Science Series
Technical Report no.138

An Ecopath model of the Irish Sea: ecosystems properties and sensitivity analysis

K. Lees and S. Mackinson

Cefas

Science Series
Technical Report no.138

An Ecopath model of the Irish Sea: ecosystems properties and sensitivity analysis

---

K. Lees and S. Mackinson

January 2007

This report should be cited as: Lees, K. and Mackinson, S., 2007. An Ecopath model of the Irish Sea: ecosystems properties and sensitivity analysis. Sci. Ser. Tech Rep., Cefas Lowestoft, 138: 49pp.

HMSO's Licensing Division
St Clements House
2-16 Colegate
Norwich
NR3 1BQ
Fax: 01603 723000
E-mail: licensing@cabinet-office.x.gsi.gov.uk

Contents

1. Introduction

Large-scale changes in the North Atlantic climate and marine community structure have been observed over the last 100 years. The 1980s represent a well-documented North Atlantic climatic and ecological regime shift (Taylor *et al.*, 1992, Taylor and Stephens, 1998; Parsons and Lear; 2001; Marshall *et al.*, 2001). The North Atlantic Oscillation Index (NAOI) and the Gulf Stream Index (GSI) and the primary indicators of North Atlantic climate variability (Marshall *et al.*, 2001; Taylor, 1995). Changes in the NAOI and the GSI have been linked to fluctuations in UK zooplankton community structure, abundance and timing of occurrence (Planque and Fromentin, 1996), timing of squid peak abundance (Sims *et al.*, 2001), and commercial fish recruitment and biomass (Beaugrand *et al.*, 2003; Hislop, 1996).

Fishing activities in the North Atlantic are also believed to impacted marine community structure and have been causatively linked to North Atlantic marine ecological regime shifts (Reid *et al.*, 2001; Pope and Macer, 1996; Jennings and Kaiser, 1998; Frid *et al.*, 2000). However, the relative roles of climatic regime shifts and fishing as drivers of marine ecological regime shifts are poorly understood. Ecosystem models such as Ecopath with Ecosim (EwE) may be useful in exploring the relative roles and interactions of climate change and fishing in driving ecological regime shifts in marine ecosystems.

The Irish Sea is influenced by the North Atlantic climate and supports a number of pelagic, demersal, and shellfish fisheries. Like other marine ecosystems, the relative impacts of North Atlantic climatic regime shifts and fishing on Irish Sea marine community structure are poorly studied and understood. An Ecopath model of the Irish Sea was constructed to aid in investigating Irish Sea ecosystem responses to climatic regime shifts and changes in fishing intensity.

The objectives of this report are to:

- Describe the construction and parameterisation of an Ecopath model representing the Irish Sea ecosystem in 1973.
- Characterise the ecosystem properties using a variety of model based ecological indicators
- Test the sensitivity and stability of the model and refine parameters to establish sensible dynamic behaviour.

2. Ecopath modelling approach

Ecopath is a static mass balanced trophic model, which was pioneered by (Polovina, 1984) and was designed for estimating biomass and food consumption of the elements (species or groups of species) of aquatic ecosystems. Since the early 1990s Ecopath has been under continuous development and has been optimised for use in evaluating fisheries management scenarios and for addressing ecological questions through the inclusion of the temporal dynamic model, Ecosim in 1995 and the spatial dynamic model, Ecospace in 1998 (Christensen *et al.*, 2000; Christensen and Walters, 2004).

Ecopath data requirements are relatively simple and are generally available from the literature, stock assessment, and ecological studies. The parameterisation of Ecopath is founded on the assumption of mass balance over a given time period (usually 1 year) and is based on satisfying two 'master' equations. The first equation describes the how the production term for each group can be divided:

Production = catch + predation + net migration + biomass accumulation + other mortality

Or, more formally:

$$P_i = Y_i + M2_i * B_i + E_i + BA_i + MO_i * B_i \qquad [1]$$

where P_i *is the production of group* $_i$; Y_i *is the total catch rate for group* $_i$; $M2_i$ *is the instantaneous predation rate for group* $_i$; E_i *is the net migration rate for group* $_i$ *(emigration – immigration);* BA_i *is the bioaccumulation rate for group* $_i$; *and* MO_i *is the other mortality rate for group* $_i$.

An Ecopath model requires diet composition, fishery parameters (landings and discards by gear type) and input of three of the following four basic parameters: biomass (B) (t km^{-2}), production/biomass ratio ($P/B.y^{-1}$) or its equivalent total mortality rate (Z), consumption/biomass ratio ($Q/B.y^{-1}$), and ecotrophic efficiency (EE) for each group ($_i$) in a model. The ideal situation is that biomass, production/biomass, and consumption/biomass are entered for all groups and ecotrophic efficiency is estimated since there is no method for its field estimation. The ecotrophic efficiency expresses the proportion of the production that is used in the system and can be considered an expression of model uncertainty rather than a meaningful ecological term (Christensen and Walters, 2004). For parameterisation, Ecopath sets up a series of linear equations for each group to solve the unknown or missing parameters establishing mass-balance in the same operation.

Energy balance is then ensured within groups by the second 'master' equation, which is based on the principle of conservation of matter within a group:

Consumption = production + respiration + unassimilated food [2]

3. Characteristics of the Irish Sea

3.1. Physical settings

The Irish Sea (ICES VIIa) lies between Britain and Ireland and covers approximately 58,000 km^2 (Vincent *et al.*, 2004) (Figure 3.1(a)). A north to south running deep-water channel (St. Georges Channel) with a maximum depth of 150 m separates the relatively shallow western and eastern regions of the Irish Sea (Figure 3.1(b)). The main flow of water through the relatively narrow western Irish Sea flows south to north from the North Channel, whilst an anti-clockwise gyre dominates circulation patterns in the eastern Irish Sea (Figure 3.1(c)). There are two main seasonal fronts in the Irish Sea: the Western Irish Sea Front, which separates mixed waters to its south-east from the stratified waters to its north-west and the Celtic Sea Front that separates the cooler, mixed waters

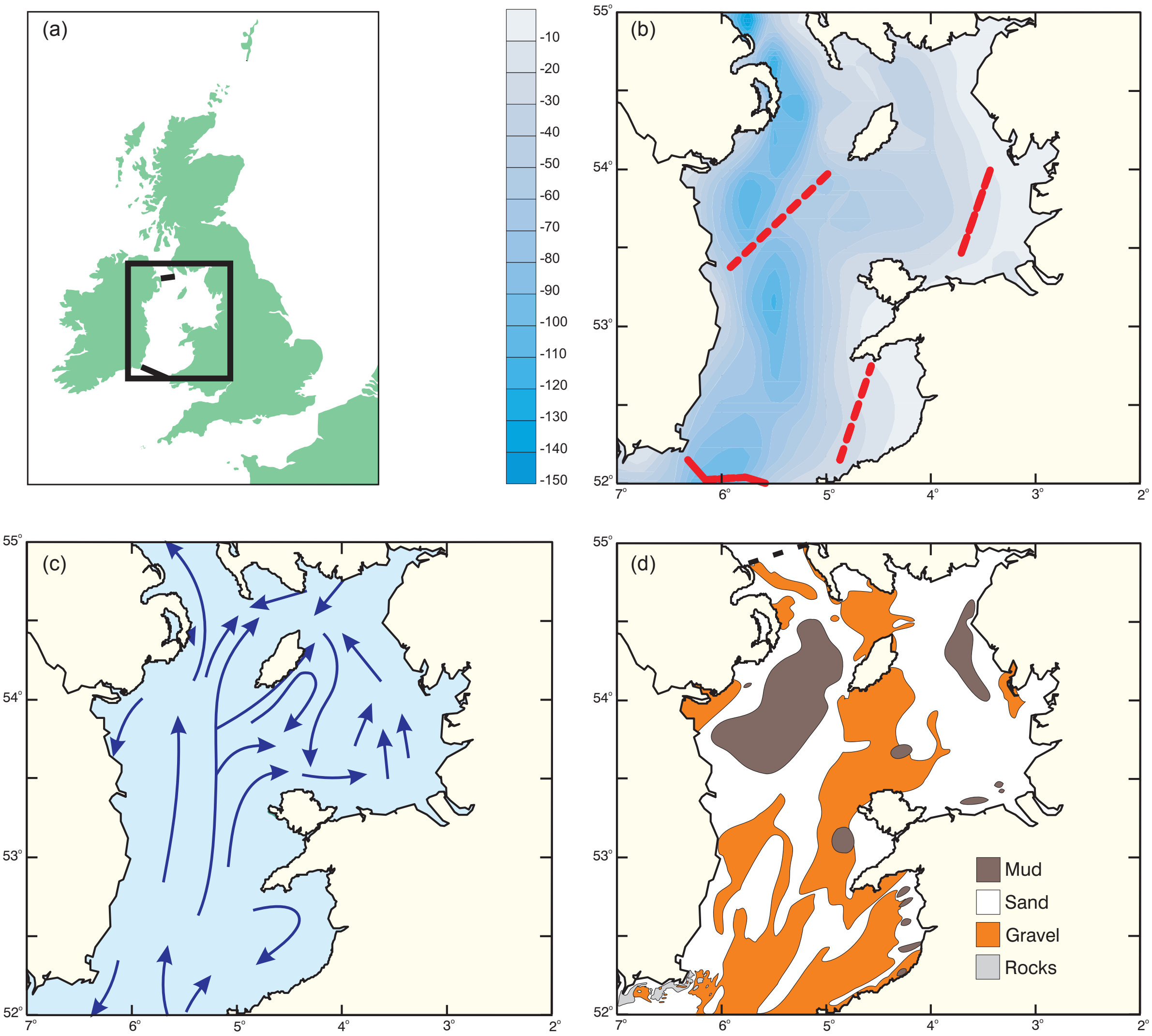


Figure 3.1. The physical characteristics of the Irish Sea (a) map of Great Britain and Ireland showing boundaries of the Irish Sea, (b) Bathymetry of the Irish Sea and front systems indicated by red lines (c) Irish Sea circulation, (d) Irish Sea sediment types. (Modified from (Parker-Humphreys, 2004).

of St. Georges Channel from the warmer surface waters of the Celtic Sea. Seasonal fronts may also occur in the eastern Irish Sea and Cardigan Bay (Figure 3.1(b)). The temperature in the Irish Sea ranges from 6ºC in the winter to 16ºC in the summer. Sand is the dominant sediment type in the western and eastern Irish Sea, whilst gravel is the prominent type in the deeper waters of the mid Irish Sea and St. Georges Channel. There are also two offshore mud grounds; one in the northeast and a more extensive one in the northwest (Parker-Humphreys, 2004) (Figure 3.1(d)). Parker-Humphreys (2004) provides a more detailed description of the physical characteristics of the Irish Sea.

3.2. Fisheries

The Irish Sea supports valuable pelagic, demersal, and inshore fisheries. Many stocks are exploited together in different combinations and often include important bycatch. *Nephrops* is one of the most valuable fisheries in the Irish Sea and occurs predominantly on the extensive mud ground in the Northwest Irish Sea (Figure 3.1(d)). Otter trawls target *Nephrops*, cod, haddock, whiting, and plaice. Important bycatch include, hake, sole, skates, and rays. Pelagic trawlers in the Irish Sea target herring. Beam trawls fisheries principally land sole, plaice, rays, brill, turbot, and anglerfish. There are also important inshore fisheries for bass, cod, grey mullet, sole, plaice, brown crabs, and lobster. (Pawson *et al.*, 2002) provides a detailed description of fisheries in the area.

4. Structure of the Irish Sea Ecopath model

Thousands of plants and animals have been recorded in the Irish Sea ranging from plankton, invertebrates, fish, marine mammals, and seabirds. Many species inhabit the Irish Sea all year round, whilst others are seasonal visitors. Representing every species known to inhabit in the Irish Sea would require an enormous amount of information, most of which is not available. Therefore many species in the Irish Sea were pooled into functional groups based on size, habitat, feeding preferences, and/or taxonomic similarities. Well-studied commercial species, for which information is readily available, are generally represented in a single species "box". The Irish Sea model is composed of 53 groups (Table 4.1).

Table 4.1. Structure of 53 box Ecopath model ("FG" is "functional group")

Marine mammals and seabirds

FG 1	Toothed Whales
FG 2	Baleen Whales
FG 3	Seals
FG 4	Seabirds

Fish groups

FG 5	Basking Sharks
FG 6	Bass
FG 7	Adult Cod 2+
FG 8	Juvenile Cod Age 1
FG 9	Adult Haddock 2+
FG 10	Juvenile Haddock Age 1
FG 11	Adult Plaice 2+
FG 12	Juvenile Plaice Age 1
FG 13	Whiting
FG 14	Sole
FG 15	Seatrout
FG 16	Sandeels
FG 17	Small Flatfish
FG 18	Medium Flatfish
FG 19	Large Flatfish
FG 20	Dragonets
FG 21	Other Large Demersals
FG 22	Gurnards
FG 23	Mackerel
FG 24	Monkfish
FG 25	Mullet
FG 26	Other Large Gadoids
FG 27	Other Small Demersal
FG 28	Other Small Gadoids
FG 29	Small Pelagic Planktivorous Fish
FG 30	Small Sharks
FG 31	Large Sharks
FG 32	Skates and Rays

Invertebrate groups

FG 33	Epifaunal Macrobenthos
FG 34	Epifaunal Mesobenthos
FG 35	Infauna (Polycheate)
FG 36	Infaunal Macrobenthos
FG 37	Infaunal Mesobenthos
FG 38	Lobster and Large Crabs
FG 39	*Nephrops*
FG 40	Cephalopods
FG 41	Prawns and Shrimp
FG 42	Sessile Epifauna
FG 43	Meiofauna
FG 44	Gelatinous Zooplankton
FG 45	Carnivorous Zooplankton
FG 46	Omnivorous Zooplankton
FG 47	Herbivorous Zooplankton

Primary producers and bacteria

FG 48	Seaweed
FG 49	Microflora
FG 50	Phytoplankton

Detritus

FG 51	Particulate Organic Matter
FG 52	Dissolved Organic Matter
FG 53	Discards

5. Basic imput parameters and data sources

5.1. Marine mammals and seabirds

Abundance estimates were available for the Irish Sea from survey data. Mean individual body weights, $P/B.y^{-1}$, and $Q/B.y^{-1}$ estimates were available from the literature and a marine mammals parameter database (Trites *et al.*, 1999 - Table 7.1). Diet composition was taken from (Pauly *et al.*, 1998 - Table 7.2). Biomass was calculated using the following equation:

$$\text{Biomass t km}^{-2} = \frac{\text{abundance*average body weight (t)}}{\text{Area of Irish Sea (58,000 km}^{-2})} \quad [3]$$

FG 1. Toothed whales

Toothed whales are composed of harbour porpoises (*Phocoena phocoena*) and common dolphins (*Delphinus delphis).* Reported sightings in the Irish Sea are available from the Irish Sea Whales and Dolphin Group for 1994-2006 from a constant effort sightings scheme and a casual sightings scheme. The constant effort sightings scheme involves a trained volunteer conducting 2 watches per month from an onshore observation station. The casual sighting scheme enables members of the public to report cetacean sightings. All records are validated and available at www.iwdg.ie. Average body weight of harbour porpoises and common dolphins were estimated to be 0.0315 t (Trites *et al.*, 1999) and 0.1 t (www.nceas.ucsb.edu), respectively. In 1994, 135 harbour porpoises and 4 common dolphins were recorded from the constant effort and the casual sightings scheme. Biomass for toothed whales was, therefore estimated to be 0.00008 t km^{-2} using equation 3.

Toothed whale diet is comprised of 1.7% benthic invertebrates, 20% cephalopods, 30% pelagics, 13.3% other invertebrates, and 35% fish (Pauly *et al.*, 1998).

FG 2. Baleen whales

The JNCC report on the distribution of seabirds and cetaceans in the water around Ireland reported just 8 Minke whale (*Balaenoptera acutorostrata*) sightings in the Irish Sea between 1981 and 1997 (Pollock *et al.*, 1997). Average Minke whale weight is estimated to be 5.251 t (Trites *et al.*, 1999a). The Irish Sea Whale and Dolphin Group sighting schemes recorded 3 minke whales in 1994. Since this was the only data available, an initial assumption that 3 Minke whales visited the Irish Sea in 1973. Baleen whale biomass was, therefore estimated to be 0.00034 t km^{-2} using equation 3.

Minke whale diet consists of 65% zooplankton, 30% small pelagic fish, and 5% other fish (Pauly *et al.*, 1998).

FG 3. Seals

Seals were composed of grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*). Grey seal abundance estimates were available from pup census data collected in Ireland and Wales and a photo-identification mark-recapture programme. Grey seal population in the Irish Sea was estimated to be around 6000 individuals (Kiely *et al.*, 2000). Average grey seal body weight is estimated to be 63 kg (Trites *et al.*, 1999). Grey seal biomass was estimated to be 0.00651 t km^{-2} using equation 3.

Harbour seal populations in the Irish Sea were estimated based on harbour seal population assessment in the Republic of Ireland and the Northern Ireland survey in 2002 (Cronin *et al.*, 2004). Mean harbour seal group size was estimated to be 69; approximately 49 groups were recorded in the Irish Sea. The number of groups was multiplied by the average group size to get an estimate of population in the Irish Sea (69*49=3381). Mean Harbour seal weight was estimated to be 0.08 t (Trites *et al.*, 1999). Biomass of harbour seals in the Irish Sea was, therefore estimated to be 0.00466 t km^{-2} using equation 3. Biomass of Grey seals and harbour seals was added together to give an estimate of seal biomass in the Irish Sea in 2002 of 0.011 t km^{-2}. This 2002 estimate is the best available data for 1973.

Seal diets is composed of 12.5% benthic invertebrates, 10% cephalopods, 75% pelagics, and 2.5% other invertebrates (Pauly *et al.*, 1998).

FG 4. Seabirds

The most dominant species of seabirds in the Irish sea are Fulmer (*Fulmarus glacialis*), Manx Shearwater (*Puffinus puffinus*), gannet (*Sula bassana*), shag (*Phalacrocorax aristotelis*), scoter (*Melanitta nigra*), common gull (*Larus canus*), lesser black backed gull (*Larus fuscus*), herring gull (*Larus argentatus argenteus*), kittiwake (*Larus tridactyla*), guillemot (*Uria aalge*), razorbill (*Alca torda*), puffin (*Fratercula arctica*), storm petrel (*Hydrobates pelagicus*) (Pollock *et al.*, 1997). Terns (Sternidae), cormorants (*Phalacrocorax pelagicus*), and great black backed gulls (*Larus marinus*) are also important seabird colonies in the Irish Sea (Pollock *et al.*, 1997). Numbers and consumption estimates were taken for the report of the working group on seabird ecology (ICES, 2002). Irish Sea seabird biomass was estimated to be 0.0511 t km^{-2} using equation 3. Seabird consumption in the Irish Sea was estimated to be around

245,000 t /58,000 = 4.224 t km^{-2} (ICES, 2002). Q/B.y^{-1} was therefore estimated to be 82.664. Since there were no P/B.y^{-1} values available P/Q.y^{-1} was estimated to be 0.013, which is close to that estimated by Ecopath in other models. Seabird diet was non-quantitative general knowledge from (Jonsson, 1993).

5.2 Fish groups

Biomass estimates for basking sharks were obtained from the literature. Biomass for bass (*Dicentrarchus labrax*), adult and juvenile cod (*Gadus morhua*), adult and juvenile haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus)*, adult and juvenile plaice (*Pleuronectes platessa*), sole (*Solea solea*), and small pelagic planktivores were taken from ICES stock assessments (ICES, 2003a; ICES, 2003b; ICES, 2004a; ICES, 2004b; ICES, 2004c). Where ICES stock assessments were not available, Cefas groundfish survey data were used to estimate biomasses. The Cefas groundfish survey used a standard GOV trawl for which the mouth width was estimated at 18 m (Jim Ellis, pers. comm.). Biomass for each species was calculated from survey data as follows:

Mean catch per hour across all stations sampled was calculated as:

Mean catch h^{-1} (t) =
Catch h^{-1} (t)/total number of stations sampled

Mean catch h^{-1} (t) was converted to total catch biomass (t km^{-2}) by multiplying by the total area towed, where

Total area towed (m^2) =
Distance towed h^{-1} (m) * Net width (m)

Therefore

Total catch biomass (t km^{-2}) =
Average CPUE (t)*Total area towed (km^2) [4]

However, many factors can influence net efficiency or catchability (q) including the size and swimming characteristics of the target species, substrate, current etc (Kaiser *et al.*, 1994). Net efficiency estimates were based on those reported by Sparholt (1990) and Kaiser *et al*. (1994). A range of catchabilities resulted in a range of biomasses (Table 5.1). An average biomass estimate was used as a starting point (Table 7.1).

Biomass (t km^{-2}) =
Total catch biomass (t km^{-2})/catchability (q) [5]

There were large discrepancies between ICES and survey biomass estimates of haddock, plaice, whiting, and sole. There are a number of possible explanations for these discrepancies. Firstly, ICES biomass estimates are for 1973, whereas Cefas groundfish survey biomass estimates represent the Irish Sea in 2004. Secondly, ICES biomass estimates are catch driven and many catch statistics are under reported, which may lead to low biomass estimates. Alternatively, the groundfish survey sampling stations are biased towards areas that can be fished, which may lead to an overestimate of Irish Sea biomasses (Robert Scott, pers. comm.).

Total mortality (Z) estimates were entered as P/B.y^{-1} ratios from ICES stock assessments where available. Z estimates were available from ICES stock assessment for bass, adult and juvenile cod, adult and juvenile haddock, whiting, adult and juvenile plaice, sole, and small pelagic planktivores were estimated (ICES, 2003a; ICES, 2003b; ICES, 2004a; ICES, 2004b; ICES, 2004c). For fish groups where ICES stock assessments are not available, Z was assumed to be the sum of fishing mortality and natural mortality (Z=F+M). ICES catch statistics (available from www.ices.dk) were used to estimate fish mortality using the following equation:

$$F = C/B \qquad [6]$$

where F is instantaneous fishing mortality rate, C is catch rate, and B is biomass (t km^{-2}) from survey data.

Where no catch statistics were available natural mortality was entered as Z. Natural mortality rate (M) of fish can be estimated from empirical relationship linking M, two parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature (Pauly, 1980).

$$M = K^{0.65} \cdot L_{\infty}-0.279 \cdot T_{c}^{0.463} \qquad [7]$$

where M is the natural mortality (/year), K is the curvature parameter of the VBGF (/year), L_{∞} is the asymptotic length in cm, Tc is the mean ambient temperature, in °C.

Parameters of the von Bertalanffy growth function values were taken from publications, calculated from survey data, or Fishbase (www.fishbase.org). Ambient temperature was assumed to be the average temperature of the Irish Sea. Where one or more of these values was not available, natural mortality was assumed to be 0.2,

Table 5.1. Biomass estimates for fish groups in the 1973 Irish Sea Ecopath model.

Group	ICES biomass (t km^{-2})	Biomass (t km^{-2}) [1]	Biomass (t km^{-2}) [2]	Average biomass (t km^{-2})
Bass	***0.0128***	0.092 (0.169)	0.148 (0.105)	0.084
Adult cod	***0.3570***	0.394 (0.145)	0.505 (0.113)	0.324
Juvenile cod	***0.1109***			0.022
Adult haddock	***0.023***	0.631 (0.292)	1.376 (0.134)	0.680
Juvenile haddock	***0.033***			0.022
Adult plaice	***0.1229***	4.119 (0.011)	2.059 (0.022)	2.078
Juvenile plaice	***0.0328***			0.011
Whiting	***0.507***	6.687 (0.191)	12.281 (0.104)	6.334
Sole	***0.110***	3.154 (0.00047)	3.294 (0.00045)	***2.174***
Sandeels		3.098 (0.00006)	0.929 (0.0002)	***2.014***
Small flatfish		0.134 (0.011)	0.066 (0.022)	***0.097***
Medium flatfish		11.892 (0.011)	5.946 (0.022)	***8.919***
Large flatfish		0.106 (0.011)	0.053 (0.022)	***0.079***
Dragonets		0.229 (0.011)	0.114 (0.022)	***0.171***
Other large demersals		0.152 (0.169)	0.246 (0.105)	***0.199***
Gurnards		0.340 (0.169)	0.548 (0.105)	***0.444***
Mackerel		48.942 (0.169)	19.577 (0.105)	***34.260***
Monkfish		0.870 (0.004)	0.435 (0.010)	***0.653***
Mullet		0.003 (0.011)	0.006 (0.022)	***0.004***
Other large gadoids		0.149 (0.169)	0.241 (0105)	***0.195***
Other small demersal		0.173 (0.169)	0.544 (0.105)	***0.360***
Other small gadoids		3.222 (0.034)	9.958 (0.011)	***6.590***
Small pelagic planktivores	***3.643***	101.577 (0.010)	184.686 (0.005)	95.863
Small sharks		2.105 (0.010)	3.388 (0.006)	***2.746***
Large sharks		0.088 (0.169)	0.142 (0.105)	***0.115***
Skates and rays		0.952 (0.169)	0.476 (0.105)	***0.714***

Number shown in ***bold italics*** are the figures entered into the model. ICES biomass estimates were taken from ICES stock assessment. Biomass (1) and (2) were calculated from the 2004 Cefas groundfish survey. Numbers shown in bracket depict the catchability estimated used. Catchability estimates from Biomass t km^{-2} (1) were taken from Sparholt (1990) IYFS and catchability estimates from Biomass t km^{-2} (2) were taken from Sparholt (1990) EGFS. Cod, haddock, and plaice biomass estimates calculated from the groundfish survey data represent the whole population, ie estimates are not age structured.

based on the rate of mortality estimated to have occurred in the absence of fishing during the Second World War.

Palomares and Pauly (1998) described a predictive model for Q/B.y^{-1} of fish using asymptotic weight, habitat temperature, a morphological variable and food type as independent variables. For cases where an estimate of total mortality, Z, (per year) is available the following relation may be used:

$$\text{Log}(Q/B.y^{-1})=5.847+0.280\text{Log}Z-0.152^{*}\log W_{\infty}-1.360^{*}T'+0.062^{*}A+0.510^{*}h+0.390^{*}d \qquad [8]$$

where W_{∞} *is the asymptotic weight (g),* T' *is an expression for the mean annual temperature of the water body, expressed using* $T' = 1000/\text{Kelvin}$ *(Kelvin = °C + 273.15), A is the aspect ratio (height*^{2}*(cm)/surface area (cm), h is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores, and 0 for herbivores and carnivores).*

For cases where Z is not available, the following relation may be used:

$$\text{Log }(Q/B.y^{-1})=7.964-0.204^{*}\text{Log}W_{\infty}-1.965^{*}T'+0.083^{*}A+0.532^{*}h+0.398^{*}d \qquad [9]$$

Where Z estimates were available from ICES stock assessments, Q/B.y^{-1} was calculated using equation 8. For groups 16-32 there were no Z estimates available. Therefore, Q/B.y^{-1} was calculated using equation 9. A weighted average was calculated where groups contained more than one species (Table 7.1).

Diet data for cod, dragonets, gurnards, haddock, large sharks, mackerel, medium flatfish, monkfish, mullet, other large demersal, other small gadoids, plaice, skates and rays, small flatfish, small pelagic planktivorous fish, small sharks, sole, and whiting were collected on survey aboard *RV Cirolana*, *RV Clione*, and *RV Scotia* between 1986 and 1994. Diet composition of the remaining fish groups were non-quantitative general knowledge from Muus and Dahlstrom (1985) (Table 7.2).

FG 5. Basking sharks

Basking shark (*Cetorhinus maximus*) biomass was calculated using equation 3. Abundance estimates were available from the Irish Sea pilot project, which reported 243 sighting in 2002 (Vincent *et al.*, 2004). The body mass of basking sharks in relation to total length is not well known on account of the difficulties associated with weighing large specimens. The mean length of basking sharks off the southwest coast has been reported as 4.06 m, which corresponds to a weight of 328 kg (Sims *et al.*, 2001). Biomass of therefore estimated to be 0.0014 t km^{-2}.

Pauly (1989) estimated Basking shark Q/B.y^{-1} for the North Sea to be 3.70. P/B.y^{-1} was taken from (Stanford and Pitcher, 2000) and based on natural mortality calculated from (Pauly, 1980). Basking shark feed on large zooplankton, diet was split evenly between the 4 zooplankton groups (Pauly *et al.*, 1998).

FG 6. Bass

Biomass estimates for bass were obtained from SURBA model outputs presented in (ICES, 2003a) for ICES areas VIIa, f, and g. Since there is a high degree of mixing between bass stocks in VIIa, f, and g and little interchange between populations in the North Sea and Biscay, it is considered reasonable to use input parameters estimated for VIIa, f, and g as an indicator of bass stock in VIIa (ICES, 2003a). Irish Sea bass spawning stock biomass was estimated to be 744,639 kg in 1985. There was no 1973 estimate available, therefore the earliest estimate was used.

SSB (t km^{-2}) =
SSB (t)/Area of Irish Sea (km^{2}) =
744.639/58000 = 0.0128 t km^{-2}

Z was estimated at 0.5 for 1995 (ICES, 2003a). Since Z was known, equation 8 was used to calculate a Q/B.y^{-1} of 2.68.

FG 7. Adult cod and FG 8. Juvenile cod

Cod were split into 2 groups: Adult (age 2+) and Juvenile (age 1) as per ICES, 2004a. Irish Sea cod spawning stock biomass was reported to be 20,753 t in 1973 (ICES, 2004a). Adult cod biomass was therefore estimated to be 0.357 t km^{-2}. The number of juvenile recruits was multiplied by the mean weight at age 1 report for 1973 (ICES, 2004a). Juvenile cod biomass was estimated to be 0.110 t km^{-2}.

P/B.y^{-1} was estimated using ICES fishing mortality (F) and natural mortality (M) estimates (ICES, 2004a). M was assumed to be 0.2 across all age groups. Mean fishing mortality was estimated to be 0.772 in 1973 for adult cod. P/B.y^{-1} was therefore estimated to be 0.972 for adult cod. Q/B.y^{-1} was estimated to be 2.00 for adult cod using equation 8. Juvenile cod P/B.y^{-1} and Q/B.y^{-1} were assumed to be double for juvenile cod (Blanchard *et al.*, 2002).

Adult cod diet is primarily composed of epifaunal macrobenthos and other demersal fish species. Juvenile diet was assumed to be largely zooplankton based.

FG 9. Adult haddock and FG 10. Juvenile haddock

Haddock were split into 2 groups: Adult (age 2+) and Juvenile (age 1) as per ICES, 2004b. ICES stock assessments on Irish Sea haddock are reported from 1993 onwards and are therefore not available from 1973. Spawning stock biomass estimates were 1,341 t in 1993 (ICES, 2004b). Adult haddock biomass was therefore estimated to be 0.020 t km^{-2}. The number of juvenile recruits (age 1) was multiplied by mean weight at age 1 in 1993 (ICES, 2004a). Juvenile haddock biomass was estimated to be 0.033 t km^{-2}.

Haddock fishing mortality was reported to be 1.221 in haddock in the Irish Sea in 1993 (ICES, 2004a). Natural mortality was assumed to be 0.2. P/B.y^{-1} was therefore estimated to be 1.421 in adult populations. Q/B.y^{-1} was estimated to be 2.58 using equation 8. Juvenile P/B.y^{-1} and Q/B.y^{-1} were assumed to be double that of adults.

Adult haddock diet largely consists of benthic invertebrates. Juvenile haddock was assumed to be primarily composed of zooplankton.

FG 11. Adult plaice and FG 12. Juvenile plaice

Plaice were split into 2 groups: Adult (age 2+) and Juvenile (age 1) as per ICES, 2004a. Spawning stock biomass estimates were 7,129 t in 1973 (ICES, 2004a). Adult plaice biomass was therefore estimated to be 0.1229 t km^{-2}. The number of juvenile recruits (age 1) was multiplied by mean weight at age 1 in 1973 (ICES, 2004a).

Juvenile plaice biomass was estimated to be 0.0328 t km^{-2}.

Mean F in adult plaice was estimated to be 0.755 (ICES, 2004a). Natural mortality was assumed to be 0.2 (ICES, 2004a). $P/B.y^{-1}$ was, therefore estimated to be 0.955 in adult plaice. Adult $Q/B.y^{-1}$ was estimated to be 3.63 using equation 8. Juvenile plaice $P/B.y^{-1}$ and $Q/B.y^{-1}$ were assumed to be double that of the adults.

Adult plaice diet data indicated that infaunal polyncheates account for 100% of their diet. Juvenile plaice was assumed to be largely composed of zooplankton groups.

FG 13. Whiting

Whiting biomass was calculated using ICES total spawning stock biomass estimates in the Irish Sea. Biomass was estimated to be 0.5074 t km^{-2} (ICES, 2004a; ICES, 2004b). $P/B.y^{-1}$ was estimated to be 0.842 based on a fishing mortality of 0.642 and a assuming a natural mortality of 0.2 (ICES, 2004b; ICES, 2004a). $Q/B.y^{-1}$ was estimated to be 2.97 for whiting using equation 8.

Whiting diet data suggested that sandeel, other small gadoids, small pelagic planktivorous fish, and epifaunal macrobenthos accounted for around half of whiting diet. The remainder was split between zooplankton, invertebrates and other fish groups.

FG 14. Sole

Sole biomass was calculated using ICES total stock biomass estimates in the Irish Sea. Biomass was estimated to be 0.110 t km^{-2} (ICES, 2004a). $P/B.y^{-1}$ was calculated based on ICES fishing and natural mortality estimates of 0.363 and 0.2, respectively (ICES, 2004a). $Q/B.y^{-1}$ was estimated to be 2.58 using equation 8.

Sole diet data indicated that epifaunal mesobenthos accounted for 100% of their diet.

FG 15. Seatrout

Average weight of an individual seatrout (*Salmo trutta*) was calculated to be 0.72 kg based on Environment Agency data (Environment Agency, 2003). Total catch numbers using net and rod methods for westcoast, English, Welsh, and Scottish rivers feeding into the Irish Sea was calculated to be 5,713 (Environment Agency, 2003; FRS, 2004). This was doubled to include migratory trout entering the Irish Sea from Irish rivers, based on advice from several experts. Although, there are probably fewer fish entering the Irish Sea from the east coast of Ireland, doubling the British westcoast data may account for under reported catches (Mike Pawson and Ted Potter, pers comm.). Total Irish Sea catch in 2002 was therefore estimated to be 65,626.

Biomass of catch (t) = 65626 * 0.72
= 47250.72 kg = 47.25 t

Exploitation rate was estimated to be 15% by assuming a mean exploitation rate of 5% for net catches and 10% for rod catches (Ted Potter, pers. comm.). Therefore biomass was estimated to be 0.005 t km^{-2}. Natural mortality was calculated to be 0.44 using equation 7. $P/B.y^{-1}$ was, therefore estimated to be 0.59. $Q/B.y^{-1}$ was estimated to be 1.99 using equation 9.

FG 16. Sandeels

Small sandeel (*Ammodytes tobianus*) and Greater sandeel (*Hyperplus lanceolatus*) comprise 47% and 53% of the sandeel group, respectively. Sandeels are planktivores and are an important food source to many commercial fish species. An average Sandeel biomass estimate of 2.014 t km^{-2} was calculated from Cefas Irish Sea ground fish survey. Natural mortality was calculated to be 1.53 using equation 7. There were no fishing mortality estimates available, therefore natural mortality was used as an estimate of total mortality. $Q/B.y^{-1}$ was estimated as 5.016 from equation 9.

FG 17. Small flatfish

Thickback sole (*Microchirus variegatus*), solenette (*Buglossidium luteum*), and scaldfish (*Arnoglossus laterna*) make up 48%, 44%, 8%, respectively. Small flatfish biomass was calculated from Irish Sea ground fish survey data and estimated to be 0.097 t km^{-2}. Natural mortality was calculated from equation 7 as $2.46.y^{-1}$. There were no fishing mortality estimates available, therefore natural mortality was assumed to be total mortality. $Q/B.y^{-1}$ was calculated from equation 9 and estimated as 5.996.

Macrobenthos groups, zooplankton, and prawns and shrimp account for over 90% of small flatfish diet composition.

FG 18. Medium flatfish

Dab (*Limanda limanda*) composed 73% of the medium flatfish group. Medium flatfish biomass data was estimated at 8.919 t km^{-2} from Irish Sea ground fish survey data. Fishing mortality was estimated as 0.014 using equation 6. Natural mortality was estimated as 2.380 using equation 7. Therefore $P/B.y^{-1}$ was estimated as 2.394. $Q/B.y^{-1}$ was estimated to be 3.642 using equation 9.

Dragonets, gurnards, monkfish, macrobenthos, and prawns and shrimp were the major components in medium flatfish diet.

FG 19. Large flatfish

Large flatfish is composed of 67% turbot (*Scophthalmus maximus*) and 33% brill (*Scophthalmus rhombus*). Large flatfish biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.0794 t km^{-2}. P/B.y^{-1} was estimated to be 1.034 from a fishing mortality of 0.064 and a natural mortality estimate of 0.92 estimated using equations 6 and 7, respectively. Q/B.y^{-1} was calculated to be 2.730 from equation 9.

FG 20. Dragonets

Dragonets are composed of 77% common dragonets (*Callionymus lyra*) and 23% spotted dragonets (*Callionymus maculatus*). Dragonet biomass data was calculated to be 0.171 t km^{-2} from Irish Sea fish survey data. Natural mortality was estimated as 1.54 using equation 7. Since there was no fishing mortality estimates available, P/B.y^{-1} was assumed to be natural mortality. Q/B.y^{-1} was estimated to be 5.154 using equation 9.

Diet data indicators that macrobenthos accounts for more than 90% of dragonets prey.

FG 21. Other large demersal fish

Other large demersal fish is largely composed of ling (Molva molva) and conger eels (*Conger conger*). Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.199 t km^{-2}. Fishing mortality was calculated to be 0.2 from ICES catch data using equation 6 and natural mortality was estimated at 1.11 using equation 7. Therefore P/B.y^{-1} was estimated to be 1.315. Q/B.y^{-1} was estimated at 3.089 using equation 9.

Prawns and shrimp, *Nephrops* (*Nephrops norvegicus*), and epifaunal macrobenthos account for 100% of other large demersal diet composition.

FG 22. Gurnards

Gurnards are composed of 72% grey gurnards (*Eutrigla gurnardus*), 21% red gurnards (*Aspitrigla cuculus*), and 7% tub gurnards (*Trigla lucerna*). Gurnard biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.444 t km^{-2}. Natural mortality was estimated to be 2.21 using equation 7. There was no estimate for fishing mortality available. P/B.y^{-1} was therefore assumed to be 2.21. Q/B.y^{-1} was estimated to be 4.104 using equation 9.

Diet data suggests that epifunal macrobenthos, prawns and shrimp, and zooplankton account for the majority of gurnards prey.

FG 23. Mackerel

Mackerel (*Scomber scombrus*) biomass data was calculated from Irish Sea ground fish survey and was estimated to be 1.623 t km^{-2}. Fishing mortality was estimated as 0.019 using equation 6 and natural mortality was estimated to be 0.400 using equation 7. P/B.y^{-1} was therefore estimated to be 0.414. Q/B.y^{-1} was estimated to be 1.73 using equation 9.

Diet data suggests that zooplankton groups make up more than 90% of mackerel diet.

FG 24. Monkfish

Monkfish is composed of 92% anglerfish (*Lophius piscatorius*) and 8% white anglerfish (*Lophius budegassa*). Monkfish biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.652 t km^{-2}. Fishing and natural mortality estimates were calculated using equations 6 and 7 and were estimated to be 0.026 and 1.22, respectively. P/B.y^{-1} was therefore calculated to be 1.246. Q/B.y^{-1} was estimated as 1.989 using equation 9.

Survey data indicates that other fish groups account for a large proportion of monkfish diet.

FG 25. Mullet

Mullet consists of red mullet (*Mullus surmuletus*) and grey mullet (*Mugil cephalus*). Biomass was calculated from Irish Sea ground fish survey data and was estimated to be 0.004 t km^{-2}. Fishing and natural mortality were estimated using equations 6 and 7 and were calculated as 0.012 and 0.56, respectively. Therefore, P/B.y^{-1} was estimated at 0.575. Q/B.y^{-1} was estimated at 2.74 using equation 9.

Stomach contents data suggests that mullet feed primarily on prawns and shrimp, infaunal polycheates, and epifunal mesobenthos.

FG 26. Other large gadoids

Other large gadoids are largely composed of Pollock (*Pollachius pollachius*). Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.194 t km^{-2}. P/B.y^{-1} was estimated to be 0.490 from fishing and natural mortality estimated using equations 6 and 7, respectively. Q/B.y^{-1} was calculated as 1.95 using equation 9.

Stomach contents data indicates that mackerel, other small gadoids, and small pelagic planktivores are important in the diet of other large gadoids.

FG 27. Other small demersal fish

Other small demersal fish are composed of 51% lesser weaver fish (*Trachinus vipera)*, 39% argentine (*Argentina* sp.), and other species such as greater weaver fish (*Trachinus draco*) and triggerfish (Balistidae). Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.360 t km^{-2}. P/B.y^{-1} was estimated to be 1.57 from fishing and natural mortality estimated using equations 6 and 7, respectively. Q/B.y^{-1} was calculated as 5.421 using equation 9.

Diet data suggests that zooplankton groups provide more than 90% of other small demersal diet.

FG 28. Other small gadoids

Other small gadoids are composed of 40% poor cod, 28% Norway pout, 26% blue whiting, and 6% bib. Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.974 t km^{-2}. Fishing mortality and natural mortality were estimated to be 0.002 and 2.33, respectively using equations 6 and 7. P/B.y^{-1} was, therefore estimated to be 2.332. Q/B.y^{-1} was estimated to be 5.235 using equation 9.

Stomach contents data indicates that prawns and shrimp and zooplankton groups are important food sources for other small gadoids.

FG 29. Small pelagic planktivorous fish

Herring (*Clupea harengus*) biomass was taken from the ICES Stock assessment and was calculated to be 105,649 t in 1973. Assuming scad (*Trachurus trachurus*), pilchards (*Sardina pilchardus*), shads (*Alosa alosa*), sprat (*Sprattus sprattus*), and anchovy (*Engraulis encrasicolus*) have around 2 times the biomass of herring, small pelagic planktivorous fish biomass was calculated to be 3.643 t km^{-2}. Fishing mortality was estimated to be 0.477 and natural mortality was estimated to be 0.25 (ICES, 2005). Therefore P/B.y^{-1} was estimated to be 0.727. Q/B.y^{-1} was estimated to be 6.516 using equation 8.

Survey data suggests that zooplankton groups account for more than 90% of the diet of small pelagic planktivorous fish.

FG 30. Small sharks

Small sharks are largely composed of lesser-spotted dogfish (*Scyliorhinus canicula*). Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 1.874 t km^{-2}. Fishing mortality and natural mortality were estimated to be 0.012 and 0.96 using equations 6 and 7, respectively. Therefore P/B.y^{-1} was estimated to be 0.972. Since there were no consumption estimates available for small sharks and there is no empirical relationship for elasmobranchs, P/Q was guessitmated to be 0.100.

FG 31. Large sharks

Large sharks include spurdogs (*Squalus acanthias*), tope (*Galeorhinus galeus*) and porbeagle (*Lamna nasus*). Biomass was calculated from Irish Sea groundfish survey and was estimated to be 0.115 t km^{-2}. Natural mortality was estimated to be 0.318 using equation 7. There were no fishing mortality estimates available, therefore P/B.y^{-1} was assumed to be natural mortality. In the absence of the availability of large shark consumption estimates, P/Q was guesstimated to be 0.100.

FG 32. Skates and rays

Skates and ray are composed of 39% thornback ray (*Raja clavata*), 17% spotted ray (*Raja montagui*), 14% painted ray (*Raja microocellata*), 9% cuckoo ray (*Leucoraja naevus*), 16% blonde ray (*Raja brachyura*), and 5% skates (*Dipturus batis*). Biomass data was calculated from Irish Sea ground fish survey data and was estimated to be 0.714 t km^{-2}. P/B.y^{-1} was estimated to be 1.60 from fishing mortalities and natural mortalities calculated using equations 6 and 7. Since there were no consumption estimates available, a P/Q of 0.100 was taken from (Stanford and Pitcher, 2000).

Diet data suggests that prawns and shrimp and epifaunal macrobenthos are important food sources for skate and rays.

5.3 Invertebrate groups

Cefas 4 m beam trawl survey data were used to estimate biomasses using equations 4 and 5. Catchability (q) estimates were derived from Kaiser *et al.* (1994), who estimated upper and lower limits to be 0.35 and 0.05, respectively (Table 5.2). Zooplankton biomass estimates were calculated from continuous plankton recorder (CPR) data. Phytoplankton biomass estimates were available in the literature (Table 7.1). There is little quantitative invertebrate diet data available for the Irish Sea; therefore non-quantitative diet information guided our decisions in producing a sensible diet matrix for invertebrate groups (Table 7.2).

Table 5.2. Biomass estimates for invertebrate groups in the 1973 Irish Sea Ecopath model

Group	Biomass (t km^{-2}) [1]	Biomass (t km^{-2}) [2]	Average biomass (t km^{-2})
Epifaunal macrobenthos	2.45 (0.35)	17.2 (0.05)	***9.8103***
Epifaunal mesobenthos	0.17 (0.35)	1.21 (0.05)	***0.6918***
Infauna (polycheates)	0.000002 (0.35)	0.000011 (0.05)	***0.000006***
Infaunal macrobenthos	0.03 (0.35)	0.19 (0.05)	***0.111***
Infaunal mesobenthos	0.02 (0.35)	0.11 (0.05)	***0.0605***
Lobster and large crabs	0.02 (0.35)	0.17 (0.05)	***0.0943***
Nephrops	0.051 (0.35)	0.35 (0.05)	***0.203***
Cephalopods	0.04 (0.35)	0.29 (0.05)	***0.1666***
Prawns and shrimp	0.01 (0.35)	0.06 (0.05)	***0.0335***
Sessile epifauna	3.49 (0.35)	24.4 (0.05)	***13.944***

Number shown in ***bold italics*** are the figures entered into the model. Biomass (1) and (2) were calculated from the 4 m Cefas beam trawl 2003 survey. Numbers shown in bracket depict the catchability estimated used. Catchability estimates from Biomass t km^{-2} (1) and Biomass t km^{-2} (2) were taken from Kaiser *et al.* (1994).

For invertebrate species F or Z estimates were rarely available. To calculate P/B.y^{-1} ratios for these groups Brey's (2002) multi-parameter P/B.y^{-1} model (version 4.04) was used to estimate annual somatic production-to-biomass ratio of benthic invertebrate populations. Mean weight for each species and a weighted average were calculated where groups contained more than one species from the survey data. Where necessary mean wet weights were converted to mean shell-free wet weight and for the purpose of calculating P/B.y^{-1}, mean body mass was converted to energy content using conversion factors provided by Thomas Brey.

Using a P/Q of 0.15 (Christensen, 1995b) Ecopath was left to estimate Q/B.y^{-1} for epifaunal macrobenthos and mesobenthos, lobsters and large crabs, *Nephrops*, prawns and shrimps, and sessile epifaunal. "(Salzwedel, 1980) estimated for a common bivalve, *Tellina fabula*, that 22% of the consumption was turned into flesh production; as detritivores may have a lower food conversion efficiency than herbivores the consumption/biomass ratio for macrobenthos was here estimated from a lower, assumed gross food conversion efficiency of 15%" (Christensen, 1995b).

FG 33. Epifaunal macrobenthos

Epifaunal macrobenthos biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 9.810 t km^{-2}. P/B.y^{-1} was estimated to be 0.561.

Epifaunal macrobenthos is comprised of 70%, 4%, and 3% common starfish (*Asterias rubens*), sandstar (*Astropecten irregularis*), and common sunstar (*Crossaster papposus*), respectively, which feed on bivalves, small crustaceans, polychaetes and other echinoderms, 10% queen scallops (*Chlamys opercularis*), which are filter feeders, 5% whelks which are carnivorous preying on dead or dying individuals, and 8% other species which also include grazers. 80% of the diet of epifaunal macrobenthos was therefore assumed to be evenly distributed between epifaunal macrobenthos and mesobenthos, infaunal macrobenthos and mesobenthos, and infaunal polycheates. The remaining 20% was split between detritus, primary production, and zooplankton groups.

FG 34. Epifaunal mesobenthos

Epifaunal mesobenthos biomass data was calculated from from the 2003 Cefas beam trawl survey data and was estimated to be 0.691 t km^{-2}. P/B.y^{-1} was estimated to be 1.062.

Hermit crabs contribute 44% of the biomass of epifaunal mesobenthos and crabs of the genus *Liocarcinus* contribute 50%. Hermit crabs are omnivorous and scavengers, whilst *Liocarcinus* are carnivorous and scavengers. Therefore 95% of the diet of epifaunal mesobenthos was equally attributed to epifaunal mesobenthos, infaunal mesobenthos, and polycheates. The remaining 5% was assumed to be seaweed.

FG 35. Infauna (polycheates)

Infauna (polycheates) biomass data was calculated from the 2003 Cefas beam trawl survey data using the method outlined above and was estimated to be 0.00063 t km^{-2}. P/B.y^{-1} was estimated to be 1.683. Polycheate diet was assumed to be split equally between benthic microfauna, dissolved organic matter, and particulate organic matter.

FG 36. Infaunal macrobenthos

Infaunal macrobenthos biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 0.111 t km^{-2}. P/B.y^{-1} was estimated to be 0.695.

Infaunal macrobenthos is composed of 66% *Philine aperta*. The remainder of the group is filter feeders. *Philine aperta* feed primarily of polychaetes, bivalves, and sea urchins. 66% of the diet was assumed to be composed of an equal amount of epifaunal macrobenthos and mesobenthos, infaunal macrobenthos and mesobenthos, and polychaetes. The remainder was allocated to planktonic groups.

FG 37. Infaunal mesobenthos

Infaunal mesobenthos biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 0.605 t km^{-2}. P/B.y^{-1} was estimated to be 1.552.

Infaunal mesobenthos is composed of 91% cut trough shell (*Spisula subtruncata*), a suspension feeder. Therefore 91% of the diet composition was divided between plankton, detritus and microfaunal groups. The remainder was split between epifaunal mesobenthos, infaunal mesobenthos, infaunal polychaetes, and discards based on the assumption that some infaunal mesobenthos would be predatory and scavengers.

FG 38. Lobsters and large crabs

Lobster and large crab biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 0.0943 t km^{-2}. P/B.y^{-1} was estimated to be 0.783.

The diet of lobsters and large crabs was assumed to be 62% detritus, 20% benthos, 15% prawns and shrimp, and 3% cannibalisms (Standford and Pitcher, 2000).

FG 39. *Nephrops*

There is considerable variation in the western Irish Sea *Nephrops* stock assessment biomass estimates (ICES, 2003b). The total estimates of biomass of *Nephrops* in the western Irish Sea ranged from 35,000 t to 102,000 t depending on the method of assessment. ICES Irish Sea *Nephrops* biomass estimates should therefore be considered preliminary (ICES, 2003b). Therefore Cefas beam trawl survey estimates were used. Biomass was estimated to be 0.203 t km^{-2}.

Natural mortality of male 0.2 and females 0.3 was based on those used in assessment of *Nephrops* stocks in the Bay of Biscay (ICES, 2004c). Fishing Mortality estimates for male is 0.48 for western Irish Sea (ICES, 2003b). Here male and female estimates are assumed to be the same. Therefore,

$$Z = 0.25+0.48=0.73$$

FG 40. Cephalopods

Cephalopods are primarily composed of northern squid (*Loligo forbesi*) and common cuttlefish (*Sepia officinalis*). Biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 0.167 t km^{-2}. Cephalopod Q/B values were taken from (Araujo *et al.*, 2005). Cephalopod diet composition was adapted from Mackinson (2001) who used indices of relative abundance in diet composition of Californian market squid (*Loligo opalescens*) published in Karpov and Calliet, 1978.

FG 41. Prawns and shrimp

Prawn and shrimp are composed of 86% pink shrimps (*Pandalus montagui*), 9% brown shrimp (*Crangon crangon*), and 5% other species. Biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 0.0335 t km^{-2}. P/B.y^{-1} was estimated to be 0.959. Prawns and shrimp diet composition from Stanford and Pitcher, 2000 and Araujo *et al.*, 2005.

FG 42. Sessile epifauna

Sessile epifauna largely consists of hornwrack (*Flustra foliacea*) and dead man's fingers (*Alycyonium digitatum*). Biomass data was calculated from the 2003 Cefas beam trawl survey data and was estimated to be 13.944 t km^{-2}. P/B.y^{-1} was estimated to be 0.066. Sessile epifaunal diet composition was assumed to be divided between plankton, microfauna, and detritus.

FG 43. Meiofauna

There are no known biomass, P/B.y^{-1}, or Q/B.y^{-1} estimates of meiofauna in the Irish Sea. Heip *et al.*, 1990 and Heip *et al.* 1984 estimated average North Sea meiofauna biomass 0.11 t km^{-2} (Heip *et al.*, 1990; Heip, 1984). This value was assumed for the Irish Sea.

Heip *et al.* (1990) estimated meiofauna P/B.y^{-1} to be 12.07 and 35.3 and (Heip, 1984) estimated P/B.y^{-1} to be 8.0 in the North Sea. An average of these values was assumed for the Irish Sea, giving a P/B.y^{-1} estimate of 18.45. Heip *et al.*, (1990) estimate North Sea Q/B.y^{-1} for meiofauna to be 150.4 and 259.9. An average of 201.6 was assumed for the Irish Sea.

Meiofauna feeds mainly on algae and organic debris with bacteria playing an important role in nutrition. Diet was assumed to be 9% meiofauna, 1% polychaetes, 0.20% particulate organic matter, and 70% microflora.

FG 44. Gelatinous zooplankton

Stanford and Pitcher (2000) estimated carnivorous zooplankton to be 1.1 t km^{-2}, which was comprised of 45% chaetognaths and 55% gelatinous zooplankton. Therefore gelatinous zooplankton was estimated to be 0.605 t km^{-2}. $P/B.y^{-1}$ was estimated to be 7.00 based on Medusae data off the coast of British Columbia (Larson, 1987; Stanford and Pitcher, 2000). $Q/B.y^{-1}$ was estimated to be 23.33 from the carnivorous jellies group in the southern British Columbia shelf model (Stanford and Pitcher, 2000). The diet composition of gelatinous zooplankton was assumed to be entirely zooplankton based on Stanford and Pitcher (2000) and was split evenly between the 4 groups.

FG 45. Carnivorous zooplankton, FG 46. Omnivorous zooplankton and FG 47. Herbivorous zooplankton

Although all zooplankton are omnivorous to some extent, they can be separated into groups based on those that are predominantly herbivorous, carnivorous or omnivorous (Anon., 2003). Biomass of carnivorous zooplankton, omnivorous zooplankton, and herbivorous zooplankton were estimated to be 0.006, 0.137, and 0.076 t km^{-2}, respectively using the following methodology.

Irish Sea raw CPR data are supplied as numbers 3 m^{-3} (SAHFOS). These were converted to dry weights using biomass indices for each taxonomic group. Conversion of individual abundance data to biomass followed equation 10.

$$\text{Biomass (mg m}^{-3}\text{)} = \frac{\text{Dry weight (mg) x Abundance (number/3 m}^3\text{)}}{3} \qquad [10]$$

to convert zooplankton density volume into area:

$$\text{Volume of the Irish Sea (m}^3\text{)} = \text{Area (m}^{-2}\text{) * average depth of Irish Sea (m)}$$

$$\text{Irish Sea zooplankton biomass (mg)} = \text{zooplankton density (mg m}^{-3}\text{) * volume of Irish Sea (m}^3\text{)}$$

$$\text{Irish Sea zooplankton biomass (t km}^{-2}\text{)} = \text{Irish Sea zooplankton biomass (t) / Area of Irish Sea (km}^2\text{)}$$

$P/B.y^{-1}$ and $Q/B.y^{-1}$ estimates were taken from (Stanford and Pitcher, 2000), which in turn were taken from Christensens' North Sea Ecopath model (Christensen, 1995a).

Herbivorous zooplankton diet was assumed to comprise 90% phytoplankton, 3% zooplankton (divided evenly between carnivorous, omnivorous, and herbivorous zooplankton groups), and 7% detritus (divided evenly between POM and DOM), omnivorous zooplankton diet was assumed to comprise an even proportion of phytoplankton, detritus, carnivorous, omnivorous, and herbvirous zooplankton, and carnivorous zooplankton diet was assumed to comprise 90% herbivorous, omnivorous, and carnivorous zooplankton, 3% phytoplankton, and 7% detritus based on the North Sea (Christensen, 1995b), the Western Channel (Araujo *et al.*, 2005; Stanford and Pitcher, 2000) and that predominantly herbivorous zooplankton species would incorporate some carnivory and vice versa (Anon., 2003).

5.4 Primary producers and bacteria

FG 48. Microflora

Stanford and Pitcher (2000) estimated benthic microflora to be 3.92 t km^{-2}, which was assumed for the Irish Sea. $P/B.y^{-1}$ of 587 was reported by Billen *et al.* (1990).

FG 49. Seaweed

Stanford and Pitcher estimated seaweed biomass to be 75 t km^{-2} and a $P/B.y^{-1}$ of 60.00.

FG 50. Phytoplankton

Gowen *et al.* (2000) estimated Irish Sea primary production to be 182 $g.C.m^{-2}$ for an enriched coastal site of Liverpool Bay and 97 $g.C.m^{-2}$ for Irish coastal waters. The lower estimated was used since areas away from the coast are not likely to be as productive and are not subject to anthropogenic nutrient enrichment. Phytoplankton was therefore estimated to be 9.667 t km^{-2}.

A $P/B.y^{-1}$ of 152.5 was taken from Stanford and Pitcher, 2000.

5.5 Detritus groups

FG 51. Particulate organic matter and FG 52. Dissolved organic matter

Particulate and dissolved organic matter detritus biomass were taken from the North Sea Ecopath model (Christensen, 1995b) which were estimated to be 50 t km^{-2} each.

FG 53. Discards
Total Irish Sea discards calculated using the Cefas discard database were divided by the area of the Irish Sea to give a discard biomass estimate of 0.309 t km^{-2} (see section 5.6).

5.6 Fishery parameters

International landings were taken from ICES Fishstat+ landings for the ICES Area VIIa database in 1973. However, this database does not have landings by gear type. Therefore the UK landings by gear type were used to calculate the percentage of each group in the model that was landed by each gear type. Gear types were grouped into 9 fleets (Table 5.3). It was assumed that all countries landed the same percentage of landings per gear type as the UK (Table 5.4). Bass fishery information was calculated from the ICES stock assessment (ICES, 2003a) based on nominal landings (t) of bass by country in ICES area VIIa, f, and g in 1985. Percentage caught by gear were based on UK best catch estimates by gear in 1985 (ICES, 2003a).

The trio discard database was used for calculating discards. The trio database contains data collected from fishing vessels greater than 10 metres. Discard officers observe around 0.25% of the UK Fishing fleet activity. This was raised to 100%, thus assuming the same rate of discarding in the remaining fleet that were not observed. The Fishstat+ database suggests that UK fishing fleets land around 58% of the Irish Sea landings. This was raised to 100% to account for other countries fishing in Irish Sea. Thereby assuming that other countries discard at the same rate of the UK fishing fleet. There were no discard estimates available for *Nephrops* trawls, dredges, other nets, or midwater trawls. Based on personal experience and similar gears, some discarding was assumed for these gear types (Table 5.5).

5.7 Detritus and discard fate

Discard fate was directed into the discards group. Detritus fate was mainly directed to particulate organic matter and dissolved organic matter, a small amount was directed to the discards groups.

Table 5.3. Gear type groups.

Gear in UK landings database	Fleets in the model
Beam trawl	Beam trawls
Heavy otter trawl	Otter trawls
Light otter trawl	Otter trawls
Bottom pair trawl	Otter trawls
Shank nets	Other nets
Hand pushed nets	Other nets
Unspecified otter trawl	Otter trawls
Twin otter trawl	Otter trawls
Triple otter trawl	Otter trawls
Midwater demersal trawl	Midwater trawls
Midwater trawl	Midwater trawls
Midwater pair trawl	Midwater trawls
Nephrops otter trawl	*Nephrops* trawl
Twin *Nephrops* otter	*Nephrops* trawl
Triple *Nephrops* otter	*Nephrops* trawl
Prawn otter trawl	Otter trawls
Danish anchor seine	Seine nets
Scottish fly seine	Seine nets
Beach seine	Seine nets
Pair fly seine	Seine nets
Purse seine	Seine nets
Ring net	Other nets
Drift net	Other nets
Unspecified gill net	Other nets
Gill net (trammel)	Other nets
Gill net (tangle)	Other nets
Hoop net	Other nets
Stake net	Other nets
Gill net (Danish)	Other nets
Fyke net	Other nets
Top opening pots	Lines and pots
Side opening pots	Lines and pots
Parlour pots	Lines and pots
Other or mixed pots	Lines and pots
Unspecified trap	Lines and pots
Cuttle trap	Lines and pots
Long lines	Lines and pots
Hand lines (inc gurdy)	Lines and pots
Rod and line	Lines and pots
Surface picking	Pickers and gatherers
Submerged picking	Pickers and gatherers
Hand dredge	Dredges
Power dredge	Dredges
Suction dredge	Dredges
Unspecified dredge	Dredges

Table 5.4. Landings by gear (t km^{-2})

Group Name	Beam trawlers	Otter trawlers	Midwater trawlers	Other nets	Seine nets	Pickers and gatherers	Pots and lines	Dredges	*Nephrops* Trawls	Total
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass 3+	0.0000	0.0003	0.0000	0.0006	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000
Adult cod 2+	0.0018	0.1950	0.0000	0.0002	0.0060	0.0000	0.0000	0.0000	0.0000	0.2030
Juvenile cod Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult haddock 2+	0.0002	0.0405	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0410
Juvenile haddock Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult plaice 2+	0.0026	0.0715	0.0000	0.0001	0.0130	0.0000	0.0000	0.0000	0.0000	0.0870
Juvenile plaice Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.0001	0.1110	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.1110
Sole	0.0040	0.0029	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.0000	0.0070
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Medium flatfish	0.0019	0.0150	0.0000	0.0149	0.0003	0.0000	0.0000	0.0000	0.0000	0.0320
Large flatfish	0.0002	0.0021	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0020
Dragonets	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0001	0.0125	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0130
Mackerel	0.0000	0.0001	0.0000	0.0000	0.0218	0.0000	0.0001	0.0000	0.0000	0.0220
Monkfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0.0001	0.0318	0.0000	0.0000	0.0000	0.0000	0.0006	0.0000	0.0000	0.0330
Other small demersal	0.0000	0.0536	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0540
Other small gadoids	0.0008	0.0063	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0070
Small pelagic planktivorous fish	0.0000	0.0366	0.4950	0.1400	0.0000	0.0000	0.0000	0.0000	0.0000	0.6720
Small sharks	0.0020	0.0216	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0240

Table 5.4. continued: Landings by gear (t km^{-2})

Group Name	Beam trawlers	Otter trawlers	Midwater trawlers	Other nets	Seine nets	Pickers and gatherers	Pots and lines	Dredges	*Nephrops* Trawls	Total
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0011	0.0695	0.0000	0.0019	0.0008	0.0000	0.0003	0.0000	0.0000	0.0740
Epifaunal macrobenthos	0.0006	0.0077	0.0000	0.0000	0.0000	0.0000	0.0017	0.2900	0.0000	0.3000
Epifaunal mesobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Infauna (polycheate)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Infaunal macrobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Infaunal mesobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Lobster and large crabs	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0073	0.0000	0.0000	0.0070
Nephrops	0.0000	0.0019	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1000	0.1020
Cephalopods	0.0000	0.0012	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010
Prawns and shrimp	0.0036	0.0000	0.0000	0.0034	0.0000	0.0000	0.0000	0.0000	0.0000	0.0070
Sessile epifauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Carnivorous zooplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Omnivorous zooplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Herbivorous zooplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seaweed	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microfuna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Particulate organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dissolved organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Discards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sum	0.0200	0.6810	0.4950	0.1610	0.0420	0.0000	0.0100	0.2900	0.1000	1.7980

Table 5.5. Discards by gear (t km^{-2})

Group Name	Beam trawlers	Otter trawlers	Midwater trawlers	Other nets	Seine nets	Pickers and gatherers	Pots and lines	Dredges	*Nephrops* Trawls	Total
Toothed whales	0	0	0.0000001	0	0	0	0	0	0	0
Baleen whales	0	0	0.000001	0	0	0	0	0	0	0
Seals	0	0	0	0	0	0	0	0	0	0
Seabirds	0	0	0	0	0	0	0	0	0	0
Basking sharks	0	0	0.0000001	0	0	0	0	0	0	0
Bass	0	0	0	0.000001	0	0	0	0	0	0
Adult cod 2+	0.000517	0.000658	0.00001	0.000041	0	0	0	0	0	0.001
Juvenile cod Age 1	0	0	0.0001	0.000001	0	0	0	0	0	0
Adult haddock 2+	0	0.000211	0.00001	0.000001	0	0	0	0	0	0
Juvenile haddock Age 1	0	0	0.00001	0.000001	0	0	0	0	0	0
Adult plaice 2+	0.0134	0	0	0	0	0	0	0	0	0.013
Juvenile plaice Age 1	0.000002	0	0	0	0	0	0	0.000001	0	0
Whiting	0.00141	0.00264	0.0001	0.000001	0	0	0	0	0	0.004
Sole	0	0.000016	0	0	0	0	0	0.000001	0	0
Seatrout	0	0	0	0	0	0	0	0	0	0
Sandeels	0	0	0	0.000001	0	0	0	0	0	0
Small flatfish	0	0.000003	0	0	0	0	0	0.001	0.000001	0.001
Medium flatfish	0.0082	0.000542	0	0	0.000038	0	0	0.0001	0.00001	0.009
Large flatfish	0.000036	0	0	0	0	0	0	0.00001	0	0
Dragonets	0.000038	0.000012	0.00002	0	0	0	0	0	0	0
Other large demersals	0	0.000808	0.00001	0	0	0	0	0	0	0.001
Gurnards	0.000008	0.000294	0.0003	0	0.000095	0	0	0	0	0.001
Mackerel	0	0.00114	0.00001	0	0	0	0	0	0	0.001
Monkfish	0.00008	0.000172	0.000001	0	0	0	0	0.00001	0	0
Mullet	0	0	0.00001	0	0	0	0	0	0	0
Other large gadoids	0.000896	0.00371	0.000001	0	0	0	0	0	0	0.005
Other small demersal	0.000018	0.000046	0	0.0000021	0	0	0	0	0	0
Other small gadoids	0.00001	0.000036	0	0	0.000006	0	0	0	0	0
Small pelagic planktivorous fish	0	0.000004	0.0001	0	0	0	0	0	0	0
Small sharks	0	0.0891	0	0	0.000274	0	0	0	0	0.089

Table 5.5. continued: Discards by gear (t km^{-2}).

Group Name	Beam trawlers	Otter trawlers	Midwater trawlers	Other nets	Seine nets	Pickers and gatherers	Pots and lines	Dredges	*Nephrops* Trawls	Total
Large sharks	0	0.000039	0	0	0	0	0	0	0	0
Skates and rays	0	0.00928	0	0	0.000064	0	0	0	0	0.009
Epifaunal macrobenthos	0.0192	0.00173	0	0	0.00002	0	0	0.0001	0.000001	0.021
Epifaunal mesobenthos	0.00789	0.00148	0	0	0.000037	0	0	0.0000001	0.00001	0.009
Infauna (polycheate)	0.000595	0.000428	0	0	0.000007	0	0	0	0	0.001
Infaunal macrobenthos	0	0	0	0	0	0	0	0.00001	0.00001	0
Infaunal mesobenthos	0	0	0	0	0	0	0	0	0	0
Lobster and large crabs	0	0.000672	0	0	0	0	0	0.00001	0	0.001
Nephrops	0	0.0154	0	0	0	0	0	0	0	0.015
Cephalopods	0.000651	0.000429	0	0	0	0	0	0	0	0.001
Prawns and shrimp	0.000532	0.000387	0	0	0	0	0	0	0.0001	0.001
Sessile epifauna	0.00215	0.000421	0	0	0.000014	0	0	0.00001	0.00001	0.003
Meiofauna	0	0	0	0	0	0	0	0	0	0
Gelatinous zooplankton	0	0	0	0	0	0	0	0	0	0
Carnivorous zooplankton	0	0	0	0	0	0	0	0	0	0
Omnivorous zooplankton	0	0	0	0	0	0	0	0	0	0
Herbivorous zooplankton	0	0	0	0	0	0	0	0	0	0
Seaweed	0.00108	0.00301	0	0	0.000009	0	0	0	0	0.004
Microflora	0	0	0	0	0	0	0	0	0	0
Phytoplankton	0	0	0	0	0	0	0	0	0	0
Particulate organic matter	0	0	0	0	0	0	0	0	0	0
Dissolved organic matter	0	0	0	0	0	0	0	0	0	0
Discards	0	0	0	0	0	0	0	0	0	0
Sum	0.057	0.133	0.001	0	0.001	0	0	0.001	0	0.193

6. Linking adult-juvenile groups

The multi-stanza feature allows users to represent multiple ontogenic stages, whereas split pools only allow for an adult/juvenile split. The Irish Sea model incorporates three multi-stanza groups: cod, haddock, and plaice that were split into two stanzas representing adults and juveniles. Adult groups are the leading stanzas and juvenile groups are non-leading stanzas. User defined diet data and P/B estimates are entered for leading and non-leading stanzas. User defined biomass and Q/B estimates are entered for leading stanzas. Biomass and Q/B for non–leading stanzas are calculated using assumptions of the von Betalanffy model.

Biomass for non-leading stanzas are calculated using the von Bertalanffy prediction of relative body weight at age a, which gives the relative biomass of each stanza. Knowing the biomass for the leading stanza and the relative biomass of each stanza, the biomass of non-leading stanzas can be calculated by first calculating the population biomass:

$$B = B_{leading}/b_{leading\ s} \qquad [11]$$

Then:

$$B_s = b_s B$$

where B is the population biomass; $B_{leading}$ *is the biomass of the leading stanza;* $b_{leading\ s}$ *is the relative biomass of the leading stanza s;* B_s *is the biomass of stanza s;* b_s *is the relative biomass of stanza s.*

Q/B of non-leading stanzas are calculated using the assumption that feeding rates vary with age as the 2/3 power of body weight (a hidden assumption in the von Bertalanffy growth model).

Based on these assumptions of the von Bertalanffy model, Ecopath estimated juvenile cod, haddock, and plaice biomasses to be 0.195 t km^{-2}, 0.174 t km^{-2}, and 0.084 t km^{-2}, respectively. Juvenile cod, haddock, and plaice Q/B.y^{-1} were estimated to be 7.765, 10.564, and 10.168, respectively. Both ICES and Ecopath juvenile cod biomass estimates are similar; the ICES estimates are higher than that of estimates generated by Ecopath for juvenile haddock and plaice. This may be explained by the inherent difficulties in studying and estimating the number of recruits leading to juvenile biomasses and feeding rate estimates that are inconsistent with adult biomass and feeding rates.

7. Model balancing

The strategy employed in balancing the model was first to examine the basic inputs and assess their credibility. This revealed that several P/Q estimates were outside of their physiological limits and invertebrate P/B estimates were too low in many cases. P/Q in most cases would be between 0.05 and 0.3, very small organisms such as bacteria may be as high as 0.5 (Christensen *et al.*, 2005) (Table 7.1). Since there were a ranges of biomass calculated in most cases, biomass estimates were the second consideration in balancing the model. A number of problems were highlighted that had resulted in both over-estimates and under-estimate of Irish Sea biomass. Model balancing remained inside the biomass ranges calculated during model construction (Tables 5.1 and 5.2. Finally, the diet matrix was scrutinised. Diet compositions provide only a snap shot of feeding habits and many prey items are very difficult to identify due to their composition and digestion processes (Tables 7.1 and 7.2).

Table 7.1. Basic input parameters for 1973 Irish Sea model. Numbers in brackets represent balanced estimates where applicable.

Group name	Trophic level	Habitat area	Biomass in habitat area (t km^{-2})	Biomass (t km^{-2})	Production/ biomass (/year)	Consumption/ biomass (/year)	Ecotrophic efficiency	Production/ consumption
Toothed whales	5.19 (4.41)	1	0.00008	0.00008	0.02	8.67	0 (0.063)	0.002
Baleen whales	4.61 (3.86)	1	0.00034	0.00034	0.02	10	0 (0.147)	0.002
Seals	4.98 (4.29)	1	0.011	0.011	0.06	14.55	0	0.004
Seabirds	4.37 (3.82)	1	0.0511	0.0511	1.075	82.664	0.77	0.013
Basking sharks	4.43 (3.59)	1	0.0014	0.0014	0.07	3.7	0 (0.001)	0.019
Bass	4.94 (4.39)	1	0.0128	0.0128	0.5	2.68	0.008 (0.84)	0.187
Adult cod 2+	5.16 (4.16)	1	0.357	0.357	0.972	2 (3)	1.332 (0.922)	0.486 (0.324)
Juvenile cod Age 1	3.77 (3.38)	1	0.11 (0.196)	0.11 (0.196)	1.944	4 (7.765)	0.993 (0.65)	0.486 (0.25)
Adult haddock 2+	4.76 (3.89)	1	0.02 (0.07)	0.02 (0.07)	1.421	2.58 (4	10.877 (0.869)	0.551 (0.355)
Juvenile haddock Age 1	3.78 (3.25)	1	0.033 (0.174)	0.033 (0.174)	2.842	5.16 (10.564)	2.235 (0.346)	0.551 (0.269)
Adult plaice 2+	4.47 (3.67)	1	0.123 (0.2)	0.123 (0.2)	0.955	3.63	1.038 (0.89)	0.263
Juvenile plaice Age 1	3.58 (3.2)	1	0.0328 (0.0835)	0.0328 (0.0835)	1.91	7.26 (10.168)	0.438 (0.289)	0.263 (0.188)
Whiting	4.89 (4.25)	1	0.507	0.507	0.842	2.97	0.855 (0.725)	0.284
Sole	4.47 (3.65)	1	0.11 (0.16)	0.11 (0.16)	0.563	2.58	4.06 (0.96)	0.218
Seatrout	4.71 (3.99)	1	0.005 (0.03)	0.005 (0.03)	0.59	1.99	4.306 (0.718)	0.296
Sandeels	3.52 (2.97)	1	2.014 (1.3)	2.014 (1.3)	1.53	5.016	0.496 (0.575)	0.305
Small flatfish	4.12 (3.55)	1	0.097 (0.134)	0.097 (0.134)	2.46	5.996 (6.5)	1.42 (0.579)	0.41 (0.378)
Medium flatfish	4.82 (4.16)	1	8.919 (0.1)	8.919 (0.1)	2.394	3.642 (6.642)	0.015 (0.902)	0.657 (0.36)
Large flatfish	4.87 (4.23)	1	0.0794 (0.0894)	0.0794 (0.0894)	1.034	2.73 (3.73)	1.059 (0.937)	0.379 (0.277)
Dragonets	4.51 (3.78)	1	0.171 (0.229)	0.171 (0.229)	1.54	5.154	19.279 (0.995)	0.299
Other large demersals	4.81 (3.68)	1	0.199 (0.152)	0.199 (0.152)	1.315	3.089 (5.089)	0.423 (0.554)	0.426 (0.258)
Gurnards	4.26 (3.57)	1	0.444	0.444	2.21	4.104 (5.74)	3.816 (0.454)	0.538 (0.385)
Mackerel	4.13 (3.58)	1	34.26 (1.143)	34.26 (1.143)	0.414	1.73	0.054 (0.901)	0.239
Monkfish	5.35 (4.65)	1	0.652 (0.125)	0.652 (0.125)	1.246	1.989 (4)	4.103 (0.939)	0.626 (0.312)
Mullet	4.31 (3.69)	1	0.004 (0.089)	0.004 (0.089)	0.575	2.74	18.415 (0.827)	0.21
Other large gadoids	4.96 (4.3)	1	0.194	0.194	0.49	1.95	1.37 (0.995)	0.251
Other small demersal	4.15 (3.59)	1	0.36 (0.544)	0.36 (0.544)	1.57	5.421	5.106 (0.872)	0.29
Other small gadoids	3.95 (3.41)	1	6.59 (1.026)	6.59 (1.026)	2.332 (1.57)	5.235	0.869 (0.517)	0.445 (0.3)
Small pelagic planktivorous fish	4.15 (3.59)	1	3.643	3.643	0.727	6.516	1.252 (0.526)	0.112

Table 7.1. continued: Basic input parameters for 1973 Irish Sea model. Numbers in brackets represent balanced estimates where applicable.

Group name	Trophic level	Habitat area	Biomass in habitat area (t km^{-2})	Biomass (t km^{-2})	Production/ biomass (/year)	Consumption/ biomass (/year)	Ecotrophic efficiency	Production/ consumption
Small sharks	5.2 (4.06)	1	2.746 (0.288)	2.746 (0.288)	0.972	9.72	0.102 (0.455)	0.1
Large sharks	5 (4.28)	1	0.115	0.115	0.318	3.18	0.002 (0.001)	0.1
Skates and rays	4.4 (3.65)	1	0.714 (0.103)	0.714 (0.103)	1.6	16	0.169 (0.65)	0.1
Epifaunal macrobenthos	4.23 (3.15)	1	9.81 (13)	9.81 (13)	0.561 (1.661)	3.74 (8.305)	5.739 (0.587)	0.15 (0.2)
Epifaunal mesobenthos	3.95 (3.11)	1	0.691 (8.975)	0.691 (8.975)	1.062 (2.062)	7.08 (9.373)	14.084 (0.99)	0.15 (0.22)
Infauna (polycheate)	2	1	0.00063 (22.726)	0.00063 (22.726)	1.683 (3.683)	11.22 (12.277)	13130.228 (0.99)	0.15 (0.3)
Infaunal macrobenthos	4.33 (2.82)	1	0.111 (8.007)	0.111 (8.007)	0.695 (2.695)	4.633 (13.475)	128.608 (0.99)	0.15 (0.2)
Infaunal mesobenthos	3.15 (2.37)	1	0.605 (24.773)	0.605 (24.773)	1.552 (2.552)	10.347 (11.6)	8.449 (0.99)	0.15 (0.22)
Lobster and large crabs	2.91 (2.59)	1	0.0943 (0.098)	0.0943 (0.098)	0.783	5.22	0.761 (0.909)	0.15
Nephrops	4.49 (2.83)	1	0.203 (0.35)	0.203 (0.35)	0.73	4.867	2.067 (0.867)	0.15
Cephalopods	4.53 (3.31)	1	0.167 (0.25)	0.167 (0.25)	1.981	15	6.099 (0.772)	0.132
Prawns and shrimp	2.82 (2.14)	1	0.0335 (4.847)	0.0335 (4.847)	0.959	6.393	360.836 (0.99)	0.15
Sessile epifauna	2.79 (2.46	1	13.944 (7.5)	13.944 (7.5)	0.066 (2.066)	0.44 (10.33)	0.019 (0.986)	0.15 (0.2)
Meiofauna	2.11	1	0.11 (6.314)	0.11 (6.314)	18.45	201.6 (61.5)	0.983 (0.99)	0.092 (0.3)
Gelatinous zooplankton	4.43 (2.7)	1	0.605 (6.333)	0.605 (6.333)	7.5	23.33 (25)	1.677 (0.99)	0.321 (0.3)
Carnivorous zooplankton	4.19 (3.02)	1	0.006 (6.585)	0.006 (6.585)	18 (10)	60 (33.333)	355.369 (0.99)	0.3
Omnivorous zooplankton	3.05 (2.62)	1	0.137 (12.183)	0.137 (12.183)	18 (17)	60 (56.667)	16.006 (0.99)	0.3
Herbivorous zooplankton	2.06 (2.04)	1	0.076 (23.374)	0.076 (23.374)	18	60	28.095 (0.99)	0.3
Seaweed	1	1	75	75	60	-	0 (0.002)	-
Microflora	1	1	3.92	3.92	587	-	0.008 (0.179)	-
Phytoplankton	1	1	9.667	9.667	152.5	-	0.002 (0.726)	-
Particulate organic matter	1	1	50	50	-	-	0 (0.082)	-
Dissolved organic matter	1	1	50	50	-	-	0 (0.134)	-
Discards	1	1	0.191 (0.193)	0.191 (0.193)	-	-	0.001 (0.624)	-
Sum	1	1	1	1	1	1	1	1

Table 7.2. Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\Predator	Toothed whales	Baleen whales	Seals	Seabirds	Basking Sharks	Bass 3+	Adult cod 2+
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0100	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0170	0.0020	0.0000	0.0000	0.0000	0.0000	0 (0.0025)
Adult cod 2+	0.0170	0.0020	0.0000	0.0100	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0170	0.0020	0.0000	0.0310	0.0000	0.0000	0.0000
Adult haddock 2+	0.0170	0.0020	0.0000	0.0050	0.0000	0.0000	0.044 (0.014)
Juvenile haddock Age 1	0.0170	0.0020	0.0000	0.031 (0.011)	0.0000	0.0000	00.005
Adult plaice 2+	0.0170	0.0020	0.0000	0.0050	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0170	0.0020	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.0170	0.0020	0.0000	0.004 (0.024)	0.0000	0.0000	0.007 (0.0295)
Sole	0.0170	0.0020	0.0000	0.0070	0.0000	0.0000	0.0000
Seatrout	0.0170	0.0020	0.0000	0.0030	0.0000	0.0000	0.0000
Sandeels	0.0990	0.1500	0.2500	0.108 (0.148)	0.0000	0.3300	0 (0.012)
Small flatfish	0.0170	0.0020	0.0000	0.0030	0.0000	0.0000	0.0050
Medium flatfish	0.0170	0.0020	0.0000	0.0100	0.0000	0.0000	0.0050
Large flatfish	0.0170	0.0020	0.0000	0.0200	0.0000	0.0000	0.0000
Dragonets	0.0170	0.0020	0.0000	0.0521 (0.012)	0.0000	0.0000	0.022 (0.01)
Other large demersals	0.0170	0.0020	0.0000	0.0260	0.0000	0.0000	0.0000
Gurnards	0.0170	0.0020	0.0000	0.0640	0.0000	0.0000	0.0020
Mackerel	0.0990	0.0020	0.2500	0.0390	0.0000	0.0000	0.0360
Monkfish	0.0170	0.0020	0.0000	0.0010	0.0000	0.0000	0.0000
Mullet	0.0170	0.0020	0.0000	0.0100	0.0000	0.0000	0.0000
Other large gadoids	0.0170	0.0020	0.0000	0.0100	0.0000	0.0000	0.0000
Other small demersal	0.0170	0.0020	0.0000	0.0040	0.0000	0.0000	0.0020
Other small gadoids	0.0170	0.0020	0.0000	0.0560	0.0000	0.0000	0.0360
Small pelagic planktivorous fish	0.0990	0.1500	0.2500	0.0060	0.0000	0.6700	0.0190
Small sharks	0.0020	0.0000	0.0000	0.0010	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0020	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0000	0.0020	0.0000	0.0040	0.0000	0.0000	0.0000
Epifaunal macrobenthos	0.0050	0.0000	0.0310	0.0520	0.0000	0.0000	0.6620
Epifaunal mesobenthos	0.0050	0.0000	0.0310	0.0520	0.0000	0.0000	0.0410
Infauna (polycheate)	0.0000	0.0000	0.0000	0.1050	0.0000	0.0000	0.0050
Infaunal macrobenthos	0.0050	0.0000	0.0310	0.0000	0.0000	0.0000	0.0000
Infaunal mesobenthos	0.0050	0.0000	0.0310	0.0000	0.0000	0.0000	0.0000
Lobster and large crabs	0.0430	0.0000	0.0080	0.0020	0.0000	0.0000	0.0000
Nephrops	0.0430	0.0000	0.0080	0.0000	0.0000	0.0000	0.0490
Cephalopods	0.1980	0.0020	0.1000	0.0000	0.0000	0.0000	0.0040
Prawns and shrimp	0.0430	0.0000	0.0090	0.1680	0.0000	0.0000	0.0550
Sessile epifauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.0000	0.1630	0.0000	0.0000	0.2500	0.0000	0.0000
Carnivorous zooplankton	0.0000	0.1630	0.0000	0.0000	0.2500	0.0000	0.0020
Omnivorous zooplankton	0.0000	0.1630	0.0000	0.0000	0.2500	0.0000	0.0020
Herbivorous zooplankton	0.0000	0.1630	0.0000	0.0000	0.2500	0.0000	0.0020
Seaweed	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Particulate organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dissolved organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Discards	0.0000	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000
Sum	1	1	1	1	1	1	1

Table 7.2. continued: Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\predator	Juvenile cod Age 1	Adult haddock 2+	Juvenile haddock Age 1	Adult plaice 2+	Juvenile plaice Age 1	Whiting	Sole	Seatrout
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult cod 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0100	0.0000	0.0000	0.0000	0.0000	0.0200	0.0000	0.0000
Adult haddock 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile haddock Age 1	0.0000	0.0000	0.0100	0.0000	0.0000	0.0200	0.0000	0.0000
Adult plaice 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0000	0.0000	0.0000	0.0000	0.0100	0.0000	0.0000	0.0000
Whiting	0.0000	0.0000	0.0000	0.0000	0.0000	0.0100	0.0000	0.0000
Sole	0.0000	0.0000	0.0000	0.0000	0.0000	0.04 (0.01)	0.0000	0.0000
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0.0400	0.0350	0.0000	0 (0.02)	0.0000	0.1100	0.0000	0.2490
Small flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0500	0.0000	0.0000
Medium flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0 (0.03)	0.0000	0.0000
Large flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dragonets	0.0000	0.0060	0.0000	0 (0.01)	0.0000	0.0060	0.0000	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0500	0.0000	0.0010
Mackerel	0.0000	0.0030	0.0000	0.0000	0.0000	0.0240	0.0000	0.0000
Monkfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0500	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other small demersal	0.0000	0.0000	0.0000	0 (0.01)	0.0000	0.0060	0.0000	0.0000
Other small gadoids	0.0000	0.0000	0.0000	0.0000	0.0000	0.1180	0.0000	0.0000
Small pelagic planktivorous fish	0.0000	0.0000	0.0000	0.0000	0.0000	0.1440	0.0000	0.1500
Small sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Epifaunal macrobenthos	0.0000	0.4670	0.0000	0.1000	0.0000	0.1160	0 (0.1)	0.2750
Epifaunal mesobenthos	0.0500	0.2100	0.0400	0.2500	0.0000	0.0170	1 (0.25)	0.1250
Infauna (polycheate)	0.1500	0.1180	0.0500	1 (0.25)	0.2100	0.0120	0.2500	0.1250
Infaunal macrobenthos	0.0000	0.0500	0.0000	0.2500	0.0000	0.0000	0.2500	0.0500
Infaunal mesobenthos	0.0000	0.0500	0.0000	0.1500	0.0500	0.0000	0.1500	0.0250
Lobster and large crabs	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Nephrops	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010	0.0000	0.0000
Cephalopods	0.0000	0.0060	0.0000	0.0000	0.0000	0.0160	0.0000	0.0000
Prawns and shrimp	0.0500	0.0430	0.0500	0.0000	0.1500	0.0850	0.0000	0.0000
Sessile epifauna	0.0000	0.0030	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000	0.0000
Carnivorous zooplankton	0.1500	0.0020	0.1500	0.0000	0.1200	0.0350	0.0000	0.0000
Omnivorous zooplankton	0.2500	0.0020	0.2500	0.0000	0.2000	0.0350	0.0000	0.0000
Herbivorous zooplankton	0.2500	0.0020	0.1500	0.0000	0.1600	0.0350	0.0000	0.0000
Seaweed	0.0000	0.0030	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0.0500	0.0000	0.2000	0.0000	0.1000	0.0000	0.0000	0.0000
Particulate organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dissolved organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Discards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sum	1	1	1	1	1	1	1	1

Table 7.2. continued: Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\predator	Sandeels	Small flatfish	Medium flatfish	Large flatfish	Dragonets	Other large demersals	Gurnards	Mackerel
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult cod 2+	0.0000	0.0000	0.0020	0.0100	0.0000	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0000	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000
Adult haddock 2+	0.0000	0.0000	0.0020	0.0100	0.0000	0.0000	0.0000	0.0000
Juvenile haddock Age 1	0.0000	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000
Adult plaice 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000	0.0100	0.0000
Sole	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0.0000	0.0000	0.0200	0.2800	0.0000	0.0000	0.0000	0.0000
Small flatfish	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000	0.0000	0.0000
Medium flatfish	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000	0.0000	0.0000
Large flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dragonets	0.0000	0.0000	0.135 (0.1)	0.0000	0.0000	0.0000	0.0180	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0000	0.0000	0.1040	0.0000	0.0000	0.0000	0.0000	0.0000
Mackerel	0.0000	0.0000	0.0050	0.0000	0.0000	0.0000	0.0000	0.0007
Monkfish	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0.0000	0.0000	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000
Other small demersal	0.0000	0.0670	0.0500	0.0010	0.0000	0.0000	0.0210	0.0000
Other small gadoids	0.0000	0.0000	0.0301 (0.065)	0.1770	0.0000	0.0000	0.0100	0.0010
Small pelagic planktivorous fish	0.0000	0.0000	0.0380	0.1220	0.0000	0.0000	0.0010	0.0090
Small sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010
Epifaunal macrobenthos	0.0000	0.2000	0.1540	0.0250	0.6420	0.5000	0.1090	0.0280
Epifaunal mesobenthos	0.0000	0.0000	0.0020	0.0250	0.0000	0.0000	0.0910	0.0090
Infauna (polycheate)	0.0000	0.2000	0.1140	0.0250	0.2860	0.0000	0.0010	0.0007
Infaunal macrobenthos	0.0000	0.0000	0.0000	0.0250	0.0000	0.0000	0.0000	0.0000
Infaunal mesobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Lobster and large crabs	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Nephrops	0.0000	0.0000	0.0009	0.0000	0.0000	0.167 (0.05)	0.0010	0.0000
Cephalopods	0.0000	0.0000	0.0070	0.1000	0.0000	0.0000	0.0030	0.0010
Prawns and shrimp	0.0000	0.2000	0.1070	0.0000	0.0000	0.333 (0.45)	0.4160	0.0000
Sessile epifauna	0.0000	0.0000	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.2000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Carnivorous zooplankton	0.1000	0.1110	0.0400	0.0000	0.0240	0.0000	0.1060	0.3120
Omnivorous zooplankton	0.2000	0.1110	0.0400	0.0000	0.0240	0.0000	0.1060	0.3120
Herbivorous zooplankton	0.1000	0.1110	0.0420	0.0000	0.0240	0.0000	0.1070	0.3130
Seaweed	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0.1000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003
Particulate organic matter	0.3000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0120
Dissolved organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Discards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sum	1	1	1	1	1	1	1	1

Table 7.2. continued: Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\predator	Monkfish	Mullet	Other large gadoids	Other small demersal	Other small gadoids	Small pelagic plank tivorous fish	Small sharks	Large sharks
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult cod 2+	0.0998 (0.01)	0.0000	0.0500	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult haddock 2+	0.0998 (0.005)	0.0000	0.05 (0.005)	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile haddock Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult plaice 2+	00.095	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.0100	0.0000	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000
Sole	0.0798 (0.04)	0.0000	0.069 (0.039)	0.0000	0.0000	0.0000	0.0000	0.0000
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0 (0.01)	0.0000	00.045	0.0000	0.0000	0.0000	0.0000	0.1340
Small flatfish	0.0858 (0.096)	0.0000	0.0010	0.0000	0.0020	0.0000	0.0000	0.134 (0.094)
Medium flatfish	0.0768 (0.097)	0.0000	0 (0.03)	0.0000	0.0030	0.0000	0.0000	0.0000
Large flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dragonets	0.0960	0.0000	0.0010	0.0000	0.0150	0.0000	0.0000	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0 (0.04)
Mackerel	0.1240	0.0000	0.1220	0.0000	0.0000	0.0000	0.0000	0.0000
Monkfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0.0100	0.0000	0.0140	0.0000	0.0000	0.0000	0.0000	0.0000
Other small demersal	0.0380	0.0000	0.0220	0.0000	0.0230	0.0100	0.0000	0.0340
Other small gadoids	0.1340	0.0000	0.1340	0.0000	0.0080	0.0000	0.0000	0.1740
Small pelagic planktivorous fish	0.0960	0.0000	0.2480	0.0000	0.0070	0.0020	0.0000	0.1540
Small sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Epifaunal macrobenthos	0.0100	0.0530	0.0150	0.0330	0.0980	0.0280	0.6650	0.3140
Epifaunal mesobenthos	0.0000	0.5200	0.0100	0.0130	0.0870	0.0060	0.0150	0.0000
Infauna (polycheate)	0.0100	0.2500	0.0000	0.0000	0.0230	0.0020	0.0350	0.0000
Infaunal macrobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2000	0.0010
Infaunal mesobenthos	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010
Lobster and large crabs	0.0070	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0400
Nephrops	0.00499 (0.003)	0.0000	0.0007	0.0000	0.0000	0.0000	0.0000	0.0000
Cephalopods	0.0000	0.0120	0.0180	0.0000	0.0020	0.0005	0.0850	0.0000
Prawns and shrimp	0.0190	0.1350	0.0760	0.0030	0.1210	0.0060	0.0000	0.0010
Sessile epifauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0100
Carnivorous zooplankton	0.0000	0.0100	0.0560	0.3170	0.1490	0.3150	0.0000	0.0010
Omnivorous zooplankton	0.0000	0.0100	0.0560	0.3170	0.1490	0.3150	0.0000	0.0010
Herbivorous zooplankton	0.0000	0.0100	0.0560	0.3170	0.1490	0.3150	0.0000	0.0010
Seaweed	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Particulate organic matter	0.0000	0.0000	0.0000	0.0000	0.1640	0.0000	0.0000	0.0000
Dissolved organic matter	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Discards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sum	1	1	1	1	1	1	1	1

Table 7.2. continued: Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\predator	Skates and rays	Epifaunal macro-benthos	Epifaunal meso-benthos	Infauna (poly-cheate)	Infaunal macro-benthos	Infaunal meso-benthos	Lobster and large crabs	*Nephrops*
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult cod 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult haddock 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile haddock Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult plaice 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.0080	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sole	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0.0040	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small flatfish	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Medium flatfish	0.0030	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dragonets	0.0180	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mackerel	0.0060	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Monkfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other small demersal	0.0570	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0070
Other small gadoids	0.0070	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0020
Small pelagic planktivorous fish	0.0080	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small sharks	0.0060	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0030	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Epifaunal macrobenthos	0.2510	0.16 (0.027)	0.0000	0.0000	0.132 (0.022)	0.0000	0.0500	0.0700
Epifaunal mesobenthos	0.0310	0.16 (0.104)	0.32 (0.01)	0.0000	0.132 (0.022)	0.025 (0.006)	0.0500	0.0700
Infauna (polycheate)	0.0210	0.16 (0.178)	0.3200	0.0000	0.1330	0.025 (0.056)	0.0000	0.0500
Infaunal macrobenthos	0.0000	0.16 (0.176)	0.0000	0.0000	0.132 (0.012)	0.0000	0.0500	0.0700
Infaunal mesobenthos	0.0000	0.16 (0.177)	0.3200	0.0000	0.1330	0.025 (0.006)	0.0500	0.0700
Lobster and large crabs	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0300	0.0000
Nephrops	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Cephalopods	0.0070	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Prawns and shrimp	0.4530	0.0000	0.0000	0.0000	0.0000	0.0000	0.1500	0.0000
Sessile epifauna	0.0000	00.006	0.0000	0.0000	0.0000	00.05	0.0000	0.1610
Meiofauna	0.0000	0.0000	0 (0.3)	0.0000	00.112	00.15	0.0000	0.0000
Gelatinous zooplankton	0.0000	0.0190	0.0000	0.0000	0.0690	0.10	0.0000	0.0000
Carnivorous zooplankton	0.0360	0.0190	0.0000	0.0000	0.068 (0.008)	0.1 (0.011)	0.0000	0.0000
Omnivorous zooplankton	0.0360	0.0190	0.0000	0.0000	0.0690	0.1 (0.011)	0.0000	0.0000
Herbivorous zooplankton	0.0360	0.0190	0.0000	0.0000	0.068 (0.018)	0.1 (0.011)	0.0000	0.0000
Seaweed	0.0000	0.018 (0.039)	0.0400	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.018 (0.037)	0 (0.01)	0.3300	0 (0.001)	0.1 (0.111)	0.0000	0.0000
Phytoplankton	0.0000	0.0190	0.0000	0.0000	0 (0.271)	0.1 (0.111)	0.0000	0.0000
Particulate organic matter	0.0070	0.018 (0.121)	0.0000	0.3400	0.068 (0.065)	0.1 (0.111)	0.6200	0.0000
Dissolved organic matter	0.0000	0.0190	0.0000	0.3300	0 (0.065)	0.1 (0.311)	0.0000	0.0000
Discards	0.0000	0.018 (0.021)	0.0000	0.0000	0.0000	0.1 (0.056)	0.0000	0.5000
Sum	1	1	1	1	1	1	1	1

Table 7.2. continued: Diet matrix showing input value. Numbers in brackets represent balanced values where applicable.

Prey\predator	Cephalopods	Prawns and Shrimp	Sessile Epifauna	Meiofauna	Gelatinous zooplankton	Carnivorous zooplankton	Omnivorous zooplankton	Herbivorous zooplankton
Toothed whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Basking sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bass	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult cod 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile cod Age 1	0.0100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult haddock 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile haddock Age 1	0.0100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adult plaice 2+	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Juvenile plaice Age 1	0.0100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Whiting	0.01 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sole	0.010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Seatrout	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sandeels	0.01 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Medium flatfish	0.010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large flatfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dragonets	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large demersals	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gurnards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mackerel	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Monkfish	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mullet	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other large gadoids	0 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other small demersal	0.01 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other small gadoids	0.01 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small pelagic planktivorous fish	0.03 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Small sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Large sharks	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Skates and rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Epifaunal macrobenthos	0.0200	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Epifaunal mesobenthos	0.0200	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Infauna (polycheate)	0.0100	0.0000	0.0000	0.0100	0.0000	0.0000	0.0000	0.0000
Infaunal macrobenthos	0.0200	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Infaunal mesobenthos	0.0200	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Lobster and large crabs	0 (0.005)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Nephrops	0 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Cephalopods	0 (0.001)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Prawns and shrimp	0 (0.01)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sessile epifauna	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Meiofauna	0.0000	0.0000	0.0000	0.0900	0.0000	0.0000	0.0000	0.0000
Gelatinous zooplankton	0.1900	0.0000	0.0000	0.0000	0.25 (0.05)	0.225 (0.125)	0.0000	0.0000
Carnivorous zooplankton	0.2 (0.125)	0.13 (0.03)	0.125 (0.099)	0.0000	0.25 (0.05)	0.225 (0.025)	0.166 (0.016)	0.0100
Omnivorous zooplankton	0.2000	0.13 (0.03)	0.125 (0.099)	0.0000	0.2500	0.225 (0.325)	0.166 (0.066)	0.0100
Herbivorous zooplankton	0.2 (0.141)	0.13 (0.03)	0.125 (0.099)	0.0000	0.25 (0.1)	0.2250	0.166 (0.466)	0.01 (0.001)
Seaweed	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Microflora	0.0000	0.0000	0.125 (0.143)	0.7000	0.0000	0.0000	0.0000	0.0000
Phytoplankton	0 (0.2)	0 (0.08)	0.125 (0.143)	0.0000	0 (0.15)	0 (0.03)	0 (0.156)	0 (0.609)
Particulate organic matter	0.0000	0.08 (0.52)	0.125 (0.143)	0.2000	0 (0.2)	0.03 (0.135)	0.166 (0.16)	0.9 (0.135)
Dissolved organic matter	0.0000	0.52 (0.31)	0.125 (0.274)	0.0000	0 (0.2)	0.035 (0.135)	0.17 (0.136)	0.035 (0.235)
Discards	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Sum	1	1	1	1	1	1	1	1

8. Characterising the UK's marine ecosystems

Ecopath is capable of generating a number of outputs for characterising ecosystem properties and states. There are three other Ecopath models of UK marine ecosystems from 1973 to the present day that can be used for comparison and thus help to characterise the Irish Sea ecosystem. The North Sea model (Mackinson and Daskalov, in prep), the English Channel model (Stanford and Pitcher, 2000), and the Western English Channel model (Araujo *et al.*, 2005). The four models vary in size, structure, and complexity. The North Sea, Irish Sea, and then the English Channel models are the order of size and complexity from largest to smallest.

Ecopath's network routine allows users to calculate energy flows between trophic levels within the system, which can be summarised in a "Lindeman spine". The Lindeman spine analysis was originally developed by Ulanowicz (1995) and reduces large complex food webs into a simple chain. The Lindeman spine shows the trophic transfer efficiencies between the 11 trophic levels represented in the Irish Sea model (Figure 8.1). Transfer efficiencies are highest a trophic level II (28.4%), remain around 20% at levels III to IX, and decrease at level XI (Figure 8.1). These efficiencies are comparable with the North Sea model, but the channel models are less efficient (Table 8.1).

The mean trophic transfer efficiencies originating from detritus and primary production are higher would be expected (Table 8.2). It is widely accepted that mean energy transfer efficiencies between trophic levels is around 10% (Pauly and Christensen, 1995). This discrepancy may be explained by the inclusion of the microbial groups in the North Sea and Irish Sea models that represent the microbial loop and is illustrated by the mean trophic transfer efficiencies originating from detritus (Table 8.2).

Ecopath incorporates a number of outputs that describe the system as a whole and act as indicators of ecosystem state and maturity (Odum, 1969) (Table 8.2). These emergent metrics relate to ecosystem size and development, community energetics, community structure, life history, nutrient cycling, selection pressure, and overall homeostasis (Odum, 1969). These metrics are useful indicators of changes in ecosystem state and maturity in temporal comparisons within systems can be made, but are more difficult to employ in cross system comparisons because they are dependent on model structure, size, and complexity.

Throughput and biomass are indicators of ecosystem size and development. Throughput is the sum of all imports and exports, consumption, respiratory flows, and flows into detritus to and from each group represented in the model (Christensen *et al.*, 2005). Total biomass excludes detritus. Throughput and biomass are expected to increase as the system matures and grow.

Primary production/respiration (Pp/R), and primary production/biomass (Pp/B) relate to the community energetic attributes of ecosystem maturity. In the early stages of ecosystem development primary production (Pp) is expected to exceed respiration (R), ie Pp/R will be greater than 1. As the system matures the ratio is expected to move towards unity. Given that respiration is expected to be less than primary production in developing systems, it follows that biomass will accumulate as the system matures. Consequently, the Pp/B ratio is expected to be high and diminish as the system matures.

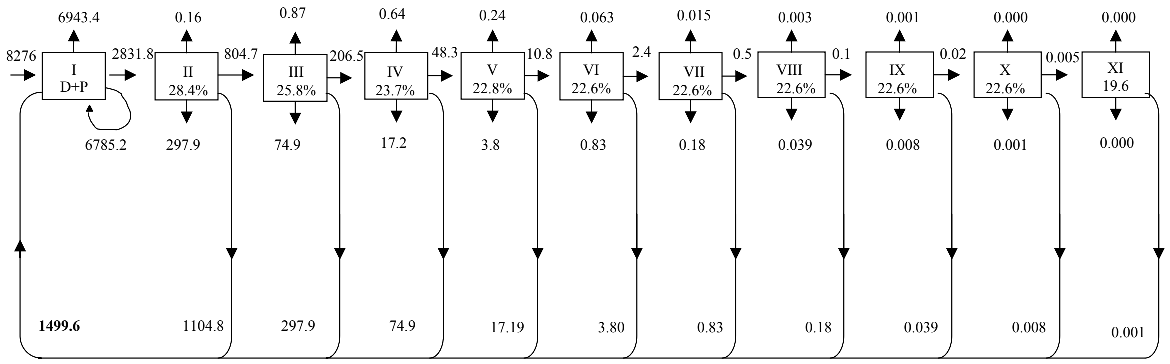


Figure 8.1. The Lindeman spine analysis. Flows out the tops of the compartment box represent export and flows out of the bottom represent respiration. Flows to detritus are recycled though the detritus and primary production (D+P) compartment at trophic level I. The percentages in the boxes represent the annual trophic transfer efficiencies (% of ingested food).

Table 8.1. Trophic transfer efficiencies flowing from producers and detritus in UK shelf Ecopath models.

Model	Trophic Level										
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Irish Sea	28.4	25.8	23.7	22.8	22.6	22.6	22.6	22.6	22.6	19.6	-
North Sea	37.1	29.1	25.6	22.6	20.8	19.8	19.3	18.0	17.7	15.7	0.2
English Channel	15.7	12.4	10.2	8.6	6.2	5.1	2.3	-	-	-	-
Western Channel	15.6	12.3	8.3	7.3	6.0	4.5	3.8	0.4	-	-	-

System trophic complexity also relates to the community energetic attributes of ecosystem maturity. Odum (1969) postulated that developing systems would shift from linear grazing to complex food webs. The connectance index (CI) and system omnivory index (SOI) can be used as a proxy of food chain complexity. Finns cycling index and path length are indicators of flow diversity and nutrient recycling capacity. These indices are expected to increase with system development (Christensen, 1995a).

Mean trophic level of catch is related to Odum's size and life cycles attributes of maturity. The catch/primary production (Y/P) ratio is a measure of gross fisheries efficiency, which is expected to increase as fishing is targeted lower down the food webs (Trites *et al.*, 1999).

A number of the metrics that might be useful for making comparison between different ecosystems are sensitive to differences in how the models are specified and so it is important to be aware of this. Ecosystem metrics that use total biomass are heavily dependent on the model's structure and complexity. Throughput is affected by user defined detritus fate, model size, and complexity. Primary production values in Table 8.2 are dependent on model structure, eg unlike the Irish Sea and Channel models, the North Sea model does not include primary production from seaweed and hence net Pp is considerably lower and ratio metrics using net Pp are not directly comparable. Indices of system trophic complexity are dependent on the detail and complexity of the diet matrix. Mean trophic level of catch may be comparable between systems, but will depend on target species, gear, and effort employed within each system. Generally speaking, straightforward single descriptors of size, trophic levels, flows, fisheries and network paths are useful for characterising system structure and state whilst ratio metrics of system energetics are more useful for comparisons of ecosystem function.

Table 8.2. Summary of Ecopath statistics.

Parameter	Irish Sea	North Sea	English Channel	Western Channel
Mean trophic transfer efficiency from detritus (%)	24.80	31.00	11.10	9.00
Mean trophic transfer efficiencies from detritus and primary production (%)	25.4	30.2	12.6	11.7
Sum of all consumption (t km^{-2} year^{-1})	3905	6212	1503	1567
Sum of all exports (t km^{-2} year^{-1})	6945	95	6797	2163
Sum of all respiratory flows (t km^{-2} year^{-1})	1330	1953	811	786
Sum of all flows into detritus (t km^{-2} year^{-1})	12837	3842	7449	2692
Total system throughput (t km^{-2} year^{-1})	25017	12102	16559	7209
Sum of all production (t km^{-2} year^{-1})	9371	4711	7834	3420
Mean trophic level of the catch	3.61	3.88	2.42	2.78
Gross efficiency (catch/net p.p.)	0.00024	0.00342	0.00048	0.00053
Calculated total net primary production (t km^{-2} year^{-1})	8275	2150	7547	2949
Total primary production/total respiration	6.22	1.10	9.31	3.75
Net system production (t km^{-2} year^{-1})	6945	197	6737	2163
Total primary production/total biomass	33.71	3.82	31.11	15.02
Total biomass/total throughput	0.010	0.047	0.015	0.027
Total biomass (excluding detritus) (t km^{-2})	245	563	243	196
Total catches (t km^{-2} year^{-1})	2.00	7.35	3.65	1.56
Connectance Index	0.223	0.222	0.129	0.170
System Omnivory Index	0.332	0.277	0.143	0.126
Finn's cycling index (% of total throughput)	0.590	5.610	0.140	0.730
Finn's mean path length	2.68	3.90	2.02	2.01

9. Model sensitivity testing

9.1 Sensitivity analysis

A simple routine for sensitivity analysis (*sensu* Majkowski, 1982) is included within Ecopath. This routine varies all four basic input parameters, ie B, P/B, Q/B, EE in steps from – 50% to + 50% to check what the effect of altering each of these would be on the "missing" parameter estimated by Ecopath during parameterisation. An increase in either biomass or P/B resulted in a decrease in the "missing" parameter value, whilst a decrease in biomass and P/B yielded an increase in the "missing" parameter estimate. "Missing" parameter values were least sensitive to increases in biomass and P/B estimates. A 50% increase in biomass resulted in a 19-33% decrease in the "missing" parameter, whilst a 50% decrease in biomass resulted in a 56-100% increase in the "missing" parameter (Figure 9.1(a)). A 50% increase in P/B resulted in a 26-33% decreased in the "missing" parameter, whilst a 50% decrease in P/B resulted in a 78-100% increase in the "missing" parameter estimate (Figure 9.1(b)). Conversely, an increase in Q/B resulted in an increase in the "missing" parameter estimate. "Missing" parameters were less sensitive to changes in Q/B than they were to changes in biomass and P/B (Figure 9.1(c)).

The sensitivity of "missing" parameters of other groups to changes in the input parameters depends on the trophic linkages between those groups. "Missing" parameters are most sensitive to changes in input parameters where predation pressure is largely from a single group. For example, a change in the input parameters of adult cod (the main predator of bass) is linearly related to changes in the ecotrophic efficiency of bass, whilst prawns and shrimps (subject to many predators) are only marginally sensitive to changes in other small gadoids input parameters (Figure 9.2).

The sensitivity analysis suggests that parameterisation of groups within the model is most sensitive to decreases in biomass and P/B estimates and that the impact of changes in the parameters of one group on another is influenced by the trophic dependency of the impacting group on the impacted group. The impacts of an increase in biomass in one group on other groups within the systems can be shown using a mixed trophic impact plot (Figure 9.3). This can be used to get an overall indication of the sensitivities and responses to reduced biomass in one group on another and the fisheries dependent upon them.

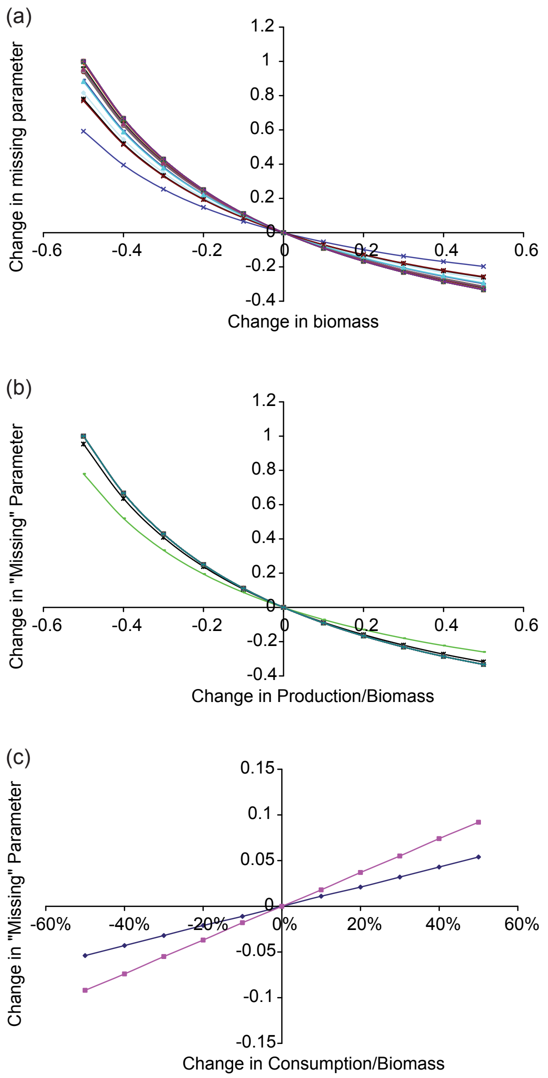


Figure 9.1. Effect of changing input parameters on missing parameters estimated by Ecopath for each groups in the model (a) biomass, (b) P/B, and (c) Q/B.

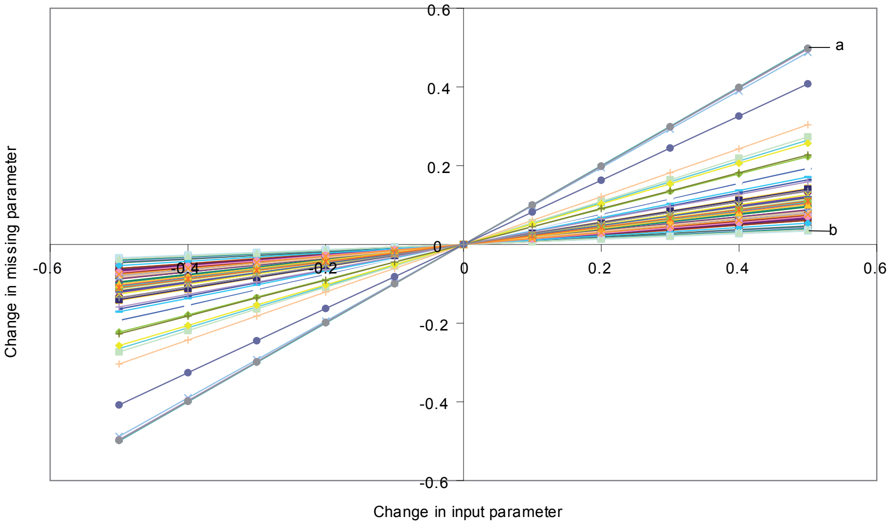


Figure 9.2. (a) Effect of a 50% increase in adult cod biomass of bass EE ("missing" parameter), (b) effect of a 50% increase in other small gadoid biomass on prawns and shrimp EE ("missing" parameter).

9.2 Ecosim parameterisation

The stability of the Irish Sea model was evaluated by examining the systems behaviour when it was disturbed from mass balance using Ecosim. Ecosim is a dynamic simulation tool for ecosystem modelling. Ecosim uses mass balance results from the base Ecopath model for parameter estimation. It also requires estimates of the vulnerability of each prey species to its predators, feeding time adjustment rate, fraction of other mortality sensitive to changes in feeding time, and predator effects on feeding time.

Model simulations are particularly sensitive to vulnerabilities. Vulnerabilities allow exploration of top-down and bottom-up control of the biomass of groups within the system. Low vulnerabilities (close to 1) means that an increase in a predator biomass will not result in an increase predation mortality exerted on its prey, ie bottom-up. Conversely, a high vulnerability (over 28) means that if a predator biomass is doubled, predation mortality exerted on it prey will be doubled i.e. top-down (Christensen *et al.*, 2005). Ecosim incorporates several approaches to estimating vulnerabilities.

Feeding time adjustment rate determines how fast organisms adjust feeding times so as to stabilize consumption rate per biomass. Setting the value to 0.0 causes feeding time (and hence time exposed to predation risk) to remain constant, all changes in consumption per biomass then result in growth rate changes. Setting it to 1.0 results in fast time response, which causes reduction in vulnerability to predation rather than increased growth rate.

The fraction of other mortality sensitive to changes in feeding time is the proportion of the unexplained natural mortality rate that is assumed to be sensitive to changes in feeding time. Setting it to 0.0 causes natural mortality to remain constant. Setting it to a higher value causes that proportion of natural mortality to vary in proportion to relative time spent feeding. Setting nonzero value along with nonzero feeding time factor generally results in density-dependent natural mortality i.e. as density increases, feeding time usually has to increase to maintain food consumption rate, and this increased feeding time leads to higher mortality rate.

Setting a nonzero value for the predator effect on feeding time parameter allows users to simulate the effect of changes in predator abundance on feeding time and food consumption rate, ie 'risk sensitive foraging behaviour'. If the value is high, it is assumed that the organism will reduce target food consumption rate (and hence time exposed to predation risk) by up to this fraction if predator abundance increases, and will correspondingly increase food consumption rate if predator abundance falls below the Ecopath baseline.

Using these parameters, Ecosim is able to simulate direct compensatory changes in juvenile recruitment via at least three alternative mechanisms or hypotheses: (1) simple density-dependence in juvenile production rate by adults, due to changes in adult feeding rates and fecundity (not a likely mechanism); (2) changes in duration of the juvenile stage and hence in total time exposed to relatively high predation risk; (3) changes in juvenile foraging time (and hence exposure to predation risk) with changes in juvenile feeding rates (Christensen *et al.*, 2005).

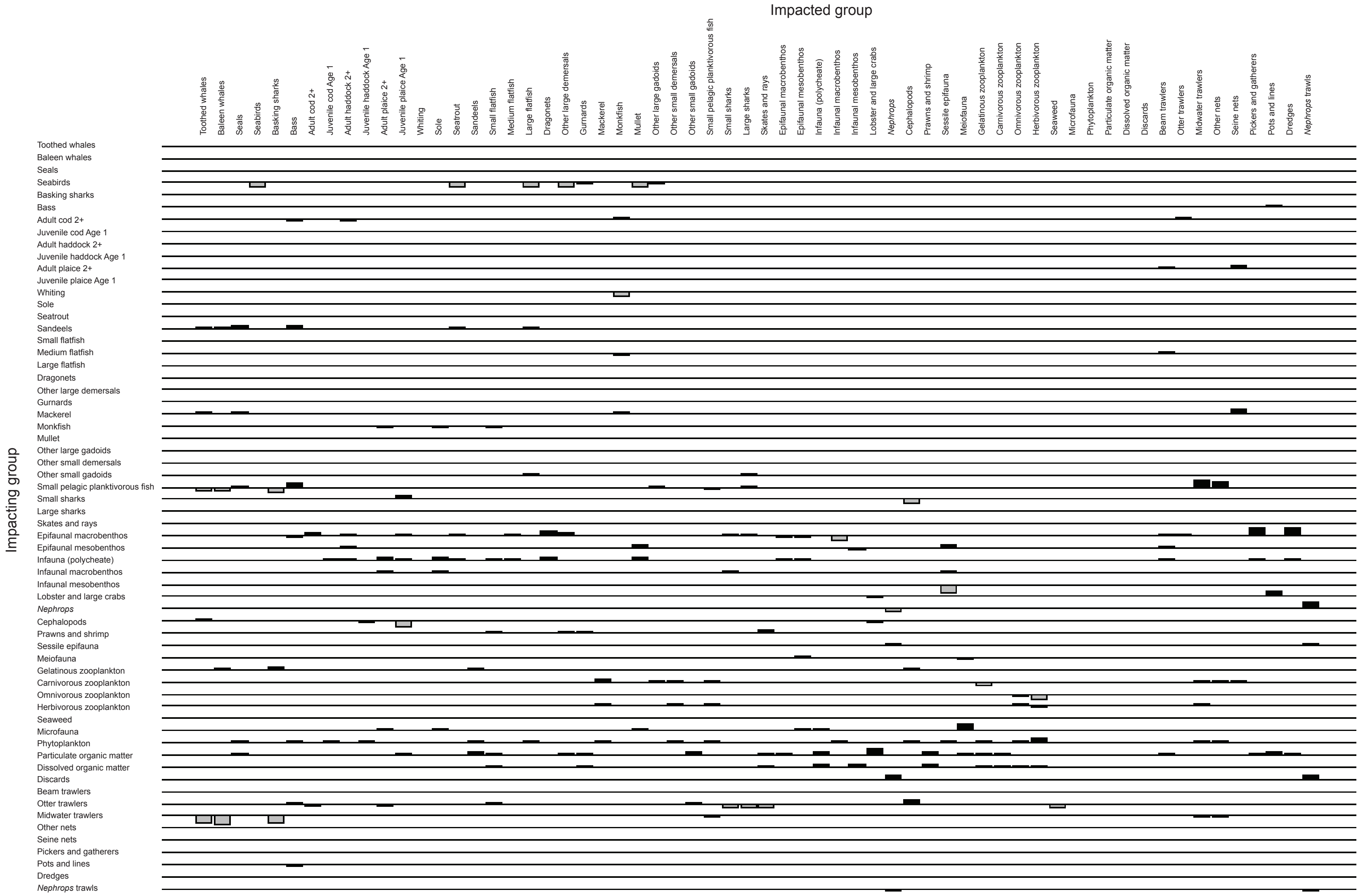


Figure 9.3. Mixed trophic impact plot. Darker shaded bar represents a positive impact whilst lighter shaded bars depict a negative impact of an increase in biomass of one group on another.

9.3 Evaluation of model dynamics

Three types of instabilities are frequently found in Ecosim: 1) predator-prey cycles and related multi-trophic level patterns; 2) system simplification (loss of biomass pools due to competition/predation effects); 3) stock-recruitment instabilities (cyclic or erratic changes in recruitment and stock size for multi-stanza groups (Christensen *et al.*, 2005). Cyclic changes in the biomass of adult and juvenile groups indicated stock recruitment instabilities in cod, haddock, and plaice. To eliminate instabilities in the model, adjustments had to be made to feeding parameters and vulnerability estimates for multi-stanza groups.

To examine the persistence of the biomass of groups represented in the model, a small disturbance in the combined fishery was created and the speed at which equilibrium was re-established was examined. A small, short-live increase in the combined fishery favoured cephalopods, small flatfish, and dragonets, whilst skates and rays, bass, small pelagic planktivorous fish, cod, haddock, plaice, whiting, *Nephrops*, other large gadoid, and small sharks were disadvantaged by the increase. All groups returned to equilibrium around ten years after the cessation of the disturbance (Figure 9.4).

In the absence of fishing skates and rays, adult cod, adult plaice, adult haddock, monkfish, other large gadoids, small pelagic planktivorous fish, whiting, small sharks, *Nephrops*, and lobsters and crabs increase in biomass. Conversely, bass, other small gadoids, bass, and cephalopods exhibit a decrease in biomass. Adult-juvenile groups exhibit apparent cyclical changes in biomass (Figure 9.5). The inclusion of age structure dynamics in Ecosim requires users to think carefully about compensatory processes relating to the 'stock-recruitment' concept. Two types of curves have commonly been used to describe SR relationships; Ricker curves and Beverton and Holt curves.

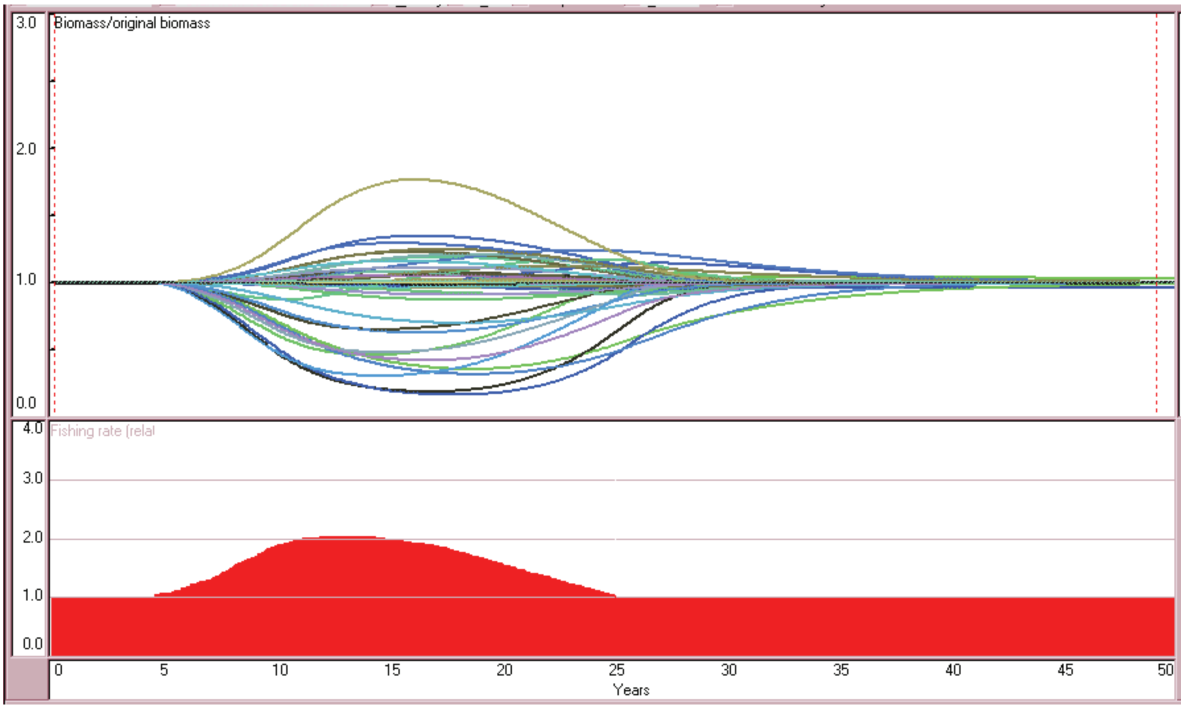


Figure 9.4. System response to a small increase in combined fishing effort. The bottom plot shows an increase in fishing effort from the baseline (1.0). The upper plot shows groups that are temporarily disturbed and their subsequent recovery.

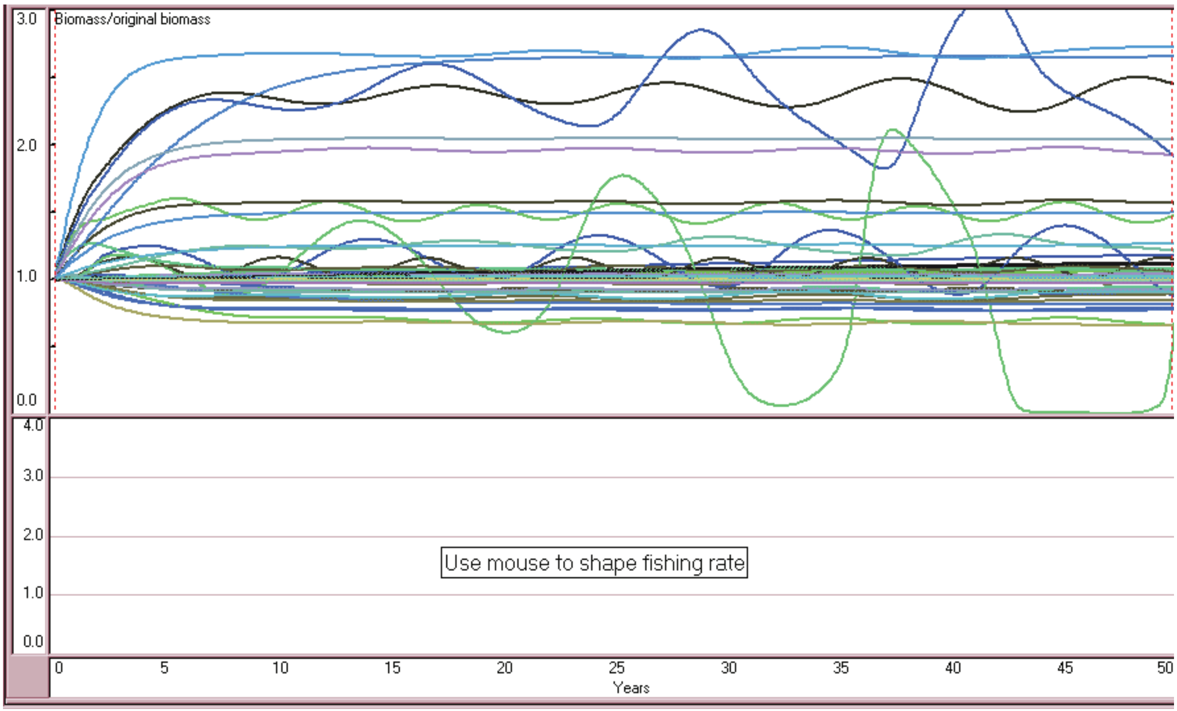


Figure 9.5. System response to cessation of fishing. Bottom plot shows fishing effort is turned off. Upper plot shows the systems response.

9.3.1 Adult-juvenile parameterisation

Ricker curves (Ricker, 1954) are domed or humped shaped curves and are said to be applicable when strong density-dependent mechanisms operate, eg

- Cannibalism by adults on the fry
- When an increase in density of the larvae means that they remain in the more vulnerable larval stage for longer
- When there is a time lag in the response of a predator to a change in its prey abundance so that a high initial density attracts (or generates) more predators without allowing for reduction of prey through exploitation (Pitcher and Hart, 1982).

Beverton-Holt curves (Beverton and Holt, 1957) are asymptotic curves and are said to be applicable when a ceiling of recruit abundance is imposed by the available food or habitat, or when a predator continually adjust its own attack rate to changes in its prey abundance (Pitcher and Hart, 1982).

Adult-juvenile parameters for cod, haddock, and plaice were set so as to produce an ‘emergent’ stock-recruitment (SR) relationship comparable to those based on ICES stock assessments. Both cod and haddock exhibited low recruitment at low and high spawning stock sizes and high recruitment at intermediate spawning stock biomass, thus resembling a Ricker curve (Figures 9.6(a) and (b). Conversely, the Irish Sea plaice SR relationship remained relatively ‘flat’ over a wide range of spawning stock sizes implying a Beverton and Holt relationship (Figure 9.6(c)).

To parameterise stock recruitment relationships fishing was switched off for 10 years, then increased gradually over a 60-year period. The emergent stock recruitment relationships for cod and plaice were erratic and none of the three species SR relationships resembled those of ICES, Beverton and Holt, or Ricker (Figures 9.7(a-c)). This suggests that the cyclic changes in biomass apparent in adult-juvenile groups may be attributed to stock recruitment instabilities within the model.

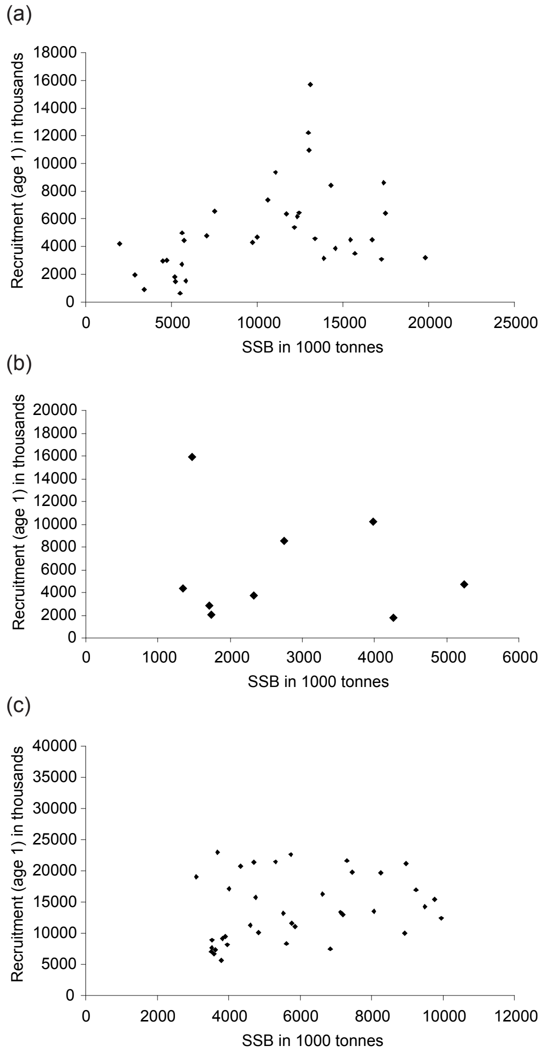


Figure 9.6. (a) ICES cod stock recruitment curve (ICES, 2004a), (b) ICES haddock stock recruitment curve (ICES, 2004a) and (c) ICES plaice stock recruitment curve.

At least two initial conditions are needed to eliminate stock recruitment instabilities and show compensatory changes in the mortality of juveniles. The juvenile group must have a relatively high total mortality rate or a relatively high EE (so that most mortality is accounted for as predation effects within the model), otherwise the user must specify a high value (close to 1.0) for the juvenile group’s fraction of other mortality sensitive to changes in feeding time parameter (Christensen *et al.*, 2005). Since all three juvenile groups had relatively low EE, the juvenile groups fraction of other mortality sensitive to changes in feeding time parameter were changed from 0 to 1.

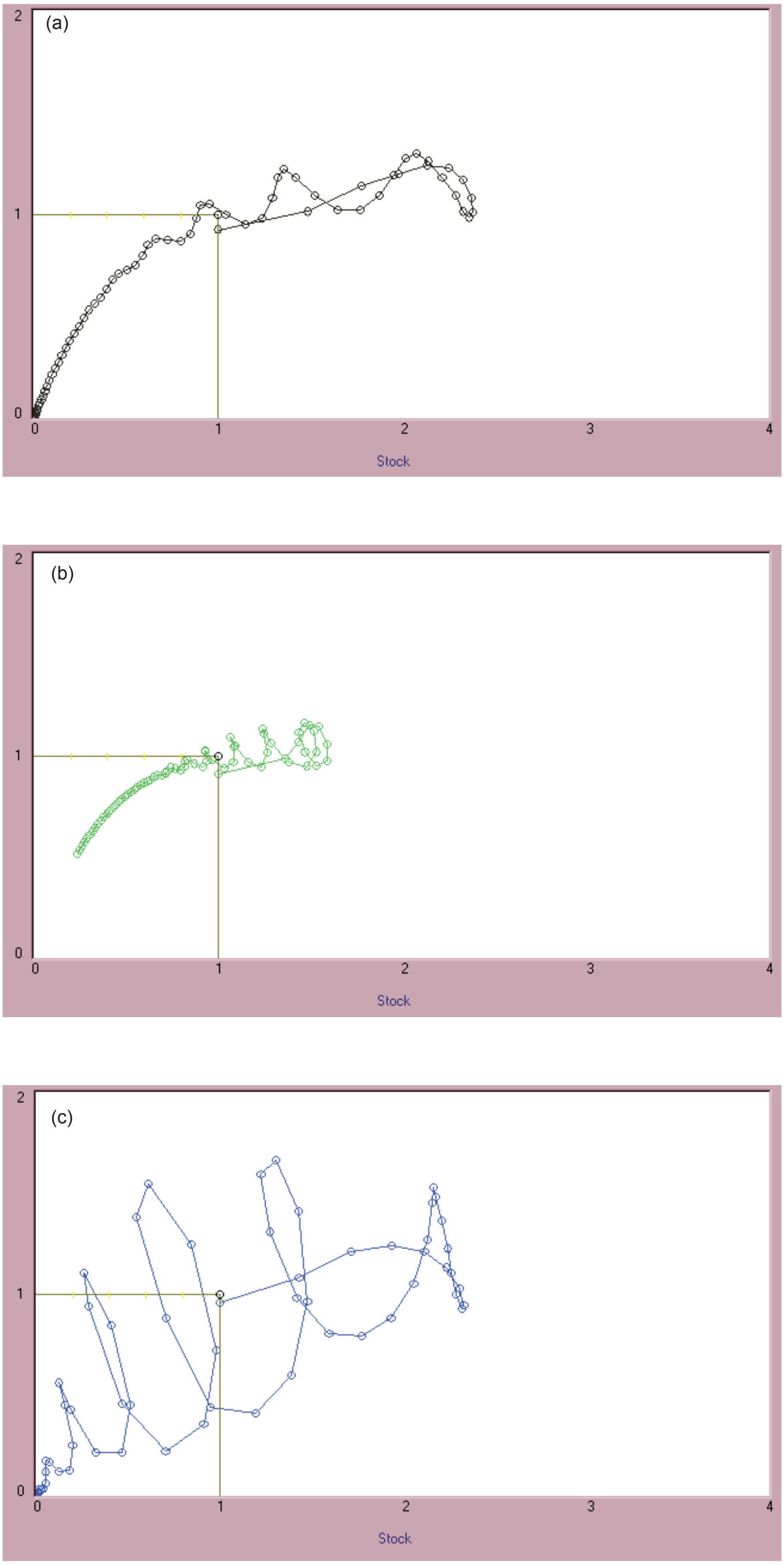
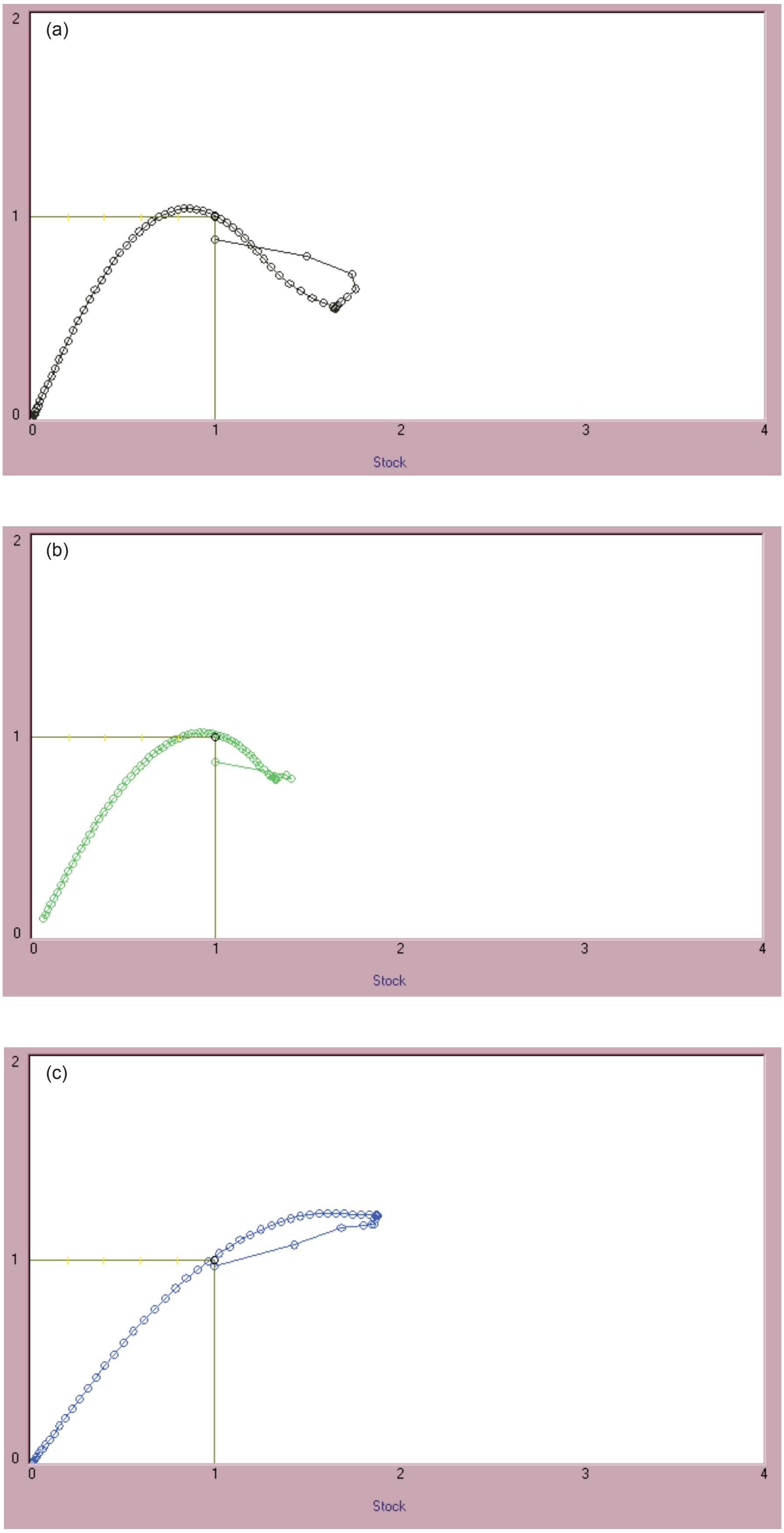


Figure 9.7. (a) model cod stock recruitment curve indicating instabilities, (b) model haddock stock recruitment curve indicating instabilities and (c) model plaice stock recruitment curve indicating instabilities.

Figure 9.8. (a) parameterised cod stock recruitment curve,(b) parameterised haddock stock recruitment curve and (c) parameterised cod stock recruitment curve.



Given these conditions, Ecosim parameters (vulnerability, feeding time adjustment rate, fraction of other mortality sensitive to changes in feeding time, and predator effect on feeding time) were manipulated to simulate compensatory changes in juvenile recruitment. Linked group dynamics were found to be sensitive to adult and juvenile feeding time adjustment rate, predator effect on feeding time, and vulnerabilities. Juvenile and adult feeding time adjustment rate was increase from 0.0 to 0.5, predator effect on feeding time for adult plaice was increased from 0 to 0.5, and adult haddock and juvenile haddock and plaice vulnerabilities were increased from the default 2.0 to 3.0, 3.7, and 5.0, respectively. This resulted in emergent SR relationship comparable to ICES in all three species (Figures 9.8(a, b, c)) and stabilised adult and juvenile biomass (Figure 9.9).

9.3.2 Model sensitivity to vulnerabilities

The effects of different vulnerability estimates on model behaviour were examined by creating an increase in fishing effort that persisted for 10 years before decreasing back to the baseline fishing mortality rate (*sensu* Blanchard *et al.*, 2002). Simulations were run for 70 years. The model was not sensitive enough to be useful with a vulnerability setting on 1 (bottom-up). For vulnerabilities in the range of 1.55 to 3.65 simulations exhibited persistence of all groups and relative stability. When vulnerabilities were increased beyond 3.65, the model exhibited erratic behaviour and extinctions occurred (Figure 9.10). Although all simulations should be carried out under a range of vulnerabilities under a range of setting for all predator-prey pairs, the simple tests performed here suggest that vulnerability settings between 1.55 and 3.5 provides reasonable dynamics and stability.

Figure 9.9. Stabilised model response to cessation of fishing. Bottom plot shows fishing effort is turned off. Upper plot shows the systems response.

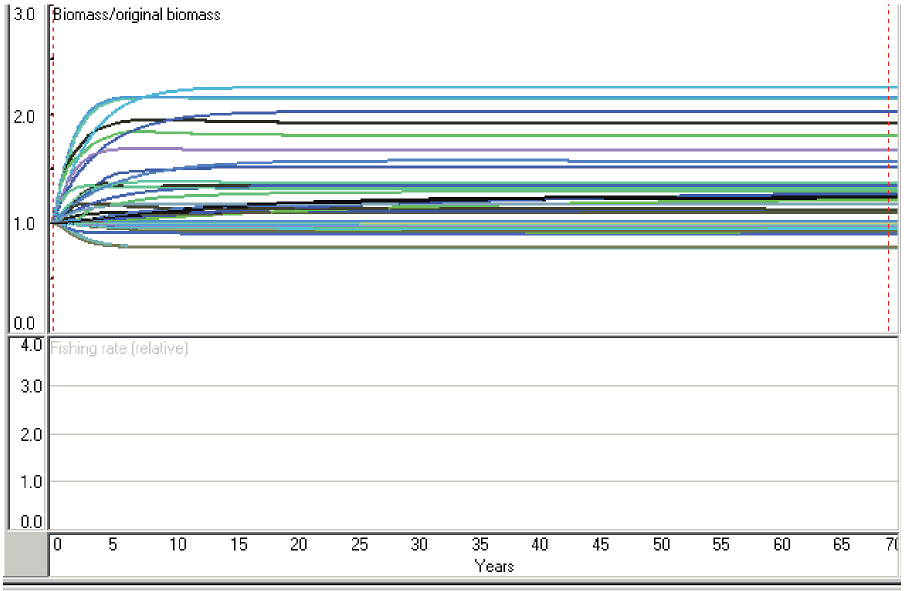
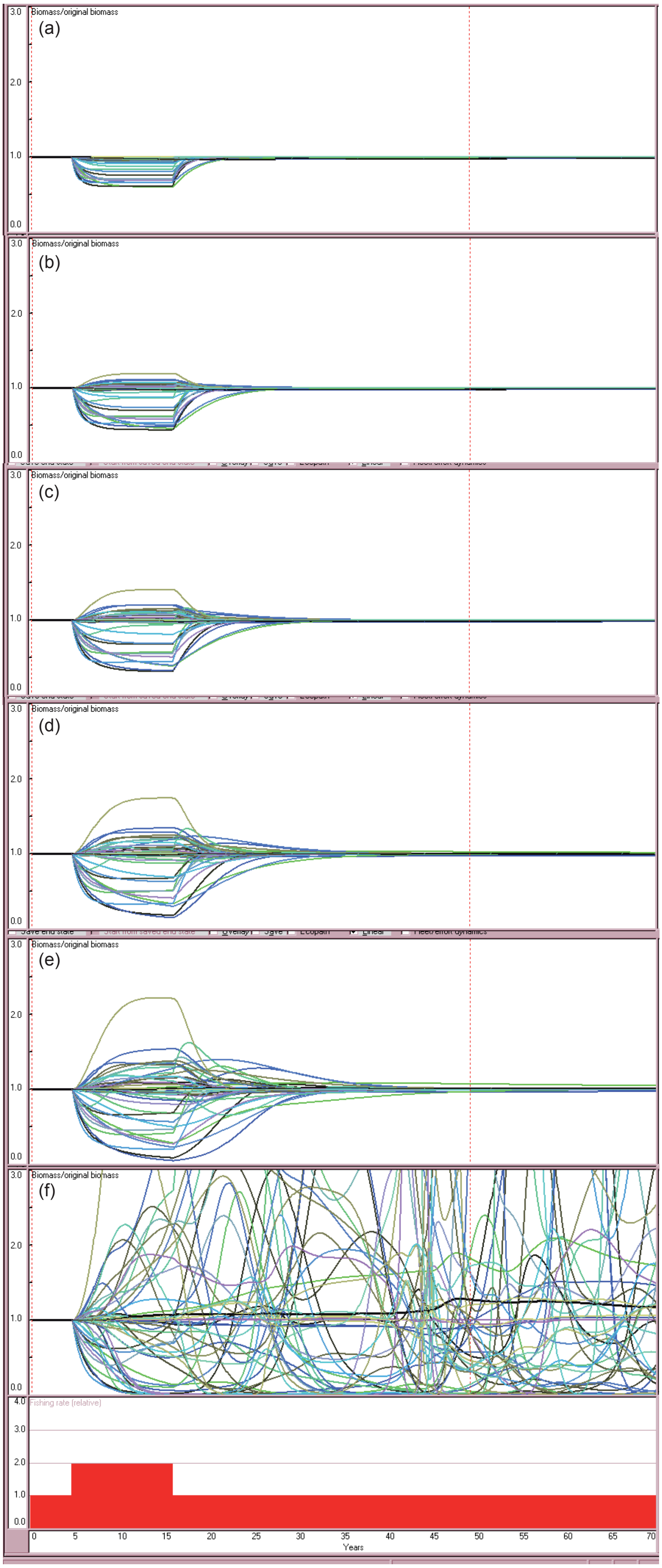


Figure 9.10. Effects on changes in the vulnerability parameter setting on the persistence of functional groups (a) v = 1.01, (b) v = 1.55, (c) v = 2.01, (d) v = 2.67, (e) v = 3.65, (f) v = 29.0.



10. References

ANON., 2003. Supplementary Material. Science, 305: 1513-1660.

ARAUJO, J.N., MACKINSON, S., ELLIS, J.R. AND HART, P.J. B., 2005. An Ecopath model of the Western Channel ecosystem with an exploration of its dynamic properties Sci. Ser. Tech Rep. Cefas Lowestoft, 125: 45pp.

BEAUGRAND, G., BRANDER, K.M., LINDLEY, J.A., SOUSSI, S. AND REID, P.C., 2003. Plankton Effect on Cod Recruitment in the North Sea. Nature, 426: 661-664.

BEVERTON R.J.H. AND HOLT, S.J., 1957. On the dynamics of exploited fish populations. London, Chapman and Hall. 533pp

BILLEN, G., SERVAIS, P. AND BECQUEVORT, S., 1990. Dynamics of Bacterioplankton in Oligotrophic and Eutrophic Aquatic Environments - Bottom-up or Top-Down Control. Hydrobiologia, 207: 37-42.

BLANCHARD, J.L., PINNEGAR, J.K. AND MACKINSON, S., 2002. Exploring maine mammal-fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea ecosystem. Sci. Ser. Tech. Rep., Cefas Lowestoft, 117: 52pp.

CHRISTENSEN, V., 1995a. Ecosystem maturity-towards quantification. Ecol. Model., 77: 3-32.

CHRISTENSEN, V., 1995b, A model of trophic interactions in the North Sea in 1981, the year of the stomach. Dana, 11: 1-19.

CHRISTENSEN, V. AND WALTERS, C.J., 2004. Ecopath with Ecosim: methods, capabilities, and limitations. Ecol. Model., 172: 109-139.

CHRISTENSEN, V., WALTERS, C.J. AND PAULY, D., 2000. Ecopath with Ecosim: a user's guide, Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia.

CHRISTENSEN, V., WALTERS, C.J. AND PAULY, D., 2005. Ecopath with Ecosim: a user's guide, Fisheries Centre, University of British Columbia, Vancouver, Canada.

CRONIN, M., DUCK, C., Ó CADHLA, O., NAIRN, R., STRONG, D. AND O'KEEFFE, C., 2004. Harbour seal population assessment in the Republic of Ireland: August 2003. 40pp Dublin National Parks and Wildlife Service, Department of Environment, Heritage and Local Governement. Irish wildlife manuals.

ENVIRONMENT AGENCY, 2003. Salmonid and freshwater fisheries statistics for England and Wales, 2002. Environment Agency, Cardiff.

FRID, C.L.J., HARWOOD, K.G., HALL, S.J. AND HALL, J.A., 2000. Long-term changes in benthic communities on North Sea fishing grounds. ICES J. mar. Sci., 57: 1303-1309.

FRS, 2004. Scottish Salmon and Seatrout Catches, 2003 Fisheries Research Services, Aberdeen.

GOWEN, R.J., MILLS, D.K., TRIMMER, M. AND NEDWELL, D.B., 2000. Production and its fate in two coastal regions of the Irish Sea: the influence of anthropogenic nutrients. Marine Ecology Progress Series, 208: 51-64.

HEIP, C., 1984. Biology of Meiofauna Proceedings of the 5th International Meiofauna Conference, Held in Ghent, Belgium, 16-20 August 1983 - Preface. Hydrobiologia, 118, R7-R7.

HEIP, C., HUYS, R., VINCX, M., VANREUSEL, A., SMOL, N., HERMAN, R. AND HERMAN, P.M.J., 1990. Composition, Distribution, Biomass and Production of North-Sea Meiofauna. Neth. J. Sea Res., 26: 333-342.

HISLOP, J.R.G., 1996. Changes in North Sea gadoid stocks. ICES J. mar. Sci., 53: 1146-1156.

ICES, 2002. Report of the working group on seabird ecology. ICES CM 2002/C:04, 72pp.

ICES, 2003a. Report of the Study Group on Sea Bass. ICES CM 2004/ACFM:04, 29pp.

ICES, 2003b. Report of the Working Group on *Nephrops* Stocks. Bergen, Norway.

ICES, 2004a. Report of the Working Group on the Assessment of Northern Shelf Demersal Stocks (WGNSDS). ICES CM 2005/ACFM:01, 714pp.

ICES, 2004b, Report of the Advisory Committee on Fisheries Management and Advisory Committee on Ecosystems 2004. ICES Advice, 1, 1544pp.

ICES, 2004c. Report of the Working Group on *Nephrops* stocks. ICES CM 2004/ACFM: 19, 441pp. Lisbon, Portugal ICES.

ICES, 2005. Report of the Herring Assessment Working Group for the Area of 62°N, 8–17 March 2005 ICES Headquarters. ICES CM 2005/ACFM:16, 599pp.

Jennings, S. and Kaiser, M.J., 1998. The effects of fishing on marine ecosysems. Adv. Mar. Biol., 34: 201-352.

Jonsson, L., 1993. Birds of Europe with North Africa and the Middle East, Christopher Helm Limited, London.

Kaiser, M.J., Rogers, S. and McCandless, D.T., 1994. Improving quantitative surveys of epibenthis communities using a modified 2 m beam trawl. Mar. Ecol. Prog. Ser., 106: 131-138.

Karpov, K.A. and Calliet, G.M., 1978. Feeding dynamics of *Loligo opalescens*. Calif. Dept. Fish Game, Fish Bull., 169: 45-65.

Kiely, O., Lidgard, K.O., McKibben, D., Connolly, N. and Baines, M., 2000. Grey seals: Status and Monitoring in the Irish and Celtic Seas. Ireland/Wales. INTERREG Report.

Larson, R.J., 1987. Daily Ration and Predation by Medusae and Ctenophores in Saanich Inlet, BC, Canada. Neth. J. Sea Res., 21: 35-44.

Mackinson, S. and Daskalov, G., in prep. An ecosystem model of the North Sea. Sci. Ser. Tech. Rep, Cefas Lowestoft.

Majkowski, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. *In*: (Pauly, D. and Murphy, G.I. (eds.)). Theory and management of tropical fishes. ICLARM.

Marshall, J., Kushnir, Y., Battisti, D., Chang, P., Czaja, A., Dickson, R., Hurrell, J., McCartney, M., Saravanan, R. and Visbeck, M., 2001. North Atlantic climate variability: Phenomena, impacts, and mechanisms. Int. J. Climatol., 21: 1863-1898.

Muus, B.J. and Dahlstrom, P., 1985. Collins Guide to the Sea Fishes of Britain and North-Western Europe., Butler and Tanner Ltd, Somerset.

Odum, E.P., 1969. The strategy of ecosystem development. Science, 104: 262-270.

Palomares, M.L. and Pauly, D., 1998. Prediciting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature, and salinity. Mar. Freshwat. Res., 49: 447-453.

Parker-Humphreys, M., 2004. Distribution and relative abundance of demersal fishes from beam trawl surveys in the Irish Sea (ICES division VIIa) 1993-2001. Sci. Ser. Tech. Rep.,120: 68pp.

Parsons, L.S. and Lear, W.H., 2001. Climate variability and marine ecosystem impacts: a North Atlantic perspective. Prog. Oceanog., 49: 167-188.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Conserv., 39: 175-192.

Pauly, D., 1989. Food consumption by tropical and temperate fish populations: some generalizations. J. Fish Biol., 35: 11-20.

Pauly, D. and Christensen, V., 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Pauly, D., Trites, A.W., Capuli, E. and Christensen, V., 1998 Diet composition and trophic levels of marine mammals. ICES J. mar. Sci., 55: 467-481.

Pawson, M.G., Pickett, G.D. and Walker, P., 2002. The coastal fisheries of England and Wales, Part IV: A review of their status 1999-2001. Sci. Ser. Tech. Rep., Cefas Lowestoft, 116: 83pp.

Pitcher, T. and Hart, P.J.B., 1982. Fisheries Ecology, Chapman and Hall, London.

Planque, B. and Fromentin, J.M., 1996. Calanus and environment in the eastern North Atlantic 1. spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser., 134: 101-109.

Pollock, C.M., Reid, J.R., Webb, A. and Tasker, M.L., 1997. The distribution of seabirds and cetaceans in the water around Ireland. JNCC Report.

Polovina, J.J.,1984. Model of coral reef ecosystems. I. The ECOPATH model and its application to French frigate shoals. Coral Reefs, 3: 1-11.

Pope J.G. and Macer C.T., 1996. An evaluation of the stock structure of North Sea cod, haddock, and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment. ICES J. mar. Sci., 53: 1157-1169.

Reid, P.C., Borges, M.F. and Svendsen, E., 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse Mackerel fishery. Fish. Res., 50: 163-171.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Bd. Canada, 11:559-623.

Salzwedel, H.,1980. Energy budgets for two populations of the bivalve *Tellina fabula* in the German Bight.Veröff. Inst. Meeresforsch. Bremerh, 18: 257-287.

Sims, D.W., Genner, M.J., Southward, A.J. and Hawkins, J., 2001. Timing of squid migration reflects North Atlantic climate variability. Proc. Roy. Soc. Lond. B, 268: 2607-2611.

Sparholt, H., 1990. An estimate of the total biomass of fish in the North Sea. J. Cons. int. Explor. Mer, 46: 200-210.

Standford, R. and Pitcher, T., 2000. The English Channel: a mixed fishery, but which mix is best? Faculty of Graduate Studies: Resource Management and Environmental Studies - Fisheries, 179.

Taylor, A.H., 1995. North-south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. ICES J. mar. Sci., 52: 711-721.

Taylor, A.H., Colebrook, J.M., Stephens, J.A. and Baker, N.G., 1992. Latitudinal displacements of the Gulf Stream and the abundance of plankton in the North-east Atlantic. J. mar. Biol. Ass. UK, 72: 919-921.

Taylor, A.H. and Stephens, J.A., 1998. The North Atlantic Oscillation and the latitude of the Gulf Stream. Tellus A: Dynamic Meteorol. Oceanog., 134-142.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M. and Pauly, D., 1999. Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and the commercial whaling hypotheses. Vancouver Fisheries Centre, University of British Columbia. 106pp.

Ulanowicz, R.E., 1995. Ecosystem Trophic Foundations: Lindeman Exonerata. *In*: (Pattern, B.C. and Jorgensen, S.E. (eds.)). Complex Ecology: the Part-Whole Relation in Ecosystems. Englewood Cliffe, New Jersey, Prentice Hall.

Vincent, M.A., Atkins, S.M., Lumb, C.M., Golding, N., Lieberknecht, L.M. and Webster, M., 2004. Marine nature conservation and sustainable development - the Irish Sea Pilot. Report to Defra by the Joint Nature Conservation Committee. JNCC Peterborough. 176pp.

Head office
Centre for Environment,
Fisheries & Aquaculture Science
Pakefield Road, Lowestoft,
Suffolk NR33 0HT, UK

Tel +44 (0) 1502 56 2244
Fax +44 (0) 1502 51 3865
Web www.cefas.co.uk
Cefas is an executive agency of Defra

ISSN 0308-5589