Evaluating food metrics of lanternfishes in waters of the southeastern Pacific Ocean

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Abstract

Using carbon and nitrogen stable isotope values, we analyzed the trophic position (TP) and the isotopic niche width of lanternfishes from three different fishing grounds in the Southern Pacific Ocean. Fishes from Perú had slightly higher δ13C values compared with fish from Chilean fisheries grounds. In contrast, δ15N values increased with latitude (North to South). Myctophids TP differed between the three fishing grounds (highest in Central Chile, lowest in Peru). Peruvian fishes had a smaller isotopic niche than the lanternfishes of the Chilean fishing grounds.

Introduction

Deep-water habitats are vast ecosystems, with an estimated biomass of approximately 10 billion metric tonnes (Goetsch et al. 2018). One of the biological components contributing to this high biomass is mesopelagic fish, which inhabit depths between 200 and 1000 meters (Moteki et al. 2017; Christiansen et al. 2018; Belcher et al. 2019). The family Myctophidae is by far the most significant fraction of the mesopelagic fish component (Espinoza et al. 2017). For example, in the Southern Pacific Ocean (SPO), myctophids (comprising 35 species) are estimated to have a biomass of up to 200 million tonnes (Lourenco et al. 2017; Saunders et al. 2018). As a result, the SPO is considered the area with the highest abundance of myctophid fish in the world. Myctophids play a crucial role in these ecosystems since they are prey for marine mammals, birds, invertebrates, and other fish (Goetsch et al. 2018; Stewart et al. 2018).

Human demands for protein from the marine environment have continued to intensify. Consequently, many fish stocks are at risk of collapse (FAO 2018), and there is a pressing need to find unexploited fish stocks that can help supply this demand. SPO myctophids have been identified as a potential resource for future exploitation (Valinassab et al. 2007), but relatively little is known about their basic biology, including their trophic ecology. Here, we use stable isotopes of carbon and nitrogen to characterize key features of the trophic ecology of South Pacific myctophids prior to their commercial exploitation, including the isotopic niche and trophic position (TP). The transfer of energy and nutrients from the bottom to top links makes TP a critical concept used to describe the functional role of consumers in a food web (Quezada-Romegialli et al. 2018).

TP has historically been estimated via stomach contents through the mass and the number of prey, but those results can be over-or under-estimated due to consumer digestive biases (Hetherington et al. 2017). In recent decades, stable isotope analyses (SIA) of nitrogen (δ^{15}N) and carbon (δ^{13}C) have been used as a complementary approach that can reduce biases associated with stomach contents analysis. Values of predator stable isotope composition revealed by SIA reflect prey assimilation (Goetsch et al. 2018). A consumer’s carbon stable ratios typically reflect the primary production mode fueling the taxa comprising its diet. Meanwhile, δ^{15}N values can be considered an indicator of TP occupied by prey and their consumers (Fry 2013). For instance, in tropical Atlantic waters, Olson and Watters (2003) examined TP in *Myctophum nitidulum* and *Symbolophorus reversus* using stomach contents, estimating a mean TP of

3.2. In contrast, stable isotopes estimated the same species to have a TP of 2.6 and 2.7, respectively (Hetherington et al. 2017).

Stable isotope values can also be used to estimate the isotopic niche - a compelling alternative to Elton's (1927) traditional definition of the trophic niche (Cherel et al. 2010). Layman et al. (2007a) developed quantitative methods using stable isotopes to measure trophic community structure. This isotopic approach is established on how individuals' chemical composition is directly influenced by what they consume. Therefore, predators with high $\delta^{15}N$ values will have a higher TP, hence a wide isotopic niche size (Herzka 2005). Thus, the variability in TP values displayed by a species could determine the size of the isotopic niche and provide a broader view of the species life history characteristics. We calculated TP and the isotope niche of the most abundant lanternfishes on three different fishing grounds in the southeastern Ocean Pacific to compare their ecological function.

Material And Methods

Samples collection

We analyzed a total of 123 individuals captured during a fisheries-independent research survey in 2015. The study area was divided into three fishing zones (Fig. 1): Peru (n = 50), Central-Chile (n = 39), and South-Chile (n = 34). A midwater trawl captured all fish from a depth range between 200 and 300 meters. After capture, they were labeled and frozen at -20°C until further analysis in the laboratory. We also collected water and zooplankton samples. For this purpose, 20 liters of water and a random set of zooplankton (plankton net WP2, ring diameter of 57 cm; mesh with 1.5 µm and length 2.6 m) were taken. The water was stored under total darkness, while the zooplankton was filtered, separated, dehydrated, and then stored under vacuum.

Lab Work

Myctophids were thawed and identified (Table 1). Approximately one gram of muscle tissue was taken from each individual. Seawater samples were filtered in the laboratory and divided into two fiberglass filters (FGP Whatman™ 1.5µm, 4.7 cm). The filter for $\delta^{13}C$ was placed in a desiccator with 20 ml of 37% HCL to remove inorganic carbon; meanwhile, the filter for $\delta^{15}N$ was put in aluminum foil at -80°C (Feuchtmayr and Grey 2003; Lorrain et al. 2003). The particulate organic matter (POM) and zooplankton left in the filters were removed and placed in individual plates. Then, all samples were dried (55°C for 48 hours) and pulverized. Subsamples of 400–500 µg were deposited in tin capsules and then analyzed in a mass spectrometer in continuous flow mode (CF) "Nu-Instruments," coupled with an elemental analyzer (EA) of Eurovector, EA-3024. Isotope radios were reported in δ notation, using standard Pee Dee Belemnite for $\delta^{13}C$ and Atmospheric Nitrogen for $\delta^{15}N$. Therefore, $\delta^{13}C$ or $\delta^{15}N = [(R\ sample/R\ standard) - 1]$, where R is $^{13}C/^{14}C$ or $^{15}N/^{14}N$, respectively. This analysis had an accuracy ± 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$.

Table 1

Summary results from δ^{13}C and δ^{15}N values of lanternfishes in the different fishing zones.

Species	**Fishing ground**	**δ^{13}C**	**δ^{15}N**	**Range C:N**	***n***
Ceratoscopelus warmingii	Perú	-18.2	10.7	3.54–3.69	20
Hygphum proximum		-18.4	11.6		20
Myctophum aurolaternatum		-18.3	11.3		10
Ceratoscopelus warmingii	Central-Chile	-17.3	17.7	3.64–6.03	10
Diogenichthys atlanticus		-18.8	15.0		5
Gymnoscopelus sp.		-18.8	15.7		5
Hintonia candens		-17.4	15.8		15
Hygphum proximum		-18.3	13.9		4
Diaphus hudsoni	South-Chile	-18.7	17.4	5.41–6.31	1
Electrona subaspera		-19.8	10.1		5
Hygphum proximum		-18.5	15.1		1
Lampadena luminosa		-18.1	13.8		3
Lampanyctodes sp.		-18.6	14.5		1
Lampanyctodes hectoris		-18.3	14.6		5
Myctophum sp.		-19.7	13.7		2
Protomyctophum tenisoni		-21.7	6.6		10
Symbolophorus boops		-18.4	13.1		5
Taaningichtys bathyphilus		-18.1	18.1		1
Baselines					
Copepods	Perú	-20.5	7.9	4.74	11*
Copepods	Central-Chile	-21.5	11.0	3.21	22*
Copepods	South-Chile	-20.7	12.5	3.75	15*
POM	Perú	-22.8	3.9	-	21*
POM	Central-Chile	-24.8	2.9	-	10*
POM	South-Chile	-24.5	4.3	-	25*
* Numbers of filters					**Total 227**

Data analysis

We calculated trophic position (TP) using two contrasting taxa as baselines based on the bulk SIA values. First, we assumed POM TP (λ) as one and copepods TP as $\lambda = 2$. Then, using the "tRophicPosition" package with Bayesian inference by the One baseline model (Quezada-Romegialli et al. 2018), we calculated myctophid TP for each of the three zones using a trophic discrimination factor (TDF) of ± SD (Δ^{15}N) of 3.4 ± 1‰ (Post 2002). Therefore, TP was calculated following this equation:

$$TP = [(\delta^{15}\mathrm{N}_M - \delta^{15}\mathrm{N}_b)/\Delta^{15}\mathrm{N}\,)] + \lambda$$

,

where $\delta^{15}N_M$ and $\delta^{15}N_b$ refer to the nitrogen values of the myctophids (M) and baseline (b), respectively, the standard ellipse area (SEA), followed by a convex-hull analysis was estimated to infer the isotopic niche's amplitude (Layman et al. 2007b). The "SIBER" package with Bayesian inference was used for this analysis (Jackson et al. 2011). A PERMANOVA: $n_{permutations}$ =9.999 test was used, based on a Euclidean similarity matrix to compare the values of δ^{15}N and δ^{13}C. A general linear model (GLM) was used to compare the values of δ^{15}N and SEA of myctophids in the different fishing zones, and a one-way ANOVA was applied to compare the mean values of POM and copepods.

Results And Discussion

Myctophids showed differences in estimated TP between the three fishing grounds. POM δ^{13}C values from the Peruvian fishing ground were ^{13}C-enriched (ANOVA; $F_{(1,24)} = 8.31$, $P = 0.029$) compared to samples from central-Chile and south-Chile (Table 1). In turn, δ^{15}N POM values were higher in south Chile (ANOVA; $F_{(1,25)} = 10.28$, $P = 0.012$). Copepod δ^{13}C and δ^{15}N did not vary among fishing grounds (ANOVA; $F_{(1,23)} = 13.58$, $P = 0.116$). However, stable isotope composition varied with the fishing ground (PERMANOVA; $F = 99.63$, $P = 0.003$). Perú is intermediated fish between the two Chilean ranges, but not significant, δ^{13}C values (Fig. 2), meanwhile the δ^{15}N values increased with latitude (Table 2). SEA not increased towards high latitudes. Indeed, SEA of central-Chile was larger than Peru and south-Chile; Peru *vs.* Central-Chile (GLM; $t_{-2.270}$; $P = 0.019$) than central-Chile *vs.* South-Chile (GLM; $t_{2.674}$; P = 0.021(Fig. 3a).

Table 2

Results of Bayesian analysis of trophic position analysis from two different baselines, POM (TP_{POM}) and Copepods ($TP_{Copepods}$)and size of the isotopic niche as standard ellipse area (SEA). SD; standard deviation and CI; credible intervals.

Fishing ground	**TP_{POM}**		**$TP_{Copepods}$**		**SEA**	
	Mean (± SD)	95% CIs	Mean (± SD)	95% CIs	Mean (± SD)	95% CIs
Peru	3.03 (0.35)	2.25, 3.73	2.87 (0.36)	2.09, 3.57	2.22 (0.31)	2.17, 2.27
Central-Chile	4.93 (0.93)	2.24, 6.25	3.57 (0.93)	2.11, 4.98	12.26 (2.40)	12.21, 12.31
South-Chile	3.85 (0.90)	2.48, 5.17	2.44 (0.90)	2.93, 3.75	7.07 (0.96)	7.02, 7.12

The average TP estimates using POM as the baseline (TP_{POM}) varied in higher ranges than those TP estimates based on copepods ($TP_{copepods}$) (Table 2). The posterior Bayesian TP calculated for Pacific myctophids for each fishing ground were similarly dependent on the baseline (Fig. 3b). This variation could be by many factors, such as feeding rates, tissues turnover rates, and/or trophic enrichment factors. Our finding to TP (~ 2.5) of lanternfishes in the SPO was similar to those obtained in other works for analogous species (Cherel et al. 2010; Bernal et al. 2015; Hetherington et al. 2017). Although the Peruvian and Chilean mesopelagic zones are considered similar oceanographically (Sutton et al. 2017), lanternfishes from the different fishing grounds showed differences in their stable isotope values. These differences likely reflect regional differences in upwelling. For example, the region of Peru sampled here has a seasonal pulse of upwelling. In contrast, the Chilean areas are subject to more permanent upwelling and, therefore, a continuous pattern of elevated primary production, explaining the isotopically enriched POM (Gutiérrez et al. 2016). Indeed, Pizarro et al. (2019) reported ^{15}N-enriched POM values in Northern Chile and associated this with upwelling.

The Southern Pacific Ocean’s lanternfishes could play an active and key role in carbon flow in the trophic web as these fishes represent prey for predators associated with different marine habitats, including surface and deep waters. In fact, Hudson et al. (2014) proposed the proportion of carbon flux carried out by the lanternfish at greater depths confirms the importance of myctophids in the biological pump of deep sea zones of the Atlantic Ocean. Olivar et al. (2019) describe secondary consumers’ role in the deep-sea ecosystem, in which some species have a vertical migration in the water column. Castro et al. (2010) found the same behavior in some lanternfishes of the SPO. This behavior results in myctophid fishes transferring energy from the upper layers of water towards the depths. Conversely, when lanternfishes migrate to the surface, they are prey for pelagic predators, including penguins, sharks, and marine mammals. However, when they migrate into deeper waters, they are prey for mesopelagic predators such as hake and squid. Therefore, our results point out that the lanternfishes from SPO likely play a primary role in the energy flow from deep waters to the surface. Nevertheless, future work is needed on lanternfishes. While myctophids are typically considered as a single homogenous guild, there are doubtless ways in which the species have differentiated. Given that our results show spatial differences in the ecological function of the guild, future studies in the SPO should compare the trophic ecology of individual species across different areas.

Declarations

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Consent to publish

This work did not have any person as a study subject.

Consent to participate

This work did not have any person as a study subject.

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Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Sebastian A. Klarian, Ivonne Quintanilla, Fernanda Vargas, Pepe Espinoza, Mauricio Zuñiga, Patricio Galvez, Rene Vargas, Alvaro Saavedra, Stephanny Curaz-Leiva. The first draft of the manuscript was written by Sebastian A. Klarian, Carolina Carcamo, Eric Schultz, Pepe Espinoza, Chris Harrod, Francisco Fernandoy, Ana Guzman, Carlos Canales-Cerro and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval

The authors from the competent authorities have obtained all necessary permissions for sampling and observational field studies. The research cruises counted all the legal authorizations for fishing research that Perú and Chile's laws maintain in their territory.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Figures

Figure 1

Study Area. In Perú, samples were collected onboard the Research vessel BIC José Olaya Balandra from the Instituto del Mar del Perú (IMARPE). In Central-Chile fish were collected by the Research vessel B/C *Abate Molina* from the Instituto de Fomento Pesquero (IFOP). In South-Chile fish were collected by the Research vessel AGS-61 *Cabo de Hornos* operated by the Chilean Navy.

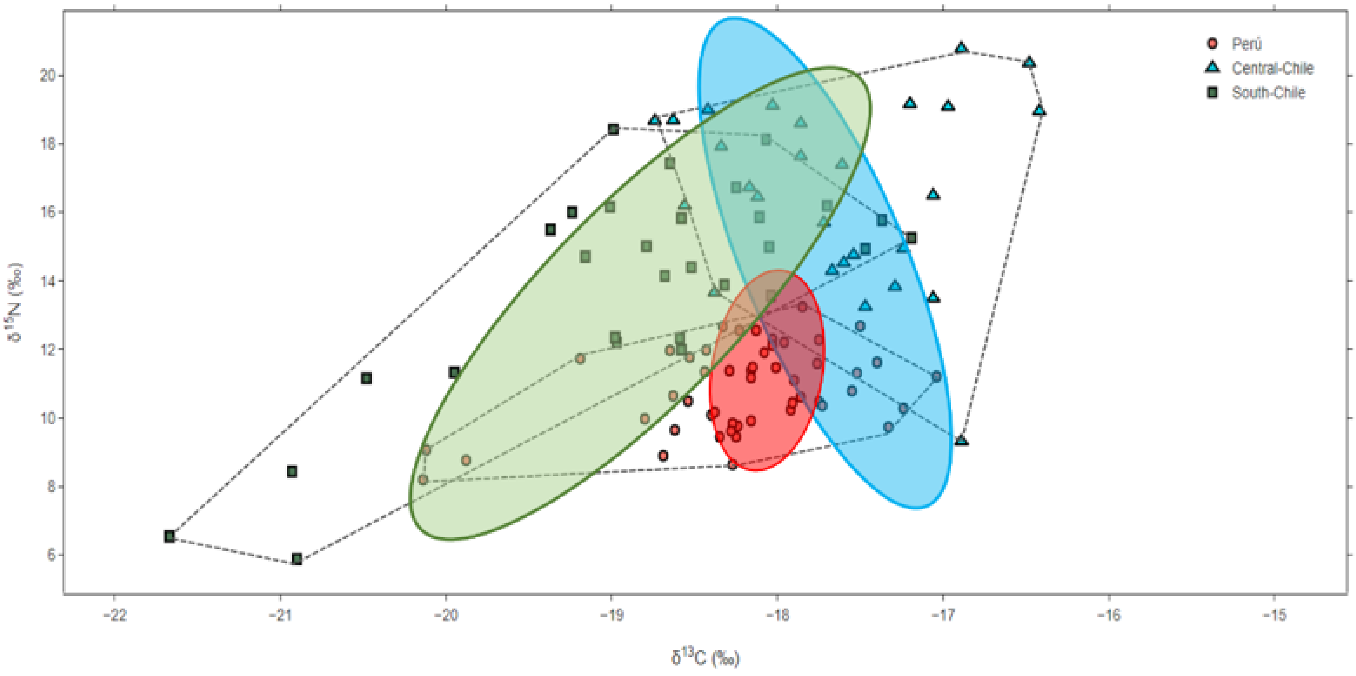

Figure 2

Biplot of δ13C and δ15N for lanternfishes caught in the different fishing grounds showing two measures of isotopic niche size - the estimated SEAc (solid lines) and the convex-hull (broken lines).

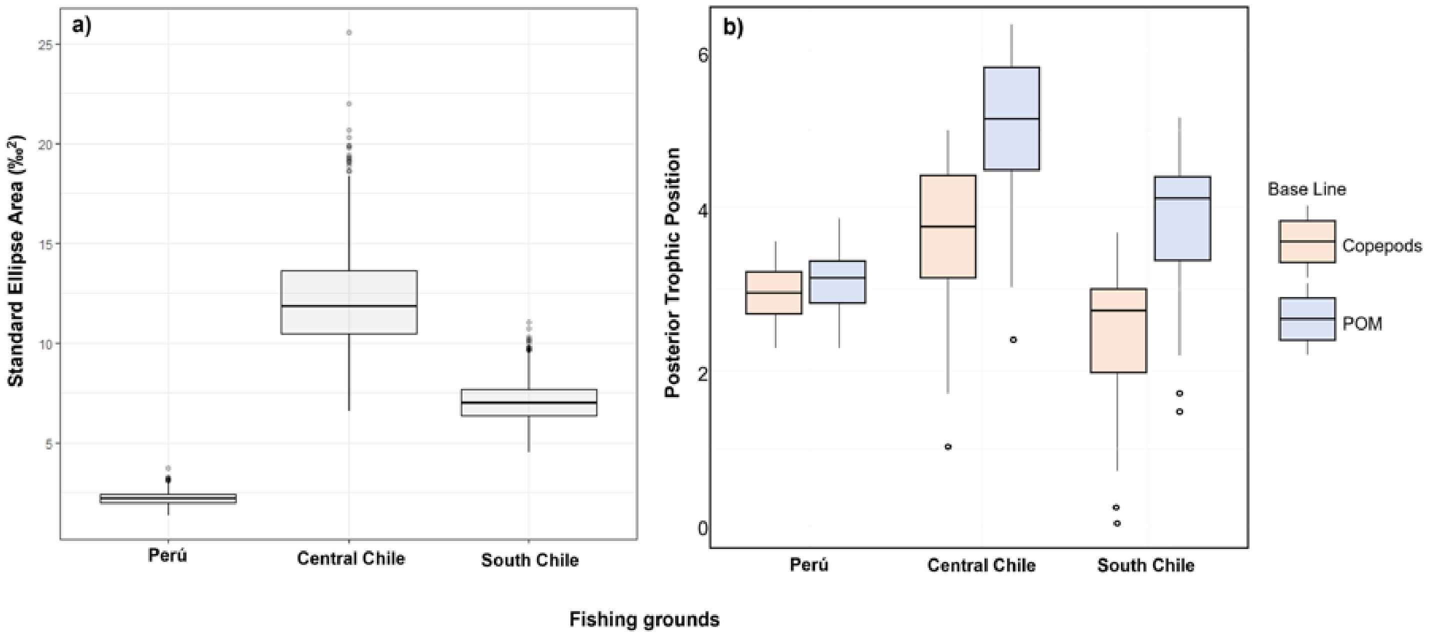

Figure 3

Box plot to the **a)** values of posterior standard ellipse area and **b)**values of the posterior trophic position (TP) inferred using two different baselines (copepods and POM).