

Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate

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North Sea environmental and biological data were analysed to examine 30-year changes in production and consumption in the fish foodweb. The analysis revealed that the demand for secondary production placed on the ecosystem by fish declined from approximately $20 \text{ g C m}^{-2} \text{ y}^{-1}$ in the 1970s to $16 \text{ g C m}^{-2} \text{ y}^{-1}$ in the 1990s. Over the same period, the proportion of demand provided by zooplankton production increased from around 70% to 75%. The overall decrease was mainly due to a reduction in piscivorous demersal fish. Average secondary production by omnivorous zooplankton was estimated to be $35 \text{ g C m}^{-2} \text{ y}^{-1}$, and annual fluctuations were positively correlated with the gross production of planktivorous fish. The results suggest a “bottom-up” control of the pelagic foodweb. Individual planktivore species have been impacted by fishing, but the populations of other functionally similar species have expanded to fill the vacant niches, thus maintaining the planktivore role in the system. In contrast, the results indicate that benthos production was more “top-down” controlled. Overall, demersal fish species have been depleted by fishing, with no obvious species expansions to fill the vacant niche, releasing the benthos from predation pressure, and leading to an increase in benthic production and fisheries for invertebrates.

Keywords: benthos, demersal fish, fish diet, fisheries, food consumption, pelagic fish, plankton, production, stock assessment.

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Introduction

The adoption of a more ecological approach to fisheries management requires the development of indicators of the current state of the marine foodweb and the environment, for comparison with baseline values (Murawski, 2000; Rice, 2000). The choices of measurements and baseline conditions pose some problems. First, the structure and function of the foodweb is affected by both fishing and climate, so baseline measurements to compare with current conditions and to assess the impact of exploitation must be standardized to the current state of the climate (Jennings and Blanchard, 2004). Second, most easily identifiable metrics of ecological conditions indicate structure and abundance, but not function or fluxes (e.g. Zwanenburg, 2000). Key measures of the state of the foodweb involve the pathways of energy flow up the web, as well as the relative magnitudes of flows through, for example, benthos

and plankton (Fogarty and Murawski, 1998; Garrison and Link, 2000). Therefore, in addition to readily identifiable abundance-based indices, there is a need for flux-based measurements and an understanding of the mechanisms by which climate and fishing may affect them.

As one of the most heavily exploited and studied shelf seas, the North Sea is an obvious subject for developing foodweb-based indices. There have been a number of attempts at estimating the flows through simplified versions of the North Sea fish foodweb, and these were reviewed by Greenstreet *et al.* (1997). In the main, they used mass-balance approaches and fixed ratios of production : biomass or production : consumption to construct snapshots of energy or carbon fluxes between functional groups of species for given years (Steele, 1974; Jones, 1982, 1984). Greenstreet *et al.* (1997) pointed out that few were constrained by the wealth of diet data available for North Sea fish, and that the implied consumption rates resulted

mainly from the imposed structure and biomass distribution across groups, and the requirement to maintain mass balance. More recently, the approach has been combined with dynamic equations, which in principle can be constrained by diet data, to forecast and hindcast future and past impacts of fishing and environmental changes (Pauly *et al.*, 2000; Christensen and Walters, 2004), though no implementation has yet been published for the North Sea.

Greenstreet *et al.* (1997) proposed a different approach that was not based on considerations of mass balance. The basic idea was to calculate the food requirements of the fish assemblage from abundance, ration, and diet data, and to compare these with estimates of the production of lower trophic levels. If the underlying data and assumptions were correct, then in a stationary system, the gross production (growth plus recruitment) of lower trophic levels should equal consumption by fish and other predators. Thus, mass balance was used as a test of the data and assumptions, rather than a constraint on the structure and fluxes. The analysis was for a snapshot in the mid-1980s, so no conclusions were drawn on the ways in which climate and fishing may have affected the fluxes so derived. In this paper, the aim is to apply the Greenstreet *et al.* (1997) approach to estimate foodweb fluxes for a series of years from 1973 to 2000, as a basis for identifying changes in the system attributable to a combination of climate change and fishing.

The approach of Greenstreet *et al.* (1997) demands extensive data on the diet, ration, and abundance of fish species. Food consumption and diet measurements exist for only a few commercially important fish species, even in an area as well studied as the North Sea, and extrapolating these to represent the fish community as a whole is a major challenge. The approach was to scale the consumption per unit biomass of a few well-studied species up to the community as a whole on the basis of the relative contributions of the studied species to total biomass. Detailed age-structured stock assessments exist for only a few (approximately ten) commercially important species of the 200 or so in the North Sea, but no detailed assessments are carried out for some species for which diet and ration data exist, such as sprat (*Sprattus sprattus*), horse mackerel (*Trachurus trachurus*), and lemon sole (*Microstomus kitt*). As a solution, Greenstreet *et al.* (1997) capitalized on the analysis of Sparholt (1990), who estimated the catchability coefficients of fish species taken by the ICES International Bottom Trawl Survey (IBTS) between 1983 and 1985, and derived the biomass of all fish species in the North Sea. They then raised the food consumption per unit biomass of a subset of well-studied species within a set of four feeding guilds up to the community as a whole, based on Sparholt's estimates of the relative contribution of the studied species to total community biomass. The contributions varied between 76% and 100%, depending on guild.

Unfortunately, the approach of Greenstreet *et al.* (1997) cannot be replicated exactly year by year over an extended

period to produce a time-series of foodweb fluxes, because the trawl survey data needed to undertake the Sparholt analysis are of variable quality, especially before the mid-1980s. An added complication is that the temporal coverage of stock assessments varies between species. For ecologically important species such as sandeel (*Ammodytes marinus*), the detailed assessments extend back only to the early 1980s, whereas for cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*), the series extend back to the 1960s. Hence, a variant of Greenstreet's approach has been developed here, based on fishery landings data. The problems associated with interpreting landings data are well documented, and relate to misreporting of catches by various sectors of the fishing fleets, discarding at sea, variations in the commercial expedience of exploiting different species, and the constraints imposed by stock conservation measures. However, these limitations should not substantially affect their use in the way described below.

Material and methods

Environmental data

Bathymetric data were required for various scaling purposes in the analysis. Average seabed depth was derived for spatial cells of 1° latitude × 2° longitude in the domain of interest (ICES fishing area IV: 51°N–62°N, 4°W–9°E), from the ETOPO5 5-min gridded elevation data set (Hirtzler, 1985). Sea surface areas within depth strata and geographical limits were estimated by integration routines in SURFER-7.

Sea temperature data were required for scaling fish feeding rates and for estimating plankton production. Monthly average temperatures for the years 1973–1999 in ICES fishing area IV, and for the depth intervals 0–30 m and from 30 m to the seabed, were estimated from hydrographic observations (standard CTD and reversing thermometer data on depth and temperature at location and time) held by ICES (see <http://www.ices.dk/ocean/>). Data collected from each 1° latitude × 2° longitude cell within the region were bin-averaged by year, month, and observation depth interval. Unsampled year/month/depth bins were filled by applying the local deviation from the long-term monthly average temperature, based on the deviations in preceding and following months.

Plankton data

Monthly averaged biomasses of omnivorous and carnivorous functional groups of zooplankton were compiled from Continuous Plankton Recorder (CPR) survey data, following a combination of the methodologies described by Broekhuizen *et al.* (1995) and Greenstreet *et al.* (1997).

CPR data on the abundances [accepted numbers per CPR sample (approximately 3 m³) at a fixed depth of approximately 7 m] of the zooplankton taxa listed by Broekhuizen *et al.* (1995; omnivores: *Evdadne* spp., *Limacina* spp., small

copepods, *Calanus finmarchicus* C5–6, *Calanus helgolandicus* C5–6, and *Calanus* spp. C1–4; carnivores: *Euchaeta* spp., *Tomopteris* spp., hyperiid amphipods, euphausiids, chaetognaths) were geometrically averaged by month over a matrix of 1° latitude × 2° longitude spatial compartments for the years 1958–1999, by the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS). The average abundance (per m³) of each taxon was then rescaled to account for undersampling, by a factor of 4 for omnivores and 1.6 for carnivores, according to Broekhuizen *et al.* (1995). Those factors are based on comparisons of zooplankton abundance estimates from a range of detailed studies in the North Sea, and the corresponding CPR samples. The numerical abundance of each taxon was then converted to carbon biomass concentration (mg C m⁻³) by applying either a month-specific or an annual mean carbon weight per individual, as described by Broekhuizen *et al.* (1995). The biomass-by-species data were then summed to derive the biomasses of the two functional groups.

The biomass concentrations of omnivores (mg C m⁻³) in the 1° × 2° compartments were integrated vertically to the mean seabed depth (as mg C m⁻²) by assuming that the CPR estimate was applicable over the upper 30 m of the water column, and that the concentration in the lower part of the column was 30% of the surface value, to reflect the typical vertical distribution of zooplankton in the North Sea (Greenstreet *et al.*, 1997). For consistency, the same integration criteria were applied to carnivores, in contrast to Greenstreet *et al.* (1997), who assumed that carnivores were uniformly distributed through the water column. Finally, the monthly values of functional group biomass (mg C m⁻²) in 1° × 2° compartments were averaged over ICES fishing area IV.

Production by the omnivorous and carnivorous zooplankton groups was derived from the monthly temperatures and carbon biomass estimates, using the Huntley and Lopez (1992) temperature relationship. The parameters of Huntley and Lopez (1992) were applied directly to estimate monthly production by omnivorous zooplankton, but the results were scaled by a factor of 0.2 to estimate the production by carnivores, as described by Greenstreet *et al.* (1997). This scaling was to take account of the fact that the Huntley and Lopez (1992) relationship was developed for copepods, whereas the carnivore group consists of larger taxa that grow more slowly. The monthly production estimates were summed over each calendar year to calculate annual carbon production.

The consumption of omnivorous zooplankton by carnivorous zooplankton was estimated by assuming a typical gross growth efficiency (i.e. production/ration) of 0.3 (Greenstreet *et al.*, 1997).

Benthos data

Greenstreet *et al.* (1997) grouped the macrobenthos of the North Sea into three functional groups – carnivores,

deposit-feeders, and filter-feeders, and estimated their biomass and production during the period 1983–1985 from the ICES North Sea Benthos Survey database (Heip *et al.*, 1992). Unlike for plankton, there are no comprehensive monitoring data on North Sea benthos that could be used to estimate year-specific annual production over a more extended period. Hence, an empirical approach had to be used.

The CPR surveys record abundance of the larvae of benthic invertebrate species, in particular echinoderms and decapods. In the absence of other data, the combined abundance of these taxa was treated as an index of benthic carnivore production. The geometric mean accepted numbers per CPR sample of echinoderm and decapod larvae were added for each year, month, and 1° × 2° compartment, and rescaled to reflect undersampling, using the same factor as for carnivorous zooplankton (1.6). The data were then converted to an index of carbon biomass (mg C m⁻³), assuming a conversion of 0.15 mg C individual⁻¹, and averaged over ICES fishing area IV. Finally, the annual average carbon biomass (mg C m⁻³) of benthic larvae was rescaled to an estimate of benthic carnivore production (p_b; g C m⁻² y⁻¹), as follows:

$$p_b = \frac{\ln(Cb_y + 1)}{\phi} \quad (1)$$

where Cb_y denotes the carbon biomass index of benthic larvae (mg C m⁻³) in year y, and φ is a parameter given by

$$\phi = \frac{(\ln(Cb_{1983} + 1), \ln(Cb_{1984} + 1), \ln(Cb_{1985} + 1))}{P_{1983-1985}} = 2.6 \quad (2)$$

where P_{1983–1985} denotes the annual production of benthic carnivores during the years 1983–1985 (1.3 g C m⁻² y⁻¹), as estimated by Greenstreet *et al.* (1997) from analyses of ICES North Sea Benthos Survey data (Duineveld *et al.*, 1991; Heip *et al.*, 1992).

The food consumption of macrobenthos carnivores was estimated by assuming a typical gross growth efficiency (production/ration) of 0.3 (Greenstreet *et al.*, 1997). The proportions of deposit- and filter-feeders in the diet were assumed constant, equal to that estimated for the period 1983–1985 by Greenstreet *et al.* (1997).

Annual fishery landings of benthic invertebrates were obtained from the STATLANT database maintained by ICES (<http://www.ices.dk/fish/statlant.asp>). These comprise yearly nominal catches of fish and shellfish officially submitted by the 19 ICES Member Countries in the Northeast Atlantic; the years 1973–2000 were used for the current purpose. The data were accessed using the FAO Fishstat+ database system.

Invertebrate species in the database were aggregated into three groups: pelagic (mainly squid), inshore benthic (mainly mussels, cockles, winkles, and oysters), and offshore

benthic invertebrates (35 taxa, mainly crabs, lobsters, prawns, shrimps, scallops, and whelks). Only landings of offshore benthic invertebrates were considered as part of this study. Inshore benthic invertebrate species were not included because their production is probably influenced by coastal conditions that may differ from those of the North Sea as a whole, so they cannot be scaled to North Sea surface area in the same way as offshore species. Pelagic invertebrate catches were <0.05% of finfish, and were also disregarded.

Each of the landed species in the offshore benthic invertebrate category was assigned to one of the three macrobenthos functional groups identified by Greenstreet *et al.* (1997): filter-feeders, deposit-feeders, and carnivores (Appendix).

Fish and fishery data

The sources of data and analysis pathways for estimating the food consumption and gross production of the fish community are shown in Figure 1.

Annual landed weights of fish for the years and areas of interest were obtained from two sources. For fish species subject to annual stock assessment, the landed weights for each assessment region were extracted from the relevant tables of ICES Stock Assessment Working Group reports (Anon., 2004a, b, c). These represent stock assessment scientists' best estimates of landings, taking into account known variations from official landing statistics. In addition, official landings of all fish species (assessed and non-assessed) were obtained from the STATLANT database (see above).

Greenstreet *et al.* (1997) assigned fish species to one of four feeding guilds (pelagic piscivores, pelagic planktivores, demersal piscivores, and demersal benthivores) on the basis of a literature survey and analyses of diet. The same guilds have been adopted in this paper, but their names require clarification. The pelagic planktivore guild includes not only pelagic fish, but also all fish for which plankton taxa constitute >80% of their diet by weight over their whole life. Hence, Norway pout (*Trisopterus esmarkii*) are classed as planktivores, despite having a more demersal distribution in the water column than, for example, sprat. Demersal benthivores are fish that feed almost exclusively on benthic invertebrates, so the guild includes plaice, but not whiting (*Merlangius merlangus*) or cod, which consume benthos but also have a high proportion of fish in their diet. Piscivores are those species for which other fish constitute more than approximately one-fifth of the diet by weight. Hence, mackerel (*Scomber scombrus*) are regarded as piscivores rather than planktivores, because sandeel constitute up to 80% of their diet at certain times of year (25% averaged over the year for ages 2 and 3; Daan, 1989). No piscivore species feed exclusively on fish, however, so the distinction between pelagic and demersal piscivores does not simply relate to the typical position in the water column or mode of fishing used for

capture. The key distinction is between species that are fundamentally piscivorous planktivores (pelagic piscivores, e.g. mackerels and tuna), and those that are piscivorous benthivores (demersal piscivores, e.g. cod and haddock, *Melanogrammus aeglefinus*).

Greenstreet *et al.* (1997) listed the guild assignments of 73 common fish species from the North Sea but, for the same region, the ICES STATLANT commercial landings database contains data on 149 finfish species over the period 1973–2000. For an expanded area of shelf seas (from the Portuguese Shelf to the northern North Sea/Faroe Islands), landings data exist for 330 finfish species. Similarly, data on the abundances of 219 species are recorded in the ICES IBTS database. The guild assignments of the 149 finfish species in the ICES STATLANT landings database listed as having been caught in the North Sea, including the 73 listed by Greenstreet *et al.* (1997), are given in the Appendix. For the many species not listed by Greenstreet *et al.* (1997), diet and habitat information were obtained from FishBase (<http://www.FishBase.org>).

Greenstreet *et al.* (1997) described in detail the analyses of diet and stomach fullness from 13 well-studied fish species (Table 1), and how these were used as the basis for estimating carbon flux between trophic levels and categories of species (Figure 2). The ration and diet composition results have been used in this paper as the basis for estimating annual fluxes during the period 1973–2000. Briefly, for each well-studied species, Greenstreet *et al.* (1997) calculated the average daily ration in each quarter of the year from stomach fullness and various temperature-dependent digestion models (according to guild assignment). This ration was then apportioned across prey taxa on the basis of the composition of stomach contents.

In this paper, the annual ration of food consumed by each well-studied species, expressed as a percentage of their biomass, was calculated from the quarterly results of Greenstreet *et al.* (1997). The results were then adjusted to the temperature applicable each year between 1973 and 2000, using a scaling factor based on the findings of Jobling (1988):

$$\frac{e^{0.097T_y}}{e^{0.092T_{1983-1985}}} \quad (3)$$

where T_y is the annual mean temperature in year y . For benthivores and demersal piscivores, the average temperature of the lower part of the water column (from 30 m deep to the seabed) was applied, and temperature in the upper 30 m was used for planktivores and pelagic piscivores.

The prey composition of this annual ration was assumed constant from year to year for each species, equal to that derived by Greenstreet *et al.* (1997). Year-specific consumption of each prey taxon per unit predator biomass was then raised to the landed weight of each well-studied species, i.e.

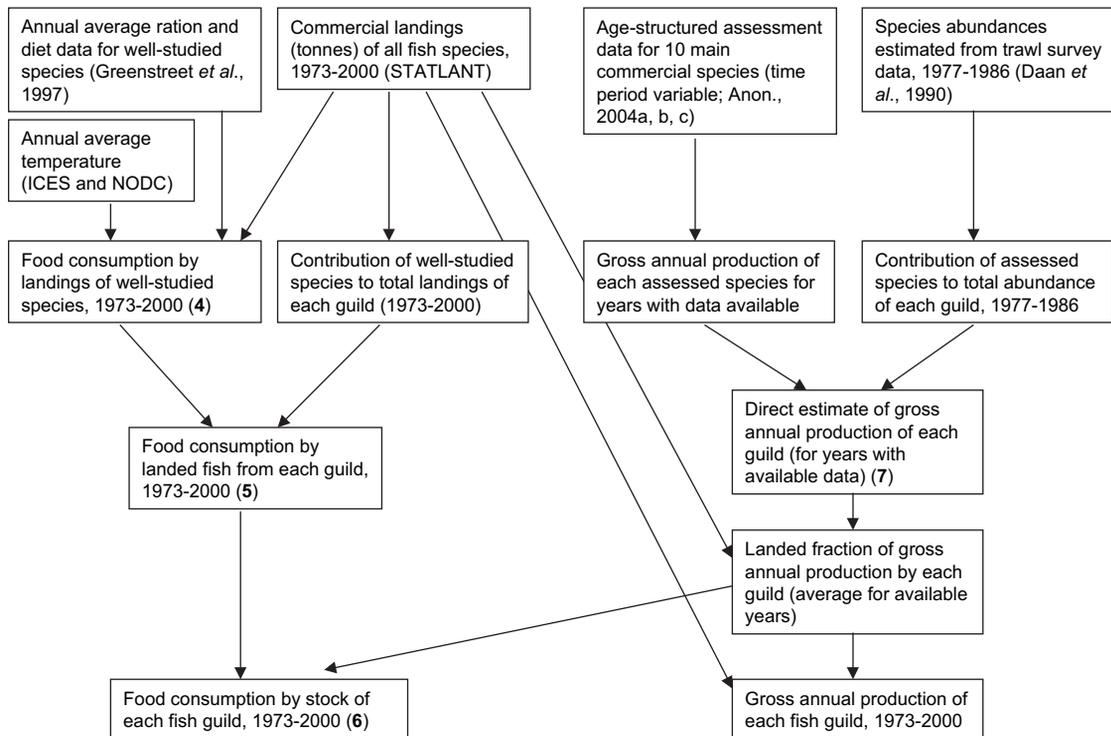


Figure 1. Sources of data and pathways for analysis, resulting in estimates of the gross production and food consumption of fish guilds in the North Sea. Numbers in parenthesis refer to equations in the text, where appropriate.

$$C_d(l)_{y,p,s} = (R_{y,p,s} \times L_{y,s}) / 2 \quad (4)$$

where $C_d(l)_{y,p,s}$ is the direct annual consumption of prey taxon p by the landed fish of well-studied species s in year y , $R_{y,p,s}$ the annual ration of a prey taxon as a fraction of the biomass of species s in year y ($g\ g^{-1}\ y^{-1}$, derived from

daily ration data presented by Greenstreet *et al.*, 1997), and $L_{y,s}$ is the landed weight of species s in year y . The factor 2 accounts for the temporal distribution of landings, as follows. Assuming that the rate of fish landings ($t\ d^{-1}$) is uniform over a year, and that the daily ration ($g\ g^{-1}\ y^{-1}$) is constant or at least varies symmetrically about the mid-date

Table 1. Well-studied, assessed, and the main non-assessed species within each fish feeding guild.

Feeding guild	Well-studied species with diet and ration data	Species with detailed stock assessment data	Well-studied species as a proportion of total guild biomass (1977–1986), according to Daan <i>et al.</i> (1990)	Assessed species as a proportion of total guild biomass (1977–1986), according to Daan <i>et al.</i> (1990)	Main non-assessed species in landings
Pelagic piscivores	Mackerel, horse mackerel	Mackerel	98–100%	28–71%	Bluefin tuna, porbeagle, tope
Demersal piscivores	Cod, haddock, saithe, whiting	Cod, haddock, saithe, whiting	66–87%	66–87%	Ling, anglerfish, hake, pollock
Planktivores	Herring, sprat, sandeel, Norway pout	Herring, sandeel, Norway pout	91–99%	70–96%	Blue whiting, pilchard, argentine, smelt, anchovy, redfish
Benthivores	Plaice, lemon sole, common dab	Plaice, common sole	70–84%	9–20%	Gurnard, turbot, flounder, bib, megrim, brill

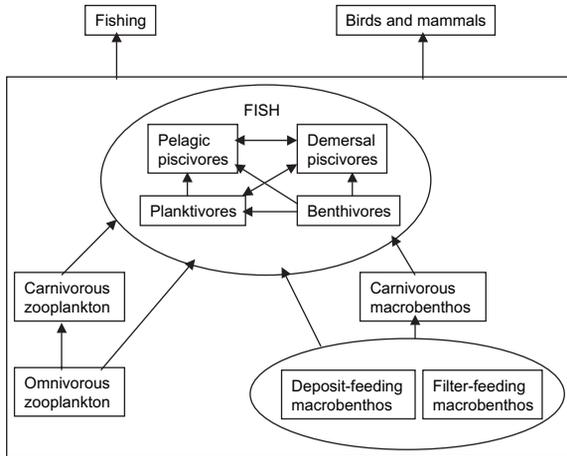


Figure 2. Foodweb components and predator–prey links that emerged from the analysis of Greenstreet *et al.* (1997). Arrows indicate fluxes from prey to predators. Removals by birds and mammals were not explicitly evaluated in that study. Omnivorous zooplankton, and macrobenthos deposit- and filter-feeders, are referred to here as “secondary producers”.

of the year, then the daily consumption of food to support the fraction of annual production destined to be landed at some point during the year decreases from a maximum at 1 January to zero at 31 December. The annual integral of the daily consumption rate will then be half the annual landed biomass times the annual ration.

Within each guild g , the weighted average rations of the well-studied species s were applied to all non-well-studied guild members, with weighting equal to the proportion of the landed catch of well-studied species. Hence, the results represent the food consumed to support the fish production landed from each guild:

$$C_d(l)_{y,p,g} = \left(\sum_{s=1}^{s=S_{\max}} C_d(l)_{y,p,s} \right) \left(L_{y,g} / \sum_{s=1}^{s=S_{\max}} L_{y,s} \right) \quad (5)$$

The range of potential prey for each guild spanned several trophic levels, including fish from the same and other guilds, carnivorous zooplankton, and macrobenthos, and at the lowest level, the “secondary producers” (omnivorous zooplankton and the macrobenthos deposit- and filter-feeders). Hence, the secondary production demand (“footprint”) of the fishery landings consists of both a direct and an indirect component. The direct component is the mass of secondary producer categories consumed directly by the landed fish, as described above. The indirect component is more complicated, comprising the mass of secondary producer categories consumed by the fish prey of landed piscivorous fish, the diet of carnivorous zooplankton and macrobenthos in turn eaten directly by landed fish, and the diet of carnivorous zooplankton and macrobenthos in turn eaten by the fish prey of landed piscivorous fish. The

indirect component attributable to the fish prey of landed fish feeding on zooplankton and benthos ($C_i(l)_{y,p,g}$, for $p =$ zooplankton and benthos) was estimated by reapplying Equations (4) and (5), the term $L_{y,s}$ being substituted by $C_d(l)_{y,p,g}$ for $p =$ each fish guild, i.e. the biomass of fish prey from each guild consumed by landed fish. The indirect component attributable to carnivorous zooplankton and macrobenthos feeding on secondary producers was estimated by assuming a fixed gross growth efficiency for the carnivores (production/ration = 0.3), that the diet of carnivorous zooplankton consisted entirely of omnivorous zooplankton, and that the carnivorous macrobenthos consumed both deposit- and filter-feeders in the annual mean proportions derived by Greenstreet *et al.* (1997).

One of the objectives of the analysis was to estimate the secondary production demand and food consumption of the whole fish assemblage, not just of the landings. The annual gross production by a fish stock (i.e. biomass gains through growth and recruitment) is balanced by losses caused by natural predation and fishing, and the net change in biomass from year to year. Hence, there should be some relatively consistent relationship between fishery catch and gross production. The total demand for secondary production, and the annual consumption of each prey category by the fish community as a whole ($C(t)_{y,p,g}$), were therefore estimated by raising the corresponding values for the landed fish ($C_d(l)_{y,p,g}$) to the gross production of each guild, assuming a factor $\Omega_{y,g}$, defined as the proportion of annual gross production by each fish guild g in year y landed by the fishery:

$$C(t)_{y,p,g} = \left(C_d(l)_{y,p,g} \right) / \Omega_{y,g} \quad (6)$$

To estimate the factor $\Omega_{y,g}$, the annual gross production of each fish guild was derived from a combination of a published summary of North Sea trawl survey data (Daan *et al.*, 1990), and data on numbers- and weight-at-age for ten North Sea fish species. The latter data were taken from catch-at-age analyses conducted annually by ICES Stock Assessment Working Groups (Anon., 2004a,b,c; Table 1).

For each assessed species, the annual growth in year y was estimated as the sum from a_R to a_{\max} of $N_{(a,y)} \times (w_{s(a+1,y+1)} - w_{s(a,y)})$, where $N_{(a,y)}$ and $w_{s(a,y)}$ are the numbers in the stock and the mean weight-at-age a in the stock, respectively, on 1 January in year y , and a_R was the youngest age class in the assessment results. Recruitment at a_R was estimated as $N_{(a_R,y)} \times w_{s(a_R,y)}$. Gross production was then the sum of growth and recruitment.

The combined contribution of the assessed species to the total gross production by each fish guild was estimated from the analysis of trawl survey data given by Daan *et al.* (1990), assuming that the production per unit biomass of the combined assessed species reflected that of the non-assessed species in each guild. Daan *et al.* (1990) published biomass estimates for 87 species for each year between 1977 and 1986, calculated using the methodology of

Sparholt (1990). For each year y , the fraction of total biomass made up by the assessed species was calculated for each guild ($\zeta_{y,g}$). The total annual production by each guild ($P_{y,g}$) was then:

$$P_{y,g} = \frac{\left(\sum_{s_a=1}^{s_a=\max} P_{y,s_a} \right)}{\zeta_{y,g}} \quad (7)$$

where s_a represents the assessed species in guild g .

There was a particular problem with extrapolating the production by mackerel and saithe (*Pollachius virens*) to the guild total for pelagic piscivores and demersal piscivores, respectively. This was because, while the assessment region for all the other assessed species was confined to the North Sea, these species are assessed over an area including waters west of the UK (and west of Ireland and the Bay of Biscay for mackerel). The only feasible way of partitioning the gross production by the total stock of each species between the North Sea and other waters was on the basis of the annual catches.

Carbon conversions

Fish biomass and ration are typically expressed in units of stock wet weight, while plankton production is usually expressed in terms of carbon per unit sea surface area. All fish biomass and flux terms were therefore converted to carbon units and scaled to unit sea surface area. Carbon content per unit wet weight (g C g WW^{-1}) of guild taxa was as quoted by Greenstreet (1996; planktivores, 0.162; benthivores, 0.107; demersal piscivores, 0.103; pelagic piscivores, 0.184; macrobenthos filter-feeders, 0.04; macrobenthos deposit-feeders and carnivores, 0.08; zooplankton omnivores and carnivores, 0.10).

Results

Changes in temperature and production by the zooplankton categories and macrobenthos carnivores are shown in Figure 3. Omnivorous zooplankton production was typically $40\text{--}60 \text{ g C m}^{-2} \text{ y}^{-1}$ over most of the period 1973–1999, but only half that from 1977 to 1983. The reduction was due almost entirely to a depressed biomass of small copepods. *Calanus finmarchicus* contributed approximately 20% of the annually averaged biomass during this period, but declined to $<2\%$ by 1999. Carnivorous zooplankton production was typically 10% of omnivore production, i.e. $4\text{--}6 \text{ g C m}^{-2} \text{ y}^{-1}$, but declined from the late 1970s to the late 1990s, mostly because of a decrease in euphausiid biomass. Chaetognaths contributed 50–60% of the biomass in the late 1990s, but only 10% in the late 1970s. Production by macrobenthos carnivores was estimated to vary between 1 and $1.7 \text{ g C m}^{-2} \text{ y}^{-1}$, with an underlying increase over the period studied.

With the exception of pelagic piscivores, the assessed species represented a relatively stable fraction of the biomass of their guilds in the fish community analysis of Daan *et al.* (1990); Figure 4a. Mackerel was the only assessed pelagic piscivore, and its biomass declined as a fraction of the guild total from 70% to 30% between 1977 and 1986, being replaced by horse mackerel (Figure 5c). The increase in assessed species contribution to the planktivore guild (approximately 10%) was due to the replacement of sprat by herring (*Clupea harengus*), as herring recovered from its collapsed state in the late 1970s.

Combining the production by assessed species with the contribution of assessed species to each guild, Equation (7) provided an estimate of gross production by each guild as a whole, assuming that the production of assessed species was representative of the non-assessed species (Figure 4b). The time-series of these direct estimates of guild-specific gross production were short, especially for planktivorous

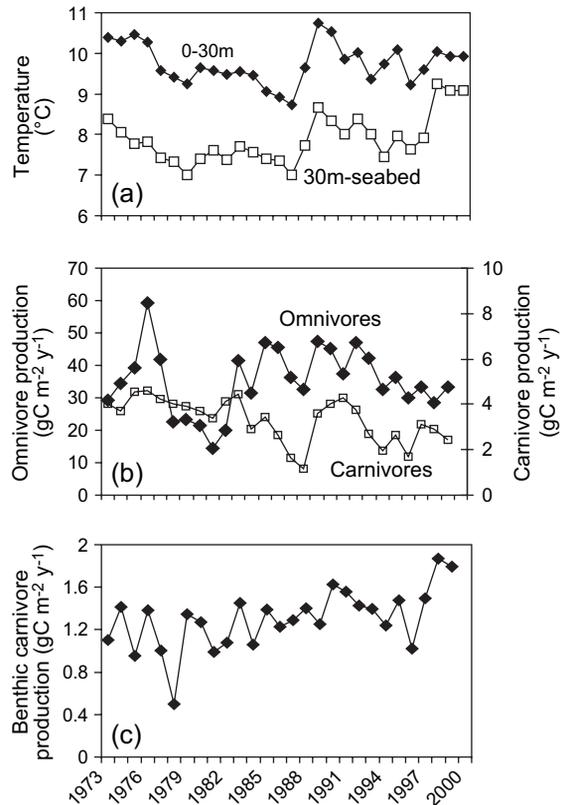


Figure 3. (a) Annual average temperature in the North Sea in the upper 30 m of the water column, and in the lower part deeper than 30 m. (b) Annual production of omnivorous and carnivorous zooplankton as derived from CPR and temperature data, according to the equation of Huntley and Lopez (1992). (c) Annual production of macrobenthos carnivores, estimated as described in text by calibrating CPR data on the abundance of decapod and echinoderm larvae with North Sea benthos survey data.

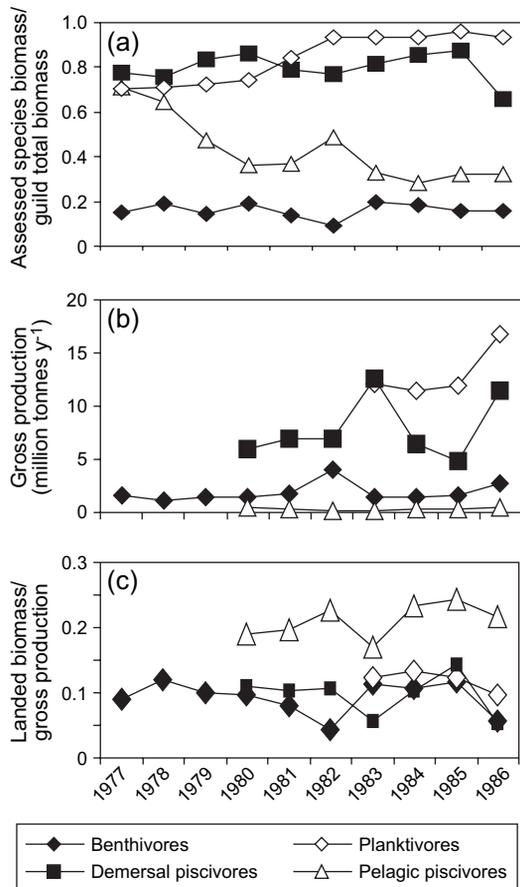


Figure 4. (a) Biomass of assessed species (see Table 1) as a fraction of the total biomass of all species in each of the four fish feeding guilds, derived from the data of Daan *et al.* (1990). (b) Gross production of each fish guild estimated by raising the combined annual production of the assessed species derived from stock assessment data to the guild total, using the biomass fraction of assessed species in each guild. (c) Landings as a fraction of gross production for each fish guild as a whole ($\Omega_{y,g}$). The series are shorter than for the assessed species alone, being limited by the duration of the data on the biomass of assessed species as a fraction of total guild biomass from Daan *et al.* (1990).

fish, because they were governed by species with the shortest duration of assessment results (e.g. sandeel and Norway pout).

The magnitude and the composition of landings of fish from each guild are shown in Figure 5. The demersal piscivore guild showed a stable species composition, with cod, saithe, haddock, and whiting contributing >90% of the landings throughout the period 1973–1999, although total landings declined steadily as the stocks became depleted. The composition of benthivores was also relatively constant, apart from a brief period in the late 1980s when grey gurnard (*Eutrigla gurnardus*) appeared as a large component of the catches. However, many more

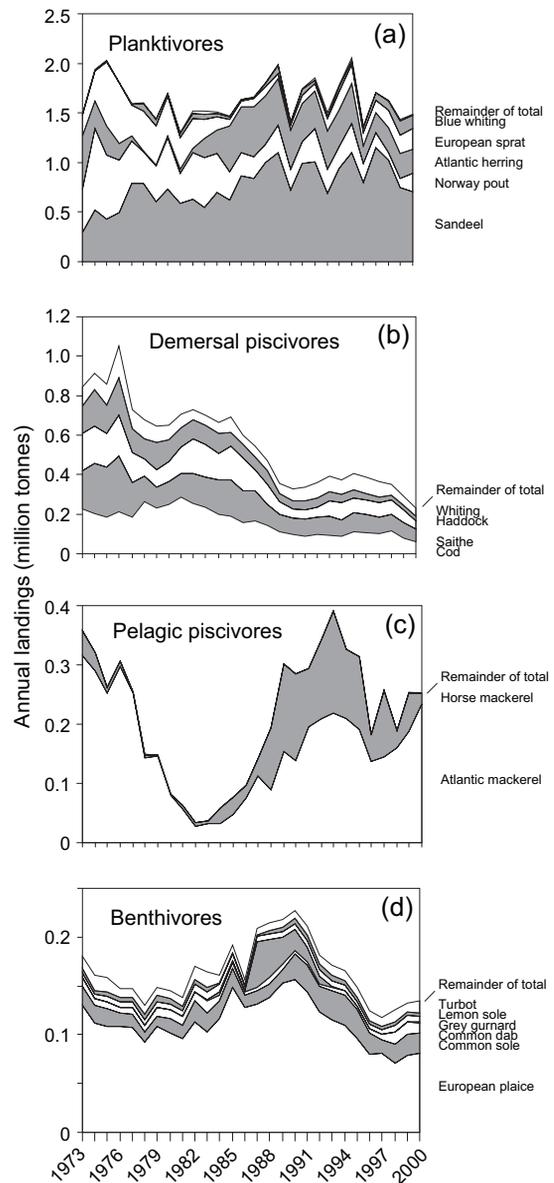


Figure 5. Composition and magnitude of annual landings of fish from each feeding guild, derived from the STATLANT database. Within each guild the species are ranked according to average annual landings over the period 1973–2000, with the highest ranked species at the bottom of each diagram. Species contributing to the landings of each guild are listed in the Appendix.

species were involved in the benthivore fishery than in demersal piscivores.

In contrast, major species substitutions took place in the planktivore and pelagic piscivore fisheries. Sprat dominated herring in the 1970s and early 1980s, but declined as the herring stock recovered. Norway pout dominated the industrial fisheries in the 1970s, but were replaced by sandeel in the 1990s. Mackerel landings in the North Sea

declined sharply in the 1980s, after which the pelagic piscivore fishery included both mackerel and horse mackerel, the latter not previously having been a significant species in the North Sea.

For the assessed demersal piscivore and benthivore species, the proportion of species-specific gross production taken as landings showed no underlying trend over the period 1973–2000. The mean levels of landings as a fraction of gross production (cod 32%, haddock 3%, whiting 13%, saithe 44%, plaice 68%, sole, *Solea solea*, 69%) reflect the perceived rates of natural mortality relative to fishing mortality assumed in the assessment procedure for each species (low natural mortality for saithe, plaice, and sole; high for haddock). In the case of planktivores, herring landings amounted to approximately 40% of gross production immediately prior to stock collapse in the late 1970s, but the landings stabilized at 10–20% from the mid-1980s, following recovery. Industrial fishery landings of Norway pout declined as a fraction of species-specific gross production between 1983 and 2000 (15%, declining to 8%), whereas sandeel landings increased from around 10% to 15% of gross production in the mid-1980s, to 20–25% in the late 1990s. For the two industrial species combined, however, the landed fraction varied around a stable value of 15–20% of production.

With the possible exception of pelagic piscivores, which were represented by a single species (mackerel), the landed fraction of gross production by the combined assessed species in each guild showed little or no underlying trend over the period of the available data. The mean levels of the landed fractions were distinctly different between guilds (10–20% for assessed planktivores and demersal piscivores, 45–85% for assessed benthivores and pelagic piscivores; Figure 6). However, the high proportion of non-assessed species in the benthivore and pelagic piscivore guilds ($\zeta_{y,g}$) meant that, when the relationship was extended to the whole guild ($\Omega_{y,g}$), landings represented a somewhat different proportion of gross production (Figure 4c). Planktivore, benthivore, and demersal piscivore annual landings were between 5% and 15% of gross production, while pelagic piscivore landings were between 17% and 24%. There were insufficient data to specify annual values of the landed fraction of gross production for each guild ($\Omega_{y,g}$) for the entire period 1973–2000, so a mean value for each guild was used in calculations, employing Equation (6) (benthivores, 0.093, s.d. 0.026; planktivores, 0.120, s.d. 0.015; demersal piscivores, 0.096, s.d. 0.032; pelagic piscivores, 0.211, s.d. 0.026). The gross production of the fish community as a whole, estimated by applying these values to the STATLANT-derived landings data, is shown in Figure 7a. Correlations between the time-series of guild gross production are shown in Table 2. The relationship between production series was significant ($p < 0.05$) only for planktivores and pelagic piscivores.

The annual average ration ($\text{g g}^{-1} \text{d}^{-1}$ wet weight) and diet compositions of the well-studied species in each guild,

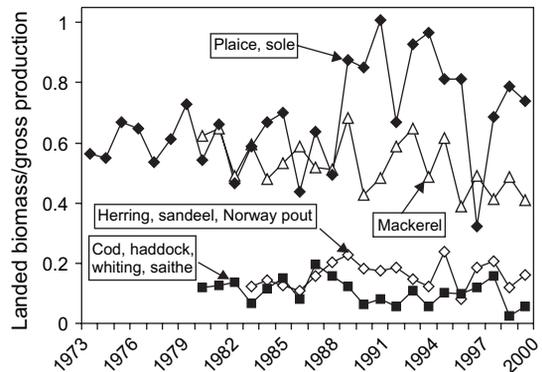


Figure 6. Landings as a fraction of gross production for assessed species only, grouped by feeding guild.

derived from the data presented by Greenstreet *et al.* (1997), are shown in Table 3. Applying those data to the annual landings of each of the well-studied species, Equation (4) provided an estimate of the direct consumption of prey needed to sustain the fishery for each species.

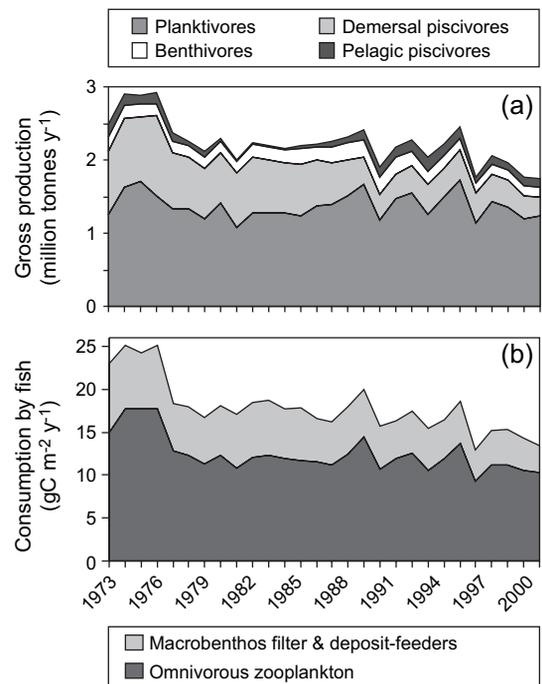


Figure 7. (a) Gross production of each fish guild estimated from the STATLANT landings data. (b) Secondary production required to support the food demands of the fish foodweb. For both omnivorous zooplankton and the macrobenthos (deposit- and filter-feeders), the consumption by fish consisted of direct and indirect consumption. Direct consumption represented fish feeding directly on secondary producers, indirect consumption represented the food requirements of carnivorous zooplankton and macrobenthos, which were themselves prey of fish.

Table 2. Cross-correlations at zero lag for time-series of gross production of each of the fish guilds. Only the cross-correlation between planktivores and pelagic piscivores was significant (r_{critical} for $p < 0.025 = 0.413$, with effective degrees of freedom, N^* , equal to 21, according to the modified Chelton method to account for serial autocorrelation; Pyper and Peterman, 1998).

Fish guild	Planktivores	Demersal piscivores	Pelagic piscivores
Benthivores	0.199	-0.104	0.160
Planktivores		0.075	0.442
Demersal piscivores			-0.252

The values were then raised to the total landings from each guild using Equation (5), and to the total production of each guild using Equation (6).

Fish feeding on fish represent a proportion of the natural mortality assumed in the demographic data for the assessed species. In any year, the difference between gross production of a guild and the sum of landings and fish predation should equal the net change in guild biomass over the year, plus losses attributable to bird and mammal predation, plus discarding from the fishery and unreported landings (Figure 8). Fish predation losses were only a small fraction of gross production, much less than landings, for pelagic piscivores. For all the other guilds, the estimated losses attributable to fish predation were greater than landings, much greater in the case of benthivorous fish. For demersal piscivores, production exceeded the sum of fish predation and landings by a factor of approximately 2 during the 1970s and early 1980s, but then declined to approximately match landings and fish predation in the 1990s. Conversely, landings and fish predation losses of planktivores were approximately equal to gross production during the mid-1970s, but declined steadily over time, mainly because of the reduction in consumption by demersal piscivores. By the late 1990s, predation and landings losses were only half gross production. Losses of benthivores to fish predation and landings exceeded the estimated production up to the mid-1980s, but thereafter predation losses declined by approximately 50%, again mainly because of the reduction in consumption by demersal piscivores.

For most of the time-series, the combined consumption of omnivorous zooplankton by fish and carnivores accounted for approximately half the omnivorous zooplankton gross production estimated from CPR and temperature data (Figure 9a). However, during the period 1977–1982, the estimated gross production apparently declined to the same level as the calculated consumption. The omnivorous zooplankton production demand of the fish community was approximately 40% of gross production, rising to 70% during 1980/1981. The gross production of omnivorous zooplankton was significantly cross-correlated

with the gross production of planktivorous fish at lags 0 and -1 year ($r = 0.365$ at lag 0, $r = 0.416$ at lag -1; $r_{\text{critical}} = 0.360$ at $p < 0.05$ with the effective degrees of freedom, N^* , equal to 20, according to the modified Chelton method documented by Pyper and Peterman, 1998; Figure 9b).

Consumption of macrobenthos carnivores by the fish community as a whole was between 50% and 60% of estimated production during the 1970s, but had declined to 15–20% by the late 1990s. The principal cause of this decline was a >50% reduction in predation by demersal piscivores (Figure 10a). During the late 1980s and early 1990s, this reduction was partly alleviated by the growth of the horse mackerel stock (pelagic piscivores), a species which, unlike mackerel, consumes benthic shrimps as a significant part of its diet.

Concurrent with the declining fish predation on macrobenthos, the surplus production of benthic carnivores (gross production less consumption by fish), and the commercial landings of benthic invertebrates in general, increased steadily from the late 1970s. There was a high inverse cross-correlation ($r = -0.423$) between invertebrate landings and macrobenthos carnivore consumption by fish. As both series exhibited extreme trends, significance tests on the cross-correlation coefficient were unreliable (Pyper and Peterman, 1998; standard inference test: d.f. = 26, $p < 0.025$; modified Chelton test: effective d.f. = 6, $r = r_{\text{critical}}$ at $p = 0.129$). Similarly, benthic invertebrate landings and surplus production were positively cross-correlated ($r = 0.503$) over the period (Figure 10b), but significance tests were again unreliable (standard inference test: d.f. = 26, $p < 0.01$; modified Chelton test: effective d.f. = 7, $r = r_{\text{critical}}$ at $p = 0.086$). The top four commercial invertebrate species in the North Sea during this period were all benthic carnivores (Figure 10c): common shrimp (*Crangon* spp.), Norway lobster (*Nephrops norvegicus*), northern prawn (*Pandalus borealis*), and edible crab (*Cancer pagurus*).

The overall demand for secondary production by the fish community (in carbon units and scaled to the sea surface area of the study region, 602 535 km²) declined from 23 to 25 g C m⁻² y⁻¹ in the 1970s to 13–15 g C m⁻² y⁻¹ by the end of the 1990s (linear trend -0.30 g C m⁻² y⁻², s.e. 0.05 g C m⁻² y⁻²; Table 4, Figure 7b). Approximately 70% of the total demand was met from zooplankton production during the 1970s, but this increased to 75% by the end of the 1990s. Secondary production demand per unit fish production (g C g C⁻¹) can be considered an inverse measure of trophic efficiency, and was highest (>7.0) for demersal piscivores, whose demand for omnivorous zooplankton and benthic filter- and deposit-feeders was mainly indirect through piscivorous feeding on planktivorous fish (Table 5). Temporal changes in demand per unit production within each guild reflected variations in temperature and, especially in the case of pelagic piscivores, variations in species composition. The partial replacement of mackerel by horse

Table 3. Annual average daily ration for the well-studied species of fish in each guild, together with the annual average proportional composition of prey categories in the diet. Values were derived from the quarterly analysis of data by Greenstreet *et al.* (1997).

Parameters for the benthivore fish guild			Plaice	Dab	Lemon sole	
Daily ration as fraction of biomass ($\text{g g}^{-1} \text{d}^{-1}$ wet weight)			0.0269	0.0101	0.0101	
Prey group contribution to annual ration (g g^{-1} wet weight)	Zooplankton	Omnivores	0	0	0	
		Carnivores	0	0	0	
	Macrobenthos	Deposit-feeders	0.8204	0.1123	0.7009	
		Filter-feeders	0.1796	0.1214	0.2225	
Fish	Fish	Carnivores	0	0.7663	0.0714	
		Benthivores	0	0	0.0052	
		Planktivores	0	0	0	
		Demersal piscivores	0	0	0	
		Pelagic piscivores	0	0	0	
Parameters for the planktivore fish guild			Herring	Sprat	Sandeel	Norway pout
Daily ration as fraction of biomass ($\text{g g}^{-1} \text{d}^{-1}$ wet weight)			0.0120	0.0145	0.0145	0.0122
Prey group contribution to annual ration (g g^{-1} wet weight)	Zooplankton	Omnivores	0.1070	1.0000	1	0.3644
		Carnivores	0.7622	0	0	0.5761
	Macrobenthos	Deposit-feeders	0.0415	0	0	0.0229
		Filter-feeders	0.0032	0	0	0.0127
Fish	Fish	Carnivores	0.0303	0	0	0.0237
		Benthivores	0.0009	0	0	0
		Planktivores	0.0536	0	0	0.0001
		Demersal piscivores	0.0013	0	0	0
		Pelagic piscivores	0	0	0	0
Parameters for the demersal piscivore fish guild			Cod	Haddock	Whiting	Saithe
Daily ration as fraction of biomass ($\text{g g}^{-1} \text{d}^{-1}$ wet weight)			0.0144	0.0130	0.0148	0.0127
Prey group contribution to annual ration (g g^{-1} wet weight)	Zooplankton	Omnivores	0	0.0028	0.0167	0
		Carnivores	0.0485	0.1090	0.0974	0.3540
	Macrobenthos	Deposit-feeders	0.0651	0.1571	0.0570	0
		Filter-feeders	0.0091	0.0719	0.0168	0.0008
Fish	Fish	Carnivores	0.2660	0.1931	0.1702	0.0010
		Benthivores	0.1639	0.2187	0.0222	0.0005
		Planktivores	0.2120	0.2464	0.5344	0.4485
		Demersal piscivores	0.2257	0.0010	0.0852	0.1951
		Pelagic piscivores	0.0097	0	0.0001	0
Parameters for the pelagic piscivore fish guild			Mackerel		Horse mackerel	
Daily ration as fraction of biomass ($\text{g g}^{-1} \text{d}^{-1}$ wet weight)			0.0048		0.0164	
Prey group contribution to annual ration (g g^{-1} wet weight)	Zooplankton	Omnivores	0.1697		0.1067	
		Carnivores	0.5306		0	
	Macrobenthos	Deposit-feeders	0.0100		0	
		Filter-feeders	0.0405		0	
Fish	Fish	Carnivores	0.0029		0.2355	
		Benthivores	0.0001		0.0059	
		Planktivores	0.2449		0.1011	
		Demersal piscivores	0.0008		0.5507	
		Pelagic piscivores	0.0004		0	

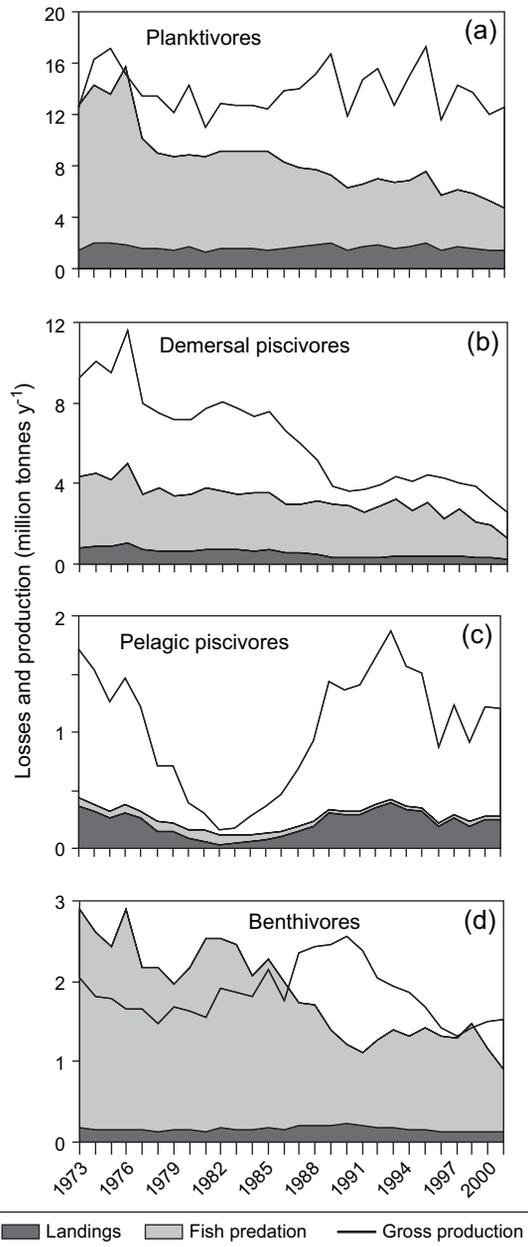


Figure 8. Annual losses to landings and fish predation from each fish guild, compared with gross annual production.

mackerel resulted in a marked increase in demand per unit production of pelagic piscivores. At a whole community level, secondary production demand per unit production declined from approximately 3.5 to 2.5 during the period 1973–2000 (Table 5, Figure 11), reflecting increasing temperature and a loss of demersal piscivores. The secondary production demand per unit landed weight of fish (all guilds combined) was in general lower than the demand per unit gross production, because the landings

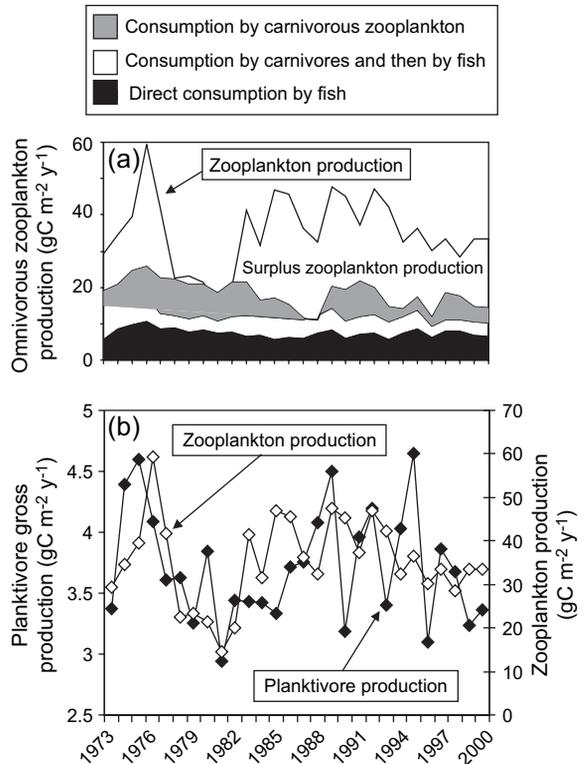


Figure 9. (a) Breakdown of the consumption of omnivorous zooplankton by fish and carnivorous plankton, compared with production. Surplus production is the difference between gross production and the total consumption accounted for by the analysis. (b) Comparison between time-series of gross production in the same year by planktivorous fish and omnivorous zooplankton. The series were significantly correlated ($r = 0.365$, $p < 0.05$, modified degrees of freedom $N^* = 20$).

contained a disproportionately large contribution from pelagic piscivores and planktivores. However, the demand per unit landed weight also declined during the study period (Table 5, Figure 11).

Discussion

Limitations and assumptions of the methodology

As with any synthesis of diverse data of variable quality, this study faced a number of problems. Perhaps the major difficulty was uncertainty about the abundance of the non-assessed fish species in the system. Trawl survey data represent the only realistic source of information on the whole fish community, but consistent data from the North Sea extend back in time only to the early 1980s. In addition, there are major issues of interpretation concerning the catchability of individual species. Catch per unit effort (cpue) certainly cannot be taken on face value as a measure

of the relative abundance of species in the sea. A few investigators have attempted to resolve the catchability issues for restricted time periods, but there is no scheme in operation for routinely updating the estimated biomass and species composition of a whole fish assemblage from annual survey results. Previously published analyses have been used here effectively to calibrate the more extensive, but also controversial, fishery landings data from the North Sea. The uncertainty regarding landings data arises principally from the extent to which they under-represent the catch by fishing fleets as a consequence of discarding at sea and misreporting at the quayside. In this study, however, landings data are used as an index of gross production by aggregations of many species, including both targeted commercial species, and non-targeted species caught incidentally. Though limited in temporal extent, the analysis presented here suggests a rather constant relationship between landings and gross production for each guild in the North Sea, though this would not necessarily be the case for individual species.

The second major limitation of the analysis was the use of fixed diet compositions and weight-specific rations (albeit temperature-adjusted) for each well-studied species. These were established from the literature and the data survey of Greenstreet *et al.* (1997), which gathered fragmentary information from a number of age classes, years, and study areas. However, changes in prey composition and abundance, and the age composition of the well-studied species must influence the population level diet and ration. There is little that can be done to avoid the assumption of a fixed diet composition in a data-based analysis such as this. Alternatives include equally uncertain assumptions about prey selectivity, and the implementation of dynamic equations to estimate consumption directly from measures of prey abundance and availability. However, the assumption of a fixed ration per unit biomass in this study is in principle partly alleviated by referencing the food consumption by the landed biomass to the gross production of each guild, rather than total biomass. There was no underlying assumption about production per unit biomass (P:B) in the estimation of gross production by the assessed species, although the P:B ratios of the non-assessed species in each guild were assumed to be the same on a year-by-year basis as for the combined assessed species. Hence, the methodology was partly capable of accounting for the trophic consequences of variations in growth rate and recruitment of the assessed species. Unfortunately, the full capability of the method was only partly realized here owing to the lack of processed information from trawl surveys to support the specification of year-specific values for $\Omega_{y,g}$ (landings/gross production) for each guild.

Assignment of fish species to guilds is always going to involve some potentially controversial decisions. There are few data on diet composition for many of the less commonly encountered species in the landings and survey data for the North Sea. In those cases, it was necessary to

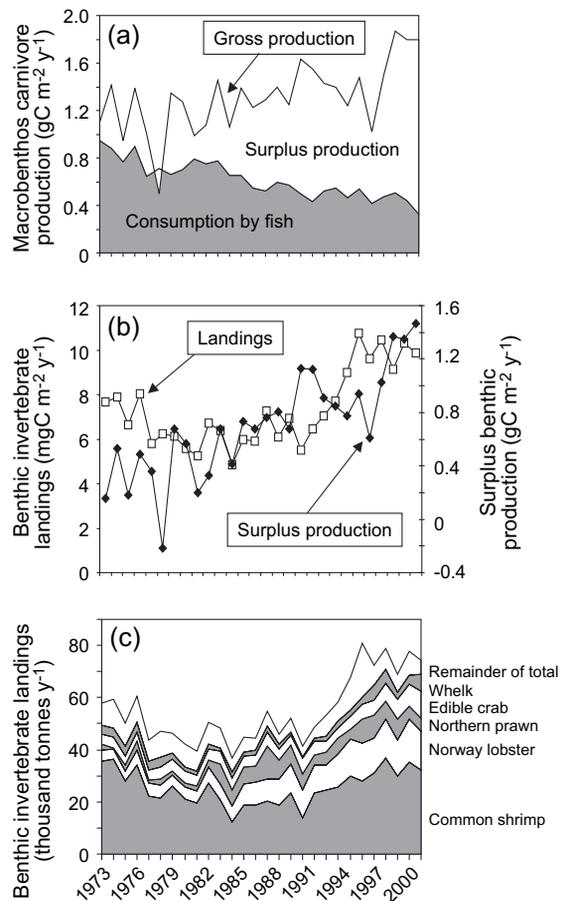


Figure 10. (a) Consumption of carnivorous macrobenthos compared with production. Surplus production is the difference between gross production and consumption accounted for by the analysis. (b) Comparison between time-series of carnivorous macrobenthos surplus production, and commercial landings of benthic invertebrates. The time-series were significantly correlated according to standard inference tests ($r = 0.503$, $d.f. = 26$, $p < 0.01$). (c) Composition and magnitude of annual landings of benthic invertebrates, derived from the STATLANT database. Species were ranked according to the annual average landings, 1973–2000, with the highest ranked species at the bottom of each diagram. Species contributing to the landings are listed in the Appendix.

reach a decision on qualitative data, often from studies outside the North Sea, on similar species or, as a last resort, on allometric considerations (e.g. Pauly, 1989). However, provided that the major species, and especially the well-studied and assessed species, were correctly assigned, then this limitation should not be critical for the analysis presented here. The first priority of the guild aggregation was to condense the taxonomic detail down to a level that still reflected the fundamental structure of the foodweb, without the intricacies of individual species. Thus, for example, regarding mackerel as a piscivore may seem unacceptable to some, but it is necessary in order to

Table 4. Decadal averages of foodweb flux ($\text{g C m}^{-2} \text{y}^{-1}$).

Parameter	Fish guild	1973–1979	1980–1989	1990–1999
Landings	Pelagic piscivore	0.0785	0.0332	0.0866
	Demersal piscivore	0.1398	0.1045	0.0614
	Planktivore	0.4568	0.4330	0.4430
	Benthivore	0.0272	0.0314	0.0285
	Benthic invertebrates	0.0070	0.0061	0.0086
	Total fish	0.7423	0.7082	0.6281
Gross production	Pelagic piscivore	0.3749	0.1587	0.4135
	Demersal piscivore	1.5383	1.1503	0.6756
	Planktivore	3.8471	3.6462	3.7301
	Benthivore	0.3070	0.3541	0.3218
	Total fish	6.0673	5.3093	5.1410
	Carnivorous zooplankton	4.1489	3.1130	2.9545
	Omnivorous zooplankton	35.7244	33.8039	36.6240
	Macrobenthos carnivores	1.1000	1.2404	1.4909
Consumption	Fish by fish	3.7709	2.6874	1.9010
	Carnivorous zooplankton by fish	3.8860	3.0651	2.5809
	Macrobenthos carnivores by fish	0.7890	0.6569	0.4853
	Omnivorous zooplankton by fish	8.4308	6.9502	7.0533
	Macrobenthos deposit- and filter-feeders by fish	2.6173	2.4659	1.9085
	Omnivorous zooplankton by carnivorous zooplankton	13.8298	10.3766	9.8484
	Macrobenthos deposit- and filter-feeders by macrobenthos carnivores	3.6668	4.1345	4.9695
Secondary production demand of the fish community	Demand for omnivorous zooplankton production	14.9075	12.0588	11.3548
	Demand for macrobenthos filter- and deposit-feeder production	6.5925	5.7957	4.4246
	Total demand for secondary production	21.5000	17.8545	15.7794

distinguish it from sandeel, sprat, and the other exclusive planktivores.

The methodology for estimating zooplankton production also involved some potentially controversial assumptions. First, the conversion of CPR data into depth-integrated abundance of plankton taxa involved a number of assumptions, including the volume filtered during each sampling interval by the CPR (Jonas *et al.*, 2004), the extent of undersampling attributable to mesh selectivity and avoidance (Broekhuizen *et al.*, 1995), the vertical distribution of plankton (Greenstreet *et al.*, 1997), and the carbon mass per individual of the taxa selected to represent the omnivore and carnivore guilds (Broekhuizen *et al.*, 1995). Then, the use of temperature-dependent weight-specific growth rates estimated from empirical relationships (Huntley and Lopez, 1992) to determine production is also debatable (Runge and Roff, 2000). With these caveats, the results indicate an average gross production rate of around $35 \text{ g C m}^{-2} \text{y}^{-1}$, roughly equivalent to $80 \text{ g dry weight m}^{-2} \text{y}^{-1}$. This value is high compared with the $44 \text{ g dry weight m}^{-2} \text{y}^{-1}$ estimated by Steele (1974). However, Steele's estimate was for herbivore production, whereas the

calculations made here represent the gross production of omnivores, and hence, include an unquantified component of recycled production within the guild attributable to carnivory. New primary production (i.e. primary production based on nitrate assimilation rather than on recycled ammonia; Dugdale and Goering, 1967) has been estimated to be around $40 \text{ g C m}^{-2} \text{y}^{-1}$ in the Dogger Bank area (Richardson *et al.*, 2000), and between 30 and $100 \text{ g C m}^{-2} \text{y}^{-1}$ in the North Sea as a whole (Steele, 1974; Richardson and Pedersen, 1998). Assuming a gross growth efficiency of 0.3, these figures imply herbivore gross production of around $10\text{--}30 \text{ g C m}^{-2} \text{y}^{-1}$, and that, for the omnivorous zooplankton production estimated in this study to be consistent with other estimates, around 40% of the gross production would have to be recycled within the guild by carnivory.

More difficult than the estimation of changes in zooplankton production was the derivation of North Sea benthic production. In this case, there were no precedents for a methodology, and few previously published estimates of production. The logic for the empirical approach adopted here was that the abundance of planktonic larvae of

Table 5. Decadal averages of the secondary production demand per unit production (g C g C^{-1}) of different fish guilds, the fish community as a whole, and landings.

Parameter	Fish guild	1973–1979	1980–1989	1990–1999
Secondary production demand of the fish community per unit fish production	Pelagic piscivores	1.267	2.173	2.550
	Demersal piscivores	7.283	7.114	7.369
	Planktivores	2.265	2.219	2.310
	Benthivores	3.375	3.323	3.523
	Total community	3.531	3.372	3.076
Secondary production demand of fish landings per unit fish landings	Total landings	3.197	3.154	2.910

macrobenthos could represent an index of the spawning population biomass and hence production, assuming a constant P:B ratio. The results indicate a trend of increasing macrobenthos production since the mid-1970s. Data from some inshore monitoring stations seem to support this conclusion (Frid *et al.*, 1996; Clark and Frid, 2001), but clearly this is a somewhat tentative aspect of the study.

Fish guild composition

The landings data show that the fishery for planktivores has remained relatively constant over time despite major fluctuations in composition. As the landings of some species declined, others expanded to take their place. For example, sprat landings increased as herring collapsed in the late 1970s, and declined again as the herring fishery recovered. Similarly, horse mackerel partially replaced mackerel in the pelagic piscivore guild during the 1990s. However, no such substitutions occurred in the demersal

piscivore guild as a result of the steady decline of cod, saithe, haddock, and whiting landings. The species composition of the benthivore guild landings also remained remarkably constant over the 30-year study period, with the exception of a brief upsurge in landings of grey gurnard in the late 1980s.

Changes in the species composition of the landings must partly reflect the underlying abundance of species in the sea, but may also be due to changes in patterns of exploitation. However, temporal trends in the intensity of exploitation of particular species (Figure 6) were small compared with changes in production or abundance, so that, for example, the substitution of sprat for herring in the landings during the 1970s and early 1980s, horse mackerel for mackerel in the 1990s, and the lack of species substitutions in demersal piscivore landings, almost certainly reflect species abundances in the sea. With regard to the sprat–herring interaction, independent data from hydroacoustic and larval surveys provide supporting evidence for the expansion of the sprat population during the period when herring were scarce, and their subsequent decline as herring recovered (McKay, 1984; McKay and Edwards, 1985). The relative stability of the species compositions of the demersal guilds is presumably related to their closer association with bathymetry and sediment habitat than pelagic species, making range expansion and species substitution more difficult. Alternatively, the results might be indicative of more intense competition for resources in the pelagic system than in the demersal.

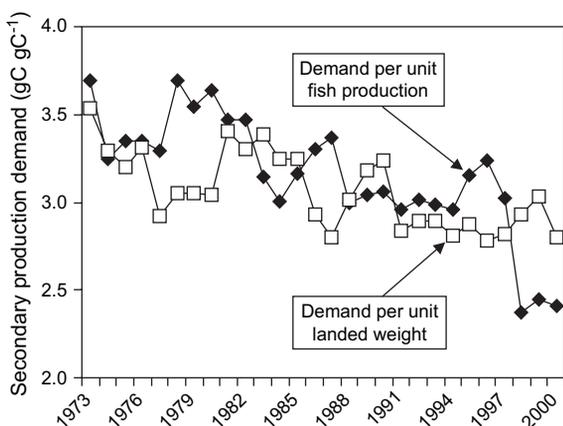


Figure 11. Annual demand for secondary production (omnivorous zooplankton plus filter- and deposit-feeding macrobenthos) by the fish foodweb in the North Sea, i.e. direct and indirect consumption. Filled symbols: demand attributable to the whole community per unit gross production. Open symbols: demand attributable to fish landings per unit landed weight.

Foodweb fluxes

The results indicate a significant decline over time in the overall demand for secondary production by the fish foodweb. Demand for both zooplanktonic and benthic secondary production declined, although demand for zooplankton production increased as a proportion of the total. Concurrently, secondary production demand per unit of fish gross production declined, indicating an increase in the efficiency of the foodweb. The pelagic guilds (planktivores and pelagic piscivores), which derive a

significant part of their food intake from feeding directly on secondary producers, had the lowest ratio of secondary production demand per unit production. The increase in overall efficiency reflected the loss of demersal guild biomass from the overall community, i.e. an increase in the proportion of pelagic guild species.

The estimated gross production of omnivorous zooplankton exceeded the combined requirements of the fish foodweb and carnivorous zooplankton by a factor of approximately 1.6 over most of the time period. This seems consistent with the implied extent of recycling within the omnivorous zooplankton guild attributable to carnivory, and suggests that the estimated plankton production demand of the fish community roughly corresponded to the available herbivore production. However, there are additional sinks for omnivorous zooplankton production in the system. Consumption by gelatinous zooplankton, which was not included in the carnivorous zooplankton group, could be important. The biomass of scyphomedusae in the North Sea was assessed in the 1970s and early 1980s by Hay *et al.* (1990). Their data indicate a typical biomass of 0.037 g C m^{-2} in July for the three main species of scyphomedusae combined. Hence, assuming a daily ration of 10% of biomass, the data imply a zooplankton consumption of $0.004 \text{ g C m}^{-2} \text{ d}^{-1}$, compared with a gross production in July (from CPR data for the same years) of $0.197 \text{ g C m}^{-2} \text{ d}^{-1}$. Therefore, the available data indicate that, North-Sea-wide during the 1970s and early 1980s, scyphomedusae consumed only around 2% of omnivorous zooplankton gross production. There are anecdotal reports, but as yet no published evidence, that the abundance of scyphomedusae may have increased in the North Sea since the 1980s, but even if it is doubled, the impact apparently remains relatively small overall.

The results indicate that, for all fish guilds combined, $3.7\times$ as much fish are eaten by other fish each year as are landed by the fishery. The ratio was higher (10) for benthivores, and lower for pelagic piscivores (0.1). It was not clear from the diet data of Greenstreet *et al.* (1997) that any of the well-studied species were significant predators on pelagic piscivores. The difference between gross production and the sum of landings and fish predation (-0.5 to 9 , average 5 million tonnes wet weight y^{-1} for planktivores) should represent losses attributable to bird and mammal predation, plus discards and misreporting. Bryant and Doyle (1992) estimated the consumption of fish (mainly planktivores) by birds and mammals in the North Sea to be between 1.0 and 1.5 million tonnes y^{-1} during the early 1980s. Tasker *et al.* (2000) estimated that at least 1.0 million tonnes y^{-1} of fish and offal are discarded from North Sea fisheries. The extent of misreported landings is very hard to estimate. However, as a conservative estimate, the sum of bird and mammal predation, discarding, and misreporting could amount to at least 3×10^6 tonnes y^{-1} . Therefore, the foodweb calculations are not unreasonable in terms of these independent (albeit crude) balancing estimates.

Controls on foodweb structure and function

The links between zooplankton and climate fluctuations are becoming increasingly clear as a result of recent research. For example, the latitudinal ranges of Subarctic zooplankton taxa and temperate copepod species in the northeastern Atlantic have both shifted northwards over the last 40 years, in concert with warming sea temperatures and changes in climate indices such as the North Atlantic Oscillation index. This has led to a major change in species composition of zooplankton in the North Sea, in particular the substitution of *Calanus finmarchicus* by smaller temperate copepod species (Beare *et al.*, 2002; Beaugrand *et al.*, 2002). At the same time, changes in the timing of seasonal patterns of abundance of plankton taxa (Edwards and Richardson, 2004), and correlations between phytoplankton and zooplankton abundances over large spatial and temporal domains (Richardson and Schoeman, 2004) indicate tight “bottom-up” control of the planktonic foodweb. The results from this study indicate that the pelagic side of the fish foodweb also appears to be controlled by production processes (“bottom-up”), while the demersal side is controlled by predation (“top-down”). Evidence for this conclusion is provided by:

- (i) the positive correlation between planktivorous fish production and the independently estimated production by omnivorous zooplankton;
- (ii) the positive correlation between planktivore and pelagic piscivore fish production;
- (iii) the inverse trends of fish predation on, and the production and commercial landings of, carnivorous macrobenthos.

If it were the case that fluctuations in regional scale zooplankton production are fundamentally controlled by predation pressure, one would expect to find an inverse relationship between consumption and production, but this was not found. Similarly, there was no inverse relationship between planktivore production and consumption by piscivores. Hence, overall production by planktivorous fish is probably not limited by predation (though individual species might be). Presumably, therefore, zooplankton and planktivore production is mostly “bottom-up” controlled by new primary production, physical oceanographic, and climate-related processes. As a caution to this conclusion, according to Lotka–Volterra dynamics (Pielou, 1969), “bottom-up” control might be expected to result in a lagged response of the planktivores to fluctuations in zooplankton production, whereas in fact there appears to be little or no lag between the two. However, Lotka–Volterra dynamics are complicated in cases, as here, of multiple predators and multiple prey (Steele, 1974), and simple lagged responses are not guaranteed.

In contrast to the plankton foodweb, macrobenthos production and landings showed a trend inverse to that of

the consumption of benthos by demersal fish guilds. This is consistent with predation being the major control on macrobenthos production, and demersal fish production being driven by fisheries rather than by secondary production in the benthos. This is not to say that climate and physical oceanographic factors play no part in the productivity of individual species in the demersal piscivore and benthivore guilds. There is clear evidence of an inverse relationship between North Sea cod and plaice recruitment rates, for example, and sea temperature, which has made those stocks more vulnerable to overfishing in a warming climate (Fox *et al.*, 2000; Clark *et al.*, 2003). Recruitment contributes to overall productivity (production per unit biomass), and because fishing mortality rates have not decreased in parallel with the warming trend, the consequence has been a net decline in production and biomass. In addition, the demersal piscivore guild as a whole is more vulnerable to fishing than that of the planktivores, owing to the apparent lack of capacity for species substitution.

The results of the current study suggest that the functioning of the fish foodweb in the North Sea has been altered by a combination of fishing and climate. Depletion of benthos-consuming fish, through a combination of fishing and climate, has shifted the structure of the secondary production demand at the base of the foodweb towards zooplankton, and released the benthos from predation pressure, causing an increase in macrobenthos production. Planktivorous fish production correlates with zooplankton production, so presumably the shift in structure will also have made the system as a whole more responsive to climate fluctuation, assuming that this is the fundamental cause of variations in plankton production. Other authors noted a change in the structure of the North Sea ecosystem during the late 1980s, principally on the basis of species composition, e.g. changes in water currents, plankton speciation, and invasion of the North Sea by horse mackerel, and some have referred to this as a regime shift (Reid *et al.*, 2001). The invasion by horse mackerel is certainly shown by the results here to be ecologically important, because it partially reverses the declining predation pressure on macrobenthos, although it is not a key issue in terms of the changing structure of the foodweb. More likely, the invasion represents an individual species response to changing environmental conditions.

The study period spans almost 30 years, but it begins in 1973 during the “gadoid outburst” in the North Sea. Stocks of all the major gadoid species were exceptionally productive by twentieth century standards during that period (Pope and Macer, 1996). There is little knowledge of the unexploited state of the North Sea, because trawl fisheries were already active in the early twentieth century when reliable catch records begin. However, Jennings and Blanchard (2004) estimated that the primary production required to support the contemporary fish community in the North Sea may be only 30% of that in an unexploited state,

and the main feature of the modern system is the near absence of large fish (>4 kg), which would be principally demersal piscivores and benthivores. The secondary production demand per unit fish production synthesizes trophic guild and species composition changes that have occurred at least since the 1970s, and hence may be a useful index of foodweb fluxes in the North Sea. Declining values of this index have reflected the loss of, in particular, demersal piscivores and the increasing dominance of planktivores, and indicate a case of “fishing down the foodweb”, in the terminology of Pauly *et al.* (1998). Secondary production demand per unit landed weight has been similar to demand per unit production over the period studied. The North Sea fisheries have, in general, harvested in proportion to production regardless of trophic guild assignment, rather than targeting particular guilds (average landings per unit production were similar across guilds, except for pelagic piscivores). In other regional seas where, for example, there are no industrial fisheries, this may not necessarily be the case. Whether the structural change reported here, towards a less piscivorous and more planktivorous regime, represents a smooth, abrupt, or discontinuous regime shift (in the terminology of Collie *et al.*, 2004) cannot yet be determined.

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Appendix

Offshore benthic invertebrate and finfish categories in the STATLANT database with catch records from the North Sea, and their assignment to macrobenthos trophic group and fish feeding guild.

Common name	Scientific name	Group
Clams	Bivalvia	Macrobenthos filter-feeder
Common European bittersweet	<i>Glycymeris glycymeris</i>	Macrobenthos filter-feeder
Crangon shrimp	<i>Crangon</i> spp.	Macrobenthos filter-feeder
Crangonid shrimp	Crangonidae	Macrobenthos filter-feeder
Craylets, squat lobsters	Galatheidae	Macrobenthos filter-feeder
Edible crab	<i>Cancer pagurus</i>	Macrobenthos filter-feeder
Great Atlantic scallop	<i>Pecten maximus</i>	Macrobenthos filter-feeder
Green crab	<i>Carcinus maenas</i>	Macrobenthos filter-feeder
Manila clam	<i>Corbicula manilensis</i>	Macrobenthos filter-feeder
Marine crabs	Brachyura	Macrobenthos filter-feeder
Marine molluscs	Mollusca	Macrobenthos filter-feeder
Queen scallop	<i>Aequipecten opercularis</i>	Macrobenthos filter-feeder
Scallops	Pectinidae	Macrobenthos filter-feeder
Striped venus	<i>Chamelea gallina</i>	Macrobenthos filter-feeder
Grooved carpet shell	<i>Ruditapes decussatus</i>	Macrobenthos deposit-feeder
Razor clams	<i>Solen</i> spp.	Macrobenthos deposit-feeder
Whelk	<i>Buccinum undatum</i>	Macrobenthos deposit-feeder
Aesop shrimp	<i>Pandalus montagui</i>	Macrobenthos carnivore
Black stone crab	<i>Menippe mercenaria</i>	Macrobenthos carnivore
Blue crab	<i>Callinectes sapidus</i>	Macrobenthos carnivore
Common prawn	<i>Palaemon serratus</i>	Macrobenthos carnivore
Common shrimp	<i>Crangon crangon</i>	Macrobenthos carnivore
European lobster	<i>Homarus gammarus</i>	Macrobenthos carnivore
King crabs	<i>Paralithodes</i> spp.	Macrobenthos carnivore
Marine crustaceans	Crustacea	Macrobenthos carnivore
Natantian decapods	Natantia	Macrobenthos carnivore
Northern prawn	<i>Pandalus borealis</i>	Macrobenthos carnivore
Norway lobster	<i>Nephrops norvegicus</i>	Macrobenthos carnivore
Pandalus shrimp	<i>Pandalus</i> spp.	Macrobenthos carnivore
Penaeus shrimp	<i>Penaeus</i> spp.	Macrobenthos carnivore
Portunus swimming crabs	<i>Portunus</i> spp.	Macrobenthos carnivore
Red crab	<i>Geryon quinquedens</i>	Macrobenthos carnivore
Sea urchins	Echinoidea	Macrobenthos carnivore
Spinous spider crab	<i>Maja squinado</i>	Macrobenthos carnivore
Starfish	Astroidea	Macrobenthos carnivore
Velvet swimming crab	<i>Necora puber</i>	Macrobenthos carnivore
Alfonsino	<i>Beryx</i> spp.	Planktivore
Allis and twaite shad	<i>Alosa alosa</i> , <i>A. fallax</i>	Planktivore
Argentine	<i>Argentina</i> spp.	Planktivore
Atlantic herring	<i>Clupea harengus</i>	Planktivore
Atlantic pomfret	<i>Brama brama</i>	Planktivore
Atlantic redfish	<i>Sebastes</i> spp.	Planktivore

(continued)

Appendix (continued)

Common name	Scientific name	Group
Atlantic salmon	<i>Salmo salar</i>	Planktivore
Basking shark	<i>Cetorhinus maximus</i>	Planktivore
Beaked redfish	<i>Sebastes mentella</i>	Planktivore
Blackbelly rosefish	<i>Helicolenus dactylopterus</i>	Planktivore
Blue whiting (= poutassou)	<i>Micromesistius poutassou</i>	Planktivore
Capelin	<i>Mallotus villosus</i>	Planktivore
Chars	<i>Salvelinus</i> spp.	Planktivore
Clupeoids	Clupeoidei	Planktivore
Cyprinids	Cyprinidae	Planktivore
European anchovy	<i>Engraulis encrasicolus</i>	Planktivore
European eel	<i>Anguilla anguilla</i>	Planktivore
European pilchard (= sardine)	<i>Sardina pilchardus</i>	Planktivore
European smelt	<i>Osmerus eperlanus</i>	Planktivore
European sprat	<i>Sprattus sprattus</i>	Planktivore
Freshwater fish	Osteichthyes	Planktivore
Garfish	<i>Belone belone</i>	Planktivore
Golden redfish	<i>Sebastes marinus</i>	Planktivore
Greater argentine	<i>Argentina silus</i>	Planktivore
Marine fish	Osteichthyes	Planktivore
Norway pout	<i>Trisopterus esmarkii</i>	Planktivore
Pelagic fish	Osteichthyes	Planktivore
Pelagic percomorphs	Perciformes	Planktivore
Salmonids	Salmonoidei	Planktivore
Sandeel (= sandlance)	<i>Ammodytes</i> spp.	Planktivore
Sea trout	<i>Salmo trutta</i>	Planktivore
Silverside (= sand smelts)	Atherinidae	Planktivore
Sticklebacks	<i>Gasterosteus</i> spp.	Planktivore
Trouts	<i>Salmo</i> spp.	Planktivore
Twaite shad	<i>Alosa fallax</i>	Planktivore
Vendace	<i>Coregonus albula</i>	Planktivore
American plaice (= long rough dab)	<i>Hippoglossoides platessoides</i>	Benthivore
Atlantic searobins	<i>Prionotus</i> spp.	Benthivore
Baird's slickhead	<i>Alepocephalus bairdii</i>	Benthivore
Black sea bream	<i>Spondyliosoma cantharus</i>	Benthivore
Blackspot (= red) sea bream	<i>Pagellus bogaraveo</i>	Benthivore
Brill	<i>Scophthalmus rhombus</i>	Benthivore
Burbot	<i>Lota lota</i>	Benthivore
Common dab	<i>Limanda limanda</i>	Benthivore
Common sole	<i>Solea solea</i>	Benthivore
Eelpout	<i>Zoarces viviparus</i>	Benthivore
European flounder	<i>Platichthys flesus</i>	Benthivore
European perch	<i>Perca fluviatilis</i>	Benthivore
European plaice	<i>Pleuronectes platessa</i>	Benthivore
Flatfish	Pleuronectiformes	Benthivore
Freshwater breams	<i>Abramis</i> spp.	Benthivore
Greater weever	<i>Trachinus draco</i>	Benthivore
Grey gurnard	<i>Eutrigla gurnardus</i>	Benthivore
Gurnards	<i>Trigla</i> spp.	Benthivore
Gurnards, searobins	Triglidae	Benthivore
Lefteye flounder	Bothidae	Benthivore
Lemon sole	<i>Microstomus kitt</i>	Benthivore
Lumpfish (= lumpsucker)	<i>Cyclopterus lumpus</i>	Benthivore
Megrin	<i>Lepidorhombus whiffiagonis</i>	Benthivore
Megrims	<i>Lepidorhombus</i> spp.	Benthivore
Porgies, sea breams	Sparidae	Benthivore
Pouting (= bib)	<i>Trisopterus luscus</i>	Benthivore

Appendix (*continued*)

Common name	Scientific name	Group
Red gurnard	<i>Chelidonichthys cuculus</i>	Benthivore
Roach	<i>Rutilus rutilus</i>	Benthivore
Rocklings	<i>Gaidropsarus</i> spp.	Benthivore
Sand sole	<i>Solea lascaris</i>	Benthivore
Scorpionfish, rockfish	<i>Scorpaena</i> spp.	Benthivore
Thickback sole	<i>Microchirus</i> spp.	Benthivore
Tub gurnard	<i>Chelidonichthys lucerna</i>	Benthivore
Turbot	<i>Psetta maxima</i>	Benthivore
Witch flounder	<i>Glyptocephalus cynoglossus</i>	Benthivore
Wrasses, hogfish,, etc.	Labridae	Benthivore
Anglerfish (= monk)	<i>Lophius piscatorius</i>	Demersal piscivore
Anglerfish	Lophiidae	Demersal piscivore
Atlantic cod	<i>Gadus morhua</i>	Demersal piscivore
Atlantic halibut	<i>Hippoglossus hippoglossus</i>	Demersal piscivore
Atlantic wolffish	<i>Anarhichas lupus</i>	Demersal piscivore
Black cardinal fish	<i>Epigonus telescopus</i>	Demersal piscivore
Black scabbardfish	<i>Aphanopus carbo</i>	Demersal piscivore
Blue ling	<i>Molva dypterygia</i>	Demersal piscivore
Blue shark	<i>Prionace glauca</i>	Demersal piscivore
Blue skate	<i>Raja batis</i>	Demersal piscivore
Cartilaginous fish	<i>Chondrichthyes</i>	Demersal piscivore
Cuckoo ray	<i>Raja naevus</i>	Demersal piscivore
Demersal percomorphs	Perciformes	Demersal piscivore
Dogfish sharks	Squalidae	Demersal piscivore
Dogfish and hounds	Squalidae, Scyliorhinidae	Demersal piscivore
Dogfish	<i>Squalus</i> spp.	Demersal piscivore
European conger	<i>Conger conger</i>	Demersal piscivore
European hake	<i>Merluccius merluccius</i>	Demersal piscivore
European sea bass	<i>Dicentrarchus labrax</i>	Demersal piscivore
European whitefish	<i>Coregonus lavaretus</i>	Demersal piscivore
Finfish	Osteichthyes	Demersal piscivore
Gadiforms	Gadiformes	Demersal piscivore
Greater forkbeard	<i>Phycis blennoides</i>	Demersal piscivore
Greenland halibut	<i>Reinhardtius hippoglossoides</i>	Demersal piscivore
Greenland shark	<i>Somniosus microcephalus</i>	Demersal piscivore
Groundfish	Osteichthyes	Demersal piscivore
Groupers, sea bass	Serranidae	Demersal piscivore
Haddock	<i>Melanogrammus aeglefinus</i>	Demersal piscivore
Lanternsharks	<i>Etmopterus</i> spp.	Demersal piscivore
Leafscale gulper shark	<i>Centrophorus squamosus</i>	Demersal piscivore
Ling	<i>Molva molva</i>	Demersal piscivore
Longnosed skate	<i>Raja oxyrinchus</i>	Demersal piscivore
Monkfish	<i>Lophius</i> spp.	Demersal piscivore
Mullet	Mugilidae	Demersal piscivore
Northern pike	<i>Esox lucius</i>	Demersal piscivore
Nursehound	<i>Scyliorhinus stellaris</i>	Demersal piscivore
Orange roughy	<i>Hoplostethus atlanticus</i>	Demersal piscivore
Picked dogfish	<i>Squalus acanthias</i>	Demersal piscivore
Pike-perch	<i>Stizostedion lucioperca</i>	Demersal piscivore
Pollack	<i>Pollachius pollachius</i>	Demersal piscivore
Portuguese dogfish	<i>Centroscymnus coelolepis</i>	Demersal piscivore
Rabbitfish	<i>Chimaera monstrosa</i>	Demersal piscivore
Rays	<i>Raja</i> spp.	Demersal piscivore
Rays and skates	Rajidae	Demersal piscivore
Red mullet	<i>Mullus surmuletus</i>	Demersal piscivore
Roughhead grenadier	<i>Macrourus berglax</i>	Demersal piscivore

(continued)

Appendix (continued)

Common name	Scientific name	Group
Roundnose grenadier	<i>Coryphaenoides rupestris</i>	Demersal piscivore
Saithe (= pollock)	<i>Pollachius virens</i>	Demersal piscivore
Sandy ray	<i>Raja circularis</i>	Demersal piscivore
Scorpionfish	Scorpaenidae	Demersal piscivore
Scorpionfish, rockfish	<i>Scorpaena</i> spp.	Demersal piscivore
Sea bass	<i>Dicentrarchus</i> spp.	Demersal piscivore
Shagreen ray	<i>Raja fullonica</i>	Demersal piscivore
Shortnose velvet dogfish	<i>Centroscymnus cryptacanthus</i>	Demersal piscivore
Small-spotted catshark	<i>Scyliorhinus canicula</i>	Demersal piscivore
Smooth-hound	<i>Mustelus mustelus</i>	Demersal piscivore
Smooth-hounds	<i>Mustelus</i> spp.	Demersal piscivore
Spotted ray	<i>Raja montagui</i>	Demersal piscivore
Spotted sea bass	<i>Dicentrarchus punctatus</i>	Demersal piscivore
Striped bass	<i>Morone saxatilis</i>	Demersal piscivore
Sturgeons	Acipenseridae	Demersal piscivore
Surmullet (= red mullet)	<i>Mullus</i> spp.	Demersal piscivore
Thornback ray	<i>Raja clavata</i>	Demersal piscivore
Tusk (= cusk)	<i>Brosme brosme</i>	Demersal piscivore
Whiting	<i>Merlangius merlangus</i>	Demersal piscivore
Wolffish (= catfish)	<i>Anarhichas</i> spp.	Demersal piscivore
Blue whiting (= poutassou)	<i>Micromesistius poutassou</i>	Pelagic piscivore
Bogue	<i>Boops boops</i>	Pelagic piscivore
Horse mackerel	<i>Trachurus trachurus</i>	Pelagic piscivore
Jack and horse mackerels	<i>Trachurus</i> spp.	Pelagic piscivore
John dory	<i>Zeus faber</i>	Pelagic piscivore
Mackerel	<i>Scomber scombrus</i>	Pelagic piscivore
Porbeagle	<i>Lamna nasus</i>	Pelagic piscivore
Shortfin mako	<i>Isurus oxyrinchus</i>	Pelagic piscivore
Tope shark	<i>Galeorhinus galeus</i>	Pelagic piscivore
Various sharks	Selachimorpha (Pleurotremata)	Pelagic piscivore

Erratum

Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate

Michael R. Heath

When this article was originally published Figure 7 was incorrect. The correct Figure 7 is printed below. The publisher regrets this error.

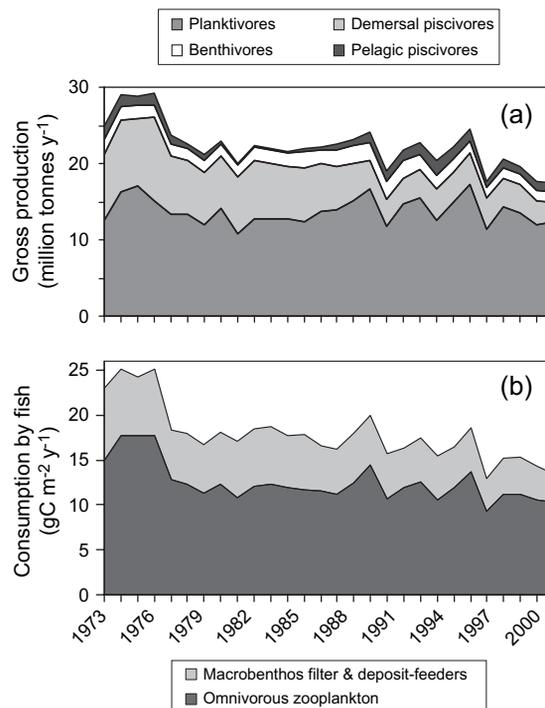


Figure 7. (a) Gross production of each fish guild estimated from the STATLANT landings data. (b) Secondary production required to support the food demands of the fish foodweb. For both omnivorous zooplankton and the macrobenthos (deposit- and filter-feeders), the consumption by fish consisted of direct and indirect consumption. Direct consumption represented fish feeding directly on secondary producers, indirect consumption represented the food requirements of carnivorous zooplankton and macrobenthos, which were themselves prey of fish.