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Patterns of trophic resource use among deep-sea shrimps in the Northern Benguela current ecosystem, Namibia

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ABSTRACT

The marine waters of Northern Benguela Ecosystem (NBE) off the Namibia support high abundances of different marine species. Seven shrimp species: *Aristeus varidens*, *Funchalia woodwardi*, *Glyphus marsupialis*, *Heterocarpus grimaldi*, *Solenocera africana*, *Plesionika martia* and *Parapeneus longirostris*, form an important trophic linkage between primary consumers and other trophic levels in the NBE. This study examined their trophic resource use patterns using their stable isotope measurements ($\delta^{15}N$, $\delta^{13}C$). Results indicated that although their trophic niche overlapped, there were some variations in their carbon sources ($\delta^{13}C$) and feeding positions ($\delta^{15}N$). *Heterocarpus grimaldi* fed at a higher trophic position, while *P. longirostris* fed at the lowest position. Latitude, body size and depth contributed to the variations observed in isotopic values of these crustaceans. This study represents the first attempt at understating trophic resource use patterns of crustaceans in the NBE using stable isotopic measurements. Further research is needed to investigate if the trophic interactions observed in this study are consistent across time and space.

The marine waters of Northern Benguela Ecosystem (NBE) off the Namibia support high abundances of different marine species, as a result of high primary production from a wind-driven upwelling phenomenon (Hutchings et al., 2009). These marine species include the stripped red shrimp *Aristeus varidens* Holthuis 1952, Woodward's pelagic shrimp *Funchalia woodwardi* Johnson 1867, kangaroo shrimp *Glyphus marsupialis* Filhol 1884, Grimald's nylon shrimp *Heterocarpus grimaldi* (A Mike Edwards and Bouvier 1900), African mud shrimp *Solenocera africana* Stebbing 1917, Golden shrimps *Plesionika martia* (A Mike Edwards 1883), and Deep-water rose Shrimp *Parapeneus longirostris* Lucas 1846. These shrimps occupy important trophic positions in the NBE food web, as they have been found in the diet of various fish (Macpherson, 1988). They also prey on various organisms such as zooplankton, polychaetes, molluscs and mysids (Bianchi et al., 1999), forming an important linkage between primary consumers and other trophic levels. Demersal surveys off the Namibia coastline have observed some of these species in the same geographic area, and in some cases occurring as mixed-species aggregations (Iitembu et al., 2014), an indication that they live at overlapping water depths (Macpherson, 1991). Although these shrimps play important trophic linkage roles in the NBE, little is known about their trophic resource use patterns including possible resource partitionings or differences in their niche preferences. Resource partitioning, whether by habitat, diet, sex or size, is known to allow for multiple species to cohabit the same environment with reduced interspecific competition for resources (Browning et al., 2014).

Our understanding of trophic resource use in marine communities has been derived from trophic interaction models (Giacomini et al., 2013) and ecosystem dynamic models such as Ecopath (Pauly et al., 2000), but these models need to be validated based on empirical data (Roux and Shannon, 2004). Traditional methods like gut-content analyses do not provide adequate trophic information for small crustaceans, as the ingested materials are mixed with very fine sediments and ground, by their gastric mill, beyond identification (Abed-Navandi and Dworschak, 2005). Over the last two decades, the use of stable isotope analysis in ecological research has increased (Post et al., 2007) and is now a commonly used method of studying trophic ecology of marine organism (Layman et al., 2007; Iitembu et al., 2012). Recently, isotope based metrics have been developed and have been used to assess potential resource use patterns in various marine species (Browning et al., 2014).

Samples of seven shrimp species: *A. varidens*, *F. woodwardi*, *G. marsupialis*, *H. grimaldi*, *S. africana*, *P. martia* and *P. longirostris* were collected during hake biomass surveys (January–February 2012) in Namibian waters on board MV Blue Sea I (Fig. 1). Trawling was done at pre-determined stations (depth range of 90–700 m) using a Gisund super two-panel bottom trawl (head length 31 m, footrope 47 m, and vertical net opening 4.5–5.5 m). Sampling per station was done with the goal of obtaining a wide size distribution of each shrimp species.

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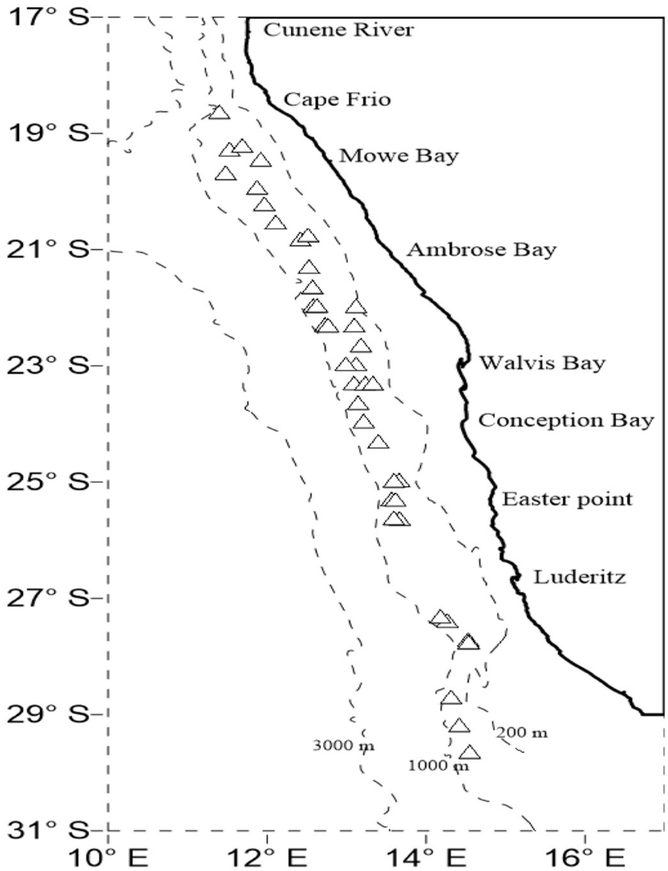

Fig. 1. Study region of the northern Benguela Current showing collection sites (△) and depth contours (dashed line).

At each sampling station, individual crustaceans (9–19 individuals) were collected and identified according to Bianchi et al. (1999). After identification, each individual shrimp was measured (total length) and the whole shrimps was immediately wrapped in aluminium foil and frozen at −20 °C on the ship.

Muscle tissues from dorsal trunk were cut, dried (60 °C, 48 h) and ground to a fine homogenous powder. All samples collected were analysed 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 ^{15}N in atmospheric nitrogen (N_2), according to the following equation:

$$\delta X\ (‰) = \left[\left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) - 1\right] \times 1000$$

where X is ^{13}C or ^{15}N and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Average analytical precision was <0.15‰ for $\delta^{13}C$ and <0.1‰ for $\delta^{15}N$. Carbon isotope measurements were mathematically corrected for lipid variations using a normalization equation from Post et al. (2007):

$$\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$$

where $\delta^{13}C_{untreated}$ was the $\delta^{13}C$ of non-lipid extracted tissue. The $\delta^{13}C$ 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 $\delta^{15}N$ values, requiring separate analyses of $\delta^{13}C$ and $\delta^{15}N$ (Sweeting et al., 2006).

The isotopic measurements ($\delta^{15}N$, $\delta^{13}C$) were, prior to analyses, tested for normality using Q-Q plots. As data did not violate parametric assumptions, analysis of variance (ANOVA) and Tukey post-hoc tests were used to assess the differences in isotopic signatures ($\delta^{15}N$, $\delta^{13}C$) between the seven species. Generalized additive models (GAM) were used to investigate if space (depth and latitude) and body size influenced the variabilities observed in isotopic signatures ($\delta^{15}N$, $\delta^{13}C$) of the shrimps. The GAMs are non-parametric generalizations of multiple linear regressions, where local smoothers are used in expressing the dependence between the response variable and the covariates (Hastie and Tibshirani, 1986). Species' isotopic signatures ($\delta^{15}N$, $\delta^{13}C$) of the shrimps were modelled as a function of depth, latitude and length. The GAM model was expressed:

$$\delta^{15}Nj/\delta^{13}Cj = sj\left(\delta^{15}N \text{ or } \delta^{13}C\right) + s\,(\text{Depth}) + s\,(\text{Latitude}) + s\,(\text{Length})$$

where ($\delta^{15}N/\delta^{13}C$) is the isotopic signatures for species j and sj ($\delta^{15}N$ or $\delta^{13}C$) represents a smooth function (cubic spline) for species j.

To investigate trophic structure of the seven crustaceans found in the NBE, quantitative population metrics (Layman et al., 2007) were derived for the each species using the Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al., 2011) model. Layman metrics included dNr, which provide information on range of trophic positions in the community and dCr, providing a univariate measure of the diversity of basal resources; total area (TA) of the convex hull, which represented niche area occupied by a population; and standard ellipse area (SEAc), which provides a bivariate measure of mean core isotopic niche (Layman et al., 2007; Jackson et al., 2011). To allow comparisons between species populations with varying sample sizes, all metrics were bootstrapped ($n = 9999$) and a small sample size correction for improving accuracy to SEA values is indicated by the subscript 'c' (Jackson et al., 2011).

A total of 92 specimens of seven shrimp species were collected and analysed for $\delta^{15}N$ and $\delta^{13}C$ isotopic measurements (Table 1). The depth from which samples were collected ranged between 255 m and 688 m (Table 1). Higher feeding position (*i.e.* $\delta^{15}N$ values) was observed in *H. grimaldi* which was caught in the northern NBE with lower feeding position being observed in the southern NBE caught crustacean *P. longirostris* (Table 1). Higher $\delta^{15}N$ values of surface sediments from the northern range of the Benguela were observed by Holmes et al.

Table 1
Mean $\delta^{15}N$ and $\delta^{13}C$ values (SD – standard deviation) of the crustaceans, together with samples size (n), body size range, average depth of collections, and average latitude of stations where samples were collected.

Species	n	Size range (cm)	Average depth (m)	Average latitude (degree south)	$\delta^{15}N$ mean ± SD	$\delta^{13}C$ mean ± SD
Aristeus varidens	17	4.2–11.6	472	−22.96	11.9 ± 1.1	−16.3 ± 1.0
Funchalia woodwardi	16	5.8–11.9	430	−24.28	11.7 ± 1.6	−16.6 ± 1.2
Glyphus marsupialis	9	5.0–9.5	499	−23.72	11.3 ± 1.7	−16.4 ± 1.3
Heterocarpus grimaldi	12	6.0–12.0	527	−21.96	12.3 ± 0.6	−16.6 ± 0.5
Parapeneus longirostris	9	9.0–13.0	485	−26.99	10.1 ± 2.0	−18.0 ± 0.9
Plesionika martia	19	5.0–8.5	478	−21.78	10.7 ± 1.1	−17.2 ± 0.9
Solenocera africana	10	6.2–8.0	348	−20.17	11.7 ± 1.1	−15.7 ± 1.1