# Cephalopods of the South-West Indian Ocean Ridge: A hotspot of biological diversity and absence of endemism

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Keywords: Cephalopod, Deep seas, South-West Indian Ocean Ridge, Biodiversity, Indian Ocean

## Abstract

A total of 68 cephalopod species belonging to 26 families (10–11% of the total known cephalopod diversity) were collected on board R/V *Fridtjof Nansen* during a research survey on the South West Indian Ocean Ridge in November–December 2009. This relatively small area extends from the Tropical front to the Subantarctic front with four distinctive cephalopod faunas and represents one of the most outstanding hotspots of cephalopod diversity reported to date. However, most of the species caught there were characterised by circumglobal distribution in the Southern Hemisphere, and no endemic species were unambiguously found, although a number of taxa could not be confidently attributed to known species. Most of the studied area was dominated by squid species reproducing in epipelagic layers (mostly Enoploteuthidae and Pyroteuthidae). Species reproducing in meso-bathypelagial whose juveniles ascend to surface water (Cranchiidae, Histioteuthidae, etc.) became gradually more and more important southward from the Tropical Zone to the Southern Peripheral Ecotone. In the latter region they were joined by near-bottom dwellers of the order Sepiolida. The epipelagic strategy of reproduction disappears completely at the Subpolar Front, where epipelagic waters were inhabited by young members of the Cranchiidae and Gonatidae hatched in deep seas. This study demonstrated the importance of conservation and management of this high-seas area, with its unique biodiversity and ecological resources, in line with recommendations by the IUCN Seamount project and Global Ocean Biodiversity Initiative.

## Introduction

Oceans cover approximately 71% of the Earth's surface, and are home to 80% of the world's biodiversity. However, oceanic biological diversity is hardly studied and only 1–2% of the world's marine habitats are protected, in contrast to approximately 12% of the land areas (UNESCO,2014; IUCN,2014). There is no single systematic sustained programme for evaluating ocean biodiversity. However, a range of major projects have been launched, such as MarBON, which intends to integrate biological levels from genes to habitats, and to link biodiversity observations to abiotic environmental variables (Duffy etal.,2014). Among numerous projects related to protection of the biological diversity, the International Union for Conservation of Nature (IUCN) initiated the Global Ocean Biodiversity Initiative (GOBI) in 2010 to help countries, as well as regional and global organisations, to use and develop data, tools, and methodologies to identify ecologically significant areas, with an initial focus on the high seas and deep sea beds beyond national jurisdiction (IUCN, 2014). One integral part of this initiative is the IUCN Seamount project, whose objective is to apply an ecosystem- based approach to fisheries management for biologically and globally significant and commercially important areas beyond national jurisdiction in the Southern Indian Ocean, focusing on seamounts, with a long-term aim to demonstrate innovative approaches for improving conservation and management of unique biodiversity and ecological resources in the high seas (IUCN, 2014).

Worldwide, there are more than 33,000 known large seamounts with elevations greater than 1000m, and a further 130,000 smaller seamounts within the elevation range of 400–1000m (Yesson et al., 2011). Large seamounts cover ~4.7% of the seafloor (17.2 million km$^2$) with smaller features making up ~16.3% (59 million km$^2$; Yesson et al., 2011), meaning that they are important ecosystems even when considered solely by surface area. While seamounts remain poorly investigated, studies to date indicate that they are often biologically distinctive oceanic habitats, hosting benthic communities that differ greatly from non-seamount habitats in their structure, species richness and bio-mass/abundance (Rogers, 1994; McClain et al., 2009, 2010; Rowden et al., 2010). Early work on benthic communities also suggested that seamount communities were characterised by high levels of endemism (Wilson and Kaufmann, 1987; De Forges et al., 2000). However, recent work has suggested that such findings may be an artefact of poor sampling in the deep ocean and that seamounts often share species with the nearest continental slope habitats, albeit with differences in relative abundance in comparison with these ecosystems (O'Hara, 2007; McClain et al., 2009; 2010; Howell et al., 2010).

Studies of the pelagic ecosystems around and above seamounts have generally indicated qualitative and quantitative differences in samples taken above seamount summits and flanks compared to the open ocean (the so-called “seamount effect”; Dower and Mackas, 1996). In some cases, increased abundances of zooplankton have been observed above the summits and flanks of sea-mounts (e.g. Fedosova, 1974; Genin and Boehlert, 1985). This was at first attributed to upwelling, associated with Taylor-column formation, and the enhancement of primary production (Genin and Boehlert, 1985; Tseytlin, 1985; Voronina and Timonin, 1986; Boehlert and Genin, 1987; Dower et al., 1992; Mouriño et al., 2001). Since this time it has been recognised that other physical processes may enhance primary production, the transport of phytoplankton over seamounts or the retention and/or supply of phytoplankton to seamount communities (see White et al., 2007 for review). However, evidence of elevated chlorophyll levels above seamounts has been infrequent and even where such observations have been made, enhanced primary production appears to be transient (e.g. Genin and Boehlert, 1985; Mouriño et al., 2001), with only a few seamounts (most notably the Northwest Georgia Rise; Meredith et al., 2003) showing enhancement of primary production over longer timescales. Other mechanisms of enhancement of zooplankton abundance have been suggested including the trapping of diurnal vertically migrating zooplankton (topographic blockage) or counter upwelling, or counter down-welling, or depth retention (Genin, 2004). In several cases, decreased density of zooplankton, micronekton or nekton have been observed above seamounts, particularly those with relatively shallow summits (e.g. Nellen, 1973; Boehlert and Seki, 1984; Genin et al., 1988; Diekmann and Piatkowski, 2004; De Forest and Drazen, 2009; Drazen et al., 2011). This has been particularly associated with diel vertical migrators (DVM) over relatively shallow features (1000 m depth) where the physical obstruction created by elevated topography is thought to reduce the density of these animals over the flanks and summits of seamounts, particularly at night (e.g. Genin et al., 1988; Diekmann et al., 2006; De Forest and Drazen, 2009).

The micronektonic and nektonic communities can also show striking differences on and off seamounts. Studies have identified populations of euphausiids, sternoptychid and myctophid fishes, and cephalopods that appear to be associated with seamounts but are relatively rare in off-seamount localities (e.g. Boehlert and Seki, 1984; Parin and Prut'ko, 1985). Furthermore, large nektonic predators, such as sharks, tuna, and billfish, as well as other aquatic predators, such as cetaceans and pinnipeds, also appear to aggregate over seamounts (e.g. Parin and Prut'ko, 1985; Haney et al., 1995; Holland and Grubbs, 2007; Litvinov, 2007; Kaschner, 2007; Morato et al., 2008, 2010; Muelbert et al., 2013). Many of these larger pelagic species, as well as seamount-resident bentho-pelgic fishes, such as *Sebastes* sp., are thought to feed on DVM or seamount-associated zooplankton and micronekton (Isaacs and Schwartzlose, 1965; Genin et al., 1988; but see Hirch and Christiansen, 2010). The activities of predators around seamounts may also reduce the densities of prey species above/around sea-mounts, accentuating the effects of physical obstruction of sea-mounts on DVM species (Diekmann et al., 2006).

Understanding the pelagic communities around seamounts along with their biological interactions and responses to the physical environment are key to resolving why seamounts host resident and/or visiting predators. This is important because these predators include both commercially valuable species (e.g. tunas and demersal species such as alfonsino, *Beryx splendens*) and those of conservation priority (e.g. sharks and cetaceans). Furthermore, benthopelagic coupling in the vicinity of seamounts may have wider, as yet unappreciated significance in open ocean ecology. One group that has been identified as probably important in the diet of predators visiting seamounts (and also as predators themselves) are cephalopods (Clarke, 2007). The life history characteristics of these animals mean that they probably have a high resilience to predation and probably aggregate around seamounts for feeding and spawning, or in some cases, by accidental drifting and retention (Boehlert and Seki, 1984; Clarke, 2007). Clarke (2007) also suggested that species that spawn on the seabed may form an important link between benthic and pelagic ecosystems as both spawning adults and egg masses may be important food sources for benthic species.

Nesis (1993) classified the cephalopods observed over sea-mounts into the following 6 main groups:

(I) Bottom- and near-bottom-living species living permanently on seamounts (e.g. sepiolids, loliginid squids and octopuses)

(II) Near-bottom and benthopelagic species that spawn on the seabed but regularly rise (or migrate upward at a specific life history stage) into the water column (e.g. *Heteroteuthis*, *Iridoteuthis*, *Sepiolina*, *Stoloteuthis*)

(III) Nerito-oceanic species that occur over seamounts as para-larvae, juveniles or sub-adults (e.g. Onychoteuthidae, Histioteuthidae)

(IV) Diel vertically migrating species that are advected over seamounts at night and descend to the bottom during the day (if the summits/flanks of the seamount lie above the depth at which they reside in daytime; e.g. Enoploteuthidae, Histioteuthidae, Octopoteuthidae, Chtenopterygyidae).

(V) Non-migrating mainly bathypelagic cephalopods advected over seamounts (e.g. members of the Chiroteuthidae, Mastigoteuthidae, *Vampyroteuthis infernalis*).

(VI) Species that avoid seamounts (e.g. large ommastrephids such as *Sthenoteuthis pteropus*, *S. oualaniensis* and *Ommastrephes bartrami*).

Clarke (2007) modified the scheme of Nesis (1993) by splitting Group I into three subgroups: Group IA comprised coastal and shelf species, Group IB bottom and near-bottom species living permanently on seamounts (e.g. *Scaeurgus* sp.), and Group IC middle and lower bathyal species living on slopes (e.g. *Benthoctopus*, *Grimpoteuthis*). Recent observations of cephalopod communities associated with seamounts have identified a predominance of oceanic species with the most important ecological groups being DVM species (Nesis Group IV; e.g. *Pyroteuthis* spp., *Abraliopsis* spp., *Selenoteuthis scintillans*, and *Chtenopteryx sicula*; Diekmann and Piatkowski, 2004; Diekmann et al., 2006). However, groups more closely associated with seamounts (e.g. *Scaeurgus unicirrhus* corresponding to Nesis Group I or Clarke Group IB) are also observed, as well as species that are thought to spawn on or close to the seabed (e.g. *Stigmatoteuthis hoylei* and other *Histioteuthis* spp., corresponding to Nesis Groups III and IV; Bower et al., 1999). Other squid are typical epipelagic, mesopelagic or bathypelagic non-DVM species and in some cases little difference hasbeen observed in the cephalopod fauna on and off seamounts (e.g. Haimovici et al., 2002).

Herein, the abundance and species richness of cephalopods both on and off seamounts of the Southwest Indian Ridge, and a single seamount on the Madagascar Ridge, are investigated. The cephalopod fauna of seamounts of the tropical Indian Ocean was previously studied during a joint cruise of two research vessels (RV *Akademik Kurchatov* and RV *Rift*) in March–May 1982. Both vessels used Isaacs-Kidd midwater trawls, doing oblique hauls from 600 m to surface, and horizontal hauls in the stratum of 1000 m (Nesis, 1986). The region around the Southwest Indian Ocean Ridge is relatively poorly known; that of the Madagascar Ridge, including Walter's Shoals, was investigated by RV *Vityaz* in December 1988 using six different trawls (Nesis, 1994). In general, all deep-sea ecosystems of the Indian Ocean apart from the Arabian Sea are also largely unknown, with seamounts being a particular gap in knowledge within this region (Banse, 1994; Demopoulos et al., 2003; Ingole and Koslow, 2005).

## 2. Material and methods

### 2.1. Sample collection

Cephalopods were collected using a pelagic fish trawl (a Norwegian “Åkra trawl”, cod-end mesh size 4 mm) at 8 stations along the Southwest Indian Ocean Ridge (SWIOR) onboard *RV Fridtjof Nansen* on 04.11.09–13.12.09 (Fig. 1). A total of 40 depth-targeted hauls were conducted on five seamounts along the ridge, a single seamount of Walter's Shoal, and on two “off-seamount” sites (station 2 on the abyssal plains between the Reunion and Atlantis seamounts, and station 7 in the sub-Antarctic convergence; Rogers et al., 2013). At each station a total of three day-time hauls (from 400–600 m to 720–1100 m) and three night-time replicates was carried out. Thus the fishing gear was sampling: (1) adults and subadults of small-bodied species, such as Enoploteuthidae, Pyroteuthidae and pelagic Sepiolida; (2) planktonic cephalopods at any ontogenetic stage, including those where mature animals generally occur deeper than 1000 m; and (3) para-larval and juvenile stages as well as smaller immature animals of large nektonic squids (Ommastrephidae, Onychoteuthidae). Some large adults of nektonic squids (*Onykia ingens*, *Todarodes filippovae*) were also captured occasionally. Thus all taxa of cephalopods occurring at seamounts might be collected by this gear, albeit at varying ontogenetic stages, except bottom-dwelling incirrate Octopoda. For descriptive characterisation of cephalopod fauna, the records were conditionally split into “juveniles” (paralarvae and immature cephalopods) and “adults” (maturing and mature animals).

All samples were stored either in buffered formalin (and then transferred into 50% ethanol) or in 70% ethanol. Several large squids (*T. filippovae*, *O. ingens*) were frozen. In most cases, a small sample of tissue was also taken and preserved in 95% ethanol for DNA studies. This tissue was usually excised from the tip of a tentacle. Cephalopods were identified to the lowest possible taxonomic level, counted and measured at a subsequent taxonomic workshop held at the South African Institute for Aquatic Sciences (SAIAB), Grahamstown, South Africa.

## 2.2. Statistical analyses

A range of statistic techniques have been used to identify cephalopod communities existing within the studied area and to compare their diversity.

Multivariate analyses were employed to examine the differences in cephalopod community structure between the stations and to reveal areas with similar cephalopod assemblages. The abundance data (number per station) were transformed as ln ($Y$+1) to reduce the influence of numerically abundant or dominant species. Cluster Analysis for Jaccard similarity (an average taken as agglomeration method), was performed at the individual species level. Principal Component Analysis (PCA) and Correspondence Analysis were performed on station-specific cephalopod abundance at the family level. Only numerically dominant families (contributing 40.5% to the overall numbers) were included, data not transformed (see: Diekmann et al., 2006). Neither of these two methods nor redundancy analysis and canonical correspondence analysis were applied because of the large number of zeros in the primary data (“zero truncation” problem, which is very common in studies of faunistic diversity; Zuur et al., 2007). A more appropriate measure of association for these data is a measure that converts all values to presence–absence, such as the Jaccard index. All estimations were done using Brodgar ver. 2.5.1 (Zuur et al., 2007).

The Shannon index (H’) (also known as either Shannon–Wiener or Shannon–Weaver index), which is commonly used to characterise species diversity in a community, was calculated as follows (see Shannon, Weaver, 1949; Diekmann et al., 2006):

$$H' = -\sum_{i=1}^{s} \frac{Ni}{N} \ln \frac{Ni}{N}$$

where *Ni* is the number of individuals of the *i*th species in the sample, *N* is the total number of identified cephalopods, and *S* is the number of species. This index was used to compare biodiversity between identified cephalopod communities.

## Results

More than 68 cephalopod species belonging to 26 families (of about 350 known species of 43 oceanic cephalopod families; Nesis, 2003) were discovered in catches. Not every specimen was identified to a species level partially because some of them were damaged, partially because of uncertainty in taxonomy of some families (Table 1). Among them ~60 were oceanic oegopsid squids, which is about 20% of the known global diversity of Teuthida (~25% of the known global diversity of oceanic squids). Most of the cephalopods encountered (69.1%) were mesopelagic with extension of the species ranges into epi- and bathypelagial, and 13.2% were bathyal slope dwellers (Table 2). Species with circumglobal distribution (at least in the Southern Hemisphere) represented 75.0%, and the bulk of cephalopods were either inhabitants of tropical and/or subtropical waters (70.6%) or mostly subtropical–notalian species (19.1%). Almost all species, if known, were pelagic spawners, including some that brood in the epipe-lagic (*Ocythoe tuberculata*, *Tremoctopus violaceus*) or meso-bathypelagic (*Gonatus antarcticus*, *Japetella diaphana*, *Bolitaena microtyla*). Only two of the encountered species (those of the order Sepiolida) are reported to lay eggs on the bottom.

Cluster analysis for Jaccard similarity (average as agglomeration method) (Fig. 2) revealed that stations could be combined into several distinctive groups differing by species composition and relative abundance in the total catch. These data are also con-firmed by results of PCA and CA with segregation at the family level (Fig. 3). The differences observed between stations 5 and 6 on one hand and Station 9 on another hand were relatively small (Figs. 2 and 3) but still statistically significant ($\chi^2$ 175.1, df 65; P<0.0001) due to the different predominating sepiolid species.

The following distinctive cephalopod faunas were found in the studied area:

### 3.1. Station 2 (tropical front area, periphery of the southern central subzone of the tropical zone)

Only seven species were recorded there, all of them either circumglobal or Indo-Pacific tropical–subtropical species apart from *Sthenoteuthis oualaniensis*, which is a purely tropical squid. Most of the catch was represented by the micronektonic enoploteuthid squid *Abraliopsis hoylei* (79.7% of specimens). Mesopelagic planktonic squids of the families Cranchiidae and Histioteuthidae were also encountered (7.2% and 4.3% respectively).

### 3.2. Stations 4 and 10 (between the tropical front and the northern extent of the subtropical convergence—south subtropical zone)

A total of 31 cephalopod species were identified in this zone, 21to species level. Tropical–subtropical species represented 48.3%of the total diversity, the rest being either purely subtropical species (10.3%) or wide-ranging tropical to temperate species (41.4%). A predominating micronektonic squid (37.2% of specimens) was *Pyroteuthis margaritifera*, followed by another pyroteuthid squid, *Pterygioteuthis gemmata* (16.2%). Nektonic juvenile epipelagic onychoteuthids represented 10.0% of specimens, and mesopelagic planktonic squids of the families Histioteuthidae and Cranchiidae were also common: 5.0 and 5.9% respectively.

### 3.3. Stations 5, 6 and 9 (subtropical Convergence–southern peripheral ecotone)

This was the zone of maximum cephalopod diversity—48 identified cephalopods, including 44 to the species level. Tropical–subtropical species still were the most diverse (63.6%), with tropical to notalian species representing a further 31.8%, and the rest being notalian. Most of them had circumglobal distribution (81.8%). Species predominating by numbers were *Pyroteuthis margaritifera* (20.1%) and *Pterygioteuthis gemmata* (10.4%), as was observed in more northerly waters of the South Subtropical Zone. However, the two benthic egg-laying species become important in this ecotone; they occurred together but with one predominating at any given location. *Heteroteuthis dagamensis* was abundant in catches at St. 5 and 6 (10.1%), whereas *Stoloteuthis* cf. *leucoptera* predominated in catches at St. 9 (21.3%). Onychoteuthids represented 12.1% of all captured squids in this zone, and histioteuthids (9.8%) and cranchiids (7.5%) were also important.

3.4. Stations 7 and 8 (subantarctic front) A total of 19 species were identified, 18 of them to the species level. About half of these (55.6%) were subtropical–temperate, some also occurring in the tropics. The rest were equally divided between wide tropical–subtropical and notalian–Antarctic species. Squids of the enoploteuthid group of families (Enoploteuthidae, Pyroteuthidae, Ancistrocheiridae) were not encountered in samples from this zone. All identified species were meso-bathypelagic (with juveniles often encountered in surface layers), a total of 88.9% with circumglobal distribution. About one third of them were known to live in close association with the bottom (*Spirula spirula*, *Stoloteuthis* cf. *leucoptera*, *Taningia danae*, *Lycoteuthis lorigera*, *Psychroteuthis glacialis*, *Onykia ingens*) and their presence resulted in twice as many species being collected at St. 8 as at “off-seamount” St. 7 (Table 1). Planktonic cranchiids and nektonic juvenile *Gonatus antarcticus* were the most abundant cephalopods (28.5 and 21.4% respectively), with onychoteuthid juveniles were also remaining important (14.3%).

Because of the gear selectivity, most of the cephalopods encountered were represented either by juveniles or species that remain small at maturity (Fig. 4). Analyses of cephalopod communities at the family level revealed that micronektonic enoploteuthid squids were associated with tropical waters, and pyroteuthids with the subtropics, while similar-sized paralarval cranchiids, gonatids, and to some extent onychoteuthids were associated with cold temperate waters (Figs. 3 and 5). Deep-sea spawning histioteuthids occurred in low numbers in every habitat. Because of such structured changes in the families' predominance across the different habitats, catches in the tropical waters of St. 2 were included mostly small-bodied adult cephalopods. In the subtropical waters of St. 4–6 and 9–10, adults of small-sized species either predominated or were occurred in similar numbers as juveniles of the entire cephalopod fauna. With the disappearance of tropical micronektonic squids near the Subantarctic front (St. 7), the cephalopod community was represented almost exclusively by juveniles of species reproducing in deep seas (Fig. 5).

## Discussion

The Norwegian 'Åkra trawl', cod-end mesh size 4 mm, used in this study was an effective means of sampling pelagic cephalopods—at least juveniles of large species and adults of small-sized squids. This is supported both by frequent collection of common species, and by several independent captures of species/genera that are distributed worldwide in subtropical or temperate waters bure rarely encountered: *Vampyroteuthis infernalis*, *Discoteuthis laciniosa*, *Pholidoteuthis massyae*, and *Asperoteuthis* sp., as well as two species that may prove new to science, *Chiroteuthis* cf. *mega* and *Enoploteuthis* cf. *semilineata*. Since the gear sampled ontogenetic stages ranging from small paralarvae to mature small-bodied squids of ca. 100 mm mantle length, species availability was likely not impacted by spawning seasonality. Most tropical and subtropical squids spawn year-round (although with some seasonal peaks; Laptikhovsky, 2002), further supporting the likely availability for collection of all species normally resident in these waters.

Because steep slopes of seamounts represent a contact zone between seafloor and different strata of the pelagic realm from epi- to bathypelagial, the so-called "mesopelagic boundary region" provides a variety of habitats for species with different life habits, temperature tolerance and vertical distribution and migrations (Young, 1995). The high productivity associated with underwater mountains and ridges supports this plethora of life.

As has been observed at other seamounts and underwater ridges, almost all cephalopod taxa encountered were represented either by juveniles or by small-bodied species (Clarke, 2007). Most of the study area was dominated by squid species reproducing in epipelagic layers, primarily from the families Enoploteuthidae and Pyroteuthidae. Species reproducing in meso-bathypelagial whose juveniles ascend to surface water (Cranchiidae, Histioteuthidae and some others) became gradually more and more important with southward shift from Tropical Zone to the Southern Peripheral Ecotone. In the latter region they were joined by near-bottom dwellers of order Sepiolida, and the epipelagic style of reproduction disappears completely at the Subpolar Front, although early juveniles of the Cranchiidae and Gonatidae, which hatch in deep seas, are frequently encountered in the epipelagic (Fig. 2).

The cephalopod fauna reported herein from the Southwest Indian Ocean Ridge and the Madagascar Ridge represents and outstanding example of cephalopod species diversity. This hotspot between 27°S and 42°S harbours at least 68 oceanic cephalopod species that were found just in one short research cruise. Previous investigations of this area (28–35°S; Nesis, 1994) reported 52 cephalopod species (including bottom-dwelling octopods), including nine species (Table 3) that were not caught in this cruise, which brings total number of cephalopod species encountered in this region to 77.

A few species were encountered in this area for the first time: *Stoloteuthis leucoptera*, the nearest known captures of which was in near southern Namibia, Kerguelen and at the Prince Edward Islands (Laptikhovsky, 1990; Villanueva and Sánchez, 1993; Reid and Jereb, 2005); *Enoploteuthis* cf. *semilineata*, very similar in morphology to specimens from central South Pacific waters (Alexeyev, 1994) but possibly an undescribed new species; *Onychoteuthis compacta*, previously known from the tropical and subtropical South Atlantic and South Pacific oceans, but not from the Indian Ocean; and a specimen of a squid genus *Chiroteuthis* that was very similar to Atlantic–Pacific *C.mega*, but with the funnel-locking apparatus of a slightly different shape and some differences in arm sucker dentition. This specimen could represent either a new species, or a local morph inhabiting the Indian Ocean, where *C.mega* has not previously been recorded. Roper and Young

(2013) reported that the genus *Chiroteuthis* might be divided into three groups, within each of which "exists considerable unexplained variation. Our knowledge of speciation in this group is minimal. Future detailed evaluation of the variation could indicate that some of the species recognised above will be synonymized (e. g., all forms in the *C. joubini* group could represent a single, highly variable species) or that additional new species will be recognised within the forms now known. We caution anyone against naming species in this genus until a better understanding of the variability is known". The *C.* cf. *mega* specimen from this study is deposited in the Natural History Museum of London, registration number 20130112. Although none of the species encountered herein could unambiguously be considered endemic to the SWIO, endemism is still a possibility for one or both of the *C.* cf. *mega* and *Enoploteuthis* cf. *semilineata*.

The cephalopod diversity reported from seamounts herein comprises about 8–9% of the total known cephalopod taxa worldwide (ca. 845 species—Hoving et al. 2014), a proportion about nearly twice the fish fauna to date consists of 798 species, or about 5% of the total number of known marine fishes; Morato and Clarke, 2007). The cephalopod diversity over SWIO is higher than the 71 or 72 oceanic species historically recorded from the Pacific shores of South America over more than twice the latitudinal range ($18^{o}$S to $56^{o}$S; Rocha, 1997; Ibanez et al., 2009). The cephalopod fauna of North Atlantic seamounts between $22^{o}$N and $44^{o}$N consists of the same number of families (26), but with just 49 species, or 6% of the world's known cephalopod diversity (Diekmann et al., 2002). Investigation of seamounts in just the tropical Indian Ocean (Error, Equator, Fred and Farquhar, 101N–111S) also encountered lower diversity: 50 cephalopod species from 23 families (Nesis, 1986).

Such a hotspot of biological diversity on the Southwest Indian Ocean Ridge could be explained by the fact that this relatively small area includes a wide range of zoogeographic features: part of the Southern Central subzone of the Tropical Zone, the South Subtropical Zone, the Southern Peripheral Ecotone (the zone of the Southern Subtropical Convergence) and part of the Notalian zone (Nesis, 2003). This area generally belongs to so-called the West Wind Drift Islands Province (Collette and Parin 1991), and its fish and cephalopod fauna includes representatives of pan-tropical, south-central and southern peripheral species, with some rare notalian species (Nesis, 1994).

The low diversity encountered around Stations 2 and 7 (7 or 8 species vs.14–35 species in other stations) could be explained by their “off-seamount” position. Sea floor and the habitats they provide were herein observed to increase pelagic cephalopod diversity about threefold, and seem to have a proportionally greater influence on cephalopod fauna than fish fauna, as discussed above. These increased diversities of cephalopods around isolated seamounts, oceanic ridges and small islands are very important. Cephalopods are sometimes the most important prey items of large predators aggregating over these features (Kaschner, 2007; Clarke, 2007; Morato et al., 2008), such as pelagic sharks, particularly blue shark (Vaske et al., 2009a, b; Markaida, Sosa-Nishizaki, 2010); swordfish and some scombroids, like big-eye tuna (Potier et al., 2007; Vaske et al., 2012); and marine mammals including sperm whales, pilot whales, elephant seals, (Clarke, 1996), and particularly beaked whales that feed primarily on deep-water squids using a unique feeding mechanism, suction feeding (Dalebout et al., 2008). Large marine predators of continental shelf upper slope waters, whose distributions do not appear correlated with seamounts and similar features, seem to be less dependent on cephalopod prey because of fish predominance in these habitats, further meta-analysis of existing literature in this area might provide additional insight.

Most of the species reported herein were characterised by circumglobal distribution in the Southern Hemisphere, and no endemic species were unambiguously found, although several taxa could also only be provisionally attributed to known species. This contrasts with the fact that the highest regional number of endemic cephalopods to date was reported nearby, in the Indian–West Pacific Tropical Region, including West Indian Ocean (Nesis, 2003). The high proportion of cosmopolitan species encountered in this study is likely due to reproductive strategies that include pelagic spawning and wide dispersal of early life stages across the southern parts of Atlantic, Indian and Pacific Oceans. These findings agree with earlier observations that many of the large deep-sea taxa frequently encountered on seamounts appear broadly distributed across the deep sea floor between highly patched environments (McClain and Hardy, 2010), and that both pelagic fish and plankton assemblages of seamounts are generally not strongly differentiated from nearby pelagic communities (Diekmann et al., 2006; Stocks and Hart, 2007). However, despite the similarity in composition between the seamount and non-seamount communities of adjacent continental margins, seamount communities may be structured differently and potentially serve as sources of larvae for suboptimal, non-seamount habitats (McClain et al., 2009).

Oceanographic retention of passive drifting early stages of invertebrates around seamounts is probably a minor factor com-pared to other processes structuring seamount communities (Brewin et al., 2009; Clark et al., 2010). Faunal communities on seamounts may be populated from a broad regional species pool, causing considerable variation among individual seamounts (Tracey et al., 2012). This phenomenon, combined with closely situated different faunistic provinces within the studied area, may have produced the surprising combination of high biological diversity and apparent absence of endemism observed herein.

## Acknowledgements

This study and data collection were undertaken as part of a research cruise on seamounts of the Southwest Indian Ocean Ridge jointly organised by the International Union for Conservation of Nature (IUCN), the Agulhas and Somali Current Large Marine Ecosystems Project (ASCLME), the UN Food and Agriculture Organisation-led EAF-Nansen Project, the Norwegian Institute of Marine Research (IMR), the African Coelacanth Ecosystem Programme (ACEP), the Zoological Society of London (ZSL) and the Marine Ecology Laboratory of Reunion University (ECOMAR). It was made possible with the funding from the Global Environment Facility through the United Nations Development Programme, the Norwegian Agency for Development Cooperation, and the National Research Foundation of South Africa. More details can be found at http://www.asclme.org, http://www.iucn.org/marine and http:// www.EAF-Nansen.org. The authors sincerely thank Dr. Paul Brewin and two anonymous reviewers for their valuable comments during the manuscript's preparation.

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**Table 1 Cephalopod species distribution, abundance (number caught) and diversity by station (Cl – Climate, Ra – Range, Ec. – Ecology)**

| **Taxon** | **St. 2** | **St. 4** | **St. 5** | **St. 6** | **St. 7** | **St. 8** | **St. 9** | **St. 10** | **Cl.** | **Ra.** | **Ec.** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Number of species** | **7** | **24** | **35** | **34** | **8** | **14** | **32** | **21** | | | |
| **Shannon - Wiener index** | **0.81** | **1.91** | **2.51** | **2.73** | **1.61** | **2.24** | **2.68** | **2.28** | | | |
| **Spirulida** | | | | | | | | | | | |
| **Spirulidae** | | | | | | | | | | | |
| *Spirula spirula* | | | 4 | 3 | | 1 | 1 | | Tr St | IWP | MBt |
| **Sepiolida** | | | | | | | | | | | |
| **Sepiolidae** | | | | | | | | | | | |
| *Heteroteuthis dagamensis* | | | 49 | 15 | | | 6 | 12 | St T | C? | MB |
| *Stoloteuthis leucoptera* | | | 8 | | | 5 | 33 | | St T | AI | Bt |
| Sepiolidae sp. indet. | | | | | | 1 | | | | | |
| **Teuthida: Oegopsida** | | | | | | | | | | | |
| **Enoploteuthidae** | | | | | | | | | | | |
| *Abralia sp. cf. andamanica* | | | 1 | | | | | | | | |
| *Abraliopsis gilchristi* | | 1 | 5 | 19 | | | 2 | | St | CS | EM |
| *Abraliopsis hoylei* | 55 | 23 | 37 | 4 | | | | 11 | Tr St | IWP | EM |
| *Abraliopsis sp* | | 22 | 1 | 2 | | | | 2 | | | |
| *Enoploteuthis cf semilineata* | | 1 | | | | | | | St | C? | EM |
| Enoploteuthidae sp. indet. | | | 2 | | | | | | | | |
| **Pyroteuthidae** | | | | | | | | | | | |
| *Pterygioteuthis gemmata* | | 24 | 38 | 31 | | | 13 | 31 | St | C | EM |
| *Pterygioteuthis giardi* | | | 2 | 4 | | | 8 | | Tr St | C | EM |
| *Pterygioteuthis sp* | | 2 | | | | | | | | | |
| *Pyroteuthis margaritifera* | 3 | 101 | 86 | 49 | | | 24 | 25 | Tr St | C | EM |
| **Ancystrocheiridae** | | | | | | | | | | | |
| *Ancistrocheirus lesuerii* | | 2 | 1 | 1 | | | | 2 | Tr St | C | MBt |
| **Histioteuthidae** | | | | | | | | | | | |
| *Histioteuthis atlantica* | | 5 | 14 | 25 | | 2 | 11 | 1 | St T | CS | MB |
| *Histioteuthis bonellii* | | 3 | 7 | 2 | | | 1 | | Tr St T | C | MB |
| *Histioteuthis corona* | | 2 | 4 | 1 | | | | | Tr St | C | MB |
| *Histioteuthis eltaninae* | | | | | 2 | | | | St T | C | MB |
| *Histioteuthis macrochista* | | | 2 | | | 4 | | | St | CS | MB |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Histioteuthis meleagroteuthis* | 2 | | | | 2 | | | | Tr St | C | MB |
| *Histioteuthis miranda* | | | 1 | | | | 1 | 2 | Tr St | C? | MB |
| *Histioteuthis pacifica* | | 4 | 3 | 3 | | | 3 | | Tr St | C | MB |
| *Stgmatoteuthis hoylei* | | 3 | 2 | 4 | | | | | Tr St | IP | MB |
| Histioteuthidae unident | 1 | 1 | 23 | 2 | | | 2 | | | | |
| **Lycoteuthidae** | | | | | | | | | | | |
| *Lycoteuthis lorigera* | | | 2 | 2 | 1 | 1 | 1 | | St T | C | MBt |
| **Octopoteuthidae** | | | | | | | | | | | |
| *Octopoteuthis rugosa* | | | 1 | 1 | | | 1 | | Tr St | IWP | MB |
| *Taningia danae* | | | | | | 2 | | | Tr St T | C | MBt |
| Octopoteuthidae sp. indet. | | | | | | | | 1 | | | |
| **Onychoteuthidae** | | | | | | | | | | | |
| *Onychoteuthis bergii* | | | | 1 | | | | | Tr St | AI | EM |
| *Onychoteuthis compacta* | | | 4 | 4 | | | 4 | | Tr St | C? | EM |
| *Onychoteuthis sp* | | 13 | 3 | 29 | 1 | | 7 | 6 | | | |
| *Notonykia sp* | | 1 | 18 | 8 | | | 5 | | Tr St | C | E |
| *N.africanae* | | | 7 | | | | | | | | E St CS |
| *Onykia ingens* | | | | 1 | 2 | | | | T | CS | EMBt |
| *Onykia sp* | | | | 4 | 3 | 2 | 3 | 1 | | | |
| *Callimachus cf. rancureli* | | 3 | 8 | 10 | | | 4 | 4 | Tr St T | CS? | EMBt? |
| Onychoteuthidae sp. indet. | | 2 | | 9 | 5 | 1 | 1 | | | | |
| **Gonatidae** | | | | | | | | | | | |
| *Gonatus antarcticus* | | | | | 9 | 12 | 1 | | T Ant | CS | EMB |
| **Chtenopterygidae** | | | | | | | | | | | |
| *Chtenopteryx sicula* | | 5 | 29 | 28 | | | 6 | 9 | Tr St | C | EM |
| **Bathyteuthidae** | | | | | | | | | | | |
| *Bathyteuthis abyssicola* | | | | | 2 | | | | St T P | C | MB |
| **Psychroteuthidae** | | | | | | | | | | | |
| *Psychroteuthis sp* | | | | | | 2 | | | T Ant | CS | MBt |
| **Neoteuthidae** | | | | | | | | | | | |
| *Neoteuthis thielei* | | 3 | | | | | | | Tr St T | C | MB |
| **Brachoteuthidae** | | | | | | | | | | | |
| *Brachioteuthis picta* | | | 1 | 2 | | | | 3 | Tr St | C | EMB |
| *Brachioteuthis riisei* | | | 1 | 1 | | | | | St T | C | EMB |
| **Ommastrephidae** | | | | | | | | | | | |
| *Ornithoteuthis volatilis* | | | | | | | | 2 | Tr St | IWP | E |
| *Sthenoteuthis oulaniensis* | 3 | | | | | | | | Tr | IP | EM |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Todarodes filippovae* | | 2 | 2 | 1 | | | | | St T | CS | EMBt |
| *Eucleoteuthis luminosa* | | | | | | 1 | | | St | C | E |
| **Architeuthidae ?** | | | | 1 | | | | | | | |
| **Lepidoteuthidae** | | | | | | | | | | | |
| *Pholidoteuthis massyae* | | 1 | | | | 1 | | | St T | C | Bt |
| **Cycloteuthidae** | | | | | | | | | | | |
| *Discoteuthis laciniosa* | | | 1 | | | | | | Tr St | C | M |
| **Chiroteuthidae** | | | | | | | | | | | |
| *Chiroteuthis mega* | | | | | | 2 | | | Tr St | C | MB |
| *Chiroteuthis sp* | | | 1 | 1 | | 3 | | | | | |
| *Chiroteuthis sp 2* | | | | 1 | | | | | | | |
| *Asperoteuthis sp* | | 4 | | | | | | 1 | | | MB |
| **Mastigoteuthidae** | | | | | | | | | | | |
| *Mastigoteuthis dentata* | | | | | | | | 1 | Tr St T | IP | B |
| *Mastigoteuthis psychrophila* | | | | | 1 | | | | T Ant | CS | B |
| Mastigoteuthidae sp. indet. | | | 1 | | 1 | | | | | | |
| **Cranchiidae** | | | | | | | | | | | |
| *Bathothauma lyromma* | | | 4 | 2 | | | 1 | | Tr St T | C | MB |
| *Belonella sp* | | | | | | | 1 | | | | MB |
| *Cranchia scabra* | 3 | 5 | | | | | 2 | 3 | Tr St | C | MB |
| *Egea inermis* | | | | | | | 1 | | Tr St | C | EMB |
| *Galiteuthis suhmi* | | | | | | 3 | 1 | 1 | St T | CS | MB |
| *Helicocranchia pfefferi* | | 1 | 6 | 13 | | | 4 | 1 | Tr St T | C | EMB |
| *Helicocranchia sp 2* | | | 3 | 5 | | | 2 | | Tr St T | C | EMB |
| *Leachia cf cyclura* | | 1 | | 2 | | | 3 | 8 | Tr St | IWP | EMB |
| *Liguriella podophtalma* | | | 1 | | | 3 | 4 | | Tr St | C | MB |
| *Liocranchia reinhardti* | 1 | | | | | | | | Tr St | C | EM |
| *Megalocranchia abyssicola* | 1 | | | | | | 1 | | Tr St | IP | MB |
| *Sandalops melancholicus* | | | | 2 | | | 1 | | Tr St | C | M |
| *Teuthowenia pellucida* | | | | | | | 1 | | St T | CS | MB |
| Taoninae sp. indet. | | 11 | 6 | 5 | 12 | 9 | 3 | 1 | Tr St | | |
| Cranchiidae sp. indet. | | 2 | 5 | 3 | | 1 | | 1 | | | |
| Oegopsida sp. indet. | | | 2 | | 1 | | 3 | 2 | | | |
| **Vampyromorpha** | | | | | | | | | | | |
| **Vampyroteuthidae** | | | | | | | | | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Vampyroteuthsi infernalis* | | | | | | | 1 | Tr St | C | B |
| **Octopoda** | | | | | | | | | | |
| **Bolitaenidae** | | | | | | | | | | |
| *Japetella diaphana* | 5 | 1 | | | | | 3 | Tr St T | C | MB |
| *Bolitaena microtyla* | | | 1 | | | | | Tr St | C | MB |
| **Amphitretidae** | | | | | | | | | | |
| *Amphitretus pelagicus* | | | 1 | | | | | Tr St | C | MB |
| **Tremoctopodidae** | | | | | | | | | | |
| *Tremoctopus violaceus* | 1 | | | | | | | Tr St | C | E |
| **Ocythoidae** | | | | | | | | | | |
| *Ocythoe tuberculata* | | | | | | 1 | 1 | St | C | E |

Climate: Tr – tropical, St – subtropical, T – temperate,  P – polar (in both hemispheres), Ant – Sub – Antarctic – Antarctic; Range: C – Circumglobal, CS – Circumglobal in the Southern Hemisphere, AI – Atlantic and Inadian Ocean, IP – Indo-Pacific, IWP – Indo- West Pacific; Ecology: E – epipelagial, M- mesopelagial, B- bathypelagial, Bt – bathyal.

Table 2. Occurrence of cephalopods with different species ranges and life styles in the studied area (abbreviations see in Table 1).

| **Climatic zone** | ***N*** | **Species Range** | ***N*** | **Habitat** | ***N*** |
|---|---|---|---|---|---|
| Tr St | 32 | C | 36 | MB | 25 |
| St T | 11 | CS | 10 | EM | 12 |
| Tr St T | 9 | IWP | 5 | EMB | 7 |
| St | 5 | C? | 4 | MBt | 5 |
| T Ant | 3 | IP | 4 | E | 5 |
| T | 1 | AI | 2 | B | 3 |
| St T P | 1 | | | M | 2 |
| Tr | 1 | | | EMBt | 2 |
| | | | | Bt | 2 |
| Not assigned | 4 | | 6 | | 4 |
| Total | 67 | | 67 | | 67 |

Table 3 Cephalopod species discovered around the Walter Ridge during previous research cruises but not in the current one (Nesis, 1994).

| Family | Species |
|---|---|
| Sepiolidae | *Sepiolina sp. cf. nipponensis* |
| Onychoteuthidae | *Onykia robsoni* |
| Ommastrephidae | *Ommastrephes bartrami* |
| Lepidoteuthidae | *Lepidoteuthis grimaldii* |
|  | *Grimalditeuthis bonplandi* |
| Cirroteuthidae | *Grimpoteuthis sp* |
| Octopodidae | *Octopus sp cf vulgaris* |
|  | *Octopus aeguina* |
| Vitreledonidae | *Vitreledonella richardi* |

Figure 1. Position of sampling sites

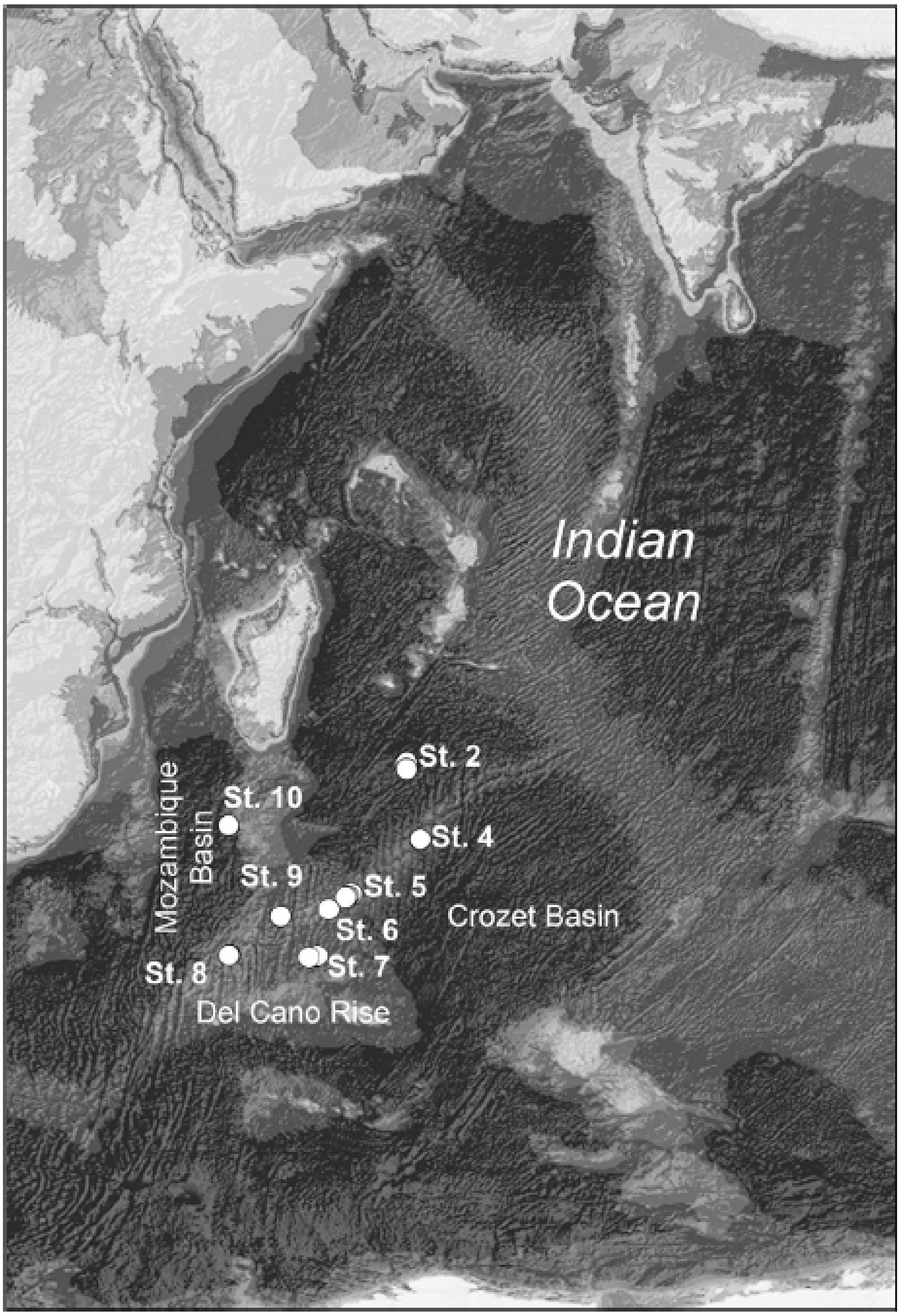

Figure 2 Dendrogram from cluster analysis for Jaccard similarity of faunistic composition.

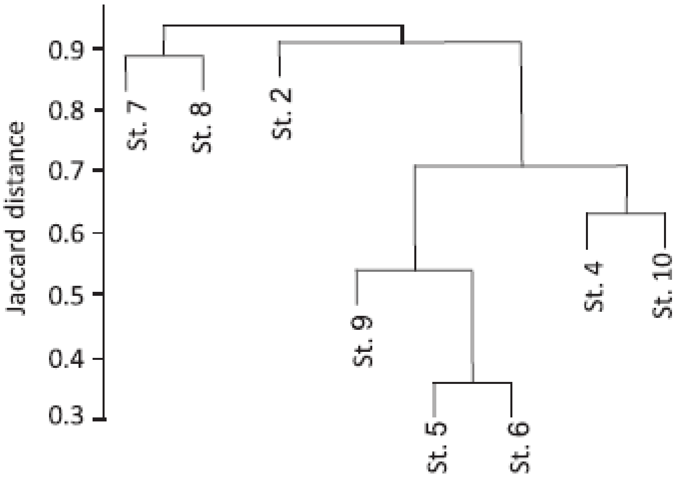

Figure 3. Principal component analysis(A) and correspondence analysis (B) ordination diagrams based on chord distances of vertically resolved cephalopod families' abundance. Only families contributing 40.5% to the overall number of specimens were included. Bra—Brachioteuthidae, Cht—Chtenopterygidae, Cra— Cranchiidae, Eno—Enoploteuthidae, Gon—Gonatidae, His—Histioteuthidae, Lyc— Lycoteuthidae, Omm—Ommastrephidae, Ony—Onychoteuthidae, Pyr—Pyroteuthidae, Sep—Sepiolidae, Spi—Spirulidae.

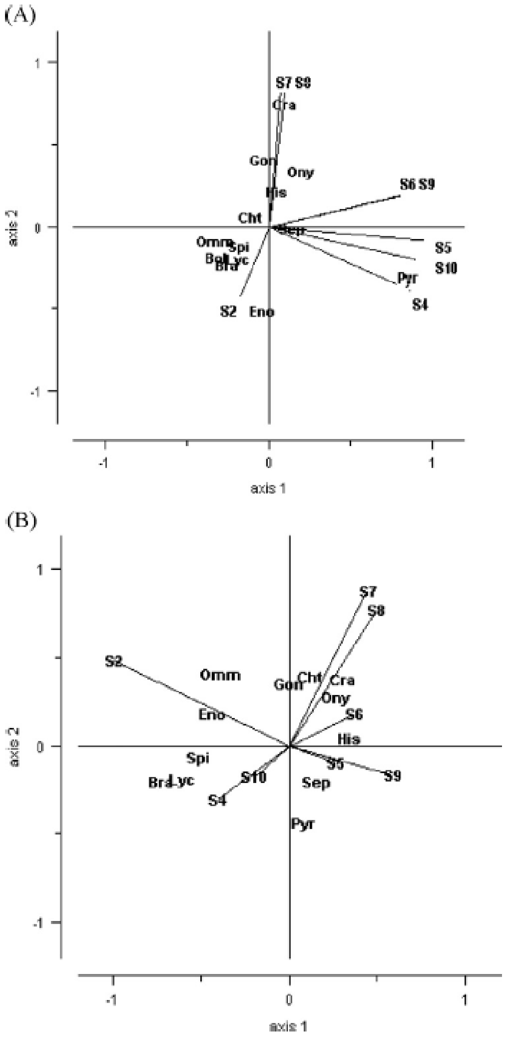

Figure 4. Occurrence of juvenile and adult cephalopods in catches per station

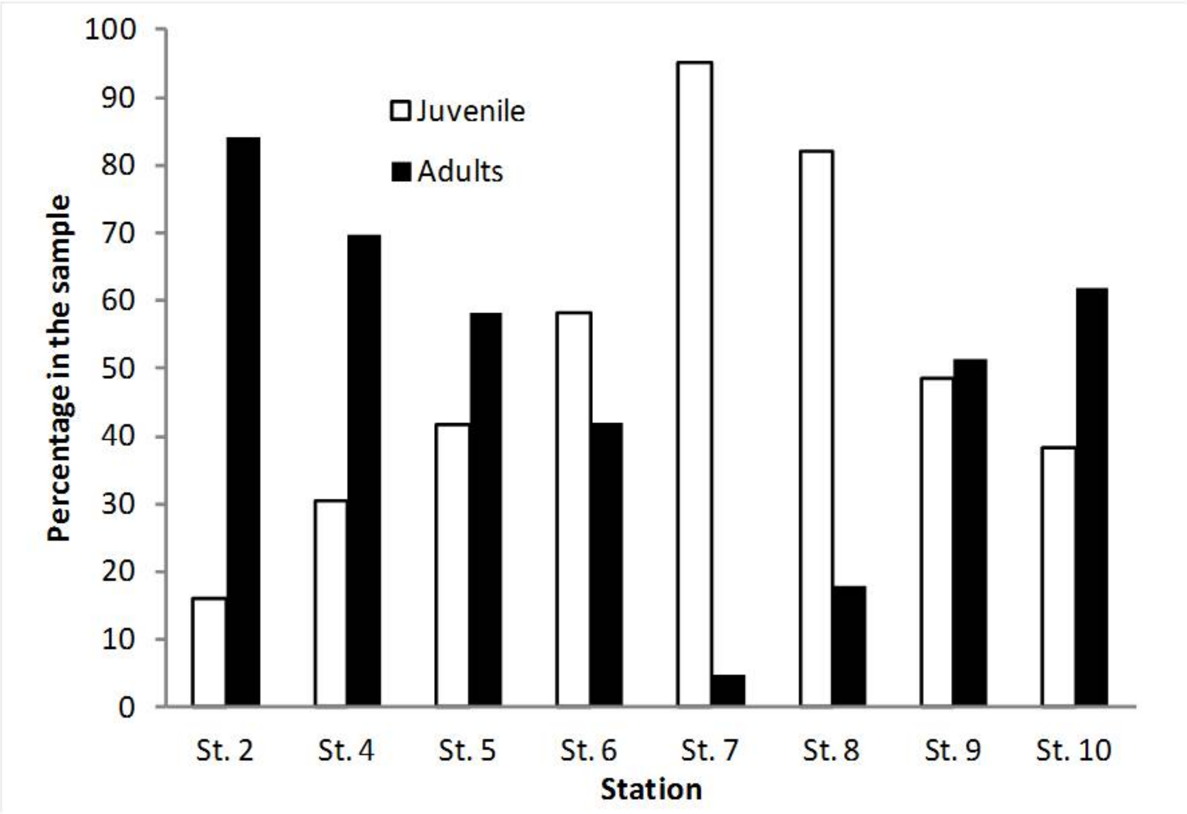

Figure 5. Occurrence of cephalopods belonging to the different ecological groups, *sensu* Nesis (1993).