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Global diversity of coastal cephalopods: hotspots and latitudinal gradients

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ABSTRACT

The present dissertation aimed to identify, for the first time, the global hotspots of coastal cephalopod diversity, namely cuttlefishes (families Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae), squids (family Loliginidae) and octopuses (family Octopodidae), and assess their latitudinal gradient of species richness (LGRS). I created a presence/absence database, according to Marine Ecoregions of the World, which revealed that the most diverse ocean was the Pacific (with 212 species), followed by the Indian (151 species) and Atlantic (103 species) Oceans. The least diverse were the Artic (13 species) and Southern (7 species) Oceans. Within the 232 ecoregions considered, the highest diversity value was reached in the Central Kuroshio Current (CKC) ecoregion, with 64 species, followed by the East China Sea (ECS, 59 species) and the Eastern Philippines (EP, 48 species). I advocate that these hotspots are linked to the "centre of origin", "centre of overlap" or "centre of accumulation" hypotheses postulated for the Indo-Australian Archipelago region, together with the particular productivity-rich conditions associated with upwelling system dynamics near CKC and ECS. Regarding the association between latitude and diversity, cephalopod peak of diversity varied among oceans, and only the squids showed a unimodal distribution with latitude. In opposition, cuttlefish, octopods and Cephalopoda revealed bimodal distributions, always with the major peak of diversity in the north hemisphere. I argue that the squid unimodal pattern may be a result of the effect of energy availability (sea surface temperature) in the organism's physiology, as proposed by the "ambient energy hypothesis". On the other hand, the widespread bimodal distributions may be linked to ocean productivity (i.e. the "species-productivity hypothesis") given that highly productive areas tend to be associated with temperate latitudes. Summing up, these findings highlight the notion that the shape and symmetry of LGRS are not universal and there are no single causal predictors to explain hotspot and latitudinal zenith locations within the same taxa.

Keywords: Macroecology, Latitudinal Gradient, Species Richness, Hotspots, Coastal Cephalopods.

RESUMO

A presente dissertação visa identificar, pela primeira vez, os *hotspots* globais de diversidade de cefalópodes costeiros, nomeadamente, de chocos (famílias Sepiidae, Sepiolidae, Sepiadariidae e Idiosepiidae), lulas (famílias Loliginidae) e polvos (família Octopodidae) e avaliar os correspondentes gradientes latitudinais de riqueza específica (GLRS). Neste âmbito, foi criada uma base de dados de presenças/ausências, de acordo com as Ecoregiões Marinhas do Mundo, na qual o Oceano Pacífico surge como sendo o mais diverso (com 212 espécies), seguido do Índico (com 151 espécies) e do Atlântico (com 103 espécies). Em contraste, os Oceanos Ártico (com 13 espécies) e Antártico (com 7 espécies) revelaram-se os menos diversos. Das 232 ecoregiões consideradas, o maior valor de diversidade específica foi obtido na ecorregião da Corrente Kuroshio Central (CKC), com 64 espécies, seguido do Mar da China Oriental (MCO), com 59 espécies, e das Filipinas (F), com 48 espécies. Advogo que a localização destes hotspots se encontra relacionada com as teorias de "centro de origem", "centro de sobreposição" ou "centro de acumulação" postuladas para a região do Arquipélago Indo-Australiano, tendo em conta as particulares condições de produtividade associadas aos dinâmicos sistemas de upwelling próximos da CKC e da ECS. Relativamente à relação entre latitude e diversidade, os picos de diversidade de cefalópodes variaram entre oceanos e apenas as lulas exibiram uma distribuição unimodal. Por outro lado, os chocos, polvos e a classe *Cephalopoda* revelaram distribuições bimodais, sendo que o maior pico de diversidade se encontrou sempre no hemisfério norte. Defendo que o padrão unimodal das lulas possa ser o resultado do efeito de disponibilidade energética (temperatura à superfície do mar) na fisiologia dos organismos, tal como proposto pela "hipótese energética do ambiente". Em contrapartida, a generalizada distribuição bimodal poderá estar associada à produtividade oceânica, tal como defendido pela "hipótese espécies-produtividade", uma vez que áreas altamente produtivas tendem a estar associadas a latitudes temperadas. Em síntese, estes resultados realçam a noção de que a forma e simetria do GLRS não são universais e que não existe um só preditor causal que explique a localização dos hotspots e dos picos de diversidade latitudinal dentro do mesmo *taxa*.

Palavras-chave: Macroecologia, Gradiente Latitudinal, Riqueza Específica, Hotspots, Cefalópodes Costeiros.

RESUMO ALARGADO

Macroecologia é o ramo da ecologia que estuda a distribuição e abundância de espécies a grande escala, tendo especial atenção à biologia, biogeografia e macroevolução das espécies em estudo com o objetivo final de melhor entender os sistemas ecológicos através de uma abordagem *top-down* (de cima para baixo, de uma visão geral para o detalhe)(Brown, 1995; Gaston & Blackburn, 1999). Apesar de os primeiros estudos macroecológicos terem sido desenvolvidos em meados do século XIX, é ainda uma área pouco explorada principalmente devido às dificuldades inerentes à escala de trabalho, tais como, a incapacidade de realizar trabalho experimental ou a complexidade de testar hipóteses macroecológicas.

A biodiversidade tem um papel fundamental no equilíbrio e no bom funcionamento dos ecossistemas e, como tal, é imperativo que sejam tomadas medidas que visem a sua conservação, nomeadamente a identificação de ameaças. Os oceanos cobrem cerca de um terço do nosso planeta e atualmente albergam 28 dos 34 filos animais conhecidos (13 dos quais endémicos). Atualmente, a degradação de habitats, sobrepesca, poluição, invasões biológicas e, em particular, as alterações climáticas constituem as maiores causas de perda de diversidade no meio marinho. O conceito de *hotspot* tem vindo a ser usado como estratégia-chave para planos de conservação global, mas tem sido pouco aplicado ao meio marinho. *Hotspots*, são geralmente, definidos com base em métricas de diversidade de espécies (tais como, riqueza específica, riqueza específica endémica ou número de espécies raras ou ameaçadas) ou, alternativamente, em métricas de diversidade funcional ou filogenética.

Os padrões globais de biodiversidade têm sido amplamente estudados e discutidos em diversos grupos taxonómicos e a diversas escalas. Desde os primórdios da ecologia que nasce o consenso universal de que a diversidade específica aumenta uniformemente dos polos em direção ao equador sendo este fenómeno denominado de Gradiente Latitudinal de Riqueza Específica (GLRE). Vários fatores foram já propostos para explicar esta tendência, tais como, heterogeneidade espacial, competição e predação, estabilidade ambiental, energia ambiente, produtividade, entre outros. Contudo, estudos indicam que, em certos grupos taxonómicos, o GLRE não é necessariamente unimodal, simétrico, nem com o seu pico de diversidade no equador.

Os cefalópodes são um grupo de moluscos exclusivamente marinhos com diversas características diferenciadoras, tais como, a redução ou mesmo ausência de concha externa, um sistema nervoso sofisticado, movimento por propulsão a jato e comportamento predatório. São um grupo com estratégias de vida bastante diversas, englobando desde espécies pelágicas a bentónicas, que habitam desde as zonas do intertidal até às profundezas abissais. Apesar da falta de estudos em macroecologia de cefalópodes, foi já descrito que a riqueza específica de cefalópodes neríticos é assimétrica entre margens do Atlântico, em termos de número, padrão e latitude dos picos de diversidade, sendo que estes últimos ocorrem a latitudes tropicais (20º N) no Atlântico ocidental e a latitudes temperadas (40º N) no Atlântico oriental. São espécies com, geralmente, um curto ciclo de vida que apresentam semelparidade, o que, aliado ao crescente interesse comercial neste grupo e às restantes ameaças atuais aos oceanos, as tornam bastante vulneráveis o que resulta em grandes flutuações e imprevisibilidade das distribuições e abundâncias.

A presente dissertação visa identificar, pela primeira vez, os *hotspots* globais de diversidade de cefalópodes costeiros, nomeadamente, de chocos (famílias Sepiidae, Sepiolidae, Sepiadariidae e Idiosepiidae), lulas (famílias Loliginidae) e polvos (família Octopodidae) e avaliar os correspondentes gradientes latitudinais de riqueza específica (GLRS). Para tal, desenvolveu-se uma base de dados de presenças/ausências de espécies de cefalópodes associadas a plataformas continentais (sendo os 200m a batimetria máxima considerada) de acordo com as Ecoregiões Marinhas do Mundo, um modelo de divisão das zonas costeiras mundiais em pequenas regiões de relativa semelhança a nível de composição faunística, mas também de características oceanográficas e topográficas.

A análise da base de dados revelou o Oceano Pacífico como sendo o mais diverso (com 212 espécies), seguido do Índico (com 151 espécies) e do Atlântico (com 103 espécies). Os Oceanos Ártico (com 13 espécies) e Antártico (com 7 espécies) revelaram-se os menos diversos. Observa-se também que, a uma escala menos refinada, podem-se definir três grandes *hotspots* de diversidade, estes sendo, o Arquipélago Indo-Australiano (AIA), o Mar Mediterrâneo e a região das Caraíbas. A grande diversidade do AIA está ligada às teorias de "centro de origem", "centro de sobreposição" ou "centro de acumulação". A primeira hipótese defende que esta área é caracteristicamente diversa por ser um local de particular especiação, a segunda sugere que é uma consequência da sobreposição das faunas

circundantes, dispersando em todas as direções a partir das suas áreas biogeográficas, e a última argumenta que, ainda que a especiação ocorra fora do AIA, as espécies sofrem dispersão unidirecional até a esta região devido às correntes predominantes. A história de isolamento das faunas do Mediterrâneo e das Caraíbas, juntamente com a demonstrada ineficácia das atuais rotas de dispersão do AIA até ao Oceano Atlântico, sugerem que a riqueza específica contemporânea destes locais foi em grande parte condicionada por eventos históricos. Em particular, pelo arrefecimento da temperatura à superfície do mar, que levou à extinção dos chocos do ocidente do Atlântico, e pela crise salina do Mediterrâneo, que provocou a extinção das espécies estenohalinas e fomentou a origem de endemismos (principalmente de chocos, que atingem a sua máxima diversidade nesta região).

Das 232 ecoregiões consideradas, o maior valor de diversidade específica foi alcançado na ecorregião da Corrente Central de Kuroshio, com 64 espécies, seguido do Mar da China Oriental, com 59 espécies, e das Filipinas, com 48 espécies. A posição em relação ao AIA destes *hotspots*, junto com as particulares condições de produtividade associadas aos sistemas dinâmicos de afloramento próximos da Corrente Central de Kuroshio e do Mar da China Oriental, justificam a riqueza específica destas ecorregiões.

Relativamente aos gradientes latitudinais, estes mostraram-se bastante variáveis entre grupos taxonómicos e oceanos. Apenas as lulas exibiram uma distribuição unimodal à escala global e no Oceano Atlântico. Defendo que o padrão unimodal das lulas possa ser o resultado do efeito de disponibilidade energética (temperatura à superfície do mar) na fisiologia dos organismos, tal como proposto pela "hipótese energética do ambiente", uma vez que os picos de diversidade dos gradientes unimodais observados se encontram em latitudes tropicais, onde as temperaturas à superfície do mar são mais elevadas. O terceiro caso de unimodalidade observado, correspondente aos polvos do Oceano Pacífico, tem o seu pico de diversidade fora dos trópicos. Tal deve-se à grande influência da ecorregião da Corrente Central de Kuroshio que se insere num panorama específico que, devido à proximidade ao AIA e às correntes quentes predominantes, possui características subtropicais particulares.

Por outro lado, os chocos, polvos e a classe *Cephalopoda* revelaram distribuições bimodais, sendo que o maior pico de diversidade se encontrou sempre no hemisfério norte. A generalizada distribuição bimodal poderá estar associada à produtividade oceânica, tal como defendido pela "hipótese espécies-produtividade", uma vez que áreas altamente produtivas tendem a estar associadas a latitudes temperadas (às quais coincidem alguns dos picos de diversidade destes gradientes bimodais). É importante realçar que nem a "hipótese energética do ambiente", para as distribuições unimodais, nem a "hipótese espécies-produtividade", para as distribuições bimodais, parecem explicar a totalidade dos padrões observados. É provável que fatores como eventos históricos e barreiras à dispersão tenham também um importante papel na definição destes padrões.

Em síntese, estes resultados realçam a noção de que a forma e simetria do GLRS não são universais e que não existe um só preditor causal que explique a localização dos hotspots e dos picos de diversidade latitudinal dentro do mesmo *taxa*.

1. INTRODUCTION

HOTSPOTS OF DIVERSITY

Macroecology is a subfield of ecology that studies the distribution and abundance of species at large scales with close attention to the biology, biogeography and macroevolution of species with the ultimate goal of understanding ecological systems through the study of the whole with a top-down approach (Gaston & Blackburn, 1999). In contrast with the traditional bottom-up approach, it has the principal advantage of looking at broader scales thus making certain particular details no longer visible nor relevant, remaining only the important generalities (Brown, 1995). Despite that the first macroecological studies could be traced back to the middle of the 19th century, it is still an unexplored field with a lot of work in need to be done greatly due to the inherent difficulties of global scale studies, such as, the incapacity of experimental work, the complexity of testing macroecological hypotheses, and also due to the lack of well-established theoretical framework (Gaston & Blackburn, 1999). Nevertheless, recent interest has arisen mainly due to the growing concern on contemporary issues occurring at global scales, such as climate change and species extinctions and invasions.

Marine habitats comprise 28 of the 34 known animal phyla (including 13 phyla that are endemic; Snelgrove *et al.*, 2017), but marine species richness may only account for 4% of global diversity (Benton, 2001). Yet, overall estimates of marine biodiversity diverge immensely, even an order of magnitude, ranging from 178.000 to more than 10 million species (Sala & Knowlton, 2006). Given the importance that biodiversity plays (Cardinale *et al.*, 2012; Hooper *et al.*, 2012), the identification of its main threats is pivotal (Hobday & Pecl, 2014; Marchese, 2015; Ramírez *et al.*, 2017). Habitat degradation, over-fishing, pollution, biological invasions and, in particular, climate change are the major causes for biodiversity loss, and the combination of all these stressors together may have already set critical transition towards a tipping point on the global ecosystem (Barnosky *et al.*, 2012). A global climate change-driven redistribution of marine species is occurring(Sunday, Bates, & Dulvy, 2012), with marine organisms having, on average, expanded their distributional limits by 72.0 ± 13.5km per decade (Poloczanska *et al.*, 2013).

The concept of hotspots has been used as a key strategy for global conservation plans, but they remain largely unexplored in marine habitats (Worm, Lotze, & Myers, 2003; Renema *et al.*, 2008; Tittensor *et al.*, 2010) due to data deficiency (Mittermeier *et al.*, 2011). Biodiversity hotspots have been usually defined using species-based metrics (e.g. species richness; endemic species richness; number of rare/threatened species) or, alternatively, focusing on phylogenetic and functional diversity metrics (Myers, 1988; Gray, 2000; Worm *et al.*, 2003; Hoekstra *et al.*, 2005). More recently, some have identified marine hotspots based on richness with metrics that incorporate both species abundances and functional traits (Stuart-Smith *et al.*, 2013) or, alternatively, based on regions that are warming more rapidly (Hobday & Pecl, 2014). According to these authors, front-line regions for climate change may be considered key areas for evaluating impacts and adaptation measures for marine ecosystems and respective ocean uses.

LATITUDINAL GRADIENT OF SPECIES RICHNESS

Global patterns of biodiversity have been widely studied and discussed over the years for a variety of taxa groups and scales ever since the early days of ecology (Darwin, 1859; Wallace, 1877). Since then, an universal consensus arose that overall species richness increases from the poles to the equator in negative correlation with latitude (Pianka, 1966; Rohde, 1992; Gaston, 2000; Lomolino, Riddle, & Brown, 2006), in what is called the Latitudinal Gradient of Species Richness (LGSR). This large-scale pattern has been described in several taxonomic groups, mainly terrestrial but also marine, namely, marine decapod crustaceans (Steele, 1988), prosobranch gastropods and bivalves (Roy *et al.*, 2000; Roy *et al.*, 1998); fish (Macpherson, 2002), among others. However, it seems that for certain groups of organisms, the LGSR is neither necessarily symmetrical and peaking at the equator (Blackburn & Gaston, 1996; Gaston & Williams, 1996; Culver & Buzas, 2000; Gaston, 2000; Gray, 2001a,b, 2002;

Hillebrand, 2004; Chaudhary, Saeedi, & Costello, 2016), nor consistent over geological ages (Mannion *et al.*, 2014) or unimodal, given that some appear to follow a bimodal trend (Chaudhary *et al.*, 2016).

Several factors have been hypothesized to explain it, such as competition and predation, spatial heterogeneity, 'Rapoport's rule', environmental stability, ambient energy, productivity, biome area, evolutionary time, energetic equivalents, Milankovitch oscillations and geometric constraints, among other possible causes (the total exceeds 30; for reviews see Rohde, 1992; Rosenzweig, 1995; Willig, Kaufman, & Stevens, 2003). Though there have been few efforts to reduce the number of explanations, the best documented contenders for a short-list of explanations are the biome and climate-based hypotheses (see Currie *et al.*, 2004).

For instance, Rosenzweig (1992, 1995) hypothesized that species richness of a certain region is a result of its geographic or biome area because of its effect on the geographic range size of the species in a given region. According to this author, species from large regions can have broader geographic ranges than species from more restricted ones making them less susceptible to extinction from accidental events or environmental changes due to their possible broader and larger populations. Given the higher possibility of isolation from geographic barriers they are also more susceptible to allopatric speciation (Blackburn & Gaston, 1997). As a result, larger regions present higher species richness. The tropics, being the largest biome or climatically similar area (as defined in Rosenzweig, 1992) and given that surface area decreases towards the poles (Gaston, 2000), it is here where species richness seem to reach its highest. However, all biomes north of the tropics have relatively the same extent and, according to Rosenzweig's hypothesis, should also have similar species richness. The fact that they do not show it is related to: i) at least in part, the geographic ranges of tropical species that reach out into the neighboring subtropical biomes and ii) the decrease in environmental productivity at higher latitudes (Blackburn & Gaston, 1997).

Energy availability is also considered as a factor determining species richness distribution and there are three main hypotheses. The freezing tolerance hypothesis, the most ancient form, states that species are limited at higher latitudes due to their incapacity to withstand winter temperatures (Hawkins, Porter, & Diniz-filho, 2014). The productivity hypothesis (Wright, 1983) claims that, energy for plants is available as sunlight and buffered by water availability, as for animals it is limited by the production of food items, plant biomass or herbivore biomass (Huston, 1994; Mittelbach *et al.*, 2001). Last, the ambient energy hypothesis (Turner *et al.*, 1987) states that diversity is shaped as a result of the environment and namely its energetic elements on the organism's physiology.

The idea that competition could be the main driver of biodiversity patterns was first described by Dobzhansky (1950), who argued that natural selection acted in different ways in temperate and tropical regions. In the former, natural selection and evolution is mainly driven through forces imposed by the environment, whereas in the tropics it is mainly driven by biological competition. Paine (1966) also claimed that diversity is driven by the proportion of predators in a region. According to the author, there are more predators (and/or parasites) in the tropics than in temperate regions, which apply such force on prey populations that levels of competition among and between them are, here, less intense. Ultimately, it translates into higher possibilities for new prey types and consequently new predators in the ecosystem.

Apart from all previous hypothesis there's also the null models category. For instance, The mid-domain effect hypothesis (Colwell & Hurtt, 1994) claims that if species ranges were randomly attributed within a geographical constrained domain, maximum species richness would tend to appear at the center of it just due to the higher chance of overlapping ranges (Colwell, Rahbek, & Gotelli, 2004). The authors assumed that species richness should be uniform along the latitudinal gradient in the absence of environmental and historical gradients.

CEPHALOPODS

Cephalopods are an unique group of marine mollusks with several differential features, such as, the reduction or even absence, in most cases, of the external shell, a sophisticated nervous system, movement through jet propulsion and predatory behavior (Boyle & Rodhouse, 2007; Judkins & Vecchione, 2010). They belong to the well-defined class of Mollusca that appeared over 450 million years ago (My), although the subclasses of the living forms recognized today originated less than 100 million years ago (Boyle & Rodhouse, 2007). It is a diverse group of exclusively marine species, with benthic to pelagic life forms, ranging from intertidal to abyssal depths, found in all marine habitats across the globe (Boyle & Rodhouse, 2007; Rosa *et al.*, 2008). Being a group with increasing fishing interest it is very important to determine and identify distribution patterns and areas of particular species richness on which to focus our management and conservation measures and programs but cephalopod populations are generally especially vulnerable to predation and environmental variables given their species short lifespan and semelparous breeding, thus resulting in great fluctuations and unpredictability of distributions and abundances (Boyle & Boletzky, 1996; Boyle & Rodhouse, 2007).

Despite the lack of large scale studies on the biogeography of cephalopods, a few have already shed some light into hotspot location and patterns of biodiversity. For instance, in the Atlantic ocean, Rosa et al., (2008) found that species richness of neritic cephalopods, is as expected, smaller in the poles than in the tropics, but some particularities were noticed, such as, the asymmetry between margins of the Atlantic in terms of number, patterns and zenith of diversity. Results showed that the peak of diversity occurs at north tropical (20º N) and temperate (40º N) latitudes, in the Western and Eastern Atlantic correspondingly, thus providing evidence that the hypothesis of the classical LGSR does not apply to this taxa.

OBJECTIVES

The present dissertation aimed to identify, for the first time, the global hotspots of coastal cephalopod diversity, in particular of cuttlefishes (families Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae), squids (family Loliginidae) and octopuses (family Octopodidae), and assess their latitudinal gradient of species richness per taxonomic group and per ocean (Atlantic, Indian and Pacific).

2. MATERIAL AND METHODS

DATABASE

The geographical ranges of coastal cephalopod species were investigated, at a global scale, by means of an exhaustive survey of primary literature (e.g. Rosa *et al.*, 2008; Judkins & Vecchione, 2010), with a special focus on the most recent FAO's Cephalopods of the World catalogues (Jereb & Roper, 2005; Jereb *et al.*, 2014, 2016). More specifically, we created a presence/absence database for all of the species belonging to the Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae, Loliginidae and Octopodidae families, according to Marine Ecoregions of the World (MEOW; Spalding *et al.*, 2007; Figure 1). According to the authors, the ecoregions are, and we quote, "*Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant biogeographic forcing agents defining the ecoregions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity*".

The present database comprised a total of 371 species (see Annexes, Table 1 for full list) that are associated with, but not restricted to, continental shelves (and depths shallower than 200 m) world-wide. Rare species and/or species with lack of significant information about geographical distribution were excluded. Some squids of the Order Oegopsida (which is mostly composed by oceanic species) are known to thrive or periodically invade the neritic province (genera *Illex, Todaropsis, Todarodes, Dosidicus*, among others), but were not included in the present database for the sake of clarity.

We used the software ArcGIS version 10.4.1 and the open source shapefiles (https://www.arcgis.com/home/item.html?id=b0ca60c9472a432f9d659b86864f3764) from Spalding *et al.*, 2007 for the identification of the hotspots of cephalopod diversity. To investigate the latitudinal gradients of species richness (LGSR), we used the methodology applied by Rosa *et al.* (2008) – i.e. species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band.

STATISTICAL ANALYSES

The latitudinal density regarding diversity of coastal cephalopods (cuttlefish, squids and octopods groups) was investigated, at a global scale and per ocean (Pacific, Atlantic and Indian Oceans), by kernel smoothing estimation. Density estimates were obtained using a Gaussian kernel function. We considered the bandwidth that is a minimizer of a smoothed bootstrap approximation to the mean integrated squared error (MISE) (following Sheather & Jones, 1991). To characterize density shape, in particular, regarding modality and symmetry patterns we found the number of local maxima and evaluated the distribution skewness. The number of local maxima allows to infer about the number of modes of the distribution, i.e., about modality. Skewness parameter sign and absolute value enables to evaluate the type and magnitude of symmetry pattern departure. Data analysis was performed using R version 3.3.2 environment (R Core Team, 2016).

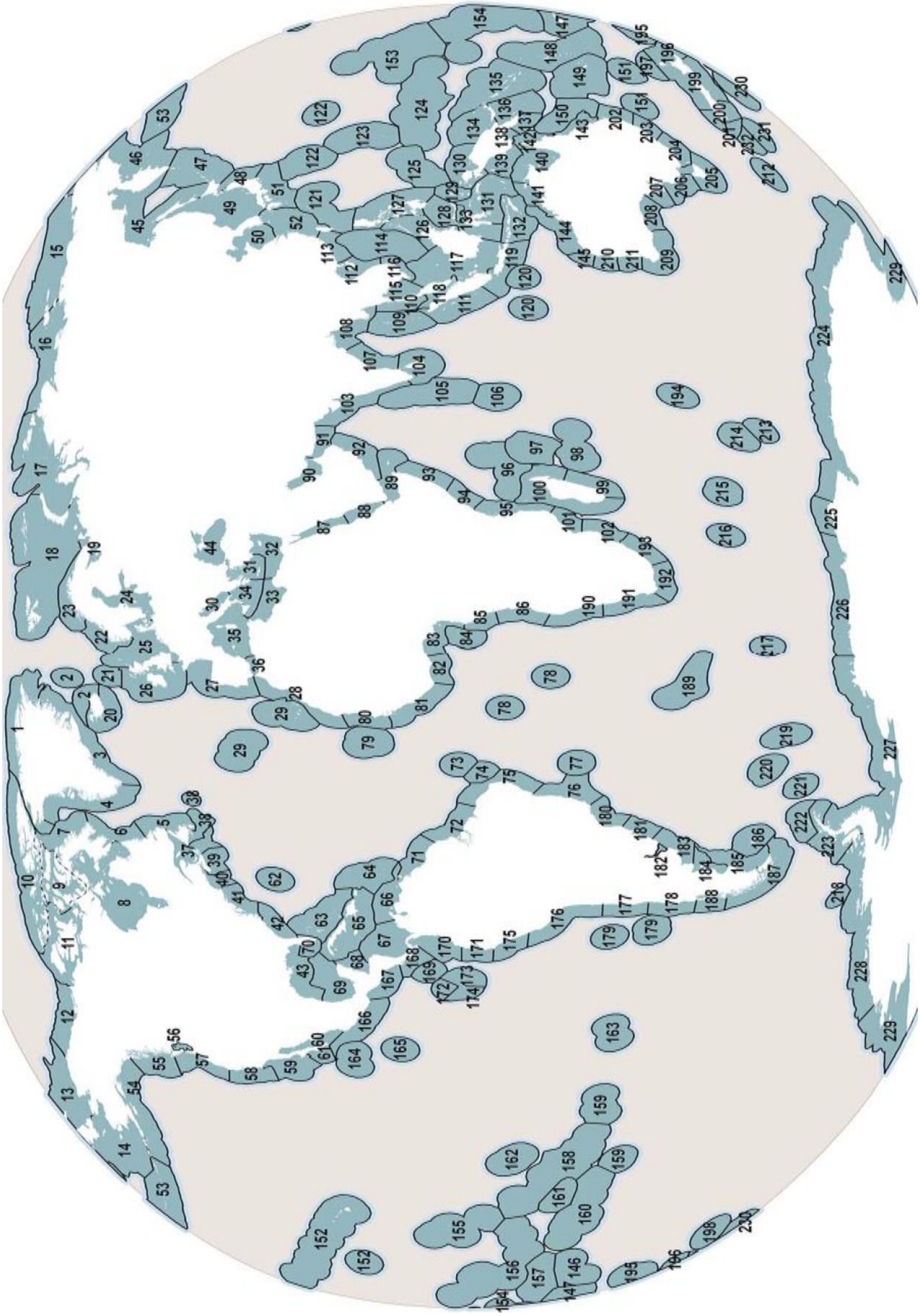

Figure 1 - Representation of the Marine Ecoregions of the World as proposed by Spalding et al. (2007).

3. RESULTS

GLOBAL DIVERSITY

The present database revealed that the most diverse ocean was the Pacific Ocean (with 212 cephalopod species), followed by the Indian (151 species) and Atlantic (103 species) Oceans (Figure 2). The least diverse were the Artic (13 species) and Southern (7 species) Oceans. This trend was mostly observed in octopuses and squids, since cuttlefish diversity was higher in the Indian (85 species) and only then followed by the Pacific Ocean (79 species). Among the 371 studied-species world-wide, 164 were octopods (family Octopodidae), 159 were cuttlefish (including the families Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae) and 48 were squids (family Loliginidae).

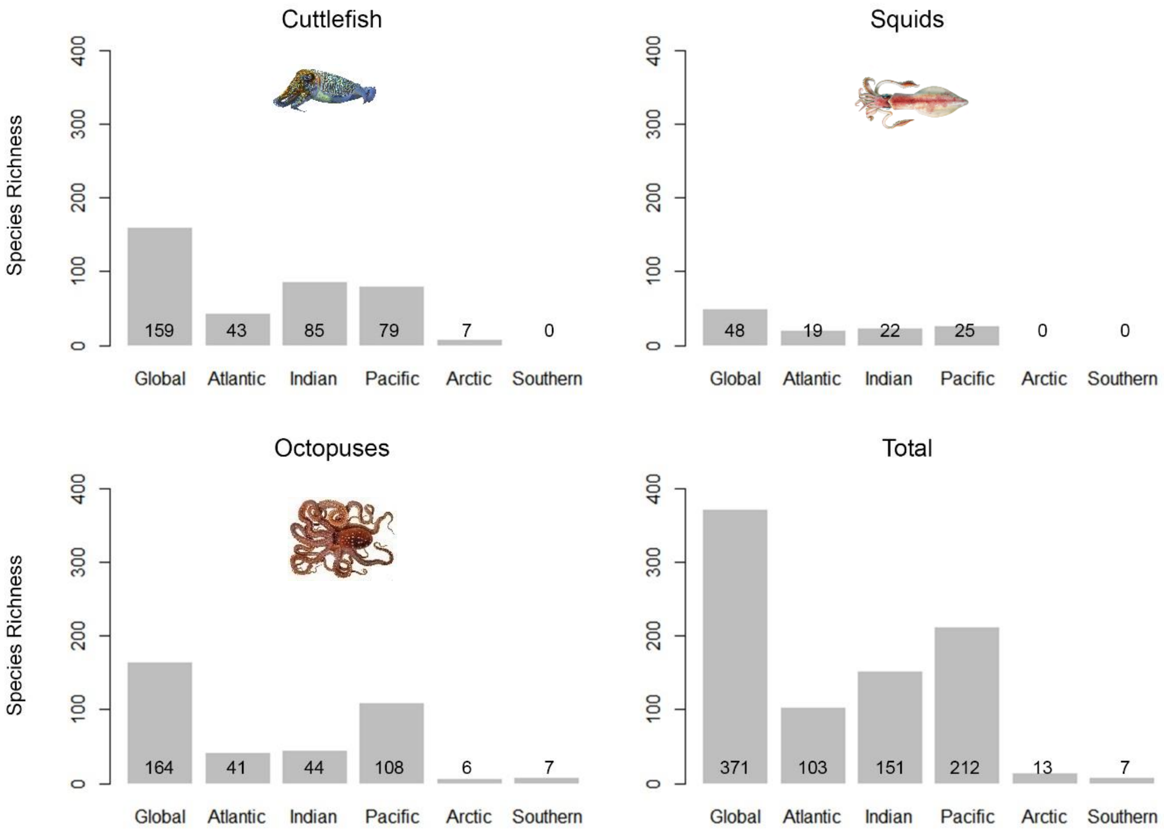

Figure 2 - Total number of species of cuttlefishes (Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae), squids (Loliginidae) and octopuses (Octopodidae) per world's oceans, used in the present study.

HOTSPOTS PER OCEAN

At a global scale, i.e., within the 232 ecoregions considered, the highest diversity (species richness) value was reached in the Pacific Ocean, namely in the Central Kuroshio Current ecoregion, with 64 species (Figure 3). It was then followed by the East China Sea (59 species) and Eastern Philippines (48 species) ecoregions. As mentioned above, the Indian Ocean was the second most diverse, and three hotspots were observed, namely the Java and Sulawesi Sea ecoregions, both with 38 species, and the Malacca Strait ecoregion with 33 species. Regarding the Atlantic Ocean, a major area of cephalopod diversity stands out, starting in the North Sea and extending down to north-western Africa, and being particularly rich in the Western Mediterranean (with 30 species) and in the Adriatic, Aegean and Ionian seas ecoregions (with 28 species). It is worth noting that the eastern Atlantic is more diverse, in part because of the members of the family Sepiidae, which were absent from the western side of the Atlantic Ocean.

The families Sepiidae, Sepiadariidae, Idiosepiidae and Loliginidae were absent from both polar regions. Only the families Sepiolidae and Octopodidae families were found in the Artic coastal areas, varying from 1 to 4 species among ecoregions. Moreover, only the family Octopodidae was found in the Southern Ocean, with diversity values ranging from 1 to 5 (depending on the ecoregion).

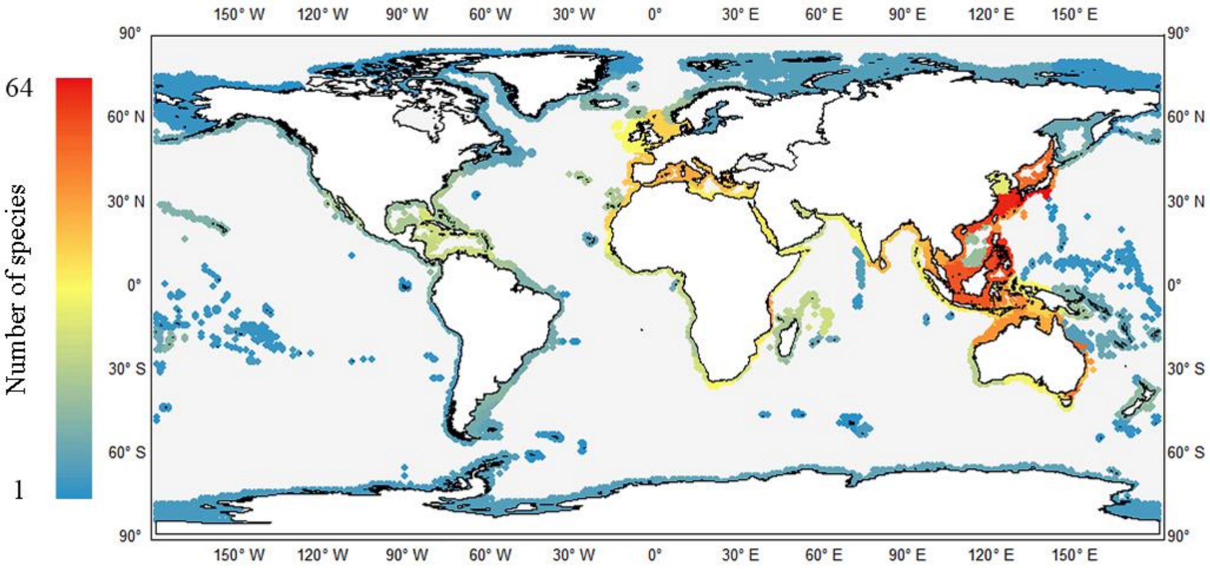

Figure 3 - Worldwide diversity (number of species per ecoregion) patterns of coastal cephalopods.

HOTSPOTS PER CEPHALOPOD GROUPS

Among cuttlefishes, the highest values of species richness in Sepiidae were observed, in the Pacific Ocean, followed by the Indian Ocean and the Atlantic Ocean. More specifically, our results clearly identified the Central Kuroshio Current and the East China Sea ecoregions as the main hotspots of Sepiidae diversity, both with a total number of 21 species (Figure 4a). Besides adjacent areas, namely from Southern China down to Vietnam (with 13 species), another hotspot was found in the East African Coral Coast (also with 13 species). A completely different scenario was observed for "bobtail" species, members of the family Sepiolidae, since the maximum diversity values were found in the Mediterranean ecoregions, especially in the western part with a total of 15 species (Figure 4b). The adjacent ecoregions, namely western Europe and north-western Africa, also showed high diversity values (13 and 11 species, respectively). Quite similar values were also observed in the East China Sea and Central Kuroshio Current ecoregions, both with 8 species.

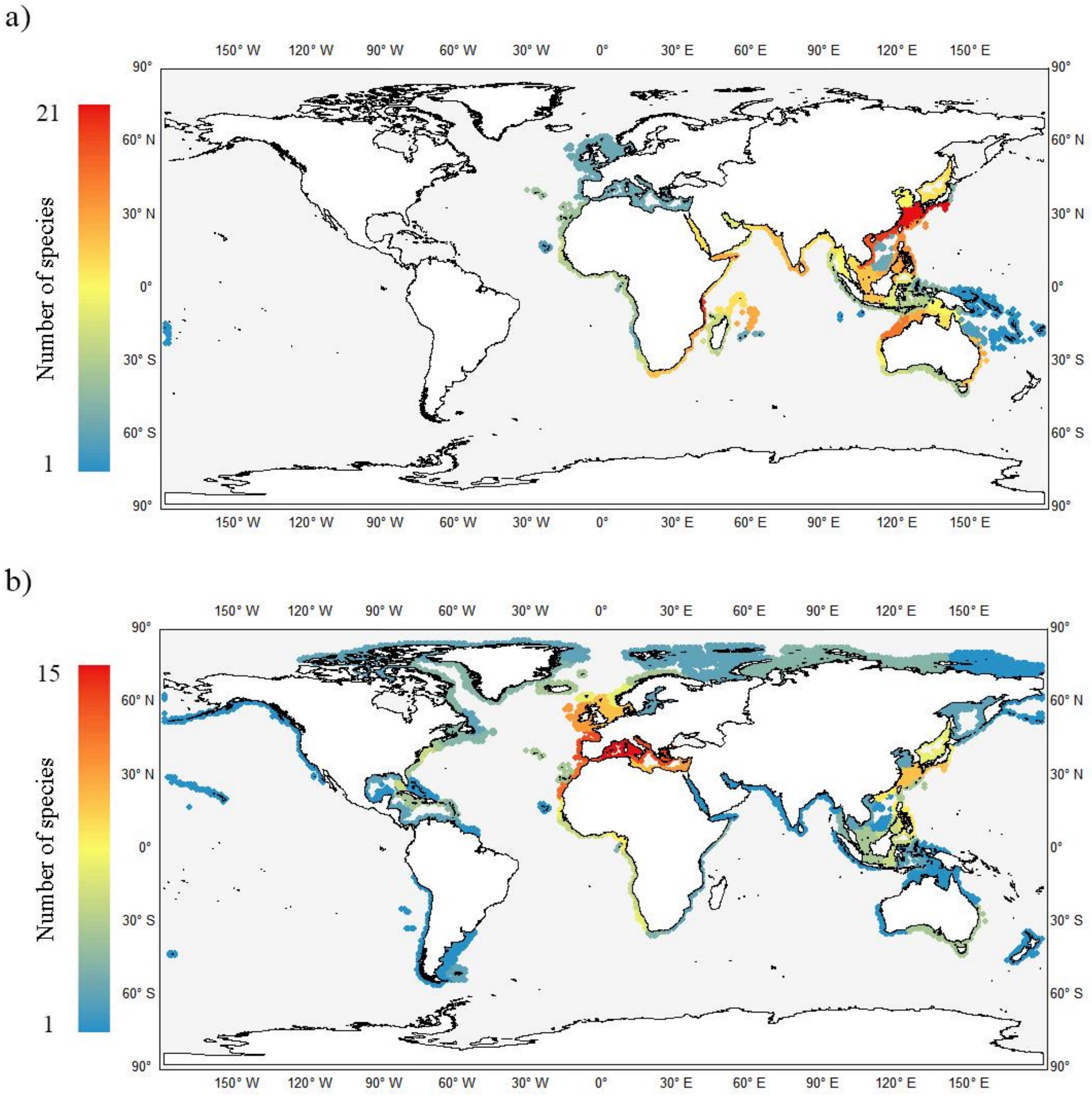

Figure 4 - Worldwide diversity (number of species per ecoregion) patterns of the families a) Sepiidae and b) Sepiolidae.

Both Sepiadariidae and Idiosepiidae were less speciose families (each only comprising a total of 7 species), and the maximum diversity values observed per ecoregion were 2 (Figure 5a and b, respectively). These values were observed in the Central Kuroshio Current, Central and Southern Great Barrier Reef and East Central Australian Shelf ecoregions for Sepiadariidae, and from north Australia up to Indonesia (comprising 9 different ecoregions) and from South Africa up to south Mozambique (comprising 3 different ecoregions) for Idiosepiidae.

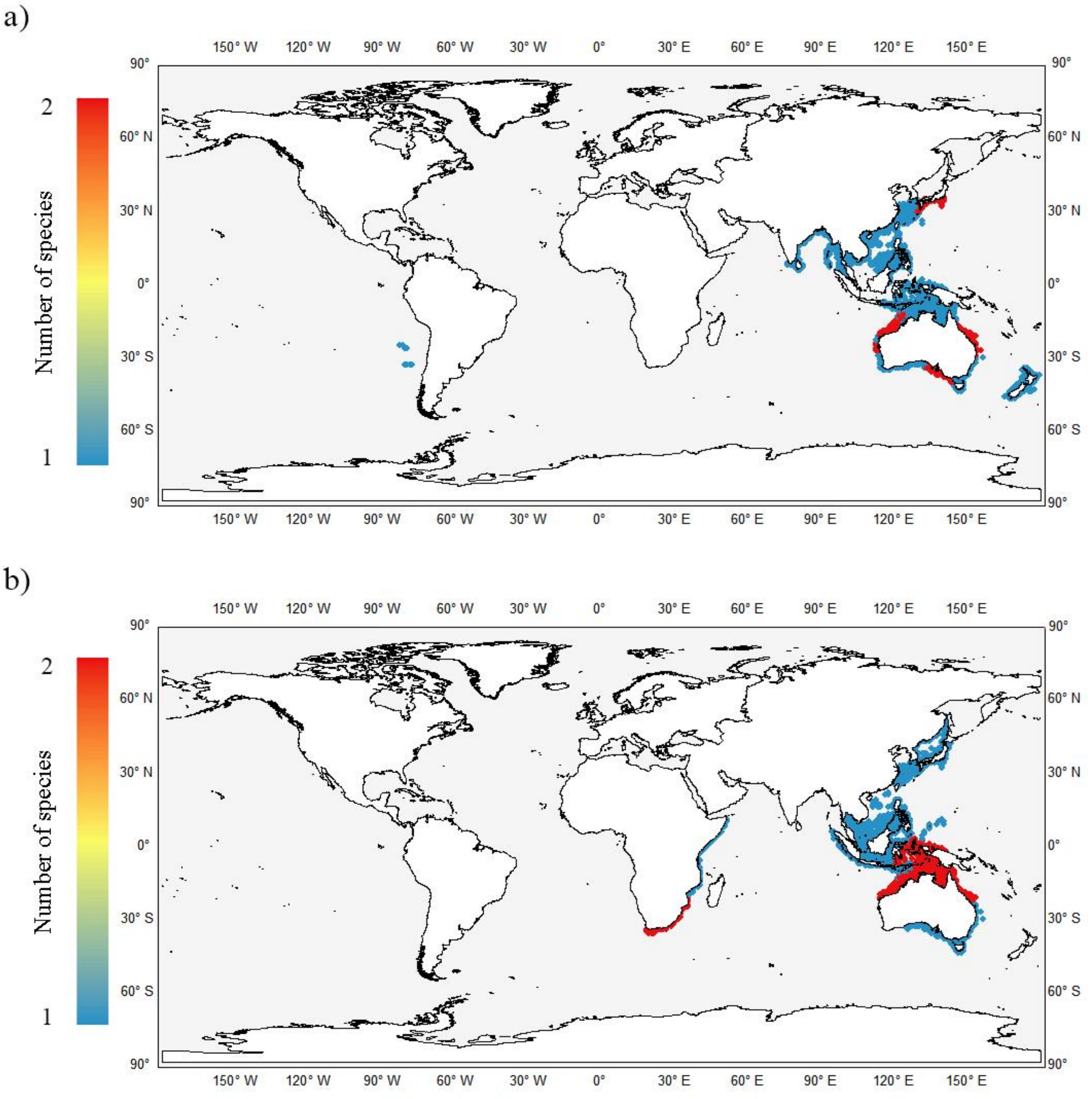

Figure 5 - Worldwide diversity (number of species per ecoregion) patterns of the families: a) Sepiadariidae, and b) Idiosepiidae.

Regarding squids, there were clear hotspots in the Indo-Pacific area, more precisely in the Java Sea ecoregion (12 species), and Malacca Strait, Palawan and Sulawesi Seas (all three regions with 11 species) (Figure 6a). On the other hand, the greatest hotspot for octopods (Octopodidae) was found in the Central Kuroshio Current, where the maximum value of 24 was reached (Figure 6b). Alongside, the East China Sea and the Eastern Philippines ecoregions also showed high diversity values, both with 18 species.

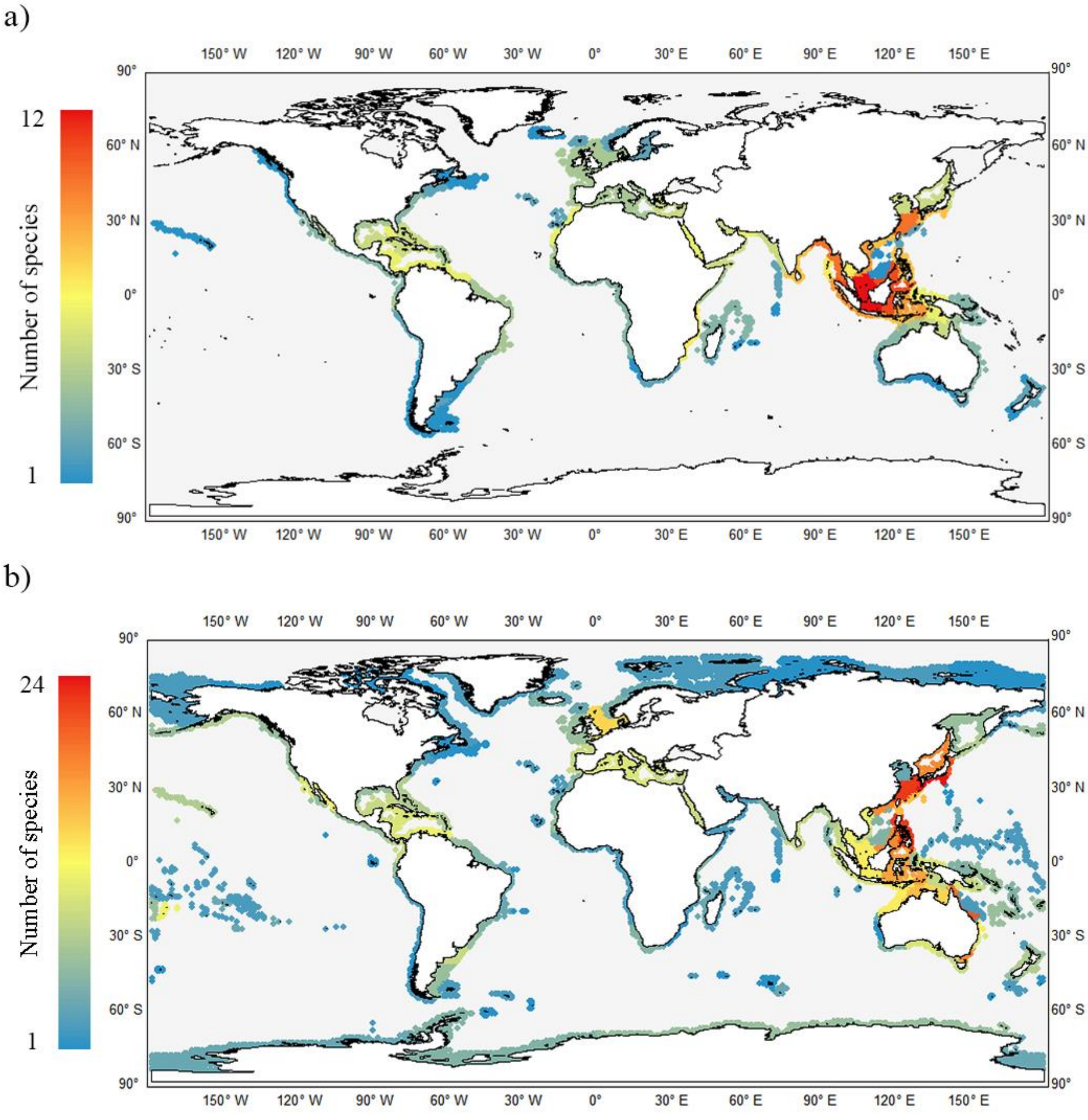

Figure 6 - Worldwide diversity (number of species per ecoregion) patterns of the families: a) Loliginidae, and b) Octopodidae.

LATITUDINAL GRADIENTS OF SPECIES RICHNESS

The association between latitude and diversity of shallow-living cuttlefish, squids and octopods, at a global scale, is shown in Figure 7, and per ocean, in Figure 11. Regarding the cuttlefish group, it was present from the 80º N/ 85º N bin to the 50 ºS/55 ºS bin, with the estimated zenith at 27 º N (Figure 7, top panels). It is worth noting that the estimated major peak of diversity varied among oceans – located at 26 ºN in the Pacific Ocean, 35 º N in the Atlantic Ocean and 15 ºS in the Indian Ocean (Figure 8).

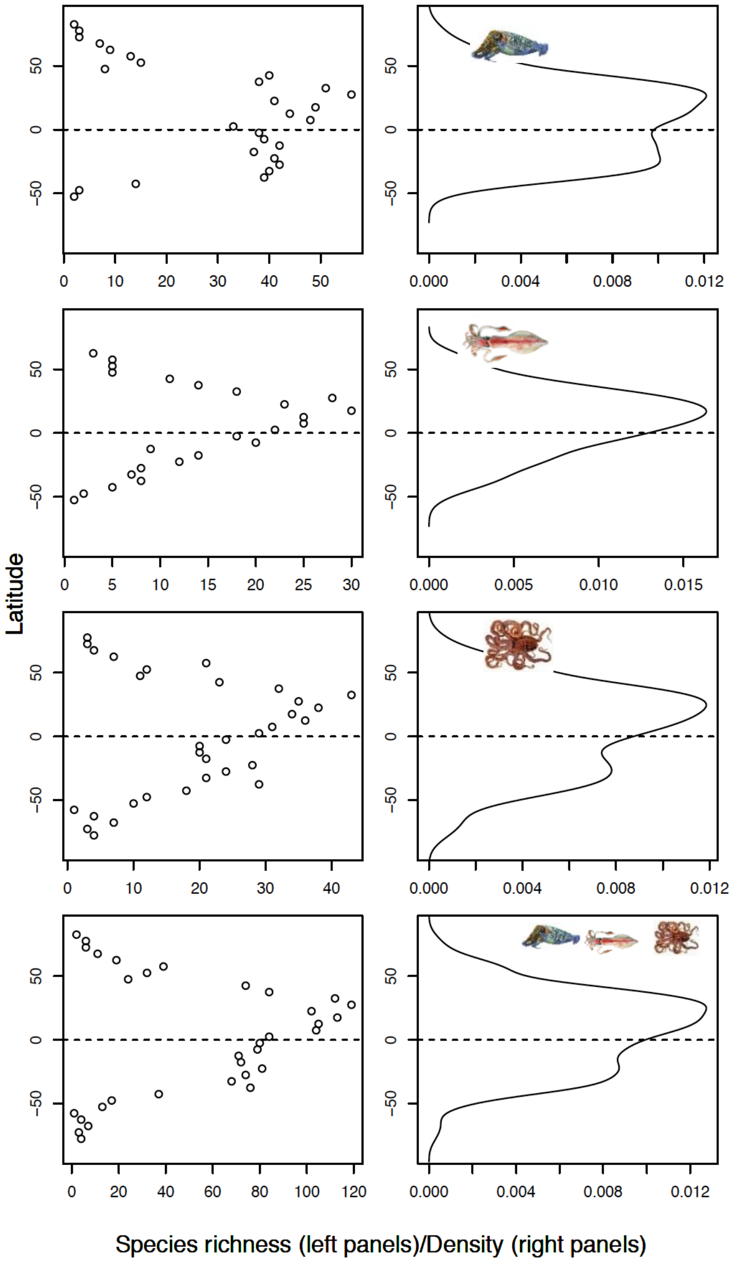

Figure 7 - Latitudinal diversity gradients of cuttlefish (top panels, families Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae), squids (middle high panels, Loliginidae) octopods (middle low panels, Octopodidae) and total cephalopods (bottom panels) at a global scale. Lefts panels: species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. Right panels: respective latitudinal densities through kernel smoothing estimation.

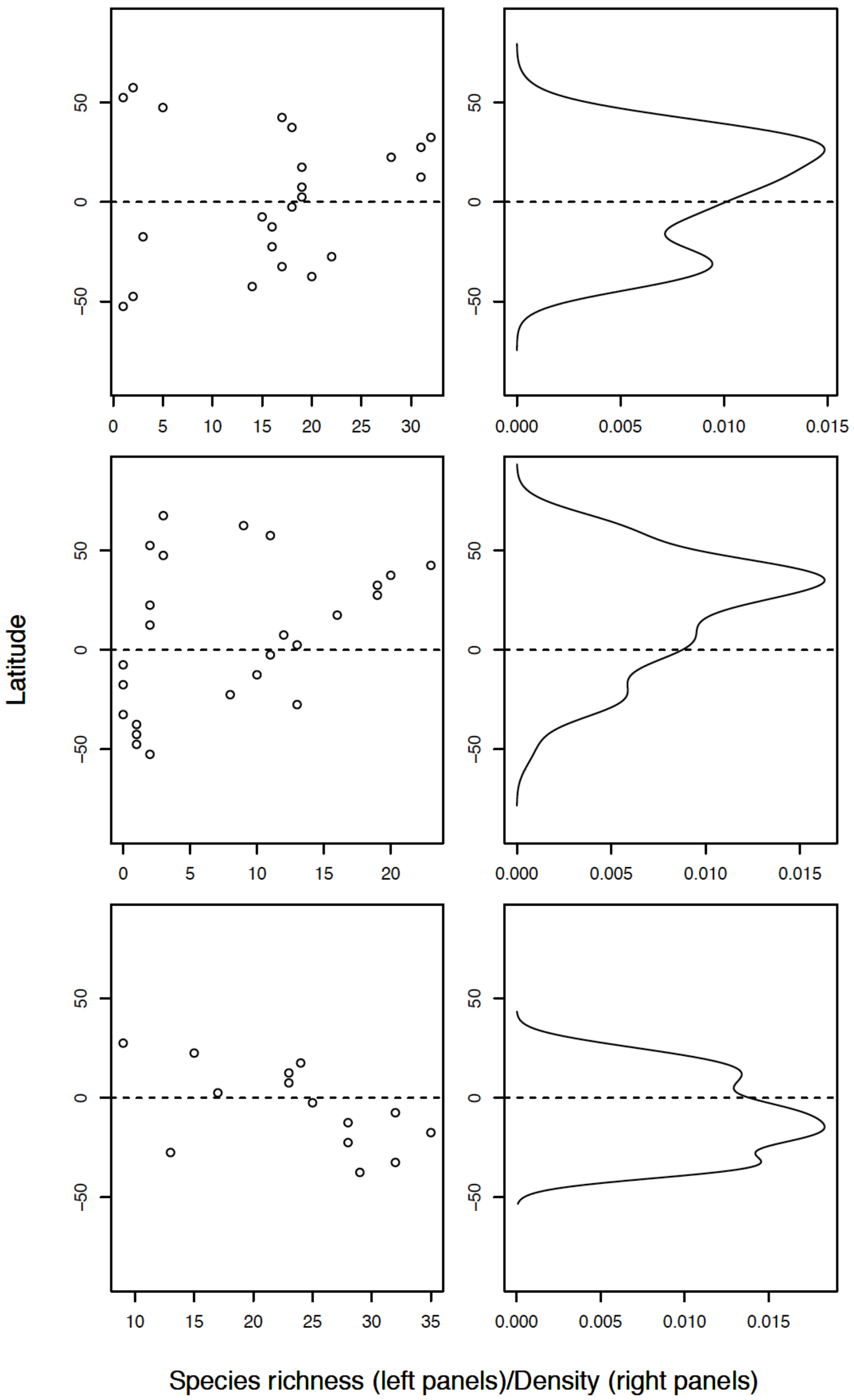

Figure 8 - Latitudinal diversity gradients of cuttlefishes (Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae) in the Pacific (top panels), Atlantic (middle panels) and Indian (bottom panels) Oceans. Lefts panels: species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. Right panels: respective latitudinal densities through kernel smoothing estimation.

Squids were present from the 55 ºN/60 ºN to the 50 ºS/55 ºS bin at a global scale, but the estimated zenith of diversity was much closer to the tropics – at 17 ºN (Figure 7, middle high panels). Again, the location of the peak of diversity also varied among oceans – at 7 ºN in the Pacific Ocean, 24 ºN in the Atlantic Ocean and 1 ºS in the Indian Ocean (Figure 9).

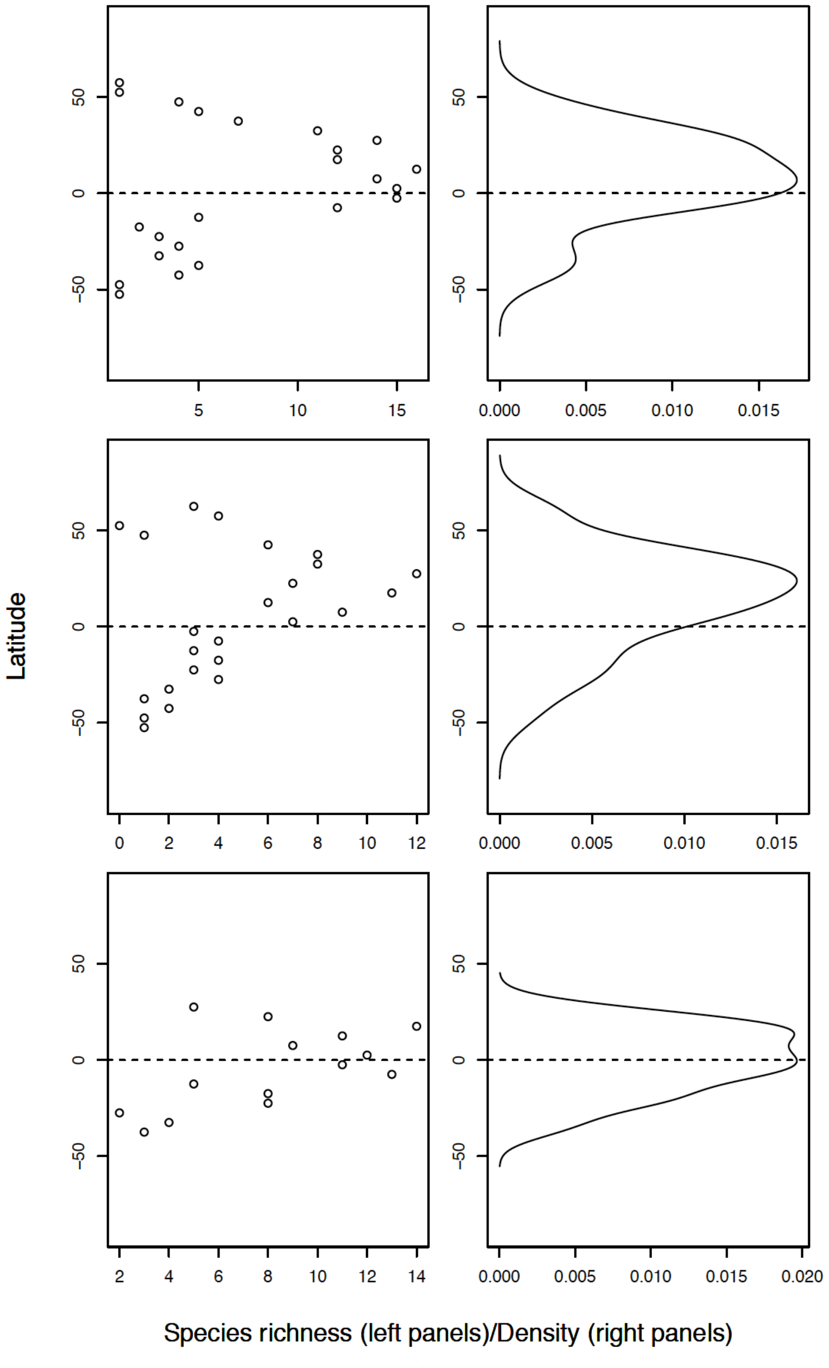

Figure 9 - Latitudinal diversity gradients of squids (Loliginidae) in the Pacific (top panels), Atlantic (middle panels) and Indian (bottom panels) Oceans. Lefts panels: species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. Right panels: respective latitudinal densities through kernel smoothing estimation.

Octopods were found from the 75 ºN/80 ºN bin to the 75 ºS/ 80 ºS with the highest estimated richness value at 25 ºN (Figure 7, middle low panels). The zenith position also changed among oceans – at 28 ºN in the Pacific Ocean, 26 ºN in the Atlantic Ocean and 4 ºS in the Indian Ocean (Figure 10).

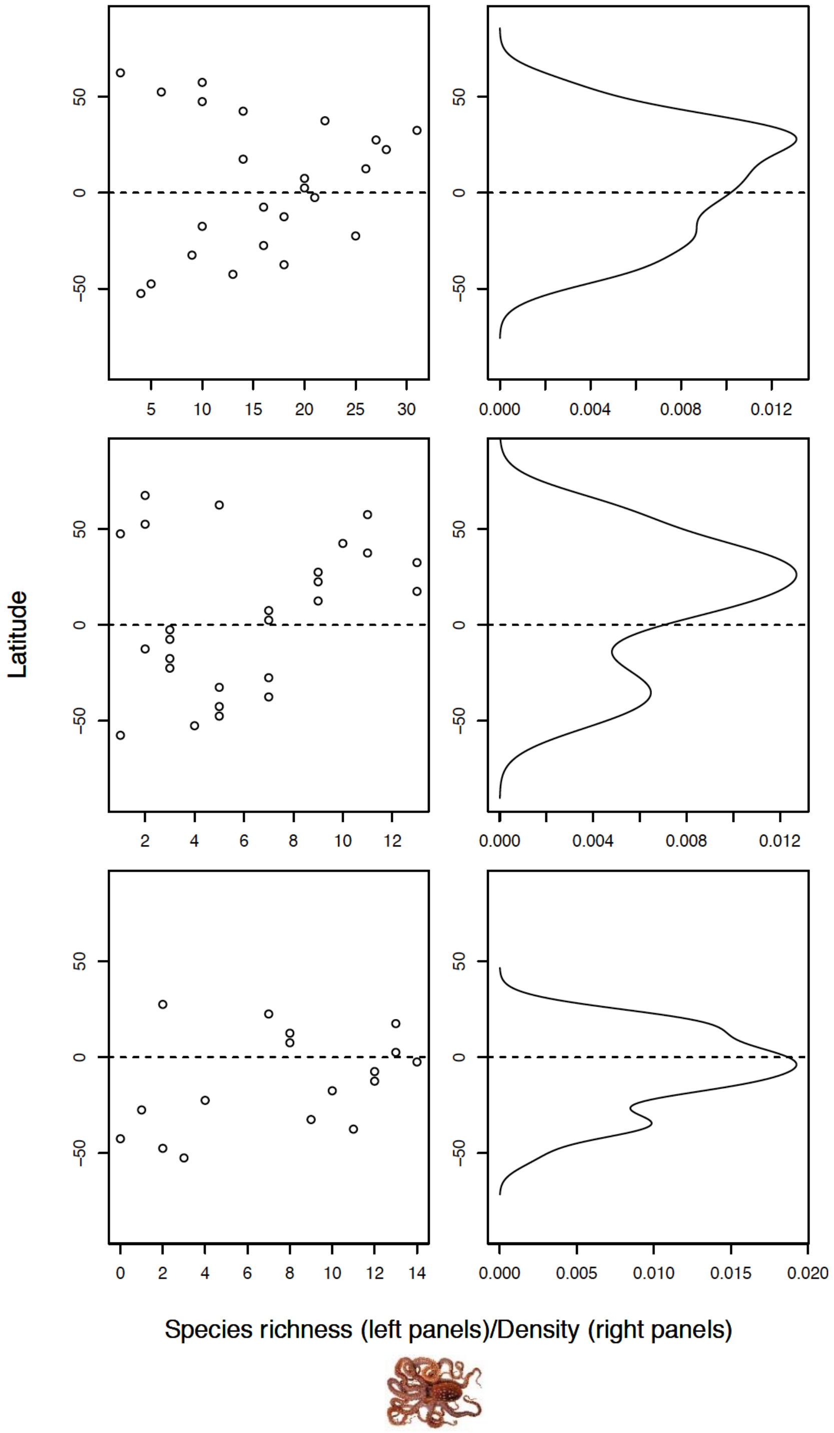

Figure 10 - Latitudinal diversity gradients of octopods (Octopodidae) in the Pacific (top panels), Atlantic (middle panels) and Indian (bottom panels) Oceans. Lefts panels: species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. Right panels: respective latitudinal densities through kernel smoothing estimation.

In the overall, cephalopods were found from the 80 ºN/85 ºN bin to the 75 ºS/80 ºS, with the global peak of diversity at 25 ºN (Figure 7, bottom panels). As expected, the cephalopod peak of diversity also varied among oceans – at 27 ºN in the Pacific Ocean, 33 ºN in the Atlantic Ocean and 7 ºS in the Indian Ocean (Figure 11).

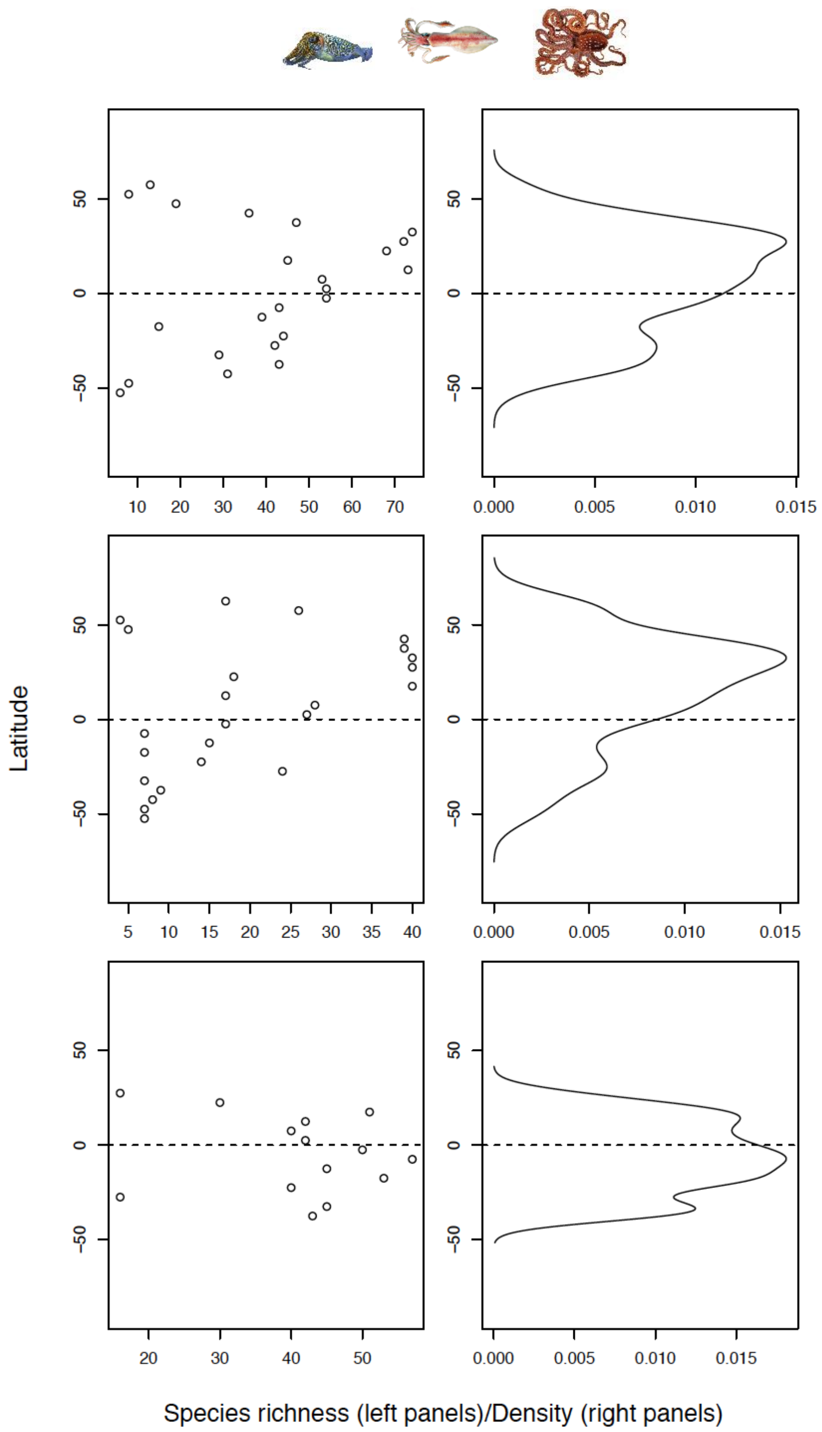

Figure 11 - Latitudinal diversity gradients of total cephalopods in the Pacific (top panels), Atlantic (middle panels) and Indian (bottom panels) Oceans. Lefts panels: species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. Right panels: respective latitudinal densities through kernel smoothing estimation.

Regarding modality patterns, and at a global scale, only the squids showed a unimodal distribution with latitude (Table 1). In opposition, cuttlefish, octopods and total cephalopods revealed bimodal distributions, always with the major peak of diversity in the north hemisphere. It is worth noting that some of these patterns changed across oceans. Last, all distributions (at a global scale and per ocean) revealed to be asymmetric and almost all were negatively skewed (Table 1).

Table 1 - Summary of the latitudinal position of the peak(s) of diversity (the major in bold), modality and shape distribution patterns of cuttlefish (families: Sepiidae, Sepiolidae, Sepiadariidae and Idiosepiidae), squids (Loliginidae), octopods (Octopodidae) and total cephalopods, per ocean and at a global scale.

Groups	**Ocean**	**Local maxima**		**Modality**	**Skewness coefficient**	**Distribution shape**
		# Peak(s)	Coordinate(s)			
Cuttlefish	Pacific	2	31º S and **26º N**	Bimodal	-0.31	Negatively skewed
	Atlantic	2	21º S and **35º N**	Bimodal	-0.49	Negatively skewed
	Indian	3	32º S, **15º S** and 12º N	Multimodal	0.15	Positively skewed
	Global	2	23º S and **27º N**	Bimodal	0.11	Positively skewed
Squids	Pacific	2	34º S and **7º N**	Bimodal	-0.46	Negatively skewed
	Atlantic	1	**24º N**	Unimodal	-0.43	Negatively skewed
	Indian	2	1º S and 13º N	Bimodal	-0.34	Negatively skewed
	Global	1	**17º N**	Unimodal	-0.25	Negatively skewed
Octopods	Pacific	1	**28º N**	Unimodal	-0.18	Negatively skewed
	Atlantic	2	35º S and **26º N**	Bimodal	-0.40	Negatively skewed
	Indian	2	34º S and **4º S**	Bimodal	-0.38	Negatively skewed
	Global	2	26º S and **25º N**	Bimodal	-0.25	Negatively skewed
Cephalopods	Pacific	2	28ºS and **27ºN**	Bimodal	-0.28	Negatively skewed
	Atlantic	2	25ºS and **33ºN**	Bimodal	-0.50	Negatively skewed
	Indian	2	34ºS, **7ºS** and 14ºN	Multimodal	-0.04	Weekly negatively skewed
	Global	2	22º S and **25º N**	Bimodal	-0.14	Negatively skewed

4. DISCUSSION

HOTSPOTS

These results clearly identify the Pacific Ocean as the most diverse, followed by the Indian, the Atlantic, the Arctic and Southern Oceans (Figure 2). Within the Pacific ocean, the Indo-Australian Archipelago (IAA) is known for being the largest global marine biodiversity hotspot for many taxa, from corals to reef fishes (Bellwood & Wainwright, 2002; Cowman & Bellwood, 2013). Such region is recognized as a site with certain characteristics, such as the broad shallow water area with great geological complexity and connectiveness with two major biogeographic regions, that might be promoting speciation processes and/or refuge (Bellwood & Wainwright, 2002; Briggs & Bowen, 2013; Cowman & Bellwood, 2013). Given that this pattern is recurrent in several taxonomic groups, it has been suggested that there must be a unifying explanation for such trend (Renema *et al.*, 2008). Three main hypotheses, based on speciation processes and dispersal, arise, attributing to the IAA a role, either as, a "centre of origin", a "centre of overlap" or a "centre of accumulation" (Bellwood & Wainwright, 2002; Mora *et al.*, 2003; Briggs & Bowen, 2013; Cowman & Bellwood, 2013). The first hypothesis suggests that the IAA is a major site of speciation from which species disperse; the second suggests that this hotspot is a consequence of the overlapping of surrounding faunas, dispersing in all directions from their biogeographic areas, and the last argues that processes of speciation occur in peripheral areas and that species extend their ranges into this area, through unidirectional dispersal from the prevailing currents (Bellwood & Wainwright, 2002; Mora *et al.*, 2003; Briggs & Bowen, 2013; Cowman & Bellwood, 2013).

The "centre of overlap" and "centre of accumulation" hypotheses are based on the assumption that species with geographic ranges, in the Indian and Pacific, usually meet in the IAA, thus making it so diverse. As so, these species should have their midpoints of longitudinal distribution outside this area, resulting in bimodal distributions. However, Mora *et al.* (2003) findings on reef fish diversity prove that species ranges show a unimodal distribution peaking in the IAA, thus excluding these two hypotheses. Still, a variation of the accumulation hypothesis, which argues that species ranges after dispersal are then reduced, is still plausible (Mora *et al.*, 2003).

Despite the lack of consensus in this matter, there is also the chance that these processes might be working together. As suggested by Mironov (2006), there are three stages (accumulation, diversification and dispersal) that characterize the development of a centre of origin. Moreover, looking at these processes at geological time scales, there is some evidence of the three stages in the IAA region (Renema *et al.*, 2008; Briggs & Bowen, 2013). In fact, the IAA started as a centre of accumulation and/or refugee of species coming from the Tethys Sea, during the loss of habitat of the late Eocene/Oligocene, became a centre of origin or diversification, starting during the Miocene, and is currently, since the Pliocene, in the stage of dispersal (Bellwood & Wainwright, 2002; Renema *et al.*, 2008; Briggs & Bowen, 2013; Cowman & Bellwood, 2013).

In contrast with the history of connectivity in the formation of the IAA, the Mediterranean and Caribbean hotspots, in the Atlantic, are a result of the early isolation from the western Tethys Sea (Parravicini *et al.*, 2013). The Caribbean is specially influenced by the cooling of the sea surface temperature, during the transition from the Eocene to the Oligocene, as it is thought to have caused the extinction of the western Atlantic cuttlefish (Rosa *et al.*, 2008). More recently, about 5.5 Ma ago, the closure of the Mediterranean Sea caused a boost on the salinity levels, the "Messinian salinity crisis", leading to the extinction of stenohaline species and origin of endemic ones (Rosa *et al.*, 2008), mainly of the Sepiidae family which is most abundant here (Figure 4 b)). Despite the early historical isolation, it is known of dispersal routes from the modern IAA, via Cape of Good Hope or Isthmus of Panama, through which species could have colonized the Atlantic region (Briggs & Bowen, 2013) but the fact that only two species are shared by the three oceans (data obtained from our database) suggests that these were not as important to these faunas the previous events.

This geological and evolutionary background explains why the IAA is such a rich region, and why the eastern Philippines are one of the most diverse ecoregions. But it does not successfully explain why the Central Kuroshio Current and the East China Sea are the two most diverse as they are outside of this area (Figure 3). This might be explained by these ecoregions being part of the subtropical gyre with predominant currents running from the IAA, thus providing dispersal, which, together with the particular environmental conditions and nutrient enrichment dynamics of the eddies and upwelling system of the area, make them particular rich (Yatsu *et al.*, 2017).

LATITUDINAL GRADIENTS OF SPECIES RICHNESS

The LGSR results (Table 1, Figures 7, 8, 9, 10 and 11) are an example of how variable latitudinal gradients are, even among taxonomically closely groups with the same Class (Cephalopoda). Here, it's shown that: i) unimodality was only detected in 3 out of the 16 latitudinal gradients analyzed, ii) bimodality was the most common trend, found in 11 gradients (providing strong evidence that exceptions to the classical LGSR do exist), iii) all distributions analyzed vary among oceans and were asymmetric between hemispheres, and iv) distributions are mostly negatively skewed (13 out of 16) with most zeniths of diversity (12 out of 16) occurring in the northern hemisphere (the only exceptions to this trend correspond to gradients in the Indian Ocean, which is latitudinally restricted at North by land).

Based on these findings I argue that unimodality, such as the one found in squids at a global scale (Table 1, Figure 7, middle high panels), may emerges as a direct result of the effect of energy-related variables that interact with the organism's physiology (namely sea surface temperature), as proposed by the ambient energy hypothesis (Turner *et al.*, 1987). The two zeniths of squid diversity corresponding to the unimodal gradients in the Atlantic (Figure 9, middle) and at global scale, occur within tropical latitudes where warmer waters are found. For example, the tropical region of the Caribbean region (Figure 4 a) and b), is clearly shaping the latitudinal unimodality in this ocean. However, as tempting as it might be to assume that this predictor would explain almost all the aspects of distribution, some evidences suggest the influence of other mechanisms might be playing a role as well. For example, the unimodal gradient of squids in the Atlantic should be broader, if ambient energy was the only predictor because warm waters are also found off the coast of Brazil. But diversity is mostly restricted to the Caribbean. As previously mentioned, history has a major role on the species pool of this region and, also, barriers such as the freshwater discharges from the Amazon river, at south, and the open ocean, at east, are known to restrict species to this area (Rosa *et al.*, 2008; Briggs & Bowen, 2013). It is also worth noting that the third unimodal gradient, corresponding to octopods of the Pacific (Figure 10, top panel), revealed a zenith of diversity outside the tropical latitudes. This could be due to the particular characteristics of the Central Kuroshio Current and East China Sea (Figure 6, b), ecoregions known to be influenced by strong and warm currents (Yatsu *et al.*, 2017).

As for the widespread bimodality pattern within cephalopods, I postulate that productivity might be the best predictor of diversity (i.e. the species-productivity hypothesis; Wright, 1983) given that highly productive areas tend to be associated with temperate latitudes. For example, cuttlefish show a bimodal gradient in the Atlantic, with a zenith at 35º N (Table 1, Figure 8, middle panel), mainly due to the contribution of species of the southwestern European and northwestern African regions (Figures 4 and 5), which are highly influenced by the Iberian and Mauritanian upwelling systems. Moreover, the second peak of diversity occurs at 21º S, which coincides with the location of the Benguela upwelling system. As another example, cuttlefish in the Western Pacific seem to be most abundant at 26º N and 31º S, in the Central Kuroshio Current and Northern Australia, correspondingly, regions known for high productivity.

Nevertheless, one cannot point for a single causal predictor because, as noted before, the Mediterranean region for instance (and their sepiolid endemism's) is clearly one of the greatest hotspot of diversity in the Atlantic influencing the resultant LGSR. Historical events play again ("Messinian salinity crisis") an important role on shaping contemporary diversity.

CONCLUSIONS

The major hotspots of coastal cephalopod species, similarly to what happens in many other taxonomic groups, are found in the Indo-Pacific, specifically in the Central Kuroshio Current, the East China Sea and in the Eastern Philippines ecoregions. I advocate that these hotspots are linked to the "centre of origin", "centre of overlap" or "centre of accumulation" hypotheses postulated for the Indo-Australian Archipelago region, together with the particular productivity-rich conditions associated to certain characteristics of the region, such as, broad shallow water area, prevailing currents and connectiveness with two major biogeographic regions, and due to nearby upwelling system dynamics. Cuttlefish are the only group that does not reach its highest diversity in the IAA but instead in the Mediterranean Sea since a period of isolation during the Miocene/Pliocene transition promote endemism appearance.

These taxonomic groups are a great example of how variable latitudinal gradients can be, given that patterns of unimodality and bimodality were both found, despite the latter being prevalent. It is also clear now that uniformity between hemispheres is not common and that the northern hemisphere is generally more diverse. Squids are the only group showing unimodal gradient at global scale and I argue it is related with the "ambient energy hypothesis" given that it seems to explain much of the patterns encountered. On the other hand, the more widespread bimodal gradients found in all other cephalopod groups, may be linked to ocean productivity (i.e. the "species-productivity hypothesis"). These findings highlight the notion that the shape and symmetry of LGRS are not universal and there are no single causal predictors to explain hotspot and latitudinal zenith locations within the same taxa.

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ANNEXES

Table 1 - Table of species of costal cephalopods used in the present study, per Order and per Family

Order Sepiida
Family Sepiidae
Metasepia pfefferi
Metasepia tullbergi
Sepia aculeata
Sepia acuminata
Sepia andreana
Sepia apama
Sepia appellofi
Sepia arabica
Sepia aureomaculata
Sepia australis
Sepia bandensis
Sepia bertheloti
Sepia braggi
Sepia brevimana
Sepia carinata
Sepia chirotrema
Sepia confusa
Sepia cottoni
Sepia cultrata
Sepia dollfusi
Sepia elegans
Sepia elliptica
Sepia elobyana
Sepia elongata
Sepia erostrata
Sepia esculenta
Sepia faurei
Sepia filibrachia
Sepia foliopeza
Sepia gibba
Sepia grahami
Sepia hedleyi
Sepia hieronis
Sepia hierredda
Sepia incerta
Sepia irvingi
Sepia ivanovi
Sepia joubini
Sepia kiensis

Sepia kobiensis
Sepia koilados
Sepia latimanus
Sepia limata
Sepia longipes
Sepia lorigera
Sepia lycidas
Sepia madokai
Sepia mascarensis
Sepia mestus
Sepia mira
Sepia mirabilis
Sepia misakiensis
Sepia murrayi
Sepia novaehollandiae
Sepia officinalis
Sepia omani
Sepia opipara
Sepia orbignyana
Sepia papillata
Sepia papuensis
Sepia pardex
Sepia peterseni
Sepia pharaonis
Sepia plangon
Sepia plathyconchalis
Sepia prabahari
Sepia prashadi
Sepia pulchra
Sepia ramani
Sepia recurvirostra
Sepia rhoda
Sepia rozella
Sepia savignyi
Sepia sewelli
Sepia simoniana
Sepia smithi
Sepia sokotriensis
Sepia stellifera
Sepia subtenuipes
Sepia sulcata
Sepia tenuipes
Sepia thurstoni
Sepia trygonina
Sepia typica
Sepia vercoi

Sepia vermiculata
Sepia vietnamica
Sepia vossi
Sepia whitleyana
Sepia zanzibarica
Sepiella cyanea
Sepiella inermis
Sepiella japonica
Sepiella mangkangunga
Sepiella ornata
Sepiella weberi
Order Sepiida
Family Sepiolidae
Subfamily Sepiolinae
Euprymna albatrossae
Euprymna berryi
Euprymna hyllebergi
Euprymna morsei
Euprymna scolopes
Euprymna tasmanica
Inioteuthis capensis
Inioteuthis japonica
Inioteuthis maculosa
Rondeletiola minor
Sepietta neglecta
Sepietta obscura
Sepietta oweniana
Sepiola affinis
Sepiola atlantica
Sepiola birostrata
Sepiola intermedia
Sepiola knudseni
Sepiola ligulata
Sepiola parva
Sepiola pfefferi
Sepiola robusta
Sepiola rondeleti
Sepiola steenstrupiana
Sepiola tridens
Sepiola trirostrata
Sepiolina nipponensis
Subfamily Rossiinae
Austrorossia australis
Austrorossia bipapillata
Austrorossia mastigophora

Neorossia caroli
Neorossia leptodons
Rossia brachyura
Rossia bullisi
Rossia macrosoma
Rossia megaptera
Rossia moelleri
Rossia pacifica pacifica
Rossia palpebrosa
Semirossia equalis
Semirossia patagonica
Semirossia tenera
Subfamily Heteroteuthinae
Heteroteuthis (Heteroteuthis) dispar
Heteroteuthis (Heteroteuthis) weberi
Heteroteuthis (Stephanoteuthis) dagamensis
Heteroteuthis (Stephanoteuthis) serventyi
Iridoteuthis maoria
Sepiolina nipponensis
Stoloteuthis leucoptera

Order Sepiida
Family Sepiadariidae
Sepiadarium auritum
Sepiadarium austrinum
Sepiadarium gracilis
Sepiadarium kochii
Sepiadarium nipponianum
Sepioloidea lineolata
Sepioloidea pacifica

Order Decapodiformes
Family Idiosepiidae
Idiosepius biserialis
Idiosepius macrocheir
Idiosepius notoides
Idiosepius paradoxus
Idiosepius picteti
Idiosepius pygmaeus
Idiosepius thailandicus

Order Myopsida
Family Australiteuthidae
Australiteuthis aldrichi

Order Myopsida

Family Loliginidae
Afrololigo mercatoris
Alloteuthis africana
Alloteuthis media
Alloteuthis subulata
Doryteuthis (Amerigo) gahi
Doryteuthis (Amerigo) ocula
Doryteuthis (Amerigo) opalescens
Doryteuthis (Amerigo) pealeii
Doryteuthis (Amerigo) surinamensis
Doryteuthis (Doryteuthis) plei
Doryteuthis (Doryteuthis) roperi
Doryteuthis sanpaulensis
Heterololigo bleekeri
Doryteuthis forbesii
Doryteuthis reynaudii
Doryteuthis vulgaris
Loliolus (Loliolus) affinis
Loliolus gotoi
Loliolus (Loliolus) hardwickei
Loliolus (Nipponololigo) japonica
Loliolus (Nipponololigo) sumatrensis
Loliolus (Nipponololigo) uyii
Loliolus (Nipponololigo) beka
Lolliguncula (Loliolopsis) diomedeae
Lolliguncula (Lolliguncula) argus
Lolliguncula (Lolliguncula) brevis
Lolliguncula (Lolliguncula) panamensis
Pickfordiateuthis bayeri
Pickfordiateuthis pulchella
Pickfordiateuthis vossi
Sepioteuthis australis
Sepioteuthis lessoniana
Sepioteuthis sepioidea
Uroteuthis (Aestuariolus) noctiluca
Uroteuthis (Photololigo) abulati
Uroteuthis (Photololigo) arabica
Uroteuthis (Photololigo) bengalensis
Uroteuthis (Photololigo) chinensis
Uroteuthis (Photololigo) duvaucelii
Uroteuthis (Photololigo) edulis
Uroteuthis (Photololigo) machelae
Uroteuthis (Photololigo) robsoni
Uroteuthis (Photololigo) sibogae
Uroteuthis (Photololigo) singhalensis
Uroteuthis (Photololigo) vossi

Uroteuthis (Uroteuthis) bartschi
Uroteuthis pickfordi
Uroteuthis reesi

Order Octopoda
Family Octopodidae
Abdopus abaculus
Abdopus aculeatus
Abdopus capricornicus
Abdopus horridus
Abdopus tonganus
Abdopus undulatus
Adelieledone adelieana
Adelieledone polymorpha
Ameloctopus litoralis
Amphioctopus aegina
Amphioctopus arenicola
Amphioctopus burryi
Amphioctopus exannulatus
Amphioctopus fangsiao
Amphioctopus kagoshimensis
Amphioctopus marginatus
Amphioctopus mototi
Amphioctopus neglectus
Amphioctopus ovulum
Amphioctopus polyzenia
Amphioctopus rex
Amphioctopus siamensis
Bathypolypus arcticus
Bathypolypus bairdii
Muusoctopus alatus
Muusoctopus hokkaidensis
Muusoctopus leioderma
Muusoctopus levis
Muusoctopus longispadiceus
Muusoctopus profundorum
Muusoctopus thielei
Muusoctopus yendoi
Callistoctopus alpheus
Callistoctopus aspilosomatis
Callistoctopus dierythraeus
Callistoctopus graptus
Callistoctopus luteus
Callistoctopus macropus
Callistoctopus nocturnus
Callistoctopus ornatus

Callistoctopus rapanui
Cistopus chinensis
Cistopus indicus
Cistopus taiwanicus
Eledone caparti
Eledone cirrhosa
Eledone gaucha
Eledone massyae
Eledone moschata
Eledone palari
Eledone schultzei
Enteroctopus dofleini
Enteroctopus magnificus
Enteroctopus megalocyathus
Enteroctopus zealandicus
Euaxoctopus panamensis
Euaxoctopus pillsburyae
Galeoctopus lateralis
Graneledone yamana
Grimpella thaumastocheir
Hapalochlaena fasciata
Hapalochlaena lunulata
Hapalochlaena maculosa
Macrochlaena winckworthi
Macrotritopus defilippi
Megaleledone setebos
Muusoctopus eureka
Muusoctopus longibrachus akambei
Muusoctopus sibiricus
Octopus abruptus
Octopus alecto
Octopus argus
Octopus australis
Octopus balboai
Octopus berenice
Octopus berrima
Octopus bimaculatus
Octopus bimaculoides
Octopus bocki
Octopus briareus
Octopus bunurong
Octopus californicus
Octopus campbelli
Octopus chierchiae
Octopus conispadiceus
Octopus cyanea

Octopus favonius
Octopus filosus
Octopus fitchi
Octopus gardineri
Octopus globosus
Octopus gorgonus
Octopus hattai
Octopus hawiiensis
Octopus hubbsorum
Octopus humilis
Octopus huttoni
Octopus incella
Octopus insularis
Octopus joubini
Octopus kaharoa
Octopus kaurna
Octopus laqueus
Octopus maorum
Octopus mariles
Octopus maya
Octopus microphthalmus
Octopus micropyrsus
Octopus micros
Octopus mimus
Octopus minor
Octopus mutilans
Octopus nanus
Octopus oculifer
Octopus ochotensis
Octopus oliveri
Octopus pallidus
Octopus parvus
Octopus penicillifer
Octopus pumilus
Octopus rubescens
Octopus salutii
Octopus selene
Octopus spinosus
Octopus superciliosus
Octopus tehuelchus
Octopus tetricus
Octopus tenuipulvinus
Octopus tsugarensis
Octopus veligero
Octopus vitiensis
Octopus vulgaris

Octopus warringa
Octopus wolfi
Octopus zonatus
Pareledone aequipapillae
Pareledone albimaculata
Pareledone aurata
Pareledone charcoti
Pareledone cornuta
Pareledone felix
Pareledone framensis
Pareledone harrissoni
Pareledone serperastrata
Pareledone subtilis
Pareledone turqueti
Paroctopus digueti
Pinnoctopus cuvierii
Pinnoctopus filholianus
Pinnoctopus fujitai
Pinnoctopus hattae
Pinnoctopus kermadecensis
Pinnoctopus lechenaultii
Pinnoctopus machikii
Pinnoctopus pardalis
Pteroctopus hoylei
Pteroctopus tetracirrhus
Robsonella fontanianus
Scaeurgus patagiatus
Scaeurgus unicirrhus
Tetracheledone spinicirrus
Thaumoctopus mimicus
Vosseledone charrua
Wunderpus photogenicus