

Research Article

Lanternfish (Myctophidae) from eastern Brazil, southwest Atlantic Ocean

**Adriana da Costa Braga¹, Paulo A.S. Costa¹, Agnaldo S. Martins²
George Olavo³ & Gustavo W. Nunan⁴**

¹Laboratório de Dinâmica de Populações Marinhas, Departamento de Ecologia e Recursos Marinhos
Universidade Federal do Estado do Rio de Janeiro, Av. Pasteur, 458, sala 410
Urca, Rio de Janeiro, 22290-240, RJ, Brazil

²Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo
Av. Fernando Ferrari, 514, Vitória, 29075-910, ES, Brazil

³Laboratório de Biologia Pesqueira, Universidade Estadual de Feira de Santana
Km-3, BR 116 Campus Universitário, s/n, Feira de Santana, 44031-460, BA, Brazil

⁴In memoriam

ABSTRACT. Twenty-nine species from 11 genera of Myctophidae were taken in daytime midwater and bottom trawl hauls off eastern Brazil (11°-22°S). Trawls were performed aboard the French R/V *Thalassa* to depths from 19 to 2271 m, including samples from shelf, slope and in the vicinity of oceanic banks and seamounts. *Diaphus garmani* was the most abundant species, accounting for 84% of all identified individuals and with four other species (*D. dumerilii*, *D. brachycephalus*, *D. perspicillatus* and *Myctophum obtusirostre*) accounted for >95% of all myctophids caught. Regarding longitudinal distribution patterns, 16 species are broadly tropical, seven tropical, three subtropical, two temperate and one amphi-Atlantic. For the most abundant and frequent species, highest abundances were associated mainly with cold waters, either South Atlantic Central Water or Antarctic Intermediate Water. Non-metric multidimensional scaling based on species presence-absence in the samples and oceanographic conditions was used to identify spatial distribution of myctophid assemblages. Three assemblages were identified in the studied area: north of Abrolhos Bank, south of Abrolhos Bank, and seamounts.

Keywords: Myctophidae, fish assemblages, seamounts, southwest Atlantic.

Peces linterna (Myctophidae) de la costa oriental de Brasil, Atlántico suroeste

RESUMEN. Veintinueve especies de 11 géneros pertenecientes a la familia Myctophidae fueron recolectados mediante faenas diurnas de arrastre de fondo y arrastre de mediana en la costa oriental brasileña (11°-22°S). Las faenas fueron realizadas con el buque oceanográfico *Thalassa* entre 19-2271 m de profundidad, cubriendo las regiones de la plataforma continental, talud, bancos oceánicos y montes submarinos. *Diaphus garmani* fue la especie más abundante (84%) y en conjunto con otras cuatro especies (*D. dumerilii*, *D. brachycephalus*, *D. perspicillatus*, *Myctophum obtusirostre*) representaron más del >95% de los mictófidios capturados. De acuerdo a los patrones de distribución longitudinal, 16 especies son de distribución tropical, siete tropical, tres son subtropicales, dos de zonas templadas y una anfi-Atlántica. Para las especies más abundantes y frecuentes, sus mayores abundancias estuvieron asociadas principalmente con aguas frías, específicamente con el Agua Central del Atlántico Sur y con el Agua Intermedia Antártica. Para definir la distribución espacial de las asociaciones de mictófidios basadas en la presencia y ausencia de las especies y su relación con las condiciones oceanográficas imperantes, se aplicó el análisis de ordenación MDS. Los resultados obtenidos indican la presencia de tres ensambles en el área de estudio: norte del Banco Abrolhos, sur del Banco Abrolhos y montes submarinos.

Palabras clave: Myctophidae, asociaciones de peces, montes submarinos, Atlántico suroeste.

INTRODUCTION

Myctophids are typically pelagic fish of the open ocean (Hartel & Craddock, 2002) and, together with members of Sternoptychidae, Gonostomatidae, Chauliodontidae and the suborder Stomiatoidei, represent the characteristic families in mesopelagic depths (Haedrich, 1997). Among these, Myctophidae is the dominant family (Nafpaktitis *et al.*, 1977) and the most speciose, including almost 250 species referred to as lanternfish due to a variety of luminous organs, among which photophores are the most characteristic (Nelson, 2006). Lanternfish range from arctic to antarctic waters, and from the surface at night to depths exceeding 2000 m (Nafpaktitis *et al.*, 1977). The family also includes species known as pseudoceanic, associated with continental shelf and slope regions and in the neighbourhood of oceanic islands (Hulley, 1981). Continental slopes are particularly important due to the topographic and hydrographic gradients, and are considered areas of dynamic tension (Merrett & Haedrich, 1997). Continental slopes also encompass a wider set of physical niches, and provide an environment for the development of a recognizable and trophically-dependent community of benthic and benthopelagic fish (Haedrich *et al.*, 1980). Down-slope zonation of lanternfish may result from the combined effects of depth and water column structure (Hulley, 1992).

Much of the current knowledge on Atlantic myctophids resulted from the study of the collections of the Woods Hole Oceanographic Institution (WHOI) (Nafpaktitis *et al.*, 1977) and Institut für Seefischerei (Hulley, 1981). In the southwestern Atlantic (0°-60°S), 79 species (22 genera) were collected during the 11th cruise of the R/V Akademik Kurchatov (Parin & Andriyashev, 1972; Parin *et al.*, 1974). The distribution of 40 of these species, with respect to the water masses between 40°30'-47°00'S, was further examined (Konstantinova *et al.*, 1994; Figueroa *et al.*, 1998). Off the coasts of Suriname and French Guiana, 15 species from 7 genera were reported (Uyeno *et al.*, 1983). In the Eastern Central Atlantic, Wienerroither *et al.* (2009) reported 52 species for the Canarian archipelago.

Although relatively few documents have been published on myctophids from low latitude oligotrophic waters (Nafpaktitis & Nafpaktitis, 1969; Hulley, 1972, 1981; Clarke, 1973; Gartner *et al.*, 1987), high diversity is apparent (Backus *et al.*, 1977). Figueiredo *et al.* (2002) and Santos (2003) reported 37 species captured in 133 midwater trawl hauls off southeastern and southern Brazil (22°-34°S), with sampling effort concentrated from 100 to 500 m. From

Rio Real, BA to Cabo São Tomé, RJ (12-22°S), 27 larval lanternfish species were identified in 658 samples collected in depths ≤ 200 m (Castro *et al.*, 2010), and Myctophidae was the most diverse family at epi- and mesopelagic depths (Braga *et al.*, 2007).

The present study provides knowledge about southwestern Atlantic lanternfish, including samples from Vitória-Trindade chain, an area understudied (Clark *et al.*, 2010), adjacent to a transition zone between tropical Atlantic and temperate South America biota. We report the occurrence and distribution of lanternfish in relation to oceanographic conditions and attempt to examine whether species associations are spatially different.

MATERIALS AND METHODS

Study area

The eastern coast of Brazil is a typical oligotrophic system (Gaeta *et al.*, 1999), and the most important oceanic surface feature is the southward flowing Brazil Current (BC: 22-27°C, 36.5-37.0 psu), the warm western boundary current of the subtropical gyre (Silveira *et al.*, 2001). The continental shelf of the study area (11-22°S) extends for only 8 km off Salvador (França, 1979) and widens to the south to form the Royal Charlotte Bank (RCB, 16°S) and the Abrolhos Bank (AB, 18°S). The Vitória-Trindade chain that extends along 20.5°S comprises seamounts that have shallow summits at depths of 34-76 m (Miloslavich *et al.*, 2011). These topographic barriers produce a complex hydrographic structure including vortices, upwellings and vertical mixing processes, which alter the oligotrophic condition mainly south of AB (Ciotti *et al.*, 2007; Valentin *et al.*, 2007). The subsurface layer beneath the BC is occupied by the cold and nutrient-rich South Atlantic Central Water (SACW: 6.0-18.5°C, 34.5-36.0 psu) flowing north, between 400-700 m (Schmid *et al.*, 1995). Periodic upwelling of SACW beyond the deep thermocline (80-120 m) enhances primary production (Nonaka *et al.*, 2000). In the subthermocline region there are three major water masses, Antarctic Intermediate Water (AAIW) near 800-900 m, North Atlantic Deep Water (NADW) centered at about 2500 m, and Antarctic Bottom Water (AABW) below about 3500 m (Hogg & Owens, 1999).

Biological sampling

The studied material was obtained with midwater and demersal trawls, both performed only during the day, on the continental shelf, continental slope and near oceanic banks and seamounts off eastern Brazil (Fig. 1). Table 1

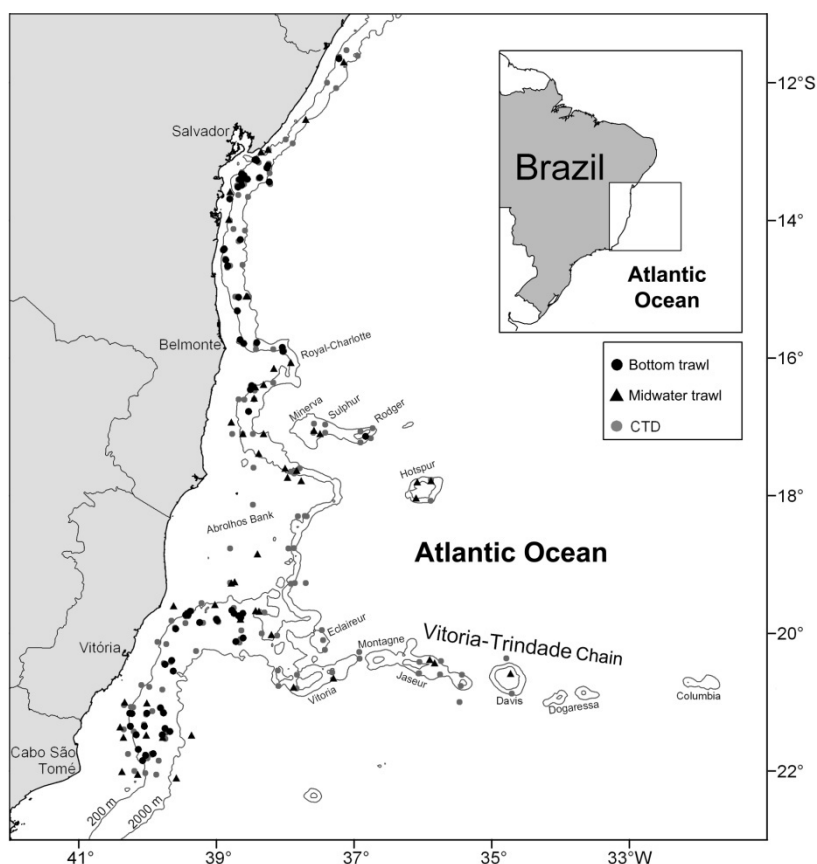


Figure 1. Study area and location of the sampling stations.

Table 1. Number of stations, depth range, effort and characteristics of nets used in midwater and demersal sampling off eastern Brazil and details of myctophids catch.

	Midwater net	Demersal net
Number of trawls	50	68
Number of stations (with myctophids)	12	53
Depth range (m)	19 - 910	100 - 2,271
Horizontal opening during operation (m)	24 - 56	28 - 45.5
Vertical opening during operation (m)	25 - 42	3 - 10.6
Net size (m)	191	80.5
Codend mesh size (mm)	20	20
Total sampling effort (hour)	40:59 h	63:41 h
Total catch (number)	28,645	2,720
Number of species	17	26
Number of exclusive species	3	12

summarizes the characteristics of midwater and demersal sampling, effort and catch of myctophids. Samples were taken aboard the French R/V *Thalassa* in May-July 1999 (midwater) and May-June 2000 (demersal). Both cruises were developed in the context of the Brazilian fishery research program REVIZEE, in scientific cooperation with IFREMER

(Institut Français de Recherche pour l'Exploitation de la Mer).

During the midwater cruise, the collections were obtained using a large midwater net (292 m circumference and 191 m long). During operations, maximum horizontal and vertical opening was 56 and 25 m, respectively. Mesh sizes were 8000 mm in the

wings and 20 mm in the cod-end. A total of 62 pelagic midwater trawls were towed at depths from 19 to 910 m, among which 50 had myctophid catches ($n = 28,645$). Hauls were undertaken on acoustically detected fish aggregations.

During the demersal cruise, the individuals were obtained using a bottom-trawl net with a 26.8 m head rope and 47.2-m foot rope, equipped with 40 rubber bobbins (rockhoppers) attached to the foot-rope. Mesh sizes were 110 mm for the wings and 20 mm for the cod-end. During the fishing operations, the horizontal and vertical mouth openings ranged between 28.0 and 45.5 m and from 3.0 to 10.6 m, respectively.

Demersal trawls were decided based on the availability of trawlable bottoms. A total of 58 stations yielded more than 45,000 specimens, from which 2,720 specimens of myctophids were recorded in 47 stations, ranging in depth from 100 to 2,271 m. On both cruises, trawl depth was acoustically controlled using SCANMAR system, which was also used to access trawl geometry, including the horizontal opening and distance from net to bottom. The vertical opening and its distance in relation to the bottom was controlled by the Ossian Trawl-Eye 49 KHz transducer fixed in the headrope. These systems allowed maintaining the net operating at specific depths during fishing and further classify the stations into different depth strata.

Water mass distribution in the study area

Temperature and salinity profiles ($n = 116$) recorded during the midwater cruise were used to analyse the horizontal distribution of temperature contours at the 200 m isobath (*e.g.*, beginning of the mesopelagic zone), throughout the studied area (11-22°S). Water masses distribution was inferred from a T-S diagram using data compiled from the National Oceanographic Data Centre (Brazilian Navy), including CTD profiles down to 5,000 m. These data was sorted from the same geographic area and period (May-July) and processed using Ocean Data View (ODV) software.

Identification of species and abundance

The ichthyological material analysed was identified using identification keys provided by Nafpaktitis *et al.* (1977), Hulley (1986), McEachran & Fechhelm (1998), and Wang & Tsung-Chen (2001). Measurements and counts were made according to Nafpaktitis & Nafpaktitis (1969). Photophore terminology followed Parr (1929) and Nafpaktitis & Nafpaktitis (1969). A representative number of specimens were deposited in the collections of Museu Nacional do Rio de Janeiro (MNRJ) and Museu Oceanográfico do Vale do Itajaí (MOVI).

Species abundance followed primarily the classification proposed by Gartner *et al.* (1987) based on total number of specimens captured [abundant (>500 individuals), common (100-500 individuals), uncommon (10-100 individuals), rare (<10 individuals)], with an additional category, extremely abundant (>2,000 individuals).

Distribution

The distribution of myctophid assemblages was analysed with non-metric multidimensional scaling (Clarke & Warwick, 2001) using the Sorensen similarity index calculated with species presence-absence in the samples. The final matrix used in the ordination was composed by 29 species and 53 samples (9 midwater and 44 demersal trawls). Stations with only one species ($n = 11$) were excluded from the matrix. A non-quantitative index was chosen due to differences in net sizes and sampling strategies between midwater and demersal fishing.

RESULTS

Water mass distribution in the study area

The thermal structure of the water column during the two cruises, both during winter, was similar. The water temperature ranged from 24-28°C at surface, 20-24°C at 100 m depth, 15.7-16.1°C at 200 m, 8-9.5°C at 500 m, and was always <3°C beyond 1,000 m depth. Tropical Water (TW) from BC ($T > 20^{\circ}\text{C}$; $S > 36.2$ psu) was present at surface (29-68 m), and the subtropical SACW with lower temperatures (6-18.5°C) and salinities (34.6-36.0 psu) occupied the subsurface layer (118-624 m) (Fig. 2).

AAIW was present mainly from 700 m (2.0-4.0°C and 34.2-34.6 psu) to eventually 1,500 m, while NADW was found at depths between 1,500-2,000 m (3.0-4.0°C; 34.6-35.0 psu). At depths greater than 2,000 m, the top layer of the AABW (3.0-3.5°C; 34.6-35.0 psu) was found.

The horizontal distribution of the water temperature at 200 m (Fig. 3) showed that this depth was occupied by SACW throughout the studied area, with an east-west gradient of decreasing temperatures. The lowest temperatures (14-15°C) were identified between 13-15°S off Salvador, and near RCB, AB and the Vitória Channel, reflecting the upwelling of SACW as a result of BC meandering along the shelf edge and seamounts.

Distribution of catches

Myctophids were more frequent in demersal (78%) than in midwater (24%) trawls, although higher

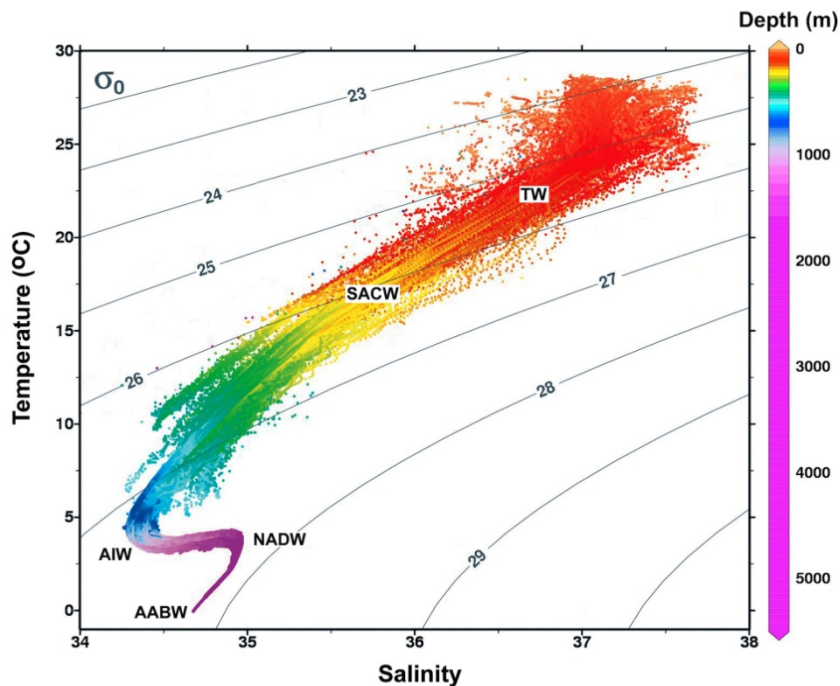


Figure 2. Water masses recorded in the present study, according to depth. TW: Tropical Water, SACW: South Atlantic Central Water, AAIW: Antarctic Intermediate Water, NADW: North Atlantic Deep Water, AABW: Antarctic Bottom Water.

abundances in midwater catches resulted from acoustically detected schools (Fig. 4). The total number of myctophids per trawl ranged from 1 to 12,415, although almost always <50 ind trawl⁻¹ occurred in demersal trawls (85%). Midwater trawl catches were mostly >200 ind trawl⁻¹, including massive catches ($>1,000$ ind trawl⁻¹) near the Royal Charlotte Bank and seamounts (Minerva, Hotspur).

The number of species/trawl ranged from 1-13 (Fig. 5), but captures of more than 5 species/trawl were more frequent in demersal trawls (21%) than in midwater trawls (17%). The maximum number of species per trawl (13) was similar in demersal and midwater trawls. Midwater trawls near seamounts south of Abrolhos Bank yielded the highest number of species (Vitória: 13 spp.; Davis: 7 spp.). Demersal trawls that yielded the highest number of species occurred at the southernmost part of the area at 624.5 m (13 spp.) and at 2,126 m off Salvador (10 spp.). Nine trawls yielded 6-9 species trawl⁻¹. Among these, six were performed between 13-14°S at depths from 522 to 1,929 m, and three were performed between 19-20°S at depths from 895 to 1,649 m.

Species data

From a total of 31,365 myctophids examined, all but 278 (0.9%) were identifiable to species. Table 2 lists

the species grouped according to abundance, along with their totals and frequency of occurrence in midwater and demersal trawls, depth of occurrence and size range. The identified material comprised 11 genera and 29 species. The top five most abundant species comprised approximately 95% of the total number of individuals. Only one species was extremely abundant, 4 were abundant, 5 were common, 8 were uncommon and 11 were rare. *Diaphus dumerilii* was the most frequent species, both in demersal (62%) and midwater (66%) trawls. The majority of species (79%) had broadly tropical and tropical affinities (as indicated by Hulley, 1981), while species with subtropical and temperate affinities were poorly represented and occurred in very low numbers (1-17 ind).

Assemblages

Three groups of trawl stations were identified in MDS ordination (Fig. 6): North of Abrolhos Bank (NAB), South of Abrolhos Bank (SAB) and Seamounts (SEAM). Assemblages were significantly different ($P = 0.02$) when similarities between SEAM x NAB ($P = 0.014$) and SEAM x SAB ($P = 0.030$) were compared (ANOSIM Global R: 0.181).

Although NAB and SAB did not significantly differ ($P = 0.255$), a change in dominance was evident

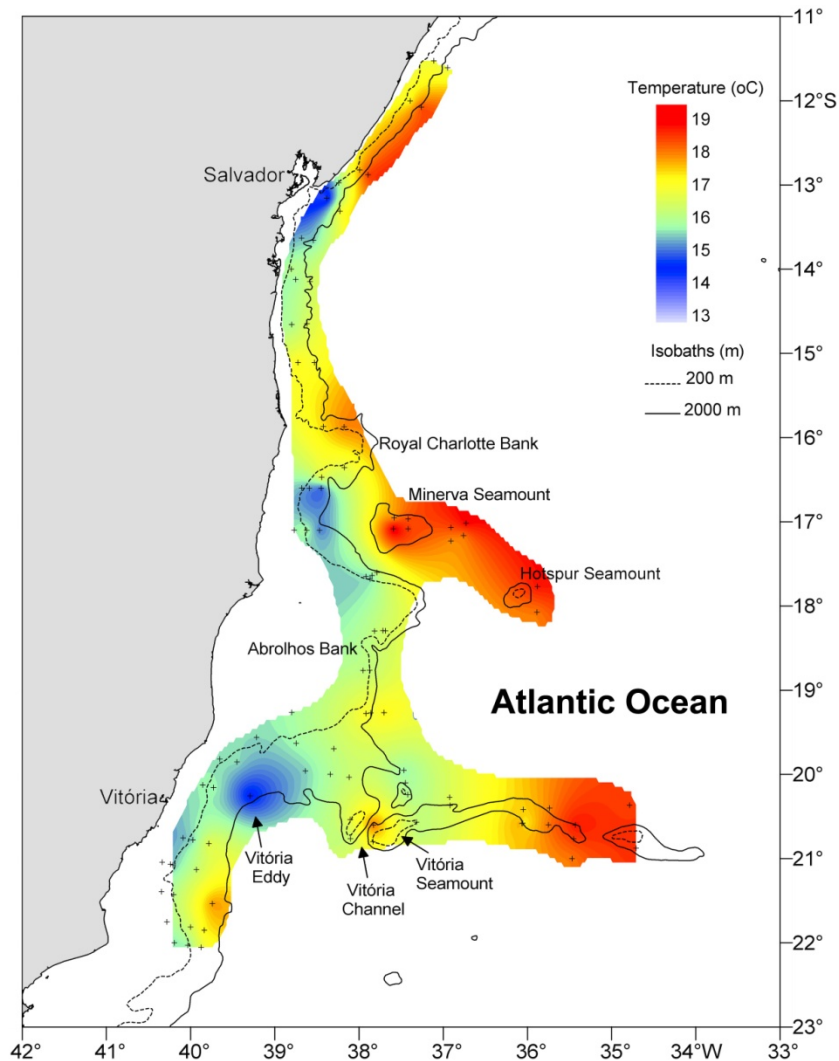


Figure 3. Distribution of temperature contours at 200 m isobath in the study area.

when mean densities (ind h^{-1}) of the nine most abundant and frequent species in midwater trawls were compared (Fig. 7). *Diaphus garmani* and *D. dumerilii* were caught throughout the area, though mostly abundant at RCB and Minerva seamount. *M. obtusirostre* occurred associated to the four seamounts sampled (Minerva, Hotspur, Vitória, and Davis). At Vitória seamount, except for *D. garmani*, the eight remaining species occurred together in catches, with yields that ranged from 4.2 to 110.2 ind h^{-1} . A monospecific school of *D. brachycephalus* caught at 15°S yielded 1,115 ind h^{-1} .

DISCUSSION

In this study, myctophids were more frequent in demersal than in midwater trawls, possibly as a result

of our exclusive daytime sampling, since under the normal diel vertical migration pattern these fishes hide from visual predators at depth during the day and forage on abundant plankton in upper waters at night (Pearre, 2003). Also, a number of specimens could have been caught during retrieval and/or deployment of the bottom trawl (the nets used were devoid of open/close mechanisms) and, for this reason, fish density estimates were not compared between midwater and demersal trawls. Moreover, the presence of myctophids in demersal trawls could represent the adoption of an adult benthopelagic life strategy, as indicated by Vinnichenko (1997). Gartner *et al.* (2008) suggested that persistent high-density near-bottom aggregations (NBAs) are a normal part of the life history of several species traditionally considered to be mesopelagic. These NBAs would enhance the probability of feeding success, as fishes could explore

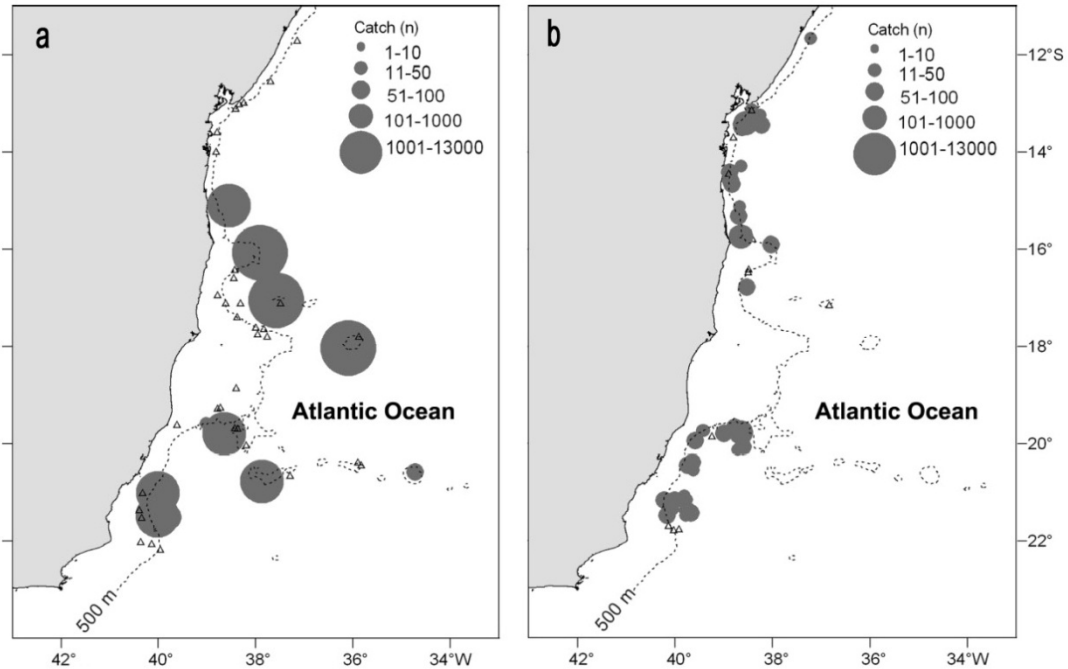


Figure 4. Total catch (in numbers) of myctophids in a) midwater trawls, b) demersal trawls. Triangles represent stations without myctophids.

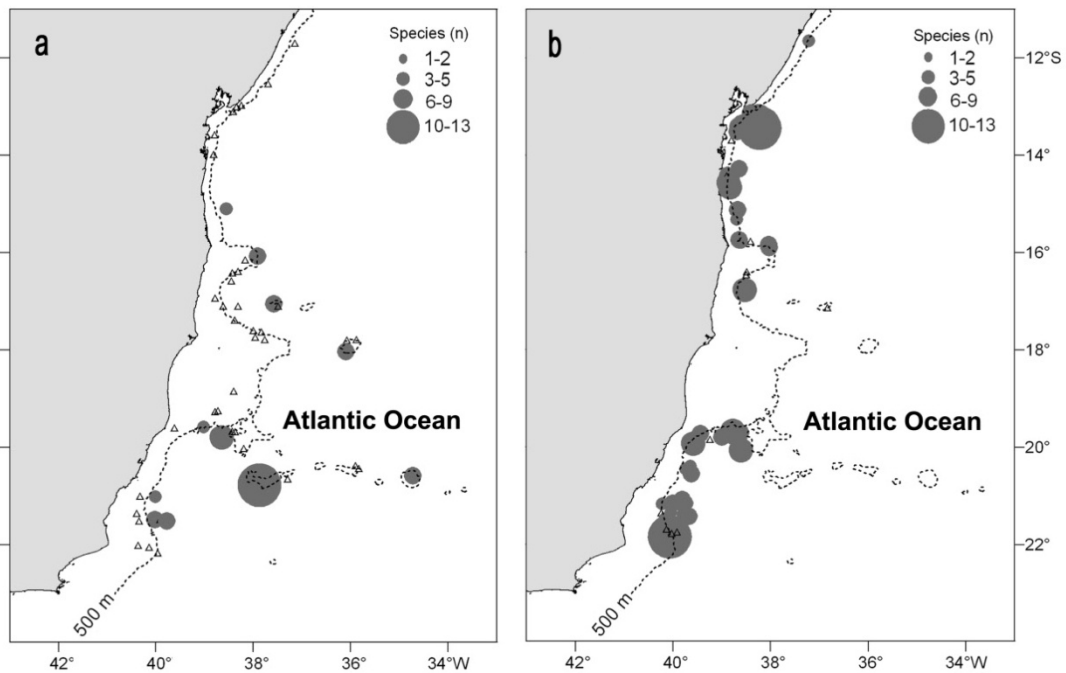


Figure 5. Number of myctophid species in a) midwater trawls, b) demersal trawls. Triangles represent stations without myctophids.

food supplies in a two dimensional search area (*i.e.*, near bottom).

Among the 29 myctophid species captured in this study, tropical and broad tropical distribution patterns

dominated. Species with temperate and subtropical affinities were restricted to hauls that sampled depths below 700 m, which is the upper limit of AAIW in the area (Hogg & Owens, 1999). Although this number is

Table 2. Lanternfish catch in midwater and demersal trawls off eastern Brazil (frequency in parentheses). Tropical: distributed only in tropical waters, Subtropical: distributed between 20° and 35° in the western South Atlantic, Broadly Tropical: distributed in both tropical and subtropical waters, Amphi-Atlantic: restricted to warm subtropical waters. Biogeographical definitions according to Hulley (1981).

	Total catch (n)	Midwater trawls (n = 12)	Demersal trawls (n = 53)	Standard length (mm)	Distribution pattern
>2,000 individuals					
<i>Diaphus garmani</i>	26,199	24,953 (6)	1,246 (21)	33-60	Tropical
500-2,000 individuals					
<i>Diaphus dumerilii</i>	1,703	1,192 (8)	511 (33)	46-105	Tropical
<i>Diaphus brachycephalus</i>	778	761 (4)	17 (6)	25-52	Broadly Tropical
<i>Diaphus perspicillatus</i>	614	436 (6)	178 (7)	40-86	Broadly Tropical
<i>Myctophum obtusirostre</i>	575	336 (6)	239 (28)	34-98	Tropical
100-500 individuals					
<i>Lepidophanes guentheri</i>	388	155 (3)	233 (5)	25-76	Tropical
<i>Ceratoscopelus warmingii</i>	171	51 (3)	120 (10)	43-76	Broadly Tropical
<i>Diaphus adenomus</i>	139	-	139 (8)	83-203	Amphi-Atlantic
<i>Diaphus problematicus</i>	107	11 (2)	96 (14)	68-95	Tropical
<i>Diaphus fragilis</i>	106	56 (1)	50 (3)	69-95	Tropical
10-100 individuals					
<i>Diaphus splendidus</i>	81	16 (3)	65 (3)	38-92	Broadly Tropical
<i>Myctophum affine</i>	42	38 (1)	4 (3)	28-44	Tropical
<i>Myctophum selenops</i>	42	20 (2)	22 (10)	48-62	Broadly Tropical
<i>Lampadena luminosa</i>	31	-	31 (14)	115-190	Tropical
<i>Diaphus lucidus</i>	28	10 (1)	18 (3)	73-103	Broadly Tropical
<i>Bolinichthys distofax</i>	17	-	17 (10)	71-85	Subtropical
<i>Bolinichthys photothorax</i>	17	-	17 (5)	40-60	Tropical
<i>Notoscopelus caudispinosus</i>	15	2 (1)	13 (6)	106-132	Broadly Tropical
<10 individuals					
<i>Symbolophorus rufinus</i>	6	6 (2)	-	50-72	Broadly Tropical
<i>Diaphus bertelseni</i>	3	-	3 (3)	44-60	Broadly Tropical
<i>Diaphus meadi</i>	3	-	3 (3)	52-59	Temperate
<i>Diaphus cf. ostenfeldi</i>	3	-	4 (2)	98-112	Temperate
<i>Hygophum reinhardti</i>	3	3 (1)	-	39-41	Broadly Tropical
<i>Lampanyctus alatus</i>	3	-	3 (1)	93-107	Broadly Tropical
<i>Lobianchia gemellari</i>	3	-	3 (3)	44-69	Broadly Tropical
<i>Myctophum nitidulum</i>	3	-	3 (3)	39-73	Broadly Tropical
<i>Notoscopelus resplendens</i>	3	-	3 (1)	54-59	Broadly Tropical
<i>Hygophum hygomii</i>	2	-	2 (2)	50-58	Subtropical
<i>Myctophum phengodes</i>	1	1 (1)	-	49	Subtropical

lower than that recorded off southeastern and southern Brazil between 22-34°S (41 species: Figueiredo *et al.*, 2002; Bernardes *et al.*, 2005), if larval occurrence is considered (Bonecker & Castro, 2006), ten more species could be added (*Benthoosema suborbitale*, *Centrobranchus nigroocelattus*, *Diaphus anderseni*, *Diogenichthys atlanticus*, *Hygophum macrochir*, *Hygophum taaningi*, *Lampanyctus nobilis*, *Lepidophanes gaussi*, *Nannobranchium cuprarium*, *Notolychnus valdiviae*) and the numbers be similar. All myctophids spend their larval stages in the productive epipelagic

zone (Sassa *et al.*, 2004), moving to the mesopelagic zone after reaching the juvenile stage (Clarke, 1973).

Eastern and south-southeastern Brazilian waters share 12 of 16 myctophid genera. Regarding the four genera exclusive within each area, broad or tropical genera (*Centrobranchus*, *Diogenichthys*, *Lampadena*, *Notolychnus*) occur between 11-22°S, while cold-water genera associated with the STC (*Electrona*, *Gymnoscopelus*, *Lampichthys*, *Scopelopsis*) occur between 22-34°S. The diversity within each area (11-22°S: 39 species, 16 genera; 22-34°S: 41 species, 16

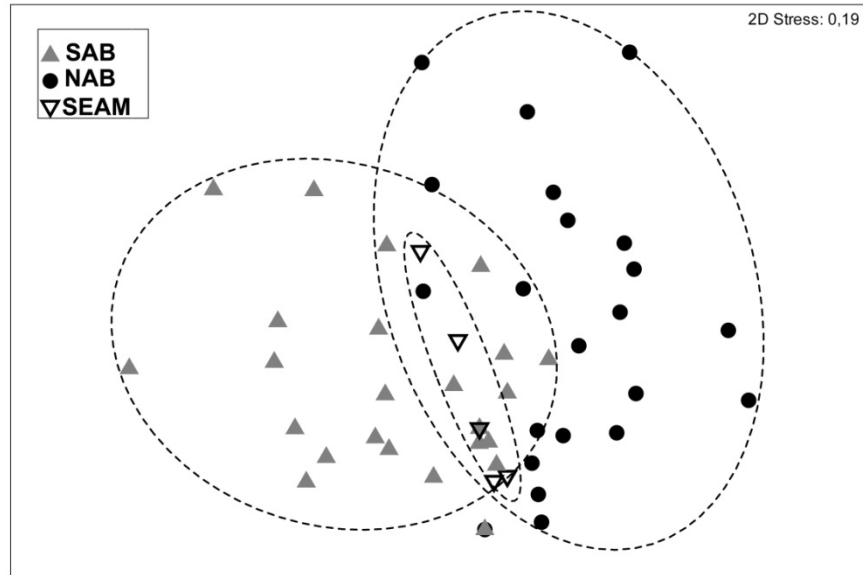


Figure 6. Multidimensional scaling ordination (MDS) plots of myctophid fishes, based on Sorensen similarity and presence-absence of species. NAB: North Abrolhos Bank $<18^{\circ}\text{S}$, SAB: South Abrolhos Bank $>19^{\circ}\text{S}$, SEAM: Seamounts.

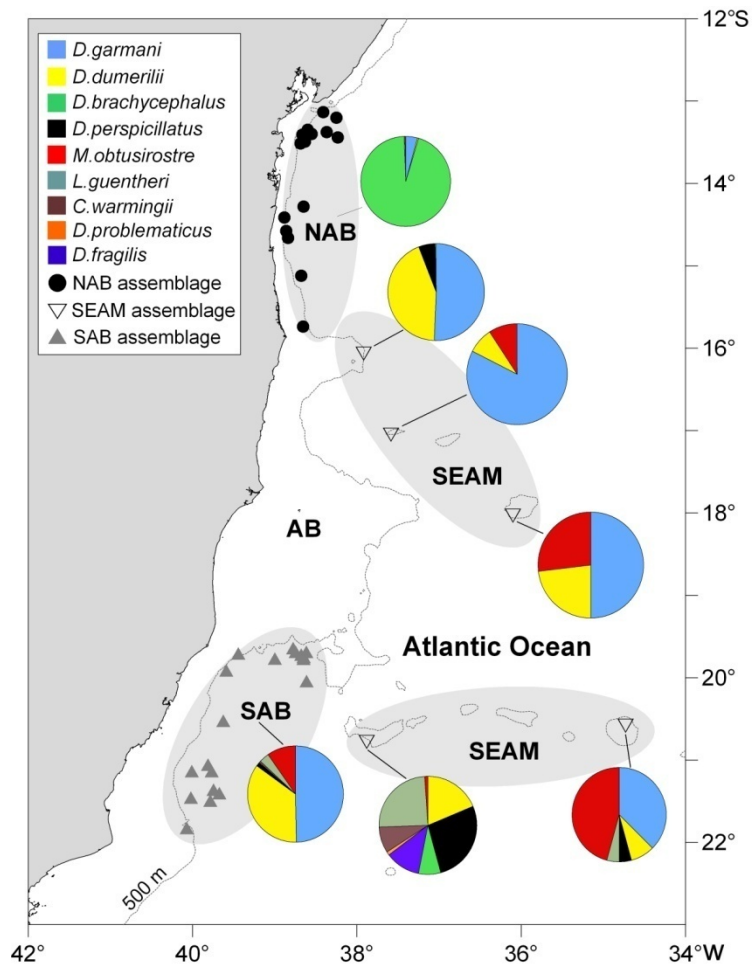


Figure 7. Relative abundance (ind h^{-1}) in percent, of the nine most abundant and frequent myctophids caught in midwater trawls. NAB: North Abrolhos Bank $<18^{\circ}\text{S}$, SAB: South Abrolhos Bank $>19^{\circ}\text{S}$, SEAM: Seamounts.

genera) is comparable to that reported for Hawaii (47 species, 18 genera; Clarke, 1973), eastern Gulf of Mexico, GOM (49 species, 17 genera; Gartner *et al.*, 1987) and north-central GOM (38 species, 17 genera; Ross *et al.*, 2010). Collectively, Brazilian waters have a high diversity of myctophids (79 species, 23 genera: Menezes *et al.*, 2003) comparable to that registered in the North Atlantic (82 species, 20 genera: Nafpaktitis *et al.*, 1977). These numbers include the 30 species reported by Hulley (1981) for waters beyond 3,000 m during the research cruises of FRV "Walther Herwig" to South America (1966-1976). Among these, many are typically associated with the STC, the frontal zone where subantarctic and subtropical waters meet, which is a circumglobal feature of the Southern Ocean (Williams *et al.*, 2001). The STC is a major biogeographic boundary, as well as a region of enhanced productivity (Pakhomov *et al.*, 2000), and much of the plankton and fish fauna in this region have a circumglobal distribution (McGinnis, 1982; Pakhomov *et al.*, 2000).

Excluding two hauls that sampled massive aggregations of *D. garmani* and captured 23,502 individuals, the top four species off eastern Brazil between 11-22°S (*D. garmani*, *D. dumerilii*, *D. brachycephalus*, *D. perspicillatus*) comprised 76.4% of the specimens caught. Off southeastern and southern Brazil between 22-34°S, the three dominant species (*D. dumerilii*, *L. guentheri*, *Symbolophorus barnardi*) comprised 74.9% (Figueiredo *et al.*, 2002; Bernardes *et al.*, 2005). Both values were similar to those reported for the contribution of the top seven species off Hawaii (75.5%; Clarke, 1973) and eastern GOM (74.7%; Gartner *et al.*, 1987), and of the top six species off north-central GOM (75.1%; Ross *et al.*, 2010). *Diaphus* is the most species among myctophid genera (60 species; Nafpaktitis *et al.*, 1977) and 19 species are reported for Brazil (Santos & Figueiredo, 2008). In ichthyoplankton surveys off eastern Brazil, *Diaphus* spp. larvae integrated the transitional and oceanic assemblages (Nonaka *et al.*, 2000; Castro *et al.*, 2010), and the numeric dominance of adults between 11-22°S probably reflects the higher sampling effort in deeper waters when compared to 22-34°S, where sampling was shallower (<500 m: Figueiredo *et al.*, 2002).

A tendency of increasing species number with depth was observed, and since temperature correlates to lanternfish distribution (Brandt, 1983), this result could be associated with the marked thermal structure of the water column. During hauls that sampled depths higher than 1,500 m between 11°-22°S, the net was towed through four waters masses (BC, SACW, AAIW, NADW), possibly increasing the probability

of catching a higher number of species. Hulley (1992) also observed an increase in lanternfish species richness and in the complexity of the distributions across the slope, possibly as the result of a higher structuring of the water column.

The presence of a variety of reliefs between 11-22°S adds topographic complexity, causing island-induced disturbance, in which upwelled nutrients promote primary and secondary production in the island wake (Bonecker *et al.*, 1992, 1993) and probably act to affect the distribution of the mesopelagic fauna. Our hydrographic results showed the occurrence of SACW at 200 m between 13-15°S, and near RCB, AB and the Vitória Channel; this possibly reflects the permanent cyclonic eddy that Schmid *et al.* (1995) detected to be formed south of the AB from the meandering movement of the BC after passing through the Vitória Channel. The spatial distribution of the SACW in the area studied seems to explain the distribution of the more speciose trawls and, for some species, the highest densities associated with seamounts and banks.

While *D. dumerilii* was the most frequent and second most abundant species in our study, it was dominant between 22-34°S (47%; Figueiredo *et al.*, 2002) and seemed to be important in the trophic relation on the slope, once it was found in the stomach contents of several demersal bony fish of STC ecosystem (Haimovici *et al.*, 1994). Near RCB this species was most abundant in rather shallow depths (25-34 m), indicating a certain degree of land association, as it was observed by Wienerroither *et al.* (2009). *Diaphus dumerilii* dominated both the water column (deep scattering layer) and the bottom (NBAs) on deep coral banks off Cape Lookout middle slope, North Carolina (Gartner *et al.*, 2008).

The occurrence of mesopelagic species in shallow waters is ascribed to the abrupt depth changeover around islands of volcanic origin (Uiblein & Bordes, 1999), and the direct interaction between pelagic and demersal organisms at the interfaces between submerged bottom features establishes an important link between epipelagic waters and the deep benthos (Marshall & Merrett, 1977). Lanternfish may be an important prey item for large pelagic species, abundant in longline catches from Vitória-Trindade seamounts (Olavo *et al.*, 2005). Future research in the area should address the study of oceanic food webs.

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REFERENCES

- Backus, R.H., J.E. Craddock, R.L. Haedrich & R.H. Robison. 1977. Atlantic mesopelagic zoogeography. In: R.H. Gibbs (ed.). *Fishes of the western North Atlantic*. Mem. Sears Found. Mar. Res., 1(7): 266-287.
- Bernardes, R.A., J.L. Figueiredo, A.R. Rodrigues, L.G. Fischer, C.M. Vooren, M. Haimovici & C.L.D.B. Rossi-Wongtschowski. 2005. Peixes da zona econômica exclusiva da região sudeste-sul do Brasil. Levantamento com armadilhas, pargueiras e rede de arrasto de fundo. Edusp, São Paulo, 295 pp.
- Bonecker, A.C.T. & M.S. Castro. 2006. Atlas de larvas de peixes da região central da zona econômica exclusiva brasileira. Museu Nacional, Rio de Janeiro (Série Livros n. 19), 216 pp.
- Bonecker, S.L.C., C.R. Nogueira, A.C.T. Bonecker, L.H.S. Santos, M.V. Reynier & D.R. Tenenbaum. 1992-1993. Estudo hidrográfico e planctológico da região entre Cabo Frio (Rio de Janeiro) e o Arquipélago de Abrolhos (BA). *Nerítica* 7(1-2): 71-86.
- Braga, A.C., P.A.S. Costa, A.T. Lima, G.W. Nunan, G. Olavo & A.S. Martins. 2007. Padrões de distribuição de teleósteos epi- e mesopelágicos na costa central (11-22°S) brasileira. In: P.A.S. Costa, G. Olavo & A.S. Martins (eds.). *Biodiversidade da fauna marinha profunda da costa central brasileira*. Museu Nacional, Rio de Janeiro, (Série Livros n. 24), pp. 63-86.
- Brandt, S.B. 1983. Temporal and spatial patterns of lanternfish (family Myctophidae) communities associated with a warm-core eddy. *Mar. Biol.*, 74: 231-244.
- Castro, M.S., W.J. Richards & A.C.T. Bonecker. 2010. Occurrence and distribution of larval lanternfish (Myctophidae) from the southwest Atlantic Ocean. *Zoologia*, 27(4): 541-553.
- Ciotti, A.M., E. Gonzalez-Rodriguez, L. Andrade, R. Paranhos & W.F. Carvalho. 2007. Clorofila-*a*, medidas bio-ópticas e produtividade primária. In: J.L. Valentin (ed.). *Características hidrobiológicas da região central da zona econômica exclusiva brasileira* (Salvador, BA, ao Cabo de São Tomé, RJ). Série Documentos REVIZEE/SCORE-Central, Ministério do Meio Ambiente, Brasília, pp. 61-72.
- Clark, M.R., A.A. Rowden, T. Schlacher, A. Williams, M. Consalvey, K.I. Stocks, A.D. Rogers, T.D. O'Hara, M. White, T.M. Shank & J.M. Hall-Spencer. 2010. The ecology of seamounts: structure, function, and human impacts. *Ann. Rev. Mar. Sci.*, 2: 253-278.
- Clarke, T.A. 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fis. B-NOAA*, 71(2): 401-433.
- Clarke, K.R. & R.M. Warwick. 2001. *Primer E (5) Computer Program*. Natural Environmental Research Council, Plymouth.
- Figueiredo, J.L., A.P. Santos, N. Yamaguti, R.A. Bernardes & C.L.D.B. Rossi-Wongtschowski. 2002. Peixes da Zona Econômica Exclusiva da região sudeste-sul do Brasil. Edusp, São Paulo, 242 pp.
- Figuerola, D.E., J.M.D. de Astarloa & P. Martos. 1998. Mesopelagic fish distribution in the southwest Atlantic in relation to water masses. *Deep-Sea Res.*, 45: 317-332.
- França, J.J.C. 1979. Geomorfologia da margem continental leste brasileira e da bacia oceânica adjacente. PETROBRAS-CENPES-DINTEP. (Série Projeto REMAC, 7) Rio de Janeiro, pp. 89-127.
- Gaeta, S.A., J.A. Lorenzetti, L.B. Miranda, S.M.B. Susini-Ribeiro, M. Pompeu & C.E.S. Araujo. 1999. The Vitória eddy and its relation to the phytoplankton biomass and primary productivity during the austral fall of 1995. *Arch. Fish. Mar. Res.*, 47(2/3): 253-270.
- Gartner, J.V., T.L. Hopkins, R.C. Baird & D.M. Milliken. 1987. The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. *Fis. B-NOAA*, 85(1): 81-98.
- Gartner, J.V., K.J. Sulak, S.W. Ross & A.M. Necaie. 2008. Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes. *Mar. Biol.*, 153: 825-841.
- Haedrich, R.L. 1997. Distribution and population ecology. In: D.J. Randall & A.P. Farrell (eds.). *Deep-Sea fishes*. Academic Press, London, pp. 79-114.
- Haedrich, R.L., G.T. Rowe & P.T. Polloni. 1980. The megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.*, 57: 165-179.
- Haimovici, M., A.S. Martins, J.L. Figueiredo & P.C. Vieira. 1994. Demersal bony fish of the outer shelf and upper slope of the southern Brazil Subtropical Convergence Ecosystem. *Mar. Ecol. Prog. Ser.*, 108: 59-77.
- Hartel, K.E. & J.E. Craddock. 2002. Order Myctophiformes. In: K.E. Carpenter (ed.). *The living*

- marine resources of the western central Atlantic. Vol. 2: Bony fishes part 1 (Acipenseridae to Grammatidae). FAO Species identification guide for fishery purposes. ASIH Spec. Publ. N°5. Rome, FAO, pp. 942-951.
- Hogg, N.G. & W.B. Owens. 1999. Direct measurement of the deep circulation within the Brazil Basin. *Deep-Sea Res.*, 46: 335-353.
- Hulley, P.A. 1972. A report on the mesopelagic fish collected during the deep-sea cruises of R.S. Africana II, 1961-1966. *Ann. S. Afr. Mus.*, 60(6): 197-236.
- 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): 1- 300.
- Hulley, P.A. 1986. Family Myctophidae. In: M.M. Smith & P.C. Heemstra (eds.). *Smith's Sea Fishes*. Springer-Verlag, Berlin, pp. 282-321.
- Hulley, P.A. 1992. Upper-slope distributions of oceanic lanternfishes (family Myctophidae). *Mar. Biol.*, 114(3): 365-383.
- Konstantinova, M.P., A.V. Remesio & P.P. Fedulov. 1994. The distribution of myctophids in the southwest Atlantic in relation to water structure and dynamics. *J. Ichthyol.*, 34(7): 151-160.
- Marshall, N.B. & N.R. Merrett. 1977. The existence of a benthopelagic fauna in the deep-sea. A voyage of discovery. *Deep-Sea Res. George Deacon 70th Anniversary Volume, (Suppl.)* 483-497.
- McEachran, J.D. & J.D. Feckhelm. 1998. *Fishes of the Gulf of Mexico. Volume I: Myxiniiformes to Gasterosteiformes*. University of Texas Press, Austin, 1120 pp.
- McGinnis, R.F. 1982. Biogeography of lanternfishes (family Myctophidae) south of 30°S. *Antarct. Res. Ser. XII*, 35: 1-110.
- Menezes, N.A., P.A. Backup, J.L. Figueiredo & R.L. Moura. 2003. *Catálogo das espécies de peixes marinhos do Brasil*. Museu de Zoologia USP, São Paulo, 160 pp.
- Merrett, N.R. & R.L. Haedrich. 1997. *Deep-sea demersal fish and fisheries*. Chapman & Hall, London, 282 pp.
- Miloslavich, P., E. Klein, J.M. Díaz, C.E. Hernández, G. Bigatti, L. Campos, F. Artigas, J. Castillo, P.E. Penchaszadeh, P.E. Neill, A. Carranza, M.V. Retana, J.M. Díaz de Astarloa, M. Lewis, P. Yorio, M.L. Piriz, D. Rodríguez, Y. Yoneshigue-Valentin, L. Gamboa, & A. Martín. 2011. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PLoS One*. 2011; 6(1): e14631. doi: 10.1371/journal.pone.0014631.
- Nafpaktitis, B.G. & M. Nafpaktitis. 1969. Lanternfishes (Family Myctophidae) collected during cruises 3 and 6 of the R/V "Anton Bruun" in the Indian Ocean. *Bull. Los Angeles County Mus. Nat. Hist., Science*, 5: 79.
- Nafpaktitis, B.G., R.H. Backus, J.E. Craddock, R.L. Haedrich, B.H. Robison & C. Karnella. 1977. Family Myctophidae. In: *Fishes of the western North Atlantic*. Mem. Sears Found. Mar. Res., 1(7): 13-265.
- Nelson, J.S. 2006. *Fishes of the world*. John Wiley & Sons, New York, 601 pp.
- Nonaka, R.H., Y. Matsuura & K. Suzuki. 2000. Seasonal variation in larval fish assemblages in relation to oceanographic conditions in the Abrolhos Bank region off eastern Brazil. *Fish. B-NOAA*, 98: 767-784.
- Olavo, G., P.A.S. Costa & A.S. Martins. 2005. Prospecção de grandes peixes pelágicos na região central da ZEE brasileira entre o Rio Real-BA e o Cabo de São Tomé-RJ. In: P.A.S. Costa, A.S. Martins & G. Olavo (eds.). *Pesca e potenciais de exploração de recursos vivos na região central da Zona Econômica Exclusiva brasileira*. Rio de Janeiro: Museu Nacional (Série Livros N°13), pp. 167-202.
- Pakhomov, E.A., R. Perissinotto, C.D. McQuaid & P.W. Foroneman. 2000. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part 1. Ecological zonation. *Deep-Sea Res. I*, 47: 1663-1686.
- Parin, N.V. & A.P. Andriyashev. 1972. Ichthyological studies during the 11th cruise of the Research Vessel Akademik Kurchatov in the South Atlantic. *J. Ichthyol.*, 12(5): 883-886.
- Parin, N.V., A.P. Andriyashev, O.D. Borodulina & V.M. Tchuvasov. 1974. Midwater fishes of the south western Atlantic Ocean. *Akad. Nauk. CCCP*, [In Russian, with English abstract.] Moscow, 98: 76-140.
- Parr, A.E. 1929. Notes on the species of myctophine fishes represented by type species in the United States National Museum. *Proc. U.S. Natl. Mus.*, 76: 1-47.
- Pearre, S. 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.*, 78: 1-79.
- Ross, S.W., A.M. Quattrini, A.Y. Roa-Varón & J.P. McClain. 2010. Species composition and distributions of mesopelagic fishes over the slope of the north-central Gulf of Mexico. *Deep-Sea Res. II*, 57: 1926-1956.
- Santos, A.P. 2003. *Estudos sobre a taxonomia e a distribuição dos peixes da família Myctophidae (Actinopterygii: Myctophiformes) no sudeste-sul do Brasil*. M.Sc. Thesis in Oceanography, Universidade de São Paulo, São Paulo, 108 pp.

- Santos, A.P. & J.L. Figueiredo. 2008. Guia de identificação dos peixes da família Myctophidae do Brasil. Edusp, São Paulo, 176 pp.
- Sassa, C., K. Kawaguchi, Y. Hirota & M. Ishida. 2004. Distribution patterns of larval myctophid fish assemblages in the subtropical-tropical waters of the western North Pacific. *Fish. Oceanogr.*, 13(4): 267-282.
- Schmid, C., H. Schäfer, G. Podestá & W. Zenk. 1995. The Vitória eddy and its relation to the Brazil Current. *J. Phys. Oceanogr.*, 25: 2532-2546.
- Silveira, I.C.A., A.C.K. Schmidt, E.J. Campos, S.S. Godoi & Y. Ikeda. 2001. A Corrente do Brasil ao largo da costa leste brasileira. *Braz. J. Oceanogr.*, 48: 171-183.
- Uiblein, F. & F. Bordes. 1999. Complex trophic interactions around oceanic islands. *Ocean Challenge*, 9: 15-16.
- Uyeno, T., K. Matsuura & E. Fujii. 1983. Fishes trawled off Suriname and French Guiana. Japan Marine Fishery Resource Research Center, Tokyo, 519 pp.
- Valentin, J.L., R. Paranhos, B.C.M.T. Faro & A.S.M. González. 2007. Massas d'Água. In: J.L. Valentin (ed.). Características hidrobiológicas da região central da Zona Econômica Exclusiva brasileira (Salvador, BA, ao Cabo de São Tomé, RJ). Sér. Doc. REVIZEE/SCORE-Central, Ministério do Meio Ambiente, Brasília, pp. 21-29.
- Vinnichenko, V.I. 1997. Russian investigations and deep water fishery on the Corner Rising seamount in subarea 6. *NAFO Sci. Countries Stud.*, 30: 41-49.
- Wang, J.T. & C. Tsung-Chen. 2001. A review of lanternfishes (Families: Myctophidae and Neoscolopelidae) and their distribution around Taiwan and the Tungsha Islands with notes on seventeen new records. *Zool. Stud.*, 40(2): 103-126.
- Wienerroither, R.M., F. Uiblein, F. Bordes & T. Moreno. 2009. Composition, distribution and diversity of pelagic fishes around the Canary Islands, eastern central Atlantic. *Mar. Biol. Res.*, 5: 328-344.
- Williams, A., J.A. Koslow, A. Terauds & K. Haskard. 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. *Mar. Biol.*, 139(6): 1177-1192.

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