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Zoogeography of the Lanternfishes (Osteichthyes, Myctophidae) of Southwest Africa

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Palabras clave: Myctophidae, zoogeografía, afloramiento, Corriente de Benguela.

SUMMARY: The lanternfishes (fam. Myctophidae) caught during five oceanographic fishing cruises carried out in the Southeast Atlantic between 1979 and 1982 are studied from the point of view of their zoogeography. Four of these cruises took place in the upwelling area of the Benguela Current off the coast of Namibia; during the fifth cruise an oceanic area was also explored, that of the Valdivia Bank, about 400 miles from the coast.

A total of 41 species were identified, 10 of which appeared only in the Benguela area, 25 only in the Valdivia Bank and 6 in both areas. The Benguela area showed a low specific diversity and the dominating species were: *Lampadena pontifex, Lampanyctus australis, Diaphus dumerilii, Symbolophorus boops, Lampanyctodes hectoris* and *Diaphus hudsoni*. The Valdivia Bank had a high level of diversity, and here the dominating species were: *Ceratoscopelus warmingii, Lampanyctus ater, Lepidophanes gaussi, Lampanyctus pusillus, Diaphus anderseni, Diaphus meadi, Scopelopsis multipunctatus* and *Notoscopelus resplendens*. This paper extends the known distribution of some of the species in the Atlantic.

The faunistics affinities of each of these two areas are analyzed. In the Benguela area, the upwelling regime imposes peculiar ecological conditions. Some of the aspects related to the lanternfishes that inhabit this area are commented upon.

RESUMEN: ZOOGEOGRAFÍA DE LOS MICTÓFIDOS (OSTEICHTHYES, MYCTOPHIDAE) DEL ÁFRICA SUDOCCIDENTAL. — Los mictófidos capturados en el curso de cinco campañas oceanográfico-pesqueras efectuadas en el Atlántico Sudoriental entre 1979 y 1982 se estudian desde el punto de vista de su zoogeografía. Cuatro de estas campañas tuvieron lugar en la zona de afloramiento de la Corriente de Benguela, frente a las costas de Namibia; en la quinta se exploró además una zona oceánica situada en el Banco de Valdivia, a unas 400 millas de la costa.

Se identificó un total de 41 especies, de las que 10 aparecieron sólo en la zona de Benguela, 25 sólo en la zona del Banco Valdivia y 6 en ambas zonas.

La zona de Benguela mostró una diversidad específica baja y las especies dominantes fueron: *Lampadena pontifex, Diaphus dumerilii, Lampanyctus australis, Symbolophorus boops, Lampanyctodes hectoris* y *Diaphus hudsoni*.

En la zona del Banco Valdivia se observó una diversidad elevada, apareciendo como especies dominantes: *Ceratoscopelus warmingii, Lampanyctus ater, Lepidophanes gaussi, Lampanyctus pusillus, Diaphus anderseni, Diaphus meadi, Scopelopsis multipunctatus* y *Notoscopelus resplendens*. Por el presente trabajo resulta ampliada la distribución en el Atlántico de algunas de las especies aparecidas.

Se analizan las afinidades faunísticas de las dos comunidades estudiadas. En la zona de Benguela, el régimen de afloramiento impone unas condiciones ecológicas peculiares, comentándose algunos de los aspectos relacionados con las especies de mictófidos que la habitan.

INTRODUCTION

The coexistence of a high number of species of the family Myctophidae in any oceanic area poses an interesting ecological problem (MOYLE and CECH, 1982), as the morphological differences between the different species are minimal and their nutrition is basically non-selective, using any planktonic prey of appropriate size (TYLER and PEARCY, 1975). There undoubtedly exists a certain bathymetric segregation, usually disguised by the catch methods used. However, as we see it, the adaptive differences of the larvae are more important for understanding the problem. As a matter of fact, the larvae of this family show a morphological diversity unreached by any other group of fishes, demonstrating a high level of specialization during this phase of their life, converging later in a general morphological type: the adult myctophid (Fig. 1). This is true to the extent that the systematic affinities within this family have been established in many cases through the study of the larval phases (MOSER and AHLSTROM, 1974).

In any case, the specific richness of this group makes it specially appropriate for zoogeographic studies similar to those carried out, more frequently, with different planktonic groups. Previous work studying myctophids in this sense are those by MCGINNIS (1982) in the Southern Ocean south of 30° S, those by BACKUS *et al.* (1977) and HULLEY (1981) in the Atlantic and by BARNETT (1984) in the Central Pacific.

The object of this particular work are the myctophids of the Namibia upwelling area and adjacent waters. The examples caught during five cruises carried out by the Instituto de Investigaciones Pesqueras de Barcelona in that area from 1979 - 1982 were studied. Four of these cruises took place in the area of the shelf and slope of the Namibian coast, covering the whole of the area, from the Cunene River to the Orange River (17° 30′ S to 29° S). The last one took place in oceanic waters near the Valdivia Bank, in an area situated about 400 miles from the coast and away from the influence of the Benguela Current, with the typical characteristics of the Subtropical Atlantic (Figure 2).

The systematics and detailed distribution of the species caught will be the object of a further paper. This paper will deal with the specific composition of the myctophids from the zoogeographic point of view and some of the aspects related to the upwelling systems in general are also commented upon.

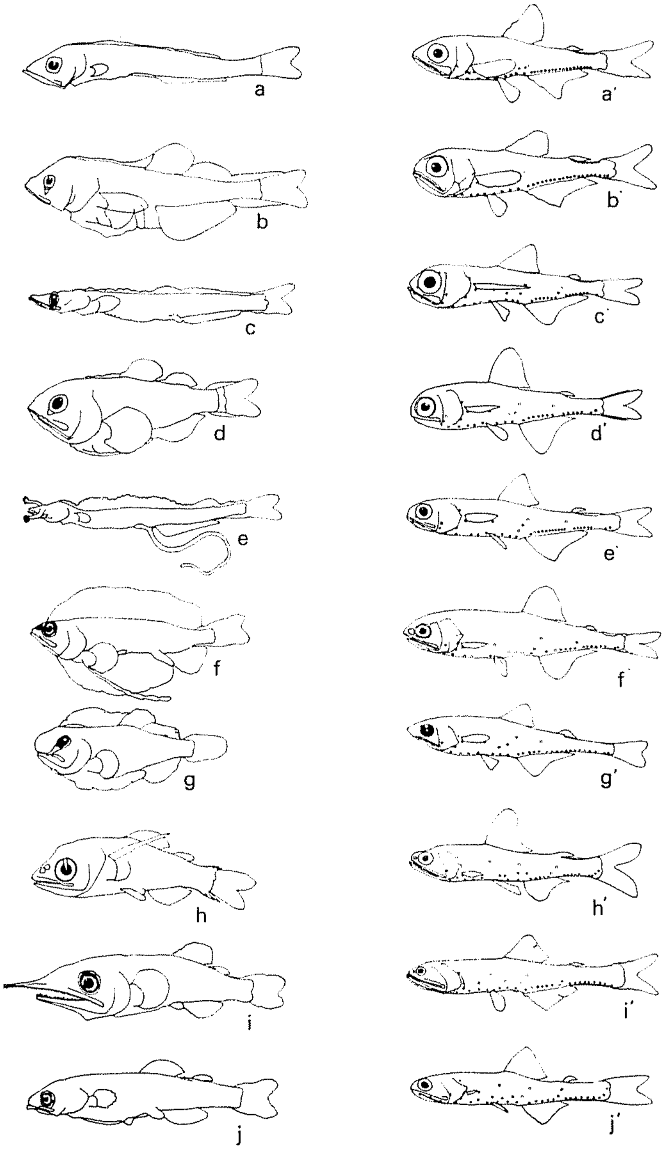

FIG. 1. — General morphology of larvae (left) and adults (right) of several species of Myctophidae: (a, a′) *Protomyctophum (P.) tenisoni*, (b, b′) *Electrona antarctica*, (c, c′) *Hygophum reinhardtii*, (d, d′) *Myctophum asperum*, (e, e′) *Myctophum aurolaternatum*, (f, f′) *Loweina rara*, (g, g′) *Centrobranchus choerocephalus*, (h, h′) *Idiolychnus urolampa*, (i, i′) *Lampanyctus achirus*, and (j, j′) *Triphoturus mexicanus*. A high morphological diversity of the larvae, showing very specialized structures, is easily observed opposite a relative uniformity of the adults. Chromatophores as well as other accessory details have been omitted and the scale is variable. a-j, from MOSER and AHLSTROM (1974) modified; a′, b′, i′, from ANDRIASHEV (1962) modified; c′, from BEKKER (1965) modified; d′, from NAFPAKTITIS and NAFPAKTITIS (1969) modified; e′, j′, from BOLIN (1939) modified; f′, from NAFPAKTITIS *et al.* (1977) modified; g′, from BEKKER (1964) modified; h′ from WISNER (1976) modified.

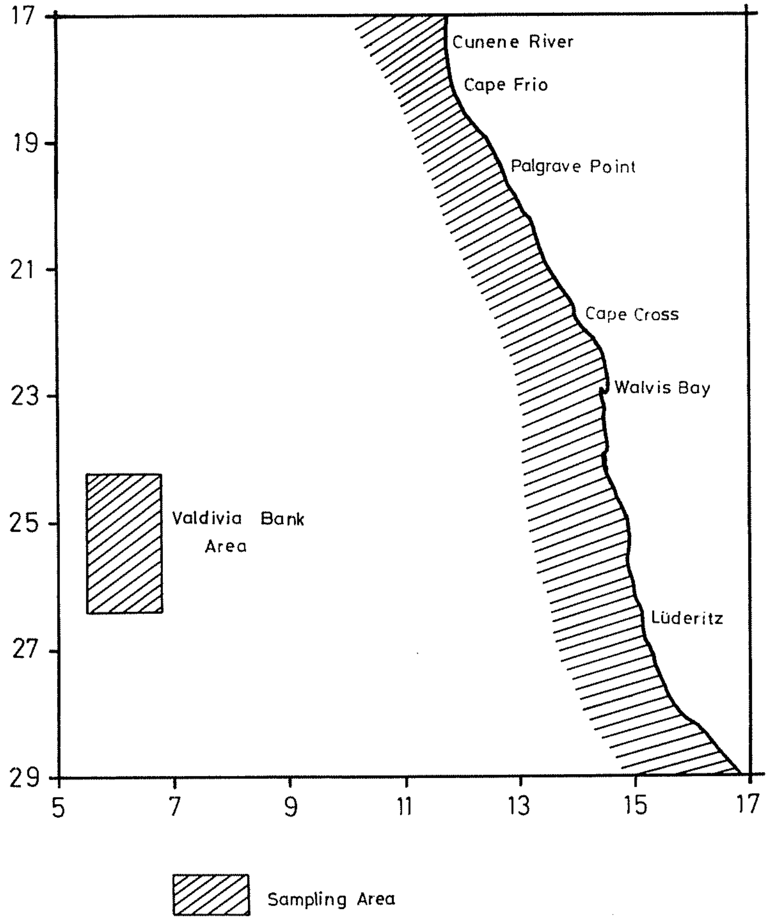

FIG. 2. — Map showing the areas covered by the samplings.

MATERIAL AND METHODS

A total of 1587 specimens were studied and their origin is given in Table 1 according to cruises, dates and areas.

Various catch methods were used, the specimens studied were distributed as follows:

— Bongo type plankton net: 13 specimens.
— IKMT type pelagic net (6 feet): 266 specimens.
— Trawl net (bottom and pelagic): 1138 specimens.
— Stomach contents of other fishes: 170 specimens.

TABLE 1

Origin of the specimens studied.

Cruise	*Date*	*Area*	*Number*
BENGUELA I	Nov. 1979	Shelf & Slope (19° 30′ S - 23° 00′ S)	42
BENGUELA II	Aug. - Sep. 1980	Shelf & Slope (17° 30′ S - 23° 00′ S)	407
BENGUELA III	Mar. - Apr. 1981	Shelf (17° 30′ S - 23° 00′ S)	269
BENGUELA IV	April 1981	Slope (17° 30′ S - 29° 00′ S)	478
VALDIVIA I	May 1982	Oceanic (Valdivia Bank) &	167
		Slope (23° 00′ S - 29° 00′ S)	180
Additional specimens from sampling onboard commercial trawlers			44
TOTAL			1587

Some of the specimens (814) were fixed and preserved in 6 % formaline and studied later in the laboratory. The remaining 773 were discarded after identification.

SPECIFIC COMPOSITION

As has already been mentioned, this study has been carried out in two areas, which, although they are very close to one another, are completely different with respect to their environmental conditions. Most of the samplings were taken in the upwelling area of the Namibian coast and 1420 of the 1587 specimens caught come from there (nearly 90 %), and the other 167 (nearly 10 %) come from the oceanic waters of the Valdivia Bank and surrounding area. This will allow us, by comparison, to observe some of the effects that the special conditions prevailing in the Benguela Current exercise on the faunistic composition of this area.

Table 2, which details the species caught in each of these areas, and their relative abundances, is worth commenting.

A total of 41 species was identified, 10 of which only appeared in Namibian waters, 25 only in the oceanic area of the Valdivia Bank, and 6 in both areas. Firstly, what stands out is the high number of species caught in the oceanic area compared to those caught in the waters of the Namibian coast, this is even more marked, bearing in mind the few castings carried out in the first of these areas, where only 10 % of the total of myctophids studied appeared. This aspect will be discussed in more detail later on.

Secondly, the small number of species common to both areas (6, repre-

TABLE 2

Specific composition of the *Myctophidae* caught in each of the two areas studied: Continental shelf and slope between 17° 30′ S and 29° S (Namibia) and Oceanic waters of the Valdivia Bank and neighbourings (Valdivia). Their relative abundance is shown by: *** very abundant, ** frequent, * scarce, — absent.

Species	*Namibia*	*Valdivia*	*Species*	*Namibia*	*Valdivia*
Metelectrona ventralis	*	—	*Lampadena pontifex*	***	—
Diogenichthys atlanticus	—	*	*Lampanyctus achirus*	—	*
Hygophum hygomii	*	*	*Lampanyctus ater*	—	***
Hygophum reinhardtii	—	*	*Lampanyctus australis*	***	*
Myctophum nitidulum	—	*	*Lampanyctus festivus*	—	*
Myctophum phengodes	*	*	*Lampanyctus intricarius*	**	*
Symbolophorus barnardi	*	*	*Lampanyctus isaacsi*	*	—
Symbolophorus boops	***	—	*Lampanyctus lineatus*	—	*
Symbolophorus evermanni	—	*	*Lampanyctus macdonaldi*	*	—
Loweina rara	—	*	*Lampanyctus pusillus*	—	***
Lobianchia dofleini	—	**	*Lampanyctus tenuiformis*	—	*
Diaphus anderseni	—	***	*Lepidophanes gaussi*	—	***
Diaphus dumerilii	***	—	*Bolinichthys indicus*	—	*
Diaphus holti	—	*	*Bolinichthys supralateralis*	*	—
Diaphus hudsoni	**	*	*Ceratoscopelus warmingii*	—	***
Diaphus meadi	—	**	*Lampanyctodes hectoris*	***	—
Diaphus ostenfeldi	*	—	*Notoscopelus caudispinosus*	—	*
Diaphus taaningi	*	—	*Notoscopelus resplendens*	—	**
Lampadena chavesi	—	*	*Lampichthys procerus*	—	*
Lampadena dea	—	*	*Scopelopsis multipunctatus*	—	**
Lampadena luminosa	—	*			

senting 15 % of the total), confirms that the two ecosystems under study are extremely different despite the fact that they are very close to one another. This will also be commented upon in more detail in the section on zoogeopraphy.

With respect to the species caught, the comments below only refer to innovations regarding their areas of distribution.

— *Metelectrona ventralis*. Typical of the area of the Subtropical Convergence of the three oceans (McGINNIS, 1982) and of the Chilean upwelling area (CRADDOCK and MEAD, 1970). This constitutes the most northern finding of this species up to date (20° 50′ S), and the first reference in the east Atlantic.

— *Symbolophorus barnardi*. Found between 30° and 40° S in the Atlantic (HULLEY, 1981) and common in the southern Benguela Current, this is the northernest reference of this species up to date (19° 30′ S).

— *Symbolophorus evermanni*. Tropical species of the Indian and Pacific Oceans (WISNER, 1976), has recently been detected in the South African east coast (HULLEY, 1984). However, this is the first time this species has been found in the Atlantic.

— *Diaphus hudsoni*. Common in the area influenced by the Benguela Current (HULLEY, 1981), this paper slightly extends its northern limit to 18° 01′ S.

— *Diaphus ostenfeldi*. Similar situation to that of *D. hudsoni*. Previously referred to in the Benguela Current (HULLEY, 1972), its northern limit is extended in this case to 18° 15′ S.

— *Lampadena luminosa*. Tropical species whose southern limit in the east Atlantic, owing to the influence of the Benguela Current, has been situated at 16° S (HULLEY, 1981). This work extends the southern limit to 25° 29′ S.

— *Lampanyctus macdonaldi*. Species of bitemperate distribution (HULLEY, 1981), registered previously in the southern region of Benguela (NAFPAKTITIS *et al.*, 1977). This is the most northern reference in this area (21° S).

— *Lampanyctus tenuiformis*. Tropical species. Catching this species at 25° 50′ S merits the same comments as those corresponding to *Lampadena luminosa*.

— *Bolinichthys supralateralis*. The same applies here as for *Symbolophorus barnardi* and *Diaphus hudsoni*, the northern limit of this species in the Benguela Current is slightly extended in this paper to 18° 14′ S.

— *Lampichthys procerus*. This is another case where catching this species at 25° 19′ S represents the northernmost reference in the Atlantic.

ZOOGEOGRAPHY

Table 3 groups the 41 species identified in this study, in accordance with their known distribution. The classification adopted is based on distributional data and criteria of previous authors, principally, WISNER (1976), BACKUS *et al.* (1977), HULLEY (1981) and BEKKER (1983).

TABLE 3

Zoogeopraphic patterns of the species of Myctophidae found during the present study, according to several authors (see the text). Left column: species caught in the Benguela area. Right column: species caught in the Oceanic area. Ranking species in each area are indicated by (*).

I. Pseudoceanic Pattern		
A. Cold Water Species		
	Lampanyctodes hectoris (*)	
B. Warm Water Species		
	Diaphus dumerilii (*)	
	Diaphus taaningi	
	Lampadena pontifex (*)	
II. True Oceanic Species		
A. Subantarctic Pattern		
	Metelectrona ventralis	*Diaphus hudsoni*
	Symbolophorus boops (*)	*Lampadena dea*
	Diaphus hudsoni (*)	*Lampanyctus achirus*
	Lampanyctus australis (*)	*Lampanyctus australis*
		Lampichthys procerus
B. Temperate Pattern		
	Diaphus ostenfeldi	*Diaphus holti*
	Lampanyctus intricarius (*)	*Diaphus meadi* (*)
	Lampanyctus macdonaldi	*Lampanyctus intricarius*
C. Subtropical Pattern		
	Hygophum hygomii	*Hygophum hygomii*
	Myctophum phengodes	*Hygophum reinhardtii*
	Symbolophorus barnardi	*Myctophum phengodes*
		Symbolophorus barnardi
		Diaphus anderseni (*)
		Lampadena chavesi
		Lampanyctus ater (*)
		Lampanyctus festivus
		Lampanyctus pusillus (*)
		Lepidophanes gaussi (*)
		Bolinichthys indicus
		Scopelopsis multipunctatus (*)
D. Subtropical-Tropical Pattern		
	Bolinichthys supralateralis	*Loweina rara*
		Lampanyctus lineatus
		Cerastoscopelus warmingii (*)
		Notoscopelus caudispinosus
		Notoscopelus resplendens (*)
E. Tropical Pattern		
	Lampanyctus isaacsi	*Myctophum nitidulum*
		Symbolophorus evermanni
		Lampadena luminosa
		Lampanyctus tenuiformis
F. Widespread Pattern		
		Diogenichthys atlanticus
		Lobianchia dofleini

1. THE OCEANIC AREA COMMUNITY (VALDIVIA)

As has already been mentioned, the most outstanding aspect is the high number of species found in the Valdivia Bank area and surrounding waters, despite the small number of samplings carried out in the area in this work.

The area under study presents the characteristics which are typical of the Subtropical Atlantic and most of the species which appeared correspond to this faunistic region. All the species marked as prevailing in Table 3, except *Diaphus meadi*, fall into the groups corresponding to Subtropical or Subtropical-Tropical distribution patterns.

The group of subantarctic species which appears in this area indicates a certain influence of the currents coming from the Convergence area. All of these species were caught in very small numbers.

Some of the tropical distribution species also reach this area sporadically. The presence of *Symbolophorus evermanni*, referred to for the first time in the Atlantic, poses a problem with respect to its origin and may be suggests a certain faunistic influence of the Indian Ocean in this area.

2. THE BENGUELA CURRENT COMMUNITY

Despite the low number of species which make up this community, the specific composition is most interesting and reflects a high heterogeneity of faunistic influences.

On the one hand there is a small group of species which, owing to their high level of dependency on the more coastal areas, is classified under the epigraph of pseudoceanic species (HULLEY, 1981). All of them reach high biomass levels. Particularly outstanding is *Lampanyctodes hectoris*, the only real inhabitant, within this group, of the waters of the Benguela Current as such. This species is partially exploited by the South African and Namibian mixed purse seine fisheries (CENTURIER-HARRIS, 1974; CRAWFORD, 1980; CRUICKSHANK, 1985) and is virtually the only shelf lanternfish from the southern end of Africa up to Walvis Bay (23° S), reaching 19° S. From Walvis Bay up north this group of pseudoceanic lanternfishes is dominated by the three species typical of warm waters (*Diaphus dumerilii*, *D. taaningi* and *Lampadena pontifex*), probably as a result of the influence of the Angola Current. It is worth mentioning that although *D. dumerilii* does not behave like a pseudoceanic species in other areas of the Atlantic, in these waters it forms an isolated population which poses systematic problems (HULLEY, 1981) and may be it merits its own taxonomic status. We should also mention that *D. taaningi*, although very scarce in our samples, is considered by O'TOOLE (1976) to be the most abundant in this area of northern Namibia, although this author does point out that the prevalence only occurs during the summer months, coinciding with the relaxing of the upwelling system and the maximum reach south of the Angola Current.

The group of truly oceanic species are dominated by species of subantarctic or temperate distribution, which here reach lower latitudes than in other Atlantic areas, thanks to the Benguela Current. The same applies here as to the previous group, the few species which make up the group nearly all form numerous populations.

Here also, as in the case of the pseudoceanic species, seasonal intrusions of the Angola Current make it possible for some subtropical and tropical elements to appear, although sporadically, and in general limited to the most northern part of the area under study.

Latitudinal distribution of the species found is not homogenous, except in some cases (*Diaphus ostenfeldi, Lampanyctus australis*). Bearing in mind only those species which appeared with certain frequency, it is possible to distinguish those which prefer the cold waters of Benguela from those which inhabit the most northern area, periodically influenced by the warm Angola current. In the same sense, ROEL *et al.* (1985) found, on analyzing the bottom fish communities, a faunistic discontinuity at 19° S. In the case of the lanternfishes, this limit seems to be somewhat further south (Fig. 3), although our data are not sufficient to specify this.

Another interesting aspect of an upwelling system such as the one we are dealing with is that, as it has environmental characteristics which are very

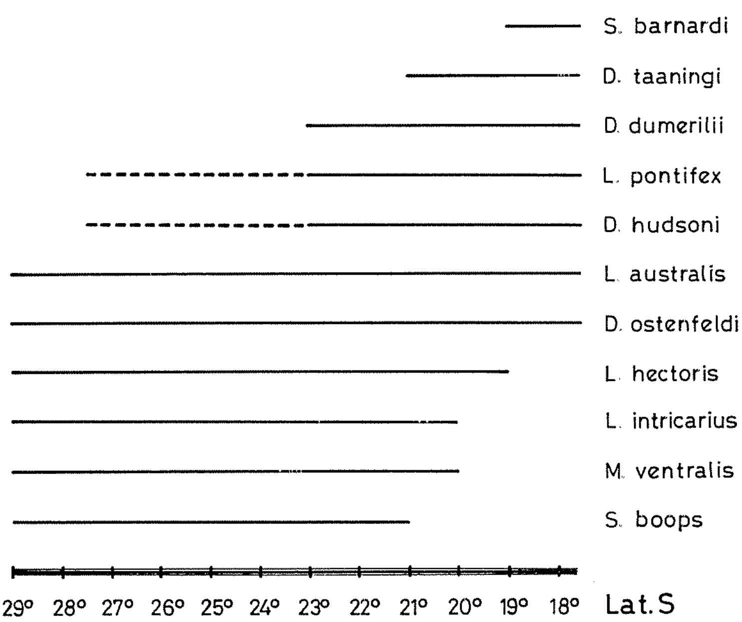

FIG. 3. — Diagram showing the latitudinal distribution found in our samplings for the significant species of Myctophidae of the northern Benguela system. Broken lines indicate sporadic findings.

different to those of the surrounding areas, the populations which inhabit it become isolated with respect to the general distribution of the species in question. This leads to speciation processes which are reflected in differences in morphological or meristic characters. *Diaphus dumerilii* has already been mentioned, in this case the Namibian population poses taxonomic problems. The same can be said for *Lampanyctus australis*, whose differences compared to populations of other areas are presently under study (RUBIÉS, under preparation), and to a lesser degree, for *Symbolophorus barnardi* and *Lampadena pontifex* also.

Finally, it would seem appropriate to make further comments regarding the low number of myctophid species which inhabit the Benguela Current. This is undoubtedly due to the restrictive conditions imposed by the upwelling system. Also as this is a high production level area, those species which manage to continue inhabiting it give rise to quite large size populations.

What are these restrictive conditions? From a very general point of view, we can argue, following the opinions expressed by MARGALEF (1978), that the upwelling centers and surrounding areas are somewhat immature systems, in which it is not possible to reach a high level of organization, where the trophic chains are kept short and where the opportunistic species (*r* strategists) are at an advantage. All this, by necessity, limits the number of species to a low level.

If we go down and look for more immediate causes, several factors can be mentioned of unknown relative importance, which hinder many species inhabiting the Benguela Current: temperature, limiting oxygen concentration at certain depths, transport and dispersion of eggs and larvae, etc. Here we will deal with only one of these factors, that related to feeding.

Table 4 includes data relative to the total number of gill rakers in the first branchyal arch obtained from the specimens studied and comparisons are made with the species caught in the Benguela system and the congeneric species caught in the oceanic area of the Valdivia Bank.

An important fact is quite evident: almost without exception, all the species in the upwelling area have a greater number of gill rakers than the congeneric species found out of it, or, in other words, for a lanternfish to inhabit the upwelling system it seems to need a high number of rakers. It is interesting to note that this is also the main difference observed between the *Diaphus dumerilii* and the *Lampanyctus australis* populations of Namibia and the populations of these species in other areas.

This anatomic feature common to all the lanternfishes of the Benguela Current must have an ecological reason. The idea of associating a well developed gill raker system with a plankton eating regime is very old, although exceptions can be mentioned which are adaptations which substitute the gill rakers as for example, the tubular mouth of the Syngnathidae (SUYEHIRO, 1942). Although a connection between gill raker modifications and the trophic position of the fishes cannot be denied, precise relationships between the type

TABLE 4

Comparison of gill rakers counts between congeneric species of lanternfishes found in the Benguela Current (Namibia) and Oceanic (Valdivia Bank) areas.

Genus	Benguela Current		Both areas		Valdivia	
Metelectrona	*M. ventralis*	23-27			*M. herwigi*	21-23
Hygophum			*H. hygomii*	20-21	*H. reinhardtii*	18-19
Myctophum	*M. phengodes*	24-27			*M. nitidulum*	15
Symbolophorus	*S. boops*	20-24	*S. barnardi*	17-19	*S. evermanni*	20
Diaphus	*D. dumerilii*	24-28			*D. anderseni*	16-18
	D. hudsoni	23-26			*D. holti*	18
	D. ostenfeldi	23-26			*D. meadi*	17-18
	D. taaningi	22-24				
Lampadena	*L. pontifex*	21-27			*L. chavesi*	21
					L. dea	20
					L. luminosa	14
Lampanyctus	*L. australis*	21-27	*L. intricarius*	13-15	*L. australis*	21
	L. isaacsi	17			*L. achirus*	16
	L. macdonaldi	23			*L. ater*	15-18
					L. festivus	14
					L. lineatus	17
					L. pusillus	12
					L. tenuiformis	14
Bolinichthys	*B. supralateralis*	21-22			*B. indicus*	14

of food and its size on the one hand, and the length, number and separation of the rakers have not been proved (HYATT, 1979). However, amongst very closely related species, as in our case, these relationships should work better and it does not seem unreasonable to assume that the higher the number of gill rakers the smaller the particles of food, at least amongst species of the same genus. This hypothesis adequately coincides with the characteristics of the plankton of an upwelling system such as the Benguela system, where there exists a great abundance of small planktonts and therefore it must be an advantage to be equipped with a system capable of retaining these particles.

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