New information from fish diets on the importance of glassy flying squid (*Hyaloteuthis pelagica*) (Teuthoidea: Ommastrephidae) in the epipelagic cephalopod community of the tropical Atlantic Ocean

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Squids of the family Ommastrephidae are a vital part of marine food webs and support major fisheries around the world. They are widely distributed in the open ocean, where they are among the most abundant in number and biomass of nektonic epipelagic organisms. In turn, seven of the 11 genera of this family (*Dosidicus, Illex, Martialia, Nototodarus, Ommastrephes, Sthenoteuthis,* and *Todarodes*) are heavily preyed upon by top marine predators, i.e., birds, mammals, and fish, and currently support fisheries in both neritic and oceanic waters (Roper and Sweeney, 1984; Rodhouse, 1997). Their commercial importance has made the large ommastrephids the target of many scientific investigations and their biology is consequently reasonably well-known (Nigmatullin et al., 2001; Zuyev et al., 2002; Bower and Ichii, 2005). In contrast, much less information is available on the biology and ecological role of the smaller, unexploited species of ommastrephids (e.g., *Eucleoteuthis, Hyaloteuthis, Ornithoteuthis,* and *Todaropsis*).

Hyaloteuthis pelagica (Bosc, 1802), the glassy flying squid, is the smallest ommastrephid, reaching a maximum mantle length of 90 mm (Nesis, 1987). It appears to be an epipelagic species that is probably distributed in all tropical and subtropical oceans (Nesis and Nigmatullin, 1979; Wormuth, 1998). *Hyaloteuthis pelagica* is rarely captured, but was caught in large numbers during a cruise off Brazil, where it was the dominant ommastrephid captured in nets (Warneke-Cremer, 1986). Almost nothing is known about its trophic relationships, either as prey or predator (Nesis and Nigmatullin, 1979). Numerous remains of *H. pelagica*—from a few intact squids to a fairly large number of accumulated beaks—were found in the stomachs of large predatory fishes during research cruises in the central Atlantic Ocean in autumn 2000. In this note, we describe the importance of *H. pelagica* in fish diets, thus adding new information about the abundance and trophic role of a poorly known ommastrephid species.

Materials and methods

Fieldwork was carried out in the central Atlantic Ocean during three cruises of the Japanese RV *Shoyo Maru* in October–December 2000 (Fig. 1). Cruise I took place in temperate waters of the north equatorial current (between 8–21°N and 42–29°W) and cruises II and III took place in tropical waters of the south equatorial divergence (between 2N–10°S and 13–26°W, and between 7–9°S and 9–24°W). Cruises were a part of the Bigeye Tuna Year Program (BETYP) that was undertaken under the auspices of the International Commission for the Conservation of Atlantic Tunas (ICCAT). The purpose of the cruises was to tag live tunas caught by longlines in order to investigate their migration pattern and behavior in relation to fish aggregating devices.

Fish were measured (eye-fork length for billfishes and fork length for other species) and dissected onboard. In the laboratory, each fish stomach was thawed, opened, and both accumulated (cephalopod beaks with no flesh attached) and fresh items were sorted. Fresh remains were divided into broad prey classes (fish, cephalopods, crustaceans, and others), and weighed to calculate their proportion by mass in the diet. Identification of cephalopod prey relied on the external morphological features of either intact specimens or beaks. Beaks

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(both lower and upper) were identified by reference to features given by Clarke (1986) and by comparison with material held in our own reference collection.

Well-preserved specimens of *H. pelagica* were identified from the special arrangement of luminous spots on the ventral side of the mantle (Nesis, 1987). Beaks from those specimens identified from the spots (reference beaks) allowed us to identify almost all ommastrephid beaks found in fish samples as belonging to *H. pelagica*. Importantly, wings of the lower beaks darkened at a small size, thus precluding misidentification with beaks of other ommastrephid species that darken at larger sizes, e.g., *Sthenoteuthis pteropus* (Clarke, 1986). Lower rostral length (LRL) of beaks was measured to 0.1 mm with a vernier caliper and the allometric equations given by Clarke (1986) were used to estimate dorsal mantle length (ML) and whole wet mass (M) from LRL. Specimens of *H. pelagica* were assumed to be adults at 46 mm ML and larger (Dunning and Brandt, 1985).

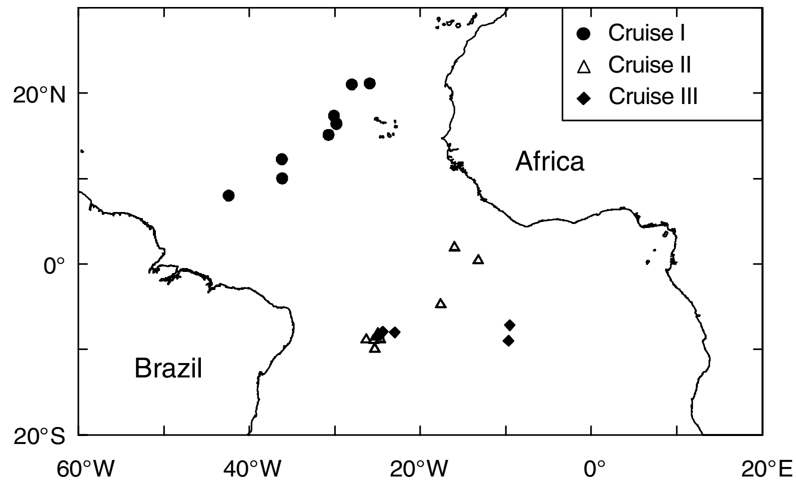

Figure 1

Locations of longline sets carried out in the central Atlantic Ocean during three cruises of the RV *Shoyo Maru* between October and December 2000.

Dietary data are presented by using two calculation techniques, namely the frequency of occurrence and the percentage by number of each prey type. Data were statistically analyzed by using SYSTAT 9 (SPSS, Chicago, IL). Values given are means (±SD).

Results

Most (97%) of the fish caught on longlines belonged to 10 different species of large oceanic predatory fishes, including longnose lancetfish (*Alepisaurus ferox*), four scombrids (wahoo [*Acanthocybium solandri*], albacore [*Thunnus alalunga*], yellowfin tuna [*T. albacares*], and bigeye tuna [*T. obesus*]), swordfish (*Xiphias gladius*), and four istiophorids (sailfish [*Istiophorus albicans*], blue marlin [*Makaira nigricans*], and white marlin [*Tetrapturus albidus*], and longbill spearfish [*T. pfluegeri*]). Most of the fish (93%) contained fresh remains in their stomachs. Fish prey dominated the diet by mass (>50%) of eight predator species (Table 1). Fish and cephalopod items were almost equally important in the diet of white marlin, whereas fish, cephalopods, and crustaceans were the main food sources of albacore.

Cephalopods amounted to slightly more than 50% of the diet by mass in one fish species (white marlin) only. They were an important prey class (>10%) in five other species and were still a minor, but significant (≥5–10%), portion of the food of the four remaining fishes (Table 1). Overall, cephalopods (both fresh and accumulated items) were found in most of the individuals (76%) and a total of 2701 cephalopod beaks were identified from the stomach of 105 fish. *Hyaloteuthis pelagica* was by far the most important cephalopod prey of the community of large predatory fishes, amounting to more than 50% of the total number of cephalopods (up to 93%) in six species (Table 2). Indeed, it was found to be the main cephalopod prey in all the fishes, except in bigeye tuna and lancetfish where it ranked second and third, respectively. *Hyaloteuthis pelagica* was much more abundant in the diet of fish caught in tropical waters (cruises II and III) than in the diet of individuals fished in temperate waters (cruise I) (n=1937 and 15 beaks, respectively).

Other important cephalopod prey (>10% by number) included the small onychoteuthid squid *Walvisteuthis* (= *Onykia*) *rancureli* in the diets of bigeye tuna and albacore, and the pelagic octopuses *Japetella diaphana* and common blanket octopus *Tremoctopus violaceus* in those of yellowfin and bigeye tunas, respectively. Three other ommastrephid squids were identified from fish stomach contents; they were two rare prey species, the Atlantic bird squid *Ornithoteuthis antillarum* and the orangeback flying squid *Sthenoteuthis pteropus*, as well as the bait, Argentine shortfin squid *Illex argentinus*.

All fishes fed upon the same size range of *H. pelagica*, including both juvenile and adult squids (Table 3, Fig. 2), but overall they segregated by preying on squids of different sizes (ANOVA on LRL, $F_{(6,907)}$=16.36, P<0.0001). *Post hoc* Tukey multiple comparison tests showed three groups of predators: yellowfin tuna and sailfish fed on smaller squids (51 mm and 3.9 g on average), bigeye tuna, white marlin, and longbill spearfish fed on larger individuals (60, 59, and 58 mm; 6.6, 6.2, and 5.7 g, respectively), and albacore and blue marlin fed on squids of intermediate sizes (54 mm and 4.7–4.8 g). Accordingly, bigeye tuna, white marlin, and longbill spearfish fed more on adult squids (89%, 92%, and 93% of the total number of *H. pelagica*, respectively) than did albacore and blue marlin (85% and 77%) and yellowfin tuna and sailfish (62% and 73%) (Table 3).

Table 1

Frequency of occurrence (FO) and proportion by mass (%) of four broad prey classes (fish, cephalopods, crustaceans, and others) recovered from the stomach contents of 10 species of predatory fishes sampled between October and December 2000 in the central Atlantic Ocean.

Species	No. of specimens	Length ±SD (cm)	No. of stomachs with fresh remains	Fish		Cephalopods		Crustaceans		Others	
				FO	Mass	FO	Mass	FO	Mass	FO	Mass
Alepisauridae											
Alepisaurus ferox	29	120 ±15	26	18	67.8	9	9.8	19	13.6	9	8.8
Scombridae											
Acanthocybium solandri	7	136 ±18	7	6	63.5	2	7.5	0	0.0	6	29.0
Thunnus alalunga	16	109 ±6	15	11	31.5	9	31.7	15	29.7	5	7.1
Thunnus albacares	6	147 ±7	6	6	77.2	5	5.8	5	12.1	2	4.9
Thunnus obesus	24	107 ±22	24	24	77.0	17	20.2	13	2.7	2	0.1
Xiphiidae											
Xiphias gladius	8	126 ±32	6	6	89.3	3	10.3	2	0.4	0	0.0
Isiophoridae											
Istiophorus albicans	4	152 ±13	4	3	85.7	4	13.1	0	0.0	1	1.2
Makaira nigricans	8	180 ±25	5	3	95.2	2	4.7	0	0.0	3	0.2
Tetrapturus albidus	7	130 ±10	7	7	48.2	6	51.2	0	0.0	4	0.6
Tetrapturus pfluegeri	30	143 ±6	29	25	86.8	23	13.0	4	0.0	4	0.1

Table 2

Number (and %composition by number) of the main cephalopod prey species found in the diet of Scombridae and Istiophoridae from the tropical Atlantic Ocean between October and December 2000. Only prey species contributing more than 5% by number are reported. *n* = number of stomachs examined.

Species	*Thunnus alalunga n=15*	*Thunnus albacares n=5*	*Thunnus obesus n=19*	*Istiophorus albicans n=4*	*Makaira nigricans n=5*	*Tetrapturus albidus n=7*	*Tetrapturus pfluegeri n=29*
Ommastrephidae							
Hyaloteuthis pelagica	194 (51.5)	133 (61.6)	45 (19.8)	78 (80.4)	101 (75.4)	481 (92.9)	897 (85.8)
Onychoteuthidae							
Onychoteuthis banksi	21 (5.6)	4 (1.9)	2 (0.9)	0 (0.0)	2 (1.5)	1 (0.2)	12 (1.1)
Walvisteuthis rancureli	63 (16.7)	5 (2.3)	62 (27.3)	1 (1.0)	9 (6.7)	0 (0.0)	7 (0.7)
Grimalditeuthidae							
Grimalditeuthis bonplandi	4 (1.1)	2 (0.9)	17 (7.5)	0 (0.0)	0 (0.0)	2 (0.4)	0 (0.0)
Tremoctopodidae							
Tremoctopus violaceus	3 (0.8)	35 (16.2)	3 (1.3)	8 (8.2)	7 (5.2)	11 (2.1)	19 (1.8)
Argonautidae							
Argonauta argo	6 (1.6)	15 (6.9)	2 (0.9)	8 (8.2)	4 (3.0)	21 (4.1)	82 (7.8)
Bolitaneidae							
Japetella diaphana	34 (9.0)	5 (2.3)	28 (12.3)	0 (0.0)	1 (0.7)	0 (0.0)	7 (0.7)
Other cephalopods	52 (13.8)	17 (7.9)	68 (30.0)	2 (2.1)	10 (7.5)	2 (0.4)	21 (2.0)
Total	377 (100.0)	216 (100.0)	227 (100.0)	97 (100.0)	134 (100.0)	518 (100.0)	1045 (100.0)

Discussion

This study is the first, to our knowledge, to point out the abundance of *H. pelagica* in the tropical pelagic ecosystem. In the central Atlantic Ocean, *H. pelagica* was found as a prey of all the fish species that were investigated. When looking at both the proportion by mass of cephalopods in the fish diet (Table 1) and the proportion by number of *H. pelagica* in their cephalopod diet (Table 2), *H. pelagica* was a major prey of white

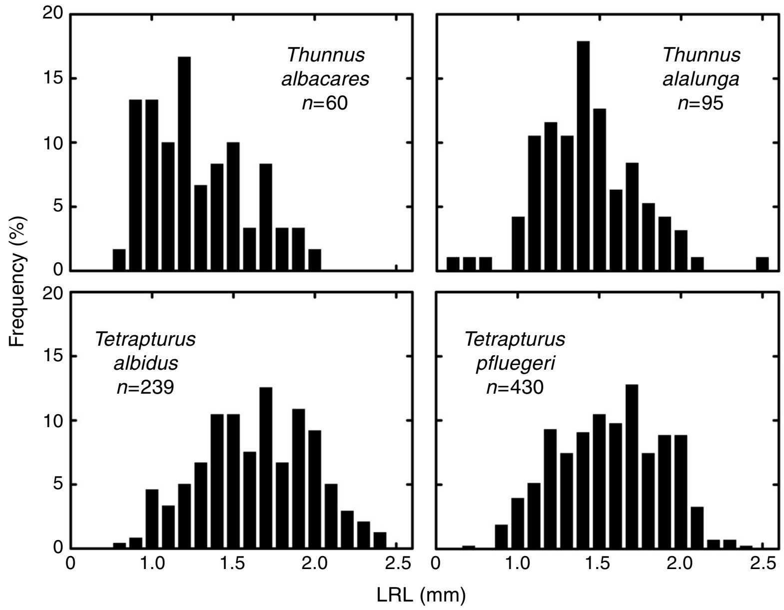

Figure 2

Frequency distribution of lower rostral lengths (LRL) (mm) of *Hyaloteuthis pelagica* glassy flying squid eaten by yellowfin tuna (*Thunnus albacares*), albacore (*Thunnus alalunga*), white marlin (*Tetrapturus albidus*), and longbill spearfish (*Tetrapturus pfluegeri*) in the tropical Atlantic Ocean.

Table 3

Characteristics of *Hyaloteuthis pelagica* eaten by large predatory fish from the tropical Atlantic Ocean. Values given are means (±SD) with ranges in parentheses. LRL=lower rostral length, ML=mantle length, M=body mass.

Species	Number (*n*)	Measured LRL (mm)	Estimated ML (mm)	Estimated M (g)	Adults (ML >46 mm) (%)
Alepisauridae					
Alepisaurus ferox	2	1.6–1.8	60–64	6.1–7.3	100.0
Scombridae					
Acanthocybium solandri	3	2.1 ±0.2 (1.9–2.3)	71 ±5 (67–77)	9.7 ±2.0 (8.5–12.0)	100.0
Thunnus alalunga	95	1.4 ±0.3 (0.5–2.5)	54 ±8 (34–81)	4.7 ±2.1 (0.8–14.0)	85.2
Thunnus albacares	60	1.2 ±0.3 (0.8–1.9)	51 ±7 (39–67)	3.9 ±1.8 (1.5–8.5)	61.7
Thunnus obesus	18	1.6 ±0.5 (0.8–2.3)	60 ±11 (39–77)	6.6 ±3.2 (1.5–12.0)	88.9
Xiphiidae					
Xiphias gladius	5	1.9 ±0.2 (1.6–2.2)	67 ±6 (59–75)	8.4 ±2.0 (5.9–11.3)	100.0
Istiophoridae					
Istiophorus albicans	33	1.3 ±0.2 (0.9–1.8)	51 ±5 (42–64)	3.9 ±1.3 (2.0–7.3)	72.7
Makaira nigricans	39	1.4 ±0.4 (0.5–2.0)	54 ±9 (34–69)	4.8 ±2.2 (0.8–9.2)	76.9
Tetrapturus albidus	239	1.6 ±0.3 (0.7–2.3)	59 ±8 (38–78)	6.2 ±2.4 (1.4–12.4)	92.1
Tetrapturus pfluegeri	430	1.5 ±0.3 (0.7–2.4)	58 ±8 (37–79)	5.7 ±2.2 (1.2–12.8)	92.6

marlin, a common food item of albacore, longbill spearfish, and sailfish and a minor prey for the remaining fishes. However, more information is needed to assess the spatiotemporal importance of *H. pelagica* in the fish community, because 1) all fish were caught during a relatively short period of time, and 2) a medium to low number of specimens per fish species were collected during the cruises.

The ommastrephid *Sthenoteuthis pteropus*, usually abundant in the tropical Atlantic Ocean, was surprisingly absent in fish diets in the present study. Two hypotheses may account for that apparent absence: either fish selected *H. pelagica* rather than *S. pteropus*, or *S. pteropus* was not an important and available nektonic prey organism at the time of sampling. The latter hypothesis is likely to be the best explanation because tunas and billfishes are known to be opportunistic predators. Moreover, the geographical distribution of *S. pteropus* shows that juvenile squids are not abundant in the central Atlantic Ocean where cruises of the present investigation took place (Warneke-Cremer, 1986; Zuev and Nikolsky, 1993). Instead, our study underlines the numerical importance of *H. pelagica*, together with *O. antillarum* (Vaske et al., 2004), in the area, and our numbers are in agreement with the large catches of the species with nets between 20°S and 31°S off Brazil during 1966 and 1968 (Warneke-Cremer, 1986).

The present study documents the largest number of *H. pelagica* ever reported, thus emphasizing the usefulness of marine predators to gain valuable information on the biology of their prey (Clarke, 1980; Cherel et al., 2004). Other ommastrephid species are important food items of various fishes, seabirds, and marine mammals (Clarke, 1996; Cherel and Klages, 1998), but *H. pelagica* was previously found only as a rare prey of squids (Shchetinnikov, 1992), fishes (Matthews et al., 1977; Okutani and Tsukada, 1988; Vaske et al., 2004), birds (Harrison et al., 1983), and cetaceans (Robertson and Chivers, 1997). In the same way, the squid *Grimalditeuthis bonplandi* and the pelagic octopods *T. violaceus* and *J. diaphana* were rarely found in significant numbers in the diet of cephalopod predators (Okutani and Tsukada, 1988; Le Corre et al., 2003), but we commonly found them as fish prey. Consequently, our study shows that these poorly known cephalopods, together with adults of *H. pelagica*, constitute a link in the transfer of energy from lower trophic levels (most likely mesozooplankton) to higher trophic levels (including tunas and billfishes) in the tropical Atlantic Ocean).

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