

Linking size-based and trophic analyses of benthic community structure

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ABSTRACT: Models of biomass size spectra assume that organisms with higher body mass feed at higher trophic levels, but explicit empirical tests of this pattern are rare. We used nitrogen stable isotopes ($\delta^{15}\text{N}$) as an index of the trophic level in a benthic fish and invertebrate size-spectrum, and demonstrated that body mass was positively and significantly related to trophic level. This pattern was consistent with the expectation that predator-prey relationships led to powerful size-based trophic structuring in marine communities and ecosystems. Further analysis of intra- and interspecific relationships between body mass and trophic level in the community showed that increases in trophic level across the size spectrum were predominantly a consequence of intra-specific increases in trophic level with body mass and not a consequence of larger species (species with greater maximum body mass) feeding at higher trophic levels. We confirmed the absence of strong inter-specific relationships between maximum body mass and trophic level with cross-species and phylogenetic comparative approaches. Size-based models are easier and cheaper to parameterise than most food-web models. Subject to the persistence of relationships between body mass and trophic level in space and time, our results suggest that size spectra could be parameterised with body mass–trophic level relationships and used to describe the trophic structure of some marine communities and ecosystems.

KEY WORDS: Size-spectra · Trophic level · Food web · Community structure · Stable isotopes · Phylogeny

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INTRODUCTION

Biomass size-spectra are widely used to describe the structure of marine ecosystems (Sheldon et al. 1972, Pope et al. 1988, Duplisea & Kerr 1995, Rice & Gislason 1996, Duplisea 1998) and models of size-spectra assume that total biomass decreases in progressively heavier body-mass classes because there is inefficient energy transfer from prey to predators (Kerr 1974, Dickie et al. 1987, Boudreau et al. 1991, Thiebaut & Dickie 1992, 1993). This implies that organisms with higher body mass feed at higher trophic levels, but explicit empirical tests of this pattern are rare (Fry & Quinones 1994, France et al. 1998).

Body mass is a fundamental attribute of any animal (Peters 1983). Species with lower adult body mass have higher intrinsic rates of increase (Schwinghamer et al. 1986), production (Brey 1990, 1999), reproductive output (Gunderson & Dygert 1988, Charnov 1993) and natural mortality (Beverton & Holt 1959, Pauly 1980). Differences in body mass within species also account for differences in growth, production and mortality, with smaller individuals growing faster and realising more production per unit body mass, but suffering higher natural mortality. Within a size spectrum, ecological processes such as production are treated solely as a function of body size, and thus a small individual of a large species is equivalent to a large individual of a small species in the same body mass class.

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Trophic level is expected to increase with increasing body size because, with the exception of parasites, most predators are larger than their prey (Cohen et al. 1993). However, this increase has been difficult to quantify since relationships between predator and prey species are highly transient in time. The transience results from the exceptional scope for growth within most marine species and the variability in growth within and among species (Brey 1999). For example, the body mass of many species increases by 5 orders of magnitude or more during their life (Cushing 1975) and a fast-growing species may begin life as a prey item for other species only to become the main predator on the same group of species within one year (Boyle & Pierce 1994, Boyle & Boletzky 1996).

The transience of predator-prey interactions, in space as well as time (Kingsford 1992), makes the study of trophic relationships a data-intensive exercise. Even studies of predator-prey relationships within small well-studied groups of commercially exploited fish species have required stomach sampling on unprecedented scales (Magnússon 1995, ICES 1999). Such species-focused approaches are unlikely to help describe trophic relationships in larger communities and ecosystems. For this reason, descriptions of trophic structure that aggregate across individuals on the basis of size rather than species may provide desirable simplifications.

One impediment to the description of links between body size and trophic level is the problem of estimating the trophic level of species that switch diet frequently, prey on species that are digested at different rates, and have gut contents that cannot be clearly identified (Polunin & Pinnegar 2002). Nitrogen stable isotope analysis provides an alternate method of estimating trophic level (Fry & Sherr 1984, Minawaga & Wada 1984, 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 et al. 1985, Peterson &

Fry 1987, Hobson & Welch 1992, Fry & Quinones 1994, Cabana & Rasmussen 1996, Post et al. 2000). Moreover, the abundance of $\delta^{15}\text{N}$ reflects the composition of assimilated diet and integrates differences in assimilated diet over time (Hobson & Welch 1992).

Nitrogen stable isotopes have already been used to provide evidence of links between trophic level and body mass in planktonic (Fry & Quinones 1994) and benthic (France et al. 1998) communities and to provide evidence for intraspecific relationships between body size and trophic level (Rau et al. 1983, Sholtodouglas et al. 1991, Wainwright et al. 1993, Hentschel 1998, Lindsay et al. 1998, Persson & Hansson 1999). We build on these observations to assess the roles of intra- and inter-specific relationships between body mass and trophic level in governing the trophic structure of a benthic community. If body size does provide a surrogate for trophic level, then analyses of size-spectra could be used to describe changes in the trophic structure of marine communities and ecosystems. The aims of this study were (1) to determine whether body size class is a good predictor of trophic level in a benthic community, and (2) to assess the role of intra- and inter-specific size-related changes in trophic level in determining trophic structure. We used $\delta^{15}\text{N}$ as an index of trophic level.

MATERIALS AND METHODS

We investigated relationships between body size and $\delta^{15}\text{N}$ in the Silver Pit region of the central North Sea (Fig. 1). The Silver Pit is predominantly 50 to 80 m deep, with a muddy-sand substratum, and is surrounded by shallower sandy areas. Epibenthic fishes and invertebrates were sampled with a 2 m beam trawl fished from the RV 'Corystes'. Three randomly located replicate tows of 5 min duration were completed in each of seven 1 × 1 nautical mile boxes (Fig. 1). The

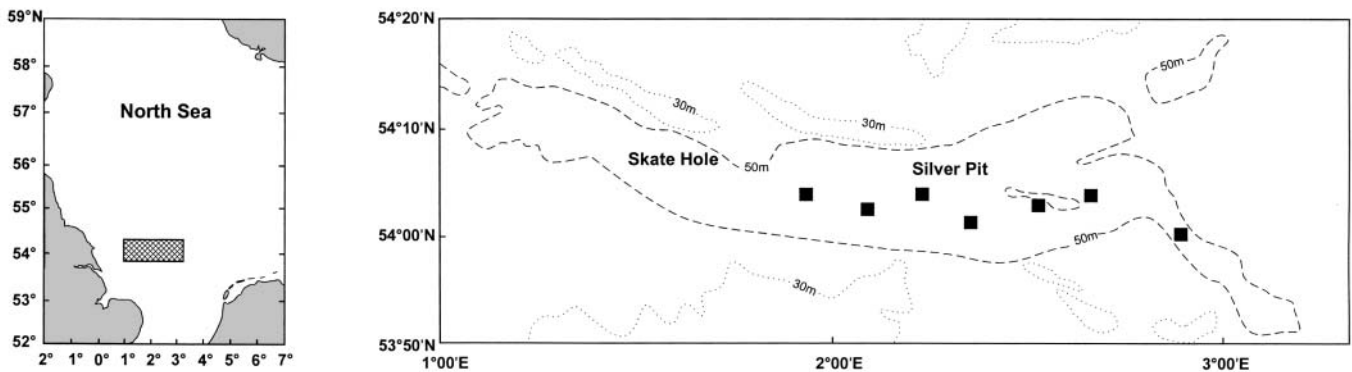


Fig. 1. The North Sea and the location of the Silver Pit study area (cross-hatched). Trawling was conducted in 7 boxes of 1 × 1 nautical mile (■). Depth contours are shown at 30 and 50 m

beam trawl was fitted with a chain mat and 2 mm mesh liner, and was towed at a speed of 1 knot (1.85 km h⁻¹) with a warp length:water depth ratio of 3:1 (Jennings et al. 1999). Each tow was timed from the moment that the net contacted the seabed until the moment of hauling from the seabed. Operational constraints meant that the distance trawled had to be confirmed retrospectively, using Sextant software linked to the ship's Differential Global Positioning System (DGPS). All sampling was conducted from 29 October 1999 to 8 December 1999.

To describe relationships between body size and trophic level for whole communities, we estimated $\delta^{15}\text{N}$ by \log_2 body mass class. Catches from the 3 tows in each 1 n mile² box were pooled, and all free-living epibenthic invertebrates and fishes were weighed and assigned to \log_2 body mass classes from 0.0625 to 32.0 g. Free-living epibenthic invertebrates were defined as species that did not anchor to shell, stone, rock or sand and that lived on the seabed or burrowed into it temporarily. Free-living species dominate epifaunal biomass in the Silver Pit (Jennings et al. 2001). Since each \log_2 size class contained many animals of many species, comparable tissues could not be sampled, and all individuals in each size class were homogenised in an electric blender, usually with added water, to produce a thoroughly mixed suspension that poured smoothly. Approximately 7 ml of this suspension was frozen to -20°C. The frozen suspension was freeze-dried to constant weight and ground to a fine powder (particles <60 µm). The powder was thoroughly mixed and a 1 mg sample weighed into a tin capsule for stable isotope analysis.

To investigate the relationship between body mass and $\delta^{15}\text{N}$ within species, we collected individuals spanning the range of observed sizes of each of the 10 most abundant species we recorded in the 2 m beam hauls (21 hauls). Individuals were collected in ten 2 m beam tows, each of 10 minutes duration. Each individual was weighed, macerated in an electric blender and frozen. Hermit crabs were removed from their shells before maceration. On return to the laboratory the frozen tissue was freeze-dried, ground and weighed into a capsule as described above.

To investigate the relationship between body mass and $\delta^{15}\text{N}$ among species, we had to extend our sampling area in space and time. A preliminary study demonstrated that variance in $\delta^{15}\text{N}$ among individuals of different sizes was greater than variance in $\delta^{15}\text{N}$ among sites for individuals of the same size. Given that individuals of the required body size (see below) could not always be caught in the Silver Pit (because they were rare), we extended our sampling time from 29 October 1999 to 4 December 2000, and our sampling area from the Silver Pit to 53° 30' - 57° 30' N and from 0

to 5° E. Individual species of invertebrates were sampled with a GOV (Grande Ouverture Verticale) demersal otter trawl and 2 m beam trawl fished from the RV 'Cirolana' and with 2 m and 4 m beam trawls fished from 'Corystes'. The GOV and 4 m beam trawls were fitted with a cod-end liner of 20 mm stretched mesh, and tows of 30 minutes duration were made at a speed of approximately 4 knots.

To investigate the relationship between body mass and $\delta^{15}\text{N}$ among species, invertebrates from different species had to be compared at a similar stage of their life history. Because key events in the life history, such as maturity, occur at a relatively constant proportion of maximum size (Charnov 1993), and because mass is a good correlate of life history attributes such as production (Brey 1990, 1999), comparing species at a fixed proportion of maximum size is equivalent to comparing them at a specific stage of their life history. We attempted to sample individuals that were 40 to 60% of their potential maximum body mass. Hermit crabs (Paguridae) were weighed after removal from their shells, but animals that secreted their own carapace were weighed with the carapace intact. Bivalve and gastropod shells were removed before maceration. Three individuals of each species were macerated to obtain tissue samples for nitrogen stable isotope analysis. The macerated tissue was placed in a vial and immediately frozen to -20°C. On return to the laboratory the frozen tissue was freeze-dried, ground and weighed into a capsule as described above. Estimates of maximum body mass were the weights of the largest individuals observed in >100 hauls with 2 m beam, 4 m beam, and GOV trawls from 29 October 1999 to 4 December 2000.

Stable isotope analysis. The ^{15}N composition of the ground tissue samples was determined using continuous flow isotope ratio-mass spectrometry (CF-IRMS) (Preston & Owens 1983, Preston 1992). Samples were oxidised and the resulting N_2 was passed to a single inlet dual collector mass spectrometer (Automated Nitrogen Carbon Analysis [ANCA] SL 20-20 or Integra systems). These were continuous-flow systems, so 2 samples of reference material (an internal standard) were analysed after every 5 tissue samples in order to calibrate the system and compensate for drift with time (ANCA-SL Dual Isotope 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 mean $\delta^{15}\text{N}$ for the infaunal or epifaunal community at each site was calculated as a weighted mean of $\delta^{15}\text{N}$ by size class. Analyses were conducted at the University of Newcastle Biomedical Mass Spectroscopy

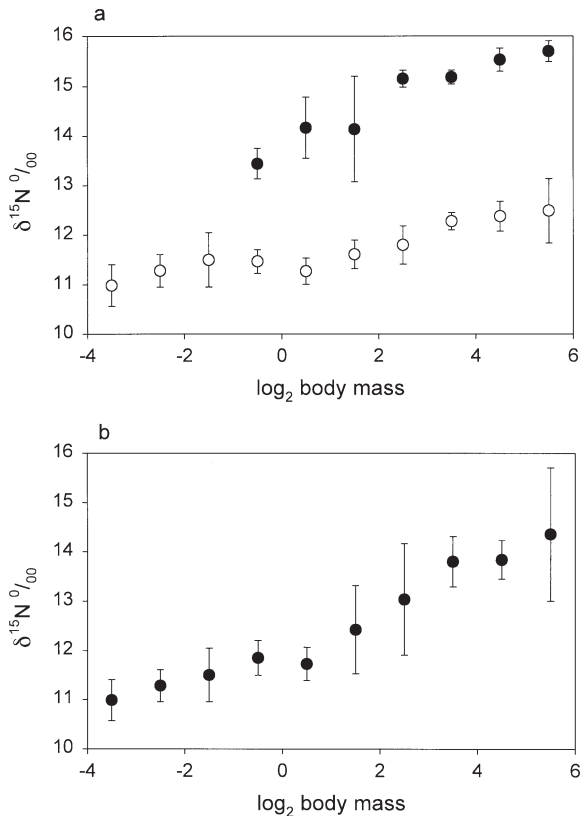


Fig. 2. Relationships between the mean $\delta^{15}\text{N}$ ($\pm 95\%$ CL) and \log_2 body mass class of (a) invertebrates (O) and fishes (●), and (b) combined invertebrates/fishes ($n \geq 5$ for all body mass classes)

Unit and at PDZ-Europa. In both laboratories, the SD for repeated $\delta^{15}\text{N}$ measurements with the reference material was $< 0.15\%$.

Data analysis. We used linear regression to explore cross-species relationships between maximum body mass 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). 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 the life histories and population biology of marine species (Jennings et al. 1998, Reynolds et al. 2001). Phylogenetic relationships among species were determined from taxonomic evidence (Hayward & Ryland 1990a,b, Howson & Picton 1997) because appropriate molecular phylogenies were not available. Independent differences (contrasts) in body mass within pairs of related species were calculated by sub-

tracting the \log_2 maximum mass of the smaller species from the \log_2 maximum mass of the larger one. Preliminary analysis of the data showed that log transformation of mass removed the effects of the relationship between body mass and location in the phylogeny (Freckleton 2000). Contrasts in $\delta^{15}\text{N}$ were then calculated for the same species pair. Contrasts in mass 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 significance of the relationship between contrast in maximum mass and contrast in $\delta^{15}\text{N}$ was assessed using binomial tests (Harvey & Pagel 1991). The null expectation is that contrasts in $\delta^{15}\text{N}$ will be randomly distributed around zero when the contrast in body mass is set to positive.

RESULTS

The relationship between $\delta^{15}\text{N}$ and body mass (M) for the invertebrate community in the Silver Pit (Fig. 2a) was $\delta^{15}\text{N} = 11.5 + 0.159 \log_2 M$, and this was significant ($r^2 = 0.45$, $F_{1,67} = 54.56$, $p < 0.001$). The relationship between $\delta^{15}\text{N}$ and body mass for the fish community was $\delta^{15}\text{N} = 13.9 + 0.364 \log_2 M$ and was also significant ($r^2 = 0.70$, $F_{1,39} = 92.63$, $p < 0.001$). The relationship between $\delta^{15}\text{N}$ and body mass for the whole epibenthic community ($\delta^{15}\text{N}$ for the invertebrate and fish samples combined; Fig. 2b) was $\delta^{15}\text{N} = 12.1 + 0.388 \log_2 M$. Again, this was significant ($r^2 = 0.59$, $F_{1,68} = 97.77$, $p < 0.001$). Note that, for the purpose of clarity, the mean $\delta^{15}\text{N}$ values ($\pm 95\%$ CL) within body mass classes are presented in Fig. 2, rather than the individual data that were used for the statistical analysis ($n \geq 5$ for all body mass classes). All relationships between mean $\delta^{15}\text{N}$ and \log_2 body mass were also significant at $p < 0.001$.

Intra-specific relationships between $\delta^{15}\text{N}$ and body mass were determined for 6 species of invertebrates and 4 species of fishes. For the invertebrates, intra-specific relationships between $\delta^{15}\text{N}$ and individual body mass were significant for 5 species at $p < 0.05$ and for all 6 species at $p < 0.1$ (Table 1). For fishes, intra-specific relationships between $\delta^{15}\text{N}$ and individual body mass were significant for 2 of 4 species at $p < 0.05$ and 3 of 4 at $p < 0.1$. The intra-specific relationship between $\delta^{15}\text{N}$ and individual body mass was not significant for *Arnoglossus laterna* (Table 1).

When the fitted relationships between $\delta^{15}\text{N}$ and body mass of the most abundant species (Table 1) were plotted on the same scale as the relationship between mass-weighted mean $\delta^{15}\text{N}$ and body mass for the whole epibenthic community (Fig. 3), it was clear that

Table 1. Regression parameters and significance of relationships between $\delta^{15}\text{N}$ and \log_2 body mass for 6 species of invertebrates and 4 species of fish

Species	a	b	n	r^2	F	df	p
Invertebrates							
<i>Ophiura ophiura</i>	11.8	0.309	11	0.38	5.43	1,9	0.045
<i>Ophiura albida</i>	12.1	0.368	11	0.41	6.34	1,9	0.033
<i>Astropecten irregularis</i>	10.5	0.198	7	0.48	4.63	1,5	0.084
<i>Pagurus bernhardus</i>	11.0	0.460	13	0.68	23.55	1,11	<0.001
<i>Liocarcinus holsatus</i>	12.9	0.480	22	0.30	8.67	1,20	0.008
<i>Nephrops norvegicus</i>	11.3	0.489	14	0.70	28.04	1,12	<0.001
Fishes							
<i>Enchelyopus cimbrius</i>	12.8	0.613	17	0.47	13.40	1,15	0.002
<i>Arnoglossus laterna</i>	15.1	0.089	7	0.32	2.29	1,5	0.190
<i>Limanda limanda</i>	13.4	0.280	14	0.25	3.91	1,12	0.071
<i>Buglossidium luteum</i>	14.6	0.226	14	0.63	20.17	1,12	<0.001

the patterns of change in $\delta^{15}\text{N}$ of abundant species mirrored those of the community. However, the $\delta^{15}\text{N}$ of abundant species in the same body mass class rarely overlapped.

The analyses of inter-specific relationships between $\delta^{15}\text{N}$ and body mass were based on 42 invertebrates species recorded in the Silver Pit (Table 2). The mean mass of individuals sampled was 31 to 68% of maximum recorded mass, although 31 species were within the 40 to 60% range. For 5 species, only 1 replicate was obtained in the acceptable size range. Inclusion or

exclusion of species outside the 40 to 60% mass range or inclusion or exclusion of those species for which there was only one replicate made no difference to the significance of our analyses. Mean $\delta^{15}\text{N}$ for the invertebrate species ranged from 6.4 to 14.2‰ (Table 2). The relationship between $\delta^{15}\text{N}$ and \log_2 maximum body mass of epibenthic invertebrates (Fig. 4) was not significant ($\delta^{15}\text{N} = 0.116 \log_2 M + 9.98$, $r^2 = 0.03$; $F_{1,40} = 1.22$; $p = 0.276$), and neither was the relationship between $\delta^{15}\text{N}$ and \log_2 mean body mass ($\delta^{15}\text{N} = 0.120 \log_2 M + 10.1$, $r^2 = 0.03$; $F_{1,40} = 1.29$; $p = 0.262$). The phylogeny for the 42 species we sampled allowed us to calculate 14 contrasts in

$\delta^{15}\text{N}$ and body mass (Fig. 5). The relationship between contrasts in $\delta^{15}\text{N}$ and contrasts in \log_2 maximum body mass was not significant at $p < 0.05$ (Fig. 6; binomial test: 10 positive, 4 negative contrasts, $p > 0.1$), in accordance with the results of the cross-species analysis.

DISCUSSION

Our analysis of the size and trophic structure of the benthic epifaunal community in the Silver Pit provides empirical evidence, in support of existing theoretical evidence, that the body mass of groups of individuals is a good predictor of their trophic level. This is in accordance with the studies of Fry & Quinones (1994) and France et al. (1998), and implies that there is a strong empirical link between community analyses based on body size distributions (e.g. Kerr 1974, Boudreau et al. 1991) and trophic structure (e.g. Pimm 1982, Hall & Raffaelli 1993).

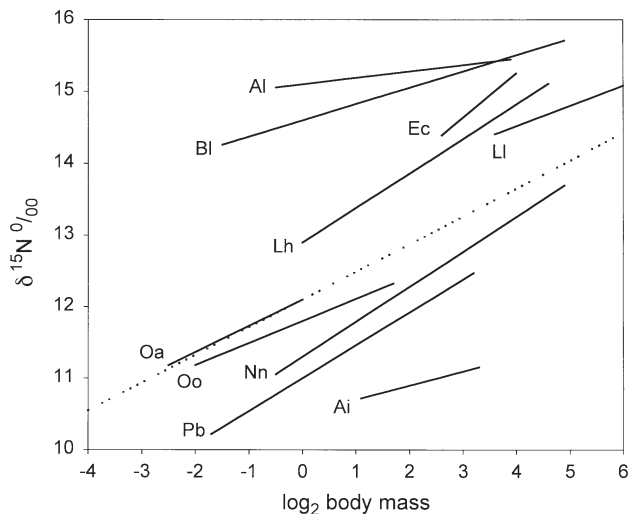


Fig. 3. Fitted linear relationship between the $\delta^{15}\text{N}$ of invertebrates/fishes and \log_2 body mass class (dotted line) and fitted linear relationships between the $\delta^{15}\text{N}$ of individual species of invertebrates or fishes and \log_2 body mass class (continuous lines). Oo: *Ophiura ophiura*, Oa: *Ophiura albida*, Ai: *Astropecten irregularis*, Pb: *Pagurus bernhardus*, Lh: *Liocarcinus holsatus*, Nn: *Nephrops norvegicus*, Ec: *Enchelyopus cimbrius*, Al: *Arnoglossus laterna*, Ll: *Limanda limanda*, and Bl: *Buglossidium luteum*

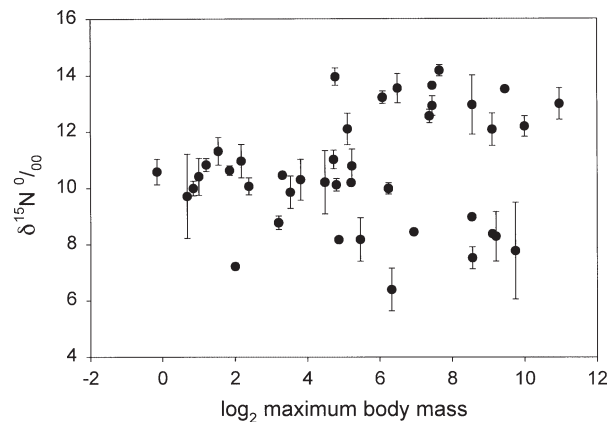


Fig. 4. Relationships between the $\delta^{15}\text{N}$ (mean \pm 95% CL) of 42 epibenthic invertebrate species and their \log_2 body mass

Table 2. Invertebrate species used to assess the relationship between body mass and $\delta^{15}\text{N}$. Mean mass: mean mass of sampled individuals (*n = 1, otherwise n = 3); Max. mass: mass of the largest individual observed; Mean mass as % of max.: mean mass of sampled individuals as a percentage of the maximum observed mass

Species	Mean mass (g) (mean \pm SD)	Max. mass (g)	Mean mass as % of max.	$\delta^{15}\text{N}$ (mean \pm SD)
<i>Aphrodita aculeata</i>	44.9 \pm 19.55	90.0	50	13.5 \pm 0.52
<i>Spirontocarus lilleborgi</i>	1.2 \pm 0.32	2.3	54	10.8 \pm 0.23
<i>Processa canaliculata</i>	1.0 \pm 0.32	1.6	60	9.7 \pm 1.49
<i>Pandalus borealis</i>	5.7 \pm 0.86	9.9	58	10.5 \pm 0.10
<i>Pandalus montagui</i>	1.9 \pm 0.42	3.6	54	10.6 \pm 0.17
<i>Crangon allmani</i>	0.9 \pm 0.00	2.9	31	11.3 \pm 0.49
<i>Pontophilus spinosus</i>	1.0 \pm 0.12	1.8	54	10.0 \pm 0.26
<i>Nephrops norvegicus</i>	85.4 \pm 14.17	165.7	52	12.6 \pm 0.24
<i>Lithodes maja</i>	600.7 \pm 168.43	1020.0	59	12.2 \pm 0.37
<i>Pagurus bernhardus</i>	42.1 \pm 7.46	67.5	62	13.2 \pm 0.22
<i>Pagurus prideaux</i>	15.6 \pm 3.90	27.8	56	10.1 \pm 0.22
<i>Munidia rugosa</i>	6.3 \pm 0.98	11.5	55	9.9 \pm 0.57
<i>Ebalia cranchii</i>	0.4 \pm 0.06	0.9	41	10.6 \pm 0.45
<i>Inarchus dorsettensis</i>	15.8 \pm 0.71	27.3	58	14.0 \pm 0.31
<i>Corystes cassevelinus</i>	19.0 \pm 2.03	34.5	55	12.1 \pm 0.56
<i>Atelecyclus rotundatus</i>	11.8 \pm 3.12	22.3	53	10.2 \pm 1.12
<i>Cancer pagurus</i>	863.3 \pm 163.57	1985.0	43	13.0 \pm 0.56
<i>Liocarcinus depurator</i>	21.7 \pm 4.74	36.9	59	10.2 \pm 0.06
<i>Liocarcinus holsatus</i>	15.4 \pm 3.57	26.4	58	11.0 \pm 0.33
<i>Colus gracilis</i>	21.3 \pm 2.17	37.4	57	10.8 \pm 0.60
<i>Buccinum undatum</i>	125.3 \pm 18.49	201.0	62	14.2 \pm 0.20
<i>Neptunia antiqua</i>	187.5 \pm 44.16	375.8	50	13.0 \pm 1.05
<i>Polinices montagui</i>	3.0 \pm 0.87	5.2	58	10.1 \pm 0.30
<i>Modiolis modiolis</i>	287.0*	552.0	52	8.4
<i>Aequipecten opercularis</i>	40.7 \pm 4.70	80.0	51	6.4 \pm 0.76
<i>Loligo forbesi</i>	369.3 \pm 109.35	550.5	67	12.1 \pm 0.58
<i>Loligo vulgaris</i>	59.0*	175.0	34	13.6
<i>Eledone cirrhosa</i>	367.0*	704.0	52	13.5
<i>Luidia ciliaris</i>	205.3*	373.0	55	9.0
<i>Astropecten irregularis</i>	29.8 \pm 6.47	44.0	68	8.2 \pm 0.77
<i>Porania pulvillus</i>	41.4 \pm 12.47	75.5	55	10.0 \pm 0.20
<i>Asterina gibbosa</i>	98.0 \pm 23.90	175.0	56	12.9 \pm 0.35
<i>Henricia sanguinolenta</i>	18.0*	29.1	62	8.2
<i>Asterias rubens</i>	175.3 \pm 28.01	376.5	47	7.5 \pm 0.39
<i>Leptasterias muelleri</i>	47.0*	122.6	38	8.4
<i>Ophiothrix fragilis</i>	5.9 \pm 0.40	9.2	64	8.8 \pm 0.24
<i>Ophiura albida</i>	1.3 \pm 0.10	2.0	65	10.4 \pm 0.65
<i>Ophiura ophiura</i>	2.9 \pm 0.10	4.5	64	11.0 \pm 0.59
<i>Echinus acutus</i>	238.0 \pm 231.62	590.0	40	8.3 \pm 0.88
<i>Echinus elegans</i>	1.7 \pm 0.17	4.0	43	7.2 \pm 0.13
<i>Echinus esculentus</i>	411.3 \pm 137.41	855.0	48	7.8 \pm 1.72
<i>Psamechinus miliaris</i>	9.3 \pm 3.51	14.0	67	10.3 \pm 0.72

The increase in trophic level with increasing body mass within the community is a response to intra-specific increases in trophic level with increasing body mass rather than, at an inter-specific level, the higher trophic levels of species with larger body mass. Comparison of changes in trophic level with body mass for the invertebrate and fish community suggest that competition for food between invertebrates and fishes of similar body mass is low, since the $\delta^{15}\text{N}$ of invertebrates is generally 2‰ lower than that of fishes of the same mass. Among the most abundant species, the relationships between $\delta^{15}\text{N}$

and body mass suggests that abundant species have separate feeding niches. Given that the $\delta^{15}\text{N}$ of the whole community increased consistently with body size, our results imply that species have evolved to feed at many trophic levels, but that small species feeding at high trophic levels will always be relatively scarce. Patterns at the community level are consistent with the expectation that predator-prey relationships led to powerful size-based trophic structuring.

If $\delta^{15}\text{N}$ increases linearly with trophic level then the strength of relationships between $\delta^{15}\text{N}$ and \log_2 body

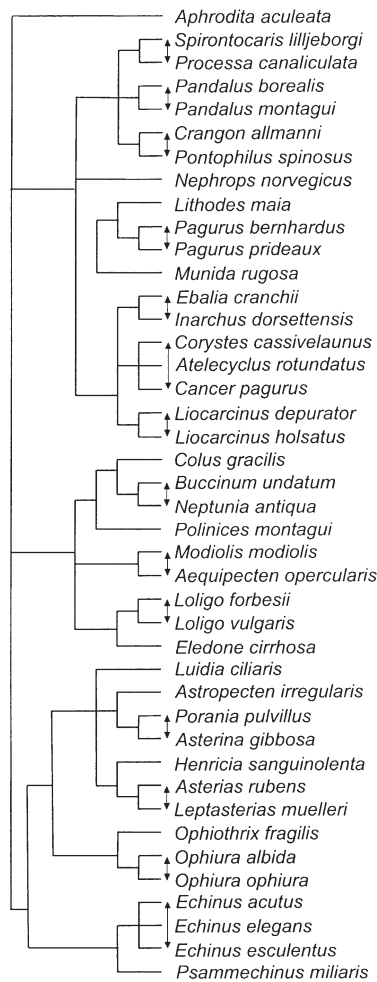


Fig. 5. Phylogenetic relationships among 42 species of epibenthic invertebrates for which $\delta^{15}\text{N}$ and maximum body mass estimates were available. Branch lengths were set to unity and vertical arrows indicate paired comparisons among species

mass class will reflect the strength of relationships between trophic level and \log_2 body mass class. If we assume a $\delta^{15}\text{N}$ enrichment of 3.4‰ for each trophic step (Minawaga & Wada 1984), then we can estimate the mean predator:prey body mass ratio in this benthic community as $2^{3.4/\text{slope}}$ or 434:1. However, the assumed $\delta^{15}\text{N}$ enrichment of 3.4‰ is a mean of many reported values (Minawaga & Wada 1984, Adams & Sterner 2000), and this has prompted calls for experimental evaluation and validation (Gannes et al. 1997, Pinnegar & Polunin 1999, Ponsard & Averbuch 1999, Schoella 1999). We cannot provide such validation for the range of complex feeding relationships that apply to the species included in this study, and regard the mean predator:prey body mass ratio as a tentative value.

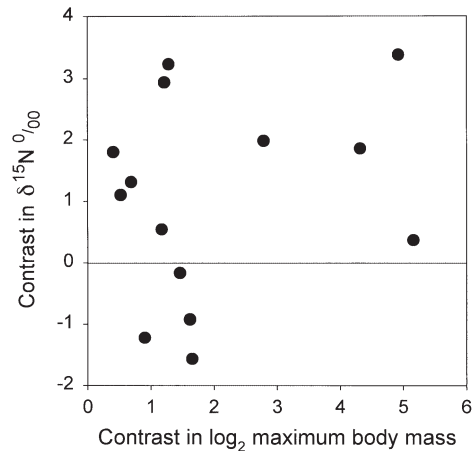


Fig. 6. Relationships between contrasts in $\delta^{15}\text{N}$ and contrasts in \log_2 body mass of epibenthic invertebrates

The observed relationship between $\delta^{15}\text{N}$ and body mass, and thus the mean predator:prey body mass ratio, will be influenced by the strength of feeding relationships between the community we sampled and species we did not sample. Benthic infauna are expected to account for a large proportion of biomass and production in muddy-sand habitats, and do not consistently increase in trophic level with body size because many of the largest infaunal species are filter- and deposit-feeding bivalves. However, the role of these bivalves in the size-based epifaunal food webs we studied is far from clear. The largest bivalves are unlikely to be widely eaten by epifauna, since species such as *Arctica islandica* have very low natural mortality and great longevity (100+ yr) (Witbaard et al. 1999). This implies that their role in benthic food webs is more likely to be associated with the production of excreted material that can be utilised by bacteria and meiofauna. Indeed, large bivalves may only become accessible to predators when they are damaged by impacts from towed fishing gears or when flatfish such as plaice bite off their siphons (Rumohr & Krost 1991, Witbaard & Klein 1994). The infauna most widely available to fishes and epibenthic species are the smaller bivalves and polychaetes. Some of the polychaetes already feed at trophic levels comparable with those of epibenthic species of a similar body mass (Jennings et al. 2001). This is because the polychaetes feed on smaller polychaetes and meiofauna as well as microbially enriched detritus (Schubert & Reise 1986, Beukema 1987).

Size-based models of some marine communities and ecosystems are relatively straightforward to develop because estimates of biomass by body mass class can be obtained from existing plankton, invertebrate or fisheries survey data (e.g. Pope et al. 1988). If relation-

ships between body mass and trophic level are consistent in space and time, these relationships could be used to predict the trophic levels of body mass classes in the size spectrum. This approach would be analogous to the existing parameterisation of size spectra with production to biomass ratios (e.g. Schwinghamer et al. 1986, Duplisea 1998). A size spectrum parameterised with trophic levels would provide a description of trophic structure, and changes in the gradient of the spectrum would reflect changes in mean trophic level. The resulting trophic spectra would have several possible applications. For example, analyses of temporal and spatial changes in size spectra could be used to detect temporal and spatial changes in trophic structure and to assess the impacts of disturbance.

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