Modelling trophic interactions, fishing and climatic variations affecting the Western English Channel ecosystem

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By

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Declaration:

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To Juracy, Carolina, Mateus and Juana

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Abstract

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Three trophic models of the Western English Channel were built using the Ecopath with Ecosim (EwE) software. A model for 1994 represented a warm period. Two models represented colder periods in 1973 and in 1985, the later coinciding with a considerable increase in fish and shellfish landings. One of the main observed differences among the models was an increase in primary production that seemed to be reflected in changes in fish biomass. Some parameters estimated indicate that (1) the ecosystem was relatively immature or disturbed, (2) despite the increase fishing effort since the 1970s, the system maturity increased in 1985 and (3) with the increased fishing mortalities operating in the system, this trend was reversed in the 1994 model.

Ecosim simulations run from 1973 to 1999 indicated that a bottom-up mechanism plays an important role in the system production. By accounting for primary production changes and by estimating the so-called vulnerability parameters, it was possible to improve the goodness of fit of the model estimates to the available biomass data by about 62 to 68% compared to fitting using only the series of fishing mortalities.

The 1994 model was used to explore the effects of the use of the EwE fishing optimization routine on profits, number of jobs and ecosystem structure. An "ideal" mixed policy configuration was found when ecosystem structure was weighted slightly higher than were profits and jobs. This scenario led to an overall reduction in effort but also to increased profits and biodiversity, with almost no lost in the number of jobs. The optimizations also showed that the average trophic level of the catches is quite conservative to changes in ecosystem structure, which contrasted with an estimated biodiversity index from Ecosim that showed huge changes as a function of the weights placed on the policy functions.

1. Introduction

1.1.Overview.

According the Food and Agriculture Organization of the United Nations (FAO), 47% of the world's main fish and shellfish stocks are fully exploited, 18% are overexploited, 10% are severely depleted or recovering from depletion, and only 25% of stocks are in an underexploited or moderate state of exploitation (FAO, 2002). There is a ongoing debate with some level of disagreement related to the role of the so-called Ecosystem Approach to Fisheries in tackling the problem of overfishing, although all parties involved in this debate agree that what is needed is an overall reduction in fishing capacity (Browman and Stergiou, 2004).

Ecosystem models play an important role in the Ecosystem Approach to Fisheries and the interest in the development of such models is not new. The ecosystem model of Andersen and Ursin (1977) is an example of a relatively early attempt to approach fisheries in an ecosystem context. However, its complexity, large input data requirements and perhaps the lack of accessibility to computer facilities have precluded its use. The progress of computation facilities that has occurred in the last 10 to 15 years, has allowed the spread of more complex methodologies, even in the context of single-species assessments (Hilborn, 2003), and has allowed the use of very different sources of information and of modelling approaches dealing with many aspects of a fishery system in a unified framework (Hilborn, 2003; Christensen et al., 2004). This, with the increased scientific community and public awareness of the problem of the impact of fisheries in other

components of the ecosystem, rather than just the common concern about sustainability of the target species, the recognition that the Ecosystem Approach to Fisheries might improve the management of aquatic systems and increased research funding both from governmental and non-governmental institutions (Browman and Stergiou, 2004), contributed to the scenario for the development of new ecosystem model methodologies to address the Ecosystem Approach to Fisheries issue.

Ecosystem models can be used as a tool 1) to provide a framework to identify potential changes in complex systems that cannot be identified with single-species models, such as counterintuitive changes in abundance when species interactions outweigh the effects of fishing impact or climate change, 2) to reveal otherwise unknown system properties, 3) to emphasize the need to improve knowledge about specific parts of the system, 4) to "test" the compatibility of data sets and 5) to serve as a useful basis for the elaboration and/or exploration of scientific hypothesis about system dynamics and functioning (Vasconcellos et al., 1997; Christensen and Pauly, 1998; Jørgensen, 1998; Pauly and Christensen, 2002; Fulton and Smith, 2004; Walters and Martel, 2004). The Ecopath with Ecosim (EwE) software (Christensen et al., 2004) is currently the most used and tested ecosystem modelling tool for addressing the issues of how ecosystems are likely to respond to changes in a fishery and to the influences of climate at the ecosystem level (Christensen and Walters, 2004; Plagányi and Butterworth, 2004). Fulton and Smith (2004) compared the results of simulations for Port Phillip Bay, Australia, from EwE with two other ecosystem-modelling tools and concluded that they lead to the same general conclusions. The EwE is the methodology adopted in this work.

1.2.The Western Channel Ecosystem.

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 the current work, they recognized 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 and also invertebrate species. There are some fish stocks that are confined to either side of the Channel and in the case of sole (*Solea solea*) presenting different long-term abundance trends. Similarly, Atlantic cod (*Gadus morhua*), presents 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.

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 50m 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 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 is 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).

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

Faunal distributions are closely correlated to physical conditions. Zooplankton species are generally less abundant in stratified waters to the west than in the vicinity of thermal fronts. The structure, abundance and distribution of benthic

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communities are correlated with depth and sediment composition. The sediment composition in the Western English Channel tends to be coarser than in 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 that are either rare or absent in the Eastern English Channel (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 has yet to be completed. 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 important to understand the spatial and temporal variation and to separate natural from artificial causes.

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 the abundance of fish and invertebrate species (see Southward et al., 1988; Southward et al., 1995; Hawkins et al., 2003, Genner et al., 2004, Southward et al., 2005). This region has been subjected to major climatic shifts, with mean sea temperature fluctuating with a range of $1.8°C$ over the last century (Southward et al., 2005). Cooler periods in the early 1900s and 1970s were followed by warming periods in the 1950s and from the 1990s to the present day, changes reflected by large-scale

patterns in temperatures observed throughout the Northern Hemisphere (Mann, 2002). In the last three decades in particular, there have been many changes in Western Channel species abundances that appear to be linked to environmental changes. Some of these events are summarized in the following paragraphs.

During the cooling phase of the 1970s and early 1980s many shoals of large mature mackerel (*Scomber scombrus*), instead of overwintering in the northwest coast of the British Isles, migrated to the southwest areas to overwinter and then supported the high catches in that region (Lockwood, 1988). Also, between 1976 and 1979, the boreal species blue whiting (*Micromesistius poutassou*) and Norway pout (*Trisopterus esmarkii*) were reported for the first time in the English Channel, coinciding with the great salinity anomaly of the seventies, which was caused by a large offshore mass of cool lower-salinity water extending down to 700 m (Cushing, 1995). Blue whiting appeared in subsequent surveys of the Marine Biological Association of the UK (MBA), but Norway pout was not reported after 1984 (Southward et al., 2005). The MBA data also shows valuable information on the abundance trends for many other species for which there is no stock assessment data available (Southward et al., 2005). Species such as poor cod (*Trisopterus minutus*), lemon sole (*Microstomus kitt*), grey gurnard (*Eutrigla gurnardus*), dragonet (*Callionymus lyra*), thickback sole (*Microchirus variegatus*) and lesser-spotted dogfish (*Scyliorhinus canicula*) have shown increasing trends in the MBA data during the last decades, coinciding with the observed warming (Genner et al., 2004; Southward et al., 2005).

The recruitment of the Western Channel plaice (*Pleuronectes platessa*) stock increased from the early 1970s up to 1986, and after that it started to decrease. This is a similar pattern to that observed in the Eastern Channel and North Sea, and shows a negative relationship with sea surface temperature between February and June (Fox et al., 2000). The International Council for the Exploration of the Sea (ICES) assessment data for the Celtic Sea stock of cod (*Gadus morhua*) (ICES divisions VIIe-k), that includes cod in the Western English Channel, shows a similar trend in recruitment, increasing from the early 1970s up to 1987, and decreasing afterwards (ICES, 2000a). Cod recruitment has been shown to have a negative relationship with the SST in the southern limits of its distribution (Planque and Fredou, 1999). It is believed that in the North Sea a bottom-up control mechanism has reduced cod recruitment, by which the increased temperature since the middle of 1980s has caused changes in the zooplankton community structure and reduced the survival of young cod (Beaugrand et al., 2003).

The recruitment of the Western Channel sole (*S. solea*) stock also increased during the 1970s, but in a different way to the Celtic Sea cod and Western Channel plaice stocks. Sole abundance increased to a maximum in 1980, and started decreasing afterwards. The relationship between sole recruitment and temperature does not seem to be so clear as it is for plaice. Rijndsdorp et al. (1992) reported a negative relationship between sole recruitment and winter and early spring temperatures in the North Sea, but this relationship was not observed for the English Channel. In contrast, Henderson and Seaby (1994) reported a positive correlation between temperature and sole abundance in Bridgwater Bay, Bristol Channel. In contrast to the Western English Channel plaice and Celtic Sea cod stock, the Western

Channel sole stock shows a stronger relationship between the spawning stock biomass and recruitment (ICES, 2000a), which suggests that mostly density-dependent processes are regulating sole recruitment in the region, while density-independent, environmentally driven mechanisms seem to be the dominant ones for cod and plaice recruitment.

A recent analysis of long-term data collected by the MBA in the Western English Channel since the early 1900s (Genner et al., 2004, Southward et al., 2005), showed that despite the increased temperature and fishing, some northern species such as cod have increased in abundance, while large southern species have decreased. It was suggested that release from food competition caused by overexploitation of other commercial species and the increase of small non-target prey species, has allowed cod to maintain its abundance despite the warming of the last years (Southward et al., 2005). These observations suggest that the response of some species to climate can be counterintuitive and that a complex interaction of factors define the trend in abundance over the years.

1.3.Objectives.

In this study we use the EwE software to build models for the Western Channel Ecosystem (1) to describe its properties, (2) to explore the effects of fishing and trophic interactions on shaping past trends in biomass and (3) to explore the effects of different fishing strategies on economic, social and ecosystem structural aspects. The first sections of the thesis describe the software and document in detail the data sources, manipulation and assumptions performed during parameterisation

of the models used to represent the system in the 1970s, 1980s and 1990s. The first model built 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 other models represent relatively colder periods, one for 1973 when the fishing effort was lower and another for 1985, which coincided with a period of considerable increase in landings. These models are then used to compare the status of the system in these time snapshots. The following section deals with the time dynamic analysis of the contribution that fishing, trophic interactions and plankton production make to explanations of the observed changes at higher trophic levels in the Western English Channel from 1973 to 1999 and discuss the results with regard to the influences of the observed climate change. This period was chosen because (1) it includes years when the best information is available; (2) it starts in a relative cold phase and ends in a considerably warmer one and; (3) there was a slight increase in cod and (4) a decrease in the abundance of some of the large southern species despite sea-temperature warming. Finally, the 1994 model is used to explore the effects of the use of the EwE fishing optimization routine on economic, social and ecological aspects of the Western English Channel fisheries and ecosystem.

2. Methods

2.1.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 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:

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

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 EE_i is the "ecotrophic efficiency" of i, the proportion of the production that is utilized in the system.

The above equation can be expressed as:

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

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 three of the following four basic parameters for 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 difficult to measure. In cases when one of the other parameters is missing, an estimate for EE is entered based on assumptions 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) is 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, isolating the biomass accumulation term, and setting up a set of differential equations of the form:

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

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 $((P/B)_i B_i (1-EE_i))$ natural mortality rate, *F$_i$* is fishing mortality rate, *e$_i$* is emigration rate, *I$_i$* is immigration rate, (and *e$_i$·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 consumption (Q) of a predator in the Ecosim simulations varies as a function of its biomass and the biomass of its prey and the "vulnerability" (v) that conceptually represents a theoretical flow rate at which the prey biomass moves from a vulnerable state to an invulnerable one. As implemented, the vulnerability is the maximum mortality that a predator can cause on a given prey, relative to the Ecopath base mortality rate, if the predator numbers were to be high. It is estimated as $v_{ij} = v'_{ij}.Q_{ij}/B_i$, where Q_{ij} is the Ecopath baseline estimate of the consumption of the species i by species j and B_i is the biomass of i. The parameter v'_{ij} that determine the maximum Q_{ij}, is also usually called vulnerability. This is an input in Ecosim and can vary from 1 (bottom-up) to ∞ (top-down control), its default value being 2. The simulations have been shown to be very sensitive to changes in the vulnerability parameter (v'_{ij}), low values cause bottom-up control, whereas high values result in top-down Lotka-Volterra predator-prey dynamics with extreme cases leading to dynamic instability (predator-prey cycles) and loss of biodiversity through the overexploitation of some functional groups by their predators. Although users can input values of v'_{ij} into Ecosim, it is not advisable to do so other than for the purposes of testing or comparing the dynamics of models, since there is little way of knowing (or measuring in the field) what these values could or should be. However, recent interpretations suggest that knowing how abundant the species is relative to its virgin abundance can provide guidance on whether the vulnerability parameter should be high or low (V. Christensen pers. comm.; Plagányi and Butterworth,

2004). Where a predator's abundance is far below its carrying capacity, high vulnerabilities of its prey means that the predator is capable of inflicting higher mortality, increasing its consumption and thus recovering more quickly. It is now advised to estimate the vulnerabilities by fitting the model estimates (e.g. biomass) to observed time series data (Walters et al., 2000; Christensen et al., 2004; Plagányi and Butterworth, 2004; Walters and Martel, 2004).

2.2. Model Building

The model structure was 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 life stages, juveniles and adults. In addition to the living groups, 2 non-living groups are included, these being detritus and discards. The fishery is represented by 9 fleet/gear types which include otter trawl, beam trawl, pelagic trawl, nets, dredges, pots, lining, seaweeds and recreational.

Many parameter estimates were taken from Stanford and Pitcher (2004). These estimates were mostly for parameters that are difficult to obtain and/or for parameters of highly aggregated functional groups, such as some invertebrates, sea birds and marine mammals. For example the diet compositions of highly aggregated functional groups that feed mainly on lower trophic levels that are also represented by highly aggregated functional groups will not differ significantly in models that

have a similar structure. Another example is the Q/B rates of invertebrate groups, which are regularly estimated in ecosystem models based on an estimation of the P/B rate and on an educated guess for the P/Q rate. So, in many cases the Q/B rate was estimated using an educated guess for the P/Q rate reported by Stanford and Pitcher (2004). On the other hand, some parameter estimates for the Western Channel used here were already available in Stanford and Pitcher (2004) since they had to compile the information from both sides of the Channel before aggregating them into a single model. In many cases, the parameters taken from Stanford and Pitcher (2004) were restricted to those species or functional groups that either had no data for either end of the Channel and represented the general rather than specific knowledge about the groups or to species for which there was only one estimate to represent the whole ecosystem. Most importantly, the parameter estimates for the big "players" in the model, i.e., the species that have the biggest effects on model estimates and simulations, were different from the ones used by Stanford and Pitcher (2004).

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 abundance and biomass data (Anon., 2001; Genner et al., 2004);

RV Corystes beam-trawl surveys of the Centre for Environment, Fisheries and Aquaculture Sciences (CEFAS) for biomass and stomach contents data;

Continuous Plankton Recorder (CPR) survey data of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (Reid et al., 2003).

For some of the most abundant species in the inshore regions in the Western English Channel, stomach contents were collected, since a great part of the information available in scientific journals is from other areas. On a CEFAS cruise in the Western English Channel on board *Corystes* between 21 of September and 5 of October 2002, about 400 stomachs were collected, of up to 30 per species, and subsequently analysed in the laboratory. For each fish the sex and maturity stage were determined, together with a record of the length (nearest cm below) and weight (g). During the diet analysis the total weight of the stomach and the contents of each diet item were recorded. The items were identified to the lowest taxonomic level possible so as to serve the main aim of using these data in the ecosystem models developed. The species for which these data was used are highlighted in section 3.4.

Parameters not available from the above were estimated using empirical equations as described in section 3.3. 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 3.4. The balanced 1994 model was used as a base upon which to build the 1973 and 1985 models. 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 and 1985 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 that was used in the 1994 was also used for the 1985 and 1973 models.

2.3. Production and consumption rate 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 detritivores, *Hd* is equal to zero for carnivores and one for herbivores and detritivores.

The growth parameters used in the above equations were taken from Froese and Pauly (2000). A mean annual sea surface temperature (SST) of 12.7 °C was used for the purpose of the mortality and consumption 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)).

2.4. Description of functional groups.

A description of the functional groups and data inputs is given below. When not specifically mentioned, the same parameters input estimates used the 1994 model were used in the 1973 and 1985 models.

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

1994 model: Estimates of *B* and *P/B* for primary producers in the Western Channel reported in Stanford and Pitcher (2004) were used as inputs for this group.

1973 and 1985 models: To estimate the biomass for these years we used the CPR phytoplankton colour index and assumed that the index is directly proportional to changes in biomass of the primary producers group.

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

1994 model: The group structure and parameter estimates, including diet composition, were based on Stanford and Pitcher (2004) and Sanchez and Olaso (2004). The estimate of B for the "carnivorous zooplankton" group reported in Stanford and Pitcher (2004) was used as input for the macrozooplanton group in this study. The estimate of B for the "zooplankton" group reported in Stanford and Pitcher (2004) and the proportions of micro- and mesozooplankton from the model of Sanchez and Olaso (2004) were used to estimate the inputs for micro- and mesozooplankton in this study. Estimates for P/B and Q/B were taken from Sanchez and Olaso (2004) and diet compositions from Stanford and Pitcher (2004).

1973 and 1985 models: To estimate the biomass for these years we used the CPR zooplankton abundance index and assumed that the index is directly proportional to changes in biomass of the zooplankton groups.

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

The input values of B for Polychaeta, Nemertina and Gastropoda groups were taken from Holme (1953) and an estimate of P/B for "deposit feeders" in the Western Channel came from Ameziane et al. (1995). The Q/B rate was left to be estimated by Ecopath based on an estimate for P/Q of 0.15 as reported in Stanford and Pitcher (2004). Diet composition was taken from Stanford and Pitcher (2004).

6. Sessile suspension feeders (cnidarians, sponges, bryozoans and ascidians).

Input values of B were taken from Holme (1953) with P/B and diet composition taken 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 as reported in Stanford and Pitcher (2004).

7. Shrimps and Prawns.

Values of B and Q/B were left to be estimated by Ecopath based on an EE of 0.95 and P/Q of 0.15 respectively as reported 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 was taken 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). A value of B for the Western Channel was estimated using the landings of the species (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 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 came from Stanford and Pitcher (2004).

1973 and 1985 model: The value of B in the 1973 model was 1.5 times higher than in the 1994 model. This is an assumption based on a lower level of beam trawl fishing in the past and that whelks were reported to have declined as a possible result of increased beam trawl fishing in the North Sea (Ten Hallers-Tjabbes et al., 1996). For the 1985 model, the B was estimated as 1.2 times larger than in the 1994 model (see section 3.5 for additional comments about the biomass estimation procedure).

9. Echinoderms.

This group included 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*. A value of B was taken from Holme (1953). The P/B, Q/B rates and diet composition were taken 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*. An estimate of B was taken from Holme (1953). Warwick and Price (1975) reported

mortality rate 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 on the effects of predation on juvenile bivalves showed annual mortality 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 an input for *P/B*. The *Q/B* rate was left to be estimated by Ecopath, based on an estimate for *P/Q* of 0.09 taken from Stanford and Pitcher (2004), which also provided the source for diet composition.

11. Scallops.

This group included great scallop *Pecten maximus*, queen scallop *Aequipecten opercularis* and variegated scallop *Chlamys varia*.

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

1973 model: A value of *B* was assumed to be 1.5 times higher than the 1994 model since there was some decline in catches during the early 1970s.

12. Small-medium sized crabs.

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

13. Large crabs.

This group included the edible crab *Cancer pagurus* and the spinous spider crab *Maja squinado*.

1994 model: The P/B rate was estimated using an F estimate of 0.4 year^{-1} and a estimate for M of 0.2 year^{-1} (Bennett, 1979). The biomass was estimated using the L/F ratio. The Q/B rate was left to be estimated by Ecopath based on an estimate for P/Q of 0.15 as in Stanford and Pitcher (2004), which also provided the source of information on diet composition.

1973 and 1985 models: The value of B in the 1973 model was assumed to be 1.5 times 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 further offshore during the 1980s to keep the same

yield levels. For 1985, biomass was assumed to be 1.2 times higher than in the 1994 model.

14. Lobsters.

This group included the European lobster *Homarus gammarus* and the common spiny lobster *Palinurus elephas*.

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

1973 model: The value of B used was assumed to be 1.5 times higher than the value in the 1994 model, since this stock seemed to be overfished (Southward and Boalch, 1992; Stanford and Pitcher, 2004). The 1985 value of biomass was assumed to be 1.2 times higher than in the 1994 model.

15. Small-medium demersal fishes.

This group included some of the main fish prey items in the model. Therefore it is a 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: The *P/B* rate was estimated using 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 had to be used, since there is substantial predation pressure on this group. The *Q/B* average used was also weighted by catch rates. *B* was estimated by Ecopath based on an *EE* of 0.9. The CPUE for small demersal fishes was about 3.5 times bigger than that for plaice in the *RV Corystes* beam trawl surveys. The commercial by-catch of small demersal fishes was estimated by assuming that the beam trawl plaice catches provide a representative index. The diet for this group was based on stomach 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 and 1985 models: There is evidence from the MBA long-term trawl data (Anon., 2001) that there was an increase in abundance of species belonging to this group, probably related to higher temperatures and the decline of large predators. Based on the same data set, it was "estimated" that the biomass in the 1973 model would be 38% and in 1985 87% of the biomass in the 1994 model (see section 3.5 for additional comments about the biomass estimation procedure). The catch time-

series was estimated assuming that the catches followed the same trend as the UK trawl fleet effort in the Western Channel reported in ICES (2000a).

16. Small gadoids (*Trisopterus* group).

This group included the small to medium-sized southern gadoids, poor cod *Trisopterus minutus* and bib *Trisopterus luscus*.

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 represented mainly by poor cod, which was by far the most abundant of the two species. The P/B rate 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. The Q/B rate was estimated using growth parameters for poor cod. Diet data come from the Irish Sea for poor cod (Armstrong, 1982) and Western Channel stomach samples collected aboard *RV Corystes* (unpublished data) supplemented with data from the Irish Sea for bib (Armstrong, 1982).

1973 and 1985 models: According to MBA data the biomass was estimated to be 55% and 74% of the 1994 level respectively.

17. Red Mullet (*Mullus surmuletus*).

1994 model: There was no published biomass estimate for red mullet, *Mullus surmuletus*. This parameter was estimated by Ecopath based on EE of 0.90. The P/B

rate was estimated using Pauly's equation for M (Pauly, 1980). Diet composition was taken from data collected in the north-eastern Mediterranean (Labropoulou et al., 1997).

1973 and 1985 model: According to the MBA data, the abundance of red mullet in 1973 would be only 16% of the abundance in the 1994 model, though this figure seemed to be low. There was an increase in catches that seems to be partially related to an abundance increase due to warmer conditions. As the average landing for 1973-80 was 50% of that in the beginning of the 1990s, it was judged that the biomass would have been 50% lower in 1973. In 1985 the biomass was estimated to be 83% of the 1994 level using the MBA data.

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

1994, 1973 and 1985 models: Values for B and the P/B ratio for sole were estimated from the ICES stock assessment data for its stock in division VIIe (Western Channel) (ICES, 2000a). Diet composition was taken from data collected in the northwest Mediterranean (Darnaude et al., 2001). The juveniles and adults were assigned the same diet composition.

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

1994 and 1985 models: Values for B and the P/B ratio for plaice were estimated from the ICES stock assessment data for its stock in division VIIe (Western Channel) (ICES, 2000a). Diet composition was taken from data collected in

Eastern Anglesey, North Wales (Basimi and Grove, 1985). The juveniles and adults were assigned the 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 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 the *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 similar to the biomass from the *RV Corystes* survey (with no corrections for catchability) and it seems very likely that the biomass estimates for dab are a good proxy for this variable. The P/B rate was taken from Stanford and Pitcher (2004) who estimated the parameter from CFSG data. Diet composition was taken from data collected in the West Coast of Scotland (Gibson and Ezzi, 1987) and Western Channel stomach samples (unpublished data).

1973 and 1985 model: The B was estimated to be to be about 40% and 85% higher respectively using MBA data.

23. Lemon sole (*Microstomus kitt*).

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

1973 and 1985 model: According to MBA data, the biomasses of lemon sole in these years were estimated to be about 37% lower and 10% higher than the 1994 level respectively. There was a huge increase in landings from 1973 up to 1983 but the MBA data does not show such an increase in catch rates. The time series of biomass estimates used in the Ecosim simulations was estimated both according to the MBA data and landing trends (see section 3.6 for additional comments about the biomass estimation procedure). The estimated series presents an increasing trend from 1973 to 1983, decreasing from 1983 to 1994 and increasing thereafter. This sequence resembles the landing trend. The catch data were first estimated using the same proportion of discards as the 1994 model. However, as it resulted in high fishing mortalities for some years of the series, the landing data (with no discards) were used to estimate the time series of fishing mortalities to drive the Ecosim simulations.

24. Large flatfish.

This group included the piscivorous species brill *Scophthalmus rhombus*, turbot *Psetta maxima* and megrim *Lepidorhombus whiffiagonis*.

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

1973 and 1985 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 to assume that there was a decline in their abundance. The B was estimated to be 2.2 and 2 times higher than in 1994 respectively using the MBA data. The P/B rate was adjusted in the 1973 model to account for a much lower fishing mortality.

25. Gurnards.

This group comprised red gurnard *Aspitrigla cuculus*, tub gurnard *Trigla lucerna* and grey gurnard *Eutrigla gurnardus*.

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

1973 and 1985 models: The B was estimated to be about 1.4 and 1.7 times higher than values for 1994 respectively based on the MBA data.

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

1994 model: Estimates of B and P/B were based on ICES stock assessment data for whiting in divisions VIIe-k (ICES, 2000). The B was estimated from the L/B ratio for the whole stock and L for VIIe. Adult diet composition was taken from data collected in the North Sea (Daan, 1989) whilst juvenile diet composition was taken from data collected in the west coast of Scotland (Gibson and Ezzi, 1987).

1973 and 1985 models: The ICES time series of VPA 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 tons in 1995 and the stock biomass remained above the average since 1993. The biomass for 1973 was estimated to be 42% the level in 1994 using the MBA data. The biomass from 1973 to 1982 was estimated based on the MBA data trend, and followed the ICES data trend onwards. For the 1985 model, the biomass was estimated to be 42% of the value in 1994 based on the ICES data (see section 3.6 for additional comments about the biomass estimation procedure).

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

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

1973 and 1985 models: The biomasses in these years were 76% and 96% of the 1994 model respectively. Inputs for the P/B (Z) of adults and juveniles were taken from ICES (2000a). Western Channel cod is treated as part of the cod stock in divisions VIIe-k, which is the Celtic Sea stock (ICES, 2000a). The landings per unit of effort in the Western Channel reported in ICES (2000a) show a similar trend to biomass time series for the whole stock. This trend was used to estimate the biomass series for the Western Channel. The catch series trend was estimated according the landings per unit of effort and effort data in the Western Channel as reported in ICES (2000a).

30. Hake (*Merluccius merluccius*)

1994 model: Values for B and P/B were based on ICES stock assessment data for northern hake stock which covers divisions IIIa, IV, VI, VII, VIIIa, b (ICES, 2000a). B was estimated from the L/B ratio for the whole stock and L for area VIIe. Diet composition was taken from data collected in the Celtic Sea (Du Buit, 1996).

1973 and 1985 models: The ICES VPA time series for the northern stock of hake starts in 1978. The biomass estimates show a declining trend. The biomass for the years between 1973 and 1978 were estimated using a regression line of biomass against time, extrapolating the trend backwards until the year in question. The catch series trend was estimated according the trend of the whole stock. The biomass for the 1973 model was 1.76 times higher than that for the 1994 model, and 1.5 times higher for the 1985 model.

31. Dogfish.

This group comprised lesser-spotted dogfish *Scyliorhinus canicula*, greater-spotted dogfish *Scyliorhinus stellaris* and spurdog *Squalus acanthias*.

1994 model: Using data from the MBA trawl surveys the catch rates for lesser-spotted dogfish and greater-spotted dogfish were estimated and then used as input for B. The value of the P/B ratio for dogfish was estimated using Pauly's equation for M (Pauly, 1980). Both P/B and Q/B were estimated using parameters for

S. canicula. Diet composition for lesser-spotted dogfish was taken from data collected in the Irish Sea (Ellis et al., 1996).

1973 and 1985 models: Using the MBA data the biomass was estimated to be 69% and 98% of the biomass in the1994 model respectively.

32. Rays.

This group included thornback ray *Raja clavata*, cuckoo ray *Leucoraja naevus*, spotted ray *Raja montagui*, blue skate *Dipturus batis*, blonde ray *Raja brachyura* and painted ray *Raja microocellata*.

1994 model: The catch rate estimated using the *Corystes* beam trawl surveys in the Western Channel was used as input for this group's biomass, *B*. Using this biomass estimate produced a value of *F* that would be at least 3 year^{-1}, which is an unrealistic estimate. So, the biomass for rays was not estimated from model independent sources but was estimated using an *EE* of 0.95 since fish in this group are heavily exploited. The estimate of *P/B* based on an average *M* of 0.28 year^{-1} for *L. naevus*, *R. montagui* and *R. clavata* and a guesstimate of $F \sim 0.3$ year^{-1}. Values of *Q/B* were averaged over values for *R. naevus*, *R. montagui* and *R. clavata*. Diet composition for cuckoo ray was taken from data collected in the Irish Sea (Ellis et al., 1996) and for thornback ray and spotted ray using averaged data from the Irish Sea (Ellis et al., 1996) and the Bristol Channel (Ajayi, 1982).

1973 and 1985 models: The biomass in these early years was estimated to be 2.5 and 1.6 times higher than 1994 respectively using MBA data.

33. Other gadoids.

This group was based mainly on *Pollachius pollachius*, but designed to "represent" saithe *Pollachius virens*, blue whiting *Micromesistius poutassou* and haddock *Melanogrammus aeglefinus* as well.

1994 model: A value of B for this group was estimated from F (C/B) for pollack taken from Stanford and Pitcher (2004) and pollack C for VIIe. The P/B ratio was estimated based on an M of 0.31 year^{-1} for pollack using Pauly's equation (Pauly, 1980) and F. The Q/B ratio was estimated using data for pollack. Diet composition was taken from data collected off the southwest of Norway for pollack (Hoines and Bergstad, 1999), and in the North Sea for saithe and haddock (Daan, 1989).

1973 and 1985 models: The biomass for the 1973 model was estimated to be 74% of the 1994 model using MBA data. In the 1985 model, it was 85% higher.

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

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

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

1973 and 1985 models: The biomass for the 1973 model was estimated to be 85% of the 1994 model using MBA data. The *P/B* rate was adjusted to account for a much lower fishing mortality. The ICES VPA time series data for Anglerfish started in 1986. The landings for anglerfish in the Western Channel showed a huge increase from 1973 up to 1983. The MBA data show a similar trend but not of the same magnitude. The biomass for the period from 1983 to 1985 was estimated using the same catch to biomass ratio of 1986 and the catches for those years. The biomass data from 1973 to 1983 were estimated assuming that the abundance steadily increased during these years. The biomass input for the 1985 model was 65% higher than in the 1994 model.

35. Large bottom dwelling fishes.

This is a general group that included ling *Molva molva*, conger *Conger conger* and others species like the greater weaver *Trachinus draco*, Forkbeard *Phycis blennioides*, eel *Anguilla anguilla* and the red-band fish *Cepola rubescens*.

1994 model: The *B* was estimated using the *L/B* ratio given in Stanford and Pitcher (2004), who used CFSG data for ling and conger, and a value of *L* for area VIIe. The *P/B* rate was estimated from an $F(C/B)$ value of 0.23 year^{-1} and on an *M* of

0.18 year^{-1}. All estimates were based on ling and conger with M and Q/B being average estimates, weighted by biomass. Diet composition was taken from data collected for conger in the Mediterranean (Macpherson, 1981) and in the Bay of Biscay (Olaso and Rodriguez-Marin, 1995). The diet of ling was based on percentage of occurrence data collected off Scotland (Rae and Shelton, 1982).

1973 and 1985 models: The biomass was estimated to be 2.5 and 2.1 times higher than 1994 respectively using MBA data. The P/B rate for the 1973 model 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: Values of B and P/B were taken from Stanford and Pitcher (2004) that used the CFSG data to make their estimates. The Q/B rate was estimated using data for black bream. Diet composition for black bream taken from Pita et al. (2002) was used as input for this group.

1973 and 1985 models: Black seabream 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 model was assumed to be

1.5 higher than the value used for the 1994 model. The biomass in the 1985 model was estimated based on an *EE* of 0.95.

37. John Dory (*Zeus faber*).

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

1973 and 1985 models: The MBA trawl data and ICES landings for this species show opposite trends. It is supposed that the observed landings increase is a result of higher abundance related to higher temperatures. So we made the assumption that in the earlier two years the biomass was about 70% and 80% of the 1994 model respectively.

38. Sandeels (*Ammodytes tobianus*).

A value of *B* was estimated by Ecopath based on a value for *EE* of 0.95 whilst the *P/B* rate was estimated from an *M* of 1.29 year^{-1} for *A. tobianus* taken from Reay (1973). Diet composition for *A. tobianus* was taken from Reay (1970).

39. Herring (*Clupea harengus*).

1994 model: It seems that there are two different herring stocks exploited in the English Channel (Ulrich et al., 2002). 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). The B was estimated using an L/B ratio for the Celtic Sea Stock and L for the Western Channel. Diet composition was taken from data collected off the west coast of Scotland (De Silva, 1973).

1973 and 1985 models: There are time series of VPA biomass estimates for the North Sea and for the Celtic Sea stocks starting in 1960. The long-term trends in biomass 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 that in the Celtic Sea stock. The biomasses in 1973 and 1985 were estimated to be 76% and 96% of the 1994 model respectively.

40. Sprat (*Sprattus sprattus*).

1994 model: A value of B was estimated by Ecopath from an EE of 0.95. The P/B ratio was taken from the North Sea model developed by Christensen (1995). Diet composition was taken from data collected off the west coast of Scotland (De Silva, 1973).

1973 and 1985 models: The biomass was estimated to be 37% and 26% of the 1994 model respectively as derived from the MBA data.

41. Pilchard (*Sardina pilchardus*).

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

1973 and 1985 models: The *B* was estimated to be 59% and 26% of the 1994 model respectively 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). Estimates of *B* and *P/B* were based on ICES stock assessment data for this stock. The *B* was estimated from the *L/B* ratio for the whole stock and *L* for VIIe. Diet composition was taken from data collected in the North Sea (Daan 1989).

1973 and 1985 models: The time series catch data for the channel shows a very different trend than 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 overwintering 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). Hence, mackerel had to be split into the regular component and the overwintering mackerel during the 70s and early 80s.

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 (see section 3.6 for additional comments about the biomass estimation procedure);

b) The overwintering mackerel component was in the Channel until 1984. From 1973 to 1984, the biomass and catch "excess" was put in the overwintering group. According to Lockwood (1988), mackerel do not eat during the overwintering 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 for the 1973 model of the regular component was estimated to be 1.2 times higher than the 1994 model. In the 1985 model it was estimated to be 92% of the 1994 estimate.

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 VIIIa, b, d, e (ICES, 1999). B and P/B rate estimates were based on data for this stock. The B was estimated using an L/B ratio for the whole stock and L for VIIe.

The diet composition was based on studies from the southern Bay of Biscay (Olaso et al., 1999) and from the North Sea (Dahl, 1987).

1973 and 1985 models: The scad ICES VPA stock assessment goes back only until 1982. The biomass data from 1973 up to 1982 were estimated based on the MBA data. From 1982 onwards the data were estimated according to the trend of the whole stock. The biomass for 1973 was estimated to be 88% of 1994 model. For 1985 it was 32% higher.

44. Bass (*Dicentrarchus labrax*).

1994 model: A value of B was estimated using the L/B ratio from Stanford and Pitcher (2004) who based their estimate on CFSG data, and L estimated for area VIIe. The P/B rate was estimated from an F (C/B) of 0.19 year^{-1} and an M of 0.24 year^{-1} estimated using Pauly's equation (Pauly, 1980). Diet composition of was taken from Cabral and Costa (2001) who give values for juveniles.

1973 and 1985 models: The B was estimated to be 1.3 and 1.1 times higher than 1994 respectively using MBA data.

45. Sharks.

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

1994 model: An estimate of *B* and the landings of this group were taken from Stanford and Pitcher (2004). The *P/B* rate was estimated from an *F* (*C/B*) of 0.06 year^{-1} and an *M* of 0.18 year^{-1}, which was estimated using Pauly's equation (Pauly, 1980) (average for tope shark, porbeagle and blue shark). The *Q/B* rate was averaged for tope shark, porbeagle and blue shark. Diet composition for tope shark was taken from data collected in the Irish Sea (Ellis et al., 1996). Porbeagle and blue shark diet compositions were taken from data collected in the northwest Atlantic (Bowman et al., 2000).

1973 and 1985 models: The biomass for 1973 was estimated to be 2.29 times and landings 2 times higher than in 1994 according to Stanford and Pitcher (2004). These estimates were based on CPUE data for blue shark taken from Vas (1990). The fishing mortalities used for 1991 to 1999 were set as the average of the estimates from 1980 to 1990. It was done because the reported landings in the last years of the series were too low, resulting in a very low level of fishing mortality. For the 1985 version of the model the biomass was set as 50% higher than the 1994 level.

46. Basking Shark. (*Cetorhinus maximus*).

All parameters were taken from Stanford and Pitcher (2004).

47. Cephalopods.

This group included cuttlefish *Sepia officinalis*, *Loligo forbesi*, *L. vulgaris* and *Illex coindetii*.

1994 model: A value of B was estimated from a catch rate estimated for cephalopods, mainly *S. officinalis*, using data collected during the *RV Corystes* 2002 beam trawl survey in the Western Channel plus the catch rates estimates for *Loligo* spp. in the Eastern Channel and available from Stanford and Pitcher (2004) (based on data from Robin et al., 1998). The P/B rate was estimated from an F (C/B) of 0.37 year^{-1} and an M of 1.69 year^{-1} (averaged by biomass). The estimate of M 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. elliptica* from Rao et al. (1993). The Q/B rate was taken from Pauly and Christensen (1996). Diet composition data were extracted from Stanford and Pitcher (2004).

1973 and 1985 models: The biomass was assumed to be about 70% and 85% of the 1994 model respectively.

48. Birds.

This group included fulmar *Fulmarus glacialis*, manx shearwater *Puffinus puffinus*, storm petrel *Hydrobates pelagicus*, gannet *Sula bassana*, cormorant

Phalacrocorax carbo, arctic skua *Stercorarius parasiticus* and Mediterranean gull *Larus melanocephalus*.

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

1973 model: The biomass was 10% lower than the 1994 model, assuming that the smaller quantity of discards would be correlated with fewer birds.

49. Toothed cetaceans.

This group included 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 and 1985 models: The biomass was 1.5 times higher than 1994 assuming a lower level of incidental fishing mortality and higher prey availability.

50. Seals.

This group included grey seals *Haliochoerus grypus* and harbour seals *Phoca vitulina*.

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

1973 and 1985 models: The biomass was 1.5 times higher than 1994 assuming higher prey availability.

2.5. Comparisons 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. Some of them are used to describe the degree of ecosystem maturity and stability (*sensu* Odum, 1969). A selection of these estimated parameters were used to compare the state of the Western Channel ecosystem in the three periods modelled. A description of the parameters used is given in the next paragraphs.

Trophic levels - The concept of trophic level was introduced by Lindeman (1942). These trophic levels are integers (i.e, 1, 2, 3, etc...). However, most species feed at several levels in the food web, therefore Odum and Heald (1975) proposed the use of fractional trophic levels (i.e., 1.3, 2.7, etc.) to better represent this fact. Ecopath has a routine to estimate these fractional trophic levels. It assigns a trophic level of 1 to producers and detritus and a trophic level of 1 + (the weighted average of the preys' trophic level) to consumers. Another routine, based on an approach suggested by Ulanowicz (1995), reverses the routine for calculation of fractional

trophic levels, and then aggregates the entire system into discrete (integer) trophic levels.

Primary production required to sustain the catches – The fraction of primary production required to sustain the catches (*PPR*) is estimated in Ecopath as:

$$PPR = \sum_{paths} \frac{C_i}{P_i} \cdot \prod_{predator, prey} \frac{Q_{predator}}{P_{predator} EE_{predator}} \cdot DC_{predator, prey}$$

where *C* is the catch of a given group *i*, *P* is production, *Q* consumption, *EE* the ecotrophic efficiency and *DC* is the diet composition for each predator/prey pair in each path.

System omnivory index – 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 index is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The omnivory index (*OI*) is calculated as the variance of the trophic level of a consumer's prey groups as:

$$OI_j = \sum_{i=1}^{n} (TL_i - (TL_j - 1))^2 \cdot DC_{ji}$$

where TL_i is the trophic level of prey *i*, TL_j is the trophic level of the predator *j*, and DC_{ji} is the proportion prey *i* constitutes to the diet of predator *j*.

System throughput and transfer efficiency - Ecopath estimates import, consumption by predators, export, flow to detritus, respiration and throughput (the sum of all previous parameters) by discrete trophic levels (*sensu* Lindeman, 1942). 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 Finn's index - This 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 average path length - This is defined as the average number of groups that an inflow or outflow passes through (Finn, 1976). It is calculated as:

Path length = Total System Throughput / ($\sum$ Export + $\sum$ Respiration)

Besides the parameters described above, the models were compared using the estimates of primary production, ratio between primary production and respiration, sum of flow into detritus, total biomass, sum of all consumption, proportion of primary production that is consumed, fish biomass, average fish production, average *P/B* of fish groups, average exploitation rates (*F/Z*), total catches, fish catches and invertebrate catches.

2.6. Modelling food web interactions, variation in plankton production and fisheries from 1973 to 1999.

The Ecosim simulations run in this work were driven whenever possible by time series of fishing mortalities by functional group. The time-series of biomass, average weight (for split groups) and fishing mortalities (F) and catches (C) were estimated using the data sources cited in previous sections.

The catch time series of species or functional group was estimated as follows:

$$C_{ei} = \frac{C_{Ii}}{C_{I1994}} \cdot C_{1994}$$

where C_{ei} represents the estimated catches for the year i; C_{Ii} and C_{I1994} represent the catches available in the ICES database for year i and 1994 respectively and C_{1994} represents the estimated catches in the 1994 model (based on the BAHAMAS database, when available). This procedure was adopted because there were huge discrepancies between the landings of some species in the BAHAMAS database (Dintheer et al., 1995; Ulrich et al., 2002, Stanford and Pitcher, 2004) and the ICES database for the years 1993 to 1995. The rationale to adopt this procedure was that the data in the BAHAMAS database is considered the best information available and there was no accurate information for the other years of the series (Stanford and Pitcher, 2004).

The biomass time series for the species for which there are virtual population analysis (VPA) estimates available were estimated as:

$$B_{ei} = \frac{B_{Ii}}{B_{I1994}} \cdot B_{1994}$$

where B_{ei} represents the estimated biomass for the year i; B_{Ii} and B_{I1994} represent the biomass estimates in the ICES reports for the years i and 1994 respectively and B_{1994} represents the estimated biomass in the 1994 balanced model. This method was used to provide time series of biomass estimates for the stocks for which the assessment data include other ICES divisions besides the Western Channel (division VIIe). For example whiting (*Merlangius merlangus*) in the Western Channel is managed as part of the Celtic Sea stock (VIIe-k) (ICES, 2000a) and by doing it, we assumed that the abundance of the species in the Western Channel followed the same trend of the whole stock.

The MBA catch (log(number+1)) per unit of effort (CPUE) data was used as an index of abundance to roughly estimate the biomass variation for some fish groups that do not have biomass estimates derived from VPA and to complement VPA series for some species that did not cover the whole period. The MBA data used was split into three groups. The 1968 to 1979 average was used to represent the relative abundance in the 1973 model; the 1983 to 1986 average was for the 1985 year. As there was no MBA surveys data for the 1990s, we used the 2000 to 2001 average and in some cases the 1983 to 2001 average as a surrogate for the 1994 model relative abundance index. For species where there was no abundance estimate available, the ratio between the abundance in the 1973 and 1994 models were based on educated guesses (see section 3.4). After the reference year's biomass had been

estimated, a linear trend was calculated to fill in the years between them and to allow the time series of fishing mortality to be estimated. Although we estimated biomass values for all years in the series to allow the estimation of fishing mortalities, when the estimates were based on the MBA data or on educated guesses, only the reference years were used to fit the model. We did this to give less weight to these data in the fitting procedure. The fishing mortality series were then estimated as C/B as that is the way it is computed in the Ecopath software.

Time series data of the average annual phytoplankton colour index and the average annual zooplankton abundance for the Western Channel were available from the CPR program. A 3-year running mean was estimated to smooth the trend. The zooplankton data were used to estimate a biomass time series for the mesozooplankton, since we assumed that the main species in the data set (general group "small copepods", <2 mm) are mostly representative of this functional group. The phytoplankton data trend was used to estimate a biomass forcing function to drive the primary producers group in the Ecosim simulations (see below). The available biomass time series for all other groups were entered in the fitting procedure as absolute values, except zooplankton, for which the series was entered as relative values, which resulted in a lower weight for this group in the fitting procedure.

Values of annual biomass accumulation rates (-0.05 or +0.05) were included in most model groups for which the simulations were driven by time series of fishing mortality. The value was set according to the biomass trend in the years following 1973.

To analyse the relative roles of fishing, trophic interactions and system productivity to account for the observed changes in biomass of different functional groups we followed a similar procedure to that described by Shannon et al. (2004). Basically, we assessed the effects of fishing mortality, primary production changes and vulnerability parameters by using the following steps:

1) The Ecosim simulation was run from 1973 to 1999 applying constant fishing mortalities (F), i.e., using the 1973 model baseline estimates. Ecosim calculated a sum of squared deviations (SS) of log observed biomass from log predicted biomass that was recorded so that it could be compared to the SS estimated in subsequent steps. Therefore, a reduction in the SS represented an improvement in the model estimates.

2) The model was run with time-varying fishing mortalities.

3) The model was run with constant fishing mortalities and including the primary production biomass forcing (PBF).

4) The model was run with time-varying fishing mortalities and including the PBF.

5) Using the settings of step 4, the Ecosim non-linear tool was used to estimate the vulnerability parameters. To assess the effects of different starting values for the vulnerabilities, we ran the non-linear search tool 8 times, starting with the default value 2, and then trying 1.5, 3, 4 and so on up to 8 to estimate the average vulnerability of the prey to each predator, i.e., assuming that the vulnerabilities to a particular predator have the same value.

6) The biomass forcing was replaced by a primary production anomaly function (PAF) estimated by the non-linear tool to "drive" the production of the

primary producers group. The PAF was estimated using the vulnerability settings estimated in step 5.

7) Alternatively to steps 4-6, the Ecosim non-linear tool was used to estimate the vulnerability parameters without the inclusion of the PBF.

8) The Ecosim non-linear tool was used to estimate a PAF.

2.7.Relating plankton production with climate.

In this case, the vulnerabilities were estimated in a slightly different way than it was descried in the section 3.6. Using the vulnerabilities default setting, the Ecosim non-linear time-series fitting tool was used to estimate the primary production anomaly function (PAF) for the period from 1973 to 1999. This PAF was used to drive the primary production in the system and under this scenario the vulnerabilities were then estimated with the non-linear time-series fitting tool. The primary producers group biomass time series estimated by Ecosim was then regressed against the average SST. To check if the relationship between SST and the biomass series was not spurious due to autocorrelation, the data set was "detrended" by first-order differencing, i.e., the lagged value of the series was subtracted from its current value (Yaffee, 2000).

2.8.Fisheries policy optimization.

The economic data (Tables 15 and 16) used in the simulations and optimization runs for this work were taken from Ulrich (2000) and Stanford and Pitcher (2004).

The optimum policy search module of Ecosim was used to search for fishing fleets configurations to optimize four policy objectives: economic, expressed in terms of maximizing profits, social, expressed as maximizing the number of jobs, assumed to be proportional to the landed value by each fishing fleet or gear type, and ecosystem structure, set to maximize a index of ecosystem maturity (*sensu* Odum, 1969) calculated as the longevity-weighted summed biomass over ecosystem groupings. The ecosystem structure function uses the inverse of the *P/B* rate of each functional group, that is an index of longevity, as a weighting factor for the group biomasses (Christensen et al., 2004). A final compromise solution was determined given similar weights to the economic, social and ecosystem criteria.

The optimum policy search module uses a nonlinear optimization procedure known as the Davidson-Fletcher-Powell method to iteratively improve an objective function by running through a series of relative fishing effort rates. As any complex non-linear system can "get stuck" in local optima, 50-year trials were run at least 30 times with random starting values of fishing effort using the batch mode of operation (Christensen and Walters, 2004). Besides the "optimum" fishing rates, the batch mode estimates the total catches, the average *TL* of the catches, and a modified version of Kempton's index of diversity estimated as $Q_{75} = S/(2 \cdot \log(B_{75}/B_{25}))$. In this, B_{75} and B_{25} are the biomass values of the upper and lower 25 percentiles and S is the number of functional groups that fall within these percentiles (Christensen and Walters, 2004). The calculation of this index includes only groups with trophic levels equal to or higher than three as it is meant to focus on the exploited part of the ecosystem (Christensen and Walters, 2004).

In the batch mode, the program can vary the weights given to a goal function. For example, in the case of optimizing ecosystem structure, the routine was set to vary the weights from 0 to 1 in steps of 0.1, while the other two functions were kept with a fixed weight of 0.2. At least 300 trials were run, 30 trials for each step. The same procedure was repeated for the profit and employment optimization searches. The best solutions of each step were selected based on the value of the objective function being optimized, except in the case for the ecosystem criteria, where the results with a higher biodiversity index were selected. In previous applications of the Ecosim optimization module, a "compromise" or mixed objective solution has been explored by using equal weights for ecological, economic and social elements. However it has been shown (Mackinson, 2002; Ainsworth et al., 2004) that giving equal weights does not allow the ecological criteria to match the relative improvement of the social and the economic ones. Hence, besides using a "compromise solution" scenario run with the weights kept fixed at 1 for all three functions, the ecosystem batch trial results were used to select the best possible combination of weights, within the range used, for the ecosystem, social and economic criteria to represent a mixed solution. In addition, the optimization routine was also used to find the same relative change in fishing effort for all fleets, i.e., if for example the effort of one fleet is changed in 10%, the same relative amount is used for other fleets. This last optimization was run just under the maximum profit scenario, i.e., given a weight of 1 to the profit function and 0.2 to the landed value and ecosystem functions. All trials were run with the module default discount rate of 0.04/year and under the mode that allows the fleets to operate under economic loss.

The rationale is that although a fleet can operate under unprofitable conditions, the sum of profits across all fleets more than compensate for those losses.

All previous runs used the vulnerabilities estimated as described in section 3.7. To test for the effects of using different vulnerability settings, the three objective function optimizations were run in a scenario with the default vulnerabilities (=2) and another scenario with vulnerabilities proportional to trophic level of the predators, using a vulnerability of 2 for the lowest trophic level and 5 for the highest. The profits optimization to find the same relative change in fishing effort for all fleets was also run under these vulnerability settings.

For the purpose of seeing how forecasted changes in climate may affect the optimization process, a temperature derived forcing function was used to drive the primary producer biomass in additional runs of the policy search routine. The relationship between primary producer biomass predicted by Ecosim and SST as estimated in the section 3.7 was used to generate the forcing function. Hulme et al. (2002) forecasted that in 2080 SSTs of the Western Channel would be 1.5-4 $^{\circ}$C higher than the 1961-1990 average, depending on whether the low emissions or high emissions scenarios are used. These estimates give an average increase of 0.02 and 0.03 $^{\circ}$C/year, considering that the model was run over a 90 years period. The lower rate was used to generate a 50-years series of SST, starting in 1994, and then to estimate the forcing function that was applied using the nutrient loading forcing function option of Ecosim. For the sake of simplicity, the forcing function was applied only for the ecosystem structure batch runs and for the simple profit optimization runs when the model was set to find the same relative change in effort

for all gears. These two sets of trials were chosen for comparisons because they were the ones that produced the most reasonable results when the forcing function was not applied.

3. Results

3.1.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.

Table 1. Data uncertainty scores (%) for the Western Channel 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 Macrozooplankton	30	30	60	100	
5 Deposit feeders	30	30	60	100	
6 Suspension feeders	30	60	60	100	
7 Shrimp 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 crab	50	20	60	100	20
14 Lobster	70	20	60	100	20
15 Small-medium demersals	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	

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

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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.

3.2. 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 other large gadoids. These strong links seemed to be inaccurate. Estimates of predation mortalities from multi-species virtual population analyses (MSVPA) in the North Sea (Jørgensen and McLay, 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, which 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 2. Basic parameters for the 1994 Western Channel 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 is presented in brackets.

Group name	TL	Biomass (t/km²)	P/ B (/year)	Q/B (/year)	EE	P/Q
1Primary producers	1	118.9	24.8-		0.26-	
2Microzooplankton	2.06	2.629	45.28	120.00	0.66	0.38
3Mesozooplankton	2.16	5.871	39.08	80.00	0.53	0.49
4Macrozooplankton	3.16	1.100	18.00	38.00	0.03	0.47
5Deposit feeders	2	13.642	3.00	20.00	0.80	0.15
6Suspension feeders	2.61	5.070	0.30	2.00	0.27	0.15
7Shrimp and Prawns	2.43	5.549	3.96	13.20	0.90	0.30
8Whelks	3.05	0.365	0.64 (0.59)	8.03	0.90 (1.43)	0.08
9Echinoderms	2.23	8.826	0.66 (0.60)	6.94	0.90 (1.12)	0.10
10Bivalves	2	17.410	0.89	9.87	0.86	0.09
11Scallops	2	0.522	0.80	8.89	0.75	0.09
12Small-medium crabs	2.3	5.157	1.95 (1.8)	12.98	0.90 (1.23)	0.15
13Large crab	2.44	0.511	0.60	4.00	0.71	0.15
14Lobster	3.11	0.010	0.52 (0.5)	5.85	0.90	0.09
15Small-medium demersals	3.1	1.825	1.57 (1.43)	9.66	0.90	0.16
16Small gadoids	3.39	1.417 (1.165)	1.27 (1.17)	5.93	0.88 (1.61)	0.22
17Red mullet	3.3	0.169	0.52	5.70	0.90	0.09
18Juvenile sole	3.01	0.015	0.75	10.06	0.50 (1.99)	0.08
19Adult sole	3.01	0.044	0.43	5.18	0.59	0.08
20Juvenile plaice	3	0.025	1.51	11.82	0.45	0.13
21Adult plaice	3	0.034	0.76	4.18	0.67	0.18
22Dab	3.19	0.033	0.75	6.00	0.79 (1.61)	0.13
23Lemon sole	3.14	0.060	0.60 (0.59)	5.32	0.90 (1.30)	0.11
24Large flatfish	3.85	0.060	0.55	4.96	0.72	0.11
25Gurnards	3.4	0.286	0.57	5.76	0.83	0.10
26Juvenile whiting	3.29	0.035	1.60	14.89	0.87 (16.8)	0.11
27Adult whiting	4.07	0.122	0.79	5.63	0.39	0.14
28Juvenile cod	3.52	0.012	1.88	8.60	0.66 (6.95)	0.22
29Adult cod	3.96	0.016	0.99	3.46	0.57	0.29
30Hake	4.42	0.026	0.53 (0.51)	3.87	0.90 (5.14)	0.13
31Dogfish	3.42	0.401 (0.626)	0.38	4.77	0.26	0.08
32Rays	3.45	0.085	0.60	4.23	0.90	0.14
33Other gadoids	3.82	0.301 (0.171)	0.82 (0.66)	4.05	0.66 (5.9)	0.20
34Anglerfish	4.18	0.151 (0.189)	0.41	2.83	0.69	0.15
35Large bottom	4.01	0.111 (0.161)	0.46 (0.41)	3.06	0.90	0.14
36Seabreams	3.01	0.118	0.61 (0.58)	4.61	0.90	0.13
37John Dory	4.22	0.015 (0.01)	0.65	4.99	0.64	0.13
38Sandeels	3.13	2.936	1.29	10.14	0.90	0.13
39Herring	3.1	0.068 (0.057)	1.00 (0.85)	6.35	0.89 (22.65)	0.16
40Sprat	3.13	0.525	1.21	9.68	0.90	0.13
41Pilchard	3.12	0.688	0.64	7.92	0.80	0.08
42Mackerel	3.44	1.363	0.36 (0.35)	6.00	0.90	0.06
43Scad	3.58	0.704 (0.879)	0.39 (0.33)	5.56	0.90	0.07
44Bass	3.47	0.065	0.42	3.91	0.44	0.11
45Sharks	4.44	0.002	0.24	2.53	0.37	0.09
46Basking shark	3.16	0.034	0.07	3.70	0.00	0.02
47Cephalopods	3.54	0.466	2.19 (2.07)	15.00	0.90	0.15
48Birds	3.55	0.001	0.40	72.12	0.01	0.01
49Toothed cetaceans	4.42	0.00384 (0.006)	0.40	13.73	0.18	0.03
50Seals	4.66	0.002	0.04	13.32	0.18	0.003
51Discarded catch	1	0.300-	-		0.07-	
52Detritus	1	1-	-		0.20-	

Table 3. Additional data necessary to represent the ontogeny of split groups in the Western Channel models. K: curvature of the von Bertalanffy growth function; Age_m: age at transition to adult stage; W_m/W_∞ : ratio between age at maturity and asymptotic weight. Estimates for Age_m based on ICES (2000a), K and W_m/W_∞ based on ICES (2000a) and Froese and Pauly (2000).

Group	K (year^{-1})	Age_m (months)	W_m/W_∞
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 Western Channel model (unbalanced model values in brackets). Values indicate % composition for each predator species.

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 Macrozooplankton												
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 crab												
14 Lobster												
15 Small-medium demersals												
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 fishes												
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 Macrozooplankton		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 Shrimp 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 crab									
14 Lobster	1.1 (1)								
15 Small-medium demersals	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 fishes									
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

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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 Macrozooplankton					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 Shrimp 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 crab								
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 fishes								
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 Macrozooplankton										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 Shrimp 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 crab	0.1	3.4 (3.2)								
14 Lobster										
15 Small-medium demersals	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 fishes							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	

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 Macrozooplankton		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 Shrimp 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 crab										
14 Lobster										
15 Small-medium demersals			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 fishes										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

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Table 5. Fisheries landings (t/km^2) in the 1994 Western Channel 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 Whelk						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 crab	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 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 fishes	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 the 1994 Western Channel model.

Group/Fleet	Otter trawl	Beam trawl	Pelagic trawl	Dredge	Net	Total
8 Whelk		1.48E-02				1.48E-02
12 Crab		1.10E-02				1.10E-02
13 Commercial crab	5.24E-04	1.76E-03		9.42E-04		3.22E-03
14 Lobster						
15 Small-medium demersals		4.23E-02				4.23E-02
16 Small gadoids	3.69E-02	4.81E-03				4.17E-02
17 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 fishes					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

3.3. Balancing the 1973 and 1985 models

The balanced 1994 model was used as a base upon which to build the 1973 and 1985 models by changing the parameters as described in the sections 3.4 and 3.5. They were balanced following the same approach used to balance the 1994 model using the automatic mass balance tool. For the 1973 model, 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 the biomass of the unbalanced groups by approximately 50%. In the 1985 model, besides of having to use the auto-balance routine as described above, the *P/B* of lemon sole was increased by 30% because of a higher fishing mortality. After these changes, sprat and pilchard were still unbalanced and their biomasses were increased by 140% and 100% respectively. There is no 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 Western Channel 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/km²)	P/ B (/year)	Q/B (/year)	EE	P/Q	C
1 Primary producers	1	80	24.8-		0.185-		1.00E-05
2 Microzooplankton	2.06	1.052	45.28	120.00	0.795	0.38	
3 Mesozooplankton	2.16	2.348	39.08	80.00	0.853	0.49	
4 Macrozooplankton	3.16	0.440	18.00	38.00	0.091	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 Shrimp and Prawns	2.43	4.885	3.96	13.20	0.90	0.30	2.51E-02
8 Whelks	3.05	0.548	0.64	8.03	0.06	0.08	2.45E-04
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	2.17E-01
11 Scallops	2	0.783	0.80	8.89	0.60	0.09	3.74E-01
12 Small-medium crabs	2.3	5.157	1.95	12.98	0.76	0.15	
13 Large crab	2.44	0.766	0.60	4.00	0.36	0.15	1.28E-01
14 Lobster	3.1	0.015	0.52	5.85	0.48	0.09	2.81E-03
15 Small-medium demersals	3.09	1.02 (0.692)	1.57	9.66	0.90 (1.94)	0.16	2.20E-02
16 Small gadoids	3.36	0.78	1.27	5.93	0.92 (1.29)	0.21	3.26E-02
17 Red mullet	3.22	0.077	0.52	5.70	0.90 (1.29)	0.09	9.90E-03
18 Juvenile sole	3.01	0.017	0.75	10.06	0.34	0.07	1.64E-03
19 Adult sole	3.01	0.049	0.43	5.18	0.33	0.08	6.80E-03
20 Juvenile plaice	3	0.016	1.51	11.82	0.49	0.13	4.70E-03
21 Adult plaice	3	0.021	0.76	4.18	0.66	0.18	8.31E-03
22 Dab	3.19	0.047	0.75	6.00	0.66	0.13	1.07E-02
23 Lemon sole	3.14	0.038	0.60	5.32	0.90 (1.11)	0.11	1.33E-02
24 Large flatfish	3.83	0.132	0.37	4.96	0.22	0.07	5.97E-03
25 Gurnards	3.34	0.400	0.57	5.76	0.68	0.10	1.34E-01
26 Juvenile whiting	3.29	0.016	1.60	14.89	0.90 (1.58)	0.11	1.77E-03
27 Adult whiting	4.05	0.055	0.79	5.63	0.51	0.14	2.11E-02
28 Juvenile cod	3.45	0.007	1.62	8.67	0.90 (1.18)	0.19	2.55E-03
29 Adult cod	3.92	0.017	0.81	3.46	0.59	0.23	8.16E-03
30 Hake	4.4	0.045	0.53	3.87	0.59	0.14	1.00E-02
31 Dogfish	3.36	0.277	0.38	4.77	0.02	0.08	1.91E-03
32 Rays	3.4	0.239	0.60	4.23	0.31	0.14	4.44E-02
33 Other gadoids	3.76	0.223	0.83	4.05	0.76	0.20	1.69E-02
34 Anglerfish	4.16	0.128	0.23	2.83	0.63	0.08	1.04E-02
35 Large bottom fishes	3.95	0.274	0.25	3.06	0.45	0.08	2.03E-02
36 Seabreams	3.01	0.177	0.61	4.61	0.70	0.13	5.28E-02
37 John Dory	4.21	0.011	0.65	4.99	0.06	0.13	4.09E-04
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	1.35E-02
40 Sprat	3.13	0.292 (0.195)	1.21	9.68	0.90 (2.56)	0.12	2.57E-02
41 Pilchard	3.12	0.406	0.64	7.92	0.95 (1.45)	0.08	2.32E-02
42 Mackerel	3.4	1.636	0.36	6.00	0.40	0.06	9.58E-02
43 Scad	3.54	0.62	0.39	5.56	0.90 (1.07)	0.07	1.74E-01
44 Bass	3.39	0.083	0.42	3.91	0.01	0.11	3.52E-04
45 Sharks	4.36	0.004	0.24	2.53	0.36	0.09	2.40E-04
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	4.65E-02
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	1.07E-04
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 Western Channel model (unbalanced model values in brackets). Values indicate % composition for each predator species.

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 Macrozooplankton														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 Shrimp 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 demersals													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 fishes														
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 Macrozooplankton										
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 Shrimp 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 crab										
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 Adult 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 fishes										
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

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

Table 9. Basic parameters for the 1985 Western Channel 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/km²)	P/B (/year)	Q/B (/year)	EE	P/Q	C
1 Primary producers	1	87.5	24.8-		0.35-		1.07E+00
2 Microzooplankton	2.06	2.629	45.28	120.00	0.64	0.38	
3 Mesozooplankton	2.16	5.871	39.08	80.00	0.53	0.49	
4 Macrozooplankton	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	0.29	0.15	
7 Shrimp and Prawns	2.43	5.570	3.96	13.20	0.91	0.30	2.10E-03
8 Whelks	3.05	0.365	0.64	8.03	0.44	0.07	1.01E-01
9 Echinoderms	2.23	8.826	0.66	6.94	0.87	0.09	
10 Bivalves	2	17.410	0.89	9.87	0.85	0.09	3.00E-02
11 Scallops	2	0.522	0.80	8.89	0.43	0.09	1.78E-01
12 Small-medium crabs	2.3	5.157	1.95	12.98	0.88	0.15	2.47E-03
13 Large crab	2.44	0.620	0.60	4.00	0.64	0.15	2.13E-01
14 Lobster	3.11	0.012	0.52	5.85	0.74	0.09	3.79E-03
15 Small-medium demersals	3.1	1.579	1.57	9.66	0.96 (1.02)	0.15	4.10E-02
16 Small gadoids	3.37	**1.173 (1.020)**	1.27	5.93	0.95 (1.36)	0.22	4.04E-02
17 Red mullet	3.3	0.140	0.52	5.70	0.95	0.09	3.90E-03
18 Juvenile sole	3.01	0.031	0.80	9.85	0.39	0.08	6.20E-03
19 Adult sole	3.01	0.063	0.54	5.18	0.59	0.08	2.00E-02
20 Juvenile plaice	3	0.042	1.65	12.02	0.37	0.13	1.71E-02
21 Adult plaice	3	0.049	0.66	4.18	0.54	0.18	1.53E-02
22 Dab	3.19	0.062	0.75	6.00	0.66	0.13	1.39E-02
23 Lemon sole	3.14	0.066	0.77 (0.60)	5.32	0.95 (1.30)	0.11	3.54E-02
24 Large flatfish	3.84	0.120	0.55	4.96	0.41	0.11	2.25E-02
25 Gurnards	3.37	0.472	0.57	5.76	0.39	0.10	7.38E-02
26 Juvenile whiting	3.29	0.017	1.80	14.24	0.94 (1.63)	0.11	1.69E-03
27 Adult whiting	4.06	0.033	1.00	5.63	0.50	0.14	1.53E-02
28 Juvenile cod	3.51	0.010	1.95	9.24	0.95 (1.04)	0.21	7.11E-03
29 Adult cod	3.94	0.018	0.81	3.46	0.76	0.23	1.10E-02
30 Hake	4.44	0.039	0.53	3.87	0.71	0.13	8.68E-03
31 Dogfish	3.41	0.394	0.38	4.77	0.25	0.08	3.74E-02
32 Rays	3.45	0.150	0.60	4.23	0.51	0.14	4.54E-02
33 Other gadoids	3.76	0.556	0.83	4.05	0.36	0.20	4.85E-02
34 Anglerfish	4.17	0.248	0.41	2.83	0.77	0.15	7.04E-02
35 Large bottom fishes	3.96	0.236	0.46	3.06	0.54	0.14	4.79E-02
36 Seabreams	3.01	0.058	0.61	4.61	0.95	0.13	9.08E-03
37 John Dory	4.25	0.012	0.65	4.99	0.27	0.13	2.13E-03
38 Sandeels	3.13	3.240	1.29	10.14	0.95	0.13	
39 Herring	3.1	0.066	1.00	6.35	0.92	0.16	1.92E-03
40 Sprat	3.13	**0.333 (0.138)**	1.21	9.68	0.95 (3.79)	0.13	4.44E-02
41 Pilchard	3.12	**0.361 (0.179)**	0.64	7.92	0.95 (3.54)	0.08	2.87E-02
42 Mackerel	3.42	1.250	0.36	6.00	0.81	0.06	2.45E-01
43 Scad	3.57	0.932	0.39	5.56	0.39	0.07	4.59E-02
44 Bass	3.47	0.072	0.42	3.91	0.42	0.11	1.28E-02
45 Sharks	4.41	0.003	0.24	2.53	0.58	0.09	3.15E-04
46 Basking shark	3.16	0.034	0.07	3.70	0.00	0.02	
47 Cephalopods	3.49	0.391	2.19	15.00	0.95	0.14	6.35E-02
48 Birds	3.51	0.001	0.40	72.12	0.02	0.01	
49 Toothed cetaceans	4.41	0.006	0.40	13.73	0.11	0.03	1.36E-04
50 Seals	4.64	0.003	0.04	13.32	0.17	0.003	
51 Discarded catch	1	0.222-	-		0.10-	
52 Detritus	1	1-	-		0.26-	

Table 10. Diet matrix for the 1985 Western Channel model (unbalanced model values in brackets). Values indicate % composition for each predator species.

Prey \ Predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1Prim. producers	94.7	78.3			10.0	8.5		5.1	50.0	50.0			8.6	0.002
2Microzooplankton	5.3	9.8			15.0	12.5								0.01
3Mesozooplankton		4.9	100.0		30.0	23.5								0.01
4Macrozooplankton														0.03
5Deposit feeders					10.0	3.0	73.5	11.2					11.9	59.1
6Suspension feed								0.5					3.3	0.04
7Shrimp and Prawns							5.6				14.6	15.2	0.3	11.5
8Whelk													0.4	
9Echinoderms							5.6	4.8					3.4	11.4
10Bivalves							11.2	5.1			8.4	20.3	24.7	14.1
11Scallops														
12Crab							4.1				0.7	1.2	45.5	2.4
13Commercial crab														
14Lobster													1.1	
15Small demersals													0.9	1.4
16Small gadoids														
17Mullet														
18Sole Juv														
19Sole Ad														
20Plaice Juv														
21Plaice Ad														
22Dab														
23Lemon sole														
24Large Flatfish														
25Gurnards														
26Whiting Juv														
27Whiting Ad														
28Cod Juv														
29Cod Ad														
30Hake														
31Dogfish														
32Rays														
33Other gadoids														
34Monkfishes														
35Large bottom fishes														
36Seabreams														
37John Dory														
38Sandeels														
39Herring														
40Sprat														
41Pilchard														
42Mackerel														
43Scad														
44Bass														
45Sharks														
46Basking shark														
47Cephalopods														
48Seabirds														
49Tooth. cetaceans														
50Seals														
51Discarded catch														
52Detritus		7.0		100.0	35.0	52.5		73.3	50.0	50.0	76.2	63.2		
53Import														
54Sum	100	100	100	100	100	100	100	100	100	100	100	100	100	100

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Table 10. Continued.

Prev \ 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	3.1							1.6 (1.5)	0.02	
4 Macrozooplankton										
5 Deposit feeders	7.0 (6.8)	48.4	84.6	84.5	48.4	48.4	65.8	68.5 (68)	5.7	25.0 (24.4)
6 Suspension feeders			1.0	1.0			19.7	3.8	0.02	
7 Shrimp and Prawns	49.8 (48.9)	15.7			0.5	0.5	3.4		18.9 (18.2)	45.2 (44.1)
8 Whelks										
9 Echinoderms	0.03	1.7			0.5	0.5	0.02	2.6 (2.5)		
10 Bivalves	8.7 (8.6)	1.3	12.7	12.7	50.6	50.6	6.4	13.3 (13.2)	0.1	0.3
11 Scallops										
12 Small-medium crabs	21.9 (21.5)	17.2	1.8	1.8			1.3		8.7 (8.3)	22.0 (21.5)
13 Large crab										
14 Lobster										
15 Small-medium demersals	4.2 (5.6)	15.7							62.0 (59.5)	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	0.05 (0.1)									0.1 (0.3)
27 Adult 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 fishes										
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 (3.8)	
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			5.0 (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

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Table 10. 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	2.9 (2.8)			3.4	17 (15.5)	
4 Macrozooplankton		0.2							
5 Deposit feeders	30.9	3.6 (3.2)	8.4	5.6 (5.3)	0.01	24.7 24.4	12.8	8.5 (7.8)	
6 Suspension feeders		0.3	0.1	0.1		1.4		0.1	
7 Shrimp and Prawns	64.4	2.3 (2.3)	47 (46.9)	0.4	0.3	5.9	26.4	3.5 (3.2)	
8 Whelks			0.1			1.4			
9 Echinoderms		0.1	0.03	0.3		2.0	0.2	6 (5.5)	
10 Bivalves		0.02 (0.01)	1.4 (1.3)	0.1		1.5	0.2	1.5 (1.3)	
11 Scallops									
12 Small-medium crabs	4.7	3.3 (2.9)	21.0	24 (22.9)		46.7 (46.1)	36.8	3.2 (2.9)	16.2 (16)
13 Large crab						0.1	3.4		
14 Lobster									
15 Small-medium demersals			18.0	21.4 (20.4)	0.3	4.0	11.0		10.1 (10)
16 Small gadoids		30.9 (27.3)	0.2 (0.4)	9.2 (8.8)	30.9 (28)	4.1	0.1 (0.2)	6.8 (13.6)	66.7 (65.8)
17 Red mullet									
18 Juvenile sole		0.01		0.3		0.1			
19 Adult sole									
20 Juvenile plaice				4.5 (4.3)		0.2			
21 Adult plaice									
22 Dab		0.02	0.4	3.6 (3.5)		0.4	0.1	0.05	0.7
23 Lemon sole				0.2					0.3 (1.4)
24 Large flatfish					0.6 (0.5)				
25 Gurnards					0.9 (0.8)				
26 Juvenile whiting		0.8 (1.4)	0.1	3.7 (7.4)	0.5 (0.4)	0.2 (0.4)	0.003	0.001	0.8 (1.6)
27 Adult whiting				1.8 (1.7)					
28 Juvenile cod		0.1	0.01	4.6 (4.4)				0.01	0.2
29 Adult cod									
30 Hake						0.1			
31 Dogfish									
32 Rays							0.01		
33 Other gadoids		7.4 (13.2)		6.8 (0.5)	5 (4.6)	0.4	0.1	0.3	
34 Anglerfish									
35 Large bottom fishes									
36 Seabreams									
37 John Dory									
38 Sandeels		26.6 (23.5)	2.8	4.8 (4.6)		1.1 (1.1)	1.5	50.3 (45.9)	
39 Herring		0.7 (0.6)		0.2	0.2	0.4	0.002	0.4 (0.3)	0.6
40 Sprat		9.8 (19.7)	0.03 (0.06)	0.8 (1.4)	3 (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)	25.1 (22.8)		1.7		2.2 (2.1)
43 Scad					27.4 (24.9)				
44 Bass									
45 Sharks									
46 Basking shark									
47 Cephalopods		2.1 (1.9)	0.4	2.5 (2.4)	0.3	4.1	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 10. Continued.

Prey \ Predator	35	36	37	38	39	40	41	42	43	44
1 Primary producers										
2 Microzooplankton					60.0	39.5	40.0	3.8	1.9 (1.8)	
3 Mesozooplankton				80.5	40.0	59.2	60.0	66.3 (65.2)	17.9 (17.4)	
4 Macrozooplankton						1.3		5.0	4.9 (4.8)	
5 Deposit feeders		98.4		19.5				0.9	10.1 (9.8)	20.7
6 Suspension feeders			0.04 (0.03)							
7 Shrimp and Prawns	10 (7.4)	0.9	1.3 (1)					1.1	39.9 (38.9)	58.9
8 Whelks										
9 Echinoderms			0.02 (0.01)							
10 Bivalves		0.3								0.3
11 Scallops										0.03
12 Small-medium crabs	20 (14.9)	0.3						1.5		1.4
13 Large crab										
14 Lobster										
15 Small-medium demersals	16 (11.9)		48.5 (36.1)						0.6	18.7
16 Small gadoids	7 (5.2)							1.2 (2.4)	5.5 (5.4)	
17 Red mullet										
18 Juvenile sole										
19 Adult sole										
20 Juvenile plaice										
21 Adult plaice										
22 Dab								0.002		
23 Lemon sole	0.9 (0.7)									
24 Large flatfish			0.7 (0.5)							
25 Gurnards									0.6	
26 Juvenile whiting	0.2							0.001	0.03 (0.05)	
27 Adult whiting										
28 Juvenile cod	0.2 (0.1)							0.003 (3.2)	0.02	
29 Adult cod										
30 Hake									0.1	
31 Dogfish										
32 Rays										
33 Other gadoids	6.2 (4.6)		2.7 (2)					0.0002	0.5	
34 Anglerfish										
35 Large bottom fishes			4.2 (3.1)							
36 Seabreams										
37 John Dory										
38 Sandeels	4.6 (3.4)		0.7 (0.5)					18 (17.7)	14.8 (14.4)	
39 Herring	1.1 (0.8)							0.1	0.2 (0.3)	
40 Sprat	17.1 (23.6)							0.5 (1)	1.3 (2.5)	
41 Pilchard	11.8 (23.6)		20.3 (40.7)						1.3 (2.5)	
42 Mackerel								0.1		
43 Scad			21.2 (15.8)							
44 Bass										
45 Sharks										
46 Basking shark										
47 Cephalopods	4.8 (3.6)		0.4 (0.3)					1.3 (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

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Table 10. Continued.

Prey \ Predator	45	46	47	48	49	50
1 Primary producers			5.7 (5.3)			
2 Microzooplankton						
3 Mesozooplankton		30.0		2.5 (2.5)		
4 Macrozooplankton						
5 Deposit feeders	1.0		0.4 (0.3)	3.6 (3.4)		
6 Suspension feeders						
7 Shrimp and Prawns						
8 Whelks						
9 Echinoderms	0.2					
10 Bivalves					0.1	
11 Scallops						
12 Small-medium crabs			64.5 (60.4)	3.6 (3.4)		
13 Large crab						
14 Lobster						
15 Small-medium demersals	4.9		13.7 (16.4)			3.6
16 Small gadoids	3.4		2.2 (4.4)	0.1		1.0
17 Red mullet			1.1			
18 Juvenile sole			0.01			
19 Adult sole						0.3
20 Juvenile plaice	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	3.6 (3.5)					
26 Juvenile whiting					0.6	1.3
27 Adult whiting						
28 Juvenile cod				1.1 (1)	0.6	0.8
29 Adult cod						
30 Hake						
31 Dogfish	1.1					
32 Rays						
33 Other gadoids					1 (0.9)	4.2
34 Anglerfish						20.7
35 Large bottom fishes						20.7
36 Seabreams			0.3		8.1 (7.3)	
37 John Dory						
38 Sandeels			8.6 (8.1)	40.7 (38.2)		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	12.7 (12.5)		0.5 (0.4)	12.2 (11.4)	10 (9)	4.4
43 Scad	7.1 (6.9)		0.6		10 (9)	1.9
44 Bass						
45 Sharks	1.1					
46 Basking shark						
47 Cephalopods	56.8 (56.9)		2.3 (2.7)		60.2 (54.2)	6.1
48 Birds	0.1					
49 Toothed cetaceans	1.5 (1.4)					
50 Seals	0.3					
51 Discarded catch	1.5			24.6 (23.1)		
52 Detritus						
53 Import		70.0		6.2		
54 Sum	100	100	100	100	100	100

3.4.Sensitivity analysis

There are different formal ways to perform a sensitivity analysis in Ecopath. The Ecopath sensitivity analysis 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, an 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 is far less significant and typically does not exceed 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 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 2. Figure 2a 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 2b

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 group 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.

Figure 2. Frequency distribution of the four basic parameters of (a) large crabs and (b) cephalopods in the Ecoranger successful runs for the 1994 Western English Channel.

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 3). 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 4).

Figure 3. Plaice population dynamics in the 1994 Western English Channel model: a) stock-recruitment relationship, b) biomass trend and c) adult plaice fishing mortality. Vulnerability of prey to juveniles = 2, juveniles P/B = 1.51 year^{-1}, K = 0.08 year^{-1}.
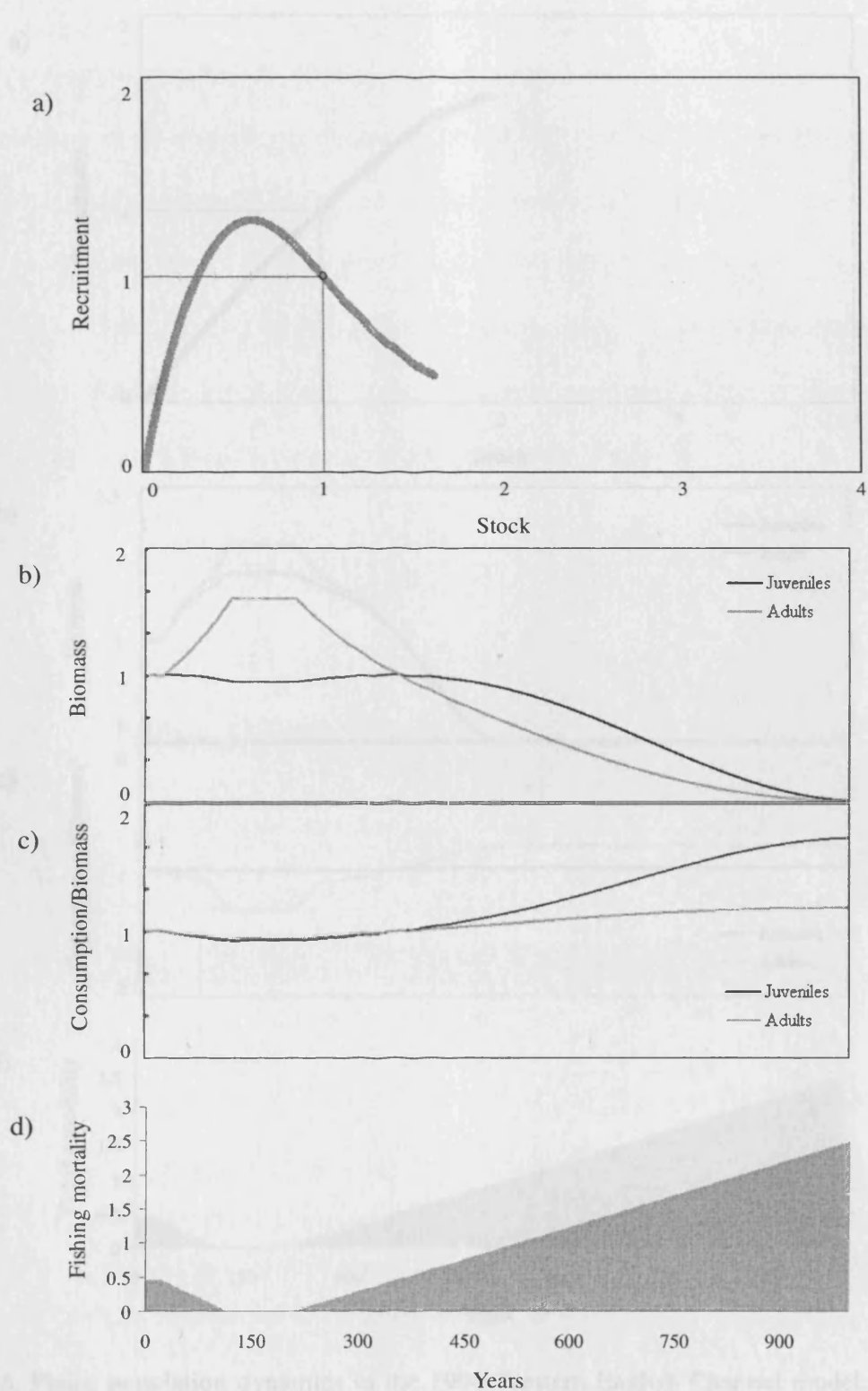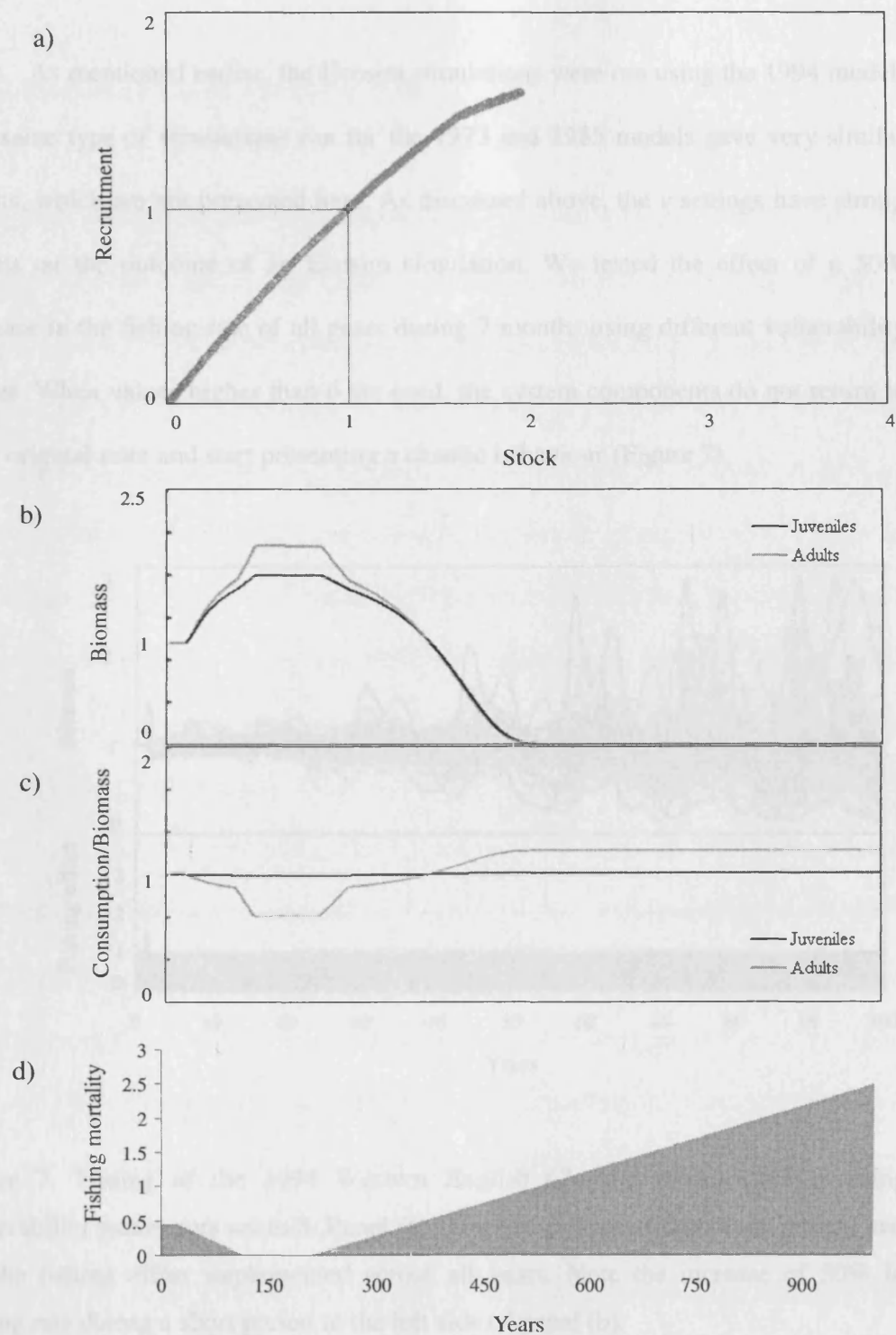
Figure 4. Plaice population dynamics in the 1994 Western English Channel model:
(a) shows stock-recruitment relationship, (b) biomass trend, (c) consumption/biomass
trend and (d) adult plaice fishing mortality. Vulnerability of prey to juveniles = 2,
juveniles P/B = 1.4 year^{-1}, K = 0.12 year^{-1}.

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 5 and 6). 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 5c and 6c). 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 preys 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 that 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 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.

Figure 5. Plaice population dynamics in the 1994 Western English Channel model: (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 6. Plaice population dynamics in the 1994 Western English Channel model: (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}.

As mentioned earlier, the Ecosim simulations were run using the 1994 model. The same type of simulations run for the 1973 and 1985 models gave very similar results, which are not presented here. As discussed above, the v settings have strong effects on the outcome of an Ecosim simulation. We tested the effect of a 50% increase in the fishing rate of all gears during 7 months 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 7).

Figure 7. Testing of the 1994 Western English Channel 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 left side of panel (b).

3.5.Comparison of ecosystem properties

The parameters used to compare the three models of the Western Channel ecosystem are presented in the Table 11. Many of the parameters presented have increased from 1973 to 1994, reflecting an overall increase in the production of the system. The total system throughput, net primary production, sum of flow into detritus and total biomass (excluding detritus) were between 67-76% and 70-84% of the 1994 level in 1973 and 1985 respectively. The sum of all consumption was about 67% of the 1994 level in 1973, but in 1995 it was nearly the same. The proportion of primary production consumed was 18, 35 and 26% in 1973, 1985 and 1994 respectively. The increase in the primary production seemed to propagate to some extent to higher trophic levels. There was an increase in the total fish biomass, which was 85% of the 1994 level in the 1973 model and 1% higher in 1985. The average fish production followed a very similar pattern. It was 76% and 98% of the 1994 level in 1973 and 1985 level respectively. The average fish P/B was 90% and 97% in the past models, showing a small shift in the fish community to smaller, more productive fish species and/or an increase in the proportion of young individuals of slow-growing species. Total catches in 1973 and 1985 were respectively about 58% and 78% of 1994 values, almost the same changes were observed for the fish catches, that were in 1973 and 1985 about 57% and 73% of the 1994 level respectively. The invertebrate catches in 1973 were about 85% of 1994 values, but only 48% of that level in 1985 because there was a great decrease in the landings of bivalves and scallops from 1973 to 1985. Although the increase in catches could be somewhat related to an increase in overall increase in biomass of several species, it was also a

consequence of increased fishing pressure, as reflected in the average fishing exploitation rate (F/Z) for fish groups, that was 71% and 73% of the 1994 level in 1973 and 1985 respectively.

Table 11. Ecosystem indices for the Western Channel. (See the text for more detailed descriptions of the indices).

Parameter/year	1973	1985	1994	Units
Sum of all consumption	1071	1588	1590	t/km²/year
Sum of all flows into detritus	1954	2074	2683	t/km²/year
Sum of all respiratory flows	539	628	796	t/km²/year
Total system throughput	5010	5832	7223	t/km²/year
Sum of all production	2235	2642	3424	t/km²/year
Calculated total net primary production	1984	2170	2949	t/km²/year
Net system production	1445	1542	2153	t/km²/year
Total biomass (excluding detritus)	151.3	166.6	197.8	t/km²
Utilization of primary production	18	35	26	%
Total primary production/total biomass	13.1	13.02	14.9	
Total fish biomass	9.94	11.81	11.72	t/km²
Total fish production	8.9	11.4	11.7	t/km²/year
Average fish P/B	0.90	0.97	1.00	year
Average fish F/Z	0.21	0.22	0.29	year
Total catches	1.965	2.638	3.378	t/km²/year
Total fish catches	0.763	0.973	1.341	
Total inv. catches	0.663	0.375	0.778	t/km²/year
Mean trophic level of the catches	2.44	2.25	2.36	
Mean trophic level of the catches (exc. pp.)	2.78	3.11	3.07	
Mean trophic level of the fish landings	3.42	3.48	3.46	
Mean fish trophic level	3.31	3.32	3.30	
Primary production required for catches	7.6	13.4	12.7	%
Total primary production/total respiration	3.7	3.5	3.7	
System Omnivory Index	0.126	0.132	0.135	
Finn's cycling index		3.5	3.7	2.9 % of total throughput
Finn's mean path length		2.5	2.7	2.4 -

There was a small decrease in the trophic level of total landings between 1973 and 1985 because the large increase in landings for seaweeds. However, when seaweeds are not taken into account the mean trophic level has actually increased slightly. The mean trophic level of the fish landings followed a similar pattern; it was higher in the 1985 model than in the other two models. The relative abundances of some high trophic level fish groups such as hake, sharks and the large bottom fish group were higher in 1973 and 1985 than in 1994. Other species such as anglerfish and cod were lower in 1973 than in 1994 but higher in 1985, showing that there was an increasing trend from 1973 to 1985 and a decreasing trend from 1985 to 1994 (Fig. 8). A summary of the changes in fish biomass is presented in Figure 9. The species represented there were regrouped in 7 categories. Small demersal and small gadoids are as defined as in the original models; the pelagic category represents scad, mackerel, herring, sprat and pilchard; gadoids represent cod, whiting, hake and other gadoids; flatfish includes sole, plaice, lemon sole and large flatfish; large demersal includes anglerfish and the large bottom fishes group; the 'other group' includes all other fish groups, that are either demersal or benthopelagic, except the group sandeels and basking sharks. As reported before, the biomass of fish groups increased from 1973 to 1985 and decreased slightly in 1994. The pelagic species were the dominant ones among the species listed above in all models. However there was a small decrease from 1973 to 1985 and this category changed from being 42% in 1973 to 34% in 1985. In 1994 the biomass of the category increased again, and it represented 38% of the total. The gadoids, flatfish and large demersal groups increased from 1973 to 1985 and decreased from 1985 to 1994. They represented 15%, 19% and 12% in those years respectively. The small demersal and small gadoids increased through the years, represented 25%, 32% and 37%. The 'other'

fish category was slightly higher in 1985 than in 1973, but decreased in 1994. It

represented 18%, 15% and 13% respectively. The biomasses of these groups are split

into discrete trophic levels (*sensu* Lindeman, 1942) in Figure 10. The trophic level III

is the dominant one, but it decreased in importance in 1985 because the increase of

high trophic level species, when it represented about 66% of the biomass, while in
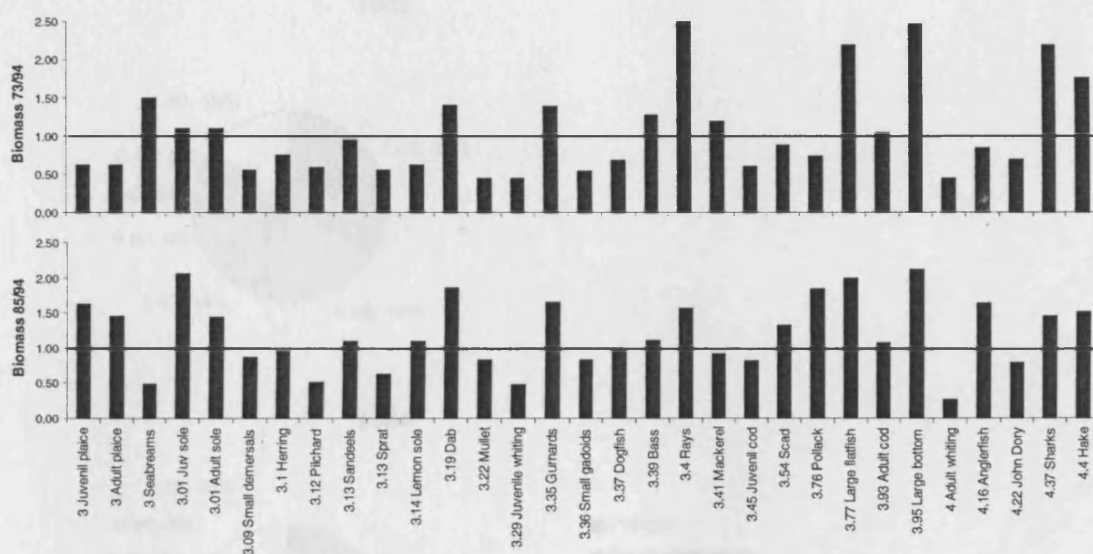
1973 and 1994 it represented about 68% and 70% respectively.

Figure 8. Biomass ratios between the 1973 and 1994 (upper panel) and between the 1985 and 1994 (lower panel) Western Channel models for all fish groups. The numbers next to group names are the estimated trophic levels.

1973

1.27; 18%

0.40; 6%

0.32; 4%

0.36; 5%

0.78; 11%

1.02; 14%

3.01; 42%

1985

1.30; 15%

0.48; 6%

0.43; 5%

0.67; 8%

1.17; 14%

1.58; 18%

2.93; 34%

1994

1.15; 13%

0.26; 3%

0.27; 3%

0.51; 6%

1.42; 16%

1.83; 21%

3.35; 38%

■ Pelagic
▧ Small demersals
▨ Small gadoids
▤ Gadoids
▨ Flatfish
▨ Large demersals
□ Other

Figure 9. Biomass of fish groups, except sandeels and basking shark, in the 1973, 1985 and 1994 Western Channel models. The original functional groups were put into 7 categories (see text for details). The values shown represent the biomass in t/km^2 and the percentage of the total fish biomass respectively.

1973

0.36; 5.0%

1.94; 27.1%

4.86; 67.9%

1985

0.47; 5.5%

2.41; 28.1%

5.69; 66.4%

1994

0.43; 4.9%

2.21; 25.2%

6.15; 69.9%

☐ V +
▨ IV
■ III

Figure 10. Biomass of fish groups, except sandeels and basking shark, split into trophic levels (*sensu* Lindeman, 1942) in the 1973, 1985 and 1994 Western Channel models. The values shown represent the biomass in t/Km^2 and the percentage of the total fish biomass respectively.

As a consequence of increased exploitation, the primary production to sustain the catches increased from 7.6% in 1973 to 13.4% in 1985, and then decreased to 12.7 in the 1994 model. These changes reflected the changes in fishing pressure and the relative dominance of groups of low and high trophic levels in the catches. The omnivory index was slightly higher in the 1994 model, suggesting a small change in the complexity of the food web. 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 was slightly smaller in 1985 than in the other two models, reflecting the increased abundance of some high trophic level species. The Finn's index was 20 and 27% higher than 1994 in 1973 and 1985 respectively. The average path length followed a similar pattern, being at its highest value in 1985.

The trophic aggregation routine estimated up to 10 trophic levels for all 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 1973 model and in all models they were at their highest levels for the flows that originated from primary producers. The proportion of the total flow originating from detritus was 50% in the 1973 model and 46% in the 1985 and 1994 models, which shows that the flows from detritus is almost as important as the flows from the primary production in this system.

Table 12. Transfer efficiencies (% of ingested food) between discrete trophic levels in the Western Channel models.

Trophic level	II	III	IV	V	VI	VII	VIII	IX	X	Geometric mean for TL II-IV
1994 model										
Producer	23.3	17.4	13.6	12.3	11.6	11	9.9			**17.7**
Detritus	13	12.4	11.5	10.7	10.1	9.8				**12.3**
All flows	19.1	16	13.2	12.1	11.4	10.9	9.9	9.8	7	**15.9**
Proportion of total flow originating from detritus: 0.46										
1985 model										
Producer	23.1	17.5	13.3	11.7	10.8	10.1	8.7			17.5
Detritus	13.1	12	10.4	9.5	8.8	8.4				11.8
All flows	19	16	12.7	11.4	10.6	9.9	8.7	8.5	8.1	15.7
Proportion of total flow originating from detritus: 0.46										
1973 model										
Producer	28.8	20.7	14.1	11.6	10.3	9.5	7.9			20.3
Detritus	11.5	10.8	9	8.1	7.5	7.1				10.3
All flows	18.7	17.2	13	11.2	10.1	9.3	7.9	7.3	4	16.1
Proportion of total flow originating from detritus: 0.5										

3.6. Modelling food web interactions, variation in plankton production and fisheries from 1973 to 1999.

Surprisingly, the inclusion of a time series of F (step 2) did not reduce the SS when compared to step 1 (Table 13). The use of the PBF with constant F (step 3) gave a better fitting than did step 2, but worse than in step 1. When the model was run with time series of F and the PBF (step 4) it resulted in a better fitting than for step 1. This version of the model was then used to estimate the vulnerabilities by further reducing the SS with the aid of the non-linear search tool (step 5).

Table 13. Ecosim runs for the Western Channel with the respective sum of squared deviations (SS) of log biomass from log predicted biomass. F = Fishing mortality; PBF = Primary producers biomass forcing, PAF = Primary producers' anomaly function, v's = vulnerabilities.

Step	Settings	SS
1	Constant F	70.92
2	Time varying F	84.84
3	Constant F + PBF	81.63
4	Time varying F + PBF	63.68
5a	Time varying F + PBF ⇒ v's	29.66
5b	Same as above but with an upper limit of 10 to v's	32.19
6	Time varying F + v's (from 5b) ⇒ PAF	26.32
7	Time varying F ⇒ v's	28.94
8	Time varying F + v's (from 7) ⇒ PAF	26.79

The final SS for each of the 8 runs of the non-linear search tool using different starting values were similar, probably because the vulnerabilities of the prey of some predators in these different runs were fairly constant. For example, the vulnerabilities of the prey of juvenile sole varied from 2.3 to 3.1. On the other hand,

some groups (mainly the groups that do not have any abundance "driver", i.e., fishing mortality) presented huge variations in the estimated vulnerabilities of their prey (Table 14). It shows that very different combinations for the vulnerabilities of the prey of some groups can result in fairly similar fittings.

We used the estimates from the run that started with the default settings and which gave the best fitting (step 5a in Table 13) to set an upper limit of 10 to the vulnerabilities, since higher values did not improve the fitting significantly and because the model was very unstable with these vulnerability settings when run in a no fishing scenario. The final SS was higher after these manipulations (step 5b in Table 13) but with these vulnerability settings the model presented a much more "stable behaviour" when run in a scenario with no fishing (results not shown). The final (capped) vulnerability settings are shown in the Table 14. The results show that the preys of most demersal fish groups tended to have higher vulnerabilities than the preys of the pelagic ones.

In the step 6, the model was run without the PBF and the non-linear search tool was used to estimate the PAF. This further improved the model fitting and the PAF showed a similar trend to the PBF's (see Fig. 11).

Finally, the SS estimated in step 7 shows that it was possible to improve significantly the fitting just by changing the vulnerabilities. The vulnerability for the prey of most groups estimated in this step were relatively similar to the ones of step 5a, but for the prey of 13 groups they differed by at least one order of magnitude. The PAF estimated in step 8 using the vulnerability settings from step 7 did not

approximate the PBF (results not shown). It implies that very different mechanism could well explain the observed variation in the biomass series.

The results of model simulations of the steps 5 and 6 for both biomass and catches are shown in figures 11 and 12 respectively. The time series data of the average annual phytoplankton colour index that was used to estimate the PBF shows an increasing trend from 1973 to 1999. The trend was not constant, showing oscillations throughout the period. Two main peaks are evident in the early 1980s and in the late 1990s respectively, with an additional but smaller peak in the late 1980s. Similarly, the zooplankton time series data shows a general increasing trend from 1973 to 1999, but the period of higher production is observed in the second half of the 1980s, coinciding with the smaller peak in the phytoplankton. Although the observed zooplankton abundance was much higher at the end than in the beginning of the series, a decreasing trend was shown over the last years, contrary to the trend shown by the phytoplankton series.

Many of the fish groups increased during these years, presenting a similar trend to the zooplankton production, with production peaking sometime during the 1980s and decreasing afterwards. For example, sole, plaice and cod, species for which there are time series of fishing mortalities derived from VPA, it is worth noting that even though F slightly increased, their biomass also increased for some time during the first years of the series. These observations suggest factors other than just fishing could be contributing to observed abundance changes for these commercial species. So, the improvement in the fit to the time series that resulted

from including the PBF shows that a bottom-up mechanism contributes to the production of high trophic levels.

Although the inclusion of the PBF improved the overall fit of the model to the biomass time series, the model generally overestimated the biomass and yield towards the end of the period. The replacement of the PBF by PAF improved somewhat the fitting. The primary production series in the PAF scenario roughly resembled the PBF ($r^2 = 0.194$, $p < 0.05$), but with lower estimates and presenting almost no trend towards the end of the period. This shows that increased primary production observed at the end of the series was not being converted into increased production for many higher trophic levels, including zooplankton, where the data from the CPR show a decreasing trend in the same period. The inclusion of the PAF also considerably improved the abundance estimates for the mesozooplankton group compared to the estimates of the PBF scenario, although the estimates show a much lower variability than the observed data ($r^2 = 0.188$, $p = 0.05$). The model also predicted a general increase of benthic, non-commercial species groups, using both PBF and PAF scenarios. The estimated trend for these groups roughly resembled the trend in the primary producers for each scenario.

Table 14. Prey-to-predator vulnerability parameter estimates for the Western Channel.

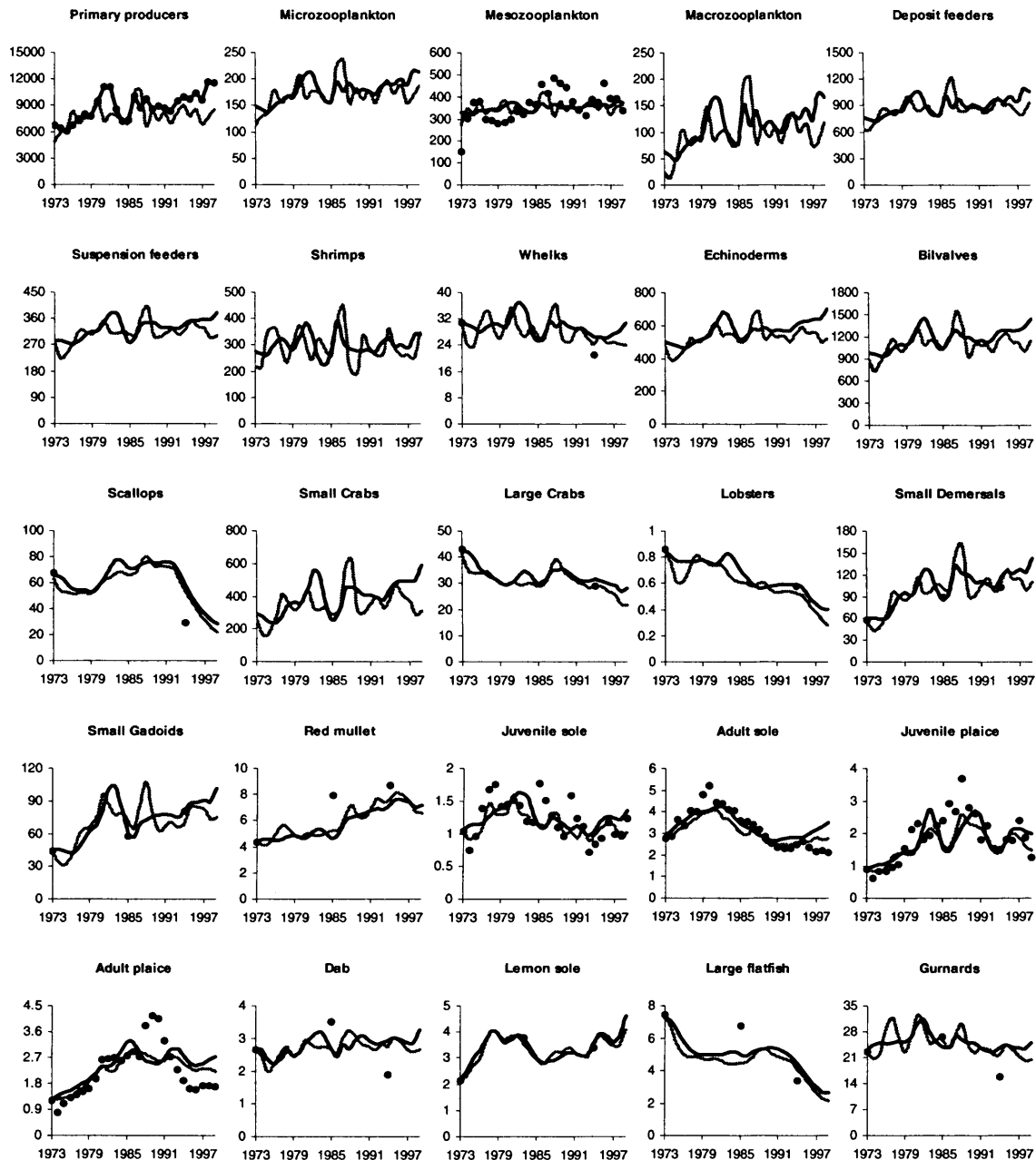| Predator/Starting v	1.5	2	3	4	5	6	7	8	Average v	SD	Final v
Microzoop.	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1	0	1
Mesozoop.	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1	0	1
Macrozoop.	12.1	10.7	16.7	20.2	>100	29.1	25.4	17.0	>100	>100	10
Deposit feeders	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1	0	1
Susp. feeders	1.0	1.0	1.0	>100	>100	>100	>100	>100	>100	>100	1
Shrimp/Prawns	1.7	1.7	1.5	1.9	3.1	4.1	4.4	1.0	2.4	1.3	1.7
Whelks	1	1.0	1.1	1.18	1.51	1.52	1.51	1.37	1.3	0.2	1.0
Echinoderms	>100	>100	>100	>100	>100	1.0	1.0	>100	>100	>100	2
Bivalves	>100	>100	>100	1.0	2.9	1.8	1.0	1.0	>100	>100	2
Scallops	>100	>100	>100	>100	>100	>100	>100	>100	>100	>100	2
S.M. crabs	94.9	41.3	>100	>100	2.0	3.5	3.0	1.0	>100	>100	10
Large crab	1.6	1.6	1.5	1.9	2.3	2.2	2.2	1.9	1.9	0.3	1.6
Lobster	1.4	1.5	1.6	1.5	1.6	1.5	1.4	1.4	1.5	0.1	1.5
S.M. demersals	4.5	4.7	3.3	4.5	2.2	3.0	2.6	4.9	3.7	1.1	4.7
Small gadoids	4.8	4.6	5.4	5.2	2.6	4.2	4.1	4.5	4.4	0.9	4.6
Red mullet	>100	>100	>100	>100	4.01	5.05	4.8	5.8	>100	>100	10
Juvenile sole	2.4	2.4	2.2	2.8	2.3	2.6	2.6	3.2	2.6	0.3	2.5
Adult sole	>100	>100	>100	>100	>100	>100	>100	>100	>100	>100	10
Juvenile plaice	8.1	8.7	5.4	8.0	5.5	6.9	8.1	6.7	7.2	1.3	8.7
Adult plaice	>100	>100	>100	>100	>100	>100	>100	>100	>100	>100	10
Dab	1	1	1	1	2.19	1.86	1.99	1	1.4	0.5	1
Lemon sole	5.0	5.0	3.9	4.1	3.9	7.0	6.7	7.2	5.3	1.4	5.0
Large flatfish	4.3	4.2	3.2	3.8	3.6	3.4	2.9	5.6	3.9	0.9	4.2
Gurnards	1.0	1.0	1.3	1.3	1.2	1.2	1.0	1.2	1.1	0.1	1
Juvenile whiting	19.3	30.3	>100	513	1.09	1	1.07	24.8	>100	>100	10
Adult whiting	1.2	1.2	1.2	1.16	>100	>100	>100	1	>100	>100	1.2
Juvenile cod	8.0	7.3	8.7	10.7	5.6	9.2	5.8	6.1	7.7	1.8	7.3
Adult cod	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1	0	1
Hake	4.6	4.5	7.3	5.8	3.9	4.3	6.7	5.2	5.3	1.2	4.5
Dogfish	3.8	3.1	6.2	6.5	11.7	14.2	12.8	9.2	8.4	4.2	3.1
Rays	1.8	1.8	1.7	1.6	1.8	1.7	1.7	1.7	1.7	0.1	1.8
Other gadoids	11.0	8.2	19.3	9.3	>100	>100	>100	43.9	>100	>100	8.2
Anglerfish	>100	>100	>100	>100	2.19	5.14	>100	>100	>100	>100	10
Large bottom	1.2	1.2	1.2	1.2	1.2	1.0	1.0	1.0	1.1	0.1	1.2
Seabreams	>100	>100	>100	>100	1	1	1	1	>100	>100	2
John Dory	>100	>100	2.1	1.2	2.5	1.7	1.0	18.5	>100	>100	5
Sandeels	3.7	4.2	2.6	2.9	2.5	1.0	1.0	2.5	2.5	1.1	4.2
Herring	1.8	1.6	2.2	1.9	5.2	3.3	3.8	2.4	2.8	1.2	1.6
Sprat	2.9	3.0	2.8	3.0	2.8	2.5	2.5	2.4	2.7	0.2	3
Pilchard	1	1	1	>100	>100	2.2	1	2.78	>100	>100	3
Mackerel	1.2	1.3	1.2	1.2	1.1	1.2	1.2	1.3	1.2	0.1	1.3
Scad	1.4	1.4	1.5	1.4	1.3	1.3	1.3	1.3	1.3	0.1	1.4
Bass	1.2	1.2	1.1	1.0	1.7	1.6	1.7	1.4	1.3	0.3	1.2
Sharks	2.0	2.0	1.7	1.7	1.5	1.4	1.4	1.5	1.7	0.2	2.0
Basking shark	>100	1	5.3	4	3.23	>100	3.96	13.9	>100	>100	2
Cephalopods	2.4	2.1	4.2	3.7	1.3	1.0	1.0	1.0	2.1	1.3	2.1
Birds	1.6	1.6	1	1	>100	>100	1.54	1	>100	>100	1.6
T. cetaceans	1	1	1	1	>100	>100	>100	>100	>100	>100	2
Seals	1	1	>100	>100	>100	>100	>100	>100	>100	>100	10

Figure 11. Biomass (thousands of tonnes) time series estimates for the Western Channel ecosystem from 1973 to 1999. Dots represent the input estimates; black lines represent Ecosim estimates using a scenario with primary producer biomass forcing (PBF) and grey lines are for the scenario using a primary producer anomaly function (PAF).
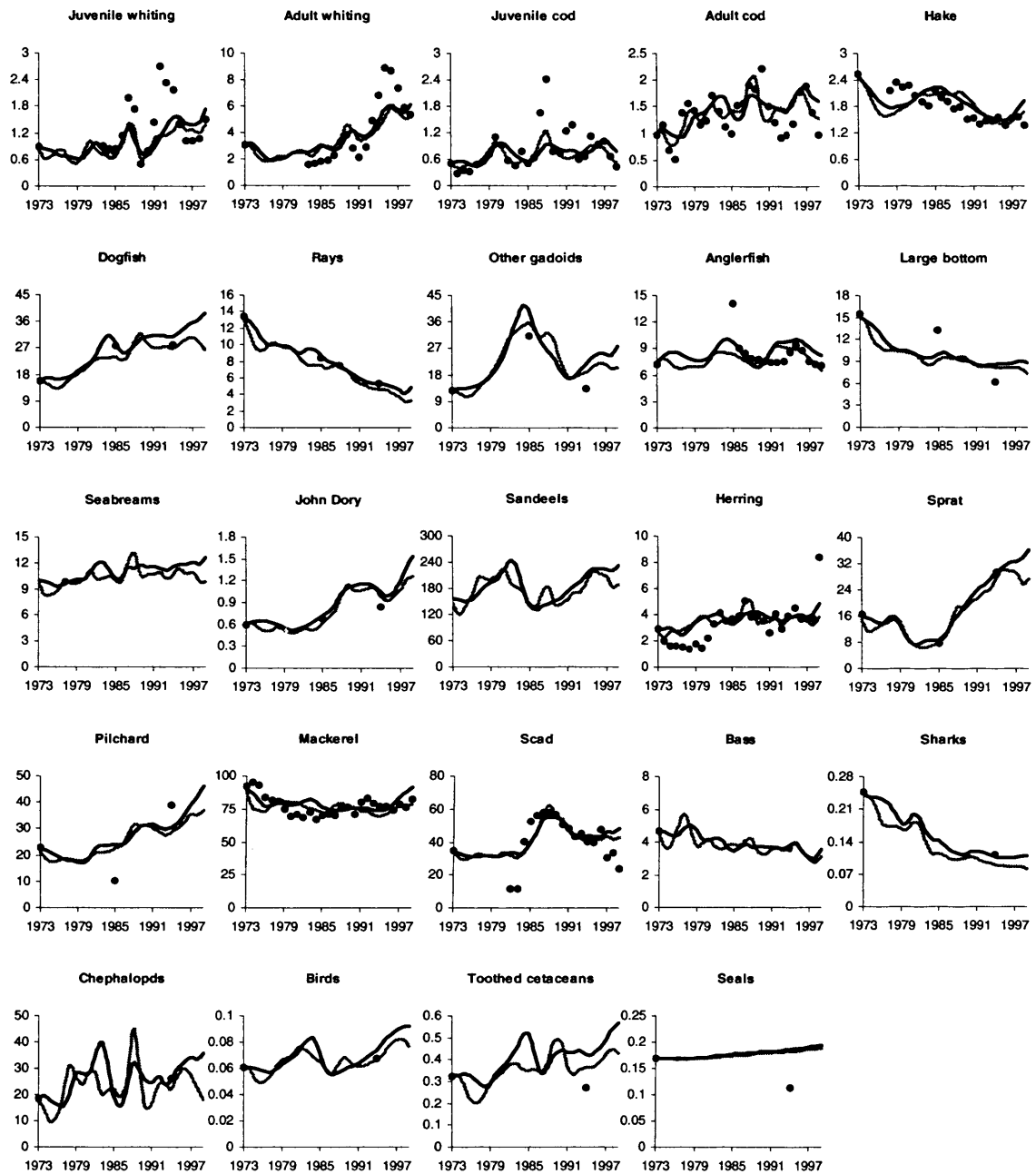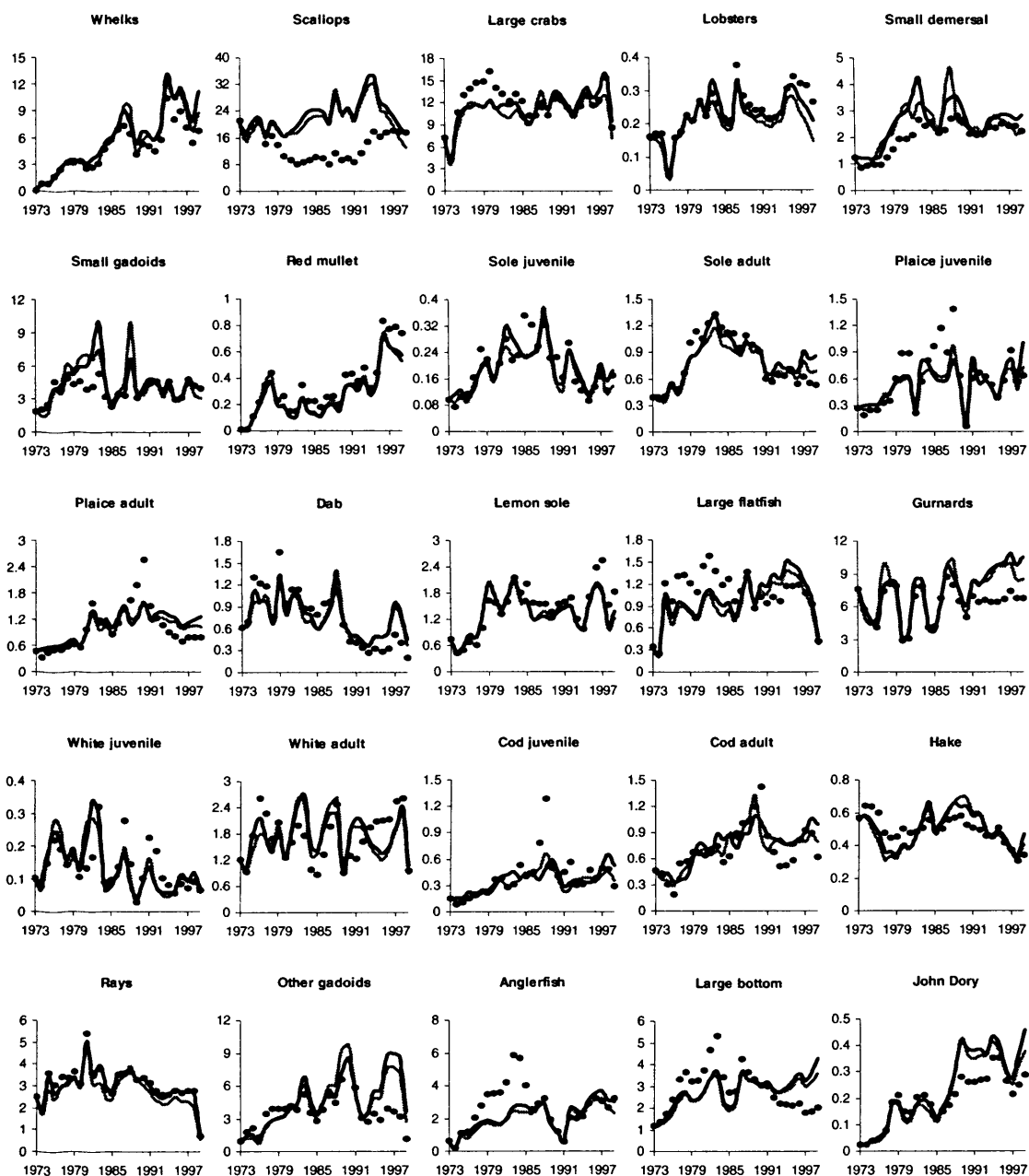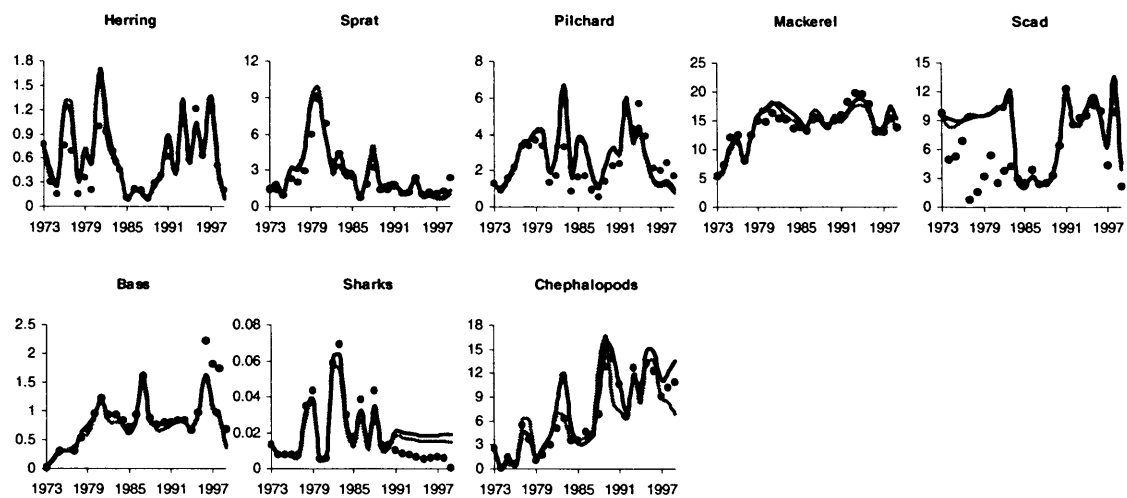
Figure 11. Continued.

Figure 12. Catch (thousands of tonnes) time series estimates for the Western Channel ecosystem from 1973 to 1999. Dots represent the input estimates; black lines represent Ecosim estimates using a scenario with primary producer biomass forcing (PBF) and grey lines are for the scenario using a primary producer anomaly function (PAF).

Figure 12. Continued.

3.7. Relating plankton production with climate.

The time series of the primary producer group biomass predicted by Ecosim for the period from 1973 to 1999 was regressed on the average SSTs for January to December (Fig. 13). In all cases, there was a negative relationship between SST and the biomass of the primary producers group generated by Ecosim. However the correlation was significant only for SST of February to May and August, with the highest value observed in March. The relationship between the primary producers biomass and the average SST from February to May was significant using either the raw or the "detrended" data (Fig. 14). This relationship was used to generate a primary production forcing function.

Figure 13. Squared Pearson coefficient (r^2) for the correlation between the primary producers biomass from 1973 to 1999 generated by Ecosim and sea surface temperature time-series (SST) (Diaz et al., 2002) in the Western English Channel when the temperature is derived from different months of the year. * p>0.05; ** p>0.01; *** p>0.001.

Figure 14. Relationship between the primary producers biomass from 1973 to 1999 generated by Ecosim and sea surface temperature time-series (SST) (Diaz et al., 2002) in the Western English Channel from February to May using the raw (A) or the "detrended" data (B).

3.8. Fisheries policy optimization.

The policy optimization routine caused big changes in the distribution of fishing effort among the fishing gears (Fig. 15). When optimizing for profits, i.e., giving a weight of 1 to the profit function and 0.2 for landed value and ecosystem structure, the model increased the effort of otter trawl, pelagic trawl, net and lining and reduced the effort of beam trawl, dredge, pot and recreational fisheries. As a result the profit increased by 46%, the landed value was 44% up and the catches were 21% higher. However, such extreme changes in effort led to huge changes in the ecosystem structure. Although the total ecosystem biomass change was very

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small, the biomass of vertebrate groups increased by 28% and 6 functional groups became extinct (Fig. 16A).

Figure 15. Changes in effort for Western English Channel fisheries resulted from optimizing for profits, landed value and ecosystem functions in the 1994 model. 1 = otter trawl; 2 = beam trawl; 3 = pelagic trawl; 4 = dredge; 5 = net; 6 = pot; 7 = lining; 8 = recreational. Compromise 1, represents the results when a weight of 1 was given to each function; compromise 2 when a weight of 0.3 was given to the ecosystem function while profits and landed value were each given 0.2 and compromise 3 is the result of optimization that included the application of the primary producer forcing function and with a weight of 0.4 given to the ecosystem function while profits and landed value were given 0.2.

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Figure 16. Biomass ratios between the end and start of a 50-years simulation for the 1994 Western Channel model. (A) Effort optimized for profits; (B) effort optimized for landed value; (C) effort optimized for ecosystem structure; (D) effort optimized for a mixed solution, i.e., given equal weights for profits, landed value and ecosystem structure; (E) effort optimized for mixed solution but with a slightly higher weight for ecosystem structure function.

Optimizing for landed value also led to extreme changes in the distribution of fishing effort. In this case, the fishing gears that had the effort increased were otter trawl, pelagic trawl and net. All other gears had the effort reduced. Also, unlike the runs where the profits were optimized, the relative changes for the gears that had the effort increased were more even. This configuration led to an increase of 89% and 87% in the landed value and catches respectively, but the profits were reduced to 79% of the baseline estimate. Under this extreme scenario, the ecosystem structure was hugely affected with a great loss of diversity. The biomass of the vertebrate groups as a whole increased by 90% but 17 of them became extinct (Fig. 16B).

When the model was set to optimize ecosystem structure, a huge decrease in fishing effort was predicted with only two fleets operating at levels close to the baseline estimates. Profits, landed value and catches dropped to 60%, 48% and 38% of the baseline level respectively. There was only a 7% increase in the biomass (Fig 16C) of vertebrate groups and an increase in diversity.

Optimizing for a mixed or a compromise solution giving a weight of 1 to the three objective functions led to a reduction in effort for all fleets except for pelagic trawl and net, for which the optimization resulted in a huge increase in effort. This configuration led to a 32% increase in profits, 31% increase in landed value and catches were 23% lower. However, there was a decrease in biodiversity with the extinction of 4 functional groups (Fig. 16D) and the biomass of the vertebrate groups increased by 40%. These results occurred because, although the final values for the three objective functions were similar when equal weights were given, the ecosystem

structure is not maintained. Some groups are lost and a few have their biomass hugely increased, and this biomass increase seems to be the factor that makes the ecosystem objective function have a high value comparable to those for the functions that maximised profits and landed value. So the batch runs of the ecosystem optimization, when the other functions were kept fixed with a weight of 0.2, and the ecosystem function weights were varied from 0 to 1, were used to select a 'better' combination of weights. The best results were obtained when the ecosystem function was given a weight of 0.3. With these weights the optimization resulted in a fleet configuration where all fleets, except lining, had their effort reduced. The changes in fishing effort were not so marked as in the optimization runs where the functions were given equal weights. Under this fleet configuration, the profits increased by 20%, the landed value remained at the same level and catches were 10% lower than the baseline model. The biomass of vertebrate groups was just 2% higher than the baseline level (Fig. 16E), but there was an increase in biodiversity.

The effects of increased weights placed on profits, landed value and ecosystem objectives on the diversity index, the average trophic level of the catches, profits and landed value are shown in Figure (17). With all functions given a weight of 0.2, the biodiversity index was 4.3, the average trophic level of the catches was 3.2, the total catches were 2.14 t/Km^2 and the profits were 35% higher than the baseline estimate. There was no clear trend for the diversity index as a function of the weight placed on profits. When optimizing for landed value, there was a huge decrease in the diversity index for weights higher than 0.3, when the index dropped to 16% of the value obtained when all functions were given weights of 0.2. For the ecosystem optimization, the diversity index increased to 75% higher than the

solution with equal weights, and remained almost constant for ecosystem function weights varying from 0.3 to 0.7. The variation for the average trophic level of the catches was not so marked as for the diversity index and presented opposite trends. This parameter increased when high weights were placed on the profit and landed value functions and decreased with increased weights on ecosystem function. Profits decreased as a function of increased weights placed on the landed value and ecosystem functions and in both cases when high weights were placed on those functions profits were lower than the baseline estimates. On the other hand, landed value presented a decreasing trend as a function of increasing weights placed on the ecosystem function but presented an increasing trend as a function of increasing weights placed on profits.

Figure 17. Results of 1994 Western English Channel ecosystem model optimizations as a function of the weight placed on profit, landed value, and ecosystem structure. Weights for the two constant objectives are set to 0.2 in all simulations. Profits and landed value results are expressed relative to the baseline estimates. * The "best" compromise solution corresponds to the results for the optimization with the ecosystem function weight set to 0.3, while profits and landed value weights were set to 0.2.

The effects of different vulnerability settings on the single policy optimizations are presented in Figure 18. The most striking differences occurred for the optimization of profits (Fig. 18A). While the optimization resulted in an increase in effort for otter trawl and lining under the vulnerabilities estimated from time-series fitting and default vulnerability scenarios, it was reduced under the scenario where the vulnerabilities were set proportional to the trophic level of the predators. In the case of the net fishery, the optimization resulted in a reduced effort under the default scenario, and an increase in the other two. The optimizations resulted in somewhat similar results for the other gears. The landed value optimizations (Fig. 18B) resulted in the same qualitative changes for all fleets, although in some cases the degree of change was considerably different among the vulnerability scenarios. The results for the ecosystem structure optimizations were fairly similar (Fig. 18C), the highest effort difference between scenarios was 7%.

When the model was run to optimize for profits using the same relative change in fishing effort for all fleets, a decrease in fishing effort was predicted irrespective of the vulnerability settings used. Effort was reduced to 78, 80 and 75% of the baseline level under the vulnerabilities estimated from time-series fitting, default vulnerabilities, and vulnerabilities proportional to the trophic level of the predators respectively. The most optimistic scenario resulted from using the vulnerabilities proportional to the trophic level of predators, when the model predicted an increase of 19% in profits, followed by the 'time-series' version (12%) and then the default vulnerabilities (11%) scenario. Beam trawl, dredge and pots had their profits increased in all scenarios, while pelagic trawl and lining had profits increased only under the scenario with the vulnerabilities proportional to trophic

levels. All other fleets had their profits reduced or not changed under these different vulnerability settings.

The application of the forcing function for primary producers caused a considerable decrease in catches and landed value. Under this scenario, the best mixed solution was found to be when a weigh of 0.4 was given to the ecosystem function, with the weights for the profits and landed value functions kept fixed at 0.2. The fishing effort estimates tended to be lower than the estimates resulted from the mixed solution without the forcing function, but were fairly similar to those. However, as the system was less productive, profits and landed value decrease to less than 70% of the baseline estimates. The profit optimization using the same relative change in fishing effort with the application of the forcing function resulted in a 30% overall decrease in effort. This result was similar to the one without the forcing function, but as the productivity was smaller, again profits and landed value decrease to less than 70% of the baseline estimates.

Figure 18. Changes in effort for the 1994 Western English Channel model as resulted from optimizing for (A) profits, (B) landed value and (C) ecosystem functions under three vulnerability settings: default (=2), proportional to trophic level of predators, varying from 2 (lowest TL) to 5 (highest) and vulnerabilities estimated with time-series fitting. 1 = otter trawl; 2 = beam trawl; 3 = pelagic trawl; 4 = dredge; 5 = net; 6 = pot; 7 = lining; 8 = recreational.

4. Discussion

4.1. Comparison of ecosystem properties

The main observed differences regarding the ecosystem state in the three models were an increase in primary production that seemed to be somewhat reflected in changes in the fish biomass. Of the models compared, the system was in its least productive state in the 1973 model. The production in the 1985 model was slightly higher than in 1994. Primary production required to sustain the fishery increased from 1973 to 1985, because of an increase in fishing effort and an increase in the abundance of some high trophic level fish. This parameter was smaller in 1994 than in 1985, as the primary production was higher and the catches of high trophic level fish decreased, following a general decrease in their abundance. There was a small increase in the omnivory index that might be related to a decrease in the abundance of some high trophic level piscivorous fish species. Small to medium fish species (including non-target) increased from 1973 to 1994. These changes were reflected in the average production and average P/B estimates of fish species, showing a small shift in the fish community to smaller, more productive fish species and/or an increase in the proportion of young individuals of slow-growing species.

Pinnegar et al. (2002) reported for the Celtic Sea a significant decline in the mean trophic level of the fish landed from 1946 to 1998 and in the trophic level of scientific survey catches from 1982 to 2000. However they did not find a significant decline for the fish landings from 1982 to 1998, the period covered by the surveys.

Although they observed a declining trend for the mean trophic level in the survey data, the series is somewhat variable and the highest value they observed occurred in 1994. The decline in the trophic level of the surveys catches for the Celtic Sea seemed to be largely related to an increase in the abundance of mackerel and boarfhish (*Capros aper*), which is not a commercial species. In the Western Channel there were very small changes in the trophic level of the fish catches, and this parameter was slightly higher in 1985 than in 1973 and 1994. The main changes in the landed trophic levels for the Celtic Sea reported in Pinnegar et al. (2002) occurred from 1946 to the middle of the 1970s. After that, there was no clear trend. A similar pattern can be seen in the Northeast Atlantic fisheries landings, where the mean trophic level seems to have stabilized after the middle of the 1970s (Pauly et al., 1998). Pinnegar et al. (2002) suggested that the differences between the landings and mean trophic level trends derived from survey might be because the changes occurring in the underlying ecosystem may be stronger than any changes observable in the fishery. It is possible that for the Western Channel the average trophic level of the fish landings and the fish in the system was already stabilized at a low level in the 1970s.

There were differences among the trophic level of some species presented in this study and the ones estimated by Pinnegar et al. (2002) using isotope analyses. They estimated trophic levels that were generally higher and with much wider variation. The lowest and the highest value reported for fish groups by them were 3.1 and 4.9 respectively, against 3 and 4.4 estimated here. In some cases the trophic level derived from isotope analyses were much higher. For example the trophic level of dab and sole were reported to be higher than 4, much higher than the values ranging

from 3 to 3.3 reported in this study and in other sources (e.g. FishBase; Froese and Pauly, 2000). They suggested that these species would have higher trophic level than expected because they are known to feed selectively on carnivorous polychaetes and that such subtleties are rarely incorporated in ecosystem models or appreciated from gut contents studies. The trophic level estimates reported here were also generally lower than the comparable groups included in the North Sea model (Christensen, 1995). However the mean trophic level of the catches for the North Sea model, which did not include invertebrate catches, was 3.4 that is similar to the mean trophic level of fish catches for the Western Channel.

The proportions of primary production consumed in the 1973, 1985 and 1994 models were 18, 35 and 26%, when the primary production was 1894, 2170 and 2949 t/Km^2 respectively. These efficiency estimates seem to be very low and suggest that the primary production could be overestimated or that the system is under a high level of exploitation. The highest estimate of primary production reported here is lower than the phytoplankton production for the 1980 North Sea model (3852 t/Km^2) (Christensen, 1995) and slightly higher than the "temperate shelves and seas" ecosystems average (2790 t/km^2) reported by Pauly and Christensen (1995). L'Helguen (1991) and Maguer et al. (1996) (cited in Hoch (1998)) and Boalch (1987) reported estimates of primary production for parts of the Western Channel of 3240, 2250 and 1350 t/Km^2 respectively. Hoch (1998) estimated using a model of nitrogen flows for the plankton food web[1] in the English Channel that only about 22% of the nitrogen output from the phytoplankton compartment flows to

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[1] The model described in Hoch (1998) includes 3 phytoplankton groups (diatoms, dinoflagellates and nanoplankton) 2 zooplankton groups (meso and microzooplankton), bacteria and detritus in the water column, dissolved nitrogen and detritus in the sediment.

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zooplankton. According to Hoch's model, the mesozooplankton plays a relatively limited role in nitrogen flow, although it is the main zooplanktonic consumer of the phytoplankton production that is in turn dominated by diatom production. On the other hand, the microzooplankton compartment plays an important role, mainly through interactions with the dissolved detritus compartment and bacteria in the water column. There is an intense nutrient recycling in the water column by bacterial activity. In the deepest areas the recycling can achieve 80% and overall it accounts for 67% of inorganic nitrogen produced. Although the interactions among microzooplankton, detritus and bacteria in the water column were not included in the present version of the Western Channel model, Hoch's results corroborates the observations made here that most of the phytoplankton production does not flow directly to the zooplankton compartments but instead almost 80% flows to detritus. These observations show however that the microzooplankton production is underestimated in the Western Channel model.

Based on Ecopath models for the Gulf of Mexico and the Eastern Central Pacific, Christensen and Pauly (1998) suggested that marine ecosystems, at least as modelled in their case studies, use the primary production quite inefficiently because of their present exploited situation, and that this should lead to increased accumulation of detritus in the sediments. However, as discussed above, the pelagic food web can be much more complex than generally it is or how it can be represented in Ecopath models. As the results from the English Channel model by Hoch (1998) suggest, most of the flow of matter can be recycled in the water column by the micropelagic food web and the interactions of this part of the web with higher trophic levels and the sediment is limited. In the southern Benguela ecosystem low

efficiency estimates, ranging from 27 to 60% use of primary production (Baird et al., 1991; Shannon and Field, 1985; Shannon et al. 2003), is thought to be partially related to the mismatch in space and time between phytoplankton blooms and zooplankton production (Baird et al., 1991) and also to the fact that some phytoplankton species are of unsuitable quality or size to be consumed by pelagic fish (Shannon and Field, 1985). Hence, the low efficiencies (<50%) with which primary production is used by high trophic level groups does not necessarily mean that the system is a long way from its carrying capacity.

Primary production required (*PPR*) to sustain the catches estimated for the Western English Channel varied from 7.6 to 13.4%. These values are lower than the range of 24.2 to 35.3%, estimated for fresh water, upwelling and shelf systems by Pauly and Christensen (1995). However, a recent compilation of *PPR* by Tudela et al. (2005) showed that the estimates for 31 models covering 19 systems in different periods ranged from 0.3 to 82.3% (mean = 19.2 ± 7). The discrepancies between these estimates can be partially explained by the fact that Tudela et al. (2005) included models of reconstructed past ecosystem states (e.g. 1880 North Sea model) when the fishing pressure was much lower and the respective *PPR* estimates were lower as well, whereas Pauly and Christensen (1995) used models for the 1990s, when the level of fishing in almost all aquatic ecosystem was already very high. However, some models of recent situations have relatively low *PPR* values (<20%) that are due to overexploitation, which would have left the reduced fish biomass unable to use the available production. Discrepancies can also be related to overestimation of primary production and/or underestimation of catches.

The use of single ecosystem indicators such as the mean trophic level of the catches for defining optimum fishing can produce ambiguous results (Murawski, 2000). Tudela (2003) proposed the combined use of *PPR* with trophic level as a quantitative index of fisheries impact because, 'given a trophic level, a fishery with a lower *PPR* would be intrinsically less disruptive than a fishery with a higher one'. Tudela et al. (2005) developed a quantitative method to set boundaries for ecosystem overexploitation based on the *PPR-* trophic level relationship. Figure 19 presents paired estimates of *PPR-* trophic level for the 1973, 1985 and 1994 Western Channel models and the 50%, 70% and 90% limit reference functions for ecosystem overexploitation as estimated by Tudela (2005). All the three models were located above the 50% (threshold) curve, showing that in all situations the system could be viewed as overexploited. The *PPR* estimated for the 1973, 1985 and 1994 models were respectively 2.3, 2.0 and 1.9 times higher than the threshold value for the corresponding trophic level. Hence, it could be inferred from these that the system was at similar levels of exploitation. However, the level of fishing has increased considerably since 1973 and it is unlikely that the system could be seen as being at a similar level of exploitation of that in 1994. The limit reference functions presented in Figure 13 are close for low trophic level. For example, for a mean trophic level of 3 and 2.5, the difference of *PPR* estimated using the 50 and 90% functions is just 4% and 1% respectively. Tudela et al. (2005) approached this point by saying that their results 'highlight the fact that ecosystem overfishing is reached sooner following an increase in *PPR* operating on low- trophic level species' and that 'disrupting energy flows lower in the trophic web has the farthest-reaching effects on the whole ecosystem'. Considering that there can be a great deal of uncertainty in primary production estimates, even relatively small errors (≤30%) would put the ecosystem in

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the 'wrong' position relative to the threshold curve. Hence, the probability of wrongly classifying an ecosystem regarding to its exploitation level, when fished at low trophic level, using this kind of approach is very high.
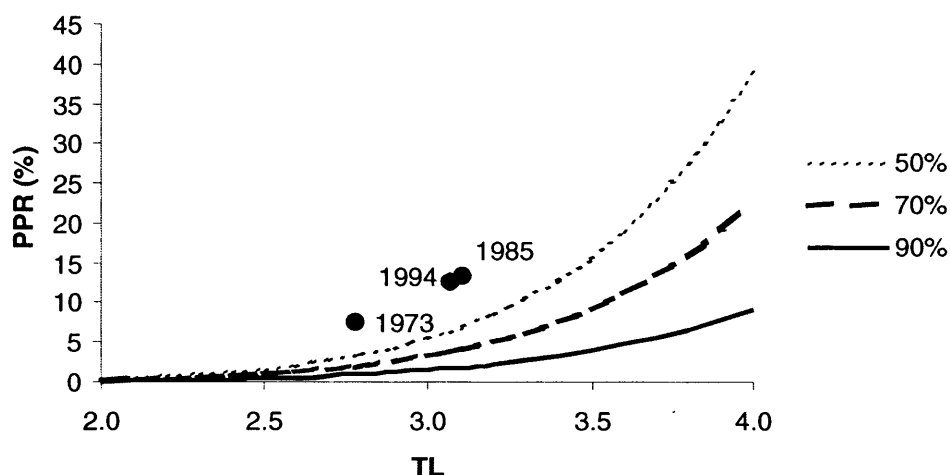

Figure 19. Paired estimates of *PPR-* trophic level for the Western English channel with reference functions related to 50%, 70%, and 90% probability belonging to a sustainable fished situation as estimated by Tudela et al. (2005).

The ratio between primary production and respiration (*PP/R*) is thought to reflect the maturity of the system, with mature or undisturbed 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 had values between 3.5 and 3.7, indicating that the system was in an immature or disturbed state in the three decades analysed. The Finn's index measures the fraction of the throughput that is recycled (Finn, 1976). The index is related to and is expected to increase with system maturity, resilience and stability. The maximum observed value for the Western English Channel was 4%, which is in line

with estimates for ecosystems under considerable levels of exploitation (Christensen and Pauly, 1998). The average path length, a parameter that is 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 estimates of this parameter for the Western Channel were, as before, similar to the ones reported by Christensen and Pauly (1998) for systems under high levels of exploitation.

Fulton et al. (2005) analysed an extensive range of ecosystem indicators using a modelling approach to explore the robustness of the indicators in the context of the level of data aggregation, resource exploitation, data quality, key groups and ecosystem type. Their results confirmed previous observations that no single indicator can give a complete description of the ecosystem state and advise that it is essential to use a selection of indicators, each focusing on different properties or attributes, and using different kinds of data and groups. They found that community and ecosystem-level indicators were generally the most informative and that indicators that are based in easily sampled data and that require just a few calculation steps, had the best performance. Indicators such as relative biomass (relative to an unexploited level or other such baseline) of sharks and target groups, total biomass (also relative to a baseline) and pelagic fish biomass to demersal fish biomass ratio were among the best indices. Model derived parameters, such as average trophic level, average ecotrophic efficiency, *PPR*, total production, total consumption, total respiration performed well only if good data are available. Contrary to previously proposed, network parameters such as ascendancy, which is generally viewed as a useful summary of system state, or dynamics often have a poor performance because of their dependence on data that are difficult to collect, on the ability to formulate

models adequately, and the need for a good knowledge of ecosystem structure, the lack of which undermines usefulness of the indices.

The ecosystem indicators estimated for the 1973, 1985 and 1994 models, such as the ratio *PP/R* and the Finn's index, discussed above, indicate that the Western English Channel was in a relatively immature or disturbed state. There has been a considerable increase in fishing effort since the 1970s in the Western Channel (ICES, 2005), however some target groups increased during the 1980s. During the same period there was also an increase in primary production and zooplankton abundance suggesting a bottom-up control of the overall system production. The net effect meant that to some extent the fishing mortality has not increased as much as it would have if the environmental conditions during the three decades had been less favourable. Using the 1973 model as a baseline for comparisons, the indicators analyzed here show that the system, despite the increase fishing effort, was in a trend of increasing maturity or stability in 1985. With the rising levels of fishing mortality operating in the system, this trend was reversed in the 1994 model. As discussed above, the robustness of some indicators are dependent on good data and good knowledge of the ecosystem structure. Shannon et al. (2003) state that Ecopath model structure constrains parameter combinations leaving little scope for values far from the ones considered to be best estimates so leaving limited combinations of parameters to describe the ecosystem. However, many indicators are functions of the primary production estimates and this parameter was not a constraining factor, as the efficiency of use of primary production were very low in the presented versions of the Western Channel model. Hence, if for example an error of ±30% in the biomass of the primary producers group occurred, it would cause respectively a change of –

20% and +40% in Finn's index, a similar amount to the observed changes in the period studied. It is clear that the models of past situations, often used as a baseline for comparisons, are often the ones with less reliable data. As there always seems to be considerable levels of uncertainty about production, biomass parameters and the structure of marine environments, any conclusions about the relative maturity or stability of the system should be taken with caution.

4.2. Modelling food web interactions, variation in plankton production and fisheries from 1973 to 1999.

The inclusion of the PBF improved the fit of the model biomass estimates to the biomass time series. As for many high trophic level groups, phytoplankton and zooplankton data show an increasing trend from 1973. However, unlike components at the higher trophic levels, the phytoplankton data show that the production kept on increasing up to the end of the time period. On the other hand, many fish groups, increased up to the 1980s, after which they started decreasing. The zooplankton data show a similar trend to the fish groups, with the period of highest production occurring in the late 1980s with a decreasing trend afterwards. An inverse relationship between air temperature from December to March and the abundance of 11 most common plankton species (mainly copepods) in the English Channel was observed by Beaugrand et al. (2000) from 1979 to 1992. They observed also that these species were negatively related to the North Atlantic Oscillation (NAO) and hypothesised that average NAO indices would be optimal for zooplankton production. However, the CPR average total zooplankton abundance series from 1958 to 2002 in the Western Channel seems to be positively related to the

phytoplankton index and the annual sea surface temperature (SST), although only the relationship between zooplankton and SST is significant (Fig. 20). So, it is possible that the observed relationship for plankton and physical variables reported by Beaugrand et al. (2000) from 1979 to 1992 does not persist when a longer series is used, although the differences described above can be also related to differences in the data sets used in these analyses. For instance, Beaugrand et al. (2000) used counts of cells as an abundance index for diatoms but the increasing trend in the late 1990s observed for the CPR phytoplankton colour index associated with higher temperatures could be associated with a shift in the phytoplankton community composition towards "unpalatable and noxious species", not diatoms, with important ramifications through the various marine trophic levels (A. Richardson pers. comm.; Edwards et al., 2001).

It has been shown to be difficult to establish a casual relationship between series of biological and physical parameters when focusing on single ecosystems. Many studies of this type now are based on meta-analysis of data for several ecosystems. For example, Richardson and Schoeman (2004), using a meta-analysis of plankton data for many areas of the Northeast Atlantic observed that there is a tight bottom-up control of zooplankton from phytoplankton, with the SST being the underlying driving force. They suggested that the relationship of SST with phytoplankton would be positive in the northern areas of the North Atlantic and negative in the southern ones, such as the North Sea and English Channel.
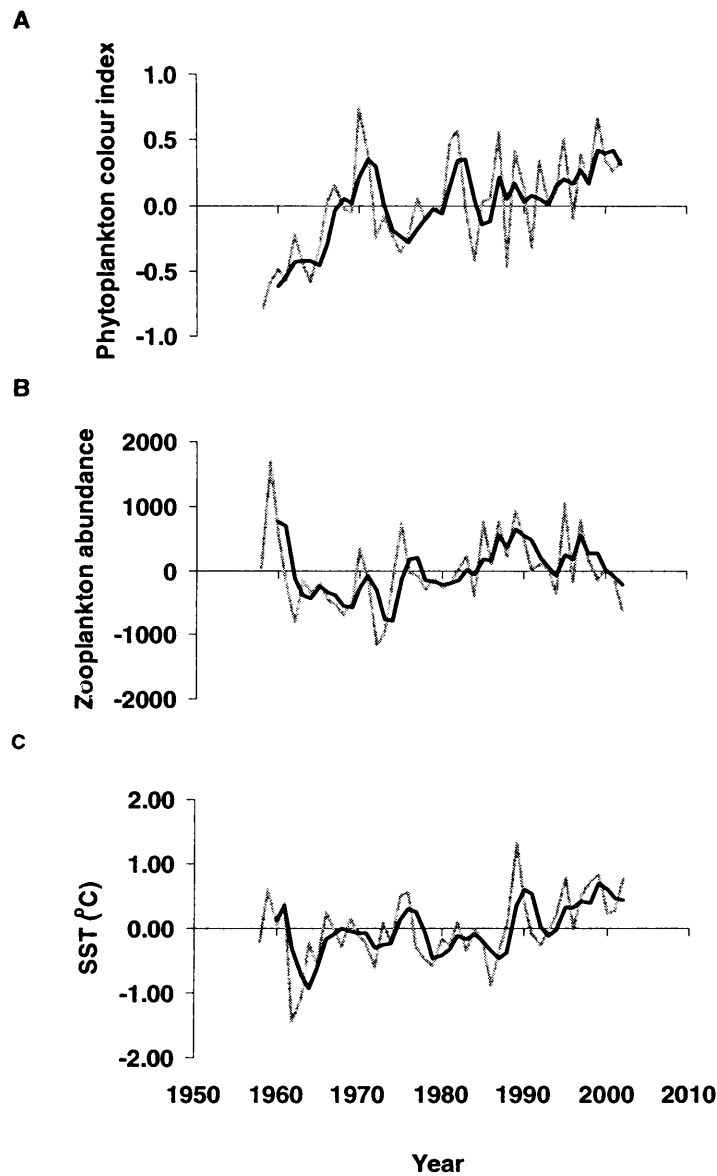
Figure 20. Normalized time series data of (A) phytoplankton colour, (B) total zooplankton abundance (Reid et al., 2003) and (C) sea surface temperature (SST) (Diaz et al., 2002) in the Western English Channel during the period 1958-2002. The bold lines represent the three-year running averages. The relationships between the variables were positive and non-significant for zooplankton and phytoplankton (r = 0.13; p = 0.41), positive and non-significant for phytoplankton and SST (r = 0.28; p = 0.06) and positive and significant for zooplankton and SST (r = 0.42; p < 0.01).

After the vulnerabilities were estimated, the model estimated a PAF that had a similar trend as the PBF, but with lower estimates for the later years. If these results are not just a model artefact, they may be seen as evidence that the production of many of the higher trophic levels is not tightly linked to the primary production. These discrepancies might be related to the fact that the zooplankton production itself is not a simple function of primary production, but also related to physical processes as discussed earlier and these processes are not modelled in Ecosim. Alternatively, the primary producers biomass may not have increased very much. We used the CPR phytoplankton colour index and assumed that the index is directly proportional to changes in biomass, but the relationship between the variation of this index and the variation in the phytoplankton biomass is presently not well understood (Edwards et al., 2001; Barton et al., 2003).

It can be argued that some species might respond very differently to environmental changes and that the use of one single mechanism to explain the overall production of the ecosystem would be misleading. A complicating factor when using an ecosystem modelling approach for the Western English Channel derives from the observation that this ecosystem is a biogeographic boundary between the northern Boreal and the southern Lusitanian fauna. The abundance of important species will not be only a function of primary and secondary production, but will also be related to distributions as a function of temperature. The change in the mackerel overwintering behaviour during the 1970s (Lockwood, 1988) is a remarkable and perhaps extreme example. Also, physical processes along with food abundance and predation mortality might regulate the survivorship in the early life stages. For example, Bradbury et al. (2001) using a model of temperature-dependent

cod egg development and mortality in Placentia Bay, Newfoundland, suggested that the effects of predation are small relative to the effects of advection, and that the interaction between advection and temperature-dependent vital rates for eggs may have dramatic consequences for the coastal retention of eggs. The mechanisms regulating the production of early stages will also differ among different species in the same ecosystem. Koster et al. (2003) observed in the Baltic Sea that for cod the period between the late egg and the early larval stage is critical for recruitment and that the potential factor affecting this stage was the prey availability for larvae. On the other hand, the period between the late larval and early juvenile stage seemed to be important for sprat recruitment. The potential causes affecting this life stage were ambient temperature and wind stress. In the North Sea, survival of young cod would be indirectly and negatively linked to temperature through changes in the zooplankton community structure, i.e. food availability (Beaugrand et al., 2003). In such a case, the increased production of some zooplankton species, not the overall production, would affect the recruitment. However the situation of the cod stock in the ICES divisions VIIe-k, that includes the Western English Channel, seems to be different. Despite the warming, the stock produced relatively good year-classes in 1999 and 2000, and the spawning stock biomass has increased slightly since then (ICES 2005), suggesting the occurrence of somewhat different mechanisms regulating the abundance of cod in this ecosystem.

Walters and Martell (2004) reported that the inclusion of a primary production anomaly helped to improve the Ecosim fittings and explained the positive covariation in abundances of different species in the West Coast Vancouver Island and Georgia Strait ecosystems. On the other hand, including such a function did not

improve the fit of models for the Central North Pacific, Gulf of Thailand and the North Sea. Shannon et al. (2004) were able to explain 4-12% of the variance in the time series data for the southern Benguela ecosystem by estimating a primary production anomaly. Cury et al. (2003) affirmed that bottom-up seems to affect most ecosystems and Ware and Thomson (2005) showed that primary production variation is highly correlated with the resident fish yield along the northeast Pacific continental margin between 34.3°N and 58.5°N. So, there is some evidence from other ecosystems to support the main observation presented here that a bottom-up mechanism has a relatively strong effect across different trophic levels in the Western English Channel ecosystem. In addition, Walters and Martell (2004) state that strong top-down control by predators appears to be relatively uncommon in marine ecosystems. In this case, predation and/or food competition release caused by removal by fishing of selected top predators would have less importance than environmentally driven changes in productivity of lower trophic levels.

In some previous work with Ecosim modelling (e.g. Harvey et al., 2003, Shannon et al., 2004), the authors have interpreted the vulnerability values estimated during the time series fitting as reflecting mechanisms of bottom-up versus top-down prey-predator dynamics. However, the vulnerabilities rather explain where group abundances are placed relative to their carrying capacities (V. Christensen pers. comm.; Plagányi and Butterworth, 2004). Hence, in the case of the present study where we have observed that the prey of many demersal predators tended to have high vulnerabilities so indicating that the predators are not close to their carrying capacity. This might be because they have been reduced from their original abundance or because of better food conditions. Although we have shown here that it

is quite possible to achieve fairly similar fittings with very different combinations of the vulnerability parameters for the prey items of some groups, implying that some very different mechanism could well explain the observed variation, the incorporation of a known process such as the observed primary production variation in the model formulation to estimate the vulnerabilities seems to give more credibility to our results. It is clear that considering the level of uncertainty of some time-series inputs used to fit the model estimates and the fact that Araújo et al. (2005) used the 1990s model diet matrix as first guess for the 1970s diets, the estimates of the vulnerabilities should be interpreted with caution. Furthermore, Aydin (2004) states that successful fitting of models does not guarantee a mechanistic explanation of the observed abundance variation and as stated by Christensen et al. (2004, page 112), many model errors can result from omissions of otherwise unknown predator-prey interactions and forcing functions representing environmental processes. According to Christensen et al. (2004), "such possible omissions are most productively viewed as alternative hypotheses about what processes and inputs have been important in shaping historical ecosystem behaviour".

We have explored in this chapter how fishing, trophic interactions and plankton production contribute to the observed variation of high trophic levels. By accounting for the phytoplankton variation observed in the CPR data, we were able to improve the goodness of fit of the model estimates to the available biomass data by about 25% compared with fitting the model by using only the series of fishing mortalities. The model fitting was further improved by changing the vulnerability settings and thus caused an overall improvement of 62% in explained variation.

These results show that, in addition to fishing, a bottom-up environmentally driven mechanism plays an important role in the system production, but complex trophic flows should be also considered for an explanation of the observed variation.

In recent years, many papers dealing with the influence of climate change on phytoplankton and zooplankton have been published. Some of these papers have dealt with time series data covering more than 40 years and the findings suggest that there is a link between plankton production and climate, although such a period can be viewed as short when analysing multi-decadal variability (Barton et al. 2003). Richardson and Schoeman (2004) provided evidence that there is a certain degree of bottom-up control of zooplankton abundance by phytoplankton over a period of 4 decades for the Northeast Atlantic. It is reasonable to suppose that these persistent changes will propagate through the food-web and affect the production at higher trophic levels, although, as stated by Genner et al. (2004), additional local environmental determinants, interspecific interactions and dispersal capacity, and we also include here differences in fishing pressure, will affect regional responses of different species and populations of the same species to changes in climate.

4.3. Fisheries policy optimization.

The results of the fisheries policy optimizations are in general similar to the ones reported in previous application of the Ecosim optimization tool (Mackinson, 2002; Stanford and Pitcher, 2004; Christensen and Walters, 2004). As in those applications, the optimization for single objectives led to the specialization of the fishing fleet, with some fleet types being almost excluded. The fleets that are kept

operating under unprofitable conditions, are so to reduce or eliminate predators and competitors of valuable species when optimization is for profits or landed value, or to reduce or eliminate predators and competitors of long-lived ones when optimization is for ecosystem structure.

The profit and landed value optimizations had qualitatively similar results. In both cases otter trawl, midwater trawl and net have increased effort after the optimization. The exception was lining, that have increased effort under the optimization for profits, but was slightly reduced under the landed value scenario. The reasons for the effort changes resulting from runs that optimized profits and landed value are not always clear. As observed by Christensen and Walters (2004), it is not always the most profitable fleet, or the fleet with the highest landed value that has its effort increased after optimization. These results can be related to the underlying biological and technical interactions and also to the level of exploitation in the baseline model. The otter trawl was the most profitable type of gear and showed the highest landed value for the baseline model, and showed an increase of effort in optimizations focussing on both economic and landed value. On the other hand, dredge and pot fisheries that are highly profitable had their effort reduced. Under the present model formulation dredges have their landed value and profits coming mainly from scallops while for pots, the catch is mainly from whelks, lobsters and large crabs groups. All these groups are under high levels of exploitation in the baseline model and they also seem to suffer little effect from changes in other functional groups. This meant that a reduction in effort led to increased profits and landed value. The beam trawl fleet had its effort reduced in all optimizations. This fleet is the least profitable and also does not have one of the highest landed values.

Some interesting or counterintuitive differences were observed among the single objective optimizations. The profits, but mainly the landed value optimizations, led to big changes in the ecosystem structure, with loss of diversity, but the overall biomass of vertebrate groups showed a considerable increase. For the objective focusing on ecosystem structure, there was an increase in biodiversity, with many long-lived groups predicted to increase, although the overall vertebrate biomass suffered just a small change. Somewhat similar results were observed for the best mixed solution.

The optimization when the ecosystem function was given a weight of 0.3, with the profit and landed value functions kept with weights of 0.2, resulted in the best mixed configuration, increasing profits and diversity, while keeping the landed value at the same level as the baseline estimates. The optimization resulted in a reduction in effort for all fleets, except lining. Although the effort for some fleet changed considerably, much smaller reductions in fishing effort would have a beneficial effect on the fishing profitability and ecosystem structure, without affecting much the final landed value, i.e., after some point, further changes in effort would cause little improvement in the optimization functions. Also, some fleets have little effect on the final result. For example, in all configurations of the optimization process, the recreational sector had in all configurations its effort much reduced mainly because this fleet had no input economic data, which gave it a lower weight in the optimizations. However if it is held at the baseline line effort while the others fleets are run with optimized efforts, the final results are not so different than when the optimized effort for this fleet is used.

The application of the effort estimated from the optimizations led in some cases to huge increase in the biomass of some species. Many species were heavily exploited in the Western Channel in 1994. For example, in 1994 sole, plaice and cod stocks were at a much lower level than their maximum biomass levels observed between the 1970s and 1980s (ICES, 2000a.). Although it has been shown that changes in primary productivity were related to the observed changes for commercial species (Araújo et al., 2006), the fishing effort has increased since the 1970s (ICES, 2000a.), and the optimization results showed that there is a lot of room, as it might be expected, to increase the biomass of commercial species through a reduction in effort.

The results of using increasing weights for the single policy functions on the average trophic level of the catches and the biodiversity index showed that the former is quite conservative to changes in the underlying system structure. Christensen and Walters (2004) observed that optimizing for value led to a steady decline of the average trophic level of the catch as the weight on value was increased, but an opposite trend to the one observed in this study. These differences might be reflecting differences of the weighting factors used for the optimization routine. Cury et al. (2005) observed that the trophic level of the catches is a conservative indicator and responds slowly to large structural changes in the ecosystem. Caddy and Garibaldi (2000) suggested changes in market demand as an alternative mechanism to interpret apparent historical changes in trophic composition. The changes in catch composition resulting from model optimizations can be seen as reflecting changes in market demand, since the fisheries are set to

satisfy certain criteria and so should not be expected to reflect changes in ecosystem structure. On the other hand, despite the high level of aggregation of the model structure, the biodiversity index presented huge changes as a function of the weights placed on the single policy functions, reflecting the changes in the system structure and then seems to be a much better candidate for a system indicator to be used in model comparisons.

Christensen and Walters (2004) performed detailed analyses of trade-offs of two objectives combined, i.e. profits vs. ecosystem, profits vs. landed value and ecosystems vs. landed value. They found that optimizing landed value is incompatible with profit and ecosystem optimization while optimizing for economic profit is consistent with ecosystem considerations. Particularly, when analysing the trade-offs between profits and ecosystem functions, they found in the parameter space a region where a clear improvement in profits was achieved, while at the same time ecosystem structure objective function was improved by a similar amount and the value of the landings was kept at the baseline level. Although such a detailed analysis was not performed here, the present analysis showed similar features. The best mixed solution extracted from the ecosystem batch runs, illustrates well these relations, where it was possible to increase profits while at the same time having positive effects on ecosystem structure and with no cost to the landed value. The results for the profits optimization when the routine was set to search for a single value of relative change in fishing effort also led to the same conclusion. In this case the profit and ecosystem structure improvements were smaller, but using this fleet configuration has the advantage that no fleet is led to operate under unprofitable conditions.

Ecosim simulations are very sensitive to the vulnerability parameters (Christensen et al., 2004). The analyses of effects of different vulnerability led to considerable changes for all settings used. The biggest differences were observed for the profits optimizations. Fulton and Smith (2004) found that economic optimizations show little sensitivity to the vulnerability settings and observed that appreciable changes in the optimal policy under economic criteria occurred only when all the vulnerability parameters are set in excess of 0.7[1]. However they compared a range of vulnerability settings using the same value for all prey at a time. Here very different settings were compared, i.e., the default (all equal to 2), vulnerability estimated with time-series fitting and vulnerabilities proportional to the trophic level of the predators, these last settings being commonly used as a short-cut when there is no time series available. When the profit optimization was set to find the same relative change in effort for all fleets the results obtained from using different vulnerabilities settings were quite similar; with all cases leading to a reduction of around 20% in fishing effort, with an increase in profit and, although small, an increase in biodiversity, while keeping the same level of the baseline landed value. Even a smaller reduction in effort, i.e. 10%, would lead to an increase in profits. However, this result seems to be mainly determined by the dredge and pots fishery that accounted for most of the profits after the optimization had been carried out and were indeed the only fleets, except for the beam trawl, to have had their profits considerably increased. These fleets had their effort always reduced in the profits optimizations for different relative changes in effort irrespective of the vulnerability settings used and seem quite insensitive to changes in other fleets.

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[1] This value is in the old Ecosim scale and is equivalent to a vulnerability of about 5.7 in the new scale.

Hence, when the optimization is for the same relative change, all other fleets are forced to a reduction as well.

The application of the temperature derived forcing function led to a fairly large reduction in profits and in the landed value. Fulton and Smith (2004) reported similar effects for their application of the optimization routine using nutrient loading forcing, where effects of the change in productivity almost overwhelm any changes attributable to the fishing strategies implemented. It has been shown that a bottom-up control temperature driven mechanism had an important effect on the overall production of the Western Channel Ecosystem from the 1970s to 1990s (Araújo et al., 2006). However, the subject of the effects of global warming is still controversial and some suggest (e.g. Bryden et al., 2005) a cooling, instead of warming, over northwest Europe with temperatures 4°C lower than at present. In a cooling scenario, as has been proposed (Richardson and Schoeman, 2004), the system productivity will be higher.

The fact that with an overall reduction in effort it would be possible to increase profits and biodiversity with almost no cost to landed value, as predicted in the compromise solution, is very positive. This can be somewhat counterintuitive, but as observed by Fulton and Smith (2004) the use of ecosystem models provides a framework to identify potential changes that cannot be identified with single-species models, such as counterintuitive changes in abundance when species interactions outweigh the effects of fishing. Although the results obtained here are conditioned to the model assumptions and input parameters and models cannot fully represent ecosystem dynamics, the present findings are encouraging considering that a 5 years

10% overall funded reduction of effort has been proposed in a recent survey with more than 100 fishermen from the South West of England (Anon., 2005).

4.4.Final overview.

In the present work, a substantial quantity of information from a variety of sources has been compiled and integrated. But as in any case of implementing such models, there will always be aspects that can be improved. The information that was generally readily available relates to the main commercial species, for example plaice, sole, cod and other finfish species, but even in such cases sometimes the situation is not ideal. In some cases for example, the biomass series derived from VPA analyses had to be complemented from other sources. There is also a great deal of uncertainty about abundance trends of top predators such as sharks and marine mammals. Interestingly, there were no long-term abundance estimates for shellfish species, which make a considerable contribution to the fishery profits in the Western Channel.

Although having many gaps and being restricted to part of the ecosystem, the MBA data was very useful to complement information for commercial species and to provide information on non-target species. The analyses of this data set published in Anon. (2001) and later in Genner et al. (2004) and Southward et al. (2005), provided a starting point for this work. Despite its undisputed value the MBA have struggled to maintain the long-term surveys due to cost restrictions (S.J. Hawkins, pers. comm.). Mace (2001) reports that United States plans for improving management indicates that the cost of monitoring all managed species would be very high, and that this may preclude comprehensive ecosystem management if the suggestions of

Larkin (1983, 1997) that research and management costs should not exceed 20-30% of the landed value of a fishery are followed. However in an ecosystem-based management context other goods and services provided by the ecosystem that cannot necessarily be priced easily should be taken into consideration. It is believed that "diverse, productive and functioning ecosystems will not only conserve aquatic wildlife and wilderness, but will also likely enhance productivity, water quality, economic options and other goods and services for human societies" (Lotze 2004). These observations and the present study highlight the importance of keeping going long-term monitoring programs such as the trawl surveys of the MBA and the CPR plankton survey. These are often hard to maintain as societies and governments have other priorities.

As widely recognised, the use of ecosystem and multispecies models has the advantage of account for trophic interaction and then are able to predict or at least provide warnings against otherwise unknown undesirable or counterintuitive responses to fishery management actions (Hollowed et al., 2000; Fulton and Smith, 2004; Walters et al., 2005). Walters et al. (2005) showed that widespread application of single-species maximum sustainable yield (MSY) fishing rates would cause severe degradation of ecosystem structure with loss of top predators. Similarly Collie and DeLong (1999) and Gislason (1999) have observed that maximizing total yield in multispecies models leads to elimination of large predators. Likewise, this kind of undesirable effect, i.e., maximizing the yields of the prey species leading to a reduction of their predator abundances, can be inferred from the study of Worm and Myers (2003), which reports on the top-down control of the shrimp *Pandalus borealis* by cod. As reported by Mace (2001), the single MSY concept changed from

being a (1) fixed amount that could be taken indefinitely, to (2) the maximum average yield that changes in response to fluctuations in stock size to (3) a limit to be avoided, a precautionary approach. However, Mace (2001) comments on the difficulties of even reducing fishing mortalities below the MSY level in the United States fisheries and that many studies suggest that if objectives such as maintenance of biodiversity, genetic diversity and reduction of bycatch and waste are considered even more substantial reductions will be necessary. These observations are corroborated by applications such as that presented in Walters et al. (2005) and the findings of the present study.

Mace (2001) highlighted the qualities of the EwE software development saying, "this is exactly the type of development I believe will move us forward towards providing ecosystem-based quantitative advice...". The issue is that is it too early to know if the EwE software is suitable for the task of being a useful management tool? The main general concerns in using this approach and other ecosystem models are the quality and quantity of data used, how to interpret the results in such complex methodology that integrates information and work on the dynamics across so many trophic levels and which level of model complexity is best when model performance is concerned. Regarding model complexity, previous studies (see Fulton et al., 2003) that there is a humped relationship between model detail and performance for ecosystem models. Plagányi and Butterworth (2004) advise that one should start simple and Fulton et al. (2003) recommend the use of multiple "minimum-realistic" models. Pinnegar et al. (2005) found, as they state, a contradictorily result regarding model complexity, with simple models shown to be more stable than a complex model when recovering from disturbance. They also

observed that including adult-juvenile linkage reduced recovery time in some types of model formulations. In addition, they state that changing the focus of different parts of the ecosystem also influences the model stability, with the models with an emphasis on a high level of aggregation of basal groups and the models focused on marine mammals (also aggregated) were the most resilient to disturbances. The main result was that sensitivity of management advice to model configuration should be taken in consideration.

It has been shown that Ecosim model behaviour is dominated by the vulnerability parameter settings rather than size/age accounting details (Walters and Martell, 2004), and by far this is the aspect that has the strongest effect on model resilience and seems to dwarf the effects of model complexity observed in studies such as that of Pinnegar et al. (2005). Walters et al. (2005) state that the step-wise procedure to fit Ecosim estimates to observed time series data by changing the vulnerability and/or estimating a primary production anomaly as it was done in this study does not mean that a fully validated model has been produced. As they state "the fitting procedure is a developing process, subject to changes over time as new information, and ideas about important interactions that may have been missed, become available". Hence, one of the biggest challenges is to improve data quality, particularly information of abundance trends of species groups across many trophic levels to improve the estimates of the vulnerability parameters that play such a critical role in Ecosim dynamics.

The input estimates used in this study are in our view the best possible and the output of the model is obviously subject to error as a result of the estimating

process. This is a widespread problem with the EwE approach and any other ecosystem modelling tool. It is also obvious that it is impossible to capture the whole complexity of an ecosystem using a modelling exercise. Different inputs of the four basic parameters of the model, namely, biomass, consumption rates, turnover rates and diet information will result in different estimates in the simulation, but the range of possible values for the input parameters is limited by mass-balance constraints in the baseline model, and this also constrains, but not always, the possible outcomes. In fact the constraining nature of the mass-balance assumption of Ecopath for initiating projections is considered by some a weakness of the approach (Plagányi and Butterworth, 2004).

According to Walters and Martell (2004) and Walters et al. (2005), fitting more complex time series data patterns, such as those observed for the Western Channel, has typically required examination of the relative role of multiple alternative hypotheses about environmental forcing, fishing and trophic interactions that might equally well explain the data. The core point of the present work is that it is one of the first to analyze system-level control factors, pitting environmental factors against fisheries. It deals with population trends for all parts of the Western Channel, and thus summarizes information at a level rarely achieved before. By accounting for changes in primary productivity we could explain a considerable part of the observed variance, but also due to the complexity of the food web and different levels of exploitation for different species, considerable changes have to be made on the vulnerability parameters to achieve a reasonable fitting. It was supposed (Southward et al. 2005), that the relative success of cod in the Western Channel was due to predation and competitive release due exploitation of other high trophic level

species, but the somewhat congruent abundance trends of many species across various trophic levels points to the fact that changes in productivity of low trophic levels seems to be a strong driving force. Of course we do not pretend to say that a definitive description of the functioning of the Western Channel ecosystem has been given. It just states what the most likely mechanism is, given the available information and assessment tools. As there is a current interest in the ecosystem impacts of fishing, more information on non-target species will become available and as a consequence the application of ecosystem models will be improved, and it is a continuous task. At the present stage the output of the application such as the fishing optimization presented here should be considered in qualitative rather than in quantitative terms as a guide to future management actions. Nonetheless it points to an overall reduction in fishing capacity, an objective widely accepted within the scientific community (Browman and Stergiou, 2004).

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