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Micronektonic fish species over three seamounts in the southwestern Indian Ocean

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ABSTRACT

Taxonomic composition, abundance and biological features of micronektonic fish were investigated using pelagic trawls conducted near and over the summits of three seamounts located in the western Indian Ocean (La Pérouse, MAD-Ridge and Walters Shoal). Mesopelagic fish from three families accounted for 80% by number of the total catch (5714 specimens, 121 taxa), namely myctophids (59%), gonostomatids (12%) and sternoptychids (9%). Whereas the gonostomatid *Sigmops elongatus* was the most abundant species around La Pérouse seamount, myctophids were the most diverse and dominant group by number in all three studied areas. Most myctophids were high-oceanic species, which included the numerically dominant *Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Diaphus perspicillatus*, *Hygophum hygomii*, and *Lobianchia dofleini*. The few remaining myctophids (*Diaphus suborbitalis* being the most abundant) were pseudoceanic fish, highlighting the association with landmasses. The study adds one myctophid species new to the Indian Ocean (*Diaphus bertelseni*), and a second record in the literature of the recently described sternoptychid *Argyripnus hulleyi*.

1. Introduction

Micronektonic fish are the most abundant fish on Earth and the most abundant vertebrates in the biosphere (Irigoien et al., 2014). They play a key role in biogeochemical cycling including in the export of organic carbon from surface waters to the deep (the 'biological pump'; Bianchi et al., 2013), and as a trophic link between zooplankton and top predators in oceanic waters (Potier et al., 2007; Cherel et al., 2010). From an economic perspective, their large biomass and nutritional quality render these fish among the few marine resources available worldwide that new commercial fisheries could exploit (Catul et al., 2011). Relatively few investigations have targeted organisms living in the oceanic domain, so contrasting with the numerous studies that have focused on coastal and neritic waters. The lack of information on micronekton is especially critical in the Indian Ocean, the less well known of the three major oceans. Moreover, because most recent oceanographic studies have tended to focus on relationships between physical oceanography and micronekton, and on the structure of the trophic web (e.g. Annasawmy et al., 2019, Annasawmy et al., 2020a, Annasawmy et al., 2020b), they do not detail the taxonomic composition of the communities, including that of mesopelagic fish.

Near landmasses, pelagic organisms enter and accumulate in the benthopelagic layer, where they interact with continental, insular and seamount slopes (Porteiro and Sutton, 2007). There, they form mesopelagic boundary communities, which consist of assemblages of open-ocean species together with pseudoceanic taxa. Pseudoceanic fish are members of primarily pelagic families that associate consistently with the benthopelagic layer of the slopes (Porteiro and Sutton, 2007). The presence of aggregations of both oceanic and pseudoceanic species over seamounts lead to a large micronektonic biomass that, in turn, favours the development of diverse benthic communities and attracts significant numbers of top predators, including large carnivorous fish and marine mammals (Pitcher et al., 2007). Consequently, seamounts are now recognized as biological hotspots that need protection and management (Rogers et al., 2017; Rogers, 2018). However, despite the pivotal trophic role of micronekton, most biological studies of seamounts have been on zooplankton or larger, commercially exploited nektonic and benthic fish, with relatively few studies on small pelagic

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fish (Moore et al., 2004; Porteiro and Sutton, 2007; Sutton et al., 2008). For example, a recent investigation of seamount communities focused only on large pelagic shrimps and mysids (Letessier et al., 2017) or cephalopods (Laptikhovsky et al., 2017), and provided no available detailed information on the co-occurring micronektonic fish, whereas they were obviously also collected by the pelagic trawl (Rogers et al., 2017).

Seamount ecosystems of the southwestern Indian Ocean are still poorly known despite decades of fisheries and research (Collette and Parin, 1991; Parin et al., 2008), and basic information on pelagic species presence, biogeography and ecology is still in short supply (Rogers et al., 2017). Within that context, the main goal of this manuscript was to detail the micronektonic fish that were collected over and close to the summits of three shallow seamounts, La Pérouse, MAD-Ridge and Walters Shoal (summit depths at ~60, ~240 and ~18 m below the sea surface, respectively). La Pérouse and Walters Shoal are well-located and named seamounts, but MAD-Ridge refers to an unnamed seamount located south of Madagascar (details in Roberts et al., 2020). Mesopelagic fish caught during three cruises were compared with data collected during the MICROTON cruise (Fig. 1) that was conducted in the open ocean of the western tropical Indian Ocean (Annasawmy et al., 2018). The present work is companion to those devoted to La Pérouse and MAD-Ridge seamounts, which present information on (i) micronekton distribution and assemblages based on acoustic and trawl data (Annasawmy et al., 2019), (ii) micronekton distribution in relation to physical oceanography (Annasawmy et al., 2020b), and (iii) the trophic structure of mesopelagic communities using the stable isotope method (Annasawmy et al., 2020a). Here, we focus on the taxonomic composition and biology of lanternfish (family Myctophidae), because they constitute the most diverse and abundant group of mesopelagic fish worldwide (Gjøsaeter and Kawaguchi, 1980).

2. Material and methods

2.1. Scientific cruises and pelagic trawling

The oceanographic cruises La Pérouse (19°43′S, 54°10′E, 15–30 September 2016, from/to La Réunion Island) and MAD-Ridge (27°28′S, 46°16′E, leg 2, Fort Dauphin, Madagascar to Durban, South Africa, 26 November–14 December 2016) were carried out in the western tropical Indian Ocean on board the RV *Antea* (more details can be found at DOI: 10.17600/16004500 and 10.17600/16004900, respectively). Totals of 10 and 17 trawls were performed during La Pérouse and MAD-Ridge, respectively. Micronekton was sampled with an open 40-m long International Young Gadoid Pelagic Trawl (IYGPT) constructed of 8 cm knotless nylon delta mesh netting at the front tapering to 0.5 cm at the codend. The trawl had a theoretical maximal mouth area of ~96 m^2 that is reduced to a smaller ellipse when deployed. The IYGPT is a non-

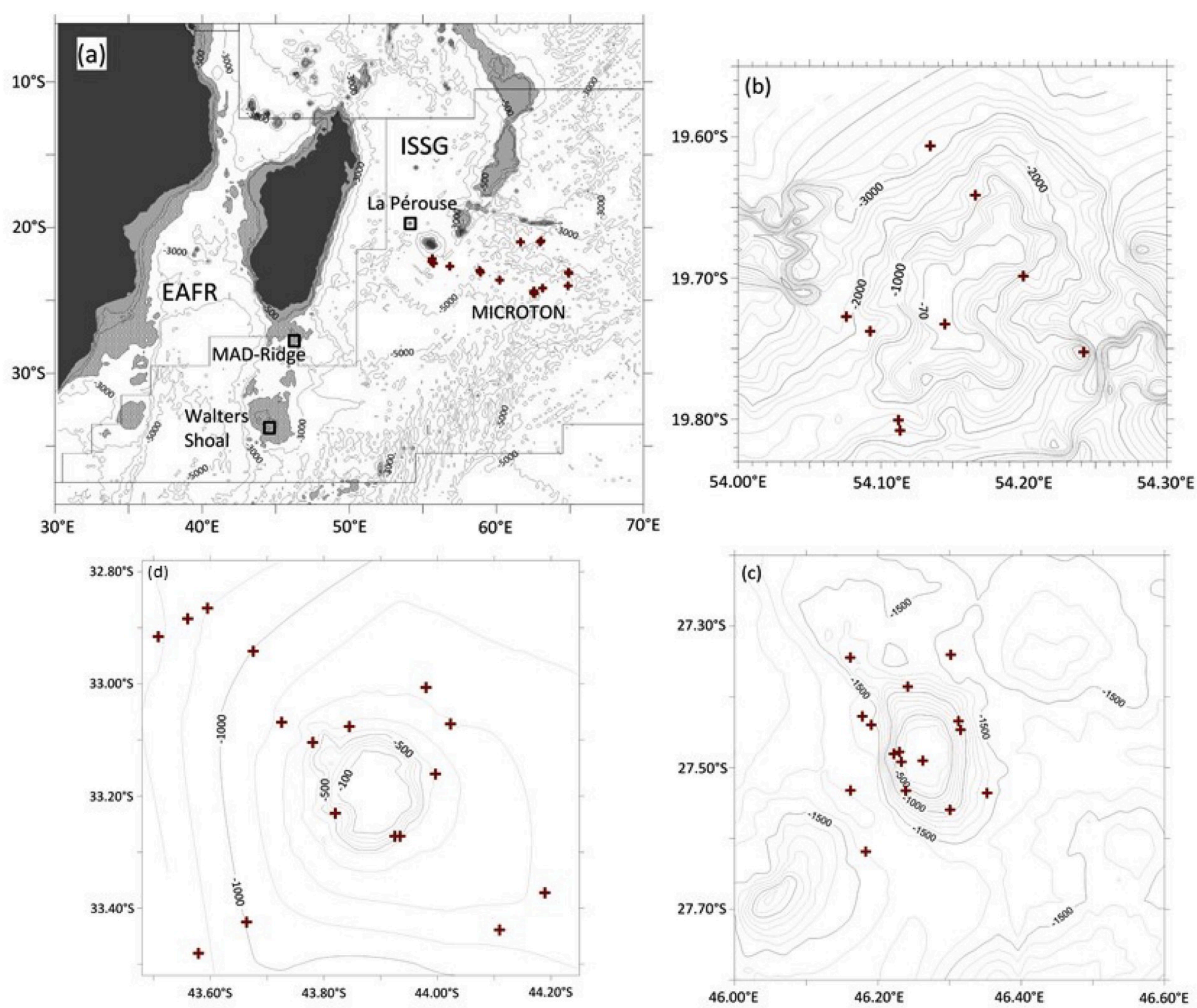

Fig. 1. (a) Map of the western Indian Ocean showing the locations of cruises and pelagic trawls (red crosses) over three seamounts: **(b)** La Pérouse, **(c)** MAD-Ridge and **(d)** Walters Shoal, and of the single open ocean investigation (MICROTON). EAFR (East African Coastal Province) and ISSG (Indian South Subtropical Gyre) refer to Longhurst (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

closing (i.e. permanently open) trawl with the principal disadvantage that it fishes from when it is shot away until it is recovered, not simply across the selected depth. However, its main advantages are its size larger than closing nets and its faster towing speed, allowing it to sample a large volume of water.

The study of the Walters Shoal seamount (33°12′S, 43°50′E, 26 Apr/May 18, 2017, MD 208, DOI: 10.17600/17002700) was conducted from the RV *Marion Dufresne II*. In all, 14 night-time hauls were performed using an Isaacs–Kidd Midwater Trawl (IKMT), because it is not possible to use trawls with doors (e.g. IYGPT) on that ship. The non-closing trawl had a mesh size reducing from 3.5 cm at its mouth to 0.5 cm at the codend and a mouth area of ~26 m^2.

The net was towed at a ship's speed of ~2–3 knots at the targeted depth for 60 min during the La Pérouse and 30 min during the MAD-Ridge and Walters Shoal cruises. Sound scattering layers (SSLs) were sampled, and trawl depth was monitored using a Scanmar depth sensor. Trawling was at night during the Walters Shoal cruise, and by night and day during the La Pérouse and MAD-Ridge cruises (n = 9 and 1, and 12 and 5, respectively). Hauls were categorized according to sampling depths as shallow (≤100 m, no less than 30 m), intermediate (from 100 to 400 m), and deep (>400 m, no more than 550 m).

An earlier cruise, MICROTON, (21°00′–24°30′S, 55°00′–64°50′E, 19 March – April 05, 2010, from/to La Réunion Island) was also conducted in the western tropical Indian Ocean on board the RV *Antea* (Fig. 1), but in the open ocean (Annasawmy et al., 2018). Micronekton on that cruise was sampled using an IYGPT within the same depth range (30–600 m), thus allowing comparison of the mesopelagic fish caught then with those collected during the La Pérouse and MAD-Ridge cruises. The main goal of the study was to compare the micronektonic fish caught either near or at seamounts with those found in oceanic waters.

2.2. Fish identification and data analyses

Micronekton was divided on board into four broad categories: gelatinous organisms, crustaceans, cephalopods (represented mostly by squid species) and fish. Fish collected during the La Pérouse and MAD-Ridge cruises were sorted to species or lowest identifiable taxon and measured before being frozen, but during the Walters Shoal cruise, fish were sorted by broad taxa and immediately frozen. Fish were kept at −20 °C until further analysis at the University of Cape Town in June 2017. There, identifications from the La Pérouse and MAD-Ridge cruises were double-checked, and fish from the Walters Shoal cruise were identified and measured. Identification was based on morphological features according to the available literature (mainly Smith and Heemstra, 1986). Special emphasis was laid on myctophid identification down to species level by combining morphological features and otolith shapes. Identification of several of the myctophids was double-checked by P.A. Hulley from the Iziko–South African Museum (Cape Town). Owing to taxonomic complexity and the lack of good identification keys, many other mesopelagic fish were determined only to genus level. Pelagic juvenile stages of non-mesopelagic fish are not detailed here and were pooled (Tables 1 and 2). Fish standard length (SL) was measured to the nearest 0.1 mm with a digital vernier caliper.

Statistical analyses were carried out using SYSTAT 13. Despite different sampling protocols depending on cruises, equality of proportion tests (large-sample tests) were performed to compare the relative numbers of each fish taxon between the La Pérouse and the MAD-Ridge cruises, with the significance level being set at $p < 0.001$. Values are reported as mean ± SD.

3. Results

Overall, 5714 micronektonic fish were identified and measured during the three cruises. Larvae/postlarvae/small juvenile stages of adult non-mesopelagic species represented 8.3% (472 individuals) of the fish communities, with leptocephali of the order Anguilliformes (n = 261, 4.6%) being the most important. A few larger fish were also caught accidently, including one *Ectreposebastes niger* (163 mm SL, Setarchidae; Fourmanoir, 1970; Paulin, 1982) during the La Pérouse cruise, and six *Cookeolus japonicus* (209–322 mm SL; Starnes, 1988), six *Neobathyclupea malayana* (219–278 mm SL, Bathyclupeidae; Prokofiev, 2014a; Prokofiev et al., 2016) and two *Promethichthys prometheus* (294–437 mm SL, Gempylidae; Nakamura and Parin, 1993) during the MAD-Ridge cruise.

3.1. Mesopelagic fish taxonomy

Overall, 121 fish taxa were identified during the three cruises, with fewer taxa caught during the Walters Shoal (n = 40) than during the La Pérouse (77) and MAD-Ridge (83) cruises. In all, 20 similar taxa were collected during all three cruises (Tables 1 and 2). When compared, fish size of those taxa depended on cruise. Smaller specimens were consistently caught during the Walters Shoal than during the La Pérouse and MAD-Ridge cruises, apparently because the smaller IKMT pelagic trawl was deployed during that cruise. The different nets precludes comprehensive comparison of the fish assemblages collected during the Walters Shoal cruise with those from the two other cruises.

Three families of mesopelagic fish accounted for 79.7% by number of the total catch, myctophids (n = 3387, 59.3%), gonostomatids (661, 11.6%) and sternoptychids (507, 8.9%) (Tables 1 and 2). Myctophids were also the most diverse group (51 taxa), and they dominated by number during the La Pérouse (49.1%), MAD-Ridge (65.4%) and Walters Shoal (68.1%) cruises. Myctophid species accounting for >5% of the catch during a given cruise were *Ceratoscopelus warmingii* (three cruises), *Diaphus suborbitalis* (La Pérouse and MAD-Ridge), *Lobianchia dofleini* (Walters Shoal), and *Hygophum hygomii* and *D. perspicillatus* (MAD-Ridge). Length-frequency distribution showed one mode of large *H. hygomii* and two size modes in *D. perspicillatus* with a predominance of large fish during the MAD-Ridge cruise (Fig. 2). Bimodality was also found in the *C. warmingii* caught, but the larger size-class dominated the La Pérouse cruise and the smaller one the MAD-Ridge cruise (Fig. 3, upper panel). Inter-cruise difference is also found for *D. suborbitalis*, with only one large size-class caught during the MAD-Ridge cruise and two size-classes during the La Pérouse cruise (Fig. 3, lower panel). Interestingly, the two modes were found in two different night hauls that contained larger and smaller fish, with no overlap in size (n = 50 and 29 measured fish, 58.1–81.9 mm and 33.6–52.1 mm SL, respectively).

Gonostomatids ranked second by number. They were more abundant during the La Pérouse cruise (21.1%) than during the MAD-Ridge cruise (6.8%), and no fish of that family were caught during the Walters Shoal cruise. By far the most abundant gonostomatid was *Sigmops elongatus*, which accounted for 20.3% by number of the catch during the La Pérouse cruise. The size of *S. elongatus* ranged widely, from 23.0 to 236 mm SL. Smaller individuals dominated during the MAD-Ridge cruise and larger ones during the La Pérouse cruise (Fig. 4, upper panel).

Sternoptychids ranked third and constituted 7.2, 10.3 and 8.8% by number during the La Pérouse, MAD-Ridge and Walters Shoal cruises, respectively. Most sternoptychids belonged to two species of hatchetfish, *Argyropelecus aculeatus* (5.9 and 6.7% during the La Pérouse and MAD-Ridge cruises, respectively) and *A. hemigymnus* (3.4 and 6.3% during the MAD-Ridge and Walters Shoal cruises, respectively). Length-frequency distribution of *A. aculeatus* showed a bimodal pattern and no inter-cruise differences between the La Pérouse and MAD-ridge cruises (Fig. 4, lower panel). By contrast, specimens of the viperfish *Chauliodus sloani* were smaller during the MAD-Ridge than during the La Pérouse cruise (Table 1).

3.2. Daytime and night-time trawls

During the La Pérouse cruise, the single daylight trawl performed in shallow water over the summit of the seamount only caught four fish, including three leptocephali. The same pattern was found during the MAD-Ridge cruise, with few fish (n = 8, six leptocephali) collected

Table 1
Micronektonic fish taxa identified from pelagic trawls during the La Pérouse and MAD-Ridge cruises on board the RV *Antea* together with their standard length. Equality of proportion tests (large-sample tests) were performed to compare relative numbers between the two cruises. Significant differences ($p < 0.001$) are highlighted in **bold**; na, not applicable.

Family	Species	Numbers						Standard length (mm)			
		La Pérouse		MAD-Ridge		Statistics		La Pérouse		MAD-Ridge	
		(n)	(%)	(n)	(%)	Z	p	(n)	mean ± SD (range)	(n)	mean ± SD (range)
SERRIVOMERIDAE	*Serrivomer beanii*			3	0.11	na	na			2	136–177
NEMICHTHYIDAE	Unidentified	14	0.62	12	0.45	0.82	0.413	13	362 ± 101 (238–614)	11	301 ± 87 (143–446)
ARGENTINIDAE	*Glossanodon* sp. (larvae/juv.)	1	0.04			na	na				
	Unidentified (larvae/juv.)	2	0.09			na	na				
STOMIIDAE	*Stomias boa*	1	0.04			na	na	1	148		
	Stomias longibarbatus	1	0.04	2	0.07	0.44	0.663	1	257	2	127–299
	Unidentified (larvae/juv.)			2	0.07	na	na				
CHAULIODONTIDAE	*Chauliodus sloani*	40	1.76	77	2.87	2.57	0.01	40	120 ± 37 (60.4–200)	75	63.3 ± 41.3 (24.5–213)
ASTRONESTHIDAE	*Astronesthes* sp.	9	0.40	18	0.67	1.31	0.19	9	69.5 ± 29.4 (26.9–117)	18	43.9 ± 22.2 (25.3–128)
IDIACANTHIDAE	*Idiacanthus atlanticus*			3	0.11	na	na			3	93.7 ± 22.0 (73.2–117)
	Idiacanthus fasciola	9	0.40	34	1.27	3.3	0.001	9	166 ± 87 (67.5–276)	31	123 ± 56 (66.4–264)
MALACOSTEIDAE	*Aristostomias* sp.			1	0.04	na	na			1	103
	Malacosteus australis			1	0.04	na	na			1	61.3
	Photostomias sp.	11	0.48	2	0.07	2.81	0.005	11	72.0 ± 18.5 (49.1–106)	2	56.9–60.2
MELANOSTOMIIDAE	*Bathophilus* sp.	4	0.18	12	0.45	1.68	0.093	3	88.7 ± 41.0 (59.4–136)	10	51.2 ± 24.1 (30.9–108)
	Echiostoma barbatum	11	0.48	11	0.41	0.39	0.697	11	45.0 ± 6.1 (34.8–54.0)	11	74.0 ± 8.6 (61.2–92.7)
	Eustomias sp.	15	0.66	13	0.48	0.82	0.412	14	86.0 ± 22.8 (63.0–126)	13	88.0 ± 14.6 (65.8–117)
	Leptostomias sp.	1	0.04			na	na	1	131		
	Melanostomias niger			1	0.04	na	na			1	239
	Melanostomias sp.	18	0.79	6	0.22	2.87	0.004	17	73.0 ± 30.8 (44.9–178)	6	87.9 ± 8.5 (75.5–98.7)
	Photonectes sp.	2	0.09	4	0.15	0.62	0.537	2	123–124	4	56.0 ± 16.7 (40.6–77.5)
	Unidentified	14	0.62	8	0.30	1.68	0.094				
PHOTICHTHYIDAE	*Ichthyococcus ovatus*			1	0.04	na	na			1	31.3
	Photichthys argenteus	2	0.09	4	0.15	0.62	0.537	2	31.5–42.2	4	91.8 ± 28.3 (67.7–129)
	Vinciguerria nimbaria	17	0.75	10	0.37	1.79	0.074	16	35.8 ± 9.7 (23.7–56.5)	10	26.9 ± 3.8 (21.1–32.4)
GONOSTOMATIDAE	*Cyclothone* sp.			52	1.94	na	na			33	28.4 ± 10.1 (13.6–60.7)
	Diplophos rebainsi			4	0.15	na	na			4	86.3 ± 17.7 (60.1–98.3)
	Diplophos taenia	13	0.57	6	0.22	1.98	0.048	13	75.0 ± 23.5 (32.8–130)	6	93.5 ± 51.3 (51.1–176)
	Gonostoma atlanticum	4	0.18	23	0.86	3.25	0.001	4	49.6 ± 6.9 (42.6–59.1)	23	44.7 ± 8.7 (26.4–61.2)
	Sigmops elongatus	461	20.29	89	3.32	**18.94**	**<0.0001**	458	121 ± 37 (23.0–236)	88	64.7 ± 39.2 (29.6–186)
	Margrethia obtusirostra			7	0.26	na	na			7	34.9 ± 6.4 (22.3–42.4)
	Unidentified	1	0.04	1	0.04	0.12	0.907				
STERNOPTYCHIDAE	*Argyropelecus aculeatus*	133	5.85	179	6.68	1.19	0.235	133	34.2 ± 14.5 (13.4–71.4)	177	39.0 ± 15.3 (13.7–80.9)
	Argyropelecus affinis			1	0.04	na	na			1	34.8
	Argyropelecus hemigymnus	15	0.66	92	3.43	**6.69**	**<0.0001**	15	20.6 ± 3.8 (14.3–28.0)	90	20.7 ± 3.5 (12.9–32.4)
	Argyropelecus sladeni	4	0.18			na	na	4	36.9 ± 6.3 (29.7–44.6)		
	Argyripnus hulleyi	4	0.18			na	na	4	74.7 ± 5.0 (70.6–82.0)		
	Sternoptyx diaphana	2	0.09			na	na	2	14.9–22.5		
	Sternoptyx sp.	1	0.04	1	0.04	0.12	0.907				
	Valenciennellus tripunctulatus	2	0.09	4	0.15	0.62	0.537	2	26.1–28.5	4	24.6 ± 6.4 (17.8–31.2)
	Unidentified	2	0.09			na	na				
SCOPELARCHIDAE	*Scopelarchus* sp.	6	0.26			na	na	6	55.3 ± 9.8 (42.6–70.3)		
NOTOSUDIDAE	*Scopelosaurus* sp.			1	0.04	na	na			1	92.4

(*continued on next page*)

Table 1 (*continued*)

Family	Species	Numbers						Standard length (mm)			
		La Pérouse		MAD-Ridge		Statistics		La Pérouse		MAD-Ridge	
		(n)	(%)	(n)	(%)	Z	p	(n)	mean ± SD (range)	(n)	mean ± SD (range)
PARALEPIDIDAE	*Lestidiops* sp.	1	0.04			na	na	1	195		
	Lestidium atlanticum			1	0.04	na	na			1	119
	Lestrolepis japonica	1	0.04			na	na	1	174		
	Unidentified (larvae/juv.)	39	1.72	15	0.56	**3.91**	**<0.0001**	36	61.3 ± 13.0 (40.8–95.3)	15	55.7 ± 29.5 (35.3–140)
EVERMANELLIDAE	*Coccorella atrata*	1	0.04			na	na	1	93.3		
	Evermanella balbo			2	0.07	na	na			2	47.4–64.6
	Evermanella indica	4	0.18			na	na	4	112 ± 8 (101–121)		
	Odontostomops normalops	1	0.04			na	na	1	90.3		
	Unidentified (larvae/juv.)	1	0.04			na	na				
MYCTOPHIDAE	*Benthosema fibulatum*			56	2.09	na	na			56	74.6 ± 7.9 (60.7–88.0)
	Benthosema suborbitale	7	0.31	26	0.97	2.85	0.004	7	29.3 ± 1.9 (26.6–31.5)	25	24.8 ± 3.3 (17.2–29.6)
	Bolinichthys photothorax	14	0.62	8	0.30	1.68	0.094	14	56.7 ± 9.5 (39.6–73.7)	8	43.9 ± 9.4 (30.2–56.7)
	Bolinichthys supralateralis			2	0.07	na	na			2	36.6–36.7
	Ceratoscopelus warmingii	346	15.23	258	9.62	**6.01**	**<0.0001**	346	50.9 ± 11.2 (23.6–68.2)	254	36.5 ± 13.6 (19.6–68.4)
	Diaphus bertelseni	1	0.04			na	na	1	65.9		
	Diaphus brachycephalus	20	0.88	10	0.37	2.29	0.022	20	33.2 ± 3.5 (26.2–38.8)	10	27.8 ± 7.0 (18.2–40.4)
	Diaphus diadematus	14	0.62	22	0.82	0.84	0.399	14	31.5 ± 3.6 (28.4–39.6)	21	31.3 ± 2.9 (23.5–35.9)
	Diaphus effulgens	1	0.04	4	0.15	1.16	0.245	1	34.5	4	79.0 ± 36.8 (28.6–107)
	Diaphus fragilis	1	0.04			na	na	1	35.3		
	Diaphus garmani	10	0.44			na	na	10	48.1 ± 3.8 (42.8–54.5)		
	Diaphus knappi			17	0.63	na	na			17	60.4 ± 18.9 (45.3–130)
	Diaphus lucidus	15	0.66			na	na	15	76.6 ± 4.7 (66.3–82.1)		
	Diaphus metopoclampus			2	0.07	na	na			2	50.1–51.4
	Diaphus mollis	16	0.70	27	1.01	1.15	0.252	16	47.6 ± 11.4 (35.8–79.4)	26	50.1 ± 10.5 (17.1–65.4)
	Diaphus parri			3	0.11	na	na			3	38.4 ± 2.2 (35.9–39.8)
	Diaphus perspicillatus	24	1.06	179	6.68	**9.94**	**<0.0001**	24	49.8 ± 10.5 (35.8–69.1)	178	48.7 ± 8.6 (17.0–63.3)
	Diaphus richardsoni	11	0.48	24	0.90	1.72	0.085	11	40.8 ± 4.2 (32.9–47.6)	24	34.3 ± 9.7 (20.1–53.5)
	Diaphus splendidus	35	1.54	1	0.04	**6.21**	**<0.0001**	35	53.1 ± 10.4 (36.4–80.9)	1	62.6
	Diaphus suborbitalis	346	15.23	586	21.86	**5.95**	**<0.0001**	80	57.3 ± 13.4 (33.6–81.9)	136	69.5 ± 5.4 (50.3–83.9)
	Diaphus sp.	10	0.44	12	0.45	0.04	0.969				
	Hygophum hygomii	5	0.22	345	12.87	**17.31**	**<0.0001**	5	42.5 ± 10.8 (29.6–55.9)	341	50.0 ± 5.9 (26.9–59.5)
	Hygophum proximum	2	0.09	1	0.04	0.72	0.470	2	39.8–43.4	1	39.7
	Lampadena luminosa	2	0.09			na	na	2	25.9–45.7		
	Lampanyctus alatus	26	1.14	53	1.98	2.33	0.020	26	43.5 ± 3.2 (38.3–50.0)	53	36.3 ± 5.4 (21.4–44.4)
	Lampanyctus lepidolychnus			5	0.19	na	na			5	82.5 ± 31.7 (33.4–113)
	Lampanyctus nobilis	30	1.32	2	0.07	**5.45**	**<0.0001**	30	71.5 ± 19.9 (47.5–118)	2	68.3–70.5
	Lampanyctus turneri	1	0.04	1	0.04	0.12	0.907	1	54.5	1	48.6
	Lampanyctus sp.	96	4.23	11	0.41	**9.20**	**<0.0001**				
	Lampichthys procerus	1	0.04			na	na	1	33.7		
	Lobianchia gemellarii	36	1.58	22	0.82	2.49	0.013	35	41.1 ± 3.2 (35.2–50.7)	22	38.2 ± 8.7 (22.6–58.7)
	Myctophum fissunovi	12	0.53	11	0.41	0.61	0.543	12	55.0 ± 8.1 (43.5–67.5)	11	62.6 ± 2.7 (59.7–69.1)
	Myctophum nitidulum	4	0.18	7	0.26	0.63	0.526	4	54.8 ± 9.4 (44.4–63.4)	7	63.7 ± 5.4 (55.1–70.8)
	Myctophum phengodes	1	0.04	2	0.07	0.44	0.663	1	62.8	2	72.1–74.0
	Myctophum selenops			2	0.07	na	na			2	53.5–59.8
	Nannobrachium atrum			1	0.04	na	na				
	Nannobrachium sp.	12	0.53			na	na	12	105 ± 17 (70.0–125)		
	Notolychnus valdiviae			3	0.11	na	na			3	

(*continued on next page*)

Table 1 (*continued*)

Family	Species	Numbers						Standard length (mm)			
		La Pérouse		MAD-Ridge		Statistics		La Pérouse		MAD-Ridge	
		(n)	(%)	(n)	(%)	Z	p	(n)	mean ± SD (range)	(n)	mean ± SD (range)
											19.8 ± 0.4 (19.4–20.1)
	Notoscopelus caudispinosus			1	0.04	na	na			1	108
	Notoscopelus resplendens			10	0.37	na	na			10	33.6 ± 3.4 (28.0–40.5)
	Scopelopsis multipunctatus			7	0.26	na	na			7	36.8 ± 5.4 (31.6–47.1)
	Symbolophorus evermanni			1	0.04	na	na			1	54.5
	Symbolophorus rufinus	1	0.04			na	na	1	74.1		
	Unidentified	16	0.70	31	1.16	1.64	0.102				
NEOSCOPELIDAE	*Neoscopelus macrolepidotus*			27	1.01	na	na			27	62.3 ± 17.9 (41.1–116)
	Neoscopelus microchir			25	0.93	na	na			25	44.6 ± 8.0 (32.1–73.4)
BREGMACEROTIDAE	*Bregmaceros macclellandii*	4	0.18	2	0.07	1.02	0.306	4	69.4 ± 4.2 (64.8–74.9)	2	39.4–40.7
	Bregmaceros sp.			4	0.15	na	na			4	32.2 ± 4.1 (27.0–37.1)
CARAPIDAE	Unidentified			1	0.04	na	na				
DIRETMIDAE	*Diretmichthys parini* (larvae/juv.)	12	0.53			na	na	12	18.5 ± 4.2 (13.9–24.6)		
	Diretmus argenteus (larvae/juv.)			2	0.07	na	na			2	30.1–30.3
MELAMPHAIDAE	*Melamphaes longivelis*	1	0.04			na	na	1	58.6		
	Melamphaes sp.			1	0.04	na	na			1	25.1
	Scopelogadus mizolepis	33	1.45			na	na	33	58.7 ± 11.1 (33.1–79.5)		
CHIASMODONTIDAE	*Chiasmodon* sp.	7	0.31			na	na	7	45.2 ± 11.6 (33.4–64.8)		
	Pseudoscopelus sp.	2	0.09	1	0.04	na	na	2	82.2–87.3	1	45.0
OTHER FISH	Indeterminate fish	1	0.04	1	0.04	0.12	0.907				
	Larvae/juv. of non-mesopelagic fish	228	10.04	161	6.01	**5.25**	**<0.0001**				
	Total	2272	100.00	2681	100.00						

during a shallow daylight trawl compared with the five shallow night-time trawls (n = 177 ± 94). The scarcity of fish in the daylight hauls led to shallower trawls only being conducted at night. During deep trawls (437–550 m) on the MAD-Ridge cruise, the same number of fish taxa was collected by night and day (53 vs. 54). The catches contained more gonostomatids (15.5 vs. 10.8% by number) and sternoptychids (28.1 vs. 19.9%) and fewer myctophids (19.8 vs. 50.7%) by day than by night. Some species were more abundant by day (e.g. *Cyclothone* sp., *Gonostoma atlanticum*), whereas others (*C. warmingii*, *Diaphus richardsoni*) were caught almost exclusively at night.

3.3. Night-time trawls at shallow, intermediate and deep depths

Fish diversity was greater in deeper hauls than in shallow ones during both La Pérouse and MAD-Ridge cruises (55 vs. 29, and 53 vs. 29 taxa, respectively). This large difference cannot be explained solely by the fact that the IYGPT is an open net that fishes also in shallow water during deep deployment. Myctophids constituted the main micronektonic fish component at each depth on all three cruises, their proportion varying from 45.6 to 83.9% of the total number of fish. Myctophid assemblages were more diverse in deeper layers, and the two commonest species (*C. warmingii* and *D. suborbitalis*) showed different depth-related patterns. *C. warmingii* was found at every sampled depth, but it was more abundant in shallow trawls. On the other hand, *D. suborbitalis* were mostly caught in two intermediate trawls during the La Pérouse (n = 316) and MAD-Ridge (n = 570) cruises. No *D. suborbitalis* were collected during the Walters Shoal cruise. For other myctophids, several *D. perspicillatus* and *H. hygomii* were caught during the MAD-Ridge cruise, with most individuals being taken in shallow trawls.

A consistent feature during the three cruises is the greater abundance of sternoptychids in deeper layers, with almost none caught in shallow trawls. *A. aculeatus* was collected in both deep and intermediate hauls, and *A. hemigymnus* almost exclusively in deep trawls. The few specimens of melamphaids and chiasmodontids were also found in deep and intermediate trawls, but were absent from shallow trawls. For gonostomatids, most of the abundant *S. elongatus* were caught in deep and intermediate hauls during the La Pérouse cruise, and fish size was related to depth. Small individuals were found ín all three depth strata, but no fish >100 mm SL were caught in shallow trawls during the La Pérouse cruise (n = 12, 28.6 ± 4.3 mm SL) or in intermediate and shallow trawls during the MAD-Ridge cruise (n = 57, 48.0 ± 16.6 mm SL).

4. Discussion

The three seamounts studied here are located in different biogeochemical provinces of the western Indian Ocean (Fig. 1), with MAD-Ridge lying within the productive East African Coastal Province (EAFR), and La Pérouse and Walters Shoal in, respectively, oligotrophic waters and at the southern boundary of the Indian South Subtropical Gyre (ISSG) (Longhurst, 2007). MICROTON was also conducted within the oligotrophic waters of the ISSG (Fig. 1), but in oceanic waters (Annasawmy et al., 2018). According to a recent global biogeographic classification of the mesopelagic zone, MICROTON, MAD-Ridge and Walters Shoal are located within the Southern Indian Ocean ecoregion and La Pérouse at the boundary between that region and the northern Mid-Indian Ocean ecoregion (Sutton et al., 2017). The Southern Indian Ocean ecoregion is oligotrophic with a mesopelagic fish diversity and biomass low relative to the rest of the Indian Ocean (Sutton et al., 2017).

Table 2
Micronektonic fish taxa identified from pelagic trawls during the Walters Shoal cruise on board the RV *Marion Dufresne II* together with their standard length.

Family	Species	Walters Shoal		SL (mm)	
		(n)	(%)	(n)	mean ± SD (range)
STOMIIDAE	*Stomias longibarbatus*	1	0.13	0	na
CHAULIODONTIDAE	*Chauliodus sloani*	13	1.71	12	75.7 ± 46.2 (42.3–184.8)
MELANOSTOMIIDAE	*Bathophilus* sp.	1	0.13	1	69.1
	Melanostomias niger	1	0.13	1	52.0
PHOTICHTHYIDAE	*Photichthys argenteus*	2	0.26	2	57.0–63.6
	Vinciguerria spp.	64	8.41	36	28.1 ± 4.3 (20.0–35.9)
STERNOPTYCHIDAE	*Argyropelecus aculeatus*	4	0.53	4	39.0 ± 12.8 (22.8–50.6)
	Argyropelecus hemigymnus	48	6.31	44	18.1 ± 4.7 (11.0–26.4)
	Valenciennellus tripunctulatus	11	1.45	5	25.9 ± 1.7 (24.8–29.0)
	Unidentified	4	0.53	0	na
NOTOSUDIDAE	Unidentified	1	0.13	1	83.1
PARALEPIDIDAE	Unidentified (larvae/juv.)	1	0.13	1	48.4
EVERMANELLIDAE	*Evermanella* sp. (larvae/juv.)	4	0.53	4	33.7 ± 5.0 (26.2–36.7)
MYCTOPHIDAE	*Benthosema suborbitale*	30	3.94	24	24.2 ± 2.6 (16.9–29.1)
	Bolinichthys indicus	21	2.76	21	21.9 ± 5.6 (17.6–39.9)
	Ceratoscopelus warmingii	39	5.12	38	26.7 ± 8.2 (19.3–60.5)
	Diaphus diadematus	4	0.53	3	27.8 ± 0.6 (27.1–28.3)
	Diaphus effulgens	7	0.92	7	45.2 ± 5.5 (38.0–53.8)
	Diaphus meadi	11	1.45	11	25.6 ± 8.3 (19.2–41.9)
	Diaphus mollis	17	2.23	17	44.0 ± 12.0 (18.9–60.1)
	Diaphus perspicillatus	6	0.79	6	47.9 ± 5.6 (41.5–56.4)
	Diaphus sp.	6	0.79	1	22.8
	Diogenichthys atlanticus	22	2.89	22	19.1 ± 1.8 (15.3–22.5)
	Gonichthys barnesi	4	0.53	4	41.4 ± 4.1 (35.7–45.2)
	Hygophum hanseni	1	0.13	1	29.9
	Hygophum hygomii	36	4.73	35	49.4 ± 5.1 (28.6–55.2)
	Lampanyctus alatus	34	4.47	33	36.8 ± 11.5 (20.0–54.2)
	Lampanyctus australis	1	0.13	1	87.2
	Lampanyctus sp.	101	13.27	93	29.9 ± 6.2 (16.2–51.4)
	Lobianchia dofleini	99	13.01	94	29.5 ± 3.1 (24.2–38.7)
	Lobianchia gemellarii	13	1.71	13	38.1 ± 8.5 (29.1–60.4)
	Myctophum phengodes	30	3.94	28	35.8 ± 10.0 (18.0–54.6)
	Myctophum selenops	1	0.13	1	43.3
	Notoscopelus caudispinosus	1	0.13	1	84.7
	Notoscopelus resplendens	9	1.18	9	58.9 ± 7.6 (40.3–64.4)
	Scopelopsis multipunctatus	2	0.26	2	51.5–52.7
	Symbolophorus evermanni	1	0.13	1	30.7
	Unidentified	22	2.89	11	18.7 ± 4.1 (11.9–27.7)
MELAMPHAIDAE	*Scopeloberyx* sp.	5	0.66	5	15.5 ± 0.6 (14.6–16.1)
OTHER FISH	Larvae/juv. of non-mesopelagic fish	83	10.91		na
	Total	761	100.00		

4.1. Mesopelagic fish taxa

Three families of mesopelagic fish accounted for the vast majority (77–83% by number) of the fish catches during the three seamount cruises, and this statement is also true for the oceanic cruise (MICROTON; 84%). Overall, myctophids ranked first (49–82%), gonostomatids second and sternoptychids third, a common pattern for micronektonic fish communities in upper oceanic waters worldwide (Bernal et al., 2015). In contrast to the three other cruises, gonostomatids were exceptionally abundant during the La Pérouse cruise, with a single species, *Sigmops elongatus*, the most numerous fish. *S. elongatus* is found throughout the world in tropical and subtropical waters (Craddock and Haedrich, 1973; Harold, 2016). It has been placed among the top three most abundant stomiiforms, *Cyclothone* excluded, and its abundance may rival the dominant species of myctophid (Lancraft et al., 1988; Moore et al., 2004). The size of *S. elongatus* ranged widely from small juveniles to adults, and different size-classes dominated during the La Pérouse and MAD-Ridge cruises. Moreover, fish size was related to depth, which is the same situation as the larger adults living and migrating in deeper layers than the smaller juveniles in the Gulf of Mexico (Lancraft et al., 1988).

All but one species (*Diaphus bertelseni*) of myctophid caught during the four cruises had been previously recorded in the Indian Ocean (Vipin et al., 2012). According to their distribution patterns (Hulley, 1981), the 49 myctophid species were partitioned either as high-oceanic or pseudoceanic. The high-oceanic group was by far the most diverse (46 species). It included the numerically dominant *Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Diaphus perspicillatus*, *Hygophum hygomii* and *Lobianchia dofleini*. The first four species in this list were collected during all cruises, but the last was caught only during the Walters Shoal cruise. The latitudinal distribution of *L. dofleini*, together with the concomitant catch of *Diaphus meadi*, *Diogenichthys atlanticus*, *Lampanyctus australis*, *Myctophum phengodes* and *Notoscopelus resplendens* (Hulley, 1986) was indicative of the more southern location of the Walters Shoal seamount than the MAD-Ridge and La Pérouse seamounts and the area covered by the earlier MICROTON cruise. Overall, *C. warmingii* was either the most abundant myctophid or numerically one of the dominant ones during each cruise, ranking first on the MICROTON cruise (56% by number), second during the La Pérouse cruise, third during the MAD-Ridge cruise and fifth during the Walters Shoal cruise. *C. warmingii* has a broadly tropical pattern (Hulley, 1981), being widely distributed in tropical and subtropical waters (Bekker, 1983; Kinzer and Schulz, 1985; Takagi et al., 2009), including in the vicinity of and over seamounts (Moore et al., 2004). The present work emphasizes its numerical importance in tropical waters of the western Indian Ocean. *C. warmingii* was caught exclusively at night, in every sampled layer, and with a bigger catch in shallow trawls, a pattern that supports the reported daylight depth range below 600 m and a night-time concentration in the upper 100 m (Robison, 1984; Kinzer and Schulz, 1985).

The three remaining myctophids (*Diaphus garmani*, *D. knappi* and

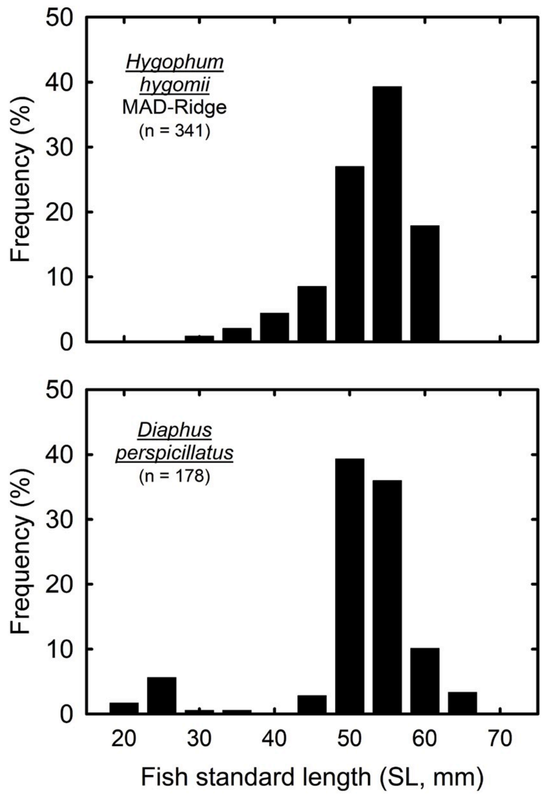

Fig. 2. Length-frequency distribution of the myctophids *Hygophum hygomii* (upper panel) and *Diaphus perspicillatus* (lower panel) caught during the MAD-Ridge cruise.

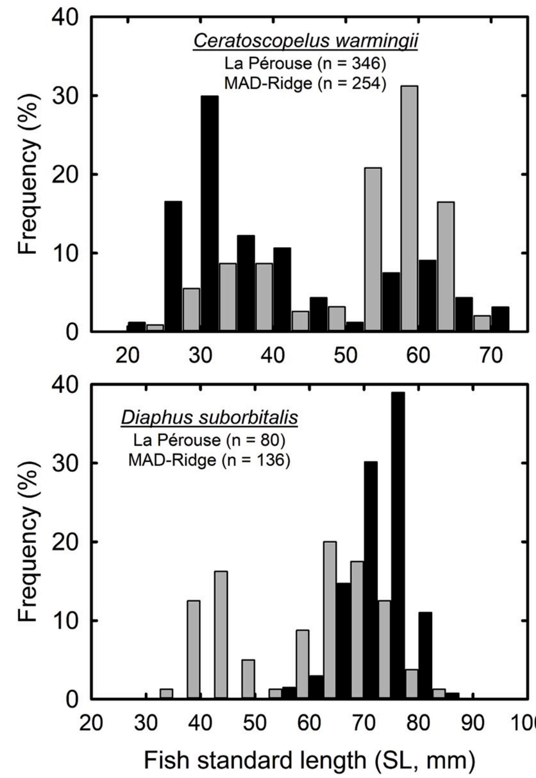

Fig. 3. Length-frequency distribution of the myctophids *Ceratoscopelus warmingii* (upper panel) and *Diaphus suborbitalis* (lower panel) caught during the La Pérouse (grey) and MAD-Ridge (black) cruises. Note that only a subset of *D. suborbitalis* was measured in two trawls containing large numbers of fish (50 and 120 of a total of 316 and 570 specimens during the La Pérouse and MAD-Ridge cruises, respectively).

D. suborbitalis) belonged to the pseudoceanic group (Hulley, 1981, 1986, pers. comm.), meaning that they interact with land environments (Kawaguchi and Shimizu, 1978; Reid et al., 1991). As expected, they were not collected during the oceanic cruise MICROTON, but they were caught together and/or in association with other known slope- and seamount-associated fish such as *Argyripnus hulleyi*, *Benthosema fibulatum*, *Cookeolus japonicus, Neobathyclupea malayana Neoscopelus macrolepidotus*, *N. microchir* and *Promethichthys prometheus* (Starnes, 1988; Bekker and Shcherbachev, 1990; Nakamura and Parin, 1993; De Forest and Drazen, 2009; Quéro et al., 2009; Prokofiev, 2014b; Roberts, 2015). The case of *D. suborbitalis* exemplifies this pattern. It was caught either (i) in moderate numbers together with the single catch of *D. garmani* (La Pérouse) or the single catch of *N. macrolepidotus*, *N. microchir* and *N. malayana* (MAD-Ridge), or (ii) in large numbers together with the single catch of *A. hulleyi* (La Pérouse) or together with *B. fibulatum* and *D. knappi* (MAD-Ridge). Elsewhere, *D. suborbitalis* is considered to be an abundant Indo-Pacific species associated with continental and oceanic island slopes, seamounts and mid-oceanic ridges (Kawaguchi and Shimizu, 1978; Bekker and Shcherbachev, 1990), where it plays a key trophic link between copepods, small *Cyclothone* fish and large predatory fish (Gorelova and Prutko, 1985; Parin and Prutko, 1985). Within that context, it is notable that the main catch of *D. suborbitalis* during the MAD-Ridge cruise was associated with two *P. prometheus*, a benthopelagic fish that is known to prey on *D. suborbitalis* over seamounts (Parin and Prutko, 1985).

Two species of the genus *Argyropelecus* accounted for most of the sternoptychid fish collected during the four cruises. Both *A. aculeatus* and *A. hemigymnus* have a worldwide distribution in tropical and temperate waters, with *A. hemigymnus* being found farther south than *A. aculeatus* (Baird, 1971). Accordingly, *A. aculeatus* was the most abundant sternoptychid during the MICROTON, La Pérouse and MAD-Ridge cruises, and *A. hemigymnus* dominated the sternoptychid catch during the Walters Shoal cruise. The two species were collected in intermediate and deep layers, supporting the belief that *Argyropelecus* species are rarely caught in the upper 100 m (Baird, 1971).

4.2. Notable records

No remarkable micronektonic fish taxa were caught during the Walters Shoal cruise, but some of the fish collected during the La Pérouse and MAD-Ridge cruises added new information to the biogeography of the species. First, four individuals of the sternoptychid *Argyripnus hulleyi* were collected during a single night trawl at intermediate depth during the La Pérouse cruise. The species was first described from nine specimens found dead at the sea surface following a volcanic eruption at La Réunion Island (Quéro et al., 2009). The La Pérouse specimens therefore constitute the second record of the species in the scientific literature, extending its occurrence to a seamount located nearby (90 nautical miles from) the holotype locality. They also raise the maximum known size of the species from 73 mm (Quéro et al., 2009) to 82 mm SL. Second, to the best of our knowledge, the single *Diaphus bertelseni* caught in a deep trawl close to the La Pérouse seamount is the first record of the species in the Indian Ocean (Vipin et al., 2012). *D. bertelseni* was previously recorded in tropical to temperate seas in the Atlantic and Pacific oceans (Paxton and Hulley, 1999; Craddock and Hartel, 2002; Robertson and Clements, 2015; Hulley and Paxton, 2016). Its presence in the western Indian Ocean extends considerably its biogeographical range and suggests that *D. bertelseni* may well have a worldwide distribution. Finally, *D. suborbitalis* has been previously caught between 7°N and 8°S in the tropical eastern and western Indian Ocean, with a few collected at 17–26°S off the eastern African and western Madagascar coasts (Nafpaktitis, 1978; Gjøsaeter and Beck, 1981; Bekker, 1983; Bekker and

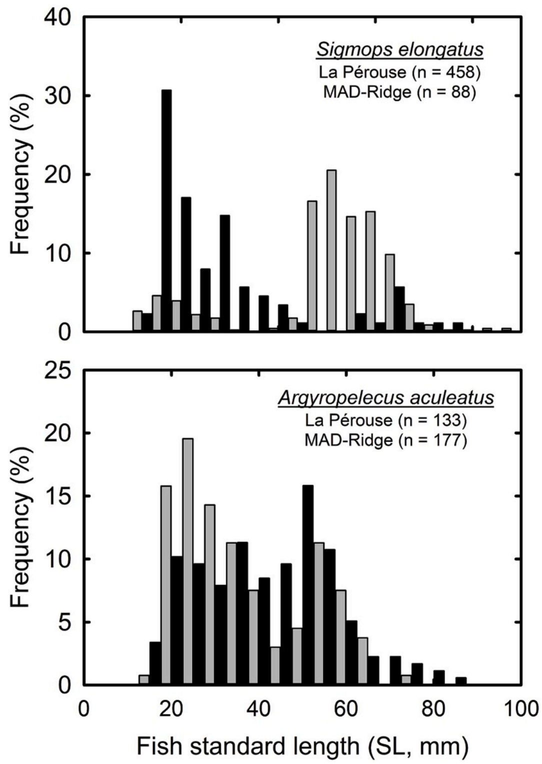

Fig. 4. Length-frequency distribution of *Sigmops elongatus* (upper panel) and *Argyropelecus aculeatus* (lower panel) caught during the La Pérouse (grey) and MAD-Ridge (black) cruises.

Shcherbachev, 1990). When compared with the records of Bekker (1983), our large catches of *D. suborbitalis* at 46°14′E 27°29′S (MAD-Ridge) and 54°06′E 19°47′S (La Pérouse) represent the southernmost and easternmost localities in the western Indian Ocean, respectively, where this species has been found. They also increased the maximum known size of *D. suborbitalis* from ~70 mm (Nafpaktitis, 1978) to 84 mm SL for the Indian Ocean.

Declaration of competing interest

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

CRediT authorship contribution statement

Yves Cherel: Conceptualization, Investigation, Writing - original draft, Formal analysis. **Evgeny V. Romanov:** Investigation, Writing - original draft. **Pavanee Annasawmy:** Investigation, Writing - original draft. **Delphine Thibault:** Conceptualization, Investigation. **Frédéric Ménard:** Conceptualization, Investigation.

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References

Annasawmy, P., Cherel, Y., Romanov, E., Le Loc'h, F., Ménard, F., Ternon, J.F., Marsac, F., 2020a. Stable Isotope Patterns of Mesopelagic Communities over Two Shallow Seamounts of the South-Western Indian Ocean. Deep-Sea Res. II (this issue, submitted).

Annasawmy, P., Ternon, J.-F., Cotel, P., Cherel, Y., Romanov, E.V., Roudaut, G., Lebourges-Dhaussy, A., Ménard, F., Marsac, F., 2019. Micronekton distributions and assemblages at two shallow seamounts of the south-western Indian Ocean: insights from acoustics and mesopelagic trawl data. Prog. Oceanogr. 178, 102161.

Annasawmy, P., Ternon, J.-F., Lebourges-Dhaussy, A., Roudaut, G., Herbette, S., Ménard, F., Cotel, P., Marsac, F., 2020b. Micronekton Distribution as Influenced by Mesoscale Eddies, Madagascar Shelf and Shallow Seamounts in the South-Western Indian Ocean: an Acoustic Approach. Deep-Sea Res. II (this issue, submitted).

Annasawmy, P., Ternon, J.-F., Marsac, F., Cherel, Y., Béhagle, N., Roudaut, G., Lebourges-Dhaussy, A., Demarcq, H., Moloney, C.L., Jaquemet, S., Ménard, F., 2018. Micronekton diel migration, community composition and trophic position within two biogeochemical provinces of the South West Indian Ocean: insight from acoustics and stable isotopes. Deep-Sea Res. I 138, 85–97.

Baird, R.C., 1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae). Bull. Mus. Comp. Zool. 142, 1–128.

Bekker, V.E., 1983. Myctophids of the World Ocean. Nauka Press, Moscow, p. 247 (in Russian).

Bekker, V.E., Shcherbachev, Y.N., 1990. Bathypelagic species of the families Neoscopelidae and Myctophidae from the Indian Ocean, with a description of a new species of *Diaphus*. J. Ichthyol. 30, 122–134.

Bernal, A., Olivar, M.-P., Maynou, F., Fernandez de Puelles, M.L., 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. Prog. Oceanogr. 135, 1–17.

Bianchi, D., Stock, C., Galbraith, E.D., Sarmiento, J.L., 2013. Diel vertical migration: ecological controls and impacts on the biological pump in a one-dimensional ocean model. Global Biogeochem. Cycles 27, 478–491.

Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to family Myctophidae. Rev. Fish Biol. Fish. 21, 339–354.

Cherel, Y., Fontaine, C., Richard, P., Labat, J.P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol. Oceanogr. 55, 324–332.

Collette, B.B., Parin, N.V., 1991. Shallow-water fishes of Walters Shoals, Madagascar ridge. Bull. Mar. Sci. 48, 1–22.

Craddock, J.E., Haedrich, R.L., 1973. The distribution of gonostomatid fishes in the western Indian Ocean. J. Mar. Biol. Assoc. India 15, 285–292.

Craddock, J.E., Hartel, K.E., 2002. Myctophidae. In: Carpenter, K.E. (Ed.), The Living Marine Resources of the Western Central Atlantic, Bony Fishes Part 1 (Accipenseridae to Grammatidae), vol. 2. FAO, Rome, pp. 944–951.

De Forest, L., Drazen, J., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. Deep-Sea Res. I 56, 232–250.

Fourmanoir, P., 1970. Notes ichtyologiques (II). Cahiers ORSTOM Sér. Océanogr. 8, 35–46.

Gjøsaeter, J., Beck, I.M., 1981. Mesopelagic fish off Mozambique. FiskDir. Skr. Ser. HavUnders. 17, 253–265.

Gjøsaeter, J., Kawaguchi, K., 1980. A review of the world resources of mesopelagic fish. FAO Tech. Pap. 193, 1–151.

Gorelova, T.A., Prutko, V.G., 1985. On feeding of *Diaphus suborbitalis* (Myctophidae, Pisces) in the equatorial Indian ocean. Okeanologya 25, 677–684 (in Russian).

Harold, A.S., 2016. Gonostomatidae. In: Carpenter, K.E., De Angelis, N. (Eds.), The Living Marine Resources of the Eastern Central Atlantic, Bony Fishes Part 1 (Elopiformes to Scorpaeniformes), vol. 3. FAO, Rome, pp. 1783–1787.

Hulley, P.A., 1981. Results of the research cruises of FRV "Walther Herwig" to south America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). Arch. Fischwiss. 31, 1–300.

Hulley, P.A., 1986. Order Myctophiformes. In: Smith, M.M., Heemstra, P.C. (Eds.), Smith's Sea Fishes. J.L.B. . Smith Institute of Ichthyology, Grahamstown, South Africa, pp. 282–322.

Hulley, P.A., Paxton, J.R., 2016. Myctophidae. In: Carpenter, K.E., De Angelis, N. (Eds.), The Living Marine Resources of the Eastern Central Atlantic, Bony Fishes Part 1 (Elopiformes to Scorpaeniformes), vol. 3. FAO, Rome, pp. 1860–1933.

Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuna, J.L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L., Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat. Commun. 5, 3271.

Kawaguchi, K., Shimizu, H., 1978. Taxonomy and distribution of the lanternfishes, genus *Diaphus* (Pisces, Myctophidae) in the western Pacific, eastern Indian oceans and the Southeast Asian seas. Bull. Ocean Res. Inst. Univ. Tokyo 10, 1–145.
Kinzer, J., Schulz, K., 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. Mar. Biol. 85, 313–322.
Lancraft, T.M., Hopkins, T.L., Torres, J.J., 1988. Aspects of the ecology of the mesopelagic fish *Gonostoma elongatum* (Gonostomidae, Stomiiformes) in the eastern Gulf of Mexico. Mar. Ecol. Prog. Ser. 49, 27–40.
Laptikhovsky, V., Boersch-Supan, P., Bolstad, K., Kemp, K., Letessier, T., Rogers, A.D., 2017. Cephalopods of the Southwest Indian Ocean Ridge: a hotspot of biological diversity and absence of endemism. Deep-Sea Res. II 136, 98–107.
Letessier, T., De Grave, S., Boersch-Supan, P.H., Kemp, K.M., Brierley, A.S., Rogers, A.D., 2017. Seamount influences on mid-water shrimps (Decapoda) and gnathophausiids (Lophogastridea) of the South-West Indian Ridge. Deep-Sea Res. II 136, 88–97.
Longhurst, A., 2007. Ecological Geography of the Sea, second ed. Academic Press, Burlington, USA, p. 542.
Moore, J.A., Vecchione, M., Collette, B.B., Gibbons, R., Hartel, K.E., 2004. Selected fauna of bear seamount (new England seamount Chain), and the presence of "natural invader" species. Arch. Fish. Mar. Res. 51, 241–250.
Nakamura, I., Parin, N.V., 1993. Snake Mackerels and Cutlassfishes of the World (Families Gempylidae and Trichiuridae), vol. 15. FAO Species Catalogue, p. 136.
Nafpaktitis, B.G., 1978. Systematics and distribution of lanternfishes of the genera *Lobianchia* and *Diaphus (Myctophidae)* in the Indian ocean. Bull. Nat. Hist. Mus. Los Ang. County 30, 1–92.
Parin, N.V., Prutko, V.G., 1985. Thalassal mesobenthopelagic ichthyocoen over the Equator submarine rise in the western tropical Indian Ocean. Okeanologia 25, 1017–1020 (in Russian).
Parin, N.V., Timokhin, I.G., Novikov, N.P., Shcherbachev, Y.N., 2008. On the composition of thalassobathyal ichthyofauna and commercial productivity of Mozambique seamount (the Indian Ocean). J. Ichthyol. 48, 361–366.
Paulin, C., 1982. Scorpionfishes of New Zealand (Pisces: Scorpaenidae). N. Z. J. Zool 9, 437–450.
Paxton, J.R., Hulley, P.A., 1999. Myctophidae. In: Carpenter, K.E., Niem, V.H. (Eds.), The Living Marine Resources of the Western Central Pacific, Batoid Fishes, Chimaeras and Bony Fishes Part 1 (Elopidae to Linophrynidae), vol. 3. FAO, Rome, pp. 1957–1965.
Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S., 2007. Seamounts: Ecology, Fisheries & Conservation. Blackwell, Oxford, UK, p. 527.
Porteiro, F.M., Sutton, T., 2007. Midwater fish assemblages and seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation. Blackwell, Oxford, UK, pp. 101–116.
Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. Fish. Res. 83, 60–72.
Prokofiev, A.M., 2014a. Fauna of deepsea herring (Perciformes: Bathyclupeidae) of the Indian ocean. J. Ichthyol. 54, 311–316.
Prokofiev, A.M., 2014b. Taxonomy and distribution of deepsea herring (Bathyclupeidae) in oceans. J. Ichthyol. 54, 493–500.
Prokofiev, A.M., Gon, O., Psomadakis, P.N., 2016. A new species of *Neobathyclupea* from the northern Indian ocean with comments on *N. malayana* (Teleostei, Perciformes, Bathyclupeidae). Zootaxa 4208, 474–484.
Quéro, J.F., Spitz, J., Vayne, J.J., 2009. *Argyripnus hulleyi*: une nouvelle espèce de Sternoptychidae (Stomiiformes) de l'île de la Réunion (France, océan Indien). Cybium 33, 39–43.
Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109, 427–440.
Roberts, C.D., 2015. Family neoscopelidae. In: Roberts, C.D., Stewart, A.L., Struthers, C. D. (Eds.), The Fishes of New Zealand, vol. 3. Te Papa Press, Wellington, pp. 610–612.
Roberts, M., Ternon, J.F., Marsac, F., Noyon, M., 2020. The MAD-Ridge Project: Bio-Physical Coupling Around a Shallow Seamount on the Northern Madagascar Ridge, Southwest Indian Ocean. Deep-Sea Res II (this issue, submitted).
Robertson, D.A., Clements, K.D., 2015. Family Myctophidae. In: Roberts, C.D., Stewart, A.L., Struthers, C.D. (Eds.), The Fishes of New Zealand, vol. 3. Te Papa Press, Wellington, pp. 613–680.
Robison, B.H., 1984. Herbivory by the myctophid fish *Ceratoscopelus warmingii*. Mar. Biol. 84, 119–123.
Rogers, A.D., 2018. The biology of seamounts: 25 years on. Adv. Mar. Biol. 79, 137–224.
Rogers, A.D., Alvheim, O., Bemanaja, E., Benivary, D., Boersch-Supan, P., Bornman, T.G., Cedras, R., Du Plessis, N., Gotheil, S., Høines, A., Kemp, K., Kristiansen, J., Letessier, T., Mangar, V., Mazungula, N., Mørk, T., Pinet, P., Pollard, R., Read, J., Sonnekus, T., 2017. Pelagic communities of the south west Indian ocean seamounts: R/V *Dr fridtjof nansen* cruise 2009-410. Deep-Sea Res. II 136, 5–35.
Smith, M.M., Heemstra, P.C., 1986. Smith's Sea Fishes. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, p. 1047.
Starnes, W.C., 1988. Revision, phylogeny and biogeographic comments on the circumtropical marine percoid Family Priacanthidae. Bull. Mar. Sci. 43, 117–203.
Sutton, T.T., Clark, M.R., Dunn, D.C., Halpin, P.N., Rogers, A.D., Guinotte, J., Bograd, S. J., Angel, M.V., Perez, J.A.A., Wishner, K., Haedrich, R.L., Lindsay, D.J., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Blachowiak-Samolyk, K., Robison, B. H., Gjerde, K.M., Pierrot-Bults, A., Bernal, P., Reygondeau, G., Heino, M., 2017. A global biogeographic classification of the mesopelagic zone. Deep-Sea Res. I 126, 85–102.
Sutton, T.T., Porteiro, F.M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C.I.H., Horne, J., Søiland, H., Falkenhaug, T., Godø, O.R., Bergstad, O.A., 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep-Sea Res. II 55, 161–184.
Takagi, K., Yatsu, A., Itoh, H., Moku, M., Nishida, H., 2009. Comparison of feeding habits of myctophid fishes and juvenile small epipelagic fishes in the western North Pacific. Mar. Biol. 156, 641–659.
Vipin, P.M., Ravi, R., Fernandez, T.J., Pradeep, K., Boopendranath, M.R., Remesan, M.P., 2012. Distribution of myctophid resources in the Indian Ocean. Rev. Fish Biol. Fish. 22, 423–436.