

Fishing effects on energy use by North Sea fishes

Simon Jennings^{a,*}, Ralf van Hal^b, Jan G. Hiddink^c, Tracy A.D. Maxwell^a

^a Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, NR33 0HT, United Kingdom

^b Wageningen IMARES, Institute for Marine Resources & Ecosystem Studies, P.O. Box 68, 1970 AB IJmuiden, The Netherlands

^c School of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Anglesey, LL59 5AB, United Kingdom

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Abstract

Fishing affects patterns of energy use in fish populations, as demonstrated by changes in population energy consumption and the size and age when energy demands are greatest. We compare theoretical predictions and observed patterns of energy use (expressed as the primary production required to support fish production) by North Sea fish, based on simple and widely applicable theory that links life history parameters, fishing mortality (F), trophic transfer efficiency and relationships between size and trophic level (as determined using nitrogen stable isotope analysis). For the demersal species that dominate total biomass, relationships between size and trophic level were quite consistent among years. There were large decreases in relative energy requirements of all exploited demersal populations except plaice *Pleuronectes platessa* during the last 3 to 4 decades. Relative energy requirements of plaice were more stable because smaller plaice, which now dominate the exploited population, feed at higher trophic levels than larger plaice. The sizes and ages when population energy demands were greatest fell with increasing fishing mortality and differences between the predicted ($F=0$) and observed ages at maximum energy demand were greater in larger species. Currently, the energy demands of most species peak early in life (1–3 years) and largely reflect patterns of recruitment, leading to a homogenisation of the trophodynamics of the fish community. The fate of energy that is no longer used by commercially exploited species is not clear, partly because of the infrequent and untargeted monitoring of species that are more resilient to fishing. However, we conducted a preliminary assessment of the energy demands of solenette *Buglossidium luteum*, a very abundant small flatfish in the central North Sea that has increased in abundance in recent years. The solenette's high abundance and resilience to fishing, suggests that it now requires 35% of primary production in part of the central North Sea, energy that may have supported larger species in a less heavily fished ecosystem.

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1. Introduction

Studies of fishing and climate effects on North Sea fish communities have proliferated in recent years, largely stimulated by an ICES group working on the ecosystem

effects of fishing activities (Gislason, 1994) and work presented at an ICES symposium on changes in the North Sea ecosystem and their causes (Daan and Richardson, 1996). Fishing is the main cause of observed changes in the size–structure of the North Sea fish community, and the role of fishing in depleting larger individuals and species (Rice and Gislason, 1996; Rijnsdorp et al., 1996), and in promoting the proliferation of smaller ones (Hessen

* Corresponding author.

E-mail address: Simon.Jennings@cefasc.co.uk (S. Jennings).

and Daan, 1996; Daan et al., 2005), has been widely described and modelled (e.g. Greenstreet and Hall, 1996; Greenstreet et al., 1998; Pope et al., 2006).

The trophic roles of, and interactions among, some fish species have been studied during the development and evaluation of multispecies virtual population analysis (Daan, 1987; Rice et al., 1991; Pope and Macer, 1996), but the trophic roles of other abundant species are not well known (Daan et al., 1990; Sparholt, 1990; Greenstreet et al., 1997). Yang (1982) estimated the trophic levels of North Sea fish from diet data and described trends in the trophic level of landings over time, but recognised the limitations of available data for many species.

The energy requirements of a population depend on the energy requirements and abundance of component individuals. Energy requirements of individuals change with body size owing to the changing allocation to metabolism, growth and reproduction with size (e.g. Ware, 1978; Clarke and Johnston, 1999). The total energy required to support any individual or population can be expressed directly in J, but is often more usefully expressed in comparative analyses as the primary production required; which takes account of the number of times that energy is transferred in the food chain (trophic level) and the efficiency of energy transfer (Cushing, 1975; Jones, 1982).

Fishing induced changes in size structure and abundance of a population will be linked to changes in trophic structure and energy use, because larger individuals tend to feed at higher trophic levels and relative energy demands fall with body size (e.g. Ware, 1978). Changes in the size and trophic level at which fish in a population have the greatest (total) energy demand thus reflect fishing effects and differences among species in the dynamics of energy use.

Here, we consider the interplay between changes in abundance, size, species composition, trophic level and energy use in North Sea fish communities, based on estimates of trophic level obtained from nitrogen stable isotope analysis (Preston and Owens, 1983). Our methods are relatively simple and demand less data than are needed to construct full energy budgets for well studied species (e.g. Daan, 1973). However, by identifying relationships between body size and trophic level and by developing simple metrics for assessing relative fishing effects on population energy use, the methods can be applied both to commercially exploited species and to other species in the North Sea fish community. The methods demonstrate that there have been relatively greater reductions in energy use by larger species and the trophic homogenisation of the North Sea fish community.

2. Methods

A simple theoretical analysis of relationships between trophic level, life history parameters and energy demands was used to investigate patterns of energy use as a function of fishing mortality and life history. Trophic level was estimated using nitrogen stable isotope analysis and information on life histories and energy demands was obtained from the literature. We considered trends in the trophic level and energy use of assessed demersal stocks and the most abundant species in the fish community. We then estimated energy use and food consumption by the solenette *Buglossidium luteum* in one area of the North Sea and compared this with benthic production in the same area. Trends in solenette abundance since 1969 were described using trawl survey data.

2.1. Energy requirements

We assumed that the energy (E) required to support metabolism, growth and reproduction scaled within species $E=cW^{0.75}$, where W is body mass and c is a constant. In reality, the $W^{0.75}$ scaling is an approximation and the value of c may differ between fish species (e.g. Ware, 1978; Clarke and Johnston, 1999; van der Meer, 2006), but we adopted our approach because we wanted to develop a generic approach that could be widely applied without having to compile complete energy budgets for each species. Assuming $E=cW^{0.75}$, then the primary production required (P_r) to meet the energy requirements of an individual at a given weight is

$$P_r = cW^{0.75} / \varepsilon^{(a+b \log_{10} W) - 1}$$

where ε is transfer efficiency and a and b are fitted parameters of the linear relationship $\lambda = a + b \log_{10} W$ where λ is trophic level (Jennings et al., 2007). This assumes that transfer efficiency in the food chains leading to individuals of all sizes and ages is the same. P_r was calculated for each individual of each species and summed across individuals in size and/or age classes to calculate total energy requirements. Differences in c among species were not known and so energy use was expressed in relative terms.

For an unfished population at equilibrium, the mean weight of the fish when the greatest quantity of energy (measured as proportion of primary production required) is needed to support a cohort (W_{mc}) is given by

$$W_{mc} = W_{\infty} \left[1 / \left(1 + \frac{M}{3k[0.75 - b(\log_e \varepsilon)(\log_{10} e)]} \right) \right]^3$$

(Jennings et al., 2007), where M is natural mortality, and k and W_∞ are the Brody growth coefficient and asymptotic weight in the von Bertalanffy Growth Equation. The advantage of expressing the relationships in this form is that both equations can be solved using an M/k ratio, which is relatively constant among species (Beverton, 1992), when M and k are not known independently. This was the case for some of the non-assessed species used in this study and M/k was assumed to be 1.5 (Beverton, 1992). The corresponding age when a cohort has the maximum energy requirements (t_{me} ; Jennings et al., 2007) is given by

$$t_{\text{me}} = t_0 + \log_e \left[1 + \frac{9}{4} \left(\frac{k}{M} \right) - 3b(\log_e \epsilon)(\log_{10} e) \left(\frac{k}{M} \right) \right]^{1/k}$$

where t_0 is the theoretical age at size=0 in the von Bertalanffy Growth Equation. Fishing effects on W_{me} and t_{me} were simulated following Jennings et al. (2007) by substituting total mortality $Z (=M+F)$ for M .

Estimates of the absolute energy requirements of solenette were based on relationships between size and oxygen consumption reported by De Morais (1985). At 11 °C, oxygen consumption (R) in ml animal⁻¹ h⁻¹ was related to weight as $\log_{10} R = 0.752 \log_{10} W - 1.33$. We assumed active metabolic rate (AMR) would be 2.5× standard metabolic rate (SMR) following Kerr (1982), but also conducted sensitivity analyses to assess the effects of this assumption. Oxygen use was converted to energy use assuming protein oxidation by a urea producing animal required 13.60 J mg⁻¹ O₂ (Elliott and Davidson, 1975; = 0.425 J mmol⁻¹ O₂). Conversions assumed were that 1 mmol O₂ weighs 0.032 g and occupies 22.42 ml. Energy requirements in J were converted to wet weight assuming that the energy content for invertebrates was 2 kJ g⁻¹ wet weight (Dauvin and Joncourt, 1989).

2.2. Trophic level

Relationships between body size and trophic level were required to estimate the trophic levels of assessed species, species caught during the North Sea English Bottom Trawl Survey and solenette. To estimate trophic level, fishes were caught at 21 stations in fixed locations in the northern North Sea, in an area from 57.5° N–61.5° N and 1° W–4° E, with a Grande Ouverture Verticale (GOV) bottom fished otter trawl net fitted with a 20 mm cod end liner and towed for 30 min at 4 knots during the North Sea English Bottom Trawl Survey. The area was sampled in late August and early September from 2002–2005. For the 12 demersal species shown to have the highest rank biomass in trawl survey data collected in this

area from 1992–2001, up to 4 individuals were collected from each of 10–13 length classes spanning the total range of total body lengths caught. Length class intervals ranged from 1 to 7 cm, depending on the range of total body lengths present. Five cm³ of white muscle tissue was dissected from the dorsal musculature of each individual and immediately frozen to –20°C and stored frozen until processing, a procedure which has no effect on the nitrogen stable isotope composition of the tissue (Sweeting et al., 2004). The tissue was subsequently freeze dried to constant mass, and ground with pestle and mortar to fine homogeneous powder. The nitrogen stable isotopic composition of the powdered samples was determined using a Europa Scientific 20–20 IRMS with a Europa Scientific Roboprep-CN preparation module at Iso-Analytical Ltd (Sandbach, UK). Two reference samples were analysed after every four to six samples of fish tissue. The ¹⁵N composition of the tissue samples was expressed in conventional delta notation ($\delta^{15}\text{N}$), relative to the abundance of ¹⁵N in atmospheric N₂. Experimental precision in all years was <0.2‰ (standard deviation of $\delta^{15}\text{N}$ for replicates of reference material). Methods are described in greater detail by Jennings et al. (2007).

To calculate trophic level (λ), and to achieve internal consistency when making year to year comparisons among individuals and species, all values of $\delta^{15}\text{N}$ were rebased to a common standard. This was the predicted $\delta^{15}\text{N}$ of an individual *Clupea harengus* (herring) of mass W_h , here taken as 200 g, and λ was calculated as

$$\lambda = \frac{\delta^{15}\text{N} - (a - b \log_{10} W_h)}{\Delta \delta^{15}\text{N}} + 4$$

where $\Delta \delta^{15}\text{N}$ is the assumed trophic fractionation of $\delta^{15}\text{N}$ (3.4‰), a and b are the fitted slope and intercept of the relationship between $\delta^{15}\text{N}$ and $\log_{10} W$ and 4 is the assumed trophic level (λ) of the herring. For the fish sampled for isotope analysis, the relationship between λ and W was described for each species in each year. The 3.4‰ value for $\Delta \delta^{15}\text{N}$ is a widely adopted mean value (Post, 2002), but there are likely to be variations in $\Delta \delta^{15}\text{N}$ due to individual and population specific differences (Sweeting et al., 2007).

For the analysis of trends in trophic level and energy use by assessed stocks, data from the four year trophic level study were pooled to calculate the body size vs trophic level relationships for each stock. For the analysis of trophic level and energy use in the northern North Sea, annual body size vs trophic level relationships were applied to species-size-abundance data for each year.

Table 1
Trophic level vs body mass relationships and life history parameters for North Sea fish species

Species Common name	Trophic level–body mass relationships					Life history parameters		
	Year	<i>n</i>	<i>a</i> ±95% CI	<i>b</i> ±95% CI	<i>p</i>	<i>W</i> _∞	<i>k</i>	<i>β</i>
<i>Trisopterus esmarki</i> Norway pout	2002	35	4.31±0.38	−0.16±0.27	0.235	68	0.52	3.12
	2003	36	4.12±0.30	0.02±0.20	0.811			
	2004	35	4.65±0.79	−0.39±0.51	0.130			
	2005	39	3.85±0.47	0.12±0.32	0.465			
	Pooled	145	4.17±0.22	−0.06±0.15	0.424			
<i>Hippoglossoides platessoides</i> Long rough dab	2002	30	3.72±0.59	0.35±0.38	0.069	133	0.34	3.20
	2003	28	3.67±0.52	0.27±0.34	0.109			
	2004	24	3.07±0.40	0.75±0.28	0.000			
	2005	25	3.98±0.69	0.21±0.46	0.367			
	Pooled	107	3.61±0.28	0.39±0.18	0.000			
<i>Limanda limanda</i> Dab	2002	34	2.97±0.30	0.71±0.17	0.000	211	0.26	3.11
	2003	31	3.42±0.33	0.55±0.19	0.000			
	2004	29	3.47±0.59	0.52±0.33	0.003			
	2005	28	3.10±0.43	0.70±0.24	0.000			
	Pooled	122	3.24±0.21	0.62±0.12	0.000			
<i>Eutrigla gurnardus</i> Grey gurnard	2002	32	5.29±0.89	−0.34±0.39	0.088	886	0.16	3.10
	2003	31	5.23±0.67	−0.28±0.31	0.074			
	2004	30	5.04±0.57	−0.22±0.27	0.095			
	2005	28	5.34±0.64	−0.31±0.29	0.037			
	Pooled	121	5.22±0.33	−0.29±0.15	0.000			
<i>Merlangius merlangus</i> Whiting	2002	43	3.88±0.26	0.44±0.12	0.000	594	0.32	3.12
	2003	35	4.11±0.29	0.35±0.13	0.000			
	2004	41	3.88±0.19	0.41±0.09	0.000			
	2005	38	4.18±0.21	0.34±0.10	0.000			
	Pooled	157	4.00±0.12	0.39±0.05	0.000			
<i>Microstomus kitt</i> Lemon sole	2002	30	2.40±1.07	0.89±0.47	0.001	551	0.42	2.76
	2003	25	2.96±0.83	0.63±0.38	0.002			
	2004	25	2.72±0.84	0.80±0.37	0.000			
	2005	27	3.06±0.77	0.67±0.34	0.000			
	Pooled	107	2.73±0.43	0.77±0.19	0.000			
<i>Pleuronectes platessa</i> Plaice	2002	13	4.59±2.07	0.06±0.88	0.889	1465	0.11	2.79
	2003	12	4.03±2.07	0.21±0.82	0.549			
	2004	14	4.72±1.41	−0.02±0.55	0.949			
	2005	18	3.94±1.52	0.29±0.61	0.327			
	Pooled	58	5.17±3.53	−0.27±1.41	0.708			
<i>Amblyraja radiata</i> Starry ray	2002	33	3.46±0.35	0.31±0.16	0.000	2348	0.23	2.90
	2003	39	3.62±0.34	0.27±0.16	0.001			
	2004	28	3.29±0.45	0.39±0.19	0.000			
	2005	21	3.43±0.78	0.39±0.33	0.025			
	Pooled	121	3.49±0.19	0.32±0.09	0.000			
<i>Melanogrammus aeglefinus</i> Haddock	2002	35	4.01±0.43	0.13±0.19	0.172	3075	0.19	3.13
	2003	35	3.99±0.33	0.25±0.14	0.001			
	2004	32	4.05±0.41	0.08±0.18	0.346			
	2005	25	4.06±0.56	0.18±0.24	0.125			
	Pooled	127	4.00±0.21	0.17±0.09	0.000			
<i>Pollachius virens</i> Saithe	2002	38	3.46±0.52	0.38±0.15	0.000	8271	0.22	2.96
	2003	23	4.00±0.79	0.23±0.25	0.068			
	2004	24	2.72±0.69	0.56±0.21	0.000			
	2005	30	3.91±0.39	0.23±0.12	0.000			
	Pooled	114	3.67±0.28	0.31±0.09	0.000			
<i>Lophius piscatorius</i> Anglerfish	2002	18	2.97±0.91	0.57±0.28	0.000	18045	0.18	3.00
	2003	27	3.21±0.84	0.56±0.28	0.000			
	2004	26	3.72±0.65	0.33±0.20	0.002			
	2005	21	3.18±0.59	0.56±0.20	0.000			
	Pooled	92	3.38±0.36	0.47±0.12	0.000			

(continued on next page)

Table 1 (continued)

Species Common name	Trophic level–body mass relationships					Life history parameters		
	Year	<i>n</i>	<i>a</i> ±95% CI	<i>b</i> ±95% CI	<i>p</i>	<i>W</i> _∞	<i>k</i>	<i>β</i>
<i>Gadus morhua</i>	2002	35	4.48±0.41	0.16±0.13	0.025	19380	0.23	3.10
Cod	2003	32	4.23±0.41	0.25±0.13	0.000			
	2004	32	4.58±0.27	0.14±0.09	0.002			
	2005	22	4.20±0.29	0.25±0.10	0.000			
	Pooled	121	4.39±0.17	0.19±0.06	0.000			

a and *b* are parameters of the relationship $\lambda = a + b \log_{10} W$ where λ is trophic level. *P* is the probability that the slope of the relationship differs significantly from zero. *W*_∞ and *k* are the asymptotic weight and Brody growth coefficient of the Von Bertalanffy Growth Equation and *β* is the exponent in the relationship $W = \alpha L^\beta$.

Solenette were sampled for stable isotope analysis in the southern North Sea on six occasions from 1 April 2005 to 29 April 2006. Several samples were collected to assess whether there were marked seasonal variations in $\delta^{15}N$, as might be expected in a very small species with relatively fast turnover time.

For solenette, trophic level was calculated as

$$\lambda = \frac{\delta^{15}N_s - \delta^{15}N_b}{\Delta\delta^{15}N} + 2.5$$

where $\delta^{15}N_s$ is the $\delta^{15}N$ of the sampled individual, $\delta^{15}N_b$ is the $\delta^{15}N$ of a base material of known trophic level, here taken to be bivalves at trophic level 2.5, and $\Delta\delta^{15}N$ is the assumed trophic fractionation of $\delta^{15}N$ (3.4‰). Bivalves were sampled on the 4 Oct 2005, 17 Feb 2006 and 29 Apr 2006 using the 2 m beam trawl described below.

2.3. Fish populations

Abundance, size and age data for Norway pout, plaice, whiting, haddock, saithe and cod were obtained from ICES stock assessments. Life history parameters for these species were also obtained from the assessment reports and existing literature (sources listed in Jennings et al., 1999a,b, 2007). Length–weight conversions were based on Coull et al. (1989) and unpublished data.

For the 12 demersal species sampled in the northern North Sea, size and abundance data were collected during the North Sea English Bottom Trawl Survey. The data used were for the same set of stations where fish samples had been collected for stable isotope analysis. The 12 selected species included assessed species. All fishes in the catch were sorted to species and weighed. All individuals in species groups or subsamples of species groups were then measured to produce raised

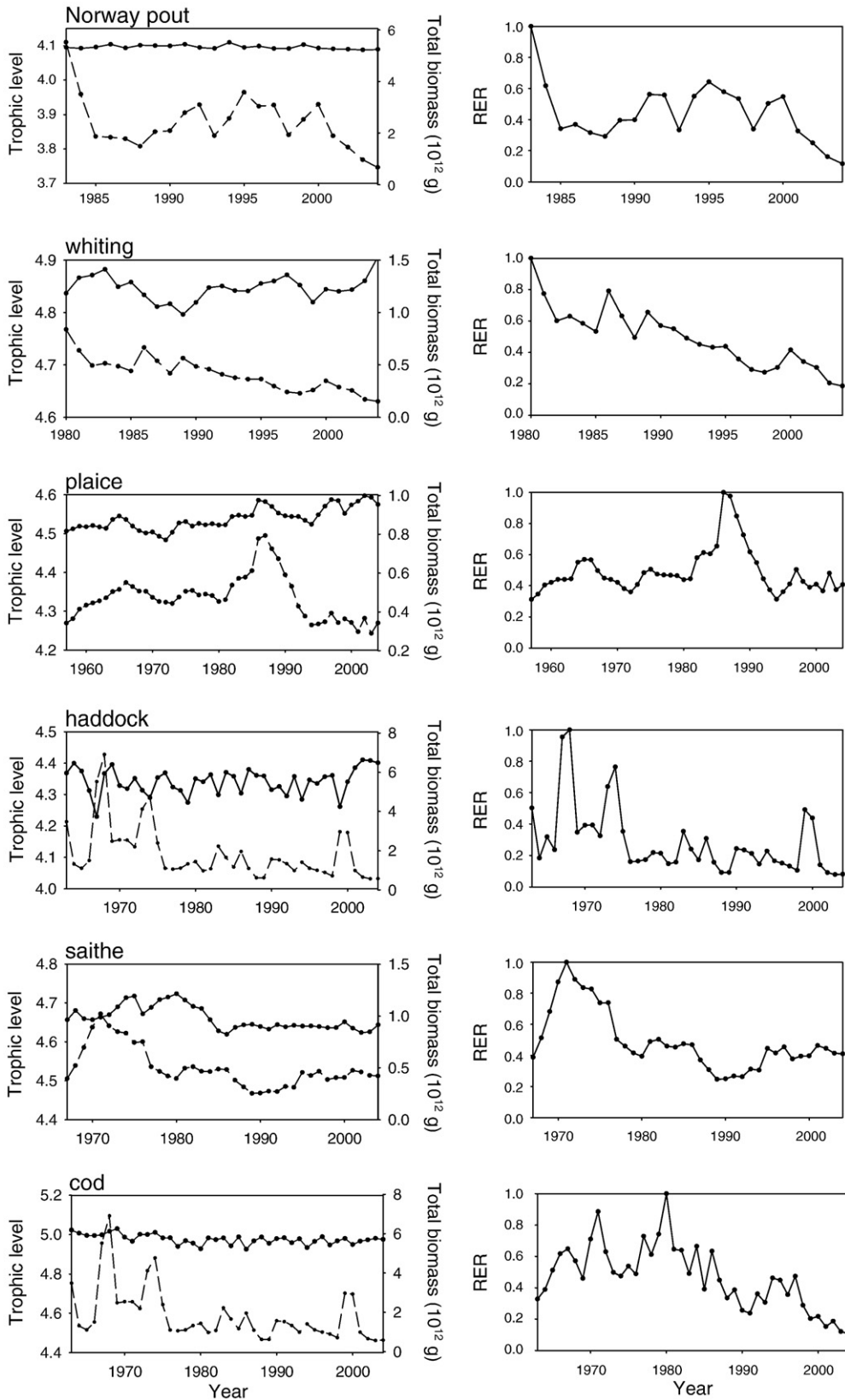
length–frequency distributions for all species. Abundance estimates were corrected for catchability by species, using the correction factors published by Sparholt (1990). Although these factors were calculated for a Granton trawl rather than a GOV trawl and apply at the population level, they remain the best available indices of catchability for most species caught by survey trawls in the North Sea.

Solenette abundance was estimated in a survey area of 7391 km² from 53°00' N to 54°00' N and 02° E–03° E using a 2-m beam trawl with 2 mm cod end of the design described by Jennings et al. (1999b). The survey area was subdivided into 36 boxes at intervals of 10' latitude and 10' longitude, with areas of 197.7 to 210.5 km². In each box, we completed 2 replicate tows of 5 min with a 2-m beam trawl. Distance was measured with DGPS from the time of arrival of the net on the seabed until it left the seabed.

All solenette were sorted from the catch, counted and weighed individually to the nearest 0.1 g on heave compensated balances. Catch rates were corrected for gear efficiency following Reiss et al. (2006) who reported a catch efficiency of 28% for solenette.

Trends in solenette abundance were described using an abundance index based on the Beam Trawl Survey (BTS) and the Sole Net Survey (SNS). These beam trawl surveys use 8 m and 6 m beams respectively, with 40 mm stretched cod end mesh. Such meshes are too small to effectively retain anything but the largest solenette and, as such, can only provide an index of relative abundance. The BTS has been conducted annually in autumn from 1985. Initially the survey was carried out only in the south-eastern North Sea, but from 1996 onwards it was expanded to cover the western, central and part of the northern North Sea. In the analyses, the only data used were for the areas east of 4° E and south of 55.5° N. The SNS has been conducted annually in autumn from 1969

Fig. 1. Interannual changes in the mean trophic level, total biomass (broken line) and relative energy requirements (RER, as a proportion of maximum value in the time series) for six North Sea fish species.



to the present. Further details of the surveys are provided in Van Beek (1997) and IMARES (2007).

Changes in solenette abundance as recorded on the surveys can reflect changes in abundance and distribution. Survey haul locations have changed from year to year and so the following model was used to account for year, survey, vessel and depth effects

$$\log(N) = Y + S + V + D + D^2$$

where N is numbers, Y is year, S is survey, V is vessel and D is depth. Year, survey and vessel are used as nominal variables. The year effect in the model was taken as an index of relative solenette abundance. BTS and SNS data were selected in preference to other series since they cover the largest areas over the longest periods with the same gear.

2.4. Benthic and primary production

Benthic and primary production in the solenette survey area of 53°00' N to 54°00' N and 02° E–03° E were estimated with a size-based benthic production model (Duplisea et al., 2002; Hiddink et al., 2006) and the European Regional Seas Ecosystem model (Allen et al., 2001).

The size-based model was used to predict the production of small soft bodied animals of wet weight 5–225 mg that were potential prey of solenette. The model accounts for the effects of environment and trawling disturbance on benthic production. Details of the development, testing and applications of the model are given in Duplisea et al. (2002) and Hiddink et al. (2006). In summary, the model contained 32 state variables, in two faunal groups (soft and hard bodied macrofauna). Growth of the population biomass in each body mass–organism type compartment was modelled by modifying Lotka–Volterra competition equations to give the population biomass flux for a compartment. The interaction between habitat type and trawling effects was modelled by including relationships between growth, mortality and the environment in the model. Thus sediment type affected trawling mortality, sediment erosion rates affected natural mortality, the effect of bed shear stress modified population growth rate and the chlorophyll a content of the sediment affected carrying capacity. The model was used to predict the production of soft bodied benthic fauna in the box where the solenette survey was conducted, based

on environment and fishing effort data from sources described in Hiddink et al. (2006). Conversions between wet weight (WW), dry weight (DW) and ash free dry weight (AFDW) for invertebrates assumed $DW = 0.198 \times WW$ and $AFDW = DW \times 0.803$.

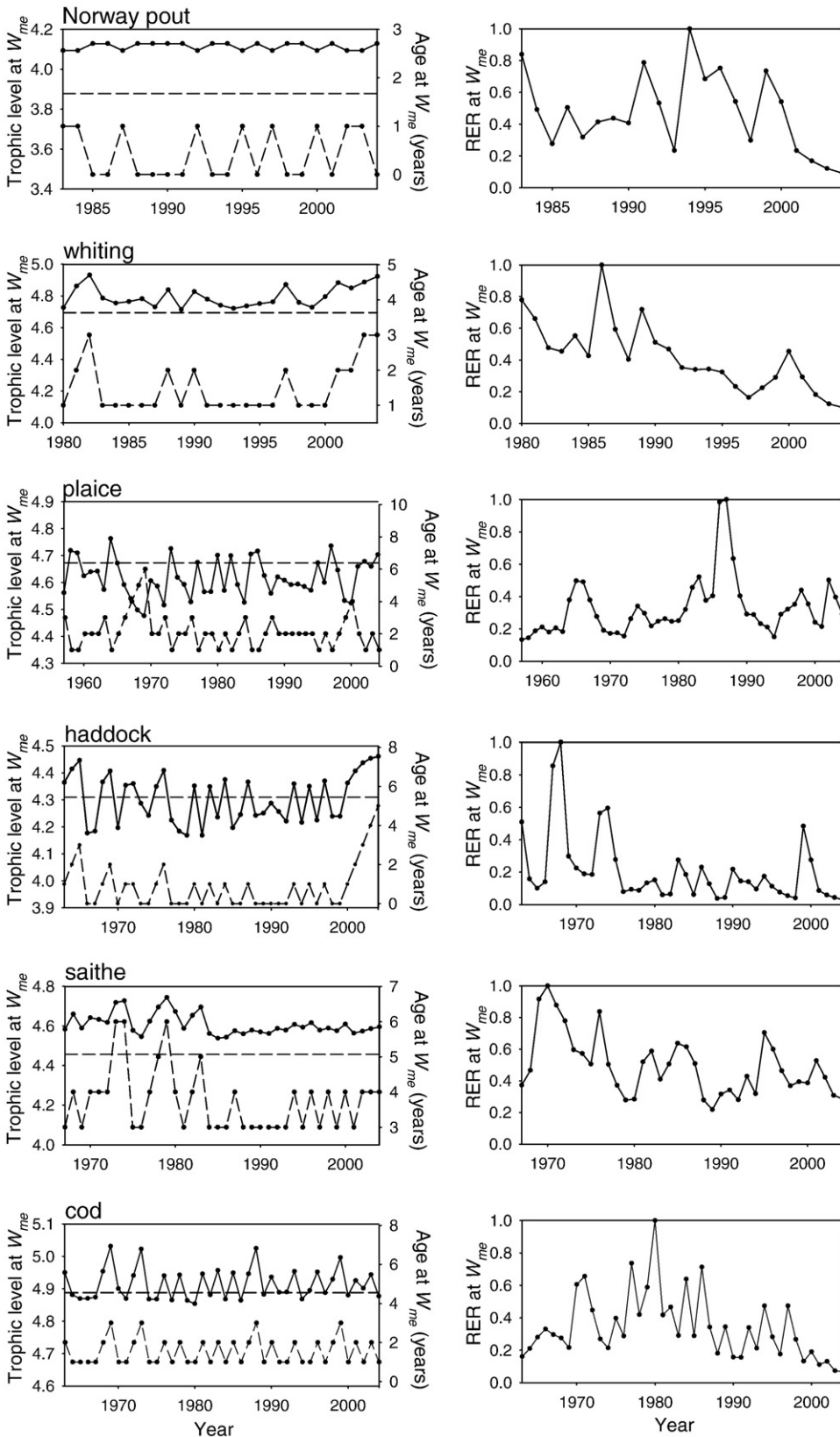
3. Results

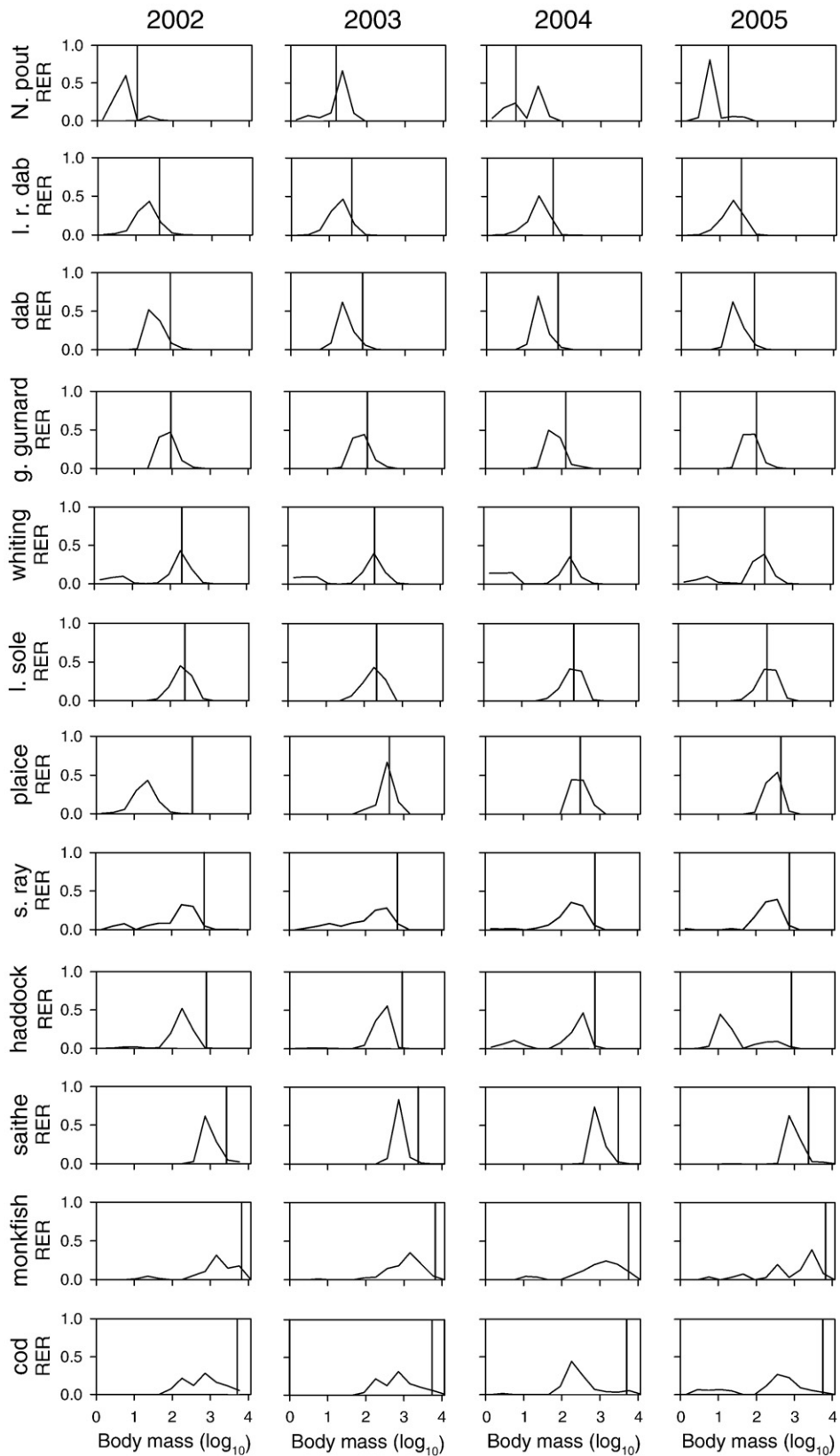
The trophic levels and changes in trophic level with size of the demersal species sampled from 2002–2005 were relatively consistent from year to year (Table 1). In energy use calculations for the stocks assessed by ICES, pooled trophic level vs size estimates were applied to all years for which assessment data were available. These analyses showed that the mean trophic level of Norway pout, whiting, haddock and cod showed no clear trend with time while the trophic level of plaice increased and that of saithe fell (Fig. 1). Total biomass of all stocks except plaice tended to decline in the same period. Relative energy requirements (RER) of all stocks except plaice tended to decrease over time (Fig. 1). Neither trophic levels at W_{me} nor t_{me} exhibited clear trends over time, except for haddock when W_{me} rose markedly post 2000 (Fig. 2). For all species except saithe, observed t_{me} was lower than predicted t_{me} (with no fishing) in all years of the time series. For saithe observed t_{me} exceeded predicted t_{me} in three years (Fig. 2). For all species except plaice, RER tended to decline through time (Fig. 2).

The RER at size of northern North Sea fishes sampled on the North Sea English Bottom Trawl Survey showed that RER usually peaked at a smaller size than would be predicted with no fishing. Patterns of RER varied within species and among years, but sizes at peak RER tended to be quite consistent within species (Fig. 3). Observed W_{me} was smaller than predicted W_{me} for almost all species in all years, and when differences between observed and predicted W_{me} were related to body weight, the differences became increasingly negative with body weight (Fig. 4). The slopes of these relationships were significantly different from zero in 2003 and 2004 ($p = 0.008$, $p = 0.006$) and near significant in 2002 and 2005 ($p = 0.150$, $p = 0.089$).

Simulations of the effects of fishing mortality on W_{me} showed how increasing fishing mortality leads to fish of different species exhibiting increasingly similar W_{me} (Fig. 5). For all species except grey gurnard and plaice, the trophic level at W_{me} decreases with F , reflecting the lower trophic levels associated with lower body size (Fig. 6).

Fig. 2. Interannual changes in trophic level at the weight of maximum energy requirements (W_{me}), age at W_{me} (broken line) and the relative energy requirements at W_{me} (RER, expressed as a proportion of the maximum value in the time series) for six North Sea fish species. The horizontal broken lines on the left panels indicate predicted age at W_{me} with no fishing.





Depths sampled in the survey box ranged from 16.7 to 45.1 m. Mean depth was 33.7 m. The biomass of solenette recorded in the survey box was $1.04 \pm 0.097 \text{ g m}^{-2} \pm 1\text{S.D.}$ The most abundant other species were dab *Limanda limanda*, common dragonet *Callionymus lyra* and scaldfish *Arnoglossus laterna* with abundances of $0.25 \pm 0.034 \text{ g m}^{-2}$, $0.20 \pm 0.070 \text{ g m}^{-2}$, and $0.11 \pm 0.012 \text{ g m}^{-2}$ respectively. Solenette food consumption was estimated to be $6.29 \pm 0.600 \text{ g wet weight m}^{-2} \text{ y}^{-1}$. Mean benthic production of small soft bodied animals of wet weight 5–225 mg was estimated to be $23.20 \text{ g wet weight m}^{-2} \text{ y}^{-1}$. Modelled primary production was $317 \text{ mg C m}^{-2} \text{ d}^{-1} = 1157 \text{ g wet weight m}^{-2} \text{ y}^{-1}$.

While there were small but significant seasonal differences in the trophic level of solenette at size (Table 2), the seasonal data were pooled to estimate the trophic level of solenette taken in the survey. The trophic level was calculated in relation to the mean $\delta^{15}\text{N}$ of bivalves of 7.90‰ ($n=55$). Based on the trophic levels assigned to solenette, an assumed transfer efficiency of 0.125 and the consumption rates calculated from oxygen demand, solenette consumed 27.1% of predicted available invertebrate production and $406.69 \text{ g m}^{-2} \text{ y}^{-1}$ or 35.1% of primary production in the box was required to support them.

Sensitivity analyses (Fig. 7) showed that reasonable assumptions about other values of transfer efficiency and the ratio AMR:SMR would all lead to the conclusion that the density of solenette in the survey area would lead to solenette using a significant (>20%) proportion of primary and benthic production. The relative abundance of solenette in the southern and central North Sea has increased since 1969 (Fig. 8).

4. Discussion

The relative energy requirements of the assessed demersal populations except plaice *Pleuronectes platessa* have fallen during the last 3 to 4 decades. Relative energy requirements of plaice were more stable because smaller plaice, which now dominate the exploited population, feed at higher trophic levels than larger plaice. This likely reflects the preference of smaller plaice for predatory polychaetes (e.g. Beukema, 1987) of higher trophic level rather than the low trophic level bivalves most frequently eaten by larger plaice and

possibly a shift in the diet of smaller and more abundant plaice away from bivalves and towards polychaetes as a consequence of the depletion of bivalves following beam trawling disturbance (Braber and De Groot, 1973; De Clerck and Buseyne, 1989; Rijnsdorp and Vingerhoed, 2001).

For the northern North Sea fish community, the sizes and ages when population energy demands were greatest fell with increasing fishing mortality and differences between the predicted ($F=0$) and observed sizes and ages at maximum energy demand were greater in larger species. This pattern was relatively consistent among years, even though the observed values of W_{me} and t_{me} depend on fluctuations in recruitment while the predicted values assume a population at equilibrium. The greater reduction in W_{me} and t_{me} of larger species with slower life histories is consistent with their lower capacity to sustain a given rate of mortality and their relatively greater depletion than related but smaller species (Jennings et al., 1999a,b). Currently, the energy demands of most North Sea species peak early in life (1–3 years), suggesting that the realised life histories and trophodynamics of the community are increasingly homogenous and fluctuations in recruitment will have a greater influence on fluctuations in energy demand than in a less heavily exploited community. The model outputs are broadly consistent with the observed patterns, with increases in F leading to greater similarities in values of W_{me} and t_{me} .

Large reductions in energy use by larger species and individuals, coupled with the observation that primary production in the North Sea has been stable or rising in recent years, suggests that a significant amount of energy once used by large individuals and species could be available to other animals. Daan et al. (2005), in the most comprehensive analysis of shifts in the size composition of fishes in the North Sea, suggested smaller species and individuals caught on the International Bottom Trawl Survey had proliferated, but this survey does not effectively sample many of the smallest species such as solenette, gobies *Gobio* spp. and scaldfish *Arnoglossus laterna*. Monitoring of these small species, that might be expected to be the most resilient to fishing, has been patchy, but they are likely to be important users of energy because they are relatively more abundant than larger fish and because smaller body size is associated with greater energy use per unit mass (Clarke

Fig. 3. Changes in the relative energy requirements (RER) of 12 North Sea fish species with body mass in the years 2002–2005. RER is expressed as a proportion of the total energy requirements of fish in all size classes. Vertical lines indicate predicted body mass at maximum RER when there is no fishing.

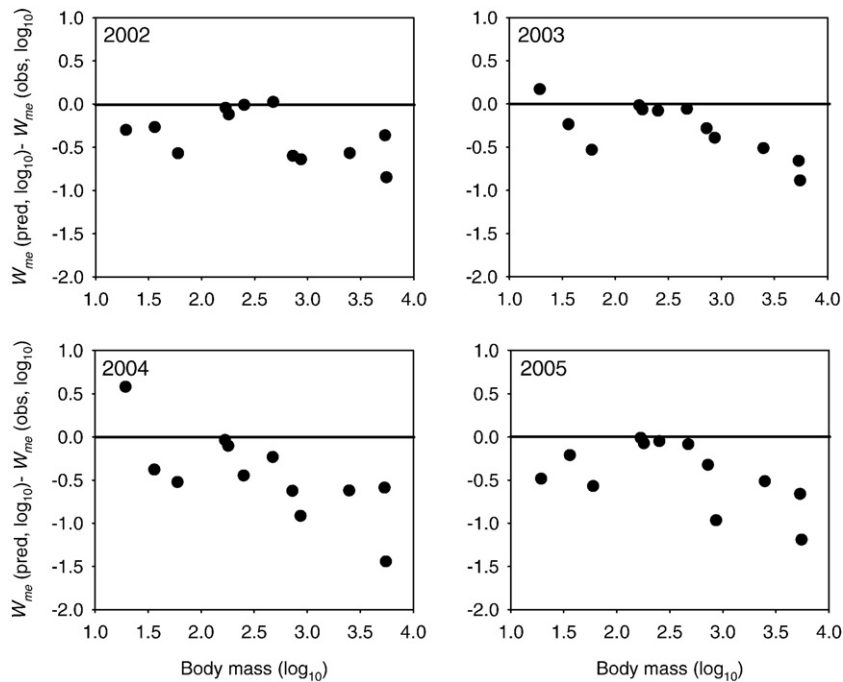


Fig. 4. Relationships between the predicted weight when energy requirements of a cohort minus the observed W_{me} ($W_{me, pred}$ and asymptotic body mass (W_{∞}) for 12 North Sea fish species for the years 2002–2005.

and Johnston, 1999). When measured as primary production required, their high rates of energy use are partly countered by the low trophic levels of smaller

fishes, but the stable isotope data suggest that solenette actually feed at relatively high trophic levels for their size (maximum body size rarely exceeds 12 cm TL; Balthus and van der Veer, 1995), consistent with a reported diet of crustaceans, polychaetes and molluscs (Amara et al., 2004).

It would be wrong to assume a direct connection between the reduced energy consumption of larger fishes and the proliferation of solenette, since the increase in solenette abundance could be influenced by many factors including climate change, reduced competition and depletion of predators. However, at least in the area of the North Sea that was studied, it is clear that this species is a very significant user of energy that may have supported, or been available to, other species in a less heavily fished ecosystem.

This was not a complete food web study and our conclusions are based on the integration of results from studies in different areas of the North Sea; but the study

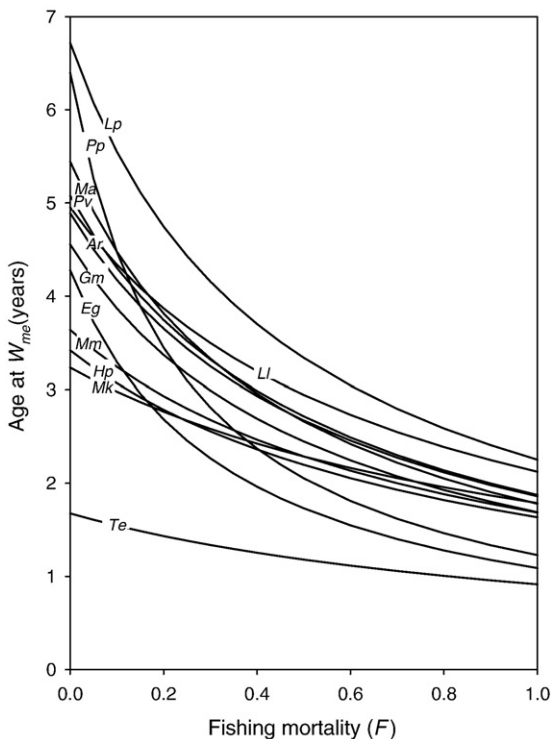


Fig. 5. Theoretical relationships between the age when energy requirements of a cohort are greatest (t_{me}) and fishing mortality (F) for 12 North Sea fish species. Species codes are Te: *Trisopterus esmarki*; Hp: *Hippoglossoides platessoides*; Ll: *Limanda limanda*; Eg: *Eutrigla gurnardus*; Mm: *Merlangius merlangus*; Mk: *Microstomus kitt*; Pp: *Pleuronectes platessa*; Ar: *Amblyraja radiata*; Ma: *Melanogrammus aeglefinus*; Pv: *Pollachius virens*; Lp: *Lophius piscatorius*; Gm: *Gadus morhua*. Common names are given in Table 1.

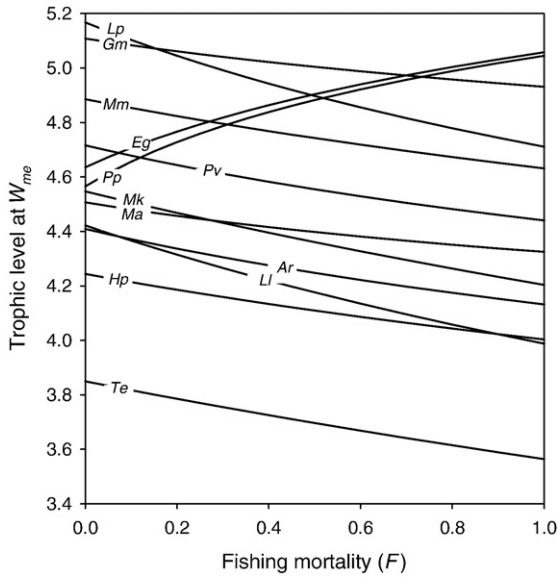


Fig. 6. Theoretical relationships between trophic level when energy requirements of a cohort are greatest (W_{me}) and fishing mortality (F) for 12 North Sea fish species. Species codes follow Fig. 5.

emphasises the potentially important role of small fish species and the relative lack of information on their ecology. The reported biomass of solenette is equivalent to approximately 20% of the total demersal benthivore biomass; estimated as 4.6 to 5.1 $g\ m^{-2}$ in the North Sea (Greenstreet et al., 1997), but energy demands would be disproportionately high given the small body size of this species. Even if total fish biomass is as high as the 10.3 to 21.6 $g\ m^{-2}$ estimated from bottom trawl survey by Sparholt (1990), solenette may contribute to 10% or more of total biomass in areas where they are abundant.

Solenette are localised to the southern and central North Sea and the depth range of the survey was largely within the range of depths where this species is known to be abundant (Balthus and van der Veer, 1995). The

Table 2

Trophic level vs body mass relationships for solenette sampled in the southern North Sea; a and b are parameters of the relationship $\lambda = a + b \log_{10} W$ where λ is trophic level and p is the probability that the slope of the relationship differs significantly from zero

Date	n	$a \pm 95\% \text{ CI}$	$b \pm 95\% \text{ CI}$	p
1 Apr 2005	16	0.27 ± 0.21	3.81 ± 0.19	0.013
25 May 2005	38	0.31 ± 0.10	3.81 ± 0.09	0.000
15 Jul 2005	20	0.36 ± 0.14	3.67 ± 0.13	0.000
4 Oct 2005	15	0.32 ± 0.19	3.71 ± 0.15	0.003
17 Feb 2006	14	0.17 ± 0.35	3.76 ± 0.24	0.323
29 Apr 2006	17	0.26 ± 0.23	3.71 ± 0.19	0.032
Pooled	120	0.34 ± 0.07	3.72 ± 0.06	0.000

limited distribution of solenette means that this very high estimate of local energy use would be much lower when expressed at the North Sea scale and we do not know if other small species are using large amounts of energy elsewhere. This is because small fishes of $\leq c.10$ cm TL are very poorly sampled on all existing surveys and surveys such as those that can be conducted with a 2 m beam trawl are required to assess long-term trends in abundance provided that the fish are available by the Netherlands in the survey area. A 2 m beam trawl survey was started “by the Netherlands” in the southern North Sea in 1999 and this will provide a valuable time series if continued.

We make a number of assumptions in our analyses. The adoption of a single exponent to describe the relationship between energy use and body mass within species ignores interspecific variation (e.g. Clarke and Johnston, 1999) and our approach will never provide the same level of information as detailed studies of feeding

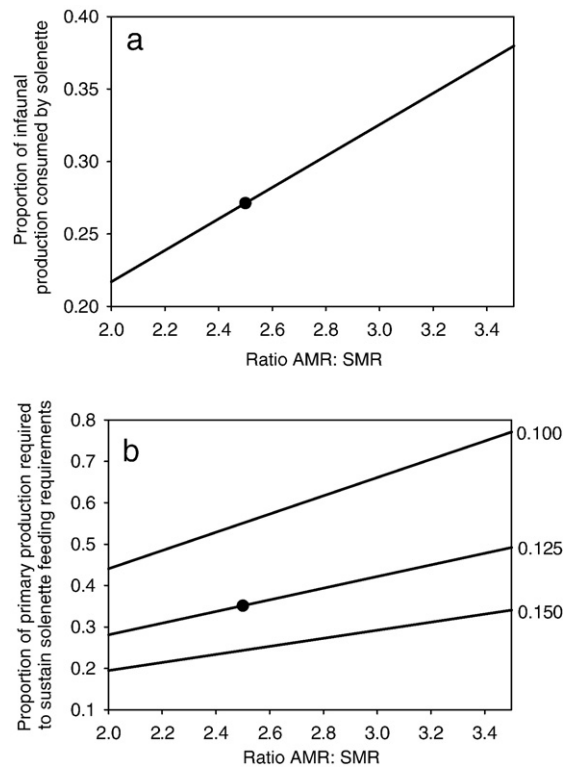


Fig. 7. Relationships between the ratio actual metabolic rate (AMR): standard metabolic rate (SMR) and the predicted proportion of benthic infaunal production consumed by solenette (a) and between AMR: SMR and the proportion of primary production required to sustain solenette feeding requirements for three values of transfer efficiency (b). The points indicate the values used in the main analyses.

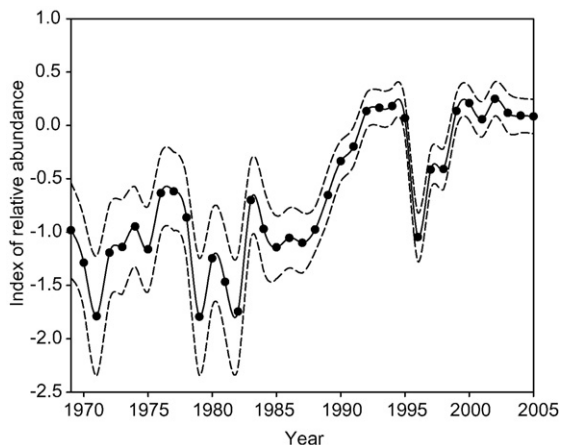


Fig. 8. Index of the relative abundance of solenette from 1969–2006 (mean \pm 95% C.I.).

(Daan, 1973; Jones, 1978) and energy allocation (Rijnsdorp, 1990). However, use of this approach does allow the application of our method to a wide range of species that have not been studied in detail. The assumptions and biases associated with using nitrogen stable isotope analysis to estimate the trophic level of fish has been extensively discussed elsewhere (Jennings et al., 2002; Sweeting et al., 2007) but despite these potential biases the short-term dietary data that are often used to assess trophic level are unlikely to be a better alternative since they may not account for diet switching, different rates of digestion, whether food is assimilated and the problems associated with identifying gut contents (Polunin and Pinnegar, 2002). The results of nitrogen stable isotope analysis also reflect the composition of tissues that have integrated fluctuations in diet over many months; even in relatively small individuals (Sweeting et al., 2005). Moreover, the use of stable isotope analysis to estimate relative trophic level avoids the need to know the trophic levels of all species in the diet.

Relationships between trophic level and size were remarkably consistent over the four year study period and we assumed that these relationships could be applied to longer time series of abundance data when calculating mean trophic levels and energy use. In the absence of a longer time series describing trophic level at size it is difficult to verify whether this assumption is acceptable, though there will be some constraints on trophic level that depend on morphology, behaviour, life history and prey size selection. The assumption of constant transfer efficiency in all food chains leading to different size classes and species of fish is also unverified, although mean transfer efficiencies are relatively consistent in different ecosystems (Ware, 2000).

The study is based on information that has been assembled from a number of different studies conducted on different time scales in different regions of the North Sea. As such, it is not a comprehensive analysis of the trophic levels and energetic roles of fish species in the North Sea food web, but the scope is sufficiently broad to conclude that the depletion of biomass of larger species has significantly reduced their energy use and that the reduction in energy use owing to declines in the mean trophic level of the population is partly countered by the increased energy demands per unit mass of smaller fish. Given that the biomass of most large species has declined at the North Sea scale (e.g. Greenstreet and Hall, 1996; Heessen and Daan, 1996; Rice and Gislason, 1996), we suggest that the relatively large declines in W_{me} and t_{me} of large species will have occurred throughout the North Sea and that the results are indicative of trophic homogenisation of the community; where populations that would have diverse life histories, trophic structures and energy demands if unfished now have increasingly similar W_{me} and t_{me} . The reduced energy demands of the exploited community will lead to changes in competition and predation; and it is clear that the solenette now use a very significant proportion of the total energy available to demersal species in one area. However, correlative studies such as this are not sufficient to establish the extent to which the increase in solenette abundance is a direct consequence of the depletion of larger predators and competitors or facilitated by other changes in the environment.

Our study also highlights the difficulties of conducting more comprehensive food web analysis to investigate interactions between small and large species, since many of the surveys currently used to provide data on fish distribution and abundance provide almost no reliable quantitative information on the smallest and potentially most abundant species and these species may therefore be ignored during model development. Given ongoing changes in the ecology of the North Sea and the potentially important role of smaller species, introducing more consistent monitoring of these animals is desirable. For demersal species this could be achieved by linking surveys using 2-m beam trawls, or other small mesh gears designed to catch animals not reliably taken by the GOV trawl, to the existing groundfish surveys.

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