

Fish abundance with no fishing: predictions based on macroecological theory

SIMON JENNINGS and JULIA L. BLANCHARD

Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK

Summary

1. Fishing changes the structure of fish communities and the relative impacts of fishing are assessed usefully against a baseline. A comparable baseline in all regions is fish community structure in the absence of fishing.
2. The structure of unexploited communities cannot always be predicted from historical data because fisheries exploitation usually precedes scientific investigation and non-fisheries impacts, such as climate change, modify ecosystems over time.
3. We propose a method, based on macroecological theory, to predict the abundance and size-structure of an unexploited fish community from a theoretical abundance–body mass relationship (size spectrum).
4. We apply the method in the intensively fished North Sea and compare the predicted structure of the unexploited fish community with contemporary community data.
5. We suggest that the current biomass of large fishes weighing 4–16 kg and 16–66 kg, respectively, is 97.4% and 99.2% lower than in the absence of fisheries exploitation. The results suggest that depletion of large fishes due to fisheries exploitation exceeds that described in many short-term studies.
6. Biomass of the contemporary North Sea fish community (defined as all fishes with body mass 64 g–66 kg) is 38% lower than predicted in the absence of exploitation, while the mean turnover time is almost twice as fast (falls from 3.5 to 1.9 years) and 70% less primary production is required to sustain it.
7. The increased turnover time of the fish community will lead to greater interannual instability in biomass and production, complicating management action and increasing the sensitivity of populations to environmental change.
8. This size-based method based on macroecological theory may provide a powerful new tool for setting ecosystem indicator reference levels, comparing fishing impacts in different ecosystems and for assessing the relative impacts of fishing and climate change.

Key-words: abundance–body mass relationships, allometry, energetic equivalence, fishing effects, metabolic scaling theory, predator–prey relationships, size spectra.

Journal of Animal Ecology (2004) **73**, 632–642

Introduction

Fisheries have dramatically changed the structure of marine ecosystems (Dayton *et al.* 1995; Hall 1999; Kaiser & de Groot 2000). Contemporary analyses of fishing impacts may underestimate the extent of these changes because the analyses are based on time-series that began after the onset of exploitation (e.g. Baum & Myers 2003) or because few ‘unfished’ control sites are

now available for study, and these are at the scale of small areas such as individual reefs rather than ecosystems (Jennings & Kaiser 1998; Jackson *et al.* 2001).

Knowledge of the structure of unexploited fish communities is required to establish baselines against which to assess current levels of impact (Steele & Schumacher 2000) and to avoid the ‘shifting baseline syndrome’ where the baseline is set with a short-term perspective and represents an increasingly exploited state over time (Pauly 1995). With the advent of an ecosystem-based approach to fishery management (e.g. Ecosystem Principles Advisory Panel 1999) and the requirement for indicators to support the ecosystem approach (Rice 2003; Rochet & Trenkel 2003), knowledge of the status

Correspondence: S. Jennings, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK. Tel: 44 01502 524363; Fax: 44 01502 513865; E-mail: S.Jennings@cefas.co.uk

of unexploited fish communities would help to set indicator reference levels (ICES 2001).

The unexploited abundance of fish communities is not necessarily the same as the historically observed state because climate has also changed over time (Walther *et al.* 2002). Indeed, it is unlikely that ecosystems today would always revert to historic states if fishing were stopped, either because phase shifts have occurred or because the environment is fundamentally different from that existing prior to human exploitation (Daan & Richardson 1996; Pinnegar *et al.* 2000).

To set a baseline for assessing fisheries impacts, it is desirable to predict the structure of fish communities subject to contemporary climatic influences but not impacted by fisheries. Here, we propose a method, based on macroecological theory and measurements of primary production and predator–prey body mass ratios, to predict total fish abundance and size structure in an unexploited ecosystem. As in all macroecology, the method is based on a number of important caveats and has to be applied to imperfect data. However, we believe the potential benefits of the approach in supporting ecosystem based fishery management are considerable and that it usefully complements and validates conventional population-based analyses that are extremely data-intensive when applied to whole communities.

The method relies on relationships between the slopes of abundance–body mass relationships (size spectra), predator–prey mass ratios and transfer efficiency (Brown & Gillooly 2003). For communities sharing a common energy source, the energetic equivalence hypothesis predicts that numerical abundance (N) scales with body mass (M) as $M^{-0.75}$ (Damuth 1981; Niklas & Enquist 2001; Belgrano *et al.* 2002; Carbone & Gittleman 2002) and therefore biomass (B) scales as $M^{0.25}$. However, in size-structured food webs all individuals do not share a common energy source, and energy available to larger individuals is constrained by inefficient energy transfer through the food chains that support them (Cyr & Pace 1993; Brown & Gillooly 2003). The rate at which available energy (E) decreases with increasing M depends on the mean predator–prey mass ratio (PPMR) and trophic transfer efficiency (TE), where TE is defined here as the proportion of prey production converted to predator production ($TE = P_c/P_p$ where P_c is predator production and P_p is prey production). If the scaling of E with M is known, then the scaling of N or B with M can be predicted (Brown & Gillooly 2003). Size-based nitrogen stable isotope analysis permits estimation of PPMR in size-structured food webs (Jennings, Mackinson & Warr 2002b), and with knowledge of TE, the scaling of E with M (Jennings & Mackinson 2003).

Abundance–body mass relationships in marine communities are commonly termed size-spectra (Kerr & Dickie 2001), and the slopes of size spectra become increasingly negative following fisheries exploitation (Duplisea & Kerr 1995; Rice & Gislason 1996). This is due to (1) the differential vulnerability of larger species, (2) within-population changes in mean body size and life

history, (3) genetic changes in life history, (4) predator–prey relationships or (5) changes in competitive interactions (Gislason & Rice 1998; Jennings, Greenstreet & Reynolds 1999; Bianchi *et al.* 2000; Law 2000). Comparing slopes of exploited size spectra with theoretical (unexploited) predictions will indicate the magnitude of fishing effects on communities (D. E. Duplisea, personal communication).

Here, we propose that macroecological theory and empirical estimates of PPMR can be used to predict slopes of unexploited size spectra. For the intensively exploited North Sea we make tentative estimates of changes in biomass, size composition, trophic level, turnover time and energy requirements of the contemporary (2001) fish community that can be attributed to fisheries exploitation.

Methods

CONTEMPORARY STRUCTURE OF FISH COMMUNITIES

The size and trophic structure of fish communities was described using trawl survey catch data collected in August and September 2001. Fish were caught at 74 sites in the North Sea (Fig. 1) with a Grande Ouverture Verticale (GOV) demersal otter trawl towed for 30 min at 4 knots. The GOV trawl was fitted with a cod-end of 20 mm stretched mesh. All fishes in the catch were weighed by species, and all individuals in species groups or subsamples of species groups were measured to produce raised length–frequency distributions.

SIZE SPECTRA

Species-size–abundance data from the trawl catches were used to compile size spectra. Body length was converted

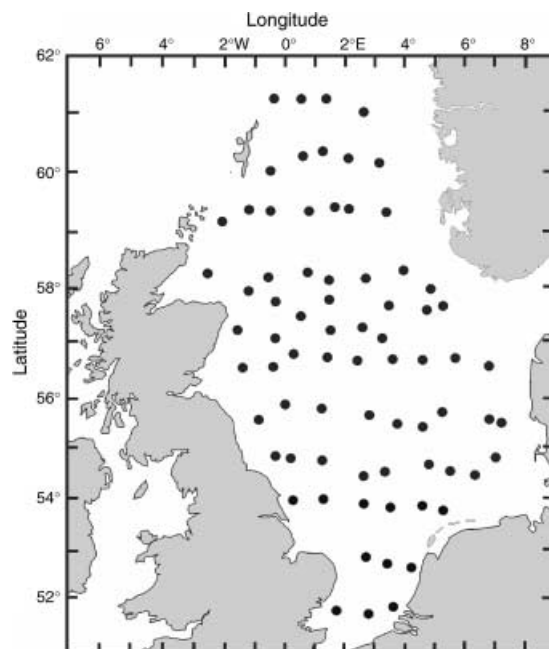


Fig. 1. Location of sample sites in the North Sea.

to body mass (M) using length–weight relationships (Bedford, Woolner & Jones 1986; Coull *et al.* 1989; CEFAS unpublished data) and fish were assigned to \log_2 M classes from 64 g to 32 kg. Total biomass (B) at M was converted to g m^{-2} of swept area, assuming a catchability of 0.25 for all species and size classes > 64 g (Jennings *et al.* 2002b). Mean B at M was calculated for the 74 sites, and the size spectrum was plotted as corrected $\log_{10} B(y)$ vs. $\log_{10} M(x)$ where $\log_{10} M$ was the midpoint of the $\log_{10} M$ class, converted from \log_2 .

PREDATOR–PREY MASS RATIOS

Predator–prey body mass ratio (PPMR) was calculated from the slope of the relationship between trophic level (estimated using nitrogen stable isotope analysis (Owens 1987; Post 2002)) (y) and M (x) for the fishes in the trawl catches. At each site, all fishes > 512 g were individually weighed and assigned to \log_2 M classes. Fishes ≤ 512 g were subsampled randomly before weighing and then assigned to \log_2 M classes. Samples of white muscle tissue, set at a fixed proportion of M, were dissected from 20 to 25 individuals in each class (all fish if < 20; Jennings *et al.* 2001). Tissue samples from each M class were combined and homogenized to produce a smooth paste. Approximately 4 g of paste were retained, frozen to -30°C and freeze-dried.

For nitrogen stable isotope analysis, freeze-dried fish tissue was ground to a fine powder (particles < 60 μm), mixed thoroughly, and weighed (1.0 mg) into a tin capsule. The ^{15}N composition was determined using continuous flow isotope ratio mass spectrometry (CF-IRMS). Samples were oxidized and the N_2 passed to a single inlet dual collector mass spectrometer [Automated Nitrogen Carbon Analysis (ANCA) Integra system, PDZ Europa (UK)]. Two samples of reference material (a standard mix of ammonium sulphate and beet sugar) were analysed after every five tissue samples to calibrate the system and compensate for drift. The ^{15}N composition was expressed in conventional delta notation ($\delta^{15}\text{N}$), relative to the level of ^{15}N in atmospheric N_2 (Owens 1987). Experimental precision was 0.1‰ (standard deviation of $\delta^{15}\text{N}$ for replicates of reference material).

Because there are large-scale spatial variations in $\delta^{15}\text{N}$ at the base of North Sea food chains (Jennings & Warr 2003a), all $\delta^{15}\text{N}$ estimates were converted to estimates of site-specific trophic level (TL) based on the assumption that the fractionation of $\delta^{15}\text{N}$ was +3.4‰ per trophic level (Post 2002) and that the TL of animals close to the base of the food chain was known (Owens 1987). Trophic level was calculated as:

$$\text{TL}_i = \left(\frac{(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{ref}})}{3.4} \right) + 2.5$$

where TL_i is TL of M class i , $\delta^{15}\text{N}_i$ is the mean $\delta^{15}\text{N}$ of M class i , and $\delta^{15}\text{N}_{\text{ref}}$ is the index of $\delta^{15}\text{N}$ in an animal close to the base of the food chain (assigned $\text{TL} = 2.5$). The $\delta^{15}\text{N}$ of this animal, a queen scallop *Aequipecten*

opercularis (Linnaeus 1758) of 55 mm shell height sampled on 1 September 2001, was predicted from the empirical relationship of Jennings & Warr (2003a):

$$\begin{aligned} \delta^{15}\text{N}_{\text{ref}} = & 208.51 - (0.009617 \times D) + (6.7729 \times T_s) \\ & - (0.31562 \times T_s^2) + (1.888 \times T_b) - (0.06505 \times T_b^2) \\ & - (13.7488 \times S) + (0.18969 \times S^2) \end{aligned}$$

where D is depth (m), T_s is mean surface temperature ($^\circ\text{C}$), T_b is mean bottom temperature ($^\circ\text{C}$) and S is mean salinity in August (‰). $\delta^{15}\text{N}_{\text{ref}}$ had to be calculated rather than determined empirically, as no single species at the base of the food chain could be sampled at every site and $\delta^{15}\text{N}$ is species- and size-specific (Jennings & Warr 2003a). PPMR was calculated from the slope b of the linear relationship $\text{TL} = a + b \log_{10} M$, where $\text{PPMR} = 10^{1/b}$ (Jennings *et al.* 2002b).

PREDICTING SLOPE AND INTERCEPT OF UNEXPLOITED SIZE SPECTRUM

In a size-based food web, E declines with M due to inefficient energy transfer from predators to prey. Thus the decrease in E with M is determined by PPMR and transfer efficiency (TE) (Cyr 2000; Brown & Gillooly 2003). The expected scaling of $\log_{10} E$ with $\log_{10} M$ was calculated as $\log_{10} \text{TE} / \log_{10} \text{PPMR}$, and a range of TE estimates were used, consistent with those reported in other marine ecosystems (Ware 2000). For the calculated scaling of E and M , we predicted the scaling of B or numerical abundance (N) and M as $M^{(\log_{10} \text{TE} / \log_{10} \text{PPMR})} \times M^{0.25}$ and $M^{(\log_{10} \text{TE} / \log_{10} \text{PPMR})} \times M^{-0.75}$, respectively.

For a size spectrum of given slope, the intercept depends on the productivity of the ecosystem (Kerr & Dickie 2001). Primary production in the North Sea was expressed as mean primary production ($\text{g C m}^{-2} \text{ year}^{-1}$) in the ICES statistical rectangle (boxes of 0.5° latitude and 1° longitude) surrounding each sample site (ICES, unpublished data) and converted to wet weight following Greenstreet *et al.* (1997). For all assumed values of TE, we calculated P_{TL} , the P at TL that the primary production (PP) would sustain, as $P_{\text{TL}} = \text{PP} \times \text{TE}^{(\text{TL}-1)}$, and converted P at TL (or equivalent M) to B at TL (or M) using the empirical relationship $P : B = 2 M^{-0.25}$, where $P : B$ is the production : biomass ratio (Banse & Mosher 1980; Ware 2000). Trophic level was expressed as M from $\log_{10} M = (\text{TL} - a)/b$, where a and b are the intercept and slope of the relationship used to derive PPMR.

COMPARING EXPLOITED AND UNEXPLOITED COMMUNITIES

The calculated slopes and intercepts of size-spectra from the 2001 trawl catch data (exploited) and the theoretical analysis (unexploited) were used to calculate B at M in M classes of 1024–4095 g (hereafter 1–4 kg), 4096–16383 g (4–16 kg) and 16384–65535 g (16–66 kg). The B of fishes in each M class during the 2001 survey

was expressed as a proportion of unexploited B when $TE = 0.100, 0.125$ or 0.150 .

The size spectra were also used to calculate mean M and mean TL of all fishes in M classes 64–65535 g (hereafter the community of fishes 64–66 kg). Mean M was calculated as $\Sigma B/\Sigma N$ where the scaling of N with M was $M^{(\log_{10} TE / \log_{10} PPMR)} \times M^{-0.75}$. Mean TL was calculated as $\Sigma(TL \times B)/\Sigma B$ for the relevant size classes. Mean turnover time was calculated as $\Sigma(T \times B)/\Sigma B$ where T is turnover time, calculated as $1/P : B$, where $P : B = 2 M^{-0.25}$ (Ware 2000). Total primary production required (PPR) to sustain the fish community was calculated as $PPR = P_{TL}/TE^{(TL-1)}$ and expressed as a proportion of the total primary production available to support the community ($1956 \text{ g WW m}^{-2} \text{ year}^{-1}$).

Results

The biomass (B) of North Sea fishes sampled in trawl survey catches declined with body mass (M) (Fig. 2). Biomass scaled as $M^{-1.0}$ in the exploited fish community (Fig. 2). Trophic level (TL) of the exploited fish community increased linearly with M (Fig. 3). The relationship between TL and M was $TL = 0.386 \log_{10} M + 3.471$ and thus mean PPMR was 390 : 1.

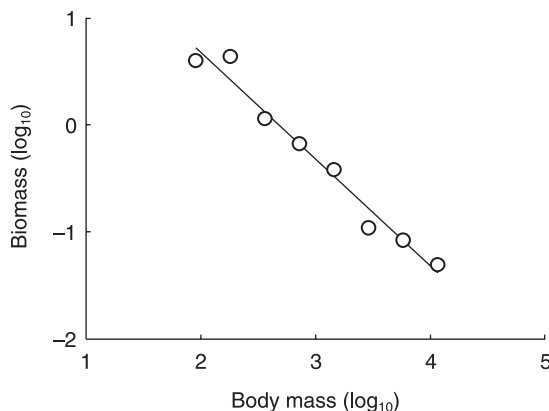


Fig. 2. Biomass size spectrum for the North Sea fish community in 2001.

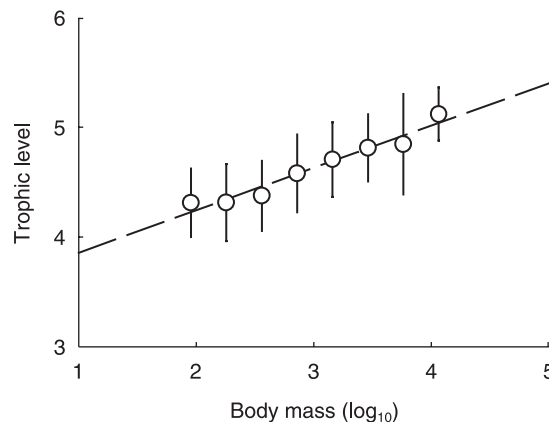


Fig. 3. Relationship between trophic level and body mass for the North Sea fish community ($\pm 95\%$ confidence intervals for mean trophic level at body mass).

Predicted scaling of B with M in an unexploited ecosystem was $M^{-0.10}$ when $TE = 0.125$ and $PPMR = 390$. The scaling was most sensitive to a given change in PPMR or TE when the values of both parameters were low (Fig. 4). Mean primary production (PP) was $1956 \pm 392 \text{ g WW year}^{-1}$ ($\pm \text{SD}$) in 2001.

To compare biomass and turnover time in the unexploited and exploited ecosystems, slopes and intercepts of unexploited size spectra were calculated for $PPMR = 390$ and $TE = 0.100\text{--}0.150$ (Fig. 5). At low TE , size spectra had lower intercepts and were steeper. For all realistic values of TE , the predicted slopes of unexploited spectra were much shallower (less negative) than the observed slope of the exploited spectrum in 2001 (Fig. 5).

Comparisons of biomass in the unexploited and exploited communities (Table 1) suggested that, for $TE = 0.125$, the biomass of 1–4 kg fishes in 2001 was 9% of that in the absence of fisheries exploitation. For M classes

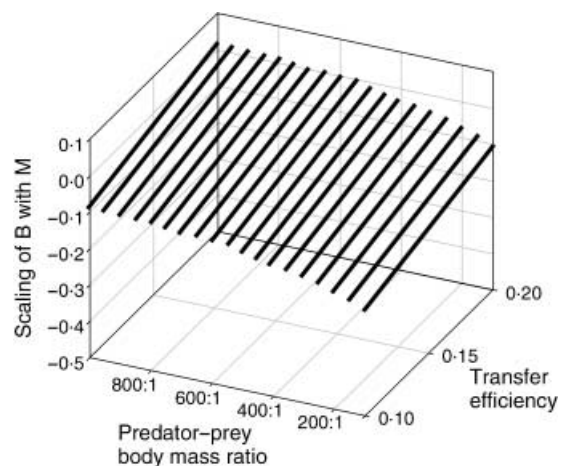


Fig. 4. Sensitivity of the slope of the biomass (B) body mass (M) relationship (unexploited biomass size spectrum) to changes in predator–prey mass ratios and transfer efficiency.

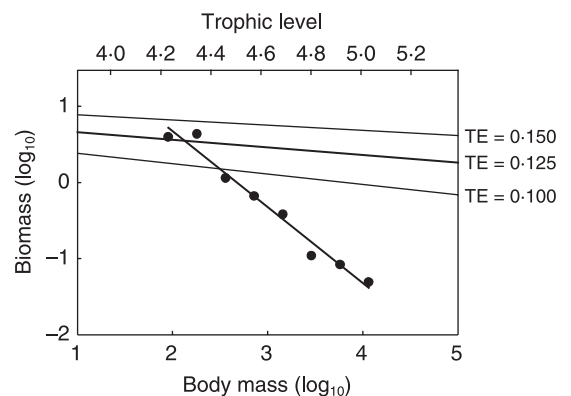


Fig. 5. Predicted slopes and locations of unexploited size spectra given primary production of $1956 \text{ g WW year}^{-1}$ and a predator–prey mass ratio of 390 : 1. Three size spectra corresponding to transfer efficiencies (TE) of 0.100, 0.125 and 0.150 are presented, with the spectrum for $TE = 0.125$ in bold ($M^{-0.10}$). Fish biomass at body mass for the North Sea fish community in 2001 (circles) and the fitted size spectrum (bold line, $M^{-1.0}$) are shown for comparison.

Table 1. Comparison of predicted fish biomass by body mass class in unexploited communities (for transfer efficiencies (TE) of 0.100–0.150) and recorded biomass in the exploited community in 2001. Values in parentheses express the 2001 biomass as a proportion of unexploited biomass

Body mass class (kg)	Biomass (g m ⁻²)			2001
	TE = 0.100	TE = 0.125	TE = 0.150	
1–4	2.35 (0.210)	5.37 (0.092)	10.71 (0.046)	0.49
4–16	1.94 (0.063)	4.68 (0.026)	9.75 (0.013)	0.12
16–66	1.61 (0.019)	4.07 (0.008)	8.87 (0.003)	0.03

Table 2. Comparison of predicted metrics for the unexploited fish community (64–66 kg, for transfer efficiencies of 0.100–0.150) and calculated metrics for the exploited community in 2001

Metric	TE = 0.100	TE = 0.125	TE = 0.150	2001
Biomass (g m ⁻²)	12.15	27.38	54.05	10.45
Mean weight of individual (g)	355	383	410	144
Mean trophic level	4.66	4.68	4.70	4.34
Mean turnover time of biomass (year)	3.33	3.45	3.56	1.89

4–16 kg and 16–66 kg the corresponding values were 2.6% and 0.8%, respectively. The evidence for low abundance of the largest fishes (16–66 kg) in the exploited ecosystem did not depend strongly on assumptions about TE. For TE = 0.100, the predicted abundance was 98.1% less than unexploited and for TE = 0.150 it was 99.7% less.

The total biomass of fishes from 64–66 kg in 2001 was less than half the predicted biomass in the unexploited community when TE = 0.125. Mean individual weight in the exploited community was 144 g, 38% of that expected when TE = 0.125 (Table 2). Mean trophic level was lower in the exploited community and the turnover time of biomass in the community was 1.9 years, as opposed to 3.5 years in an unexploited community with TE = 0.125 (Table 2). The reduction in turnover time exceeded 40% for all values of TE.

The primary production required (PPR) to sustain the community was 1956 g m⁻² year⁻¹ in the absence of fisheries exploitation. In 2001, estimated PPR was 1265 g m⁻² year⁻¹ for TE = 0.100, 598 g m⁻² year⁻¹ for TE = 0.125 and 324 g m⁻² year⁻¹ for TE = 0.150. Thus, for all assumed values of TE, a large proportion of primary production could not be used by the exploited fish community.

Discussion

Our predictions suggest that the biomass of large fishes (16–66 kg) in the North Sea is around two orders of magnitude lower than expected in the absence of fisheries exploitation. The results suggest that the true extent of depletion of large fishes by fishing exceeds that described in many short time-series, consistent with the observation that many large species regarded formerly as abundant are rarely caught in contem-

porary fisheries or surveys (Holden 1978). The scarcity of large fishes means that the power of surveys and analyses to determine changes in population biomass or occupancy will be very low (Nicholson & Fryer 1992; Nicholson & Barry 1995), and it will be difficult or impossible to assess further declines or population recovery on time-scales relevant to managers. The decrease in biomass of large fishes is associated with an increase in mean turnover time of the exploited community. Fast turnover at low abundance will lead to greater interannual instability in biomass and production, complicating management action and increasing the sensitivity of populations and communities to environmental change.

Our approach for describing size and abundance in unexploited food webs provides a baseline description of ecosystem structure in the absence of fisheries exploitation. This baseline is not subject to the biases associated with 'historical' baselines, which are rarely based on data collected prior to fisheries exploitation and in which non-fisheries (e.g. climate change) and fisheries impacts are often confounded. Whether a subsequent cessation of exploitation would allow the fish community to revert to the unexploited abundance–body mass structure is another issue, determined by whether large species that can reproduce successfully are still found in the exploited ecosystem (Dulvy, Sadovy & Reynolds 2003), cultivation effects (Walters & Kitchell 2001), depensation (Liermann & Hilborn 2001), phase shifts (Pinnegar *et al.* 2000), genetic selection for small body size (Law 2000) and interspecies interactions (Hutchings 2000).

While the collection of time-series abundance data usually began after the onset of fisheries exploitation, recorded changes in abundance do help us to determine

whether our predictions are realistic. Clearly, for very large species and individuals (16–66 kg), our predictions of a 100-fold declines in biomass due to exploitation do not seem erroneous. Brander (1981) reported the regional extinction of the common skate *Dipturus batis* (Linnaeus 1758) from the Irish Sea by the 1970s, when this species had been described as abundant in all parts of the Irish Sea in the 1800s. Indeed, local (scale 10^3 – 10^5 km²) and regional (scale $> 10^5$ km²) losses of large skate, ray and shark species have been reported in many areas where they were once abundant (Walker & Heessen 1996; Casey & Myers 1998; Walker & Hislop 1998; Rogers & Ellis 2000; Stevens *et al.* 2000; Dulvy & Reynolds 2002) and landings data for the Bassin d'Arcachon on the western coast of France show that landings of the angel shark *Squatina squatina* (Linnaeus 1758) fell by $> 98.5\%$ from 1850 to 1996, despite a large increase in fishing effort and the catch efficiency of fishing gear (Quero 1998).

Even for intermediate-sized species and individuals (4–16 kg), reductions to 1/10–1/100th of unexploited biomass do not seem improbable. Based on trawl survey data, spurdog *Squalus acanthias* Linnaeus 1758 abundance fell 18-fold between 1901 and 1907 and 1989 and 1997 in the Irish Sea (Rogers & Ellis 2000) and by 10-fold from 1929 to 1993 in the North Sea (Greenstreet & Hall 1996). The entire Irish Sea and North Sea were already accessible to trawlers by 1900, so significant fishing effects would also have occurred well before the first of these surveys took place (Jennings & Kaiser 1998). Virtual population analyses have also shown that declines in the abundance of intermediate-sized North Sea cod *Gadus morhua* Linnaeus 1758 (7–10-year-old fish *c.* 9–13 kg) exceeded 90% in the 30 years since 1970 (ICES 2002).

Even for some of the smaller species, long-term changes in fishery catch per unit effort (CPUE) suggest that fisheries can reduce unexploited biomass by 90% or more. Thus CPUE statistics for the sole *Solea solea* (Linnaeus 1758), a relatively small flat fish with a maximum size of 3 kg, caught in the Bristol Channel (Irish Sea) have been collected since the 1920s, when the stock had already been fished for at least 200 years. Even in the period 1924–90, CPUE (catch weight per hour) fell by around 90%, despite increases in the catching efficiency of the fishing fleet (Horwood 1993).

While climatic effects as well as fishing can contribute to trends in abundance (O'Brien *et al.* 2000), consistent declines in the abundance of larger species and individuals relative to their smaller phylogenetic relatives or conspecifics (Jennings *et al.* 1999) show that fisheries exploitation is the primary cause of changes in overall biomass and size-structure of the fish community.

Large-scale analyses are inevitably ambitious and rely on assumptions that could be avoided when working at small scales in controlled situations. However, large-scale analyses provide insights into the effects of human activities on the scales at which they impact the marine environment. Thus ecosystems are defined on scales

of 10⁶ km² or more (Sherman, Alexander & Gold 1993) and few areas in these ecosystems are inaccessible to national or international fishing fleets (FAO 1993). Given that the ecosystem effects of fishing are ideally assessed at large scales (Pauly & Christensen 1995; Jennings & Kaiser 1998; Pauly *et al.* 1998), we consider that the trade-off between the scale and the rigour of our analysis is both appropriate and necessary to assess the extent of large-scale changes in fish communities.

Our approach is based on several assumptions, principally (1) that the predator–prey mass ratio (PPMR) is independent of body mass (*M*) and predominantly influenced by the environment rather than fishing, (2) that our estimates of transfer efficiency (TE) are realistic, (3) that the steep scaling of the size spectrum in 2001 does not result from a negative relationship between catchability and *M*, (4) that the fish community accounts for most of the biomass in the food web in the size classes considered and (5) that the procedure for estimating trophic level (TL) is reliable.

Available evidence suggests that PPMR is independent of *M* in the *M* classes we considered, because the relationship between TL and *M* is linear. Previous analyses that include both fish and invertebrates from 2 to 2048 g (invertebrates account for an increasingly large proportion of the biomass of the community at *M* < 64 g) have also shown that the relationship is linear (Jennings *et al.* 2002b) and a projection of the PPMR we predict here to TL = 2 and TL = 1 implies mean *M* of 10^{−4} g (95% confidence limits 10^{−2.6}–10^{−5.6} g) and 10^{−6.4} g (95% confidence limits 10^{−4.8}–10^{−9.0} g) at TL = 2 and TL = 1, respectively. The 95% confidence limits encompass the size ranges of many omnivorous zooplankton and larger phytoplankton (Ware 2000).

For fishes significantly larger than those included in our projections (*M* $> c.$ 66 kg) it is unlikely that mean TL would continue to increase linearly with *M*, and thus mean PPMR would increase. This is because the largest predators often feed further down the food web on smaller and more productive size classes of prey. For example, when blue-fin tuna *Thunnus thynnus* (Linnaeus 1758) were common in the North Sea, they fed predominantly on herring (Tiews 1978). The reduction in *B* of these large (*M* to 500 kg) and heavily exploited predators feeding at low trophic levels cannot be predicted using our size-based approach. Thus our estimates of biomass loss will be conservative.

There are few estimates of mean PPMR in food webs, although those presented here are consistent with assumed ratios of 1 : 10²–10³ (Cushing 1975) and the sizes of prey selected by fish predators (Ursin 1973; Hahm & Langton 1984; ICES 1988). The valid application of our method requires that PPMR is insensitive to fishing effects. While spatial comparisons among areas subject to significant (> 20 -fold) variation in fishing intensity do suggest that PPMR is influenced primarily by environmental variation and not by fishing (Jennings & Warr 2003b), this relationship should be validated in time as well as space. Nevertheless, we predict that

PPMR is unlikely to be influenced strongly by fishing in the North Sea, as animals are killed at all trophic levels [as catches, discards and due to the direct impacts of fishing gear on benthic communities (Kaiser & de Groot 2000)] and overall mortality and biomass depletion are strongly size-related. Thus, larger predators will be depleted more than their prey and the total consumption of predators will fall relative to prey production. This (time averaged) surplus of prey production is unlikely to lead to predators consistently targeting prey of otherwise suboptimal M . Fishing could, however, affect PPMR in ecosystems where fishing selectively targets a few intermediate size classes and our approach for estimating the slope of the unexploited size-spectrum would have to be applied with caution.

Our estimate of TE is realistic (Ware 2000), but it is more likely to be too low than too high for the size-spectrum as a whole because TE in the plankton community may approach 20% (Greenstreet *et al.* 1997; Ware 2000). Indeed, in a detailed analysis of the North Sea food web, Greenstreet *et al.* (1997) estimated omnivorous zooplankton production (based on a temperature-dependant weight-specific production model applied to size-abundance data) of $426 \text{ g WW m}^{-2} \text{ year}^{-1}$. This is rather higher than the production of $244 \text{ g WW m}^{-2} \text{ year}^{-1}$ at $\text{TL} = 2$ from our assumed $\text{TE} = 0.125$, and would imply that fishing effects on the B of large fishes are greater than reported. An assumed $\text{TE} = 0.125$ corresponds well with other values reported in the literature (Ware 2000). Ware (2000) suggests that TE will be slightly higher at lower TL, although the available data are inadequate to develop a function linking TE and M . If TE was related inversely to M , and PPMR was constant, then the unexploited size spectrum would be curvilinear.

The steep scaling of the size spectrum in 2001 could be attributed to the low catchability of larger fishes, and our application of a single catchability value to all M classes and species $> 64 \text{ g}$ is clearly not desirable. However, the abundance estimates for all M classes and species could not be corrected to account for catchability [even if size- and species-specific catchability were known (Sparholt 1990)] unless TL was also weighted by size, species and abundance at all sites. This would require species-specific M vs. TL relationships at all sites; a logistic and financial impossibility at present. As such, we do not know the extent to which the negative slope of the size spectrum in 2001 is a function of catchability. Nevertheless, we do know that many of our sites have been fished with the same trawl gear on annual surveys since 1982, and the slope of the size spectrum has become progressively steeper in recent years as large fishes have become scarce (Jennings *et al.* 2002a) (Fig. 6; slope in 1982 scales $M^{-0.75}$). Moreover, smaller commercial trawls and survey nets fished at slower speeds in the early 1990s caught large numbers of large and sexually mature bottom-dwelling fishes such as skates (*Dipturus batis* and *Raja clavata* Linnaeus 1758), halibut *Hippoglossus hippoglossoides* (Linnaeus 1758), cod *Gadus morhua* and spurdog *Squalus acanthias*, spe-

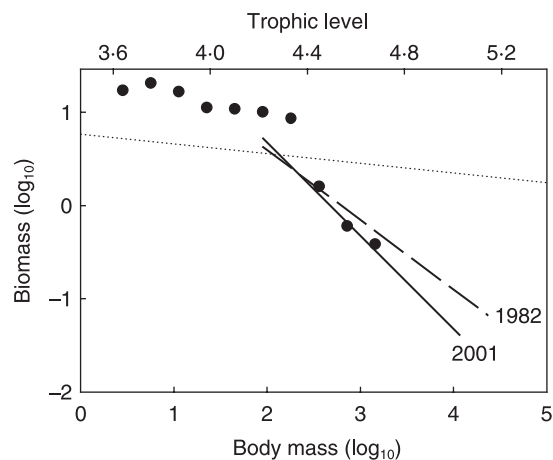


Fig. 6. Predicted slopes of an unexploited size spectrum when transfer efficiency = 0.125 (dotted line) and of size spectra for the exploited North Sea in 2001 (solid line) and 1982 (dashed line). Circles indicate biomass at body mass for the entire food web (fish and invertebrates) in the central North Sea in 2001 (Jennings *et al.* 2002b). The size-spectrum for 1982 is calculated from data in Jennings *et al.* (2002a).

cies largely absent in survey catches today (Holden 1978; Greenstreet *et al.* 1998; Walker & Hislop 1998). Given the change in slope of the spectrum from 1982 to 2001, and that Scottish fisheries survey data compiled by Greenstreet & Hall (1996) show the slope of the size-spectrum for the central and northern North Sea demersal community becoming increasingly negative (steeper) as a linear function of time from 1925 to 1996 (Jennings *et al.* 2002a), we conclude that the steep slope of the spectrum in 2001 reflects predominantly the effects of fishing on the fish community. Indeed, if the rate of change in slope observed from 1982 to 2001 ($-0.0125 \text{ years}^{-1}$) had been linear since 1925, the slope in 1925 would be approaching that expected in an unexploited community. Notwithstanding, it is still necessary to improve the rigour of all population, community and ecosystem assessments that require absolute abundance data by correcting for gear type [or visual census method (Kulbicki 1998)], size-, species- and time-specific catchability.

Marine mammals and seabirds can consume a significant proportion of zooplankton and fish production. Many marine mammal and some seabird species would be more abundant in the absence of human impacts (e.g. Roman & Palumbi 2003). These species feed predominantly on smaller size classes in the size spectrum and therefore use energy that might otherwise be available to larger fish predators. Thus, marine mammal and seabird predation would modify the height rather than the slope of the size spectrum and affect estimates of abundance rather than changes in mean size and turnover time. If estimates of the unimpacted abundance of marine mammals and seabirds in the North Sea were available, we could modify our approach to account for the effects of different rates of marine mammal or seabird predation at different trophic levels.

Trophic level can be estimated from $\delta^{15}\text{N}$ because the $\delta^{15}\text{N}$ of predators is enriched relative to their prey (Post 2002). In some circumstances nitrogen stable isotope analysis is preferable to diet analysis for estimating TL because the $\delta^{15}\text{N}$ of a predator reflects the composition of assimilated diet and integrates differences in assimilated diet over time (Post 2002). Diet analysis also provides inadequate information on the TL of species that switch diet frequently, prey on species that are digested at different rates, regurgitate food on capture, feed intermittently or have gut contents that cannot be identified (Polunin & Pinnegar 2002). We assumed a $\delta^{15}\text{N}$ enrichment of 3.4‰ per TL. However, many factors influence isotopic fractionation and this has prompted calls for further experimental validation (Harvey *et al.* 2002; Olive *et al.* 2003). Such validation has not been completed in a complex open sea food web.

Experimental manipulations of temperature, dietary nitrogen content and other factors can be shown to affect $\delta^{15}\text{N}$ fractionation. In the food web as a whole, species are living in their normal temperature ranges on a nitrogen rich marine diet. On average, they are unlikely to experience the extreme conditions imposed on animals in feeding experiments. Indeed, 18 months experimental rearing of bass *Dicentrarchus labrax* (Linnaeus 1758) fed on sandeel *Ammodytes marinus* (Raitt 1834) and dab *Limanda limanda* (Linnaeus 1758) diets at a range of ambient North Sea temperatures has shown that mean fractionation with both diets was 3.4–3.9‰ (Sweeting unpublished data). The effects of variation in fractionation on estimates of PPMR can be determined from the relationship $\text{PPMR} = 10^{r/b}$, where r is the trophic fractionation in $\delta^{15}\text{N}$ and b is the slope of the relationship $\delta^{15}\text{N} = a + b \log_{10} M$. The effects of variation in PPMR on the predicted scaling of B and M is given in Fig. 4. Small changes in mean fractionation (< 0.5‰) would have a minimal impact on our conclusion that the slope of the size spectrum is significantly steeper in the exploited community.

It is essential to express TL relative to a reference animal, as most of the large-scale spatial variation in $\delta^{15}\text{N}$ at M is determined by the environment (Jennings & Warr 2003a). However, the TL assigned to reference animals, in this case filter-feeding scallops (TL = 2.5), will determine predicted P and B at higher trophic levels. Thus, if the scallop fed on pure phytoplankton (TL = 1) we would underestimate the intercept of the size spectrum because the food chain leading to B at a given M would be shorter than predicted and the losses due to TE lower. Conversely, if the scallop fed on material of TL > 1.5 (diet rich in small zooplankton or meiofauna) the intercept would be overestimated. Without site-specific information on the feeding strategies of the scallops it is impossible to know the extent of any bias, although scallops which fed at a lower TL (a diet richer in phytoplankton) would have the same effect on our results as an increase in TE and lead to an underestimate of the reduction in fish biomass due to fishing.

The slope of the exploited size-spectrum may provide a useful indicator of fishing effects (Rochet & Trenkel 2003). For spectra based on relatively large fishes, the slope of the size-spectrum becomes steeper in response to increased fisheries exploitation, but the spectrum tends to remain linear (Pope *et al.* 1988; Murawski & Idoine 1992; Rice & Gislason 1996; Bianchi *et al.* 2000; Dulvy *et al.* 2004). How changes in slope propagate to smaller M classes has not been clear, but our approach may provide some new insights.

Reductions in the abundance of large fishes reduce the amount of primary production required (PPR) to sustain them. Theoretically, the energy not used by large fishes can be used by smaller fishes, which may then proliferate. However, because mean TL increases linearly with M, mean PPMR is independent of M and as the relative abundance of large fish is reduced more by fishing, fishes in high M classes will experience the greatest reductions in predation mortality. Fishes in these classes will also be more vulnerable to fishing. As a result, any benefits from reduced predation mortality will not be evident until M is sufficiently low that the balance between fishing mortality and P/B allows fish in a M class to proliferate.

Comparison of the 2001 size-spectrum (fishes > 64 g) with a size spectrum for all animals of 2–2048 g in the central North Sea (Jennings *et al.* 2002b) suggests that fishing leads to a relatively abrupt change in slope when a M class no longer has sufficient refuge from fishing mortality (in space or time) to benefit from reduced predation. The few available data (Fig. 6) suggest this may occur at around 250 g in the North Sea, since the size spectrum for animals < 256 g is relatively linear and has a slope consistent with that predicted from energy equivalence theory (the predicted slope in the central North Sea is slightly steeper than for the whole North Sea because PPMR was smaller in the central North Sea (Jennings *et al.* 2002b)). The intercept of the central North Sea size-spectrum for animals of 2–256 g is higher than that predicted from PP in this study. Because PP in the central North Sea is not higher than the mean PP for the North Sea (PP estimate of 1935 g WW $\text{m}^{-2} \text{year}^{-1}$ in the central North Sea study area of 54°00′–55°00′ N and 00°30′–02°00′ E vs. 1956 g WW $\text{m}^{-2} \text{year}^{-1}$ in the whole North Sea), the increase in intercept may reflect increases in abundance of M classes that are released from predation mortality and have high enough P : B, or low enough fishing mortality, to allow proliferation. This empirical evidence suggests that size-selective fishing mortality causes an increase in the steepness of the size spectrum at large M while, at small M, the second-order effects of fishing are manifest as changes in the height of the spectrum rather than changes in slope. Unfortunately, changes in slope or intercept at small M cannot be studied with most trawl survey data, as the surveys under-represent B at M and do not sample small pelagic fishes or benthic invertebrates that often dominate B.

The size-based approach does not allow us to estimate the biomass of the largest fishes in unexploited

ecosystems, as these may feed down the food web (e.g. tunas or plankton feeding sharks with high PPMR, as above). Predictions of B for these fishes would require knowledge of the function linking PPMR and M, and an understanding how their consumption rates would influence the energy available to smaller competitors. The lack of B predictions for the largest fishes, coupled with the observation that these fishes are effectively absent in the exploited North Sea, leads to conservative estimates of fishing effects on B. Conversely, the analysis of fishing effects on mean TL overestimates the decrease in TL. Given that size-based and trophic responses to fishing can become decoupled, and that first-order size-based responses of populations and communities to fishing mortality are governed by very well-established links between M (or related life-history parameters) and the capacity to withstand elevated mortality (Beverton & Holt 1959; Myers, Bowen & Barrowman 1999), changes in mean TL due to fishing (Yang 1982; Pauly *et al.* 1998; Jennings *et al.* 2002a; Pinnegar *et al.* 2002) are a less sensitive indicator of fishing effects than changes in size structure.

The intercept of the size-spectrum increases with increased PP. Our estimate of PP (1956 g WW m⁻² year⁻¹) is consistent with other recent estimates for the North Sea, such as those of Christensen (1995) and Reid *et al.* (1990). Primary production in the North Sea has fluctuated in space and time since records were first collected in the early 1900s, and this will be a key driver of potential production at higher trophic levels (Reid *et al.* 1998).

Prediction of the slope of the unexploited size spectrum requires fewer untestable assumptions than prediction of slope and intercept since (1) the M range over which PPMR is applied is closer to that over which it is calculated, (2) TE is less likely to be a function of M, (3) no estimate of PP is required and (4) slope estimation is independent of TL at the base of the food chain (only fractionation in $\delta^{15}\text{N}$ with TL needs to be known, not absolute TL). Empirical description of slope requires estimates of relative rather than absolute B at M, but these estimates are still problematic when size- and species-specific catchability are poorly known. The difference between predicted (unexploited) and exploited slopes provides an indicator of fishing impacts that would be applicable in all ecosystems where predator–prey interactions are strongly size-based. The difference in slopes, however, indicates changes in the B ratio of small and large individuals, rather than total B. This would not be a concern in most fisheries, where higher M classes are generally subject to higher fishing mortality, but would be a concern if the difference between slopes was adopted as an indicator of fishing impacts (Rice 2003) and was subsequently manipulated by increasing the fishing mortality on low M classes rather than reducing fishing mortality at high M.

We conclude that fishing effects on abundance, size structure, trophic structure and turnover time are larger

than predicted from the analysis of many time-series data. This is not surprising when exploitation usually precedes scientific investigation and the first effects of fishing in a previously unexploited ecosystem, predominantly the ‘mining’ of large and old individuals, are usually the most profound (Jennings & Kaiser 1998; Jackson *et al.* 2001). Our approach is grounded in well-established allometric and life-history theory (Peters 1983; Charnov 1993; Brown & West 2000; Kerr & Dickie 2001) and takes specific account of the strongly size-based predator–prey interactions in marine ecosystems; where many species grow in mass by five orders of magnitude during their life cycle and cross-predation, cannibalism and transient predator–prey interactions are common (Cushing 1975; Pope, Shepherd & Webb 1994). Used in conjunction with the analysis of time-series species-size–abundance data, the approach provides a potentially powerful new tool for assessing the relative impacts of fishing and climate change on community structure, comparing the magnitude of fishing impacts in different ecosystems and for setting reference levels for ecosystem indicators.

Acknowledgements

We thank Richard Ayers, Trevor Boon, Grant Course, Tracy Dinmore, Chris Firmin, Karema Warr and the officers and crew of *RV Cirolana* for their efforts at sea, Steph Cogan for sample preparation, Anne Bruce and Rowan White for conducting the stable isotope analyses and Nick Dulvy and John Pinnegar for helpful comments on the manuscript. We thank Defra (MF0729, MF0731) and the US National Science Foundation (SCOR IOC NMFS WG 119) for funding this project.

References

- Banase, K. & Mosher, S. (1980) Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs*, **50**, 355–379.
- Baum, J.K. & Myers, R.A. (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, **7**, 135–145.
- Bedford, B.C., Woolner, L.E. & Jones, B.W. (1986) *Length–Weight Relationships for Commercial Fish Species and Conversion Factors for Various Presentations*. Fisheries Research Data Report 10. MAFF Fisheries Laboratory, Lowestoft, UK.
- Belgrano, A., Allen, A.P., Enquist, B.J. & Gillooly, J.F. (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecology Letters*, **5**, 611–613.
- Beverton, R.J.H. & Holt, S.J. (1959) A review of the lifespan and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquia on Ageing*, **5**, 142–180.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F. & Zwanenburg, K. (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, **57**, 558–571.

- Brander, K. (1981) Disappearance of common skate, *Raia batis*, from the Irish Sea. *Nature*, **290**, 48–49.
- Brown, J.H. & Gillooly, J.F. (2003) Ecological food webs: high-quality data facilitate theoretical unification. *Proceedings of the National Academy of Sciences of the USA*, **100**, 1467–1468.
- Brown, J.H. & West, G.B., eds (2000) *Scaling in Biology*. Oxford University Press, Oxford.
- Carbone, C. & Gittleman, J.L. (2002) A common rule for the scaling of carnivore density. *Science*, **295**, 2273–2276.
- Casey, J.M. & Myers, R.A. (1998) Near extinction of a large, widely distributed fish. *Science*, **281**, 690–692.
- Charnov, E.L. (1993) *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford University Press, Oxford.
- Christensen, V. (1995) A model of trophic interactions in the North Sea in 1981, the year of the stomach. *Dana*, **11**, 1–28.
- Coull, K.A., Jermyn, A.S., Newton, A.W., Henderson, G.I. & Hall, W.B. (1989) *Length/Weight Relationships for 88 Species of Fish Encountered in the North East Atlantic*. Department of Agriculture and Fisheries for Scotland, Aberdeen.
- Cushing, D.H. (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge.
- Cyr, H. (2000) Individual energy use and the allometry of population density. *Scaling in Biology* (eds J.H. Brown & G.B. West), pp. 267–295. Oxford University Press, Oxford.
- Cyr, H. & Pace, M.L. (1993) Allometric theory: extrapolations from individuals to communities. *Ecology*, **74**, 1234–1245.
- Daan, N. & Richardson, K., eds (1996) Changes in the North Sea ecosystem and their causes: Arhus 1975 revisited. *ICES Journal of Marine Science*, **53**, 879–1226.
- Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.
- Dayton, P.K., Thrush, S.F., Agardy, M.T. & Hofman, R.J. (1995) Environmental effects of marine fishing. *Aquatic Conservation*, **5**, 205–232.
- Dulvy, N.K., Polunin, N.V.C., Mill, A.C. & Graham, N.A.J. (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences*, in press.
- Dulvy, N.K. & Reynolds, J.D. (2002) Predicting extinction vulnerability in skates. *Conservation Biology*, **16**, 440–450.
- Dulvy, N.K., Sadovy, Y. & Reynolds, J.D. (2003) Extinction vulnerability in marine populations. *Fish and Fisheries*, **4**, 25–64.
- Duplisea, D.E. & Kerr, S.R. (1995) Application of a biomass size spectrum model to demersal fish data from the Scotian shelf. *Journal of Theoretical Biology*, **177**, 263–269.
- Ecosystem Principles Advisory Panel (1999) *Ecosystem-Based Fishery Management*. NOAA National Marine Fisheries Service, Silver Spring, MD.
- FAO (1993) *Marine fisheries and the law of the sea: a decade of change*. FAO Fisheries Circular 853.
- Gislason, H. & Rice, J.C. (1998) Modelling the response of size and diversity spectra of fish assemblages to changes in exploitation. *ICES Journal of Marine Science*, **55**, 362–370.
- Greenstreet, S.P.R., Bryant, A.D., Broekhuizen, N., Hall, S.J. & Heath, M.R. (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES Journal of Marine Science*, **54**, 243–266.
- Greenstreet, S.P.R. & Hall, S.J. (1996) Fishing and ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, **65**, 577–598.
- Greenstreet, S.P.R., Spence, F.E. & McMillan, J.A. (1998) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in the structure of the North Sea groundfish species assemblage between 1925 and 1996. *Fisheries Research*, **40**, 153–183.
- Hahm, W. & Langton, R. (1984) Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. *Marine Ecology Progress in Series*, **19**, 1–5.
- Hall, S.J. (1999) *The Effects of Fishing on Marine Ecosystems and Communities*. Blackwell Science, Oxford.
- Harvey, C.J., Hanson, P.C., Essington, T.E., Brown, P.B. & Kitchell, J.F. (2002) Using bioenergetics models to predict stable isotope ratios in fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 115–124.
- Holden, M.J. (1978) Long-term changes in landings of fish from the North Sea. *Rapports et Procès-Verbaux Des Réunions, Conseil International Pour l'Exploration de la Mer*, **172**, 11–26.
- Horwood, J.W. (1993) The Bristol Channel sole (*Solea solea* L.): a fisheries case study. *Advances in Marine Biology*, **29**, 215–367.
- Hutchings, J.A. (2000) Collapse and recovery of marine fishes. *Nature*, **406**, 882–885.
- ICES (1988) *Report of the multispecies assessment group*. International Council for the Exploration of the Sea, Committee Meeting, 1988/Assess 23.
- ICES (2001) *Report of the Working Group on Ecosystem Effects of Fishing Activities*. International Council for the Exploration of the Sea, Committee Meeting, 2001/ACME: 09.
- ICES (2002) *Report of the Advisory Committee on Fisheries Management*. International Council for the Exploration of the Sea. ICES Co-operative Research Report, **255**.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjørndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–638.
- Jennings, S., Greenstreet, S.P.R., Hill, L., Piet, G.J., Pinnegar, J.K. & Warr, K.J. (2002a) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size-spectra and community metrics. *Marine Biology*, **141**, 1085–1097.
- Jennings, S., Greenstreet, S.P.R. & Reynolds, J.D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617–627.
- Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.
- Jennings, S. & Mackinson, S. (2003) Abundance–body mass relationships in size-structured food webs. *Ecology Letters*, **6**, 971–974.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934–944.
- Jennings, S. & Warr, K.J. (2003a) Environmental correlates of spatial variation in $\delta^{15}\text{N}$. *Marine Biology*, **142**, 1131–1140.
- Jennings, S. & Warr, K.J. (2003b) Smaller predator–prey body size ratios in longer food chains. *Proceedings of the Royal Society: Biological Sciences*, **270**, 1413–1417.
- Jennings, S., Warr, K.J. & Mackinson, S. (2002b) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator–prey body mass ratios in food webs. *Marine Ecology Progress in Series*, **240**, 11–20.
- Kaiser, M.J. & de Groot, S.J., eds (2000) *The Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation Socio-Economic Issues*. Blackwell Science, Oxford.
- Kerr, S.R. & Dickie, L.M. (2001) *The Biomass Spectrum: a Predator–Prey Theory of Aquatic Production*. Columbia University Press, New York.

- Kulbicki, M. (1998) How the acquired behaviour of commercial fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology*, **222**, 11–30.
- Law, R. (2000) Fishing, selection and phenotypic evolution. *ICES Journal of Marine Science*, **57**, 659–668.
- Liermann, M. & Hilborn, R. (2001) Depensation: evidence, models and implications. *Fish and Fisheries*, **2**, 33–58.
- Murawski, S.A. & Idoine, J.S. (1992) Multispecies size composition: a conservative property of exploited fishery systems. *Journal of Northwest Atlantic Fishery Science*, **14**, 79–85.
- Myers, R.A., Bowen, K.G. & Barrowman, N.J. (1999) Maximum reproductive rates of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Science*, **56**, 2404–2419.
- Nicholson, M. & Barry, J. (1995) Inferences from spatial surveys about the presence of an unobserved species. *Oikos*, **72**, 74–78.
- Nicholson, M.D. & Fryer, R.J. (1992) The statistical power of monitoring programmes. *Marine Pollution Bulletin*, **24**, 146–149.
- Niklas, K.J. & Enquist, B.J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences of the USA*, **98**, 2922–2927.
- O'Brien, C.M., Fox, C.J., Planque, B. & Casey, J. (2000) Climate variability and North Sea cod. *Nature*, **404**, 142.
- Olive, P.J.W., Pinnegar, J.K., Polunin, N.V.C., Richards, G. & Welch, R. (2003) Isotope trophic-step fractionation: a dynamic equilibrium model. *Journal of Animal Ecology*, **72**, 608–617.
- Owens, N.J.P. (1987) Natural variations in ^{15}N in the marine environment. *Advances in Marine Biology*, **24**, 389–451.
- Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, **10**, 34.
- Pauly, D. & Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, **374**, 255–257.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998) Fishing down marine food webs. *Science*, **279**, 860–863.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pinnegar, J.K., Jennings, S., O'Brien, C.M. & Polunin, N.V.C. (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, **39**, 377–390.
- Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G. & Pipitone, C. (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*, **27**, 179–200.
- Polunin, N.V.C. & Pinnegar, J.K. (2002) Ecology of fishes in marine food-webs. *Handbook of Fish and Fisheries* (eds P.J. Hart & J.D. Reynolds), pp. 301–320. Blackwell Science, Oxford.
- Pope, J.G., Shepherd, J.G. & Webb, J. (1994) Successful surfing on size spectra: the secret of survival in the sea. *Philosophical Transactions of the Royal Society*, **343**, 41–49.
- Pope, J.G., Stokes, T.K., Murawski, S.A. & Idoine, S.I. (1988) A comparison of fish size composition in the North Sea and on Georges Bank. *Ecodynamics: Contributions to Theoretical Ecology* (eds W. Wolff, C.J. Soeder & F.R. Drepper), pp. 146–152. Springer Verlag, Berlin.
- Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology*, **83**, 703–718.
- Quero, J.C. (1998) Changes in the Euro-Atlantic fish species composition resulting from fishing and ocean warming. *Italian Journal of Zoology*, **65**, 493–499.
- Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E. & Weichart, G. (1990) Phytoplankton in the North Sea and its dynamics: a review. *Netherlands Journal of Sea Research*, **26**, 295–331.
- Reid, P.C., Planque, B. & Edwards, M. (1998) Is observed variability in the long-term results of the CPR survey a response to climate change? *Fisheries Oceanography*, **7**, 282–288.
- Rice, J.C. (2003) Environmental health indicators. *Ocean and Coastal Management*, **46**, 235–259.
- Rice, J.C. & Gislason, H. (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES Journal of Marine Science*, **53**, 1214–1225.
- Rochet, M.-J. & Trenkel, V.M. (2003) Which community indicators can measure the impact of fishing? a review and proposals. *Canadian Journal of Fisheries and Aquatic Science*, **60**, 86–99.
- Rogers, S.I. & Ellis, J.R. (2000) Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science*, **57**, 866–881.
- Roman, J. & Palumbi, S.R. (2003) Whales before whaling in the North Atlantic. *Science*, **301**, 508–510.
- Sherman, K., Alexander, L.M. & Gold, B.D., eds (1993) *Large Marine Ecosystems: Stress, Mitigation and Sustainability*. American Association for the Advancement of Science Press, Washington.
- Sparholt, H. (1990) An estimate of the total biomass of fish in the North Sea. *Journal du Conseil, Conseil International Pour l'Exploration de la Mer*, **46**, 200–210.
- Steele, J.H. & Schumacher, M. (2000) Ecosystem structure before fishing. *Fisheries Research*, **44**, 201–205.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, **57**, 476–494.
- Tiews, K. (1978) On the disappearance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. *Rapports et Procès-Verbaux Des Réunions, Conseil International Pour l'Exploration de la Mer*, **172**, 301–309.
- Ursin, E. (1973) On the prey size preferences of cod and dab. *Medd Komm Dan Fisk-Havunders Series Fiskeri*, **7**, 85–98.
- Walker, P.A. & Heessen, H.J.L. (1996) Long-term changes in ray populations in the North Sea. *ICES Journal of Marine Science*, **53**, 1085–1093.
- Walker, P.A. & Hislop, J.R.G. (1998) Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES Journal of Marine Science*, **55**, 392–402.
- Walters, C. & Kitchell, J.F. (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Science*, **58**, 39–50.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-C., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Ware, D.M. (2000) Aquatic ecosystems: properties and models. *Fisheries Oceanography: an Integrative Approach to Fisheries Ecology and Management* (eds P.J. Harrison & T.R. Parsons), pp. 161–194. Blackwell Science, Oxford.
- Yang, J. (1982) A tentative analysis of the trophic levels of North Sea fish. *Marine Ecology Progress in Series*, **7**, 247–252.