

Uncommon pelagic and deep-sea cephalopods in the Mediterranean: new data and literature review

A. QUETGLAS¹, F. ORDINES¹, M. GONZÁLEZ², N. ZARAGOZA¹, S. MALLOL¹, M. VALLS¹ and A. DE MESA¹

¹ Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, 07015 Palma, Spain

² Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Puerto Pesquero s/n, 29640 Fuengirola, Spain

Corresponding author: toni.quetglas@ba.ieo.es

Received: 5 December 2011; Accepted: 22 November 2012; Published on line: 21 February 2013

Abstract

Compared with their shelf-living relatives, the biology and ecology of most pelagic and deep-sea cephalopods are presently relatively little known because of the difficulty in catching them. To compensate for the lack of information regarding these cephalopods, scientists have had to make use of the limited and fragmentary data gathered from different sources, such as sporadic captures, strandings or stomach contents of their predators. In this study, we provide some biological and ecological information on eleven uncommon pelagic and deep-sea cephalopods collected over more than fifteen years of fishery surveys in the western Mediterranean Sea. The cephalopods investigated include two epipelagic octopuses (*Ocythoe tuberculata* and *Tremoctopus violaceus*), one deep-sea cirrate octopus (*Opisthoteuthis calypso*), the sepiolid *Stoloteuthis leucoptera* and seven teuthoid species inhabiting, preferentially, the mesopelagic and bathypelagic waters (*Abraliopsis morisii*, *Ancistrocheirus lesueurii*, *Brachioteuthis riisei*, *Chroteuthis veranyi*, *Ctenopteryx sicula*, *Onychoteuthis banksii* and *Taonius pavo*). Although all of these species are either cosmopolitan or present a wide distribution in other oceans, they are nevertheless relatively rare in catches, and therefore, remain lesser known. The finding of *T. pavo* represents the first record of this cephalopod in the Mediterranean waters.

Keywords: cephalopods, pelagic, deep-sea, first record, review.

Introduction

There are two points of general consensus among the researchers involved in the study of the biology and ecology of cephalopods (e.g. Clarke, 1996b; Piatkowski *et al.*, 2001; Cherel *et al.*, 2009). The first refers to the key role played by these molluscs in the marine trophic chains, either as voracious predators or as important prey of a large set of predators, including fishes, other cephalopods, marine mammals and seabirds. According to this view, the study of cephalopods assumes primary importance to analyse the structure and dynamics of marine food webs, particularly in the deep waters. The second point concerns the generalised lack of information on the pelagic and deep sea species compared with their demersal relatives distributed on the continental shelf, in particular, those of commercial importance. Indeed, according to Clarke (1996b), the shelf species only represent a small percentage (15%) of all cephalopod genera.

The dearth of data on these oceanic species reflects the inadequacy of the current fishing gears to catch them, as the stomach content analyses of their predators clearly indicate that these cephalopods are highly abundant along the water column (Cherel & Hobson, 2005; Clarke,

1996a). To compensate for the deficiency in data on the pelagic and deep sea cephalopods, we should utilise the limited and fragmentary data collected from different sources such as sporadic findings from experimental surveys and catches of the commercial fishing vessels, strandings or the stomach content studies of the teuthophagous species. With this as our aim, we report some pertinent biological and ecological data on eleven cephalopod species that are rarely caught, not only in the Mediterranean Sea, but also on a worldwide level. The present work is based on a limited number of individuals collected during the fishery surveys conducted over the last fifteen years in the western Mediterranean basin. It should be emphasized, however, that the rarity of them being caught could be the result of the inefficiency of standard bottom trawl gears in capturing the pelagic species (e.g. Bello, 2000).

One of these rare findings represents the first record of the mesopelagic cephalopod *Taonius pavo* (Lesueur, 1821) in the Mediterranean Sea. Very little is known about this species, to the point that the currently available information is exclusively a result of the stomach content analyses of the cetaceans (e.g. Mintzer *et al.*, 2008; Santos *et al.*, 2007; Yatabe *et al.*, 2010). This paucity of knowledge also applies to the other species reported in the present study,

which increases the value of the limited information presented here. The recently published monograph by Jereb & Roper (2010) reviewed and up-dated the available data for most of the species dealt with in this study. To avoid duplication, we have reviewed the bibliography of only those species not included in that monography or those specific aspects not treated in it. In any case, a revision of the literature currently available on all of the species reported in this study clearly reveals the dearth of information worldwide regarding these pelagic and deep-sea cephalopods.

Material and Methods

The material analysed arises from different sources: 1) scientific surveys conducted between 1994 and 2010, in the western Mediterranean (except for two pelagic trawl surveys in December 2009 and July 2010, all other surveys were done using bottom trawl gears); 2) samplings on board commercial trawlers operating around the Balearic Islands during the same time period (Fig. 1); and 3) other sources (two specimens were obtained, one from a stranding and the other from a commercial purse-seiner). A GOC73 trawl gear was used in the surveys (Bertrand *et al.*, 2002) with 20 mm mesh size in the codend and horizontal and vertical openings (estimated using the SCANMAR system) of 16.4 and 2.8 m, on an average, respectively. In the two pelagic surveys conducted during 2009 and 2010, otter board mid-water trawl gears with an estimated mouth area of 280 and 112 m², respectively were used. The commercial bottom trawling fleet used a conventional “huelvano” type gear (Guijarro & Massuti, 2006) with 40 mm mesh size and average horizontal and vertical openings of 25.0 and 2.0 m, respectively. For each haul, the total catch per species (numbers and biomass) was recorded, together with the data on the samplings, such as date, location and depth. Once captured, specimens were frozen and later brought to the laboratory where the following biological parameters were noted: mantle length (ML, to the nearest mm), total weight (TW, to the nearest 0.1 g), sex and maturity stage based on the three macroscopic stages (immature, maturing and mature) described by Quetglas *et al.* (2009). Whenever possible, other parameters including gonad weight (GW), digestive gland weight (DGW) and stomach weight (SW) were also recorded (all to the nearest 0.01 g). In this case, the following indices were calculated: gonadosomatic index ($GSI=100 \cdot GW/(TW-GW)$), digestive gland index ($DGI=100 \cdot DGW/(TW-DGW)$) and fullness weight index ($FWI=100 \cdot SW/(TW-SW)$). The remains from the stomach contents were analysed and the preys were identified to the lowest possible taxon. Other relevant information, pertaining to the egg sizes of mature females, nidamental gland weight or the arm lengths in some species, was also noted.

To determine the rarity of the cephalopods reported in the study area, the frequency of occurrence (F) of all the

cephalopod species caught during the bottom trawl scientific surveys mentioned above were analysed. The value of F was obtained taking into consideration the entire set of hauls (N=2470) for the epipelagic species inhabiting the superficial waters of both the shelf and slope, but exclusively considering the hauls done at a mean depth higher than 200 m (N=961) for all the other species (mesopelagic and bathypelagic). This was because during the daylight hours they typically inhabit the water column above the slope grounds.

In order to determine if some unusual findings were related to specific oceanographic conditions, environmental different variables such as sea surface temperature (SST), wind speed and chlorophyll (Chla) concentration were analysed. Satellite images of these variables were downloaded from the NOAA webpage Ocean Watch (<http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php>). Oceanographic conditions during the month of the findings were compared with the conditions present during the same month of the previous and subsequent years to investigate the occurrence of some anomaly.

Whenever possible, we finally obtained the length-weight relationships for each species by combining the published data with our own data. The parameters of the power equation $TW=aML^b$ were calculated with a non-linear estimation using the Levenberg-Marquardt estimation method available in the STATISTICA package (version 6).

Results

A total of eleven uncommon pelagic cephalopod species, including a first record for the Mediterranean, are reported in this work (Table 1). No individual of two out of the eleven species was caught during the scientific surveys analysed, and the frequency of occurrence was lower than 3% in all other cases. The findings include two epipelagic octopuses (*Ocythoe tuberculata* and *Tremoctopus violaceus*), one deep-sea cirrate octopus (*Opisthoteuthis calypso*), the sepiolid *Stoloteuthis leucoptera* and seven teuthoid species inhabiting, preferentially, the mesopelagic and bathypelagic waters (*Abraliopsis morisii*, *Ancistrocheirus lesueurii*, *Brachiotheuthis riisei*, *Chirotheuthis veranyi*, *Ctenopteryx sicula*, *Onychoteuthis banksii* and *Taonius pavo*). Information on each species, listed in alphabetical order, is given below. Information on the entire set of species reported is presented in: 1) Supplementary Material, which lists the individual biological data such as size, weight, sex, maturity stage and different indices (GSI, DGI, and FWI) together with data on the findings (date, location and source) is available on the on-line edition only; 2) Figure 2, which records the mean capture depth of each individual finding; and 3) Table 2, which contains the length-weight relationships for nine out of the eleven species investigated. Although the length-weight relationships were calculated using a very small number

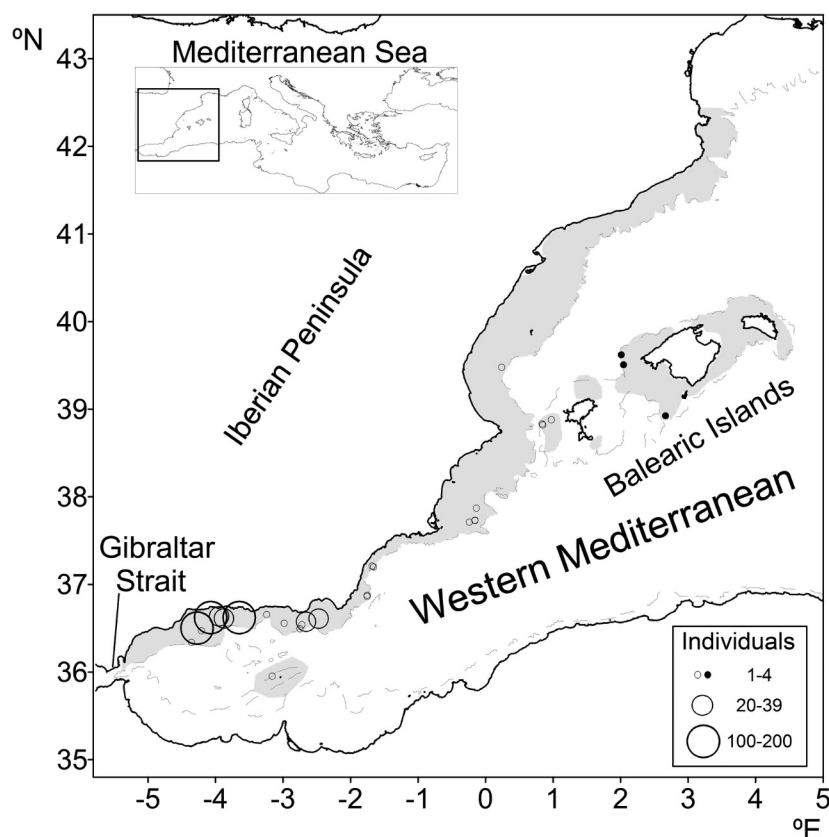


Fig. 1: Map of the western Mediterranean showing the study area prospected by different bottom trawl surveys undertaken between 1994 and 2010 in grey. The findings of the uncommon pelagic cephalopod *Brachioteuthis riisei* are also shown. Specimens taken from scientific surveys and samplings on board commercial vessels are shown as open and filled symbols, respectively. The bathymetric line represents 800 m depth.

of individuals (between 6 and 40), the lack of any relationship for most species in the bibliography justifies the presentation of these preliminary estimates. In two cases

(*A. morisii* and *T. pavo*), we could not find additional data in the literature to calculate the relationship.

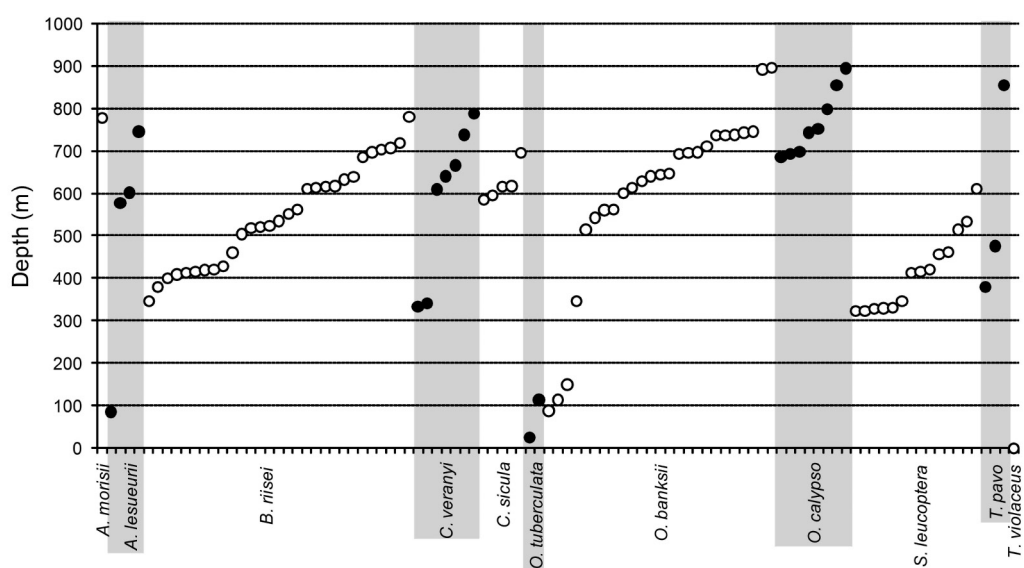


Fig. 2: Bathymetric distribution of the eleven uncommon pelagic cephalopods from the western Mediterranean studied in this paper. Species are arranged in alphabetical order. The epipelagic octopus *Tremoctopus violaceus* was found stranded dead on a beach.

Table 1. Total number of individuals (N), frequency of occurrence (F) and depth (mean and ranges) of the pelagic cephalopods collected during the scientific surveys conducted in the western Mediterranean between 1994 and 2010. Species are arranged in the increasing order of F. The eleven species reported in this study are shown in bold, including the two species absent in the samplings from those scientific surveys but caught during samplings on board commercial vessels.

Species	N	F	Depth (m)
<i>Abraliopsis morisii</i>	—	—	—
<i>Tremoctopus violaceus</i>	—	—	—
<i>Ocythoe tuberculata</i>	1	0.04	113.0
<i>Ancistrocheirus lesueurii</i>	2	0.10	414.5 (85-744)
<i>Chtenopteryx sicula</i>	1	0.10	586.0
<i>Taonius pavo</i>	1	0.10	855.0
<i>Chroteuthis veranyi</i>	3	0.31	721.3 (643-855)
<i>Opisthoteuthis calypso</i>	12	0.83	764.3 (685-894)
<i>Onychoteuthis banksii</i>	20 ¹	1.46	578.4 (88-897)
<i>Stoloteuthis leucoptera</i>	25	1.46	415.5 (324-612)
<i>Brachoteuthis riisei</i>	544	2.71	537.7 (347-782)
<i>Loligo forbesi</i>	4747	8.22	248.6 (38-760)
<i>Heteroteuthis dispar</i>	151	9.99	584.7 (147-855)
<i>Histioteuthis bonnellii</i>	183	10.51	565.0 (136-774)
<i>Neorossia caroli</i>	545	13.11	435.4 (48-770)
<i>Ancistroteuthis lichtensteinii</i>	409	13.74	580.3 (86-896)
<i>Rondeletiola minor</i>	3140	15.19	233.0 (41-715)
<i>Todaropsis eblanae</i>	1055	16.13	271.9 (37-760)
<i>Pteroctopus tetracirrhus</i>	449	16.75	292.5 (79-750)
<i>Histioteuthis reversa</i>	381	17.59	601.4 (329-896)
<i>Rossia macrosoma</i>	848	20.71	300.0 (67-751)
<i>Octopus salutii</i>	817	22.89	326.9 (74-897)
<i>Abralia veranyi</i>	3908	23.00	389.8 (41-798)
<i>Bathypolypus sponsalis</i>	1166	33.51	552.9 (63-896)
<i>Sepietta oweniana</i>	22777	35.17	239.0 (26-785)
<i>Todarodes sagittatus</i>	1935	50.57	476.6 (54-858)

¹Including a mature female, that was earlier classified as a separate species, *Chaunoteuthis mollis*.

Abraliopsis morisii

This species has never been caught during the scientific surveys conducted between 1994 and 2010. A single immature female of 22 mm ML was collected at a mean depth of 778 m during samplings on board the commercial trawlers around the Balearic Islands in April 1996.

Ancistrocheirus lesueurii

Eight individuals were caught, two of them during the scientific surveys analysed (F=0.10) and six during samplings on board the commercial trawlers in waters around

the Balearic Islands. Seven individuals were taken using bottom trawl gears between April and September 2001 at 577-745 m depth, and the remaining one with a pelagic trawl gear working at 80-90 m depth in July 2010. All individuals were mature females with 165 to 290 mm ML. The ovarian egg sizes in three out of four individuals taken in August 2001 were between 2.5 and 3.5 mm. Other biological data were recorded only for the individual caught in 2010 because the other individuals were in a bad state: 1) GSI=5.68%; 2) DGI=4.24%; and 3) stomach empty. Stomachs were analysed in five individuals, but only one of them (ML=290 mm) contained the remains of an indeterminate fish.

Brachoteuthis riisei

The species was quite rare in the waters around the Balearic Islands (F=1.38) and the eastern Mediterranean coast off the Iberian Peninsula (F=1.59), where single individuals were sporadically captured (only in two cases were two individuals caught in the same haul). No individual was ever caught east of 03°E or north of 40°N (Fig. 1). It was more frequent (F=5.52) in the Alboran Sea (east of the Strait of Gibraltar), where the captures contained many individuals in some cases, as during the summer of 2005 when 128, 150 and 198 individuals, respectively, were taken in each of the three different hauls performed between 345 and 420 m depth. The mean squid weight in these three hauls (2.0, 2.2 and 0.9 g, respectively) indicate that the samples were made up of small-sized individuals. Oceanographic conditions during this event (June 2005) showed that there was an episode of high Chla concentration in the Alboran Sea at the sites where the individuals were caught, compared with the conditions present during June of the previous and subsequent years (Fig. 3).

The species was caught through a wide bathymetric range, ranging from 347 to 782 m depth. Individuals from the Alboran Sea (4.5 ± 2.5 g) were smaller in size than those from the eastern Iberian coast (5.7 ± 2.1 g) and the Balearic Islands (10.0 ± 3.5 g). Biological data were available from only three individuals caught by the commercial trawlers from the Balearic Islands, two indeterminate individuals (44 and 65 mm ML) caught in July and August 1996, and a mature male (73 mm ML) caught in September 2008.

Chroteuthis veranyi

A total of seven individuals were picked up around the Balearic Islands, three of which were taken during scientific surveys (F=0.31%), while the remaining four were picked up during samplings on board the commercial trawlers. In all cases, a single individual per haul was captured. Two individuals were taken at 332-340 m depth and the remaining five between 609 and 855 m. Biological data was available for only six individuals with a size range of 47-119 mm ML. This sample included four males, two of

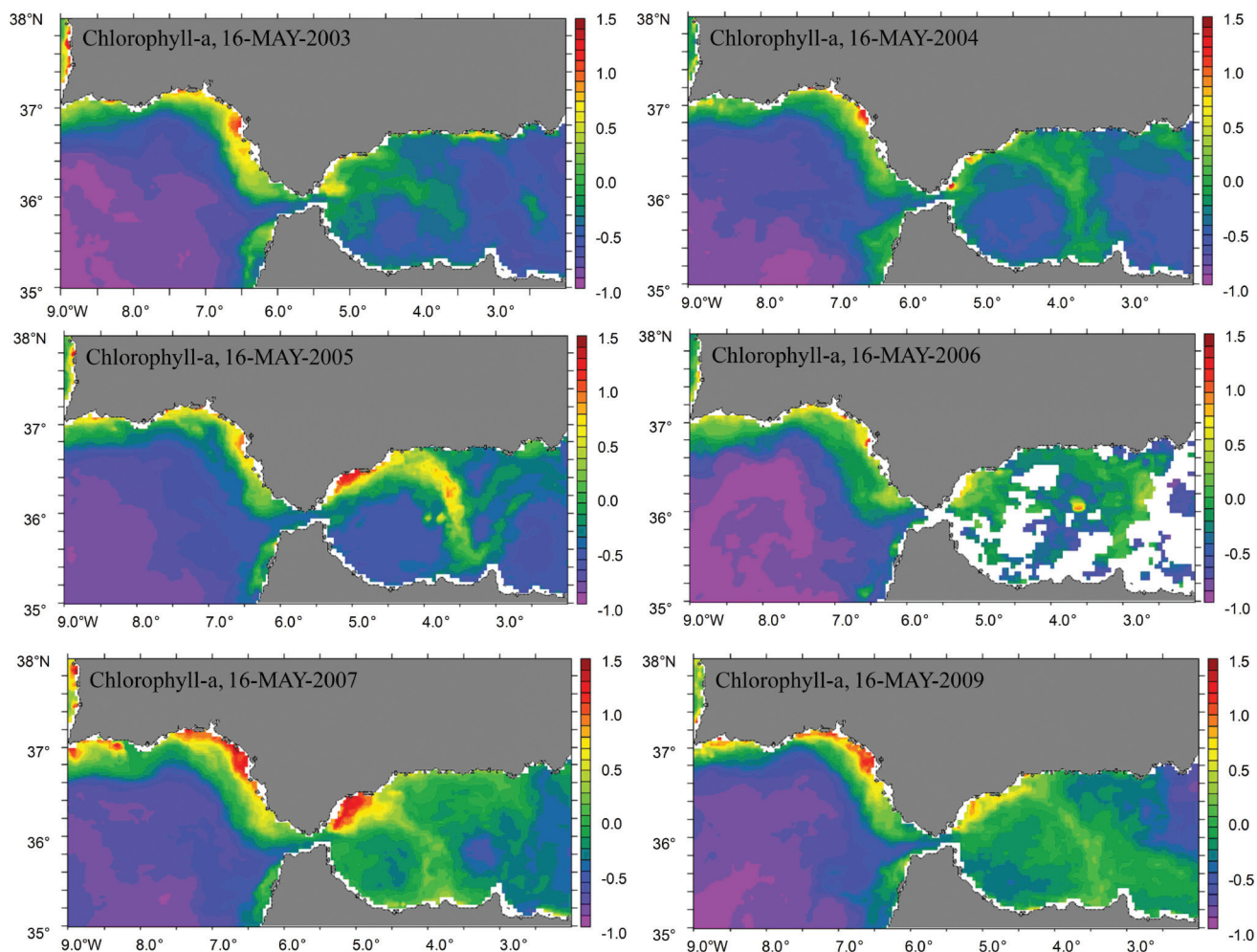


Fig. 3: Oceanographic conditions (chlorophyll a concentration, Chla) during May 2005, when uncommonly large numbers of the pelagic cephalopod *Brachioteuthis riisei* were obtained in the Alboran Sea (east of Gibraltar Strait), compared with the conditions during May of the previous (2003 and 2004) and following (2006, 2007 and 2009) years. The year 2008 is not listed because the data is not complete. Images have been downloaded from the NOAA Ocean Watch webpage <http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php>.

which (caught in July) were sexually mature, one immature female and one unsexed individual.

Ctenopteryx sicula

Five females and a male (40-70 mm ML) were recorded, of which one individual was caught during a scientific survey ($F=0.10$), while the remaining five were taken on board commercial trawlers. All the individuals were caught in the waters off the Balearic Islands within a narrow depth range (586-698 m), and all but one, in July. A single stomach from the largest female was analysed ($FWI=0.08\%$), which contained three individuals of the natantian crustacean *Gennades elegans*.

Ocythoe tuberculata

Only two individuals were caught, one at 115 m depth in a scientific survey ($F=0.04$) off the northeast Mediterranean coast of the Iberian Peninsula and another by a purse

seiner fishing vessel in the superficial waters (about 25 m depth) off the Balearic Islands. Both octopuses were mature females with a total body weight of 1326 g and 1502 g, respectively. Other biological data from the individual caught by the purse seiner (ML=24 cm) were also recorded: 1) $GSI=5.43\%$; 2) nidamental gland weight: 45.33 g; 3) $DGI=10.34\%$; 4) stomach empty; and 5) arm lengths I (425 mm), II (365 mm), III (315 mm), and IV (425 mm).

Onychoteuthis banksii

A total of 20 individuals were taken during the scientific surveys conducted between 1994 and 2010 ($F=1.46\%$). Another sample of 13 individuals was caught around the Balearic Islands during samplings on board the commercial trawlers. Most individuals were picked up at between 500 and 750 m depth, although a lesser number were also caught in the shallower (three individuals at 114, 150 and 347 m, respectively) and deeper waters (two individuals at 894 and 897 m, respectively). Biological data was

Table 2. Parameters of the length-weight relationships ($TW=a \cdot ML^b$) for nine of the eleven cephalopod species reported in this study obtained combining own data and data from the literature. Intercept and slope estimates are given with their corresponding 95% confidence intervals. The sources of the data are shown below, specifying the number of individuals of each source.

Species	Intercept (a)	Slope (b)	r	N	Size range (mm)
<i>Ancistrocheirus lesueurii</i> ¹	$5.74 \cdot 10^{-4}$ ($-4.42 \cdot 10^{-4}$, $1.59 \cdot 10^{-3}$)	2.57 (2.27, 2.88)	0.915	40	122-435
<i>Brachioteuthis riisei</i> ²	$3.70 \cdot 10^{-4}$ ($-4.38 \cdot 10^{-4}$, $1.18 \cdot 10^{-3}$)	2.42 (1.89, 2.94)	0.987	8	35-73
<i>Chroteuthis veranyi</i> ³	$7.57 \cdot 10^{-4}$ ($-2.17 \cdot 10^{-3}$, $3.69 \cdot 10^{-3}$)	2.50 (1.67, 3.33)	0.962	9	36-119
<i>Chtenopteryx sicula</i> ⁴	$1.16 \cdot 10^{-4}$ ($-3.46 \cdot 10^{-4}$, $5.79 \cdot 10^{-4}$)	2.97 (2.04, 3.90)	0.986	6	40-79
<i>Ocythoe tuberculata</i> ⁵	$3.14 \cdot 10^{-3}$ ($-9.27 \cdot 10^{-3}$, $1.55 \cdot 10^{-2}$)	2.45 (1.75, 3.16)	0.906	19	77-335
<i>Onychoteuthis banksii</i> ⁶	$1.26 \cdot 10^{-3}$ ($4.99 \cdot 10^{-3}$, $2.02 \cdot 10^{-2}$)	1.74 (1.63, 1.85)	0.995	14	57-301
<i>Opisthoteuthis calypso</i> ⁷	$6.25 \cdot 10^{-3}$ ($-1.67 \cdot 10^{-2}$, $2.92 \cdot 10^{-2}$)	2.60 (1.64, 3.57)	0.868	17	13-54
<i>Stoloteuthis leucoptera</i> ⁸	$3.86 \cdot 10^{-4}$ ($1.08 \cdot 10^{-4}$, $6.64 \cdot 10^{-4}$)	3.12 (2.88, 3.35)	0.995	13	10-25
<i>Tremoctopus violaceus</i> ⁹	$1.62 \cdot 10^{-4}$ ($-2.17 \cdot 10^{-4}$, $5.42 \cdot 10^{-4}$)	3.06 (2.62, 3.49)	0.994	9	75-230

¹This work (8), Bello *et al.* 1994 (1), D'Onghia *et al.* 1997 (10), dos Santos and Haimovici 2001 (1), Hoving *et al.* 2006 (19), Colabuono and Vooren 2007 (1); ²This work (3), D'Onghia *et al.* 1995 (3), Lefkaditou *et al.* 2000 (1), Piatkowski and Diekmann 2005 (1); ³This work (8), Tursi *et al.* 1994 (1); ⁴This work; ⁵This work (1), Biagi 1980 (1), Sánchez 1980 (1), Corsini & Lefkaditou 1995 (3), Laptikhovsky and Salman 2003 (1), Lefkaditou & Kallianiotis 2006 (4), Honma *et al.* 2007 (2), Caballero-Alfonso *et al.* 2009 (2), Tutman *et al.* 2008 (3), Salman & Akalin (2012); ⁶This work; ⁷This work (10), Cuccu *et al.* 2009 (3), Sartor and Belcari 2009 (4); ⁸This work; ⁹This work (1), Zeidler 1989 (1), Lozano-Soldevilla 1991 (2), Laptikhovsky and Salman 2003 (5).

available for 14 individuals, including for an indeterminate individual and males and females at all three stages of maturity. The single mature female (ML=301 mm), which was formerly classified as *Chaunoteuthis mol-lis*, was taken at 893 m depth during a scientific survey conducted in December 2009. Biological indices were calculated by sex and maturity stage; 1) females: immature (GSI=0.41±0.15%; DGI=5.25±1.29%), maturing (DGI=6.74%), mature (GSI=14.53%; DGI=6.57%); 2) males: immature (GSI=0.17%), maturing (GSI=1.65%), mature (GSI=2.90±0.93%; DGI=12.26±2.27%).

Opisthoteuthis calypso

In all, 12 individuals were caught between 685 and 895 m depth during the scientific surveys (F=0.83%); one of them in the Alboran Sea and the rest around the Balearic Islands. Biological information was available for ten of the individuals, ranging from 13 to 40 mm ML, of which only eight could be sexed (2 males, 6 females). The sample contained females at varying maturity stages: immature (GSI=0.74%; DGI=2.52%), maturing (GSI=3.36±0.28%; DGI=1.62±0.33) and mature (GSI=9.42±1.38%; DGI=2.76±0.63). The males were maturing (GSI=0.55%; DGI=1.09%) and mature (no weights available). The ma-

ture individuals were caught in July, August and November. Considering the stomach weights available (N=7), the mean FWI (±SD) was 0.72±0.24%.

Stoloteuthis leucoptera

A total of 25 individuals were caught between 324 and 612 m depth, all of which occurred during the scientific surveys conducted in 2001 and between 2003 and 2006 (F=1.46%). The species occurred more frequently in the Alboran Sea (F=3.25%) than in the eastern coast of the Iberian Peninsula and the Balearic Sea (F=0.66%). However, no individual was caught north of 40°N and east of 2°E. In most cases, a single individual per haul was taken, but captures of two and five individuals occurred in three and two hauls, respectively. Biological information was available for only 13 individuals, nine immature females and four males (two mature and two maturing individuals, all caught during May).

Taonius pavo

A total of four individuals were captured within the depth range of 380-609 m; one (153 mm ML) during a scientific survey in July 2010 (F=0.10%) off the Balearic Islands (Fig. 4) and the other (ML=97, 106, 173 mm) on

board a commercial trawler near the Gulf of Lion in June 1998. It is of great interest to note that three individuals caught by the commercial vessel were captured within a few days in the same location, two of them during the same haul. None of the four individuals could be sexed. Apart from the biological information shown in the Supplementary Material, we recorded the following data from the individual caught in 2010: arm length I (27.0 mm), II (33.3 mm), III (37.3 mm), IV (41.3 mm), and tentacles (right: 120.2 mm; left: 140.3 mm); eye width (25.0 mm) was greater than the mantle width (18.5 mm) and the fin width (17.0 mm). The stomach weighed 0.13 g (FWI=2.47%) and its contents could not be identified.

Tremoctopus violaceus

The single individual reported was found dead, stranded on a beach of the Balearic Islands, in July 2000. The 110 mm ML specimen was a mature female with the following biological data: 1) GSI=3.00%; 2) DGI=13.28%; and 3) FWI=3.49%. The arm length was: I (210 mm), II (226 mm), III (122 mm), and IV (128 mm). The eggs in the ovary measured between 2.0 and 2.5 mm. The stomach content analysis revealed the presence of *Posidonia oceanica* and the algae *Flabellia petiolata*, *Ceramium* sp. and an indeterminate Rhodophyta, all of them were sessile benthic organisms. Knowing the pelagic habits of this octopus, however, such remains could have been consumed by the moribund specimen and carried by the currents into the shallow waters.

Discussion

The analysis of a large bulk of bottom trawl hauls undertaken during the scientific surveys conducted between 1994 and 2010 in the western Mediterranean Sea, prompted a further investigation of the eleven cephalopods which are considered as rare or very rare species based on their low frequency of occurrence (<3% in all cases). As mentioned earlier, however, such infrequency most probably reflects the inefficiency of the sampling gears, which are not designed to collect oceanic cephalopods, because the stomach content analyses of their predators indicate that they are abundant in the open waters (e.g. Bello, 2000; Cherel & Hobson, 2005). Furthermore, there could be differences in capturing them even between the experimental and commercial bottom trawlers using different mesh sizes and vertical openings (Maiorano *et al.*, 1999; Lefkaditou *et al.*, 2003a,b). In the following paragraphs, the biological and ecological aspects of each species are discussed, based upon our own data and published literature.

Abraliopsis morisii Vérany, 1839

Although according to Nesis (1987) this species was misidentified as *A. pfefferi*, Bello (2005) showed that *A. morisii* is the valid binomen to indicate one of the two

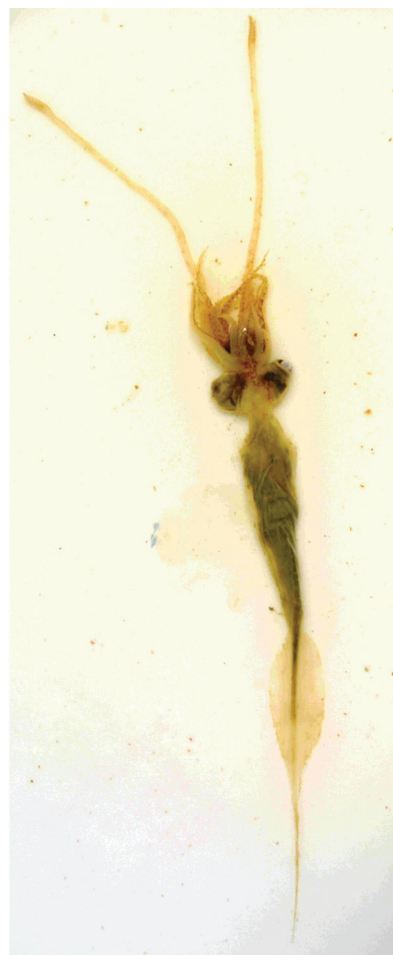


Fig. 4: Specimen of the pelagic cephalopod *Taonius pavo* (153 mm ML) caught in July 2010 in a scientific survey conducted aboard a commercial trawler in the waters off the Balearic Islands (western Mediterranean).

Atlantic species and the only one present in the Mediterranean. The species is found distributed in the tropical to warm temperate Atlantic Ocean, including the Gulf of Mexico, and Mediterranean Sea (Tsuchiya, 2009). However, little is known regarding the biology or ecology of this species, which appears to occur in the mesopelagic layers during the day but moving to the epipelagic waters at night (Murzov, 1986). Arkhipkin (1996) studied the age and growth from 29 individuals caught at night, between 25 and 300 m along the central east Atlantic. According to his samples (20 to 33 mm ML), *A. morisii* is a short-lived squid (<5.5 months) and, most likely, a multiple spawner, producing two or three generations per year. Laptikhovsky (1999) analysed the reproductive aspects, including the fecundity and oocyte sizes from the 13 specimens (22-39 mm ML) picked up in the north Atlantic. Kear (1994) included *A. morisii* in a study on the morphology and function of the mandibular muscles of 23 cephalopods. In the experiments dealing with light attraction on pelagic cephalopods undertaken around Madeira, Clarke & Pascoe (1998) found that sizes of *A. morisii* increased with an increase in the wattage of the lights.

In the Atlantic Ocean, *A. morisii* has been reported in the northwest (Lu & Roper, 1979), the northeast (Clarke & Lu, 1975) and the subtropical waters of the Brazil Current (Rodhouse *et al.*, 1992). The species was also reported in the Indian Ocean (Adam, 1954; Silas, 1968), however, according to the present information on the distribution of the genus *Abraliopsis* (Tsuchiya, 2009), such records should belong to another species. From a sample of 3731 paralarval and juvenile cephalopods of 44 generic and specific taxa collected during 21 western North Atlantic cruises, Vecchione *et al.* (2001) studied 21 specimens of *A. morisii* and showed that, besides the oceanic areas, this species was also found on the continental shelf over the bottom depths as shallow as 66 m. The specimens taken by Roper (1972), ranging between 6 and 36 mm ML, showed a trend for the adults to occur deeper than the larvae during the day (375–675 m vs. 100 m).

As indicated, the single specimen found in our samplings between 1994 and 2010, shows that *A. morisii* is rarely caught in the Mediterranean and the number of records is very limited. In most cases, the reports refer to the sporadic findings of single individuals, such as the one reported by Mangold-Wirz (1973), in the north western basin or the specimen taken by Maiorano *et al.* (2010), at 558 m depth, in a trawl survey series undertaken between 1985 and 2006 in the Ionian Sea. The species, however, could be abundant, as it is the predominant prey of different predators captured in this area, including the giant red shrimp and two species of dolphins (Bello & Pipitone, 2002; Blanco *et al.*, 1995, 2006). Of note is the species was not found to be the prey of teuthophagous predators from outside the Mediterranean, in the literature reviewed. Furthermore, Roper (1972) found that this species was the third most abundant cephalopod in the juvenile and paralarval stages captured along the Mediterranean, although Sánchez & Molí (1985) found a single paralarva of 2.3 mm ML in one sampling station at 0–100 m depth in the western basin.

Ancistrocheirus lesueurii Orbigny, 1842

This species is distributed worldwide in the tropical and temperate open ocean waters (Roper *et al.*, 1984). According to Nesis (1993), the paralarvae, juveniles and subadults inhabit the epipelagic and mesopelagic deep-waters although the adults spawn on or near the bottom. The transition from the epipelagic and mesopelagic to the bathypelagic waters is reflected in the statolith growth increments (Arkhipkin, 1997).

Paralarvae have been reported both in the western and eastern Atlantic as well as in the Mediterranean. In an exhaustive study of the micronektonic cephalopod assemblage (2215 individuals of 47 species) from the eastern Gulf of Mexico at sampling depths of 0–1000 m, Passarella & Hopkins (1991) found that the daytime occurrences of *A. lesueurii* were deeper than at night. Moreno *et al.* (2009) caught two paralarvae with 3.0 and 5.3 mm ML in January and March, respectively, off the western Iberian Peninsula,

one of which was collected at 20 m depth near the shore. In the Mediterranean, two single paralarvae were picked up at 250 m (5 mm ML, Lefkaditou *et al.*, 1999) and 350 m depth (2.5 mm ML, Salman *et al.*, 2003) in July and May, respectively.

The species has been cited several times in the Mediterranean and, to our knowledge, with the only exception of the two paralarvae aforementioned, all the individuals reported to date were mature females. Adults have been caught in the mesopelagic waters close to the bottom using bottom trawl gears (500–580 m, D'Onghia *et al.*, 1997; 577–745 m, this work), as well as in the epipelagic waters using squid jigs (70 m, Bello *et al.*, 1994) and pelagic trawl gears (85 m, this work). In spite of the rarity of this species, the presence of both the early life stages (Lefkaditou *et al.*, 1999; Salman *et al.*, 2003) and spawning females (D'Onghia *et al.*, 1997; this work) suggest that reproduction occurs in the Mediterranean (Bello *et al.*, 1994). The fact that all of our specimens were mature females, and that seven out of the eight findings were caught in the same year, could indicate irregular movements of the female shoals, related to reproduction. Egg sizes in our sample (between 2.5 and 3.5 mm) were larger than those previously reported (1.3–2.6 mm, D'Onghia *et al.*, 1997; 2.0–2.2 mm, Laptikhovsky, 1999).

Brachioteuthis riisei Steenstrup, 1882

Very little is known regarding this squid, to the point that currently there is not even a single publication on its biology or ecology. In fact, the entire family Brachioteuthidae currently requires revision and the available literature only refers to sporadic findings. According to Guerra (1992), *B. riisei* occurs worldwide; however, the limits of its distribution remain uncertain. Although juveniles, including the early juvenile stages, are abundant in the northeast Atlantic, adults are rarely caught. From a total of 592 cephalopods collected during the surveys conducted between 1979 and 1999 off the western coast of Scotland and Ireland, only two adults were caught (Collins *et al.*, 2001). In the same area, however, the early life stages were abundant in the surface waters over the continental slope deeper than 200 m (Collins *et al.*, 2002). In the southern waters, however, the abundance of the paralarvae appears to decrease as Moreno *et al.* (2009) and Salman *et al.* (2003), respectively, found only one paralarva off the Iberian Peninsula (3.5 mm ML over a bottom depth of 500 m) and the Mediterranean Sea (3.2 mm ML at 968 m).

In the Mediterranean, where the species has regularly been recorded since more than a hundred years ago (e.g. Jatta, 1896; Naef, 1923; Degner, 1926), *B. riisei* is sporadically caught both in the western (González & Sánchez, 2002; Quetglas *et al.*, 2000) and eastern (D'Onghia *et al.*, 1995; Lefkaditou *et al.*, 2000) basins. All of our specimens were captured at depths between 350 and 780 m using bottom trawl gears. Besides the data provided in our study, the recent findings containing biological information include

the three males (one mature and two maturing) ranging between 5.2 and 6.0 mm ML caught at 540-590 m depth in the Ionian Sea (D'Onghia *et al.*, 1995), and the mature female with 66 mm ML picked up at 380-418 m depth in the Aegean Sea (Lefkaditou *et al.*, 2000). The presence of the paralarvae (Salman *et al.*, 2003) and sexually mature individuals of both sexes suggests that reproduction takes place through the entire Mediterranean.

The higher frequency of occurrence in the Alboran Sea (east of the Strait of Gibraltar) than along the eastern Mediterranean coast of the Iberian Peninsula and the Balearic Islands suggests an Atlantic origin of the individuals captured in the Mediterranean, besides the specimens of Mediterranean origin. Furthermore, the increase in individual size with increasing distance from the Strait of Gibraltar could indicate an ontogenetic migration towards the eastern waters. The findings of large aggregations of small-sized individuals during the times of high primary production, such as the one reported here in the Alboran Sea, could also indicate that shoals, at least those of juveniles move in search of those food-rich events. Such events could be the result of upwelling conditions, as the pelagic cephalopods are known to be associated with hydrographic regimes (Coelho, 1985).

Chiroteuthis veranyi Férussac, 1835

This species occurs in the Atlantic, including the Mediterranean, between 60°N and 25°S, and the subtropical areas of the Pacific and Indian Oceans (Guerra, 1992). Very little is known regarding the biology or ecology of this species, and the only currently available scientific literature comprises taxonomic descriptions of material collected in the Southern Ocean (Rodhouse & Lu, 1998) and around the New Zealand waters (Mensch, 2010). It is a typical oceanic squid, where the adults live in the bathypelagic and mesopelagic depths down to 2000 m rising to the surface only at night, while the juveniles and paralarvae are scattered through the entire water column (Guerra, 1992).

Paralarvae have been collected in the Pacific and Atlantic Oceans, including the Mediterranean. Okutani & McGowan (1969) reported data on the systematics, distribution and abundance of the larval stages of cephalopods from 28 cruises undertaken between 1954 and 1957 in the California Current by the California Cooperative Oceanic Fisheries (CalCOFI). A total of 103 individuals of *C. veranyi* ranging from 7 to 25 mm ML appeared in 76 of the 3895 tows undertaken; data on seasonal abundances indicated that the species is a summer spawner. Moreno *et al.* (2009) took four paralarvae offshore, ranging between 4.8 and 16.8 mm ML, over the bottom depths of 210-3000 m, between January and March in the northeast Atlantic. In the Mediterranean, Sánchez & Molí (1985) found a paralarva with 3.1 mm ML during samplings between the surface and 200 m depth in the western basin, whereas Lefkaditou *et al.* (1999) collected four paralarvae ranging between 16 and 31 mm ML between 250 and 750 m depth

in the eastern basin. In his samplings of larval and juvenile cephalopods throughout the Mediterranean, Roper (1972) caught only four individuals with 40-52 mm ML at different depths.

The species has been recorded in the Mediterranean since more than a hundred years ago (e.g. Lozano-Rey, 1905; Degner, 1926), where it was sporadically caught both in the western (Quetglas *et al.*, 2000; González & Sánchez, 2002) and eastern (Kaspiris & Tsiambao, 1984; Salman *et al.*, 2002) basins. Together with the data provided in our study, the findings containing some biological data include: 1) Morales (1958) reported two individuals caught in the summer, an indeterminate specimen of 60 mm ML and a mature female of 92 mm ML with egg sizes ranging between 0.07 and 0.15 mm; 2) Kaspiris & Tsiambao (1984) collected six specimens ranging from 41 to 64 mm ML with a commercial trawler, working up to a maximum depth of 320 m; 3) Tursi *et al.* (1994) found an immature individual of 36 mm ML at 627 m depth in the Ionian Sea; 4) Salman *et al.* (2003) took a specimen of 54 mm ML at 650 m in the Aegean Sea. The presence of early life stages and sexually mature individuals of both sexes would indicate that reproduction occurs in the Mediterranean. Considering the mature female reported by Morales (1958) and the two mature males caught by us in July, reproduction could also take place during the summer, as has been suggested for the Pacific populations (Okutani & McGowan, 1969).

Chtenopteryx sicula Vérany, 1851

This species is widespread in the tropical and subtropical oceans, including the Mediterranean (Guerra, 1992). Very little is known about its life cycle or ecology and the only currently available publications deal with just the taxonomical aspects, bathymetric distribution and ontogenetic changes during the paralarval stages. The taxonomic studies (Young, 1991; Brierley *et al.*, 1996) conclude that the species is more related to the myopsid loliginid species than to the oegopsids under which it has been traditionally classified. Shea & Vecchione (2002) found discontinuities at three different sizes in the paralarval development, which appear to be related to their locomotor ability. The paralarval daytime depth distribution showed a gradual, ontogenetic descent into the deeper waters with increasing size, whereas at night, all individuals, regardless of size, were taken in the upper 200-300 m (Shea & Vecchione, 2010).

Adults are typical oceanic squids inhabiting depths of 500-1000 m during the day and rising at night to feed in the shallower waters (Norman, 2003). The species is quite abundant off the Namibian waters compared with the central and western South Atlantic (Nesis, 1991) waters, where Roeleveld *et al.* (1992) reported the species off eastern South Africa. Vecchione *et al.* (2010) reported 14 specimens from 10 to 69 mm ML collected in the northern Mid-Atlantic Ridge. In the Mediterranean, *C. sicula*

is sporadically caught by bottom trawl gears (Quetglas *et al.*, 2000; González & Sánchez, 2002; Lefkaditou *et al.*, 2003a,b). Villanueva (1992b) collected one female with 54 mm ML at 1099 m depth in the western basin. The fact that five out of the six squids in our samples were caught in July could indicate the different availability to bottom trawl gears related to certain life cycle characteristics, probably reproduction, because maturing and mature females were present in the samples. Furthermore, the only individual taken in March was clearly smaller (40 mm ML) than the ones caught in July (57-79 mm ML).

Paralarvae have been found in the Pacific and Atlantic oceans and the Mediterranean. In the Pacific, Okutani & McGowan (1969) found a single specimen with 8 mm ML on analysing the 3895 tows undertaken by the CalCOFI between 1954 and 1957. Vecchione *et al.* (2001) collected 37 specimens in the northwest Atlantic, and noted that, although not particularly abundant, the ubiquity of this species contrasted with the paucity of adults in the trawl surveys. Sampling down to 1000 m depth in the Gulf of Mexico, Passarella & Hopkins (1991) collected only this species in the shallow waters (0-200 m) at night. Moreno *et al.* (2009) found a single paralarva with 2.1 mm ML in the high seas, at over a 2000 m bottom depth in the north-east Atlantic. Roper (1974) collected up to 21 juvenile or paralarval stages (5-25 mm ML) along the Mediterranean using a net-closing device, most of them during summertime and restricted to night samplings undertaken in depths shallower than 150 m. Two occurrences of a single paralarva have been reported in the Mediterranean, a paralarva of 3.1 mm ML collected during the daytime between 0 and 200 m in the western basin (Sánchez & Molí, 1985), and another one with 9.0 mm ML collected at 100 m depth in the eastern basin (Salman *et al.*, 2003).

Ocythoe tuberculata Rafinesque, 1814

This is a cosmopolitan epipelagic octopus inhabiting the tropical and subtropical waters (Guerra, 1992). Biological information on this species exists from the records of their sporadic findings, most of which are in the Mediterranean. In the western basin, Morales (1958) found two females of 115 and 230 mm ML; the first caught in June by a commercial bottom trawler had an hectocotylus stuck to their arms, while the second one was caught in April by a purse seiner at 29 m depth; Sánchez (1980) reported a single female (290 mm ML) caught during June, in the surface coastal waters; and Pretus & De Pablo (1993) reported a female (250 mm ML) taken by trammel nets in March at 80-90 m depth. In the eastern basin, Tutman *et al.* (2008) caught three females, an immature octopus of 77 mm ML in March, and two mature specimens with 178 and 202 mm ML collected in May and June, respectively, and reported the information on fecundity ($18 \cdot 10^4$ - $22 \cdot 10^4$ eggs), oocyte size (0.1-3.9 mm) and stomach contents (remains of fish and gelatinous plankton organisms); Lapikhovsky & Salman (2003) also presented data on fecun-

dity ($20 \cdot 10^4$ eggs) and oocyte size (0.1-3.7 mm) from a single mature female (170 mm ML) caught in September; Salman & Akalin (2012) reported two females taken in April and May (ML=285 and 335 mm, respectively), the second one being the biggest individual collected worldwide and showing the highest known fecundity for an octopod ($\sim 10^6$ eggs).

In the North Atlantic, Caballero-Alfonso *et al.* (2009) reported two females with 188 and 245 mm ML caught at the sea surface by live bait boats in June and July, respectively, off the northwest Iberian Peninsula. Such uncommon findings north of the Azores (41°-45°N) were found to be related to a seasonal warming process and an anomalous peak abundance of jellyfish; males and young females are sometimes found inhabiting the tests of salps (Naef, 1923; Okutani & Osuga, 1994). Vecchione *et al.* (2010) reported two specimens with 9 and 71 mm ML collected in the northern Mid-Atlantic Ridge. In the South Atlantic, Nesis (1991) found *O. tuberculata* off the Namibian waters at depths shallower than 100 m. In the Pacific, Honma *et al.* (2007) histologically examined the ovary and associated appendages from a single female caught in February, off Japan.

Including the two mature females reported in the present study, most mature individuals were found during May-June, which could indicate a peak in reproduction. During that period, mature females would approach the coastal waters and becoming more vulnerable to fishing or stranding. Paralarvae of the species were first described by Sweeney *et al.* (1992). However, the paralarvae had never been identified in the eastern Atlantic or Mediterranean, until Moreno *et al.* (2009) reported the collection of a single individual (6 mm ML), in June, in the top 200 m layer of the high seas off the western Iberian Peninsula, over a bottom depth of 4318 m. The arm formula of our specimen (I=IV.III.II) differs from that (I=IV.II=III) presented by Guerra (1992).

Onychoteuthis banksii Leach, 1817

The systematics and phylogeny of the family Onychoteuthidae has been extensively reviewed during recent years (Bolstad, 2007, 2008, 2010; Bonnaud *et al.*, 1998; Nesis, 2000). Prior to these reviews, and owing to the systematic disarray of the genus *Onychoteuthis*, *O. banksii* was believed to be composed of a complex of sympatric species with similar morphology and ecology inhabiting the Pacific, Atlantic and Indian Oceans. Furthermore, also until recent years, the mature females of *O. banksii* were considered a separate species on its own, *Chaunoteuthis mollis*, based on the marked morphological differences with respect to the males and young females due to sexual maturation (Arkhipkin & Nigmatullin, 1997; Bello, 1998). However, *O. banksii* is now considered to be restricted to the Central and North Atlantic, including the Gulf of Mexico, occurring commonly at the surface, at night, but down to 800 m during the day (Bolstad, 2008).

Arkhipkin & Nigmatullin (1997) studied the various biological and ecological aspects (age, growth, reproduction, diet and parasites) of the *O. banksii* complex from individuals collected in the Gulf of Guinea, the southeast Pacific and northwest Atlantic. Stomach contents revealed an opportunistic predator, showing an ontogenetic shift in diet from small crustaceans during the young stages to a diet including fish and squid when they reached adulthood. The length-weight relationship of this *O. banksii* complex indicated higher growth rates ($a=2.11 \cdot 10^{-1}$, $b=2.18$; Arkhipkin & Nigmatullin, 1997) when compared with the Mediterranean samples ($a=1.26 \cdot 10^{-3}$, $b=1.74$; this study).

According to Bello (1998) only four mature females, earlier known as *C. mollis*, had been reported in the Mediterranean before our finding; all these specimens were found floating dead on the water surface. In our case, however, a mature female was caught near 900 m depth using a pelagic trawl gear, although most of our *O. banksii* specimens were found in the shallower waters between 500 and 750 m. The good condition in which we found our mature female, together with the high GSI value (14.5%) suggests that it was in the late maturation stages or close to spawning, which consequently could take place at such great depths.

Compared with the scarcity of such adult captures, *O. banksii* is rather abundant in the samplings of paralarval and juvenile stages. In the northwest Atlantic (Vecchione *et al.*, 2001), the species was found to constitute one of the most abundant cephalopods (94 individuals of 2-7 mm ML). In a sample of 591 individuals (5-75 mm ML) taken using net-closing devices in the Mediterranean, *O. banksii* was the most abundant species both in summer and winter, along a broad vertical range, although the heaviest concentrations occurred in the upper 100 m, both during the day and night (Roper, 1974). Sánchez & Molí (1985) found 13 paralarvae ranging between 2.6 and 8.9 mm ML at depths between 0 and 300 m in the western Mediterranean. Moreno *et al.* (2009) collected six paralarvae ranging from 6.8 to 11.2 mm ML in the top 200 m ocean layer, over bottom depths of 230 to 3000 m in the northeast Atlantic. Sampling down to 1000 m depth in the Gulf of Mexico, Passarella & Hopkins (1991) took this species only in the shallow waters (0-200 m) at night, and the stomachs of 52 individuals smaller than 3 mm ML were found to contain mainly the remains of fishes and euphausiids. Okutani & McGowan (1969) analysed 132 specimens ranging from 2 to 47 mm ML from the CalCOFI material and found that the paralarvae were more abundant during the spring and summer; the specimen studied by these authors, however, was misidentified as *O. banksii* because it is now known that this species does not occur in the Pacific (Bolstad, 2008).

Opisthoteuthis calypso Villanueva, Collins, Sánchez and Voss, 2002

Up to the description of *O. calypso* as a new species (Villanueva *et al.*, 2002), the specimens inhabiting the east

Atlantic and the Mediterranean waters were misidentified as *O. agassizii*. After this review, however, the species inhabiting the northwest Atlantic between 10° and 40°N (*O. agassizii*) was considered to be taxonomically different from the species found in the east Atlantic, including the western Mediterranean, between 50°N and 30°S (*O. calypso*). Roeleveld *et al.* (1992) report finding the species off eastern South Africa.

Several aspects of the biology of this species including distribution, reproduction and diet, have been studied from the samples collected in the east Atlantic (off Namibia, Villanueva, 1992a; Villanueva & Guerra, 1991), off Portugal (Rosa *et al.*, 2009) and the Mediterranean (Cuccu *et al.*, 2009; Sartor & Belcari, 2009). Reproduction apparently occurs throughout the year in the Namibian waters (females showed continuous egg production over the entire adult life) and considerable growth occurred in both sexes following the onset of sexual maturity (Villanueva, 1992a). This could also be the case in the Mediterranean, as both maturing and mature individuals have been caught throughout a protracted period of time (January, May and September, Cuccu *et al.*, 2009; September, Sartor & Belcari, 2009; July, August and November, this study). Ovarian oocyte size distributions indicate a continuous-spawning reproductive pattern both in the Namibian (Villanueva, 1992a) and Mediterranean (Cuccu *et al.*, 2009; Sartor & Belcari, 2009) waters.

Individuals found off Namibia are clearly larger (4-5400 g TW, Villanueva, 1992a) than those collected off Portugal (5-522 g TW, Rosa *et al.*, 2009) and the Mediterranean (18-243 g TW, Cuccu *et al.*, 2009; 48-162 g TW, Sartor & Belcari, 2009; 1-137 g TW, this study) and appear to inhabit the shallower waters. Such size differences among locations of findings could explain the decrease of the slope value in the length-weight relationship from Namibia ($b=3.10$, Villanueva & Guerra, 1991), Portugal ($b=2.74$, Rosa *et al.*, 2009) and the Mediterranean ($b=2.60$, this study). Most individuals were picked up at 365-570 m depth off Namibia (Villanueva, 1992a), while at 775-815 m off Portugal (Rosa *et al.*, 2009) and between 685-2208 m in the Mediterranean (871-1420 m, Cuccu *et al.*, 2009; 710 m, Sartor & Belcari, 2009; 1204-2208 m, Villanueva, 1992a; 685-895 m, this study). Although Villanueva (1992a) observed a tendency for the specimens of both sexes to increase in weight, and consequently reach the sexual maturity stage, with depth, Rosa *et al.* (2009) did not discover any such tendency. The species preys upon small epibenthic and suprabenthic crustaceans, mostly amphipods and mysids, and polychaetes (Villanueva *et al.*, 2002; Cuccu *et al.*, 2009; Sartor & Belcari, 2009). In our bibliographic searches we did not find a single record of the paralarva of this species nor any indication of its presence as a prey item in the stomach contents of any predator.

The species, however, appears regularly in the studies on cephalopod assemblages from the Mediterranean Sea covering middle slope depths (Villanueva, 1992b; Quetglas

et al., 2000; González & Sánchez, 2002). However, together with Cuccu *et al.* (2009) and Sartor & Belcari (2009), a few authors report some biological data regarding this octopus: 1) Morales (1962) reported two individuals caught in August (43 mm ML) and September (18 mm ML) at 670-690 m and 560-576 m, respectively; 2) Villanueva (1992b) collected three males, one female and three unsexed specimens ranging between 17 and 35 mm ML at depths between 1204 and 2208 m; and 3) Orsi-Relini *et al.* (2001) found a juvenile with 20 mm ML at 600 m depth.

Stoloteuthis leucoptera Verrill, 1878

Very little is known about this sepiolid, to the point that currently not a single study on its biology or ecology exists today. Although it frequently occurs in the northwest Atlantic (Cairns, 1976; Roper & Young, 1975; Vecchione *et al.*, 1989; Vecchione & Roper, 1991), reports from other areas are scarce. Villanueva & Sánchez (1993) found the species in the Benguela Current off Namibia and provided a detailed morphological description of this species. In samplings of paralarval cephalopod assemblages conducted throughout the year in the northwest Atlantic, Vecchione *et al.* (2001) found this sepiolid only in the winter where the bottom depths exceeded 138 m. However, it is noteworthy that *S. leucoptera* was the most common cephalopod consumed by the onychoteuthid squid *Moroteuthis ingens* collected in the Southern Ocean, appearing in 25% of the stomachs and comprising 74% of the identifiable cephalopod remains (Phillips *et al.*, 2003).

This sepiolid has been recorded several times in the western Mediterranean (Sánchez *et al.*, 1998; Wurtz *et al.*, 1995). The following publications included some data on the specimens captured: 1) Orsi-Relini & Massi (1991) reported three individuals (8.5, 9.5 and 11.5 mm ML, respectively) taken by commercial bottom trawlers at between 250 and 400 m depth, which were considered a recent immigration from the east Atlantic; 2) Volpi *et al.* (1995) collected a male of 18 mm ML at 461 m depth in the Ligurian Sea; and 3) Cuccu *et al.* (2010) took two mature females of 10.4 and 14.5 mm ML at 550 and 360 m depth in summer and winter, respectively. A total of 25 individuals taken between 324 and 612 m depths were found in our samples, most of them in the Alboran Sea, east of the Strait of Gibraltar where the Mediterranean connects with the Atlantic. Although our samplings were undertaken between 1994 and 2010, the species was present only in 2001, and later, between 2003 and 2006. However, the oceanographic conditions (SST, Chla, wind speed) during these years did not reveal any special variations when compared with the remaining years, which could indicate that the findings are the result of sporadic, irregular events of immigration from the Atlantic. According to Bello (2011), *S. leucoptera* currently has a stable self-sustaining population in the western Mediterranean, after entering through the Strait of Gibraltar and reaching the Liguro-Provençal basin in the mid-1980s.

Taonius pavo LeSueur, 1821

Similar to the previous species, very little is known about this squid and there is no existing study on its biology or ecology. According to Voss (1980), who included *T. pavo* in her revision of the family Cranchiidae, the species has a circumglobal distribution between the subantarctic and subarctic waters and inhabits waters from the subsurface to depths greater than 2000 m. The species shows an ontogenetic migration to the deeper waters, as the paralarvae live at depths of 300-400 m, juveniles at 600-650 m and adults deeper than 700 m (Lu & Roper, 1979). Moreno *et al.* (2009) collected eleven paralarvae ranging between 2.5 and 15.6 mm ML within the top 200 m of the water column, between depths of over 800 to 4000 m in the northeast Atlantic. Sampling done between the surface and 1000 m depth in the Pacific Ocean off Oregon, showed that the species was more abundant at 0-500 m than at 0-200 or 0-1000 m (Pearcy, 1965). Abbes (1970) captured two individuals (52 and 72 mm ML) between 1280 and 4000 m depth in the northeast Atlantic and gave a detailed morphological description of the species. Vecchione *et al.* (2010) reported 23 specimens from 72 to 300 mm ML collected in the northern Mid-Atlantic Ridge.

Previous to our finding, the species had not been reported in the Mediterranean (e.g. Bello, 2008). The paucity of other findings in the area, in spite of the regular samplings undertaken since 1994, plus the fact that three out of the four individuals were collected in the same month, could suggest, as in the case of other species, sporadic events of immigration from the Atlantic. Although the scarcity of findings of adults or juveniles in the adjoining Atlantic waters does not concur with this idea, this species was among the most abundant paralarvae of the deep-sea squids in the Gulf of Cadiz (Moreno *et al.*, 2009). It could also be a fact that, although very rare, the species was actually a permanent member of the Mediterranean teuthofauna. In fact, the species could go unnoticed because, at least in our case, it was not easy to distinguish a cephalopod with such a soft, transparent body once it reached the boat deck. Although the species of the genus *Taonius* are large squids reaching up to 660 mm ML (Young & Mangold, 2011), our specimens were small-sized, undetermined juveniles between 97 and 173 mm ML. Hatching in the east Atlantic would occur at the end of the year according to the paralarvae collected in January-February by Moreno *et al.* (2009). The arm formula of our individual taken in 2010 (IV.III.II.I) did not concur with that (III.II.IV.I) given by Voss (1980), although it is closer to the formula (III.IV.II.I) reported by Abbes (1970).

By contrast to the dearth of findings of live specimens, *T. pavo* appears frequently in the stomach contents of the teuthophagous predators in all world oceans, especially in whales (Yatabe *et al.*, 2010) and also in fur seals (Field *et al.*, 2007), seabirds (Cooper & Klages, 2009), oceanic squids (Watanabe *et al.*, 2004) and deep-sea fishes (Bergstad *et al.*, 2010).

Tremoctopus violaceus Delle Chiaje, 1830

This is an epipelagic octopus occurring in the Atlantic between 40°N and 35°S, including the Gulf of Mexico, Caribbean Sea and Mediterranean Sea (Thomas, 1977). This species is characterised by being the most extreme example for sexual size-dimorphism in a non-microscopic animal (Norman *et al.*, 2002) and its associations with coelenterates such as *Physalia* as an offensive and defensive mechanism (Jones, 1963).

Here, we review the records of the live specimens collected after the excellent work of Thomas (1977), which in most cases come from the Mediterranean. Lozano-Soldevilla (1991) reported two immature females with 150 and 110 mm ML taken in May in the northeast Atlantic. Biagi & Bertozzi (1992) reported an unusual capture of 10-20 females through a period of 20 days during July 1990 by a purse-seiner in the boundary between the Ligurian and Tyrrhenian Seas. Bello (1993) found the remains of a mature female (estimated size 90 mm ML and eggs measuring 1.1x0.9 mm) in the stomach contents of a swordfish captured in the Adriatic Sea. Laptikhovsky & Salman (2003) studied the reproductive biology from five individuals taken in July of different years (between 1990 and 1996) in the Aegean Sea. In this study, we report a single mature female found stranded on a beach of the Balearic Islands in July 2000. The fact that most findings of mature females occur in July would indicate that they approach the coastal waters for reproduction during the summer, showing an increased vulnerability to fishing or stranding as in the case of the epipelagic octopus *O. tuberculata*. However, we did not find any record of the paralarvae of this octopus in the literature.

Once again, the arm formula of our specimen (II.I.III.IV) did not concur with those (II.I.IV.III or I.II.IV.III) reported by Guerra (1992). Laptikhovsky & Salman (2003) classified the species as an intermittent terminal spawner based on oocyte size distributions and fecundity estimates ($1 \cdot 10^5$ - $3 \cdot 10^5$); oocyte sizes from our individual (2.0-2.5 mm) were similar to the sizes reported by those authors for mature and spawning females. Findings of live specimens in other areas include the Andaman Sea in the Indian Ocean (Nabhitabhata *et al.*, 2009), Arabian Sea (Chesalin & Zuyev, 2002) and the south Australian and New Zealand waters (Norman *et al.*, 2002; Zeidler, 1989).

Concluding remarks

Although the pelagic cephalopods are some of the main faunal components of the oceanic ecosystems, they are also some of the most poorly understood, largely due to the inability of the present day sampling equipment to catch them (Lansdell & Young, 2007). The very low number of published studies focused specifically on the pelagic species reported here is a clear reflection of this paucity of knowledge. The scarcity of the captures worldwide represents the disadvantage to fully understand the

life-history of these species. Therefore, scientists should benefit from the limited and fragmentary information reporting sporadic findings from different sources, as done in the present study. Here, we have compiled data on eleven pelagic cephalopod species, which are considered very rare on a global level, collected during more than fifteen years of fishery surveys in the western Mediterranean. Although limited, we believe the information provided in this study will greatly enhance the available knowledge on the biology and ecology of these rather lesser known pelagic species.

Acknowledgements

We are grateful to all the participants in the scientific surveys BALAR-MEDITS, IDEA (REN2002-04535-C01-02/MAR) and IDEADOS (CTM2008-04489-C03-01/MAR), as well as to the fishermen of the Balearic Islands for their kindness during the sampling collection on board the commercial vessels. Our thanks are due especially to Dr. G. Bello for providing bibliography and information, as well as for making useful suggestions to improve the manuscript. We are very grateful to Dr. R. Villanueva for providing bibliography.

References

- Abbes, R., 1970. Remarques sur quelques céphalopodes mésopélagiques du Golfe de Gascogne. *Revue des Travaux de l'Institut des Pêches Maritimes*, 34 (2), 195-204.
- Adam, W., 1954. Cephalopoda. 3e Partie. IV. Cephalopodes à l'exclusion des genres *Sepia*, *Sepiella* et *Sepioteuthis*. *Siboga Expeditions Monographie*, 33c, 123-193.
- Aguiar dos Santos, R., Haimovici, M., 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21-34° S). *Fisheries Research*, 52 (1), 99-112.
- Arkhipkin, A.I., 1996. Age and growth of the squid *Abraliopsis pfefferi* (Oegopsida: Enoploteuthidae) from the central-east Atlantic based on statolith microstructure. *Scientia Marina*, 60 (2-3), 325-330.
- Arkhipkin, A.I., 1997. Age and growth of the mesopelagic squid *Ancistrocheirus lesueurii* (Oegopsida: Ancistrocheiridae) from the central-east Atlantic based on statolith microstructure. *Marine Biology*, 129 (1), 103-111.
- Arkhipkin, A.I., Nigmatullin, C.M., 1997. Ecology of the oceanic squid *Onychoteuthis banksi* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the UK*, 77 (3), 839-869.
- Bello, G., 1993. *Tremoctopus violaceus* (Cephalopoda: Tremoctopodidae) in the stomach content of a swordfish from the Adriatic Sea. *Bolletino Malacologico*, 29, 45-48.
- Bello, G., 1998. *Chaunoteuthis mollis*: re-examination of a Mediterranean specimen and its identity with *Onychoteuthis banksii* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the UK*, 78 (3), 1027-1030.

- Bello, G., 2000. How rare is *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) in the eastern Mediterranean Sea? *Journal of Molluscan Studies*, 66, 575-577.
- Bello, G., 2005. *Abraliopsis morisii* vs. *Abraliopsis pfefferi* (Cephalopoda: Eupoloteuthidae): which is the right name? *Journal of Conchology*, 38, 561-565.
- Bello, G., 2008. Cephalopoda. *Biologia Marina Mediterranea*, 15 (Suppl.), 318-322.
- Bello, G., 2011. The “alien” status of the cephalopods in the Checklist of the flora and fauna of the Italian seas: a matter of terminology. *Bollettino Malacologico*, 48, 131-134.
- Bello, G., Pipitone, C., 2002. Predation on cephalopods by the giant red shrimp *Aristaeomorpha foliacea*. *Journal of the Marine Biological Association of the UK*, 82 (2), 213-218.
- Bello, G., Potoschi, A., Berdar, A., 1994. Adult of *Ancistrocheirus lesueurii* caught in the Straits of Messina (Cephalopoda: Ancistrocheiridae). *Bollettino Malacologico*, 29 (9-12), 259-266.
- Bergstad, O.A., Gjelsvik, G., Schander, C., Hoines, A.S., 2010. Feeding ecology of *Coryphaenoides rupestris* from the Mid-Atlantic Ridge. *Plos One*, 5 (5), e10453. doi:10.1371/journal.pone.0010453.
- Bertrand, J.A., Leonori, I., Dremière, P.Y., Cosimi, G., 2002. Depth trajectory and performance of a trawl used for an international bottom trawl survey in the Mediterranean. *Scientia Marina*, 66 (Suppl. 2), 169-182.
- Biagi, V., 1980. Sul rinvenimento e la cattura di un esemplare vivente di *Ocythoe tuberculata* (Raf.) femmina (Cephalopoda-Octopoda) nelle acque del canale di Piombino. *Bollettino Malacologico*, 16 (3-4), 41-52.
- Biagi, V., Bertozzi, A., 1992. Presenza stagionale di *Tremoctopus violaceus* Delle Chiaie, 1830 (Cephalopoda: Octopoda) nel mare di Piombino (Li). *Bollettino Malacologico*, 28 (1-4), 47-54.
- Blanco, C., Aznar, J., Raga, J.A., 1995. Cephalopods in the diet of the striped dolphin *Stenella coeruleoalba* from the Western Mediterranean during an epizootic in 1990. *Journal of Zoology*, 237 (1), 151-158.
- Blanco, C., Raduan, M.A., Raga, J.A., 2006. Diet of Risso's dolphin (*Grampus griseus*) in the western Mediterranean Sea. *Scientia Marina*, 70 (3), 407-411.
- Bolstad, K.S., 2007. Systematics and distribution of the New Zealand onychoteuthid fauna (Cephalopoda: Oegopsida), including a new species, *Notonychia nesi* sp. nov. *Reviews in Fish Biology & Fisheries*, 17 (2-3), 305-335.
- Bolstad, K.S., 2008. Two new species and a review of the squid Genus *Onychoteuthis* Lichtenstein, 1818 (Oegopsida: Onychoteuthidae) from the Pacific Ocean. *Bulletin of Marine Science*, 83 (3), 481-529.
- Bolstad, K.S., 2010. Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Zootaxa*, 2696, 1-186.
- Bonnaud, L., Rodhouse, P.G., Boucher-Rodoni, R., 1998. A phylogenetic study of the squid family Onychoteuthidae (Cephalopoda: Oegopsida). *Proceedings of the Royal Society B: Biological Sciences*, 265 (1407), 1761-1770.
- Brierley, A.S., Clarke, M.R., Thorpe, J.P., 1996. *Ctenopteryx sicula*, a bathypelagic loliginid squid? *American Malacological Bulletin*, 12, 137-143.
- Caballero-Alfonso, A.M., Ganzedo-López, U., Díez-Díez, G., Castro, J.J., 2009. New record of *Ocythoe tuberculata* (Cephalopoda: Ocythoidea) in the North-east Atlantic related to sea warming. *Marine Biodiversity Records*, 2, e79. doi: <http://dx.doi.org/10.1017/S1755267209000657>. (Published online).
- Cairns, S., 1976. Cephalopods collected in the Straits of Florida by the R/V Gerda. *Bulletin of Marine Science*, 26 (2), 233-272.
- Cherel, Y., Fontaine, C., Jackson, G.D., Jackson, C.H., Richard, P., 2009. Tissue, ontogenic and sex-related differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the oceanic squid *Todarodes filipovae* (Cephalopoda: Ommastrephidae). *Marine Biology*, 156 (4), 699-708.
- Cherel, Y., Hobson, K.A., 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proceedings of the Royal Society B: Biological Sciences*, 272 (1572), 1601-1607.
- Chesalin, M.V., Zuyev, G.V., 2002. Pelagic cephalopods of the Arabian Sea with an emphasis on *Sthenoteuthis oualensis*. *Bulletin of Marine Science*, 71 (1), 209-221.
- Clarke, M.R., 1996a. The role of cephalopods in the world's oceans: an introduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351 (1343), 979-983.
- Clarke, M.R., 1996b. The role of cephalopods in the world's oceans: general conclusion and the future. *Philosophical Transactions of the Royal B: Biological Sciences*, 351 (1343), 1105-1112.
- Clarke, M.R., Lu, C.C., 1975. Vertical distribution of cephalopods at 18°N 25°W in the North Atlantic. *Journal of the Marine Biological Association of the UK*, 55 (1), 165-182.
- Clarke, M.R., Pascoe, P.L., 1998. The influence of an electric light on the capture of oceanic cephalopods by a midwater trawl. *Journal of the Marine Biological Association of the UK*, 78 (2), 561-575.
- Coelho, M.L., 1985. Review of the influence of oceanographic factors on cephalopod distribution and life cycles. *NAFO Scientific Council Studies*, 9, 47-57.
- Colabuono, F.I., Vooren, C.M., 2007. Diet of black-browed *Thalassarche melanophrys* and Atlantic yellow-nosed *T. chlororhynchus* albatrosses and white-chinned *Procellaria aequinoctiales* and spectacled *P. conspicillata* petrels off Southern Brazil. *Marine Ornithology*, 35 (1), 9-20.
- Collins, M.A., Yau, C., Allcock, L., Thurston, M.H., 2001. Distribution of deep-water benthic and benthic-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association of the UK*, 81 (1), 105-117.
- Collins, M.A., Yau, C., Boyle, P.R., Friese, D., Piatkowski, U., 2002. Distribution of cephalopods from plankton surveys around the British Isles. *Bulletin of Marine Science*, 71 (1), 239-254.
- Cooper, J., Klages, N.T.W., 2009. The winter diet of the great-winged petrel *Pterodroma macroptera* at sub-Antarctic Marion Island in 1991. *Marine Ornithology*, 37 (3), 261-263.
- Corsini, M., Lefkaditou, E., 1995. Occurrence of *Ocythoe tuberculata* (Cephalopoda: Ocythoidea) in Greek waters. *Bollettino Malacologico*, 30, 304-310.
- Cuccu, D., Mereu, M., Cannas, R., Follesa, M.C., Cau, A. et al., 2009. Morphology, biology and molecular characterizations of *Opisthoteuthis calypso* (Cephalopoda: Octopoda) from the Sardinian Channel (central western Mediterranean). *Journal of the Marine Biological Association of the UK*, 89 (8), 1709-1715.
- Cuccu, D., Mereu, M., Masala, P., Cau, A., Jereb, P., 2010. First record of *Stoloteuthis leucoptera* (Cephalopoda: Sepiolidae)

- in the Sardinian waters. p. 306-307. In: *41st Congress of the Società Italiana di Biologia Marina, Rapallo (GE), 7-11 June 2010*.
- Degner, E., 1926. Cephalopoda. *Report on the Danish Oceanographic Expeditions 1908-10 to the Mediterranean and adjacent seas. 9, Vol. II. Biology*, C1, 1-94.
- D'Onghia, G., Maiorano, P., Panetta, P., 1995. *Octopoteuthis sicula* (Rüppell, 1844) and *Brachioteuthis riisei* (Steenstrup, 1882) (Cephalopoda: Teuthoidea) from the northwestern Ionian Sea. *Bolletino Malacologico*, 31 (5-8), 137-142.
- D'Onghia, G., Maiorano, P., Tursi, A., 1997. Morphometric and biological data on *Ancistrocheirus lesueurii* (Orbigny, 1842) from the middle-eastern Mediterranean Sea. *Scientia Marina*, 61 (3), 389-396.
- Field, I.C., Bradshaw, C.J.A., van den Hoff, J., Burton, H.R., Hindell, M.A., 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology*, 150, 1441-1452.
- González, M., Sánchez, P., 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Scientia Marina*, 66 (Suppl. 2), 199-208.
- Guerra, A., 1992. Mollusca, Cephalopoda. *Fauna Ibérica. Vol. I*. Museo Nacional de Ciencias Naturales, CSIC, Madrid, 327 pp.
- Guijarro, B., Massutí, E., 2006. Selectivity of diamond- and square-mesh codends in the deepwater crustacean trawl fishery off the Balearic Islands (western Mediterranean). *ICES Journal of Marine Science*, 63 (1), 52-67.
- Honma, Y., Ushiki, T., Takeda, M., Nakamura, Y., 2007. Notes on the histology of ovarian eggs of the epipelagic octopus *Ocythoe tuberculata* caught off Naoetsu port, Niigata Prefecture, Sea of Japan. *Venus*, 65 (4), 345-353.
- Hoving, H.J.T., Roeleveld, M., Lipinski, M.R., Videler, J.J., 2006. Nidamental glands in males of the oceanic squid *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae) - sex change or intersexuality? *Journal of Zoology*, 269 (3), 341-348.
- Jatta, G., 1896. I Cefalopodi viventi nel Golfo di Napoli. *Fauna e Flora del Golfo di Napoli: Monografia della Stazione Zoologica di Napoli, No. 23*. R. Friedländer & Sohn, Berlin, 268 pp.
- Jereb, P., Roper, C.F.E. (Eds), 2010. Cephalopods of the world: an annotated and illustrated catalogue of species known to date. Vol. 2. Myopsid and Oegopsid Squids. *FAO Species Catalogue for Fishery Purposes, No. 4*. FAO, Rome, 605 pp.
- Jones, E.C., 1963. *Tremoctopus violaceus* uses *Physalia* tentacles as weapons. *Science*, 139 (3556), 764-766.
- Kaspiris, P., Tsiambao, S.P., 1984. Some uncommon cephalopods from western Korinthiakos Gulf (Mollusca: Dibranchiata). *Bilješke-Notes*, 62, 1-4.
- Kear, A.J., 1994. Morphology and function of the mandibular muscles in some coleoid cephalopods. *Journal of the Marine Biological Association of the UK*, 74 (4), 801-822.
- Lansdell, M., Young, J., 2007. Pelagic cephalopods from eastern Australia: species composition, horizontal and vertical distribution determined from the diets of pelagic fishes. *Reviews in Fish Biology & Fisheries*, 17 (2-3), 125-138.
- Laptikhovskiy, V., Salman, A., 2003. On reproductive strategies of the epipelagic octopods of the superfamily Argonautoidea (Cephalopoda: Octopoda). *Marine Biology*, 142 (2), 321-326.
- Laptikhovskiy, V.V., 1999. Fecundity and spawning in squid of families Enoplateuthidae and Ancistrocheiridae (Cephalopoda: Oegopsida). *Scientia Marina*, 63 (1), 1-7.
- Lefkaditou, E., Kallianiotis, A., 2006. New findings of female *Ocythoe tuberculata* in the Northeastern Mediterranean. p. 84. In: *Cephalopod International Advisory Council Symposium 2006 (CIAC '06), 6-10 February 2006, Hobart, Tasmania*.
- Lefkaditou, E., Mytilineou, Ch., Maiorano, P., D'Onghia, G., 2003a. Cephalopod species captured by deep-water exploratory trawling in the north-eastern Ionian Sea. *Journal of Northwest Atlantic Fishery Science*, 31, 431-440.
- Lefkaditou, E., Papaconstantinou, C., Anastasopoulou, K., 1999. Juvenile cephalopods collected in the midwater macroplankton over a trench in the Aegean Sea (Northeastern Mediterranean). *Israel Journal of Zoology*, 45, 395-405.
- Lefkaditou, E., Peristeraki, P., Bekas, P., Tserpes, G., Politou, C.Y. et al., 2003b. Cephalopods distribution in the southern Aegean Sea. *Mediterranean Marine Science*, 4 (1), 79-86.
- Lefkaditou, E., Politou, C.Y., Papaconstantinou, C., 2000. Notes on *Brachioteuthis riisei* (Steenstrup, 1882) and *Onychoteuthis banksi* (Leach, 1817) (Cephalopoda: Teuthoidea) found in the Aegean Sea. *Belgian Journal of Zoology*, 130 (Suppl. 1), 69-73.
- Lozano Rey, L., 1905. Cefalópodos de Cataluña y Baleares. *Revista de la Real Academia de Ciencias Exactas, Físicas y Naturales de Madrid*, 3, 1-62.
- Lozano-Soldevilla, F., 1991. Primera cita de *Tremoctopus violaceus violaceus* Delle Chiaje, 1830 (Octopoda: Tremoctopodidae) en aguas Canarias. *Scientia Marina*, 55 (3), 547-549.
- Lu, C.C., Roper, C.F.E., 1979. Cephalopods from Deepwater Dumpsite 106 (Western Atlantic): vertical distribution and seasonal abundance. *Smithsonian Contributions to Zoology, No. 288*. Smithsonian Institution Press, Washington, 36 pp.
- Maiorano, P., Mastrototaro, F., Casamassima, F., Panetta, P., 1999. Comparative analysis of teuthofauna caught by two different trawl nets. *Biologia Marina Mediterranea*, 6 (1), 579-583.
- Maiorano, P., Sion, L., Carlucci, R., Capezzuto, F., Giove, A. et al., 2010. The demersal faunal assemblage of the north-western Ionian Sea (central Mediterranean): current knowledge and perspectives. *Chemistry & Ecology*, 26 (Suppl.), 219-240.
- Mangold-Wirz, K., 1973. Les cephalopodes récoltés en Méditerranée par le "Jean-Charcot" campagnes Polymede I et II. *Revue des Travaux de l'Institut des Pêches Maritimes*, 37 (3), 391-395.
- Mensch, R., 2010. *A systematic review of the squid genus Chiroteuthis (Mollusca: Cephalopoda) in New Zealand waters*. MSc Thesis. Auckland University of Technology, New Zealand, 130 pp.
- Mintzer, V.J., Gannon, D.P., Barros, N.B., Read, A.J., 2008. Stomach contents of mass-stranded short-finned pilot whales (*Globicephala macrorhynchus*). *Marine Mammal Science*, 24 (2), 290-302.
- Morales, E., 1958. Cefalópodos de Cataluña.I. *Investigación Pesquera*, 11, 3-32.
- Morales, E., 1962. Cefalópodos de Cataluña II. *Investigación Pesquera*, 21, 97-111.
- Moreno, A., Santos, A., Piatkowski, U., Santos, A.M.P., Cabral, H., 2009. Distribution of cephalopod paralarvae in relation

- to the regional oceanography of the western Iberia. *Journal of Plankton Research*, 31, 73-91.
- Murzov, S.A., 1986. Fauna and vertical distribution of squids in the upper epipelagia of the south-east Atlantic. p. 144-145. In: *Abstracts of the 4th All-Union Conference on Commercial Invertebrates, April 1986, Sevastopol, Kiev*.
- Nabhitabhata, J., Sukhsangchan, C., Wongkamhaeng, K., 2009. First record of two pelagic octopods, *Argonauta argo* and *Tremoctopus violaceus* Cf. *gracilis* from the Andaman Sea, Thailand. *Vie et Milieu – Life & Environment*, 59 (1), 39-45.
- Naef, A., 1923. Die Cephalopoden. *Fauna e Flora del Golfo di Napoli: Monografia della Stazione Zoologica di Napoli*, No. 35, R. Friedlaender, Berlin, 863 pp.
- Nesis, K.N., 1987. *Cephalopods of the World*. T.F.H. Publications, Neptune City N.J., 351 pp.
- Nesis, K.N., 1991. Cephalopods of the Benguela upwelling off Namibia. *Bulletin of Marine Science*, 49 (1-2), 199-215.
- Nesis, K.N., 1993. Cephalopods of seamounts and submarine ridges. p. 365-373. In: *Recent advances in cephalopod biology*. Okutani, T., O'Dor, R.K., Kubodera, T. (Eds). Tokai University Press, Tokyo.
- Nesis, K.N., 2000. Squids of the family Onychoteuthidae: Phylogeny, biogeography, and way of life. *Zoologicheskyy Zhurnal*, 79 (3), 272-281.
- Norman, M., 2003. *Cephalopods: a world guide*. Conch Books, Hackenheim, 320 pp.
- Norman, M.D., Paul, D., Finn, J., Tregenza, T., 2002. First encounter with a live male blanket octopus: the world's most sexually size-dimorphic large animal. *New Zealand Journal of Marine & Freshwater Research*, 36, 733-736.
- Okutani, T., McGowan, J.A., 1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current, April 1954-March 1957. *Bulletin of the Scripps Institution of Oceanography*, No. 14. University of California Press, Berkeley & Los Angeles, 90 pp..
- Okutani, T., Osuga K., 1994. A peculiar nesting behavior of *Ocythoe tuberculata* in the test of a gigantic salp, *Tethys vagina*. *Venus*, 45, 67-69.
- Orsi-Relini, L., Mannini, A., Rossi, M., Fiorentino, F., 2001. Un cefalopode nuovo nella fauna italiana: *Opisthoteuthis agassizii* Verril, 1883 (Octopoda, Cirrata, Opisthoteuthidae). *Biologia Marina Mediterranea*, 8, 749-752.
- Orsi-Relini, L., Massi, D., 1991. The butterfly squid *Stoloteuthis leucoptera* in the Mediterranean. *Journal of the Marine Biological Association of the UK*, 71 (1), 47-51.
- Passarella, K.C., Hopkins, T.L., 1991. Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bulletin of Marine Science*, 49 (1-2), 638-659.
- Pearcy, W.G., 1965. Species composition and distribution of pelagic cephalopods from the Pacific Ocean off Oregon. *Pacific Science*, 19, 261-266.
- Phillips, K.L., Jackson, G.D., Nichols, P.D., 2003. Temporal variations in the diet of the squid *Moroteuthis ingens* at Macquarie Island: stomach contents and fatty acid analyses. *Marine Ecology Progress Series*, 256, 135-149.
- Piatkowski, U., Diekmann, R., 2005. A short note on the cephalopods sampled in the Angola Basin during the DIVA-1 expedition. *Organisms Diversity & Evolution*, 5 (Suppl. 1), 227-230.
- Piatkowski, U., Pierce, G.J., Morais da Cunha, M., 2001. Impact of cephalopods in the food chain and their interaction with the environment: preface. *Fisheries Research*, 52 (1-2), 1.
- Pretus, J.L., De Pablo, F., 1993. Nota sobre la captura d'*Ocythoe tuberculata* Rafinesque, 1814 (Cephalopoda: Ocythoidae) en aigües de Menorca. *Bolletí de la Societat d'Història Natural de les Balears*, 36, 61-63.
- Quetglas, A., Carbonell, A., Sánchez, P., 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (north-western Mediterranean). Biological aspects of some deep-sea species. *Estuarine, Coastal & Shelf Science*, 50 (6), 739-749.
- Quetglas, A., Ordines, F., González, M., Franco, I., 2009. Life history of the bathyal octopus *Pteroctopus tetracirrhus* (Mollusca, Cephalopoda) in the Mediterranean Sea. *Deep-Sea Research Part I: Oceanographic Research Papers*, 56 (8), 1379-1390.
- Rodhouse, P.G., Lu, C.C., 1998. *Chiroteuthis veranyi* from the Atlantic sector of the Southern Ocean (Cephalopoda: Chiroteuthidae). *South African Journal of Marine Science*, 20, 311-322.
- Rodhouse, P.G., Symon, C., Hatfield, E.M.C., 1992. Early life-cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series*, 89, 183-195.
- Roeleveld, M.A., Lipiński, M.R., Augustyn, C.J., Stewart, B.A., 1992. The distribution and abundance of cephalopods on the continental slope of the eastern South Atlantic. *South African Journal of Marine Science*, 12 (1), 739-752.
- Roper, C.F.E., 1972. Ecology and vertical distribution of Mediterranean pelagic cephalopods. p. 282-344. In: *Mediterranean Biological Studies, Final Report, Part 5*. Smithsonian Institution Press, Washington, D.C.
- Roper, C.F.E., 1974. Vertical and seasonal distribution of pelagic cephalopods in the Mediterranean Sea: preliminary report. *Bulletin of the American Malacological Union*, May 1974, 27-30.
- Roper, C.F.E., Young, R.E., 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology*, No. 209. Smithsonian Institution Press, Washington, DC, 49 pp.
- Roper, C.F.E., Sweeney, M.J., Nauen, C.E., 1984. FAO species catalogue Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis*, No. 125. FAO, Rome, 277 pp.
- Rosa, R., Pereira, J., Moreno, A., 2009. Bathymetric range, density and reproductive biology of the deep-sea cirrate octopus *Opisthoteuthis calypso* in the Portuguese continental slope. *Journal of the Marine Biological Association of the UK*, 89 (1), 131-134.
- Salman, A., Katağan, T., Benli, H.A., 2002. Cephalopod fauna of the Eastern Mediterranean. *Turkish Journal of Zoology*, 26, 47-52.
- Salman, A., Katağan, T., Benli, H.A., 2003. Vertical distribution and abundance of juvenile cephalopods in the Aegean Sea. *Scientia Marina*, 67 (2), 167-176.
- Salman, A., Akalin, M., 2012. A rare pelagic cephalopod *Ocythoe tuberculata* (Octopoda: Argonautoidae): the record fecundity for Octopoda and new data on morphometry. *Turkish Journal of Fisheries & Aquatic Sciences*, 12, 339-344.
- Sánchez, P., 1980. Nueva cita de *Ocythoe tuberculata* (Raf., 1814) (Cephalopoda: Ocythoidae) en las costas catalanas. *Investigación Pesquera*, 44 (1), 111-117.
- Sánchez, P., Belcari, P., Sartor, P., 1998. Composition and spatial

- distribution of cephalopods in two north-western Mediterranean areas. *South African Journal of Marine Science*, 20 (1), 17-24.
- Sánchez, P., Molí, B., 1985. An annotated list of the cephalopod larvae collected off the Mediterranean coast of Spain, 1976-1981. *Vie et Milieu*, 35 (3-4), 171-173.
- Santos, M.B., Martin, V., Arbelo, M., Fernández, A., Pierce, G.J., 2007. Insights into the diet of beaked whales from the atypical mass stranding in the Canary Islands in September 2002. *Journal of the Marine Biological Association of the UK*, 87 (1), 243-251.
- Sartor, P., Belcari, P., 2009. *Opisthoteuthis calypso* (Cephalopoda: Octopoda) collected on bathyal bottoms of the northern Tyrrhenian Sea (western Mediterranean). *Bolletino Malacologico*, 45 (Suppl. 8), 17-21.
- Shea, E.K., Vecchione, M., 2002. Quantification of ontogenetic discontinuities in three species of oegopsid squids using model II piecewise linear regression. *Marine Biology*, 140 (5), 971-979.
- Shea, E.K., Vecchione, M., 2010. Ontogenetic changes in diel vertical migration patterns compared with known allometric changes in three mesopelagic squid species suggest an expanded definition of a paralarva. *ICES Journal of Marine Science*, 67 (7), 1436-1443.
- Silas, E.G., 1968. Cephalopoda of the west coast of India collected during the cruises of the research vessel Varuna, with a catalogue of the species known from the Indian ocean. p. 277-359. In: *Proceedings of the Symposium on Mollusca, MBI, 12-16 January 1968, Cochin*.
- Sweeney, M.J., Roper, C.F.E., Mangold, K.M., Clarke, M.R., Boletzky, S.V. (Eds), 1992. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, No. 513. Smithsonian Institution Press, Washington, DC, 282 pp.
- Thomas, R.F., 1977. Systematics, distribution, and biology of cephalopods of Genus *Tremoctopus* (Octopoda: Tremoctopodidae). *Bulletin of Marine Science*, 27 (3), 353-392.
- Tsuchiya, K., 2009. *Enoplateuthis Orbigny in Rüppell 1844*. Version 23 July 2009 (under construction). <http://tolweb.org/Enoplateuthis/19641/2009.07.23>. In The Tree of Life Web Project. <http://tolweb.org/>.
- Tursi, A., D'Onghia, G., Matarrese, A., Panetta, P., Maiorano, P., 1994. Finding of uncommon cephalopods (*Ancistroteuthis lichtensteinii*, *Histioteuthis bonnellii*, *Histioteuthis reversa*) and first record of *Chiroteuthis veranyi* in the Ionian Sea. *Cahiers de Biologie Marine*, 35 (3), 339-345.
- Tutman, P., Krstulović Šifner, S., Dulčić, J., Pallaoro, A., Gavrilović, A. et al., 2008. A note on the distribution and biology of *Ocythoe tuberculata* (Cephalopoda: Ocythoidae) in the Adriatic Sea. *Vie et Milieu – Life & Environment*, 58 (3-4), 215-221.
- Vecchione, M., Roper, C.F.E., 1991. Cephalopods observed from submersibles in the Western North Atlantic. *Bulletin of Marine Science*, 49 (1-2), 433-445.
- Vecchione, M., Roper, C.F.E., Sweeney, M.J., 1989. Marine flora and fauna of the eastern United States. Mollusca: Cephalopoda. *NOAA Technical Report NMFS 73*. U.S. Department of Commerce, 23 pp.
- Vecchione, M., Roper, C.F.E., Sweeney, M.J., Lu, C.C., 2001. Distribution, relative abundance and developmental morphology of paralarval cephalopods in the Western North Atlantic Ocean. *NOAA Technical Report NMFS 152*. U.S. Department of Commerce, 54 pp.
- Vecchione, M., Young, R.E., Piatkowski, U., 2010. Cephalopods of the northern Mid-Atlantic Ridge. *Marine Biology Research*, 6 (1), 25-52.
- Villanueva, R., 1992a. Continuous spawning in the cirrate octopods *Opisthoteuthis agassizii* and *Opisthoteuthis vossi*: features of sexual maturation defining a reproductive strategy in cephalopods. *Marine Biology*, 114 (2), 265-275.
- Villanueva, R., 1992b. Deep-sea cephalopods of the north-western Mediterranean: indications of up-slope ontogenic migration in two bathybenthic species. *Journal of Zoology*, 227 (2), 267-276.
- Villanueva, R., Collins, M.A., Sánchez, P., Voss, N.A., 2002. Systematics, distribution and biology of the cirrate octopods of the genus *Opisthoteuthis* (Mollusca, Cephalopoda) in the Atlantic Ocean, with description of two new species. *Bulletin of Marine Science*, 71 (2), 933-985.
- Villanueva, R., Guerra, A., 1991. Food and prey detection in two deep-sea cephalopods, *Opisthoteuthis agassizii* and *O. vossi* (Octopoda, Cirrata). *Bulletin of Marine Science*, 49 (1-2), 288-299.
- Villanueva, R., Sánchez, P., 1993. Cephalopods of the Benguela Current off Namibia: New additions and considerations on the Genus *Lycoteuthis*. *Journal of Natural History*, 27, 15-46.
- Volpi, C., Borri, M., Zucchi, A., 1995. Notes on the family Sepiolidae (Mollusca, Cephalopoda) off the Northern Tuscany coast. *Bulletin de l'Institut Océanographique, Monaco*, 16, 27-34.
- Voss, N.A., 1980. A generic revision of the Cranchiidae (Cephalopoda, Oegopsida). *Bulletin of Marine Science*, 30 (2), 365-412.
- Watanabe, H., Kubodera, T., Ichii, T., Kawahara, S., 2004. Feeding habits of neon flying squid *Ommastrephes bartramii* in the transitional region of the central North Pacific. *Marine Ecology Progress Series*, 266, 173-184.
- Wurtz, M., Matricardi, G., Repetto, N., 1995. Sepiolidae (Mollusca: Cephalopoda) from the lower Tyrrhenian Sea, Central Mediterranean. *Bulletin de l'Institut Océanographique, Monaco*, 16, 35-39.
- Yatabe, A., Kubo, N., Otsuka, M., Shima, S., Kubodera, T. et al., 2010. Stomach contents and structure of a longman's beaked whale (*Indopacetus pacificus*) stranded in Kyushu, Japan. *Aquatic Mammals*, 36 (2), 172-177.
- Young, J.Z., 1991. *Ctenopteryx* the comb-fin squid is related to *Loligo*. *Bulletin of Marine Science*, 49 (1-2), 148-161.
- Young, R.E., Mangold, K.M., 2011. *Taonius Steenstrup, 1861*. Version 08 March 2011 (under construction). <http://tolweb.org/Taonius/19558/2011.03.08>. In The Tree of Life Web Project. <http://tolweb.org/>.
- Zeidler, W., 1989. The pelagic octopus *Tremoctopus violaceus* Delle Chiaje, 1830, from Southern Australian Waters. *Véliger*, 32 (2), 166-170.