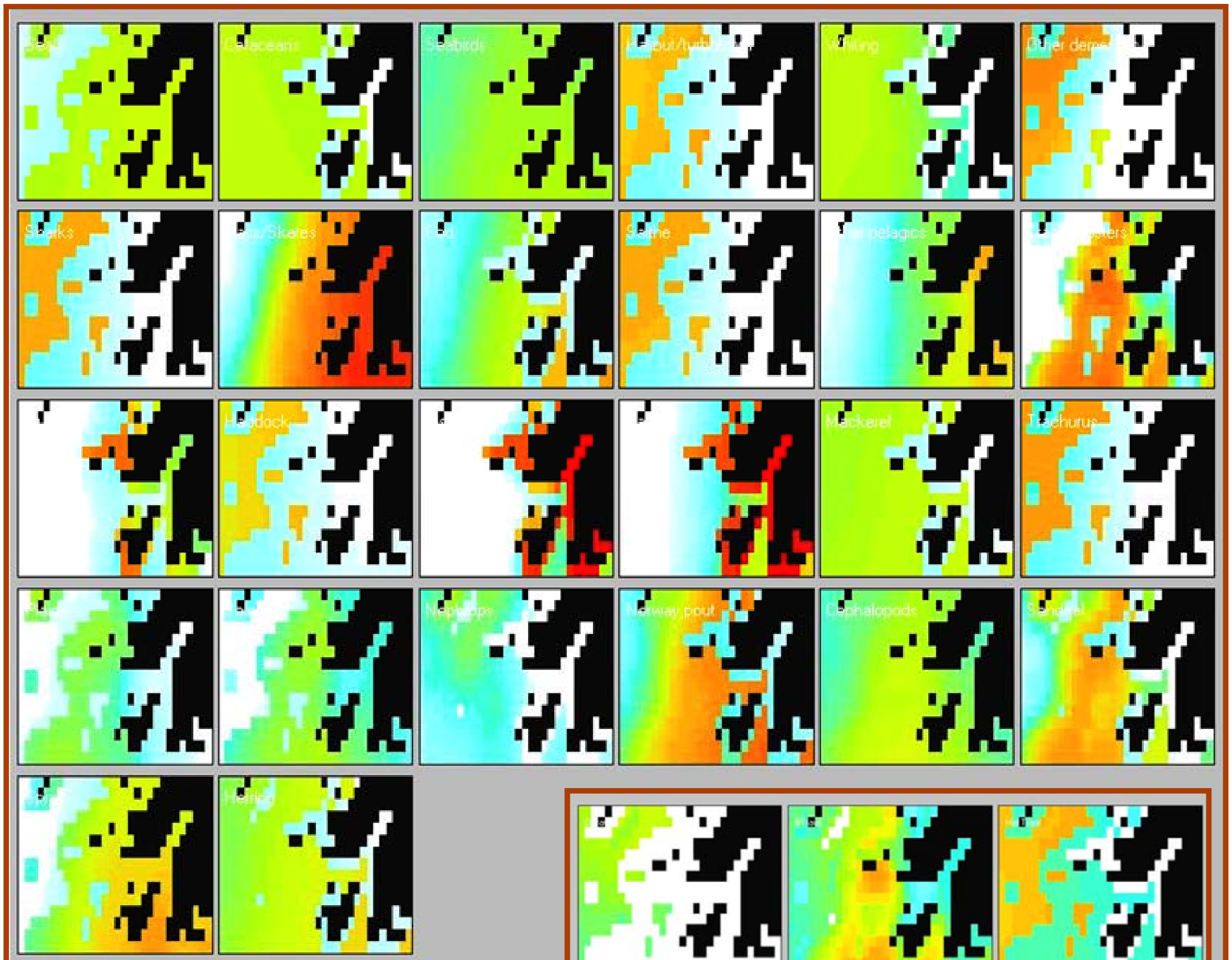
Spatial Representation of Fisheries

The eight fisheries in the preliminary west coast of Scotland ecosystem model are allocated to the *Ecospace* habitats in Table 11. Costs of steaming from port or differences in relative catching power and efficiency are not included in this version. This table would also show fishery management zones (no-take or restricted by gear type), but none have been set up at this stage of the work. Since for each time step in *Ecospace*, fishing effort is proportional to the overall profitability of fishing in a cell, it is critical that fishery costs and the landed prices per fishery gear type and model group be entered in the basic *Ecopath* model.

Output zones. Tabulated *Ecospace* results (biomass and catch per zone per model group) can be obtained either at the end of a simulation (red broken line on screen), or for full results during the simulation using the 'save'; button. Example output zones are illustrated in Figure 21 (right panel).

Demonstration *Ecospace* Results

Results in the form of spatial distributions of biomass relative to starting values for 26 of the ecosystem model groups at the end of a 50-year *Ecospace* simulation are shown in Figure 22. The lower panel shows relative fishing effort for the eight gear types. (Labels identifying the model groups and gear types are in white text and are pasted from a screen capture, and hence are hard to read). It should be noted that this simulation merely sets up a baseline equilibrium allocation of biomass with which other scenarios may be compared after the overall *Ecosim* model is adjusted; in other words, at this early stage of development of the west coast of Scotland model, these spatial simulations are best used as diagnostics with which to adjust model



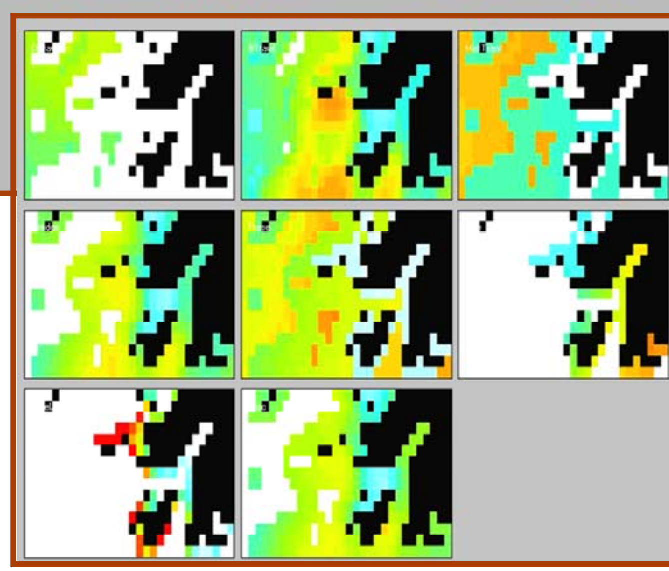


Figure 22. Upper panel shows relative biomass of 26 model functional groups at the end of a 50-year *Ecospace* simulation, using the basic *Ecosim* and *Ecopath* parameters for West Scotland. Lower panel shows relative fishing effort at end state for the 8 simulated gear types. This simulation establishes a baseline spatial equilibrium with which other scenarios may later be compared. Although white text labels for the model groups and the gear types are not visible, the groups can be inferred from their position: reefs are in the upper left hand corner, detritus in the lower right, other groups in between.

structure and parameters. For example, abundance gradients for small pelagics, skate, Norway pout, cephalopods, sandeels and discontinuous distributions for *Trachurus*, saithe, haddock, halibut, sharks all need to be evaluated, ground-truthed and checked and the habitat parameters adjusted accordingly. Biomass and catch per output zone may be determined, but there is not much point in doing this with this preliminary work.

MODEL DEVELOPMENT AND APPLICATION

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Abstract

In the absence of good local data for most species, the preliminary west coast of Scotland ecosystem model relies heavily on other models. Specific recommendations are made on how the model might be improved and extended to answer a range of research and fisheries management priorities.

Introduction

The absence of good local data for almost all species is a recurring theme. For example, gurnard are the only finfish species in the model for which local biomass data were available. All others were calculated by the software. Key parameters for most species were derived from other models, some of which, in turn, relied on other models. Path length is a good thing in ecosystems but of questionable value in model lineage.

On the credit side, the results demonstrate the power of the *Ecopath* approach to create an ecosystem model that is 'possible' in terms of the basic criterion of sufficient prey for all groups. Input obtained from local experts during a 2 day research visit, email iterations and a course in Oban were important in identifying and removing the more egregious errors. That said, the model is, as advertised, preliminary and would benefit from a great more ground truthing from local scientists, fishers, birders and others fortunate enough to spend their lives on or beside the waters of the west coast of Scotland (at least during the summer months).

Discussion

Given the high degree of uncertainty associated with dynamic predictions, we should continue to modify and advance the models as new data become available. Of particular importance is time series information, with which we can compare predicted results to improve the *EwE* initialization. A sensitivity analysis would also help determine which data elements are most critical to dynamic functioning and allow us to explore the effect of alternate estimates for key parameters. Although much more can be done to improve *Ecosim*, preliminary testing does suggest a reasonable representation of broad-scale ecosystem dynamics. This reliability, unusual for a new model, has likely been inherited from the existing (tested) models that inform its basic structure.

That said, the biomass accumulation graphs in Figure 17 suggest that mackerel, whiting, halibut/turbot/brill and horse mackerel appear to be overexploited, while other demersals, crabs, haddock, inshore fish and gurnards are fully exploited. Herring, sprat, cod, rays, sharks, skates and salmon appear to be underexploited according to the parameters in this preliminary model. For many of these groups this is far from the case and so, clearly, we need a reality check with these groups.

The behaviour of each functional group under dynamic simulation will be greatly influenced by the initial relative level of exploitation represented in the basic *Ecopath* model. Review of the equilibrium graphs in Figure 17 by fisheries experts in the west coast of Scotland area should help us to gauge whether production and mortality parameters are properly assigned in the basic *Ecopath* model.

The major sources of data uncertainty in *Ecopath* lie in the biomass and the production of all groups, especially fish. It is common to have models with sparse information on benthos or fish species that are not commercially targeted. However, more information is usually available for commercially important species, on which more research and census are normally carried out (Morissette 2005).

Haggan, N. and Pitcher, T.J. 2005. Model Development and Application. *In*: Haggan, N. and Pitcher, T.J. (eds) Ecosystem Simulation Models of Scotland's West Coast and Sea Lochs, pp. 54-57. UBC Fisheries centre Research Reports 13(4), 67pp

Using ecotrophic efficiencies from other models does not reliably represent the real density of each species modelled, although setting *EE* to 0.9 or so provides a rough way of obtaining preliminary biomasses for sparsely documented groups. Very little diet information was found specific to the study area but all species for which a diet or consumption study was available were included in the model's database. Where no local diet information was available, the extensive diet composition literature reviews in Morissette *et al.* (2003) and Mackinson (2001) were used.

As biomasses were calculated by *Ecopath* based on other models, it is likely that our estimates are high for crab, lobsters, and mackerel and low for whiting, demersal fish, sharks, cod, and plaice;

The Q/B for crabs and lobsters appear to be overestimated in the Scottish model. Our value of 30 is estimated by the P/Q ratio and is thus less accurate. We should compare with other temperate region models (North Sea, English Channel, Newfoundland, British Columbia, etc.) for a more accurate estimation.

The lack of local information used in the preliminary model creates an important uncertainty for the simulations with *Ecosim*, although in terms of comparisons among alternative scenarios, such models have been found to be reasonably robust. Our *Ecosim* model needs to be improved to include better estimates of main dynamic parameters for the functional groups. This may be achieved by fitting to as much time series data on biomass, fishing mortality and survey information as possible in order to tune the vulnerability parameters, here set as proportional to trophic level as a first approximation improvement from the baseline assumption of equality.

Model pedigree could have been increased by reducing the number of groups, thereby reducing dependence on other models necessitated by absence of local data. However, this would reduce the utility of the model in capturing essential ecological processes when it comes to be adapted to sea lochs and human-made and natural rocky reefs. There is no substitute for further consultation with local experts and additional surveys and studies to fill remaining data gaps.

Over-aggregated groups in the model (Table 1) include cetaceans, inshore fish, cephalopods, small zooplankton, epifauna and infauna. These groups should be split in later versions of the model. Other groups to consider are sea gooseberries, pelagic sea squirts and other jellies, chaetognaths and the microbial loop organisms.

In subsequent versions of the model, it would be useful to make the targetted *Nephrops* demersal trawl a separate gear type.

More precise discard values should be easily obtainable with the help of experts on the local fisheries.

One important development would be to set up more juvenile/adult split pool groups so that ecology of juvenile stages can be better included as indicated in Table 1. A new development here, the 'multi-stanza' approach in which several life history stages can be represented, and which has proven especially valuable for marine mammals, would be worth attempting.

Considerable effort also needs to be put into improving the *Ecospace* dispersal parameters and to setting up more realistic habitats and migrations. But in addition to parameter improvements, using *Ecosim* and *Ecospace* in their diagnostic modes with feedback to basic *Ecopath* parameters, model structure, diet and *Ecosim* dynamics is an essential and time-consuming step before time series fitting can be attempted with any confidence of success. In addition, human-made reefs, additional benthic organisms, such as crabs, encrusting colonial animals, benthic algae, ascidians crinoids and sponges will likely have to be modelled more explicitly.

Next Steps

Model development

Workshops with scientific and lay experts familiar with the study area and the major migratory species and oceanographic influences are essential to improve model quality. This process will cross-validate or reject model parameters and identify new sources of data. Questions posed by the model can contribute to the design of research projects to fill data gaps. Some research questions and potential projects that arose during the research and course in Oban are identified. Priorities for model development arising from the *Ecosim* and *Ecospace* simulations include:

- Review of equilibrium graphs produced by *Ecosim* by local fisheries experts to gauge whether production and mortality parameters are properly assigned in the basic *Ecopath* model;
- Tuning the vulnerability matrix and improving the dynamic behaviour of *Ecosim* as time series data is collected for WCS.

Back to the Future on the West Coast of Scotland

A new approach called Back to the Future (BTF) uses ecosystem models of the past to quantify the effect of fisheries and other factors on biodiversity, abundance and trophic structure over time. Models of northern British Columbia for the 1750s, 1900s, 1950s and 2000, constructed with input from Aboriginal people, historians, archaeologists and other sources show a significant decline in abundance (Ainsworth *et al.* 2002a and Figure 23).

The existing models and the availability of a comprehensive dataset going back to the 1920s create an important opportunity to establish benchmarks of productive potential. Applying the Back to the Future approach to the west coast of Scotland will require a multidisciplinary team including resource economists. Experience and recent success achieved in teasing out the interactions between interspecies competition, fisheries and ocean regime in the north Pacific indicate that data reconstruction and modelling projects of this magnitude require full-time attention, ideally by two post-docs and a series of workshops with scientists and lay experts to build intellectual capital in the model and social capital between the scientists, fishers, managers and other collaborators. The end goal is to build consensus on re-investment in natural capital.

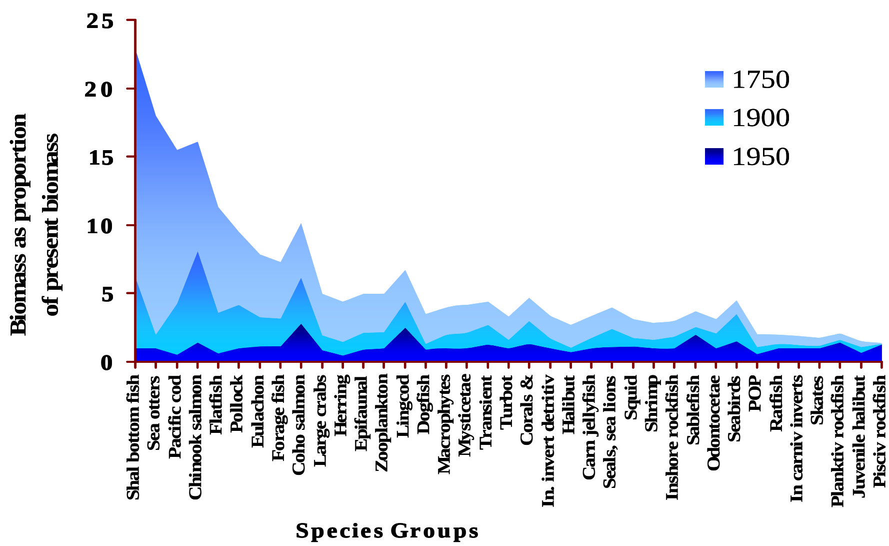

Figure 23. Percentage change in biomass of major species in northern British Columbia modelled by Ainsworth *et al.* (2002a).

Essential Fish Habitat / Sustainable Marine Bioresources

This project requires a GIS-based whole loch model that mixes predictive modelling with a statistical approach at fine scale. The project is in line with a planned extension of the modelling methodology to avail of fine-scale data available from GIS. In essence, *Ecospace* would allocate biomasses to normal large cells. Within *Ecospace* cells, GIS habitat mapping would allocate biomass pools to detailed small mapped habitats using a preference list. The project would require substantial programming.

Artificial reef colonisation

This project would avail of significant fieldwork and statistical analysis under way (Jenny Beaumont PhD thesis). Like the preceding, it would require programming of *Ecospace* to allow a new 'cast of characters' and to accommodate changing habitats. As a fallback, reef scenarios can be tackled with development of the present model, ideally with some programming capacity in the project.

Sandeel/forage fish links with seabird breeding success

Heavy fishing on sandeels is raising concern about the effect on seabird breeding success in Shetland and other critical seabird colonies in the north of Scotland. The existing models can be adapted to partition seabirds properly but this has rarely been done in EwE and may need some special algorithms/programming for seabird breeding when feeding chicks. Potential partners include the north Atlantic Fisheries College of the University of the Highlands and Islands and local fishers and communities.

Models and algorithms developed in one or more of the above projects would enable a number of other projects suggested at the September 2004 modelling course in Oban and described below.

Impact of salmon and mussel farms on sea lochs

Salmon and mussel farms may have significant impact on nutrient fluxes in enclosed waterbodies such as sea lochs. Macrophytes will be an important consideration. The FLABAY model (Hollings *et al.* 1994) might be a better approach than *Ecospace*. Potential UBC Fisheries Centre collaborators include Dr Steve Martell with links through Dr Tony Pitcher and PhD candidate Robyn Forrest to the *Atlantis* modelling approach being developed and applied in Australia.

Sealice emulation model using Ecosim

The question of transference of sealice from farmed to wild salmon is hotly debated on both sides of the Atlantic and in the Pacific northwest. Modelling an ectoparasite in *Ecosim* would be a neat challenge, and could also be done in *Ecospace* but would need a lot of special programming. A cooperative SAMS / UBC workshop on the Atlantic and Pacific dimensions and case studies would be a good starting point and should be easy to fund given the political profile of the issue.

Loch Etive - a unique repository of biodiversity

Loch Etive is of high ecological interest because of unique hydrography, relict populations of arctic species and *Calanus* populations of special interest. Loch Etive is relatively data-rich as it has been the site of a long-established marine laboratory. There is concern about the effect of aquaculture on the unique biota. As Loch Etive is close to a self-contained system, *Ecosim* could be used if programmed to accept a changing cast of players as in the impact of salmon and mussel farm project above.

Nutrient loading, point source pollution

This project would add modelling of aquatic biota to a Rural Economy and Land Use (RELU) project. As it stands, the Macaulay Institute in Aberdeen is doing the terrestrial side, with some oceanographers modelling the aquatic side. This is a bit of a 'long shot' for *Ecosim*. A better case could be made for using CSIRO's *Atlantis* model.

Ecotrace for Sellafield waste plume / Dounreay decommissioning

The Ecotrace routine in EwE can be used to trace persistent pollutants through aquatic food webs (Dalsgaard *et al.* 1998) and has been applied to track radionuclides from the US Atomic Bomb testing programme on Enewetak Atoll (Dalsgaard 1998). The project would apply recent advances in the software to model the paths of radioactive waste and their likely impact on environmental and human health.

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Appendix 1. *Ecopath* Diet Matrix

Prey \ Predator	Crabs/lobsters	Gurnards	Haddock	Inshore fish	Salmo	Mackerel	Trachurus	Plaice	Sole	*Nephrops*	Norway pout	Cephalopods
Seals												
Cetaceans												
Seabirds												
Halibut/turbot/brill		0.00086										
Whiting		0.07384			0.01004	0.011						
Other demersals	0.10474	0.0304	0.03993			0.0066					0.00278	
Sharks												
Rays/Skates												
Cod		0.01268			0.0001	0.00532						
Saithe					0.0001							
Other pelagics		0.0148	0.01847			0.01						0.00191
Crabs/lobsters	0.005			0.1								0.00191
Gurnards			0.00324									0.00191
Haddock		0.00349	0.00043		0.0002	0.007	0.01319					0.00382
Inshore fish												0.01911
Salmo												
Mackerel					0.00696							
Trachurus						0.02						0.01911
Plaice		0.00005										0.00764
Sole		0.00005										0.00764
Nephrops	0.10473											0.00191
Norway pout		0.00401	0.0093		0.0002	0.01	0.01649					0.00382
Cephalopods												
Sandeel		0.08207	0.03		0.051	0.01						0.01911
Sprat		0.00575	0.08		0.012	0.01008	0.01649					0.00382
Herring		0.0304	0.00059		0.25	0.02						0.01911
Echinoderms	0.20947	0.05428	0.12	0.1				0.16882	0.03227	0.16138	0.052	
Other benthic inverts	0.20947	0.04343	0.212	0.4				0.31211	0.06848	0.1272		0.00191
Prawns/shrimps	0.15711	0.37244	0.36984	0.1	0.10987	0.185	0.10286	0.13232	0.57274		0.19322	
Euphausiids					0.45	0.41	0.42081		0.07218	0.1765	0.202	
Large zooplankton		0.21717			0.10953	0.19	0.20572			0.32278	0.55	0.59233
Polychaetes	0.10474	0.05428	0.1162	0.1		0.005	0.00936	0.38675	0.25433	0.05075		0.0198
Small zooplankton						0.1	0.21508			0.16139		0.27323
Epifauna	0.05237			0.1								0.00191
Infauna	0.05237			0.1								
Phytoplankton												
Detritus												
Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1
	12	13	14	15	16	17	18	19	20	21	22	23

Appendix 1, continued

Prey \ Predator	Sandeel	Sprat	Herring	Echinoderms	Other benthic inverts	Prawns/shrimps	Euphausiids	Large zooplankton	Polychaetes	Small zooplankton	Epifauna	Infauna
Seals												
Cetaceans												
Seabirds												
Halibut/turbot/brill	0.001											
Whiting												
Other demersals												
Sharks												
Rays/Skates												
Cod												
Saithe												
Other pelagics												
Crabs/lobsters												
Gurnards												
Haddock												
Inshore fish												
Salmo												
Mackerel												
Trachurus												
Plaice												
Sole												
Nephrops												
Norway pout												
Cephalopods												
Sandeel			0.0005									
Sprat			0.00026									
Herring												
Echinoderms				0.08								
Other benthic inverts				0.24	0.0597	0.009						
Prawns/shrimps	0.403	0.22822	0.15376			0.11						
Euphausiids	0.015	0.01	0.18775			0.02181						
Large zooplankton	0.579	0.76178	0.65121			0.04361	0.02381					
Polychaetes	0.001			0.04	0.02303	0.00496			0.03558			
Small zooplankton	0.001				0.09808	0.21062	0.22619	0.05333		0.03		
Epifauna				0.4	0.31507							
Infauna					0.12603							
Phytoplankton			0.00652			0.2	0.57	0.85057	0.49948	0.8	0.25	0.025
Detritus				0.24	0.37809	0.4	0.18	0.0961	0.46494	0.17	0.75	0.975
Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1
	24	25	26	27	28	29	30	31	32	33	34	35

Appendix 1, continued

Prey \ Predator	Seals	Cetaceans	Seabirds	Halibut/turbot/brill	Whiting	Other demersals	Sharks	Rays/Skates	Cod	Saithe	Other pelagics
Seals		0.00054					0.005				
Cetaceans							0.00001				
Seabirds	0.0005	0.00098					0.001				
Halibut/turbot/brill	0.0005		0.00009		0.001		0.0005	0.001	0.001	0.001	0.00101
Whiting	0.38259	0.00098	0.00435	0.1406	0.04841	0.008	0.029				
Other demersals	0.34279	0.06301	0.09289	0.02108	0.12305	0.02	0.0202				
Sharks		0.0001		0.00105			0.041				
Rays/Skates	0.0001					0.05	0.001				
Cod	0.01005	0.00185	0.00299	0.09342	0.009	0.05	0.02347		0.07709	0.052	
Saithe		0.00098	0.00043		0.00664		0.0005		0.01572		
Other pelagics		0.6364	0.00043		0.12	0.1		0.01	0.10723	0.012	0.03407
Crabs/lobsters	0.001		0.05	0.00526		0.04	0.00939	0.024			
Gurnards			0.004			0.003	0.001	0.005	0.0017		0.00495
Haddock	0.01005	0.0001	0.00041	0.02377	0.0136		0.00224		0.02013	0.037	0.00248
Inshore fish	0.0005	0.00098	0.00043			0.08	0.00051				
Salmo	0.00499	0.0049					0.004		0.0005		
Mackerel	0.01382	0.00098				0.03	0.01663		0.00597		
Trachurus	0.04955				0.0133		0.01			0.06	0.03
Plaice	0.001		0.033			0.008		0.02	0.03787	0.02	0.05817
Sole	0.001		0.002			0.006		0.02		0.008	0.01272
Nephrops			0.00043	0.00951		0.08		0.13	0.01403		0.09539
Norway pout	0.0005		0.00405	0.00421	0.02		0.00224	0.01	0.01482	0.2	0.00495
Cephalopods	0.0174	0.00492		0.23162			0.15049		0.01822	0.005	0.02727
Sandeel	0.02362	0.07627	0.1		0.05	0.05	0.02041	0.05	0.0435	0.03	0.02727
Sprat	0.001	0.00492	0.1		0.13	0.048	0.09642	0.04	0.001	0.09	0.0065
Herring	0.13904	0.00097	0.295		0.34	0.03	0.31629	0.13	0.09261	0.15	0.02727
Echinoderms			0.11	0.16211		0.05		0.04	0.01404		0.13633
Other benthic inverts		0.00049	0.00425	0.20632	0.07	0.164	0.1086	0.1	0.05332		0.23178
Prawns/shrimps		0.00165	0.00425	0.10105	0.035	0.09	0.1	0.38	0.40689	0.115	0.09539
Euphausiids					0.02	0.008	0.04			0.2	
Large zooplankton		0.12934				0.05				0.02	0.03407
Polychaetes			0.18			0.03	0.0001	0.04	0.07436		0.13631
Small zooplankton		0.06964									0.03407
Epifauna			0.011			0.005					
Infauna											
Phytoplankton											
Detritus											
Import											
Sum	1	1	1	1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	10	11

Appendix 2. Prey-predator vulnerability settings

	Seals	Cetaceans	Seabirds	Halibut/turbot/brill	Whiting	Other demersals	Sharks	Rays/Skates	Cod	Saithe	Other pelagics	Crabs/lobsters	Gurnards	Haddock	Inshore fish	Salmo	Mackerel	Trachurus	Plaice	Sole	Nephrops	Norway pout	Cephalopods	Sandeel	Sprat	Herring	Echinoderms	Other benthic inverts	Prawns/shrimps	Euphausiids	Large zooplankton	Polychaetes	Small zooplankton	Epifauna	Infauna
Seals		2					2																												
Cetaceans							2																												
Seabirds	2	2					2																												
Halibut/turbot/brill	2		8.4		2		2	2	2	2	2		2											2											
Whiting	10	2	8.4	8.1	7.8	2	7.6						6.3			5.9	5.9																		
Other demersals	10	8.5	8.4	8.1	7.8	7.6	7.6					6.6	6.3	6.3			5.9					5													
Sharks		2		8.1			7.6																												
Rays/Skates	2					7.6	2																												
Cod	2	8.5	8.4	8.1	7.8	7.6	7.6		7	2			6.3			5.9	5.9																		
Saithe		2	8.4		7.8		2		7							5.9																			
Other pelagics		8.5	8.4		7.8	7.6		7.1	7	7	6.6		6.3	6.3			5.9						2												
Crabs/lobsters	2		2	8.1		7.6	7.6	7.1				6.6			6								2												
Gurnards			8.4			2	7.6	7.1	7		6.6			6.3									2												
Haddock	10	2	8.4	8.1	7.8		7.6		7	7	6.6		6.3	6.3		5.9	5.9	5.7					4.9												
Inshore fish	2	2	2			2	2																4.9												
Salmo	2	2					2		2																										
Mackerel	10	2				2	7.6		7							5.9																			
Trachurus	10				7.8		2			7	6.6						5.9						4.9												
Plaice	10		8.4			7.6		7.1	7	7	6.6		2										4.9												
Sole	2		8.4			7.6		2		2	6.6		2										4.9												
Nephrops			2	8.1		7.6		7.1	7		6.6	6.6											2												
Norway pout	2		8.4	8.1	7.8		7.6	7.1	7	7	6.6		6.3	6.3		5.9	5.9	5.7					4.9												
Cephalopods	10	2		8.1			7.6		7	2	6.6																								
Sandeel	10	8.5	8.4		7.8	7.6	7.6	7.1	7	7	6.6		6.3	6.3		5.9	5.9						4.9			4.7									
Sprat	2	2	8.4		7.8	2	7.6	2	2	7	6.6		6.3	2		5.9	5.9	5.7					4.9			4.7									
Herring	10	2	8.4		7.8	7.6	7.6	7.1	7	7	6.6		6.3	6.3		5.9	5.9						4.9												
Echinoderms			2	8.1		7.6		2	7		6.6	6.6	6.3	6.3	6				5.6	5.3	5.1	5					4.2								
Other benthic inverts		2	2	8.1	7.8	7.6	7.6	7.1	7		6.6	6.6	6.3	6.3	6				5.6	5.3	5.1		2				4.2	3.2	2.7						
Prawns/shrimps		8.5	2	8.1	7.8	7.6	7.6	7.1	7	7	6.6	6.6	6.3	6.3	6	5.9	5.9	5.7	5.6	5.3		5		4.9	4.7	4.7			2.7						
Euphausiids					2	2	7.6			7						5.9	5.9	5.7		5.3	5.1	5		4.9	4.7	4.7			2.7						
Large zooplankton		8.5				7.6				2	6.6		6.3			5.9	5.9	5.7			5.1	5	4.9	4.9	4.7	4.7			2.7	2					
Polychaetes			2			7.6	7.6	2	7		6.6	6.6	6.3	6.3	6		5.9	5.7	5.6	5.3	5.1		4.9	2			4.2	3.2	2.7			1.3			
Small zooplankton		8.5									6.6						5.9	5.7			5.1		4.9	2				3.2	2.7	2	1.4		1.3		
Epifauna			2			2						6.6			6								2				4.2	3.2							
Infauna												6.6			6													3.2							
Phytoplankton																										4.7			2.7	2	1.4	1.3	1.3	1.2	1.2
Detritus																											4.2	3.2	2.7	2	1.4	1.3	1.3	1.2	1.2