

The consumption of zooplankton by early life stages of fish in the North Sea

Michael R. Heath

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Previous work has shown that during the 1970s, fish and carnivorous macrozooplankton together consumed $\sim 22 \text{ gC m}^{-2} \text{ year}^{-1}$ of mesozooplankton, principally copepods. Consumption declined to $\sim 17 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1990s, mainly because of a reduction in fish production. The zooplankton production required to meet this demand seems to be approximately accounted for by estimates of new primary production, but there are additional sinks for zooplankton production attributable to predation by, for example, gelatinous species. Additionally, the consumption of zooplankton by early life stages of fish is difficult to assess and could be larger than implied by the earlier analysis. Here, the role of fish early life stages in zooplankton consumption is re-assessed, and found to be approximately double that previously estimated. Some 28% of the zooplankton consumption by fish is now estimated to be attributable to early life stages, resulting in an estimate of zooplankton consumption by the fish community as a whole 14% higher. Taken overall, the consumption of zooplankton production by fish and other planktivorous predators is now estimated to be $19\text{--}25 \text{ gC m}^{-2} \text{ year}^{-1}$.

Keywords: fish diet, fish larvae, fisheries, food consumption, plankton, production, stock assessment.

M. R. Heath: Fisheries Research Services, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK; tel: +44 1224 876544; fax: +44 1224 295511; e-mail: heathmr@marlab.ac.uk

Introduction

Previous work (Heath, 2005) revealed marked changes since the early 1970s in production and consumption within the North Sea fish foodweb. The production of fish was translated into a direct and indirect (i.e. through predator-prey links) demand for secondary production by mesozooplankton and filter and deposit feeding benthos. This demand was estimated to have declined from $\sim 20 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1970s to $16 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1990s. Over the same period, the proportion of demand provided by zooplankton production increased from $\sim 70\%$ to 75% , as planktivorous fish became more dominant in the fish community. Annual fluctuations in the estimates of mesozooplankton production were positively correlated with the gross production of planktivorous fish, and this was interpreted as suggesting bottom-up control of the pelagic foodweb. In contrast, benthos production was interpreted as being more top-down controlled, and benthic invertebrate production was estimated to have increased as predation pressure from fish declined.

The pelagic foodweb analysed by Heath (2005) was represented by two zooplankton functional groups, omnivores and carnivores, each of which was potentially preyed on by four fish feeding guilds (planktivores, demersal piscivores, pelagic piscivores, and benthivores). Consumption by fish was estimated from diet and ration data for a set of well-studied species, scaled to the gross production of each fish guild by landings, stock assessment, and trawl survey data. The results suggested that the total food consumption by fish amounted to between 10 and $20 \text{ gC m}^{-2} \text{ year}^{-1}$ (1973–1999

average = $14.3 \text{ gC m}^{-2} \text{ year}^{-1}$), of which $5.8 \text{ gC m}^{-2} \text{ year}^{-1}$ (average $6.7 \text{ gC m}^{-2} \text{ year}^{-1}$) was contributed by omnivorous mesozooplankton. The remainder was made up of carnivorous zooplankton (average $2.8 \text{ gC m}^{-2} \text{ year}^{-1}$), benthos (average $2.4 \text{ gC m}^{-2} \text{ year}^{-1}$), and piscivory (average $2.4 \text{ gC m}^{-2} \text{ year}^{-1}$). In contrast, $8.14 \text{ gC m}^{-2} \text{ year}^{-1}$ (average $11.0 \text{ gC m}^{-2} \text{ year}^{-1}$) of omnivorous mesozooplankton were estimated to be consumed by carnivorous zooplankton (euphausiids and macroplankton). Therefore, total annual consumption of omnivorous mesozooplankton was $17.18 \text{ gC m}^{-2} \text{ year}^{-1}$.

New primary production (i.e. primary production based on nitrate assimilation rather than on recycled ammonia; Dugdale and Goering, 1967) is estimated to be $\sim 40 \text{ gC m}^{-2} \text{ year}^{-1}$ in the Dogger Bank area (Richardson *et al.*, 2000), and between 30 and $100 \text{ gC m}^{-2} \text{ year}^{-1}$ in the North Sea as a whole (Steele, 1974; Richardson and Pedersen, 1998). Assuming a gross growth efficiency of 0.3 , these values imply herbivorous zooplankton gross production of $\sim 10\text{--}30 \text{ gC m}^{-2} \text{ year}^{-1}$, consistent with the estimated consumption of zooplankton by fish and carnivorous zooplankton.

Although the predation losses of mesozooplankton appear to match approximately the likely production based on knowledge of new primary production, there remains an issue as to whether there are significant sources of predation on zooplankton unresolved by the analysis of Heath (2005). The main candidates are probably gelatinous taxa, which were not included in the carnivorous zooplankton group, and early life history stages of fish, which were only included crudely in the fish predation calculations. 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 gC m^{-2} during July for the three main species of scyphomedusae combined. Assuming a daily ration of 10% of biomass (Hay *et al.*, 1990), these data imply a zooplankton consumption rate of $0.004 \text{ gC m}^{-2} \text{ d}^{-1}$, compared with a gross production rate during July (from CPR data for the same years) of $0.197 \text{ gC m}^{-2} \text{ d}^{-1}$. Therefore, the available data indicate that North Sea wide scyphomedusae consumed $\sim 2\%$ of omnivorous zooplankton gross production during the 1970s and early 1980s. 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 doubled, the overall impact apparently remains relatively small.

Heath (2005) assumed that the biomass of fish between 3 and 9 months old (depending on species) entering the stock each year was representative of prerecruit production and hence food consumption. On this basis, food consumption by prerecruits represented between $<1\%$ and 30% of the population total, depending on species. In contrast, Sissenwine *et al.* (1984) estimated consumption by prerecruits (fish up to ~ 12 months old) on Georges Bank to be approximately the same as that by the exploitable stock. This discrepancy requires investigation, because the larvae of most fish are exclusively zooplanktivorous, so an alternative representation of their food consumption could significantly alter the perception of predation loading on the plankton.

The few field studies in which the predatory impact of the whole larval fish community has been estimated (e.g. Munk and Nielsen, 1994; Nielsen and Munk, 1998; Rasmussen, 2004) provide little basis for an evaluation of budget calculation. Field data have been, of necessity, restricted to a small area (typically $30 \times 30 \text{ km}$) and a short interval (typically $10\text{--}20 \text{ d}$) relative to the entire spatial and temporal domain of the distributions of fish larvae in an area such as the North Sea. Hence, extrapolation of field estimates of community consumption up to regional scale annual consumption is fraught with uncertainties. The purpose here is to re-assess the predation loading on zooplankton by fish in the North Sea, by explicitly simulating the role of fish larvae and prerecruit juveniles.

Material and methods

Model formulation

The weight specific growth rate (G , d^{-1}) of an individual is defined as

$$G_t = \frac{\log_e(W_{t2})}{t2} - \frac{\log_e(W_{t1})}{t1}, \quad (1)$$

where W_{t1} and W_{t2} are individual body weights, at the start (age $t1$) and end (age $t2$) of a development interval, respectively. Houde and Zastrow (1993) and Houde (1996) derived generalized bioenergetic relationships between temperature and rates of growth and food consumption for typical marine fish larvae, and estimated gross growth efficiency to be 3.23, i.e.

$$C_t = 3.23(G_t), \quad (2)$$

where C is the daily consumption per unit body weight, $\text{g g}^{-1} \text{ d}^{-1}$. This relationship is independent of temperature.

Following from the above, the weight of food ingested by a cohort of identical individuals (I_t , g) over the growth interval W_{t1} to W_{t2} is given by

$$I_t = 3.23(N_{tW})(W_{t2} - W_{t1}), \quad (3)$$

where N_{tW} is the number of individuals at the age of the mean body weight over the growth interval W_{t1} – W_{t2} . Assuming that the number of individuals (N_t) declines with age as a consequence of mortality according to

$$N_t = N_{t1}e^{-M(t-t1)}, \quad (4)$$

where M is the instantaneous mortality rate (d^{-1}), then N_{tW} is equivalent to the mean number of individuals in the cohort over the age interval $t1$ – $t2$, i.e.

$$\begin{aligned} N_{tW} &= \left(\frac{1}{t2 - t1} \right) \int_{t1}^{t2} N_{t1}e^{-M(t-t1)} dt \\ &= \left(\frac{N_{t1}}{M(t2 - t1)} \right) (e^{-M(t2-t1)} - 1). \end{aligned} \quad (5)$$

For fish larvae, both M and G vary systematically with body size (W) and hence with age. Houde (1997) derived a generalized relationship describing the allometry of mortality rate as

$$M_t \approx 1.5W_t^{-0.5}. \quad (6)$$

The weight specific growth rate (G) varies according to a more complicated relationship. Growth in weight may be positive or negative according to feeding conditions, whereas growth in length is governed more by the underlying allometry. In this case, the requirement is to represent the age dependence of mean weight specific growth rate, but the underlying model is length dependent, according to von Bertalanffy (1938):

$$L_t = L_{\text{hatch}} + L_{\infty}(1 - e^{-k(t)}), \quad (7)$$

where L_{hatch} and L_{∞} are the length at hatching ($t=0$) and the asymptotic length, respectively, and k is the growth velocity parameter (d^{-1}). Scaling between body length and body weight, to facilitate the estimation of weight increments over given age intervals, takes a standard function of the form

$$W_t = aL_t^b. \quad (8)$$

The pathways for simulating daily food consumption by an annual cohort of early life stages of a given species, based on the equations above, is shown in Figure 1.

Data sources

The model was parameterized for each of the main assessed North Sea fish species: planktivore guild herring (*Clupea harengus*), sandeel (*Ammodytes* spp.), Norway pout (*Trisopterus esmarkii*); demersal piscivore guild cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*); pelagic piscivore guild Atlantic mackerel (*Scomber scombrus*); benthivore guild plaice (*Pleuronectes platessa*), sole (*Solea solea*). The parameters a and b of the

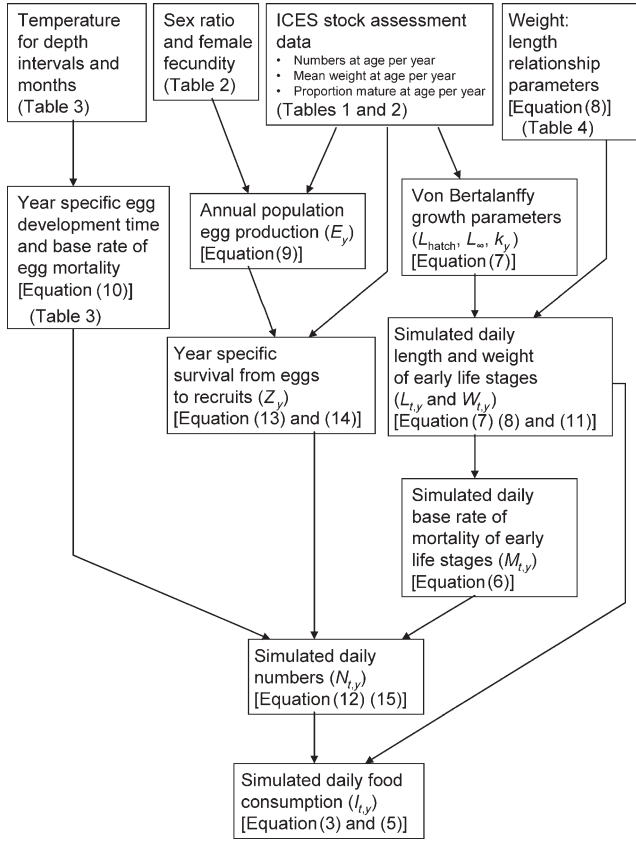


Figure 1. Flow diagram showing the connections between the input data and the resulting simulations of daily food consumption by an annual cohort of early life stages of a given species. Numbers in brackets within each cell refer to equations in the text.

weight length relationship [Equation (8)] for these species were taken from Coull *et al.* (1989).

Numbers at age, proportion mature at age, and mean weights at age in the stock for each species, for each year in the assessments, were obtained from the relevant ICES North Sea Assessment Working Group documentation (ICES, 2004a, b, c). In general, the assessment outputs took the form of estimated numbers at age on 1 January each year, and mean weights at age over the subsequent calendar year. However, the youngest age class included in the assessment, and the assumptions regarding the date at which this class was assessed, varied from species to species (Table 1). The earliest year for which data were available in the assessments also varied between species. The shortest sequence was for sandeel and Norway pout, for which the earliest year was 1983, whereas for plaice and sole the assessments extended back to 1957.

Egg production

The number of eggs produced each year (E_y) by the stock of each species was estimated from the assessed numbers at age class ($N_{a,y}$), proportion mature at age class ($p_{a,y}$), mean weight at age class ($W_{a,y}$), sex ratio ($S_{a,y}$), and relative fecundity ($F_{a,y}$):

$$E_y = N_{a,y} p_{a,y} W_{a,y} S_{a,y} F_{a,y}. \quad (9)$$

The resolution of year on year variability in proportion mature at age class varied between species. All assessments

incorporate age dependence, although some only by a knife edge function (Table 2). Only the herring assessments routinely incorporate interannual variability. However, data on year dependence of proportion mature at age class for cod and haddock (Pouling, 1997) were incorporated into the analysis here. Similar data exist for plaice and sole up to 1988 (Rijnsdorp *et al.*, 1991), but extensions of these analyses to the late 1990s are apparently not yet available in the literature.

Sex ratio was assumed to be 1:1 for all species, age classes, and years. Estimating realized fecundity is a complex issue for many species, especially batch spawners such as mackerel (e.g. ICES, 2005), and beyond the scope of this study. However, a variety of literature data indicate that annual potential relative fecundity (eggs kg female⁻¹) can reasonably be assumed constant with respect to age for most species (e.g. plaice, Rijnsdorp, 1991). An exception is haddock, for which 2 year old fish have a lower relative fecundity than older fish (Hislop, 1988). Long term trends and interannual variability in fecundity have been recorded for a number of species (cod: Yoneda and Wright, 2004; plaice: Horwood *et al.*, 1986; Rijnsdorp, 1991; Rijnsdorp *et al.*, 1991). However, even for the better studied species, the data were fragmentary and insufficient to include as a time series in this study. For the less well studied species (e.g. sandeel, saithe), there are no detailed studies of trends in fecundity. Hence, the relative fecundity of each species ($F_{a,y}$) was assumed constant with respect to time (Table 2).

Egg development period

Mortality rates were assumed to be constant with age during the egg stage, and distinct from the rates for larvae and juveniles derived from Equation (6). Bunn *et al.* (2000) list estimates of rates of egg mortality for five of the assessed species (herring 0.05 d⁻¹; cod 0.03–0.40 d⁻¹; haddock 0.21–0.54 d⁻¹; plaice 0.02–0.20 d⁻¹; and sole 0.20–1.00 d⁻¹), but it was difficult to identify appropriate values to use in the simulation. Instead, a generic relationship with temperature (T , °C), derived from published field studies (Pepin, 1991), was used to obtain a base rate of egg mortality for each species in any given year:

$$M_{\text{egg}} = e^{-3.520+0.178T}. \quad (10)$$

In contrast, relationships between egg development times and temperature, or the data to derive such relationships, were available in the literature for seven of the ten species (herring, sandeel, cod, haddock, plaice, sole, mackerel; Table 3). For saithe, the sparse data on egg development times indicated a similarity to the relationship for haddock, which was therefore used as a substitute for that for saithe (egg development time 9 d at 9.4°C for saithe compared with 8.9 d at 9.4°C from the fitted relationship for haddock). No data could be found for whiting or Norway pout egg development times, so the generic size and temperature based relationship of Pauly and Pullin (1988) was used, assuming mean egg diameters of 1.14 mm for both species (Russell, 1976).

Temperature data appropriate to the spawning months for each species (Table 3) were derived from hydrographic observations (standard CTD and reversing thermometer data on depth and temperature at location and time) held by ICES (<http://www.ices.dk/ocean/>). Data collected in each 1° latitude × 2° longitude cell within ICES fishing Area IV (North Sea) were bin averaged by year, month, and observation depth interval (sea surface to 30 m, and 30 m to seabed). Unsampled year/month/depth bins were

Table 1. Basic properties of the North Sea stock assessment data (ICES, 2004a, b, c) used in the analysis.

Guild	Assessed species	Number of age classes	Youngest age class	Assumed hatching date	Age corresponding to numbers-at-age of youngest class (months)	Age corresponding to weight-at-age of youngest class (months)
Planktivores	Herring ^a	10	0	1 October	9	12
	Sandeel ^b	5	0	1 April	3	6
	Norway pout ^b	5	0	1 April	3	6
Demersal piscivores	Cod	7	1	1 April	9	15
	Haddock ^c	8	0	1 April	3	6
	Whiting	6	1	1 April	9	15
Benthivores	Saithe	10	1	1 April	9	15
	Plaice	10	1	1 April	9	15
Pelagic piscivores	Sole	10	1	1 April	9	15
	Mackerel ^d	13	0	1 April	3	6

^aAccording to the herring assessment literature, the date corresponding to the numbers-at-age of the youngest age class is 1 January, when the individuals concerned are ~3 months old. However, the annual rate of natural mortality assumed for the youngest age class (1.0) is more representative of the 6-monthly mortality assumed for the 0-group of other species, so in this study, the date corresponding to 0-winter-ring herring numbers-at-age assessment is taken to be 1 July.

^bFor sandeel and Norway pout, the assessments are carried out quarterly rather than annually, so the data used here have been selected such that the date corresponding to 0-group numbers-at-age assessment is 1 July, and 1 January for older classes.

^cThe natural mortality rate applied to 0-group haddock in the assessments is assumed to apply for 6 months, so the date corresponding to the 0-group numbers-at-age assessment is 1 July.

^dFormally, the youngest age class in the mackerel assessment is 0-group, but the assumed natural mortality rate is the same for all age classes (0.15), and for the 0-group, this is probably unrealistically low. Hence, the assessed numbers of 0-group must be underestimated and were discarded in this study.

filled by applying the local deviation from the long term monthly average temperature based on the deviations in preceding and following months. The temperature of the North Sea for each year/month/depth combination was taken as the mean over all latitude/longitude bins. For each species, the temperature relevant to the egg development time in a given year was a 2 or 3 monthly average centred on the approximate spawning months given by Russell (1976). For this purpose, the North Sea

herring were assumed to be autumn spawners. Data from the 30 m to seabed depth bins were used to represent conditions for the demersal spawning species (herring and sandeel), and surface to 30 m data for the other species (Table 3).

Larval and juvenile growth simulation

The asymptotic length (L_{∞}) and the mean von Bertalanffy growth velocity parameter (k) were estimated for each species by non

Table 2. Fecundity and maturity-at-age data for the assessed species.

Guild	Assessed species	Annual potential relative fecundity (eggs kg ⁻¹)	Proportion mature at age class							
			0	1	2	3	4	5	6	7+
Planktivores	Herring ^a	303 782	0	0	v	v	1	1	1	1
	Sandeel ^a	783 255	0	0	1	1	1			
	Norway pout ^a	528 382	0	0.1	1	1	1			
Demersal piscivores	Cod ^b	87.041[(W/1.15) ^{1.248}]	0	v	v	v	v	v	v	1
	Haddock ^c	274 000 ages ≤2; 493 000 ages ≥3	0	v	v	v	v	v	v	1
	Whiting ^a	1 140 664	0	0.11	0.92	1	1	1	1	
	Saithe ^d	434 650	0	0	0	0	0.15	0.7	0.9	1
Benthivores	Plaice ^a	320 515	0	0	0	1	1	1	1	1
	Sole ^a	590 724	0	0	0	1	1	1	1	1
Pelagic piscivores	Mackerel ^a	749 561	0	0.08	0.6	0.9	0.97	0.97	0.99	1

An entry of v in the maturity table indicates that the values were variable between years; otherwise the values were year-independent.

^aRelative fecundity derived from fecundity at 50% mature and length at 50% mature as cited by Rickman *et al.* (2000). Length at 50% maturity was transformed to weight at 50% maturity using the wet weight: length relationships of Coull *et al.* (1989). Maturity-at-age data from stock assessment reports (ICES, 2004a, b, c).

^bCod fecundity was estimated from wet weight (W , g) using the equation given, which originates from data on Icelandic cod by Marteinsdottir (see also Marteinsdottir and Begg, 2002). This was not significantly different from that estimated in 1970 for cod samples in the eastern North Sea and west of Scotland by West (1970) (fecundity = 167.8 $W^{1.1689}$). Cod maturity-at-age data from Poulting (1997).

^cHaddock fecundity from Hislop (1988), and maturity-at-age data from Poulting (1997).

^dNo fecundity data could be located for saithe, so the value for cod derived from the data presented by Rickman *et al.* (2000) was used instead on the grounds that saithe and cod have similar values of L_{∞} . Maturity-at-age data from stock assessment reports (ICES, 2004b).

Table 3. Equations assembled from the literature relating egg development times to temperature for each of the assessed species, together with the months and depths for averaging the temperature data relevant for each species.

Guild	Assessed species	Relationship between time from fertilization to hatching (d) and temperature (T, °C)	Relevant period and depth interval for temperature data in the North Sea	References
Planktivores	Herring	$e^{6.000} T^{-1.422}$	August–October, seabed 30 m	Parameterized from data in Blaxter (1956) and Gamble <i>et al.</i> (1985)
	Sandeel	$e^{4.653} T^{-0.758}$	February–March, seabed 30 m	Parameterized from data in Winslade (1971) and Field (1988)
	Pout	Generic relationship: $CF[10^{7.1+(0.608 \log(ED) - 4.09(\log(T+26))}] CF^a = 1.1$, egg diameter (ED) = 1.14 mm	March–April, sea surface 30 m	Pauly and Pullin (1988). ED from Russell (1976)
Demersal piscivores	Cod	$10^{1.871}(T+2)^{0.790}$	March–April, sea surface 30 m	Page and Frank (1989; as revised by Geffen <i>et al.</i> , 2006)
	Haddock	$10^{1.890}(T+2)^{0.890}$	March–April, sea surface 30 m	Page and Frank (1989)
	Whiting	Generic relationship: $CF[10^{7.1+(0.608 \log(ED) - 4.09(\log(T+26))}] CF^a = 1.1$, egg diameter (ED) = 1.14 mm	March–April, sea surface 30 m	Pauly and Pullin (1988). ED from Russell (1976)
	Saithe	As haddock, based on single record of saithe egg development (9 d at 9.4°C)	March–April, sea surface 30 m	Breder and Rosen (1966)
Benthivores	Plaice	$43.853 - 14.427 \log_e T + 1.5$	March–April, sea surface 30 m	Relationship for Irish Sea plaice with an offset of 1.5 d relative to North Sea plaice according to Fox <i>et al.</i> (2003)
	Sole	$e^{4.926} T^{-1.328}$	March–April, sea surface 30 m	Fonds (1979)
Pelagic piscivores	Mackerel	$e^{8.877} T^{-1.579}$	April–May, sea surface 30 m	Mendiola <i>et al.</i> (2006) ^b

^aCF is a calibration factor defined as the mean ratio of egg stage durations of cod and haddock according to the relationship of Pauly and Pullin (1988), assuming egg diameters of 1.52 and 1.50 mm, respectively (Russell, 1976), relative to the values for these species estimated according to Page and Frank (1989), at temperatures of 5°C, 6°C, and 7°C.

^bParameter values after correcting errors in the original publication.

linear regression using Simplex optimization of the average over all years of the lengths at mean weight at age from the stock assessment data. Lengths were calculated by back transforming the mean weight at age data in the assessment outputs [Equation (8)]. Assumed lengths at hatching (L_{hatch}), and ages from hatching corresponding to mean weights in the assessment data are given in Tables 1 and 4.

Year specific von Bertalanffy growth velocity parameter values (k_y) were estimated by scaling the mean value (k) for each species with the year specific mean weight of the age class 1 in the assessments. The scaling factor ϕ (such that $k_y = \phi k$) was calculated as

$$\frac{(\ln(1 - (L_{a1} - L_{\text{hatch}})/L_{\infty}))/t_{a1}}{(\ln(1 - (\bar{L}_{a1} - L_{\text{hatch}})/L_{\infty}))/t_{a1}}, \quad (11)$$

where $a1$ corresponds to the age from hatching represented by the weight of age class 1.

For each species, the parameters k_y , L_{∞} , and L_{hatch} (assumed constant over time), and the parameters a and b of the weight length relationship allowed the individual body weight at age (W_t) to be calculated at daily intervals from hatching to the minimum age at which the weight at age was accounted for in the stock assessment data [15 months or 455 d in the case of cod, whiting, saithe, plaice, and sole; younger for the other species (Table 1)].

Early life stage mortality simulation

Post hatch, the base rate of daily mortality was given by Equation (6). These values were also year specific, depending on the simulated daily weights at age. The year specific cumulative base rate mortality from the beginning of the egg stage to the age at which population numbers were first estimated by the stock assessments was then the sum of the daily values, including egg stages:

$$\zeta_y = \sum_{\text{spawning}}^{\text{age 1st assessment}} M_{t,y}. \quad (12)$$

In contrast, the actual year specific rate of mortality (Z_y) was estimated as

$$Z_y = \ln(E_y) - \ln(N_{0,y}) \quad (13)$$

for sandeel, Norway pout, and haddock for which the youngest assessed age class was age 0, and

$$Z_y = \ln(E_y) - \ln(N_{1,y+1}) \quad (14)$$

for herring, cod, whiting, saithe, mackerel, plaice, and sole.

Finally, the base rates of daily mortality rate ($M_{t,y}$) in each year were scaled by the ratio (Z_y/ζ_y), and the numbers of eggs or larvae

Table 4. Weight length relationship parameters from Coull *et al.* (1989) ($W = \text{constant} \times L^{\text{exponent}}$, W in g, L in cm).

Guild	Assessed species	Weight length constant	Weight length exponent	Assumed length at hatch (cm)	Fitted von B. L_{∞} (cm)	Fitted mean von B. growth velocity (year^{-1})	Corrected r^2 for von B. fitting
Planktivores	Herring	0.00603	3.0904	0.5	33.3	0.464	0.996
	Sandeel	0.00124	3.3200	0.4	18.2	0.875	0.996
	Norway pout	0.00920	3.0265	0.3	17.0	1.102	0.978
Demersal piscivores	Cod	0.02048	2.8571	0.3	124.5	0.205	0.991
	Haddock	0.01821	2.8268	0.3	64.7	0.240	0.979
	Whiting	0.01051	2.9456	0.3	34.9	0.668	0.996
Benthivores	Saithe	0.02832	2.7374	0.3	115.1	0.147	0.960
	Plaice	0.02301	2.7901	0.3	39.1	0.617	0.907
	Sole	0.00360	3.3133	0.3	33.9	0.710	0.951
Pelagic piscivores	Mackerel	0.00300	3.2900	0.4	38.0	0.576	0.983

von Bertalanffy (von B.) growth in length parameters fitted by Simplex optimization to mean length-at-age data back-transformed from the weight-at-age data available from the stock assessments.

at daily ages ($N_{t,y}$), simulated as

$$N_{t,y} = N_{t-1,y} e^{-(Z_y/\zeta_y)M_{t,y}} \quad (15)$$

for $t = 1$ to 455, where $N_{0,y} = E_y$.

Early life stage ingestion simulation

For each species and year, the weight of food ingested at daily intervals ($I_{t,y}$) by the annual cohort of larvae was calculated from Equation (3), based on the simulated numbers at age ($N_{t,y}$) and body weights at age ($W_{t,y}$). Food consumption of eggs was set to zero. The integrated food consumption over successive 3 month intervals from hatching (I_m) was the sum of the daily ingestion values over successive 91 d intervals from hatching.

Diet composition of prerecruit life stages

Working from the North Sea fish diet data summaries of Greenstreet (1996), percentage contributions by weight of prey species to the diet of age classes 0 and 1 of each of the assessed fish species, in each quarter of the year, were accumulated into categories of mesozooplankton (principally copepods), carnivorous zooplankton (principally euphausiids), filter and deposit feeding benthos (principally Annelida), benthic carnivores (principally *Crangon* spp.), and fish. For all species except herring, age 0 fish in quarter 3 were considered to represent juveniles 3–6 months old, age 0 in quarter 4 to represent 6–9 months old, etc. No data were available for larvae and juveniles 0–3 months old, so those stages were regarded as feeding exclusively on mesozooplankton. Herring were treated differently, being predominantly autumn/winter spawners rather than spring spawners. Age 0 herring in quarter 1 were regarded as being 3–6 months old, and so on to age 0 in quarter 4 being 12–15 months old.

Estimation of post-recruit food consumption

Beyond the minimum age represented in the stock assessment outputs, fish were regarded as being post recruits. Numbers at age and mean weight at age in the stock were available at annual intervals from the assessment data. Equations (3) and (5) were applied directly to the annual interval data on

numbers at age and mean weights at age in the stock from the assessment outputs, to estimate food consumption of each age class in each year. The gross efficiency (C/G) of the immature post recruit age classes [Equation (3)] was assumed to be the same as for larvae and juveniles (3.23). However, a growth efficiency of 8.9 was applied for the proportion of each age class given as mature in the assessment data. This value takes account of the additional cost of reproduction over and above those of growth for mature fish (Sissenwine *et al.*, 1984; Mateo, 2007). The results were summed over age classes within each year to estimate the annual food consumption of post recruits.

Regional correction of saithe and mackerel data

There was a particular problem with estimating the consumption by mackerel and saithe. This was because, although the assessment region for all 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 ingestion by populations of mackerel and saithe between the North Sea and other waters was on the basis of annual landings, as described by Heath (2005).

Carbon conversions

Fish biomass and ingestion are typically expressed in units of wet weight, whereas 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 (gC gW W^{-1}) of guild taxa were as quoted by Greenstreet (1996; planktivores 0.162; benthivores 0.107; demersal piscivores 0.103; pelagic piscivores 0.184).

Results

Mean egg development times estimated from the various relationships assembled from the literature (Table 3) varied from 10 d for Norway pout and whiting to 25 d for sandeel (Figure 2). Within each species, year on year differences in temperature generated further variability, with an average range (maximum minimum) across all species of 7 d (Figure 2). Egg mortality rates predicted from the temperature data varied between 0.06

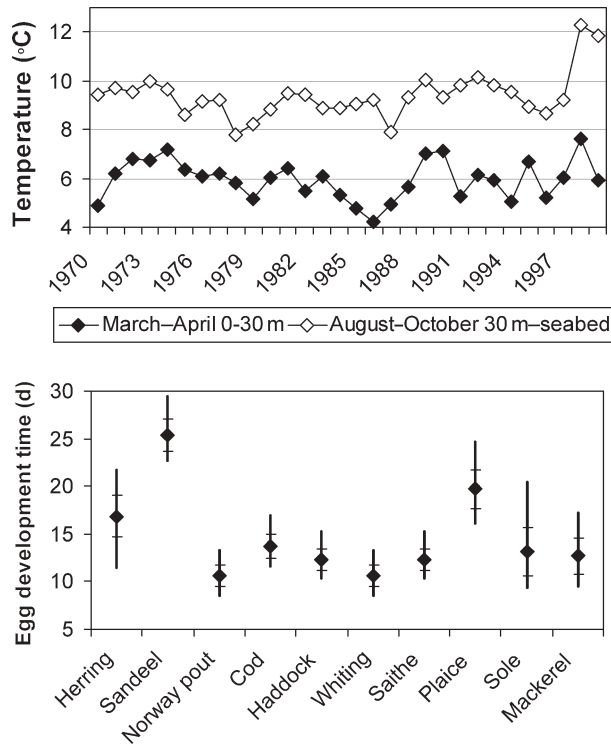


Figure 2. (Upper panel) North Sea average temperatures, 1970–1999, for sea surface to 30-m depth during March and April (filled symbols) and 30 m to seabed during August–October (open symbols). (Lower panel) Average egg incubation period (filled symbols), 1973–1999, maximum to minimum range (vertical lines), and standard deviation (horizontal tick-marks) for each species.

and 0.11 d^{-1} for Norway pout, cod, haddock, whiting, saithe, plaice, and sole, from 0.08 to 0.11 d^{-1} for sandeel, from 0.09 to 0.15 d^{-1} for mackerel, and from 0.12 to 0.27 d^{-1} for herring.

L_{∞} and the mean von Bertalanffy growth velocity parameter (k) estimates for each of the assessed species, derived from the assessment data, are shown in Table 4. Early life stage mortality rates, standardized to the interval between spawning and age 91 d after hatching $[(\xi_y/Z_y) \sum_t^{91\text{d}} M_{t,y}]$, averaged over the years 1983–2000, showed some relationship with the von Bertalanffy parameters (Figure 3). The species with the smallest L_{∞} (sandeel and Norway pout) exhibited the fastest growth and least early life mortality, whereas the species with largest L_{∞} (cod and saithe) exhibited the slowest growth and the highest mortality.

Taking herring as an example, simulated trajectories of body weight (g), number of individuals, and daily food consumption ($\text{gC m}^{-2} \text{d}^{-1}$) after hatching are shown in Figure 4. During the first 10 d after hatching, mortality rates exceeded growth rates, and cohort food consumption declined. Thereafter, growth rates were higher than mortality rates, and cohort consumption increased. The year showing the highest rates of cohort food consumption (1985) exhibited lower mortality and higher egg production and growth rates than the year of lowest food consumption (1974). However, in neither year were any of the mortality, growth, or egg production rates the extremes in the time series.

Considering the cumulative cohort food consumption over the first 15 months from hatching, the balance between consumption during the first 6 months and that during the later months varied

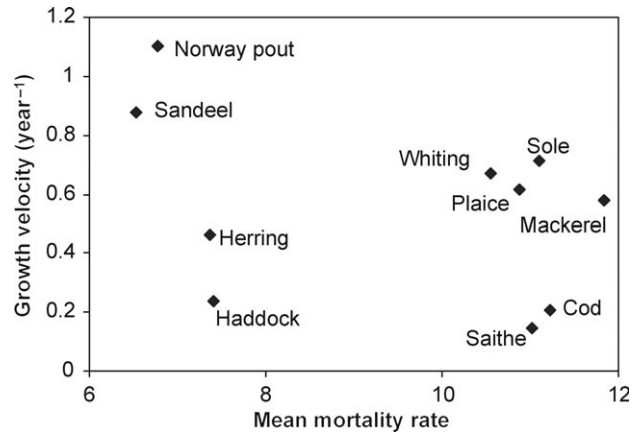


Figure 3. Fitted von Bertalanffy growth velocity parameter in relation to the mean early life stage mortality rate over the first 3 months of life, for each of the assessed fish species.

between species, depending on the pattern of growth and the balance between growth and mortality (Figure 5). For all species, the rate of cohort food consumption (I_m) increased up to 6 months of age. However, the cohort food consumption rate of Norway pout, sandeel, whiting, and plaice peaked within the first 15 months, and then declined. For all other species, the

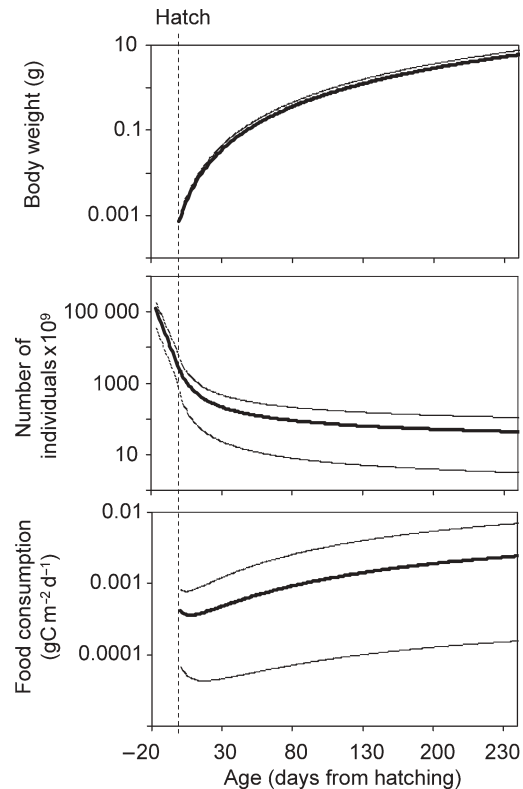


Figure 4. Trajectories of body weight (g) (upper panel), numbers of individuals (middle panel), and cohort daily food consumption (lower panel) for simulations of herring early life history. The heavy line in each plot indicates the mean trajectory over the period 1970–2000. Thin lines indicate results for the maximum and minimum food consumption years in the time-series.

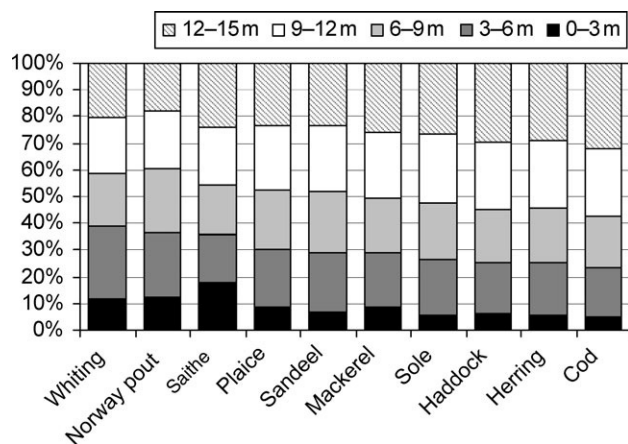


Figure 5. Mean proportion of food consumption during the first 15 months by 3-month interval for each of the assessed species, estimated by the simulation model.

cohort food consumption rate was still increasing with age at 12–15 months, but the rate of increase $[d(I_m)/dt]$ peaked by 9 months even for cod, haddock, and saithe.

The age from hatching at which fish were first included in the stock assessments varied between species (Table 1). For each year and species, the cumulative cohort food consumption up to this age estimated from the early life stage simulations (prerecruit food consumption) was added to the annual food consumption similarly estimated from the assessment data on numbers at age and weight at age of post recruit age classes. The proportion of annual food consumption taken by prerecruits varied between species (Table 5). The proportions for whiting and herring were significantly ($p < 0.05$) higher than those for sandeel, haddock, saithe, and mackerel. However, there were no significant ($p < 0.05$) linear trends over the period 1983–2000, these being the years for which assessment data were available for all species. Summing the data across feeding guilds (i.e. taking account of the relative abundances of each species), the proportion of consumption taken by prerecruits varied from 3% for pelagic piscivores to 26% for benthivores (Figure 6, Table 5). The simple

method for calculating prerecruit food consumption used by Heath (2005; prerecruit production = biomass of the incoming recruit year class) led to lower estimates of the proportion of total annual food consumption taken by all prerecruits except flatfish species (Table 5).

Considering the first 12 months of life, rather than the prerecruit stages as defined by the stock assessments, the proportion of annual food consumption taken by early life stages varied from 7% to 17% for long lived (Table 1), large L_∞ (Table 4) species (cod, saithe, and mackerel), and from 35 to 56% for the short lived, low L_∞ species such as Norway pout, sandeel, and whiting (Table 6).

Heath (2005) calculated the total food consumption by each fish guild (all species combined rather than just the 10 assessed species; Equation (6), and Table 4 of Heath, 2005) resolved by various prey categories (other fish, zooplankton, and benthos). These data were apportioned into pre and post recruit consumption using the original, simple estimates of prerecruit/total consumption upon which they were based. The post recruit components were summed across prey categories for each guild, and the new ratios of guild specific prerecruit/total consumption (Table 5) were applied to estimate revised values for guild level prerecruit food consumption for all prey categories combined. The results indicated that prerecruit fish consumed $4.87 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1970s, declining to $3.56 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1990s.

Percentage diet compositions by weight for each assessed species in 3 monthly age intervals up to 15 months (Table 7) were used to apportion the simulated total food consumption between prey categories. All species were assumed to feed exclusively on mesozooplankton up to 3 months old, but thereafter additional prey categories appeared in the diet. The benthivore species (plaice and sole) switched to a diet exclusively of benthos, whereas the demersal piscivores fed on a mixed diet of carnivorous zooplankton, benthos, and other fish. The 3 monthly age classes regarded as being prerecruits with respect to the stock assessments varied between species (Table 1), and the prey consumption by those classes were summed for each species, then across species within each fish feeding guild, and finally across guilds, to estimate the prerecruit community

Table 5. Average food consumption of prerecruit fish, 1983–2000, as a proportion of the total population food consumption estimated from the simulations described here, and compared with the simple estimates from Heath (2005).

Guild	Assessed species	Species-specific prerecruit consumption/total	s.d. of prerecruit consumption/total	Prerecruit consumption/total, summed over assessed species	Prerecruit consumption/total as estimated by Heath (2005)
Planktivores	Herring	0.308	0.101	0.240	0.068
	Sandeel	0.150	0.067		
	Norway pout	0.249	0.087		
Demersal piscivores	Cod	0.245	0.107	0.189	0.107
	Haddock	0.112	0.045		
	Whiting	0.434	0.105		
Benthivores	Saithe	0.112	0.062	0.260	0.315
	Plaice	0.249	0.080		
Pelagic piscivores	Sole	0.244	0.157	0.027	<0.001
	Mackerel	0.030	0.010		

The guild-level prerecruit consumption relative to the total for the guild took account of the relative abundances of the species comprising each guild.

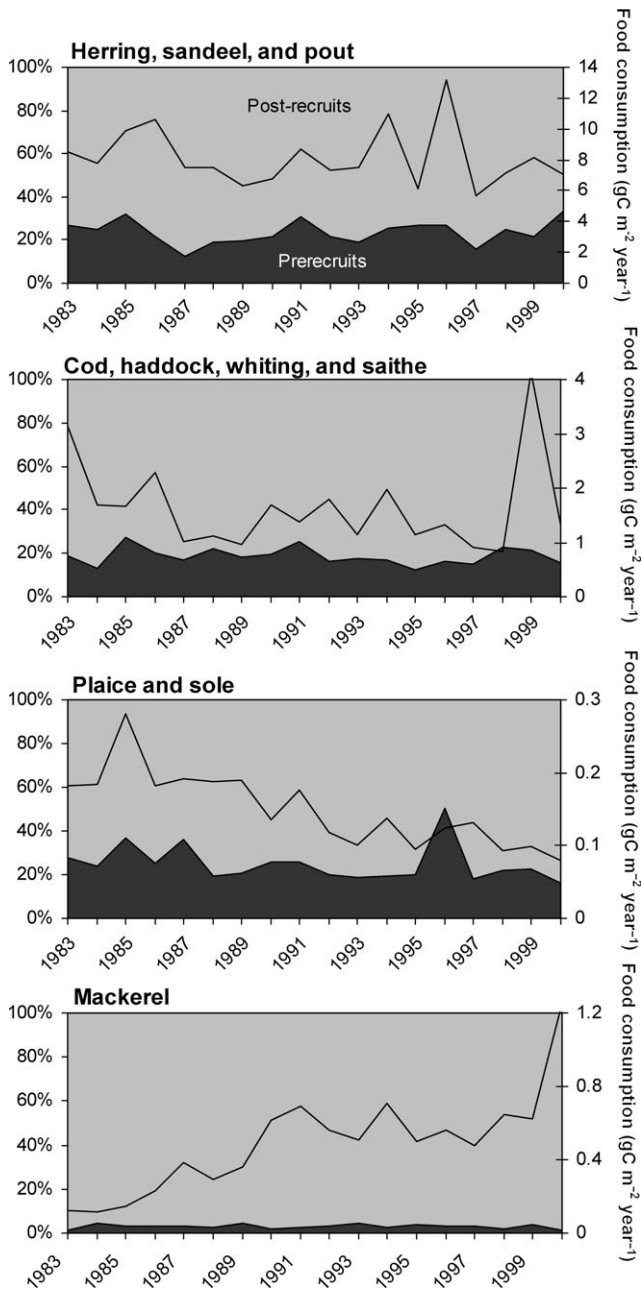


Figure 6. Time-series of annual food consumption by the combined pre- and post-recruit populations of assessed fish species, grouped by feeding guild (line plot and right scale). The dark and pale grey shaded areas (left scale) show the percentage contributions of pre- and post-recruits, respectively, to the total annual food consumption.

consumption of prey. These results represented only a minimum estimate of the prerecruit food consumption, because they did not include any of the non assessed species in each guild. There was no practical way of estimating the contribution of non assessed species, so the consumption values for each prey category based on assessed species were treated as relative indices, and their proportions applied to the revised guild level prerecruit total consumption values derived from Table 5. The results (Table 8) indicated that the revised estimates of prerecruit food consumption

were $\sim 2.3 \times$ higher than the previous estimates of Heath (2005). Planktivory represented $\sim 90\%$ of the consumption (mesozooplankton 70%, carnivorous zooplankton 20%), with benthivory and piscivory contributing 5% each. The revised food consumption by the whole fish community, including both pre and post recruits was $22.4 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1970s, declining to $16.2 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1990s, with 22–23% being taken by prerecruits. Combining the previous estimates of mesozooplankton consumption by post recruit fish and carnivorous zooplankton with the revised estimates for consumption by prerecruits gave annual ecosystem consumption rates of mesozooplankton of $24.9 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1970s, declining to $18.9 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1990s, $\sim 10\%$ higher than that derived by Heath (2005).

Uncertainties in egg development times, egg mortality rate, and the allometry of larval and juvenile mortality rates will all contribute to the way in which total mortality from spawning to first assessment is apportioned across development stages in the model, and hence to the simulated pattern of cohort food requirements with age. To gain an indication of sensitivity to assumptions about the egg stages, the simulations were re run assuming a constant egg development time of 10 d for all species and all years, and a relatively extreme constant egg mortality rate of 0.225 d^{-1} , based on field observation of cod and plaice eggs in the southern North Sea (Rijnsdorp and Jaworski, 1990) and a synthesis of data for other species (Bunn *et al.*, 2000). These assumptions resulted in 14–15% lower estimates of the food consumption for the community of prerecruits ($4.14 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1970s compared with $4.87 \text{ gC m}^{-2} \text{ year}^{-1}$, and $3.05 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1990s compared with $3.56 \text{ gC m}^{-2} \text{ year}^{-1}$).

Discussion

Sissenwine *et al.* (1984) and Steele *et al.* (2005) appear to have been the only previous authors to have attempted to estimate the ecosystem impact of feeding by larval and prerecruit stages of the fish community, in both cases on Georges Bank (NW Atlantic). Sissenwine *et al.* (1984) estimated the total food consumption of the fish community to be $13.24 \text{ gC m}^{-2} \text{ year}^{-1}$ during the period 1964–1975, of which 40–45% was due to pre exploited stages defined as ranging from first feeding larvae to 8 months old for haddock, and larvae to 14 months for herring and yellow tail flounder (*Limanda ferruginea*). Steele *et al.* (2005) estimated the Georges Bank fish community food consumption to be $14.19 \text{ gC m}^{-2} \text{ year}^{-1}$ over the period 1973–2002, of which 25–35% was due to prerecruits. By comparison, I estimate the food consumption by fish in the North Sea to be $16.22 \text{ gC m}^{-2} \text{ year}^{-1}$, 22–23% of which was by prerecruits. Hence, on face value, the three studies appear to give similar results.

The derivations of consumption rates for prerecruits, however, differ radically between Sissenwine *et al.* (1984), Steele *et al.* (2005), and the present study. Sissenwine *et al.* (1984) developed an approach that accounted for the metabolic balance of the fish, but simplified the key equations by assuming that G and M were time invariant, and that $G = M$ over the interval from spawning to recruitment. The implication of the latter assumption is that cohort biomass remains constant over time. From the work of Beyer (1989) and Houde (1996), we know that there is little justification for such assumptions, and that a model which takes account of ontogenetic and interannual variations in M/G is required, such as presented here. Interannual differences in

Table 6. Average food consumption of fish up to 12 months of age, 1983–2000, as a proportion of the total population food consumption, derived from the simulations.

Guild	Assessed species	Species-specific consumption by fish <12 months old relative to total	s.d. of <12 months consumption/ total	Consumption by fish <12 months old relative to total, summed over assessed species
Planktivores	Herring	0.308	0.101	0.408
	Sandeel	0.384	0.179	
	Norway pout	0.561	0.207	
Demersal piscivores	Cod	0.167	0.072	0.319
	Haddock	0.303	0.135	
	Whiting	0.348	0.083	
Benthivores	Saithe	0.084	0.044	0.197
	Plaice	0.190	0.060	
Pelagic piscivores	Sole	0.179	0.114	0.068
	Mackerel	0.074	0.027	

The guild-level consumption by fish <12 months old relative to the total for the guild took account of the relative abundances of the species constituting each guild.

mean M/G should be inversely related to cohort food consumption of prerecruits per unit of egg production, and ontogenetic changes in mortality relative to growth have the potential to alter the balance of cohort food consumption between larval and juvenile stages.

Steele *et al.* (2005) took a simple approach to estimating food consumption by prerecruits. They assumed that the piscivorous diet of recruited fish was exclusively prerecruits, on which they were the dominant predators, and that the consumption of fish by the recruited stocks was therefore an estimate of prerecruit production. Then, the food consumption of prerecruits was estimated by assuming a production: consumption ratio of 0.3. This approach is essentially similar to that of Heath (2005), in which prerecruit production was assumed to be equal to the biomass of recruits joining the assessed stocks each year. Clearly, neither can provide a complete perspective of prerecruit production or consumption.

The methodology presented here also contains a number of assumptions, in particular the values for gross growth efficiency, allometric relationships for mortality, and temperature dependence of egg mortality and development time. However, the results were relatively insensitive to assumptions about species and interannual variability in egg development times and mortality rates. The main driver of the simulated cohort numbers at age, and hence the food demand, was the scaling ratio (Z_y/ζ_y) derived from the stock assessment data. Hence, the results must be vulnerable to the uncertainties inherent in the fishery catch at age based analyses of stock numbers performed for each of the assessed species. In particular, the rates of natural mortality of the youngest age classes assumed in the assessments can have a great effect on the estimated numbers of recruits. For purposes of fisheries advice, where the major requirement is to estimate trends in spawning stock biomass, recruitment, and fishing mortality, this sensitivity is not critical. However, for exercises such as described here, it is important to bear in mind that the assumed rates of natural mortality are at best very poorly known. In some cases, for example mackerel, where the same annual rate of natural mortality (0.15) is applied to all age classes in the assessment, the absolute assessed numbers of the

0 group must be highly questionable. In that case, the effect would be to inflate the prerecruit mortality estimate, leading to an underestimate of larval and juvenile food consumption. However, for most assessed species in the North Sea, more reasonable age dependent profiles of natural mortality are assumed, based on the outputs from multispecies model simulations performed periodically for the region.

Independent estimates of food consumption by the prerecruit fish community, e.g. from field observations, are scarce in the literature. Nielsen and Munk (1998) derived the grazing rate of the larval fish community (principally cod, whiting, Norway pout, sandeel, common dab *Limanda limanda*), long rough dab *Hippoglossoides* spp., and gobies *Crystallogobius* spp.) on copepod species in a frontal area of the central North Sea during late May 1992. Estimates ranged from $5.5 \text{ mgC m}^{-2} \text{ d}^{-1}$, close to the front where ichthyoplankton were most abundant, to $2.0 \text{ mgC m}^{-2} \text{ d}^{-1}$ in shallower inshore waters. The principal copepod prey species were *Calanus finmarchicus*, *Temora longicornis*, and *Pseudocalanus* spp. For the northern North Sea, Rasmussen (2004) calculated day by day food consumption by a larval fish community sampled at intervals of 6 h during a 10 d drift study in May 1996. In that case, the community consisted mainly of larval and pelagic juvenile sandeel, Norway pout, saithe, whiting, haddock, cod, and witch (*Glyptocephalus cynoglossus*), and all prey taxa were considered. Mean daily consumption was estimated to be $1.3 \text{ mgC m}^{-3} \text{ d}^{-1}$ in the upper 40 m of the water column, equivalent to $\sim 50 \text{ mgC m}^{-2} \text{ d}^{-1}$ (maximum daily value equivalent to $147 \text{ mgC m}^{-2} \text{ d}^{-1}$). However, for comparison with the results of Nielsen and Munk (1998), only 30% of the consumption consisted of copepodites and copepod nauplii. The remainder was mainly invertebrate eggs, with some gastropods and fish eggs. Taken together, the results from these two studies imply that, during May, the average consumption rate of zooplankton by the prerecruit fish community in the North Sea should be in the range $5\text{--}50 \text{ mgC m}^{-2} \text{ d}^{-1}$. By comparison, the average annual consumption of mesozooplankton by prerecruit fish during the 1990s, as estimated here ($2.16 \text{ gC m}^{-2} \text{ year}^{-1}$; Table 8), represents a mean daily rate of $12 \text{ mgC m}^{-2} \text{ d}^{-1}$ assuming that most of the mesozooplankton

Table 7. Diet percentage composition by weight of prerecruit stages of assessed species, in 3-month age intervals, for five prey groups.

Guild	Assessed species	Age interval from hatching				
		0 3 months	3 6 months	6 9 months	9 12 months	12 15 months
Mesozooplankton prey						
Planktivores	Herring	100	100	100	23	52
	Sandeel	100	100	100	100	100
	Norway pout	100	49	20	20	48
Demersal piscivores	Cod	100	12	14	8	12
	Haddock	100	23	31	42	48
	Whiting	100	26	29	23	9
	Saithe	100	0	10	13	1
Benthivores	Plaice	100	0	0	0	0
	Sole	100	0	0	0	0
Pelagic piscivores	Mackerel	100	54	77	2	17
Carnivorous zooplankton prey						
Planktivores	Herring	0	0	0	74	45
	Sandeel	0	0	0	0	0
	Norway pout	0	47	80	80	47
Demersal piscivores	Cod	0	3	0	3	11
	Haddock	0	24	6	9	16
	Whiting	0	1	2	27	37
	Saithe	0	27	47	40	26
Benthivores	Plaice	0	0	0	0	0
	Sole	0	0	0	0	0
Pelagic piscivores	Mackerel	0	7	9	85	1
Filter and deposit feeding benthos prey						
Planktivores	Herring	0	0	0	0	0
	Sandeel	0	0	0	0	0
	Norway pout	0	0	0	0	0
Demersal piscivores	Cod	0	7	5	19	13
	Haddock	0	10	14	30	22
	Whiting	0	11	6	5	2
	Saithe	0	0	0	0	0
Benthivores	Plaice	0	100	100	100	100
	Sole	0	100	100	100	100
Pelagic piscivores	Mackerel	0	0	0	0	0
Benthic carnivore prey						
Planktivores	Herring	0	0	0	0	0
	Sandeel	0	0	0	0	0
	Norway pout	0	4	0	0	4
Demersal piscivores	Cod	0	49	57	42	18
	Haddock	0	2	7	8	5
	Whiting	0	55	21	0	0
	Saithe	0	0	0	0	0
Benthivores	Plaice	0	0	0	0	0
	Sole	0	0	0	0	0
Pelagic piscivores	Mackerel	0	9	0	0	0
Fish prey						
Planktivores	Herring	0	0	0	3	3
	Sandeel	0	0	0	0	0
	Norway pout	0	0	0	0	0
Demersal piscivores	Cod	0	29	24	27	46

Continued

Table 7. Continued

Guild	Assessed species	Age interval from hatching				
		0 3 months	3 6 months	6 9 months	9 12 months	12 15 months
Benthivores	Haddock	0	40	42	10	8
	Whiting	0	8	42	44	52
	Saithe	0	72	43	47	73
	Plaice	0	0	0	0	0
	Sole	0	0	0	0	0
Pelagic piscivores	Mackerel	0	31	15	12	82

predation is during the first 3 months of life. Hence, it is concluded that the simulation results are broadly consistent with the very limited observational data available.

It seems clear that the simplistic representation of fish prerecruit food consumption in the foodweb analysis of Heath (2005)

Table 8. Decadal average estimates of food consumption ($\text{gC m}^{-2} \text{year}^{-1}$) from Heath (2005), and updated values resulting from the simulations presented here.

Food consumption	Parameter	1973 1979	1980 1989	1990 1999
According to Heath (2005)	Total food by post recruit fish	17.54	14.20	12.59
	Consisting of			
	Mesozooplankton	7.75	6.41	6.54
	Carnivorous zooplankton	3.56	2.81	2.39
	Filter and deposit feeding benthos	2.15	1.98	1.50
	Benthic carnivores	0.70	0.59	0.44
	Other fish	3.38	2.41	1.73
	Total food by prerecruit fish	1.95	1.62	1.34
	Mesozooplankton by carnivorous zooplankton	13.83	10.38	9.85
	Total consumption of mesozooplankton by fish and carnivorous plankton	22.26	17.33	16.90
Revised, by prerecruit fish	Total food by prerecruit fish	4.87	4.14	3.56
	Consisting of			
	Mesozooplankton	3.26	2.77	2.52
	Carnivorous zooplankton	1.08	0.92	0.73
	Filter and deposit feeding benthos	0.16	0.14	0.08
	Benthic carnivores	0.11	0.09	0.07
	Other fish	0.26	0.22	0.17
	Total consumption of mesozooplankton by fish pre and post recruits and carnivorous plankton	24.84	19.56	18.91

led to approximately a $2 \text{ gC m}^{-2} \text{year}^{-1}$ (10%) lower estimate of the annual consumption of omnivorous mesozooplankton in the North Sea. Implementing the revised analysis brings the annual consumption by fish and carnivorous zooplankton up to between 19 and $25 \text{ gC m}^{-2} \text{year}^{-1}$, still within the range that might be anticipated from the rather uncertain knowledge of North Sea wide new primary production. Total primary production estimates for the North Sea are reasonably well established but, as stated earlier, the proportion that is nitrate based, and hence does not include within year recycling, is less well known.

Heath (2005) attempted to estimate mesozooplankton production from monthly averaged carbon biomass derived from scaled Continuous Plankton Recorder (CPR) data, using temperature relationships based on those of Huntley and Lopez (1992). The results suggested that average omnivorous zooplankton production was $\sim 35 \text{ gC m}^{-2} \text{year}^{-1}$, somewhat higher than earlier estimates (e.g. $44 \text{ g dry weight m}^{-2} \text{year}^{-1}$, equivalent to $\sim 24 \text{ gC m}^{-2} \text{year}^{-1}$; Steele, 1974), and higher than implied by the new primary production estimates. Also, the value of $35 \text{ gC m}^{-2} \text{year}^{-1}$ exceeded the combined predation requirements of the fish foodweb and carnivorous zooplankton by a factor of ~ 1.6 over most of the time period studied. The revision of consumption estimates by fish presented here does not account for this apparent surplus of production over consumption. Therefore, accepting that there is no major predation loading remaining unaccounted for (i.e. that the consumption by gelatinous predators is relatively small), the weight of evidence points towards an overestimation of zooplankton production using the CPR and Huntley and Lopez (1992) equations.

Heath (2005) argued that the apparent excess of zooplankton production estimated from CPR data might be due to omnivory, such that the values include an unquantified component of recycled production within the guild attributable to carnivory. For this argument to be consistent with the new primary production estimates, earlier estimates of herbivore production around 40% of the CPR based omnivore gross production would have to be recycled within the guild by carnivory. However, the methodology used by Heath (2005) for estimating zooplankton production also involved some potentially controversial assumptions in areas lacking any generally accepted methodology. 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; Pitois and Fox, 2006), 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). Therefore, 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). In particular, Hirst and Lampitt (1998) compiled a more comprehensive dataset on copepod growth and egg production than was available to Huntley and Lopez (1992), and produced new growth rate relationships depending on spawning type, body size, and temperature. For the smaller copepods ($\sim 4 \mu\text{gC individual}^{-1}$), these equations yield similar estimates of production to those of Huntley and Lopez (1992) at $< 6^\circ\text{C}$, but lower estimates, by a factor of 2, at $> 12^\circ\text{C}$. Overall, it seems clear that a fresh look at estimating North Sea regional zooplankton production is required.

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