

Dietary success of a 'new' key fish in an overfished ecosystem: evidence from fatty acid and stable isotope signatures

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ABSTRACT: The bearded goby *Sufflogobius bibarbatatus* has become a key component of the pelagic food web off Namibia following the crash in pelagic fish populations during the 1970s, and its biomass is increasing despite significant predation pressure and apparent life-history constraints. The integrated feeding of the bearded goby was studied from samples collected during April 2008, using stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) and fatty acids, to resolve conflict amongst previous dietary studies based on gut-content analysis and to understand how diet could influence its success within the region. Isotopes of carbon and nitrogen suggest that the now abundant jellyfish could contribute up to 74 % of the diet, and $\delta^{34}\text{S}$ signatures indicate that the diatom- and bacteria-rich sulphidic sediments on the central shelf may contribute around 15 % to the diet. Fatty acid analyses provided support for sulphur bacterial and jellyfish-feeding amongst gobies, and further suggest that small gobies fed more on zooplankton while large gobies fed more on sedimented diatoms. Both data sets suggest that ontogenetic changes in diet were linked to changes in habitat: pelagic when small, more demersal when large. The study highlights the value of using multiple tracers in trophic studies and indicates that the dietary flexibility of the bearded goby, in conjunction with its behaviour and physiology, likely contributes to its success within the northern Benguela ecosystem.

KEY WORDS: Benthic–pelagic coupling · Keystone species · Disturbed ecosystem · Feeding · *Aequorea forskalea* · *Chrysaora fulgida*

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INTRODUCTION

The northern Benguela ecosystem has undergone a number of profound changes over the last few decades (Heymans et al. 2004). Sardines *Sardinops sagax* were the most abundant pelagic fish species in the region during the 1960s (Boyer & Hampton 2001), but their populations crashed off Namibia during the 1970s due to a combination of overfishing and environmental change (Boyer et al. 2001, Cury & Shannon 2004). Sar-

dines were replaced by several other fishes, including horse mackerel *Trachurus trachurus capensis* and the bearded goby *Sufflogobius bibarbatatus*, and to a much lesser extent by anchovy *Engraulis encrasicolus* (Cury & Shannon 2004). Many higher predators (including piscivorous fishes, seabirds and seals) that had once fed on sardines started to feed on gobies instead (Crawford et al. 1985). Recently, the effects of 'fishing down the marine food web' (Pauly et al. 1998) appear to have resulted in an increase in the biomass of jelly-

fish *Chrysaora fulgida* (Reynaud, 1830) and *Aequorea forskalea* (Forskål, 1775) (Bakun & Weeks 2006, Lynam et al. 2006). These jellyfish have changed the transfer and flow of energy through the system, with most energy now thought to be channelled from jellyfish directly to the detrital food web (Heymans et al. 2004). The scarcity of sardines has also resulted in an increased sedimentation of primary production (Bakun & Weeks 2006), which contributes to increased regional anoxia (Monteiro et al. 2006).

*Sufflogobius bibarbatu*s is an unlikely 'winner' in the changed ecosystem off Namibia, as it is a relatively large, slow-growing gobiid that can attain 140 mm total length (TL) and an age of at least 6 yr (Melo & Le Clus 2005). Reproductive maturity is attained only at 2 to 3 yr of age, and although it is considered to be a serial batch spawner, overall fecundity is not high (Melo & Le Clus 2005). The species is discontinuously distributed between Southern Angola and the Eastern Cape (South Africa), with peaks in abundance mirroring the distribution of the diatomaceous mud belt off central Namibia (Staby & Krakstad 2006). Juvenile gobies generally occur inshore of the 200 m isobath, while larger individuals are more common offshore (O'Toole 1978). Although *S. bibarbatu*s displays diel vertical migration, smaller individuals are predominantly pelagic, whereas large individuals are largely demersal (D'Arcangues 1977).

Previous studies on the diet of *Sufflogobius bibarbatu*s have been conducted using gut-content analyses of generally small sample sizes. The results of these studies are conflicting, but suggest that it is an opportunistic predator. Barber & Haedrich (1969) noted that juvenile gobies feed primarily on diatoms, an observation in agreement with the findings of Crawford et al. (1985) and O'Toole (1978). In contrast, D'Arcangues (1977) noted that adult and juvenile gobies feed primarily on zooplankton, whilst Macpherson & Roel (1987) highlighted that benthic infauna can form a numerically important part of the diet. Hundt (2009) has recently shown that the diet varies with the food environment, with the diet of inshore animals being dominated by diatoms and infauna, and that of offshore animals by zooplankton and benthic infauna. Cedras (2009) has shown changes in the diet that are assumed to be linked to ontogenetic changes in the habitat occupied: smaller, more pelagic individuals fed primarily on zooplankton, whilst larger, demersal animals fed mainly on benthic infauna.

Here, we used stable isotope ratios of carbon, nitrogen and sulphur in conjunction with fatty acid analyses to resolve conflicts among previous studies on the diet and trophic position of *Sufflogobius bibarbatu*s off Namibia, and to determine whether the feeding biology of the goby might contribute to its current success

within the region. Stable isotope and fatty acid signatures provide a temporally and spatially integrated view of feeding history and trophic structure (Minagawa & Wada 1984, Peterson & Fry 1987, Hobson et al. 1995, Pitt et al. 2007), since they reflect assimilation of the elements into the soma. Consumers differentially accumulate heavier isotopes (Peterson & Fry 1987) resulting in a predictable trophic enrichment (fractionation) in heavy isotopes. This fractionation is negligible for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ but ranges between 3 and 4‰ for $\delta^{15}\text{N}$ (Minagawa & Wada 1984, Peterson & Fry 1987), which means that stable nitrogen ratios ($^{15}\text{N}/^{14}\text{N}$) can be used to determine the relative trophic level of a particular individual (Minagawa & Wada 1984, Peterson & Fry 1987). Stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) are commonly used to provide information on the primary source of organic matter sustaining a food web (Peterson & Fry 1987), while stable sulphur isotope ratios are commonly used to make inferences about possible links to the detrital or benthic food web (Thomas & Cahoon 1993). Fatty acids are also valuable tools to explore trophic relationships in aquatic systems, as different food sources can display distinctive fatty acid profiles that are transferred to consumer tissues (Budge et al. 2006, Pitt et al. 2009). The combination of stable isotopes and fatty acid markers, as used here, is widely seen as the way forward in trophic investigations (e.g. El-Sabaawi et al. 2010), as each provides slightly different sets of information.

MATERIALS AND METHODS

Field sampling and study site. The study was based on samples collected from a 48 h anchor station off Walvis Bay between 4 and 5 April 2008, using the RV 'G. O. Sars'. This anchor station (23° 30' S, 13° 40' E; referred to as Stn B in Supplement 1) was situated at the outer edge of the continental shelf at a depth of ~180 m. Vertical profiles of the water column were constructed from CTD (Sea-Bird SBE 19) casts and indicated that the temperature decreased from a maximum of 18°C at the surface to a minimum of 13°C at 90 m (remaining constant thereafter to the bottom), and that the water column was approximately isohaline throughout (35.26 PSU; A. C. Utne-Palm et al. unpubl. RV 'G. O. Sars' cruise report). Oxygen levels at the surface were close to 6 ml dissolved oxygen (DO) l⁻¹, and these decreased evenly to 1 ml l⁻¹ at around 100 m: only near the seafloor did DO concentrations drop to less than 0.4 ml l⁻¹ (A. C. Utne-Palm et al. unpubl. cruise report). Additional material was collected from an inshore station (23° 20' S, 14° 12' E; referred to as Stn A in Supplement 1) at 120 m depth.

Fish and jellyfish (*Chrysaora fulgida*, *Aequorea forskalea*) intended for isotope and fatty acid analysis

Table 2. Sample sizes (n and mean dry weight, DW) analysed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$ and fatty acid signatures. MZ 150–1000: mixed zooplankton of sizes 150–1000 μm

Sample	Stable isotopes (C, N) ^a		Stable isotopes (S,C,N) ^b		Fatty acids	
	n	Mean DW (mg)	n	Mean DW (mg)	n	Mean DW (mg)
Sediment	2	5.9 ± 0.01	3	5.31 ± 0.40	2+8 ^c	196.38 ± 52.01
Pteropod shells	5	0.63 ± 0.04	–	–	6	130.94 ± 49.39
Amphipods	–	–	–	–	2	33.25 ± 1.41
Pteropods	4	0.65 ± 0.02	–	–	9	159.93 ± 53.86
Adult euphausiids	6	0.63 ± 0.05	–	–	6	209.13 ± 83.54
MZ 150–1000	–	–	8	5.47 ± 0.41	–	–
MZ 150	–	–	–	–	2	44.40 ± 24.74
MZ 200	2	0.63 ± 0.02	–	–	2	59.74 ± 10.94
MZ 250	–	–	–	–	2	130.26 ± 28.47
MZ 500	4	0.64 ± 0.03	–	–	4	123.42 ± 50.25
MZ 1000	8	0.63 ± 0.02	–	–	5	189.89 ± 23.74
<i>Aequorea forskalea</i>	11	1.07 ± 0.61	3	5.45 ± 0.66	9	373.59 ± 98.90
<i>Chrysaora fulgida</i>	11	0.99 ± 0.30	5	5.54 ± 0.42	22 ^c	261.01 ± 75.50
Gobies	–	–	7	5.80 ± 0.34	–	–
Goby large	15	0.65 ± 0.03	–	–	20	35.21 ± 11.12
Goby medium	21	0.64 ± 0.03	–	–	20	68.39 ± 28.48
Goby small	41	0.64 ± 0.04	–	–	20	179.61 ± 51.51

^aAnalysed at the University of Cape Town, South Africa; ^banalysed at the University of Stockholm, Sweden; ^csamples collected from inshore station (Stn A)

For fatty acid analysis, samples of >20 mg of homogenised, freeze-dried fish white muscle, jellyfish tissue, zooplankton and sediment (insufficient polychaete material was available) were preserved in 2 ml chloroform under nitrogen at -20°C . The methods used for total lipid extractions and transesterification follow Budge et al. (2006) using 23:0 (tricosanoic acid $\geq 98.5\%$ GC; FLUKA) as an internal standard. Fatty acid methyl esters (FAMES) of total extracted lipids suspended in hexane were injected (1 μl aliquots) into a gas chromatograph (Hewlett Packard 5890 series II, equipped with a ZB-Waxplus 320 column), with helium as the carrier gas. The injector and detector temperatures were maintained at 250°C and 260°C , respectively, and the oven was set at 150°C for the first 5 min, raised to 225°C at $2.5^{\circ}\text{C min}^{-1}$ and held for 5 min. FAME peaks were integrated using ClarityLite 2.6.2 software, and identified by comparison with known standards (polyunsaturated fatty acid, PUFA no. 1 and a 37 component FAME mix; Supelco). Each fatty acid was measured as a proportion of the total identified fatty acids (%TFA) and quantitatively as μg fatty acid mg^{-1} dry weight (DW).

Fatty acids that are required for the biological functioning of membranes and organs but are not effectively synthesised de novo by animals, termed the essential fatty acids (EFAs), include the PUFAs 20:5 ω 3, 22:6 ω 3 and 20:4 ω 6. These fatty acids must be obtained from the diet, and as such are commonly used as biomarkers for algal consumption (Budge et al. 2006). There is some uncertainty with regards to the discriminatory power of such biomarkers measured in total

lipid fractions in metazoan consumers, especially since no single fatty acid is exclusive to any particular algal group. However, as the phytoplankton community in the Benguela upwelling region is dominated first by diatoms and then dinoflagellates (Fréon et al. 2009), we utilised 2 independent ratio markers to assess the prevalence of diatoms in the goby diet: $\Sigma(16:1\omega 7 + 16:1\omega 5)/16:0$ ($\Sigma 16:1/16:0$; Graeve et al. 1994) and 20:5 ω 3/22:6 ω 3 (Parrish et al. 2000). The reverse ratio of 22:6 ω 3/20:5 ω 3 was used to assess the relative dominance of dinoflagellates relative to diatoms (Parrish et al. 2000). Bacterial fatty acids (BAFAs) include odd-numbered carbon chains and *iso-* (*i-*) and *anteiso-* (*ai-*) branched forms (Budge & Parrish 1998), and the sums of long chain monounsaturated fatty acids (MUFAs, $\Sigma[20:1\omega 9 + 22:1\omega 11]$) were used to indicate potential consumption of calanoid copepods ($\Sigma[20:1 + 22:1]$; Sargent & Falk-Petersen 1988).

Statistical methods. For both stable isotope and fatty acid analyses, gobies were categorised as small (<57 mm), medium (58 to 90 mm) and large (>90 mm) based on a visual inspection of a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ versus total length plot (Fig. 1) of goby signatures. The sample sizes of each group used for both analyses are summarised in Table 2. While we acknowledge the circularity of the methods used to delimit size classes here, there is a clear relationship between age and length (Melo & Le Clus 2005) and there is a clear change in tracer signature over the continuous size gradient examined here.

A 1-way analysis of variance (ANOVA) was used to analyse potential differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sig-

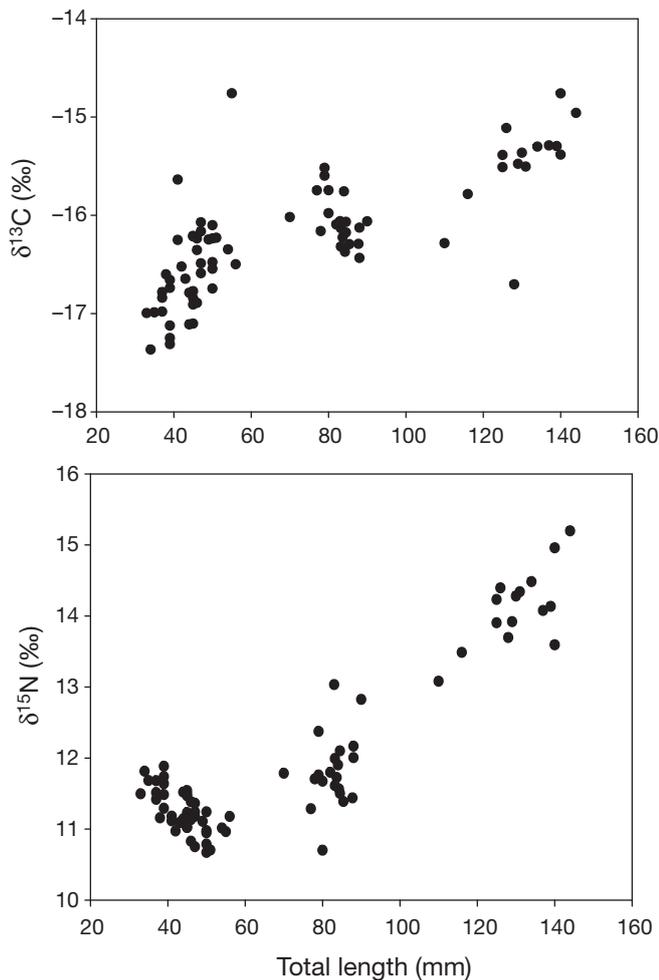


Fig. 1. *Sufflogobius bibarbatus*. Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures with size of the bearded goby off Namibia at 180 m depth. Small gobies: <57 mm total length (TL); medium-sized gobies: 58–90 mm TL; large gobies: >90 mm TL

natures among the different goby size classes. To establish from which food types gobies were deriving nutrition, we calculated ranges in isotope values expected for all food types and used these values to draw 'trophic-shift boxes' in 2-dimensional $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space. Fauna that derive 100% of their diet from jellyfish, sediment and zooplankton are expected to cluster within the trophic boxes for the respective food sources (Demopoulos et al. 2007). For these calculations, we assumed no trophic-level fractionation for $\delta^{13}\text{C}$ (France & Peters 1997), and a +3‰ increase in $\delta^{15}\text{N}$ per trophic level for jellyfish, sediment and zooplankton (Demopoulos et al. 2007).

A multisource mixing model (IsoSource) was used to estimate minimum and maximum proportional contributions of potential prey items to the goby diet (Phillips & Gregg 2003). To do this, $\delta^{15}\text{N}$ -corrected and uncor-

rected $\delta^{13}\text{C}$ faunal isotope measurements were plotted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space and a 5-sided polygon drawn narrowly around the data (see Fig. S1 in the Supplement 1 at www.int-res.com/articles/suppl/m428p219_supp.pdf). The apices of the polygon represent the average isotope signatures that must be available to support the gobies. Apices were allocated for adult euphausiids, shrimp, *Aequorea forskalea*, *Chrysaora fulgida* 1 and *C. fulgida* 2, of which *C. fulgida* 1 had lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures relative to *C. fulgida* 2, perhaps as a consequence of natural variation. *C. fulgida* 1 and 2 end members were defined as possible food resources since isotope values of jellyfish of the same species can be distinct (Towanda & Thuesen 2006, Pitt et al. 2009). Therefore, we used 2 *C. fulgida* end members. Isotopic signatures of gobies and food source end members were then used in the 5-source mixing model (Fig. S1), in order to calculate the proportional contributions of all food sources to goby diet (Demopoulos et al. 2007, Utne-Palm et al. 2010). Source increment was set at 1‰, with a tolerance level of 0.05‰. Spearman rank correlations (Zar 1999) with subsequent sequential Bonferroni corrections (Quinn & Keough 2002) were used to correlate fish size with prey source contributions.

To determine the contribution of benthic and pelagic food sources to the diet of *Sufflogobius bibarbatus*, a 2 end member linear mixing model was employed (Levin & Michener 2002) using $\delta^{34}\text{S}$ signatures. Ultimately, the 'enriched $\delta^{34}\text{S}$ food source' (mixed zooplankton and jellyfish) was used as 1 end member and the 'reduced $\delta^{34}\text{S}$ food source' (benthic sediment containing diatoms, sulphur bacteria and/or benthic meiofauna) as the other end member. However, a precise allocation of the benthic $\delta^{34}\text{S}$ end member signature is difficult, because the process of freeze-drying removes part of the porewater hydrogen sulphide and precipitates isotopically heavy porewater sulphate. We selected 2 values to estimate the benthic contribution: an average value of +5.75‰ versus VCDT was used as the isotopically light end member representing spatially pooled freeze-dried sediment containing diatoms, benthic meiofauna and sulphur bacteria. An alternative value of -15‰ versus VCDT was used as the second end member based on previous measurements at a shelf station at 23° 45.5'S, 14° 16.0'E in 114 m water depth (Dale et al. 2009). We based the use of this value on the fact that sulphur available to grazing gobies is porewater hydrogen sulphide, organic sulphur and elemental sulphur stored in sulphur bacteria, but not mineral sulphides and inorganic sulphate. The origin of the sulphides and elemental sulphur is through production by sulphate-reducing bacteria, which fractionate porewater sulphate to derive hydrogen sulphide with a value of -15‰ (Dale et al. 2009).

The fatty acid data were analysed quantitatively ($\mu\text{g mg}^{-1}$ DW relative to a standard, 23:0) and qualitatively (as percentage of TFA), the latter being useful in situations where samples vary greatly in their TFA content. The effects of ontogeny on key fatty acids and entire fatty acid profiles of gobies were determined using a series of 1-way ANOVAs, with subsequent Bonferroni correction (Quinn & Keough 2002) and principal component analysis (PCA), respectively, following normalisation of the quantitative fatty acid data using a mix of \log_{10} and square root transformations. Relationships between the composition of potential dietary items (taxa or size classes of taxa) and gobies were also explored using non-metric multidimensional scaling (NMDS) in PRIMER v6 (Clarke & Warwick 2001).

RESULTS

Stable isotopes

Small, medium and large gobies were significantly different from each other in terms of their $\delta^{13}\text{C}$ ($F = 37.55$, $p < 0.05$, $n = 41$, $n = 21$ and $n = 15$, respectively) and $\delta^{15}\text{N}$ signatures ($F = 255$, $p < 0.05$, $n = 41$, $n = 21$ and $n = 15$, respectively). Gobies became more enriched in the heavier carbon isotope as they increased in size (Fig. 1). Small gobies fed at the same average trophic level ($\delta^{15}\text{N} = 11.24 \pm 0.05\text{‰}$ SE; $n = 41$) as medium gobies ($\delta^{15}\text{N} = 11.82 \pm 0.11\text{‰}$; $n = 21$), but small and medium gobies fed at a lower trophic level compared to large gobies ($\delta^{15}\text{N} = 14.12 \pm 0.14\text{‰}$; $n = 15$; Fig. 1).

Small and medium-sized gobies were similar to *Chrysaora fulgida* in their $\delta^{13}\text{C}$ signatures (Fig. 2). Based on $\delta^{15}\text{N}$ signatures, *Aequorea forskalea* fed at the same average trophic level as small and medium-sized gobies but lower than large gobies and higher than *C. fulgida* (Fig. 2).

Shrimp, benthic polychaetes, sediments and adult euphausiids had carbon isotope signatures closest to that of the goby. Pteropods (*Cymbulia* sp.) possessed similar $\delta^{15}\text{N}$ -signatures compared to mixed zooplankton, which suggests that they feed at similar trophic levels (Fig. 2). However, nitrogen isotope signals indicated that pteropods feed at a lower trophic level compared to small gobies, medium gobies, benthic polychaetes and shrimp, which all appeared to feed at approximately the same average trophic level (Fig. 2).

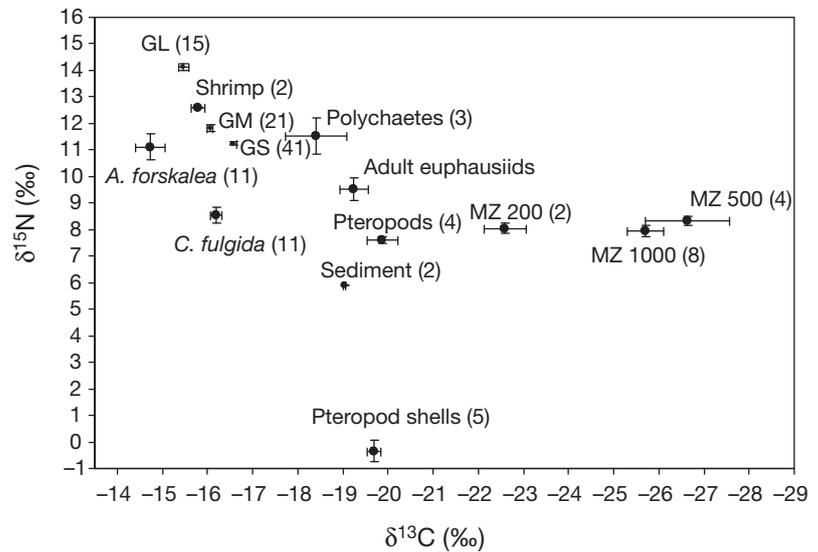


Fig. 2. *Sufflogobius bibarbatus*. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of different size classes of bearded goby and potential dietary sources off Namibia, n in parentheses. A.: *Aequorea*; C.: *Chrysaora*; GS: small gobies; GM: medium-sized gobies; GL: large gobies; MZ 200–1000: mixed zooplankton of sizes 200–1000 μm

Spatially pooled sediment had the lowest $\delta^{34}\text{S}$ signatures ($\delta^{34}\text{S} = 5.75 \pm 0.99\text{‰}$; $n = 3$), followed by that of gobies ($\delta^{34}\text{S} = 16.45 \pm 0.41\text{‰}$; $n = 7$), mixed zooplankton ($\delta^{34}\text{S} = 19.78 \pm 0.64\text{‰}$; $n = 8$), *Aequorea forskalea* ($\delta^{34}\text{S} = 21.44 \pm 0.21\text{‰}$; $n = 3$) and *Chrysaora fulgida* ($\delta^{34}\text{S} = 21.50 \pm 0.12\text{‰}$; $n = 7$; Fig. 3). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of sediment were $-16.35 \pm 1.10\text{‰}$ and $6.19 \pm 0.37\text{‰}$, respectively.

Based on trophic shift boxes, gobies appeared to receive only a small part of their diet from sediment, as

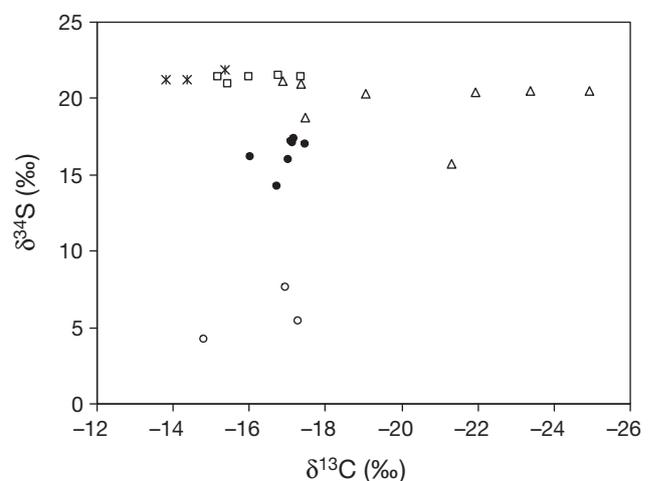


Fig. 3. Cross-plot of $\delta^{13}\text{C}$ versus $\delta^{34}\text{S}$ of individual samples of sediment (open circles), *Aequorea forskalea* (stars), *Chrysaora fulgida* (open squares), mixed zooplankton (open triangles) and *Sufflogobius bibarbatus* (closed circles) collected off the Namibian shelf during April 2008. Modified from Utne-Palm et al. (2010)

their $\delta^{15}\text{N}$ signatures were outside the range of the diatomaceous mud (also known to contain large sulphur bacteria and diatoms; Fig. 4). Gobies fed on *Aequorea forskalea* and *Chrysaora fulgida*, although it appeared that the very large gobies fed almost exclusively on *A. forskalea* (upper leftmost symbols in Fig. 4 and see Fig. 5) while possibly supplementing their diet with shrimp (Fig. 4).

The results of the IsoSource model indicate that the maximum contribution of *Aequorea forskalea* was positively correlated with fish size ($R = 0.91$, $p < 0.05$, $n = 76$; Fig. 5), with average source contributions reaching a maximum of 70.36% in large gobies (Table 3). *Chrysaora fulgida* with lighter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures was negatively correlated with fish size ($R = -0.82$, $p < 0.05$, $n = 76$; Fig. 5), and potentially reached an average maximum contribution of 73.85% in small fish (Table 3).

The $\delta^{34}\text{S}$ signatures indicated that contributions of the benthic sediment (which may include diatoms and bacteria) to the diet of the goby were on average $34.2 \pm 2.5\%$, if the average value of $+5.75\%$ versus VCDT for freeze-dried sediment is used as the end member (Table 4). If an average value of -15% versus VCDT is chosen for the biologically available sulphur fraction (see Discussion), then the dietary contribution of the benthos is $15.0 \pm 1.1\%$ (Table 4).

Fatty acids

All raw qualitative (Tables S1 to S4) and quantitative (Tables S5 to S8) individual and summary fatty acids are presented in Supplement 1 at www.int-res.com/articles/suppl/m428p219_supp.pdf, and all essentially indicate similar patterns.

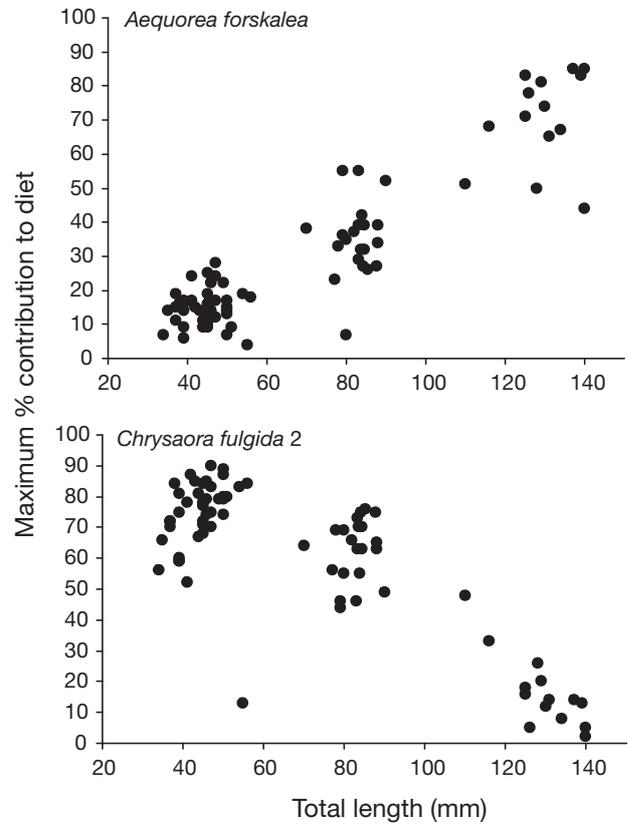


Fig. 5. *Sufflogobius bibarbatu*s. Changes in maximum percentage contribution of *Aequorea forskalea* and *Chrysaora fulgida 2* to the diet of bearded goby with fish size (total length, mm)

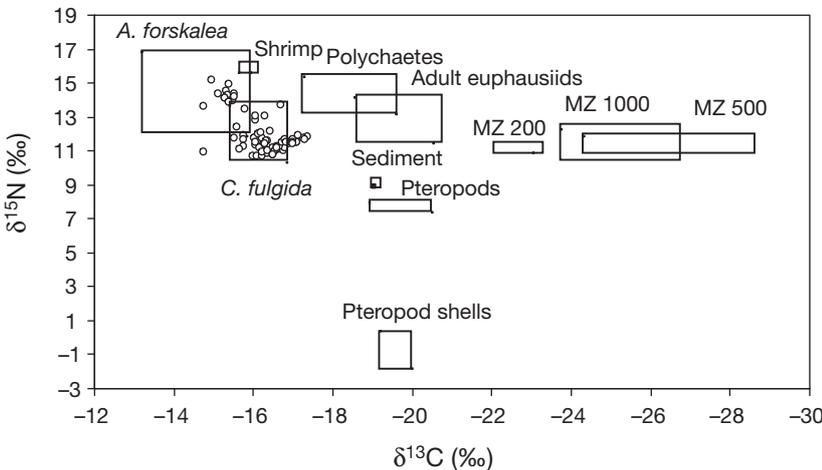


Fig. 4. *Sufflogobius bibarbatu*s. Trophic-shift boxes of gobies collected off Namibia during 2008, related to the upper and lower limits of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of potential prey items. A.: *Aequorea*; C.: *Chrysaora*; MZ 200–1000: mixed zooplankton of sizes 200–2000 μm

[com/articles/suppl/m428p219_supp.pdf](http://www.int-res.com/articles/suppl/m428p219_supp.pdf), and all essentially indicate similar patterns.

NMDS results based on fatty acid profiles suggested that gobies were not deriving nutrients from sediment or pteropod shells, but that large gobies were potentially feeding on jelly-fish (Fig. 6). As a group, gobies could also be deriving nutrition from a combination of pteropods (soft tissue), amphipods, euphausiids and mixed zooplankton (Fig. 6). PCA of the quantitative fatty acid profiles of the gobies suggested that the diet of small gobies differed from that of large gobies, with medium gobies representing a transitional and variable developmental stage (Fig. 7). The PCA loadings demonstrated that the saturated fatty acids (SFAs) 14:0, 16:0 and 18:0, the MUFAs 16:1 ω 7, 18:1 ω 7, 18:1 ω 9 and 20:1 ω 9, and the PUFAs 18:2 ω 6, 20:5 ω 3 and 22:6 ω 3 were strongly associated

Table 3. Average (\pm SE) minimum and maximum percentage contribution of different prey to the diet of *Sufflogobius bibarbatus* of different size, as determined from a 5 end member IsoSource model (see 'Materials and methods' for more details)

Prey source	Fish size (mm)	n	Percent contribution	
			Min.	Max.
Adult euphausiids	<57	41	8.17 \pm 1.73	26.85 \pm 1.87
	58–90	21	0	33.14 \pm 1.93
	>90	14	1.71 \pm 1.64	18 \pm 3.89
Shrimp	<57	41	0	12.44 \pm 0.62
	58–90	21	0	27.05 \pm 2.2
	>90	14	11.14 \pm 4.18	58.64 \pm 4.34
<i>Aequorea forskalea</i>	<57	41	0	14.73 \pm 0.85
	58–90	21	0	35.1 \pm 2.39
	>90	14	12.07 \pm 5.55	70.36 \pm 3.68
<i>Chrysaora fulgida</i> 1	<57	41	3.85 \pm 2.18	29.56 \pm 2.29
	58–90	21	3.81 \pm 1.74	55.05 \pm 2.03
	>90	14	0.79 \pm 0.79	26.79 \pm 2.62
<i>C. fulgida</i> 2	<57	41	44.1 \pm 1.99	73.85 \pm 2.1
	58–90	21	9.29 \pm 3.07	62.48 \pm 2.21
	>90	14	0	16.71 \pm 3.28

Table 4. Relative percentage dietary contribution from benthic sediment, porewater hydrogen sulphide and pelagic 'enriched $\delta^{34}\text{S}$ food sources' to the diet of gobies as calculated from a 2 end member mixing model (Scenario 1: $\delta^{34}\text{S}_{\text{sediment}} = 5.8\text{‰}$ vs. VCDT; Scenario 2: $\delta^{34}\text{S}_{\text{H}_2\text{S}} = -15\text{‰}$ vs. VCDT). See 'Materials and methods' for more details. Mean \pm SE values for benthic and 'enriched $\delta^{34}\text{S}$ food source' contributions are indicated. VCDT: Vienna-Canyon Diablo Troilite

$\delta^{34}\text{S}$ (‰)	Benthic contribution to diet	
	Scenario 1	Scenario 2
16.0	37.0	16.3
17.1	30.0	13.2
17.2	29.8	13.1
17.4	28.6	12.6
16.2	35.6	15.6
17.0	30.5	13.4
14.3	47.6	20.9
Benthic contribution	34.2 \pm 2.5	15.0 \pm 1.1
'Enriched pelagic' contribution	65.8 \pm 2.5	85 \pm 1.1

with small gobies (Fig. 7). The PUFAs 16:2 ω 4, 16:3 ω 3, 16:3 ω 4 and 20:4 ω 6 distinguished the large gobies in the PCA (Fig. 7). A PCA using summary fatty acid profiles of quantitative data (not shown) indicated the greatest fatty acid content (TFA, SFA, MUFA, PUFA, EFA, BAFA and $\Sigma[22:1+20:1]$), as well as larger ratios of the traditional dinoflagellate marker 22:6 ω 3/20:5 ω 3 in small gobies, whereas traditional diatom markers $\Sigma 16:1/16:0$ and 20:5 ω 3/22:6 ω 3 were elevated in the tissues of large gobies (Table S7).

No marker specific to jellyfish was identified during this study, but both gobies and jellyfish had elevated ratios of 22:6 ω 3/20:5 ω 3 (Tables S7 & S8). *Aequorea forskalea* and *Chrysaora fulgida* were proportionally high in *i*-17:0 (1.16 and 1.14 % TFA, respectively) and 19:0 (1.27 and 1.34 % TFA, respectively) compared to other prey items (Fig. 8). Similarly, elevated proportions of these fatty acids were seen in the tissues of small, medium and large gobies (Fig. 8). Sediment was dominated by 16:0 (20.28 % TFA), 18:1 ω 7 (14.27 % TFA) and 16:1 ω 7 (12.92 % TFA; Table S2). Sediment was substantially higher in *ai*-15:0 (3.13 to 5.41 % TFA), 24:0 (1.29 to 5.59 % TFA), 16:1 ω 7 (6.24 to 12.92 % TFA), 18:1 ω 7 (6.66 to 14.27 % TFA; Tables S1 & S2) and BAFA (12.06 to 14.3 % TFA; Tables S3 & S4) when compared to most other food sources.

DISCUSSION

Herbivory or detritivory?

The $\delta^{34}\text{S}$ results suggest that spatially pooled benthic sediment contributed to the diet of the goby. The source apportionment depends critically on the isotope composition of benthic endmembers and potential sulphur isotope trophic shifts. It is difficult to assign a specific sulphur isotope value to the benthic diet based on a bulk measurement of freeze-dried sediment. Only a fraction of the freeze-dried sediment likely comprises the food source for gobies considering that the diatomaceous sediment contains iron sulphide mineral grains and seawater sulphate that will pass unused through the gut of the goby. Therefore, only selective organic sulphur compounds and sulphur stored in bacterial biomass form part of the sulphur in the goby diet. Based on individual sulphur species isotope studies, the sulphur isotope composition of these fractions is significantly lighter and varies between -10 and -20‰ in the top 3 cm of sediment (Dale et al. 2009). Such a light sulphur isotope diet diminishes the benthic diet contribution. The Namibian shelf sediment is known to contain diatoms and sulphur-storing bacteria such as *Thiomargarita* sp. (Schulz et al. 1999), and previous studies have all highlighted diatoms as being major components of the diet of gobies collected inshore along the Namibian coast (Barber & Haedrich 1969, O'Toole 1978, Crawford et al. 1985, Hundt 2009). The

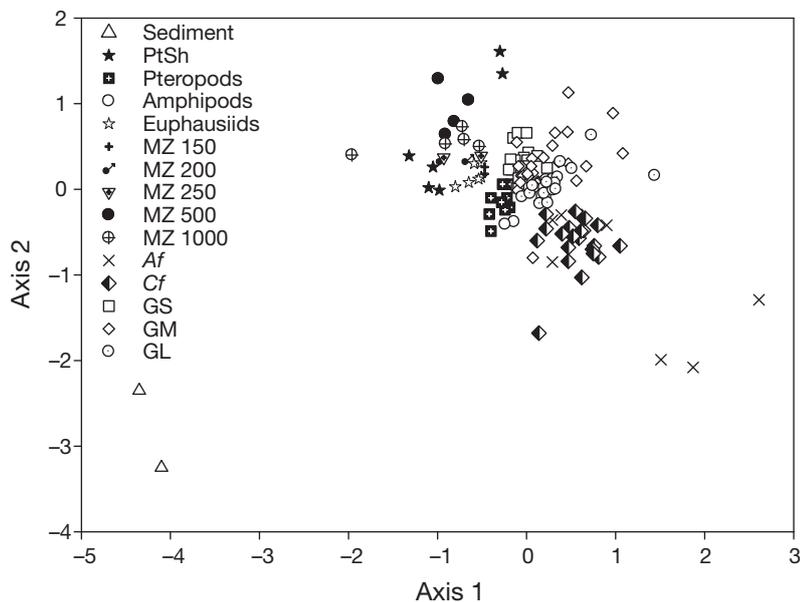


Fig. 6. *Sufflogobius bibarbat*. Non-metric multidimensional scaling (NMDS) ordination of the qualitative individual fatty acid profiles of bearded goby and its potential prey. PtSh: pteropod shells; MZ 150–1000: mixed zooplankton sized 150–1000 μm ; Af: *Aequorea forskalea*; Cf: *Chrysaora fulgida*; GS: small gobies; GM: medium gobies; GL: large gobies. All samples were collected at the offshore station, but *C. fulgida* are from the inshore station

short, widely spaced gill rakers of gobies render them unable to filter feed on diatoms directly in the water column (Utne-Palm et al. 2010), in contrast to other specialist filter feeding fishes such as sardine (van der Lingen et al. 2009). Considering that the contribution of the benthic diet may be closer to 15%, the benthic C and N contribution to the goby diet is so small that it does not affect the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the gobies significantly. This interpretation fits well with the observation that the $\delta^{15}\text{N}$ values of the sediment, which were similar to the observations (-20 to -21‰ , and 5.5 to 7‰ , respectively) recorded by Struck et al. (2002) off Namibia (but see below), are very different from each other.

Results of trophic sulphur isotope shifts have been variable and showed fractionations between -3 and $+4\text{‰}$ for individual taxa (Connolly et al. 2004). On average, however, no significant isotope shifts have been observed when multiple taxa were considered (McCutchan et al. 2003, Connolly et al. 2004). Support for minor trophic isotope shifts also come from the small variation of sulphur isotope values for all zooplankton and jellyfish ($20.5 \pm 1.6\text{‰}$, $n = 19$), which, despite their different trophic levels, all have sulphur isotope values close to the sulphur isotope composition of seawater sulphate (20.7‰).

Analyses of the fatty acids showed that the tissues of large gobies contained greater diatom marker ratios

$\Sigma 16:1/16:0$ and $20:5\omega 3/22:6\omega 3$ compared to small and medium gobies (Fig. 8, Table S7). These data suggest that large gobies ingested more diatom-rich sediment than small gobies, which is in agreement with ontogenetic changes in vertical habitat use (D'Arcangues 1977). Although it is possible that large gobies may have derived their algal fatty acids from ingesting zooplankton that were high in diatom markers, absolute concentrations of the copepod markers $20:1\omega 9$ and $22:1\omega 11$ showed a general decrease with increasing goby size (Table S5). As such, small and medium-sized gobies may have acquired fatty acids characteristic of diatoms by feeding on zooplankton as well as benthic sediments.

Sediment was dominated by $16:0$, $18:1\omega 7$ and $16:1\omega 7$ (Table S2), whereas branched fatty acids such as *i*- $17:0$ typically found in sulphate-reducing bacteria (Taylor & Parkes 1983, Zhang et al. 2002) were minor components. Sediment fatty acid profiles in the Northern Benguela ecosystem are consistent with those of *Thioploca* sp., *Beggiatoa* sp. and other sulphur-oxidising bacteria, for which $16:1\omega 7$ and $18:1\omega 7$ have been proposed as signature biomarkers in H_2S -rich marine sediments (Jacq et al. 1989, McCaffrey et al. 1989, Zhang et al. 2005). Besides $16:1\omega 7$ and $18:1\omega 7$, *ai*- $15:0$ and $24:0$ were also found in higher proportions in sediment compared to animal prey (Tables S1 & S2), suggesting that gobies were opportunistic detritivores deriving these fatty acids from bacteria in the sediment.

Carnivory

Mixed zooplankton (primarily copepods and juvenile euphausiids) were not significantly assimilated by gobies according to the stable carbon and nitrogen analyses (Fig. 4), contrasting with earlier stomach content data (D'Arcangues 1977, O'Toole 1978, Macpherson & Roel 1987). In our study, euphausiids were generally of secondary importance, and their consumption was not significantly correlated with goby size (Fig. 5a); these findings are in agreement with those of both Cedras (2009) and Hundt (2009).

Whereas isotopes of carbon and nitrogen could not identify links between gobies and zooplankton, fatty acid analyses (particularly the quantitative data) suggested that gobies may have derived much of their

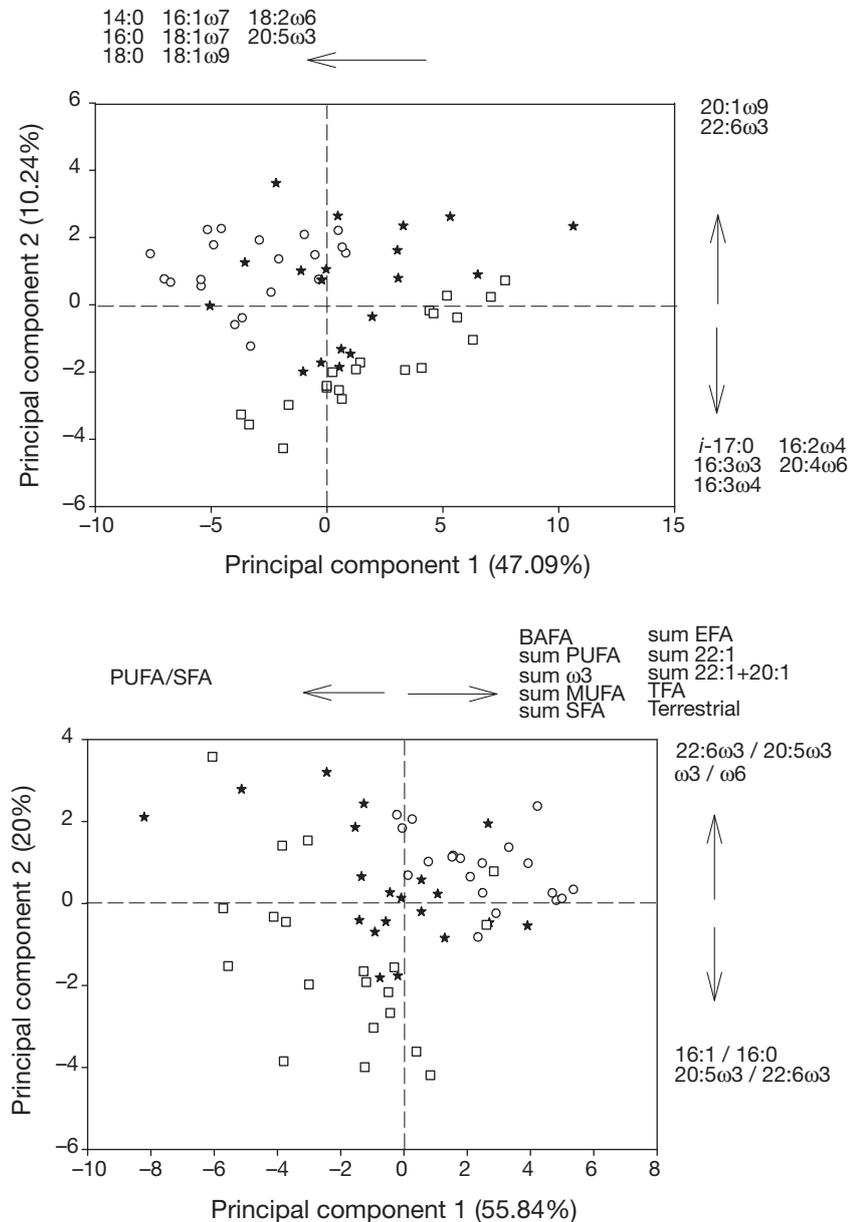


Fig. 7. *Sufflogobius bibarbatus*. Principal component plots of the transformed quantitative fatty acid composition ($\mu\text{g mg}^{-1}$ dry weight, DW) of small (circles), medium (stars) and large (squares) gobies collected off the coast of Namibia during April 2008. (a) All individual fatty acids, (b) summary fatty acids. Arrows running parallel to axes represent the most influential fatty acids with loading values greater than 0.2. Dashed lines denote the origin. Percentage values represent the proportion of the variance explained by each principal component. BAFA: bacterial fatty acid; MUFA: monounsaturated fatty acid; PUFA: polyunsaturated fatty acid; SFA: saturated fatty acid; EFA: essential fatty acid

EFA from zooplankton, of which the largest fractions contained mean EFA totals $>30 \mu\text{g mg}^{-1}$ DW (Table S7). Small gobies had greater dietary contributions from copepods compared to medium and large gobies, as indicated by their significantly higher

absolute concentrations of 20:1 ω 9 and 22:1 ω 11 (Table S5). Cedras (2009) recently showed a negative relationship between goby size and the frequency of copepod consumption, which he suggested was a reflection of the more pelagic habitat of younger gobies.

Based on isotopic data, the diet of small gobies was dominated by *Chrysaora fulgida*, with depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ -signatures (maximum contribution of 73.85%), while the diet of large gobies was dominated by *Aequorea forskalea* (70.36%; Table 3). Trophic links have not previously been made between gobies and jellyfish. While it is possible that this simply reflects the recent nature of the increases in jellyfish biomass, it more likely reflects the fast digestion rate of jellyfish tissue (Arai et al. 2003, Arai 2005) and prolonged and inefficient sample storage (Arai 2005). Jellyfish had very low lipid contents, although both gobies and jellyfish had elevated ratios of the dinoflagellate marker 22:6 ω 3/20:5 ω 3 (Tables S7 & S8), which agrees with dietary observations by Flynn & Gibbons (2007). It is thus possible that the dinoflagellate fatty acid signature present in *Sufflogobius bibarbatus* is an indirect reflection of their consumption of jellyfish, as gobies are unlikely to graze directly on dinoflagellates in the water column. Both jellyfish species were proportionally higher in *i*-17:0 and 19:0 when compared to other prey items (Fig. 8), as were goby tissues (Fig. 8). These specific fatty acids, along with the multivariate analysis of the fatty acid profiles (Fig. 6), together suggest that gobies could have been feeding on jellyfish in very high quantities to compensate for the low nutritional value of this easily digested tissue (Arai et al. 2003). Although the close association between jellyfish and gobies in the water column (Utne-Palm et

al. 2010) may help the non-specialist gobies avoid other predators while feeding on abundant prey, we should be careful in our interpretation because it is equally possible that the gobies were eating moribund jellyfish on the seafloor.

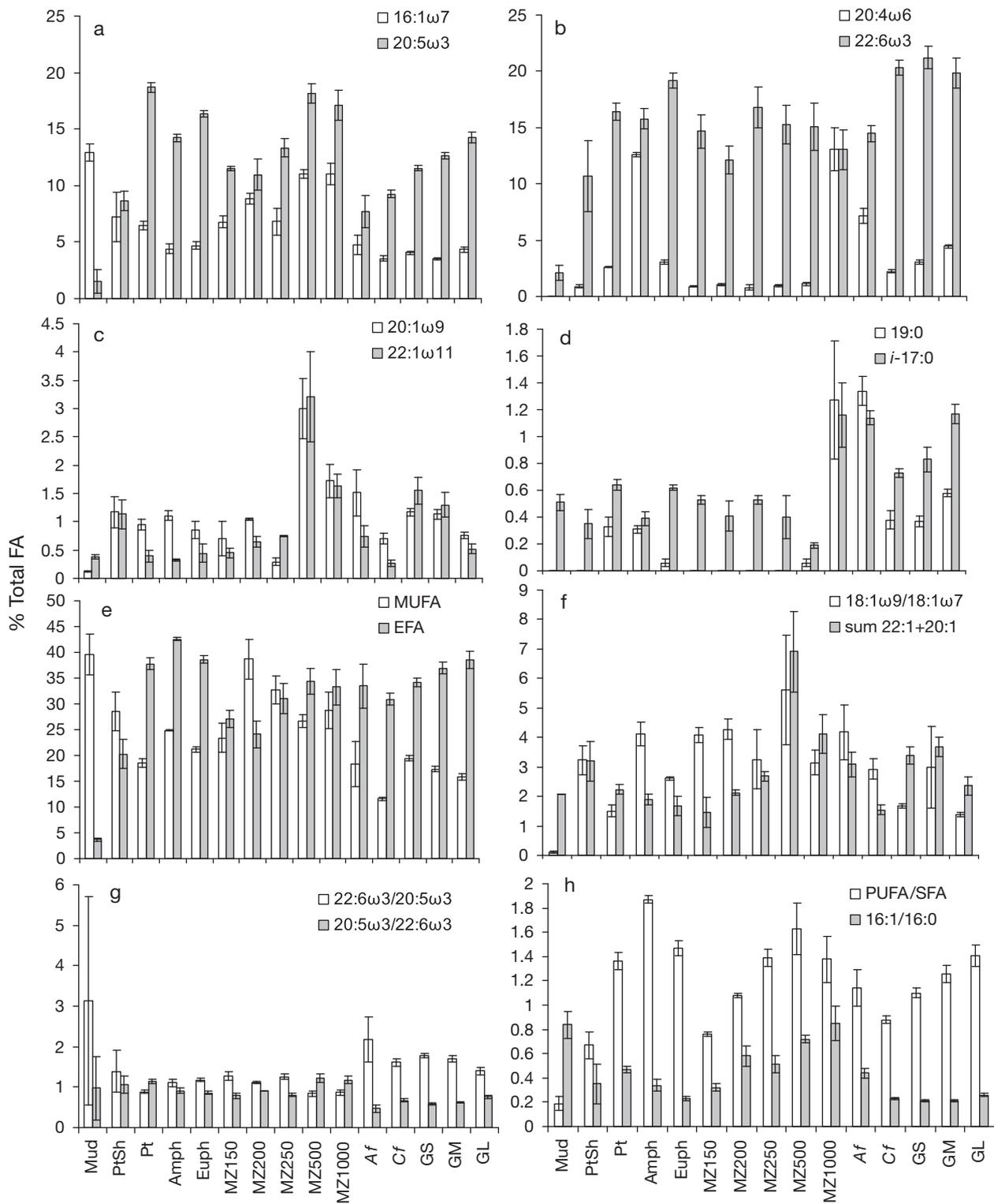


Fig. 8. *Sufflogobius bibarbatius*. Qualitative comparison (% total fatty acids) of the key fatty acids: (a) 16:1 ω 7 and 20:5 ω 3; (b) 20:4 ω 6 and 22:6 ω 3; (c) 20:1 ω 9 and 22:1 ω 11; (d) 19:0 and *i*-17:0; and sums/ratios of (e) monounsaturated fatty acids (MUFA) and essential fatty acids (EFA); (f) 18:1 ω 9/18:1 ω 7 and Σ (22:1+20:1); (g) 22:6 ω 3/20:5 ω 3 and 20:5 ω 3/22:6 ω 3; and (h) polyunsaturated/saturated fatty acids (PUFA/SFA) and Σ 16:1/16:0 of gobies and their potential food sources. Values are mean \pm SE. PtSh: pteropod shells; Pt: pteropods; Amph: amphipods; Euph: adult euphausiids; MZ150–1000: mixed zooplankton of sizes 150–1000 μ m; Af: *Aequorea forskalea*; Cf: *Chrysaora fulgida*; GS: small gobies; GM: medium gobies; GL: large gobies. All samples were collected at the offshore station, but *C. fulgida* were from the inshore station

Ontogenetic shift in goby diet

There appear to be gradual changes in the diet of the goby as it increases in size: small gobies fed primarily on *Chrysaora fulgida* with depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and supplemented their diet with prey enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, including *C. fulgida*, *Aequorea forskalea* and adult euphausiids (Fig. 5, Table 3). Fatty acid data suggest that small gobies also fed on copepods (20:1 ω 9 and 22:1 ω 11; Table S5), and as they grew in size they developed a diet dominated by *A. forskalea*, supplemented by *C. fulgida*, adult euphausiids (Fig. 5, Table 3) and diatom (sediment) input (Fig. 8g,h, Tables S5 & S7).

Whilst caution should be exercised in the interpretation of signature variations with size, which might be artefacts arising from size-dependent effects on metabolic turnover or accumulation of specific biochemical components (Rossi et al. 2004), a number of studies have shown ontogenetic changes in the diet of gobies (Gibson 1970, del Norte-Campos & Temmings 1994, Maruyama et al. 2001, Sorensen & Hobson 2005). These changes have been attributed to shifts in metabolic demands (Levy 1990), morphology, habitat, prey availability (Grossman 1980) or behaviour (Grossman et al. 1980). Cedras (2009) highlighted the importance of habitat change, noting that smaller gobies fed primarily on plankton, whilst larger individuals fed mostly in the benthos. Small gobies are more pelagic, frequently migrating vertically in the water column (D'Arcangues 1977, Staby & Krakstad 2006). Large gobies are primarily demersal and migrate infrequently (D'Arcangues 1977, Staby & Krakstad 2006), which coincides with the increased dietary contribution from benthic diatoms but decreased contributions from pelagic copepods, as indicated by the fatty acid results (Tables S5 & S7).

The apparent ontogenetic change in the composition of the jellyfish component (*Chrysaora fulgida* to *Aequorea forskalea*) of the goby diet coincides with cross-shelf distribution patterns: *C. fulgida* tends to be more abundant than *A. forskalea* closer to the shore, whilst the opposite situation is found offshore (as here) (Sparks et al. 2001, Utne-Palm et al. 2008). Small gobies are more common closer to the coast than larger fish (O'Toole 1978) and likely move offshore with increasing age and size, as do many other demersal species within the region (e.g. Gordo et al. 1995). Interestingly, both species of jellyfish are found throughout the water column but reach highest densities near the surface (Buecher et al. 2001, Sparks et al. 2001), which suggests either that large gobies scavenge moribund jellyfish on the seafloor (as e.g. Lebrato & Jones 2009), or that they move into near surface waters to consume them.

CONCLUSIONS

Isotopic comparisons among gobies, anchovy and sardines in the Benguela ecosystem suggest that *Sufflogobius bibarbatus* feeds at the same average trophic level as anchovy ($\delta^{15}\text{N} \approx 12\text{‰}$, C. D. van der Lingen & T. Miller pers. comm.), but that both gobies ($\delta^{15}\text{N} \approx 12\text{‰}$) and anchovy feed at a higher trophic level than sardines ($\delta^{15}\text{N} \approx 9.5\text{‰}$, C. D. van der Lingen & T. Miller pers. comm.). Anchovies (van der Lingen et al. 2009) and gobies feed mainly on zooplankton and zooplankton and jellyfish, respectively, but sardines are more omnivorous and are able to filter feed on phytoplankton when abundant (van der Lingen et al. 2009). Interestingly, however, gobies are substantially lighter in $\delta^{13}\text{C}$ ($\delta^{13}\text{C} \approx -16.3\text{‰}$) compared to both sardines and anchovy (both $\delta^{13}\text{C} \approx -13\text{‰}$, C. D. van der Lingen & T. Miller pers. comm.), which is likely due to the consumption of bacteria-rich sediment. A number of studies have shown that sulphur-bacteria have very depleted levels of $\delta^{13}\text{C}$, ranging from -40 to -26.1‰ (Levin & Michener 2002, Gilhooly et al. 2007, Levin et al. 2009), and this impacts the structure of basal components of the food webs so based.

Although many higher predators within the Benguela ecosystem off Namibia have now replaced sardines in their diet with gobies (e.g. Crawford et al. 1985), it is clear that gobies have not assumed the role of sardines or anchovy within the system. Despite relatively slow growth rates and late maturity, a comparatively long life-span (Melo & Le Clus 2005), and a high level of predation pressure, the regional biomass of *Sufflogobius bibarbatus* is increasing (Staby & Krakstad 2006). Although its adaptations to a physiologically stressful environment are remarkable (Utne-Palm et al. 2010), its success within the altered ecosystem off Namibia must also reflect its flexible diet and an ability to use both the huge jellyfish biomass found there (Lynam et al. 2006) and the benthos. Indeed, by tapping into both of these (previously considered) dead-end resources (Sommer et al. 2002, Heymans et al. 2004), the bearded goby provides a mechanism by which commercial fish biomass and production can be stabilised. It provides a key link in the food web off Namibia, and its populations should be managed accordingly.

The results generated in this study demonstrate the utility of using a suite of tracers in trophic studies. For example, the stable carbon and nitrogen isotope ratios indicate that jellyfish are an important dietary source for gobies, but that zooplankton and sediment are not. This is in contrast to the results of the fatty acid analyses, which do not strongly support a medusivorous diet (lipid concentrations in jellyfish are extremely low), but they do suggest that zooplankton are impor-

tant for small gobies and that (sedimented) diatoms are more important for large gobies. The results of the stable sulphur isotope analyses indicate that diatom-, and sulphur bacteria-rich sediments are an important source of food for gobies, which is supported by the fatty acid data and (weakly) by the generally low (by comparison with pelagic fishes) levels of $\delta^{13}\text{C}$ (see above). In other words, complementary, and supportive, information about the diet of the bearded goby are provided by the different types of analyses.

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