

Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities

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Summary

1. Body size determines rates of respiration and production, energy requirements, mortality rates, patterns of predation and vulnerability to mortality. Body size distributions are often used to describe structure and energy flux in communities and ecosystems.
2. If clear relationships can be established between body size and trophic level in fishes, they may provide a basis for integrating community and ecosystem analyses based on size spectra, food webs and life histories.
3. We investigated relationships between the body sizes (weight and length) of north-east Atlantic fishes and their trophic level. The abundance of ^{15}N , as determined by stable isotope analysis, was used as an index of trophic level.
4. Cross-species and comparative analyses demonstrated that body size was unrelated or weakly related to trophic level. Thus allometric relationships between body size and trophic level could not be used to predict the trophic structure of fish communities.
5. The results of the cross-species analyses contrasted with patterns in the size and trophic structure of entire fish communities. When fish communities were divided into size classes, there were strong positive relationships between size class and trophic level. The slope suggested a mean predator : prey body mass ratio of 496:1
6. Our results suggest that body size does not provide a useful surrogate of trophic level for individual species, but that body size is an excellent predictor of trophic level within the community, providing an empirical basis for integrating community analyses based on models of trophic structure and body size distributions.

Key-words: allometry, body size, food web, life history, phylogeny, trophic level.

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Introduction

Body size is an obvious and important feature of any animal (Peters 1983; Cohen *et al.* 1993). It determines potential predators and prey (Peters 1983), rates of production and natural increase (Banse & Moser 1980; Schwinghamer *et al.* 1986; Brey 1999) and vulnerability to mortality (Adams 1980; Jennings, Reynolds & Mills 1998). Body size distributions have been used to describe structure and energy flux in ecosystems (Sheldon, Prakash & Sutcliffe 1972; Kerr 1974; Platt & Denman 1978; Dickie, Kerr & Boudreau 1987; Boudreau, Dickie & Kerr 1991), and are correlated with species

diversity and abundance in communities (Blackburn, Harvey & Pagel 1990; Cotgreave & Harvey 1992, 1994; Siemann, Tilman & Haarstad 1996).

Since body size determines the range of prey sizes a predator can consume (Cohen *et al.* 1993), larger individuals are expected to feed at higher trophic levels. Studies of size distributions in marine ecosystems are consistent with this hypothesis (Sholtodouglas *et al.* 1991; Fry & Quinones 1994; France, Chandler & Peters 1998). However, these analyses do not explore relationships among species. If such relationships exist, size could provide an easily measured surrogate of trophic level. Moreover, if changes in the size structure of exploited communities (Pope *et al.* 1988; Duplisea & Kerr 1995; Rice & Gislason 1996) reflect changes in their trophic level (Pauly *et al.* 1998; Pauly, Christensen

& Walters 2000) then size-based analyses would provide a simple and effective means of assessing the impacts of exploitation on trophic structure.

If there is a relationship between trophic level and body size then this would indicate that there are relationships between trophic level and other life history parameters. This is because maximum body size is correlated negatively with growth, age at maturity, reproductive output and natural mortality (Beverton & Holt 1959; Beverton 1963, 1987; Pauly 1980; Jennings & Beverton 1991, 1992; Charnov 1993; Sadovy 1996; Stamps, Mangel & Phillips 1998), due to trade-offs among life history allocations (Stearns 1976, 1992). Body size is often used as a surrogate for other life history parameters because for many species the detailed population data needed to describe maturation and growth are difficult and costly to gather (Froese & Binohlan 2000).

One impediment to the study of the relationships between body size and trophic level has been the paucity of trophic level estimates for many species. Trophic level has often been estimated from dietary studies (Yang 1982), but massive research effort is needed to obtain dietary data (Greenstreet 1996) and research on fish has tended to focus on a few abundant species of commercial significance (Rice *et al.* 1991; Christensen 1995). However, nitrogen stable isotope analysis can also be used to estimate trophic level (Fry & Sherr 1984, 1989; Owens 1987) because the abundance of $\delta^{15}\text{N}$ in the tissues of consumers is typically enriched by 3‰ relative to their prey (Peterson, Howarth & Garritt 1985; Peterson & Fry 1987; Hobson & Welch 1992; Fry & Quinones 1994). The main benefits of assessing trophic level using stable isotopes are that the abundance of $\delta^{15}\text{N}$ reflects the composition of the assimilated diet and integrates differences in assimilated diet over time (Hobson & Welch 1992).

The aims of this paper are (i) to describe empirical relationships between trophic level and body size of marine fishes; (ii) to test whether empirical species-based relationships between trophic level and body size can be used to predict the trophic structure of fish communities; and (iii) to describe the trophic structure of entire fish communities based on body size distributions.

Methods

SAMPLING INDIVIDUAL SPECIES

Individual species of fish were sampled in the Celtic and North Seas with a modified Portuguese High-Headline Trawl and Grande Ouverture Verticale (GOV) demersal trawl, respectively (Knijn *et al.* 1993; Warnes & Jones 1995). The trawls were fished from the research vessel 'Cirolana' and fitted with a cod-end of 20 mm stretched mesh. Tows of 30 min duration were made at a speed of approximately 4 knots. Sixty-one sites in the Celtic Sea were fished during February and March 2000, and 75 sites in the North Sea were fished during August and September 2000 (Fig. 1). In both the Celtic and North

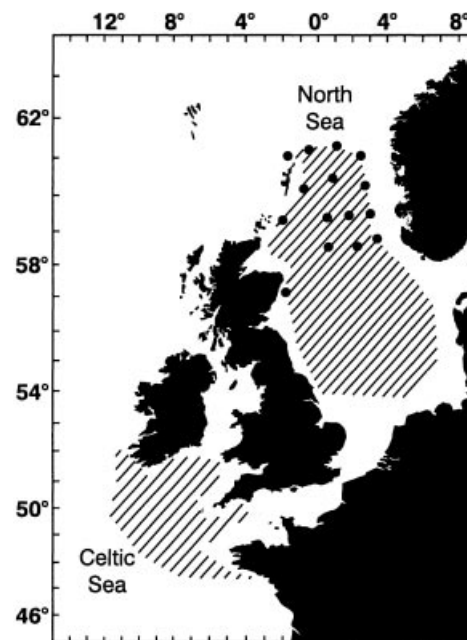


Fig. 1. The regions (hatched) in the Celtic and North Seas from which individual species of fish were collected. The trophic structure of the entire fish community was investigated at 15 North Sea sites (circles).

Seas, three fish of each species caught were dissected to obtain tissue samples for nitrogen stable isotope analysis. Approximately 2 g of white muscle were dissected from the dorsal musculature of each fish, placed in a vial and immediately frozen to $-30\text{ }^{\circ}\text{C}$. On return to the laboratory the frozen tissue was freeze-dried and ground to a fine powder (particles $< 60\text{ }\mu\text{m}$). This was mixed thoroughly and a 0.7-mg sample was weighed into a tin capsule for stable isotope analysis.

Since trophic level increases with body size within species, fish from different species had to be compared at an equivalent stage of their life history. In the absence of detailed maturity and growth data for all species, we always attempted to sample fish that were between 60% and 80% of the maximum recorded length. Because key events in the life history, such as maturity, occur at a relatively constant proportion of maximum size (Beverton & Holt 1959; Beverton 1963, 1992; Charnov 1993), comparing fishes at a fixed proportion of maximum size is equivalent to comparing them at a specific stage of their life history.

SAMPLING THE COMMUNITY

To describe relationships between body size and trophic level for multispecies fish communities, we estimated the ^{15}N content of the entire multispecies catch by \log_2 body mass class at 15 sites in the northern North Sea during September 2000 (Fig. 1). Catches were made with a GOV trawl, towed for 30 min at approximately 4 knots.

All fish of all species were assigned to \log_2 size classes. Fish $> 512\text{ g}$ total weight were assigned directly

Table 1. Proportion of body mass sampled by size class

Size class (g)	% individual body mass sampled	Composition of sample	Number of fish sampled in size class
> 1–2	20%	Whole fish excluding head, tail and guts	20–25 (all in catch if < 20)
> 2–4	20%	Whole fish excluding head, tail and guts	20–25 (all in catch if < 20)
> 4–8	20%	White muscle and skin	20–25 (all in catch if < 20)
> 8–16	20%	White muscle and skin	20–25 (all in catch if < 20)
> 16–32	10%	White muscle and skin	20–25 (all in catch if < 20)
> 32–64	5%	White muscle	20–25 (all in catch if < 20)
> 64–128	5%	White muscle	20–25 (all in catch if < 20)
> 128–256	2%	White muscle	20–25 (all in catch if < 20)
> 256–512	1%	White muscle	20–25 (all in catch if < 20)
> 512–1024	0.5%	White muscle	All in catch
> 1024–2048	0.2%	White muscle	All in catch
> 2048–4096	0.1%	White muscle	All in catch
> 4096–8192	0.05%	White muscle	All in catch
> 8192–16384	0.05%	White muscle	All in catch
> 16384–32768	0.05%	White muscle	All in catch

to size classes while fish weighing ≤ 512 g were more abundant and had to be subsampled randomly before assignment (fish from all species were combined within size classes). We dissected tissue from 20–25 randomly selected individuals in each size class (or all the fish in the size class if < 20 were caught). The limits on the number of fish processed were imposed by the practicality of dissecting tissue before spoilage had started to occur.

A sample of white muscle tissue was dissected from the dorsal musculature of each fish for stable isotope analysis. Each fish was weighed before the sample was dissected, and the size of the sample retained was set at a fixed percentage of body weight in each size class (Table 1). For fish smaller than 32 g, we cut the largest possible fillet from the dorsal musculature of each fish, and for fish smaller than 4 g we kept all the tissue that remained after removing the head and guts. The tissue from fish in each size class was homogenized in a blender, or crushed and ground manually, to produce a smooth paste. Approximately 4 g of paste were retained and immediately frozen to -30 °C. On return to the laboratory the frozen tissue was freeze-dried and ground to a fine powder (particles < 60 μ m). This was thoroughly mixed and a 0.7-mg sample was weighed into a tin capsule for stable isotope analysis.

STABLE ISOTOPE ANALYSIS

The ^{15}N composition of the samples was determined using continuous flow isotope ratio mass spectrometry (CF-IRMS) (Preston & Owens 1983; Preston 1992). Weighed samples of 0.7–1.0 mg ground material were oxidized and the N_2 passed to a single inlet dual collector mass spectrometer (Automated Nitrogen Carbon Analysis (ANCA) SL 20–20 system). This was a continuous flow system, so two samples of reference material (an internal standard) were analysed after every five tissue samples in order to calibrate the system and compensate for drift with time (ANCA-SL Dual Isotope v3.4 software).

Ratios of $^{15}\text{N} : ^{14}\text{N}$ were expressed relative to N_2 in air for nitrogen and calculated as:

$$\delta^{15}\text{N} = \left(\frac{{}^{15}\text{N} : {}^{14}\text{N}_{\text{sample}}}{{}^{15}\text{N} : {}^{14}\text{N}_{\text{standard}}} - 1 \right) \times 1000$$

The SD for the repeated $\delta^{15}\text{N}$ measurements made with the reference material was 0.1%.

BODY SIZE AND LIFE HISTORIES

The biology and ecology of many fishes in the Celtic and North Seas is poorly known, and detailed growth and maturity data were not always available. For most species, we used maximum recorded body size as a surrogate for other life history parameters (Froese & Binohlan, 2000). Maximum body sizes were taken from Wheeler (1969), Knijn *et al.* (1993) and unpublished data. Transformations between weight and length were made using conversion factors (Bedford, Woolner & Jones 1986; Coull *et al.* 1989; CEFAS, unpublished).

Fish communities in the Celtic and North Sea are heavily exploited and the maximum observed size of many species has fallen in recent years. In many cases, this has been associated with reductions in the age and size at maturity and increases in growth rate (Torensen 1990; Rijnsdorp 1993; Millner & Whiting 1996; Rijnsdorp & van Leeuwen 1996). This is the combined effect of genetic and phenotypic responses to fishing mortality (Law & Rowell 1993; Rowell 1993; Stokes & Blythe 1993; Law & Stokes, 2001). In reporting maximum sizes we tried to select those that were indicative of the maximum sizes seen in the fish community at the present time. In many cases, therefore, they are smaller than those reported historically.

DATA ANALYSIS

We used linear regression to explore relationships between maximum body size (as length or weight) and

$\delta^{15}\text{N}$. In order to confirm that any significant relationships were not confounded by the non-independence of data used in the cross-species analysis, the significance of relationships between body size and trophic level was also assessed using a comparative approach (Felsenstein 1985; Harvey & Pagel 1991; Harvey 1996). Phylogenetically based analyses overcome the fact that related taxa may share traits due to common ancestry and yield data which are statistically independent (Harvey & Pagel 1991). The comparative approach has already been used to assess links between life

histories and vulnerability to fishing (Jennings *et al.* 1998; Reynolds, Jennings & Dulvy 2001) and life histories and recruitment variation (Rickman *et al.* 2000).

Phylogenetic relationships among species were determined from published taxonomic and molecular evidence (Wheeler 1969; Cohen 1989; Cohen *et al.* 1990; Nelson 1994). Phylogenetically independent differences (contrasts) in body size within pairs of related species were calculated by subtracting the \ln maximum length of the smaller species from the larger one. Preliminary

Table 2. Species recorded in the Celtic Sea, their maximum lengths and weights, and the length and $\delta^{15}\text{N}$ of individuals that were sampled. Groups of related species that were used to calculate independent contrasts in the phylogenetic analysis have the same numeric code under 'contrast'. Three individuals were sampled from each species except *, where $n = 1$

Scientific name	Common name	Contrast	Maximum length (mm)	Maximum weight (g)	Sample length (mm) mean \pm SD	Mean sample length as % maximum	$\delta^{15}\text{N}\text{‰}$ mean \pm SD
<i>Scyliorhinus canicula</i>	Lesser spotted dogfish		880	2763	647 \pm 18	74	15.0 \pm 0.91
<i>Galeorhinus galeus</i>	Tope	1	1670	23948	1090 \pm 164	65	17.0 \pm 0.82
<i>Mustelus asterias</i>	Starry smooth hound	1	1700	25429	1115 \pm 15	66	14.0 \pm 0.22
<i>Squalus acanthias</i>	Spurdog		1000	4251	628 \pm 40	63	12.0 \pm 0.57
<i>Raja montagui</i>	Spotted ray	2	790	3418	626 \pm 18	79	13.7 \pm 0.93
<i>Leucoraja naevus</i>	Cuckoo ray	2	920	5232	641 \pm 30	70	13.6 \pm 0.44
<i>Clupea harengus</i>	Herring	3	315	257	246 \pm 1	78	13.3 \pm 0.23
<i>Sardina pilchardus</i>	Pilchard	3	250	126	190 \pm 17	76	12.6 \pm 0.59
<i>Sprattus sprattus</i>	Sprat	3	170	40	126 \pm 6	74	14.3 \pm 1.26
<i>Engraulis encrasicolus</i>	Anchovy		200	70	139 \pm 9	70	14.6 \pm 0.95
<i>Argentina phyraena</i>	Lesser argentine		270	124	198 \pm 7	73	12.1 \pm 0.22
<i>Lophius piscatorius</i>	Anglerfish		1060	18045	653 \pm 45	62	14.3 \pm 0.72
<i>Gadiculus argenteus</i>	Silvery pout	5	150	29	118 \pm 7	79	10.2 \pm 0.26
<i>Gadus morhua</i>	Cod		1100	14024	735 \pm 99	67	15.2 \pm 0.77
<i>Melanogrammus aeglefinus</i>	Haddock		680	3157	490 \pm 30	72	12.6 \pm 0.85
<i>Merlangius merlangus</i>	Whiting	6	420	608	306 \pm 15	73	17.2 \pm 1.24
<i>Micromesistius poutassou</i>	Blue whiting		340	315	240 \pm 10	71	11.1 \pm 0.64
<i>Molva molva</i>	Ling	4	1400	16495	1107*	79	15.3
<i>Phycis blennoides</i>	Forkbeard	4	650	3067	426 \pm 31	66	13.3 \pm 0.50
<i>Pollachius virens</i>	Saithe	6	1400	19860	1054 \pm 28	75	14.4 \pm 0.60
<i>Trisopterus esmarki</i>	Norway pout	7	230	122	168 \pm 12	73	13.7 \pm 1.03
<i>Trisopterus minutus</i>	Poor cod	7	200	80	146 \pm 5	73	12.9 \pm 1.12
<i>Merluccius merluccius</i>	Hake	5	1200	13046	863 \pm 120	72	13.5 \pm 0.29
<i>Beryx splendens</i>	Beryx		400	319	241 \pm 2	60	10.8 \pm 0.85
<i>Zeus faber</i>	John dory	8	500	2214	356 \pm 40	71	14.7 \pm 0.74
<i>Capros aper</i>	Boarfish	8	160	52	116 \pm 5	73	10.4 \pm 0.20
<i>Helicolenus dactylopterus</i>	Bluemouth		460	1750	311 \pm 17	68	13.5 \pm 0.26
<i>Aspitrigla cuculus</i>	Red gurnard	9	400	655	258 \pm 15	65	13.2 \pm 0.11
<i>Eutrigla gurnardus</i>	Grey gurnard	9	460	886	325 \pm 27	71	12.8 \pm 0.23
<i>Dicentrarchus labrax</i>	Bass	10	1000	11530	639 \pm 3	64	15.8 \pm 0.42
<i>Trachurus trachurus</i>	horse mackerel	10	500	1344	347 \pm 22	69	13.8 \pm 0.41
<i>Sponyllosoma cantharus</i>	Black sea bream		500	2068	302 \pm 22	60	15.2 \pm 0.85
<i>Mullus surmuletus</i>	Red mullet	11	400	940	280 \pm 20	70	15.3 \pm 0.82
<i>Echiichthys vipera</i>	lesser weaver	11	160	30	106 \pm 8	66	15.1 \pm 0.21
<i>Hyperoplus immaculatus</i>	Corbins sandeel	11	340	151	267 \pm 5	79	12.2 \pm 0.87
<i>Callionymus lyra</i>	Dragonet	11	230	74	158 \pm 14	69	12.7 \pm 0.40
<i>Scomber scombrus</i>	Mackerel	11	399	555	289 \pm 4	72	12.7 \pm 1.26
<i>Lepidorhombus boscii</i>	Four-spot megrim	12	410	556	284 \pm 17	69	11.9 \pm 0.12
<i>Lepidorhombus whiffiagonis</i>	Megrim	12	600	1970	394 \pm 38	66	12.5 \pm 0.74
<i>Arnoglossus imperialis</i>	Imperial scaldfish		250	93	165 \pm 8	66	10.9 \pm 0.14
<i>Glyptocephalus cyanoglossus</i>	Witch	13	460	736	299 \pm 24	65	13.6 \pm 0.51
<i>Hippoglossoides platessoides</i>	Long rough dab		250	133	180 \pm 10	72	14.1 \pm 0.16
<i>Limanda limanda</i>	Dab		310	325	193 \pm 17	62	14.7 \pm 1.66
<i>Microstomus kitt</i>	Lemon sole	13	440	1102	239 \pm 14	54	12.9 \pm 2.00
<i>Platichthys flesus</i>	Flounder	14	460	1231	315 \pm 3	68	13.5 \pm 1.17
<i>Pleuronectes platessa</i>	Plaice	14	510	1454	336 \pm 13	66	12.9 \pm 0.97
<i>Microchirus variegatus</i>	Thick back sole	15	300	314	202 \pm 3	67	13.5 \pm 0.73
<i>Solea solea</i>	Sole	15	480	1339	329 \pm 38	69	14.6 \pm 0.71

analysis of the data showed that log transformation removed the effects of the relationship between body size and location in the phylogeny (Freckleton 2000). Contrasts in trophic level were then calculated for the same species pair. The significance of the relationship between contrast in maximum length and contrast in trophic level was assessed using binomial tests (Harvey & Pagel 1991).

We analysed the North Sea and Celtic Sea data separately. Contrasts in body size were set to positive since the body size of the smaller species was always subtracted from the larger. If phylogenetic relationships between species could not be resolved, we calculated all $(n^2 - n)/2$ contrasts for each group and presented mean values. The null expectation in this analysis is that the

contrasts in trophic level will be randomly distributed around zero when the contrast in body size is set to positive.

Results

SPECIES-BASED ANALYSIS

Forty-three species were sampled in the North Sea and 48 species in the Celtic Sea (Tables 2 and 3). The mean length of individuals sampled was 50–77% of maximum length in the North Sea. For five species, only one replicate was obtained in the acceptable size range (Table 2). In the Celtic Sea, mean length of individuals sampled was 54–79% of maximum length, and only

Table 3. Species recorded in the North Sea, their maximum lengths and weights, and the length and $\delta^{15}\text{N}$ of individuals that were sampled. Groups of related species that were used to calculate independent contrasts in the phylogenetic analysis have the same numeric code under 'contrast'. Three individuals were sampled from each species except *, where $n = 1$

Scientific name	Common name	Contrast	Maximum length (mm)	Maximum weight (g)	Sample length (mm) mean \pm SD	Mean sample length as % maximum	$\delta^{15}\text{N}$ % mean \pm SD
<i>Scyliorhinus canicula</i>	Lesser spotted dogfish		880	2763	657 \pm 49	75	14.1 \pm 0.86
<i>Leucoraja naevus</i>	Cuckoo ray	1	920	4220	550*	60	12.7
<i>Raja radiata</i>	Starry ray	1	660	2450	433 \pm 17	66	14.3 \pm 0.38
<i>Clupea harengus</i>	Herring	2	340	326	262 \pm 3	77	12.1 \pm 0.53
<i>Sprattus sprattus</i>	Sprat	2	170	38	127 \pm 9	75	13.3 \pm 0.42
<i>Argentina sphyraena</i>	Lesser argentine		270	124	197 \pm 9	73	13.3 \pm 0.16
<i>Lophius piscatorius</i>	Anglerfish		1060	18045	672 \pm 99	63	15.3 \pm 0.81
<i>Brosme brosme</i>	Torsk	3	890	8464	550*	62	14.3
<i>Gadiculus argenteus</i>	Silvery pout	4	160	35	120 \pm 9	75	11.3 \pm 0.87
<i>Gadus morhua</i>	Cod		1230	17650	816 \pm 94	66	16.5 \pm 1.83
<i>Melanogrammus aeglefinus</i>	Haddock		720	3515	434 \pm 3	60	14.7 \pm 0.23
<i>Merlangius merlangus</i>	Whiting	5	540	1360	271 \pm 4	50	14.8 \pm 0.28
<i>Micromesistius poutassou</i>	Blue whiting		370	410	283 \pm 12	77	11.3 \pm 0.22
<i>Molva molva</i>	Ling	3	1400	16495	730 \pm 17	51	13.6 \pm 0.58
<i>Pollachius virens</i>	Saithe	5	1550	23609	1070 \pm 10	76	15.2 \pm 0.52
<i>Enchelyopus cimbrius</i>	Four bearded rockling		330	182	222 \pm 8	67	13.3 \pm 0.17
<i>Trisopterus esmarki</i>	Norway pout	6	230	122	166 \pm 3	72	13.6 \pm 0.54
<i>Trisopterus luscus</i>	Bib	6	420	1095	227 \pm 6	54	16.8 \pm 0.27
<i>Trisopterus minutus</i>	Poor cod	6	200	80	153 \pm 6	76	17.3 \pm 0.32
<i>Merluccius merluccius</i>	Hake	4	1100	10950	591 \pm 37	54	14.4 \pm 0.71
<i>Capros aper</i>	Boarfish	7	140	40	93 \pm 11	67	11.9 \pm 0.39
<i>Sebastes viviparus</i>	Norway haddock	8	360	876	237 \pm 38	66	12.5 \pm 0.85
<i>Eutrigla gurnardus</i>	Grey gurnard	7	460	886	325 \pm 25	71	15.3 \pm 0.08
<i>Myxocephalus scorpius</i>	Bull rout	8	350	838	250*	71	16.5
<i>Agonus cataphractus</i>	Pogge	8	180	37	132*	73	14.1
<i>Cyclopterus lumpus</i>	Lumpsucker	8	500	5780	371*	74	12.1
<i>Trachurus trachurus</i>	Horse mackerel	9	500	1344	347 \pm 13	69	17.9 \pm 0.49
<i>Echiichthys vipera</i>	Lesser weaver	9	160	35	96 \pm 9	60	15.1 \pm 0.10
<i>Anarhichas lupus</i>	Wolffish	9	1000	10392	714 \pm 144	71	12.8 \pm 0.06
<i>Ammodytes marinus</i>	Raitt's sandeel	10	240	48	172 \pm 22	72	13.6 \pm 0.40
<i>Hyperoplus lanceolatus</i>	Greater sandeel	10	350	154	226 \pm 7	64	14.4 \pm 0.51
<i>Callionymus lyra</i>	Dragonet		300	148	227 \pm 16	76	12.7 \pm 0.58
<i>Scomber scombrus</i>	Mackerel	9	399	555	268 \pm 19	67	12.4 \pm 0.56
<i>Lepidorhombus whiffiagonis</i>	Megrim	11	610	2059	357 \pm 19	58	12.1 \pm 1.09
<i>Phrynorhombus norvegicus</i>	Norwegian topknot	11	140	24	101 \pm 12	72	13.8 \pm 0.30
<i>Arnoglossus laterna</i>	Scaldfish		160	38	109 \pm 7	68	15.2 \pm 0.51
<i>Glyptocephalus cyanoglossus</i>	Witch	12	470	696	308 \pm 39	65	12.9 \pm 0.29
<i>Hippoglossoides platessoides</i>	Long rough dab		250	133	181 \pm 24	72	13.4 \pm 0.28
<i>Limanda limanda</i>	Dab	13	330	400	190 \pm 10	58	15.5 \pm 0.22
<i>Microstomus kitt</i>	Lemon sole	12	457	1181	267 \pm 15	58	13.8 \pm 0.79
<i>Pleuronectes platessa</i>	Plaice	13	580	2157	361 \pm 7	62	15.3 \pm 0.78
<i>Buglossinium luteum</i>	Solenette	14	130	22	93 \pm 6	72	14.5 \pm 0.37
<i>Solea solea</i>	Sole	14	460	950	278 \pm 30	60	16.8 \pm 0.11

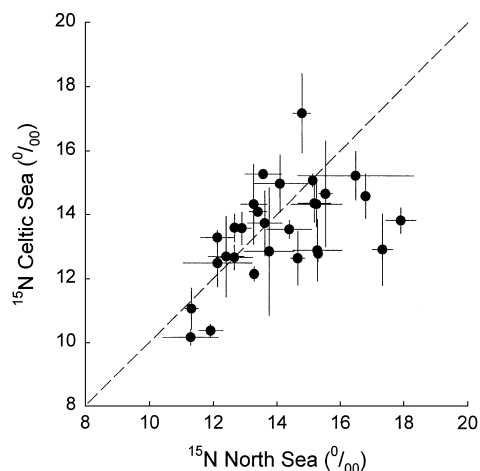


Fig. 2. Relationship between the $\delta^{15}\text{N}$ of white muscle tissue in Celtic and North Sea fishes of the same species (means \pm 95% CL).

one replicate was obtained for the ling *Molva molva* (Table 3).

In the North Sea, there was a significant relationship between the mean length of individuals sampled as a proportion of maximum length (L_p) and maximum length ($F_{1,41} = 5.15$, $P = 0.029$). Given that body size and $\delta^{15}\text{N}$ can be correlated positively within species (e.g. Sholtodouglas *et al.* 1991), the significant relationship between L_p and maximum length could have affected the results of subsequent analyses. Further exploration of the data showed that the significance of the relationship between L_p and maximum length was due to the small ling that were sampled (Table 2, maximum length 1400 mm, $P = 51\%$). When the data for ling were excluded, the relationship between L_p and maximum length was not significant ($F_{1,40} = 2.38$, $P = 0.131$). In subsequent analyses, the inclusion or exclusion of the North Sea ling did not affect on the significance of our results. Moreover, for both the North Sea and Celtic Sea fishes, the inclusion or exclusion of species for which $L_p \neq 60\text{--}80\%$, or the inclusion or exclusion of those species for which only one replicate was caught, made no difference to the significance of any results that we report. The relationship between L_p and maximum length was not significant for the Celtic Sea ($F_{1,46} = 0.41$, $P = 0.523$).

Mean $\delta^{15}\text{N}$ ranged from 11.3 to 17.9 in the North Sea and 10.2–17.2 in the Celtic Sea. The $\delta^{15}\text{N}$ values for the 29 species that occurred in both the North and Celtic Seas (Fig. 2) were significantly but weakly correlated ($r = 0.53$, d.f. = 27; $P < 0.01$). The relationship between \log_2 maximum body mass or \log_{10} maximum length and $\delta^{15}\text{N}$ (Figs 3 and 4) was not significant for North Sea fishes (mass: $r^2 = 0.03$; $F_{1,41} = 1.16$, $P > 0.1$ length: $r^2 = 0.02$; $F_{1,41} = 0.86$, $P > 0.1$) but was significant for Celtic Sea fishes (mass: $\delta^{15}\text{N} = 0.249 \log_2 \text{mass} + 11.1$, $r^2 = 0.21$; $F_{1,46} = 11.84$; $P = 0.001$ length: $\delta^{15}\text{N} = 2.24 \log_{10} \text{length} + 7.55$; $r^2 = 0.17$; $F_{1,46} = 9.58$; $P = 0.003$). When the relationships between \log_2 maximum body

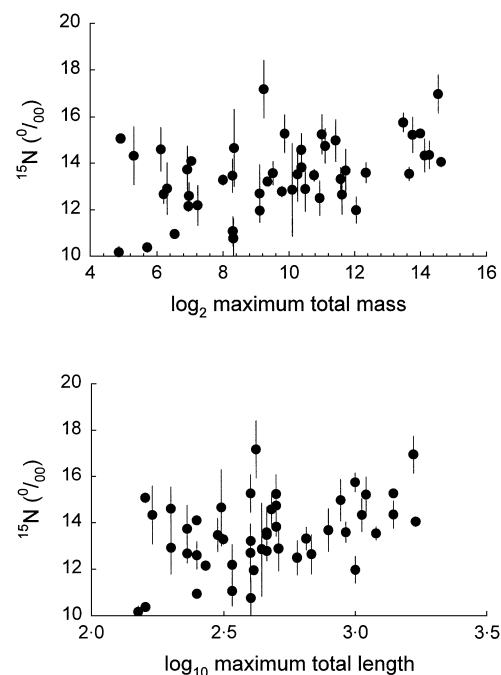


Fig. 3. Relationships between the $\delta^{15}\text{N}$ of white muscle tissue (mean \pm 95% CL) and maximum weight (upper panel) or total length (lower panel) in Celtic Sea fishes.

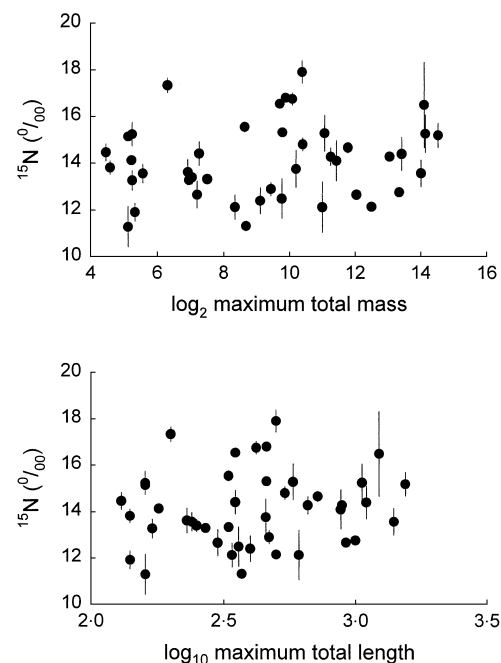


Fig. 4. Relationships between the $\delta^{15}\text{N}$ of white muscle tissue (mean \pm 95% CL) and maximum weight (upper panel) or total length (lower panel) in North Sea fishes.

mass or \log_{10} maximum length and $\delta^{15}\text{N}$ were investigated using a phylogenetic comparative approach (Fig. 5), the results were not significant in both the North Sea (binomial test: mass: 6 positive, 8 negative contrasts, $P > 0.1$; length: 5 positive, 9 negative contrasts $P > 0.1$) and Celtic Sea (mass: 8 positive, 7 negative

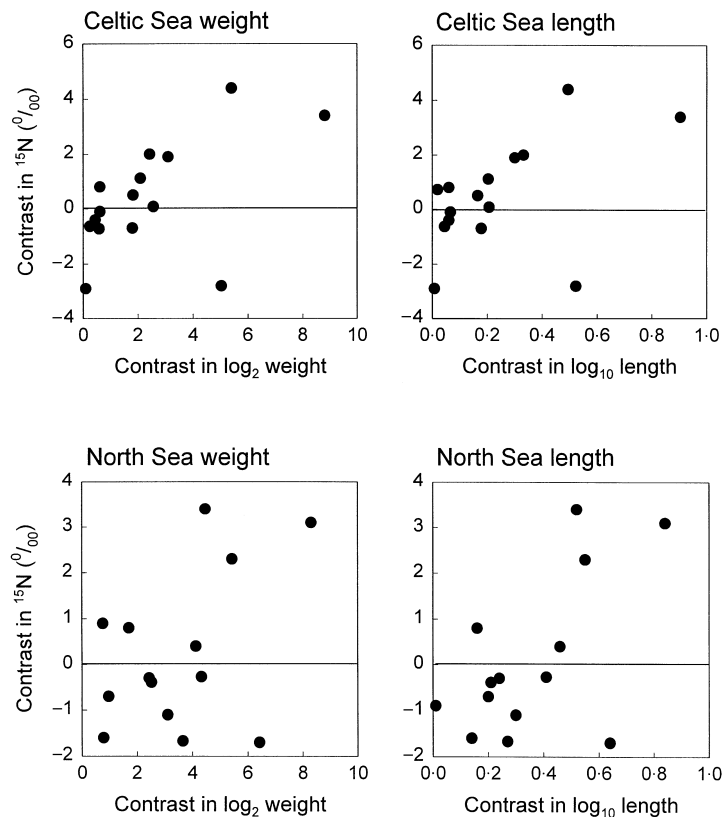


Fig. 5. Relationships between contrasts in the $\delta^{15}\text{N}$ of white muscle tissue and contrasts in maximum weight and length for Celtic Sea fishes (upper panels) and North Sea fishes (lower panels).

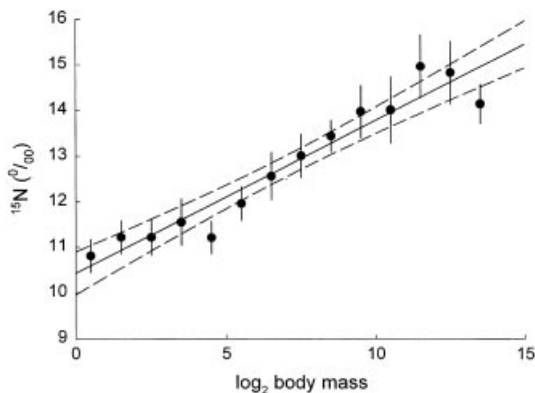


Fig. 6. Relationship between the $\delta^{15}\text{N}$ of white muscle tissue and size class for the northern North Sea fish community.

contrasts, $P > 0.1$; length: 9 positive, 6 negative contrasts, $P > 0.1$).

COMMUNITY-BASED ANALYSIS

At the 15 sites where relationships between $\delta^{15}\text{N}$ and body mass in the entire community were investigated, there were significant positive relationships between these variables. The pooled data (Fig. 6) showed a significant increase in $\delta^{15}\text{N}$ with body size in the community as a whole ($r^2 = 0.93$, $F = 147.8$, d.f. = 1,12; $P < 0.0001$). The relationship was given by the equation $\delta^{15}\text{N} = 0.335 \log_2 \text{body mass} + 10.4$. There was very

little variation around the mean $\delta^{15}\text{N}$ at size among sites, suggesting similar structuring of the fish communities.

Discussion

Cross-species relationships between $\delta^{15}\text{N}$ and body size were weak or non-significant, in accordance with the results of the comparative analyses. However, the $\delta^{15}\text{N}$ of the whole community increased consistently and significantly with body size, implying that small species feeding at high trophic levels were relatively scarce. Patterns at the community level were consistent with the expectation that predator–prey relationships lead to powerful size-based trophic structuring.

Body size is used widely to predict production: biomass ratios, natural mortality and respiration rates of animals (Banse & Moser 1980; Schwinghamer *et al.* 1986; Brey 1999). However, our relationships between body size and $\delta^{15}\text{N}$ were too weak to provide precise predictions of trophic level. The relationships could be weak (i) because the maximum body size of a species does not constrain its trophic level; (ii) because there are large spatial and temporal differences in the $\delta^{15}\text{N}$ of the same species that reduce the power of our analyses; or (iii) because $\delta^{15}\text{N}$ is not a good index of trophic level. We favour (i) and reject (ii) and (iii) for the following reasons.

A large sampling area is needed to catch a range of species of comparable size, while a small sampling area

is needed to avoid spatial variance in $\delta^{15}\text{N}$ among individuals. If the sampling area is reduced, then the number of species that can be included in the analysis will fall. We consider that it is more important to catch fish from narrow and comparable size classes (60–80% of maximum length in this study) than to be overly concerned about spatial variation, since the effects of ontogenetic shifts in $\delta^{15}\text{N}$ and low replication dramatically reduce the power of our analyses. For example, studies of fishes taken from a single trawl tow (*c.* 2 nautical miles in length) show a 2% increase in $\delta^{15}\text{N}$ between the smallest and largest individuals of the same species (S.J., unpublished data), while variation among individuals of the same species and same size is much less (Tables 2 and 3). Moreover, we demonstrated significant correlations between the $\delta^{15}\text{N}$ of the same species in two widely separated sea areas, suggesting that fishes at the same life history stages are feeding at similar trophic levels.

In our analyses we assumed that $\delta^{15}\text{N}$ was linearly related to trophic level. We did not attempt to assign actual trophic levels to the fishes, since this requires that the trophic level of a group of animals closer to the base of the food chain is known. Assigning trophic levels to phytoplankton or zooplankton, or species that consume them, is exceedingly difficult, because pure phytoplankton cannot be extracted from plankton samples to make $\delta^{15}\text{N}$ measurements and because the trophic level of zooplankton can vary by two or more trophic levels due to the effects of the microbial food loop (Azam *et al.* 1983). We assume a $\delta^{15}\text{N}$ enrichment of around 3% for each trophic step (e.g. Cabana & Rasmussen 1994; Zanden, Casselman & Rasmussen 1999; Post, Pace & Hairston 2000). However, Adams & Sterner (2000) have commented that the fractionation of 3.4% reported by Minagawa & Wada (1984) was actually the numerical mean of reported values between 1.3 and 5.3%, and this has prompted calls for experimental evaluation and validation (e.g. Gannes *et al.* 1997; Pinnegar & Polunin 1999; Ponsard & Averbuch 1999; Schoella 1999; Adams & Sterner 2000). We cannot provide such validation for all the complex feeding relationships that apply to the species included in this study, but the choice of value will not affect the conclusions of our analyses unless the increase in $\delta^{15}\text{N}$ is a non-linear function of trophic level. There is no existing evidence for this.

If there is a linear increase of 3% $\delta^{15}\text{N}$ per trophic level, our community-based analysis can be used to estimate the mean predator : prey body mass ratio. The slope of the relationship between \log_2 body mass and $\delta^{15}\text{N}$ (0.335) suggests that predators in this North Sea fish community have a mean mass approximately 496 times greater than that of their prey. This assumes that predator-prey relationships in the community occur predominantly among the species sampled. Clearly, many of the smaller size classes will eat plankton and benthos, but larger ones are predominantly piscivorous.

Attempts to assign trophic levels to small fishes and invertebrates using diet data have been fraught with difficulty, because gut contents can be virtually indistinguishable and diet studies require a massive sampling commitment (Polunin & Pinnegar 2002). If body size could be used as a surrogate for trophic level in marine communities, then size-spectra could be analysed to investigate changes in trophic structure as well as production. It is well known that the size structure of the biota in a marine ecosystem follows regular patterns (Sheldon *et al.* 1972) and the relationship between body size (as classes) and total biomass by size class can be predicted by theoretical models of energy flow from prey to predators (Kerr 1974; Platt & Denman 1978; Dickie *et al.* 1987). Size spectra have been used widely to describe aquatic community structure (Kerr 1974; Dickie *et al.* 1987; Pope *et al.* 1988; Boudreau *et al.* 1991; Thiebaut & Dickie 1992; Sprules & Stockwell 1995) and to investigate the effect of perturbations on community structure (Boudreau & Dickie 1992; Duplisea & Kerr 1995; Rice & Gislason 1996). The present study provides empirical evidence, in support of existing theoretical evidence, that size alone is a useful predictor of trophic level in the community. This provides a basis for integrating studies of body size distributions and food webs (e.g. Cohen *et al.* 1993; Hall & Raffaelli 1993) and for assessing the impacts of fishing on the marine ecosystem (e.g. Hall 1999).

Size-based analyses have shown that fishing leads to predictable changes in the size structure of fish communities (Pope *et al.* 1988; Boudreau & Dickie 1992; Duplisea & Kerr 1995; Rice & Gislason 1996), while ecosystem models based on trophic relationships suggest that fishing may reduce the trophic level of fish communities (Christensen & Pauly 1992; Walters, Christensen & Pauly 1997; Pauly *et al.* 1998, 2000). Size-based models of fishing effects are far easier to parameterize than ecosystem models, and our results suggest that size spectra could be reparameterized using relationships between body size and trophic level for the community. This provides a link between the use of size spectra to examine the effects of exploitation on community structure and the use of ecosystem models. The next step is to investigate the stability of relationships between community size structure and trophic level in space and time. If such relationships are stable, then the increases in the slope of size spectra that result from fishing (Pope *et al.* 1988; Rice & Gislason 1996), will indicate decreases in the trophic level of the community.

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