



## Migratory patterns, vertical distributions and diets of *Abralia veranyi* and *Abraliopsis morisii* (Cephalopoda: Enoploteuthidae) in the eastern North Atlantic

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### ABSTRACT

*Abralia veranyi* and *Abraliopsis morisii* were the most abundant cephalopods caught during epipelagic and mesopelagic surveys off the Canary Islands and accounted for 26% and 35% of the cephalopod catch, respectively. Diel vertical migration patterns were observed in both species. At night, *A. veranyi* was recorded at depths as shallow as 38–90 m, whereas *Abraliopsis morisii* occurred at depths of 98–219 m. As individuals grow in mantle length, their diet changes substantially. *Abraliopsis morisii* showed ontogenetic shifts at 22.9 mm and 35.3 mm dorsal mantle length (DML), while *A. veranyi* showed ontogenetic shifts at 20.5 mm and 30.9 mm DML. Prior to the first ontogenetic shift, both species fed mainly on copepods and mysids. After this shift they fed on larger prey, such as decapods and fish; the diets of larger individuals also contained cephalopods.

### INTRODUCTION

Cephalopods are common inhabitants of the mesopelagic zones of the ocean and occupy key roles in many marine ecosystems, both as predators and prey (Clarke, 1996; Piatkowski, Pierce & Morais da Cunha, 2001; Boyle & Rodhouse, 2005). Although mesopelagic cephalopods are globally widespread, they live in inaccessible environments, so little is known about their behaviour. According to Xavier *et al.* (2015), knowledge about noncommercially exploited oceanic cephalopods is scarce, with most of this knowledge having been obtained from the analysis of the stomach contents of predators (e.g. Hernández-García, 1995; Clarke, 1996). As has also been reported for fish and planktonic crustaceans (Torres *et al.*, 2018), many mesopelagic cephalopod species migrate vertically over hundreds of meters to feed near the surface during the night, returning to deep water at dawn (Clarke & Lu, 1974; Roper & Young, 1975). This behaviour facilitates the transfer of energy and organic matter from productive shallow waters to the deep ocean (Ariza, 2015).

While the importance of mesopelagic cephalopods in oceanic ecosystems has been described by several authors (Clarke, 1969; Clarke & Lu, 1974; Vecchione & Roper, 1991; Shea *et al.*, 2017), their role in the trophic relationships of open-ocean ecosystems is poorly understood (Clarke, 1962; Rocha & Cheikh, 2015). The enoploteuthids are likely to be ecologically particularly important. They constitute a large biomass at depths between 200 and 400 m (Laptikhovsky, 1999) and are an important and abundant prey

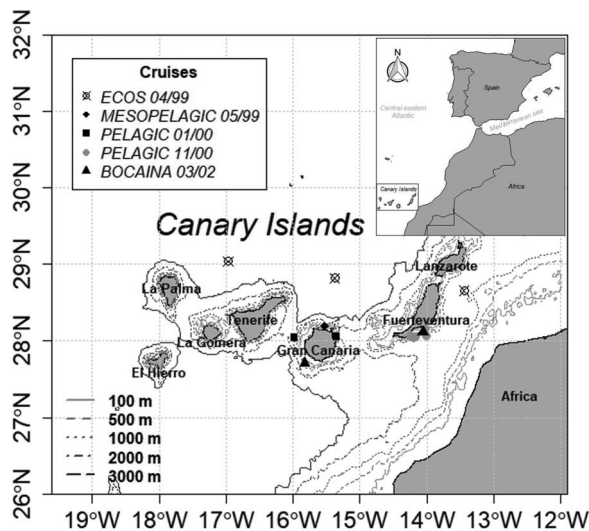
source for many predators (Anastasopoulou *et al.*, 2013; Kousteni *et al.*, 2018).

The enoploteuthids *Abralia veranyi* (Rüppel, 1844) and *Abraliopsis morisii* (Vérany, 1839) are important components of the mesopelagic fauna of the warm waters of the Atlantic Ocean, including the Mediterranean Sea and the Gulf of Mexico (Nesís, 1987). Despite this, the feeding behaviour of these two species, particularly in the eastern North Atlantic, is still poorly known. Using data gathered in the Canary Current region of the eastern North Atlantic, we describe the diets of *A. veranyi* and *Abraliopsis morisii* and detail the daily migratory patterns and distribution of these species in the water column.

### MATERIAL AND METHODS

#### Sampling

Cephalopods were collected off the Canary Islands (eastern North Atlantic) during five research surveys carried out by the vessel R/V LA BOCAINA between 1997 and 2002 (Fig. 1). Depths ranging from 8 to 1,035 m were sampled. *Abralia veranyi* ( $n = 763$ ) and *Abraliopsis morisii* ( $n = 1,026$ ) were caught using a commercial semi-pelagic otter trawl net (5 mm mesh size at the cod-end). Trawling was carried out at different times of the day, and both diurnal and nocturnal trawls were conducted. The net used was an open net lacking closing doors. The net was dropped from the ship until it



**Figure 1.** Map of the Canary Islands, showing locations sampled on the research cruises of the R/V LA BOCAINA.

sank to a particular trawl depth, after which trawling was carried out at a constant depth (capture depth). The trawls were monitored through acoustic telemetry using a SCANMAR net-sensor system; this system measured parameters such as depth, position, speed and both the vertical and horizontal opening of the net's mouth (see Bordes *et al.*, 1997, 2002). Once the trawling was finished, the ship came to a complete halt and the net was hoisted vertically. At the moment of hoisting, the bulk of the net was pulled down by its own weight to form a bag and this closed the mouth of the net; the mouth of the net was demarcated by lines of buoys and plumbs. The hoisting speed was adjusted to prevent the mouth of the net from accidentally opening.

Captured cephalopods were classified and preserved in 70% ethanol for later analysis. Specimens of *Abraliopsis morisii* and *A. veranyi* were identified with the aid of the key developed by Nesis (1987). For each individual, the following measurements were taken in the lab: (1) dorsal mantle length (DML), measured to the nearest 0.1 mm; (2) total wet weight (TW) to the nearest 0.1 g; (3) head weight (HW), including the arms and tentacles, to the nearest 0.1 g; and (4) weight of the stomach contents (i.e. following extraction from the stomach) to the nearest 0.001 g. Length frequency distributions were quantified for the different depths of fishing, and the trawls were separated into nocturnal and diurnal captures. The DML data for the analysed specimens were not normally distributed in relation to depth; thus, a nonparametric test was used to determine if there were significant differences or not. The diet of the two species was analysed for samples of multiple individuals (*A. veranyi*,  $n = 119$ ; *Abraliopsis morisii*,  $n = 119$ ).

#### Breakpoint analysis

A model II piecewise linear regression (PLR) was carried out to detect possible ontogenetic shifts (Shea & Vecchione, 2002) in the growth of *Abraliopsis morisii* and *A. veranyi*. The relationship between TW and HW was analysed to detect possible growth-related differences in diet. This was done by  $\log_e$  transforming the variable HW and plotting it against  $\log_e$  TW. Following Shea & Vecchione (2002), we used the reduced major axis regression model and changed the LOSS default function to  $LOSS = (y - (a + bx))^2 / ABS(b)$ , where  $x$  is the independent variable,  $y$  is the dependent variable and  $a$  and  $b$  are the intercept and slope of the line, respectively.

To analyse the breakpoints, a simple linear regression (SLR) was plotted using model II; *A. veranyi* and *Abraliopsis morisii* showed a patterned residual and this allowed possible breakpoints to be

deduced. Subsequently, an iterative PLR model was employed, with the first test breakpoint being used to analyse multiple subsequent breakpoints (for each iteration the breakpoint increased by 0.1). The number of iterations performed was 22 for *Abraliopsis morisii* and 26 for *A. veranyi*. For each iteration,  $R^2$ , LOSS and residues were saved.

As more than one breakpoint was observed for both species, the values of  $R^2$  and LOSS for each segment were analysed to see if the PLR segments were better adapted to the data than the SLR segment. After obtaining the two possible breakpoints, the equation for each segment and its 95% confidence intervals (CI) were calculated. The slopes were considered different if the slope of segment 2 was outside the CI of segment 1 and the slope of segment 3 was outside the CI of segment 2.

If the slope analysis showed that the  $R^2$  and LOSS values, along with their respective residuals, improved in comparison with SLR results, but the slope was within the 95% CI, the breakpoint was rejected. If, however, the new segments were associated with improved values of  $R^2$ , LOSS and residuals of the SLR model, and the slope of the new segment was not in the 95% CI of the previous segment, the breakpoint was accepted. Allometric parameters were calculated for each segment (Table 1). All statistical analyses were carried out using R v. 3.4.2 (R Core Team, 2019).

#### Diet analysis

The stomach fullness index (SF) was calculated using the following equation:

$$SF = \left( \frac{\text{wet weight of stomach content}}{\text{wet weight of individual}} \right) \times 100$$

Prey items (hard and soft tissues) were identified to the lowest possible taxonomic level. However, due to the heavily digested state of food items, identification to the family or species level was usually not possible. Plankton and decapod taxa were identified using the guides by Zariquiey (1968), Estrada & Genicio (1970) and Newell & Newell (1970). The index of relative importance (% IRI) was calculated as described by Pinkas, Oliphant & Iverson (1971):

$$IRI_i = (N_i + WW_i) \times O_i,$$

where  $N$  = numerical frequency,  $WW$  = % wet weight,  $O$  = frequency of prey occurrence for all stomach analyses (including empty stomachs) and  $i$  = number of prey analysed.

A Kruskal–Wallis test was used to test for significant differences between the SF index of individuals captured during nighttime and daytime hours. This was followed by a post hoc Tukey honestly significant difference (HSD) test to determine at exactly which hours there were significant differences in the SF index. On the basis of the breakpoint analysis, individuals of both species were grouped into three length classes and growth-related differences in diet were analysed (See Results for further details); a  $\chi^2$  test was used to assess if differences in diet were significant.

## RESULTS

A total of 20 species of cephalopods were identified from the mesopelagic and epipelagic trawl samples taken at depths ranging from 8 to 1,035 m. Enoploteuthids represented 65.4% of the captured cephalopods, with *Abraliopsis morisii* being the most frequently captured species (35.1%). Other sampled enoploteuthid species included *A. veranyi* (26.1%) and *Enoploteuthis anapsis* (0.1%). Small individuals (DML <12 mm) were scarce in the trawl samples (11 and 4 individuals of *Abraliopsis morisii* and *A. veranyi*, respectively). This may possibly have been due to the fine mesh size of the trawl net, with specimens of DML <5 mm generally not been captured. Most of the small specimens captured had been damaged in the cod-end (i.e. due to the weight of the rest of the catch).

**Table 1.** Allometric parameters and breakpoints for *Abraliopsis morisii* and *Abralia veranyi* for the relationship between  $\log_e$  TW and  $\log_e$  HW.

Species	Breakpoints (TW, g)	Allometric parameters								
		Segment 1			Segment 2			Segment 3		
		Intercept	Slope	95% CI	Intercept	Slope	95% CI	Intercept	Slope	95% CI
<i>Abraliopsis morisii</i>	0.9 & 2.58	−0.83	0.94	0.47–1.12	−0.71	1.26	1.15–1.36	−0.88	0.67	0.49–0.87
<i>Abralia veranyi</i>	1.2 & 2.35	−0.99	0.58	0.27–1.14	−0.87	1.27	1.07–1.37	−0.48	0.70	0.37–1.22

The relationship consists of three segments: 1, points < breakpoint 1; 2, points between breakpoints 1 and 2; 3, points > breakpoint 2. Intercept and slope for the regression result for each segment are also given. When the slope = 1 the growth is isometric. 'CI' is the confidence interval.

**Table 2.** Number of individuals of *Abraliopsis morisii* and *Abralia veranyi* (by length class) caught at different depths during nighttime (00.00–06.30 and 18.30–00.00) and daytime (06.30–18.30) sampling.

Time (UTC)	Depth (m)		
<b><i>Abraliopsis morisii</i></b>	<b>DML &lt;22.9 mm</b>	<b>DML = 22.9–35.3 mm</b>	<b>DML &gt;35.3 mm</b>
00.00–06.30	38–40 m (n = 11)	38–40 m (n = 2)	38–40 m (n = 2)
06.30–18.30	356–402 m (n = 5)	356–402 m (n = 10)	–
18.30–00.00	38–49 m (n = 7)	38–90 m (n = 49)	38–90 m (n = 33)
<b><i>Abralia veranyi</i></b>	<b>DML &lt;20.6 mm</b>	<b>DML = 20.6–30.9 mm</b>	<b>DML &gt;30.9 mm</b>
00.00–06.30	–	–	–
06.30–18.30	308–1,035 m (n = 19)	308–1,035 m (n = 39)	308–1,035 m (n = 15)
18.30–00.00	98–219 m (n = 4)	98–219 m (n = 27)	98–219 m (n = 15)

We analysed the capture depth of *Abraliopsis morisii* and *A. veranyi* as a function of hour of the day (Table 2). Specimens of *Abraliopsis morisii* were caught during the night at depths of 38–90 m. While this represented 87.4% of the total number of individuals obtained for this species, 12.6% were caught during the day at depths ranging from 356 to 402 m. Similarly, for *A. veranyi*, 63.0% of individuals were captured during the night (between depth of 98–219 m) and 37.0% were obtained during the day (depth of 308–1,035 m). A Kruskal–Wallis test indicated nonsignificant differences in the vertical distribution of the DML of *A. veranyi* ( $H = 116.11$ ,  $df = 114$ ,  $P = 0.43$ ) and *Abraliopsis morisii* ( $H = 113.22$ ,  $df = 111$ ,  $P = 0.42$ ). Both enoploteutid species were caught during nighttime hours by deep-water trawls and during daytime hours by near-surface trawls, indicating that these cephalopods show a clear diel migratory pattern.

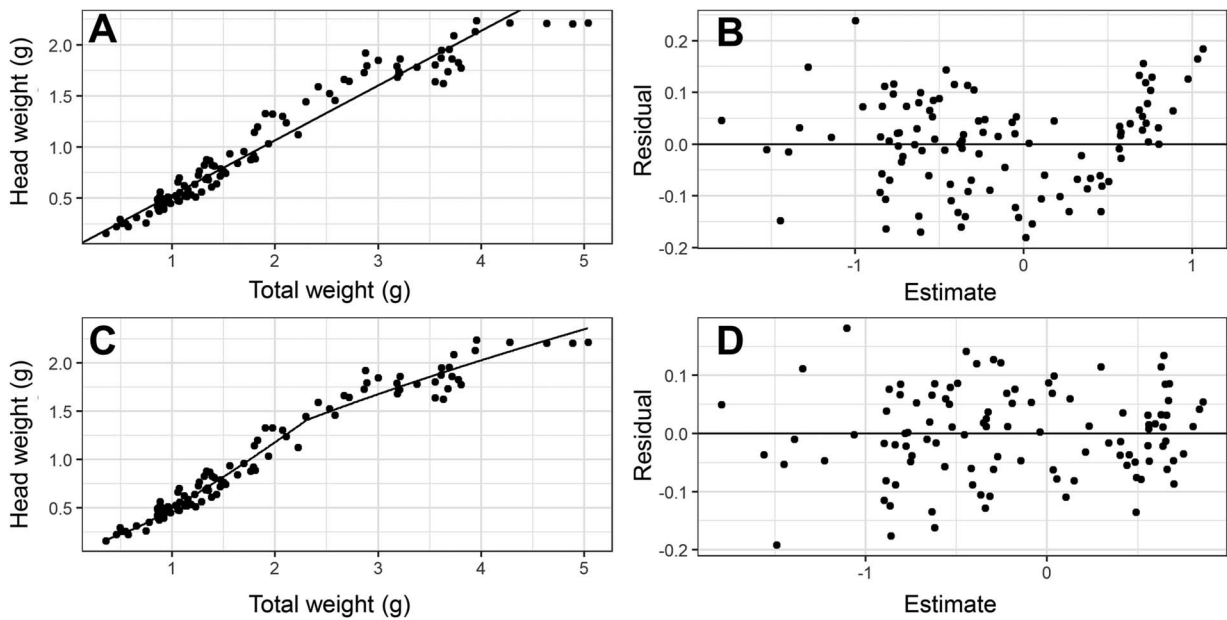
The breakpoint analysis showed significant morphometric changes during ontogeny for both *Abraliopsis morisii* (SLR:  $R^2 = 0.95$ , LOSS = 1.43; PLR:  $R^2 = 0.97$ , LOSS = 1.38; Fig. 2) and *A. veranyi* (SLR:  $R^2 = 0.96$ , LOSS = 2.51; PLR:  $R^2 = 0.97$ , LOSS = 2.01; Fig. 3). The relationship between  $\log_e$  TW and  $\log_e$  HW showed that for both species there were two morphometric changes during growth. *Abraliopsis morisii* had two ontogenetic changes at a TW of 0.68 g and 2.29 g, respectively, while for *A. veranyi* these occurred at a TW of 0.81 g and 2.27 g, respectively (Figs 2, 3). In both species, the rate of increase of HW relative to TW was high after the first slope change, but declined after the second slope change (Figs 2, 3). These ontogenetic changes show that *Abraliopsis morisii* has its first morphometric change at 22.9 mm and the second one at 35.3 mm DML, while in *A. veranyi* they occur at 20.6 mm and 30.9 mm DML (Figs 2, 3). On the basis of the breakpoint analysis, each of the two species was grouped into three length classes: small (corresponding to data points occurring in the plot up to the first slope shift), medium-sized (data points between the first and second slope change) and large (data points after the second/last observable slope change).

Study of stomach contents showed that prey belonged to four taxa (Table 3). While a maximum of three prey items was found

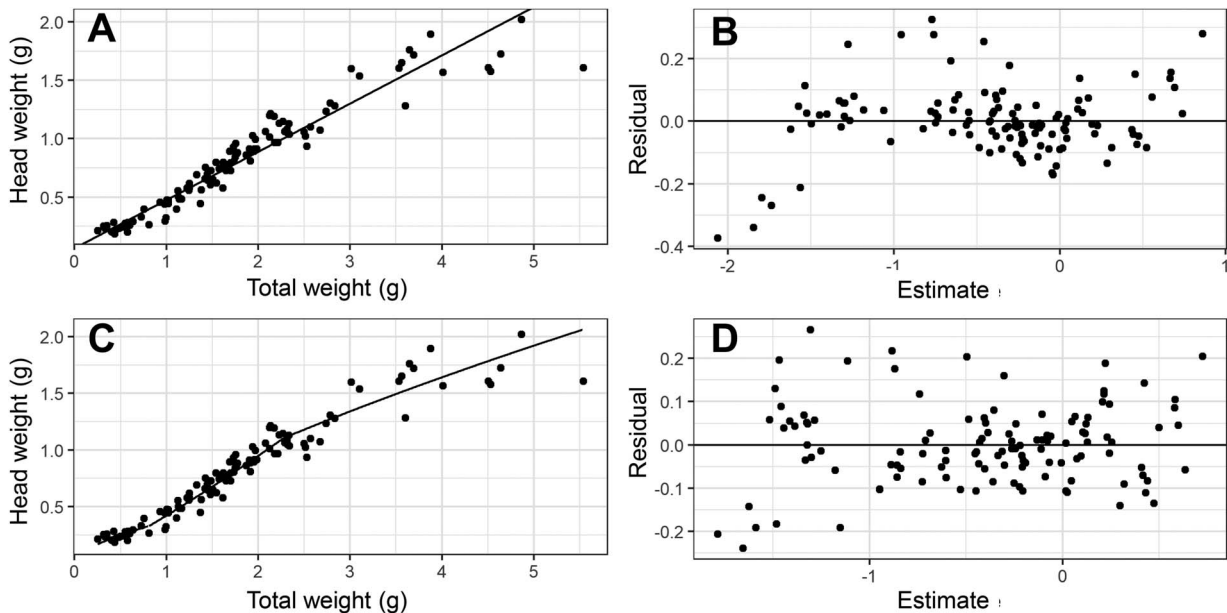
in a single stomach (this stomach appeared to be distended to maximum capacity), the stomach of 79.7% and 86.8%, respectively, of *Abraliopsis morisii* and *A. veranyi* individuals contained only a single prey item. Stomach fullness was quite variable, but typically lower during the day than at night (Fig. 4), indicating nocturnal feeding. A Kruskal–Wallis test showed significant differences in stomach fullness between nighttime and daytime for both *A. veranyi* ( $H = 54.51$ ,  $n = 119$ ,  $P < 0.00001$ ) and *Abraliopsis morisii* ( $H = 12.30$ ,  $n = 119$ ,  $P = 0.015$ ). A Tukey HSD *post hoc* test ( $\alpha = 0.05$ ) also found significant differences between daytime and nighttime in both species ( $P < 0.03$ ; Fig. 4).

Crustaceans were the most abundant prey items in the stomachs of both species. Food items, when present, were heavily digested, making identification of prey species difficult. Nonetheless, we found that decapods constituted a large proportion of the crustaceans. A  $\chi^2$  test showed highly significant differences in the diet of the three length (DML) classes of *Abraliopsis morisii* ( $P < 0.01$ ). The smallest specimens (DML <22.9 mm) of *Abraliopsis morisii* were shown to feed mainly on copepods (IRI = 83.7%), unidentified crustaceans (IRI = 14.4%) and mysids (IRI = 1.9%), while individuals in the medium-sized length class (DML = 22.9–35.3 mm) preyed almost exclusively on decapods (IRI = 91.0%). The largest specimens (DML >35.3 mm) also preyed mainly on crustaceans (IRI = 78.3%), but fish (IRI = 16.7%) and cephalopods (5.0%) were prevalent components of their diets. The possibility that the cephalopods were preyed upon when the captured study animals were in the net was rejected. This was because prey items were found to be in an advanced state of digestion, despite the fact that the stomachs containing them were extracted and preserved (in 70% ethanol) immediately after the capture of individuals of *Abraliopsis morisii* and *A. veranyi*. *Abraliopsis morisii* showed a high stomach fullness index at night, indicating that this species feeds preferentially during nocturnal hours (Table 3).

As with *Abraliopsis morisii*, a  $\chi^2$  test showed highly significant differences in diet among the three length classes of *A. veranyi* ( $P < 0.0001$ ). The diet of the smallest individuals (DML <20.6 mm) consisted mainly of copepods (IRI = 59.9%), other



**Figure 2.** Breakpoint analysis for *Abraliopsis morisii*. **A.** Linear regression (SLR) for the relationship between total weight and head weight ( $R^2 = 0.946$ ,  $LOSS = 1.43$ ). **B.** Plot showing residuals from the SLR. **C.** PLR showing regression line with two breakpoints at 0.68 g and 2.29 g TW (corresponding to 22.9 mm and 35.3 mm DML, respectively;  $R^2 = 0.967$ ,  $LOSS = 1.38$ ). **D.** Plot showing residuals from the PLR. Note the lack of a pattern. Graphs shown in **A** and **B** are plotted with untransformed data for clarity; graphs **C** and **D** are plotted with  $\log_e$  transformed data.



**Figure 3.** Breakpoint analysis for *Abralia veranyi*. **A.** Linear regression (SLR) for the relationship between total weight and head weight ( $R^2 = 0.957$ ,  $LOSS = 2.51$ ). **B.** Plot showing residuals from the SLR. **C.** PLR showing regression line with two breakpoints at 0.81 g and 2.27 g TW (corresponding to 20.6 mm and 30.9 mm DML, respectively;  $R^2 = 0.969$ ,  $LOSS = 2.012$ ). **D.** Plot showing residuals from the PLR. Note the lack of a pattern. Graphs shown in **A** and **B** are plotted with untransformed data for clarity; graphs **C** and **D** are plotted with  $\log_e$  transformed data.

unidentified crustaceans (IRI = 18.0%) and mysids (IRI = 7.0%), while medium-sized individuals (DML = 20.6–30.9 mm) preyed more frequently on decapod crustaceans (IRI = 85.3%), other crustaceans (IRI = 10.7%) and, to a much lesser extent, fish (IRI = 2.5%). The diet of the largest specimens (DML > 30.9 mm) of *A. veranyi* consisted of fish (IRI = 49.3%), crustaceans, mainly in the form of decapods (IRI = 26.8%), and cephalopods (IRI = 10.6%; Table 3). In contrast to *Abraliopsis morisii*, medium-sized individuals and adults of *A. veranyi* preyed on fish at any time of the day, but on cephalopods only during daylight hours (Table 3).

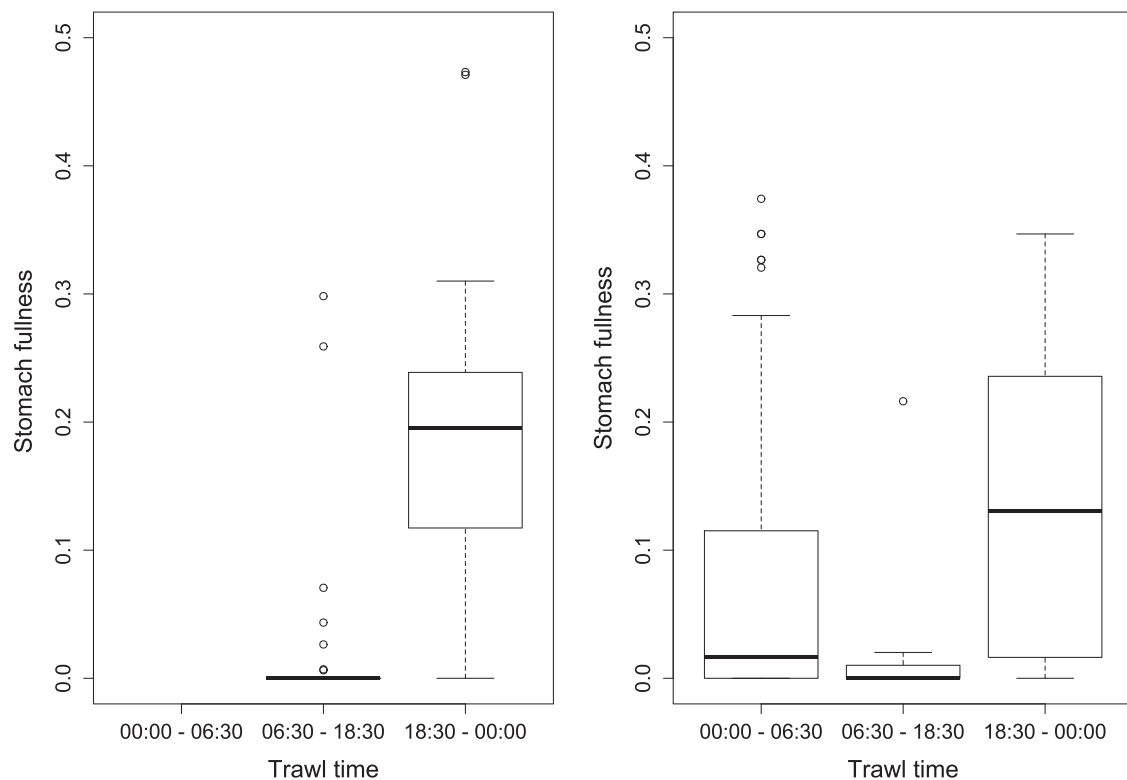
Figure 4 shows the prey composition of the diet in relation to depth for both species. Crustaceans were recovered from the stomach of individuals caught across the whole depth range sampled (8–1,035 m depth). While copepods (27% and 42% IRI for *A. veranyi* and *Abraliopsis morisii*, respectively) were the most abundant prey in the diet of individuals caught in the upper 200 m of the sea, decapods predominated in the diet of individuals from waters between 200 and 500 m, reaching an IRI value of 88.7% for *A. veranyi*, but only 1% for *Abraliopsis morisii* at that same depth interval. In relation to depth intervals, fish were more abundant in



**Table 3.** Relative importance index (IRI) for the different prey taxa found in the stomach contents of *Abraliopsis morisii* and *Abralia veranyi* during daytime and nighttime.

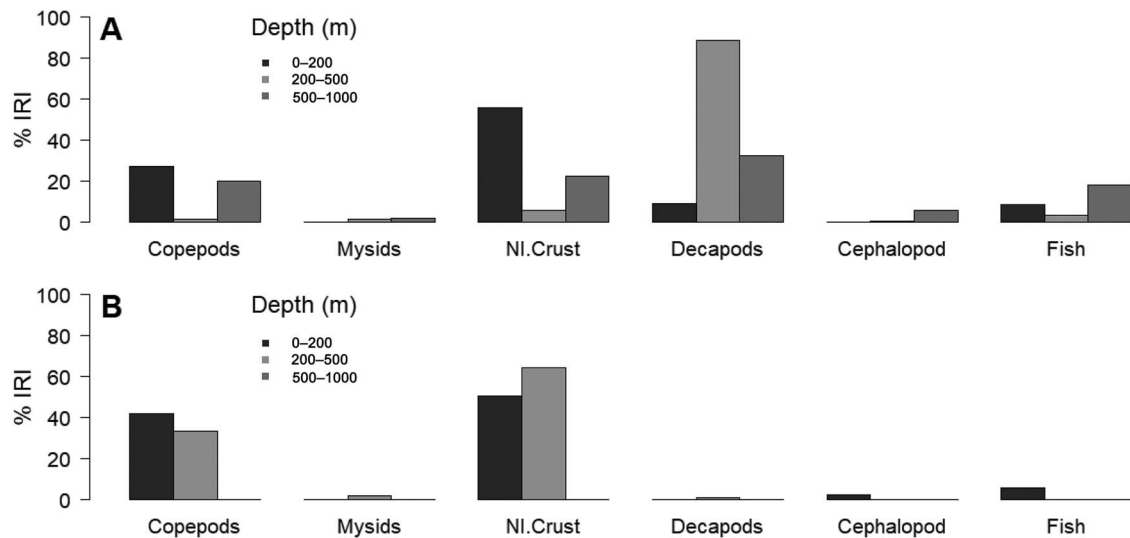
	DML <22.9 mm			DML = 22.9–35.3 mm			DML >35.3 mm		
	% IRI			% IRI			% IRI		
	Total (n = 20)	Night (n=15)	Day (n = 5)	Total (n = 64)	Night n = 51)	Day (n = 13)	Total (n = 35)	Night (n=35)	Day (n = 0)
<b><i>Abraliopsis morisii</i></b>									
Copepods	83.7	35.3	80.0						
Mysids	1.9	12.7							
NI crustacea	14.4	1.8	20.0	76.2	98.6	98.1	78.3	80.2	
Decapod crustacea				23.5	0.0	1.9			
Cephalopods				0.2	0.7		5.0	5.6	
Fish				0.1	0.7		16.7	14.2	
<b><i>Abralia veranyi</i></b>									
	DML <20.6 mm			DML = 20.6–30.9 mm			DML >30.9 mm		
	% IRI			% IRI			% IRI		
	Total (n = 23)	Night (n = 4)	Day (n = 19)	Total (n = 66)	Night (n=27)	Day (n = 39)	Total (n = 30)	Night (n=15)	Day (n = 15)
Copepods	59.9		59.9	0.8		0.9			
Mysids	7.0		7.0	0.7		0.8			
NI crustacea	18.0		18.0	10.7	78.6	5.0	13.2	57.3	9.6
Decapod crustacea	15.1		15.1	85.3	14.5	91.5	26.8		31.3
Cephalopods				0.04		0.1	10.6		12.4
Fish				2.5	6.9	1.7	49.3	42.7	46.7

Data are presented in relation to the length classes of the two species. 'NI crustacea' indicate non-identified crustacea.

**Figure 4.** Relationship between stomach fullness and trawl time. **A.** *Abralia veranyi* (n = 119). **B.** *Abraliopsis morisii* (n = 119).

the stomach contents of *A. veranyi* caught between depths of 500–1,000 m (18.2% IRI) than in the stomach contents of individuals from shallower waters. In the case of *Abraliopsis morisii*, fish were only present in the stomach contents of individuals caught in shallower waters (0–200 m depth; IRI of 5.7%). Mysids and cephalopods were

relatively scarce in the diet of both species; they were most common in *A. veranyi* caught at depths of 500–1000 m. For *Abraliopsis morisii*, cephalopods were found only in the stomachs of individuals from depths between 0 and 200 m and mysids were recorded only from individuals caught between depths of 200–500 m (Fig. 5).



**Figure 5.** Relationship between taxa found in the stomach contents and depth. **A.** *Abralia veranyi* ( $n = 119$ ). **B.** *Abraliopsis morisii* ( $n = 119$ ). Non-identified crustacea are indicated by 'NI.Crust'.

## DISCUSSION

*Abralia veranyi* and *Abraliopsis morisii* feed mainly on zooplankton, particularly on copepods, mysids and the early growth stages of decapod crustaceans. Despite similar feeding behaviour, these two enoploteuthid species differ in the prey composition of their diets. Moreover, the diet of both species showed variability in relation to their circadian cycles; this was particularly marked in *Abraliopsis morisii*.

Our observations indicate that the diet of both species changes significantly with growth, with the diets of larger individuals containing a greater share of other cephalopods and fish than smaller individuals. During ontogeny, individuals of both enoploteuthid species undergo two changes in the growth cycle and these probably relate to rapid changes in the ecology of these species; similar changes have been described by Castro & Hernández-García (1995) and Shea & Vecchione (2002) for other cephalopod species. As the body and head increase in size during growth, the buccal mass also increases in size. This facilitates the capture and consumption of larger, more robust prey, and studies have shown a direct relationship between the size of individuals and the type of prey consumed (Castro & Hernández-García, 1995; Sugimoto & Ikeda, 2013). The capacity to feed on larger prey is also associated with a significant increase in swimming speed and mode of hunting (Sugimoto & Ikeda, 2013). These changes in ontogenetic growth and diet may also be indicative of growth-related habitat shifts or the capacity for greater vertical movement through the water column (Shea & Vecchione, 2010).

The presence of copepods in the diet of smaller individuals of *Abraliopsis morisii* and *A. veranyi* can be explained by the relatively high abundance of this zooplankton group in surface waters. Hernández-León, Gómez & Aristegui (2007) have shown that copepods are extremely abundant in the shallow waters off the Canary Islands, where they represent c. 90% of the zooplankton community. Although the presence of members of the family Enoploteuthidae in epipelagic waters (0–200 m depth) has been reported by Roper (1972), our observations indicate that smaller individuals (DML < 12 mm) of both *Abraliopsis morisii* and *A. veranyi* occur in surface waters, particularly at night. However, we did not find significant differences in depth distribution among small, medium-sized and large individuals of the two species. Nevertheless, it is obvious that increases in body musculature allow these species to migrate into the deeper mesopelagic layer (Röpke, Nellent & Piatkowski, 1993). This ontogenic change in behaviour is believed to result from reduced

visual predator–prey interactions in the light-limited deep sea, as has been described for other cephalopod species (Hunt & Seibel, 2000).

Changes in the prey composition of the diet in relation to ontogenetic shifts have been reported for mesopelagic fish (Watanabe, Kawaguchi & Hayashi, 2002; Bernal *et al.*, 2015) and epipelagic cephalopods (Castro & Hernández-García, 1995; Mouat, Collins & Pompert, 2001). As we observed, *Abraliopsis morisii* and *A. veranyi* are distributed throughout the mesopelagic layer during the daytime and ascend at night to the epipelagic region to feed (the two species feed at different depth levels and this may reduce interspecific competition). This feeding migration resembles that described by Sassa *et al.* (2002), Yatsu *et al.* (2005) and Takagi *et al.* (2009) for mesopelagic fish.

We found heavily digested prey items in the stomach of most of the individuals investigated and this suggests that most individuals had fed during the hours prior to capture. Contrastingly, we also found that many individuals had empty stomachs, indicating that these individuals had yet to feed. Sassa *et al.* (2002) has reported vertical migratory behaviour for mesopelagic fish, with some myctophid fish species being shown to have a diel vertical migratory pattern related to feeding. Most studies of vertical migration have focused on fish (McClatchie & Dunford, 2003; D'elia *et al.*, 2016) and comparable data on the migration of mesopelagic cephalopods are scarce (Young, 1995; Hernández-García, Bordes-Caballero & Almonacid, 2006). Vertical migration to feed during nocturnal hours is common in mesopelagic fish (Yatsu *et al.*, 2005; Takagi *et al.*, 2009), but has been less extensively described in mesopelagic cephalopods (Passarella & Hopkins, 1991). Our study has shown that the cephalopods *Abraliopsis morisii* and *A. veranyi* feed between dusk and dawn in the epipelagic zone (0–200 m depth), pointing to the possibility that these species play a key role in the oceanic food web (Clarke, 1996; Ariza, 2015) and in the sequestration of carbon. We found that individuals of both species exhibited greater stomach fullness during nighttime hours compared with daytime hours, and this observation is consistent with vertical migration to the surface at night to feed.

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