Predation on cephalopods by the giant red shrimp
Aristaeomorpha foliacea

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The stomachs of 427 giant red shrimps, *Aristaeomorpha foliacea*, caught in the Strait of Sicily (Mediterranean Sea) during four seasonal surveys contained 73 cephalopods, or 8.6% of prey. Cephalopods ranked third as prey following crustaceans (49.2% of prey) and bony fish (20.5% of prey). The following cephalopod taxa were identified: *Heteroteuthis dispar*, *Sepietta oweniana*, *Brachioteuthis* sp., *Abraliopsis morisii*, *Onychoteuthis banksii*, *Ancistroteuthis lichtensteinii*, *Histioteuthis bonnellii*, *H. reversa*, Taoniinae sp., Octopodidae sp.; the dominant species was *Heteroteuthis dispar* (13 specimens). All remains pertained to small and very small specimens, including early juveniles; rostral length of 13 beaks (=17.8% of cephalopods) measured <1 mm. Early juveniles were found in stomach contents only in summer and winter. Cephalopod size was found to be positively correlated to shrimp size. No seasonal nor predator sex-related differences were found in the quantities and frequencies of ingested cephalopods.

INTRODUCTION

The giant red shrimp *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea: Aristeidae) is a bathyal species occurring in many temperate and tropical areas around the world. In the Mediterranean its depth range spans from 120 to 1300 m, but it occurs more frequently above 700 m (Holthuis, 1987). Because of its size (up to 17 cm in total length in males and 22.5 cm in females) it attains a very high market price among Mediterranean shrimps, hence it is a major target species for several Mediterranean deep-water fisheries (Bianchini & Ragonese, 1994).

Unlike the other commercially important Mediterranean aristeid shrimp, *Aristeus antennatus* (Risso, 1816), published information on the diet and feeding behaviour of *Aristaeomorpha foliacea* is scant and is included in a few papers dealing with the deep water shrimp assemblages of the north-western Mediterranean Sea (Brian, 1931; Maurin & Carries, 1968; Cartes, 1995), Atlantic coast of Morocco (Lagardère, 1972, 1977) and north-western Australia (Rainer, 1992). Pipitone et al. (1994) reported some preliminary results of the stomach content analysis of *A. foliacea* collected in the Strait of Sicily, using the same batch of specimens used herein. In all previous papers, cephalopods are not dealt with in detail; indeed, to the best of our knowledge, no identification of cephalopod remains from the stomach contents of *A. foliacea* was attempted before the present study.

The purpose of this paper was first to estimate the contribution of cephalopods to the diet of *A. foliacea*, and second to investigate the predatory behaviour of this shrimp with respect to cephalopods.

MATERIALS AND METHODS

The giant red shrimps were collected during daylight hours in the Strait of Sicily, during four trawl surveys carried out on a seasonal basis from September 1990 to June 1991, at depths from 350 to 740 m (Figure 1). A total of 427 specimens were examined; their sizes ranged from 15 to 64 mm CL (carapace length, measured from the eye socket to the median dorsal edge of carapace); mean CL=37.5 mm, SD=8.33 (Figure 2).

The shrimps were frozen on board soon after capture. Within the following month, in the laboratory, they were defrosted and dissected, and their stomachs were preserved in 5% buffered formalin. The stomach contents were sorted according to higher taxonomic categories with the
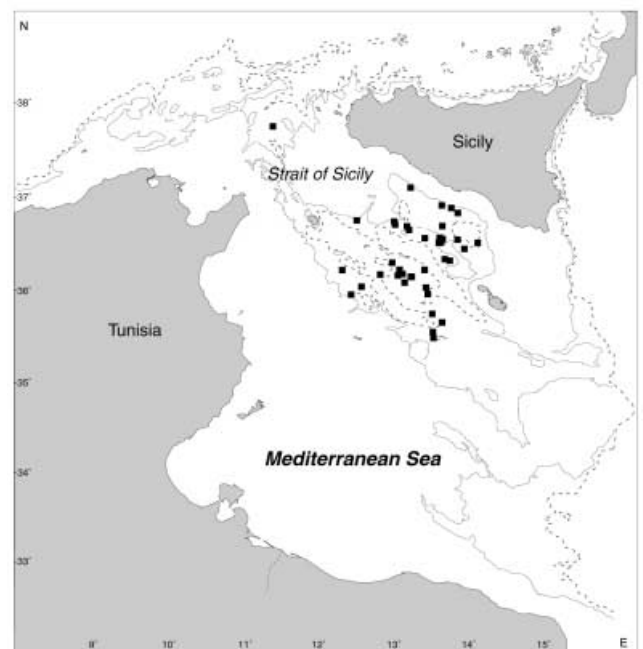

Figure 1. Giant red shrimp, *Aristaeomorpha foliacea*, fishing area in the Strait of Sicily. Squares represent capture localities for examined specimens.
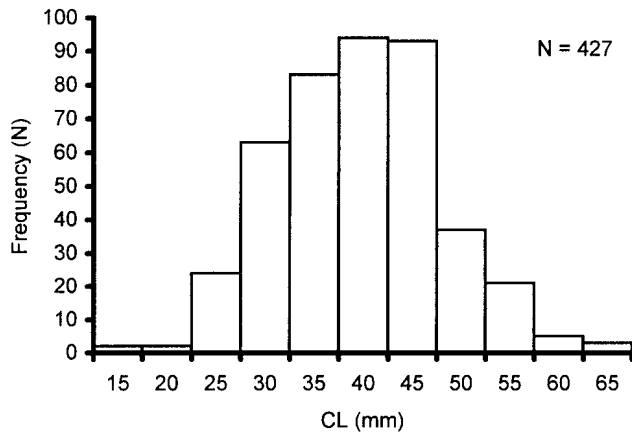
Figure 2. Carapace length (CL)–frequency distribution of examined giant red shrimps, *Aristaeomorpha foliacea*.

aid of a dissecting microscope. Identification at the species level was carried out only for cephalopods.

In order to give a broad picture of the diet of the giant red shrimp, the yearly coefficients of prey frequency ($F_p = (S_c/S_p) \times 100$ where S_c is the number of stomachs containing cephalopods and S_p is the number of stomachs containing any prey) and coefficients of prey numerical dominance ($F_n = (N_c/N_p) \times 100$ where N_c is the number of prey-cephalopods and N_p is the total number of prey items) were calculated for all prey-taxa, except F_n for foraminiferans because their abundance (45.6% of total prey items) regardless of whether they were intentionally ingested of not, would heavily overestimate their dietary importance (cf. Lagardère, 1972; Cartes, 1995).

To assess the role of cephalopods in the diet of *Aristaeomorpha foliacea*, the total giant red shrimp sample was sub-divided according to sex, size ('small' < 40 mm CL, 'large' ≥ 40 mm CL; cf. Cartes, 1995) and season of capture. The statistical significance of differences in prey frequency and numerical dominance between these sub-groups was tested by the Yates-corrected χ^2 test.

Cephalopod remains consisted mostly of hard parts (beaks, sucker rings, sucker hooks, and eye-lenses), therefore identification was carried out on the beaks using the

key provided by Clarke (1986) and, especially for the beaks belonging to early juvenile stages, by comparing them with the collection of voucher beaks of one of the authors (G.B.). Both lower and upper beaks were used for identification purposes. Beak measurements were recorded following Clarke (1962, 1986): LRL, lower rostral length; URL, upper rostral length; LHL, lower hood length; UHL, upper hood length.

Mantle lengths of some subadult and adult prey-teuthoids were estimated (EML) using the regression equations reported by Clarke (1986); to estimate mantle lengths of *Heteroteuthis dispar* the equation given by Orsi-Relini (1995) was used. In the case of early juvenile beaks, EMLs were not calculated because of the unavailability of suitable equations.

RESULTS

Forty-nine stomachs (11.48%) were empty. In the stomachs examined, 844 prey items (foraminiferans excluded) were found, of which 73 were cephalopods. Most stomachs with any cephalopods contained remains of just one cephalopod; four stomachs contained remains from two cephalopods, and one stomach contained remains from three cephalopods. Considering the yearly overall results (Table 1), cephalopods ranked third as prey of the giant red shrimp ($F_p = 17.7$; $F_n = 8.6$), following crustaceans ($F_p = 80.2$; $F_n = 49.2$) and bony fish ($F_p = 45.5$; $F_n = 20.5$).

Table 2 reports the F_p and F_n values for cephalopods (yearly overall and sex, size and seasonal sub-groups) and the relative results of χ^2 test applied to cephalopod sub-groups. Shrimp size appeared to have some bearing on catching and ingesting cephalopods; on the contrary, no statistically significant differences in prey frequency and prey numerical dominance were found between seasonal and sex sub-groups (Table 2).

Table 1. *Importance of prey taxa in the diet of the giant red shrimp,* Aristaeomorpha foliacea.

	F_p	F_n
Foraminiferans	34.9	–
Siphonophores	11.9	5.3
Polychaetes	2.6	1.2
Gastropods	9.0	5.0
Bivalves	4.2	2.3
Cephalopods	17.7	8.6
Crustaceans	80.2	49.2
Bony fish	45.5	20.5
Unidentified	17.7	7.9

F_p, yearly overall coefficient of prey frequency; F_n, yearly overall coefficient of prey numerical dominance.

Table 2. *Importance of cephalopods in the diet of the giant red shrimp,* Aristaeomorpha foliacea, *by sex, size and season of capture, and χ^2-test for differences between sub-groups.*

	S_c	S_p	F_p	N_c	N_p	F_n
Yearly overall	67	378	17.72	73	844	8.65
Males	34	190	17.89	36	410	8.78
Females	33	188	17.55	37	434	8.53
	$\chi^2 = 0.008$; P, ns			$\chi^2 = 0.017$; P, ns		
Small	25	198	12.63	26	436	5.96
Large	42	180	23.33	47	408	11.52
	$\chi^2 = 7.412$; $P < 0.01$			$\chi^2 = 8.235$; $P < 0.005$		
Summer	29	142	20.42	33	277	11.91
Autumn	13	85	15.29	13	194	6.70
Winter	15	80	18.75	17	192	8.85
Spring	10	71	14.08	10	181	5.52
	$\chi^2 = 1.756$; P, ns			$\chi^2 = 6.914$; P, ns		

F_p, coefficient of prey frequency $= (S_c/S_p)100$ where S_c is the number of stomachs containing cephalopods and S_p is the number of stomachs containing any prey; F_n, coefficient of prey numerical dominance $= (N_c/N_p)100$ where N_c is the number of cephalopods and N_p is the total number of prey items; ns, not significant.
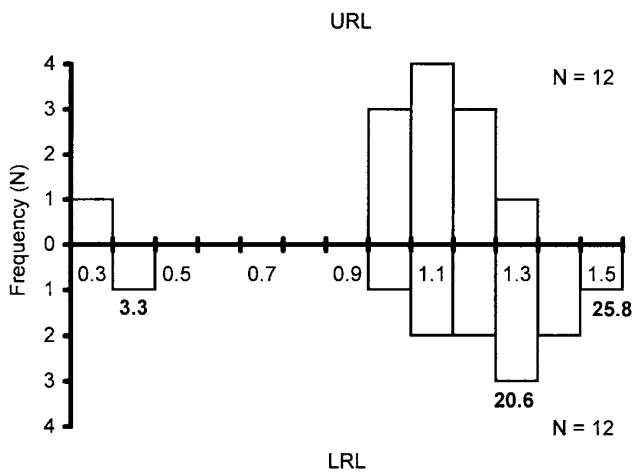
Figure 3. Upper (URL) and lower (LRL) rostral length–frequency distributions, and estimated mantle lengths (EML) at selected LRL values (lowest, mode, highest) for *Heteroteuthis dispar* beaks found in the giant red shrimp stomach contents; EML in boldface; all measurements in mm.

All remains consisted of small fragments of the body, mostly hard parts; pieces of flesh were found in only four cases (5.5%). The fragmentation of prey items was due to the powerful mincing activity of the shrimp. For instance, many beaks were broken in pieces or missed some portions even from their hardest part, i.e. the rostrum. Because of such a condition, prey identification was not possible in more than half of the instances.

Table 3 summarizes the diversity, abundance, and type of remains of cephalopods in the stomach contents of the giant red shrimp. In several instances beak size was not measurable, and hence was not given, because of poor beak conditions. In the case of *Heteroteuthis dispar*, which was the most abundant cephalopod, the distributions of LRLs and URLs and the EMLs are reported in Figure 3; the mean URL/LRL ratio, calculated on 11 pairs of beaks,
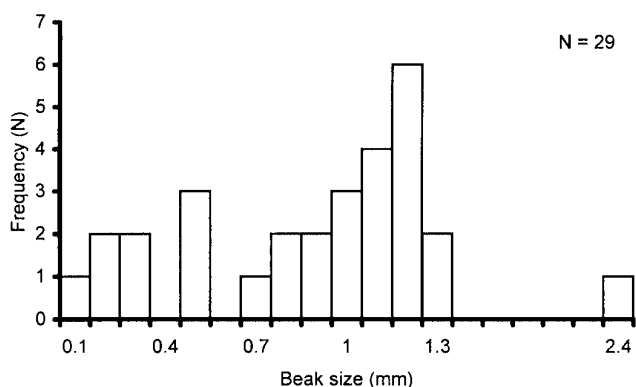

Figure 4. Beak size–frequency distribution for all cephalopods found in the giant red shrimp stomach contents (beak size is the average of upper and lower rostral lengths of pairs of beaks, or rostral length of the only available beak).

was 0.89. Comments on certain cephalopod remains are reported hereafter.

The lower beak ascribed to *Brachioteuthis* sp., although distinctive of the genus, differs from another Mediterranean beak of *Brachioteuthis* described by Bello (1995a) because of the presence of a knob on the wing, which makes it look very much like that of *B. picta* figured in Clarke (1986; figure 44C).

Only one species of *Abraliopsis* is known to live in the Mediterranean Sea (Mangold & Boletzky, 1988; Bello, 1995b), which has been variously named either *A. morisii* or *A. pfefferi* Joubin, 1896. The beaks found in the shrimp stomach contents pertain to this unique Mediterranean species, whichever is its right name (any nomenclatural discussion is beyond the scope of the present paper; however see comments of Young et al. (1998) on *A. morisii*).

The early juvenile lower beaks of *Histioteuthis bonnellii* and *H. reversa* were identified thanks to their typical lateral wall ridges, fin-like and square in profile respectively. A tiny beak (LRL=0.2 mm) of the former species already shows a hint of the peculiar fin-like ridge on the lateral wall below the hood.

The beaks ascribed to unidentified taoniine (Table 3) pertain to the group *Teuthowenia+Galiteuthis* (Cranchiidae: Taoniinae), the lower beaks of which genera cannot be distinguished from one another (Clarke, 1986). The only species belonging to these genera known to occur in the Mediterranean Sea are *Teuthowenia megalops* and *Galiteuthis armata* (Mangold & Boletzky, 1988; Bello, 1995b); hence the remains found in the shrimp stomachs are most probably from one of these species.

The presence of a ridge on the lateral wall of the octopodid early juvenile lower beak suggests that this is either an octopodine or a bathypolypodine.

The taxonomic composition of the cephalopods according to the fully and partially identified remains was as follows: Sepiolidae, N=14 or 46.7%; Teuthoidea, N=15 or 50.0%; Octopoda, N=1 or 3.3%.

Most preyed upon cephalopods were small specimens, either adults of small-sized species or juveniles of large-sized species, as suggested by the observation of beak sizes (Figure 4). In particular, several remains were from early juveniles; rostral length of 13 beaks, or 17.8% of cephalopods, measured less than 1.0 mm (Figure 4); such remains were found in the shrimp stomach contents only in summer and winter (Table 4) (note that the quantity of early juveniles among unidentified cephalopods is most probably underestimated).

Lastly, cephalopod size (rostral length, RL, i.e. LRL or URL when LRL was not available) was found to be positively correlated to shrimp size (CL). The correlation of RL to CL was best described by the power curve model; the predictive equation was derived and the curve was fitted to the scattergram of the points (CL, RL) (Figure 5) according to such a model (Sokal & Rohlf, 1981):

$$RL = 0.00039CL^{2.052} \qquad (1)$$

$$N = 29; \ r = 0,432; \ P < 0.0002.$$

Table 3. *Diversity, abundance, and type of cephalopod remains in the stomach contents of the giant red shrimp,* Aristaeomorpha foliacea.

	N	Early juvenile (N)	Type of remains	Beak size and estimated mantle length (mm)	Shrimp size (mm)	Depth range of shrimp capture (m)
Sepiolioidea						
Sepiolidae						
Heteroteuthis dispar (Rüppell, 1844)	13	1	2 pairs of beaks+fragments of flesh; 9 pairs of beaks; 1 upper beak; 1 lower beak	See Figure 3	35–58	472–688
Sepietta oweniana (d'Orbigny, 1841)	1	—	pair of beaks	URL=0.9, LRL=1.0	48	472–501
Teuthoidea						
Brachioteuthidae						
Brachioteuthis sp.	1	—	lower beak close to maturity	LRL=2.4, EML=65	42	611–719
Enoploteuthidae						
Abraliopsis morisii (Verany, 1839)	1	—	pair of fully mature beaks	URL=1.1, LRL=1.3, EML=42	40	653–688
Onychoteuthidae						
Onychoteuthis banksii (Leach, 1817)	1	1	pair of beaks	LRL=0.8	41	653–688
Ancistroteuthis lichtensteinii (Férussac, 1835)	1	—	pair of beaks	URL=0.95, LRL=1.4+	48	561–598
Histioteuthidae						
Histioteuthis bonnellii (Férussac, 1835)	2	2	1 pair of beaks; 1 lower beak	URL=0.9, LRL=0.6+; LRL=0.2	27–49	399–613
Histioteuthis reversa (Verrill, 1880)	1	1	pair of beaks	URL=0.5, LRL=0.5	36	488–560
Cranchiidae						
Unidentified taoniine	2	2	1 pair of beaks+1 arm+13 sucker rings; 1 lower beak	URL=0.45, LRL=0.55; LRL=0.58	37–38	488–625
Unidentified oegopsid squids	6	1	fragments of beaks, sucker rings, sucker hooks		32–61	472–667
Octopoda						
Octopodidae						
Unidentified octopodid	1	1	pair of beaks	UHL=1.3, LHL=0.8	43	606–613
Unidentified cephalopods	43	4	fragments of flesh, eye lenses, fragments of beaks	—	29–54	488–737

URL, upper rostral length; LRL, lower rostral length; EML, estimated mantle length; UHL, upper hood length; LHL, lower hood length.

Table 4. *Seasonal occurrence of cephalopod remains in the stomach contents of* Aristaeomorpha foliacea.

	Yearly total	Summer	Autumn	Winter	Spring
Heteroteuthis dispar	13	3*	3	1	6
Sepietta oweniana	1	1			
Brachioteuthis sp.	1			1	
Abraliopsis morisii	1			1	
Onychoteuthis banksii	1			1*	
Ancistroteuthis lichtensteinii	1		1		
Histioteuthis bonnellii	2	1*		1*	
Histioteuthis reversa	1	1*			
Unidentified taoniine	2	2**			
Unidentified oegopsid squid	6	3*		2	1
Unidentified octopodid	1			1*	
Unidentified cephalopods	43	22****	9	8	4

*, quantity of asterisks indicates quantity of early juveniles; Summer: 3–15 September; Autumn: 5–10 December; Winter: 27 February–13 March; Spring: 11–12 June.
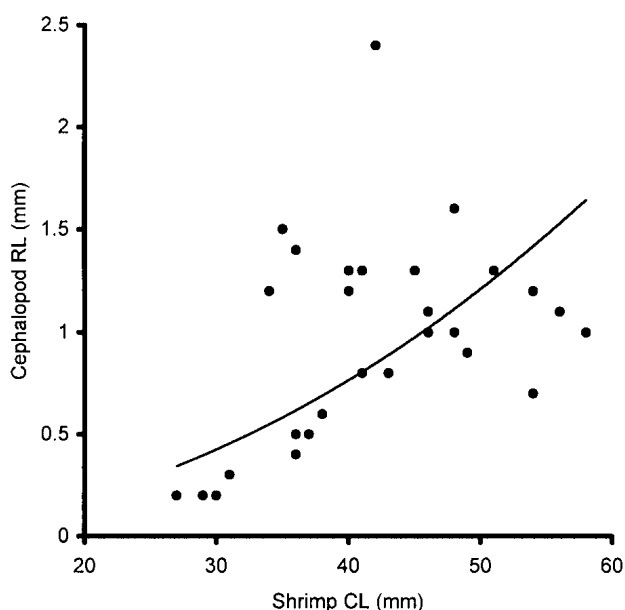
Figure 5. Correlation of cephalopod beak rostral length (RL) to shrimp carapace length (CL).

DISCUSSION

Cephalopods do not play a major role in the diet of the giant red shrimp from the Strait of Sicily. Their coefficients of prey frequency (F_p=17.7) and numerical dominance (F_n=8.6) ranked third well after the crustacean and bony fish coefficients (Table 1). Such a minor role agrees with the results of dietary studies carried out on *Aristaeomorpha foliacea* from other areas: Atlantic coast of Morocco (Lagardère, 1972, 1977), north-western Australian coast (Rainer, 1992) and Catalan Sea (Cartes, 1995). However, according to the present results, the relative importance of cephalopods in the diet of giant red shrimps from the Strait of Sicily was higher than in giant red shrimps from the other areas. Such a difference may be due either to actual geographical differences or sampling procedures, i.e. distribution in time and space of samples and quantity of shrimps sampled in different studies; for instance, our overall shrimp sample was several-fold larger than samples collected elsewhere (Lagardère, 1972, 1977; Rainer, 1992; Cartes, 1995).

Other benthopelagic shrimps such as *Aristeus antennatus*, *Parapeneaus longirostris* (Lucas, 1846), *Plesionika* spp. and *Solenocera membranacea* (Risso, 1816), occurring in the western Mediterranean Sea on the upper and middle slope, feed also on cephalopods, but only as a minor food item (Cartes & Sardá, 1989; Cartes, 1993a, 1995). A thorough comparison, as far as cephalopods are concerned, between the diet of the giant red shrimp and the diet of other benthopelagic shrimps, as well as between the diets of *Aristaeomorpha foliacea* from different geographical areas is made impossible by the lack of any cephalopod identification beyond the class level in previous studies.

All identified cephalopods from the stomachs of *A. foliacea* are oceanic, except *Sepietta oweniana* (however see Bello & Biagi (1995) about the capabilities of sepioline squid of accomplishing vertical migrations in the water column), and one may safely assume that they

were most probably preyed upon in the water column. Some species, such as the cranchiids and *Onychoteuthis banksii*, are known to perform an ontogenetic descent from the sea surface towards deeper waters (Rodhouse & Piatkowski, 1995; Arkhipkin & Nigmatullin, 1997), hence most early juvenile cephalopods were caught by the giant red shrimp well above the sea-floor. Furthermore, the fact that *A. foliacea* in the Strait of Sicily undergoes a nocturnal upward migration in the water column (Bianchini et al., 1998) makes us suppose that all or most cephalopods were preyed upon during night-time; such a hypothesis is also corroborated by the low percentage of cephalopod fleshy remains in giant red shrimps caught during daytime. It is likely that the nocturnal vertical migration towards more superficial water layers is dictated by the search for food. The same conclusion was reached by Pipitone et al. (1994), based on the presence of siphonophores and midwater crustaceans in the stomach contents of the same batch of giant red shrimps.

Lagardère (1972) stressed the importance of pelagic prey and suggested a diurnal feeding for *A. foliacea*. Indeed, it should be pointed out that the stomachs of the Sicilian giant red shrimps also contained strictly benthic prey (polychaetes, gastropods, bivalves; Table 1) in addition to pelagic prey. It appears that in the Strait of Sicily *A. foliacea* feeds in the water column during night-time and on the sea-floor during daytime, which is in agreement with Rainer's (1992) results. Alimentary rhythms linked to diel vertical migrations are known to occur to different extents in several other bathyal shrimps, and they are probably correlated to bottom geomorphology and to seasonal variations of available prey (Cartes, 1993b).

The significant differences between the number of cephalopods eaten by 'small' and 'large' giant red shrimps (Table 2) and the significant correlation of the size of cephalopods to the size of their predators ($P<0.0002$), show that there is a predator-size effect. Only medium and large shrimps are capable of catching and subduing larger cephalopods (Figure 5).

The cephalopods found in the stomach contents of *A. foliacea* fit two categories of about the same numerical importance. About half of them died of predation by *A. foliacea* as subadults and adults, viz. *Heteroteuthis dispar*, *Sepietta oweniana*, *Brachioteuthis* sp., and *Abraliopsis morisii*, whereas the remaining fraction of cephalopods were eaten in the earliest stages of their life. Teuthoid squid produce a large number of offspring to withstand high juvenile mortality rates. The present study shows that, in the Mediterranean oceanic food webs, *Aristaeomorpha foliacea* is one of the predators that contributes to the mortality of juvenile cephalopods; indeed very little is known about the causes of mortality of cephalopod earliest life stages. Conversely, juvenile teuthoid squid may be important to oceanic food webs. In fact some beaks observed in this study are among the smallest ever recorded in predation research. Somewhat larger pelagic cephalopods are preyed upon by the albacore, *Thunnus alalunga*, which is another predator feeding on juvenile cephalopods (Bello, 1999).

As for *H. dispar*, the most important cephalopod in the diet of *A. foliacea*, this study corroborates once more its keystone role in Mediterranean food webs (Bello, 1999): it has been found in the stomachs of a vast array of predators,

from the comparatively small-sized giant red shrimp (present results) to large-sized swordfish and dolphins (e.g. Bello, 1997).

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