

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ elucidation of size-structured food webs in a Western Arabian Sea demersal trawl assemblage

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ABSTRACT: In aquatic systems, predators are usually larger in body size than their prey, and within a species larger individuals tend to occupy higher trophic levels. This has led to the expectation that communities are strongly size-structured. In the present study, we tested whether size structuring was present in a demersal trawl assemblage from the Western Arabian Sea. Nitrogen and carbon stable isotopes were used to describe trophic level and basal resource utilisation and were assessed against body size (\log_2 size class) at both the community (species independent) and species levels. Nitrogen and bulk carbon isotopic values were significantly and positively related to body mass at the community level. Despite sampling over 15 \log_2 mass classes (0.001 to 32.8 kg), the trawl assemblage spanned approximately 1 trophic level. The community relationship between $\delta^{13}\text{C}$ and \log_2 body mass was associated with higher lipid content in smaller size classes. In contrast, comparisons of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of species at a similar stage of their life history (55 to 80% of maximum length) were independent of body size, suggesting reduced niche overlap at different sizes. While some small species feed at high trophic levels and vice versa, they contributed comparatively little to the sampled community biomass, and overall, the community was size-structured in terms of trophic level.

KEY WORDS: Food chain · Fractionation · Stable isotopes · Trophic level · Predation · Community structure

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INTRODUCTION

Size is an important ecological characteristic in most aquatic species, which may increase in mass by over 5 orders of magnitude during their lifetime (Jennings et al. 2002a). Size dictates an individual's predator–prey interactions via gape (Mumby et al. 2006), body dimensions and swimming speed (Schmidt-Nielsen 1984), such that predators are usually 3 to 4 times larger than their prey, and larger fish usually feed at a higher trophic levels (Jennings et al. 2002a). Size is also an important ecological determinant influencing species diversity and abundance within communities (France et al. 1998, Jennings et al. 2001, 2002a,b). Thus, changes in the size structure of a community (e.g. through fisheries exploitation, Dulvy et al. 2004)

can influence the trophodynamics of aquatic organisms and entire marine communities (Pauly & Watson 2005). This suggests that coupled analyses of body size and trophic level (TL) may be used to assess the impacts of exploitation on trophic structure (Jennings et al. 2002a).

TL has traditionally been calculated based on the average trophic composition of prey items identified through stomach content (Hyslop 1980) or other dietary analyses, such as the examination of preserved hard parts in feces. Obtaining such dietary data for a wide range of species within a community requires a large sampling effort due to the high variability of stomach contents in space and time (Jennings et al. 2001) and high levels of stomach vacuity (Hyslop 1980). Detailed dietary information is often limited to

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commercially or ecologically important species and tends to be absent on community-wide scales. Notable exceptions are the 1981 and 1991 North Atlantic 'years of the stomach' (Daan 1989, Hislop et al. 1997).

Stable isotope analyses provide an alternative approach for estimating TL on both species and community scales (France et al. 1998, Jennings et al. 2001). While not providing the dietary resolution obtained from gut content analyses, stable isotopes provide time- and space-averaged trophic estimates that can be used to describe trophic linkages within and among species (Davenport & Bax 2002, Harvey et al. 2002).

The utility of stable isotope techniques depends primarily on differences in the isotopic ratios ($^{15}\text{N}:^{14}\text{N}$ or $^{13}\text{C}:^{12}\text{C}$) among consumers and their diet. These differences arise due to the excretion of lighter isotopes during respiration and excretory processes (DeNiro & Epstein 1978, 1981). This leads to a relative increase in the natural abundance of ^{15}N and ^{13}C as a function of TL (trophic enrichment Δ). Since $\Delta\delta^{15}\text{N}$ is often assumed to increase consistently with TL, averaging ca. 3.4‰ (Vander Zanden & Rasmussen 2001, Post 2002), $\delta^{15}\text{N}$ is widely used to estimate TL relative to a baseline $\delta^{15}\text{N}$ value (Post 2002). The $\delta^{13}\text{C}$ values of consumers relative to their prey are usually enriched by ca. 1.0‰ (DeNiro & Epstein 1978). Therefore, $\delta^{13}\text{C}$ values of consumers remain similar to basal values throughout a food web and can be used to identify carbon sources and trace carbon flow (Fry & Sherr 1984).

The use of stable isotope data has reinforced the idea that TL tends to increase as a function of size in aquatic food webs (Jennings et al. 2001); however, the strength of this relationship appears to vary. Within species, TLs may increase, decrease or remain constant in relation to body size (Jennings et al. 2001). However, at the community level, strong positive relationships have been observed between body mass and $\delta^{15}\text{N}$ values, (Jennings et al. 2001) despite a weak relationship between maximum length (L_{max}) and TL at the species level. The study of Jennings et al. (2001) of the North Sea demersal fish assemblage is unique in the literature; thus, the extent to which such structuring occurs in other systems is unclear.

Layman et al. (2005) have suggested that positive relationships between body size and TL may be a feature of comparatively simple food webs, but that in diverse food webs where both predator and prey cover a wide range of body sizes, predators may exploit short productive food chains and TL may be independent of body size. However, conclusions were drawn at the species level, and potentially fail to account for observations that small-bodied high-TL species and large-bodied low-TL species could represent only a minor proportion of community biomass (as observed in Jennings et al. 2001). Therefore, it remains uncertain

whether size structuring is an exclusive feature of simple food webs.

As TL increases, the basal energy required to sustain a unit of biomass also increases, the result of inefficient transfer of energy at each trophic step (Pauly & Christensen 1995). Numerous isotope-based studies have used $\delta^{13}\text{C}$ differences among species to illustrate that among species, a wide range of primary production sources can be utilised (Yamamuro et al. 1995, Darnaude et al. 2004). However, species feeding at higher TL tend to show limited variation in $\delta^{13}\text{C}$ values, which may result from averaging energy obtained from 2 or more sources or the domination of 1 source (Darnaude et al. 2004, Darnaude 2005). Community-scale patterns in $\delta^{13}\text{C}$ as a function of size, analogous to those of Jennings et al. (2001) for $\delta^{15}\text{N}$, remain untested. However, where 1 source of production dominates, a linear relationship of body size with $\delta^{13}\text{C}$ would be expected if TL ($\delta^{15}\text{N}$) relates to body size. Several sources of primary production would tend to weaken or even negate a body size– $\delta^{13}\text{C}$ relationship at the community level.

This study examined whether body mass–TL relationships are restricted to simple food webs or are a more generic feature of marine food webs. Specifically, we tested the hypotheses that $\delta^{15}\text{N}$ is related to body mass at (1) community (species independent) and (2) species (mature adult individuals) scales in the upwelling-influenced food web of the Western Arabian Sea that is characterized by a significant overlap in predator and prey body sizes. Further, we tested whether $\delta^{13}\text{C}$ is related to body size at (3) community and (4) species scales to examine possible patterns of production utilisation at different scales and (5) relate these to observations for $\delta^{15}\text{N}$.

MATERIALS AND METHODS

Study site. The Western Arabian Sea is a tropical water body subject to a reversal in the SW/NE monsoonal wind that results in a seasonal (May to September) upwelling during the SW monsoon. Sea surface temperature ranges from 21 to 28°C and drops to about 18°C during the upwelling season (Morrison et al. 1998). The increased availability of nutrients during the SW monsoon increases zooplankton biomass 5 times compared to during the late NE reversal (Luo et al. 2000).

Experimental trawling was conducted from a commercial trawler (FV 'IXTHUS 5') using a demersal otter trawl with a 110 mm cod end and 20 mm liner. Trawling was undertaken in 2 areas, north and south of Ras Madrakah (Oman) (Fig. 1), on fishing grounds utilised by a multi-species trawl fishery mainly targeting dem-

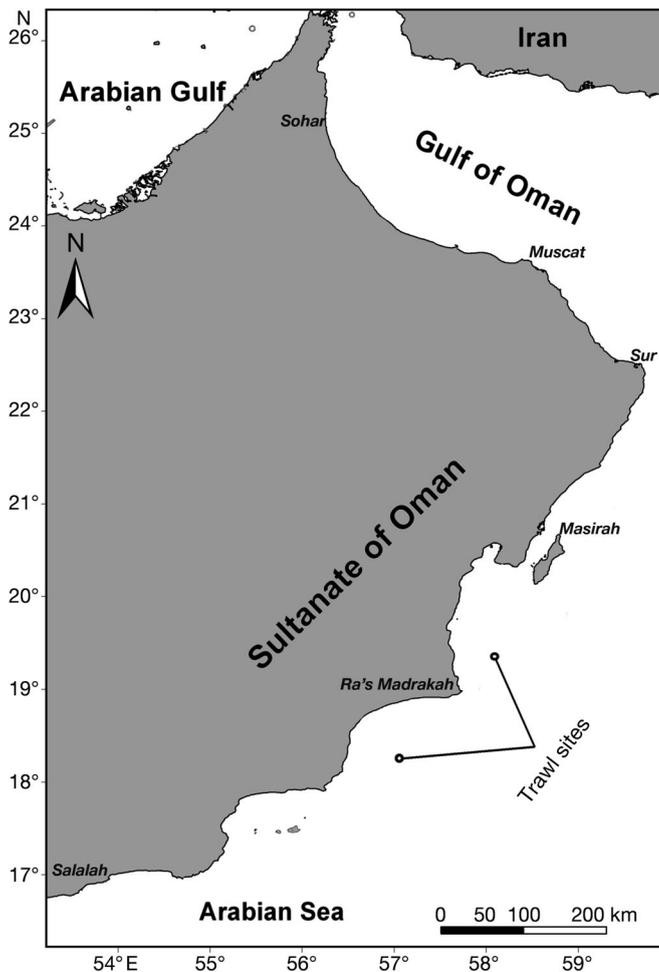


Fig. 1. Sampling sites within the Sultanate of Oman

ersal species (MAF 2000). Four hauls were conducted at each of 3 replicate sites within each area over 4 time periods: May 2003, January 2004, May 2004 and January 2005. Trawls were of 1 hr duration at 3 to 3.5 knots and ranged in depth from 13 to 64 m.

Community scale sampling. For community analyses, the catch was sorted on board into \log_2 body weight classes, and up to 25 individuals were randomly selected from each size class regardless of species. Individuals were weighed, and then up to 5 g of dorsal white muscle were excised from each individual. For small individuals with insufficient muscle tissue, the guts and head were removed and the rest of the body was analyzed. All samples were placed in glass vials and frozen to -29°C . Samples were freeze-dried and ground for stable isotope analysis.

One mg of powder per individual was placed into a tin capsule for nitrogen and carbon analysis. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were determined using a Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS) con-

nected to an Automated Nitrogen Carbon Analysis Solids/Liquid Preparation Module (PDZ Europa). After every 5 samples, a pair of internal reference samples (cod muscle) were used to calibrate the machine and check for machine drift. Isotopic compositions were expressed in terms of δ notation relative to international reference standards, which were atmospheric N_2 ($\delta^{15}\text{N}$) and Pee Dee Belemnite (PDB) ($\delta^{13}\text{C}$). Based on the standard deviation of the internal standard, precision of both nitrogen and carbon were $\pm 0.2\%$.

The community level isotopic signature for each size class was calculated as the average isotopic value of all individuals within a size class weighted to account for body mass:

$$\delta^{15}\text{N}_{\text{comm}} = \frac{\delta^{15}\text{N}_1 \times Wt_1 + \delta^{15}\text{N}_2 \times Wt_2 + \delta^{15}\text{N}_{\dots i} \times Wt_{\dots i}}{\sum Wt_{1\dots i}} \quad (1)$$

where $\delta^{15}\text{N}$ is the isotopic signatures of individuals 1 to i and Wt is their respective mass.

This approach was chosen over that of Jennings et al. (2001) where muscle samples were macerated together in proportion to catch prior to isotopic analysis, because the isotopic signature of certain species (e.g. parrotfish) were believed to be important in interpreting the results. This method produced results virtually identical to those derived by following the method of Jennings et al. (2001) in a pilot study conducted in May 2003 (S. H. Al-Habsi unpubl. data).

Species-specific sampling. To examine whether size was a significant predictor of isotopic signature among species, 3 individuals of the 20 most common species captured at between 55 and 80% of L_{max} (Froese & Pauly 2006) were selected from the catch. This allowed for the comparison of individuals at a similar stage of their life history (Jennings et al. 2001). Samples of muscle were frozen at -29°C for further analysis upon reaching the laboratory. Samples were thawed enough to excise 2 g of dorsal white muscle from each individual. Samples were then freeze-dried and ground to powder for stable isotope analysis as above.

Data analysis. As this study was primarily interested in the large-scale annual ecosystem trends and aimed to identify any evidence of size structuring in the system, both species and community data were pooled across years, seasons and areas (Layman et al. 2005). Such averaging is important for 2 reasons. Firstly, small species or individuals represent isotopic signatures over shorter temporal scales than do larger individuals and species, the result of differences in isotopic turnover rate. This is particularly important in an upwelling environment where the pooling of samples averages out seasonal variation in basal isotopic signatures such that all size classes represent comparable temporal scales. Without such an approach, any com-

munity analysis would be confounded by the effect of season in the small size classes. Secondly, species differ in mobility; thus, individuals reflect spatial variation in isotopic signatures as a function of their mobility and isotopic turnover rate. Averaging isotopic signatures over space reduced such spatial variation.

For accurate interpretation of $\delta^{13}\text{C}$ it is sometimes necessary to account for variations in tissue lipid content. Lipids are depleted in ^{13}C relative to proteins (DeNiro & Epstein 1977), and thus systematic trends in $\delta^{13}\text{C}$ can be induced by variation in lipid content alone. To correct for lipid content, we apply the species-independent lipid normalisation techniques of McConnaughey & McRoy (1979) as adapted by Kiljunen et al. (2006) to all $\delta^{13}\text{C}$ data:

$$L = \frac{93}{1 + (0.246 \times (\text{C:N}) - 0.775)^{-1}} \quad (2)$$

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + D \times \left(I \frac{3.90}{1 + 287/L} \right) \quad (3)$$

where L = the proportional lipid content of the sample and $\delta^{13}\text{C}'$ is the lipid-normalised value of the sample; C and N are the proportions of carbon and nitrogen in the sample; $\delta^{13}\text{C}$ is the measure value of the sample; D is the isotopic difference between protein and lipid (7.018 ± 0.263); and I is a constant (0.048 ± 0.013). To standardize within and among species, all $\delta^{13}\text{C}$ data were lipid-normalised to $\delta^{13}\text{C}'$. Trends were examined in both lipid-normalised and bulk $\delta^{13}\text{C}$.

Because the community and species level analyses were performed on mass-based size classes, the maximum

weight for each species was derived from length data using published length–weight relationships (Table 1). Where species-specific data were not obtainable (only *Rhinobatos punctifer*), a mean value for all obtainable species within the genus was applied. Predator prey mass ratios (PPMR) were determined following Jennings et al. (2002b) as $\text{PPMR} = 2^{3.4 \times \text{slope}}$.

Statistical analyses were performed using Minitab14 statistical software. All data were tested for normality and homogeneity of variance prior to analysis. Linear regressions were used to determine relationships between body mass and $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$. Pearson's correlation coefficient was used to test correlations among variables. Significance was set at $p = 0.05$ in all cases. All errors are reported as ± 1 SD unless otherwise stated.

RESULTS

Community isotopic size spectra

There was a significant positive relationship between body mass and weighted mean $\delta^{15}\text{N}$ at the community level ($\delta^{15}\text{N} = 0.263 \pm 0.031 \log_2$ body mass + 14.23 ± 0.26 , $r^2 = 0.835$, $p < 0.001$, $F_{1,14} = 71.64$) (Fig. 2a). Mean $\delta^{15}\text{N}$ ranged from $14.09 \pm 1.19\text{‰}$ for the 1 to 2 g size class to $18.98 \pm 4.16\text{‰}$ for the largest size class in the trawl assemblage (Fig. 2a), a range of 4.89‰ ; i.e. ~ 1.5 TLs. The regression slope suggests a mean dif-

Table 1. Species of the same standardized length (55 to 80%) of the maximum recorded length (L_{max}) and their mean (\pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Code = species code used in Fig. 3, n = sample size, a & b = parameters of length–weight relationship ($W = aL^b$)

Species	Common name	Code	n	L_{max} (cm)	a	b	\log_2 max. weight	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Argyrops filamentosus</i>	King soldierbreem	13	1	70	0.1203	2.5800	12.62	16.56	-16.57
<i>A. spinifer</i>	King soldierbreem	17	3	70	0.0337	2.8900	12.76	17.10 ± 0.32	-15.91 ± 0.10
<i>Atractoscion aequidens</i>	Geelbeck croaker	5	2	130	0.0083	2.8580	14.24	15.62 ± 0.21	-16.04 ± 0.30
<i>Carangoides chrysophrys</i>	Longnose trevally	15	3	60	0.0193	3.0040	11.89	16.96 ± 0.16	-16.93 ± 0.31
<i>C. coeruleopinnatus</i>	Coastal trevally	12	1	40	0.0077	3.1310	10.49	16.56	-17.37
<i>Cheimerius nufar</i>	Santer breem	14	3	75	0.0180	2.9400	12.86	16.77 ± 0.33	-16.25 ± 0.09
<i>Diagramma pictum</i>	Painted sweetlips	18	3	60	0.0001	3.6110	11.47	17.24 ± 0.15	-15.65 ± 0.07
<i>Decapterus russelli</i>	Indian shad	20	3	39	0.095	2.1000	7.70	15.510 ± 0.41	-16.778 ± 0.14
<i>Epinephelus diacanthus</i>	Thornycheek grouper	9	3	55	0.0169	3.0490	11.20	16.12 ± 0.09	-16.41 ± 0.07
<i>E. gabriellae</i>	Brownspotted grouper	19	3	75	0.0350	2.8100	13.02	17.38 ± 0.08	-15.66 ± 0.11
<i>Lethrinus nebulosus</i>	Spangled emperor	11	3	80	0.0830	2.6410	12.93	16.56 ± 0.27	-15.72 ± 0.14
<i>Nemipterus mesoprion</i>	Redfilament threadfin breem	10	3	30	0.0183	3.0000	8.91	16.50 ± 0.19	-16.28 ± 0.10
<i>Pagellus affinis</i>	Arabian Pandora	1	3	37	0.2750	2.6250	10.30	14.84 ± 0.46	-17.48 ± 0.13
<i>Pomadasys commersonnii</i>	Smallspotted grunt	7	1	80	0.0281	2.8860	12.61	15.91	-14.66
<i>Rhinobatos punctifer</i>	Guitarfish	3	3	80	0.0084	3.0100	11.18	15.03 ± 0.01	-16.11 ± 0.02
<i>Scarus ghobban</i>	Flame parrotfish	6	3	75	0.0385	2.8785	13.10	15.74 ± 0.88	-16.25 ± 0.34
<i>Scomber japonicus</i>	Chub mackerel	2	3	54	0.0310	2.9470	11.81	15.01 ± 0.22	-17.06 ± 0.27
<i>Sepia pharaonis</i>	Cuttlefish	4	3	43	0.0456	2.7000	12.38	15.58 ± 0.41	-16.43 ± 0.11
<i>Sufflamen fraenatus</i>	Masked triggerfish	8	1	38	0.0073	3.2863	10.45	15.92	-17.14
<i>Trichiurus lepturus</i>	Largehead hairtail	16	3	234	0.0225	2.9320	15.13	17.01 ± 0.13	-16.77 ± 0.19

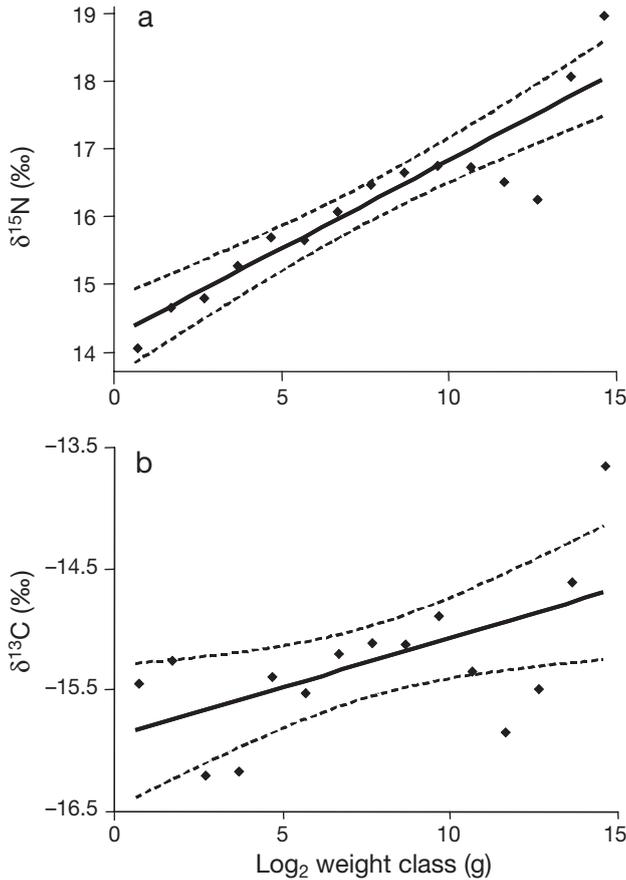


Fig. 2. Relationship of (a) $\delta^{15}\text{N}$ (mean \pm SD) and (b) bulk $\delta^{13}\text{C}$ (mean \pm SD) against \log_2 body mass (g) for the Western Arabian Sea trawl assemblage. Solid line: least squares regression, dashed lines: 95% CI

ference of 3.6‰ in $\delta^{15}\text{N}$ between the smallest and largest size classes; thus, despite sampling individuals with mass spanning over 5 orders of magnitude, species spanned just 1 to 1.5 TL. Notional predator:prey body mass ratio in the assemblage was 7792:1. Both size classes 12 and 13 exhibited high residual values. Examination of species composition highlighted relatively large numbers of parrotfishes with low $\delta^{15}\text{N}$, particularly in size class 13. Excluding size classes with parrotfishes from the analysis did not alter the conclusions, although the regression slope increased to 0.304.

The mean size class $\delta^{13}\text{C}$ exhibited a significant positive relationship with body mass ($\delta^{13}\text{C} = 0.081 \pm 0.031 \log_2$ body mass -15.88 ± 0.27 , $r^2 = 0.292$, $p = 0.022$, $F_{1,14} = 6.75$) (Fig. 2b). Mean $\delta^{13}\text{C}$ ranged from $-15.42 \pm 1.30\text{‰}$ for the smallest size class to $-13.64 \pm 3.07\text{‰}$ for the largest class in the trawl assemblage, although size class 3 had the lowest $\delta^{13}\text{C}$ ($-16.18\text{‰} \pm 0.25$).

With the exception of size class 12, mean C:N ratio decreased with size class (C:N = $-0.023 \log_2$ body mass $+ 3.54$, $r^2 = 0.552$, $p = 0.002$, $F_{1,13} = 14.78$). Size class 12 was an outlier with the highest C:N of all size classes.

Tuna with high lipid content contributed significantly to this size class and its inclusion resulted in a non-significant relationship of C:N to body mass ($p = 0.092$, $F_{1,14} = 3.31$). Lipid-normalised mean $\delta^{13}\text{C}$ showed no significant relationship with body mass ($p = 0.148$, $F_{1,14} = 3.31$), although the trend was positive.

There was a strong correlation between mean $\delta^{15}\text{N}$ and mean $\delta^{13}\text{C}$ at the community level ($r = 0.768$, $p = 0.001$). Slopes of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ suggest a relative trophic fractionation within the community of 3.2:1, which is close to commonly-assumed 3.4‰ and 1.0‰ trophic enrichment values. $\delta^{15}\text{N}$ still correlated with lipid-normalised $\delta^{13}\text{C}$ ($r = 0.522$, $p = 0.046$) but more weakly. Slope of $\delta^{15}\text{N}$ and lipid-normalised $\delta^{13}\text{C}$ gave relative community trophic fractionation values of 3.2:0.6 (trend slope of 0.045).

Species isotopic analyses

Twenty species were sampled in the assemblage, 4 of which consisted of only 1 replicate within the size range of 55 to 80% of L_{\max} (Table 1). Mean $\delta^{15}\text{N}$ of the Arabian Sea species ranged from $14.84 \pm 0.8\text{‰}$ for *Pagellus affinis* to $17.38 \pm 0.08\text{‰}$ for *Epinephelus gabrielae*, and mean bulk $\delta^{13}\text{C}$ ranged from $-17.48 \pm 0.13\text{‰}$ for *Pagellus affinis* to -14.66‰ for *Pomadasys commersonnii* (Table 1, Fig. 3). Relationships of mean $\delta^{15}\text{N}$ ($F_{1,19} = 2.70$, $p = 0.118$) (Fig. 4a), mean bulk $\delta^{13}\text{C}$ ($F_{1,19} = 2.03$, $p = 0.172$) (Fig. 4b) and mean lipid-normalised $\delta^{13}\text{C}$ ($F_{1,19} = 0.53$, $p = 0.475$) with \log_2 maximum body mass were all non-significant. Excluding samples with less than 3 replicates made no difference to the results and neither did the exclusion of *Pomadasys commersonnii* (species 7), the isotopic signature of which appears to be an outlier (Fig. 3). There was no correlation between $\delta^{15}\text{N}$ and bulk $\delta^{13}\text{C}$ at the species level ($r = 0.314$, $p = 0.177$) (Fig. 3), although this changed after the removal of *Pomadasys commersonnii* ($r = 0.458$,

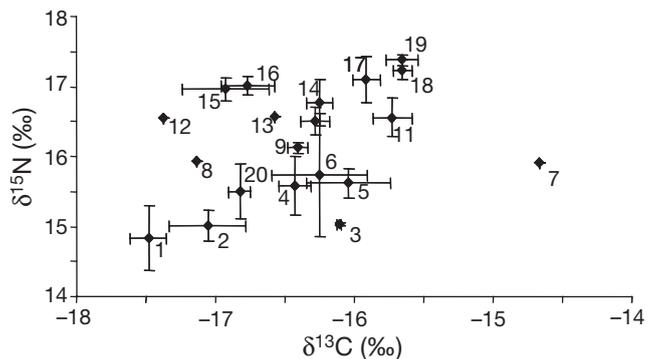


Fig. 3. Bivariate bulk $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ for the Arabian Sea trawl assemblage. Numbers refer to species codes in Table 1. Error bars represent ± 1 SD

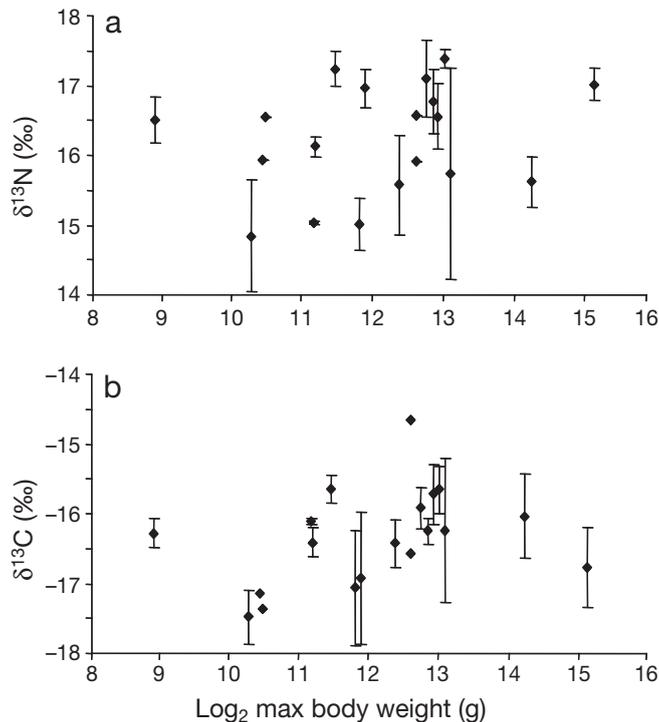


Fig. 4. (a) $\delta^{15}\text{N}$ (mean \pm SD) and (b) bulk $\delta^{13}\text{C}$ (mean \pm SD) against \log_2 of maximum total weight for 20 fish species

$p = 0.049$), which had an unusually heavy ^{13}C signature. Accounting for lipid content strengthened the correlation ($r = 0.818$, $p < 0.001$).

DISCUSSION

Species $\delta^{15}\text{N}$

That species $\delta^{15}\text{N}$ was independent of maximum body size is consistent with previous studies (Jennings et al. 2001, Layman et al. 2005). Such patterns may occur if there are large spatial and temporal differences in species $\delta^{15}\text{N}$ or because maximum size does not constrain TL. Experimental design specifically accounted for potential spatial or temporal variation in basal isotopic signatures through pooling of locations and seasons. This was essential as it allows comparison of isotopic signatures among sizes where turnover rate is inversely related to the size of individuals and species (McIntyre & Flecker 2006). In the absence of pooling, the different spatial or temporal scale represented in the isotopic signature would confound any analysis. Therefore, we conclude that maximum size does not constrain TL.

The independence of TL from body size has been attributed to the utilisation of a wide variety of niches in complex systems (Layman et al. 2005). However,

results presented by Jennings et al. (2001) suggest that this feature is not exclusive to complex food webs. The trawl assemblage studied in this paper is intermediate in its complexity compared to the systems studied by Layman et al. (2005) and Jennings et al. (2001).

Results presented in this paper highlight that either (1) niche specialisation at body size has occurred in 3 very different aquatic systems (Western Arabian Sea, North Sea and Cinaruco River, Venezuela), which allows for the exploitation of a range of TLs for any particular body size class, or (2) omnivory is widespread, resulting in broad niches which differ little in extent with respect to L_{max} . It need not be the same process occurring at all locations; isotope data alone cannot resolve one process from the other.

Another possibility is that our results are an artefact of the sampling regime, and that there is an influence from seasonal and/or annual variation of the baseline. However, given the comparatively slow turnover observed in the fish muscle of juveniles $<30\%$ L_{max} (Hesslein et al. 1993, Sweeting et al. 2005) and the fact that turnover decelerates rapidly with age as reduction in growth-based dilution diminishes (Witting et al. 2004), such variation is unlikely to strongly influence analysis of fish at 55 to 80% L_{max} .

Community $\delta^{15}\text{N}$

Trawl assemblage $\delta^{15}\text{N}$ values increased with \log_2 body mass with a slope of 0.263, despite non-significant relationships with body size at the species level, which implies size structuring within the community. Reconciling species and community level results suggests that while small species feeding at high TL and vice versa are viable feeding strategies, they contribute comparatively little to the sampled community biomass. Furthermore, fishes exhibiting a decrease in TL with body size are likely to be rare. Further work is required to determine the relative importance of change in species composition and size-based (or ontogenetic) changes in diet for a particular species in driving community size structuring.

Community size structuring and weak cross-species relationships are comparable to findings from the North Sea fish community (Jennings et al. 2001), although estimates of slope were lower in the Western Arabian Sea trawl assemblage (slope = 0.263) than for both the fish community (slope = 0.335; Jennings et al. 2001) and for mixed faunal groups (slope = 0.50; Jennings et al. 2002a) in the North Sea, suggesting weaker size structuring in the Western Arabian than in the North Sea. The slope derived in this study is remarkably similar to that for a component of the Galician upwelling pelagic food web (slope 0.28; Bode et al. 2003).

Predator:prey mass ratio

PPMR was calculated for the Western Arabian Sea trawl assemblage as 7792:1, close to that derived for the Galician upwelling pelagic assemblage (ca. 4500:1; Bode et al. 2003), although new data for the Iberian Peninsula increased PPMR (slope = 0.195, PPMR = 1.8×10^5) in the region (Bode et al. 2006). All are of greater magnitude than observed in the North Sea fish community (PPMR = 1136:1; Jennings et al. 2001) and 1 order of magnitude greater than North Sea mixed faunal groups (PPMR = 109:1).

Steeper slopes of the relationship between community \log_2 body mass and $\delta^{15}\text{N}$ leads to a reduction of PPMR. In the Western Arabian Sea, the presence of large herbivores (e.g. parrotfishes) may reduce the weighted mean $\delta^{15}\text{N}$, and thus reduce the community $\delta^{15}\text{N}$ slope and increase apparent PPMR. The presence of such large animals feeding on smaller and more productive size classes of prey may mask or weaken the size-based analyses. Indeed, excluding parrotfish from size classes 12 and 13 increased the slope to 0.304, with an associated reduction in PPMR from 7792:1 to 2327:1.

A PPMR of 7792:1 is outside the majority of estimates for marine systems, but PPMR is affected by both the estimate of trophic fractionation and by the slope of the $\delta^{15}\text{N}$ size-based analysis. It is possible that the applied trophic fractionation was too high, as PPMR decreases with decreasing trophic fractionation. Mean $\Delta\delta^{15}\text{N}$ has been estimated as $3.4\text{‰} \pm 0.98$ (Post 2002), and $\Delta\delta^{15}\text{N}$ values as low as 2.5‰ (PPMR 1214:1) are therefore not unreasonable. Using the trophic fractionation of 3.2‰ derived from the slope of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, PPMR = 4599:1. Furthermore, fractionation may alter with temperature (Bosley et al. 2002, Power et al. 2003) and differ among systems (France & Peters 1997). It is unclear at present whether different fractionation estimates should be applied to temperate and tropical systems.

Short food chains

Jennings & Warr (2003) correlated food chain length with the mean PPMR, where a smaller mean PPMR indicates a longer food chain. This suggests that the food chains in the Western Arabian Sea are particularly short, in agreement with other upwelling areas (Bode et al. 2003, 2006).

The $\delta^{15}\text{N}$ -body mass slope suggests that from the smallest to the largest body mass size classes the assemblage spans only 1 TL (assuming trophic fractionation of 3.4‰ ; Vander Zanden & Rasmussen 2001, Post 2002). The span is only slightly larger (4.49‰ or 1.3 TLs) when considering minimum and maximum observed values. TL span will vary depending on assumption of trophic

fractionation; however, fractionation estimates between 3.0 and 3.4‰ are robust for fish and have little impact on conclusions (Sweeting et al. 2007). Therefore, most species caught in the trawl assemblage existed within 1 TL.

Shorter food chains have often been thought to characterize upwelling ecosystems (3 TLs) as opposed to those of the open ocean (5 TLs) (Ryther 1969, Bode et al. 2003). In contrast, Pimm (1982) argued that very productive oceanic areas (e.g. upwelling areas) should exhibit longer food chains because productivity at lower TLs could maintain a longer energy flux to higher TLs. However, examples from productive lakes do not show long food chains (see Vander Zanden et al. 1999), and results presented here support the first theory (Ryther 1969).

Species $\delta^{13}\text{C}$

Among species, $\delta^{13}\text{C}$ was independent of maximum body size, regardless of whether or not $\delta^{13}\text{C}$ was normalised for lipid content or not. Given that in most species C:N ratios (a good proxy for lipid content in fish; Sweeting et al. 2006) were low, $<3.5:1$, the effect of lipid content was expected to be small relative to feeding and behaviour-induced variation in $\delta^{13}\text{C}$. We discounted spatial and temporal variation for the same reasons as for species $\delta^{15}\text{N}$. The most likely explanation therefore is that multiple production sources support multiple individual food chains, which is consistent with size-independent niche segregation implied for $\delta^{15}\text{N}$. Mean $\delta^{13}\text{C}$ of production sources ranged from -28.28‰ (mangrove) to -18.62‰ (phyto- and zooplankton $<500\ \mu\text{m}$) to -7.47‰ (macrophytes, range -15.01 to -7.47‰ ; S. H. Al-Habsi unpubl. data), and the assemblage contained both planktivores (e.g. *Scomber japonicus*) and algal herbivores (e.g. *Scarus ghobban*), supporting the suggestion that multiple food chains based on differing production sources exist.

Community $\delta^{13}\text{C}$

Patterns in the trawl assemblage $\delta^{13}\text{C}$ were similar to those of $\delta^{15}\text{N}$, in that community $\delta^{13}\text{C}$ also increased with body mass, while species data at the among-species level did not. This relationship was driven in part by lower lipid content in large individuals, although a non-significant positive trend still remained between lipid-normalised $\delta^{13}\text{C}$ and size. Variation in $\delta^{13}\text{C}$ between the smallest and largest body mass was within the published enrichment values for $\delta^{13}\text{C}$ of $\sim 1\text{‰}$ per TL (DeNiro & Epstein 1978). Given the low trophic enrichment and variation in $\delta^{13}\text{C}$ among sources of production, the R^2 for $\delta^{13}\text{C}$ with body mass was low.

Despite this, the linear nature of community $\delta^{13}\text{C}$ size-based analysis and the fact that slopes were consistent with a 0.6‰ trophic enrichment for $\delta^{13}\text{C}$ (assuming $\Delta\delta^{15}\text{N} = 3.4\text{‰}$) suggest that production supporting the community biomass is dominated by only 1 source, with $\delta^{13}\text{C}$ in the region of -18‰ ($\delta^{15}\text{N} \approx 10\text{‰}$). Isotopic composition of primary producers can be averaged out in top consumers even when different food sources at the base of the food web have similar isotopic signatures. Values are consistent with those of the phytoplankton–zooplankton assemblage (90 to 500 μm).

The conclusions presented here are based on catch data from the Arabian Sea demersal trawl assemblage, and thus represent only one component of the total Arabian Sea continental shelf community. Data interpretation is therefore constrained to that assemblage, and it would be desirable to test whether observed size structuring and cross-species relationships hold true across the whole community as observed in the North Sea (Jennings et al. 2002b). Additional seasonal sampling with gears specifically targeting small size classes not efficiently sampled here would also be valuable for providing insight into patterns in size structuring introduced by the upwelling event at finer temporal resolution.

Towards the ecosystem approach to fisheries management

Size-based techniques such as size-spectra analysis (abundance–size relationships) have been increasingly promoted as useful metrics in assessing the impacts of fishing and disturbance at the community level (Rochet & Trenkel 2003, Jennings & Dulvy 2005). Such metrics have demonstrated predictable changes in response to fishing for temperate demersal fisheries (Gislason & Rice 1998). It is likely that similar responses will be apparent for tropical demersal fisheries; due to less consistent datasets and potentially higher growth rates, the trends may not be as strong (Bianchi et al. 2000, Stobberup et al. 2005). As suggested by Jennings et al. (2001) for the North Sea, this study suggests that size alone is also a useful predictor of TL in tropical short food chain fish communities. It may therefore be possible to parameterise size spectra with TL (as suggested by Jennings et al. 2001, 2002a) to assess changes in trophic structure in response to fishing, management scenarios or other pressures on the system. Clearly, with increasing acceptance that fisheries should be managed at the ecosystem level and the majority of such work occurring in temperate waters, more research on the use of such indicators in tropical continental shelf fisheries is essential.

CONCLUSIONS

The present study suggested that even in aquatic systems with large ranges of predator and prey body sizes, the community is size structured, despite weak cross-species relationships between body size and TL. Our findings also suggest that although a wide range of production sources may be utilised in a complex system such as that of the Western Arabian Sea, and as a result of niche specialisation, the community biomass may be largely reliant on only 1 source. Trophic size structuring at the community level in such a complex system lends further support to the use of size-based models to assess the effects of fishing at the ecosystem level.

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