

Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics

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Previous North Sea food web studies are reviewed. These studies used estimates of primary production and fish energy requirements, then manipulated the energy flow pathway between the two to balance the budget. The resulting pathways largely ignored actual fish diets and consumption rates. In the present paper, North Sea biomass flow food webs are constructed for each quarter of the year from published estimates of fish abundance, diet and daily food consumption, and using long-term Continuous Plankton Recorder and North Sea benthos survey data. Estimates of daily production of each component of the web are derived from specific daily growth and gross growth efficiency measurements. The flow of biomass from secondary production to fish is sufficient to supply the food requirements of planktivorous pelagic fish and benthivorous demersal fish. Piscivorous pelagic fish obtain much of their food requirements from outside the North Sea. The food requirements of piscivorous demersal fish also do not appear to be adequately supplied from within the North Sea, but, in this case, immigration is not thought to provide the shortfall. The high predation pressure on demersal piscivores may explain why this group appears to be especially vulnerable to fishing. The supply of biomass from primary production to secondary producers appears to be sufficient without the need to postulate import into the North Sea. Indeed, the supply to the benthos is such that a detritivore trophic level can be inserted between organic settlement and production of macrobenthos.

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Introduction

Several attempts have been made to describe the flow of energy through simplified North Sea food webs (Steele, 1974; Jones, 1982, 1984; Cohen *et al.*, 1982). In each case the webs were constrained in order to achieve a balanced energy budget. This paper examines the structure of these food webs, and the validity of their constraints, in

the light of more recent data on the biomass, diet and food consumption rates of fish in the North Sea. Since the earlier food web studies were published, several major investigations have provided additional data and so make a reassessment worthwhile.

First, several studies provide estimates of the biomass of the 200 or so non-commercial species, in addition to the 11 main commercial species (Yang, 1982; Sparholt, 1990; Daan *et al.*, 1990); neither Steele's (1974) nor Jones' (1982, 1984) webs specifically accounted for the energy requirements of non-commercial fish. Secondly, during the 1980s and 1990s the diets of numerous species of fish in the North Sea have been described, particularly from the 1981 and 1991 ICES stomach sampling

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programmes. In these the diet, by age and/or size class, of the five main piscivorous predators, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*), was described, by area and quarter year, throughout the North Sea (Daan, 1989). The diets of many other fish species have also been described, but generally in less detail (e.g. Hamerlynck *et al.*, 1986; Creutzberg and Duineveld, 1986; Creutzberg and Witte, 1989). Numerous laboratory studies have also been undertaken to estimate stomach evacuation rates (e.g. Daan, 1973; Jones, 1974, 1978; Elliott and Persson 1978; Jobling, 1981; Mehl and Westgard, 1983a; Basimi and Grove, 1985a). By combining these data with information on food composition and the mean weight of stomach contents, food consumption rates can be estimated (e.g. Mehl and Westgard, 1983b; Basimi and Grove, 1985b; Hislop *et al.*, 1991). This approach provides a valuable contrast with that used in the earlier studies where consumption rates were inferred from estimates of energetic requirements. We can therefore turn the question around from, "How much energy do fish theoretically require and in what form can this energy be made available?", to "How much energy do fish actually consume and from what sources do they obtain it?"

The third development which makes a re-evaluation worthwhile is the large body of recent work on the abundance and distribution of the various benthic and planktonic species which make up the food of fish in the North Sea (e.g. Heip *et al.*, 1992; Broekhuizen and McKenzie, 1995). These data, and better information on the growth, reproduction and general productivity of fish prey species, allow us to determine whether estimates of local food abundance and productivity are sufficient to support estimated fish feeding rates throughout the year.

In this paper we first review the findings of previous efforts to construct energy flow food webs for the North Sea. We then use the new information that has become available to construct our own biomass flow food webs by estimating the consumption rates by fish of all major prey categories for each quarter of the year, using stomach contents and digestion rate data. We then compare these consumption rate estimates with estimates of prey production to determine whether the demands of the fish assemblage can be met from within the North Sea, or whether significant import from outside must be inferred. Finally, we compare our food webs with the earlier webs of Steele (1974) and Jones (1982, 1984).

Review of previous food web energy budgets

Steele (1974) constructed the first North Sea energy flow food web. He assumed that total annual fish production

was equivalent to total annual fish yield (the sum of the biomass of fish removed by fishing and the biomass dying of natural causes in a year). Assuming an energy transfer efficiency of 10% (e.g. Slobodkin, 1961), so multiplying total annual fish yield by ten, fish energy consumption estimates of $127 \text{ kcal m}^{-2} \text{ yr}^{-1}$ were obtained. After reviewing several published studies (e.g. Steeman Nielsen, 1952; Steele and Baird, 1961), Steele (1974) used a value of $900 \text{ kcal m}^{-2} \text{ yr}^{-1}$ for annual primary production. As later pointed out by Jones (1984), these values imply that there could only be one intermediate trophic level between fish and phytoplankton, i.e. fish could only feed on herbivorous zooplankton or benthic detritivores. Furthermore, no energy would be available for carnivores other than fish.

Steele (1974) resolved this inconsistency by balancing the energy budget only for the secondary producers and higher trophic levels in his web. Assuming a production: biomass (P:B) ratio of 7 and annual average herbivorous zooplankton densities of 25 kcal m^{-2} , Steele estimated herbivorous zooplankton production to be $175 \text{ kcal m}^{-2} \text{ yr}^{-1}$; implying a phytoplankton to zooplankton energy transfer efficiency of 19.4% and effectively doubling the amount of energy available to higher trophic levels! With exploited pelagic fish requiring at least $85 \text{ kcal m}^{-2} \text{ yr}^{-1}$, $90 \text{ kcal m}^{-2} \text{ yr}^{-1}$ remained available for consumption by pelagic invertebrate carnivores. In turn, some of the pelagic invertebrate carnivore production was then available for consumption by pelagic fish, thereby allowing them to feed at two trophic levels.

Steele estimated macrobenthos production at between 20 and $50 \text{ kcal m}^{-2} \text{ yr}^{-1}$ (from annual average densities of between 0.6 and 1.6 gC m^{-2} , $1 \text{ gC}=10 \text{ kcal}$, and a P:B ratio of between 2 and 5). In order to supply $30 \text{ kcal m}^{-2} \text{ yr}^{-1}$ to the demersal fish, and leave $20 \text{ kcal m}^{-2} \text{ yr}^{-1}$ for other benthic carnivores, Steele (1974) had to use a value at the top end of the estimate range. Meiobenthos production was estimated to be $20 \text{ kcal m}^{-2} \text{ yr}^{-1}$ (from an annual average density of 2 kcal m^{-2} and a P:B ratio of 10) giving a total benthic production of $70 \text{ kcal m}^{-2} \text{ yr}^{-1}$. Steele (1974) suggested that approximately 66% of the $900 \text{ kcal m}^{-2} \text{ yr}^{-1}$ ingested by herbivorous zooplankton would be assimilated; $300 \text{ kcal m}^{-2} \text{ yr}^{-1}$ of primary production therefore settled to the seabed in the form of zooplankton faeces to become available to the demersal part of the web. Even if this faecal material were immediately available to the benthos, an energy transfer efficiency of over 23% would be required. But much of the detritus passes through a bacterial/meiobenthos detritivore trophic level before it is utilized by the macrobenthos (Kuipers *et al.*, 1981). The existence of this extra trophic level between the detritus and benthos suggests that this part of the energy budget might not balance unless unrealistically high transfer efficiencies are assumed.

Since Steele's (1974) estimate of fish consumption was based on the catch taken by fishing, consumption by non-exploited species was not explicitly accounted for. Jones (1982) revised Steele's (1974) energy flow food web, producing two webs, one for the early 1960s when the fish assemblage was dominated by pelagic species, and one for the late 1960s following the decline of the herring (*Clupea harengus*) stock. Based on maintenance, growth, and reproduction energy requirements, Jones and Richards (1976) suggested that the annual energy requirement of a fish stock would be 3.8 times the energy biomass of the stock. Jones (1982) therefore multiplied estimates of the recruited stock biomass (in kcal) of the major, assessed, commercial species by 3.8 to determine annual energy consumption by adult fish. In addition, Jones (1982) accounted for the energy requirements of the adults of "30 minor species taken commercially" by assuming a food/production ratio of 0.20 and that the landings of these species was half their total production. Norway pout (*Trisopterus esmarki*), sprat (*Sprattus sprattus*), sandeels (*Ammodytes* spp.) and the non-recruited juveniles of other species were included in an "other primary carnivore" group. Jones (1982) estimated the fish component of energy consumption by this group under a variety of exploitation and initial mortality scenarios, the most realistic of which assumed 90% initial mortality (Jones and Hall, 1973) combined with observed levels of exploitation mortality. Under this scenario Jones' total energy requirement for the whole fish assemblage was $111 \text{ kcal m}^{-2} \text{ yr}^{-1}$ during the early 1960s period, and $85 \text{ kcal m}^{-2} \text{ yr}^{-1}$ during the late 1960s. Despite the addition of the minor species energy requirements, Jones' (1982) estimates of fish energy requirement were still lower than Steele's (1974) estimate of $127 \text{ kcal m}^{-2} \text{ yr}^{-1}$. However, the food requirements of non-exploited species remained unconsidered.

Jones (1982) used the same estimates of secondary production as Steele (1974), except that, because of his reduced fish energy requirements, he was able to use an estimate of macrobenthos production of $30 \text{ kcal m}^{-2} \text{ yr}^{-1}$, midway between the previously suggested range of values. Only $10 \text{ kcal m}^{-2} \text{ yr}^{-1}$ were required by the adult demersal fish, the remaining $20 \text{ kcal m}^{-2} \text{ yr}^{-1}$ being left for the other benthic carnivores. He concluded that his energy flow food webs could be balanced without "having to make any unreasonable assumptions". However, in so doing he continued to ignore the problem already identified in Steele's (1974) web regarding the source of primary production energy utilized by the macro- and meiobenthos, and the possible role played by bacteria as an intermediate step. Jones (1984) later revised his earlier webs after reviewing the literature concerned with primary production estimation. He concluded that the estimate of $900 \text{ kcal m}^{-2} \text{ yr}^{-1}$ was

too low and that a value of $1300 \text{ kcal m}^{-2} \text{ yr}^{-1}$ was more representative of the whole North Sea over the whole year. He directed the $400 \text{ kcal m}^{-2} \text{ yr}^{-1}$ so gained through the pelagic side of the food web, however, and so did nothing to alleviate any shortfall in the benthos energy supply.

Jones' (1982) primary concern was to balance the energy budget under two contrasting scenarios; the pelagic fish dominated system of the early 1960s and the demersal fish dominated system of the late 1960s. Jones (1984) was also concerned by the fact that earlier food webs unrealistically restricted the diet of fish almost exclusively to secondary producers. With higher estimates of primary production and assuming energy transfer efficiency rates of 15% through herbivorous zooplankton and 20% through other primary carnivores, sufficient energy was available to enable fish to feed at more than one trophic level. Thus, he considered that in the early 1960s adult pelagic fish obtained their energy from other primary carnivores as well as directly from the herbivorous zooplankton. In the late 1960s the increased energy demands of adult demersal fish appeared to be met by greatly increased predation on the other primary carnivore group (which included the fish species sandeels, Norway pout, and sprats). More of this resource was available to adult demersal fish in the late 1960s web because of the reduced requirements of the smaller biomass of adult pelagic fish.

It is clear that these webs (Jones, 1982, 1984) make implicit assumptions regarding fish diet. However, the diet presented in the webs is totally hypothetical, and completely elastic, being determined by the quantity of energy entering the system and the amount of energy required by the fish. The energy flow pathway within the web, and hence fish diet, is simply manipulated so as to maintain an overall energy balance within the system. In the early 1960s web, adult pelagic fish apparently obtained 74% of their energy from herbivorous zooplankton and 26% from other primary carnivores. In the late 1960s web, these percentages changed relatively little; to 76% and 24% respectively (Jones, 1984). However, in order to balance the energy budgets of the two webs, major changes were required in the diet of adult demersal fish. In the early 1960s web, adult demersal fish were required to have a diet of 83% benthic detritivores and 17% other primary carnivores, while in the late 1960s web these percentages had to change to 52% and 48% respectively (Jones, 1984). That adult demersal fish diet was the most affected by the changes in demersal and pelagic fish population sizes perhaps reflects the fact that the benthos-adult demersal fish side of the webs so far described appears short of energy, while the plankton-adult pelagic fish sides appear abundantly supplied.

Table 1. Biomass and biomass density of each trophic guild in the North Sea in each quarter of the year.

Total biomass (tonnes WW)	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Demersal Piscivore	1 961 013	2 143 494	2 326 758	2 510 878
Demersal Benthivore	2 842 000	2 929 269	2 861 444	2 638 524
Pelagic Piscivore	161 996	736 130	1 450 377	2 304 667
Pelagic Planktivore	3 645 992	4 285 440	4 939 087	5 606 931
Whole fish assemblage	8 611 000	10 094 333	11 577 666	13 061 000
Macro-benthos Carnivore	4 050 000	4 050 000	4 050 000	4 050 000
Macro-benthos Deposit-feeder	14 575 000	14 575 000	14 575 000	14 575 000
Macro-benthos Filter-feeder	8 364 000	8 364 000	8 364 000	8 364 000
Whole benthos assemblage	26 989 000	26 989 000	26 989 000	26 989 000
Meso-zooplankton Carnivore	3 101 469	5 403 985	1 888 601	2 706 705
Meso-zooplankton Omnivore	2 773 317	6 904 301	7 566 953	4 519 154
Mero-plankton	No data	No data	No data	No data
Whole zooplankton assemblage	5 874 786	12 308 286	9 455 554	7 225 859
Biomass density (gWW m ⁻²)	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Demersal Piscivore	3.44	3.76	4.08	4.41
Demersal Benthivore	4.99	5.14	5.02	4.63
Pelagic Piscivore	0.28	1.29	2.55	4.04
Pelagic Planktivore	6.40	7.52	8.67	9.84
Whole fish assemblage	15.11	17.71	20.31	22.91
Macro-benthos Carnivore	7.11	7.11	7.11	7.11
Macro-benthos Deposit-feeder	25.57	25.57	25.57	25.57
Macro-benthos Filter-feeder	14.67	14.67	14.67	14.67
Whole benthos assemblage	47.35	47.35	47.35	47.35
Meso-zooplankton Carnivore	5.44	9.48	3.31	4.75
Meso-zooplankton Omnivore	4.87	12.11	13.28	7.93
Mero-plankton	No data	No data	No data	No data
Whole zooplankton assemblage	10.31	21.59	16.59	12.68

Estimation of standing crop biomass (Table 1)¹

In the following sections, recent data on North Sea biota are compiled to produce estimates of the biomass of trophic groups.

Fish

Sparholt (1990) estimated the average (1983–1985) total biomass of fish in the North Sea at 8.6 million tonnes on

1 January (quarter 1) and 13.1 million tonnes on 1 October (quarter 4). For the present analysis each species was assigned to one of four fish feeding guilds; Demersal Piscivores, Demersal Benthivores, Pelagic Piscivores and Pelagic Planktivores (see Appendix 1). Linear change in biomass between quarters 1 and 4 was assumed to estimate the biomass in quarters 2 and 3. Jones (1982) gives the area of the North Sea as 570 000 km², allowing biomass density (gWW m⁻²) to be determined.

Benthos

Biomass density and total North Sea biomass of the macrobenthic community were estimated from the ICES North Sea Benthos Survey database (Heip *et al.*, 1992; Basford *et al.*, 1993; see also Bryant *et al.*, 1995), with additional reference to Eleftheriou and Basford (1989) and Basford *et al.* (1990). The survey was carried out in April and, in the absence of seasonal data, it was assumed to be valid for the whole year. Ash-free dry weight was assumed to be 13.6% of wet weight (Rumohr *et al.*, 1987; Eleftheriou and Basford, 1989).

¹In all the tables, and throughout the text, the values presented show the actual estimate derived. In many cases the number of significant digits given suggests a level of precision that is unwarranted. For example, Table 1 shows the biomass of pelagic planktivorous fish in quarter 1 as 3 645 992 tonnes WW. The precision of this particular estimate is unlikely to be less than ± 5000 tonnes WW, the Pelagic Planktivore biomass is therefore probably between 3 640 000 and 3 650 000 tonnes WW. The actual derived estimates have been presented throughout the paper to prevent the accumulation of rounding errors as calculations progress, leading to apparent discrepancies which might hinder comprehension. Readers wishing to use particular data presented should consult the text and relevant cited literature in order that a reasonable degree of precision might be assessed.

The total macrobenthic biomass was apportioned between three guilds, carnivores, deposit feeders and filter feeders following Bryant *et al.* (1995). However, while these authors assigned between 2% and 5% of the total biomass to the macrobenthos carnivore group, we now believe this to be an underestimate. Given the benthic species trophic guild assignments listed in Appendix 2, we have assumed that 15% of the total benthos biomass should belong to the carnivore guild. We have correspondingly reduced the proportions assigned to the deposit and filter-feeding guilds to 54% and 31% respectively. These proportions are roughly in line with crude estimates derived from data given by Heip *et al.* (1992) knowing the contributions of these taxa to the macrobenthos biomass at various latitudes, and the relative area of each latitude band in the North Sea.

Our estimate of the average standing crop wet weight biomass of the macrobenthos filter-feeder and deposit feeder guilds combined is 40.24 gWW m⁻². Assuming a conversion factor to ash-free dry weight of 0.136 (see above) and carbon fraction of ash-free dry weight of 0.6 (e.g. Bryant *et al.*, 1995), this is equivalent to 5.47 gAFDW m⁻² and 3.28 gC m⁻². These values are in close agreement with other recent estimates of the average density of these organisms in the North Sea, which after adjustment to exclude benthic carnivore biomass, range between 4.3 gAFDW m⁻² (Duineveld *et al.*, 1991) and 6.0 gAFDW m⁻² (Heip *et al.*, 1992). Steele's (1974) benthos production estimates were based on a macrobenthos carbon density approaching 1.6 gC m⁻². Heip *et al.* (1992) acknowledged that their benthic biomass estimates were at least twice as high as that assumed by Anderson and Ursin (1977) for their North Sea model, which in turn was higher than the estimate used by Steele (1974), and later by Jones (1982, 1984). Heip *et al.* (1992) considered that these previous estimates were unrealistic because they were based on rather limited data. The data quoted by Steele (McIntyre, 1961) were mainly collected from the northern part of the North Sea where benthic biomass density is generally lowest; in the southern North Sea benthic biomass density may be as much as an order of magnitude higher (Heip *et al.*, 1992). In addition early benthic biomass estimates may have been underestimated through the use of less efficient grabs (Zijlstra, 1988). It would appear that the webs of both Steele and Jones seriously underestimated the macrobenthos standing crop biomass.

Plankton

Whilst there are many short-term studies in which localized estimates of zooplankton abundance have been made (e.g. Williams and Lindley, 1980a; Krause and Trahms, 1982; Franz and Diel, 1984; Franz and Gieskes, 1984; Franz *et al.*, 1984; Kjørboe and Johansen, 1986; Roff *et al.*, 1988; Hay *et al.*, 1991), there

are very few which span the entire annual cycle. The only data set which has the spatial and temporal coverage for our purposes is that from the Continuous Plankton Recorder (CPR) programme (e.g. Edinburgh Oceanographic Laboratory, 1973). The CPR device samples a large variety of planktonic organisms which fall into one or other of our omnivore and carnivore classes; our analysis was restricted, however, to only the most abundant of these taxa.

We estimated the abundance of omnivores from the CPR counts of "small copepods" and copepodite stages 5 and 6 of *Calanus* spp. Carnivore biomass was estimated from the CPR counts of "total euphausiids" and "total hyperiids". The raw, average monthly counts for each taxa were smoothed, using the methods described in Broekhuizen and McKenzie (1995) and Broekhuizen *et al.* (1995), to yield smoothed monthly estimates of abundance. Daily copepod biomass estimates for the period 1982 to 1985 were calculated by deriving daily abundance values by cubic spline interpolation and converting these to daily surface water biomasses using individual dry weight estimates provided by H. G. Hunt (Sir Alister Hardy Foundation, MBA Plymouth) and assuming dry weight to be 15% of wet weight (Corner and O'Hara, 1986). The tendency of the CPR device to undersample smaller copepods was taken account of by means of an empirically derived re-scaling relationship (see Broekhuizen *et al.*, 1995). No re-scaling was done on the CPR carnivore data. Since the CPR only samples at a nominal depth of 7 to 10 m (Hays and Warner, 1993), it was assumed that the biomass of copepods estimated at 10-m depth held throughout the surface (0–30 m) interval, and that below this depth the biomass was 30% of this value (Krause and Trahms, 1982; Franz *et al.*, 1984). The carnivore biomass was assumed to be homogeneous throughout the water-column.

Steele (1974) quotes a range of values for the herbivorous zooplankton biomass of 3 to 10 gDW m⁻². He used a value of 6.25 gDW m⁻² which represented the average value over the period April to October; the situation in his web over winter is unclear. Our equivalent estimate of the average biomass of the meso-zooplankton omnivore group in quarters 2 and 3 of 12.7 gWW m⁻², or 2 gDW m⁻², is lower than Steele's estimate; however the CPR data also suggest an average standing crop of 6.4 gWW m⁻², or 1 gDW m⁻², over the winter period. Determining which estimates to use is difficult because of the enormous annual, seasonal and spatial variation in zooplankton abundance in the North Sea. Our estimate of meso-zooplankton omnivore abundance attempts to take this variability into account. The CPR data were analysed for 10 separate regions through four quarters of the year, and then averaged over five years (see Broekhuizen and McKenzie, 1995; Broekhuizen *et al.*, 1995). However, we recognize that the algorithm used to rescale the CPR data to account for undersampling of the smallest zooplankton

Table 2. Daily production and production density of each trophic guild in the North Sea in each quarter of the year.

Total production (tonnes WW d ⁻¹)	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Demersal Piscivore	5447	5193	7641	8977
Demersal Benthivore	7894	7096	9397	9434
Pelagic Piscivore	408	801	- 272	- 1868
Pelagic Planktivore	18 022	27 452	28 545	- 9319
Whole fish assemblage	32 022	40 542	45 311	7224
Macro-benthos Carnivore	16 440	18 384	25 620	22 461
Macro-benthos Deposit-feeder	61 360	67 550	92 100	82 200
Macro-benthos Filter-feeder	33 400	38 350	55 500	47 200
Whole benthos assemblage	111 200	124 284	173 220	151 861
Meso-zooplankton Carnivore	279 337	540 708	265 031	347 660
Meso-zooplankton Omnivore	237 912	728 031	1 195 454	604 480
Mero-plankton	No data	No data	No data	No data
Whole zooplankton assemblage	517 249	1 268 739	1 460 485	952 140
Production density (gWW m ⁻² d ⁻¹)	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Demersal Piscivore	0.0096	0.0091	0.0134	0.0157
Demersal Benthivore	0.0138	0.0124	0.0165	0.0166
Pelagic Piscivore	0.0007	0.0014	- 0.0005	- 0.0033
Pelagic Planktivore	0.0321	0.0482	0.0501	- 0.0163
Whole fish assemblage	0.0562	0.0711	0.0795	0.0127
Macro-benthos Carnivore	0.0288	0.0323	0.0449	0.0394
Macro-benthos Deposit-feeder	0.1076	0.1185	0.1616	0.1442
Macro-benthos Filter-feeder	0.0586	0.0673	0.0974	0.0828
Whole benthos assemblage	0.1951	0.2180	0.3039	0.2664
Meso-zooplankton Carnivore	0.0980	0.1897	0.0930	0.1220
Meso-zooplankton Omnivore	0.4174	1.2772	2.0973	1.0605
Mero-plankton	No data	No data	No data	No data
Whole zooplankton assemblage	0.9075	2.2259	2.5623	1.6704

size classes tends to underestimate the true abundance of small copepods when their abundance is high, and to overestimate their abundance when they are scarce. Seasonal variation is thus reduced and consequently our biomass estimates for quarters 2 and 3 are possibly low, while those for quarters 1 and 4 may be too high. Despite this, our abundance estimates are in close agreement with values observed in several studies (Williams and Lindley, 1980b; Franz and Gieskes, 1984; Franz *et al.*, 1984; Hay *et al.*, 1991; Hay, 1995), while other studies suggest spring/summer abundance values more in line with Steele's estimates (Krause and Martens, 1990). Perhaps the zooplankton standing crop biomass values we have used in our webs in quarters 2 and 3 might be considered minimum values, and Steele's (1974) estimate a maximum.

Our estimates of the standing crop biomass of meso-zooplankton carnivores compare closely with observed euphausiid densities in the "Flex" box in the north-western North Sea in 1976 (Williams and Lindley, 1980a), but are approximately two to four times higher than annual average euphausiid biomass density estimates for the whole North Sea in the late

1960s (Lindley, 1982a,b). Lindley's data suggest, however, that the average biomass density of euphausiids in the North Sea might vary by at least a factor of four between years (Lindley, 1982a). In addition, our zooplankton carnivore group also includes hyperiid amphipods as well as euphausiids.

Estimation of daily production (Table 2)

Fish

Weight-at-age data in each quarter of the year for key species in each fish guild were those used in the Multi-Species Virtual Population Analysis (MSVPA) model for the key run of the 1990 meeting of the ICES Multi-Species Working Group (Anon, 1991; P. A. Kunzlik, Marine Laboratory, Aberdeen, Pers. Comm.). These data indicate the weight gains of individual fish with increasing age, in quarter years, and so provide estimates of specific growth rate. By applying these rates to population biomass-at-age data, potential population daily production in the absence of exploitation could be

estimated. Potential daily production rates for each fish guild were determined using the average of the key species rates weighted by relative population biomass. Data were available for cod, haddock, whiting, and saithe in the Demersal Piscivore guild, for mackerel in the Pelagic Piscivore guild and for Norway pout, herring, sprat, and sandeel in the Pelagic Planktivore guild. Quarterly daily production rates of the Demersal Benthivore guild were assumed to be the same as for the Demersal Piscivore guild, as a percentage of standing crop biomass. Quarterly daily production rates varied between -0.2 and 0.7% of population biomass depending on fish guild and season, well in line with observed daily growth rates in fish (Checkley, 1984; Hawkins *et al.*, 1985; Hall, 1988), particularly in younger fish (Daan, 1973).

Benthos

Mean annual production was estimated from biomass on the basis of the empirical relationships given by Brey (1990). Seasonal variation in whole community production in sub-tidal and especially deeper water benthos is largely unknown, which poses a problem for our quarterly analysis. In intertidal and estuarine habitats, most of the annual production occurs in the second and third quarters of the year (Steele and Baird, 1968; Asmus, 1982). As a conservative estimate (Duncan and Klekowski, 1975) a $Q_{10}=2$ was used to weight the annual production means to give quarterly production figures (using temperatures from the Pohlmann hydrodynamic model, Pohlmann, 1996). The quarterly production estimates for macrobenthos filter feeders and deposit feeders given here indicate an annual macrobenthos P:B ratio of 1.9, at the lower end of the range suggested by Steele (1974). Our estimate of annual production in the whole benthos community is marginally higher (1.2 times) that of Duineveld *et al.* (1991).

Plankton

Daily meso-zooplankton omnivore production was estimated for the period 1982 to 1985 to applying the Huntley and Lopez (1992) temperature-dependent weight-specific copepod production model to CPR data (see Broekhuizen *et al.*, 1995). Daily region-specific temperatures were derived from the Pohlmann hydrodynamic model of the European shelf seas (Pohlmann, 1991, 1996). Our meso-zooplankton production estimates are therefore driven by seasonal variation in water temperature and the impact that this has on daily specific growth rates. They are broadly similar to those determined in a number of other studies (Fransz and Gieskes, 1984; Fransz *et al.*, 1984; Hay, 1995; Roff *et al.*, 1988). Our daily production estimates indicate an annual production of $66.4 \text{ gDW m}^{-2} \text{ yr}^{-1}$, 34% higher

than the value of $43.8 \text{ gDW m}^{-2} \text{ yr}^{-1}$ used by Steele (1974), and they imply specific daily growth rates varying from 0.086 in quarter 1 to 0.158 in quarter 3, in line with daily growth rates observed in the North Sea (Fransz and Diel, 1984; Fransz *et al.*, 1984; Fransz *et al.*, 1991; Hay, 1995). Such high specific production rates take no account of mortality, but give a measure of the potential productivity if all individuals were to reach full size. However, the majority of individuals are preyed on at an early stage of development so population production never reaches these levels. Daily production estimates that take mortality into account are generally a factor of two or more lower (e.g. Evans, 1977; Martens, 1980; Fransz *et al.*, 1991).

The Huntley and Lopez (1992) model, being based on copepods, is, strictly speaking, not really suitable for estimating the daily production of the much larger carnivorous zooplankton such as euphausiids. However, obtaining such estimates from the literature is difficult owing to a scarcity of data on seasonal variation, and because of the extreme variability between different estimates. Data showing temporal variation in euphausiid mean length in three North Sea areas are given by Lindley (1982a). When these data are converted to dry weight using length-weight regressions (Lindley, 1978), estimates of daily specific growth rates as high as 0.40 are obtained in quarter 3 for euphausiids in their earliest stages of development. Daily specific growth in the older generation euphausiids is much slower at around 0.02 to 0.04 in quarters 2, 3, and 4. Other studies have recorded daily specific growth rates from 0 to 0.02 for new generation, and between -0.004 and 0.005 for old generation *Meganyctiphanes norvegica* in cold deep water off western Norway (Bamstedt, 1976), while values as high as 0.03 have been reported for *Euphausia pacifica* held at 10°C in the laboratory (Lasker, 1966). Other components of the zooplankton carnivore group may have higher specific growth rates than euphausiids; specific daily growth rates in *Sagitta hispida* for example may be as high as 0.05 to 0.10 (Reeve and Walter, 1972).

To circumvent these problems, and to attain a basis from which to proceed, we applied the Huntley and Lopez (1992) copepod growth model to the CPR data for hyperiids and euphausiids. This suggested daily specific growth rates of between 0.09 and 0.14 and a total potential annual production in the absence of mortality of $34 \text{ gDW m}^{-2} \text{ yr}^{-1}$. Since the specific growth rates of euphausiids are unlikely to exceed those of the much smaller bodied copepods, we considered these values to be the upper limits to any estimates of meso-zooplankton carnivore production. Lindley (1982a,b) estimates average annual euphausiid production at $1.5 \text{ gDW m}^{-2} \text{ yr}^{-1}$; approximately 5% of our value. However, Lindley's figures, based on Allen curves (Edmonson and Winberg, 1971), do not take into

Table 3. Daily food consumption by four fish guilds in each quarter of the year.

	Quarter (tonnes WW d ⁻¹)				Quarter (mgWW m ⁻² d ⁻¹)			
	1	2	3	4	1	2	3	4
Demersal Piscivores								
Phyto-plankton Flagellate	0.3	0.0	0.0	0.0	0.00	0.00	0.00	0.00
Meso-zooplankton Omnivores	3.4	118.4	456.7	133.6	0.01	0.21	0.80	0.23
Meso-zooplankton Carnivores	3627.7	6225.2	6803.7	3971.8	6.36	10.92	11.94	6.97
Macro-benthos Filter-feeders	579.5	715.2	886.0	1409.4	1.02	1.26	1.55	2.47
Macro-benthos Deposit-feeders	1776.0	1626.4	3026.6	2840.5	3.12	2.85	5.31	4.98
Macro-benthos Carnivores	3303.0	3584.4	5764.5	5707.7	5.80	6.29	10.11	10.01
Pelagic Planktivores	9116.8	9972.0	14 779.6	13 946.7	15.99	17.50	25.93	24.47
Pelagic Piscivores	0.2	0.9	71.7	109.1	0.00	0.00	0.13	0.19
Demersal Benthivores	1209.3	3087.0	4319.9	3613.6	2.12	5.42	7.58	6.34
Demersal Piscivores	2212.9	3103.4	5862.1	2636.5	3.88	5.45	10.28	4.63
Total	21 829.0	28 433.0	41 970.7	34 368.9	38.30	49.88	73.63	60.30
Demersal Benthivores								
Macro-benthos Filter-feeders	3711.0	6466.4	10 204.5	5205.2	6.51	11.35	17.90	9.13
Macro-benthos Deposit-feeders	12 939.8	29 986.8	16 982.2	18 160.4	22.70	52.61	29.79	31.86
Macro-benthos Carnivores	10 013.5	14 364.5	16 937.2	20 576.3	17.57	25.20	29.71	36.10
Demersal Benthivores	10.1	18.4	19.3	5.1	0.02	0.03	0.03	0.01
Total	26 674.4	50 836.2	44 143.2	43 947.0	46.80	89.19	77.44	77.10
Pelagic Piscivores								
Meso-zooplankton Omnivores	10.4	1613.7	2542.6	2823.5	0.02	2.83	4.46	4.95
Meso-zooplankton Carnivores	457.7	492.1	758.4	1100.0	0.80	0.86	1.33	1.93
Mero-Plankton	0.1	11.6	24.0	27.1	0.00	0.02	0.04	0.05
Macro-benthos Filter-feeders	10.2	41.0	222.5	192.6	0.02	0.07	0.39	0.34
Macro-benthos Deposit-feeders	0.2	6.1	43.3	65.5	0.00	0.01	0.08	0.12
Macro-benthos Carnivores	17.8	2048.7	4549.8	4818.7	0.03	3.59	7.98	8.45
Pelagic Planktivores	43.8	1882.9	2920.0	2739.9	0.08	3.30	5.12	4.81
Pelagic Piscivores	0.0	5.4	0.0	0.0	0.00	0.01	0.00	0.00
Demersal Benthivores	0.4	51.5	107.5	120.7	0.00	0.09	0.19	0.21
Demersal Piscivores	36.9	4787.0	9931.3	11 213.4	0.07	8.40	17.42	19.67
Total	577.5	10 940.0	21 099.3	23 101.3	1.01	19.19	37.02	40.53
Pelagic Planktivores								
Meso-zooplankton Omnivores	20 139.4	43 333.8	51 169.0	37 565.1	35.33	76.02	89.77	65.90
Meso-zooplankton Carnivores	17 126.2	25 278.5	28 803.3	22 535.4	30.05	44.35	50.53	39.54
Mero-Plankton	56.2	3.2	4.3	166.0	0.10	0.01	0.01	0.29
Macro-benthos Filter-feeders	1013.6	433.9	323.3	2067.9	1.78	0.76	0.57	3.63
Macro-benthos Deposit-feeders	380.7	726.8	826.6	1800.3	0.67	1.28	1.45	3.16
Macro-benthos Carnivores	27.1	822.3	779.8	26.4	0.05	1.44	1.37	0.05
Pelagic Planktivores	858.1	523.8	794.2	1649.4	1.51	0.92	1.39	2.89
Demersal Benthivores	24.9	0.0	0.0	37.8	0.04	0.00	0.00	0.07
Demersal Piscivores	23.6	14.9	13.0	14.8	0.04	0.03	0.02	0.08
Total	39 650.0	71 137.3	82 713.5	65 891.9	69.56	124.80	145.11	115.60

account the production required to support mortality losses, which can exceed 90% in early life stages and can also be high in adults following breeding (Lindley, 1978). We therefore adjusted the results of the Huntley and Lopez (1992) model downwards by a factor of five to bring them in line with Lindley's (1982a) data (see above). This gave us daily specific growth rates varying between 0.018 and 0.028 through the year and a total potential annual production, before mortality losses, of 6.9 gDW m⁻² yr⁻¹. This approach provides estimates of meso-zooplankton carnivore production and growth which, while comparable with other published data, are, to some extent, driven by carnivorous zooplankton data and so exhibit a degree of seasonality.

Estimation of daily food consumption (Table 3)

Fish

Daily food consumption rates were estimated for key species within each fish guild through literature review; the remaining species within each guild were assumed to have a similar daily ration, as a percentage of biomass, and a composite diet. The key species in the Demersal Piscivore Guild were cod, haddock, whiting and saithe, making up between 75% and 80% of the total biomass (Sparholt, 1990). Their quarterly diets at age were estimated with reference to Cranmer (1986), Daan (1973, 1989), Hislop *et al.* (1983, 1991), Robb (1981),

Robb and Hislop (1980), and Veá Salvanes (1986). Daily rations were determined by applying Jones' (1974) digestion model to stomach weight data given in Daan (1989). Sea temperature was assumed to be 6°C in quarter 1, 7°C in quarter 2, 10°C in quarter 3, and 8°C in quarter 4 (Daan, 1989). The MSVPA program was used to determine the mean weight and proportion of biomass at age in each quarter.

Plaice (*Pleuronectes platessa*), common dab (*Limanda limanda*), and lemon sole (*Microstomus kitt*) were the key species in the Demersal Benthivore guild, accounting for between 78% and 86% of the guild's biomass throughout the year (Sparholt, 1990). Their diets were estimated with reference to Basimi and Grove (1985a), Braber and De Groot (1973), Creutzberg and Duineveld (1986), De Clerck and Buseyne (1989), De Clerck and Torneele (1988), Duineveld and van Noort (1986), Knust (1986), and Rae (1956). Plaice daily consumption rates in each quarter of the year given in Basimi and Grove (1985a) were used after adjustment for seasonal variation in plaice feeding activity, and for North Sea water temperatures. Data in Creutzberg and Duineveld (1986) were used to estimate an annual average daily consumption rate for dab as a percentage of the population biomass. Gwyther and Grove's (1981) function relating digestion to water temperature was used to modify this rate to provide daily consumption rates in each quarter. These were further adjusted to take into account seasonal variation in dab feeding activity (Knust, 1986). The quarterly rates estimated for dab, taking into account the effect of water temperature only, were also used for lemon sole after further modification to account for the different seasonal variation in feeding activity (Rae, 1956).

The Pelagic Piscivore guild consists of only two species, horse mackerel (*Trachurus trachurus*) and mackerel (Sparholt, 1990); their diets were estimated with reference to Daan (1989), Dahl and Kirkegaard (1986, 1987), and Kirkegaard *et al.* (1987). Mackerel daily food consumption was calculated by applying Mehl and Westgard's (1983a,b) digestion model to mean stomach weight data given in Daan (1989). Mean weight-at-age and the proportion of the total mackerel biomass belonging to each age group in each quarter were obtained from the MSVPA. Horse mackerel daily consumption rates observed in a Danish study carried out in autumn (Dahl and Kirkegaard, 1986, 1987; Kirkegaard *et al.*, 1987) were extrapolated to the whole North Sea population and considered to vary seasonally in a similar manner to mackerel.

Four key species, Norway pout, herring, sprat and sandeel, made up between 97% and 100% of the biomass of the Pelagic Planktivore guild (Sparholt, 1990). Their diets were estimated with reference to Albert (1991), Hardy (1924), Last (1982, 1989), Macer (1966), Raitt and Adams (1965), Robb (1981), Robb and Hislop (1980), Savage (1937), and Wilson and Bailey (1991).

Albert's (1991) diet and stomach weight data for Norway pout were all given as dry weight values. These had to be converted to wet weight data using suitable water content conversions (Omori, 1969; Raymont *et al.*, 1971; Bamstedt, 1981; Rumohr *et al.*, 1987). Herring diet was described as percent contribution of each prey item by number (Last, 1989). However, the relative weight of each prey item could be estimated from the data presented, allowing the percent contribution to the diet of each prey item by wet weight to be calculated. Jones' (1984) digestion model was applied to the Norway pout mean stomach content wet weight values to estimate their daily food consumption rates. Herring stomach contents weight data were obtained from Koster *et al.* (1990), and Daan's (1973) digestion model was used to estimate daily consumption rates. A gastric emptying time of 12 h was assumed (Koster *et al.*, 1990), but times as fast as 6 h have been observed (Daan *et al.*, 1985). Sprats were considered to have the same daily consumption rate (as a percentage of the total population biomass) as that part of the herring population up to 15 cm in length. The same population daily consumption rates were applied to sandeels also.

The prey items recorded in the diet studies cited above were assigned to one of 12 prey guilds (see Appendix II). More detail as to how these figures for total daily consumption of each prey guild by each fish predator guild in each quarter of the year were derived is given by Greenstreet (1996).

The estimated quantities of food consumed daily by the whole fish assemblage represented between 1.0% and 1.6% of the total fish assemblage biomass, in line with published data obtained from both field and laboratory studies (Daan, 1973; Basimai and Grove, 1985a; Hall, 1987; Hislop *et al.*, 1991; Santos and Jobling, 1992). As might be expected, food consumption is highest in the warmer summer months when metabolic rates are raised (e.g. Swenson and Smith, 1973), more food is available, and fish populations are augmented by the presence of young fish with their higher relative food requirements (e.g. Daan, 1973; Hamerlynck and Hostens, 1993).

The annual consumption of food by the whole fish assemblage, as calculated from Table 3, amounts to some 55.4 million tWW yr⁻¹, or 97.2 gWW m⁻² yr⁻¹, approximately five times the annual average fish assemblage standing crop biomass (see Table 1), and very similar to the ratio implicit in Jones (1982). When Jones' (1982) factors for converting grams wet weight to kilo-calories are taken into account, 1.36 for mackerel and herring, 1.10 for sprats, sandeels, and Norway pout, and 1.00 for all other species, then an energy requirement/stock energy content ratio of 3.8 represents a food mass/stock biomass ratio of 4.9 in Jones' early 1960s period and 4.3 in his late 1960s period. Assuming, for the moment, an average grams biomass to kilo-calories energy conversion factor of 1.0 for the food consumed by fish (e.g. Steele, 1974)

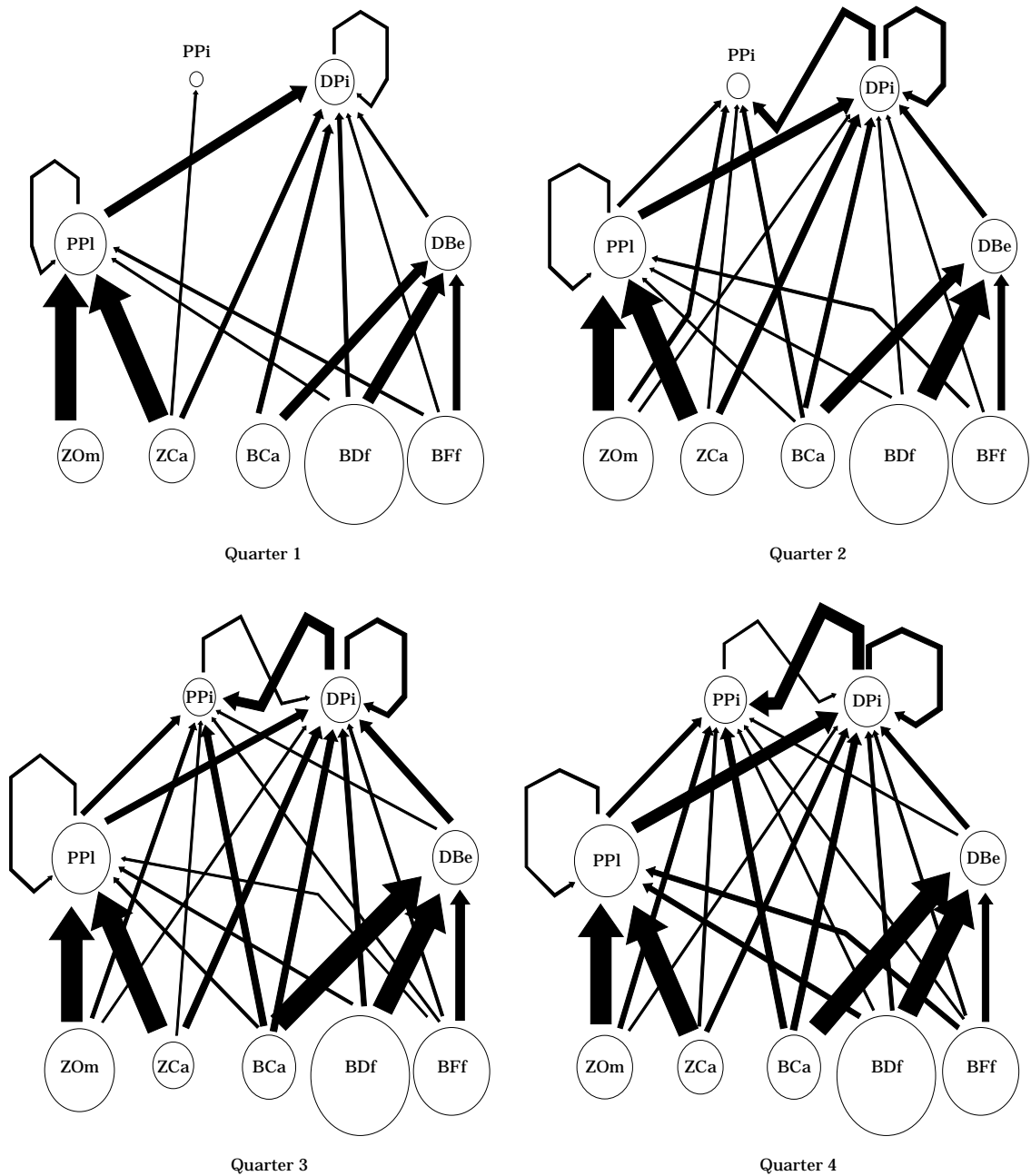


Figure 1. North Sea food webs for each quarter of the year. The area of each circle is proportional to the standing crop biomass of each trophic guild (gWW m^{-2}). The arrows indicate the major trophic links ($>0.0001 \text{ gWW m}^{-2} \text{ d}^{-1}$) for the fish guilds and arrow width is approximately proportional to the quantity of food consumed by each fish guild per day ($\text{gWW m}^{-2} \text{ d}^{-1}$). (PPi=Pelagic Piscivores; PPI=Pelagic Planktivores; DPi=Demersal Piscivores; DBe=Demersal Benthivores; ZOm=Meso-zooplankton Omnivores; ZCa=Meso-zooplankton Carnivores; BCa=Macro-benthic Carnivores; BDf=Macro-benthic Deposit feeders; BFf=Macro-benthic Filter feeders).

our annual fish food requirement of $97 \text{ gWW m}^{-2} \text{ yr}^{-1}$ is in close agreement with Jones' (1982) figures of between 85 and $111 \text{ kcal m}^{-2} \text{ yr}^{-1}$, depending on time period, and initial mortality, as well as with Steele's (1974) estimate of $127 \text{ kcal m}^{-2} \text{ yr}^{-1}$.

Initial food web construction (Fig. 1)

The data presented in Tables 1 to 3 were used to construct simple food webs for the North Sea in each quarter of the year (Fig. 1). Connecting links where the

biomass transfer between prey guild and predator guild was less than $0.0001 \text{ gWW m}^{-2} \text{ d}^{-1}$ are excluded. Relatively unimportant prey guilds (as far as fish are concerned), such as phyto-plankton and mero-plankton, are also ignored.

Discussion

Fish diet

Our food webs differ noticeably from previous North Sea webs in the trophic level(s) at which fish feed (Fig. 2). In extracting comparative figures from Jones' (1982) paper the following rules were applied:

- (i) 66% of Other Primary Carnivore prey consumed by adult herring and mackerel consisted of fish (e.g. sandeels, sprat, fish larvae, etc.).
- (ii) The remaining 34% of Other Primary Carnivore prey consumed by adult herring and mackerel was carnivorous meso-zooplankton (e.g. euphausiids).
- (iii) All Other Primary Carnivore prey taken by adult demersal fish consisted of fish (e.g. sandeels, sprat, juvenile fish).
- (iv) Figures were derived using Jones' data assuming an energy efficiency transfer of 10%, rather than 5%, through the Other Primary Carnivore group (see Jones, 1984).

These rules, based on the results of our literature survey of fish diet (see above), tended to raise the trophic levels at which fish components of Jones' (1982) webs were feeding. Thus, in terms of comparison with our study, these rules were "conservative", tending to minimize differences.

Our web most closely resembles Jones' (1982) late 1960s web, when demersal fish were dominant. The amount of fish and lower trophic level macrobenthos consumed by fish are very similar. Our data suggest that over the year 18% of the diet of fish consisted of fish (seasonal variation of 15 to 22%) and 21% of macrobenthos (seasonal variation of 17 to 25%), compared with Jones' (1982) figures of 17.5% and 20% respectively. The most notable difference lies in the quantity of food supplied to fish by meso-zooplankton herbivores/omnivores; 60% in Jones' (1982) late 1960s web compared with our annual average of 26% (seasonal variation 23 to 29%). To compensate, carnivorous zooplankton supply 19% of fish food (seasonal variation 17 to 24%) compared with 3% in Jones' web. A further major difference between the two webs is our inclusion of an additional benthic group, the macrobenthos carnivores, a trophic level not even considered by Jones (1982), which supplies 15% of the food consumed by fish over the year (seasonal variation 13 to 19%). Steele's (1974) food web is not too dissimilar from Jones' (1982) late 1960s web; pelagic fish rely on herbi-

vores for 88.5% of their food, while demersal fish are even more dependent on the lower trophic order macrobenthos, which contributes 83% of their food.

Divergence between our food webs and that of Jones (1982) is more apparent when the two main food chains, plankton to pelagic fish and benthos to demersal fish, are considered separately (Fig. 3). However, the difference between the two demersal food chains is not as large as first impressions suggest. If rule (iii) above is relaxed so that some of the Primary Carnivore group taken by adult demersal fish in Jones' food chain consists of carnivorous invertebrates, then the fractions of fish and carnivorous invertebrates in the two chains become quite close. Combining the benthic carnivores with the lower trophic level benthos indicates that the fraction of the diet originating from the benthos is at least similar in the two chains, but in our food chain, this benthic derived food passes through one additional trophic step. Differences between the two pelagic food chains are more profound and indicative of quite different energy flow pathways. In Jones' (1982) webs, sprats, sandeels, and Norway pout are placed in the Other Primary Carnivore Group, and since this group does not feed on itself, the diet of these fish species is restricted solely to herbivorous zooplankton. Our literature survey indicates that this is far from being the case, since these fish species, placed in our Pelagic Planktivore group, consume large quantities of prey considered to be meso-zooplankton carnivores. In addition, the diets of adult mackerel and herring consist of far more meso-zooplankton carnivore prey than Jones' (1982) webs allow. A large fraction of the energy reaching pelagic fish does so via an intermediate trophic step, meso-zooplankton carnivores, rather than passing directly from herbivorous zooplankton.

Food supply to fish

Daily production and daily fish predation losses of each of the main trophic guilds are indicated in Figure 1. These data are summarized in Table 4 and daily production surplus/deficits are calculated. Production of lower trophic level guilds easily supports their fish predation losses, but problems towards the top end of the food web are clearly evident. As in previous North Sea food webs, the greatest difficulty in satisfying the food requirements of fish is to be found in the benthos to demersal fish food chain.

The plankton-pelagic fish food chain (Table 5)

Daily production of the meso-zooplankton omnivore group is such that, after accounting for the observed changes in standing crop biomass and supplying the food requirements of fish, a large surplus of production remains in each quarter of the year. This surplus is available for consumption by meso-zooplankton carnivores, a predator-prey link not shown in Figure 1. Gross

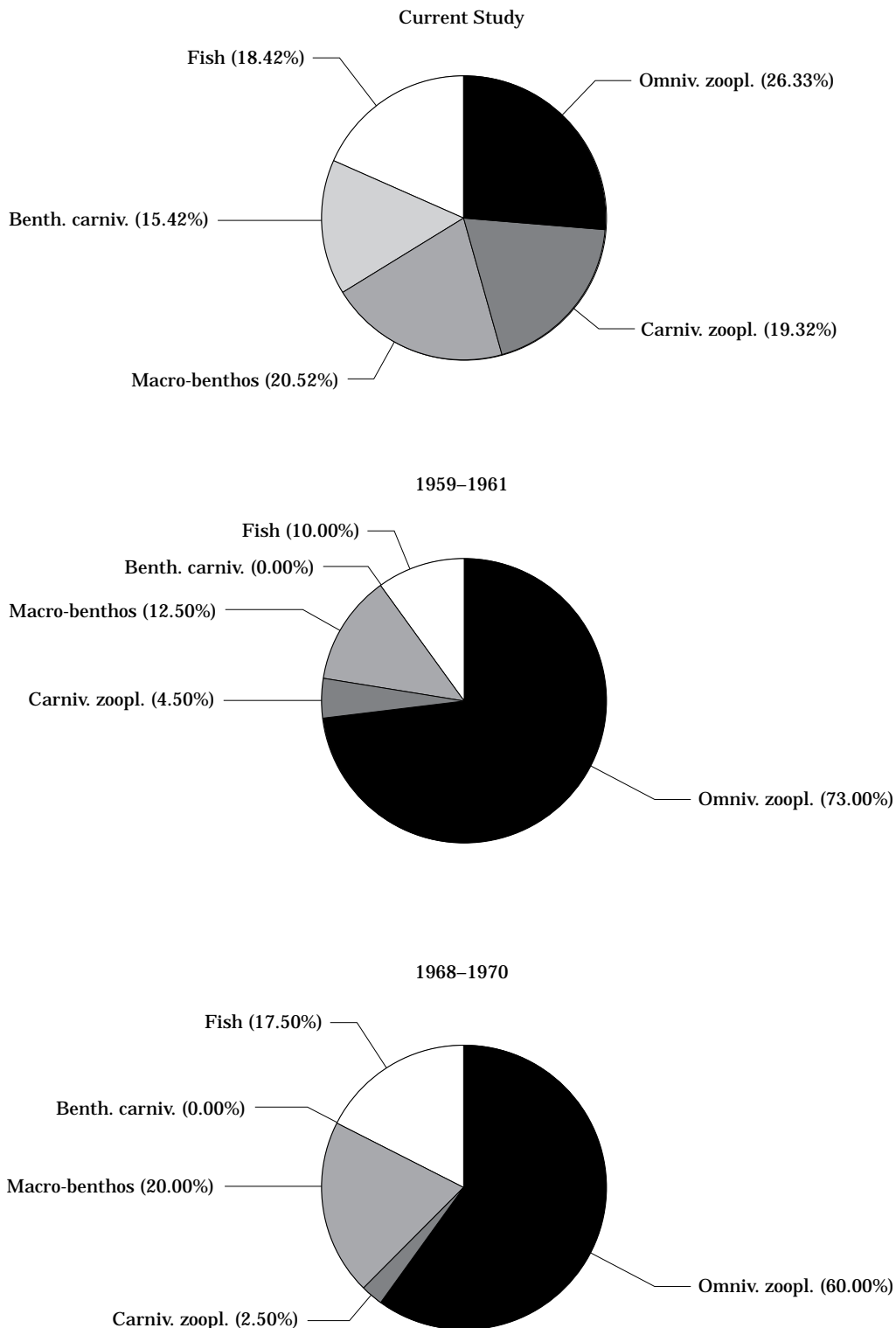


Figure 2. Comparison of fish diet between our food webs and Jones' (1982) food webs.

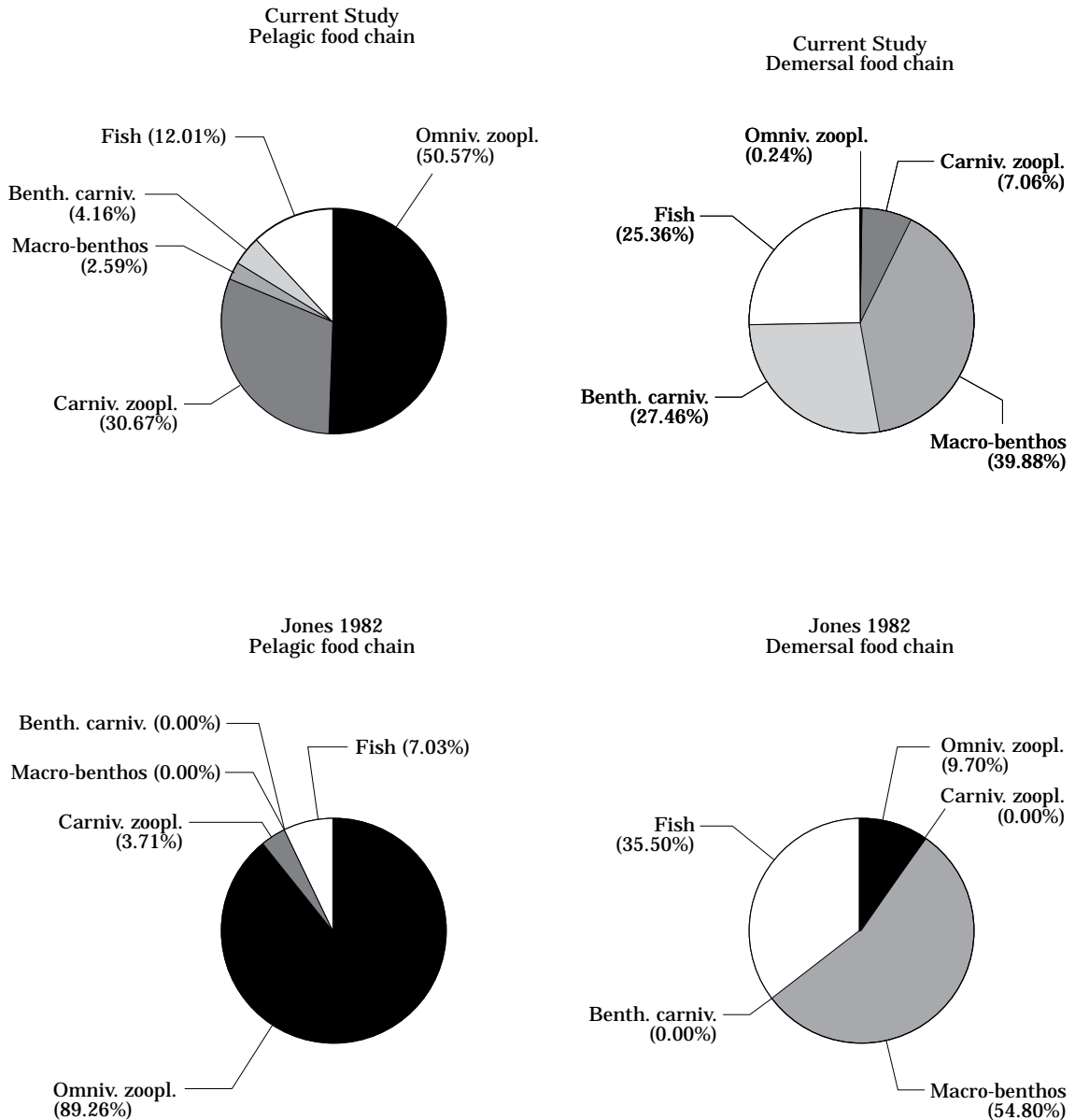


Figure 3. Comparison of fish diet in the plankton to pelagic fish and benthos to demersal fish food chains between our food webs and Jones' (1982) food webs.

growth efficiencies are high in carnivorous zooplankton (Raymont, 1983). Values in the order of 30% appear reasonable over a range of species and development stages (Lasker, 1966; Reeve, 1973). The consumption of meso-zooplankton omnivores by meso-zooplankton carnivores is therefore 3.33 times carnivore production in each quarter.

Even when carnivore predation has been accounted for, omnivore production is still sufficient to leave a large surplus in quarters 2, 3, and 4. The small deficit of omnivore production in quarter 1, when standing crop

biomass is actually increasing, suggests that import is important in early spring. Our figures suggest that, at other times of the year, the North Sea has the potential to be a net omnivore exporter, but this of course depends upon whether there is sufficient phyto-plankton food available to allow maximum potential omnivore production to be achieved.

Production of the meso-zooplankton carnivore guild exceeds demand throughout the year. By far the largest surplus occurs in quarter 2, when the highest production rates coincide with a large decline in the standing crop

Table 4. Daily fish predation losses, daily production and production surplus or deficit over fish predation losses (gWW m⁻² d⁻¹) for each prey guild in each quarter of the year.

Daily consumption by fish	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Meso-zooplankton omnivores	0.0354	0.0791	0.0950	0.0711
Meso-zooplankton carnivores	0.0372	0.0561	0.0638	0.0484
Macro-benthos filter-feeders	0.0093	0.0134	0.0204	0.0156
Macro-benthos deposit-feeders	0.0265	0.0567	0.0366	0.0401
Macro-benthos carnivores	0.0234	0.0365	0.0492	0.0546
Pelagic Planktivores	0.0176	0.0217	0.0324	0.0322
Pelagic Piscivores	0.0000	0.0000	0.0001	0.0002
Demersal Benthivores	0.0022	0.0055	0.0078	0.0066
Demersal Piscivores	0.0040	0.0139	0.0277	0.0244
Total	0.1556	0.2830	0.3332	0.2932
Daily production	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Meso-zooplankton omnivores	0.4174	1.2772	2.0973	1.0605
Meso-zooplankton carnivores	0.0980	0.1897	0.0930	0.1220
Macro-benthos filter-feeders	0.0586	0.0673	0.0974	0.0828
Macro-benthos deposit-feeders	0.1076	0.1185	0.1616	0.1442
Macro-benthos carnivores	0.0288	0.0323	0.4490	0.0394
Pelagic Planktivores	0.0321	0.0482	0.0501	-0.0163
Pelagic Piscivores	0.0007	0.0014	-0.0005	-0.0033
Demersal Benthivores	0.0138	0.0124	0.0165	0.0166
Demersal Piscivores	0.0096	0.0091	0.0134	0.0157
Total	0.7667	1.7561	2.5737	1.4616
Production – consumption	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Meso-zooplankton omnivores	0.3820	1.1982	2.0023	0.9894
Meso-zooplankton carnivores	0.0608	0.1336	0.0292	0.0736
Macro-benthos filter-feeders	0.0493	0.0538	0.0770	0.0672
Macro-benthos deposit-feeders	0.0812	0.0618	0.1249	0.1041
Macro-benthos carnivores	0.0054	-0.0043	-0.0042	-0.0152
Pelagic Planktivores	0.0145	0.0264	0.0176	-0.0485
Pelagic Piscivores	0.0007	0.0014	-0.0006	-0.0035
Demersal Benthivores	0.0117	0.0069	0.0087	0.0099
Demersal Piscivores	0.0056	-0.0048	-0.0143	-0.0086
Total	0.6111	1.4731	2.2405	1.1684

biomass. Euphausiids reproduce in the late winter–early spring following which most of the mature adults die (Lindley, 1978, 1982a; Mauchline, 1980, 1984). The high production rates in quarter 2 can therefore be attributed to large numbers of young in the population, while the population decline is associated with the loss of the adults that make up the bulk of the population in late winter. This suggests that a large fraction of the surplus carnivore biomass in quarter 2 remains in the North Sea, becoming available to the benthic food chain. At other times of the year waste material associated with moulting also passes down to the benthic food chain, but the North Sea may also be a net exporter of carnivorous zooplankton.

Over the first three quarters of the year, pelagic planktivore daily production is sufficient to sustain fish predation losses, to allow the standing crop biomass to

increase, and still leave a small production surplus in each quarter. Relatively high individual gross growth efficiencies are required if the observed potential production rates are to be achieved given the observed daily food ration. However, when mortality losses are taken into account these equate to ecological transfer efficiencies of around 20%, or less. Furthermore, in estimating daily rations for the pelagic planktivores we assumed a conservative stomach emptying time of 12 h. This gave food intake rates of between 1.1% and 1.7% of body-weight in quarters 1 to 3. If a time of 6 h were adopted (see earlier text) then daily food rations would be approximately doubled and the gross growth efficiencies halved. In the discussion above it is clear that the potential zooplankton production is sufficient to support these higher predation rates. In quarter 4, pelagic planktivorous fish stop growing and may actually lose weight

Table 5. Daily biomass flux budget for components of the plankton to pelagic fish food chain.

Meso-zooplankton Omnivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	4.8655	12.1128	13.2754	7.9283
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0794	0.0127	-0.0586	-0.0336
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0354	0.0791	0.0950	0.0711
Production gWW m ⁻² d ⁻¹ (P)	0.4174	1.2772	2.0973	1.0605
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.3026	1.1854	2.0609	1.0230
Biomass consumed by carnivores gWW m ⁻² d ⁻¹ (C)	0.3267	0.6324	0.3100	0.4066
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F-C)	-0.0241	0.5530	1.7509	0.6163
Meso-zooplankton Carnivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	5.4410	9.4810	3.3130	4.7490
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0443	-0.0676	0.0157	0.0076
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0372	0.0561	0.0638	0.0484
Production gWW m ⁻² d ⁻¹ (P)	0.0980	0.1897	0.0930	0.1220
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0165	0.2012	0.0135	0.0660
Gross growth efficiency (GGE)	0.3000	0.3000	0.3000	0.3000
Daily ration gWW m ⁻² d ⁻¹ (R=P/GGE)	0.3267	0.6324	0.3100	0.4066
Pelagic Planktivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	6.3960	7.5180	8.6650	9.8370
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0123	0.0126	0.0128	-0.0377
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0176	0.0217	0.0324	0.0322
Production gWW m ⁻² d ⁻¹ (P)	0.0321	0.0482	0.0501	-0.0163
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0022	0.0139	0.0048	-0.0108
Daily ration gWW m ⁻² d ⁻¹ (R)	0.0696	0.1248	0.1451	0.1156
Gross growth efficiency (P/R)	0.4609	0.3859	0.3451	-0.1414
Pelagic Piscivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	0.2840	1.2910	2.5450	4.0430
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0110	0.0137	0.0164	-0.0412
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0000	0.0000	0.0001	0.0002
Production gWW m ⁻² d ⁻¹ (P)	0.0007	0.0014	-0.0005	-0.0033
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	-0.0103	-0.0123	-0.0170	0.0377
Daily ration gWW m ⁻² d ⁻¹ (R)	0.0010	0.0192	0.0370	0.0405
Gross growth efficiency (P/R)	0.7064	0.0732	-0.0129	-0.0809

(Bryant *et al.*, 1995), and this negative production, combined with predation losses, results in a fall in the standing crop biomass. Negative production in fish still feeding gives rise to negative gross growth efficiencies reflecting continuing metabolic costs.

That the pelagic piscivore figures initially seem rather confusing can be explained by the migratory nature of the two species, mackerel and horse mackerel, which make up this guild. These fish have few fish predators so predation losses are always low. Since it is mainly adult fish that migrate into the North Sea their production rates are relatively low; the faster growing youngest fish are found in the north-east Atlantic. The unrealistically high gross growth efficiency value in quarter 1 probably reflects the fact that few pelagic piscivorous fish are left in the North Sea at this time and those sampled seemed to have very low

feeding rates. However, outside the North Sea the main bulk of these populations were continuing to grow. The steady increase in standing crop biomass through the year cannot be balanced by production; the resulting biomass deficits in quarters 1, 2, and 3, are therefore made up by immigration. These fish leave the North Sea in early winter, hence the fall in standing crop biomass and the biomass surplus in quarter 4. This guild exploits the food resources of the North Sea, but contributes very little back.

The benthos-demersal fish food chain (Table 6)

Throughout the year there is sufficient production within the filter-feeder and deposit-feeder guilds to sustain the consumption demands of fish predators, and still leave a surplus available for benthic carnivores. A gross growth efficiency of 30% is assumed for benthic carnivores

Table 6. Daily biomass flux budget for components of the benthos to demersal fish food chain.

Macro-benthos Filter-feeders	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	14.6737	14.6737	14.6737	14.6737
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0000	0.0000	0.0000	0.0000
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0093	0.0134	0.0204	0.0156
Production gWW m ⁻² d ⁻¹ (P)	0.0586	0.0673	0.0974	0.0828
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0493	0.0538	0.0770	0.0672
Biomass consumed by carnivores gWW m ⁻² d ⁻¹ (C)	0.0346	0.0387	0.0539	0.0473
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F-C)	0.0147	0.0151	0.0230	0.0200
Macro-benthos Deposit-feeders	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	25.5702	25.5702	25.5702	25.5702
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0000	0.0000	0.0000	0.0000
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0265	0.0567	0.0366	0.0401
Production gWW m ⁻² d ⁻¹ (P)	0.1076	0.1185	0.1616	0.1442
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0812	0.0618	0.1249	0.1041
Biomass consumed by carnivores gWW m ⁻² d ⁻¹ (C)	0.0615	0.0688	0.0959	0.0841
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F-C)	0.0196	-0.0070	0.0291	0.0200
Macro-benthos Carnivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	7.1053	7.1053	7.1053	7.1053
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0000	0.0000	0.0000	0.0000
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0234	0.0365	0.0492	0.0546
Production gWW m ⁻² d ⁻¹ (P)	0.0288	0.0323	0.0449	0.0394
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0054	-0.0043	-0.0042	-0.0152
Gross growth efficiency (GGE)	0.3000	0.3000	0.3000	0.3000
Daily ration gWW m ⁻² d ⁻¹ (R=P/GGE)	0.0961	0.1075	0.1498	0.1314
Demersal Benthivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	4.9860	5.1391	5.0201	4.6290
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0017	-0.0013	-0.0043	0.0039
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0022	0.0055	0.0078	0.0066
Production gWW m ⁻² d ⁻¹ (P)	0.0138	0.0124	0.0165	0.0166
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0100	0.0082	0.0130	0.0060
Daily ration gWW m ⁻² d ⁻¹ (R)	0.0468	0.0892	0.0774	0.0771
Gross growth efficiency (P/R)	0.2959	0.1396	0.2129	0.2147
Demersal Piscivores	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Standing crop biomass gWW m ⁻² (B)	3.4404	3.7605	4.0820	4.4050
Biomass change gWW m ⁻² d ⁻¹ (δB)	0.0035	0.0035	0.0035	-0.0106
Biomass consumed by fish gWW m ⁻² d ⁻¹ (F)	0.0040	0.0139	0.0277	0.0244
Production gWW m ⁻² d ⁻¹ (P)	0.0096	0.0091	0.0134	0.0157
Biomass surplus/deficit gWW m ⁻² d ⁻¹ (P-δB-F)	0.0021	-0.0083	-0.0179	0.0019
Daily ration gWW m ⁻² d ⁻¹ (R)	0.0383	0.0499	0.0736	0.0603
Gross growth efficiency (P/R)	0.2495	0.1826	0.1821	0.2612

(Carefoot, 1967; Crisp, 1984), enabling the daily ration required to fuel their daily production to be estimated. In all four quarters the production surplus within the two lower trophic order guilds is sufficient to supply the carnivores this food ration. The small deficit among deposit feeders in quarter 2 is easily compensated by the surplus in filter feeders.

The carnivore group is not quite so well balanced. The surplus of production over predation losses in quarter 1 is not sufficient to sustain the deficits observed in quarters 2 to 4, although, throughout the year, these differences are very small. The simplest explanation is that our assignment of benthic species to trophic guilds is still slightly suspect. We have probably assigned a greater

proportion of the benthic prey recorded in fish stomachs to the carnivore guild than has been the case in assigning biomass to the three guilds from the benthic survey data. If all three benthic groups are combined, production is more than sufficient to meet the predation demands of fish throughout the year.

Benthivorous demersal fish production is sufficient to produce the observed changes in standing crop biomass and meet the predation requirements of their fish predators. The ratios of production to food ration give gross growth efficiencies of between 14 and 29% over the year, in line with observed values (Edwards *et al.*, 1969; Pandian, 1970; Chesney and Estevez, 1976; Williams and Caldwell, 1978; Jobling, 1982). The situation in the piscivorous demersal fish guild is, however, not as promising. Production in quarters 2 and 3 is insufficient to sustain predation losses and produce the observed changes in standing crop biomass. Neither is this summer deficit compensated by the small production surpluses in quarters 1 and 4. Our figures suggest that, rather than increasing by $1 \text{ gWW m}^{-2} \text{ yr}^{-1}$, the demersal piscivore standing crop biomass should be declining by $2 \text{ gWW m}^{-2} \text{ yr}^{-1}$ over the year. Gross growth efficiencies of between 18 and 26% are similar to values recorded in the literature (Daan, 1975; Jones and Hislop, 1978; Hawkins *et al.*, 1985; Hall, 1988), suggesting that our daily production rates are about as high as could be expected given the daily ration values. Our figures indicate that predation on piscivorous demersal fish is quite severe, perhaps suggesting that these fish are less capable of sustaining high fishing mortality levels; a premise apparently substantiated by fisheries assessment data (Daan *et al.*, 1990).

Food supply to secondary producers

Steele (1974) assumed an average annual primary production of $90 \text{ gC m}^{-2} \text{ yr}^{-1}$. Jones (1982) only considered secondary producers and higher trophic levels in his webs, but implicitly went along with Steele's primary production value, in that he used identical figures for secondary production. Jones' (1984) later paper reviewed more recent estimates of primary production, which varied from 54 to $212 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Russell *et al.*, 1971; Cushing, 1973; Gieskes and Kraay, 1980), with daily values as high as $2 \text{ gC m}^{-2} \text{ d}^{-1}$ during bloom periods (Tijssen and Eijgenraam, 1980). More recently Reid *et al.* (1990) suggested that annual primary production may exceed $200 \text{ gC m}^{-2} \text{ yr}^{-1}$ over the whole North Sea, while Joint and Pomroy (1993) suggest a lower figure of around $150 \text{ gC m}^{-2} \text{ yr}^{-1}$. It seems likely therefore that Steele (1974) underestimated primary production.

We assume a primary production of $170 \text{ gC m}^{-2} \text{ yr}^{-1}$; an average daily production of $0.465 \text{ gC m}^{-2} \text{ d}^{-1}$. Primary production during bloom periods can be

twice as high as during other times (Jones, 1984). To force some seasonality into our primary production estimates we assign primary production values of $0.62 \text{ gC m}^{-2} \text{ d}^{-1}$ to quarters 2 and 3 and $0.31 \text{ gC m}^{-2} \text{ d}^{-1}$ to quarters 1 and 4. Assuming the same carbon to wet weight ratio as zooplankton, these figures equate to 10.3 and $5.2 \text{ gWW m}^{-2} \text{ d}^{-1}$ respectively. Gross growth efficiency in herbivorous/omnivorous copepods is highly variable, with values ranging from 20% to 45% over the whole life cycle (Conover, 1964; Mullin and Brooks, 1973; Raymont, 1983), and is dependent on development stage, temperature and food availability (Raymont, 1983). We assume values of 25% in quarters 1 and 4 and 35% in quarters 2 and 3. Assuming all the primary production is taken up by zooplankton secondary producers (e.g. Joiris, 1978), then maximum secondary production is $1.3 \text{ gWW m}^{-2} \text{ d}^{-1}$ in quarters 1 and 4, and $3.61 \text{ gWW m}^{-2} \text{ d}^{-1}$ in quarters 2 and 3. As can be seen from Table 4, our estimates of omnivore production are actually lower than this throughout the year; there appears to be sufficient potential primary production to drive the secondary production required to fuel our plankton to pelagic fish food chain.

Steele (1974) assumed that 30% of primary production reached the benthic food chain, mainly in the form of zooplankton faeces. Assimilation efficiency in zooplankton is extremely variable with values ranging from 50 to 80%, depending on food type and abundance, temperature, etc., and an average value of 70% does not seem unreasonable (Raymont, 1983). Davies (1975) observed organic settlement to the sediments approximately equal to 30% of primary production in the overlying water column.

Assuming then that 30% of primary production feeds into the benthic food chain, this represents inputs of $1.56 \text{ gWW m}^{-2} \text{ d}^{-1}$ in quarters 1 and 4, and $3.09 \text{ gWW m}^{-2} \text{ d}^{-1}$ in quarters 2 and 3. Further assuming gross growth efficiencies of 0.3 in benthic filter- and deposit-feeders (Crisp, 1984), this allows for maximum production in the two lower trophic order benthic guilds combined of $0.47 \text{ gWW m}^{-2} \text{ d}^{-1}$ and $0.93 \text{ gWW m}^{-2} \text{ d}^{-1}$ respectively. Reference to Table 6 shows that actual estimated production varies between 28 and 50% of this potential maximum. When one further considers the potentially large input to the benthic food chain provided by the meso-zooplankton carnivore guild (see above), secondary production in the benthos appears rather inefficient. However, none of the food webs previously discussed allows for an extra trophic level between settlement of organic matter to the sea bed and production in the macrobenthos. Inclusion of a bacteria/meiobenthos detritivore trophic level would account for most of the slack. Other studies have suggested that a considerable fraction of the energy flow to the benthos passes through such a component (Kuipers *et al.*, 1981).

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Appendix I

Species with biomass estimates provided in Sparholt (1990) and the fish feeding guild to which each species has been assigned.

Scientific name	Common name	Feeding guild
<i>Scyliorhinus caniculus</i>	Dogfish	Demersal Piscivore
<i>Galeus melastomus</i>	Black-mouthed Dogfish	Demersal Piscivore
<i>Galeorhinus galeus</i>	Tope	Demersal Piscivore
<i>Mustelus mustelus</i>	Smooth hound	Demersal Piscivore
<i>Squalus acanthias</i>	Spurdog	Demersal Piscivore
<i>Etmopterus spinax</i>	Velvet belly	Demersal Piscivore
<i>Raja brachyura</i>	Blonde ray	Demersal Benthivore
<i>Raja clavata</i>	Roker	Demersal Benthivore
<i>Raja montagui</i>	Spotted ray	Demersal Benthivore
<i>Raja radiata</i>	Starry ray	Demersal piscivore
<i>Raja batis</i>	Skate	Demersal Benthivore
<i>Raja fullonica</i>	Shagreen ray	Demersal Benthivore
<i>Raja circularis</i>	Sandy ray	Demersal Benthivore
<i>Raja naevus</i>	Cuckoo ray	Demersal Benthivore
<i>Chimaera monstrosa</i>	Rat fish	Demersal Piscivore
<i>Clupea harengus</i>	Herring	Pelagic Planktivore
<i>Sprattus sprattus</i>	Sprat	Pelagic Planktivore
<i>Alosa alosa</i>	Allis shad	Pelagic Planktivore
<i>Salmo trutta</i>	Sea-trout	Demersal Piscivore
<i>Argentina sphyraena</i>	Argentine	Pelagic Planktivore
<i>Argentina silus</i>	Greater argentine	Pelagic Planktivore
<i>Lophius piscatorius</i>	Angler	Demersal Piscivore
<i>Gadus morhua</i>	Cod	Demersal Piscivore
<i>Gadiculus argenteus</i>	Silvery pout	Pelagic Planktivore
<i>Melanogrammus aeglefinus</i>	Haddock	Demersal Piscivore
<i>Merlangius merlangus</i>	Whiting	Demersal Piscivore
<i>Trisopterus minutus</i>	Poor cod	Demersal Piscivore
<i>Micromesistius poutassou</i>	Blue whiting	Pelagic Planktivore
<i>Trisopterus luscus</i>	Bib	Demersal Piscivore
<i>Trisopterus esmarki</i>	Norway pout	Pelagic Planktivore
<i>Pollachius pollachius</i>	Pollock	Demersal Piscivore
<i>Pollachius virens</i>	Saithe	Demersal Piscivore
<i>Brosme brosme</i>	Torsk	Demersal Piscivore

Appendix I

(Continued)

Scientific name	Common name	Feeding guild
<i>Ciliata septentrionalis</i>	Northern rockling	Demersal Piscivore
<i>Enchelyopus cimbrius</i>	Four-bearded rockling	Demersal Piscivore
<i>Gaidropsarus vulgaris</i>	Three-bearded rockling	Demersal Piscivore
<i>Molva molva</i>	Ling	Demersal Piscivore
<i>Molva dypterygia</i>	Blue ling	Demersal Piscivore
<i>Merluccius merluccius</i>	Hake	Demersal Piscivore
<i>Zoarces viviparus</i>	Viviparous blenny	Demersal Benthivore
<i>Sebastes marinus</i>	Red-fish	Demersal Piscivore
<i>Sebastes viviparus</i>	Norway haddock	Demersal Piscivore
<i>Trigla lucerna</i>	Tub gurnard	Demersal Piscivore
<i>Eutrigla gurnardus</i>	Grey gurnard	Demersal Piscivore
<i>Trigloporus lastoviza</i>	Streaked gurnard	Demersal Benthivore
<i>Myoxocephalus scorpius</i>	Bull-rout	Demersal Benthivore
<i>Taurulus bubalis</i>	Sea-scorpion	Demersal Benthivore
<i>Agonus cataphractus</i>	Hooknose	Demersal Benthivore
<i>Cyclopterus lumpus</i>	Lumpsucker	Demersal Benthivore
<i>Liparis liparis</i>	Sea-snail	Demersal Benthivore
<i>Trachurus trachurus</i>	Horse mackerel	Pelagic Piscivore
<i>Echiichthys vipera</i>	Lesser weever	Demersal Benthivore
<i>Trachinus draco</i>	Greater weever	Demersal Benthivore
<i>Anarhichas minor</i>	Spotted catfish	Demersal Benthivore
<i>Lumpenus lampretaeformis</i>	Snake blenny	Demersal Benthivore
<i>Pholis gunnellus</i>	Butterfish	Demersal Benthivore
<i>Ammodytes tobianus</i>	Sandeel	Pelagic Planktivore
Callionymidae	Dragnet	Demersal Benthivore
Gobiidae	Gobies	Demersal Benthivore
<i>Scomber scomber</i>	Mackerel	Pelagic Piscivore
<i>Scophthalmus rhombus</i>	Brill	Demersal Piscivore
<i>Scophthalmus maximus</i>	Turbot	Demersal Piscivore
<i>Lepidorhombus whiffiagonis</i>	Megrim	Demersal Piscivore
<i>Arnoglossus laterna</i>	Scaldfish	Demersal Benthivore
<i>Pleuronectes platessa</i>	Plaice	Demersal Benthivore
<i>Platichthys flesus</i>	Flounder	Demersal Benthivore
<i>Limanda limanda</i>	Dab	Demersal Benthivore
<i>Microstomus kitt</i>	Lemon sole	Demersal Benthivore
<i>Glyptocephalus cynoglossus</i>	Witch	Demersal Benthivore
<i>Hippoglossides platessoides</i>	Long rough dab	Demersal Benthivore
<i>Hippoglossus hippoglossus</i>	Halibut	Demersal Benthivore
<i>Solea solea</i>	Sole	Demersal Benthivore
<i>Buglossidium luteum</i>	Solenette	Demersal Benthivore

Appendix II

Prey items found in stomach samples examined in fish diet studies and the prey life-history guild to which each item has been assigned.

Scientific name	Common name	Life history guild
Phaeophyta	Phytoplankton	Phytoplankton flagellate
Appendicularia	Oikopleura	Meso-zooplankton omnivore
Porifera	Sponges	Macrobenthos filter feeder
Cnidaria	Cnidarians	Meso-zooplankton carnivore
Hydrozoa	Hydroids	Macrobenthos filter feeder
Ctenophora	Comb jellies	Meso-zooplankton carnivore
Platyhelminthes	Flatworms	Macrobenthos carnivore
Nemertea	Ribbon worms	Macrobenthos carnivore
Gephyrea	Group name of Pseudocoelomate phyla	Macrobenthos deposit feeder

Appendix II

(Continued)

Scientific name	Common name	Life history guild
Priapulida	Priapulid worms	Macrobenthos deposit feeder
Unidentified mollusca		Macrobenthos filter feeder
Polyplacophora	Chitons	Macrobenthos deposit feeder
Gastropoda	Footed shells	Macrobenthos deposit feeder
Scaphopoda	Tusk shells	Macrobenthos deposit feeder
Bivalvia	Bivalve shells	Macrobenthos filter feeder
<i>Cultellus pelucidus</i>	Bivalve	Macrobenthos filter feeder
<i>Ensis ensis</i>	Bivalve	Macrobenthos filter feeder
<i>Abra alba</i>	Bivalve	Macrobenthos deposit feeder
Cephalopoda	Squids, Octopi	Meso-zooplankton carnivore
Annelida	Segmented worms	Macrobenthos deposit feeder
Polychaeta	Segmented worms	Macrobenthos deposit feeder
<i>Pectinaria koreni</i>	Polychaeta	Macrobenthos deposit feeder
<i>Nephtys</i> spp.	Polychaeta	Macrobenthos deposit feeder
Echiura	Spoon worms	Macrobenthos deposit feeder
Sipuncula	Peanut worms	Macrobenthos deposit feeder
Unidentified Crustacea		Macro-Benthos carnivore
Copepoda	Copepods	Meso-zooplankton omnivore
Calanoida	Copepod	Meso-zooplankton omnivore
<i>Paracalanus parvus</i>	Copepod	Meso-zooplankton omnivore
<i>Pseudocalanus elongatus</i>	Copepod	Meso-zooplankton omnivore
<i>Calanus finmarchius</i>	Copepod	Meso-zooplankton omnivore
<i>Centropages typicus</i>	Copepod	Meso-zooplankton omnivore
<i>Temora longicaudata</i>	Copepod	Meso-zooplankton omnivore
<i>Euchaeta norvegica</i>	Copepod	Meso-zooplankton carnivore
<i>Paraeuchaeta norvegica</i>	Copepod	Meso-zooplankton carnivore
Leptostraca		Macro-benthos deposit feeder
Mysidia	Opossum shrimps	Macro-benthos deposit feeder
<i>Amblyops abbreviata</i>	Mysid	Macro-benthos deposit feeder
<i>Boreomysis arctica</i>	Mysid	Macro-benthos deposit feeder
<i>Boreomysis nobilis</i>	Mysid	Macro-benthos deposit feeder
<i>Pseudomma affine</i>	Mysid	Macro-benthos deposit feeder
<i>Pseudomma roseum</i>	Mysid	Macro-benthos deposit feeder
<i>Erythrops serrata</i>	Mysid	Macro-benthos deposit feeder
Ostracoda	Seed shrimps	Meso-zooplankton omnivore
Cumacea	Cumaceans	Macro-benthos deposit feeder
Lampropidae	Cumacean	Macro-benthos deposit feeder
Tanaidacea	Tanaidaceans	Macro-benthos deposit feeder
Isopoda	Isopods	Macro-benthos deposit feeder
Flabellifera	Isopod	Macro-benthos deposit feeder
Valvifera	Isopod	Macro-benthos deposit feeder
Asellota	Isopod	Macro-benthos deposit feeder
Amphipoda	“Sandhoppers”	Macro-benthos filter feeder
Gammaridea	Amphipod	Macro-benthos filter feeder
<i>Parathemisto abyssorum</i>	Amphipod	Macro-benthos filter feeder
Hyperiidea	Amphipod	Macro-benthos filter feeder
Caprellidea	Amphipod	Macro-benthos filter feeder
Euphausiacea	Euphausiids	Meso-zooplankton carnivore
<i>Meganyctiphanes norvegica</i>	Euphausiid	Meso-zooplankton carnivore
<i>Thysanoessa raschii</i>	Euphausiid	Meso-zooplankton carnivore
Decapoda	Shrimps, crabs and lobsters	Macro-benthos carnivore
Decapoda zoea	Young decapods	Meroplankton
Caridea	Prawns and Shrimps	Macro-benthos carnivore
Pandalidae	Prawns	Macro-benthos carnivore
<i>Pandalus borealis</i>	Prawn	Macro-benthos carnivore
Crangonidae	Shrimps	Macro-benthos carnivore
<i>Crangon crangon</i>	Shrimp	Macro-benthos carnivore
<i>Pontophilus norvegicus</i>	Shrimp	Macro-benthos carnivore
Pasiphaeidae	Shrimps	Meso-zooplankton carnivore
<i>Pasiphaea tarda</i>	Shrimp	Meso-zooplankton carnivore
Macrura	Lobsters	Macro-benthos carnivore

Appendix II

(Continued)

Scientific name	Common name	Life history guild
<i>Nephrops norvegica</i>	Norway lobster	Macro-benthos carnivore
<i>Upogebia</i> spp.	Burrowing prawn	Macro-benthos filter feeder
Anomura	Squat lobsters and Hermit crabs	Macro-benthos carnivore
Galatheidae	Squat lobsters	Macro-benthos carnivore
<i>Munida sarsi</i>	Squat lobsters	Macro-benthos carnivore
Brachyura	Crabs	Macro-benthos carnivore
Oxystomata	Crabs	Macro-benthos carnivore
Oxyrhyncha	Crabs	Macro-benthos carnivore
Brachyrhyncha	Crabs	Macro-benthos carnivore
Cancridea	Crabs	Macro-benthos carnivore
Pycnogonida	Sea spiders	Macro-benthos carnivore
Chaetognatha	Arrow worms	Meso-zooplankton carnivore
<i>Sagitta setosa</i>	Arrow worm	Meso-zooplankton carnivore
Echinodermata	Echinoderms	Megabenthos
Ophiuroidea	Brittle stars	Megabenthos
Urochordata	Tunicates and salps	Macro-Benthos filter feeder
Ascidiace	Sea squirts	Macro-benthos filter feeder
Cephalochordata	Lancelets	Macro-benthos filter feeder
TELEOSTEI	Fish	
Unidentified fish eggs		Meroplankton
Unidentified fish post-larvae		Demersal Piscivore
Clupeidae	Unidentified Clupeoids	Pelagic Planktivore
Clupeoid post-larvae		Pelagic Planktivore
<i>Clupea harengus</i>	Herring	Pelagic Planktivore
<i>Sprattus sprattus</i>	Sprat	Pelagic Planktivore
Argentinidae	Argentines	Pelagic Planktivore
<i>Maurolicus muelleri</i>	Pearl-side	Pelagic Planktivore
Gadidae	Unidentified gadoids	Demersal Piscivore
<i>Gadus morhua</i>	Cod	Demersal Piscivore
<i>Gadiculus argenteus</i>	Silvery pout	Pelagic Planktivore
<i>Melanogrammus aeglefinus</i>	Haddock	Demersal Piscivore
<i>Merlangius merlangus</i>	Whiting	Demersal Piscivore
<i>Trisopterus minutus</i>	Poor cod	Demersal Piscivore
<i>Trisopterus esmarki</i>	Norway pout	Pelagic Planktivore
Norway pout post-larvae		Pelagic Planktivore
Unidentified Rocklings		Demersal Piscivore
<i>Merluccius merluccius</i>	Hake	Demersal Piscivore
<i>Gasterosteus aculeatus</i>	Stickleback	Demersal Benthivore
<i>Syngnathus</i> spp.	Pipe fish	Demersal Benthivore
<i>Sebastes viviparus</i>	Norway haddock	Demersal Piscivore
Triglidae	Unidentified gurnards	Demersal Piscivore
<i>Trachurus trachurus</i>	Scad	Pelagic Piscivore
<i>Echiichthys vipera</i>	Lesser weever	Demersal Benthivore
Blenniidae	Unidentified blennies	Demersal Benthivore
<i>Anarhichas lupus</i>	Wolf fish	Demersal Benthivore
Ammodytidae	Sandeels	Pelagic Planktivore
<i>Crystallogobius linearis</i>	Crystal goby	Pelagic Planktivore
Gobiidae	Unidentified gobies	Demersal Benthivore
Goby post-larvae		Demersal Benthivore
<i>Scomber scombrus</i>	Mackerel	Pelagic Piscivore
<i>Pleuronectes platessa</i>	Plaice	Demersal Benthivore
Plaice eggs		Meroplankton
<i>Limanda limanda</i>	Dab	Demersal Benthivore
<i>Microstomus kitt</i>	Lemon sole	Demersal Benthivore
<i>Glyptocephalus cynoglossus</i>	Witch	Demersal Benthivore
<i>Hippoglossus platessoides</i>	Long rough dab	Demersal Benthivore
<i>Solea solea</i>	Sole	Demersal Benthivore
Unidentified flatfish		Demersal Benthivore
Flatfish larvae		Meroplankton