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Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopod and giant squid

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Although deep-sea cephalopods are key marine organisms, their feeding ecology remains essentially unknown. Here, we report for the first time the trophic structure of an assemblage of these animals (19 species) by measuring the isotopic signature of wings of their lower beaks, which accumulated in stomachs of stranded sperm whales. Overall, the species encompassed a narrow range in $\delta^{13}\text{C}$ values (1.7‰), indicating that they lived in closely related and overlapping habitats. $\delta^{13}\text{C}$ values can be interpreted in terms of distribution with the more ^{13}C -depleted species (e.g. *Stigmatoteuthis arcturi*, *Vampyroteuthis infernalis*) having a more pelagic habitat than the more ^{13}C -enriched, bathyal species (e.g. *Todarodes sagittatus* and the giant squid *Architeuthis dux*). The cephalopods sampled had $\delta^{15}\text{N}$ values ranging 4.6‰, which is consistent with the species spanning approximately 1.5 trophic levels. Neither the giant octopod (*Haliphron atlanticus*) nor the giant squid reached the highest trophic position. Species $\delta^{15}\text{N}$ was independent of body size, with large squids having both the highest (*Taningia danae*) and lowest (*Lepidoteuthis grimaldii*) $\delta^{15}\text{N}$ values. Their trophic position indicates that some species share the top of the food web, together with other megacarnivores such as the sperm whale.

Keywords: marine predator; North Atlantic; pelagic ecosystem; sperm whale; trophic level

1. INTRODUCTION

Cephalopods play a major role in the marine ecosystems, as underlined by their global standing stock and annual consumption of resources (Rodhouse & Nigmatullin 1996). Squids and octopods dominate the cephalopod biomass in the deep sea, and determining their trophic relationships is a key issue in

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understanding the structure of this poorly known environment. The role of cephalopods as prey is demonstrated by their importance in the diet of predators (Clarke 1996), but knowledge of their diet is limited by lack of data (Rodhouse & Nigmatullin 1996). A new tool to investigate cephalopod feeding ecology has recently been developed, by combining the use of their predators as biological samplers together with measurements of the stable isotopic signature of their chitinized beaks (Cherel & Hobson 2005). The basic concept is that an animal's isotopic composition is directly influenced by what it consumes. In the marine environment, stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) are indicators of the foraging areas and trophic levels of consumers, respectively (e.g. Cherel & Hobson 2005).

Here, we report the trophic structure of an assemblage of deep-sea cephalopods by measuring the isotopic signature of beaks that accumulated in the stomach of sperm whales. We used whales that stranded together as samplers, because it is the only way to collect large numbers of coexisting cephalopod species. Stable isotopes were analysed in wings of lower beaks, because they retain the most recent growth bands, thus indicating the isotopic signal of the more recently assimilated food (Cherel & Hobson 2005; Hobson & Cherel 2006). The assemblage is made of 19 species that are representative of the large taxonomic, size range and lifestyle diversity of deep-sea cephalopods worldwide. It includes 17 oceanic squids, one octopod and the only species of the order Vampyromorpha. Fast-swimming muscular cephalopods are represented by the ommastrephid *Todarodes sagittatus* and the onychoteuthid *Ancistroteuthis lichtensteini*, but the assemblage is mainly composed of ammoniacal and gelatinous species (including the giant octopod *Haliphron atlanticus*; see the electronic supplementary material).

2. MATERIAL AND METHODS

Beaks were collected from three immature male sperm whales that stranded in the Bay of Biscay (44°13' N, 01°18' W) in December 2001. The three whales fed on the same cephalopod assemblage, as indicated by the overall similar percentages by number of the different beaks found in their stomachs (J. Spitz, Y. Cherel & V. Ridoux 2009, unpublished data). Cephalopods were identified from the morphology of their beaks. Lower rostral length of squid beaks and lower hood length of octopod beaks were measured, and allometric equations were used to estimate their dorsal mantle length (Clarke 1986; Lu & Ickeringill 2002). Lower beaks were wholly darkened, indicating maturing and/or adult cephalopods. However, most *Architeuthis* beaks (all but three large ones) had no wings and their size indicated juveniles. Consequently, a piece of the outer corner of the lateral wall was used for isotopic analyses. When available, 10 beaks from each species were randomly selected for isotopic analyses. Pieces of lower beaks were cleaned, dried and cut into small pieces. Relative abundance of stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) was determined with an elemental analyzer connected online to an isotope ratio mass spectrometer. Results are presented in the usual δ notation relative to PeeDee belemnite marine fossil limestone and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. To help interpret the isotopic signature of cephalopods, the muscle $\delta^{15}\text{N}$ values of top consumers living in the Bay of Biscay/eastern North Atlantic were used (Das *et al.* 2000, 2003). Since beaks were depleted in $\delta^{15}\text{N}$ when compared with soft tissues, their signatures were corrected by adding 3.5‰ at their $\delta^{15}\text{N}$ values (Cherel *et al.* 2009). Values are mean \pm s.d. Data were statistically analysed using SYSTAT v. 9 for Windows.

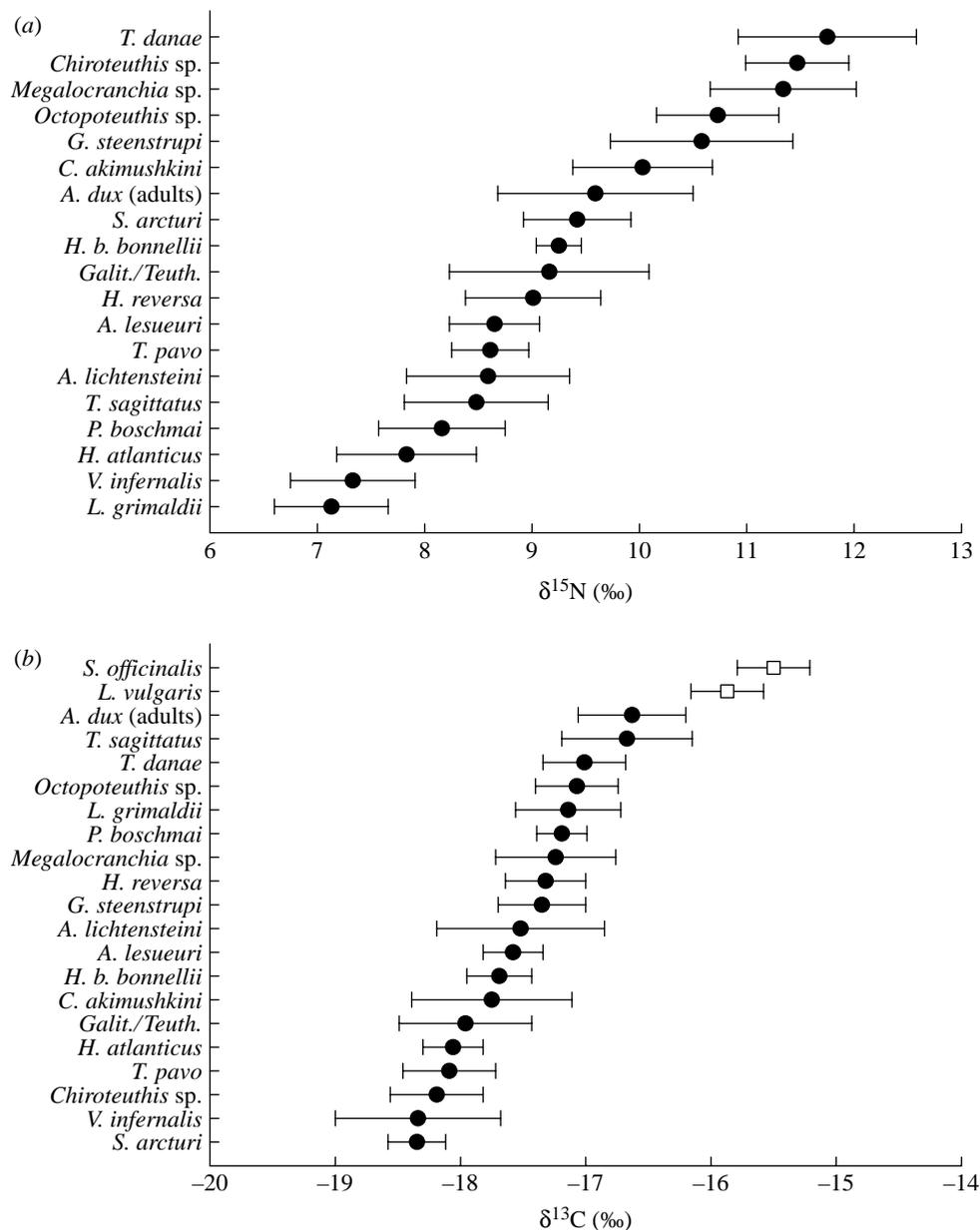


Figure 1. (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ values of lower beak wings of cephalopods eaten by sperm whales (filled circles). Open squares refer to control species living in neritic waters. Values are mean \pm s.d.

3. RESULTS

Cephalopods were segregated by the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of their beak wings (Kruskal–Wallis, $H=146$ and 111, respectively, both $p<0.0001$; see the electronic supplementary material). Species were deliberately placed in trophic sequence according to their nitrogen signatures to illustrate the trophic structure of the assemblage (figure 1). As indicated by their $\delta^{15}\text{N}$ values, coexisting deep-sea cephalopods from the North Atlantic fed along a continuum of less than two trophic levels (4.6‰) from $7.1\pm 0.5\text{‰}$ (*Lepidoteuthis grimaldii*) to $11.7\pm 0.8\text{‰}$ (*Taningia danae*). They had a more restricted range (1.7‰) in $\delta^{13}\text{C}$ values, with all the 19 species showing a gradual enrichment in ^{13}C from $-18.3\pm 0.2\text{‰}$ (*Stigmatoteuthis arcturi*) to $-16.6\pm 0.4\text{‰}$ (the giant squid *A. dux*). The $\delta^{13}\text{C}$ values of cephalopods eaten by sperm whales were impoverished in ^{13}C when compared with two control species living in neritic

waters, the myopsid *Loligo vulgaris* and the cuttlefish *Sepia officinalis* (figure 1). Overall, estimated mantle lengths were different between cephalopod species ($H=152$, $p<0.0001$). Mantle length encompassed a large range within the assemblage (approx. 1.3 m), from the small *Histioteuthis reversa* to the giant squid (5.8 ± 0.3 and 134 ± 3 cm, respectively). Values of $\delta^{15}\text{N}$ did not correlate with size ($F_{1,15}=0.21$, $p=0.656$), but $\delta^{13}\text{C}$ values increased linearly with mantle length ($F_{1,15}=10.70$, $p=0.005$; figure 2).

The two gigantic forms were segregated by their stable isotope signatures, with beak wings of the giant octopod having lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than those of the giant squid (Mann–Whitney, both $U=30$ and $p=0.01$). Juvenile and adult giant squids were segregated by their stable isotope signatures, with juveniles having lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than adults ($U=30$ and 27 $p=0.011$ and 0.043 , respectively). Finally, the three histioteuthids were

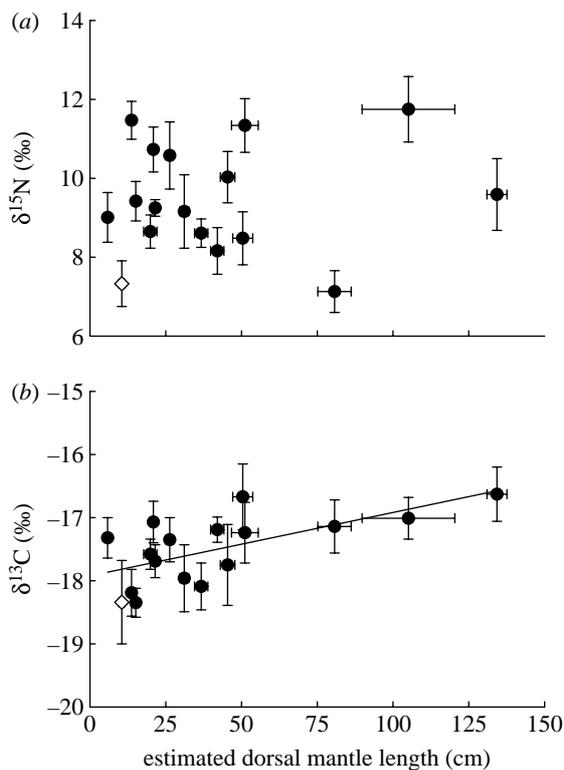


Figure 2. (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ values of lower beak wings versus estimated mantle length of cephalopods eaten by sperm whales. Values are mean \pm s.d. Open diamond refers to *Vampyroteuthis infernalis* and filled circles refer to squids ($y=0.010x-17.92$, $r=0.65$, $p=0.005$).

segregated by their habitats ($\delta^{13}\text{C}$ values; ANOVA, $F_{2,27}=36.34$, $p<0.0001$, *post hoc* Tukey's honestly significantly different multiple comparison tests, all $p\leq 0.012$) but not their trophic positions ($\delta^{15}\text{N}$ values; $F_{2,27}=1.84$, $p=0.178$), while the two octopoteuthids had different $\delta^{15}\text{N}$ values but identical $\delta^{13}\text{C}$ values (two-sample *t*-test, $t=3.19$ and 0.38 , $p=0.005$ and 0.712 , respectively).

4. DISCUSSION

Here, we report for the first time the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of beak wings of adult/subadult squids eaten by sperm whales that stranded together, thus focusing on the recent feeding habits of coexisting cephalopods that characterize the deep-sea teuthofauna. All the 19 cephalopod species encompassed a narrow range, with a small variance in their $\delta^{13}\text{C}$ values. They were, moreover, impoverished in ^{13}C when compared with the signatures of the neritic loliginid and cuttlefish, thus indicating that neither squids nor octopods recently foraged over the shelf but, instead, that they lived in oceanic waters. The small but significant $\delta^{13}\text{C}$ gradient between species can nevertheless be interpreted in terms of horizontal/vertical distribution, with the more ^{13}C -depleted species (e.g. *S. arcturi*, *Vampyroteuthis infernalis*) having a more pelagic lifestyle than, for example, *T. sagittatus* that lives primarily above the slope and at the bottom near the slope (Nesis 1987). Interestingly, $\delta^{13}\text{C}$ values were positively related to cephalopod size, suggesting that giant squid, *T. danae* and *L. grimaldii*, lived in the

bathyal. Indeed, large specimens of the three species seem to be associated with, but not restricted to, the bottom (Nesis 1987), indicating that some cephalopods adopt a benthopelagic or demersal lifestyle as they age. There, the fast-growing cephalopods would benefit from enhanced food supplies, due to the persistent near-bottom aggregations of mesopelagic organisms and of benthopelagic and demersal predators feeding on them (Gartner *et al.* 2008). Finally, the small and continuous $\delta^{13}\text{C}$ gradient indicates that the species lived in closely related and overlapping isotopic habitats. This allows the comparison of their nitrogen signatures as reflecting their relative trophic position, with no deleterial effect linked to different $\delta^{15}\text{N}$ baseline levels.

The trophic structure of the assemblage showed a continuum of $\delta^{15}\text{N}$ values that amounted to 4.6‰, corresponding to approximately 1.5 trophic levels (e.g. Hobson & Cherel 2006). Interestingly, neither the giant octopod nor the giant squid reached the highest $\delta^{15}\text{N}$ values, and large species occupied both the highest (*T. danae*) and lowest (*L. grimaldii*) trophic positions. That between-species differences in $\delta^{15}\text{N}$ were independent of body size is consistent with previous studies on fishes and contradicts species size-based trophic structuring in communities (Layman *et al.* 2005). This does not preclude a structuring effect of size within species, however, as the nitrogen signature of cephalopod beaks increase during ontogeny (Cherel *et al.* 2009). Indeed, beaks of adult giant squids were more ^{15}N -enriched than those of juveniles by 1.7‰, i.e. approximately half a trophic level. Their $\delta^{15}\text{N}$ values nevertheless indicated that giant squids are not positioned at the top of the food web, either in the Southern Ocean (Cherel & Hobson 2005) or in the North Atlantic, where, surprisingly, some fragile smaller forms (e.g. *Chiroteuthis* spp.) have a similar or even higher trophic position.

Comparison of corrected isotopic signatures of cephalopods with the $\delta^{15}\text{N}$ values of other top consumers (Das *et al.* 2000, 2003) shed a new light on the trophic structure of the oceanic ecosystem. The nitrogen signature of *T. danae* is close to that of the sperm whale, indicating that the species has a trophic position similar to that of some top marine consumers. This is in agreement with the recent finding that *T. danae* is an aggressive and tenacious predator rather than a sluggish, inactive squid, as previously thought (Kubodera *et al.* 2007). Histioteuthids are one of the main prey of sperm whales worldwide (Clarke 1996) and, accordingly, their $\delta^{15}\text{N}$ values were lower than the nitrogen signature of their predator. Finally, the cephalopods with the lowest trophic positions (*L. grimaldii* and *V. infernalis*) are comparable with common and striped dolphins (*Delphinus delphis* and *Stenella coeruleoalba*), showing that the assemblage of deep-sea cephalopods overall encompassed the same range of trophic positions than the most common oceanic mammals in the area.

Isotopic niches of cephalopods illustrate the different mechanisms allowing species coexistence. The three histioteuthids segregate by their $\delta^{13}\text{C}$ values, suggesting a habitat gradient from more

pelagic *S. arcturi* to more bathyal *Histioteuthis bonnellii bonnellii*, while octopoteuthids segregate by different $\delta^{15}\text{N}$ values, with *T. danae* occupying a higher trophic position than *Octopoteuthis* sp., as would be expected from its much greater size. It is also noteworthy that the two gigantic forms of the assemblage segregate by both their habitat and trophic position. Their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggest that the giant octopod is a more pelagic species, feeding on low-trophic-level prey, and the giant squid a more bathyal species feeding at a higher trophic position.

In summary, beak $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of squids and octopods eaten by sperm whales reveal new information about the trophic relationships of deep-sea cephalopods. Importantly, the stable isotopic signature of beaks accumulated in predators' stomachs is one of the few tools available to gather meaningful biological information on oceanic cephalopods that are rarely collected in the field. In this way, a further promising step should be to look at trace elements in beaks to better characterize cephalopod habitats, and to sample sequentially along the beak growth increments to produce a chronological record of trace elements and isotopic information, allowing for reconstruction of an individual's trophic history.

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