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An attempt at modelling the diets of two sympatric species of hake (*Merluccius capensis* and *Merluccius paradoxus*) off the coast of Namibia: isotope mixing model approach

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Abstract

Two species of hake, Merluccius capensis and Merluccius paradoxus, are the most important secondary consumers in the Benguela current ecosystem. To better understand hake diets in the northern Benguela (Namibia), the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of their muscles, and that of their prey (Hake, $n = 115$ and prey, $n = 299$) were analysed. Results indicated that their diets were dominated by *Plesionika martia, Chlorophthamus agazizi, Myctophids* and *Euphausiids.* The highest contributor to the diet of *M. paradoxus* varied with length, while the diet of *M. capensis* was dominated by *myctophids* at all length classes. Cannibalism accounted for less than 6% and less than 4% in the diets of *M. capensis* and *M. paradoxus* respectively. Isotope based estimates of prey dietary contributions differed from that of previous gut content analyses. Overall, the results support the hypothesis that the two species have similar diets. Application of a Bayesian mixing isotope model can be improved to allow for improved hake consumption (i.e. annual) estimates to be made.

Keywords:Stable Isotopes, diets, hake, Namibia, mixing models, *Merluccius capensis, Merluccius paradoxus.*

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1 Introduction

Predators feed on the most abundant prey in their surroundings (Mesa et al., 1994) or they can choose specific prey from those available (Schlacher and Wooldridge, 1996). Feeding ecology of exploited fish species has seldom been considered in evaluating their population dynamics in fisheries management (Jaworski and Ragnarsson, 2006). General consensus has emerged among fisheries scientists that fish feeding ecology represents a major aspect of food web linkages, and it warrants consideration when managing fisheries resources (Gascuel et al., 2005; Shannon et al., 2010).

Merluccius capensis and *M. paradoxus* are important predators in marine waters off Namibia (Macpherson and Roel, 1987; Roel and Macpherson, 1988). Early attempts to investigate at their diets indicated that they feed on a variety of fishes and crustaceans (Assorov and Kalinina, 1979). Payne et al. (1987) reported that crustaceans, mesopelagic fish and hake are the most important prey organisms in the majority of length classes of hake studied. In the marine waters off Namibia, Roel and Macpherson(1988) described hake diet as consisting of mainly small crustaceans, fish and cephalopods. On the west coast of South Africa hake fed mainly on crustaceans, with anchovy being the dominant dietary item of juvenile *M. capensis*, a reflection of the increased availability of anchovy at the time of the surveys (Punt et al., 1992). At sites abundant in zooplankton, hake fed preferentially on large crustaceans [amphipods, euphausiids and shrimp (*Pasiphaea semispinosa*)], while at a site dominated by recruits of anchovy (*Engraulis capensis*), the hake were almost exclusively piscivorous (Pillar and Barange, 1993).

On the south coast of South Africa, fish remains in hake stomach contents accounted for 92% of prey by mass, 5% for crustaceans and 3% for cephalopods, contrasting with that documented for the West Coast of South Africa (Pillar and Wilkinson, 1995). For small hake, especially *M. paradoxus*, euphausiids were consumed more frequently in summer and mesopelagic fish were of more dietary importance in winter, with hake-on-hake predation a more prominent feature in *M. capensis* (Pillar and Barange, 1997). Macpherson and Gordoa (1994) observed that in large *M. capensis*, cannibalism is not related to the density of the small conspecifics, nor to the density of alternative prey, but rather that large hake have a dietary preference for small conspecifics. The most recent study of hake diet off Namibia, indicated that crustaceans and cephalopods were of minor importance compared to fish in *M. capensis*, but they contributed relatively more to the diet of *M. paradoxus* (Traut, 1996). The same study also found hake was a more important prey item for *M. capensis* than for *M. paradoxus*.

The above studies showed that the relative importance of prey in the diets of *M. capensis* and *M. paradoxus* varies both seasonally and geographically. The opportunistic nature of hake feeding, which changes with prey availability, plays a major role in determining contributions of prey in their diets. The use of only stomach content analyses in studying these dynamics is confounded by the fact that such data are limited temporally because they represent only snapshots of recent feeding, and quantitatively because of biases resulting from variability in the digestion rates of different prey (Cortés 1997)

The increased use of stable isotopes (δ^{15}N and δ^{13}C) in trophic research (Taka et al., 2007; Stowasser et al., 2009; Iitembu et al., 2012) has led to the development of isotope mixing models (Phillips and Gregg, 2003; Parnell et al., 2010;). These mixing model approaches are based on the idea that a predator's tissues are an isotopic mixture of its dietary sources and can indicate the proportional contributions of these sources to its diet (Phillips and Gregg, 2003; Parnell et al., 2010). Feasible contributions of different prey to the isotopic mixture of the predator's tissues have been used as a proxy of their dietary contributions (Boyle et al., 2012; Hopkins III and Ferguson, 2012; Quevedo et al., 2012). Results from mixing models reduce biases associated with stomach content analyses because of the use of time and space-integrated isotopic data (Layman and Allgeier, 2012). This study contributes to the research efforts in understanding the contributions of different prey to *M. capensis* and *M. paradoxus* diet off Namibia. I used an isotope mixing model to determine the feasible contributions of prey to the isotopic mixture of hake and assessed how it varied with fish length. I hypothesized that the temporally integrated dietary representations of the two species diets are similar, given that based on stomach content analyses they both feed on small fishes and crustaceans.

2 Methods and materials

2.1 Field sampling

Samples of hake and their potential prey were collected in the northern Benguela upwelling system (Namibia). The collection was done during hake biomass surveys (11th January-25th February 2011) on board MV Blue Sea I and a monkfish biomass survey (16th-27th December 2011) on board RV Welwitchia (Fig 1). These surveys were done mainly for the estimation of biomass and size composition of the hake and monkfish stocks off Namibia, therefore sampling followed survey pre-determined stations and was confined within the borders of Angola (latitude 17°12'S) and South Africa (29°30'S) at a depth range of 90-700 m (Fig 1). Sampling was opportunistic, with the general goal of obtaining a wide size distribution of each species. At each sampling station, individual fish (up to 10 specimens when available) were chosen from the largest, middle and smallest size groups. After identification, each fish was measured (total length, cm), and a small section of white muscle (4-6 g) was removed from the anterior-dorsal region of each specimen. Skin was removed from the muscle, and the muscle was immediately wrapped in aluminium foil and frozen at -20°C on board.

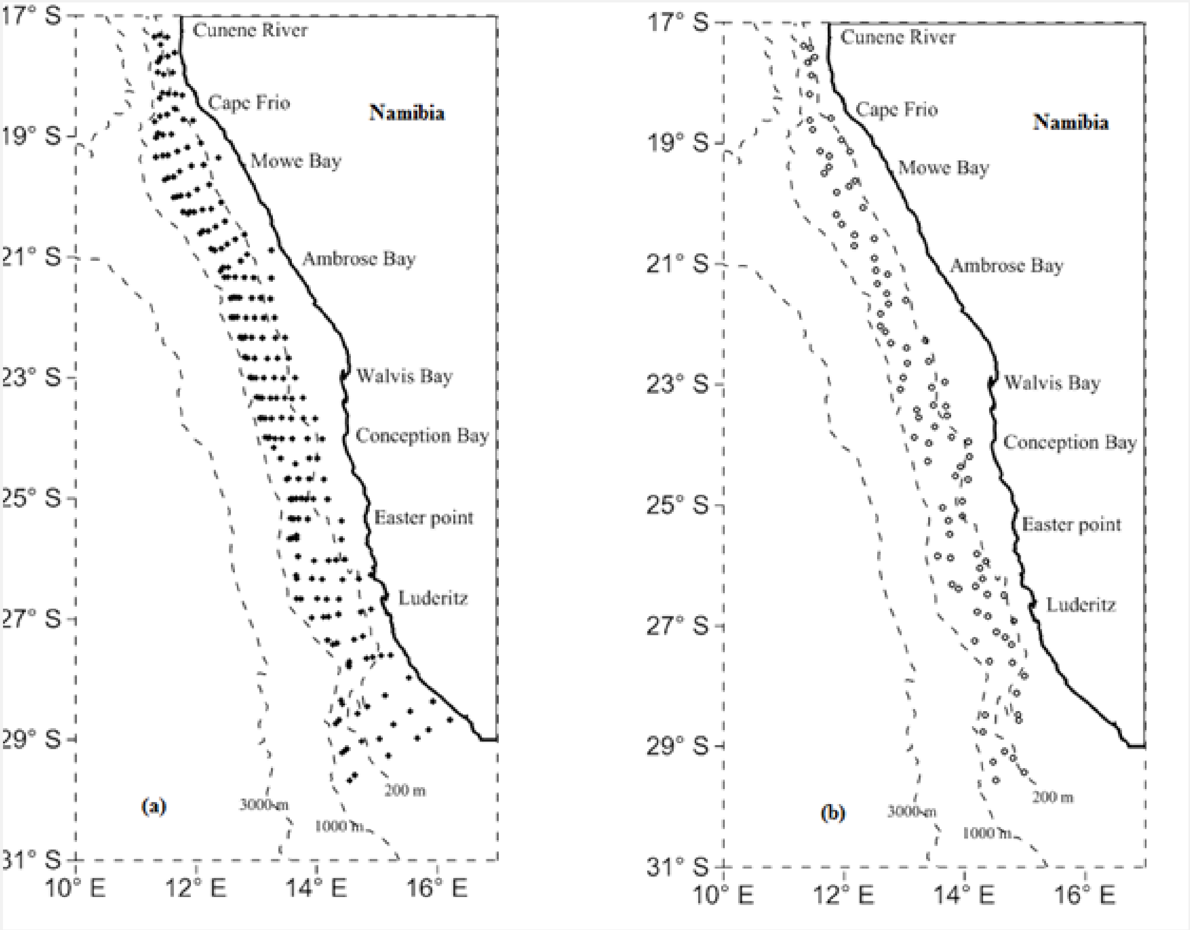

Figure 1: A map showing the Coverage of (a) hake and (b) monkfish biomass surveys off the coast of Namibia.

2.2 Laboratory analysis

Tissue samples were dried in an oven for 48 hours at 60°C, ground to a fine powder using a mortar and pestle, and placed in polyethylene vials for storage. All isotopic analyses were done at IsoEnvironmental cc (Grahamstown, South Africa) using a Europa Scientific Elemental Analyzer coupled to a 20-20 Isotope Ratio Mass Spectrometer (IRMS). Beet sugar, ammonium sulfate and casein were used as in-house standards calibrated against International Atomic Energy Agency (IAEA) standards CH-6 and N-1.

The ^{12}C/^{13}C and ^{14}N/^{15}N isotope measurements were expressed in the delta notation relative to the levels of ^{13}C in Pee Dee Belemnite and 15N in atmospheric nitrogen (N2), according to the following equation:

$$\delta X = \{(R_{sample}/R_{standard}) - 1\} \times 1000$$

where:
X is ^{13}C or ^{15}N and
R is the ratio of the heavy to light isotope for the sample (R_{sample}) and standard ($R_{standard}$) in units of parts per thousand (‰).

Because carbon isotope ratios can be altered by changes in lipids irrespective of the carbon source (McConnaughey & McRoy 1979), measurements were mathematically corrected for lipid variations using a normalization equation by Post et al. (2007):

$$\delta^{13}\mathrm{C}_{normalized} = \delta^{13}\mathrm{C}_{untreated} - 3.32 + 0.99 \times C:N$$

where:
$\delta^{13}\mathrm{C}_{untreated}$ was the δ^{13}C of non-lipid extracted tissue.

The δ^{13}C of samples having C:N ratios < 3.5 do not benefit from lipid normalization (Post et al. 2007), therefore only samples expressing C:N ratios > 3.5 were lipid normalized. Lipid extraction was not performed as it can alter δ^{15}N values, requiring separate analyses of δ^{13}C and δ^{15}N analysis (Sweeting et al. 2006) The mathematical lipid correction method has worked successfully for lipid correction of δ^{13}C in deep-sea fishes (Hoffman & Sutton 2010).

To calculate the relative trophic level (TL) of each species, the following equation was used:

$$TL = \frac{(\delta^{15}\mathrm{N}_{consumer} - \delta^{15}\mathrm{N}_{base})}{\Delta\delta^{15}\mathrm{N}} + 2.0$$

where:
$\delta^{15}\mathrm{N}_{consumer}$ is the signature of the consumer,
$\delta^{15}\mathrm{N}_{base}$ is the baseline value of the food web,
$\Delta\delta^{15}$N is the trophic enrichment factor, and
the value 2.0 indicates the trophic level of the organism used to establish the $\delta^{15}\mathrm{N}_{base}$ [in this case, bivalves *Choromytilus meridionalis* collected from Lüderitz (south coast, $n = 6$), Swakopmund (central coast, $n = 6$) and Henties Bay (northern coast, $n = 6$) during the same time frame; mean of 9.8‰]. The mytilid bivalves ($TL = 2.0$) were used as the base level because bivalves are primary consumers that have protracted isotopic turnover rates that can integrate seasonal variability (Lorrain et al. 2002; Fukumori et al. 2008). The trophic enrichment factor was set at 3.4‰ per trophic level (Minagawa & Wada 1984; Post 2002).

2.3 Statistical analysis

Mean isotopic composition and its standard deviation (SD) were calculated for hake species and their prey. The significance differences among ^{15}N and ^{13}C values of the prey species were investigated using an analysis of variance (ANOVA) test with a Tukey HSD (Tukey Honest Significant Difference) post hoc test to perform multiple comparisons. Data were examined for normality and homogeneity of variance using a Shapiro-Wilk and Levene test. Violations of homogeneity and normality were addressed through log transformations. A Bayesian stable-isotope mixing model, termed Stable Isotope Analysis in R (SIAR) (Parnell et al., 2010), was used to obtain the feasible contributions of the different species to the isotopic signatures of the two hake species. The fractionation factors of 3.2±1.28‰for δ^{15}N (Sweeting et al., 2007a) and 1.56±1.10‰for δ^{13}C (Sweeting et al., 2007b) were used. In addition to 14 prey species (see Table 1), hake (*M. capensis* and *M. paradoxus*) of ≤ 40 cm were also used as prey to account for cannibalism. The numbers of prey were chosen based on accounts of published hake stomach content results (Payne et al., 1987; Roel and Macpherson, 1988; Traut, 1996). All the analyses were done in R (R Development Core Team 2012, Vienna Austria).

3 Results

3.1 Isotopic characteristics of the prey

Samples from 299 individuals of fish were analysed to derive their stable isotope ratios (δ^{15}N and δ^{13}C). Crustaceans (5 species), teleost fish (9 species) and cephalopods (2 species) were used as prey for the two hake species (Table 1). *Merluccius capensis* sizes ranged from 18 cm to 69 cm, while *M. paradoxus* sizes ranged from 22cm to 65 cm. The prey species sizes ranged from the smallest crustaceans (euphausiids) of 4 cm to a teleost (*Nezumia micronychodon*) of 24 cm. Among the prey considered, a teleost (*N. micronychodon*) had the most enriched δ^{15}N (14.87‰), while *C. agazizi* had the most depleted δ^{15}N (9.84‰) (Table 1). The prey relative trophic levels ranged from 1.99 for *C. agazizi* to 3.4 for *N. micronychodon* (Table 1).

To determine whether isotopic signatures were different among potential prey, two ANOVA were run (one for nitrogen and one for carbon), followed by Tukey HSD post hoc tests to identify any specific differences. There was a significant difference among species' δ^{15}N (ANOVA, $p < 0.05, F(17.131) = 8.81$). In term of δ^{15}N, *N. micronychodon* was significantly different from all the prey species ($p < 0.05$). *Epigonus denticulatus* was significantly different from *Funchalia woodwardi* ($p < 0.001$), euphausiids ($p < 0.001$) and *Plesionika martia* ($p < 0.001$).

Table 1: Summary mean (±SD) values of nitrogen and carbon stable isotopes of species from the study, with respective sample sizes(n), L (average length), $\delta^{13}C_n$ (lipid normalized) and standard deviation, C:N ratios and trophic level (TL).

Prey categories	Family	n	L(cm)	δ^{15}N	δ^{13}C	$\delta^{13}C_n$	C:N	TL
Crustaceans								
Aristeus varidens	Aristeidae	19	9	11.80 (1.05)	-16.16(0.99)		3.15	2.57
Solenocera africana	Solenoceridae	10	7	11.71 (1.09)	-15.66 (0.07)		3.13	2.55
Plesionika martia	Pandalidae	19	7	10.71 (1.09)	-17.16 (0.94)		3.15	2.25
Euphausiids(krill)	Euphusidae	16	4	10.91 (0.56)	-16.93 (0.24)		3.28	2.33
Funchalia woodwardi	Penaeidae	16	8	11.70 (1.70)	-16.58 (1.20)		3.15	2.54
Teleosts								
Chelidonichthys capensis	Triglidae	6	23	11.09(0.56)	-13.96 (0.38)		3.25	2.93
Chlorophthamus agazizi	Chlorophthalmidae	5	11	9.84 (2.72)	-16.38 (0.73)		3.28	1.99
Emmelichthys nitidus nitidus	Emmelichthydae	4	21	13.02(0.25)	-17.23 (0.27)		3.44	3.22
Epigonus denticulatus	Epigomidae	5	16	14.05 (0.19)	-16.81(0.17)		3.23	2.83
Etrumeus whiteheadi	Clupeidae	8	20	12.67(0.33)	-16.82 (0.02)		3.46	2.83
Helicolenus dactylopterus	Scorpaenidae	4	15	12.20 (2.12)	-16.09 (1.72)		3.19	2.69
myctophids	Myctophidae	12	5	12.62(0.51)	-18.99 (0.47)	-15.60(0.48)	6.78	2.81
Nezumia micronychodon	Macrouridae	5	24	14.87(0.60)	-15.82 (0.44)		3.12	3.40
Paracallionymus costatus	Callionymidea	5	24	13.52(0.32)	-17.43(0.62)	-17.07(0.55)	3.71	3.04
Phosichthys argenteus	Phosichthyidae	11	17	12.83(0.78)	-17.84(0.28)		3.08	2.87
Sufflogobius bibartus	Gobidae	5	11	12.74 (0.45)	-15.62 (0.32)		3.39	2.85
Synagrops microlepis	Acropomatidae	26	9	10.21(0.84)	-16.94(1.84)	-15.81(0.58)	4.50	2.10
small hake (<15 cm)	Merluccidae	10	12	12.41(0.28)	-16.73 (0.42)		3.23	2.74
M. paradoxus (<40 cm)	Merluccidae	26	33	13.06(0.64)	-16.65(0.5)		3.20	2.94
M. capensis(<40 cm)	Merluccidae	34	27	12.87(0.82)	-16.62(1.0)		3.19	2.88
M. paradoxus (>40 cm)	Merluccidae	26	48	13.57(0.42)	-16.58 (0.56)		3.31	3.10
M. capensis(>40 cm)	Merluccidae	19	52	13.26 (0.74)	-15.76(0.52)		3.23	3.02
Cephalopods								
Todarodes sagittatus	Ommastrephidae	2	44	12.79(0.88)	-16.70(0.24)		3.26	2.86
Todaropsis eblanae	Ommastrephidae	6	13	11.95(0.52)	-17.10(0.47)		3.43	2.61

Euphausiid nitrogen signatures were significantly different from those of *Emmelichthys nitidus nitidus* ($p = 0.003$), *Phosichthys argenteus* ($p = 0.03$) and *Paracallionymus costatus* ($p = 0.009$) and *Plesionika martia* was significantly different from small hake ($p = 0.002$), *P. costatus* ($p = 0.001$), *P. argenteus* ($p = 0.007$) and *Todarodes sagittatus* ($p = 0.03$).

There was a significant difference among species' δ^{13}C (ANOVA, $p < 0.05, F(17.131) = 2.66$). In terms of δ^{13}C of prey species, *C. capensis* had the most enriched δ^{13}C (17.84‰) while *P. argenteus* had the lowest δ^{13}C (13.96‰) (Table 1). ANOVA followed by a Tukey HSD post hoc test indicated that *C. capensis* was significantly different from *F. woodwardi* ($p = 0.013$), *E. denticulatus* ($p < 0.001$), *E. nitidus nitidus* ($p = 0.001$), euphausiids ($p = 0.002$), myctophids ($p < 0.001$), *P. argenteus* ($p < 0.001$), *P. costatus* ($p < 0.001$), *P. martia* ($p < 0.001$) and small hake [< 15 cm, $p = 0.008$)]. Myctophids were significantly different from *A. varidens* ($p < 0.001$), *P. argenteus* ($p = 0.02$), *F. woodwardi* ($p < 0.001$), *Helicolenus dactylopterus* ($p < 0.001$), euphausiids ($p = 0.01$), *N. micronychodon* ($p < 0.001$) and *Solenocera africana* ($p < 0.001$). *Phosichthys argenteus* was significantly different from *Aristeus varidens* ($p = 0.02$), *N. micronychodon* ($p = 0.003$) and *S. africana* ($p = 0.002$). *Plesionika martia* was significantly different from *S. africana* ($p = 0.003$).

3.2 Prey dietary contributions

Feasible contributions of different prey to the isotopic mixtures of the two hake species (all size-pooled) showed dietary overlap between the hake (Table 1). For both species, *S. microlepis* was the highest feasible contributor to their isotopic mixtures, with credible intervals of 4.77-34.24% and 4.04 -38.68% for *M. paradoxus* and *M. capensis*, respectively. *Plesionika martia*, *C. agazizi*, myctophids and euphausiids had notable feasible contributions to the isotopic mixtures of the two species (Table 2). The contributions of small hake (< 15 cm) were 0-4% for *M. paradoxus* and 0 - 6% for *M. capensis.* The contributions of medium size hake (<40 cm), as prey, averaged at 1.21% for *M. paradoxus* and at 1.6% for *M. capensis.* The contribution of small and medium size hake represented cannibalism of less 6% and 4%, for *M. capensis* and *M. paradoxus* respectively (Table 2).

Table 2: Mode, mean and 95% credible intervals (CI) of feasible contributions of the prey categories into the isotopic mixtures of *M. capensis* and *M. paradoxus*, respectively, all sizes of hake were pooled.

Prey categories	*M. paradoxus*				*M. capensis*			
	Mode	Mean	95% CI		Mode	Mean	95 %CI	
			Low	High			Low	High
Crustaceans								
Aristeus varidens	0.63	1.82	0.00	4.83	0.49	2.24	0.00	6.79
Solenocera africana	0.59	1.48	0.00	3.98	0.79	2.08	0.00	5.11
Plesionika martia	9.38	12.08	1.51	25.58	10.42	13.28	0.94	23.55
Euphausiids(krill)	9.26	7.77	0.00	16.80	7.70	7.76	0.04	15.30
Funchalia woodwardi	0.83	2.50	0.00	5.727	0.72	3.37	0.00	8.81
Teleosts								
Chelidonichthys capensis	0.74	1.13	0.00	2.56	0.41	1.30	0.00	3.63
Chlorophthamus agazizi	18.54	18.32	4.24	30.88	13.92	15.71	1.41	27.70
Emmelichthys nitidus nitidus	0.23	1.54	0.00	3.75	0.62	2.38	0.00	6.77
Epigonus denticulatus	0.99	1.22	0.00	2.99	0.27	1.19	0.00	3.41
Etrumeus whiteheadi	0.54	1.70	0.00	4.80	0.80	2.08	0.00	5.65
Helicolenus dactylopterus	0.46	1.36	0.00	3.78	0.32	1.74	0.00	4.91
myctophids	5.09	14.30	0.00	36.10	10.03	11.19	0.17	22.76
Nezumia micronychodon	0.23	0.64	0.00	1.49	0.27	0.79	0.00	2.13
Paracallionymus costatus	0.38	1.59	0.00	4.61	0.83	1.89	0.00	4.99
Phosichthys argenteus	0.74	3.25	0.00	8.81	0.76	3.34	0.00	8.65
Sufflogobius bibartus	0.19	1.03	0.00	2.37	0.32	1.29	0.00	3.76
Synagrops microlepis	19.34	19.56	4.77	34.24	16.74	17.20	4.04	28.68
small hake (< 15 cm)	0.46	1.71	0.00	4.12	1.01	2.16	0.00	6.16
M. paradoxus (<40 cm)	0.25	1.20	0.00	3.38	0.36	1.61	0.00	4.76
M. capensis(<40 cm)	0.23	1.31	0.007	3.28	0.40	1.67	0.00	4.96
Cephalopods								
Todarodes sagittatus	0.31	1.65	0.00	4.25	0.34	1.87	0.00	5.31
Todaropsis eblane	0.64	2.85	0.00	7.69	1.07	3.86	0.00	9.31

The contributions of different prey species per length classes indicated that *P. martia,* *C. agazizi*, myctophids and euphausiids were dominant contributors to both hake species (Tables 3 & 4). For hake in the 20-29 cm length class, myctophids contributed more than all other prey (modal contributions of 6.72% for *M. capensis* and 6.78% for *M. paradoxus*). In all length classes of *M. capensis*, myctophids had higher modal contributions than all prey, while for *M. paradoxus* larger than 30 cm, *Synagrops microlepis* was the highest contributor to the isotopic mixture.

In hake between 20-29 cm, three crustacean species (*P. martia*, euphausiids, and *F. woodwardi*) had modal contributions of more than 3% for *M. paradoxus.* For *M. capensis*, only *P. martia* and euphausiids had modal contributions more that 3% at 20-29 cm length classes. Of the cephalopods, *Todaropsis eblanae* had modal contributions of more than 3% in the length classes of 30-39 cm for *M. capensis* and 20-29 cm for *M. paradoxus.*

Helicolenus dactylopterus had the widest 95% credible interval (CI) of their dietary feasible contributions (0-11.18%) for *M. paradoxus* in 20-29 cm length class. In 30-39 cm length class, myctophids had the widest CI (0.0-15.92%) while in 40-49 cm length class, *C. agazizi* had the CI (0.0-17.68%) and in >50 cm length class, *S. microlepis* had the CI (0.00-10.70%). Myctophids had the widest CI of their feasible contributions at all length classes of *M. capensis.* Small hake (<15 cm), *M. paradoxus* (<40 cm) and M. capensis (<40 cm) all had modal contributions of around 1% in all length classes for both species, with their upper level CI around 9% (Tables 3 & 4).

4 Discussion

Studies of feeding ecology of *M. capensis* and *M. paradoxus* in the Benguela Current region have previously been done using stomach content analyses (Payne et al., 1987; Roel and Macpherson, 1988; Traut, 1996). Estimates of hake feeding using gut contents are imprecise in identifying the relative contributions of different prey because of the opportunistic feeding behaviours of hake (Punt et al., 1992), and the natural variability associated with prey densities (Macpherson and Gordoa 1994). In this study, I utilized stable isotope mixing models to assess the contributions of different prey to the isotopic mixture of each hake species. The temporally-integrated estimates of their diets from my results differed from those of previous data derived from stomach content analyses, which appeared to have overestimated the contributions of certain prey to the diets of hake.

Potential prey collected consisted of small fish, crustaceans and cephalopods identified in previous studies (Payne et al., 1987; Roel and Macpherson, 1988; Traut, 1996). Prey sizes ranged from the smallest crustaceans (euphausiids) of 4 cm to a teleost (*N. micronychodon*) of 24 cm. Among the prey, *N. micronychodon* had the most enriched δ^{15}N, indicating

Table 3: Mode and 95 % credible intervals (CI) of feasible contributions of the prey in the isotopic mixtures of *M. paradoxus* in different length classes

M. paradoxus	20-29 cm			30-39 cm			40-49 cm			>50 cm		
	Mode	95% CI		Mode	95 %CI		Mode	95% CI		Mode	95% CI	
		Low	High		Low	High		Low	High		Low	High
Crustaceans												
Aristeus varidens	1.22	0.00	9.44	1.04	0.00	9.79	1.04	0.00	9.76	1.17	0.00	9.63
Solenocera africana	1.42	0.00	9.22	0.91	0.00	9.03	0.92	0.00	8.88	1.08	0.00	9.38
Plesionika martia	5.49	0.00	10.69	6.63	0.00	13.84	6.73	0.00	16.03	6.21	0.00	10.46
Euphausiids(Krill)	4.54	0.00	10.26	3.98	0.00	12.75	6.37	0.00	14.83	5.12	0.00	10.23
Funchalia woodwardi	3.51	0.00	9.74	1.31	0.00	10.63	1.12	0.00	10.99	1.62	0.00	9.92
Teleosts												
C. capensis	0.86	0.00	8.50	0.75	0.00	7.68	0.70	0.00	7.29	0.98	0.00	9.06
C. agazizi	4.22	0.00	9.71	6.05	0.00	14.06	6.94	0.00	17.68	6.33	0.00	10.65
E. nitidus nitidus	1.54	0.00	9.24	1.11	0.00	9.97	1.04	0.00	9.52	1.94	0.00	9.55
Epigonus denticulatus	1.13	0.00	9.67	0.76	0.00	8.17	0.70	0.00	7.11	0.94	0.00	9.08
Etrumeus whiteheadi	1.19	0.00	9.23	1.05	0.00	9.68	0.95	0.00	9.21	1.33	0.00	9.50
H. dactylopterus	0.98	0.00	11.88	0.93	0.00	8.95	0.90	0.00	9.07	1.07	0.00	9.31
Myctophids	6.78	0.00	8.39	7.22	0.00	15.92	7.55	0.00	16.35	5.95	0.00	10.52
N. micronychodon	0.92	0.00	9.66	0.59	0.00	6.50	0.49	0.00	5.36	0.91	0.00	8.52
P. costatus	1.40	0.00	10.34	1.05	0.00	9.55	0.85	0.00	8.96	1.08	0.00	9.33
Phosichthys argenteus	4.57	0.00	8.89	1.60	0.00	11.55	1.34	0.00	11.04	1.53	0.00	9.87
Sufflogobius bibartus	1.06	0.00	10.76	0.77	0.00	7.90	0.74	0.00	7.23	0.85	0.00	9.04
Synagrops microlepis	5.59	0.00	9.58	7.32	0.00	14.70	8.11	0.04	17.82	6.21	0.00	10.70
Small hake (<15 cm)	1.01	0.00	9.32	1.12	0.00	9.79	0.96	0.00	9.72	1.23	0.00	9.50
M. paradoxus(<40 cm)	1.10	0.00	9.25	0.96	0.00	8.89	0.87	0.00	8.33	1.04	0.00	9.21
M. capensis(<40 cm)	1.42	0.00	10.30	1.05	0.00	9.08	0.91	0.00	8.57	1.97	0.00	9.20
Cephalopods												
Todarodes sagittatus	1.21	0.00	9.53	1.08	0.00	9.34	0.83	0.00	8.74	1.76	0.00	9.25
Todaropsis eblane	3.15	0.00	10.08	1.58	0.00	11.20	1.97	0.00	11.50	4.09	0.00	9.84

that it feeds at a higher relative trophic position to all other prey collected in this study. The estimated trophic position of *N. micronychodon* was higher than the average estimated for larger *M. paradoxus* and *M. capensis*. It is possible that *N. micronychodon*, being the largest prey, among prey used in this study, is too large to be consumed by the two hake species. However, fish from the Macrouridae family have been found in hake stomachs (Roel and Macpherson, 1988), and the feeding range of some hake species (e.g. *Merluccius gayi*) included prey more than half their length (Konchina, 1983). *C. agazizi* had the most depleted δ^{15}N, with an estimated trophic position of 1.99.

In terms of δ^{13}C, *C. capensis* had the most depleted ^{13}C values, and it represented the pelagic and off-shore ecosystem, as benthic and near shore species have more enriched ^{13}C values relative to those from pelagic and off-shore environments (France, 1995). *Phosichthys argenteus*, with the most enriched 13C values, represent species from the benthic/near shore

Table 4: Mode and 95 % credible intervals (CI) of feasible contributions of the prey in the isotopic mixtures of *M. capensis* in different length classes

M. capensis	20-29 cm			30-39 cm			40-49 cm			>50 cm		
	Mode	95% CI		Mode	95 %CI		Mode	95% CI		Mode	95% CI	
		Low	High		Low	High		Low	High		Low	High
Crustaceans												
A. varidens	1.00	0.00	9.86	1.05	0.00	9.41	1.33	0.00	9.30	1.08	0.00	9.32
S. africana	1.03	0.00	9.03	0.92	0.00	8.74	0.98	0.00	8.95	0.96	0.00	9.09
P. martia	6.34	0.00	13.69	5.67	0.00	12.60	4.82	0.00	11.30	5.93	0.00	12.38
Euphausiids(Krill)	5.66	0.00	12.70	4.86	0.00	11.92	3.48	0.00	10.80	5.68	0.00	11.31
F. woodwardi	1.15	0.00	10.47	1.17	0.00	10.26	1.62	0.00	10.19	1.11	0.00	10.16
Teleosts												
C. capensis	0.80	0.00	7.96	0.65	0.00	7.41	0.76	0.00	7.49	0.72	0.00	7.66
C. agazizi	5.10	0.00	13.96	3.82	0.00	11.83	3.96	0.00	10.45	4.39	0.00	11.31
E. nitidus nitidus	1.14	0.00	9.68	1.14	0.00	9.92	1.16	0.00	10.20	1.12	0.00	10.08
E. denticulatus	0.81	0.00	8.22	0.94	0.00	8.92	1.13	0.00	9.26	0.99	0.00	8.93
E. whiteheadi	0.93	0.00	9.77	1.13	0.00	9.60	1.63	0.00	9.69	1.15	0.00	9.67
H. dactylopterus	1.00	0.00	9.15	0.91	0.00	9.237	1.03	0.00	9.21	1.09	0.00	9.18
Myctophids	6.72	0.00	14.48	7.31	0.00	16.02	7.24	0.13	12.96	7.38	0.00	14.57
N. micronychodon	0.64	0.00	6.68	0.72	0.00	7.38	0.93	0.00	8.14	0.78	0.00	7.65
P. costatus	0.93	0.00	9.43	1.27	0.00	10.33	1.63	0.00	10.30	2.03	0.00	10.18
P. argenteus	3.72	0.00	10.96	5.27	0.00	11.82	6.60	0.00	11.05	5.26	0.00	11.13
S. bibartus	0.92	0.00	8.21	0.78	0.00	8.18	0.84	0.00	8.47	0.89	0.00	8.45
S. microlepis	6.61	0.00	14.33	6.32	0.00	13.30	5.027	0.00	11.17	5.58	0.00	12.45
Small hake (<15 cm)	0.99	0.00	9.87	1.13	0.00	9.69	1.09	0.00	9.84	1.19	0.00	9.79
M. paradoxus (<40 cm)	0.96	0.00	8.76	0.94	0.00	9.22	1.05	0.00	9.38	0.99	0.00	9.26
M. capensis(<40 cm)	0.97	0.00	8.97	1.00	0.00	9.22	1.03	0.00	9.54	0.89	0.00	9.34
Cephalopods												
T. sagittatus	0.98	0.00	9.15	0.93	0.00	9.35	1.20	0.00	9.61	1.06	0.00	9.34
T. eblane	1.37	0.00	11.42	4.75	0.00	10.96	1.48	0.00	10.35	2.09	70.00	10.66

environment (Miller et al., 2008). Although the difference in ^{13}C provided evidence of habitat related carbon source (phytoplankton vs. benthic primary production) separation of ^{13}C values of prey, some of the variations can be from lipid content (Post et al., 2007), and geographical differences in plankton biosynthesis and metabolism (Rau et al., 1989). The ranges of prey δ^{15}N in this study therefore represented multiple trophic positions, while their δ^{13}C ranges represented diverse basal resources.

Some prey were not statistically different from each other in terms of either δ^{13}C or δ^{15}N. The similarities of δ^{13}C and δ^{15}N may be a result of mixing of cross-shelf and offshore waters through upwelling, resulting in homogeneous mixture of food sources available to the various prey. Holmes et al.(1998) observed little change in δ^{13}C and δ^{15}N values in surface sediments up to 200 km off shore. The similarities in the isotopic values among prey may present a problem, as different combinations of prey species can produce the same isotope signatures. However, the ability of the SIAR model to incorporate variations of isotope values reduces the impact of overlapping or similar isotope ratios of prey (Parnell et al., 2010).

Feasible contributions of different prey to hake isotopic mixtures (all sizes-pooled) showed that the two hake species' diets overlapped. This confirmed the findings of previous studies using stomach contents (Payne et al., 1987; Roel and Macpherson, 1988). *Synagrops microlepis* was the highest feasible contributor to both species isotopic mixture, with credible intervals of 4.77-34.24% and 4.04 -38.68% for *M. paradoxus* and *M. capensis*, respectively. These specific results contrast the previous findings obtained using stomach content analyses, which indicated that crustaceans were the main food for both species (Roel and Macpherson, 1988). The differences could be a result of the temporally-integrated nature of isotope data, in which signatures are assimilated over a longer period (Haines, 1976; West et al., 2006), as opposed to gut contents which are 'snap shots' of recent feeding (Paine, 1988). *Plesionika martia*, *C. agazizi*, myctophids and euphausiids also made considerable contributions to the diets of the two hake species. Results in my study indicated that the diets of the two hakes were not dominated by a single taxon, i.e. fish, a finding similar to that based on gut contents (Roel and Macpherson, 1988). Cannibalism accounted for less than 6% and less than 4% in the diets of *M. capensis* and *M. paradoxus*, respectively. The greater degree of cannibalism in *M. capensis* confirms patterns observed by Traut (1996). The cannibalism estimates from most studies utilising gut contents (Macpherson and Gordoa, 1994; Roel and Macpherson, 1988; Traut, 1996) were, however, much higher than my own estimates. Cannibalism is possibly overestimated by stomach contents analyses. The two hake species occur in great numbers in the marine waters off Namibia (Burmeister, 2001). Prey patch characteristics such as local densities of hake at the times of feeding (Benoit-Bird et al., 2013) can, therefore, bias their contributions to overall diet. Payne et al. (1987) also concluded that much of the feeding is not true cannibalism because adult *M. capensis* feed largely on small *M. paradoxus* where the latter co-occurs in great numbers.

The contributions of prey to the isotopic mixtures of hake (sizes-pooled) might not reflect their correct dietary representations, as fish feeding patterns change during growth (Emmerson and Raffaelli, 2004; Persson and De Roos, 2003). The ontogenic trophic shift of hake species (Iitembu et al., 2012) can result in different prey contributions with different size classes, which necessitated the separation of hake into different length classes. The contributions of different prey to different length classes of hake indicated that for both species, *P. martia, C. agazizi*, myctophids and euphausiids are dominant contributors, findings similar to those of the pooled size classes for hake. For small hake (20-29 cm), myctophids contributed more than all other prey, with modal contributions of 6.72% for *M. capensis* and 6.78% for *M. paradoxus.* Myctophids had higher modal contributions than all other prey to all length classes of *M. capensis*, which differ from Roel and Macpherson's (1988) findings of myctophid feeding decreasing with hake length. Myctophids were dominant only in *M. paradoxus* less than 30 cm, while in large ones, *S. microlepis* had the highest modal contributions to their isotopic mixture. The dietary differences between the two hake species are also shown by the 95% CI, where in *M. paradoxus* of the 20-29 cm length class, *H. dactylopterus* had the widest CI. In *M. paradoxus* between 30-39 cm, myctophids had the widest CI. In the 40-49 cm length class of *M. paradoxus*, *C. agazizi* had the widest feasible co-contributions, while in *M. paradoxus* of > 50 cm *S. microlepis* had the widest CI. *M. paradoxus* appears to feed on more diverse prey in comparison to *M. capensis*, and the importance of prey changed as they grew in length. Myctophids had the widest CI in all length classes of *M. capensis*, indicating their importance to the diet of *M. capensis*.

Contributions of crustaceans to the diets of hake indicated that, in the 20-29 cm length class, *F. woodwardi* with *P. martia* and euphausiids had modal contributions of more than 3% for *M. paradoxus*. For *M. capensis* of the same size, only *P. martia* and euphausiids modal contributions of more than 3%. The above dietary contributions shows that while the smaller hake species are isotopically indistinguishable (Iitembu et al., 2012), they differed in terms of dietary contributions of prey species. It is possible for two species feeding on different prey to have similar stable-isotope signatures, especially if the prey consumed have similar isotopic signatures (Thomson et al., 2012).

Payne et al. (1987) found cephalopods were important food for hake from a length of 50 cm in the west coast of South Africa. In my study, contributions of cephalopods to the diets of both hake were very low, not exceeding 3% in many of the length classes. *Todarodes eblanae* had modal contributions of more than 3% to the length classes of 30-39 cm for *M. capensis* and 20-29 cm for *M. paradoxus*. Increased cannibalism has mostly been reported in larger hake (>60 cm total length) (Biology et al., 1994), although cannibalism by *M. capensis* was observed in small (10-20 cm) hake (Pillar and Wilkinson, 1995). Small hake ($<$ 15 cm), *M. paradoxus* ($<$ 40 cm) and *M. capensis* (<40 cm) all had modal contributions of around 1% at all length classes for both hake species, with their upper level CI around 9%.

While the model provided a time-integrated view of the contributions of different prey to the hake diets, the consumption of any prey is also dependent on the prey biomass available to hake. The biomass of the prey used in the model were not determined, therefore a prey biomass survey will help to make inferences on how the prey affects the dynamic of the hake diets and population. The prey biomass survey results could also then be used with isotope mixing models to make inferences on the importance of particular prey to the diet of hake.

The model used (SIAR) allowed for robust dietary solutions of hake species to be derived as the consumer mixture and putative prey items as sources (Parnell et al. 2010). Although I am confident in my findings because of the putative nature of the prey used, an increase in sample size of prey would help increase the precision of the model output. Isotope mixing model like SIAR have a number of important limitations as they function on the assumption that all sources are equally available, source parameters are known, trophic fractionation or discrimination is estimated without errors, and that isotope ratios are uncorrelated and they do not allow the diet proportion vector to depend on covariates, such as time (Parnell et al.

2010; Galva et al. 2012). The findings of mixing models are also limited by the uncertainties associated with the fractionation factors which are assumed and the isotopic turnover rates which are not known for both hake species. Future research should therefore focus on determining the species-specific fractionation factors and isotopic turnover rates for the two hake species and their major prey. Accurate use of fractionation factors and turnover rates are crucial for quantitative diet estimates from mixing models to help direct future research and improve parameters (i.e. natural mortality) for stock assessment models. Efforts have been made to include as many prey of hake based on published gut content results (Payne et al., 1987; Roel and Macpherson, 1988; Traut, 1996) in the model. The inclusion of many hake prey was done to reduce the effect of missing source biases (Parnell et al. 2013); however because of the compositional nature the models results dietary contribution estimates were limited by the constant sum constraint (Aitchison 1986; Kucera and Malmgren 1998). Future modelling studies are needed to explore ways in which the feasible contributions of different sources are allowed to vary independently in the models. The application of additional independent techniques to assess hake diets such as fatty acids will also further refine our understanding of the feeding dynamics of hake species.

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Conflicts of Interest
The authors declare no conflict of interest

References

[1] Aitchison J. The Statistical Analysis of Compositional Data. Chapman and Hall., London (1986).

[2] Benoit-Bird KJ, Battaile BC, Heppell S, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom,C A, Paredes R, Suryan RM, Waluk CM, Trites AW. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies (2013). PLoS One 8, e53348.doi:10.1371.

[3] Boyle MD, Ebert DA, Cailliet GM. Stable-isotope analysis of a deep-sea benthic-fish assemblage: evidence of an enriched benthic food web. J. Fish Biol. 80, 1485-1507 (2012).

[4] Burmeister, L.-M. Depth-stratified density estimates and distribution of the Cape hake *Mer-*

luccius capensis and *M. paradoxus* off Namibia deduced from survey data, 1990âĂŞ1999. S. Afr. J. Mar. Sci. 23, 347-356 (2001).

[5] CortÃľs E. A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. C. J. Fish. Aqu. Sci. 54, 726-738. (1997)

[6] Emmerson MC, Raffaelli D. Predator-prey body size, interaction strength and the stability of a real food web. J. Anim. Ecol. 73, 399-09 (2004).

[7] France RL. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnol. Oceanogr. 40, 1310-1313 (1995).

[8] Galva DE, Sweeting CJ, Polunin NVC. Methodological uncertainty in resource mixing models for generalist fishes. Oecologia (2012). DOI 10.1007/s00442-012-2273-4.

[9] Gascuel D, Bozec Y, Chassot E, Colomb A, Laurans M. The trophic spectrum: theory and application as an ecosystem indicator. ICES J. Mar. Sci. 62, 443-452 (2005).

[10] Haines EB. Relation between the stable carbon isotope composition offiddler crabs, plants, and soils in a salt marsh. Limnol. Oceanogr. 21, 880-883 (1976).

[11] Holmes ME, Mueller PJ, Schneider RR, Segl M, Wefer G. Spatial variations in euphotic zone nitrate utilization based on delta super(15)N in surface sediments. GeoMarine Lett. 18, 58-65 (1998).

[12] Hopkins III J, Ferguson J. Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. PLoS One 7 (2012), e28478. doi:10.1371/journal.pone.0028478

[13] Iitembu JA, Miller TW, Ohmori K, Kanime A, Wells S. Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. Fish. Oceanogr. 21, 215-225 (2012).

[14] Jaworski A, Ragnarsson SA. Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES J. Mar. Sci. 63, 1682-1694 (2006).

[15] Konchina GV.The feeding niche of the hake *Merluccius gayi* (Merlucciidae), and the jack mackerel, *Trachurus symmetricus* (Carangidae) in the trophic system of the Peruvian coastal upwelling. J. Ichthyol. 23, 87-98 (1983).

[16] Kucera M, Malmgren BA. Logratio transformation of compositional data: A resolution of the constant sum constraint. Mar. Micr. 34, 117-120 (1998)

[17] Layman CA, Allgeier J. Characterizing trophic ecology of generalist consumers: A case study of the invasive lionfish in The Bahamas. Mar. Ecol. Prog. Ser. 448, 131-141 (2012).

[18] Macpherson E, Gordoa A. Effect of prey densities on cannibalism in Cape hake (*Merluccius capensis*) off Namibia. Mar. Bio. 119, 145-149 (1994).

[19] Macpherson E, Roel B.A. Trophic relationships in the demersal fish community off Namibia. S. Afri. J. Mar. Sci. 5, 585-596 (1987).

[20] Mesa MG, Poe TP, Gadomski DM, Petersen JH. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. J. Fish Biol. 45, 81-96 (1994).

[21] Miller TW, Brodeur RD, Rau GH. Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. Limnol. Oceanogr. 53, 1493-1503 (2008).

[22] Paine RT. Road maps of interactions or grist for theoretical developmentâĂŕ? Ecology 69, 1648-1654 (1998).

[23] Parnell AC, Inger R, Bearhop S, Jackson AL. Source partitioning using stable isotopes: Coping with too much variation. PLoS One 5.(2010) e9672. doi:10.1371/journal.pone.0009672

[24] Payne AIL, Rose B, Leslie RW. Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. S. Afri. J. Mar. Sci. 5, 37-41(1987).

[25] Persson L, De Roos AM. Adaptive habitat use in size-structured populations: Linking individual behavior to population processes. Ecology 84, 1129-1139 (2003).

[26] Phillips DL, Gregg JW. Source partitioning using stable isotopes: Coping with too many sources. Oecologia 136, 261-269 (2003).

[27] Pillar SC, Barange M. Diel variability in bottom trawl catches and feeding activity of the Cape hakes off the west coast of South Africa. ICES J. Mar. Sci. 485-499 (1997).

[28] Pillar SC, Barange M. Feeding selectivity of juvenile Cape hake *Merluccius capensis* in the southern Benguela. S. Afr. J. Mar. Sci. 13, 255-268 (1993).

[29] Pillar SC, Wilkinson IS. The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. S. Afr.J. Mar. Sci. 15, 225-239 (1995).

[30] Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J and Montaña CG. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179-89 (2007).

[31] Punt AE, Leslie RW, Du Plesis S. Estimation of the annual consumption of food by cape hake *Merlucius capensis* and *M. paradoxus* off the South African west coast. S. Afr. J. Mar. Sci. 12, 611-634 (1992).

[32] Quevedo D, Aguilar A, Cardona L, Irene A. Massive consumption of gelatinous plankton by mediterranean apex predators. PLoS One 7 (2012). e31329. doi:10.1371/journal.pone.0031329.

[33] Rau GH, Takahashi T, Des Marais DJ. Latitudinal variations in plankton d13C: implication for CO and productivity in past oceans. Nat. 341, 516-518 (1989).

[34] Roel BA, Macpherson E. Feeding of *Merluccius capensis* and *M. paradoxus* off Namibia. S. Afr. J. Mar. Sci. 6, 227-243 (1988).

[35] Scharf FS, Buckel JA, Juanes F, Conover DO. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. Can. J. Fish. Aquat. Sci. 55, 1695-1703 (1998).

[36] Schlacher TA, Wooldridge TH. Patterns of selective predation by juvenile, benthivorous fish on estuarine macrofauna. Mar. Biol. 125, 241-247 (1996).

[37] Shannon LJ, Jarre A, Petersen SL. Developing a science base for implementation of the ecosystem approach to fisheries in South Africa. Prog. Oceanogr. 87, 289-303 (2010).

[38] Stowasser G, Mcallen R, Pierce GJ, Collins MA, Moffat CF, Priede IG, Pond DW. Trophic position of deep-sea fish -Assessment through fatty acid and stable isotope analyses. Deep Sea Res : Part I, Oceanogr. Res. Pap. 56, 812-826 (2009).

[39] Sweeting CJ , Polunin NVC and Jennings S. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rap. Com. Mas. Spe. 20, 595-601 (2006)

[40] Sweeting CJ, Barry J, Polunin NVC., Jennings S. Effects of body size and environment on diet-tissue δ^{13}C fractionation in fishes. J. Exp. Mar. Bio. Ecol. 252, 165-176 (2007a).

[41] Sweeting CJ, Barry J, Barnes C, Polunin NVC, Jennings S. Effects of body size and environment on diet-tissue δ^{15}N fractionation in fishes. J. Exp. Mar. Bio. Ecol. 340, 1-10 (2007b).

[42] Taka N, Hirose N, Osawa T, Hagiwara K, Kojima T, Okazaki Y, Kuwae T, Taniuch T, Yoshihara K. Carbon source and trophic position of pelagic fish in coastal waters of south-eastern Izu Peninsula, Japan, identified by stable isotope analysis. Fish. Sci. 73, 593-608 (2007).

[43] Thomson J, Heithaus MR, Burkholder D, Vaudo J, Wirsing A, Dill L. Site specialists, diet generalists? Isotopic variation, site fidelity, and foraging by loggerhead turtles in Shark Bay, Western Australia. Mar. Ecol. Prog. Ser. 453, 213-226 (2012).

[44] Traut, P. Diet and annual composition for the Cape hakes on the Namibian shelf, with special reference to cannibalism. University of Bergen, Bergen, Norway (1996).

[45] West JB, Bowen GJ, Cerling TE, Ehleringer JR. Stable isotopes as one of nature's ecological recorders. Trends Ecol. Evol. 21, 408-414 (2006).