

Tracking habitat and resource use for the jumbo squid *Dosidicus gigas*: a stable isotope analysis in the Northern Humboldt Current System

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Abstract To determine the habitat and resource use of *Dosidicus gigas* in the Northern Humboldt Current System, we analysed carbon and nitrogen stable isotopes of 234 individuals collected during 2008–2010. Large variations in mantle stable isotope ratios were recorded, with values ranging from -19.1 to -15.1 ‰ ($\delta^{13}\text{C}$) and from 7.4 to 20.5 ‰ ($\delta^{15}\text{N}$). Most of the variation was explained by latitude, followed by distance to shelf break for carbon and by squid size for nitrogen. Latitudinal variations with increasing values from north to south were also found in zooplankton samples and were related to changes in isotope baseline values probably due to oxygen minimum zones that occur off Peru. This similar latitudinal trend in both zooplankton and *D. gigas* samples reveals that *D. gigas* is a relatively resident species at the scale of its isotopic turnover rate (i.e. a few weeks), even if this is not necessarily the case at the scale of its life. A small but significant size effect on $\delta^{13}\text{C}$ values suggests that jumbo

squid perform offshore–onshore ontogenic migration, with juveniles distributed offshore. For nitrogen, the high inter-individual variability observed with mantle length indicates that *D. gigas* can prey on a high variety of resources at any stage of their life cycle. This large-scale study off the coast of Peru provides further evidence that *D. gigas* have the capability to explore a wide range of habitats and resources at any stage of their life.

Introduction

Cephalopods, and particularly squid, are a central component in marine food webs worldwide. They are a valuable prey source for fish, marine mammals and birds and are a voracious predator of a wide variety of prey, including fish, crustaceans and other squid (Clarke 1996; Croxall and Prince 1996; Klages 1996; Smale 1996). Because of their high feeding rates and generalist feeding strategy, squid can potentially exert trophodynamic control on the recruitment of the early life stages of fish (Dawe 1988; Rodhouse and Nigmatullin 1996; Hunsicker and Essington 2008). Determining and quantifying their trophic relationships is therefore a key issue in understanding the structure and functioning of marine ecosystems. The trophic role of cephalopods has been examined mainly by stomach contents analysis. However, cephalopod trophodynamic studies based on such methods are hampered because the ingested prey are often rapidly digested, rejected and more usually eaten in parts, making species identification difficult (Rodhouse and Nigmatullin 1996; Cherel and Hobson 2005). Additionally, stomach content analysis is time-consuming and represents the last feeding events only, with no indication of long-term dietary habits (Jackson et al. 2007).

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Stable isotope analysis (SIA) has emerged as a common and alternative tool in ecology and has proven especially useful in the study of squid trophic ecology (Ruiz-Cooley et al. 2006; Cherel and Hobson 2005; Lorrain et al. 2011). Carbon isotopes ($\delta^{13}\text{C}$) are natural markers reflecting migrations routes and foraging habitats (Rubenstein and Hobson 2004), while stable isotopes ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) provides insight into trophic positioning (Post 2002; McCutchan et al. 2003; Vanderklift and Ponsard 2003). Indeed, in contrast to $\delta^{15}\text{N}$ values, which show a stepwise enrichment from prey to predators, carbon isotope values shows little variations with trophic level and may act as a good indicator of sources of production (Fry and Sherr 1984; McCutchan et al. 2003). Stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of animal tissues reflect the composition of assimilated food and provide a long-term indication of feeding strategy by integrating any differences in assimilated food over time (Hobson and Welch 1992, 1994).

However, ratios of stable isotopes are the additive result of a complex series of chemical and biological processes that are characteristic of a particular environment during carbon fixation for example, or nutrient cycling. Within marine ecosystems, $\delta^{13}\text{C}$ has been shown to differentiate between benthic and pelagic-derived production (Davenport and Bax 2002) and between nearshore and offshore productivity (Kline 1999; Perry et al. 1999), with nearshore and benthic systems being more enriched in ^{13}C (Cherel and Hobson 2007). Indeed algal-based food webs also tend to be enriched in ^{13}C compared with phytoplankton-based food webs (e.g., France 1995). $\delta^{15}\text{N}$ records changes in the nutrient dynamic in the water column and biological transformations of nitrogen under oxic or anoxic conditions that can alter the isotopic composition (Brandes et al. 1998). $\delta^{15}\text{N}$ of NO_3^- from anoxic water masses, where denitrification occurs, is significantly heavier than oxygenated waters (Liu and Kaplan 1989). This signature in turn would affect the $\delta^{15}\text{N}$ of marine plankton and propagate up to the food web (Graham et al. 2010). In oxygen minimum zones (OMZ), as off Peru, both intense denitrification and anaerobic ammonium oxidation (anammox) occur (Kuypers et al. 2005; Thamdrup et al. 2006; Hamersley et al. 2007; Lam et al. 2009; Lam and Kuypers 2011), which would lead to high $\delta^{15}\text{N}$ values of the isotopic baseline. Denitrifiers preferentially consume $^{14}\text{NO}_3^-$ leaving the residual oceanic NO_3^- pool strongly enriched in the heavier ^{15}N , with N isotope enrichment factors between 20 and 30 ‰ (Altabet et al. 1999; Voss et al. 2001; Graham et al. 2010). The isotope signature of anammox has not yet been determined. Since many isotope estimates were derived from field studies in which the isotope effect was estimated from the total nitrogen loss, they implicitly include the effect of anammox (Galbraith et al. 2008).

Dosidicus gigas is the largest and most abundant ommastrephid squid in the eastern Pacific and plays an important trophic role in the oceanic and neritic ecosystem (Nesis 1983). *D. gigas* is found from California (37° N) to southern Chile (47° S), and the highest concentrations are in the middle of its range, particularly in waters related to the areas of high productivity where zooplankton and meso- and bathypelagic fish are abundant (Nesis 1970, 1983; Nigmatullin et al. 2001; Waluda et al. 2006; Argüelles et al. 2008). The rich Peruvian waters are thus a region where *D. gigas* is abundant and exploited by an important fishery (Yamashiro et al. 1998; Taïpe et al. 2001). During the period 1991–1999, *D. gigas* had a wide distribution along the Peruvian sea, with the highest concentrations to the north (03–09°S), while the lowest concentrations were found between 13 and 16°S (Taïpe et al. 2001). The species is fast growing and short lived (Arkhipkin and Murzov 1986; Masuda et al. 1998; Argüelles et al. 2001; Markaida et al. 2004) with the age of most individuals no more than 1 year. However, it seems that the age of largest individuals could be underestimated and may be longer than 2 years (Nigmatullin et al. 2001). Likewise, other studies found variability in growth, longevity and maximum size among different cohorts (Keyl et al. 2011). *D. gigas* are thought to inhabit primarily mesopelagic depths (800–1,000 m) during daylight and to ascend close to the surface at night to feed in the southeast Pacific (Yatsu et al. 1999; Nigmatullin et al. 2001). Horizontal movement pattern is related to feeding migration of growing squid in the austral summer and autumn (Nesis 1970). More recently Lorrain et al. (2011) found a large inter-individual variability in horizontal movements, showing a high degree of plasticity of this species to adapt to environmental changes. However, precise migration patterns are not known along the coast of Peru. The diet of *D. gigas* has been regularly assessed by stomach contents analysis (Shchetinnikov 1989; Markaida and Sosa-Nishizaki 2003; Markaida 2006; Field et al. 2007) showing that it feeds on a wide range of species with mesopelagic fish being the most important prey in the northeast Pacific (Markaida and Sosa-Nishizaki 2003; Markaida 2006) and southeast Pacific (Shchetinnikov 1989; Rosas-Luis et al. 2011). Cannibalism can also be important in this species (Ibañez and Keyl 2009) but its amount can be overestimated depending of the fishing gear used for capture (Ibañez et al. 2008). Using stable isotopes, Ruiz-Cooley et al. (2006, 2010) showed that *D. gigas* trophic position increased with mantle length in the Gulf of California. However, in the Northern Humboldt Current System (NHCS), Lorrain et al. (2011) showed that at an individual level, *D. gigas* can decrease its trophic level at large sizes.

In this study, we analysed stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in *D. gigas* muscle samples in Peruvian waters

according to size, latitude and longitude in order to analyse the main important factors controlling these isotopic variations at the scale of the NHCS. We aimed to gain better insight into *D. gigas* foraging strategies.

Materials and methods

Dosidicus gigas and zooplankton sampling for isotopic analysis

A total of 234 *D. gigas* with mantle length (ML) ranging between 2.2 and 98.8 cm were analysed. Samples were obtained from 03.48 to 18.31°S, and up to 813 km from the shelf break from the commercial jigging fleet and research vessels within three successive years (from 31 May 2008 to 20 April 2010) (Table 1; Fig. 1). Each specimen was measured (ML in mm), and a small piece of muscle (1 × 1 cm) was collected from the anterior dorsal margin of the mantle. Samples were fixed and stored in ethanol (70 %) as storage in ethanol does not significantly alter the isotopic composition of tissues (Hobson et al. 1997), including the mantle of squid (Ruiz-Cooley et al. 2011). Thirty-four samples of zooplankton were collected during research surveys performed in 2008 using a Hensen net of 0.33-m² mouth area with a 300-μm mesh, in vertical hauls between 0 and 50 m. They were stored frozen until further processing.

Dosidicus gigas and zooplankton isotopic analysis

Before isotopic analysis, squid muscle and zooplankton samples were dried in an oven at +60 °C. They were then ground to a fine powder, and lipids were extracted with cyclohexane (Kojadinovic et al. 2008). Zooplankton samples were also acidified to remove any residual carbonates from cuticles and then rinsed with distilled water (Riera et al. 2000). Relative abundance of stable isotopes of carbon and nitrogen was determined by continuous-flow isotope-ratio mass spectrometry (Micromass at Department of Marine Biology, La Rochelle, France). Results are presented in the usual notation relative to PDB belemnite and atmospheric N₂ (Air) for δ¹³C and δ¹⁵N, respectively. Reference gas calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N1, IAEA-N2, IAEA-N3, IAEA-600 for nitrogen). Analytical precision based on isotope values of the acetanilide (Thermo Scientific) used to estimate C and N content for each sample series was <0.1 ‰ both for carbon and nitrogen.

Statistical analyses

We investigated potential relationships between dependent variables (δ¹⁵N and δ¹³C) and independent variables

(latitude (Lat), ML, distance to shelf break (DSB), Year, Season). As the relationships were likely to be nonlinear and multivariate, we used generalized additive models (GAM; Hastie and Tibshirani 1990) with the statistical computing software R. GAM is a nonparametric regression technique that generalizes multivariate linear regression by relaxing the assumptions of linearity and normality, replacing regression lines by smooths. We used ‘GCV.Cp’ as smoothing parameter estimation method. To find the best alternative distribution, we used the best-fitting Tweedie distribution with maximum likelihood estimation for model power (the Tweedie.profile function in the R statistical package; Dunn and Smyth 2008). The Tweedie set of distributions are two-parameter distributions that include a range of distributions including the normal, Poisson, gamma and mixed gamma–Poisson models. Since the Year and the Season had no significant effect in the complete model, these variables were removed from further analysis.

Classification and regression trees (CART, Brieman et al. 1984) were used to assess the relative importance of Year, latitude, size (ML) and DSB on squid δ¹⁵N and δ¹³C values. In CART, the dependent variables were modelled as a function of covariates. CART divides the data set through a sequence (tree) of binary splits on the values of one of the covariates at a time such that the overall variance in the dependent variable is minimized at each split. The resulting CART is usually simplified (‘pruned’) for the clarity of explanation. For pruning the tree and validating the robustness of the CART results, we used the recursive partitioning method (rpart; De’ath and Fabricius 2000). This method divides the data set into a number of subgroups (we used 10 groups following De’ath and Fabricius 2000) and then repeats the CART analysis sequentially, removing one subgroup each time. This replication gives a measure of robustness in the node splits in CART. Using a graph of the relative performance (i.e. the total model variance plus the number of nodes multiplied by a weighting factor, against the weighting factor), we chose a weighting factor such that the relative performance did not improve markedly with the addition of more nodes.

Results

Stable isotope analysis

The δ¹³C values of *D. gigas* muscle tissue ranged between –19.1 and –15.1 ‰, while δ¹⁵N ranged between 7.4 and 20.5 ‰ over the sampled size range (2.2–98.8 cm ML, Table 1).

GAMs (Fig. 2; Table 2) showed that the variables latitude, ML and DSB explained up to 77 and 82 % of the

Table 1 Data description and minimum, maximum and mean stable isotope values (‰) of carbon, nitrogen and mantle length (cm) of *Dosidicus gigas* analysed

Date	Lat		Long	DSB	N	Mantle length (cm)		
	South	West				km	Min	Max
31-May-08	3.7	80.9	−14	1	22.0	22.0	22.0	
18-Jun-08	7.7	80.1	−4	1	91.2	91.2	91.2	
2-Jul-08	15.9	76.2	100	13	13.2	38.3	23.1 (\pm 7.3)	
9-Nov-08	5.0	84.2	313	10	8.3	13.6	10.5 (\pm 2.1)	
10-Nov-08	5.3	83.6	239	8	15.0	16.8	15.9 (\pm 0.6)	
13-Nov-08	6.8	83.1	224	3	20.1	24.4	21.6 (\pm 2.4)	
18-Nov-08	7.9	80.5	29	1	53.9	53.9	53.9	
19-Nov-08	8.2	80.5	42	9	34.9	81.2	49.7 (\pm 15.9)	
19-Nov-08	8.6	80.7	79	7	61.2	72.2	67.2 (\pm 4.5)	
28-Feb-09	3.5	82.0	82	10	2.2	6.4	4.3 (\pm 1.4)	
7-Mar-09	6.4	81.4	37	5	2.7	9.0	5.1 (\pm 2.5)	
15-Mar-09	9.2	79.2	−39	10	2.9	4.4	3.7 (\pm 0.5)	
5-May-09	6.6	81.2	30	3	51.3	59.6	54.4 (\pm 4.5)	
11-May-09	5.5	81.8	57	4	60.7	83.3	76.9 (\pm 10.8)	
17-May-09	5.6	81.6	35	3	87.4	93.5	90.7 (\pm 3.1)	
11-Mar-10	17.6	72.4	55	10	69.0	82.5	76.4 (\pm 4.5)	
12-Mar-10	16.9	76.6	225	8	35.1	54.0	44.7 (\pm 6.5)	
15-Mar-10	7.5	81.1	52	20	27.0	59.0	41.2 (\pm 6.9)	
22-Mar-10	13.0	77.6	69	10	15.0	17.9	16.7 (\pm 1.1)	
23-Mar-10	13.7	77.0	36	10	11.2	17.9	13.2 (\pm 1.9)	
28-Mar-10	15.4	75.8	35	1	77.5	77.5	77.5	
1-Apr-10	16.7	73.4	19	18	14.9	23.0	19.6 (\pm 2.3)	
2-Apr-10	17.2	73.4	67	5	14.6	15.6	15.2 (\pm 0.4)	
2-Apr-10	15.2	77.0	112	11	41.5	98.8	66.7 (\pm 25.1)	
3-Apr-10	16.9	72.6	−12	6	19.9	26.6	23.9 (\pm 2.4)	
3-Apr-10	17.1	72.2	10	7	16.2	34.4	20.8 (\pm 6.4)	
4-Apr-10	18.3	71.7	68	5	13.8	16.4	15.0 (\pm 1.0)	
5-Apr-10	17.3	73.7	97	5	61.0	78.9	70.8 (\pm 7.3)	
6-Apr-10	17.6	72.5	71	5	80.7	93.0	87.8 (\pm 5.2)	
7-Apr-10	18.3	71.1	31	2	19.2	33.5	26.4 (\pm 10.1)	
14-Apr-10	16.9	76.6	219	6	37.0	49.6	42.7 (\pm 4.7)	
15-Apr-10	17.4	78.7	406	6	35.3	51.0	45.0 (\pm 6.1)	
17-Apr-10	18.0	83.0	813	6	34.1	45.0	38.2 (\pm 3.9)	
20-Apr-10	17.7	72.7	88	5	83.5	90.5	86.8 (\pm 2.7)	
Total				234	2.2	98.8		

Date	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			C/N		
	Min	Max	Mean (\pm SD)	Min	Max	Mean (\pm SD)	Min	Max	Mean (\pm SD)
31-May-08	9.1	9.1	9.1	−17.6	−17.6	−17.60	3.1	3.1	3.1
18-Jun-08	12.6	12.6	12.6	−15.9	−15.9	−15.90	3.1	3.1	3.1
2-Jul-08	13.8	18.5	16.4 (\pm 1.9)	−18.1	−16.4	−17.4 (\pm 0.5)	3.0	3.2	3.1 (\pm 0.04)
9-Nov-08	8.1	9.1	8.6 (\pm 0.3)	−18.0	−17.0	−17.5 (\pm 0.3)	3.2	3.3	3.2 (\pm 0.05)
10-Nov-08	7.4	8.2	7.8 (\pm 0.3)	−18.9	−18.4	−18.7 (\pm 0.2)	3.0	3.1	3.1 (\pm 0.05)
13-Nov-08	9.0	10.4	9.8 (\pm 0.7)	−18.5	−17.1	−17.8 (\pm 0.7)	3.2	3.3	3.2 (\pm 0.06)
18-Nov-08	16.1	16.1	16.1	−16.2	−16.2	−16.20	3.2	3.2	3.2
19-Nov-08	11.3	17.7	12.8 (\pm 1.9)	−16.7	−15.6	−16.1 (\pm 0.4)	3.2	3.3	3.2 (\pm 0.05)

Table 1 continued

Date	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			C/N		
	Min	Max	Mean (\pm SD)	Min	Max	Mean (\pm SD)	Min	Max	Mean (\pm SD)
19-Nov-08	11.5	14.8	13.0 (\pm 1.3)	-16.6	-15.3	-16.1 (\pm 0.5)	3.2	3.3	3.2 (\pm 0.04)
28-Feb-09	8.5	10.4	9.3 (\pm 0.6)	-19.1	-17.3	-18.7 (\pm 0.5)	3.2	3.3	3.2 (\pm 0.04)
7-Mar-09	10.4	11.5	10.9 (\pm 0.4)	-17.3	-16.5	-16.9 (\pm 0.3)	3.2	3.3	3.3 (\pm 0.05)
15-Mar-09	14.3	14.7	14.5 (\pm 0.2)	-16.6	-16.1	-16.3 (\pm 0.2)	3.2	3.3	3.3 (\pm 0.05)
5-May-09	12.4	15.4	13.5 (\pm 1.6)	-16.3	-15.5	-16.0 (\pm 0.4)	3.2	3.4	3.3 (\pm 0.10)
11-May-09	11.3	12.8	11.8 (\pm 0.7)	-17.4	-16.4	-16.9 (\pm 0.4)	3.3	3.4	3.3 (\pm 0.05)
17-May-09	11.9	12.9	12.2 (\pm 0.5)	-17.0	-16.3	-16.6 (\pm 0.4)	3.2	3.4	3.3 (\pm 0.10)
11-Mar-10	16.0	20.0	18.3 (\pm 1.2)	-17.8	-16.7	-17.4 (\pm 0.4)	3.0	3.1	3.1 (\pm 0.03)
12-Mar-10	12.1	17.1	14.4 (\pm 1.8)	-17.9	-17.2	-17.6 (\pm 0.2)	3.1	3.2	3.1 (\pm 0.05)
15-Mar-10	8.9	13.8	11.4 (\pm 1.1)	-17.7	-16.2	-17.1 (\pm 0.4)	3.1	3.3	3.2 (\pm 0.08)
22-Mar-10	12.5	14.3	13.4 (\pm 0.6)	-17.2	-15.4	-16.2 (\pm 0.5)	3.1	3.2	3.2 (\pm 0.04)
23-Mar-10	13.1	14.2	13.5 (\pm 0.4)	-17.1	-15.1	-16.0 (\pm 0.6)	3.1	3.2	3.2 (\pm 0.05)
28-Mar-10	15.4	15.4	15.4	-15.7	-15.7	-15.70	3.1	3.1	3.1
1-Apr-10	11.7	16.5	14.0 (\pm 1.6)	-17.5	-15.6	-16.6 (\pm 0.4)	3.1	3.2	3.2 (\pm 0.53)
2-Apr-10	15.3	19.1	17.2 (\pm 1.3)	-17.7	-16.5	-17.3 (\pm 0.4)	3.1	3.3	3.2 (\pm 0.09)
2-Apr-10	12.1	20.3	16.5 (\pm 3.1)	-17.3	-16.1	-16.8 (\pm 0.4)	3.0	3.2	3.1 (\pm 0.06)
3-Apr-10	14.0	18.3	16.1 (\pm 1.7)	-16.9	-16.3	-16.7 (\pm 0.2)	3.1	3.3	3.2 (\pm 0.08)
3-Apr-10	12.8	18.7	16.9 (\pm 2.1)	-17.5	-16.7	-17.2 (\pm 0.3)	3.1	3.3	3.2 (\pm 0.06)
4-Apr-10	16.9	18.9	17.8 (\pm 0.7)	-17.2	-16.5	-16.9 (\pm 0.3)	3.1	3.2	3.1 (\pm 0.04)
5-Apr-10	17.2	18.4	17.7 (\pm 0.6)	-18.0	-16.5	-17.2 (\pm 0.6)	3.1	3.2	3.2 (\pm 0.05)
6-Apr-10	17.5	20.2	18.9 (\pm 1.0)	-17.3	-16.3	-16.7 (\pm 0.4)	3.1	3.1	3.1 (\pm 0.00)
7-Apr-10	16.1	18.5	17.3 (\pm 1.7)	-17.2	-16.8	-17.0 (\pm 0.3)	3.0	3.5	3.3 (\pm 0.35)
14-Apr-10	13.7	17.5	15.9 (\pm 1.3)	-17.7	-17.0	-17.4 (\pm 0.3)	3.1	3.2	3.2 (\pm 0.05)
15-Apr-10	14.6	18.9	17.9 (\pm 1.6)	-17.9	-16.5	-17.2 (\pm 0.5)	3.1	3.2	3.1 (\pm 0.04)
17-Apr-10	16.0	17.7	16.5 (\pm 0.6)	-17.7	-17.2	-17.4 (\pm 0.2)	3.1	3.1	3.1 (\pm 0.00)
20-Apr-10	17.9	20.5	19.3 (\pm 1.0)	-17.5	-17.0	-17.2 (\pm 0.2)	2.9	3.1	3.0 (\pm 0.09)
Total	7.4	20.5		-19.1	-15.1		2.9	3.5	

Negative values of distance to the shelf break (DSB) indicate location over the continental shelf

variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, with all effects being significant. Latitude had the most important effect on $\delta^{15}\text{N}$ values (45 %) but was also important for $\delta^{13}\text{C}$ values (34 %). ML was the second most important factor for $\delta^{15}\text{N}$ values (29 %), but with much less effect on $\delta^{13}\text{C}$ values (8 %). Finally, DSB explained only 6 % of the variability in $\delta^{15}\text{N}$ values but 34 % (main effect) for $\delta^{13}\text{C}$ values (Table 2). The effect of latitude on $\delta^{13}\text{C}$ was bell shaped with an increasing trend between 03 and 12°S then a decreasing trend between 12 and 18°S. $\delta^{13}\text{C}$ values showed a linear increasing trend with size (with high variability for a given ML) and a decreasing trend with DSB (Fig. 2). The relationship between $\delta^{15}\text{N}$ and latitude was positive and almost linear with higher $\delta^{15}\text{N}$ values at higher latitude (south, Fig. 2). The ML also had a positive effect on $\delta^{15}\text{N}$ (in particular at sizes greater than 20 cm), but this trend was associated with a high variability in $\delta^{15}\text{N}$ values at a given ML. The effect of DSB on $\delta^{15}\text{N}$ was

U-shaped with a decreasing trend until 50 km to the shelf break and after that a positive trend (Fig. 2).

CART analysis showed that latitude had the greatest effect on $\delta^{13}\text{C}$, with the highest values south of 3.59°S (Fig. 3). The second cut was also due to latitude with lower values south of 15.61°S and the third cut due to latitude and DSB that show maximum values farther than 43 km offshore (Fig. 3). Latitude also had the greatest effect on $\delta^{15}\text{N}$ (Fig. 4). The highest $\delta^{15}\text{N}$ values were observed south of 14.48°S. The second cuts were due both to latitude (with significant lower $\delta^{15}\text{N}$ values north of 7.59°S) and to size (with a significantly higher $\delta^{15}\text{N}$ signature for larger organisms (>48.3 cm, south of 14.48°S).

For euphausiids, $\delta^{13}\text{C}$ values ranged between -20.5 and -17.7 ‰ and $\delta^{15}\text{N}$ values between 7.7 and 11.5 ‰, while copepods $\delta^{13}\text{C}$ values ranged between -21.6 and -18.4 ‰ and $\delta^{15}\text{N}$ values between 6.4 and 10.1 ‰ (Table 3). The relationships between $\delta^{13}\text{C}$ values and latitude were linear,

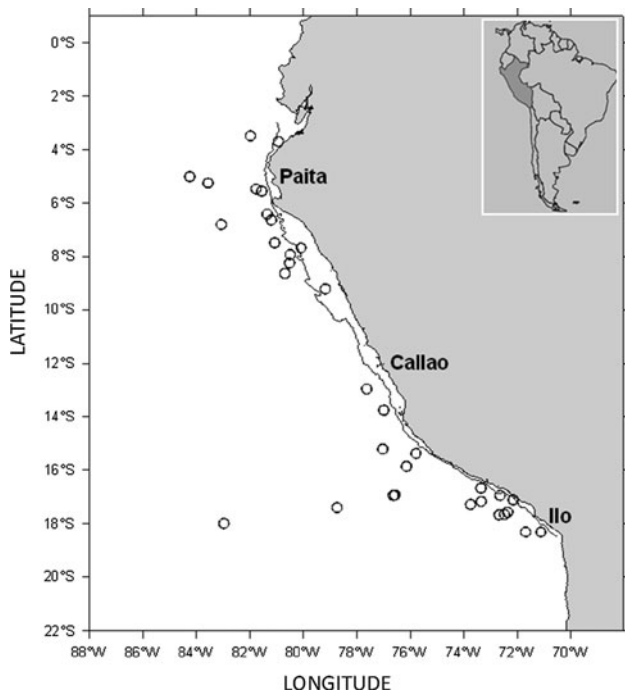


Fig. 1 Sampling sites where *Dosidicus gigas* were collected for isotopic analysis. The continuous parallel line to the coast indicates the 200-m isobath

positive and significant ($\delta^{13}\text{C} = 0.355 \text{ latitude} - 22.89$, $r^2 = 0.655$, $p < 0.05$) in copepods (between 03 and 12°S), but no significant linear correlation was observed for euphausiids and *D. gigas* (Fig. 5). Between 03 and 12°S, the increase in $\delta^{13}\text{C}$ values was 2.82, 2.76 and 2.50 ‰ for euphausiids, copepods and *D. gigas*, respectively. The relationships between $\delta^{15}\text{N}$ values and latitude were linear, positive and significant in euphausiids ($\delta^{15}\text{N} = 0.469 \text{ latitude} + 5.647$, $r^2 = 0.987$, $p < 0.001$), copepods ($\delta^{15}\text{N} = 0.395 \text{ latitude} + 5.112$, $r^2 = 0.852$, $p < 0.001$) and *D. gigas* ($\delta^{15}\text{N} = 0.539 \text{ latitude} + 7.404$, $r^2 = 0.670$, $p < 0.001$) (Fig. 6). Between 03 and 12°S, the increase in $\delta^{15}\text{N}$ values was 3.86, 3.62 and 4.08 ‰ for euphausiids, copepods and *D. gigas*, respectively. The slopes of the relationship between $\delta^{15}\text{N}$ in zooplankton, *D. gigas* and latitude were not significantly different (t test, $t = 1.174$, $p > 0.05$).

Discussion

Isotope variability and habitat

In this study, the isotopic variation in mantle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Dosidicus gigas* was analysed considering latitude, mantle size, distance to the shelf break (the effects of the Year and the Season were not significant). For carbon, distance to shelf break and latitude were the main

explaining factors. The decreasing $\delta^{13}\text{C}$ values with increasing distance to the shelf break are consistent with higher $\delta^{13}\text{C}$ values corresponding to highest productivity in coastal waters than in oceanic waters (Pennington et al. 2006; Miller et al. 2008). In turn, the latitudinal variation in $\delta^{13}\text{C}$ values in the mantle of *D. gigas* showed a clear bell-shaped trend with lowest values north of Peru and highest values in central Peru. The latitudinal variation in $\delta^{13}\text{C}$ values in *D. gigas* muscles and in zooplankton samples could then be related to the upwelling off Peru and reflect latitudinal changes in productivity. Indeed, the richest nearshore area ranges between 7 and 15°S where the highest $\delta^{13}\text{C}$ values are observed (Guillén and Calienes 1981; Echevin et al. 2008). Takai et al. (2000) reported for another squid species (*Sthenotheutis oualaniensis*) with high $\delta^{13}\text{C}$ values at low latitudes and low $\delta^{13}\text{C}$ values at higher latitudes along a large latitudinal scale (>60°). They explained these variations by large differences in temperature and CO_2 concentration. This hypothesis is not directly applicable to our study as the latitudinal range is small along the coast off Peru (~15° range).

$\delta^{13}\text{C}$ values also increased with organism size (ML, Fig. 2), and this agrees with Ruiz-Cooley et al. (2006) who found an increasing trend of $\delta^{13}\text{C}$ with mantle length in *D. gigas* in the Gulf of California. Several studies showed that carbon isotopic changes primarily reflect increases in body mass (e.g. Hesslein et al. 1993; Herzka 2005). Related with food web, carbon differences in $\delta^{13}\text{C}$ occur primarily at primary production, with small increases with increasing trophic level (0.4 ‰; Post 2002). Therefore, hypothesizing that $\delta^{13}\text{C}$ values only reflect changes in habitat, the increasing trend of $\delta^{13}\text{C}$ values with ML would suggest that *D. gigas* might change of habitat while growing. However, the high variability in $\delta^{13}\text{C}$ by size in our work suggests that *D. gigas*' juveniles and adults distribute over a large range of habitats. Nesis (1970, 1983) and Nigmatullin et al. (2001) indeed reported that if *D. gigas* seasonally migrates to coastal waters to grow, mature and feed, they could return to oceanic waters to spawn.

Latitude strongly affected $\delta^{15}\text{N}$, with increasing values from north to south (nearly 8 ‰ $\delta^{15}\text{N}$ difference from 3 to 18°S, Fig. 2). These latitudinal differences also have been observed in the northeast Pacific for *D. gigas* (Ruiz-Cooley et al. 2010) with an approximately 6 ‰ difference between 40 and 0°N. Takai et al. (2000) also reported high $\delta^{15}\text{N}$ values (16.3 ± 0.6 ‰) for another squid species (*Sthenotheutis oualaniensis*) off Peru (14°S), which corresponded to a 6 ‰ difference from Japan to Peru, and is similar to the value we found for *D. gigas* at this latitude. The $\delta^{15}\text{N}$ difference we found in our study is however of higher magnitude than the two other studies on squid with latitude (higher $\delta^{15}\text{N}$ range over a lower latitudinal range). Both studies attributed these large differences in $\delta^{15}\text{N}$

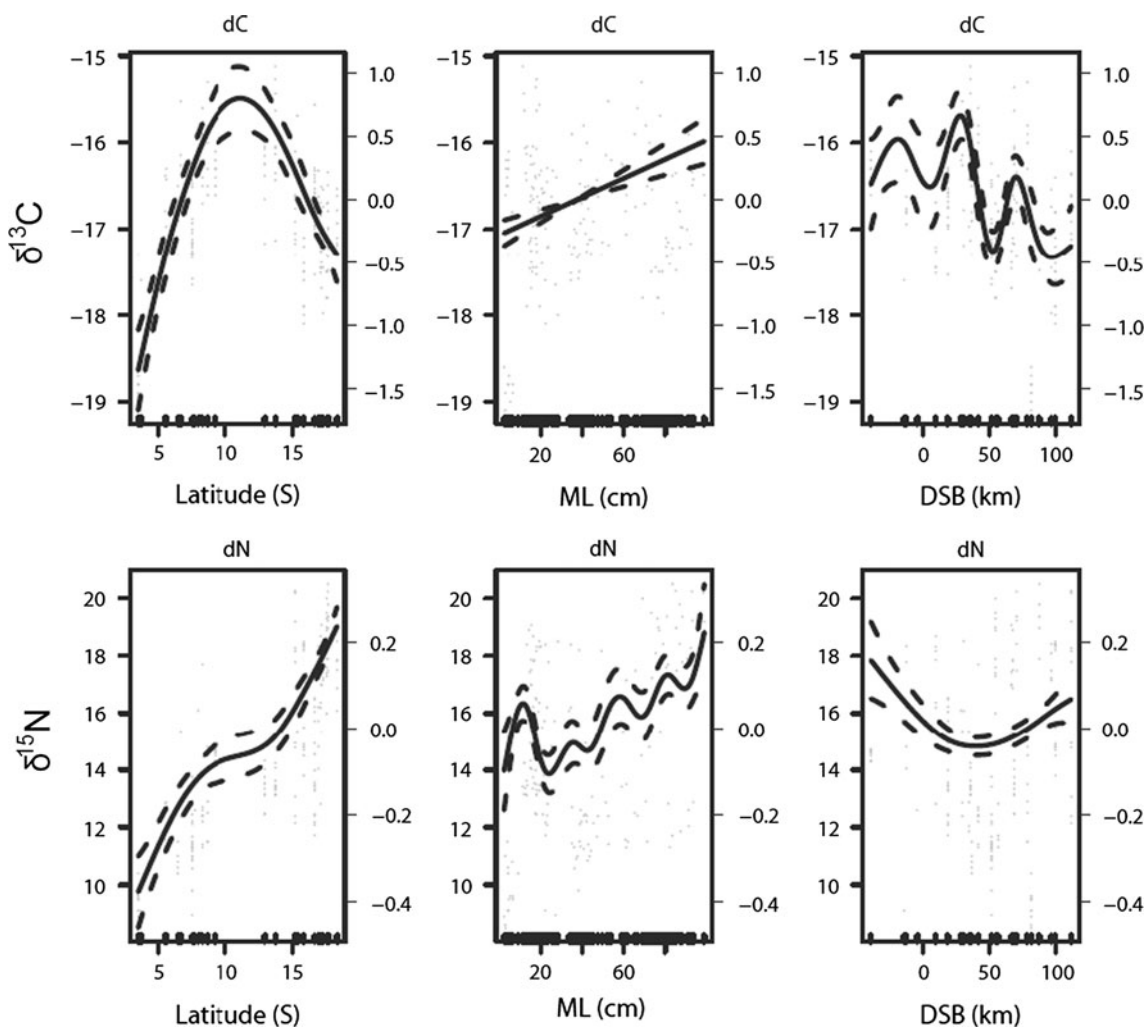


Fig. 2 GAMs of muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as a function of latitude, mantle length (ML) and distance to shelf break (DSB)

Table 2 Statistical outputs of GAMs based on mantle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Dosidicus gigas*

Variable	Source	e.d.f	F	p	% explained
$\delta^{13}\text{C}$	Lat	3.768	37.780	<2 e-16	34.40
	Size	1.000	26.500	7.10 e-07	7.80
	DSB	8.283	12.830	7.77 e-15	34.43
	Model			<2 e-16	76.63
$\delta^{15}\text{N}$	Lat	3.629	59.419	<2 e-16	45.33
	Size	8.763	9.945	3.46 e-12	28.72
	DSB	2.853	7.366	4.19 e-05	6.15
	Model			<2 e-16	82.20

among regions to regional differences in nitrogen metabolism. Indeed, if the $\delta^{15}\text{N}$ of animal tissues are used as an indicator of trophic position in marine food webs, variation in $\delta^{15}\text{N}$ values in consumers may not only result from the

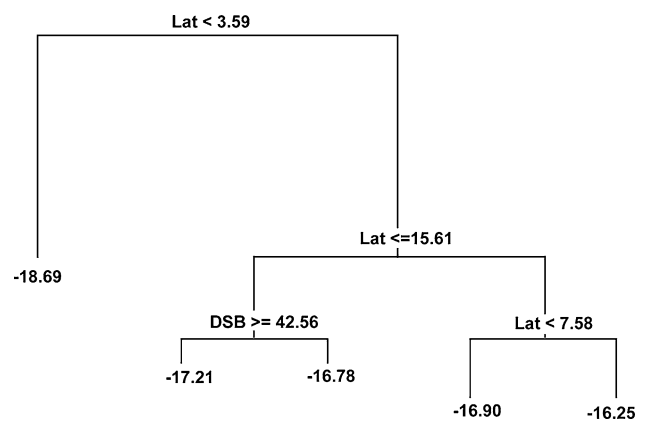


Fig. 3 Results of the classification and regression tree assessing the relative importance of latitude, mantle length and distance of the shelf break to muscle $\delta^{13}\text{C}$ values. The tree is split off on the values of one covariate at a time such that the overall variance in the dependent variable is minimized at each split

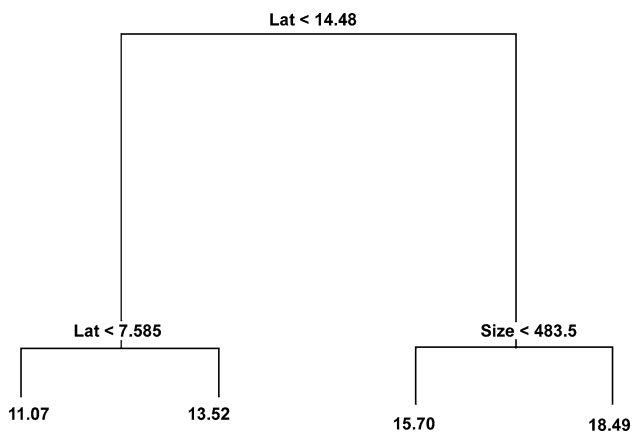


Fig. 4 Results of the classification and regression tree assessing the relative importance of the latitude, mantle length and distance of the shelf break to muscle $\delta^{15}\text{N}$ values. The tree is split off on the values of one covariate at a time such that the overall variance in the dependent variable is minimized at each split

trophic level at which they feed, but also from changes at the base of the food web (Fry 2006). It is important to consider that the dissolved inorganic nitrogen acts to set the baseline isotopic composition of the marine plankton and its signature is directly related with the environmental conditions and particularly associated with oxygen conditions. Indeed, spatial and temporal changes in the nutrient source at the base of a food web can also affect the overall nitrogen isotope values of consumers (e.g., O'Reilly et al. 2002). In Peruvian waters, nitrogen concentration (particularly nitrates) shows latitudinal variability, with a decreasing trend from north to south (Codispoti 1981; Graco et al. 2007) with higher values north of 15°S (Guillen and Yzaguirre de Rondan 1973; Silva et al. 2009). These differences in the latitudinal concentrations can be associated with the biogeochemical activity in deficient oxygen conditions that contributes to intense nitrate reduction (Fiadeiro and Strickland 1968; Ward et al. 1989). The Northern Humboldt Current System (NHCS) encompasses one of the most intense and shallow OMZ of the world ocean (Chavez et al. 2008; Paulmier and Ruiz-Pino 2009). These OMZs are generally the site of intense

nitrogen loss (Ward et al. 1989; Naqvi et al. 2000) that is known to increase the baseline $\delta^{15}\text{N}$ values (Sigman et al. 1999; Helly and Levin 2004; Graham et al. 2010). The trend in the intensification of this oxygen deficient condition to the south (Fuenzalida et al. 2009; Bertrand et al. 2010) can therefore contribute to latitudinal gradients in the $\delta^{15}\text{N}$ baseline values, with highest denitrification and therefore highest $\delta^{15}\text{N}$ values in the south. High nitrate $\delta^{15}\text{N}$ values were recovered in the eastern tropical Pacific due to water column denitrification processes (Liu and Kaplan 1989). Popp et al. (2007) and Olson et al. (2010) also reported a strong isotope baseline effect on nitrogen isotopic value in yellowfin tuna (*Thunnus albacares*) around the eastern tropical Pacific with increasing $\delta^{15}\text{N}$ values while latitude increases. In both studies, these variations paralleled the ones in mesozooplankton, used as an approximation of the isotopic values at the baseline, and were linked to the effect of strong denitrification in this region. A similar trend between $\delta^{15}\text{N}$ values and latitude in Peruvian waters was also observed in our work for zooplankton organisms (euphausiids and copepods) (Fig. 6), which suggests that baseline isotopic values are also the main drivers of $\delta^{15}\text{N}$ values in jumbo squid muscles. As the slopes did not differ significantly between zooplankton organisms and jumbo squid samples according to latitude, we can hypothesize that squid of a same size have a similar trophic position whatever the latitude.

The latitudinal and DSB effects are strong for this species in the Peruvian waters as environmental gradients shaping the baseline (i.e. oxygen minimum zones) are particularly important and variable along the coast. Furthermore, the isotopic turn over rate of *D. gigas* muscle is high (i.e. a few weeks as the animal is growing very rapidly); and even if squid perform large range migrations over their life (Nesis 1970, 1983), the muscle isotopic signature really reflects the last weeks of an individual's life. Ruiz-Cooley et al. (2010) reported that a jumbo squid of 40 cm ML would reach equilibrium to new dietary items after approximately 80 days. The similar latitudinal trend of isotope values of zooplankton and *D. gigas* in the study

Table 3 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton collected in Peruvian waters

Years	Zooplankton	Latitude South	Data number	$\delta^{15}\text{N}$ Mean ($\pm\text{SD}$)	$\delta^{13}\text{C}$ Mean ($\pm\text{SD}$)	C/N Mean ($\pm\text{SD}$)
2008	Euphausiids	3	1	7.7	-20.5	3.7
2008	Euphausiids	5	3	8.1 (± 0.2)	-19.5 (± 1.4)	3.6 (± 0.04)
2008	Euphausiids	7	1	9.4	-18.5	3.5
2008	Euphausiids	12	1	11.5	-17.7	3.7
2008	Copepods	3	1	6.4	-21.6	5.1
2008	Copepods	4	1	6.7	-21.6	5.7
2008	Copepods	5	10	7.4 (± 0.7)	-20.8 (± 1.0)	4.7 (± 0.6)
2008	Copepods	7	3	8.0 (± 0.2)	-20.3 (± 1.0)	5.1 (± 1.0)
2008	Copepods	12	5	10.1 (± 0.4)	-18.4 (± 0.8)	5.9 (± 1.1)

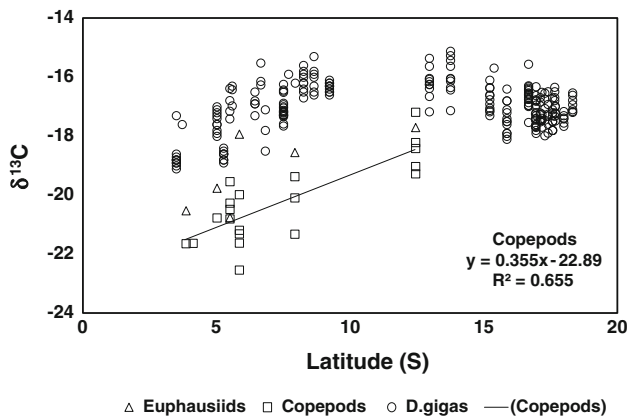


Fig. 5 Latitudinal variation in $\delta^{13}\text{C}$ values of zooplankton and *D. gigas* in Peruvian waters

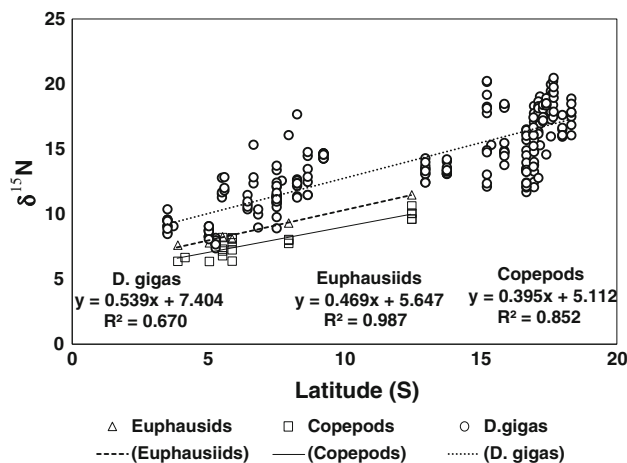


Fig. 6 Latitudinal variation in $\delta^{15}\text{N}$ values of zooplankton and *D. gigas* in Peruvian waters

reveals that the jumbo squid is a relatively resident species at a temporal scale of a few weeks. Indeed, if an individual has a similar isotopic value as the local isotopic baseline, then the predator is a resident, whereas if the individual and baseline isotopic values are distinctly different, the predator is an immigrant from another, isotopically distinct region (see Graham et al. 2010 for a review). This does, however, not diminish the possibility that *D. gigas* perform migrations during ontogeny, since *D. gigas* in the South-eastern Pacific seems to carry out seasonal migrations, moving into coastal waters to feed (to the southeast and east of the spawning grounds) and then migrate to the spawning grounds (northwest and west of the feeding areas) (Nesis 1970, 1983; Nigmatullin et al. 2001). At the population level, the very high variability in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at a given DSB or latitude (Fig 2) illustrates that squid in a given area may come from different places and therefore have different life histories in terms of habitats.

Isotope variability and diet

In this study, size, after latitude, was the second explaining factor of $\delta^{15}\text{N}$ variations, suggesting that diet still explains part of the observed variability. We first show an overall increase in $\delta^{15}\text{N}$ values with ML greater than 20 cm (~ 4 ‰ increase, Fig. 2), suggesting that there is an increase in trophic level with ontogeny for this species. Our results agree with those of Ruiz-Cooley et al. (2006, 2010) who found a significant increasing trend of $\delta^{15}\text{N}$ with mantle length. The increasing trend of values in Peruvian waters was also associated with a very high variability of $\delta^{15}\text{N}$ values with mantle length. As already proposed (Ruiz-Cooley et al. 2010; Lorrain et al. 2011), we suggest that this is due to highly opportunistic foraging strategies in jumbo squid. For example, a given squid with a ML of 20 cm can have a similar $\delta^{15}\text{N}$ values than a squid with a ML of 80 cm (Fig. 2, grey markers and Table 1), which suggests that during its ontogeny *D. gigas* can prey on the same resources. This is consistent with Lorrain et al. (2011) who reported using stable isotopes in jumbo squid *gladii* off Peru that, even if the trophic level globally increases with squid size; this trend was not systematic. Indeed, analysing the most recent part of two large individuals, these authors hypothesized that their similar proximal $\delta^{13}\text{C}$ value indicated that they foraged in similar habitats, and their very different nitrogen isotopic values indicated feeding on distinct trophic levels (i.e. euphausiids vs. fish). This is also corroborated by stomach content data that show that large and small jumbo squid forage on the same prey spectra and can feed from euphausiids or mesopelagic fish at any size (see Table 3 in Lorrain et al. 2011). Other feeding ecology studies based on stomach content analysis in the northeastern Pacific (Markaida and Sosa-Nishizaki 2003; Markaida 2006), and south-eastern Pacific (Shchetinnikov 1989; Ibañez et al. 2008) also reported a wide variety of prey species all along their life, and even on euphausiids at large sizes (Ibañez et al. 2008).

Stable isotopes studies in other squid species (*T. filippovae*, *O. bartramii* and *S. oualaniensis*) reported such a large increase in $\delta^{15}\text{N}$ values with size both in field (Cherel and Hobson 2005; Parry 2008; Cherel et al. 2009) and experimental studies (Hobson and Cherel 2006) and also attributed it to the trophic plasticity and opportunism of these voracious and fast-growing ommastrephid squid, which prey on various proportions of crustaceans, mesopelagic fish and on their own species (Rodhouse and Nigmatullin 1996). However, given the high proportion of cannibalism in *Dosidicus gigas* (Markaida and Sosa-Nishizaki 2003; Markaida 2006; Ibañez et al. 2008) and its very high growth rate, with one-year-old individuals having mantle lengths >1 m, one could have expected larger $\delta^{15}\text{N}$ changes than in other species.

As already explained, the high inter-individual variability in foraging strategies through ontogeny has already

been observed by Lorrain et al. (2011) off Peru. However, this study was based on only five large individuals and over a limited spatial range over the coast of Peru. Our study therefore confirms with a much higher number of samples and a large geographical range (from 3 to 18°S) that *D. gigas* is a highly opportunistic species (Shchetinnikov 1989; Markaida and Sosa-Nishizaki 2003; Markaida 2006; Field et al. 2007; Ibañez et al. 2008; Ruiz-Cooley et al. 2010) with a wide trophic niche (from euphausiids to cephalopods and fish, sensu Newsome et al. 2009). This species have therefore the capability to explore a wide range of habitats and resources at any stage of their life.

Summary

Our results showed a very high variability in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at a given DSB, latitude or size which illustrates that squid captured in a given area may have very different life histories. The similar latitudinal trend of isotope values of zooplankton and *D. gigas* in the study area suggests that *D. gigas* is a relatively resident species at the scale of its isotopic turnover rate (i.e. a few weeks). The increasing trend of $\delta^{13}\text{C}$ values with mantle length and the strong relation between $\delta^{13}\text{C}$ values and distance to shelf break suggest that *D. gigas* migrate from oceanic to coastal waters, changing its foraging areas between juvenile and adults, although no significant diet shift seems to occur. Our results furthermore reinforce the idea that there is no systematic increase in trophic position with size and that latitude is the main driving factor on $\delta^{15}\text{N}$ values off Peru. Caution must then be taken when comparing individuals of different sizes in different environments. Further study should implement combined stable isotope and stomach content analyses over large spatial scales together with compound-specific isotope analysis of amino acids that have shown great potential to decipher trophic versus habitat on nitrogen isotope values (see Popp et al. 2007; Olson et al. 2010).

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