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An Ecopath model of the Western English Channel ecosystem with an exploration of its dynamic properties

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1. ABSTRACT

Two trophic models of the Western English Channel (ICES Division VIIe) were developed; one representing the ecosystem in a warm period (1994) and another representing a cold period (1973). The purpose of this technical report is to document in detail the data sources, manipulation and assumptions performed during parameterisation of the models and to compare the status of the system in these two years. The ecosystem indices for the two models were generally alike, partially because the same basic inputs for primary producers, and diet composition data were very similar. The main differences were an increase in the fish biomass (mainly non-target species), an increase in the primary production required to sustain fishery catches and a small increase in the omnivorous index that might be related to a decrease in the abundance of some high trophic level piscivorous fish species. The ecosystem indicators suggest that the Western English Channel is a relatively immature system. However, many of these indicators are functions of the primary production and consumers biomass and are therefore dependent on the reliability of those estimates. Consequently, any conclusions about the 'relative maturity' of the system should be taken with caution. For the purpose of sensitivity testing and refining the Ecopath model parameters, temporal dynamics of the models were explored using Ecosim. The 1994 model was used to examine the emergent stock-recruitment functions produced from linked juvenile-adult groups. An interesting outcome of this analysis was that the vulnerability of the prey to the juveniles group has a dramatic influence on the shape of the stock-recruitment relationship. The analysis showed that the vulnerability settings also determine the size of the spawning stock at which maximum recruitment occurs. The higher the vulnerability value the higher the adult stock size at which recruitment attains its maximum. It implies that the vulnerability parameter values used in Ecosim for linked adult-juvenile groups should in part be based on empirical evidence of the size of the spawning stock at which maximum recruitment occurs, not solely on biological/behavioural assumptions regarding the maximum mortality rate a predator can exert on a prey (relative to the Ecopath baseline value). Future work will include estimation of the vulnerabilities parameters by fitting model predictions to observed time series of biomass and subsequently using the model to explore 3 hypotheses about temperate-related ecosystem change in the Western English Channel.

2. INTRODUCTION

The Western English Channel ecosystem is considered an important biogeographic boundary between northern Boreal and southern Lusitanian fauna and has been subject to many studies regarding the effects of climate change on abundance of fish and invertebrate species (Southward *et al*., 1988; Southward *et al*., 1995; Hawkins *et al*., 2003; Genner *et al*., 2004). A recent analysis of long-term data collected by the Marine Biological Association of the UK (MBA) in the Western English Channel (Genner *et al*., 2004), has led to some hypotheses about the responses of northern and southern species to climate changes and fishing pressure:

1. Competitive and/or predation release has led to a slight increase in the abundance of northern species such Atlantic cod (*Gadus morhua*) despite the increase in the water temperature and fishing pressure.
2. High fishing mortality has inhibited the expansion of large southerly species in response to climate change.
3. Habitat disturbance may have influenced the response of cod to increased fishing by increasing food availability in the form of dead invertebrates and fish. Alternatively, observed increases in small-bodied species, in response to climate change, may have provided more food for northern species.

At present these hypotheses have not been tested further.

To enable us to test these hypotheses and to explore the effects of climate change on the ecosystem of the Western Channel, we have developed two trophic models using Ecopath with Ecosim 5.1 software (Christensen *et al*., 2004). The first model represents the ecosystem in a warm period for the years 1993 to 1995, hereafter called the 1994 model. The period was selected on the rationale that there were 'high quality' fisheries data available, which were collected by the Channel Fisheries Study Group (CSFG) (Dintheer *et al*., 1995). The second model is for a cold period represented by the year 1973.

The purpose of this technical report is to document in detail the data sources, manipulation and assumptions performed during parameterisation of the models and to compare the status of the system in these two years. Subsequent publications will report on application of the models to testing the 3 hypotheses about ecosystem change in the Western English Channel.

2.1. The Western English Channel Ecosystem

The English Channel is a shallow continental shelf system with a relatively flat bottom. The depth varies from 100 m in the westernmost part to 40 m in the Dover Straits. The Western English Channel is generally deeper than the Eastern English Channel, with the inshore zone more steeply shelving, and most of the Western English Channel is more than 50 m deep. The currents system is mainly tidal in nature. There is a gradient related to the vertical mixing in the English Channel during the summer, varying from

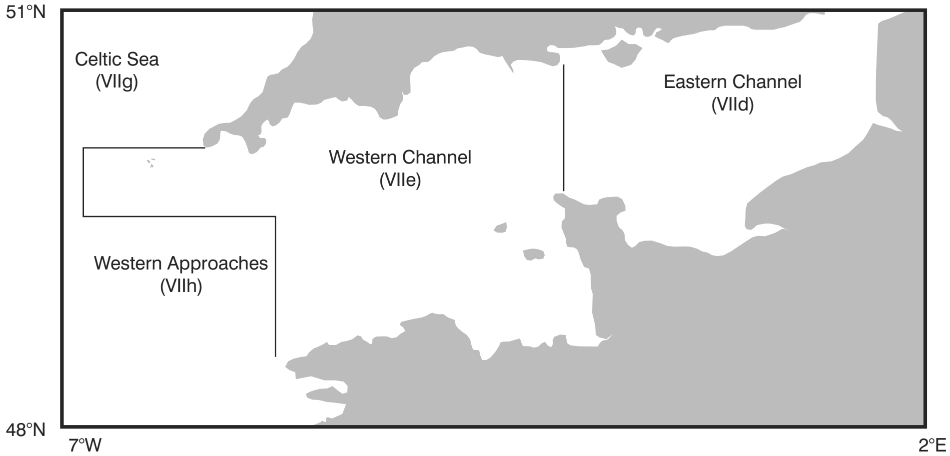


Figure 1. Western English Channel and adjacent waters. Roman numerals represent ICES areas

stratified waters in the west, where there are deeper waters and weaker currents, to relatively better mixed waters in the east, where the system is shallower and stronger currents occur. Between these extremes there are a gradient of transitional conditions, with the occurrence of thermal fronts. The general circulation of water is characterized by a 'river' from the Atlantic to the North Sea, passing through the Celtic Sea and English Channel (Pawson, 1995). The Western Channel accounts for 63% of the English Channel, covering approximately 56,452 km^2 (Stanford and Pitcher, 2004) (Figure 1).

Faunal distributions are closely correlated to physical conditions. Zooplankton are generally less abundant in stratified waters to the west than in the vicinity of thermal fronts. The structure, abundance and distribution of benthic communities are correlated with depth and sediment composition. The Western English Channel tends to be coarser than the Eastern English Channel, and there is a decrease in benthic species from west to east (Pawson, 1995). Indeed, there are several species of invertebrate and fish that are common in the Western English Channel and that are either rare or absent in the Eastern English Channel (e.g. Holme, 1961, 1966; Pawson, 1995; Ellis, 2001). Ellis (2001) described five species assemblages for the English Channel and Sanvicente-Anorve *et al.* (2002) defined four benthic macrofaunal assemblages in the Eastern Channel. A detailed study about the relationships of benthic fauna and fish assemblages in the Western English Channel is yet to be done. Although the relationship between hydrographical and climatic conditions, sediment and benthic communities play an important role in structuring fish assemblages, changes caused by fishing activity need to be addressed as well. Rogers *et al.* (1998) stressed that information on the distribution of fishing effort is very important to understand the spatial and temporal variation and to separate natural from artificial causes.

The fisheries of the English Channel have been studied in some detail in the last decade. Economic, technical interactions and biological aspects have been described and been subject to modelling studies. It may be regarded as a large and diverse multi-country, multi-gear and multi-species artisanal fishery (Ulrich *et al.*, 2001; Ulrich *et al.*, 2002; Stanford and Pitcher, 2004). The model developed by Ulrich *et al.*, (2002) explores the technical interactions by dividing the fishery in different sectors or 'métiers' (gear x target species x fishing area) but does not account for trophic interactions. Although Stanford and Pitcher (2004) developed a trophic model for the English Channel as a whole with the same methodology applied in this work, they recognize that "there would certainly be a rationale for making two models, separating the Western from the Eastern Channel, because of their distinctiveness". This distinctiveness seems to be reflected in the distribution and population parameters of many fish species. There are some fish stocks that are confined to either side of the Channel and in the case of sole (*Solea solea*) presenting very different long-term abundance trends. Similarly, Atlantic cod (*Gadus morhua*), presents very different long term trends in the western and eastern part of the Channel (ICES, 2000a; ICES, 2000b). The Western Channel cod is treated as part of the Celtic Sea stock and the Eastern Channel cod is managed as part of the North Sea stock.

2.2. The Ecopath with Ecosim software

The Ecopath with Ecosim (EwE) model (Christensen *et al.*, 2004) is built on a system of linear equations describing the average flows of mass and energy between the species groups during a period of time, normally a year. The 'mass balance' term means that the model parameters describing an ecosystem are under the physical constraint that the total flows of mass (or energy) into each species group must equal the flow out of the group.

The flow to and from each functional group is described by the following equation:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

[Equation 1],

where P_i is the total production; Y_i is the total fishery catch rate; B_i the biomass; $M2_i$ is the predation mortality rate; E_i the net migration rate (emigration - immigration), BA_i is the biomass accumulation rate and EEi is the 'ecotrophic efficiency' of *i*, the proportion of the production that is utilized in the system.

Equation 1 can be expressed as:

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

[Equation 2],

where P/B_i is the production/biomass ratio of *i*, B_j is the biomass of consumers or predators *j*, $(Q/B)_j$ is the consumption per unit of biomass of *j* and DC_{ji} is the fraction of *i* in the diet of *j*.

To parameterize an Ecopath model, the user must input (at least in principle) three of the following four parameters basic parameters all trophic groups in the ecosystem:

- biomass;
- production/biomass ratio;
- consumption/biomass ratio; and
- ecotrophic efficiency.

Besides those three basic parameters, the following information must be entered for all groups:

- catch by group and fleet type;
- net migration rate (the default value is zero);
- biomass accumulation rate (the default value is zero);
- unassimilated food/consumption ratio (default is 0.2) and
- diet composition.

Although Ecopath can estimate *B* or *P/B*, when an estimated value of *EE* for a group is entered, ideally the user should enter estimates for the first two parameters and let the program estimate *EE*, since it is very difficult to measure. In cases when one of the other parameters is missing, a guesstimate for *EE* is entered based on assumptions/estimates about the level of predation and/or fishing mortality of a functional group. For example, in an exploited system, small pelagic fish are either eaten or fished and just a small proportion die of old age. So, species that are heavily consumed or exploited will have values close to one (0.90-0.99), whereas top predators such as sharks and marine mammals would have lower values. On the other hand, when *Q/B* for a group is missing, it can be estimated given that estimates for the gross food conversion efficiency, *P/Q*, and *P/B* are provided.

The EwE 5.1 version used in this work (Christensen *et al*., 2004), allows the user to enter multiple life stages, for a trophic group in the basic input table, rather than splitting the group just into juvenile adult stages as implemented in the Ecosim module of the previous versions. The user must enter the estimates of *P/B*, *B*, *Q/B* and *BA* for one stage and *P/B* for the remaining ones. In addition, estimates for the growth parameter *K* of the Von Bertalanffy growth function, the starting age in months of each stage, and the ratio between the average weight at maturity and the asymptotic weight must be entered. As *B* of the other stage(s) are then estimated by Ecopath, the user can vary the inputs to have an approximation of the observed *B* for them.

Ecosim is the time dynamic version of Ecopath. It can be used to simulate the ecosystem effects of fishing mortality changes and environmental forcing over time. The process is based on the set of linear equations used in Ecopath (Equation 1), isolating the biomass accumulation term, and setting up a set of differential equations of the form:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i$$

[Equation 3],

where dB_i/dt represents the growth rate of group (*i*) during the time interval *dt* in terms of its biomass, B_i, g_i is the net growth efficiency (production/consumption ratio), M_i the non-predation ($(P/B)_i B_i(1\text{-}EE_i)$) natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate, (and $e_i \cdot B_i - I_i$ is the net migration rate). The two summations estimate consumption rates, the first expressing the total consumption by group (*i*), and the second the predation by all predators on the same group (*i*).

Ecosim uses the parameter estimates from the Ecopath basic model as input for time simulations. It has some additional parameters, set with default starting values that are described in detail in Christensen *et al*. (2004). The most important one is the so-called vulnerability parameter (*v*), specified for each predator-prey interaction. The vulnerability is the maximum mortality that a predator could cause on a given prey (relative to the Ecopath base mortality rate). It is a mortality rate multiplier. Conceptually it represents a theoretical flow rate at which the prey biomass moves from a vulnerable state (*V*) to an invulnerable one (*B-V*). Low values cause bottom-up control, whereas high values (all prey available all the time) lead to Lotka-Volterra predator-prey dynamics (Christensen *et al*., 2004). The vulnerability parameters are estimated as $v_{ij} = v'_{ij} \times M2_{ij}$, where, $M2_{ij}$ is the Ecopath base estimate of the predation mortality. The parameter

v'_{ij} parameter is specified in Ecosim by the user and varies from 1 (bottom-up) to ∞ (top-down control). The Ecosim simulations are very sensitive to changes in the vulnerability parameters, and these parameters are used in fitting the model estimates to observed time series data.

3. MODEL BUILDING

The model structure and some parameter estimates were based on previous models developed by Stanford and Pitcher (2004) for the whole English Channel. A total of 50 functional groups was used to represent the Western Channel ecosystem. These include, one primary producer group, 13 invertebrate groups, 32 fish groups, one cephalopod group, one seabird group and 2 marine mammal groups. Four fish species (sole, plaice, whiting and cod) are represented by two functional groups or live stages, juveniles and adults. In addition to the living groups, 2 non-living groups are included: detritus and discards. The fishery is represented by 9 fleets/gear types (otter trawl, beam trawl, pelagic trawl, nets, dredges, pots, lining, seaweeds and recreational). To complement the information taken from Stanford and Pitcher (2004), new data were gathered from the following sources:

- ICES reports on stock assessment (ICES, 1979, 1999, 2000a, 2000b, 2000c) and the electronic landings database (ICES, 2001);
- 'Base Halieutique pour une Manche Stratifiée' (BAHAMAS), an electronic landings database developed by the Channel Fisheries Study Group (CFSG) (Dintheer *et al*., 1995; Ulrich *et al*., 2002);
- MBA long-term trawl data (Anon., 2001; Genner *et al*., 2004);
- *RV CORYSTES* beam-trawl surveys (CEFAS);

or estimated using empirical equations as described in the next section. Diet composition and some other parameters were compiled from a variety of sources detailed specifically in the description of each functional group given in section 3.2. The balanced 1994 model was used as a base upon which to build the 1973 model. When not stated, the landings data used in the 1994 model were taken from the BAHAMAS database and from Ulrich *et al*. (2002). The 1973 model landings were based on the ICES database (ICES, 2001). Discards were estimated based on the ratio between discards and landings in Stanford and Pitcher (2004) and allocated to juveniles in the case of split groups. The same level (proportion) of discards was used for the 1994 and 1973 models.

3.1. Production and consumption rates estimation for fish groups

Annual production rate (*P/B*) equals the total mortality (*Z*) under some assumptions (Allen, 1971). For most of the fish groups, estimates of *Z* were derived from stock assessments. In some cases when a total mortality estimate was not directly available, it was estimated by summing the estimates of natural mortality (*M*) and the fishing mortality (*F*). When not available from other sources, *M* was estimated using the empirical relationship (Pauly, 1980):

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot T_c^{0.463}$$

where, *M* is the natural mortality (year^{-1}), *K* (year^{-1}) is the curvature parameter of the Von Bertalanffy growth function, L_{∞} is the asymptotic length (cm) in the same function, and T_c is the mean water temperature, in °C.

The annual fishing mortality (*F*) was estimated when possible directly from the ratio between catch (*C*) and biomass (*B*) as computed in Ecopath (*C=F/B*).

Annual consumption rates (*Q/B*) of fish were estimated using the empirical relationship (Palomares and Pauly, 1989):

$$Q/B = 10^{6.73} \cdot 0.0313\ Tk \cdot W_{\infty}^{0.168} \cdot 1.38^{Pf} \cdot 1.89^{Hd}$$

where *Tk* is 1000/average temperature in Kelvin, W_{∞} is the asymptotic weight (g) of the Von Bertalanffy growth function, *Pf* is equal to one for carnivores and zero for herbivores and dentrivores, *Hd* is equal to one for herbivores and dentrivores and zero for carnivores.

A mean annual sea surface temperature (SST) of 12.7°C was used for the purpose of these estimations which corresponds to the mean annual water temperature at the beginning of the 1990s in the Western English Channel, (International Comprehensive Ocean-Atmosphere Data Set (ICOADS) (Diaz *et al*., 2002)).

3.2. Description of functional groups

Below a description of the functional groups and data inputs is given. When not specifically mentioned, the same parameters estimates were used in both 1994 and 1973 models.

1. Primary producers (phytoplankton, macro-algae and micro-phytobentos)

B and *P*/*B* for primary producers were estimated using data for the Western Channel presented in Stanford and Pitcher (2004).

2,3,4. Micro-, meso- and macro-zooplankton

The group structure and parameter estimates, including diet composition, were based on Stanford and Pitcher (2004) and Sanchez and Olaso (2004).

5. Deposit feeders (worms, gastropods and small invertebrates such as amphipods)

B for Polychaeta, Nemertina and Gastropoda groups from Holme (1953) and *P*/*B* for 'deposit feeders' in the Western Channel from Ameziane *et al*. (1995) were used as inputs for this group. *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.15 in Stanford and Pitcher (2004). Diet compositon from Stanford and Pitcher (2004).

6. Sessile suspension feeders (cnidarians, sponges, byozoans and acidians)

B from Holme (1953). *P*/*B* and diet composition from Stanford and Pitcher (2004). The *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.15 in Stanford and Pitcher (2004).

7. Shrimps and Prawns

B and *Q*/*B* left to be estimated by Ecopath based on an *EE* of 0.95 and P/Q of 0.15 respectively in Stanford and Pitcher (2004). An estimate of total mortality for *Crangon crangon* from Port Erin Bay, Isle of Man, Irish Sea (Oh *et al*. 1999) was used as input for *P*/*B*. Diet composition from Stanford and Pitcher (2004).

8. Whelks (mainly *Buccinum undatum*)

1994 model: Biomass and total mortality estimates for the English Channel (CFSG data) were available in Stanford and Pitcher (2004). *B* for the Western Channel was estimated using its landings (*L*) divided by the ratio between landings and biomass (*L*/*B*) for the whole Channel. Savini *et al*. (2002) estimated daily consumption for the rapa whelk *Rapana venosa* preying on the hard clams *Mercenaria mercenaria* varying from 0.8% to 3.6% of their body weight. These values were converted to annual *Q*/*B* of 2.92 and 13.14 year^{-1}. The average of 8.03 year^{-1} was used. This resulted in a gross food conversion (*P*/*Q*) of 0.07 that seems to be reasonable. Diet composition from Stanford and Pitcher (2004).

1973 model: *B* was 1.5 larger than in the 1994 model. This is an assumption based on a lower level of beam trawl fishing in the past and that whelk was reported to have declined as a possible result of increased beam trawl fishing in the North Sea (Ten Hallers-Tjabbes *et al*., 1996).

9. Echinoderms

Includes species such as *Asterias rubens*, *Ophiura* spp., *Psammechinus miliaris*, *Astropecten irregularis*, *Luidia ciliaris*, *L. sarsi*, *Porania pulvillus*, *Anseropoda placenta*, *Marthasterias glacialis*, *Echinus acutus*, *Echinus esculentus* and *Spatangus purpureus*. *B* estimate was taken from Holme (1953). *P*/*B*, *Q*/*B* and diet composition from Stanford and Pitcher (2004).

10. Bivalves

Some of the species represented are *Nucula* spp., *Venus* spp, *Cardium* spp, *Dosinia lupinus*, *Ensis* spp, *Abra* spp, *Mytilus edulis*, *Glycymeris glycymeris*, *Cerastoderma edule*, flat oyster *Ostrea edulis*, Pacific oyster *Crassostrea gigas*. *B* estimate was taken from Holme (1953). Warwick and Price (1975) reported mortality rates estimates for *Cerastoderma edule* and *Mya arenaria* of 0.2 and 0.5 year^{-1} respectively from an estuary in the Western Channel. However, experimental studies about the effects of predation on juveniles bivalves showed annual mortalities rates as high as 1.96 year^{-1} (Nakaoka 1996; Masski and Guillou 1999). The average (0.89 year^{-1}) of these values was used as input for *P*/*B*. *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.09 in Stanford and Pitcher (2004). Diet compostion from Stanford and Pitcher (2004).

11. Scallops

Composed by great scallop *Pecten maximus*, queen scallop *Aequipecten opercularis*, variegated scallop *Chlamys varia*.

1994 model: *B* for the Western Channel was estimated based on an mean *F* of 0.6 year^{-1} estimated by Ulrich (2000). The *P*/*B* estimate was taken from same source. *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.09 in Stanford and Pitcher (2004). Diet composition taken from this source as well.

1973 model: *B* was assumed to be 1.5 higher than the 1994 model since there was some decline in catches over the past years.

12. Small-medium sized crabs

This group includes green crab (*Carcinus maenas*), swimming crabs (*Necora puber* and *Liocarcinus* spp), hairy crab (*Pilumnus hirtellus*), hermits crab (*Pagurus bernhardus*), squat lobsters and spider crabs. *B* estimate taken from Holme (1953) and *P*/*B* from Jarre-Teichamann and Guenette (1996). *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.15 in Stanford and Pitcher (2004). Diet composition was taken from the same source.

13. Large crabs

Composed by the edible crab *Cancer pagurus* and the spinous spider crab *Maja squinado*.

1994 model: *P*/*B* was estimated using an *F* estimate of 0.4 year^{-1} and a gesstimate for *M* of 0.2 year^{-1} (Bennet, 1979). The biomass was estimated using the *L*/*F* ratio. *Q*/*B* was left to be estimated by Ecopath based on an estimate for *P*/*Q* of 0.15 as in Stanford and Pitcher (2004). Diet composition come from the same source.

1973 model: *B* assumed to be 1.5 higher as in Stanford and Pitcher (2004). This is partially justified by the fact that, although the catches have being sustained, Southward and Boalch (1992) reported that the boats had to go during the 1980s further offshore to keep the same yield levels.

14. Lobster

The european lobster *Homarus gammarus* and common spiny lobster *Palinurus elephas*.

1994 model: *P*/*B* for *H. gammarus* from Stanford and Pitcher (2004). This estimate was based on an *F* of 0.4 year^{-1} for the south-west stock (Bannister and Addison, 1984) and *M* assumed to be 0.1 (ICES, 1979). *B* estimated using the *L*/*F* ratio. *Q*/*B* taken from Stanford and Pitcher (2004). Diet composition for *Homarus americanus* from Gulf of St. Lawrence, eastern Canada (Sainte-Marie and Chabot, 2002).

1973 model: *B* assumed to be 1.5 higher as in Stanford and Pitcher (2004), since this stock seemed to be overfished (Southward and Boalch, 1992).

15. Small-medium demersal

This group includes some of the main fish prey items in the model. Therefore it is a very general group designed to include many different species. Some of them are the most abundant species that occurred in the beam trawl surveys recently carried out on the Western Channel. They were: pogge *Agonus cataphractus*, common dragonet *Callionymus lyra*, scaldfish *Arnoglossus laterna*, solenette *Buglossidium luteum* and thickback sole *Microchirus variegatus*. The parameters and diets were based on these species

1994 model: *P*/*B* was estimated using the Pauly's equation for natural mortality (Pauly, 1980) (weighted by catch rates). The estimates varied from 0.75 to 1.43 year^{-1} (mean = 1.02 year^{-1}). The highest value was used, since there is a big predation pressure on this group. *Q*/*B* average was also weigheted by catche rates. *B* was estimated by Ecopath based on *EE* of 0.9. The CPUE for small demersal were about 3.5 times bigger than that for plaice in the CEFAS beam trawl surveys. The small demersal catch was estimated assuming that the beam trawl plaice catches are a good index for it. The diet for this group was based on stomachs samples collected in the Western Channel aboard *RV CORYSTES* (unpublished data) and from information from Darnaude *et al*. (2001), Gibson and Robb (1996) and Gibson and Ezzi (1987) as well.

1973 model: There are evidences from the long-term trawl data (MBA) (Anon., 2001) that there was an abundance increase of species pertained to this group, probably related to higher temperatures and the declining of large predators. Based on the same data set, it was 'estimated' that the biomass would be 2.6 times lower.

16. Small gadoids (*Trisopterus* group)

The small medium sized southern gadoids poor cod, *Trisopterus minutus* and bib *Trisopterus luscus* compose this group.

1994 model: The mean catch rate in the Western Channel estimated using the MBA otter trawl survey data (Anon., 2001), was used as the biomass input for the group. It was represent mainly by poor cod that was by far the most abundant of the two species. The *P*/*B* was calculated using an *M* of 1.1 year^{-1} for poor cod (Menon, 1950) and *F* of 0.07 year^{-1} estimated as the *L*/*B* ratio. *Q*/*B* was estimated using growth parameters for poor cod. Diet data come from Irish Sea for poor cod (Armstrong, 1982) and Western Channel stomach samples collected aboard *RV CORYSTES* (unpublished data) and Irish Sea for bib (Armstrong, 1982).

1973 *model*: The biomass was estimated to be 55% of 1994's level according to MBA data.

17. Red Mullet (*Mullus surmuletus*)

1994 model: There was no biomass estimate for red mullet, *Mullus surmuletus*. This parameter was estimated by Ecopath based on *EE* of 0.90. The *P*/*B* was estimated using the Pauly's equation for *M*. Diet composition come from north-eastern Mediterranean. (Labropoulou e*t al*., 1997).

1973 model: According to MBA data, the biomass would be only 16% of 1994 model, but it seems to be very low. There was an increase in catches that seems to be partially related to an abundance increase due warmer conditions. As average landing for 1973-80 was 50% of that in the beginning of the 1990s, it was guesstimated that the biomass was 50% lower.

18, 19. Juvenile and adult Sole (*Solea solea*)

1994 and 1973 models: B and *P*/*B* ratio for sole, were estimated based on the ICES stock assessment data for its stock in division VIIe (Western Channel) (ICES, 2000a). Diets data come from north-west Mediterranean (Darnaude *et al*., 2001). The juveniles and adults were set with the same diet composition.

20, 21. Juvenile and adult Plaice (*Pleuronectes platessa*)

1994 model: *B* and *P*/*B* ratio for plaice were estimated based on the ICES stock assessment data for its stock in division VIIe (Western Channel) (ICES, 2000a). Diets data come from Eastern Anglesey, North Wales (Basimi and Grove, 1985). The juveniles and adults were set with same diet composition.

1973 model: The ICES time series data for plaice starts in 1976. So, we estimated *B* for 1973 using the average *L*/*B* ratio (yield) for the period 1976-80 and the landings for 1973.

22. Dab (*Limanda limanda*)

1994 model: The catch rate estimated for dab using data collected aboard *RV CORYSTES* beam trawl survey in 2002 was used as the biomass input for dab. The biomass estimates of ICES VPA for sole and plaice are very similar to biomass from *CORYSTES* Survey (even no corrections for q) and it seems very likely that the biomass estimates for dab are a good proxy for this parameter. *P*/*B* was taken from Stanford and Pitcher (2004) (estimated based on CFSG data). Diet data come from West Coast of Scotland (Gibson and Ezzi, 1987) and Western Channel stomachs samples (unpublished data).

1973 model: *B* was estimated to be to be about 40% higher using MBA data.

23. Lemon sole (*Microstomus kitt*)

1994 model: *B* was estimated based on the same *L*/*B* ratio and biomass estimates from Stanford and Pitcher (2004) (based on CFSG data). *P*/*B* was estimated based on an *F* (*C*/*B*) of 0.39 year^{-1} and a guesstimate for *M* of 0.2 year^{-1} (as used for megrim *Lepidorhombus whiffiagonis* in ICES reports (ICES 2000a)). *Q*/*B* was estimated using data for megrim, since we could not find estimates for lemon sole and they have similar maximum sizes. Diet data come from Iceland (Steinarsson, 1979) and Scotland (Rae, 1965).

1973 model: The biomass was estimated to be about 63% of 1994 according to MBA data.

24. Large flatfish

Composed by the piscivorous species brill *Scophthalmus rhombus*, turbot *Psetta maxima* and megrim *Lepidorhombus whiffiagonis*.

1994 model: *B* for megrim was estimated using ICES stock assessment data in Sub-area VII and divisions VIIIa,b,d,e (ICES, 2000a) from *L*/*B* ratio for the whole stock and *L* for the division VIIe. The estimates for the others two species were based on *B* and *L*/*B* ratio from Stanford and Pitcher (2004) (CFSG data) for the English Channel (VIId and e) and *L* for VIIe. *P*/*B* was based on ICES data for megrim (ICES, 2000a). *Q*/*B* was averaged using biomass as weighting factor. The average diet composition (weight by consumption) was based on megrim data (mainly juveniles) from Gulf of Valencia, Spain (Morte *et al*., 1999) and turbot and brill data (juveniles) from the Belgium coast (Beyst *et al*., 1999).

1973 model: the MBA long term trawl data show a decreasing trend in the catch rates for this group. As these are large species that in general are more vulnerable to fishing pressure it seemed reasonable assume that was a declining in their abundance. *B* was estimated to be 2.2 times higher than in 1994 using the MBA data. *P*/*B* was adjusted to account for a much lower fishing mortality.

25. Gurnards

Composed by red gurnard *Aspitrigla cuculus*, tub gurnard *Trigla lucerna* and grey gurnard *Eutrigla gurnardus*.

1994 model: *B* was estimated based on the same *L*/*B* ratio and *B* estimates from Stanford and Pitcher (2004) (based on CFSG data). *P*/*B* taken from Stanford and Pitcher (2004) (CFSG data). *Q*/*B* was estimated using data for red gurnard. Diet composition based on data for red gurnard in the Western Channel (unpublished data) and for grey gurnard in the North Sea (De Gee and Kikkert, 1993).

1973 model: Biomass estimated to be 1.4 times higher than 1994 using the MBA data.

26,27. Juvenile and adult whiting (*Merlangius merlangus*)

1994 model: *B* and *P*/*B* based on Ices stock assessment data for whiting in divisions VIIe-k (ICES, 2000). *B* was estimated from *L*/*B* ratio for the whole stock and *L* for VIIe. Adults diet data come from North Sea (Daan, 1989). Juveniles diet from west coast of Scotland (Gibson and Ezzi, 1987).

1973 model: The ICES' VPA time series data for whiting in divisions VIIe-k starts in 1982. The average estimated biomass for the whole period is 53,503 tons. There was an increase since 1982. The highest biomass was estimated to be 96,150 in 1995 and the stock biomass remained above the average since 1993. The biomass for 1973 was estimated to be 42% of 1994 using the MBA data.

28, 29. Juvenile and adult cod (*Gadus morhua*)

1994 model: *B* and *P*/*B* based on ICES stock assessment data for cod in divisions VIIe-k (ICES 2000a). *B* was estimated from *L*/*B* ratio for the whole stock and *L* for VIIe. Diets composition data for both adults and juveniles come from North Sea (Daan, 1989).

1973 model: The biomass for 1973 was 76% of the 1994 model. New inputs for adults and juveniles *P*/*B* were entered.

30. Hake (*Merluccius merluccius*)

1994 model: *B* and *P*/*B* based on ICES stock assessment data for northern hake stock (divisions IIIa, IV, VI, VII, VIIIa,b) (ICES, 2000a). *B* was estimated from *L*/*B* ratio for the whole stock and *L* for VIIe. Diet composition data come from the Celtic Sea (DuBuit, 1996).

1973 model: The ICES' VPA time series data for the hake northern stock start in 1978. The biomass estimates show a declining trend. The biomass for 1973 was estimated using a regression line of biomass against time, extrapolating the trend backwards until that year. The biomass was 1.76 higher than that for the 1994 model.

31. Dogfish

Composed by lesser-spotted dogfish *Scyliorhinus canicula*, greater-spotted dogfish *Scyliorhinus stellaris* and spurdog *Squalus acanthias*.

1994 model: The catch rate for lesser-spotted dogfish and greater-spotted dogfish estimated using data from the MBA trawl surveys was used as input for *B*. *P*/*B* for dogfish was estimated using Pauly's equation for *M*. Both *P*/*B* and *Q*/*B* were estimated using parameters for *S. canicula*. Diet composition data for lesser-spotted dogfish from Irish Sea (Ellis *et al*., 1996)

1973 model: The biomass was estimated to be 69% of 1994 model using MBA data.

32. Rays

Composed by thornback ray *Raja clavata*, cuckoo ray *Leucoraja naevus*, spotted ray *Raja montagui*, blue skate *Dipturus batis*, blonde ray *Raja brachyura*, painted ray *Raja microocellata*.

1994 model: The catch rate estimated using the *CORYSTES* Beam Trawl surveys in the Western Channel was used a input for *B*. With this biomass, the *F* would be at least 3 year^{-1}, an unrealistic estimate. So, the biomass for rays was left blank, estimated using and *EE* of 0.95 since they are heavily exploited. *P*/*B* based on average *M* of 0.28 year^{-1} for *L. naevus*, *R. montagui*, *R. clavata* and a guesstimate of *F* ~ 0.3 year^{-1}. *Q*/*B* was averaged for *R. naevus, R. montagui*, *R. clavata*. Diet composition for cuckoo ray come from Irish Sea (Ellis *et al*., 1996) and for thornback ray and spotted ray using averaged data from Irish Sea (Ellis *et al*., 1996) and Bristol Channel (Ajayi, 1982).

1973 model: The biomass was estimated to be 2.5 times higher than 1994 using MBA data.

33. Other gadoids

Based mainly on *Pollachius pollachius*, but designed to 'represent' saithe *Pollachius virens*, blue whiting *Micromesistius poutassou* and haddock *Melanogrammus aeglefinus* as well.

1994 model: *B* estimated from *F* (*C*/*B*) for pollack in Stanford and Pitcher (2004) and pollack *C* for VIIe. *P*/*B* was estimated based on *M* of 0.31 year^{-1} for pollack using Pauly's equation and *F*. *Q*/*B* estimated using data for pollack. Diet composition come from south-western of Norway for pollack (Hoines and Bergstad, 1999), and from North Sea for saithe and haddock (Daan, 1989).

1973 model: The biomass was estimated to be 74% of the 1994 model using MBA data.

34. Anglerfish (*Lophius piscatorius* and *L. budegassa*)

Although *L. Piscatorius* is the dominant anglerfish in VIIe, we have combined the two species.

1994 model: *B* and *P*/*B* were estimated based on ICES stock assessment data for anglerfish in Divisions VIIb–k and VIIIa,b (ICES, 2000a). *B* was estimated from *L*/*B* ratio for the whole stock and *L* for VIIe. Diet composition data come from Irish Sea (Crozier, 1985).

1973 model: The biomass was estimated to be 85% of the 1994 model using MBA data. *P*/*B* was adjusted to account for a much lower fishing mortality.

35. Large bottom

Very general group composed by ling *Molva molva*, conger *Conger conger* and others species like Greater weaver *Trachinus draco*, Forkbeard *Phycis blennioides*, Eel *Anguilla anguill*a and red-band fish *Cepola rubescens*.

1994 model: *B* estimated using *L*/*B* ratio as in Stanford and Pitcher (2004) (CFSG data for ling and conger assuming same *L*/*B*) and *L* for VIIe. *P*/*B* was estimated based on *F*(*C*/*B*) of 0.23 year^{-1} and on *M* of 0.18 year^{-1}. All estimates were based on ling and conger (*M* and *Q*/*B* are average estimates, weighted by biomass). Diet composition data for conger come from Mediterranean (Macpherson, 1981) and Bay of Biscay (Olaso and Rodriguez-Marin, 1995). The diet of ling was based on percentage of occurrence data from Scotland (Rae and Shelton, 1982).

1973 model: The biomass was estimated to be 2.5 higher than 1994 using MBA data. *P*/*B* was adjusted to account for a much lower fishing mortality.

36. Seabreams

This group represents mainly black seabream *Spondyliosoma cantharus*, but was designed to also include gilthead seabream *Sparus aurata* and red seabream *Pagellus bogaraveo*.

1994 model: *B* and *P*/*B* was taken from Stanford and Pitcher (2004) (estimated based on CFSG data). *Q*/*B* was estimated using data for black bream. Diet composition for black bream (Pita *et al*., 2002).

1973 model: Black bream seems to be overexploited. The landings in the beginning of the series were higher and fell suddenly. After that, the landings increased slightly. So, the biomass for the 1973 was assumed to be 1.5 higher.

37. John Dory (*Zeus faber*)

1994 model: The catch rate for John Dory in the MBA trawls survey was used as input for *B*. *P*/*B* was estimated from the *L*/*B* ratio. The diet composition data come from the Portuguese coast (Silva, 1999).

1973 model: The MBA trawl data and ICES landings show opposite trends. It is supposed that the observed landings increase is a result of higher abundance related to higher temperatures. So we decide to follow the ICES data trend as an index of abundance and set the biomass to be about 70% of the 1994 model.

38. Sandeels (*Ammodytes tobianus*)

B was left to be estimated by Ecopath based on *EE* of 0.90. *P*/*B* was based on an *M* of 1.29 year^{-1} for *A. tobianus* from Reay (1973). Diet for *Ammodytes tobianus* from Reay (1970).

39. Herring (*Clupea harengus*)

1994 model: It seems that there are two different herring stocks exploited in the English Channel. The Eastern Channel herring is managed as part of the North Sea Downs stock. The Western Channel stock is considered to be a local unit with landings much lower than in the eastern part (Ulrich *et al*., 2002). In the absence of direct biomass data for the Western Channel, it was decided to base the *B* and *P*/*B* estimates on ICES stock assessment data for Celtic Sea stock (ICES, 2000c). *B* was estimated using *L*/*B* for the Celtic Sea Stock and *L* for the Western Channel. Diet composition data come from west coast of Scotland (De Silva, 1973).

1973 model: There are time series of VPA biomass estimates for the North Sea and for the Celtic Sea stocks since 1960. The biomass long-term trends of these two stocks are very similar. As the Western Channel is between these two areas, it seemed quite reasonable to assume that herring stock in this area followed a similar pattern to the Celtic Sea stock. The biomass in 1973 was estimated to be 76% of 1994 model.

40. Sprat (*Sprattus sprattus*)

1994 model: *B* left to be estimated by Ecopath based on *EE* of 0.95. *P*/*B* was taken from the North Sea Model (Christensen, 1995). Diet composition data come from west coast of Scotland (De Silva, 1973).

1973 model: Biomass estimated to be 37% of the 1994 model according to MBA data.

41. Pilchard (*Sardina pilchardus*)

1994 model: *B* estimate taken from Stanford and Pitcher (2004). This parameter was estimated based on numbers estimates of 10,000 km^{-2} taken from Cushing (1957) and Southward (1963) and a mean body weight of 68.8 g for pilchard in the Western Channel. *Z* for pilchard in ICES divisions VIIIc and IXa (ICES, 1999) was used as input for *P*/*B*. Diet composition from Moreno and Castro (1995).

1973 model: *B* was estimated to be 59% of the 1994 model using the MBA data.

42. Mackerel (*Scomber scombrus*)

1994 model: The mackerel caught in the Western Channel is considered part of the huge Western mackerel stock that is exploited in the ICES areas II, III, IV, V, VI, VII and divisions VIIIa and VIIIb (ICES, 1999). *B* and *P*/*B* estimates were based on ICES stock assessment data for this stock. *B* was estimated from *L*/*B* ratio for the whole stock and *L* for VIIe. Diet composition data come from North Sea (Daan 1989).

1973 model: The time series catch data for the channel shows a very different trend that from the whole stock. It is, at least in part, the consequence of a different stock distribution (migration) pattern from the previous years throughout the 1970s and early 1980s. During this period many shoals of large mature fish, instead of overwinter in the northern areas, migrated to the southwest coast of England to overwinter there and then supported the higher catches in that region (Lockwood, 1988). So, mackerel had to be split into the regular component and the overwinter mackerel during the 1970s and early 1980s.

To estimate the biomass and landings for the 1973 model, the following assumptions were made:

a) The biomass and catches trend for mackerel in the channel followed the same pattern of the Western stock. These parameters were estimated as relative values of that in 1994 (1993-1995);

b) The overwinter mackerel component was in the channel until 1984. From 1973 to 1984, the biomass and catch 'excess' was put in the overwinter group. According to Lockwood (1988), mackerel do not eat during the overwinter period, and so, this group was not included in the model, as it would have little or no effect on simulations. A similar approach was used by Stanford and Pitcher (2004). The biomass of the regular component was estimated to be 1.2 times higher than the 1994 model.

43. Scad (*Trachurus trachurus*)

1994 model: The scad caught in the Western Channel is considered part of the Western scad stock that is exploited in the ICES divisions IIa, IVa, Vb, VIa, VIIa-c,e-k and VIIIabde (ICES, 1999). *B* and *P*/*B* estimates were based on data for this stock. *B* was estimated using *L*/*B* ratio for the whole stock and *L* for VIIe. The diet composition was based on a study from the southern Bay of Biscay (Olaso *et al*., 1999) and from the North Sea (Dahl, 1987).

1973 model: The scad ICES VPA stock assessment goes back only until 1982. The landings time series data for the Western Channel and for the whole stock show a similar pattern. However, the Channel scad landings gathered by the CFSG (Dintheer *et al*., 1995; Ulrich *et al*., 2002) for the period 1993-1995 were much lower than that available in the ICES electronic database for the same area. Since there seems to be no accurate information for other years, we assumed that the landings trend for scad in the channel followed the same pattern of the whole stock. So, it was used the ICES landings data for the Western Channel as relative values, with 1994 set to 1, and the 1973 landings were estimated using the respective relative value and the mean landings estimated for 1994 from CFSG data. The biomass for 1973 was estimated to be 88% of 1994 model on the MBA trawl data.

44. Bass (*Dicentrarchus labrax*)

1994 model: *B* estimated using *L*/*B* ratio from Stanford and Pitcher (2004) (CFSG data) and *L* for VIIe. *P*/*B* was estimated based on *F* (C/B) of 0.19 year^{-1} and a *M* of 0.24 year^{-1} estimated using Pauly's equation. Diet composition (juvenile data) from Cabral and Costa (2001)

1973 model: *B* was estimated to be 1.28 higher than 1994 using MBA data.

45. Sharks

Composed by smooth-hound *Mustelus mustelus*, starry smoothhound *M. asterias*, tope shark *Galeorhinus galeus*, porbeagle *Lamna nasus* and blue shark *Prionace glauca*.

1994 model: *B* and landings were taken from Stanford and Pitcher (2004). *P*/*B* was estimated based on a *F* (*C*/*B*) of 0.06 year^{-1} and a *M* of 0.18 year^{-1} estimated using Pauly's equation (average for tope shark, porbeagle, blue shark). *Q*/*B* was averaged for tope shark, porbeagle, blue shark. Diet composition data for tope shark come from Irish Sea (Ellis *et al*., 1996). Porbeagle and blue shark diet data come from north west Atlantic (Bowman *et al*., 2000).

1973 model: The biomass was estimated to be 2.29 times and landings 2 times higher than 1944 according to Stanford and Pitcher (2004). These estimates were based on CPUE data for blue shark taken from Vas (1990).

46. Basking Shark (*Cetorhinus maximus*)

All parameters taken from Stanford and Pitcher (2004).

47. Cephalopods

Composed by cuttlefish *Sepia officinalis*, *Loligo forbesi*, *L. vulgaris* and *Illex coindetii*.

1994 model: *B* was estimated using catch rate estimated for cephalopods, mainly *S. officinalis*, using data collected during the *CORYSTES* 2002 beam trawl survey in the Western Channel plus the catch rates estimates for *Loligo* spp. in the Eastern Channel available from Stanford and Pitcher (2004) (based on data from Robin *et al*., 1998). *P/B* was estimated based on a *F* (*C*/*B*) of 0.37 year^{-1} and a *M* of 1.69 year^{-1} (averaged by biomass). *M* estimate was taken from Stanford and Pitcher (2004) and was calculated using empirical relationship for *Loligo forbesi* as 2 year^{-1} (Pierce *et al*., 1996), and for *S. officinalis* as 1.5 year^{-1} based on values for *S. aculeata* and *S. elliptic*a from Rao *et al*., (1993). *Q*/*B* was taken from Pauly and Christensen (1996). Diet composition data as in Stanford and Pitcher (2004).

1973 model: The biomass was assumed to be about 70% of the 1994 model.

48. Birds

Composed by fulmar *Fulmarus glacialis*, manx shearwater *Puffinus puffinus*, storn petrel *Hydrobates pelagicus*, gannet *Sula bassana*, cormorant *Phalacrocorax carbo*, arctic skua *Stercorarius parasiticus*, mediterranean gull *Larus melanocephalus*, etc…

1994 model: All parameters and diet composition taken from Stanford and Pitcher (2004).

1973 model: The biomass of the 70 was 10% lower than the 1994 model, assuming that with less discards would be less birds.

49. Toothed cetaceans

Composed by harbour porpoise *Phocoena phocoena*, common dolphin *Delphinus delphis* and long-finned pilot whale *Globiecephala melas*.

1994 model: All parameters and diet composition taken from Stanford and Pitcher (2004).

1973 model: The biomass was 1.5 higher than 1994 assuming a lower level of incidental fishing mortality and a higher prey availability.

50. Seals

Composed by grey seals *Haliochoerus grypus* and harbour seals *Phoca vitulina*.

1994 model: All parameters and diet composition taken from Stanford and Pitcher (2004).

1973 model: The biomass was 1.5 higher than 1994 assuming higher prey availability.

4. MODEL BALANCING

4.1. Balancing the 1994 model

The strategy used to balance the model was first to make big changes in the diet matrix since diet compositions are only snapshots of the feeding habits and because much of the information used to build the matrix was taken from studies carried out in different ecosystems and periods. Only after this, were the biomass and/or production rates changed. The magnitudes of the changes were based on the reliability of the input data. The classification of the data was based on the 'pedigree' tables available in the EwE software (Christensen *et al*., 2004). This routine allows the user to classify the data origin using a pre-defined table for each type of input parameter, and attributing a guesstimate of the confidence intervals based on their origin. The scales used to give data inputs scores were modifications of the Ecopath default tables. The scale of uncertainty that was constructed is presented in Table 1.

After the first attempt to parameterize the model, 12 groups were 'unbalanced' (Table 2), i.e., their ecotrophic efficiencies exceeded one. Mostly values exceeded one because the excessive mortality caused by predation by scad on other groups such as whiting, cod, pollack and hake. The model was balanced using the automated mass balance procedure that was recently developed and included in the EwE software (Kavanagh *et al*., 2004). This routine was run using the parameter variation intervals in the pedigree tables (e.g. Table 1). Balancing was done in two steps. In the first, the automated procedure was run two times to change the diet matrix only. Where further changes were required to balance the model, the procedure was run to alter the B and P/B parameters.

Table 1. Data uncertainty scores (%) for the 1994 model

	Group	B	P/B	Q/B	Diets	Catch
1	Primary producers	30	30			20
2	Microzooplankton	30	60	60	100	
3	Mesozooplankton	30	60	60	100	
4	Marozooplankton	30	30	60	100	
5	Deposit feeders	30	30	60	100	
6	Suspension feeders	30	60	60	100	
7	Shrimps and Prawns	80	20	60	100	20
8	Whelks	30	10	60	100	20
9	Echinoderms	30	60	60	100	
10	Bivalves	30	30	60	100	40
11	Scallops	50	10	60	100	20
12	Small-medium crabs	30	60	60	100	
13	Large crabs	50	20	60	100	20
14	Lobster	70	20	60	100	20
15	Small-medium demersal	80	50	50	100	60
16	Small gadoids	50	60	50	30	20
17	Red mullet	80	50	50	100	20
18	Juvenile sole	10	10	50	100	20
19	Adult sole	10	10	50	100	20
20	Juvenile plaice	10	10	50	100	20
21	Adult plaice	10	10	50	100	20
22	Dab	50	10	50	100	20
23	Lemon Sole	50	30	60	100	20
24	Large flatfish	50	20	50	100	20
25	Gurnards	50	20	50	30	20
26	Juvenile whiting	30	20	50	100	20
27	Adult whiting	30	20	50	100	20
28	Juvenile cod	30	20	50	100	20
29	Adult cod	30	20	50	100	20
30	Hake	50	20	50	100	20
31	Dogfish	50	30	50	30	20
32	Rays	80	60	50	100	20
33	Other gadoids	80	30	50	100	30
34	Anglerfish	30	10	50	100	20
35	Large bottom	70	50	50	100	20
36	Seabreams	50	10	50	100	40
37	John Dory	30	50	50	100	20
38	Sandeels	80	20	50	100	
39	Herring	70	20	50	100	20
40	Sprat	80	50	50	100	20
41	Pilchard	50	20	50	100	20
42	Mackerel	50	20	50	100	20
43	Scad	50	20	50	100	20
44	Bass	30	50	50	100	20
45	Sharks	80	50	50	100	50
46	Basking shark	80	20	50	100	
47	Cephalopods	30	50	60	100	20
48	Birds	80	60	60	100	
49	Toothed cetaceans	80	60	60	100	50
50	Seals	80	60	60	100	

Table 2. Basic parameters for the 1994 model. Those estimated by Ecopath (outputs) are underlined. Functional groups with inputs changed are in bold, with the original value in brackets. The Ecotrophic Efficiency (EE) of groups in the unbalanced model are presented in brackets

Group name	TL	Biomass (t km^{-2})	P/ B (/year)	Q/B (/year)	EE	P/Q
2 Microzooplankton	2.06	2.629	45.28	120.00	0.66	0.38
3 Mesozooplankton	2.16	5.871	39.08	80.00	0.53	0.49
4 Marozooplankton	3.16	1.100	18.00	38.00	0.03	0.47
5 Deposit feeders	2	13.642	3.00	20.00	0.80	0.15
6 Suspension feeders	2.61	5.070	0.30	2.00	0.27	0.15
7 Shrimps and Prawns	2.43	5.549	3.96	13.20	0.90	0.30
8 Whelks	3.05	0.365	**0.64 (0.59)**	8.03	0.90 (1.43)	0.07
9 Echinoderms	2.23	8.826	**0.66 (0.60)**	6.94	0.90 (1.12)	0.09
10 Bivalves	2	17.410	0.89	9.87	0.86	0.09
11 Scallops	2	0.522	0.80	8.89	0.75	0.09
12 Small-medium crabs	2.3	5.157	**1.95 (1.8)**	12.00	0.90 (1.23)	0.15
13 Large crabs	2.44	0.511	0.60	4.00	0.71	0.15
14 Lobster	3.11	0.010	**0.52 (0.5)**	5.85	0.90	0.09
15 Small-medium demersal	3.1	1.825	**1.57 (1.43)**	7.13	0.90	0.15
16 Small gadoids	3.39	**1.417 (1.165)**	**1.27 (1.17)**	4.58	0.88 (1.61)	0.22
17 Red mullet	3.3	0.169	0.52	4.13	0.90	0.09
18 Juvenile sole	3.01	0.015	0.75	7.29	0.50 (1.99)	0.08
19 Adult sole	3.01	0.044	0.43	3.75	0.59	0.08
20 Juvenile plaice	3	0.025	1.51	8.56	0.45	0.13
21 Adult plaice	3	0.034	0.76	3.03	0.67	0.18
22 Dab	3.19	0.033	0.75	4.35	0.79 (1.61)	0.13
23 Lemon sole	3.14	0.060	**0.60 (0.59)**	3.85	0.90 (1.30)	0.11
24 Large flatfish	3.85	0.060	0.55	3.62	0.72	0.11
25 Gurnards	3.4	0.286	0.57	3.86	0.83	0.10
26 Juvenile whiting	3.29	0.035	1.60	10.79	0.87 (16.8)	0.11
27 Adult whiting	4.07	0.122	0.79	4.08	0.39	0.14
28 Juvenile cod	3.52	0.012	1.88	8.89	0.66 (6.95)	0.21
29 Adult cod	3.96	0.016	0.99	3.85	0.57	0.32
30 Hake	4.42	0.026	**0.53 (0.51)**	2.81	0.90 (5.14)	0.13
31 Dogfish	3.42	**0.401 (0.626)**	0.38	3.46	0.26	0.08
32 Rays	3.45	0.085	0.60	3.06	0.90	0.14
33 Other gadoids	3.82	**0.301(0.171)**	**0.82 (0.66)**	2.94	0.66 (5.9)	0.20
34 Anglerfish	4.18	**0.151 (0.189)**	0.41	2.05	0.69	0.15
35 Large bottom	4.01	**0.111 (0.161)**	**0.46 (0.41)**	2.22	0.90	0.14
36 Seabreams	3.01	0.118	**0.61 (0.58)**	3.34	0.90	0.13
37 John Dory	4.22	**0.015 (0.01)**	0.65	3.62	0.64	0.13
38 Sandeels	3.13	2.936	1.29	7.35	0.90	0.13
39 Herring	3.1	**0.068 (0.057)**	**1.00 (0.85)**	4.60	0.89 (22.65)	0.16
40 Sprat	3.13	0.525	1.21	7.02	0.90	0.13
41 Pilchard	3.12	0.688	0.64	5.74	0.80	0.08
42 Mackerel	3.44	1.363	**0.36 (0.35)**	4.34	0.90	0.06
43 Scad	3.58	**0.704 (0.879)**	**0.39 (0.33)**	4.03	0.90	0.07
44 Bass	3.47	0.065	0.42	2.84	0.44	0.11
45 Sharks	4.44	0.002	0.24	1.83	0.37	0.09
46 Basking shark	3.16	0.034	0.07	3.70	0.00	0.02
47 Cephalopods	3.54	0.466	**2.19 (2.07)**	15.00	0.90	0.14
48 Birds	3.55	0.001	0.40	72.12	0.01	0.01
49 Toothed cetaceans	4.42	**0.00384 (0.006)**	0.40	13.73	0.18	0.03
50 Seals	4.66	0.002	0.04	13.32	0.18	0.003
51 Discarded catch	1	0.300	-	-	0.07	-
52 Detritus	1	1	-	-	0.20	-

4.2. Refining the1994 balanced model

After balancing the model, the Ecosim routine was run under a no-fishing scenario and under a 100% increase in the fishing rate of all fleets to check for unusual or extreme model predictions. Under the non-fishing scenario, the model predicted a biomass increase of more than 50 times the input value for John Dory and about 18 times for rays. The observed problem of John Dory was probably related to the fact that it does not have any predator in the model so that fishing mortality accounts for about 98% of the total mortality, which in Ecopath is equivalent to its production rate, *P*/*B*. The problem was overcome by changing the biomass input to 0.015 t km^{-2}, which was within the confidence interval estimated for the catch rate data from the MBA trawl surveys. The problem with the predictions on ray biomass was overcome by changing the ecotrophic efficiency from 0.95 to 0.8. These changes reduced the ratio between fishing mortality and *P*/*B* for both groups, and so the model predicted more realistic changes under a non-fishing scenario.

When fishing effort was doubled, surprisingly the biomass of commercial species such as cod and large other gadoids had a large increase. Inspection of the Ecopath mortalities rates revealed that the predation caused by scad on these groups was very high, accounting for more than 70% of the predation mortality. When scad biomass was decreased by more than 80% as the fishing was increased, it caused a huge response in the biomass of cod and large other gadoids. These strong links seemed to be inaccurate. Estimates of predation mortalities from multi-species virtual population analyses (MSVPA) in the North Sea (Anon., 2003), do not show such a strong trophic link. The results observed here are likely the consequences of using scad diet data that, although being a good indication of the general feeding habits of the species, are not representative of the Western Channel. To remove this artefact, we manually overrode the changes to the diet matrix made by the autobalance routine. The sandeel group was used as a 'buffer' during the balancing/refining process, accounting for a significant part of the fish consumed in the model. As a consequence, sandeel biomass became very high and this group should be viewed as a kind of 'other prey' group, that account for any species not explicitly accounted for in the model.

Finally we increased the *P*/*B* of all groups that had very high *EE* (>0.9) so as to reduce the *EE* to 0.9. It is just a technicality that seemed to improve the performance of an Ecopath tool, Ecoranger, that was used as way to perform a sensitivity analysis and is presented in section 6. The parameters of the 1994 model are presented in Tables 2 to 6.

Table 3. Additional data necessary to represent the ontogeny of split groups. K: curvature of the von Bertalanffy growth function; Age$_m$: age at transition to adult stage; W$_m$/W$_\infty$: ratio between age at maturity and asymptotic weight. The same data were used in both 1994 and 1973 models. Estimates for Age$_m$ based on ICES (2000a), K and W$_m$/W$_\infty$ based on ICES (2000a) and Froese and Pauly (2000)

Group	K (year^{-1})	Age$_m$ (months)	W$_m$/W$_\infty$
Sole	0.30	36	0.19
Plaice	0.08	36	0.05
Whiting	0.18	24	0.12
Cod	0.20	26	0.08

Table 4. Diet matrix for the 1994 model (unbalanced model values in brackets)

Prey\Predator	2	3	4	5	6	7	8	9	10	11	12	13
1 Primary producers	94.7	78.3			10.0	8.5		5.1 (5)	50.0	50.0		
2 Microzooplankton	5.3	9.8			15.0	12.5						
3 Mesozooplankton		4.9	100.0		30.0	23.5						
4 Marozooplankton												
5 Deposit feeders					10.0	3.0	73.5 (70)	11.2 (10.2)				
6 Suspension feeders								0.5				
7 Shrimp and Prawns							5.6 (5)				14.6 (14.9)	15.2 (14.9)
8 Whelks												
9 Echinoderms							5.6 (5)	4.8 (6)				
10 Bivalves							11.2 (10)	5.1 (5)			8.4 (7.9)	20.3 (19.8)
11 Scallops												
12 Small-medium crabs							4.1 (10)				0.7 (3)	1.2 (3)
13 Large crabs												
14 Lobster												
15 Small-medium demersal												
16 Small gadoids												
17 Red mullet												
18 Juvenile sole												
19 Adult sole												
20 Juvenile plaice												
21 Adult plaice												
22 Dab												
23 Lemon sole												
24 Large flatfish												
25 Gurnards												
26 Juvenile whiting												
27 Adult whiting												
28 Juvenile cod												
29 Adult cod												
30 Hake												
31 Dogfish												
32 Rays												
33 Other gadoids												
34 Anglerfish												
35 Large bottom												
36 Seabreams												
37 John Dory												
38 Sandeels												
39 Herring												
40 Sprat												
41 Pilchard												
42 Mackerel												
43 Scad												
44 Bass												
45 Sharks												
46 Basking shark												
47 Cephalopods												
48 Birds												
49 Toothed cetaceans												
50 Seals												
51 Discarded catch												
52 Detritus		7.0		100.0	35.0	52.5		73.3 (72.7)	50.0	50.0	76.2 (74.3)	63.2 (62.3)
53 Import												
54 Sum	100	100	100	100	100	100	100	100	100	100	100	100

Table 4. continued

Prey\Predator	14	15	16	17	18	19	20	21	22
1 Primary producers	8.6 (7.9)	0.002							
2 Microzooplankton		0.01	2.8 (2.7)						
3 Mesozooplankton		0.01	3.1 (3)						
4 Marozooplankton		0.03							
5 Deposit feeders	11.9 (11)	59.1 (57.1)	6.8 (6.6)	48.4 (33.9)	84.6 (83.1)	84.6 (83.1)	48.4	48.4	65.8 (64.8)
6 Suspension feeders	3.3 (3)	0.04			1.0 (0.9)	1.0 (0.9)			19.7 (19.2)
7 Shrimps and Prawns	0.3	11.5 (11)	48.9 (47.3)	15.7 (11)			0.5	0.5	3.4 (3.3)
8 Whelks	0.4 (8)								
9 Echinoderms	3.4 (3.1)	11.4 (10.9)	0.03	1.7 (1.2)			0.5	0.5	0.02
10 Bivalves	24.7 (22.8)	14.1 (13.5)	8.6 (8.3)	1.3 (0.9)	12.7 (11.7)	12.7 (11.7)	50.6	50.6	6.4 (6.2)
11 Scallops									
12 Small-medium crabs	45.5 (42)	2.4 (6.1)	21.5 (20.8)	17.2 (42.1)	1.8 (4.3)	1.8 (4.3)			1.3 (3.2)
13 Large crabs									
14 Lobster	1.1 (1)								
15 Small-medium demersal	0.9	1.4 (1.3)	5.6 (7.4)	15.7 (11)					
16 Small gadoids			0.3 (0.9)						
17 Red mullet									
18 Juvenile sole									
19 Adult sole									
20 Juvenile plaice									
21 Adult plaice									
22 Dab									
23 Lemon sole									
24 Large flatfish									
25 Gurnards									
26 Juvenile whiting			0.1 (0.5)						
27 Adult whiting									
28 Juvenile cod									
29 Adult cod									
30 Hake									
31 Dogfish									
32 Rays									
33 Other gadoids									
34 Anglerfish									
35 Large bottom									
36 Seabreams									
37 John Dory									
38 Sandeels			0.1						
39 Herring									
40 Sprat			0.4 (0.6)						
41 Pilchard									
42 Mackerel									
43 Scad									
44 Bass									
45 Sharks									
46 Basking shark									
47 Cephalopods			1.9 (1.8)						3.4 (3.4)
48 Birds									
49 Toothed cetaceans									
50 Seals									
51 Discarded catch									
52 Detritus									
53 Import									
54 Sum	100	100	100	100	100	100	100	100	100

Table 4. continued

Prey\Predator	23	24	25	26	27	28	29	30
1 Primary producers								
2 Microzooplankton	0.9	0.02			4.8 (3.6)	0.01		
3 Mesozooplankton	1.5	0.02			5.5 (4.1)	0.02	2.8 (2)	
4 Marozooplankton						0.2 (0.1)		
5 Deposit feeders	68.0 (67.4)	5.7 (5.3)	24.4 (21.5)	30.9 (28.1)	3.2 (2.4)	8.4 (8.1)	5.3 (3.8)	0.01
6 Suspension feeders	3.8 (3.7)	0.02			0.3 (0.2)	0.1	0.1	
7 Shrimps and Prawns		18.2 (16.8)	44.1 (38.9)	64.4 (60.5)	2.0 (1.5)	46.9 (45.3)	0.4 (0.3)	0.3 (0.1)
8 Whelks						0.1 (1)		
9 Echinoderms	2.5				0.1	0.03	0.3 (0.2)	
10 Bivalves	13.2 (13)	0.1	0.3		0.01	1.3	0.1	
11 Scallops								
12 Small-medium crabs		8.3 (7.7)	21.5 (30.6)	4.7 (11.4)	2.9 (2.2)	21.0 (20.2)	22.9 (16.4)	
13 Large crabs								
14 Lobster								
15 Small-medium demersals		59.5 (55.9)	2.3 (2)			18.0 (17.3)	20.4 (14.6)	0.3 (0.1)
16 Small gadoids					27.3 (20.4)	0.4 (0.8)	8.8 (6.3)	28.0 (10.6)
17 Red mullet								
18 Juvenile sole					0.01		0.3 (0.2)	
19 Adult sole								
20 Juvenile plaice							4.3 (3.1)	
21 Adult plaice								
22 Dab					0.015 (0.03)	0.4 (1.5)	3.5 (8.4)	
23 Lemon sole							0.2 (0.3)	
24 Large flatfish								0.5 (0.2)
25 Gurnards								0.8 (0.3)
26 Juvenile whiting			0.3		1.4 (4.6)	0.1 (1.1)	7.4 (11)	0.4 (2.9)
27 Adult whiting							1.7 (1.2)	
28 Juvenile cod			0.2		0.1 (04)	0.01 (0.1)	4.4 (4.7)	
29 Adult cod								
30 Hake								0.1 (0.7)
31 Dogfish								
32 Rays								
33 Other gadoids					6.5 (14.1)		6.5 (15.7)	4.6 (42.3)
34 Anglerfish								
35 Large bottom								
36 Seabreams								
37 John Dory								
38 Sandeels	8.4 (8.3)				23.5 (17.6)	2.8 (2.7)	4.6 (3.3)	
39 Herring	0.05 (0.9)	0.3 (7)			0.6 (12.7)		0.2 (4)	0.2 (2.5)
40 Sprat	0.6 (0.9)	7.6 (7)			19.7 (14.7)	0.1	1.4 (1)	6.1 (2.3)
41 Pilchard	0.9	0.2						10.8 (4.1)
42 Mackerel					0.1		2.1 (1.5)	22.8 (16.1)
43 Scad								24.9 (17.6)
44 Bass								
45 Sharks								
46 Basking shark								
47 Cephalopods			7 (6.2)		1.9 (1.4)	0.4	2.4 (1.7)	0.3 (0.1)
48 Birds								
49 Toothed cetaceans								
50 Seals								
51 Discarded catch								
52 Detritus								
53 Import								
54 Sum	100	100	100	100	100	100	100	100

Table 4. continued

Prey\Predator	31	32	33	34	35	36	37	38	39	40
1 Primary producers			0.1							
2 Microzooplankton									60.0	39.5
3 Mesozooplankton		3.4 (3.2)	15.5 (11.6)					80.5	40.0	59.2
4 Marozooplankton										1.3
5 Deposit feeders	24.4 (23.3)	12.8 (12)	7.8 (5.8)			98.4 (98.1)		19.5		
6 Suspension feeders	1.4 (1.3)		0.1				0.03 (0.02)			
7 Shrimps and Prawns	5.9 (5.6)	26.3 (24.7)	3.2 (2.4)		7.4 (5.0)	0.9 (0.8)	1.0 (0.6)			
8 Whelks	1.4 (3.9)									
9 Echinoderms	2.0 (1.9)	0.2	5.5 (4.1)				0.01			
10 Bivalves	1.5 (1.4)	0.2	1.3 (1)			0.3				
11 Scallops										
12 Small-medium crabs	46.1 (44)	36.8 (34.5)	2.9 (2.2)	16.0 (11.2)	14.9 (10)	0.3 (0.8)				
13 Large crabs	0.1	3.4 (3.2)								
14 Lobster										
15 Small-medium demersal	4.0 (3.8)	11 (10.3)		10.0 (7.0)	11.9 (8)		36.1 (22.2)			
16 Small gadoids	4.1 (3.9)	0.2 (4)	13.6 (22.8)	65.8 (46.1)	5.2 (3.5)					
17 Red mullet										
18 Juvenile sole	0.1 (0.2)									
19 Adult sole										
20 Juvenile plaice	0.2									
21 Adult plaice										
22 Dab	0.4 (0.6)	0.1 (0.3)	0.05 (0.1)	0.7 (1.5)						
23 Lemon sole				1.4 (2.8)	0.7 (1.2)					
24 Large flatfish							0.5 (0.3)			
25 Gurnards										
26 Juvenile whiting	0.4 (0.6)	0.003 (0.03)	0.001 (0.7)	1.6 (15.9)	0.2 (2.3)					
27 Adult whiting										
28 Juvenile cod			0.01 (0.04)	0.2 (1.8)	0.1 (1.2)					
29 Adult cod										
30 Hake										
31 Dogfish										
32 Rays		0.01								
33 Other gadoids	0.4 (1.1)	0.1 (2.1)	0.3 (5.7)		4.6 (16.5)		2.0 (39.7)			
34 Anglerfish										
35 Large bottom							3.1 (1.9)			
36 Seabreams										
37 John Dory										
38 Sandeels	1.0	1.5 (1.4)	45.9 (34.3)		3.4 (2.3)		0.5 (0.3)			
39 Herring	0.4 (1.1)	0.002 (0.04)	0.3 (6.6)	0.6 (11.1)	0.8 (15.9)					
40 Sprat	1.1	0.02 (0.04)	2.5 (1.9)		23.6 (15.9)					
41 Pilchard	1.1	0.04			23.6 (15.9)		40.7 (25.0)			
42 Mackerel		1.7 (1.6)		2.1 (1.5)						
43 Scad							15.8 (9.7)			
44 Bass										
45 Sharks										
46 Basking shark										
47 Cephalopods	4.1 (3.9)	2.2 (2.1)	0.8 (0.6)	1.7 (1.2)	3.6 (2.4)		0.3 (0.2)			
48 Birds										
49 Toothed cetaceans										
50 Seals										
51 Discarded catch										
52 Detritus										
53 Import										
54 Sum	100	100	100	100	100	100	100	100	100	100

Table 4. continued

Prey\Predator	41	42	43	44	45	46	47	48	49	50
1 Primary producers							5.3 (4.8)			
2 Microzooplankton	40.0	3.8 (3.4)	1.8 (1.3)							
3 Mesozooplankton	60.0	65.2 (58.8)	17.4 (12.5)			30.0		2.4 (2.2)		
4 Marozooplankton		5.0 (4.4)	4.8 (3.4)							
5 Deposit feeders		0.9 (0.8)	9.8 (7)	20.7 (20.6)	1.0 (0.9)		0.3	3.4 (3.1)		
6 Suspension feeders										
7 Shrimps and Prawns		1.1 (1)	38.9 (27.8)	58.8 (58.7)						
8 Whelks										
9 Echinoderms					0.2					
10 Bivalves				0.3					0.1	
11 Scallops				0.03						
12 Small-medium crabs		1.5 (1.3)		1.4 (1.8)			60.4 (55.3)	3.4 (3.1)		
13 Large crabs										
14 Lobster										
15 Small-medium demersal			0.6 (0.4)	18.7 (18.6)	4.9 (4.3)		16.4 (14.9)			3.6 (2.5)
16 Small gadoids		2.4 (4.6)	5.4 (7.7)		3.4 (6.2)		4.4 (8.3)	0.1		1.0 (0.7)
17 Red mullet							1.1 (1)			
18 Juvenile sole							0.01 (0.2)			
19 Adult sole										0.3 (0.2)
20 Juvenile plaice					2.1 (1.9)		0.02 (0.2)			
21 Adult plaice										5.4 (3.7)
22 Dab		0.002 (0.005)			0.7 (1.9)					0.1
23 Lemon sole										2.9 (5.2)
24 Large flatfish										7.6 (5.2)
25 Gurnards			0.6 (0.4)		3.5 (3.1)					
26 Juvenile whiting		0.001 (0.01)	0.05 (14.6)						0.6 (5.7)	1.3 (12.6)
27 Adult whiting										
28 Juvenile cod		0.003 (0.03)	0.02 (2.5)					1.0	0.6 (5.7)	0.8 (7.5)
29 Adult cod										
30 Hake			0.1 (1.2)							
31 Dogfish					1.1 (1.0)					
32 Rays										
33 Other gadoids		0.0002 (0.02)	0.5 (5.5)						0.9 (5.7)	4.2 (11.5)
34 Anglerfish										20.7 (14.2)
35 Large bottom										20.7 (14.2)
36 Seabreams							0.3		7.3 (5.7)	
37 John Dory										
38 Sandeels		17.7 (19.9)	14.4 (6.4)				8.1 (7.3)	38.2 (35.2)		19.1 (13.1)
39 Herring		0.1 (2.5)	0.3 (5.3)		0.3 (6.1)		0.1 (4)	0.1 (1.7)	0.3 (7)	0.045 (0.9)
40 Sprat		1.0 (2)	2.5 (1.8)		3.0 (2.6)			9.1 (13.8)	9.0 (7)	
41 Pilchard			2.5 (1.8)					1.8 (1.7)	9.0 (7)	
42 Mackerel		0.1			12.5 (11.1)		0.4	11.4 (10.6)	9.0 (7)	4.4 (3)
43 Scad					6.9 (6.2)		0.6 (0.5)		9.0 (7)	1.9 (1.3)
44 Bass										
45 Sharks					1.1					
46 Basking shark										
47 Cephalopods		1.2 (1.1)	0.4 (0.3)		55.9 (49.6)		2.7 (2.5)		54.2 (42.2)	6.1 (4.2)
48 Birds					0.1					
49 Toothed cetaceans						1.4 (1.3)				
50 Seals					0.3 (1.3)					
51 Discarded catch					1.5 (1.4)			23.1		
52 Detritus										
53 Import						70.0		6.2		
54 Sum	100	100	100	100	100	100	100	100	100	100

Table 5. Fisheries landings (t km^{-2}) in the 1994 model

Group/Fleet	Otter trawl	Beam trawl	Pelagic trawl	Dredge	Net	Pot	Lining	Seaweed	Recreational	Total
1 Primary producers	4.76E-03							1.03E+00		1.03E+00
7 Shrimp and Prawns	3.36E-04					1.10E-03				1.43E-03
8 Whelks						1.69E-01				1.69E-01
10 Bivalves				1.05E-01						1.05E-01
11 Scallops	1.11E-02	2.02E-03		3.00E-01						3.13E-01
12 Small-medium crabs	1.20E-05	2.00E-05		9.09E-04	6.80E-05	7.21E-03				8.22E-03
13 Large crabs	4.17E-03	2.01E-04		8.94E-04	9.95E-03	1.86E-01				2.01E-01
14 Lobster						4.09E-03				4.09E-03
16 Small gadoids	3.53E-02	3.21E-03	8.01E-04		8.01E-04					4.01E-02
17 Red mullet	4.68E-03	4.84E-04	3.50E-05		1.39E-04					5.33E-03
18 Juvenile sole	5.32E-04	1.01E-03		1.34E-04	9.30E-05					1.77E-03
19 Adult sole	3.37E-03	6.42E-03		8.49E-04	5.86E-04					1.12E-02
20 Juvenile plaice	2.20E-03	3.12E-03		1.27E-04	6.20E-05					5.51E-03
21 Adult plaice	6.32E-03	8.95E-03		3.65E-04	1.78E-04					1.58E-02
22 Dab	1.23E-03	5.17E-04								1.74E-03
23 Lemon sole	1.41E-02	2.69E-03	1.30E-05	1.38E-04	2.30E-05	1.00E-06	1.00E-06			1.70E-02
24 Large flatfish	7.24E-03	6.97E-03	1.30E-05	2.37E-04	5.70E-04	3.00E-05	1.30E-05			1.51E-02
25 Gurnards	5.71E-02	2.08E-03	2.08E-03							6.13E-02
26 Juvenile whiting	5.63E-04		5.10E-05							6.14E-04
27 Adult whiting	3.43E-02	1.38E-03	2.07E-04	1.20E-05	6.34E-04	3.00E-06	1.93E-04			3.67E-02
28 Juvenile cod	5.11E-03									5.11E-03
29 Adult cod	5.18E-03	2.73E-04	2.73E-04		3.55E-03					9.27E-03
30 Hake	3.86E-03				3.86E-03					7.72E-03
31 Dogfish	3.07E-02	9.00E-05	4.90E-04	1.10E-04	2.57E-03	8.20E-05	5.05E-03			3.90E-02
32 Rays	3.03E-02	2.65E-03	2.34E-04	2.03E-04	4.00E-03	1.25E-04	1.21E-03			3.87E-02
33 Other Gadoids	1.71E-02				1.40E-02		1.55E-03			3.26E-02
34 Anglerfish	2.00E-02	6.07E-03		8.25E-04	7.45E-03					3.43E-02
35 Large bottom	1.31E-02	1.42E-03			8.75E-03		1.16E-02			3.49E-02
36 Seabreams	1.60E-02		6.60E-03							2.26E-02
37 John Dory	5.81E-03	3.90E-04			5.20E-05					6.25E-03
39 Herring	4.80E-04		9.12E-03							9.60E-03
40 Sprat			3.77E-02							3.77E-02
41 Pilchard	9.49E-04		9.53E-02							9.63E-02
42 Mackerel	3.68E-03		2.94E-01				1.69E-02			3.15E-01
43 Scad	1.36E-02		1.43E-01							1.57E-01
44 Bass	2.99E-03		7.48E-04		1.50E-03		2.99E-03		3.74E-03	1.20E-02
45 Sharks									1.20E-04	1.20E-04
47 Cephalopods	1.43E-01	2.37E-02	6.35E-04	1.19E-03	3.37E-04	4.57E-03	3.13E-04			1.74E-01
Sum	4.99E-01	7.36E-02	5.92E-01	4.11E-01	5.91E-02	3.72E-01	3.99E-02	1.03E+00	3.86E-03	3.08E+00

Table 6. Discards (t km^{-2}) in the1994 model

Group/Fleet		Otter trawl	Beam trawl	Pelagic trawl	Dredge	Net	Total
8	Whelks		1.48E-02				1.48E-02
12	Small-medium crabs		1.10E-02				1.10E-02
13	Large crab	5.24E-04	1.76E-03		9.42E-04		3.22E-03
14	Lobster						
15	Small-medium demersal		4.23E-02				4.23E-02
16	Small gadoids	3.69E-02	4.81E-03				4.17E-02
17	Red mullet	4.45E-04					4.45E-04
18	Juvenile sole				2.17E-04	2.17E-04	4.34E-04
20	Juvenile plaice	2.88E-03	2.88E-04		5.76E-04		3.75E-03
22	Dab	2.69E-03	4.75E-04			7.92E-04	3.96E-03
23	Lemon sole	1.13E-03	5.10E-03				6.24E-03
24	Large flatfish	1.01E-03	4.52E-03				5.53E-03
25	Gurnards	5.09E-02	1.04E-03				5.19E-02
26	Juvenile whiting	7.16E-04	1.02E-04				8.18E-04
28	Juvenile cod	4.11E-04					4.11E-04
30	Hake	2.21E-04					2.21E-04
32	Rays	6.19E-03	5.16E-04		5.16E-04		7.22E-03
33	Other gadoids	2.79E-02					2.79E-02
34	Anglerfish				2.14E-03	7.12E-04	2.85E-03
35	Large bottom					2.91E-03	2.91E-03
36	Seabreams	1.70E-02		9.43E-04			1.79E-02
39	Herring			6.00E-04			6.00E-04
40	Sprat			4.71E-03			4.71E-03
41	Pilchard			4.63E-03			4.63E-03
42	Mackerel	1.18E-02		2.04E-02			3.23E-02
43	Scad	8.63E-03		3.70E-03			1.23E-02
44	Bass	7.50E-05					7.50E-05
47	Cephalopods	1.06E-03					1.06E-03
49	Toothed cetaceans		2.00E-04			2.00E-04	
	Sum	1.70E-01	8.67E-02	3.52E-02	4.39E-03	4.63E-03	3.01E-01

4.3. Balancing the 1973 model

The balanced 1994 model was used as a base upon which to build the 1973 model by changing the parameters as described in the section 3.2. It was balanced following the same approach used to balance the 1994 model using the automatic mass balance tool. First the auto-balance routine was run allowing a maximum of 50% of change in the diet matrix parameters. After this run, the small demersal and sprat were still unbalanced. To resolve this, it was necessary to increase their biomass by approximately 50%. There is not data that can be used to help validate these changes. The parameter estimates are presented in the Tables 7 to 10.

Table 7. Basic parameters for the 1973 model. Those estimated by Ecopath (outputs) are underlined. Functional groups with inputs changed are in bold, with the original value in brackets. The EE of groups in the unbalanced model are presented in brackets

Group name	TL	Biomass (t km^{-2})	P/ B (/year)	Q/B (/year)	EE	P/Q
1 Primary producers	1	118.9	24.8	-	0.26	-
2 Microzooplankton	2.06	2.629	45.28	120.00	0.63	0.38
3 Mesozooplankton	2.16	5.871	39.08	80.00	0.51	0.49
4 Marozooplankton	3.16	1.100	18.00	38.00	0.04	0.47
5 Deposit feeders	2	13.642	3.00	20.00	0.69	0.15
6 Suspension feeders	2.61	5.070	0.30	2.00	0.27	0.15
7 Shrimps and Prawns	2.43	4.885	3.96	13.20	0.90	0.30
8 Whelks	3.05	0.548	0.64	8.03	0.06	0.08
9 Echinoderms	2.23	8.826	0.66	6.94	0.76	0.10
10 Bivalves	2	17.410	0.89	9.87	0.79	0.09
11 Scallops	2	0.783	0.80	8.89	0.60	0.09
12 Small-medium crabs	2.3	5.157	1.95	12.98	0.76	0.15
13 Large crabs	2.44	0.766	0.60	4.00	0.36	0.15
14 Lobster	3.1	0.015	0.52	5.85	0.48	0.09
15 Small-medium demersal	3.09	**1.02 (0.692)**	1.57	9.66	0.90 (1.94)	0.16
16 Small gadoids	3.36	0.78	1.27	5.93	0.92 (1.29)	0.22
17 Red mullet	3.22	0.077	0.52	5.70	0.90 (1.29)	0.09
18 Juvenile sole	3.01	0.017	0.75	10.06	0.34	0.08
19 Adult sole	3.01	0.049	0.43	5.18	0.33	0.08
20 Juvenile plaice	3	0.016	1.51	11.82	0.49	0.13
21 Adult plaice	3	0.021	0.76	4.18	0.66	0.18
22 Dab	3.19	0.047	0.75	6.00	0.66	0.13
23 Lemon sole	3.14	0.038	0.60	5.32	0.90 (1.11)	0.11
24 Large flatfish	3.83	0.132	0.37	4.96	0.22	0.08
25 Gurnards	3.34	0.400	0.57	5.76	0.68	0.10
26 Juvenile whiting	3.29	0.016	1.60	14.89	0.90 (1.58)	0.11
27 Adult whiting	4.05	0.055	0.79	5.63	0.51	0.14
28 Juvenile cod	3.45	0.007	1.62	8.67	0.90 (1.18)	0.19
29 Adult cod	3.92	0.017	0.81	3.46	0.59	0.23
30 Hake	4.4	0.045	0.53	3.87	0.59	0.14
31 Dogfish	3.36	0.277	0.38	4.77	0.02	0.08
32 Rays	3.4	0.239	0.60	4.23	0.31	0.14
33 Other gadoids	3.76	0.223	0.83	4.05	0.76	0.20
34 Anglerfish	4.16	0.128	0.23	2.83	0.63	0.08
35 Large bottom	3.95	0.274	0.25	3.06	0.45	0.08
36 Seabreams	3.01	0.177	0.61	4.61	0.70	0.13
37 John Dory	4.21	0.011	0.65	4.99	0.06	0.13
38 Sandeels	3.13	2.786	1.29	10.14	0.90	0.13
39 Herring	3.1	0.052	1.00	6.35	0.90 (1.20)	0.16
40 Sprat	3.13	**0.292 (0.195)**	1.21	9.68	0.90 (2.56)	0.13
41 Pilchard	3.12	0.406	0.64	7.92	0.95 (1.45)	0.08
42 Mackerel	3.4	1.636	0.36	6.00	0.40	0.06
43 Scad	3.54	0.62	0.39	5.56	0.90 (1.07)	0.07
44 Bass	3.39	0.083	0.42	3.91	0.01	0.11
45 Sharks	4.36	0.004	0.24	2.53	0.36	0.09
46 Basking shark	3.16	0.034	0.07	3.70	0.00	0.02
47 Cephalopods	3.43	0.326	2.19	15.00	0.90 (1.05)	0.15
48 Birds	3.51	0.001	0.40	72.12	0.03	0.01
49 Toothed cetaceans	4.36	0.006	0.40	13.73	0.12	0.03
50 Seals	4.63	0.003	0.04	13.32	0.27	0.003
51 Discarded catch	1	0.185	-	-	0.10	-
52 Detritus	1	1	-	-	0.20	-

Table 8. Diet matrix for the 1973 model (unbalanced model values in brackets)

Prey\Predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Primary producers	94.7	78.3			10.0	8.5		5.1	50.0	50.0			8.6	0.002
2 Microzooplankton	5.3	9.8			15.0	12.5								0.01
3 Mesozooplankton		4.9	100.0		30.0	23.5								0.01
4 Marozooplankton														0.03
5 Deposit feeders					10.0	3.0	73.5	11.2					12.0 (11.9)	59.5 (59.1)
6 Suspension feeders								0.5					3.3	0.04
7 Shrimps and Prawns							5.6				14.2	15.2	0.3	11.6 (11.5)
8 Whelks													0.4	
9 Echinoderms							5.6	4.8					3.4	11.5 (11.5)
10 Bivalves							11.2	5.1			8.5	20.3	24.8 (24.7)	14.2 (14.1)
11 Scallops														
12 Small-medium crabs							4.1				0.7	1.2	45.7 (45.5)	2.4
13 Large crab														
14 Lobster													1.1	
15 Small-medium demersal													0.4 (0.9)	0.7 (1.4)
16 Small gadoids														
17 Red mullet														
18 Juvenile sole														
19 Adult sole														
20 Juvenile plaice														
21 Adult plaice														
22 Dab														
23 Lemon sole														
24 Large Flatfish														
25 Gurnards														
26 Juvenile whiting														
27 Adult whiting														
28 Juvenile cod														
29 Adult cod														
30 Hake														
31 Dogfish														
32 Rays														
33 Other gadoids														
34 Anglerfish														
35 Large bottom														
36 Seabreams														
37 John Dory														
38 Sandeels														
39 Herring														
40 Sprat														
41 Pilchard														
42 Mackerel														
43 Scad														
44 Bass														
45 Sharks														
46 Basking shark														
47 Cephalopods														
48 Birds														
49 Toothed cetaceans														
50 Seals														
51 Discarded catch														
52 Detritus		7.0		100.0	35.0	52.5		73.3	50.0	50.0	76.6	63.2		
53 Import														
54 Sum	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Table 8. continued

Prey\Predator	16	17	18	19	20	21	22	23	24	25
1 Primary producers										
2 Microzooplankton	2.9 (2.8)							0.9	0.02	
3 Mesozooplankton	3.2 (3.1)							1.9 (1.5)	0.02	
4 Marozooplankton										
5 Deposit feeders	7.1 (6.8)	52.9 (48.4)	84.6	84.5	48.4	48.4	65.8	68.5 (68)	6.0 (5.7)	25.6 (24.4)
6 Suspension feeders			1.0	1.0			19.7	3.8	0.02	
7 Shrimps and Prawns	50.5 (48.9)	17.2 (15.7)			0.5	0.5	3.4		18.9 (18.2)	46.4 (44.1)
8 Whelks										
9 Echinoderms	0.03	1.9 (1.7)			0.5	0.5	0.02	2.6 (2.5)		
10 Bivalves	8.9 (8.6)	1.4 (1.3)	12.7	12.7	50.6	50.6	6.4	13.3 (13.2)	0.1	0.4 (0.3)
11 Scallops										
12 Small-medium crabs	22.2 (21.5)	18.8 (17.2)	1.8	1.8			1.3		8.7 (8.3)	22.6 (21.5)
13 Large crabs										
14 Lobster										
15 Small-medium demersals	2.8 (5.6)	7.8 (15.7)							62.0 (59.5)	1.1 (2.3)
16 Small gadoids	0.2 (0.3)									
17 Red mullet										
18 Juvenile sole										
19 Adult sole										
20 Juvenile plaice										
21 Adult plaice										
22 Dab										
23 Lemon sole										
24 Large flatfish										
25 Gurnards										
26 Juvenile whiting	0.1									0.1 (0.3)
27 WAdult whiting										
28 Juvenile cod										0.1 (0.2)
29 Adult cod										
30 Hake										
31 Dogfish										
32 Rays										
33 Other gadoids										
34 Anglerfish										
35 Large bottom										
36 Seabreams										
37 John Dory										
38 Sandeels	0.1							8.5 (8.4)		
39 Herring								0.05	0.4 (0.3)	
40 Sprat	0.2 (0.4)							0.3 (0.6)	3.8 (7.6)	
41 Pilchard								0.5 (0.9)	0.1 (0.2)	
42 Mackerel										
43 Scad										
44 Bass										
45 Sharks										
46 Basking shark										
47 Cephalopods	1.9						3.4			3.7 (7)
48 Birds										
49 Toothed cetaceans										
50 Seals										
51 Discarded catch										
52 Detritus										
53 Import										
54 Sum	100	100	100	100	100	100	100	100	100	100

Table 8. continued

Prey\Predator	26	27	28	29	30	31	32	33	34
1 Primary producers								0.1	
2 Microzooplankton		5.4 (4.8)	0.01						
3 Mesozooplankton		6.2 (5.5)	0.02	3.0 (2.8)			3.6 (3.4)	17.0 (15.5)	
4 Marozooplankton		0.2							
5 Deposit feeders	30.9	3.6 (3.2)	9.4 (8.4)	5.7 (5.3)	0.01	25.9 (24.4)	13.6 (12.8)	8.5 (7.8)	
6 Suspension feeders		0.3	0.1	0.1		1.4		0.1	
7 Shrimps and Prawns	64.4	2.3 (2)	52.2 (46.9)	0.4	0.4 (0.3)	6.2 (5.9)	28.0 (26.3)	3.5 (3.2)	
8 Whelks			0.1			1.4			
9 Echinoderms		0.1	0.03	0.3		2.1 (2)	0.2	6.0 (5.5)	
10 Bivalves		0.02	1.5 (1.3)	0.1		1.6 (1.5)	0.2	1.5 (1.3)	
11 Scallops									
12 Small-medium crabs	4.7	3.3 (2.9)	23.3 (21)	24.5 (22.9)		48.9 (46.1)	39.1 (36.8)	3.2 (2.9)	16.2 (16)
13 Large crabs						0.1	3.6 (3.4)		
14 Lobster									
15 Small-medium demersals			9.0 (18)	21.8 (20.4)	0.4 (0.3)	2.0 (4)	5.5 (11)		10.1 (10)
16 Small gadoids		30.9 (27.3)	0.2 (0.4)	9.4 (8.8)	38.1 (28)	2.0 (4.1)	0.1 (0.2)	6.8 (13.6)	66.7 (65.8)
17 Red mullet									
18 Juvenile sole		0.01		0.3		0.2 (0.1)			
19 Adult sole									
20 Juvenile plaice				4.6 (4.3)		0.2			
21 Adult plaice									
22 Dab		0.02	0.5 (0.4)	3.7 (3.5)		0.4	0.1	0.05	0.7
23 Lemon sole				0.2					0.9 (1.4)
24 Large flatfish					0.7 (0.5)				
25 Gurnards					1.1 (0.8)				
26 Juvenile whiting		0.7 (1.4)	0.1	3.7 (7.4)	0.6 (0.4)	0.2 (0.4)	0.004	0.001	0.8 (1.6)
27 Adult whiting				1.8 (1.7)					
28 Juvenile cod		0.1	0.01	2.2 (4.4)				0.01	0.2
29 Adult cod									
30 Hake					0.2 (0.1)				
31 Dogfish									
32 Rays							0.01		
33 Other gadoids		7.4 (6.5)		6.9 (6.5)	6.2 (4.6)	0.4	0.1	0.3	
34 Anglerfish									
35 Large bottom									
36 Seabreams									
37 John Dory									
38 Sandeels		26.7 (23.5)	3.1 (2.8)	4.9 (4.6)		1.1 (1)	1.6 (1.5)	50.3 (45.9)	
39 Herring		0.7 (0.6)		0.2	0.2	0.3 (0.4)	0.002	0.4 (0.3)	0.6
40 Sprat		9.8 (19.7)	0.03 (0.1)	1.5 (1.4)	3.0 (6.1)	0.6 (1.1)	0.01 (0.02)	1.3 (2.5)	
41 Pilchard					5.4 (10.8)	0.6 (1.1)	0.02 (0.04)		
42 Mackerel		0.1		2.2 (2.1)	30.9 (22.8)		1.8 (1.7)		2.2 (2.1)
43 Scad					12.4 (24.9)				
44 Bass									
45 Sharks									
46 Basking shark									
47 Cephalopods		2.1 (1.9)	0.5 (0.4)	2.5 (2.4)	0.4 (0.3)	4.3 (4.1)	2.4 (2.2)	0.9 (0.8)	1.7
48 Birds									
49 Toothed cetaceans									
50 Seals									
51 Discarded catch									
52 Detritus									
53 Import									
54 Sum	100	100	100	100	100	100	100	100	100

Table 8. continued

Prey\Predator	35	36	37	38	39	40	41	42	43	44
1 Primary producers										
2 Microzooplankton					60.0	39.5	40.0	3.9 (3.8)	1.9 (1.8)	
3 Mesozooplankton				80.5	40.0	59.2	60.0	68.2 (65.2)	18.5 (17.4)	
4 Marozooplankton						1.3		5.2 (5.0)	5.1 (4.8)	
5 Deposit feeders		98.4		19.5				0.9	10.4 (9.8)	23.1 (20.7)
6 Suspension feeders			0.05 (0.03)							
7 Shrimps and Prawns	10.1 (7.4)	0.9	1.4 (1)					1.2 (1.1)	41.4 (38.9)	65.6 (58.9)
8 Whelks										
9 Echinoderms			0.02 (0.01)							
10 Bivalves		0.3								0.3
11 Scallops										0.04
12 Small-medium crabs	20.3 (14.9)	0.3						1.5		1.6 (1.4)
13 Large crabs										
14 Lobster										
15 Small-medium demersal	16.2 (11.9)		53.5 (36.1)						0.3 (0.6)	9.3 (18.7)
16 Small gadoids	7.1 (5.2)							1.2 (2.4)	2.7 (5.4)	
17 Red mullet										
18 Juvenile sole										
19 Adult sole										
20 Juvenile plaice										
21 Adult plaice										
22 Dab								0.002		
23 Lemon sole	0.3 (0.7)									
24 Large flatfish			0.7 (0.5)							
25 Gurnards									0.6	
26 Juvenile whiting	0.1 (0.2)							0.001	0.04 (0.1)	
27 Adult whiting										
28 Juvenile cod	0.1							0.003	0.02	
29 Adult cod										
30 Hake									0.1	
31 Dogfish										
32 Rays										
33 Other gadoids	6.3 (4.6)		2.9 (2)					0.0002	0.6 (0.5)	
34 Anglerfish										
35 Large bottom			4.6 (3.1)							
36 Seabreams										
37 John Dory										
38 Sandeels	4.7 (3.4)		0.7 (0.5)					16.1 (17.7)	15.3 (14.4)	
39 Herring	0.5 (0.8)							0.1	0.1 (0.3)	
40 Sprat	12.1 (23.6)							0.5 (1)	1.3 (2.5)	
41 Pilchard	17.4 (23.6)		23.0 (40.7)						1.3 (2.5)	
42 Mackerel								0.1		
43 Scad			12.6 (15.8)							
44 Bass										
45 Sharks										
46 Basking shark										
47 Cephalopods	4.9 (3.6)		0.5 (0.3)					1.0 (1.2)	0.4	
48 Birds										
49 Toothed cetaceans										
50 Seals										
51 Discarded catch										
52 Detritus										
53 Import										
54 Sum	100	100	100	100	100	100	100	100	100	100

Table 8. continued

	Prey\Predator	45	46	47	48	49	50
1	Primary producers			6.1 (5.3)			
2	Microzooplankton						
3	Mesozooplankton		30.0		2.5 (2.4)		
4	Marozooplankton						
5	Deposit feeders	1.0		0.4 (0.3)	3.6 (3.4)		
6	Suspension feeders						
7	Shrimps and Prawns						
8	Whelks						
9	Echinoderms	0.2					
10	Bivalves					0.2 (0.1)	
11	Scallops						
12	Small-medium crabs			69.6 (60.4)	3.6 (3.4)		
13	Large crabs						
14	Lobster						
15	Small-medium demersal	5.1 (4.9)		8.5 (16.4)			3.7 (3.6)
16	Small gadoids	3.6 (3.4)		2.2 (4.4)	0.1		1.0
17	Red mullet			0.7 (1.1)			
18	Juvenile sole			0.01			
19	Adult sole						0.3
20	Juvenile plaice	2.2 (2.1)		0.02			
21	Adult plaice						5.4
22	Dab	0.7					0.1
23	Lemon sole						2.9
24	Large flatfish						7.6
25	Gurnards	3.7 (3.5)					
26	Juvenile whiting					0.7 (0.6)	1.3
27	Adult whiting						
28	Juvenile cod				1.1 (1)	0.7 (0.6)	0.8
29	Adult cod						
30	Hake						
31	Dogfish	1.2 (1.1)					
32	Rays						
33	Other gadoids					1.1 (0.9)	4.2
34	Anglerfish						20.9 (20.7)
35	Large bottom						20.9 (20.7)
36	Seabreams			0.3		8.7 (7.3)	
37	John Dory						
38	Sandeels			9.3 (8.1)	40.7 (38.2)		19.3 (19.1)
39	Herring	0.3		0.1	0.1	0.4 (0.3)	0.05
40	Sprat	1.5 (3)			4.5 (9.1)	4.5 (9)	
41	Pilchard				0.9 (1.8)	4.5 (9)	
42	Mackerel	13.2 (12.5)		0.5 (0.4)	12.2 (11.4)	10.6 (9)	4.4
43	Scad	3.5 (6.9)		0.3 (0.6)		4.5 (9)	0.9 (1.9)
44	Bass						
45	Sharks	1.2 (1.1)					
46	Basking shark						
47	Cephalopods	59.0 (55.9)		2.0 (2.7)		64.2 (54.2)	6.2 (6.1)
48	Birds	0.1					
49	Toothed cetaceans	1.5 (1.4)					
50	Seals	0.3					
51	Discarded catch	1.6 (1.5)			24.6 (23.1)		
52	Detritus						
53	Import		70.0		6.2		
54	Sum	100	100	100	100	100	100

Table 9. Fisheries landings (t km^{-2}) for the 1973 model

Group/Fleet	Otter trawl	Beam trawl	Pelagic trawl	Dredge	Net	Pot	Lining	Seaweed	Recreational	Total
1 Primary producers	5.00E-08							1.00E-05		1.00E-05
7 Shrimps and Prawns	5.89E-03					1.92E-02				2.51E-02
8 Whelks						2.25E-04				2.30E-04
10 Bivalves				2.17E-01						2.17E-01
11 Scallops	1.33E-02	2.41E-03		3.58E-01						3.74E-01
13 Large crabs	2.61E-03	1.26E-04		5.59E-04	6.22E-03	1.16E-01				1.26E-01
14 Lobster						2.81E-03				2.81E-03
16 Small gadoids	1.41E-02	1.28E-03	3.20E-04		3.20E-04					1.60E-02
17 Red mullet	7.98E-05	8.26E-06	6.00E-07		2.37E-06					9.00E-05
18 Juvenile sole	4.02E-04	7.66E-04		1.01E-04	7.02E-05					1.34E-03
19 Adult sole	2.04E-03	3.89E-03		5.15E-04	3.56E-04					6.80E-03
20 Juvenile plaice	1.12E-03	1.58E-03		6.45E-05	3.15E-05					2.80E-03
21 Adult plaice	3.32E-03	4.70E-03		1.92E-04	9.35E-05					8.31E-03
22 Dab	2.30E-03	9.70E-04								3.27E-03
23 Lemon sole	8.07E-03	1.53E-03	7.41E-06	7.87E-05	1.31E-05	5.70E-07	5.70E-07			9.70E-03
24 Large flatfish	2.10E-03	2.02E-03	3.77E-06	6.87E-05	1.65E-04	8.70E-06	3.77E-06			4.37E-03
25 Gurnards	6.77E-02	2.46E-03	2.46E-03							7.26E-02
26 Juvenile whiting	1.17E-03		1.06E-04							1.28E-03
27 Adult whiting	1.97E-02	7.91E-04	1.19E-04	6.91E-06	3.65E-04	1.73E-06	1.11E-04			2.11E-02
28 Juvenile cod	2.25E-03									2.25E-03
29 Adult cod	4.56E-03	2.40E-04	2.40E-04		3.12E-03					8.16E-03
30 Hake	4.78E-03				4.78E-03					9.56E-03
31 Dogfish	1.50E-03	4.39E-06	2.39E-05	5.37E-06	1.25E-04	4.00E-06	2.46E-04			1.91E-03
32 Rays	2.93E-02	2.57E-03	2.27E-04	1.97E-04	3.87E-03	1.21E-04	1.17E-03			3.75E-02
33 Other gadoids	4.75E-03				3.89E-03		4.32E-04			9.07E-03
34 Anglerfish	5.61E-03	1.70E-03		2.32E-04	2.09E-03					9.63E-03
35 Large bottom	7.04E-03	7.60E-04			4.69E-03		6.24E-03			1.87E-02
36 Seabreams	2.09E-02		8.59E-03							2.95E-02
37 John Dory	3.80E-04	2.55E-05			3.40E-06					4.10E-04
39 Herring	6.36E-04		1.21E-02							1.27E-02
40 Sprat			2.28E-02							2.28E-02
41 Pilchard	2.18E-04		2.19E-02							2.21E-02
42 Mackerel	1.01E-03		8.12E-02				4.66E-03			8.69E-02
43 Scad	1.39E-02		1.47E-01							1.61E-01
44 Bass	8.75E-05		2.19E-05		4.37E-05		8.75E-05		1.09E-04	3.50E-04
45 Sharks									2.40E-04	2.40E-04
47 Cephalopods	3.81E-02	6.32E-03	1.70E-04	3.16E-04	9.00E-05	1.22E-03	8.36E-05			4.63E-02
Sum	2.79E-01	3.40E-02	2.97E-01	5.77E-01	3.00E-02	1.40E-01	1.30E-02	1.00E-05	3.00E-04	1.37E+00

Table 10. Discards (t km^{-2}) for the 1973 model

Group/Fleet	Otter trawl	Beam trawl	Pelagic trawl	Dredge	Net	Total
8 Whelks		2.00E-05				2.00E-05
13 Large crabs	3.27E-04	1.10E-03		5.88E-04		2.02E-03
15 Small-medium demersal		2.20E-02				2.20E-02
16 Small gadoids	1.47E-02	1.92E-03				1.66E-02
17 Red mullet	8.00E-06					1.00E-05
18 Juvenile sole				1.50E-04	1.50E-04	3.00E-04
20 Juvenile plaice	1.46E-03	1.46E-04		2.93E-04		1.90E-03
22 Dab	5.05E-03	8.91E-04			1.49E-03	7.43E-03
23 Lemon sole	6.47E-04	2.91E-03				3.56E-03
24 Large flatfish	2.91E-04	1.31E-03				1.60E-03
25 Gurnards	6.03E-02	1.23E-03				6.15E-02
26 Juvenile whiting	4.30E-04	6.00E-05				4.90E-04
28 Juvenile cod	2.98E-04					3.00E-04
30 Hake	4.46E-04					4.50E-04
32 Rays	5.99E-03	5.00E-04		5.00E-04		6.99E-03
33 Other gadoids	7.78E-03					7.78E-03
34 Anglerfish				6.02E-04	2.01E-04	8.00E-04
35 Large bottom					1.56E-03	1.56E-03
36 Seabreams	2.21E-02		1.23E-03			2.33E-02
39 Herring			7.95E-04			8.00E-04
40 Sprat			2.85E-03			2.85E-03
41 Pilchard			1.07E-03			1.07E-03
42 Mackerel	3.26E-03		5.63E-03			8.89E-03
43 Scad	8.87E-03		3.80E-03			1.27E-02
44 Bass	2.00E-06					2.00E-06
47 Cephalopods	2.41E-04					2.40E-04
49 Toothed cetaceans			1.07E-04			1.10E-04
Sum	1.32E-01	3.20E-02	1.50E-02	2.00E-03	3.00E-03	1.84E-01

5. COMPARISON OF ECOSYSTEM PROPERTIES

The EwE program estimates several parameters or system statistics that describe the ecosystem and allow the user to make comparisons with other similar systems or the same system in different periods. A selection of these estimated parameters for the two models of the Western Channel ecosystem are presented in the Table 11 and some of them are used to describe the degree of ecosystem maturity and stability (*sensu* Odum, 1969). Most of these parameters are very similar in both years modelled, partly because the same basic inputs for some groups and the input diet composition for the 1973 model were the same as those of the 1994 balanced model. Table 11 also shows estimates of some of these parameters for the Northern Benguela (Heymans *et al*., 2004) and Barents Sea (Blanchard *et al*., 2002) ecosystems for comparative analyses.

There was a small decrease in the trophic level of total catches between 1973 to 1994 because the large increase in landings for seaweeds. However, when seaweeds are not taken into account the mean trophic level has actually increased. Taking only fish into account, the mean trophic level of catches has remained the same. Although the abundance of some high trophic level fish groups, such as hake, sharks and large bottom species, have decreased, others like anglerfish and cod have increased over the period (Figure 2) and the total fish biomass has increased.

Table 11. System statistics for the Western Channel (this study), Northern Benguela (Heymans et al., 2004) and Barents Sea (Blanchard et al., 2002) ecosystems

Parameter/Ecosystem	Western Channel		Northern Benguela			Barents Sea	Units
	1994	1973	1970s	1980s	1990s	1995	
Sum of all consumption	1590	1550	3214	11743	4477	2401	t km^{-2} year^{-1}
Sum of all exports	2153	2172	6124	1021	4452	37	t km^{-2} year^{-1}
Sum of all respiratory flows	796	777	1550	6070	1731	1063	t km^{-2} year^{-1}
Sum of all flows into detritus	2683	2693	6555	3973	5591	1701	t km^{-2} year^{-1}
Total system throughput	7223	7192	17443	22806	16251	5201	t km^{-2} year^{-1}
Sum of all production	3424	3413	8264	9808	7379	1920	t km^{-2} year^{-1}
Mean trophic level of the catch	2.44	2.78	2.85	3.25	3.1	4.11	
Mean trophic level of the catch (exc. pp.)	3.08	2.78					
Mean trophic level of the fish catch	3.48	3.43					
Mean fish trophic level	3.31	3.32					
Calculated total net primary production	2949	2949	7675	7091	6183	1100	t km^{-2} year^{-1}
Total primary production/total respiration	3.7	3.8	4.95	1.17	3.57	1.04	
Net system production	2153	2163	6124	1021	4452		t km^{-2} year^{-1}
Total primary production/total biomass	14.9	15.1	27	20	16	9.3	
Total biomass/total throughput	0.027	0.027	0.016	0.016	0.023	0.023	
Total biomass (excluding detritus)	197.8	195.9	282	361	381	118.8	t km^{-2}
Total fish biomass	11.27	9.68	33.5	47.2	23.5		t km^{-2}
Total catches	3.378	1.556	6.555	6.652	3.441	0.305	t km^{-2} year^{-1}
Primary production required for catches	12.7	7.9	4.98	5.94	4.28		%
Connectance Index	0.17	0.170	0.258	0.285	0.301		
System Omnivory Index	0.135	0.126	0.152	0.172	0.117	0.228	
Ascendency	36.9	37.1	41.7	24.1	31.7		% of capacity
Overhead	63.0	62.9	58.3	75.9	68.3		% of capacity
Throughput cycled (excluding detritus)	43.5	43.3	274	1766	567		t km^{-2} year^{-1}
Predatory cycling index	2.4	2.4	6.32	12.12	11.19		% of throughput w/o detritus
Throughput cycled (including detritus)	207	212	56	33	37		t km^{-2} year^{-1}
Finn's cycling index	2.9	3.0	2.8	23.0	9.5	13.6	% of total throughput
Finn's mean path length	2.4	2.4	2.3	3.3	2.6	4.7	-
Finn's straight-through path length	2.3	2.3	2.6	2.1	2.6		without detritus
Finn's straight-through path length	2.4	2.4	2.2	2.5	2.4		with detritus

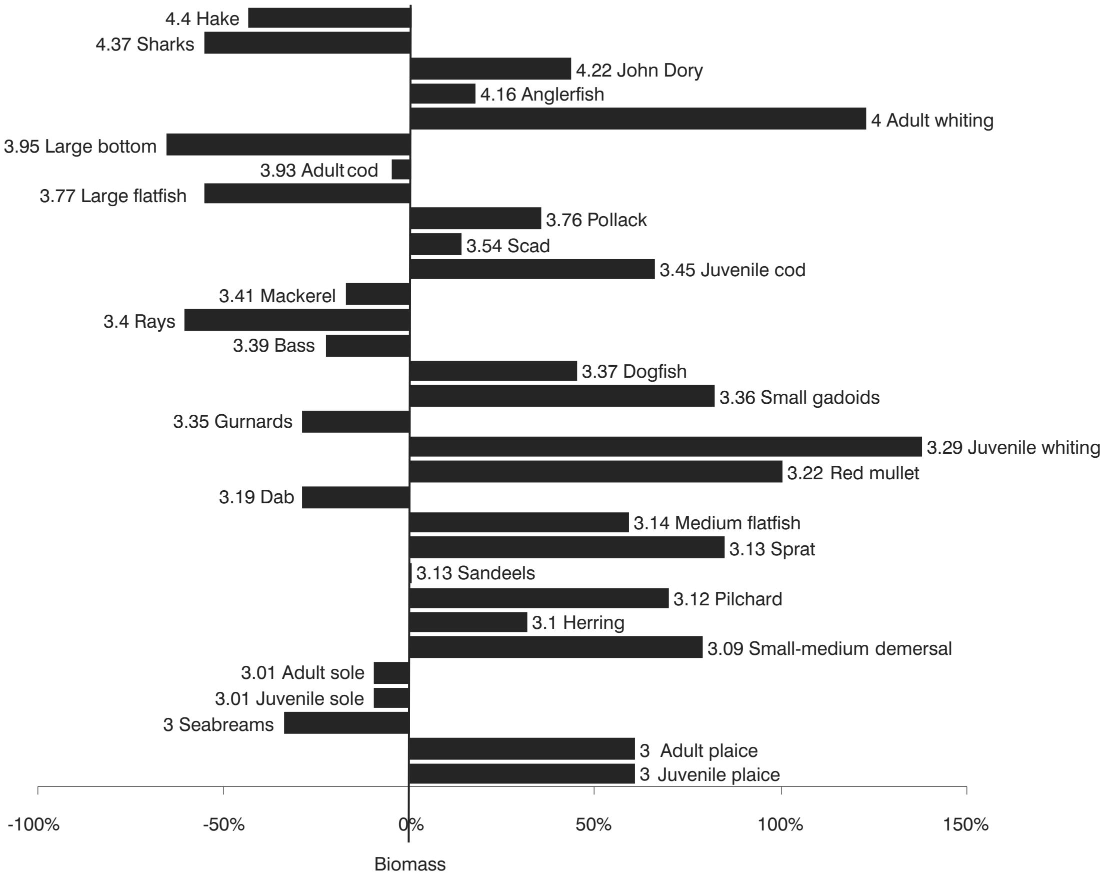


Figure 2. Biomass differences between the 1994 and 1973 Western Channel models for all fish groups. The numbers next to bars are the estimated trophic levels

As a consequence of increased exploitation, the primary production to sustain the catches increased from 7.9% in the 1973 model to 12.7% in the 1994 model. These estimates are lower than the range, from 24.2 to 35.3%, estimated for shelf systems by Pauly and Christensen (1995). These relatively low values could be due to factors as (1) overestimation of primary production, (2) underestimation of catches and (3) overfishing, which would had left the reduced fish biomass unable to use the available production.

The omnivory index was slightly smaller in the 1994 model, suggesting a small change in the complexity of the food web. The omnivory index describes the degree of "linearity of the energy course" in the food web or can be seen as a measure of how the feeding interactions are distributed between trophic levels (Christensen *et al.*, 2004). The small increase is probably associated with the decrease in the abundance of species that are mainly piscivorous and have a less diversified diet, for instance hake, large bottom and large flatfish groups.

The ratio between primary production and respiration (*PP*/*R*) is thought to reflect the maturity of the system, with mature systems having values close to one. Christensen and Pauly (1993) reported this parameter for 41 aquatic systems and found that in most of them it fell in the range 0.8-3.3. The Western English Channel has a value of 3.8, indicating that the system is an immature state.

The Finn index measures the fraction of the throughput that is recycled (Finn, 1976). It is related to and expected to increase with system maturity, resilience and stability. The comparison of this parameter with those of the Northern Benguela and Barents Sea presented in Table 11 suggests, as did the previous parameter, that we are dealing with a relatively immature system. The Western English Channel has a value of about 3%, much lower than the estimates for the 1980s Benguela and Barents Sea models. Both of these models have the *PP*/*R* very close to 1 and so can be regarded as mature systems.

The average path length, a parameter that is strongly correlated with the Finn Index (Christensen and Pauly, 1993) and to some extent with the *PP*/*R*, also is related to ecosystem stability (Vasconcellos *et al.*, 1997). The estimate of this parameter for the Western Channel was lower than those for the 1980s Benguela and Barents Sea model.

Table 12. Transfer efficiencies (% of ingested food) between discrete trophic levels

Trophic level	II	III	IV	V	VI	VII	VIII	IX	X	Weighed mean
1994 model										
Producer	23.3	17.4	13.6	12.3	11.6	11	9.9	9.8	7	21.9
Detritus	13	12.4	11.5	10.7	10.1	9.8				12.9
All flows	19.1	16	13.2	12.1	11.4	10.9	9.9	9.8	7	18.4
Proportion of total flow originating from detritus: 0.46										
1973 model										
Producer	22.4	16.8	12.5	10.9	9.9	9.2	7.6	7.3	4	21.0
Detritus	11.6	10.5	8.9	8.1	7.4	7.1				11.4
All flows	17.9	15.1	11.9	10.5	9.7	9.1	7.5	7.3	4	17.4
Proportion of total flow originating from detritus: 0.46										

The ecosystem indicators estimated by Ecopath, such as the primary *PP*/*R* and the Finn index, discussed above, indicate that the Western English Channel is a relatively immature system. However, these indicators are functions of the production and biomass estimates and so depend on the reliability of those estimates. For example a change of +30% and –30% in the biomass of the primary producers group would cause respectively a change of about +30% and –30% in the *PP*/*R* and –20% and +40% in the Finn index. As there always seems to be some level of uncertainty about production and biomass parameters for marine environments, any conclusions about the 'relative maturity' of the system should be taken with caution.

Besides the estimates of fractional trophic levels, Ecopath estimates discrete trophic levels (*sensu* Lindeman, 1942). Ecopath then can estimate import, consumption by predators, export, flow to detritus, respiration and throughput (the sum of all previous parameters) by these discrete trophic levels. In addition, Ecopath calculates the transfer efficiencies between trophic levels, by dividing the sum of the exports from a given trophic level, plus the flow that is transferred to the next level, by the throughput at that level. The trophic aggregation routine estimated up to 10 trophic levels for both 1994 and 1973 models, but the sum of the throughput of the highest levels (>III) represent less than 1% of the total system throughput. The transfer efficiencies (Table 12) were slightly higher in the 1994 model and in both models they were at their highest levels for the flows that originated from primary producers. In both models the proportion of the total flow originating from primary producers was 54% and from detritus it was 46%, what shows that primary production have a slightly higher importance than secondary production from detritus in this system.

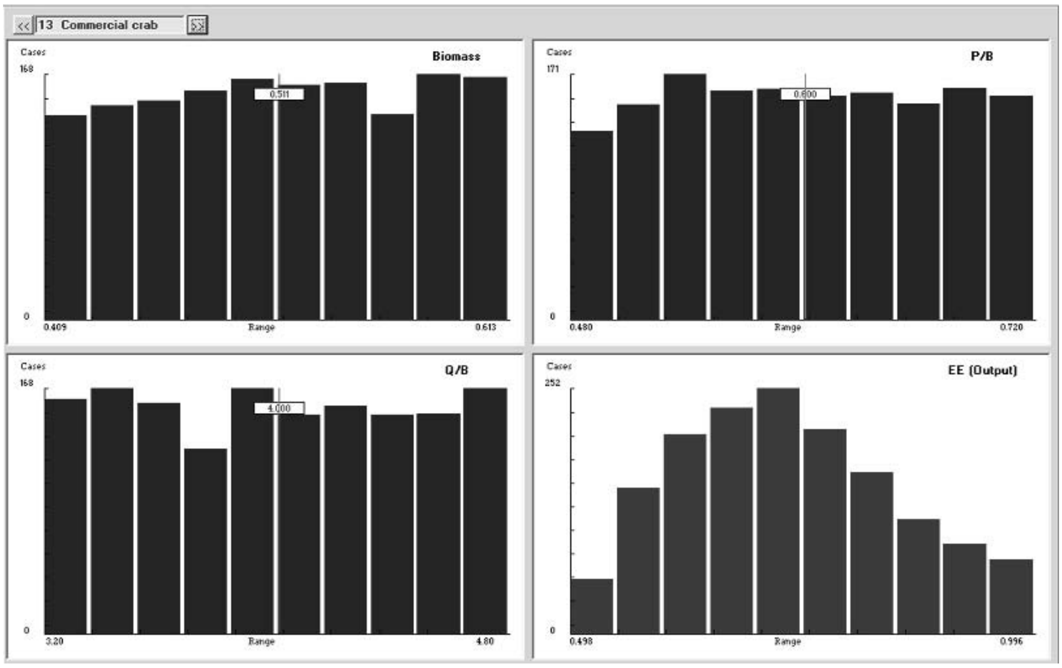
6. SENSITIVITY ANALYSIS

There are different formal ways to perform a sensitivity analysis in Ecopath. The Ecopath 'sensitivity routine' varies the basic input parameters (*B*, *P*/*B*, *Q*/*B*, *EE*) to check for the effects of the changes on the missing parameters of each functional group. We performed this simple sensitivity analysis for the 1994 model. Generally, a increase of 50% in one of the three inputs of a group, for instance *B*, causes a 33% decrease in its missing parameter, for instance *EE*. A decrease of 50% causes a 100% decrease. These results are very similar in magnitude and direction, irrespective of the input and the missing parameter. The effect that changing a parameter of a group has in other's group parameter are far less significant and typically does not exceeds 30%.

Ecopath includes a routine called Ecoranger that allows entry of a range and mean or mode for all basic parameters and diet compositions and the kind of frequency distribution (uniform, triangular or normal) for those parameters. Random input parameters are taken from the defined parameter space and the resulted model is rejected if any group has the *P/Q* >0.6 and/or *EE* >1. The process is repeated many times and the routine generates using the successful runs a frequency distribution for the basic parameters (*B*, *P*/*B*, *Q*/*B* and *EE*). We ran Ecoranger for the 1994 model assuming parameters to have a uniform distribution with a variability of 20%. The routine was set to run up to 1 million times and to a maximum of 2 thousand successful runs. Ecoranger found 1557 (0.16%) successful runs. Two examples of the Ecoranger results are presented in Figure 3. Figure 3a shows the results for large crabs, a group that the posterior frequency distributions for the input parameters (*B*, *P*/*B* and *Q*/*B*) are very similar to the prior distribution and

Figure 3b is for cephalopods, that had the posterior distributions for two of its inputs (*P*/*B*, *Q*/*B*) markedly different from the priors that were assumed to be uniform. So, it means that cephalopods inputs have both strong effects on models solutions and are constrained by other groups parameters. Cephalopods and large crabs are extreme examples. The cephalopods group has a relatively high biomass and has many trophic links, including many fish groups, and high ecotrophic efficiency. All these features limit the number of successful solutions. On the other hand, large crabs group has just a few links in the model representation and a lower ecotrophic efficiency, so there is more ‘room’ to changes in its parameters.
The successful Ecoranger solutions can be treated as different hypothesis about the ecosystem state with their associated probability determined by the posterior parameter distributions given the priors (parameters values and distribution) and Ecopath constraints. These results can be used as well to identify the parameters that have the strongest effects on model solutions and ‘deserve’ more effort to be refined.

(a)



(b)

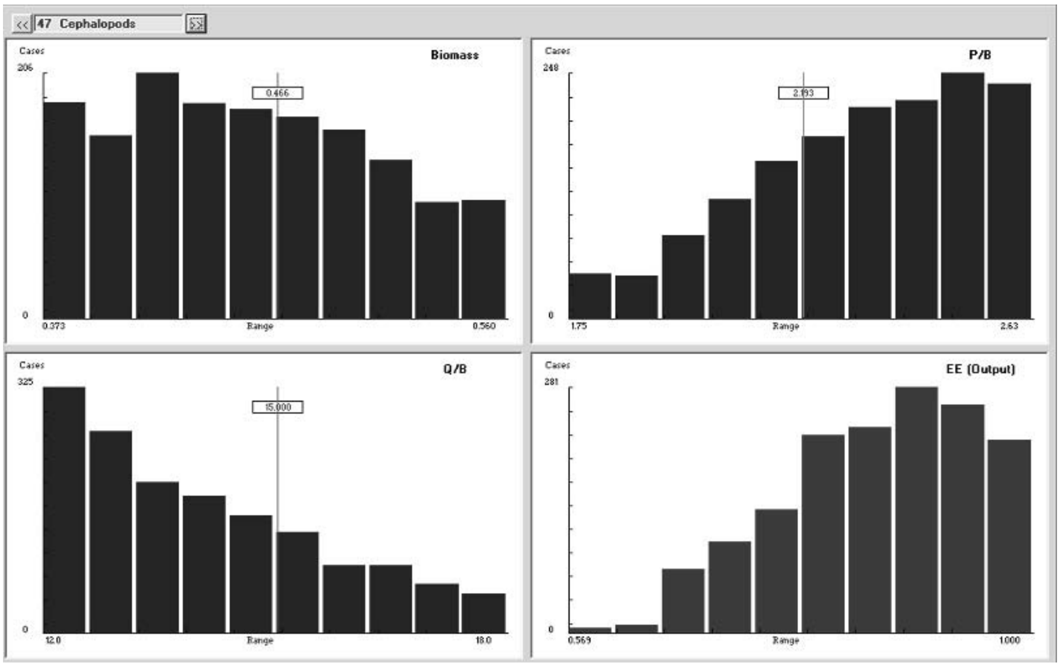


Figure 3. ***Frequency distribution of the four basic parameters of (a) large crabs and (b) cephalopods in the Ecoranger successful runs***

As part of the sensitivity analysis the emergent stock-recruitment relationships for the split juvenile-adult groups was tested in the 1994 model by simulating in Ecosim conditions of very high and very low abundance. This was achieved by altering the fishing mortality of the adult component of a species by first decreasing it to zero for a period allowing the stock to increase and subsequently steadily ramping up the fishing mortality to levels that would result in the disappearance of the functional group from the system. All groups except plaice, showed stock-recruitment relationships that qualitatively resembled the empirical data for these species, i.e., the relationships are flat over a range of spawning stock sizes (Beverton-Holt type curves). However, for plaice, there was a kind of dome-shaped, strongly compensatory relationship (Figure 4). We 'adjusted' this feature by increasing the parameter K of the von Bertalanffy function from 0.08 to 0.12 year^{-1} and decreasing the P/B ratio for juvenile plaice from 1.51 to 1.4 year^{-1}. After these changes the emergent stock-recruitment relationship seemed more reasonable (Figure 5).

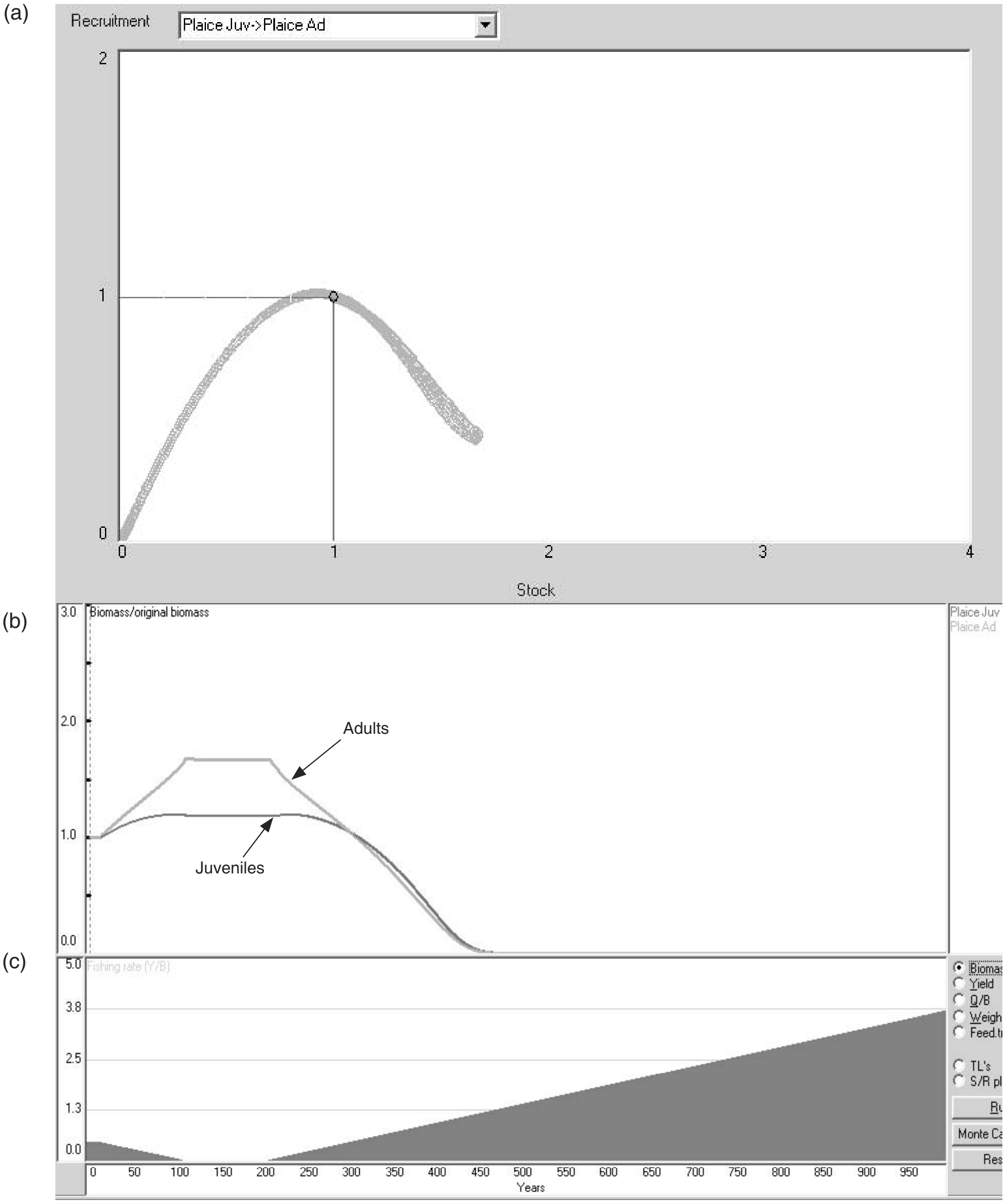


Figure 4. ***Plaice population dynamics: (a) stock-recruitment relationship, (b) biomass trend, (c) adult plaice fishing mortality. Vulnerability of prey to juveniles = 2, juveniles P/B = 1.51 year^{-1}, K = 0.08 year^{-1}***

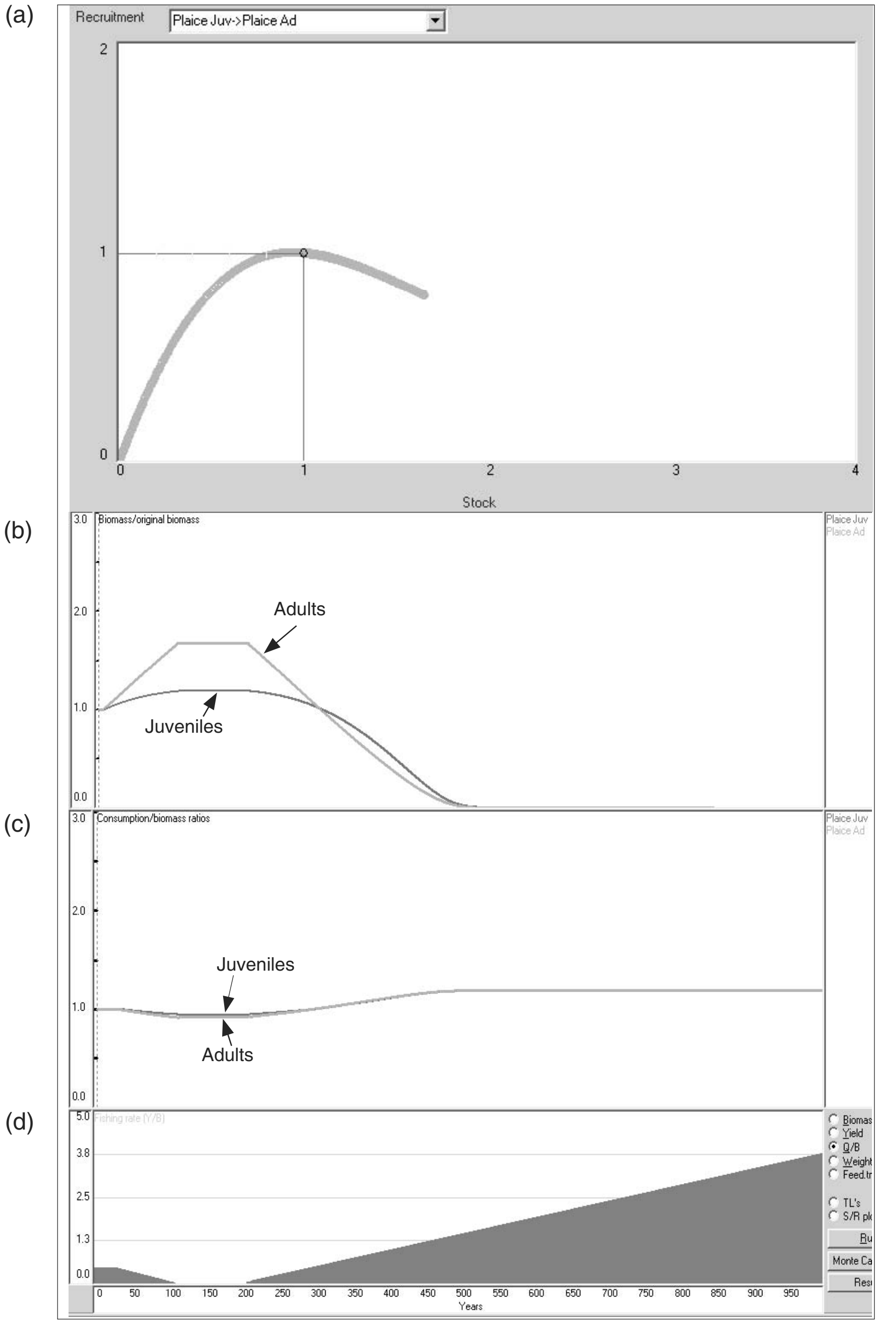


Figure 5. Plaice population dynamics. Panel (a) shows stock-recruitment relationship, (b) biomass trend, (c) consumption/biomass trend and (d) adult plaice fishing mortality. Vulnerability of prey to juveniles = 2, juveniles P/B = 1.4 year^{-1}, K = 0.12 year^{-1}

The effects of changes in the vulnerability (*v*) parameters on the emergent stock-recruitment relationship were investigated using plaice as an example. The most critical factor in determining the shape of the stock-recruitment function are the *v* parameters assigned to prey of the juvenile group; only the results related to them are shown here (Figures 6 and 7). Besides the default value results presented before, we first set the *v* parameter of the prey of juvenile plaice to 1.25 and after to 20, keeping the *v* of preys of the adult group at the default value. As can be seen the vulnerability parameters have a large effect on the shape of the stock-recruitment relationship. With low values, a dome-shaped (strongly compensatory) pattern emerges again. On the other hand, if the vulnerabilities are too high, the relationship is almost a straight line, with little compensation. These patterns are related to how the level of mortality that juvenile plaice can have on its prey (the *v* parameter) influences the consumption rates of juvenile plaice (Figures 6c and 7c). Under the low vulnerability settings (low relative mortality on prey), the juveniles *Q*/*B* presents a considerable increase when their biomass is lower then the Ecopath base line estimation. This is because when the prey have low vulnerability and the biomass of juveniles is in decline as a result of fishing on adults, there is a greater availability of food per unit biomass of juvenile plaice. This results in a strong compensation effect which reduces the velocity of the juvenile biomass decrease, and the maximum recruitment is achieved at a stock level lower than the Ecopath base line estimate. This compensation can be noticed as well by comparing the relative positions of the juveniles and adult biomass curves under different vulnerability settings. With low *v* values, the distance between the juveniles and adults biomass curves when the stock is at low levels is higher then under the default parameters scenario. Under the high *v* values scenario, the juveniles *Q*/*B* is almost constant at different biomass levels and causes almost no compensation effects. In this case the

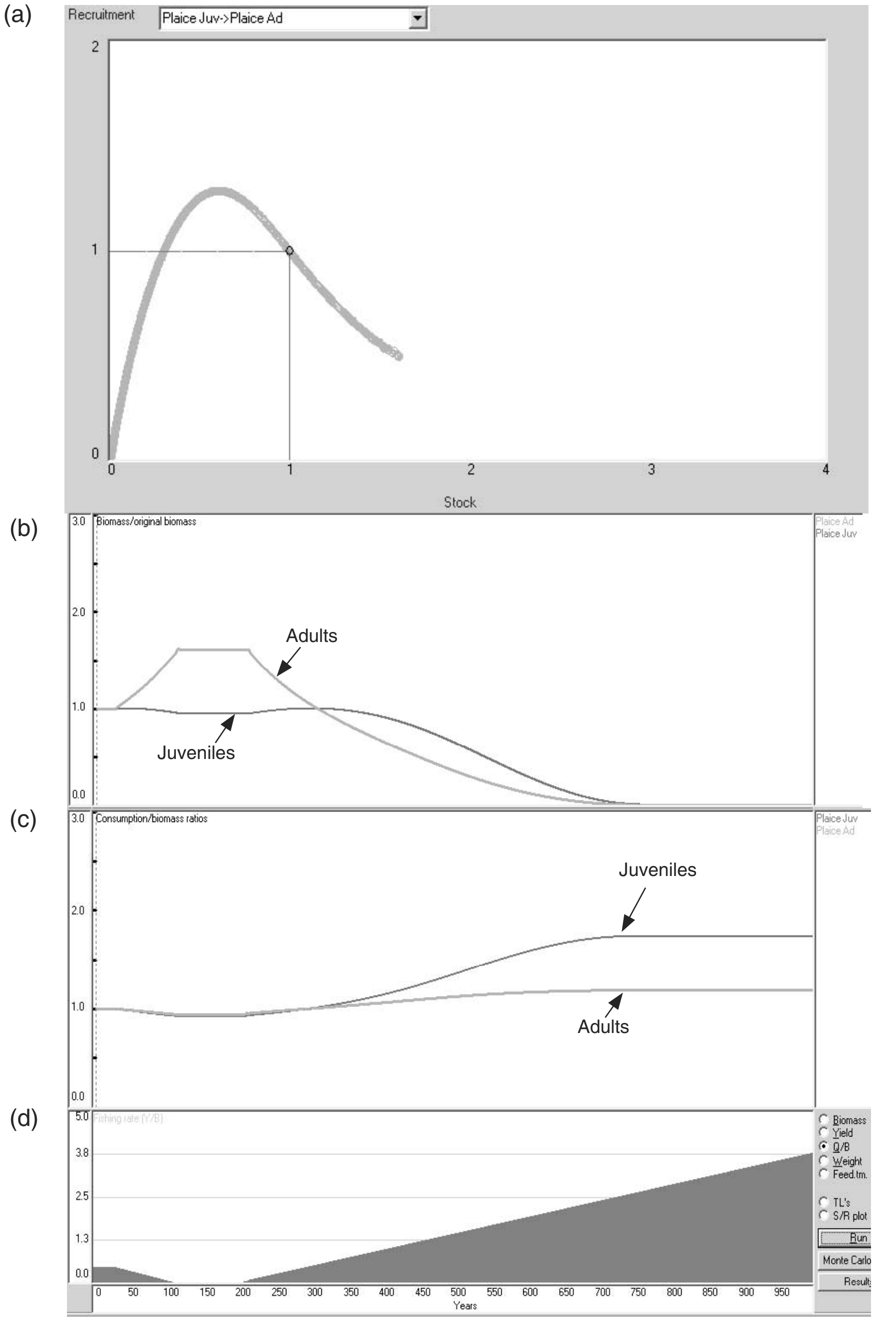


Figure 6. ***Plaice population dynamics. Panel (a) shows stock-recruitment relationship, (b) biomass trend, (c) consumption/biomass trend and (d) adult plaice fishing mortality. Vulnerability of prey to juveniles = 1.25, juveniles P/B = 1.4 year^{-1}, K = 0.12 year^{-1}***

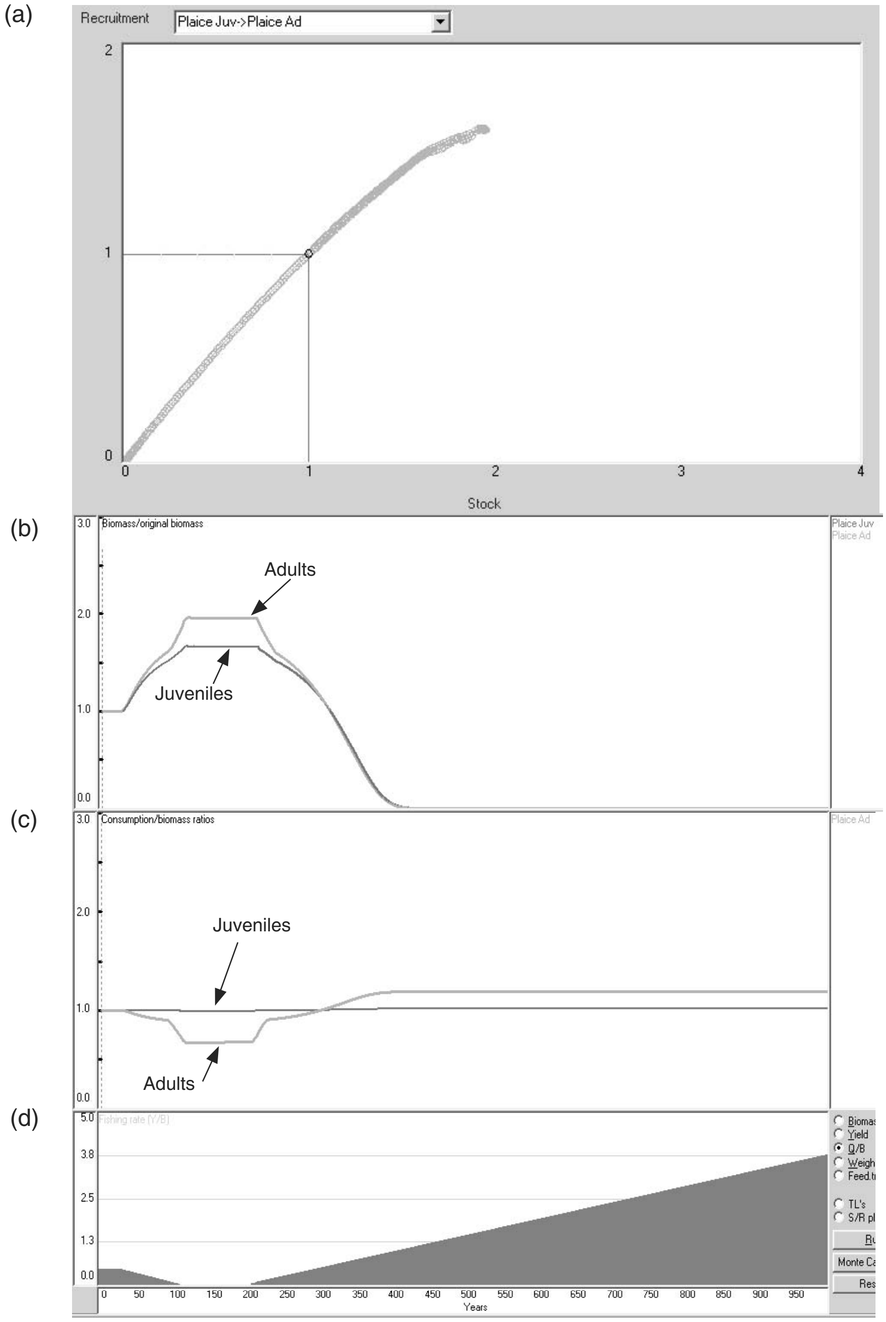


Figure 7. ***Plaice population dynamics: Panel (a) shows stock-recruitment relationship, (b) biomass trend, (c) consumption/biomass trend and (d) adult plaice fishing mortality. Vulnerability of prey to juveniles = 20, juveniles P/B = 1.4 year^{-1}, K = 0.12 year^{-1}***

maximum recruitment rate is not determined by the juvenile group as before, but by the maximum possible adult biomass, that is limited by the *v* parameters to the adult group.

As mentioned earlier, the Ecosim simulations were run using the 1994 model. The same type of simulations run for the 1973 model gave very similar results which are not presented here. As discussed above, the *v* settings have strong effects on the outcome of a Ecosim simulation. We tested the effect of a 50% increase in the fishing rate of all gears during 7 years using different vulnerability values. When values higher than 6 are used, the system components do not return to their original state and start presenting a chaotic behaviour (Figure 8).

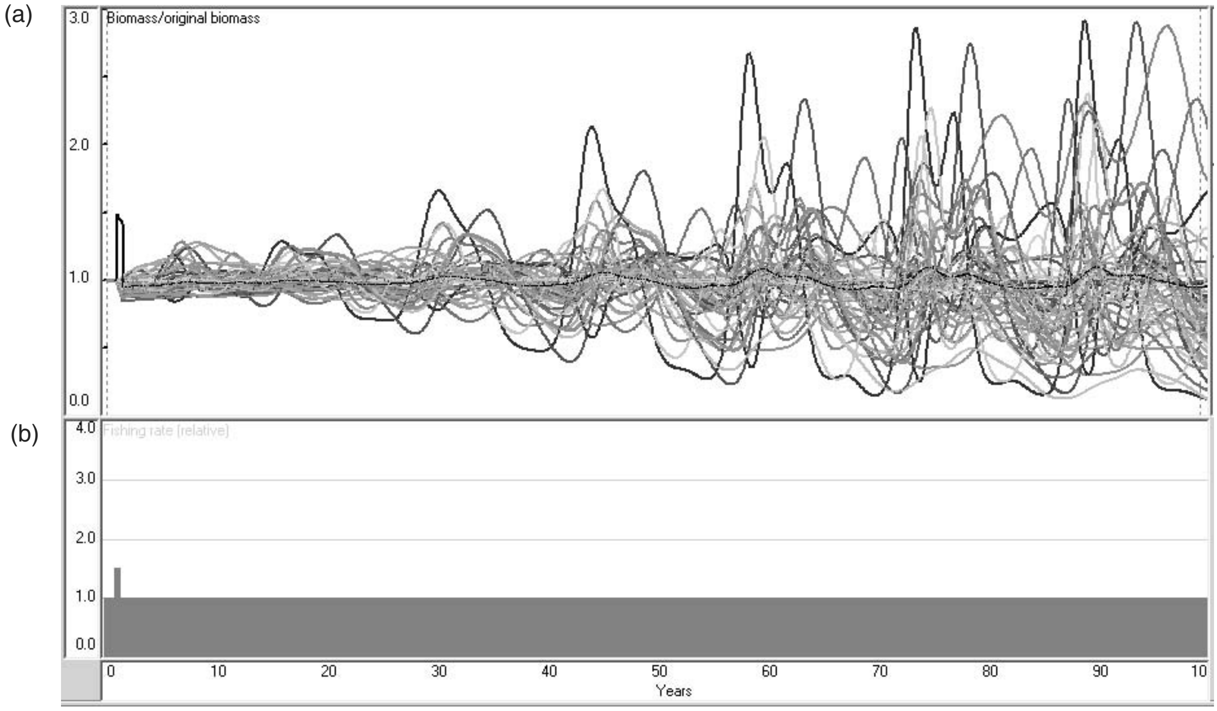


Figure 8. ***Testing of model stability using vulnerability parameters set to 8. Panel (a) shows responses of functional groups and (b) the fishing effort implemented across all gears. Note the increase of 50% in fishing rate during a short period in the right side of panel (b)***

7. CONCLUSIONS

The ecosystem indices for the 1994 and 1973 model were generally very similar, partially because the same basic inputs for primary producers, and diet composition data were very similar. The main differences were an increase in the fish biomass (mainly non-target species), an increase in the primary production required to sustain fishery catches and a small increase in the omnivorous index that might be related to a decrease in the abundance of some high trophic level piscivorous fish species.

An interesting outcome of the sensitivity analysis was that of the effects of the vulnerability parameters on the emergent stock-recruitment relationship. The results showed that vulnerability settings have a dramatic influence on the shape of the kind of stock-recruitment relationship. Assuming a value of 2 for the vulnerabilities of prey to juveniles, roughly means that the maximum rate of recruitment occurs at the Ecopath base line estimate for the spawning stock biomass. The higher the vulnerability value the higher the adult stock size (relative to baseline) at which recruitment attains its maximum. When too high values are used, recruitment increases linearly with stock size. When too low values are used, the compensation in recruitment at low stock levels is spuriously high. Plagányi and Butterworth (2004) explored the impacts of ‘foraging arena’ theory on stock-recruitment functions and stressed that the selection of the vulnerability parameter should be based on knowledge of the long term trends in stock. They added that it is unsatisfactory to use the vulnerability default settings for all functional groups, since it is very likely that the predators are in ‘different stages of their exploitation histories’, i.e. the stock sizes would be at different levels relative to their pre-exploitation levels. These results, highlighting the sensitivity of stock-recruitment relationships for multiple life stage groups, are important for users to take into consideration when applying the method of estimating vulnerability parameters by fitting model predictions to observed time series data (Christensen *et al*., 2004). Realism in stock-recruitment relationships should be tested after model fitting.

Constructing ecosystems models can lead to a better understanding of the interactions of the multiple factors affecting fish abundance. Future work will include estimation of the vulnerabilities parameters by the fitting of model predictions to observed time series of biomass and subsequently using the model to explore 3 hypotheses about temperate-related ecosystem change in the Western English Channel.

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