

REVIEW OPEN ACCESS

Understanding Biogeographic Patterns in Sepiolidae (Cephalopoda)

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ABSTRACT

The biogeography of the bobtail squid family Sepiolidae is reviewed. Species of the Sepiolinae subfamily are only found in coastal waters of the ‘Old World’, with a high degree of diversification in the Mediterranean Sea and the Coral Triangle in the Indo-Pacific region. The Rossiinae subfamily inhabits coasts of both the Old and New Worlds. Finally, the Heteroteuthinae subfamily exhibits widespread distribution patterns in the oceans of the whole world. The Mediterranean and Coral Triangle waters correspond to hotspots of biodiversity for the family, with 24.1% and 19.0% of the species, respectively, and with a high predominance of Sepiolinae species (17.7% and 13.9%) compared to Rossiinae (2.5% and 1.3%) and Heteroteuthinae (3.8% and 3.8%). The Sepiolinae species inhabit shallow, coastal, benthic habitats, and their paralarvae have a nectobenthic paralarvae strategy with a planktonic stage limited in time, which quickly adopts the benthic lifestyle. The Rossiinae species are adapted to benthic habitats in deeper waters on continental shelves and slopes. They lay large eggs, and the newly hatchlings have a Direct Nectobenthic Juvenile strategy, adopting a benthic lifestyle with only a very brief, if any, planktonic stage. Heteroteuthinae species occupy pelagic habitats, lay small eggs associated to seamounts, islands and continental slopes and give birth to hatchlings that adopt a pelagic paralarvae strategy with a planktonic larval stage. The biogeographic patterns of the Sepiolidae family show the remarkable adaptability of this group to both coastal and oceanic environments. However, some species still have unknown distribution patterns and are seemingly cryptic. Understanding these biogeographical patterns is a useful tool for identifying potential cryptic species and, consequently, for improving the management of conservation measures for species affected by phenomena such as climate change.

1 | Introduction

The family Sepiolidae Leach, 1817 (Superfamily Sepioloidea Leach 1817) is composed of three subfamilies (Heteroteuthinae Appellöf 1898, Rossiinae Appellöf 1898 and Sepiolinae Leach 1817) and one species (*Choneteuthis tongaensis*) that does not fit clearly into any of the currently recognized subfamilies (Lu and Boucher-Rodoni 2006). The family systematic status has been revised by several authors (Khromov 1990, 1991; Boletzky 1995; Sweeney and Roper 1998), confirming its validity (Sweeney and Roper 1998) based on genetic (Bonnaud et al. 1996; Carlini and

Graves 1999), electrophoretic and immunological (Boucher-Rodoni et al. 1995; Bonnaud et al. 1996) evidences. Sepiolidae is one of the most diverse groups of cephalopods from the ecological standpoint, with representatives in all the world's oceans and in a wide depth range (Roper et al. 1984; Bello 2019; Sánchez et al. 2021). This group comprises 80 nominal species (WoRMS 2026), although the actual number of sepiolid species is unknown, as many species and morphotypes still need to be described in detail. The accurate identification of sepiolids, which requires knowledge of their morphology, as well as their distribution patterns, ecology and behaviour, is essential for

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the effective implementation of conservation measures for both populations and species of cephalopod (Braid and Bolstad 2019). This is especially relevant due to the recognized impact of climate change on species biodiversity and ecosystems (Coelho et al. 2023).

Sepioids can grow to 10 cm in mantle length, and they can all be easily recognized by their short, oval and round-ended mantle, and by its rounded fins inserted at mid-length of the mantle (Guerra 1992; Jereb and Roper 2005). Although several species are exploited locally, this family has low fishery interest (Jereb and Roper 2005). On the other hand, this group is ecologically important because they represent an intermediate position in the trophic webs. This is because sepioids are eaten by a large number of species and prey actively on molluscs, crustaceans and fish (Clarke 1996; Luna et al. 2026). However, many aspects of the group are poorly understood. This may be due to its low economic value, to the difficulty of observing it because its small size and to the fact that most of them are nocturnal (Nesis 1987). Added to this, normally, the trawl nets – both commercial and scientific- designed with a bigger mesh size excluding the catch of these small cephalopods (Bello 2019), which makes it yet more difficult their capture and report (A. Luna, unpubl. data). It should be noted that cephalopods tend to twist and escape from the meshes of the nets (Clarke 2007). Plankton or trawl nets specially designed for these sizes are needed to catch them.

The distribution patterns of this family should be related to both the displacement and habitat capacity of the adults, as well as the dispersal capacity of their larval stages. In the case of cephalopods, this last factor is determined by the size of the egg, which defines the size of the newborn paralarva and the duration of this phase, as well as by its “planktonic” or “benthic” character (Bello and Biagi 1995; Laptikhovsky et al. 2009). Characteristics of reproduction and ecology differ in each subfamily whose ecology and life cycle are poorly known for many of those species (Bello and Biagi 1995; Jereb and Roper 2005).

This review analyses the biogeographic patterns of sepioid species based on their known distributions and biological characteristics.

2 | Materials and Methods

A systematic review of data on the Sepiidae family was conducted in accordance with the PRISMA (Page et al. 2021) and SWiM (Campbell et al. 2020) methodological recommendations. For this review, a systematic search was carried out of scientific works, databases and web pages related to cephalopods. First, a complete compilation of valid sepioid species and distribution was made using Roper et al. (1984), Nesis (1987, 1993), Bello (1995), Nateewathana (1997), Sweeney and Roper (1998), Bello (2003), Jereb and Roper (2005), De Heij et al. (2017) and Bello (2020) publications. The WoRMS (2026) database was also used to corroborate the validity of the species and their updated scientific names. Sepioid publications were searched in the BioCephaLab bibliographic collection (which includes almost 3600 papers and books about cephalopods), the internet repositories (such as Google Academic, ResearchGate and Web of Science) and the University of Vigo's bibliographical

resources (including access to major scientific journals). The reviewed publications include the reproductive characteristics and habitats of sepioids, as well as the distribution characteristics of each species, analysed by genus and subfamily, including descriptions and reports of their presence or absence, and their geographic and bathymetric distribution. Genetic and morphological studies on species identity, distribution and phylogenetic relationships were also reviewed. Species were analysed looking for wide and restricted distributions. In the latter case, we consider a species to be endemic when its distribution is limited to a specific area.

For distribution patterns analyses, the classification of marine regions and biogeographical provinces by Toonen et al. (2016) was used. The biogeographical characterization of the zones in which sepioid species are distributed followed the studies of Briggs (2003, 2006), Mironov (2006), Spalding et al. (2007), Bowen et al. (2013), Bowen et al. (2013) and Toonen et al. (2016), among others. Twelve general studies about cephalopods species distribution, including a paper about species richness in coastal cephalopods (Rosa et al. 2019) and 115 scientific papers on sepioids, were selected. From these papers, information about each species was analysed in order to obtain data on their distribution, bathymetric range, habitat, reproductive characteristics and phylogenetic relationships, among other relevant details for the study. Where citations regarding the distribution of a species were considered doubtful, the information was cross-checked and validated with data from other studies. If a species is likely to be present in an area but this has not yet been clearly confirmed, this data was included in the tables and maps as ‘doubtful’, indicating this where appropriate.

To avoid making this review too long and repetitive, the results and the discussion were combined into a single section. This streamlines and optimizes the reading experience.

3 | Results and Discussion

The list of 80 species analysed, including their full scientific name and authorship, distribution and bathymetric range, is shown in Table S1. The species *Heteroteuthis* sp.1 and *Iridoteuthis* sp.1, which were reported in Sala y Gómez Archipelago and the Nazca Ridge, in the southern Pacific Ocean by Nesis (1993), were not included in the analysis. This is because their taxonomic identity is still unclear.

The family Sepiidae is generally distributed on the continental shelf and slope, at depths between the surface and 3000 m. The Sepiinae species are the most coastal and live associated with the bottom, mainly on the continental shelf and slope at depths of over 500 m; although some of the species from this subfamily, such as *Sepietta oweniana*, inhabit a wide depth range, from the surface to over 1000-m depth (Jereb and Roper 2005; Drerup 2022). The species of Rossiinae live associated to the bottom, mainly on the continental shelf, slope, and in deep waters from the surface to 1800 m (Drerup 2022). On the other hand, the Heteroteuthinae representatives show a lifestyle associated mainly to the water column in open ocean environments, inhabiting deeper waters from surface to 3000 m (Jereb and Roper 2005; Drerup 2022).

3.1 | Geographical Distribution Patterns

Members of Sepiolidae have distributions ranging from restricted to wide, from coastal benthic (Sepiolinae and Rossiinae) to oceanic habitats (Heteroteuthinae). The Atlantic Ocean and Mediterranean Sea (40.5% and 22.8% of species, respectively) and the Indo-Pacific region and western Pacific Ocean (30.4% and 34.2% of species) show the largest number of species in this family (Figure 1).

3.1.1 | Subfamily Sepiolinae

Within this family, the subfamily Sepiolinae is the largest group of sepiolids, comprising 11 genera and 39 species. It is

distributed throughout the coasts of the eastern Atlantic, Indian and western Pacific Oceans, in tropical, temperate and cold waters (Figures 2–4). This ‘Old World’ pattern is very similar to the Sepiidae distribution (Khromov 1998; Young et al. 1998), but differs in that Sepiolinae are found in Hawaiian waters (*Euprymna scolopes*), while Sepiidae are absent there (Voss 1974; Khromov 1998; Jereb and Roper 2005).

The Lusitanian and Indo-Polynesian provinces show the highest number of Sepiolinae species, with 21 (14 in the Mediterranean and 10 in the Atlantic) and 12 species, respectively, mainly belonging to the *Sepiolo* and *Euprymna* genera. However, the latter genera show different distribution patterns: *Sepiolo* spp. can be found in both the Indo-Polynesian (one species) and the Lusitanian (11 species) provinces; in

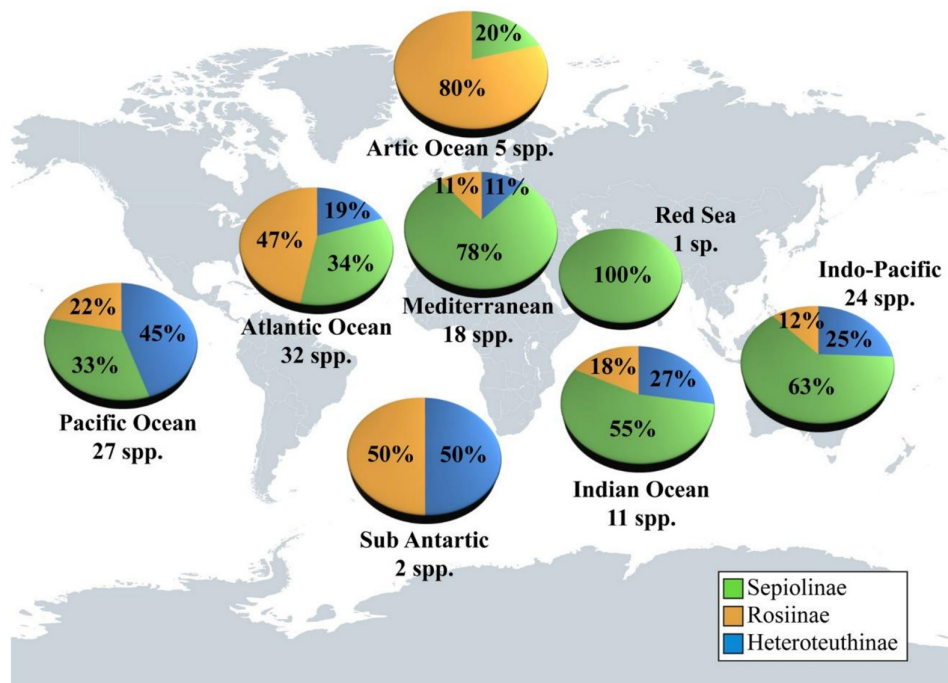


FIGURE 1 | Sepiolidae species abundance distribution in the principal oceans and seas.

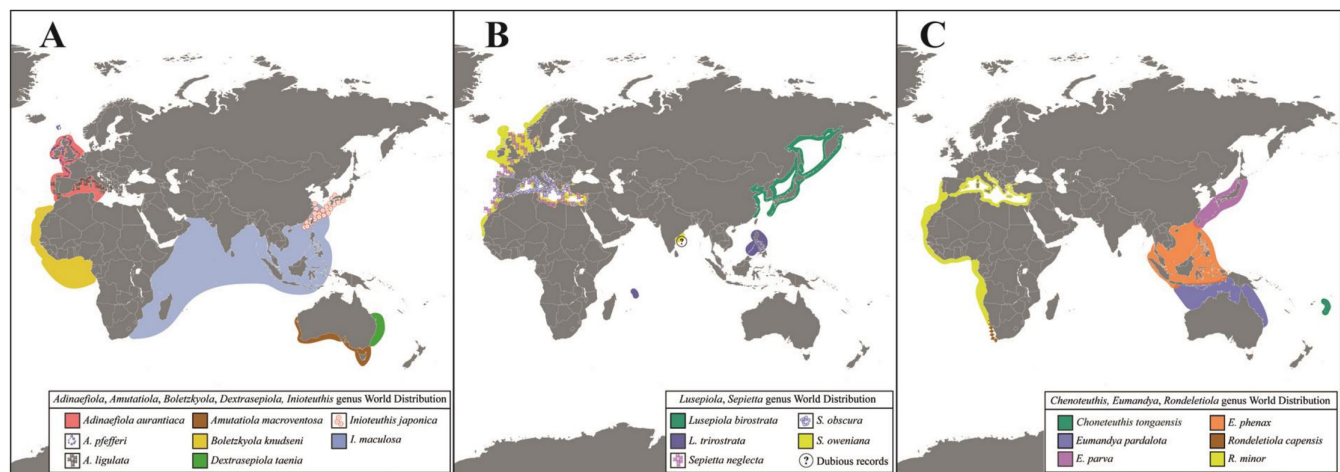


FIGURE 2 | Distribution of species of the subfamily Sepiolinae. (a) Genera *Adinaefiola*, *Amutatiola*, *Boletzkyola*, *Dextrasepiola* and *Inioteuthis*. (b) Genera *Lusepiola* and *Sepietta*. (c) Genera *Eumandya* and *Rondeletiola*. In addition, *Choneteuthis* genus distribution is shown.

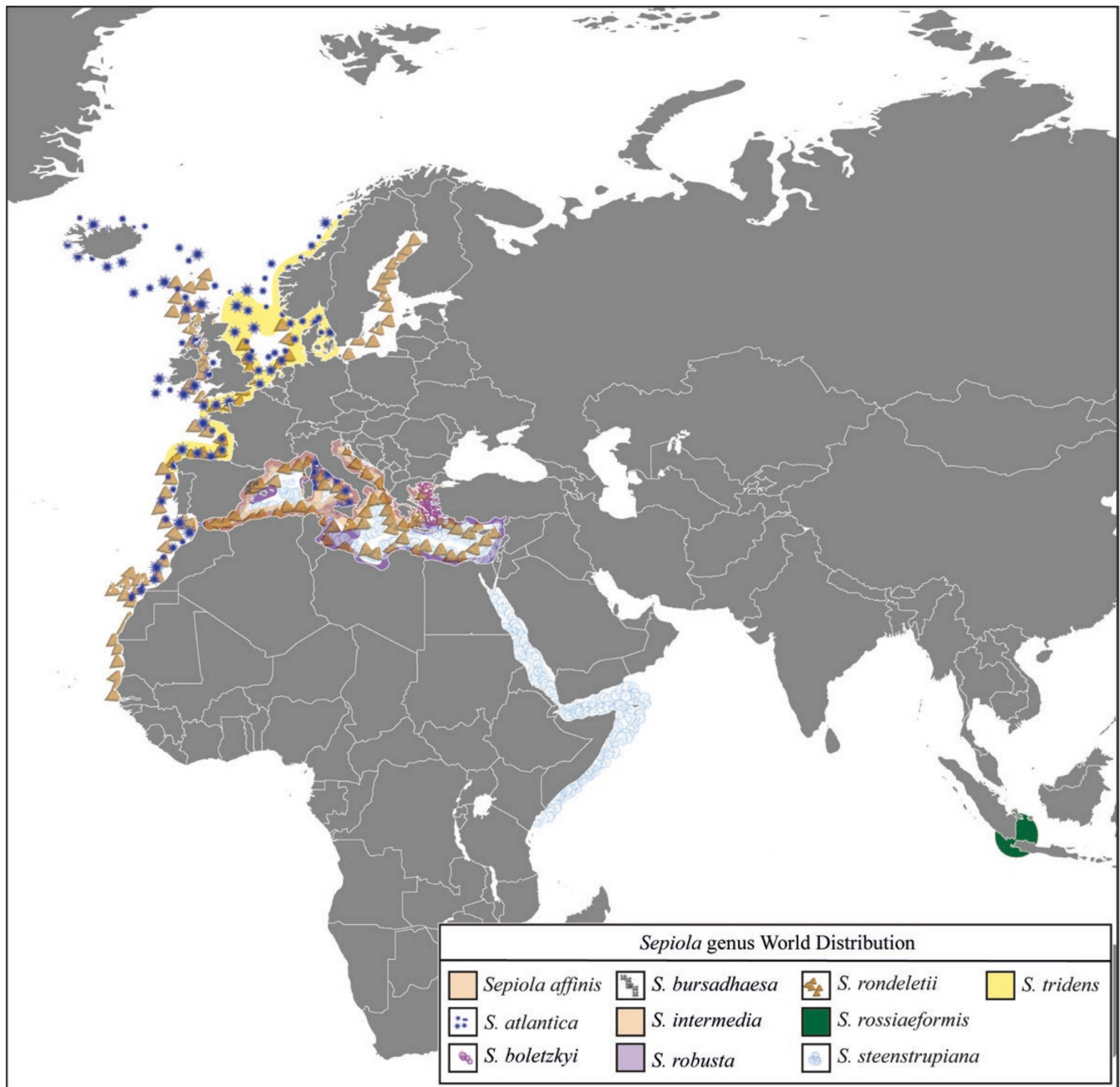


FIGURE 3 | Distribution of species belonging to the genus *Sepioloidea* (subfamily Sepioloidea). Since *Sepioloidea affinis* and *Sepioloidea intermedia* have the same distribution pattern, both species are indicated with the same colour.

contrast, *Euprymna* spp. are present in the Indo-Pacific province (six species), but absent in the Lusitanian one (Table 1; Figures 3 and 4).

Sepioloidea atlantica is restricted to the Atlantic Ocean (Jereb and Roper 2005; Rodrigues, Garci, et al. 2011) (Figure 3). Würtz et al. (1995) cited one specimen of this species in the Mediterranean, but its presence there is currently doubtful (Bello 2019). These findings raise the question of whether the newly discovered species have been present in the Mediterranean for a long time without being officially recognized, or if the animals only recently entered the Mediterranean through the Strait of Gibraltar or the Suez Canal (Salman et al. 1999). Although sepiolid diversity would

thus increase in Mediterranean waters as a result, we prefer to disregard this record because it refers to only one specimen, which may have entered the Mediterranean accidentally. Nevertheless, this record could exemplify how a species' distribution pattern may occur. In addition, this species is a good example to illustrate the confusion surrounding the nomenclature and classification of sepiolids (Bello 2011).

Another example is *Sepioloidea tridens*, which was discovered thanks to genetic techniques (De Heij and Goud 2010), and only afterwards discriminated morphologically from *S. atlantica*.

Sepietta oweniana is a well-documented and abundant species present in the northeast Atlantic and the Mediterranean (Jereb

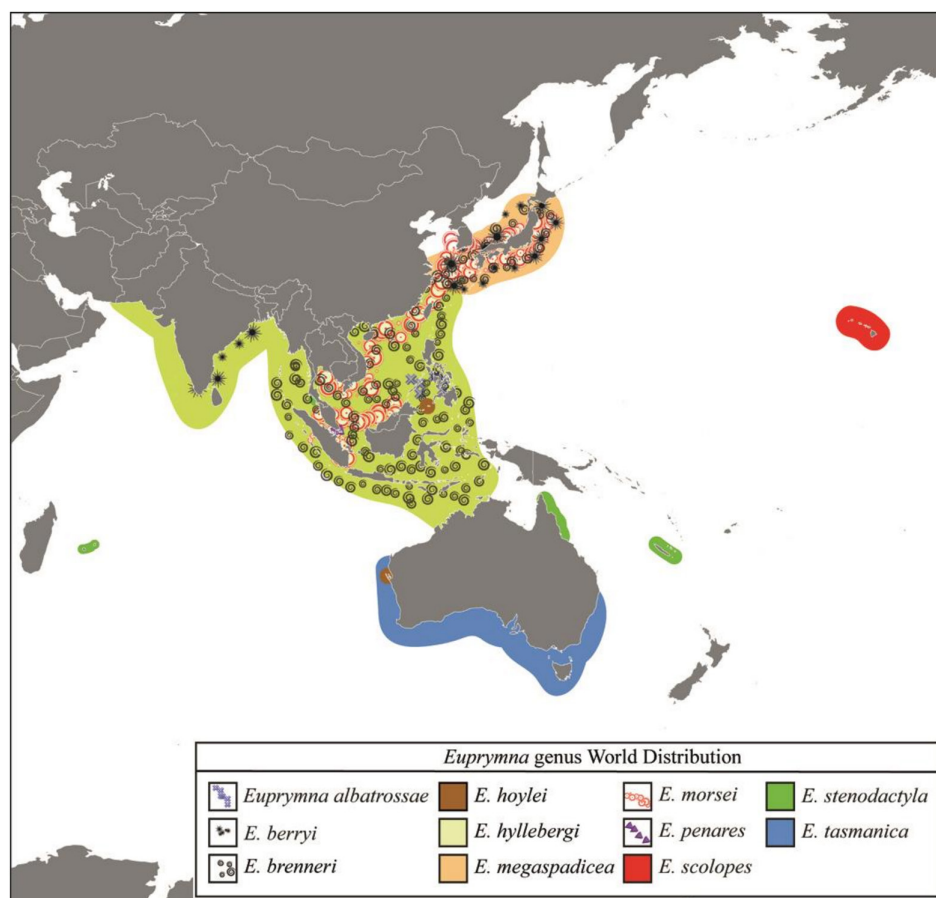


FIGURE 4 | Distribution of species belonging to the genus *Euprymna* (subfamily Sepiolinae).

and Roper 2005; Bello 2019). Although its distribution seems to be clear, Mohan and Rao (1978) cited the species in the western coast of Gulf of Bengal (India). Given that the morphologic description of the specimens in this paper is unclear and that this record has not been confirmed by new citations for the area, the presence of *S. oweniana* in Indian waters must be considered dubious until further confirmation. Its distribution in northern waters has recently expanded to the Barents Sea in the Arctic, probably due to Arctic warming (Golikov et al. 2014).

The distribution of the *Euprymna* and *Eumandya* genera is remarkable. Assuming no significant data on their distribution has been ignored, the distribution patterns of these genera could indicate that they originated in the Indo-Polynesian and Sino-Japanese provinces (Figures 2c and 4), which have a relatively recent origin (Norman and Lu 1997), given that *Eumandya* is only present here and *Euprymna* is scarce outside this area. Consequently, the greater diversity of the Indo-Polynesia and Sino-Japanese provinces could mean that they act as Briggs's 'species origin centers', exporting species outside the provinces (Briggs 1999a, 2003, 2006). This would be the case of *E. scolopes* in Hawaiian Islands (Berry 1914; Anderson and Mather 1996) or *Euprymna stenodactyla* in Mauritius Island (Voss 1963). For example, *E. stenodactyla* is known with certainty to be found on Mauritius Island, although it has been reported in the Indo-West Pacific, north of Australia and Solomon Islands (Nesis 1993; Nootmorn and Chotiyaputa 2002), albeit these records arise some doubt (Jereb and Roper 2005).

Furthermore, considering the widest distribution of *Euprymna morsei*—that overlaps almost every other *Euprymna* spp. distribution—according to Briggs (1999a, 2003) criteria, we could hypothesize that it is the oldest species of the genus. Competitive speciation phenomena may have occurred in animals living at the limits of this species' range, with the new resulting species being younger or later evolved (Briggs 1999a, 2003). This could explain the sympatric distributions observed in *Euprymna hoylei*, *Euprymna hyllebergi*, *Euprymna albatrossae*, *Euprymna phenax* and *Euprymna berryi*. In comparison, *E. berryi* and *E. stenodactyla* exhibit vicariant (allopatric) distributions, which may have been produced by the formation and/or destruction of biogeographic barriers during the Pleistocene glacial and interglacial periods (Potts 1983; Benzie and Williams 1997; Briggs 1999a). These phenomena could also have created cryptic species in the area (Benzie and Williams 1997), explaining the genetic differences between morphologically similar individuals of *Euprymna tasmanica* found in Australian waters (Norman and Lu 1997).

As in some octopods and cuttlefish, the high diversity of sepiolids, particularly *Euprymna*, can be explained by the near-total absence of a paralarval planktonic stage (Voight 1998; Young et al. 1998). This reduces genetic flux and dispersion capacity, consequently representing an advantage for increased speciation and diversity. However, there is a species of *Euprymna* that has colonized Hawaii in spite of the genus's reduced dispersion capacity. This species, *E. scolopes*, has been intensely studied

TABLE 1 | Sepiolineae distribution by biogeographic provinces by genus, indicating the number of species in each province.

Ocean	Provinces	Sepiolineae										Total	
		<i>Adinaeffiola</i>	<i>Amutatiola</i>	<i>Boletzkyola</i>	<i>Dextrasepiola</i>	<i>Eumandya</i>	<i>Euprymna</i>	<i>Inioteuthis</i>	<i>Lusepiola</i>	<i>Rondeletiola</i>	<i>Sepietta</i>		<i>Sepiola</i>
Indian Ocean	Agulhas									1			1
	Western Indian Ocean					2		1				1	4
	Red Sea											1	1
Indo-Pacific	Indo-Polynesian					2	6	1	1			1	12
	Southwestern Australia	1					1						2
	Southeastern Australia	1		1			2						4
	Tasmanian	1					1						2
Pacific Ocean	Sino-Japanese				1	4		2	1				8
	Oriental				1			1	1				3
	Okhotsk								1				1
	Kuril								1				1
Atlantic Ocean	Hawaiian						1						1
	Eastern Atlantic	2								2	3		7
	Lusitania (Atlantic)	2								1	3	3	9
	Lusitania (Mediterranean)	2								1	3	7+1 ^a	13+1 ^a
	Tropical East Atlantic			1						1	1	1	4
	Benguela									2			2
	Arctic										1		1

^aSpecies reported but whose presence is doubtful.

(Sánchez et al. 2021), revealing that it has a planktonic stage lasting 1–4 weeks and a life cycle of 10 months (Singley 1983; Hanlon et al. 1997; Claes and Dunlap 2000). Its hatchlings spend long periods of the day buried and only swim during hunting activities (Hanlon et al. 1997). However, none of these features explains how this species reached Hawaii (Berry 1914; Anderson and Mather 1996). In any case, the dispersionist or the vicarionistic paradigms could explain it. First, the dispersionist hypothesis, known as ‘stepping-stone dispersal’, involves the dispersal of the species by currents, mainly across the East Pacific Rise. This premise has been used to explain the allopatric distribution of some marine species, such as a number of trans-Pacific distributions (Rosenblatt and Waples 1986; Brown and Lomolino 1998; Briggs 2003, 2006). Here, only a few individuals were able to cross long distances and colonize far-off coasts from expansive nuclei. Due to their limited life cycle, daily habitats and activities, it seems very unlikely that this theory can be applied in this case. One possible method of dispersal could be oceanic rafting, which plays a fundamental role in the colonization of isolated biotas by ‘non-dispersive’ species (Thiel and Gutow 2005; Fraser et al. 2011). Second, the vicarionistic hypothesis argues that taxa dispersion is not a random process but occurs following the movement of tectonic plates (Heads 2005). In this way, the distribution of *E. scolopes* would represent a population separated from the remaining *Euprymna* species of Indo-West Pacific by the tectonic formation of the East Pacific Barrier.

The Sepiolineae subfamily also includes endemic species with restricted distributions. This could be the case for representatives of two monospecific genera, *Amutatiola macroventosa* and *Dextrasepiola taenia*, both of which are found only in Australian waters (Lu and Okutani 2022). *Sepiola steenstrupiana* is considered an endemic species of Mediterranean Sea (Bello 2019). However, this species was previously cited in the Red Sea (Adam 1973) and the coast of Somalia (Rocha et al. 1998) (Figure 3), suggesting that it may have colonized the Indian Ocean through an anti-Lessepsian migration. There are only a few cases of this type of migration from the Mediterranean to the Red Sea (Rocha et al. 1998; Bello 2019). Generally, it occurs in the opposite direction, from high to low diversity ecosystems (Briggs 1974; Vermeij 1991; Briggs 1999b). The other species of the subfamily considered endemic are *Rondeletiola capensis* (from South Africa), *Inioteuthis japonica* (from Japan and China) and *Sepietta obscura* (from Mediterranean) (Voss 1962; Jereb and Roper 2005; Bello 2019).

3.1.2 | Subfamily Rossiinae

The Rossiinae subfamily comprises four genera and 21 species, which are found in all oceans except Antarctic and Hawaiian waters (Figure 5). Contrary to the Sepiolineae, Rossiinae species can also be found in American waters, associated with the continental shelf and slope, showing a more extensive distribution pattern than the Sepiolineae. The Atlantic Ocean shows the highest species abundance (Table 2). Some authors consider this subfamily to be mainly distributed in cold waters (Young et al. 1998) because the Arctic region has four species. However, this subfamily is also widely distributed in temperate and tropical waters, with six species in tropical Caribbean waters (Table 2).

The four Rossiinae genera are widely distributed, although *Semirossia* appears to be limited to the American coast (Figure 5b), which could indicate that the group originated there. On the other hand, some species of *Semirossia*, *Austrorossia* and *Neorossia* exhibit discontinuous distributions along the coast (Figure 5). This may be a consequence of the lack of data from areas where specimens of these genera have not yet been found or described. This is the case of *Semirossia tenera*, with a widespread distribution in the Atlantic coast of America from Nova Scotia to Caribbean Sea (Figure 5b). This species is possibly also present in the South America coast from Surinam to Uruguay coast, but this distribution must be confirmed (Jereb and Roper 2005).

Austrorossia mastigophora is distributed in both African coast of Atlantic and Indian Oceans, from Guinea to Somalia (Jereb and Roper 2005; Luna et al. 2021). Guerra et al. (2011) report the species in Patagonian shelf waters (southwest Atlantic Ocean) and Rocha (1997) cited the species on the coast of central Chile (Pacific Ocean). Both records could be considered doubtful (Figure 5a). This, because Rocha (1997) cannot examined the specimens. Instead, Guerra et al. (2011) record is based on a female caught and examined by the authors, but no morphological data on the specimen were showed.

Until recently, the geographic distribution of *Neorossia caroli* encompassed the Mediterranean Sea, the North Atlantic Ocean (along the coasts of both Europe and North America), the Atlantic coast of Africa as far south as Namibia and the Patagonian continental slope and Falkland Islands in the southwestern Atlantic (Jereb and Roper 2005). However, records of *N. caroli* on the American coast, between Newfoundland Bank and the Gulf of Mexico, could be considered doubtful (Jereb and Roper 2005). On the other hand, Nesis et al. (2001) reported *N. caroli* in the southwestern Atlantic, considering that the population present there corresponds to the subspecies *N. caroli jeannae*. Recently, Bonavita et al. (2026) determined that this population corresponded to a new species, *Neorossia jeannae*, meaning that *N. caroli* is no longer found in the southwestern Atlantic Ocean (Figure 5b).

The subfamily Rossiinae contains several endemic or restricted-distribution species, such as *Rossia moelleri* (from the Arctic Province), *Rossia brachyura* (from the Caribbean) or *Semirossia patagonica* (from the Pacific and Atlantic coasts of South America) (Voss 1955; Rodhouse et al. 1992; Rocha 1997; Nesis 2001). On the contrary, *Rossia pacifica* shows a wide trans-oceanic distribution (Figure 5c) on both sides of the North Pacific Ocean (Jereb and Roper 2005). This is a well-known species studied in both laboratory and wild conditions (Summers 1985b; Anderson 1991; Laptikhovsky et al. 2008). The paralarvae of this species have a very short planktonic stage, and the hatchlings quickly adopt the adult lifestyle (Summers 1985b; Summers and Colvin 1989; Anderson 1991). These characteristics—a short life cycle and a nearly absent planktonic phase—make large-scale migrations difficult to conceive (Summers 1985a). Once again, the vicarionistic hypothesis explanation seems to be more plausible (Rosenblatt and Waples 1986; Brown and Lomolino 1998; Briggs 2003; Thiel and Gutow 2005; Briggs 2006; Fraser et al. 2011). Mangold et al. (1998) indicated that there could be two different subspecies of *R. pacifica*, distributed on the eastern

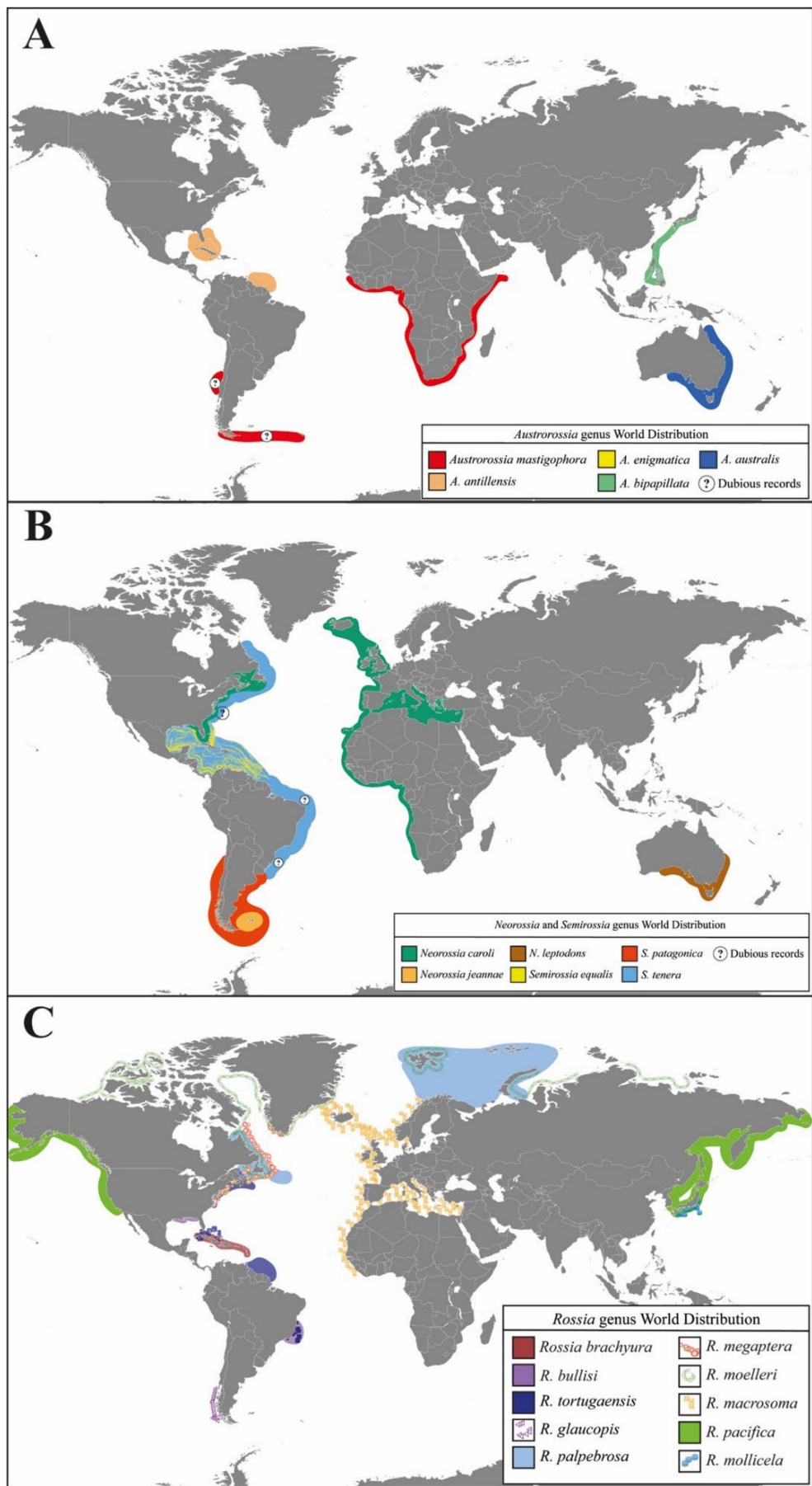


FIGURE 5 | Distribution of species of the subfamily Rossiinae. (a) Genus *Austrorossia*. (b) Genera *Neorossia* and *Semirossia*. (c) Genus *Rossia*.

TABLE 2 | Rossiinae distribution by biogeographic provinces by genus, indicating the number of species in each province.

Ocean	Provinces	Rossiinae				Total Rossiinae
		<i>Austrorossia</i>	<i>Neorossia</i>	<i>Rossia</i>	<i>Semirossia</i>	
Indian Ocean	Agulhas	2				2
	Western Indian Ocean	1				1
Indo-Pacific	Indo-Polynesian	1				1
	Southwestern Australia	1	1			2
	Southeastern Australia	1	1			2
	Tasmanian	1	1			2
Pacific Ocean	Sino-Japanese	1		2		3
	Oriental			1		1
	Okhotsk			1		1
	Kuril			1		1
	Aleutian			1		1
	Oregon			1		1
	CTZ			1		1
	California			1		1
	Southern Chile	1 ^a		1	1	3
	Tierra del Fuego	1 ^a		1	1	3
	Southern Argentina				1	1
Atlantic Ocean	Falkland Islands		1		1	2
	Argentinian				1	1
	Brazilian			1	1 ^a	1 + 1 ^a
	Western Atlantic		1 ^a	3	1	4 + 1 ^a
	Caribbean	1		2	2	5
	Carolina		1 ^a	1	2	3 + 1 ^a
	Eastern Atlantic		1	2		3
	Lusitania (Atlantic)		1	1		2
	Lusitania (Mediterranean)		1	1		2
	Tropical East Atlantic	1	1			2
	Benguela	2	1			3
Arctic Ocean	Arctic			5		5
Atlantic and Indian Oceans	Sub-Antarctic group	1				1

^aSpecies reported but whose presence is doubtful.

and western Pacific sides, since there are probably at least two different populations.

3.1.3 | Subfamily Heteroteuthinae

The Heteroteuthinae subfamily comprises six genera and 19 species distributed in the Atlantic, Pacific and Indian Oceans (Table 3; Figure 6). Young et al. (1998) suggested that it exhibits different distribution patterns than the Sepiolineae and

Rossiinae. This is mainly due to Heteroteuthinae species being pelagic (Nesis 1987; Rotermund and Guerrero-Kommritz 2010; Drerup 2022). Species such as *Heteroteuthis dispar* present an amphi-Atlantic and Mediterranean distribution in both coastal and open ocean waters (Jereb and Roper 2005; Luna et al. 2021). In addition, most species of the subfamily have been identified as inhabiting oceanic seamount and ridge habitats—e.g., Hawaii (Harman and Seki 1990), Nazca Ridge, Sala y Gómez Ridge, Discovery Seamount, Mascarene Ridge and Walters Shoals (Nesis 1993, 1994)—despite their wide

TABLE 3 | Heteroteuthinae and uncertain subfamily species distribution by biogeographic provinces and genus, indicating the number of species in each province.

Ocean	Provinces	Heteroteuthinae						Total		Uncertain subfamily
		<i>Amphorateuthis</i>	<i>Heteroteuthis</i>	<i>Iridoteuthis</i>	<i>Nectoteuthis</i>	<i>Sepiolina</i>	<i>Stoloteuthis</i>	Heteroteuthinae	<i>Chonoteuthis</i>	
Indian Ocean	Agulhas		1					1		
	Western Indian Ocean	1	1					2		
Indo-Pacific	Indo-Polynesian		2	1		1	1	5		1
	Southwestern Australia		1			1		2		
	Southeastern Australia		2		1			3		
	Tasmanian		1	1				2		
Pacific Ocean	Kuril					1		1		
	Oriental		2			1		3		
	Sino-Japanese		3			2	1	6		
	Kermadec		1					1		
	Auckland			2			1	3		
	New Zealand			2			1	3		
	Hawaiian		1	1				2		
	Eastern Island						1	1		
Atlantic Ocean	Western Atlantic						1	1		
	Caribbean		2		1			3		
	Carolina		2		1		1	4		
	Brazilian		2					2		
	Argentinian		1					1		
	Eastern Atlantic		1					1		
	Lusitania (Atlantic)		1				2	3		

(Continues)

TABLE 3 | (Continued)

Ocean	Provinces	Heteroteuthinae						Total	Uncertain subfamily
		<i>Amphorateuthis</i>	<i>Heteroteuthis</i>	<i>Iridoteuthis</i>	<i>Nectoteuthis</i>	<i>Sepiolina</i>	<i>Stoloteuthis</i>		
Atlantic and Indian Oceans	Lusitania (Mediterranean)		1				1	2	
	Tropical East Atlantic		1				1	2	
	Benguela		1				1	2	
	Sub-Antarctic group						1	1	

Note: Eastern Island Province represents Sala y Gómez Ridge and Nazca Ridge areas.

distribution in the open ocean (Drerup 2022). According to Drerup (2022), Heteroteuthinae species, independent of their open-ocean lifestyle, can be associated with the sea bottom during at least part of their life cycle, probably during the spawning period. This is based on the large number of specimens found in the stomach contents of demersal or continental slope habitat predators (Bello 1997, 1999; Kousteni et al. 2018).

The distribution patterns of most Heteroteuthinae species are poorly known, probably due to their pelagic lifestyle. Species identified only in oceanic seamounts or ridges likely have a broader distribution that goes undetected due to inadequate sampling. For example, there are significant gaps in the distribution of *Heteroteuthis dagamensis*, which has been found in the eastern and western South Atlantic, in the Gulf of Mexico (North Atlantic) and the Kermadec Islands (Pacific Ocean) (Rotermund and Guerrero-Kommritz 2010; Judkins et al. 2016; Braid and Bolstad 2019). As the specimen identifications in these zones were carried out using both morphological and DNA barcoding methods, it is unlikely that they correspond to misidentifications. In consequence, *H. dagamensis* most probably has a wide distribution, comprising Atlantic, Pacific waters and probably the Indian Ocean as well (Figure 6b).

The case of *Stoloteuthis leucoptera* is different. This is a widely distributed pelagic species in Atlantic Ocean that is uncommon in the open ocean (Nesis 1987; Vecchione et al. 1989; Sweeney et al. 1992; Nesis 1993). *S. leucoptera* has been cited in the Mediterranean Sea (Salman et al. 1999), first in 1991 (Orsi-Relini and Massi 1991), and has been cited repeatedly there since (Volpi, Borri, and Zucchi 1995; Würtz et al. 1995). However, Fernández-Álvarez et al. (2021), using morphometric and genetic analysis, identified a new species, *Stoloteuthis cthulhui*, in the Mediterranean Sea. These authors determined that specimens previously identified as *S. leucoptera* in these waters correspond to *S. cthulhui*, and *S. leucoptera* is restricted only to the Atlantic Ocean.

Several species of Heteroteuthinae can be considered endemic: *Iridoteuthis iris* inhabits the Hawaiian archipelago and several Pacific Ocean seamounts (Harman and Seki 1990; Nesis 1993), *S. cthulhui* that seems to distribute only in the Mediterranean Sea (Fernández-Álvarez et al. 2021) and *Stoloteuthis weberi* is only cited for central Indonesia (Nesis 1987). However, the latter species could have a wider distribution due to the pelagic habitat of the genus. Young et al. (2007) discovered a new species, *Amphorateuthis alveatus*, in Tanzanian waters. Kubodera et al. (2009) discovered another new species belonging to this genus, *Heteroteuthis ryukyuensis*, in Japan.

3.2 | Insular and Submarine Ridges Species Distribution

A total of 22 species of Sepiolidae were found in the waters surrounding isolated islands and submarine ridges (Table 4). According to Nesis (1987), at least two other unidentified species of Heteroteuthinae are associated with this kind of distribution. This 'insular pattern' is most frequent in the Heteroteuthinae species (40.9%), followed by Sepiolinae (36.4%) and Rossiinae (18.2%). In addition, *C. tongaensis* (4.5%) is included here,

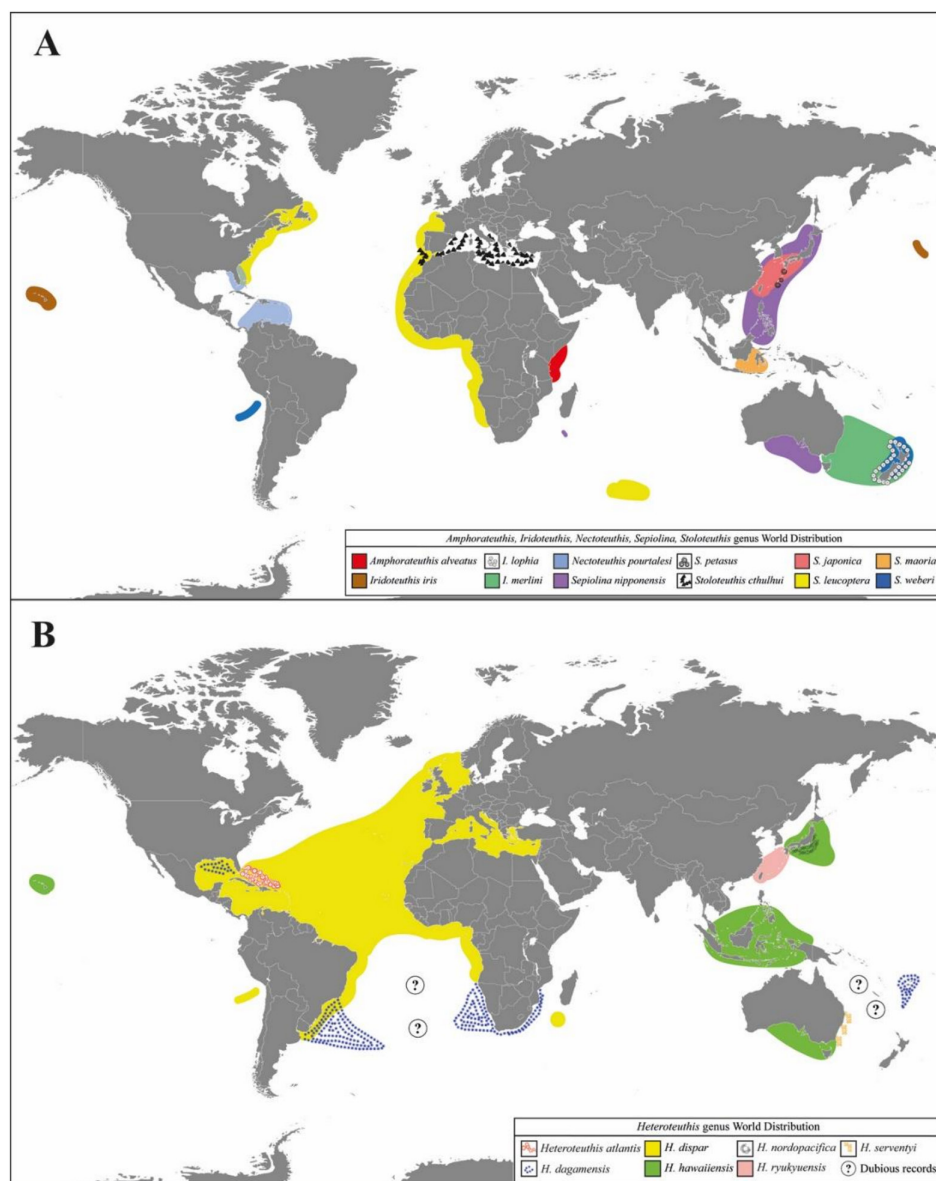


FIGURE 6 | Distribution of species of the subfamily Heteroteuthinae. (a) Genera *Amphorateuthis*, *Iridoteuthis*, *Nectoteuthis*, *Sepiolina* and *Stoloteuthis*. (B) Genus *Heteroteuthis*.

although its current taxonomic subfamily is uncertain (Lu and Boucher-Rodoni 2006).

Nesis (1993) indicated that the cephalopod fauna found on oceanic islands can be explained by the dispersionistic, but not by the vicarionistic, paradigm. For example, the fauna on the seamounts of the Nazca and Sala y Gómez ridges is clearly an offshoot of the Indo-West Pacific fauna, which is only compatible with the dispersionistic point of view (Nesis 1993). This may apply to Heteroteuthinae species (Jereb and Roper 2005; Drerup 2022). Due to their pelagic habitat and wide oceanic distributions, they are apparently able to colonize oceanic islands, seamounts, and submarine ridges as it is both the case of *H. dispar* and *H. dagamensis* (Rotermund and Guerrero-Kommritz 2010; Judkins et al. 2016; Braid and Bolstad 2019). Other species in this group that have been described in these environments could also have wider distributions. Nonetheless, these distributions are currently unknown due to a lack of information or records.

However, the distribution of Sepiolinae and Rossiinae species, which presumably lack pelagic stages (Jereb and Roper 2005; Drerup 2022), must be explained by a different mechanism (Nesis 1993). Probably, the most plausible explanation is the vicariant one. Again, one possible dispersal method is oceanic rafting. Here, the ocean currents transport the sepiolids to the location, on floating macroalgae, pieces of wood or another flotsam that have become detached from the bottom. This phenomenon has been documented for a great number of 'non-dispersive' and sessile marine species (Thiel and Gutow 2005; Fraser et al. 2011), including cephalopods such as *Pteroctopus tetracirrhus* in the Atlantic Ocean (Villanueva et al. 2020), *Lusepiola birostrata* and others near Japan (Hirosaki 1964) and several other species of cephalopods around the world (Thiel and Gutow 2005). Both the Sepiolinae and the Rossiinae species lay their eggs attached to objects on the bottom, including various substrates such as rocks, sponges, algae, bryozoans and man-made objects (Okutani and Sasaki 2007; Drerup 2022; Jolly

TABLE 4 | Sepiolidae species present in isolated Islands and submarine ridge waters.

Subfamily	Specie	Location
Sepiolinae	<i>Adinaefiola pfefferi</i>	Faroe Islands
	<i>Euprymna scolopes</i>	Hawaii Islands
	<i>Euprymna stenodactyla</i>	Mauritius Island Solomon Islands
	<i>Lusepiola tristrostrata</i>	Saya de Malha Bank
	<i>Sepietta oweniana</i>	Madeira Islands
	<i>Sepiola atlantica</i>	Faroe Islands
	<i>Sepiola rondeletii</i>	Faroe Islands
Rossiinae	<i>Austrorossia mastigophora</i>	Error Seamount
	<i>Neorossia caroli</i>	Azores Island Falkland Islands
	<i>Rossia macrosoma</i>	Azores Island Faroe Islands
	<i>Semirossia patagonica</i>	Falkland Islands
	<i>Heteroteuthis dagamensis</i>	Kermadec Islands Mascarene Ridge
Heteroteuthinae	<i>Heteroteuthis dispar</i>	Azores Island Bermuda Islands Canary Islands Madeira Islands Nazca Ridge Sala y Gómez Ridge Walters Shoals
	<i>Heteroteuthis hawaiiensis</i>	Combe Shoal Ogasawara Island Hawaii Islands
	<i>Iridoteuthis iris</i>	Colahan Seamount Hawaii Islands Hancock Seamount Kammu Seamount
	<i>Sepiolina nipponensis</i>	Walters Shoals
	<i>Sepiolina petasus</i>	Kume-shima Island
	<i>Stoloteuthis japonica</i>	Kume-shima Island
	<i>Stoloteuthis leucoptera</i>	Kerguelen Island
	<i>Stoloteuthis maoria</i>	Nazca Ridge Sala y Gómez Ridge
	<i>Choneteuthis tongaensis</i>	Tonga Islands
Uncertain subfamily		

et al. 2022), some of which can break off from the seabed and be carried by ocean currents.

3.3 | Bathymetric Distribution Patterns

Sepiolinae and Rossiinae are mainly benthic, whereas Heteroteuthinae is pelagic (Nesis 1987; Sweeney et al. 1992; Villanueva 1995; Young et al. 1998) with nektonic properties (Volpi, Borri, and Zucchi 1995). Heteroteuthinae likely

approaches the bottom during the spawning period to spawn (Drerup 2022). Most Sepiolidae species perform bathymetric migrations (Drerup 2022) and can move to the surface during the night to spawn when they are close to the coast (Nesis 1987). In fact, specimens of *Sepiola*, *Sepietta*, *Euprymna* and *Rossia* can be collected in zooplankton and water column samples (Vecchione 1987; Bello and Biagi 1995).

The subfamily Sepiolinae is constituted mainly by small, benthic species living between the surface and a depth of 1000 m,

most species inhabiting the continental shelf in the upper 200 m (Nesis 1987; Sweeney et al. 1992; Young et al. 1998; Jereb and Roper 2005; Bello 2019) (Figure 7). *Rondeletiola minor* and *S. oweniana* are the Sepiolinae that reach the greatest depths, being the most abundant between depths of 150 and 500 m (Villanueva 1995). *S. oweniana* has the widest bathymetric range, occurring between 8 and 1000 m (Table S1) and is considered the most eurybathic sepioline (Drerup 2022). Orsi-Relini and Bertuletti (1989) and Bello (2019) believed that *Sepiola rondeletii*, *Sepiola affinis* and, probably, *S. steenstrupiana*, are shallow water species. Moreover, these authors considered *Sepiola robusta* and *Adinefiola ligulata* as circumlittoral species, *Sepiola intermedia* as eurybathic and *Adinaefiola aurantiaca* as bathyal species. *S. obscura* inhabits neritic waters, and *Sepietta neglecta* can reach bathyal depths (Orsi-Relini and Bertuletti 1989).

The species of the subfamily Rossiinae show a more extended vertical distribution (Nesis 1987; Sweeney et al. 1992; Young et al. 1998; Jereb and Roper 2005; Drerup 2022). Most Rossiinae live deeper than Sepiolinae, at depths between 200 and 600 m (Figure 7). For example, *R. pacifica* can be found from the surface to 1200 m, and *N. caroli* is distributed between 120 and 1744 m of depth (Table S1), both species exhibiting ontogenetic vertical migration (Villanueva 1992, 1995; Jereb and

Roper 2005). *Neorossia* spp. have characteristics similar to those of abyssal species, such as the absence of an ink sac and luminous organs (Boletzky 1971).

Heteroteuthinae species inhabit pelagic or nectobenthic environments (Roper and Young 1975; Nesis 1987; Orsi-Relini and Massi 1991; Sweeney et al. 1992; Young et al. 1998; Drerup 2022). These species are distributed primarily in the bathyal zone, mainly between 200 and 1000 m, being able to reach considerable depths (Figure 7). *H. dispar* shows both diel and ontogenetic vertical migrations (Nesis 1987; Vecchione 1987; Orsi-Relini 1995). The adult individuals migrating to the surface at night (Roper 1974). In addition, its paralarvae have been reported from mesopelagic and bathypelagic zones between 1500 and 3000 m, but adults commonly occur at depth between 200 and 300 m (Jereb and Roper 2005). As indicated by Drerup (2022), Heteroteuthinae species can be less pelagic than it was supposed, at least during part of their life cycle. For example, *Heteroteuthis hawaiiensis* and *I. iris* seem to be associated with submarine ridges (Harman and Seki 1990; Okutani and Tsuchida 2005), and it is likely that the Heteroteuthinae species move close to the bottom during the reproductive period near continental slopes, seamounts and submarine ridges, despite their wide open-ocean distribution (Nesis 1993; Drerup 2022).

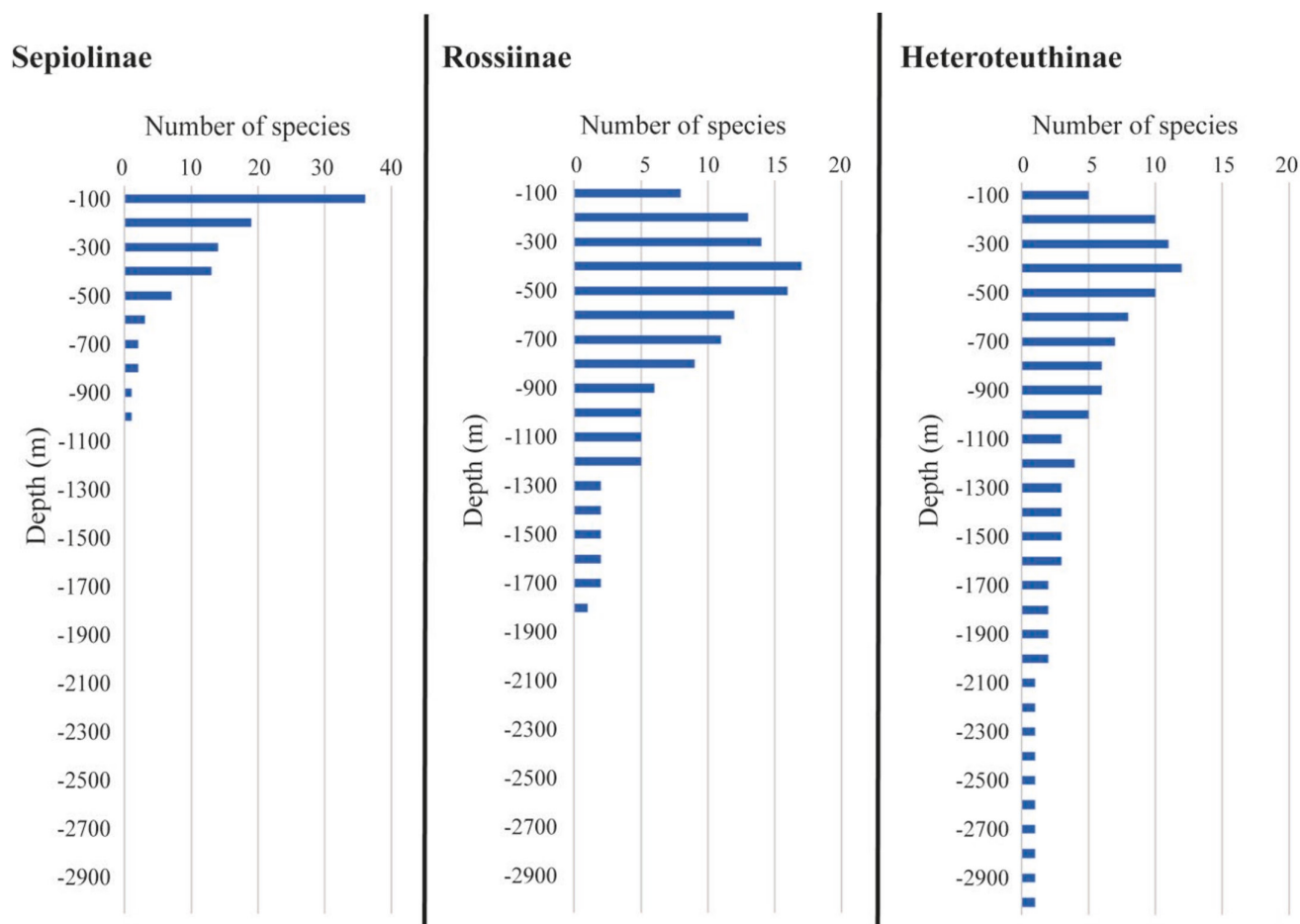


FIGURE 7 | Bathymetric distribution range of Sepiolinae, Rossiinae and Heteroteuthinae subfamilies. The number of species present in each 100-m-deep interval is indicated.

3.4 | Paralarvae Distribution Patterns

As far as is known, Sepiolineae and Rossiinae lay benthic eggs on the bottom, either close to or farther from the coast, depending on the species (Jereb and Roper 2005). The eggs are attached to different substrates and organisms (such as algae or corals), arranged in small groups or individually (Drerup 2022). Little is known about how Heteroteuthinae species lay their eggs, since they have not yet been observed in the wild or in captivity (Drerup 2022). Only a record of one egg of *Heteroteuthis* sp. collected on a muddy bottom (540 m deep) from Banyuls in Mediterranean Sea has been reported (von Boletzky 1978). In addition, *H. dispar* and *H. hawaiiensis* have been seen swimming near the bottom, which suggests that they may also lay benthic eggs (Orsi-Relini 1995; Okutani and Tsuchida 2005). The oocyte sizes of Sepiolidae species range from as small as 0.4-mm oocytes in diameter of *Eumandya pardalota* to 12-mm oocytes of *Neorossia leptodons* (Reid 1991, 2011). On the other hand, the egg sizes of Sepiolidae in egg-laying vary from 1.0 mm in *E. morsei* to 19.6 mm in *R. pacifica* (Shevtsov et al. 2000; Jolly et al. 2022). It is necessary to emphasize that the literature about the size of 'eggs' in cephalopods is quite ambiguous, because authors name as 'eggs' the mature oocytes (present in the ovary or oviduct) and the spawned eggs. This is important because the spawned eggs are covered by protective membranes that increase the size of the egg. For this reason, it is necessary to distinguish between oocyte and spawned egg when we consider the size of sepiolids 'eggs' (Table 5).

In general, Sepiolidae species seems to have hatchlings associated with three main strategies: (1) Direct Nectobenthic Juveniles: large eggs whose hatchlings are practically juveniles, with a short or non-existent larval period. (2) Nectobenthic paralarvae: medium-sized eggs whose hatchlings have a larval period associated with the bottom. (3) Pelagic paralarvae: medium- to small-size eggs whose hatchlings have a pelagic larval stage.

The Direct Nectobenthic Juveniles strategy in Sepiolidae comprises species with a distribution limited to coastal areas or continental slope bottoms above 1800-m depth, with large eggs and paralarvae with little dispersal capacity, nectobenthic or benthic, which quickly adopt adult life habits. Most species in the subfamily Rossiinae (Table 5) would present this pattern, inhabiting a much more limited, coastal distribution, and the largest egg sizes among the three subfamilies (spawned eggs ranging from 7.0 to 19.6 mm, corresponding to 17.5%–28.3% of the species' maximum dorsal mantle length [DML]) (Shevtsov et al. 2000; Okutani and Sasaki 2007; Hastie et al. 2009). On the other hand, these species have a bathymetric distribution ranging from the surface to depths of 1000–2000 m, enabling them to inhabit more oceanic waters, but with relatively shallow bottoms. According to Salman (2011), Rossiinae species have developed this 'holobenthic strategy' living directly in the benthic zone without a pelagic phase, which provides them with a stable habitat (Boletzky 1986). The strategy involves species with asynchronous ovulation that produces large eggs in small consecutive spawning batches (Summers 1985b; Laptikhovsky et al. 2008; Önsöy et al. 2008; Salman 2011). Little is known about the growth of Rossiinae species during reproductive process, but Summers (1985b) reported that

TABLE 5 | Sepiolidae oocytes and eggs characteristics and paralarvae-juvenile distributions patterns.

	Mean DML (mm)	Oocyte/egg	Mean size (mm)	Mean percentage of DML	Known habitat of paralarvae	Depth range (m)	Total number of species
Sepiolineae	32.8 ± 14.3	Oocyte (No = 11) Egg (Ne = 14)	3.7 ± 1.2 3.7 ± 1.2	12.3 ± 6.6 14.8 ± 9.2	Nectobenthic associated to coastal continental shelf	0–500	19
Rossiinae	62.2 ± 21.5	Oocyte (No = 11) Egg (Ne = 3)	8.8 ± 2.4 12.3 ± 6.5	13.9 ± 4.8 22.5 ± 5.5	Nectobenthic or benthic in bottoms associated to continental shelf and slope	0–1000	13
Heteroteuthinae	21.2 ± 4.5	Oocyte (No = 8) Egg (Ne = 1)	1.9 ± 0.4 2.5	9.4 ± 2.8 10.0	Pelagic ^a probably mesopelagic and abyssopelagic, far from the coast	0 ^a –3000	8
						Total	40

Note: The number of total species could not coincide with the sum of No + Ne. No: number of species where the size of oocytes was recorded. Ne: number of species where the size of spawned eggs was recorded.

Abbreviation: DML, dorsal mantle length.

^aProbable habitat or depth limit, but this information must be confirmed.

R. pacifica maintains its growth during spawning. Therefore, most species of this subfamily could develop the multiple spawning (Rocha et al. 2001) and Direct Nectobenthic Juvenile strategies.

R. pacifica is an example of a species with a bathymetric range between 30 and 550 m, inhabiting muddy and sandy coastal substrates on the continental shelf, although it can be found swimming in the water column at night (Jereb and Roper 2005). Very little information is available on the larval stages of this species but it has been established that it has a nectobenthic paralarvae lacking a planktonic stage (Summers and Colvin 1989; Jereb and Roper 2005; Villanueva et al. 2016). This is consistent with the spawned egg size (14.0–19.6 mm according to Shevtsov et al. 2000) and characteristics of this subfamily, as well as the paralarvae strategy proposed here. This pattern has also been observed in two other species in this subfamily, namely, *N. caroli* and *Rossia macrosoma*. They lay big eggs measuring 10 mm (12% of DML) and 9.2 mm (10.8% of DML), respectively, and they are distributed between the surface and depth of up 1800 m (Collins et al. 2001; Jereb and Roper 2005; Cuccu et al. 2007).

The nectobenthic paralarvae strategy evolved in Sepiolineae species (Table 5) with coastal distribution, associated with the continental shelf and slope, inhabiting the bottom up to a maximum depth of 1000 m (Bello 1995; Jereb and Roper 2005; Villanueva et al. 2016). They would have planktonic paralarvae that quickly acquire the nectobenthic lifestyle, especially in the case of the species with large eggs. Depending on the species, these paralarvae and juveniles have limited or moderate dispersal capacity, resulting in a distribution range that may be extensive but is always limited to shallow coastal areas (e.g., Collins et al. 2002; Olmos-Pérez et al. 2018). These species would have small to medium size spawned eggs from 1.0 to 4.9 mm, corresponding to 2.3%–23.8% of maximum DML (Rodrigues et al. 2012; Jolly et al. 2022; Deickert and Bello, in press). It is necessary to point out that Reid (2011) reported that *E. pardalota* has 0.4-mm oocytes. However, this data is based on the measurement of a single egg, and no gonad study was conducted. It is possible that it corresponds to an immature oocyte and the real size of mature eggs is larger, similar to the 2.0-mm size of mature oocytes observed in the congeneric species *E. parva* (Sánchez et al. 2019). The strategy comprises species with asynchronous ovulation that produces eggs into consecutive spawning batches (Gabel-Deickert 1995; Lefkaditou and Kaspiris 1998; Bello and Deickert 2003; Salman and Önsoy 2004; Rodrigues, Garcí, et al. 2011; Rodrigues et al. 2012; Önsoy et al. 2013). At least, in several species of Sepiolineae, females grow between egg batches (Rodrigues, Garcí, et al. 2011; Jolly et al. 2022). Therefore, most species of this subfamily could develop the Intermittent Terminal Spawning strategy (Rocha et al. 2001), and their new hatchling individuals use the nectobenthic paralarvae strategy.

Examples of this pattern are *S. affinis*, *S. robusta*, *S. intermedia* and *S. obscura*, with intermediate-sized eggs, nectobenthic paralarvae and coastal distribution in Mediterranean waters. *S. affinis* is endemic to the Mediterranean and has a depth range from 20 to 178 m, although it is typically abundant in shallow waters (15–30 m) over sandy or muddy bottoms. These species lay 2.2–3.2-mm eggs in intermittent batches with benthic clutches (Jereb and Roper 2005; Laptikhovskiy et al. 2008). *S. robusta* is

distributed between 26- and 498-m depth in the Mediterranean, has benthic 3.5–4.5-mm eggs (Boletzky 1983) that are spawned more than once and has nectobenthic paralarvae (Salman and Önsoy 2004; Jereb and Roper 2005; Bello 2019). The distribution of *S. intermedia* is restricted to the continental shelf between 8 and 200 m (Jereb and Roper 2005; Bello 2019). Its eggs are 4.9 mm long (Deickert and Bello, in press), and it is considered that they laid benthic clutches divided into intermittent batches (Gabel-Deickert 1995; Salman 2014). *S. obscura* is a littoral species that lives in shallow waters on sandy or muddy bottoms of the Mediterranean and Atlantic coast of the Iberian Peninsula between 27 and 376 m (Jereb and Roper 2005; Bello 2019). This species lay 3.7–4.5-mm eggs in intermittent batches (Jereb and Roper 2005; Deickert 2009). Together with *S. oweniana* and *S. neglecta*, *S. obscura* aquarium-kept has been observed to present oocytes at various stages of maturation in its oviducts, being considered multiple spawners (Deickert 2009).

In Atlantic waters, we can find other Sepiolineae species such as *S. atlantica*, *S. neglecta* and *S. oweniana* (De Heij et al. 2017). They have planktonic or nectobenthic paralarvae and are distributed in areas further offshore, but always within the continental shelf and slope. *Sepiola atlantica* is an epibenthic species restricted to the continental shelf that has been found in mid-water both during the day and at night. It is an intermittent bottom egg-laying (Gabel-Deickert 1995; Rodrigues, Garcí, et al. 2011; Rodrigues et al. 2012), with 3.7-mm eggs long (Rodrigues, Garcí, et al. 2011) and planktonic-nectobenthic paralarvae that, when they grow, gradually become epibenthic, burying themselves in the sand (Collins et al. 2002; Rodrigues et al. 2010). *S. neglecta* is a mainly mud-bottom species with a bathymetric range of 25–475 m on the continental shelf of Europe and North Africa in the Atlantic Ocean (Jereb and Roper 2005). According to Lefkaditou and Kaspiris (1998), it lays 1.4–2.8-mm eggs in intermittent batches (Deickert 2009). Its paralarvae are nectobenthic, and its individuals cover themselves with sand during the day, starting to feed in the early morning (Von Boletzky and Von Boletzky 1970). *S. oweniana* is the largest species of the genus and lives mainly in deep waters between 8 and 1000 m (common between 100 and 400 m), laying between 90- and 120-m depth (Jereb and Roper 2005), although its eggs can be found deeper (Cuccu et al. 2010). It is a multiple egg-laying with 2.1–2.5-mm spawned eggs (Bello and Deickert 2003), and a planktonic-nectobenthic paralarvae (Bergström and Summers 1983). After hatching, it swims actively day and night, spending short periods on the bottom, but its behaviour gradually changes adopting the typical adult nectobenthic lifestyle (Cuccu et al. 2010).

In Sepioidae, the Pelagic Paralarvae strategy comprises pelagic distribution species with small eggs, pelagic paralarvae and wide bathymetric distribution range (0–3000 m). This is characteristic of the subfamily Heteroteuthinae (Table 5) with wide oceanic distribution patterns and small size 1.5–2.8-mm oocytes (7.0%–15.6% of DML) (Villanueva and Sánchez 1993; Kubodera and Okutani 2011), whose spawned eggs (2.5 mm in *Heteroteuthis* sp.) could represent 10.0% of its DML (von Boletzky 1978). Little is known about reproduction in Heteroteuthinae, but it seems that some species lay benthic egg clutches associated with the continental slope on the seabed (von Boletzky 1978; Drerup 2022). Its paralarvae are clearly mesopelagic and abyssopelagic, always distributed far from the coast between 1500- and 3000-m depth

(Jereb and Roper 2005). Data on *H. dispar* and *H. dagamensis* show that the ovary exhibits a wide range of oocyte sizes, indicating an asynchronous ovulation pattern (Hoving et al. 2008; Rotermund and Guerrero-Kommritz 2010). Hoving et al. (2008) also indicated that *H. dispar* presents a total fecundity 5–10 times higher than Sepiolineae and Rossiinae species, together with asynchronous ovulation, with oocytes ovulating one by one and accumulating in the oviduct, resulting in continuous spawning. Accordingly, the species of this subfamily could develop the continuous spawning strategy (Rocha et al. 2001), and the new hatchling individuals use the pelagic paralarvae strategy.

3.5 | Hotspots of Biodiversity

The Sepiidae species show at least two biodiversity hotspots: Mediterranean Sea and the Indo-Pacific and North West Pacific waters of Philippines, Vietnam, Malaysia, Taiwan and Japan. Rosa et al. (2019) also identified these areas as high diversity cephalopods marine ecoregions, with a high Sepiolineae species richness in the North Atlantic and Mediterranean waters.

The Mediterranean Sea has a high species diversity, representing 24.1% of the total sepiolids, with a high predominance of Sepiolineae (17.7%) in comparison with Rossiinae (2.5%) and Heteroteuthinae (3.8%) species. According to Mangold and Boletzky (1988) and Bello (2003, 2013, 2019), after the Messinian salinity crisis that dried up almost completely the Mediterranean, the cephalopod fauna, including sepiolid species, would have migrated to the Mediterranean from Atlantic waters (Por 1975; Hsü 1976; Adams et al. 1977). Due to the reduction of the sea level six million years ago, the previous Mediterranean fauna most probably became extinct or migrated away, and it was replaced by incoming species (Hsü 1976). Por (1975) indicated that two types of fauna colonized the Mediterranean: the first one originated in Arctic-Boreal areas during the glacial periods; the second one originated in tropical regions of Western Africa during the interglacial periods. Thus, present-day Mediterranean fauna probably has these two origins. In addition, new cephalopod species have recently migrated into the Mediterranean via the Suez Canal or in ship ballast waters (Salman 2002; Bello 2019).

The Mediterranean shows also high level of species endemism (Bello 2019; Rosa et al. 2019). The genera *Sepioida* and *Adinaefiola* have the highest number of endemic species here, as is the case with *S. affinis*, *S. robusta* and *A. aurantiaca* (Sánchez and Morales-Seguí 1986; Volpi, Borri, and von Boletzky 1995; Volpi, Borri, and Zucchi 1995; Jereb and Roper 2005). Endemisms must have been established after the Sepiidae migrated into the Mediterranean as a consequence of their reproductive strategies and life cycles: namely, low fecundity, short lifespans and benthic activity (Bello 2019). The discovery that three *Sepioida* species from the Mediterranean (*S. affinis*, *S. intermedia* and *S. rondeletii*) have a recent common ancestor (Gabel-Deickert 1995) may indicate that these processes are still active. This may explain why, even though the Mediterranean Sea is one of the most studied places in terms of cephalopod richness, new species are

still being described there (Bello 2013; Bello and Salman 2015; Fernández-Álvarez et al. 2021).

The North Atlantic waters also show a high level of Sepiolineae species (16.5% of the total). According to Bello (2013, 2019), most sepiolids in the Mediterranean and Atlantic are morphologically similar and grouped together in the 'Atlantic group' *sensu* Naef (1923). This coincides with the genetic studies of Sánchez et al. (2021) that grouped the Mediterranean and Atlantic sepiolid species into the 'tribe Sepioline'. In consequence, Mediterranean hotspot must be considered associated to adjacent North Atlantic waters as high diversity Sepiidae species region (Rosa et al. 2019).

The second sepiolid biodiversity hotspot corresponds to the Indo-Pacific and Northwest Pacific areas, which includes the named Coral Triangle. In particular, the Coral Triangle is a well-known marine centre of speciation and the largest global marine biodiversity hotspot for many taxa (Briggs 1999a; Bowen et al. 2013; Briggs and Bowen 2013; Rosa et al. 2019). In addition, Rosa et al. (2019) indicated that it shows the greatest values of coastal cephalopod richness. Coral Triangle waters include 19.0% of Sepiidae species, with highest predominance of Sepiolineae (13.9%), followed by Heteroteuthinae (3.8%) and Rossiinae (1.3%). The genus *Euprymna* shows several endemic species such as *E. albatrossae*, *E. hoylei* and *Euprymna penares* (Norman and Lu 1997; Jereb and Roper 2005). However, several sepiolid species in this area have been described only from one locality (Nesis 1987), or their original descriptions have been inadequate or incomplete, or their type specimens have been lost (Norman and Lu 1997). According to Rosa et al. (2019), this cephalopod biodiversity hotspot would be the centre of origin from which species would disperse to adjacent areas, especially via ocean currents.

The adjacent area of the North West Pacific (Taiwan and Japan waters, corresponding to Sino-Japanese province; Toonen et al. 2016) also exhibits a high abundance of Sepiidae species (20.3%), where Sepiolineae are the most abundant (8.9%), followed by Heteroteuthinae (7.6%) and Rossiinae (3.8%). Rosa et al. (2019) pointed out that Taiwan and Japan waters would correspond to an 'accumulation center'. Here, the speciation would occur when species extend their distribution from a hotspot carried by ocean currents or other mechanisms (Mironov 2006; Bowen et al. 2013; Gaither and Rocha 2013). Indo-Pacific area seems to be the dispersion and speciation centre of *Inioteuthis*, *Euprymna*, *Lusepiola* and *Eumandya* genera. According to Sánchez et al. (2021), these taxa are phylogenetically close so to be gathered into the tribe Euprymini separately from the Mediterranean species (tribe Sepioline). In addition, Sánchez et al. (2021) postulated that both Mediterranean-Atlantic and Indo-Pacific lineages overlap during the early Eocene, and their separation and diversification coincide with the end of the Tethys Sea, which separated the Indo-Pacific from the Mediterranean-Atlantic regions (Rögl 1998; Cowman and Bellwood 2013).

Both Mediterranean and Indo-Pacific hotspots represent diversification areas for Sepiolineae species. However, Rossiinae and Heteroteuthinae do not show a wide species diversity in these areas. This can depend on the lifestyle of these species.

According to Mironov (2006), the Mediterranean and Indo-Pacific hotspots are centres of diversification and redistribution for shallow water marine fauna, which would correspond to the habitat of Sepiolinae species. Rossiinae and Heteroteuthinae inhabit deeper waters or pelagic habitats, and this could explain why their biodiversity is not higher in these hotspots.

A likely hotspot for Rossiinae and Heteroteuthinae species is the Caribbean and Gulf of Mexico waters (Caribbean and Carolina provinces, Toonen et al. 2016), with the 15.2% of the species (8.9% for Rossiinae and 6.3% for Heteroteuthinae). Rosa et al. (2019) also reported a high number of cephalopod species and endemism level in this area. According to Mironov (2006) and Bowen et al. (2013), it represents a centre of biodiversity and redistribution for marine species, producing and exporting species or accumulating biodiversity produced in peripheral habitats. In the case of Rossiinae, a possible biodiversity hotspot could be also in the North Atlantic waters (Western and Eastern Atlantic provinces; Toonen et al. 2016) with 7.6% of the species. Nesis (2003) stated that *Rossia* genus probably had an Atlantic origin and radiated from this zone (e.g., to the Pacific Ocean throughout the Arctic waters using the Bering Strait).

4 | Conclusion

The sepiolids are undoubtedly a very interesting group in terms of their ecological role and distribution patterns. The 80 species currently recognized exhibit distribution patterns that reflect different lifestyles and ecological strategies. Although several aspects of their biology and phylogeny are becoming increasingly well understood (Sánchez et al. 2019; Fernández-Álvarez et al. 2021; Reid 2021; Sánchez et al. 2021), today, it is difficult to evaluate the true number, distribution and origin of all sepiolid species. This is due to the lack of data on distribution, abundance and population of several of them, as well as their taxonomic status. One important point is the high degree of misidentifications made in this family and the presence of possible cryptic species complex (Fernández-Álvarez et al. 2021; Reid 2021). These aspects do not aid in correctly identifying new or established species and represent an impediment to implementing conservation measures for this group. In this regard, Braid and Bolstad (2019) indicate that this aspect is fundamental for conservation efforts because 'both a lack of recognition of distinct taxa and oversplitting can have important consequences for the future of the species involved'. In this sense, it is highly recommended the joined use of both molecular and morphological methods for species identification in order to reveal all the hidden cryptic diversity in this group.

The geographic and bathymetric distributions of species depend on historical, oceanographic and ecological factors that determine their presence or absence in an area (Brown and Lomolino 1998; Rögl 1998; von Boletzky 1999). For example, Young et al. (1998) indicated that factors such as temperature, depth and geographic distance influence the Sepiolinae distribution in oceanic basins. Assuming this is correct, the age of these factors could provide a key for dating the family origin. In this respect, the use of both genetic and morphological analysis to identify and study the Sepiolidae species (Groenenberg et al. 2009; Judkins et al. 2016; Braid and Bolstad 2019; Sánchez

et al. 2019; Fernández-Álvarez et al. 2021) is of interest, given the great number of them inhabiting continental and oceanic islands. These studies could reveal whether new species exist and whether genetic variation and flux occur between populations.

Considering the distribution patterns of Sepiolidae species, their absence in tropical East-Pacific is particularly interesting. This may be due to two alternative causes: First, Sepiolidae species are present in the area, but there, its absence of records is caused by sampling bias or the lack of specialized studies in the area. Second, Sepiolidae have not yet colonized the tropical East-Pacific. In the latter case, several possibilities would exist. Firstly, Sepiolidae dispersion across the Pacific was unable to reach the tropical coast of America from the west Pacific or South America. Alternatively, for any reason, the species were unable to colonize these waters from Atlantic before the Panama Isthmus was formed. Other possibility is that Sepiolidae colonized tropical eastern Pacific waters, but they were extinct due to environmental changes generated by the Isthmus formation (Savin and Douglas 1985; Coates and Obando 1996; Cronin and Dowsett 1996). However, the latter option seems less likely, considering that there are other cephalopod species that have colonized both Atlantic and Pacific areas before the Panama Isthmus in each coast of Central America (Voight 1988; Pérez-Losada et al. 2002).

In general, Sepiolidae species appear to have adapted to three life strategies that determine their habitats and biogeographic patterns. First, there are the species of the subfamily Sepiolinae, which live in shallow coastal benthic habitats and whose paralarvae have a nectobenthic paralarvae strategy with a limited planktonic stage, which adopt the benthic life quickly. This coastal 'Old World' group exhibits a wide diversity of species and a high degree of diversification originated from the Mediterranean and the Coral Triangle in the Indo-Pacific, which are known as biodiversity hotspots for species of shallow coastal habitats (Mironov 2006; Rosa et al. 2019). A second pattern is observed in the subfamily Rossiinae. Their species have adapted to benthic habitats in deeper waters on continental shelves and slopes. They lay large eggs, and the newly hatched have a Direct Nectobenthic Juvenile strategy adopting the benthic lifestyle without or with only a very brief planktonic stage. The coastal Old and New World Rossiinae species have a significant presence in the Atlantic and Arctic Oceans. Finally, the subfamily Heteroteuthinae exhibits a third strategy, occupying pelagic habitats with wide distributions in the oceans, both near and far from the coast. Although little is known about their reproductive strategies, these species lay small eggs on bottoms associated with seamounts, islands or continental slopes. Here, the hatchlings adopt a pelagic paralarvae strategy with a planktonic larval stage that allows for broad dispersal patterns, carried by ocean currents.

The biogeographic patterns of species in the Sepiolidae family demonstrate the remarkable adaptability of this group of small cephalopods to both coastal and oceanic environments. Furthermore, although they play an important role in the ecosystems, many aspects of their biology and ecology remain poorly understood. Some species even have an unknown distribution,

are indistinguishable from other sepiolids or belong to cryptic species. This must be clarified to gain a complete understanding of their taxonomic and conservation status, especially in relation to alterations in species distribution and abundance that could be induced by climate change, or alterations in the ecosystem they live. Therefore, future studies should focus first on these points to clarify the existing uncertainties regarding the identity and distribution of these species.

Author Contributions

Francisco Rocha: supervision, conceptualization, investigation, formal analysis, writing – original draft, writing – review and editing, methodology, data curation, validation. **Amanda Luna:** writing – review and editing, investigation, methodology, formal analysis, data curation, validation. **Leonardo Mantilla-Aldana:** methodology, visualization, writing – review and editing, resources, formal analysis, validation, software.

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The data supporting the findings of this review are accessible in the article itself, or in the References, as well as in the additional [Supporting Information](#).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Systematic list of Sepiolidae species, including their distribution and deep range according to literature data.