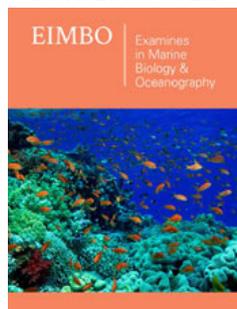


# Beaks And Gladii of Oegopsid Squids to Understand Their Trophic Ecology Around American Waters: A Review of The Stable Isotope Analysis

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## Abstract

The trophic ecology of squids has been studied using traditional methods of stomach content identification, there are reports of the diet of species of the order Oegopsida that described the prey and consumption of these predators in oceanic waters. Recently, the trophic ecology studies have included the analysis of hard tissues and the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to identify changes in the contribution of prey to the diet of squids, and to describe the trophic niche and overlap probability between species. This review analyzed the bibliographic references that used beaks and gladii to understand the trophic ecology of squids that inhabit in the marine waters of America. Results demonstrate that the beak of 14 oegopsid squid families have been included in this kind of analysis. The most studied squid was the Ommastrephid *Dosidicus gigas* in the Pacific Ocean, but many squid families (13) were analyzed in the Atlantic Ocean. The gladius was included in the hard tissue analysis, and it was reported that in addition to beaks, they are useful to describe the habitat, use of prey for squids, and feeding changes through ontogeny. As squids are fast moving predators, the use of these tissues in the isotope analysis help researchers to identify hot spots in the ocean, because these areas are the main refuges for feeding and for the development of these populations. Sympatric species can be identified by using hard tissue and isotopic analysis, as these tissues recorded the use of habitat and feeding behavior.

**Keyword:** Isotopes; Oegopsid squids; Trophic niche; Trophic ecology; American oceans

## Introduction

Squids are widely distributed in the oceans and are important sources for fisheries [1,2] they are abundant species from the south to the north hemisphere [1]. The relative increase of the squid abundance has been explained by the fishing down of the food web that causes the depletion of stocks of groundfish and other predatory fishes [3], by the expansion of fisheries into new areas such as South America countries [1,4] and by the cephalopod's adaptability to climate change [5,6]. Thus, it is necessary to find relations or differences in habitat use of these species that favor the creation of management strategies of their fisheries.

The most important squid species caught in the Pacific and Atlantic Oceans correspond to the order Oegopsida: the family Ommastrephidae with *Dosidicus gigas* (d'Orbigny 1835), *Todarodes pacificus* (Steenstrup 1880), *Illex argentinus* (Castellanos, 1960), and the order Myopsida: the family Loliginidae with the genus *Doryteuthis* and *Loligunculla* reported in fisheries [1]. These pelagic species are prey of sharks, fish, seabirds, marine mammals, and other squids [7-11] and they are active predators of fish, mollusks, and crustaceans [12-18]. These species are important transfers of energy and mass from basic to high levels of the food chain [19].

The study of distribution, migration, and trophic ecology of squids is difficult because they are fast-moving species, the large area they inhabit, and their horizontal and vertical movements [20]. A proxy to understand movements, use of habitat, and trophic interactions is the stable isotope analysis of carbon and nitrogen [21]. Stable isotopes of nitrogen ( $\delta^{15}\text{N}$ )

and carbon ( $\delta^{13}\text{C}$ ) have been reported to understand the trophic ecology of squids [17,22-24]. According to McCutchan et al. [25] and Vanderklift & Ponsard [26], the  $\delta^{15}\text{N}$  values show the trophic position of consumers, the  $\delta^{15}\text{N}$  values are higher in consumers relative to consumed prey. In addition, the latitudinal variation of  $\delta^{15}\text{N}$  is relatively low in oceanic waters of the Southern Ocean, and seasonal variation is integrated and buffered throughout the food web, from short-lived phytoplankton to long-lived predators [27]. The  $\delta^{13}\text{C}$  values indicate the inshore/pelagic versus offshore/benthic contribution to food in the diet of consumers [22,23,28]. In the giant squid *Architeuthis dux* (Steenstrup 1857), the more positive  $\delta^{13}\text{C}$  values indicate the use of waters to the north of the subtropical front to the Kerguelen waters in Southern Oceans [22], and for *Doryteuthis gahi* (d'Orbigny 1835) the more positive  $\delta^{13}\text{C}$  values indicate the use of shallow waters [17].

The isotope analysis in squids has been performed using mantle muscle tissue [17,29-31] beaks [32-36], gladii [37-39], statoliths [40], and eye lenses [41-43]. Each tissue allows the isotope analysis in a determinate time; two months approximately for muscle tissue, and life history for beaks, gladii, and eye lenses [29,41,44]. In general, the use of hard tissue in the isotope analysis resulted in the description of the trophic preferences and ontogenetic changes [40], the habitat characterization [34], spatial variation [45], and

the life history [37,38,46]. Beaks and gladii are hard structures composed of chitin, which grow adding chemical components during ontogeny, these components could be related to the food and areas where squids inhabits and growth [22].

Since beaks and gladii are good indicators and recorders of the life history, the use in the isotope analysis resulted adequate to understand the behavior and trophic ecology of squids. Thus, this review revised the published information for oegopsid squids and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the American Pacific and Atlantic Oceans to resume and compare the data published and evidence research necessities and future challenges in the isotope studies with hard structure of squids.

## Materials And Methods

### Data

Data related to  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of beaks and gladii were compiled from published sources (Table S1 & S2). Data were organized by Atlantic and Pacific oceans. The mean and standard deviation (SD) were calculated for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for each species. For *D. gigas*  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values allowed the analysis by size group and by country. For gladii, the myopsid squid *D. gahi* was included in the analysis to compare with other species.

**Supplementary material Table 1:** Mean±standard deviation SD of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of squid species. UN means unidentified. Logan and Lutcavage, 2013. 2 Staudinger et al. [32], Queirós et al. [36], Trasviña-Carrillo et al. [40], Ruiz-Cooley et al. [47], Liu et al. [34], Hu [33].

Species	n	Collection Year	Size	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Trophic Position	Tissue	Reference
<b>North Atlantic Ocean</b>								
Architeuthidae UN	5	2001-2002		-17.1±1.0	5.9±1.8		beaks	1
Chiroteuthidae UN	15	2001-2002	7.4±2.2	-18.0±0.3	7.4±0.8		beaks	1
<i>Megalocranchia</i> sp.	9	2012	9.9±6.0	-18.3±1.2	9.7±3.1	3.9	beaks	2
<i>Taonius pavo</i>	22	2012	18.0±5.1	-18.1±0.6	10.5±1.1	4.1	beaks	2
<i>Leachia atlantica</i>	7	2012	6.1±1.1	-17.9±0.4	8.5±0.0	3.5	beaks	2
Cycloteuthidae UN	1	2001-2002		-17.4±0.0	6.3±0.0		beaks	1
<i>Abrialiopsis morisii</i>	12	2012	2.8±0.8	-18.3±0.4	7.9±1.0	3.4	beaks	2
Gonatidae UN	2	2001-2002		-17.2±0.9	8.1±0.4		beaks	1
Histioteuthidae UN	12	2001-2002		-18.7±1.0	5.1±1.1		beaks	1
<i>Stigmatoteuthis arcturi</i>	3	2012	3.2±0.1	-18.6±0.2	9.4±0.7	3.8	beaks	2
<i>Histioteuthis bonnellii</i>	5	2012	3.6±3.4	-18.3±0.4	9.7±0.3	2.7	beaks	2
<i>Histioteuthis meleagroteuthis</i>	8	2012	5.0±1.1	-18.2±0.3	8.9±0.8	3.7	beaks	2
<i>Histioteuthis corona</i>	4	2012	4.2±0.1	-18.1±0.2	9.8±0.6	3.9	beaks	2
<i>Histioteuthis reversa</i>	8	2012	6.0±5.0	-17.8±0.2	11.4±1.1	4.4	beaks	2
<i>Joubiniteuthis portieri</i>	5	2012	6.1±0.0	-17.1±0.3	12.6±0.3	3.6	beaks	2
<i>Mastigoteuthis agassizii</i>	7	2012	7.7±1.6	-17.7±0.2	13.5±0.4	3.8	beaks	2
<i>Mastigopsis hjorti</i>	3	2012	6.3±0.0	-17.5±0.2	11.3±1.5	3.2	beaks	2
<i>Mastigoteuthis magna</i>	15	2012	13.0±7.6	-17.4±0.3	12.7±0.9	3.6	beaks	2
<i>Octopoteuthis sicula</i>	14	2012	7.5±4.6	-17.8±0.4	10.9±2.3	4.3	beaks	2
<i>Ornithoteuthis antillarum</i>	11	2012	5.0±2.1	-19.0±0.4	7.3±0.6	3.2	beaks	2

<i>Sthenoteuthis pteropus</i>	11	2012	7.5±3.2	-18.9±0.7	6.4±0.7	2.9	beaks	2
Ommastrephidae UN	20	2001-2002		-18.8±0.5	15.0±0.8		beaks	1
<i>Illex</i>	3	2001-2002		-18.3±0.4	13.4±0.3		beaks	1
<i>Illex illecebrosus</i>	4	2012	25.6±4.9	-17.8±0.4	11.7±0.8	4.5	beaks	2
<i>Ommastrephes bartramii</i>	6	2012	13.9±1.9	-17.6±0.4	5.8±0.7	2.8	beaks	2
<i>Onychoteuthis banksii</i>	8	2012	3.2±1.5	-18.7±0.1	7.2±1.1	3.2	beaks	2
Onychoteuthidae UN	4	2001-2002		-17.2±0.8	6.3±0.3		beaks	1
<i>Pyroteuthis margaritifera</i>	8	2012	2.4±0.0	-18.8±0.6	9.0±0.2	3.7	beaks	2
<b>South Atlantic Ocean</b>								
<i>Illex argentinus</i>	18	2015	21.5±2.9	-17.8±0.7	7.2±1.3		beaks	3
<b>North Pacific Ocean</b>								
<i>Dosidicus gigas</i>	66	2007	56.0±12.5	-17.06±0.6	12.1±1.4		beaks	4
<i>Dosidicus gigas</i>	153	2009	44.0±7.5	-17.3±0.6	13.3±1.8		beaks	4
<i>Dosidicus gigas</i>	10	1996-1999	60.2±15.2	-15.6±0.3	13.0±1.0		beaks	5
<i>Dosidicus gigas</i>	8	1996-1999	23.9±2.8	-17.3±0.5	10.6±0.7		beaks	5
<i>Dosidicus gigas</i>	17	2009-2013	31.1±1.4	-17.9±0.1	6.9±0.5		beaks	6
<i>Dosidicus gigas</i>	28	2009-2013	29.5±2.1	-19.0±0.1	3.6±0.5		beaks	6
<b>South Pacific Ocean</b>								
<i>Dosidicus gigas</i>	147	2013		-18.4±0.5	8.8±2.0		beaks	7
<i>Dosidicus gigas</i>	20	2009-2013	35.0±10.2	-17.0±0.6	9.7±2.6		beaks	6
<i>Dosidicus gigas</i>	17	2009-2013	43.0±5.9	-16.6±0.3	15.5±0.8		beaks	6
<i>Dosidicus gigas</i>		2013	31.7±4.2	-18.3±0.5	8.8±2.0		beaks	7
<i>Dosidicus gigas</i>		2014	40.7±8.2	-18.3±0.6	11.4±2.9		beaks	7
<i>Dosidicus gigas</i>		2015	37.7±6.4	-17.3±0.5	7.8±1.9		beaks	7
<i>Dosidicus gigas</i>		2014		-18.2±0.6	10.6±2.9		beaks	7
<i>Dosidicus gigas</i>		2015		-17.7±0.5	7.8±1.3		beaks	7
<i>Dosidicus gigas</i>		2014		-18.7±0.2	13.9±0.7		beaks	7
<i>Dosidicus gigas</i>		2015		-17.1±0.4	7.7±2.4		beaks	7
<i>Dosidicus gigas</i>	73	2013-2014		-18.1±0.6	13.2±2.7		beaks	6
<i>Dosidicus gigas</i>	73	2013-2014		-17.7±0.6	14.1±2.3		beaks	6
<i>Dosidicus gigas</i>	73	2013-2014		-18.6±0.9	10.7±3.8		beaks	6
<i>Dosidicus gigas</i>	73	2013-2014		-18.5±0.8	11.9±3.5		beaks	6
<i>Dosidicus gigas</i>	73	2013-2014		-18.8±0.9	11.3±4.0		beaks	6

### Prey groups

Reports of the feeding habits of squids were used to identify prey species and groups (Table S2 & S3). Prey species were

organized in Myctophid fishes, other fishes, Euphausiids, Copepods, Amphipods, and other crustaceans. After the revision, the mean and SD of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of prey were compiled (Table S2 & S3) [9,10, 12,14,15,16,18, 30,33,34,36, 35,40,47-60].

**Supplementary Table 2:** Mean±standard deviation SD of C values of prey groups reported for squids, and bibliographic references. Myc is Myctophid fish, Eup is euphausiid, Cop is copepods, Ceph is cephalopod, Amp is amphipods, and Oth crus is other crustacean. Regueira et al. 2014, Passarella & Hopkins 1991, Guerra-Merrero et al. [51], Squires [59], Rosas-Luis et al. [16], Parry 2006, Arkhipkin et al. [49], Merten et al. [18], Arkhipkin & Nigmatullin [12], Markaida et al. [14], Trasviña-Carrillo et al. [40], Ruiz-Cooley et al. [47], Argüelles et al. [30], Rosas-Luis et al. [48], Olivar et al. [56], Miller TW et al. [55], Loch and Hily [53], Bode et al. [50], Silva et al. [58], Olson et al. [15], López-Ibarra et al. [54], Logan & Lutcavage [32], Staudinger et al. [35], Liu et al. [34], Kaufman et al. [52], Tripp-Valdez et al. [60], Paiva et al. [57].

Predator/Prey	Myc	Other Fishes	Eup	Cop	Ceph	Amp	Oth crus	Diet reference	Isotope references
Atlantic ocean									

Architeuthidae									
<i>Architeuthis</i>		-16.65±0.1			-17.81±0.8			1	17, 22
Chiroteuthidae		-19.31±1.1						2	15
Enoploteuthidae									
<i>Abraliopsis morisii</i>			-21.15±0.9	-22.12±0.8	-17.90±0.4			3	19, 23
Histioteuthidae									
<i>Histioteuthis corona</i>		-19.31±1.1	-21.15±0.9	-21.83±2.3				2	15, 19
Mastigoteuthidae									
<i>Mastigoteuthis</i>		-19.31±1.1	-21.15±0.9	-22.12±0.8				2	15
Ommastrephidae									
<i>Illex</i> North		-19.31±1.1	-21.15±0.9					4	15, 19
<i>Illex argentinus</i> South	-21.8	-18.72±0.3	-28.76±1.4			-23.1		5	5
<i>Ommastrephes bartramii</i>	-18.58±0.1	-19.98±0.4			-18.30±0.6			6	15, 23
<i>Ornithoteuthis antillarum</i>	-19.31±1.1	-19.98±0.4	-21.15±0.9	-22.12±0.8	-18.20±0.3	-22.00±0.9		2, 7	15, 19, 25
<i>Sthenoteuthis pteropus</i>	-19.67±1.1	-19.49±1.8	-21.15±0.9		-18.20±0.7			8	15, 18, 19, 23, 27
Octopoteuthidae									
<i>Octopoteuthis</i>					-17.90±0.4			2	23
Onychoteuthidae									
<i>Onychoteuthis banksii</i>	-19.31±1	-19.98±0.4		-21.98±0.2	-18.00±0.7	-22.00±0.9		9	15, 23, 25
Pyroteuthidae									
<i>Pyroteuthis margaritifera</i>		-19.31±1	-21.15±0.9	-21.98±0.2	-17.90±0.4			2	15, 19, 23
<b>Pacific ocean</b>									
<i>Dosidicus gigas</i> North	-19.70±1.4	-18.75±0.5	-19.49±2.1	-21.23±1	-16.96±0.4		-17.68	10, 11, 12	12, 16, 20, 26
<i>Dosidicus gigas</i> South	-19.70±1.4		-21.00±0.8	-20.4	-18.51±0.8			13, 14	16, 24

**Supplementary Table 3:** Mean±standard deviation SD of N values of prey groups reported for squids. Myc is Myctophid fish, Eup is euphausiid, Cop is copepods, Ceph is cephalopod, Amp is amphipods, and Oth crus is other crustaceans.

Predator/Prey	Myc	Other Fishes	Eup	Cop	Cep	Amp	Oth crus
<b>Atlantic ocean</b>							
Architeuthidae							
<i>Architeuthis</i>		11.05±0.1			5.60±0.4		
Chiroteuthidae		7.85±1.2					
Enoploteuthidae							
<i>Abraliopsis morisii</i>			9.19±1.2	6.20±0.4	8.50		
Histioteuthidae							
<i>Histioteuthis corona</i>		7.85±1.2	9.19±1.2	8.28±1.1			
Mastigoteuthidae							
<i>Mastigoteuthis</i>		7.85±1.2	9.19±1.2	6.20±0.4			
Ommastrephidae							
<i>Illex</i> North		7.85±1.2	9.19±1.2				
<i>Illex argentinus</i> South	8.40	12.03±0.5	3.15±0.6			5.60	
<i>Ommastrephes bartramii</i>	7.34±1.1	9.16±0.3			8.46±3.5		

<i>Ornithoteuthis antillarum</i>	7.85±1.2	9.16±0.3	9.19±1.2	6.20±0.4	8.48±1.4	12.50	
<i>Sthenoteuthis pteropus</i>	8.13±1.1	10.64±1.1	9.19±1.2		9.33±3.8		
Octopoteuthidae							
Octopoteuthis					8.50		
Onychoteuthidae							
<i>Onychoteuthis banksii</i>	7.85±1.0	9.16±0.3		7.24±1.5	7.38±1.1	12.50	
Pyroteuthidae							
<i>Pyroteuthis margaritifera</i>		7.85±1.2	9.19±1.2	7.24±1.5	8.50		
<b>Pacific ocean</b>							
<i>Dosidicus gigas</i> North	14.70±0.8	14.00±2.0	12.01±3.1	9.56±1.4	12.26		12.40
<i>Dosidicus gigas</i> South	14.70±0.8		9.80±0.7	8.50	11.94		

### Isotopic mixing model

A stable isotope analysis in R (SIAR) was applied [61] to describe the potential contributions of different prey groups to the beak of each squid species. The SIAR model uses  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the consumer and its potential prey group to calculate the assimilation in proportion of each prey in the tissue analyzed. This model runs in the free software R [62] and allows the inclusion of variability in the stable isotope ratios of the predator and the potential prey [61].

To run the SIAR model, values of six prey groups (myctophid fish, other fish, euphausiids, copepods, cephalopods, and amphipods; Table 1) reported as prey in the diet of each species were used (bibliographic references are included in the Table S2). Trophic enrichment factors (TEF) of  $3.4\pm 1$  for  $\delta^{15}\text{N}$  and  $0.4\pm 1.3$  for  $\delta^{13}\text{C}$  were used due to the facility to compare these results with previous reports of cephalopod species [63,64]. Potential prey contribution was used to generate a graphical network using the Food Web Designer software [65].

**Table 1:** Mean±standard deviation SD of C and N values of prey groups reported as components in the diet of squids.

Prey group	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean	SD	Mean	SD
<b>North Atlantic Ocean</b>				
Myctophids	7.8	0.3	-19.2	0.5
Other fish	8.8	1.2	-19.3	0.9
Euphausiids	9.2	1.2	-21.2	0.9
Copepods	7.1	0.9	-22	0.1
Amphipods	12.5	1.0	-22	0.9
Cephalopods	8.1	1.1	-18	0.2
<b>South Atlantic Ocean</b>				
Myctophids	8.4	1.0	-21.8	1.0
Other fish	12	0.5	-18.7	0.3
Euphausiids	3.2	0.6	-28.8	1.4
Amphipods	5.6	1.0	-23.1	1.0
<b>North Pacific Ocean</b>				
Myctophids	14.7	1.0	-19.7	1.4
Other fish	14	2	-18.8	0.5
Euphausiids	12	3.1	-19.5	2.1
Copepods	9.6	1.4	-21.2	1.0
Cephalopods	12.3	0.1	-17	0.4
<b>South Pacific Ocean</b>				
Myctophids	14.7	0.8	-19.7	1.4
Euphausiids	9.8	0.7	-21	0.8
Copepods	8.5	1.0	-20.4	1.0
Cephalopods	11.9	3.5	-18.5	0.8

**Results**

**Beaks reports**

A total of eight reports of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values related to beaks of oegopsid squids in America were accounted, with three related to the Atlantic Ocean and five to the Pacific Ocean (Table S1).

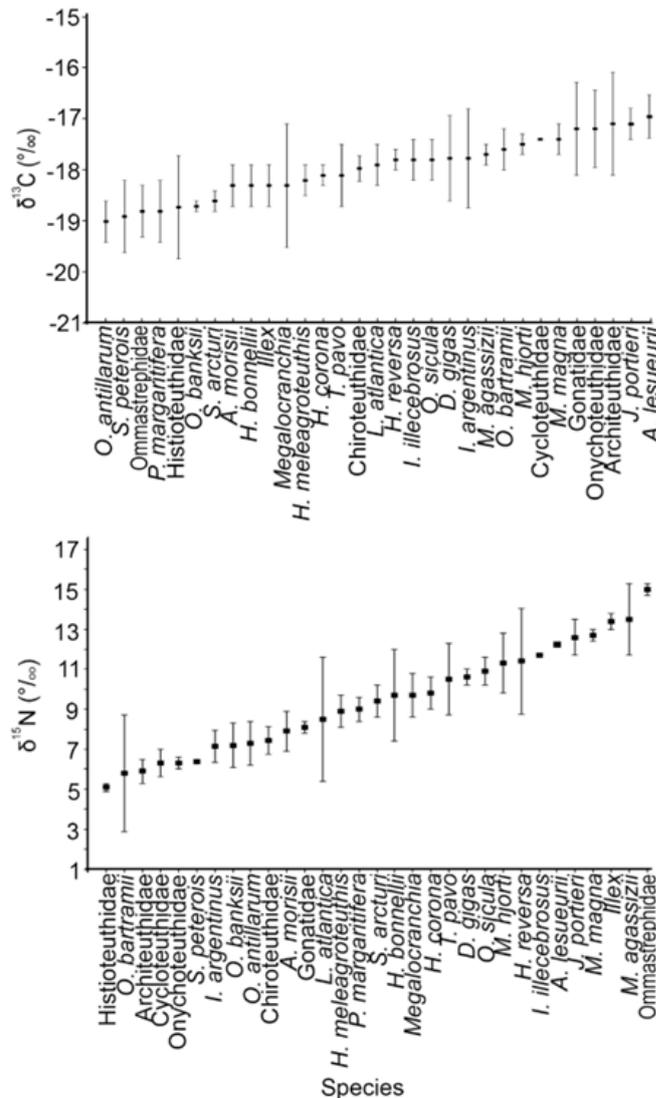
**Gladii reports**

Four reports of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in gladii, Lorrain et al. [37] and Li et al. [66], Rosas-Luis et al. [38], and Kato et al. [39] were included in the revision. For the Pacific Ocean the squid *D. gigas* and *Ommastrephes bartramii* (Lesueur, 1821), and for the Atlantic Ocean *I. argentinus* and *D. gahi* were used in isotope reports.

**General description of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values**

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of 14 oegopsid squid families were described in the Pacific and Atlantic Oceans around America. The Atlantic Ocean has been better studied with the families,

Architeuthidae, Chiroteuthidae, Cranchiidae, Cycloteuthidae, Enoploteuthidae, Gonatidae, Histoteuthidae, Joubiniteuthidae, Mastigoteuthidae, Octopoteuthidae, Ommastrephidae, Onychoteuthidae, and Pyroteuthidae, included in the isotope analysis. For the Pacific Ocean only two families, Ommastrephidae and Ancistrocheiridae, had reports of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Mean values of  $\delta^{13}\text{C}$  ranged from -19.0 and -17.0‰ (Figure 1 & 2). *Ancistrocheirus lesueurii* (d'Orbigny, 1842) and *Joubiniteuthis portieri* (Joubin, 1916) showed the highest  $\delta^{13}\text{C}$ , *D. gigas*, *Octopoteuthis sicula* (Rüppell, 1844), *Illex illecebrosus* (Lesueur, 1821), *Histoteuthis reversa* (Verrill, 1880), *Leachia atlantica* (Degner, 1925), *Taonius pavo* (Lesueur, 1821), *Histoteuthis corona* (N. A. Voss & G. L. Voss, 1962), *Histoteuthis meleagroteuthis* (Chun, 1910), and *Megalocranchia* sp. (Pfeffer, 1884) showed medium values around -18.0‰, and *Ornithoteuthis antillarum* (Adam, 1957), *Sthenoteuthis pteropus* (Steenstrup, 1855), *Pyroteuthis margaritifera* (Rüppell, 1844), and *Onychoteuthis banksi* (Leach, 1817) showed the lowest values around -19.0‰ (Figure 1).



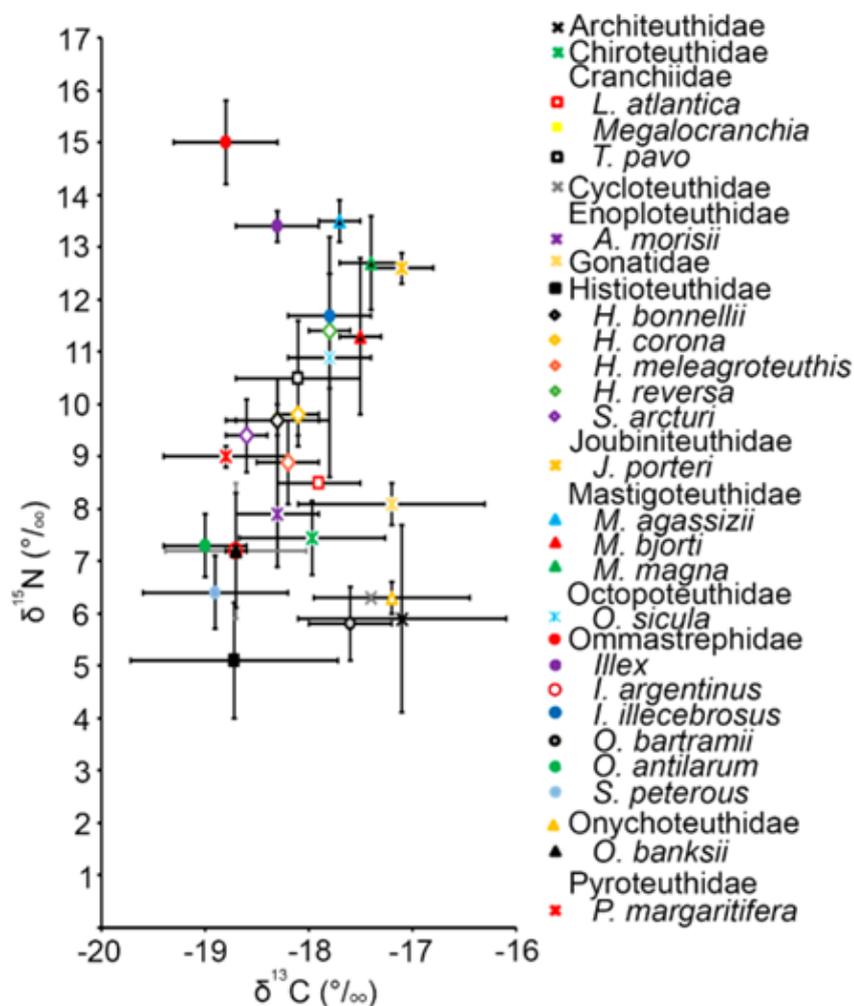
**Figure 1:** Mean and standard deviation of Carbon and Nitrogen isotope values for the lower beak of Oegopsid squids analyzed around America.

The mean  $\delta^{15}\text{N}$  values ranged from 5 to 15% (Figure 1). *Mastigoteuthis agassizii* (Verrill, 1881), *Illex* sp. (Steenstrup, 1880), *Mastigoteuthis magna* (Joubin, 1913), *J. portieri*, and *A. lesueurii* showed the highest values (between 12 and 15%), *H. meleagroteuthis*, *P. margaritifera*, *Stigmatoteuthis arcturi* (Robson, 1948), *Histioteuthis bonnellii* (Férussac, 1834), *Megalocranchia* sp. (Pfeffer, 1884), and *H. corona* showed medium values between 9 and 10%, and *O. bartramii* and *S. pteropus* with the lowest values between 5 and 7% (Figure 1).

### $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Atlantic Ocean squids

Squids, *S. pteropus*, *I. argentinus*, Architeuthidae UN, Histioteuthidae UN, Onychoteuthidae UN, Gonatidae UN, showed

the highest standard deviation for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Figure 2), the lowest values were reported for *M. agassizii*, *J. portieri*, and *S. arcturi* (Figure 2). The most positive  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were reported for *J. portieri*, *M. magna*, *M. agassizii*; the highest  $\delta^{13}\text{C}$  and the lowest  $\delta^{15}\text{N}$  values were reported for Architeuthidae UN, Onychoteuthidae UN, and Cycloteuthidae UN; the lowest  $\delta^{13}\text{C}$  and the highest  $\delta^{15}\text{N}$  values were reported for Ommastrephidae UN and *Illex*; the lowest  $\delta^{13}\text{C}$  and the lowest  $\delta^{15}\text{N}$  values were reported for Histioteuthidae UN, *S. pteropus*, *O. antillarum*, *O. banksii*, and *I. argentinus*; the other squid species had medium values (Figure 2). The Ommastrephidae UN segregated from the other species, with the highest  $\delta^{15}\text{N}$  values, and *O. bartramii* had low  $\delta^{15}\text{N}$  values close to 5% (Figure 2).

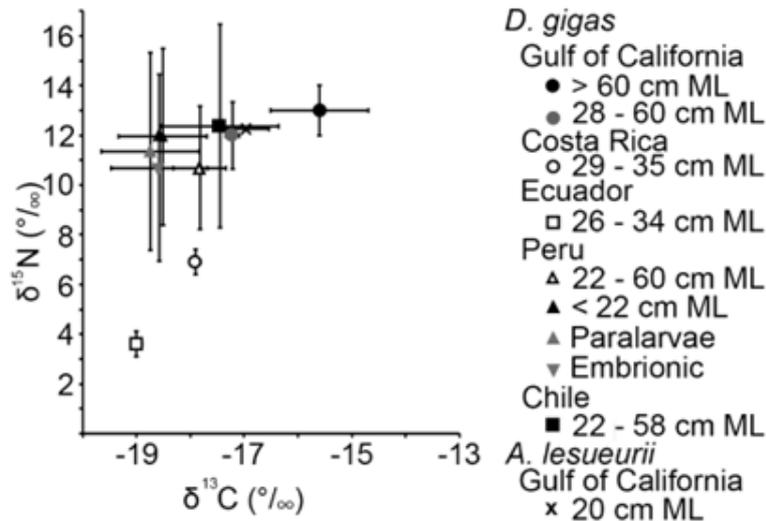


**Figure 2:** Mean and standard deviation of C and N values of cephalopod's lower beaks of the America's Atlantic Ocean.

### $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pacific Ocean squids

In the Pacific Ocean, two species were reported for isotope analysis, *D. gigas* and *A. lesueurii*. The Gulf of California showed the highest  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for *D. gigas* and *A. lesueurii* (Figure 3). For *D. gigas*, Costa Rica and Ecuador showed the lowest values;

Chile and Peru showed medium values (Figure 3). The graphical analysis by size allowed the presentation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for *D. gigas*, the  $\delta^{13}\text{C}$  values increases according to the size of squids, from embryonic to adult stage (Figure 3). Medium sized squids from Costa Rica and Ecuador showed the lowest  $\delta^{15}\text{N}$  values (Figure 3).



**Figure 3:** Mean and standard deviation of C and N values of *Dosidicus gigas* and *Ancistrocheirus lesueurii* lower beaks of the America’s Pacific Ocean.

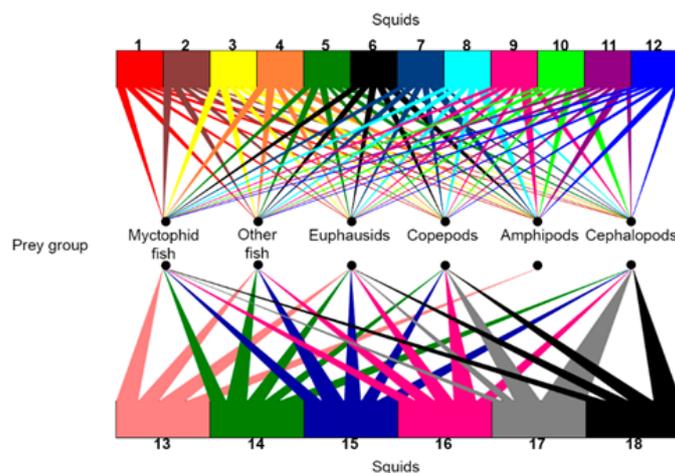
**Potential prey contribution to the diet of squids**

The amphipods were found as the most important contributor prey group for Architeuthidae UN, Chiroteuthidae UN, *A. morisii*, *H. corona*, *Octopoteuthis* sp., *O. antillarum*, *S. pteropus*, *O. bartramii*, *O. banksii*, and *P. margaritifera* (Figure 4). Cephalopods were the most important contributor prey for *Mastigoteuthis* spp. (Verrill, 1881), *Illex* spp., and *D. gigas* (in the Gulf of California, Costa Rica, Peru and Chile) (Figure 4). Euphausiids were the most important contributor prey for *I. argentinus* (Figure 4). Copepods were the most important contributor prey for *D. gigas* in Ecuador (Figure 4).

The second most important contributor prey group for *A. morisii*, *H. corona*, *Octopoteuthis* sp., *O. antillarum*, *S. pteropus*, *O. banksii*, *P. margaritifera*, *D. gigas* in Ecuador, and Architeuthidae

UN, Chiroteuthidae UN, was the myctophid fishes (Figure 4). Amphipods were the second contributor group in importance for *Mastigoteuthis* spp., *Illex* spp., and *I. argentinus* (Figure 4). Other fishes were the second most important contributor prey group for *O. bartramii* and for *D. gigas* in the Gulf of California and Costa Rica, and copepods for *D. gigas* in Peru and Chile (Figure 4).

The third contributor group in importance for *A. morisii*, *H. corona*, *Mastigoteuthis* spp. *Octopoteuthis* sp., *O. antillarum*, *S. pteropus*, *Illex* spp., *O. banksii*, *P. margaritifera*, *D. gigas* in Ecuador, Architeuthidae UN, and Chiroteuthidae UN, were other fishes (Figure 4). Myctophids were the third contributor group in importance for *O. bartramii*, *I. argentinus*, and *D. gigas* in Costa Rica, Peru and Chile (Figure 4). Euphausiid were the third contributor group in importance for *D. gigas* in the Gulf of California (Figure 4).



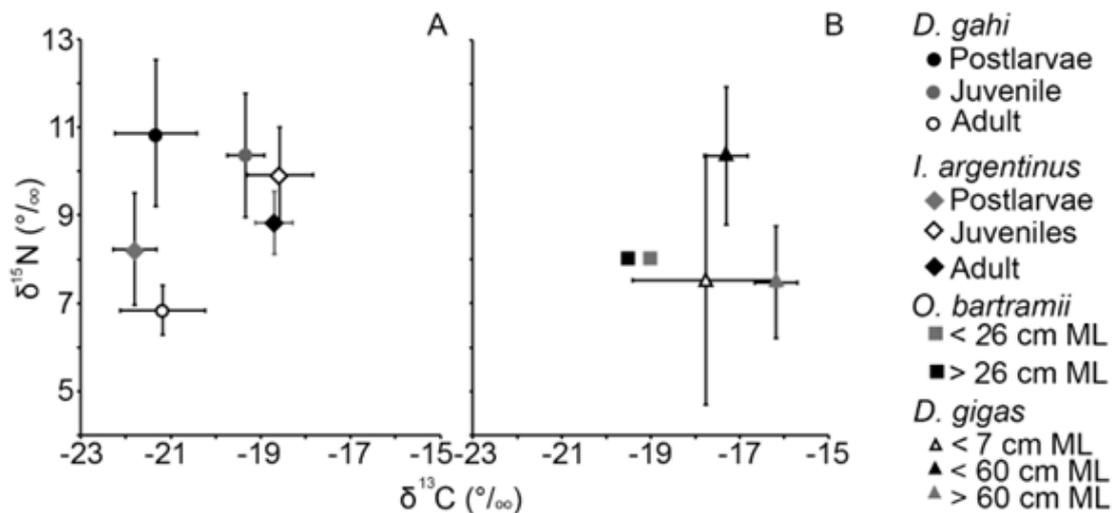
**Figure 4:** Potential prey contribution to the beak tissue of squid. 1 Architeuthidae UN, 2 Chiroteuthidae UN, 3 *Abraliopsis morisii*, 4 *Histioteuthis corona*, 5 *Mastigoteuthis* spp., 6 *Octopoteuthis* sp., 7 *Ornithoteuthis antillarum*, 8 *Sthenoteuthis pteropus*, 9 *Ommastrephes bartramii*, 10 *Illex* spp., 11 *Onychoteuthis banksii*, 12 *Pyroteuthis margaritifera*. 13 *Illex argentinus*, 14 *Dosidicus gigas* (Gulf of California), 15 *Dosidicus gigas* (Costa Rica), 16 *Dosidicus gigas* (Ecuador), 17 *Dosidicus gigas* (Peru), 18 *Dosidicus gigas* (Chile).

## The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in gladii

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of gladii of three oegopsid squids have been reported. In the south Atlantic Ocean, the isotope values of *I. argentinus* were reported (Figure 5). A segregation between postlarvae and juveniles and adult stages was reported; the  $\delta^{13}\text{C}$  values were lowest for postlarvae stage (Figure 5). In the same ecosystem, the juvenile stage of *D. gahi* was found with higher  $\delta^{13}\text{C}$  values than the juvenile and adult stage (Figure 5). The  $\delta^{15}\text{N}$  values of the adult stage for both species was lower than the other stages

(Figure 5).

In the Pacific Ocean, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of *O. bartramii* and *D. gigas* were reported. For *O. bartramii*, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values allowed the analysis between two groups, squids larger than 26cm ML and shorter than 26cm ML (Figure 5), values were similar for both size groups. For *D. gigas*, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values showed an overlap with large SDs (Figure 5). The  $\delta^{15}\text{N}$  values of the adult stage of *D. gigas* was lower than the medium size group (Figure 5).



**Figure 5:** Mean and standard deviation of C and N values of oegopsid squid's gladius (*Illex argentinus*, *Ommastrephes bartramii*, and *Dosidicus gigas*) and the myopsid squid *Doryteuthis gahi*. A represents values for the South Atlantic Ocean, and B represents values for the North Pacific - *Ommastrephes bartramii* and South Pacific - *Dosidicus gigas*. ML means mantle length. The values of *O. bartramii* were reported by Kato et al. [39], for *D. gigas* were reported by Lorrain et al. [37] and Li et al. [66], and for *I. argentinus* and *D. gahi* were reported by Rosas-Luis et al. [38].

## Discussion

The revision of reports of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, in hard tissues (beaks) of oegopsid squids related to America, highlights the need to increase research in the Pacific Ocean and to include more species in this kind of analysis. Since the first report in 2006 in the North Pacific Ocean for *D. gigas* [47], only three squids have been used to describe the isotope concentrations for the Pacific Ocean, they include *D. gigas*, *O. bartramii* and *A. lesueurii*, while in the Atlantic Ocean 27 squids have been reported. The highest number of species for the Atlantic were reported by Staudinger et al. [35] and corresponded to the North Atlantic Ocean. In the Pacific Ocean, all the reports used *D. gigas* as main squid in the analysis. This difference in the number of species is a result of the importance of squid species in fisheries. In the Pacific Ocean, *Dosidicus gigas* is the main fishery source in the Humboldt Current, in the Gulf of California and California Current, and a well-developed fishery industry is reported for Chile, Peru, Ecuador and Mexico [1,67]. In the Atlantic Ocean, a formal fishery industry is reported for *I. argentinus*, but no for other species [68]. Despite the need of more research, this revision organized the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of squids

and the discussion is based in the differences of values between species reported in the Atlantic Ocean and the values of different size groups and countries where *D. gigas* and *A. lesueurii* were captured in the Pacific Ocean.

## General description of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Values of  $\delta^{13}\text{C}$  in beaks showed a wide range indicating that squid species may use different  $\delta^{13}\text{C}$  baseline areas as previously reported by Navarro et al. [23]. In this review the results showed that the highest values were reported for *A. lesueurii* and *J. portieri*, and the lowest values were for *O. antillarum*, *S. pterois* and *P. margaritifera*. Squid species are voracious organisms looking for food at any time, this behavior could be evidenced with the  $\delta^{13}\text{C}$  values reported for *A. lesueurii* and *J. portieri*, which are neritic-oceanic species that can occur in association with seamounts and submarine ridges where upwelling events promote concentration of primary producers [69,70] and coinciding with the assumption that the highest values of  $\delta^{13}\text{C}$  are related to high productive areas in the ocean [63,71]. The lowest  $\delta^{13}\text{C}$  values reported for *O. antillarum*, *S. pterois* and *P. margaritifera* could be related to the oceanic areas where these species dwell, including the epipelagic to mesopelagic zones, and

related to general patterns for these species that are related to the use of the surface layer between 0 to 100m depths during early and juvenile stages [72]. Medium  $\delta^{13}\text{C}$  values were reported for *D. gigas*, *I. argentinus*, *T. pavo*, *L. atlantica*, among others, these values could be related to the habitat where these species are caught. For *D. gigas*, the distribution area included the east Pacific Ocean from the southern Chile to the North in Canada [73], this species is characterized to inhabit areas with high primary production as the Gulf of California, the Humboldt Current and the California current, and probably medium  $\delta^{13}\text{C}$  values vary in function of the vertical and horizontal migrations that these squid perform during day and night and between different areas for feeding as it was reported for *D. gigas* that moves from the coast to oceanic waters in the east Pacific Ocean [74].

Regarding the  $\delta^{15}\text{N}$  values, the highest values were reported for *M. agassizii*, *M. magna*, *Illex* sp., and the lowest values were reported for *O. bartramii* and Architeuthidae, indicating that the  $\delta^{15}\text{N}$  source is not related to the size of predator. Large species didn't show the highest values. These results indicate that the general rule that the size of prey increases with the size of predators does not apply for squids. Reports on the feeding habits of Ommastrephid's squids documented the variation in prey consumption between small to large squids, highlighting the consumption of small crustaceans in adult stages [74]. As the  $\delta^{15}\text{N}$  is accumulated through the food chain and depends in the source consumed by predators, the use of different feeding sources during squid ontogeny modified the mean  $\delta^{15}\text{N}$  values.

The description of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in squids of the American waters confirmed their plasticity, natural behavior and predatory strategies which are variate between species and promoting their interaction in the ecosystem through different trophic levels [23], minimizing competition and allowing their coexistence.

### $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Atlantic Ocean squids

An overlap in the  $\delta^{13}\text{C}$  for squids in the Atlantic Ocean is evidenced and related to the area where they were caught (Northwest Atlantic Ocean) for almost all species, the difference was found in the  $\delta^{15}\text{N}$  values. The highest values were showed for the squids of the family Ommastrephidae in the north Atlantic and the lowest values for the families Histiotuthidae and Architeuthidae. It is important to mention that the standard deviation reported for squids allowed the segregation between species, and that the accumulation in  $\delta^{15}\text{N}$  isotopes resulted in the increase of the trophic level of species, but for squids it cannot be related to the size of predators. The trophic levels assumed with the  $\delta^{15}\text{N}$  allowed the categorization of these species as medium trophic level predators, which corresponds with similar trophic levels calculated by Chérel & Hobson [22]. These squids showed a large range of  $\delta^{15}\text{N}$  with small variances that encompasses at least three trophic levels suggesting a greater diversity in their feeding habits. The exploratory analysis using potential prey indicated that segregation in prey consumption can be identified, squids feeding mainly on myctophids, squids feeding mainly on amphipods and euphausiids, and squids feeding

mainly on copepods. The feeding partitioning resulted as the main factor that allows the coexistence of squid species. Feeding segregation was previously reported by Chérel & Hobson [22] for squid species in the subantarctic Kerguelen Islands, and results for the American waters coincide with their conclusion asseverating that the main feeding strategy of squids are related to transitions between crustaceans and fish-eaters, with omnivore the dominant strategy. In contrast, the findings in this review indicates that the contribution of Cephalopods in the diet of the Ommastrephids *Illex* sp. in the Northwest Atlantic Ocean is important. This finding must be analyzed in future research and include a better description of the feeding habits of this and other species, a lack in the trophic ecology studies was identified for the Northwest Atlantic Ocean resulting in a bad description of their feeding sources and predatory strategies.

### $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Pacific Ocean squids

*Dosidicus gigas* is the main species used in the isotope analysis for the Pacific Ocean, this species has been described as a squid with high abundances in areas where the upwelling events favored the enrichment of primary production in the Humboldt Current and in the Gulf of California [75]. Thus, their highest  $\delta^{13}\text{C}$  values in the Gulf of California are good indicators of the feeding activity that this squid maintains with coastal areas in their distribution area [76]. *D. gigas* is a squid species that consumes prey at deep waters during daytime [48] and during night this species moves to surface water where their diet could include other prey related to coastal and surface waters [48,74], that was evidenced with a wide range of isotope values compared with other species in this review. As *A. lesueurii* was collected at the same time that the samples of *D. gigas* [47] it can be assumed that they are inhabiting the same area as isotopes coincided for both species.

Isotope values of *D. gigas* of Ecuador and Costa Rica segregated from the other samples in Chile, Peru and Mexico, the difference was found in the  $\delta^{15}\text{N}$  values. These samples showed the lowest  $\delta^{15}\text{N}$  values, probably related to the area where these samples were taken (open oceanic waters) [45]. Unfortunately, there are no feeding reports of this species in open waters in these two countries, thus the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  contributions found in this review must be confirmed with feeding description of the diet, and the confirmation of these prey as important for *D. gigas*. The findings in this review indicates that the contribution of cephalopods in the diet of *D. gigas* for the eastern Pacific Ocean is relevant for Peruvian and Chilean waters reinforcing the assumption made by Bruno et al. [77] where crustaceans and cephalopods are the main prey consumed by this species in Chile. This finding must be analyzed in future research because it is coincident with reports of the importance of cannibalism in *D. gigas* [77,78], and generally it is discarded in trophic ecology studies, enforcing the idea that this species prey on fishes.

### The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in gladii

Reports of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  descriptions in gladii are scarce in American waters, four reports including *I. argentinus* [38],

*O. bartramii* [39] and *D. gigas* [37,52] were found. These reports highlighted the importance to analyze segments of the hard tissue to compare the values through ontogeny. In general, the analysis of gladii allowed the identification of habitat use, in the three oegopsid species analyzed and in the myopsid squid *Doriteuthis gahi* [44], related to different mature stages. Segments related to the postlarvae stage of *I. argentinus* had the lowest  $\delta^{13}\text{C}$  values suggesting an habitat with low primary production, and a migratory movement to highly productive areas for juveniles and adults [63,71]. For *D. gigas* a segregation in the habitat use could not be evidenced, but it is important to note that segments related to the largest size (>60cm ML) had lower  $\delta^{15}\text{N}$  values than medium size squids, confirming the finding reported in stomach contents [74,76].

### Final Considerations

As the isotope analysis in beaks has been applied using a single sample (a mixed sampled) it is not possible to identify the size or the stage that is represented in the isotope values, thus an error can be assumed quantifying the isotopes and relating them to a specific size or stage. The analysis of isotope contribution using prey reported in the diet and generating potential groups of prey allowed the identification of the crustaceans and fishes as main feeding sources for many squid species, but cephalopods resulted as important contributors for the diet of the Ommastrephids *Illex* sp. in the Northwest Atlantic Ocean and *D. gigas* for the eastern Pacific Ocean. That highlights the necessity to describe the feeding habits and isotope contribution through ontogeny using a wide range of sizes and increase the isotope analysis along the beaks, gladii, or eye lenses. As the author mentioned before, this finding must be analyzed in future research because it is coincident with reports of the importance of cannibalism in *D. gigas* [77,78]. Another topic that must be included in future research is the analysis of segments along the beak, this will allow the comparison between stages and the inferences will result in the characterization of movements, feeding habits, and areas where squids inhabit, as it was performed in eye lenses [46] and gladii [38,79].

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