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New contribution to the knowledge of the mesopelagic cephalopod community off the western Canary Islands slope

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ABSTRACT

Cephalopods are a key component of the marine food webs. Nevertheless, the deep-sea cephalopods are still poorly studied worldwide. The distribution and composition of the mesopelagic cephalopod's community in different deep scattering layers from the Canary Islands (North-eastern Atlantic) are described here. The results of a mesopelagic fishing survey (CETOBAPH) at the western slopes of three islands of the Canary archipelago (El Hierro, La Palma and Tenerife) are reported. A total of 3,717 specimens of 17 families were caught at different acoustic scattering layers previously detected in depth. The pelagic families Pyroteuthidae, Enoploteuthidae, Onychoteuthidae and Cranchiidae comprised 91% of the total cephalopod catch. Species belonging to these families were responsible for the differences found in the cephalopod community assembly between the shallow sound scattering layers, situated at night in the epipelagic zone and deep sound scattering layers in the mesopelagic zone. No differences were observed in the cephalopod community composition among the three sampled islands. The species richness among islands were similar with 32, 30 and 31 species collected for El Hierro, La Palma and Tenerife, respectively. These results suggest the existence of vertical but no horizontal segregation of small cephalopod species at the mesoscale level in the Canary Islands.

1. Introduction

Cephalopods that live deeper than 200 m, particularly squids, are the most diverse taxonomic group with *ca.* 300 species (Hoving et al., 2014). Ecologically, they are widely recognized as an important component in marine food webs, being voracious predators of fish, crustaceans, zooplankton and detritus (Clarke, 1996). Cephalopods are also preys for marine apex predators such as seabirds, sharks and marine mammals (e.g. Croxall and Prince, 1996; Smale, 1996). Due to their high food consumption, rapid growth and short life history, squids transfer a large amount of energy from lower to high trophic levels, producing a top-down and bottom-up control on populations of its preys and predators, respectively (Coll et al., 2013; Hunsicker et al., 2010; Rodhouse and Nigmatullin, 1996). In addition, several species perform vertical migrations between depth to shallow waters, with the subsequent contribution to the active flux of nutrients and carbon between ocean compartments (Longhurst and Harrison, 1988). On the other hand, some oceanic cephalopods have fishery interest such as, Ommastrephids (e.g. *Dosidicus gigas*, *Illex* spp., *Todarores* spp.) that reach an annual total catch of about 4 million tons (FAO, 2021). Despite its importance in the marine ecosystem and fisheries, many aspects of their bioecology, systematics and biogeography remain poorly understood (Hoving et al., 2014).

Oceanic islands and seamounts offer a great opportunity to study deep-sea and mesopelagic cephalopods, since neritic, pelagic, mesopelagic, slope, benthopelagic and benthic habitats are in close proximity, promoting a great species richness in relative small areas (Young, 1995; Reid et al., 1991). In this sense, the Canary Islands with depths over 2000 m close to shore,

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offer a unique opportunity for studying the deep-sea and oceanic ecosystems, its ecological processes and biodiversity, which are relatively accessible to shore-based research stations at low cost. Canarian mesopelagic cephalopods remain overlooked compare to neritic and deep-sea fishes, corals, echinoderms and other groups, (Brito, 1991; Gómez and Pérez, 1997; Brito and Ocaña, 2004; Brito et al., 2002; Hernández et al., 2013; Moro, 2015). Historically, knowledge about the mesopelagic cephalopods of the Canary Islands is based mainly on a discrete number of scientific cruises. In 1965, the SOND cruise was the first expedition that reported a systematic list of mesopelagic cephalopods caught from surface to 900 m depth on the Fuerteventura Island slope (Clarke, 1969; Foxton, 1969). Later, Clarke (2006) reported catch data from two mesopelagic surveys conducted during 1961 and 1976, close to the southwest coast of Tenerife. Finally, Bordes et al. (2009) reported catch data from six pelagic surveys carried out around the Canary Islands between 1997 and 2002. None of these previous studies focused on the cephalopod species assemblages as a whole community nor its vertical distributions in relationship with the sound scattering layers during their diel vertical migrations.

We aim to fill this gap of information in the study region. In this sense, we carried out an acoustic-trawl survey in the western Canary Islands of El Hierro, La Palma and Tenerife to explore horizontal and diel vertical variations in the distribution of species and relative abundance of cephalopods within different sound scattering layers.

2. Material and methods

2.1. Mesopelagic survey

The research cruise CETOBAPH was conducted in April 2012 and performed mesopelagic fishing between the 1000 and 2000 m isobaths off three western Canary Islands: southwest off El Hierro (EH), W off La Palma (LP) and SW off Tenerife (TF) (Canary Islands, NE Atlantic Ocean), (Fig. 1). Hydrographic and acoustic data, as well as cephalopods samples, were collected on board the R/V *Cornide de Saavedra*. Cephalopods were catched using a pelagic trawl with a 300 m^2 mouth area and 45 m length. The mesh size was 80 cm near the opening, decreasing to 1 cm in the cod end. Hauls were horizontally deployed within the acoustic scattering layers detected with a hull-mounted Simrad EK60 echosounder emitting at 18 and 38 kHz. Two main sets of acoustic layers were detected, the deep scattering layers (DSLs) situated between 200 and 1000 m depth and the shallow scattering layers (SSLs) from the surface to 200 m (see Ariza et al. (2016)) (Fig. 2). All hauls were standardized to 1 h of effective fishing towing at 2–3 knots. Hauls data are summarized in Table 1.

Cephalopods were frozen on board at −20 °C. Once in the laboratory all specimens were identified to the lowest possible taxonomic level. When the mantle was not too damaged, the dorsal mantle length (DML) of the specimen was measured to the nearest mm and weighed to the nearest 0.1 g.

2.2. Cephalopods community assemblage analysis

Total cephalopods species richness by island and Simpson diversity index (D) for each trawl were calculated. Differences in the Simpson diversity index grouping trawls by island (EH, LP, TF) was explored by applying a Monte-Carlo permutation test with 9999 permutations and a significance level of $p = 0.05$. A permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), based on a Bray–Curtis dissimilarity distance of previous log (x+1) transformed abundance data matrix was used to test the null hypothesis of no difference in cephalopods assemblage structure among islands, scattering layers and between sampling periods (day, night). The factor "island" was analyzed as an orthogonal fixed factor with three levels (EH (El Hierro), LP (La Palma) and TF (Tenerife)), while the factor "scattering layer" and "period" was analyzed as a fixed factor with 2 levels: DSL–SSL and day–night, respectively. Significance was set at $p = 0.05$ and p-values were obtained using 3999 permutations, with permutation of residuals under a reduced model following the PERMANOVA method. In addition, a non-metric multidimensional scaling (n-MDS) analysis was used to visualize grouping among trawls. The cephalopod species responsible for dissimilarity in the assemblage structure were identified with the similarity percentages routine (SIMPER) (Clarke, 1993). PRIMER v.6+ PERMANOVA software was used for all multivariate routines.

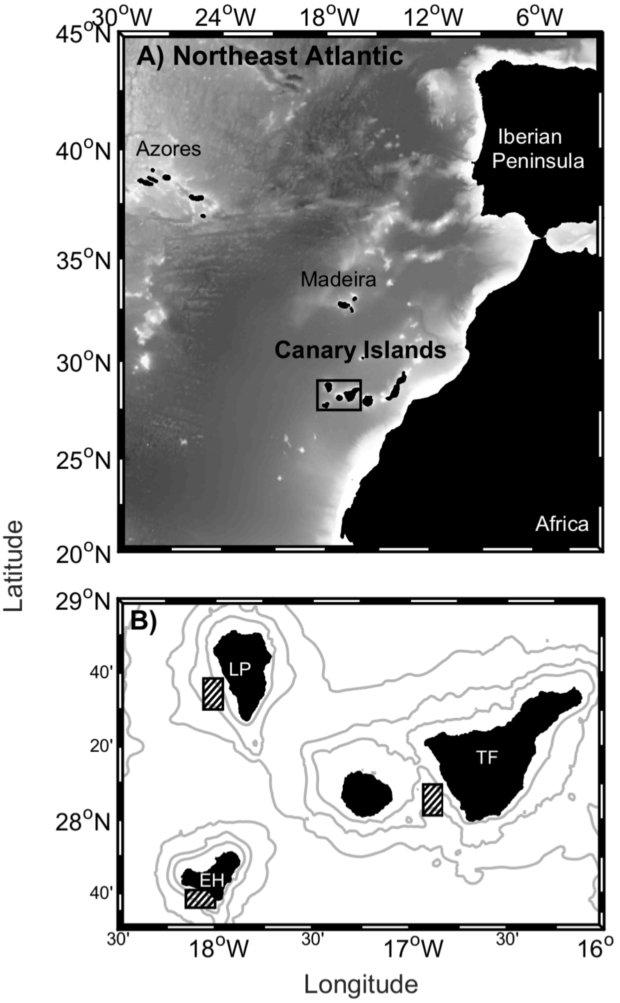

Fig. 1. Map of the study area, boxes represent the fishing areas during CETOBAPH cruise.

3. Results

During the CETOBPAH cruise a total of 3717 cephalopods specimens of 17 families were captured. Captures included two octopods, one spirulid, one sepiid and 33 oegopsids species (Table 2). The most abundant families were Pyroteuthidae (n = 1875 individuals), Enoploteuthidae (n = 1137), Onychoteuthidae (n = 407), Cranchiidae (n = 57) and Histioteuthidae (n = 56). The most abundant species were *Pyroteuthis margaritifera*,

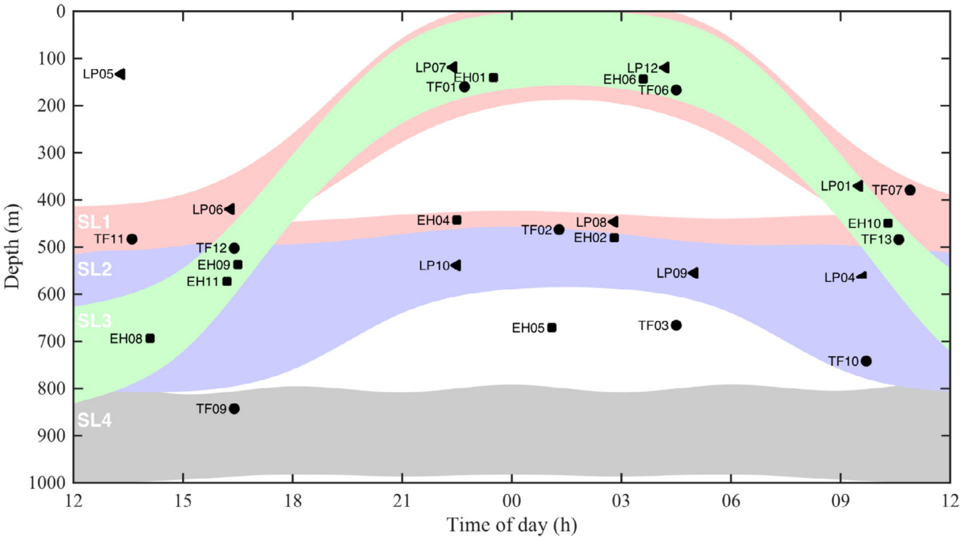

Fig. 2. Schematic of acoustic scattering layers throughout the diel cycle in the study region, according to Ariza et al. (2016), and hauls targeting these layers. EH, LP and TF stand for El Hierro, La Palma, and Tenerife locations. Hauls depth and timing can be derived from the plot. Different acoustic scattering layers and their diel vertical movements detected during a 24-h period in the study area, are shown. SL1: a scattering layer characterized by a high backscattering at 18 kHz roughly between 400 and 500 m depth. SL2: a permanent layer mainly visible at 38 kHz between 500 and 600 m depth DSL. SL3: a weak backscattering zone at 18 and 38 kHz between 600 and 800 m depth and SL4: a permanent weak echo at 18 kHz approximately from 800 to 1000 m detected.

Table 1
Details of locations and depths of trawls conducted during the CETOBAPH survey at western Canary Islands. DA: depth average (meters).

Hauls	Island	Date	Time	Latitude (N)	Longitude (W)	DA (m)
EH01	El Hierro	04/05/12	23:30	27º 38.860′	018º 02.450′	130.5
EH02	El Hierro	04/06/12	02:50	27º 39.610′	018º 04.870′	470.0
EH04	El Hierro	04/06/12	22:30	27º 39.570′	018º 04.740′	433.0
EH05	El Hierro	04/07/12	01:06	27º 39.580′	018º 04.733′	661.0
EH06	El Hierro	04/07/12	03:37	27º 38.940′	018º 03.423′	134.0
EH07	El Hierro	04/08/12	10:10	27º 39.000′	018º 03.421′	420.0
EH08	El Hierro	04/08/12	14:04	27º 39.300′	018º 04.113′	684.0
EH09	El Hierro	04/08/12	16:32	27º 36.366′	018º 01.910′	527.0
EH10	El Hierro	04/09/12	10:22	27º 39.900′	018º 05.900′	440.0
EH11	El Hierro	04/09/12	16:16	27º 39.900′	018º 05.700′	563.0
LP01	La Palma	04/10/12	09:30	28º 33.600′	017º 57.700′	380.5
LP04	La Palma	04/11/12	09:40	28º 34.524′	018º 00.106′	574.0
LP05	La Palma	04/11/12	13:20	28º 35.100′	018º 00.100′	143.0
LP06	La Palma	04/11/12	16:21	28º 32.600′	018º 00.098′	430.0
LP07	La Palma	04/12/12	22:25	28º 35.200′	018º 00.100′	129.0
LP08	La Palma	04/12/12	02:50	28º 33.930′	018º 00.100′	457.0
LP09	La Palma	04/13/12	05:00	28º 32.200′	018º 00.100′	565.0
LP10	La Palma	04/14/12	22:28	28º 34.304′	018º 00.171′	549.0
LP11	La Palma	04/14/12	01:31	28º 33.280′	018º 00.055′	481.0
LP12	La Palma	04/14/12	04:12	28º 35.400′	018º 00.200′	130.0
TF01	Tenerife	04/14/12	22:40	28º 05.681′	016º 50.305′	150.0
TF02	Tenerife	04/15/12	01:20	28º 04.670′	016º 49.440′	453.0
TF03	Tenerife	04/15/12	04:30	28º 03.800′	016º 47.800′	656.0
TF06	Tenerife	04/16/12	04:30	28º 04.216	016º 49.063′	149.0
TF07	Tenerife	04/17/12	10:53	28º 04.900′	016º 49.400′	369.0
TF09	Tenerife	04/17/12	16:25	28º 05.000′	016º 49.900′	833.0
TF10	Tenerife	04/18/12	09:41	28º 05.600′	016º 50.100′	732.0
TF11	Tenerife	04/18/12	13:18	28º 05.960′	016º 50.430′	473.0
TF12	Tenerife	04/18/12	16:23	28º 04.363′	016º 49.259′	492.0
TF13	Tenerife	04/19/12	10:35	28º 04.300′	016º 49.300′	474.0

Abraliopsis moriisi, *Onychoteuthis banksii* and *Pterygioteuthis giardi*, comprising 91% of the total caught. These species were the most dominant spatially, being catched at all stations and scattering layers sampled. The average mantle length of these four species was 21.6 ± 4.4 mm, 24.7 ± 4.6 mm, 34.8 ± 7.8 mm and 22.2 ± 3.4 mm, respectively.

Nocturnal hauls targeting the SSLs captured 2803 specimens (56% of the total catches) of 23 species included in 13 families. In contrast, hauls targeting DSLs between 400–800 m depth catched only 914 specimens, but captures were more diverse: 33 species comprising 16 families. The average of Simpson diversity index (D) for the hauls performed in each island was 0.60 ± 0.25 for El Hierro, 0.58 ± 0.19 for La Palma and 0.65 ± 0.27 for Tenerife, whilst species richness was also similar among islands: 32, 30 and 31 taxa, respectively.

No statistical evidence of differences among islands was found in the cephalopod community structure nor when considering the interaction between islands and scattering layers. However, there was a significant difference in the cephalopod community structure between scattering layers (SSL and DSL) (PERMANOVA; $p < 0.005$) (Table 3), Fig. 3. The average dissimilarity between scattering layers was high (66.52%) (SIMPER, Table 4) and due

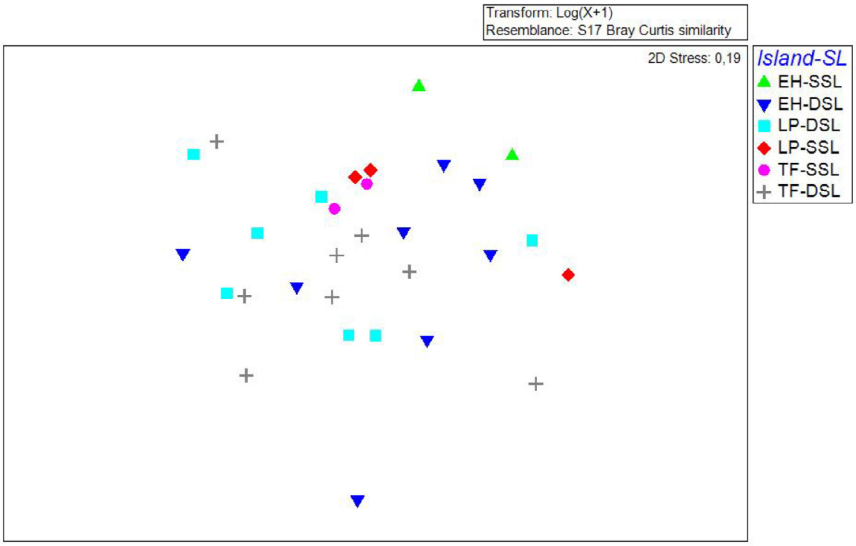

Fig. 3. n-MDS analysis of the trawls perform during the CETOBAPH mesopelagic survey in El Hierro (EH), La Palma (LP) and Tenerife (TF) island, Canary Islands at different acoustics scattering layers detected, Shallow Scattering Layer (SSL) and Deep Scattering Layer (DSL).

mainly to the change of dominant species abundance. Four dominant species, *P. margaritifera*, *A. moriisi*, *O. banksii* and *P. giardi* contributed to 49.5% of the differences between the epipelagic SSL and DSLs mesopelagic scattering layers. *P. margaritifera* accounted for 42.2% and 28.7% of the total catches in the SSL and DSL, respectively. Similarly, *A, moriisi* was more abundant in the SSL with 31.3% of the total catches, while it accounted for 26.1% of the total catches in the DSL. Likewise, *O. banksii* was more abundant in the SSL (12.9%) than in DSL (4.9%). In contrast, *P. giardi* catches were more abundant in DSL (21%) than in SSL (8.4%) layers (Table 4).

4. Discussion

Several types of fishing nets have been used to study the oceanic cephalopod community and all of them have their advantages and disadvantages (Wormuth and Roper, 1983; Clarke, 2005). In this study, a commercial open-mouth net of 300 m^2 and 45 m in length with a mesh size of 80 cm near the opening, decreasing to 1 cm in the cod end, was used. Large nets with large mouth openings favor the catch of larger individuals, as well as greater diversity than smaller nets such as the Isaac-Kidd Midwater trawl (IKMT), but are more vulnerable to catch contaminating species from other depth horizons, mainly during descent or ascent to the desired discrete sampling depth, than open/close net systems (Clarke, 2005). In our study, it is possible that some species found in deep hauls came from contamination of upper layers due to the lack of an opening–closing system in our trawl. This problem was minimized by increasing the speed of deploying and lifting maneuvers reducing the time that trawl crossed other scattering layers (<5 min) compared to the horizontal trawling times at the targeted scattering layer (60 min). This represented less than 10% of the effective fishing time. The identification of 37 cephalopods species in only 30 pelagic trawls performed during this study makes this comparatively the most profitable in terms of cephalopods richness, respect to previous largest surveys conducted in the Canary Islands with smaller nets like IKMT, Rectangular Midwater Trawls (RMT), Ring net and smaller comercial trawls, that reported 32, 22 and 18 cephalopods species, respectively (Clarke, 1969, 2006; Bordes et al., 2009). Despite the high species richness in our samples, large cephalopods species were poorly represented being dominated by the micronektonic fraction of the cephalopod community. Hence, the contribution to the cephalopod community of families with high movement capabilities and large sizes, such as Ommastrephidae, Pholidoteuthidae, Onychoteuthidae or Thysanoteuthidae were possibly underestimated and only represented by juveniles.

In this study, we found a typical oceanic cephalopod community dominated by several species of the families Pyroteuthidae, Enoploteuthidae, Onychoteuthidae, Cranchiidae and Histioteuthidae. During the night, cephalopods caught in the SSLs were strongly dominated by recognized nyctoepipelagic synchronous diel vertical migrating species, i.e. the Pyroteuthids as *P. margaritifera* and *P. giardi* occurs mainly at 250 to 500 m during the day and ascends to 50 to 250 m at night (Jereb and Roper, 2010; Judkins and Vecchione, 2020). In the same manner, *A. morisii* have been reported at 610–650 m during daytime and 50–100 m at night (Roper and Young, 1975). Finally, juveniles of the Onychoteuthid *O. banksii* also have been reported to perform migrations to upper 100 m at night from a daytime habitat of between 400 and 700 m (Watanabe et al., 2006). Our results are similar to those found in other surveys carried out in the region. Bordes et al. (2009), who also used large midwater trawls, capturing 32 species of 20 families, where dominant families in numbers of specimens were Enoploteuthidae and Pyroteuthidae. These observations suggest that Pyroteuthidae, Enoploteuthidae and Onychoteuthidae families form the bulk of the mesopelagic cephalopod community in the Canary Islands. Similar communities with these families are known from tropical or subtropical regions, such as the Gulf of México, Sargasso Sea, SW Indian Ocean (Haimovici et al., 2002; Clarke, 2006; Laptikhovsky et al., 2015; Lischka et al., 2017; Judkins et al., 2017; Judkins and Vecchione, 2020). Despite the dominance of these families in the world's temperate and tropical oceans SSL, scarce studies have investigated their ecological role. The abundance of these vertical migrant squid species may play an important and underestimated role in the active vertical fluxes of carbon and nitrogen in the marine ecosystem (Clarke, 1996). These squids are able to rapidly convert their food into biomass (top-down effect) and also represent an important source of energy to predators (bottom-up effect) (Bustamante et al., 1998). These organisms are able to fill the gap between small fish (*e.g.* myctophids) and large pelagic organisms (*e.g.* small-pelagics), linking secondary production with high trophic levels (*e.g.* strict carnivores) (Olson and Watters, 2003; Coll et al., 2013).

Table 2
List of cephalopods caught during the CETOBAPH cruise on western Canary Islands. Size range of mantle length (ML) of the specimens collected.

Family	Species	Number of specimens	Size range ML (mm)	Distribution	Habitat
Argonautidae	*Argonauta argo* Linnaeus, 1758	1	–	Worldwide	Oceanic
Bolitaenidae	*Japetella diaphana* Hoyle, 1885	2	–	Worldwide	Oceanic
Sepiolidae	*Heteroteuthis dispar* (Rüppell, 1844)	32	10.8–22.5	Atlantic	Oceanic
Spirulidae	*Spirula spirula* (Linnaeus, 1758)	2	30.6–34.2	Worldwide	Oceanic
Ancistrocheiridae	*Ancistrocheirus lesueurii* (d'Orbigny, 1842)	1	106.5	Worldwide	Slope
Brachioteuthidae	*Brachioteuthis picta* Chun, 1910	2	60	Worldwide	Oceanic
	Brachioteuthis riisei (Steenstrup, 1882)	8	16–65	Worldwide	Oceanic
	Brachioteuthis spp.[a]	4	–	–	–
Chiroteuthidae	*Chiroteuthis mega* (Joubin, 1932)	1	137.4	Atlantic	Oceanic
	Chiroteuthis veranii (Férussac, 1834)	2	49.3–113	Worldwide	Oceanic
	Chiroteuthis spp.[a]	2	–	–	–
Chtenopterygidae	*Chtenopteryx canariensis* (Salcedo-Vargas and Guerrero-Kommritz, 2000)	2	27–43	Atlantic	Oceanic
	Chtenopteryx sicula (Vérany, 1851)	55	18–43	Worldwide	Oceanic
	Chtenopteryx spp.[a]	4	–		
Cranchiidae	*Bathothauma lyromma* Chun, 1906	2	32.9–45	Worldwide	Oceanic
	Cranchia scabra Leach, 1817	10	27.3–113.2	Worldwide	Oceanic
	Helicocranchia pfefferi Massy, 1907	2	55–56.8	Worldwide	Oceanic
	Leachia atlantica (Degner, 1925)	14	43–92	Eastern North Atlantic	Oceanic
	Liocranchia reinhardtii (Steenstrup, 1856)	2	91–102.2	Worldwide	Oceanic
	Megalocranchia oceanica (Voss, 1960)	24	44.1–250	Atlantic	Oceanic
	Taonius pavo (Lesueur, 1821)	3	21	Atlantic	Oceanic
Enoploteuthidae	*Abralia veranyi* (Rüppell, 1844)	1	22.4	Atlantic–Mediterranean	Oceanic
	Abraliopsis morisii (Vérany, 1839)	1119	14.9–41	Atlantic	Oceanic
	Enoploteuthis cf. anapsis Roper, 1964	10	19–63	Atlantic	Oceanic
	Enoploteuthis cf. leptura (Leach, 1817)	7	18–26.8	Atlantic-Indian-West Pacific	Oceanic
Histioteuthidae	*Histioteuthis cf. celetaria* (Voss, 1960)	3	21.6–28	Atlantic	Oceanic
	Histioteuthis corona corona (Voss & Voss, 1962)	19	10–33.1	Atlantic	Oceanic
	Stigmatoteuthis arcturi Robson, 1948	9	13–48.7	Tropical–Subtropical Atlantic	Oceanic
	Histioteuthis meleagroteuthis (Chun, 1910)	14	3.7–65.8	Worldwide	Oceanic
	Histioteuthis reversa (Verrill, 1880)	1	–	Atlantic–Mediterranean	Oceanic
	Histioteuthis spp.[a]	10	–	–	–
Lycoteuthidae	*Lampadioteuthis megaleia* Berry, 1916	5	18.2–40	North Atlantic–Southwestern Pacific	Oceanic
	Selenoteuthis scintillans Voss, 1959	3	22–38.4	North Atlantic	Oceanic
Mastigoteuthidae	*Mastigopsis hjorti* (Chun, 1913)	18	12.2–108.4	North Atlantic–Central Pacific–Indian Ocean	Oceanic
	Mastigoteuthid[a]	7	–		
Octopoteuthidae	*Octopoteuthis sicula* Rüppell, 1844	1	90	Worldwide	Oceanic
	Octopoteuthis leviuncus (Kelly, 2019)	3	97–140	North Atlantic	Oceanic
Ommastrephidae	*Ommastrephes caroli* (Furtado, 1887)	1	220.2	Worldwide	Oceanic
	Todarodes sagittatus (Lamarck, 1798)	25	13–170	Eastern Atlantic–Mediterranean	Oceanic
	Ommastrephid[a]	3	–	–	–
Onychoteuthidae	*Onychoteuthis banksii* (Leach, 1817)	407	40.7–15	Worldwide	Oceanic
Pyroteuthidae	*Pterygioteuthis giardi* Fischer, 1896	427	14–30.1	Worldwide	Oceanic
	Pterygioteuthis spp.[a]	3	–	–	–
	Pyroteuthis margaritifera (Rüppell, 1844)	1445	9.7–41.3	Worldwide	Oceanic
Total: 17	**39**	**3717**			

[a] Specimens not identified at species level due its poor preservation conditions.

The three main components in biomass of the DVM community in the Canary Islands and in other subtropical regions are fishes (70%), mostly myctophids, whereas the second and third components are disputed by crustaceans and cephalopods. In the Canary Islands, cephalopods represent 20% of the SSL whilst the crustaceans correspond to 9% in biomass (Ariza et al., 2016). Active flux of nutrients and carbon have been traditionally calculated in zooplankton and the micronektonic fish, mainly in myctophids and the crustacean components of de DVM community (*e.g.*, Ariza et al., 2015; Cotté et al., 2022). This flux is mediated by respiration, egestion of faecal pellets, excretion of metabolic dissolved nitrogen and carbon compounds and body carcasses after mortality of the migratory animals during the daylight permanence at depth (Ducklow et al., 2001). Cephalopods respiration rates are 1.5 to 1.7 times higher than those of fish (Ikeda, 2016) and that they are a live-fast, die-young group of animals with short lifespan cycles of few months to a year in comparison with 1 to 5 years lifespan in myctophids in temperate-subtropical oceans (Arkhipkin, 1996, 2004; Catul et al., 2011). Hence, their contribution to the carbon active flux should be taken into consideration, as it may be comparable to that of micronectonik fishes. Future research studies on this topic are needed to shed light on this gap of knowledge.

A few species were encountered in this area for the first time during this survey. Namely, the Octopoteuthid *Octopoteuthis*

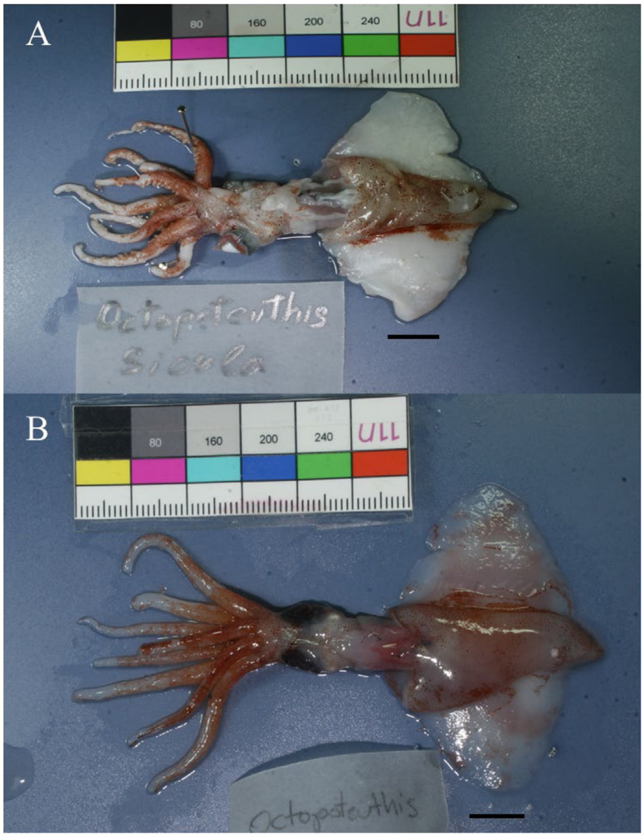

Fig. 4. Species caught from Octopoteuthidae family, ventral view of (A) *Octopoteuthis sicula* and (B) *Octopoteuthis leviuncus*. Scale bar 1 cm.

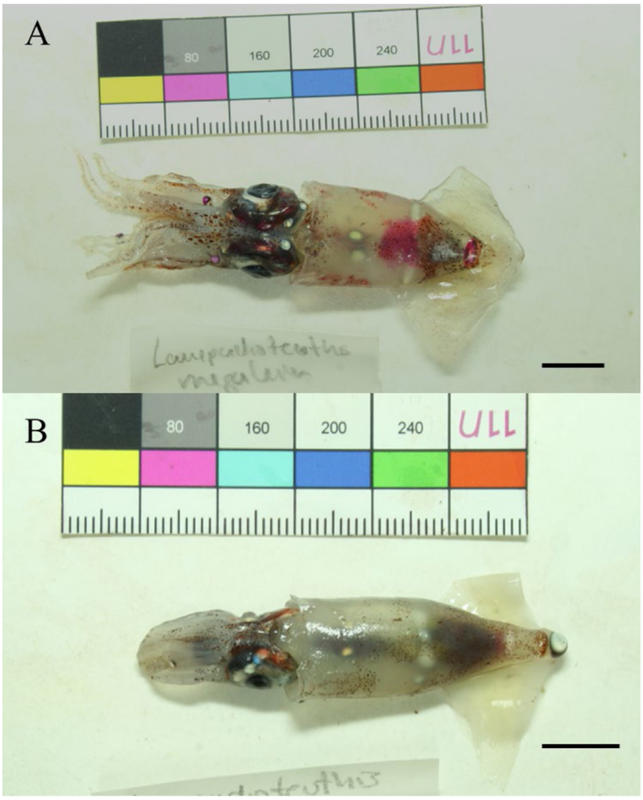

Fig. 5. Lycoteuthids caught during CETOBAPH cruise. (A) Ventral view of a *Lampadioteuthis megaleia* (B). Ventral view of a *Selenoteuthis scintillans*. Scale bar 1 cm.

Table 3
Summary of PERMANOVA results for the analysis of differences in assemblage structure across different factors. Factors: Islands (EH: El Hierro, TF: Tenerife, LP: La Palma). Acoustic layers; Deep Scattering Layer (DSL), Shallow Scattering Layer (SSL).

Factor	df	MS	Pseudo-F	p
Islands (EH,TF,LP)	2	2934.3	1.3932	0.134
Acoustic layer (SSL, DSL)	1	2.8433	2.8433	0.0058*
Islands × Acoustic layer	2	0.67129	0.67129	0.8305
Residuals	24			
Total	29			

*Significant results.

Table 4
SIMPER analysis for cephalopods abundance per scattering layer type (SSL. DSL). AVA: average abundance; av. sim.: average similarity; cum. sim. (%): cumulative percentage of similarity.

Species	AVA SSL	AVA. DSL	Av. Sim.	Cum. Sim. (%)
Average similarity: 50.16%				
P. margaritifera	4.26		12.75	25.43
A. moriisi	3.48		11.18	47.71
O. banksii	2.91		7.59	62.84
P. giardi	2.61		5.82	74.45
H. dispar	1.12		3.09	80.60
T. sagittatus	1.03		2.84	86.26
M. oceanica	0.96		1.78	89.82
H. meleagroteuthis	0.66		1.63	93.08
Average similarity: 33.19%				
P. magaritifera		1.80	12.39	37.31
A.moriisi		1.52	6.76	57.69
P. giardi		1.43	6.31	76.69
H. dispar		0.39	1.72	81.87
O. banksii		0.61	1.60	86.70
L. atlantica		0.32	1.10	90.02
Average dissimilarity: 66.52%				
P. margaritifera	4.26	1.80	10.05	15.10
A. moriisi	3.48	1.52	8.37	27.69
O. banksii	2.91	0.61	7.43	38.85
P. giardi	2.61	1.43	7.08	49.49
T. sagittatus	1.03	0.18	3.36	54.54
C. sicula	0.99	0.27	2.93	58.95
M. oceanica	0.96	0.21	2.88	63.28
H. dispar	1.12	0.39	2.81	67.51

leviuncus recently described by Kelly (2019) was represented in the catches by 3 specimens, one catched in El Hierro and two in Tenerife (Fig. 4). This species has a single embedded posterior ventral mantle photophore and two embedded photophores on both recti-abdominis muscles and hooks on arms without accessory claws. This species is widely distributed on both sides of the temperate-tropical Atlantic from about 35°S to 35°N and the closest previous records to the Canary Islands were around Madeira Island (Portugal) (Kelly, 2019). In addition to these new records, other infrequent species for the region were reported, i.e. the Lycoteuthids *Selenoteuthis scintillans* and *Lampadioteuthis megaleia* with 3 and 5 specimens, respectively (Fig. 5). The first species is only known from the tropical and subtropical North Atlantic, whilst *L. megaleia* is known from the subtropical North Atlantic, South Pacific and Southwestern Pacific. In the Canary Islands, *S. scintillans* was previously reported by Clarke (2006) after the revision of the specimen's collection fished during a research cruise carried out in 1966 nearby Fuerteventura. On the other hand, the first record of *L. megaleia* for the Canary Islands corresponded to specimens captured in 1970 by an expedition of the Woods Hole Oceanographic Institution, which were later deposited in the collection of the National Museum of Natural History. The Enoploteuthid *Ancistrocheirus lesueurii*, a single specimen was catched at 650 m of depth in the

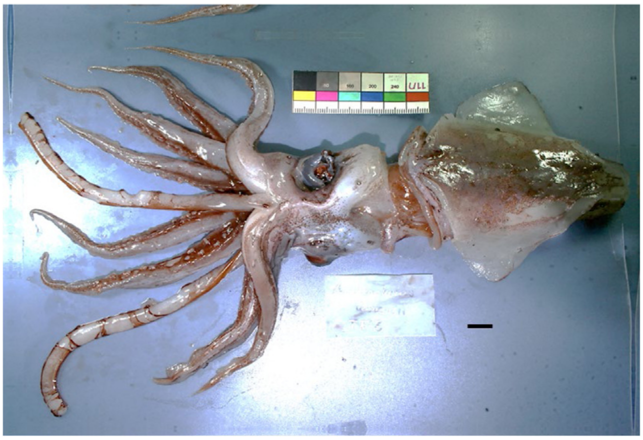

Fig. 6. Specimen of *Ancistrocheirus lesueurii* caught in Tenerife. Scale bar 1 cm.

southwest slope of Tenerife during early morning (Fig. 6). This species has a pantropical and pansubtropical distribution and is believed to be a species complex with more than one species due to differences in paralarval morphology between Atlantic and Pacific Oceans (Young et al., 1992). Previous records of this species were made from Fuerteventura during the SOND expedition as well from beaks found in the stomach contents of a sperm whale stranded in Fuerteventura (Clarke, 2006; Fernández et al., 2009). The Cranchiid, *Bathothauma lyromna* with 2 specimens, has rarely been catched in the archipelago, reporting only seven and two paralarvaes in Clarke (2006) and Bordes et al. (2009), respectively. Finally, *Chtenopteryx canariensis* represented by 2 individuals is a scarce species only known from the Canary Islands and one more specimen from the Sargasso sea (Salcedo-Vargas and Guerrero-Kommritz, 2000; Escánez et al., 2018).

5. Conclusions

This study has revealed a high diversity within the cephalopod mesopelagic community of the Canary Islands (39 species), yet with few dominant species being responsible for most of the differences in the abundance and composition between the two main acoustic scattering layers (SSL and DSL) observed in waters around occidental islands of the Canary archipelago (El Hierro, La Palma and Tenerife). These species were nyctoepipelagic sychronus diel vertical migrators, i.e. *P. giardi*, *P. margatifera*, *A. moriisi* and *O. banksii*, belonging to the Pyroteuthidae, Enoploteuthidae and Onychoteuthidae families. In view of our own results and previous studies in the region, we suggest that these species form the bulk of the mesopelagic cephalopod community in the Canary Islands. In addition, it was observed a homogeneous mesopelagic cephalopod community among islands with similar species richness.

The gear used during this study, an open pelagic trawl introduced a methodological bias affecting the representativeness of the large and highly mobile species that were caught in lower numbers in contrast with micronektonic species. Despite this, this mesopelagic survey caught 45.8% (39 species) of the known cephalopod's species richness for the Canary Islands (85 species) (Escánez et al., 2021) in only 30 trawls, being one the most efficient surveys in terms of cephalopods catch, performing in the region.

The species *Octopoteuthis leviuncus* was first recorded for the Canary archipelago. This collection also has provided valuable specimens of poorly known species such as *C. canariensis, L. megaleia* and *S. scintillans,* among others, which will allow us to perform molecular analyses to resolve its taxonomy, as well as other aspects of their ecology. These results emphasize the need to continue exploring the deep sea around Canary Islands and other macaronesian archipelagos such as Madeira, Azores and Cape Verde in order to increase knowledge on diversity, biology, ecology and distribution of these ecologically important species. Additionally, to go deeper and less explored bathyal zones between 1000–4000 m in both pelagic and benthic environments. This further research should be combining different sampling methods, including classical fishing methods (*e.g.* scientific trawls), molecular approaches such as environmental DNA analysis and new technologies such deep-water baited remote underwater video systems (BRUVS), and remotely operated vehicles (ROVs) (*e.g.* Merten et al., 2021).

We suggest that the Canary Islands represent a strategic emplacement to conduct research on the ecological role of pelagic cephalopods in marine ecosystems of oceanic islands.

CRediT authorship contribution statement

Alejandro Escánez: Data curation and database organization, Writing – original draft, Formal analysis, Investigation. **Ángel Guerra:** Data curation, Investigation, Writing – review & editing, Resources. **Rodrigo Riera:** Writing – original draft, Writing – review & editing. **Alejandro Ariza:** Methodology, Data curation, Writing – review & editing. **Ángel F. González:** Data curation, Writing – review & editing. **Natacha Aguilar de Soto:** Research conceptual framework, Data collection, Resources, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx.doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Ariza, A., Garijo, J.C., Landeira, J.M., Bordes, F., Hernández-León, S., 2015. Migrant biomass and respiratory carbon flux by zooplankton and micronekton in the subtropical northeast Atlantic Ocean (Canary Islands). Prog. Oceanogr. 134, 330–342. http://dx.doi.org/10.1016/j.pocean.2015.03.003.

Ariza, A., Landeira, J.M., Escánez, A., Wienerroither, R.M., Aguilar, N., Røstad, A., Kaartvedt, S., Hernández-León, S., 2016. Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands. J. Mar. Syst. 157, 82–91. http://dx.doi.org/10.1016/j.jmarsys.2016.01.004.

Arkhipkin, A.I., 1996. Age and growth of the squid *Abraliopsis pfefferi* (Oegopsida: Enoploteuthidae) from the Central-East Atlantic based on statolith microstructure. Sci. Mar. 60 (2–3), 325–330.

Arkhipkin, A.I., 2004. Diversity in growth and longevity in short-lived animals: squid of the suborder Oegopsina. Mar. Freshw. Res. 55 (4), 341–355. http://dx.doi.org/10.1071/MF03202.

Bordes, F., Wienerroither, R., Uiblein, F., Moreno, T., Bordes, I., Hernández, V., 2009. CatáLogo de Especies Meso y Batipelágicas. Peces, Moluscos y Crustáceos. Colectadas con Arrastre en las Islas Canarias Durante las Campañas Realizadas a Bordo del B/E la Bocaina. Instituto Canario de Ciencias Marinas.

Brito, A., 1991. Catálogo de los Peces de las Islas Canarias. Eds.: Francisco Lemus, La Laguna, Spain.

Brito, A., Ocaña, B., 2004. Corales de las Islas Canarias: Antozoos con Esqueleto de los Fondos Litorales y Profundos. Francisco Lemus, Editor, Spain.

Brito, A., Pascual, P., Falcón, J.M., Sancho, A., González, G., 2002. Peces de las Islas Canarias: Catálogo Comentado e Ilustrado. Eds.: Francisco Lemus, La Laguna, Spain.

Bustamante, P., Caurant, F., Fowler, S.W., Miramand, P., 1998. Cephalopods as a vector for the transfer of cadmium to top marine predators in the north-east Atlantic ocean. Sci. Total Environ. 220 (1), 71–80. http://dx.doi.org/10.1016/S0048-9697(98)00250-2.

Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to the family Myctophidae. Rev. Fish Biol. Fish. 21 (3), 339–354. http://dx.doi.org/10.1007/s11160-010-9176-4.

Clarke, M.R., 1969. Cephalopoda collected on the SOND cruise. J. Mar. Biol. Assoc. U.K. 49 (04), 961–976.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Aust. J. Ecol. 18, 117–143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Clarke, M.R., 1996. Cephalopods in the world's oceans: cephalopods as prey. III. Cetaceans. Philos. Trans. R. Soc. Lond. B Biol. Sci. 351, 1053–1065. http://dx.doi.org/10.1098/rstb.1996.0093.

Clarke, M.R., 2005. Searching for deep sea squids. Phuket Mar. Biol. Cent. Res. Bull. 66, 27–38.

Clarke, M.R., 2006. Oceanic cephalopod distribution and species diversity in the eastern north Atlantic. Arquipél. Life Mar. Sci. 23A, 27–46.

Coll, M., Navarro, J., Olson, R., Christensen, V., 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Res. II 95, 21–36. http://dx.doi.org/10.1016/j.dsr2.2012.08.020.

Cotté, C., Ariza, A., Berne, A., Habasque, J., Lebourges-Dhaussy, A., Roudaut, G., Espinasse, B., Hunt, B.P.V., Pakhomov, E.A., Henschke, N., Péron, A., Koedooder, C., Izard, L., Cherel, Y., 2022. Macrozooplankton and micronekton diversity and associated carbon vertical patterns and fluxes under distinct productive conditions around the Kerguelen Islands. J. Mar. Syst. 226, 103650. http://dx.doi.org/10.1016/j.jmarsys.2021.103650.

Croxall, J.P., Prince, P.A., 1996. Cephalopods as Prey. I. Seabirds. Phil. Trans. R. Soc. Lond. B 351, 1023–1043. http://dx.doi.org/10.1098/rstb.1996.0091.

Ducklow, H.W., Steinberg, D.K., Buesseler, K.O., 2001. Upper Ocean carbon export and the biological pump. Oceanography 14, 50–58. http://dx.doi.org/10.5670/oceanog.2001.06.

Escánez, A., Á, Guerra., Riera, R., Rocha, F.J., 2021. Revised species records reveal the Canary Islands as a cephalopod biodiversity hotspot. Reg. Stud. Mar. Sci. 41, 101541. http://dx.doi.org/10.1016/j.rsma.2020.101541.

Escánez, A., Roura, Á., Riera, R., González, Á.F., Guerra, Á., 2018. New data on the systematics of comb-fin squids *Chtenopteryx* spp. (Cephalopoda: Chtenopterygidae) from the Canary Islands. Zool. Stud. 57, http://dx.doi.org/10.6620/ZS.2018.57-40.

F.A.O., 2021. FAO Yearbook. Fishery and Aquaculture Statistics 2019/FAO Annuaire. Statistiques des Pêches et de l'Aquaculture 2019/FAO Anuario. Estadísticas de Pesca y Acuicultura 2019. Rome/Roma.

Fernández, R., Santos, M.B., Carrillo, M., Tejedor, M., Pierce, G.J., 2009. Stomach contents of cetaceans stranded in the Canary Islands 1996–2006. J. Mar. Biolog. Assoc. U.K. 89 (5), 873–883. http://dx.doi.org/10.1017/S0025315409000290.

Foxton, P., 1969. SOND Cruise 1965 Biological sampling methods and procedures. J. Mar. Biolog. Assoc. U.K. 49 (03), 603–620. http://dx.doi.org/10.1017/S0025315400037176.

Gómez, R., Pérez, J.M., 1997. Moluscos Bivalvos de Canarias. Ediciones del Cabildo Insular de Gran Canaria, Spain.

Haimovici, M., Piatkowski, U., dos Santos, R.A., 2002. Cephalopod paralarvae around tropical seamounts and oceanic islands off the north-eastern coast of Brazil. Bull. Mar. Sci. 71 (1), 313–330.

Hernández, J.C., Clemente, S., Tuya, F., Pérez-Ruzafa, A., Sangil, C., Moro-Abad, L., Bacallado-Aránega, J.J., 2013. Echinoderms of the Canary Islands, Spain. In: Echinoderm Research and Diversity in Latin America. Springer, Berlin, Heidelberg, pp. 471–510.

Hoving, H.J., Perez, J.A., Bolstad, K., Braid, H.E., Evan, A.B., Fuchs, D., Judkins, H., Kelly, J.T., Marian, J.E.A.R., Nakajima, R., Piatkowski, U., Reid, A., Vecchione, M., Xavier, J., 2014. The Study of Deep-Sea Cephalopods Advances in Marine Biology, 2014. Vol. 67. pp. 235–359, Chapter 3.

Hunsicker, M.E., Essington, T.E., Watson, R., Sumaila, U.R., 2010. The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? Fish Fish (Oxf.) 11 (4), 421–438. http://dx.doi.org/10.1111/j.1467-2979.2010.00369.x.

Ikeda, T., 2016. Routine metabolic rates of pelagic marine fishes and cephalopods as a function of body mass, habitat temperature and habitat depth. J. J. Exp. Mar. Biol. Ecol. 480, 74–86. http://dx.doi.org/10.1016/j.jembe.2016.03.012.

Jereb, P., Roper, C.F.E., 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. 2. Myopsid and Oegopsid squids. FAO Species Cat. Fish. Purp. 4 (2), 1–605.

Judkins, H., Vecchione, M., 2020. Vertical distribution patterns of cephalopods in the northern Gulf of Mexico. Front. Mar. Sci. 7 (47), http://dx.doi.org/10.3389/fmars.2020.00047.

Judkins, H., Vecchione, M., Cook, A., Sutton, T., 2017. Diversity of midwater cephalopods in the northern Gulf of Mexico: comparison of two collecting methods. Mar. Biodivers. 47 (3), 647–657. http://dx.doi.org/10.1007/s12526-016-0597-8.

Kelly, J.T., 2019. Systematics of the Octopoteuthidae Berry, 1912 (Cephalopoda: Oegopsida) (Ph.D. thesis). Auckland University of Technology.

Laptikhovsky, V., Boersch-Supan, P., Bolstad, K., Kemp, K., Letessier, T., Rogers, A.D., 2015. Cephalopods of the Southwest Indian Ocean ridge: a hotspot of biological diversity and absence of endemism. Deep-Sea Res II 1–38. http://dx.doi.org/10.1016/j.dsr2.2015.07.002.

Lischka, A., Piatkowski, U., Hanel, R., 2017. Cephalopods of the Sargasso Sea: distribution patterns in relation to oceanography. Mar. Biodivers. 47 (3), 685–697. http://dx.doi.org/10.1007/s12526-016-0629-4.

Longhurst, A.R., Harrison, W.G., 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. I 35 (6), 881–889. http://dx.doi.org/10.1016/0198-0149(88)90065-9.

Merten, V., Bayer, T., Reusch, T.B., Puebla, O., Fuss, J., Stefanschitz, J., Lischka, A., Hauss, H., Neitzel, P., Piatkowski, U., Czudaj, S., Christiansen, B., Denda, A., Hoving, H.J.T., 2021. An integrative assessment combining deep-sea net sampling, in situ observations and environmental DNA analysis identifies cabo verde as a cephalopod biodiversity hotspot in the Atlantic Ocean. Front. Mar. Sci. 9, http://dx.doi.org/10.3389/fmars.2021.760108.

Moro, L.E., 2015. Moluscos Opistobranquios Bentónicos de las Islas Canarias y su Entorno (Ph.D. thesis). Universidad de La Laguna, Spain.

Olson, R.J., Watters, G.M., 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. Bull. I-ATCC 22, 133–217.

Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109 (3), 427–440. http://dx.doi.org/10.1007/BF01313508.

Rodhouse, P., Nigmatullin, C.M., 1996. Role as consumers. Philos. Trans. R. Soc. Lond. B: Biol. Sci. 351, 1003–1022.

Roper, C.F., Young, R.E., 1975. Vertical distribution of pelagic cephalopods. Smithsonian contributions to zoology.

Salcedo-Vargas, M.A., Guerrero-Kommritz, J., 2000. Three New Cephalopods from the Atlantic Ocean, Vol. 97. Mitteilungen aus dem Hamburgischen Zoologische Museum und Institut Hamburg, pp. 31–44.

Smale, M.J., 1996. Cephalopods as prey. 4. Fishes. Philos. Trans. R. Soc. Lond. B Biol. Sci. 351, 1067–1081. http://dx.doi.org/10.1098/rstb.1996.0094.

Watanabe, H., Kubodera, T., Moku, M., Kawaguchi, K., 2006. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Mar. Ecol. Prog. Ser. 315, 187–197. http://dx.doi.org/10.3354/meps315187.

Wormuth, J.H., Roper, C.F.E., 1983. Quantitative sampling of oceanic cephalopods by nets: Problems and recommendations. Biol. Oceanogr. 2 (2–4), 357–377.

Young, R.E., 1995. Aspects of the natural history of pelagic cephalopods of the Hawaiian mesopelagic-boundary region. Pac. Sci. 49 (2), 143–155.

Young, R.E., Mangold, K.M., Vecchione, M., 1992. The enoploteuthid group of families. In: Larval and Juvenile Cephalopods: a Manual for Their Identification. In: Smithson. Contrib. Zool., vol. 513, pp. 187–210.