Deep-Sea Research II ■ (■■■■) ■■■–■■■

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Cephalopods of the Southwest Indian OceanRidge: A hotspot of biological diversity and absence of endemism

V. Laptikhovsky [a,*], P. Boersch-Supan [b,c], K. Bolstad [d], K. Kemp [e], T. Letessier [f], A.D. Rogers [b]

[a] CEFAS, Pakefield Rd., Lowestoft NR33 0HT, U.K.
[b] Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.
[c] The University of St Andrews, Fife KY16 9AJ, U.K.
[d] Institute for Applied Ecology New Zealand (AENZ), Auckland University of Technology, New Zealand
[e] Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, U.K.
[f] The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Perth, Australia

ARTICLE INFO

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 onboard R/V *Fridtjof Nansen* during a research survey on Southwest 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.

1. 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 et al., 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 seabeds 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 1000 m, and a further >130,000 of smaller seamounts with in the elevation range of 400–1000 m) (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

* Corresponding author.

http://dx.doi.org/10.1016/j.dsr2.2015.07.002
0967-0645/

Please cite this article as: Laptikhovsky, V., et al., Cephalopods of the Southwest Indian OceanRidge: A hotspot of biological diversity and absence of endemism. Deep-Sea Res. II (2015), http://dx.doi.org/10.1016/j.dsr2.2015.07.002

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 biomass/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 seamounts (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 downwelling, 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 is 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 seamounts, accentuating the effects of physical obstruction of seamounts 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 seamounts 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 paralarvae, 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 has