

## **Trophic Dynamics of Pelagic Nekton in the Southern Benguela Current Ecosystem: Calibrating Trophic Models with Stable Isotope Analysis**

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**Abstract**—We measured the stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) in tissue collected from some important components of the pelagic food web of the southern Benguela ecosystem, including small pelagic fish, mackerels, squid, hakes, and sharks. The relative trophic level of these species estimated from their mean observed  $\delta^{15}\text{N}$  value was then compared to the trophic level derived for those species in Ecopath models developed for the southern Benguela, using the lowest level species (sardine) as the isotopic baseline and assuming a 3.4‰ increase in  $\delta^{15}\text{N}$  per trophic level. The rate of increase in  $\delta^{15}\text{N}$  value with increasing trophic level was less for observations than predicted by the model, indicating that the two diverged most at higher trophic levels. Possible reasons for differences between model and observations are discussed, the utility of this approach in calibrating trophic models is assessed, and future work is outlined.

**Keywords:** ecosystem models, nitrogen, pelagic nekton, southern Benguela, stable isotopes, trophic levels

### INTRODUCTION

Ecosystem models such as Ecopath are mass-balance trophic models that have been developed to investigate food web structure and functioning in marine ecosystems (Walters *et al.*, 1997). In such models important species, or functional groups of species that have the same or similar trophic level, are modeled as individual boxes that are trophically linked (Shannon *et al.*, 2003). Initial state input data required for each box include estimates of biomass, production, consumption, catches, and dietary composition, and models provide a static food web linkage pattern that can be altered over time through dynamic simulation. Ecopath models have been used to explore responses of food webs to changed fishing pressure (e.g. Travers *et al.*, 2010), and may also be useful in assessing the

impacts of climate change on ecosystem structure and functioning (Shannon *et al.*, 2008).

In some instances knowledge of the dietary composition and trophic interactions of species or functional groups in Ecopath models is poor or may be biased. This will reduce the accuracy of such models and impair their utility, and improved understanding of the relative trophic level of important species can assist in this regard. Knowledge of the trophic dynamics of pelagic nekton in the southern Benguela ecosystem (Fig. 1) has been inferred from stomach content analyses and can be considered to be relatively good (see Shannon *et al.*, 2003), but these studies are by their very nature limited to a “snapshot” of the diet and are generally also spatially and temporally limited. In contrast, stable isotope analysis (SIA) of  $\delta^{15}\text{N}$  provides a more time-integrated measure of an organism’s relative trophic level, because the isotopes are assimilated into an organism from metabolic and anabolic processes. In fish this temporal integration can vary substantially from weeks to years. Stable isotope analyses of southern Benguela pelagic nekton are limited, but data have recently been collected as part of a larger project to compare pelagic ecosystem structure across several regions (Miller *et al.*, 2010). In this paper we present mean  $\delta^{15}\text{N}$  values observed for several species of pelagic nekton in the southern Benguela. We then compare their relative trophic level (derived from SIA) with that derived from a recent Ecopath model of the southern Benguela (Osman, 2010).

#### MATERIALS AND METHODS

Samples for SIA were collected primarily during research surveys conducted around South Africa’s coast by the Department of Agriculture, Forestry and Fisheries (DAFF) between 2008 and 2010. Sardine, anchovy, round herring, chub and horse mackerels, squid and hakes were collected from either midwater or demersal trawls, and blue and mako shark were collected via long-lining. Table 1 shows the number of stations sampled, the date and season of sampling, and the number and size range of sampled individuals for each species. The locations of stations where samples were collected are shown in Fig. 1. Tissue samples were taken fresh from sharks and larger hake and then frozen, whilst for other species the whole fish was frozen soon after collection and subsequently processed ashore. In the laboratory fish were thawed, measured, and the tissue (dorsal musculature for fish and sharks, mantle for squid) removed, dried on aluminum foil for 48–96 h at 60°C, and sent from South Africa to Japan in sealed plastic bags. Sample processing involved pulverizing all tissue to a fine powder using a mortar and pestle, from which sub-sample aliquots were subsequently weighed and encapsulated into tin cups for SIA. Stable isotopes were measured for  $\delta^{13}\text{C}$  (data not shown in this study) and  $\delta^{15}\text{N}$  at the Center for Marine Environmental Studies using a Carlo Erba Elemental Analyzer 2500 coupled to a Finnigan MAT Delta Plus stable isotope ratio mass spectrometer via a ConFlo-III continuous flow interface (measurement error for  $\delta^{15}\text{N} \pm 0.3\text{‰}$ ). Calculation of the ratios relative to the standard for nitrogen ( $\text{N}_2$ ) was done by the standard equation  $\delta X = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \times 1000$ , where R is the ratio of the heavy to light

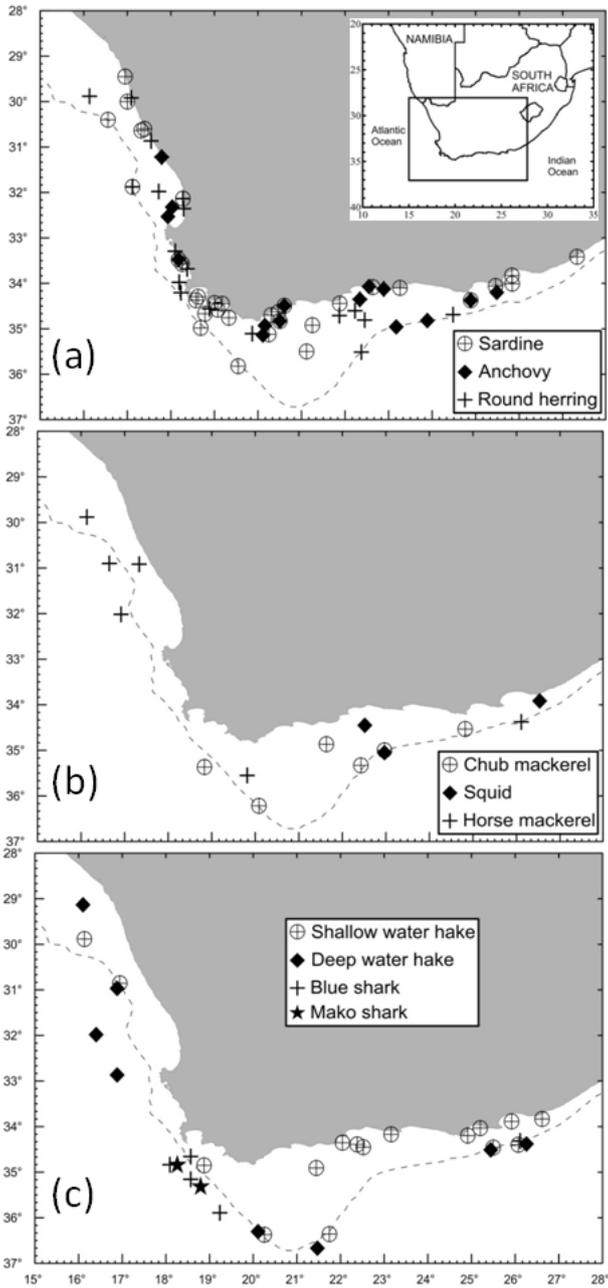


Fig. 1. Locations of sampling sites for (a) sardine, anchovy and round herring, (b) chub mackerel, horse mackerel, and squid, and (c) shallow and deep water hakes and blue and mako sharks. The dashed line indicates the position of the 200 m isobath, and the insert in (a) shows the mapped region relative to the whole of South Africa.

Table 1. Initial state trophic level of various species of pelagic nekton estimated by an Ecopath model of the southern Benguela (from Osman, 2010), and the number and dates of stations sampled, number of specimens and their mean size, and mean  $\delta^{15}\text{N}$  value. Species are listed in order of increasing trophic level (except for hakes); note that the trophic level for squid is that derived for “cephalopods”, and that for blue and mako sharks is that for “pelagic feeding chondrichthyans”, in the Ecopath model. CL = caudal length, FL = fork length, and TL = total length.

Species	Derived trophic level	No. (and dates) of stations sampled	n	Mean ( $\pm$ std. dev.) size (and range; mm)	Mean ( $\pm$ std. dev.) $\delta^{15}\text{N}$
Sardine ( <i>Sardinops sagax</i> )	2.99	34 (May/June and Nov./Dec. 2009)	232	139 $\pm$ 48 (52–213) CL	11.145 $\pm$ 0.526
Anchovy ( <i>Engraulis encrasicolus</i> )	3.54	15 (May/June and Nov./Dec. 2009)	100	103 $\pm$ 27 (43–137) CL	11.498 $\pm$ 0.699
Round herring ( <i>Etrumeus whiteheadi</i> )	3.64	22 (May/June and Nov./Dec. 2009)	123	137 $\pm$ 49 (42–207) CL	12.236 $\pm$ 0.877
Horse mackerel ( <i>Trachurus capensis</i> )	3.67	6 (Nov. 2008, Jan. 2009)	50	239 $\pm$ 39 (154–321) FL	13.785 $\pm$ 0.599
Chub mackerel ( <i>Scomber japonicus</i> )	3.82	6 (Sep. 2008, Nov. 2008)	60	236 $\pm$ 24 (147–320) FL	11.513 $\pm$ 0.605
Squid ( <i>Loligo vulgaris reynaudii</i> )	4.08	3 (Jan. 2009)	27	238 $\pm$ 70 (120–255) ML	13.782 $\pm$ 0.391

Species	Derived trophic level	No. (and dates) of stations sampled	<i>n</i>	Mean ( $\pm$ std. dev.) size (and range; mm)	Mean ( $\pm$ std. dev.) $\delta^{15}\text{N}$
Deep water hake ( <i>Merluccius paradoxus</i> )					
Small (<40 cm TL)	3.87	(Jan. 2009, Apr. 2010)	61	312 $\pm$ 69 (148–398) TL	13.659 $\pm$ 0.538
Large (>40 cm TL)	4.52		58	520 $\pm$ 90 (400–780) TL	15.190 $\pm$ 1.218
Shallow water hake ( <i>Merluccius capensis</i> )					
Small (<40 cm TL)	3.95	(Jan. 2009, Apr. 2010)	57	314 $\pm$ 48 (185–399) TL	13.992 $\pm$ 0.888
Large (>40 cm TL)	4.64		62	528 $\pm$ 119 (410–541) TL	15.307 $\pm$ 0.971
Blue shark ( <i>Prionace glauca</i> )	4.94	5 (July 2009)	29	1676 $\pm$ 514 (736–2900) TL	14.271 $\pm$ 0.632
Mako shark ( <i>Isurus paucus</i> )	4.94	2 (July 2009)	5	1521 $\pm$ 217 (1258–1786) TL	15.185 $\pm$ 0.361
Range or total	2.99–4.94	140 (spring, summer, autumn, winter, 2008–2010)	864	42–2900	11.145–15.307

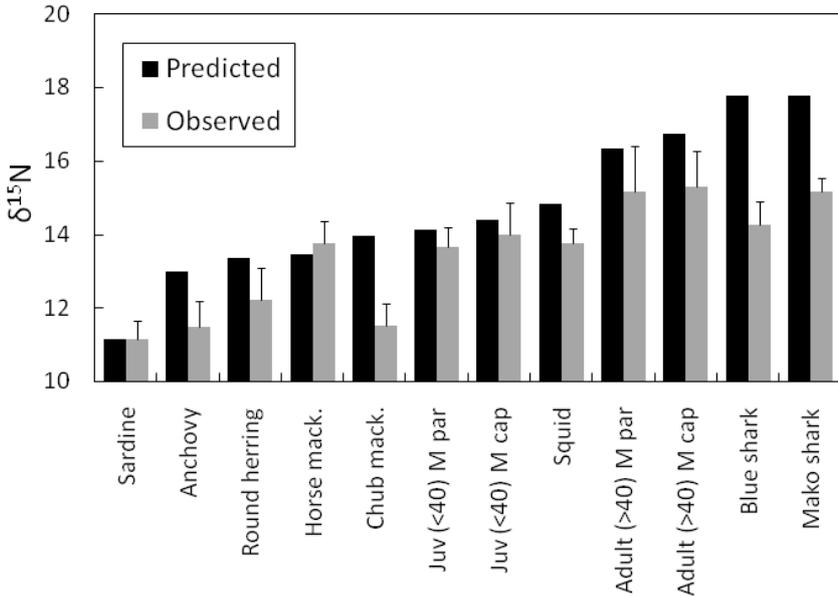


Fig. 2. Predicted and observed  $\delta^{15}\text{N}$  values for southern Benguela pelagic nekton species (ranked by model-derived trophic level). Standard deviations are shown with observations.

isotope for the sample ( $R_{\text{sample}}$ ) and standard ( $R_{\text{standard}}$ ) in units of parts per mil (‰).

Because we lacked  $\delta^{15}\text{N}$  data for primary consumers (herbivorous zooplankton) and in order to explicitly compare model-derived trophic levels with those inferred from observations of  $\delta^{15}\text{N}$  values, we used sardine as the isotopic baseline and assumed that both its model-derived trophic level and its mean observed  $\delta^{15}\text{N}$  value (see Section “Results”) were accurate, i.e.,  $\text{TL } 2.99 = 11.145\text{‰ } \delta^{15}\text{N}$ . We then assumed a 3.4‰ increase in  $\delta^{15}\text{N}$  per trophic level (Vander Zanden and Rasmussen, 2001; Post, 2002) to calculate  $\delta^{15}\text{N}$  values for successive trophic levels (such that  $\text{TL } 3.99 = 14.545$  and  $\text{TL } 4.99 = 17.945$ ) and used the linear regression between these three points ( $y = 3.4x + 0.9786$ ) to predict a  $\delta^{15}\text{N}$  value for the model-derived trophic level of each species.

## RESULTS

Model-derived trophic level and mean  $\delta^{15}\text{N}$  values are compared for each species (and size class for hakes) in Table 1 and Fig. 2. Whereas observations conform in general to the expected pattern of increasing  $\delta^{15}\text{N}$  value with trophic level, the rate of increase was less for data than for the model. The ratio of observed/predicted  $\delta^{15}\text{N}$  values showed a significant ( $F = 4.96$ ,  $n = 12$ ,  $r^2 = 0.332$ ;  $p = 0.05$ ) linear decrease with trophic level (Fig. 3), indicating that either

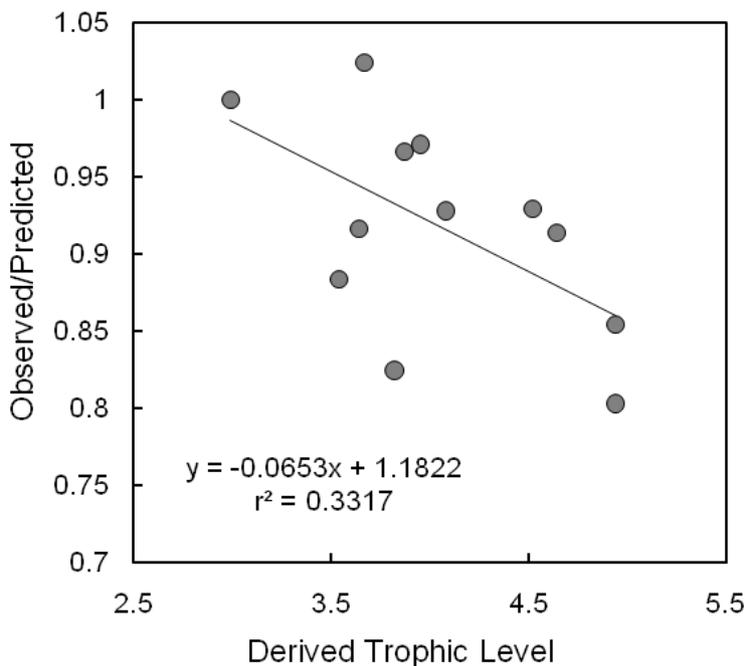


Fig. 3. Scatterplot of observed/predicted  $\delta^{15}\text{N}$  values ratio against derived trophic level for southern Benguela pelagic nekton species; the significant ( $p = 0.05$ ) linear regression and equation parameters are shown.

observations underestimated  $\delta^{15}\text{N}$  at higher trophic levels, or that model-derived trophic levels overestimate relative trophic position.

Of the small pelagic species, observed values were lower than predicted for anchovy and round herring (Fig. 2), and whereas both of these species have higher  $\delta^{15}\text{N}$  values than sardine, anchovy appear more similar isotopically to sardine than they are to round herring (Table 1). Observed  $\delta^{15}\text{N}$  was much lower than predicted for chub mackerel, and for both shark species (Fig. 2).

## DISCUSSION

Mean  $\delta^{15}\text{N}$  values calculated for the three small pelagic and two hake species came from large samples that had a wide spatial and seasonal coverage (Table 1; Fig. 1). A large portion of the observed size range of these species was also sampled, hence their mean  $\delta^{15}\text{N}$  values can be considered robust estimators of their nitrogen isotopic value during the period (2008–2010) sampled. For other species sample sizes were moderate but coverage was less spatially and seasonally extensive. For all species the small (2–8%) CV values are indicative of the

precision with which  $\delta^{15}\text{N}$  was estimated.

The slower increase in observed  $\delta^{15}\text{N}$  values with increasing trophic level compared to those predicted from model-derived trophic level may be due to several reasons. Firstly, the assumptions made in the comparison between observed and predicted  $\delta^{15}\text{N}$  values could be incorrect. These could be tested by sensitivity analysis to varying the model-derived trophic level of sardine, and to varying the trophic fractionation value, the latter being particularly important since “estimates of trophic position are very sensitive to assumptions about the trophic fractionation of  $\delta^{15}\text{N}$ ” (Post, 2002). Secondly, small sample sizes at the higher trophic levels (particularly for blue shark [ $n = 29$ ] and mako shark [ $n = 5$ ]) could have resulted in a poor (in this instance under-) estimation of their mean  $\delta^{15}\text{N}$  values. Further, comparison of these species groups with the corresponding model chondrichthyan group (pelagic-feeding chondrichthyans consisting of a wide variety of sharks, skates and rays) is a source of uncertainty in itself. However, sample size was not small for hakes ( $n = >100$  for each species) and observed  $\delta^{15}\text{N}$  values were lower than predicted for both size classes of both species, suggesting that observation error is not a strong cause of the mismatch between observed and predicted values. Thirdly, models based on dietary analyses alone may be vulnerable to the spatial and temporal limitations mentioned earlier, but bias may also arise due to differential digestive rates of different prey types by upper trophic level species. Large prey such as fishes tend to be digested at a slower rate, and hence persist longer in stomach contents, than do smaller, lower trophic level species such as zooplankton (Jobling, 1987). Where high trophic level predators are able to consume a broad range of prey, from zooplankton to other fishes, differential digestion rates mean that that large, higher trophic level prey items may be over-estimated in predator diet. This would result in a higher trophic level being assigned to a predator than is actually the case. If this third reason for the discrepancy in observed and predicted  $\delta^{15}\text{N}$  values is largely true then it has significant implications for trophic models of the southern Benguela, and suggests that model-derived trophic levels of higher trophic level species may require a downward revision by enhancing the contribution of low TL prey items (zooplankton) in model diets. It also indicates that given the limitations of dietary studies, greater integration between those studies and stable isotope analysis is needed, with more focus being placed the importance of mixed diets in higher trophic level species.

The greater difference in mean  $\delta^{15}\text{N}$  values between anchovy and round herring than between sardine and anchovy is surprising, since whilst sardine feed primarily on small zooplankton both anchovy and round herring feed primarily on large zooplankton (Wallace-Fincham, 1987; van der Lingen *et al.*, 2006). The higher  $\delta^{15}\text{N}$  values for round herring may reflect increased feeding on euphausiids compared to anchovy, or possibly a higher level of predation on fish. This observed difference has significant implications for Ecopath models, both because the model estimates a similar trophic level for the two species (see Table 1) based on their assumed diet compositions but also because of their large populations in the southern Benguela and hence important role in the foodweb.

Observed  $\delta^{15}\text{N}$  values for chub mackerel were substantially lower than predicted, but this is likely due to the fact that primarily small fish (see Table 1) that feed predominantly on zooplankton were sampled in this study, whilst the model-derived trophic level incorporates piscivory by larger fish (Baird, 1978). However, dietary studies were conducted at a time when chub mackerel was more abundant in the system than at present, and large individuals of this species are now seldom captured (Fairweather, 2009). Hence, consideration should be given to modifying Ecopath models of the southern Benguela to reflect the lower trophic level of the chub mackerel population in this system in recent years.

Further work will focus on expanding sampling at both the lower and upper ends of the trophic spectrum. Herbivorous zooplankton (copepods) and euphausiids will be collected across a large spatial scale to establish alternate isotopic baselines. Using primary consumers (copepods) as baseline indicators is particularly important in order to minimize error in estimates of the trophic position of higher level species (Vander Zanden and Rasmussen, 2001). In addition we aim to increase predator coverage, and will sample local tuna species and increase sample sizes for hakes and sharks. Ultimately, nitrogen and carbon isotope values and inferred food web structure will be linked with satellite-derived measures of chlorophyll a and water temperature for the southern Benguela and compared to similar data for other systems, so as to assess ecosystem-scale differences in the trophic dynamics of their pelagic zones (Miller *et al.*, 2010).

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