Planktonic stages of lanternfishes (Osteichthyes, Myctophidae) in the Benguela upwelling region*

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Key words: Lanternfishes, ichthyoplankton, development, distribution, Benguela upwelling
Palabras clave: Mictófidos, icrioplancton, desarrollo, distribución, afloramiento de Benguela

SUMMARY: A comprehensive survey of the planktonic stages of the myctophids in the Benguela upwelling region has been carried out. Plankton samples collected on a total of thirteen cruises effected in different seasons of the year between 1979 and 1986 were examined. This paper sets out the species whose eggs or larvae were identified and contains descriptions of species not previously reported in the region together with a detailed discussion of the identification process for each. In addition, information is provided on the egg and larval distribution and abundance of each species. Larvae of 26 distinct myctophid species were found, 16 of which were identified to species level. Detailed descriptions of the larvae of Hygophum macrochir, Protonycotothypum (Hierops) chilensis and various species of the genera Hygophum, Lampangiuctes and Notoseopelus are included. The distribution and abundance of myctophid larvae in the Benguela region coincided rather closely with the distribution and abundance pattern for myctophid adults, with greatest species diversity and larval concentrations over the continental slope, although the eggs and larvae of Lampanyctodes hectoris were also extremely abundant on the continental shelf outside the 200 m isobath.

RESUMEN: ESTADOS PLANCTONICOS DE LOS MICTOFIDOS EN LA REGION DEL AFLORAMIENTO DE BENGUELA. Se ha realizado un estudio exhaustivo de las fases planctónicas de los mictófidos del afloramiento de Benguela. Se han examinado las muestras de plancton obtenidas en un total de 13 campañas realizadas en diferentes estaciones del año entre 1979 y 1986. En este trabajo se presenta la lista de especies identificadas como huevos o larvas, y se incluyen descripciones de las larvas de aquellas especies que no habían sido citadas previamente en la región y una amplia discusión sobre la identidad de cada una de ellas. Por otra parte, se ofrece información sobre la distribución y abundancia de dichos huevos y larvas. Han sido identificadas las larvas de 26 especies distintas de mictófidos, 16 de las cuales pudieron llegar a reconocerse a nivel específico. Se presentan descripciones detalladas de las larvas de Hygophum macrochir, Protonycotothypum (Hierops) chilensis y de varias especies de los géneros Hygophum, Lampanyctes y Notoseopelus. Por lo que se refiere a sus patrones de distribución y abundancia, se concluye que la distribución de las larvas de mictófidos en la región de Benguela coincide bastante bien con la señalada para los adultos, presentándose tanto la mayor diversidad de especies como las mayores concentraciones de sus larvas sobre el talud continental, aunque los huevos y las larvas de Lampanyctodes hectoris son también muy abundantes en la región de la plataforma, desde la isobata de 200 m.

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INTRODUCTION

Myctophids are mesopelagic or bathypelagic fishes, the biomass of which may be higher than that of all other families of marine vertebrates combined (AHLSTROM et al., 1976). This group of fishes is extremely abundant in all oceans. Myctophid larvae are caught practically in every plankton haul from the open sea and commonly make up a substantial share of plankton samples (AHLSTROM, 1971, 1972; NELLEN, 1973; RICHARDS, 1974; JOHN, 1985). In the Benguela region myctophids are the primary food source for a large number of fish species (CENTURIER-HARRIS, 1974; CRAWFORD, 1980; MACPHERSON, 1983).

According to HULLEY (1986a, b), up to 125 different species of lanternfish may be present in the waters off South Africa. In the Benguela Current region, and more specifically over the continental shelf, *Lampanyctodes hectoris* (GUNTHER, 1876), stands out because of its abundance. This species is used for fish meal (CENTURIER-HARRIS, 1974). The Benguela upwelling region contains other myctophid species, among which *Symbolophorus boops* (RICHARDSON, 1845), *Lampanyctus ater* TÄNING, 1928, *Diaphus hudsoni* Zurbrig & Scott, 1976, and *Lampanyctus australis* TÄNING, 1932 are significant in view of their abundance (HULLEY, 1981; RUBIES, 1985).

To the North of Walvis Bay in the northern most part of the Benguela region, the myctophid fauna changes substantially and is dominated by warm-water species, such as *Lampadena pontifex* Krefft, 1970, *Diaphus dumetilii* (BleeKer, 1856) and *D. taansing* Norman, 1930 (RUBIES, op. cit.).

HULLEY (1981, 1986a) and RUBIES (personal communication) provide the most extensive compilations dealing with myctophids in the Benguela upwelling region. AHLSTROM et. al. (1976), OLIVAR and RUBIES (1986) and OLIVAR (1987), have considered the systematics of myctophid larvae, while AHLSTROM et al. (1976), OLIVAR (1985) and SHELTON (1986), have reported on larval distribution and abundance.

The most common myctophid in this study was *Lampanyctodes hectoris*, the eggs and larvae of which were present in most samples and at most stations. The list of species recorded in the study is given in table I.

The distribution of myctophid larvae in the Benguela region coincides with that reported for the adults, and corresponds fairly closely with the 200 m depth contour. The greatest densities have been recorded in deeper oceanic waters (CRUICKSHANK, 1985).

The criteria used to identify larvae were those used by MOSER and AHLSTROM (1970, 1972, 1974) and MOSER et al. (1984). Not all larvae could be identified to species level, sometimes because only very few or very small larvae were caught, as in the case of the genera *Benthoemia, Electrona, Boli- nichthys, Ceratoscopelus, Diaphus, Gymnoscopelus, Lampadena,* and Lepido-
phanes, other times because the larvae collected did not match exactly any previously described species and not enough transformation stages were available as with the specimens grouped as Lampanyctus sp. and Notsocopelus sp.

**TABLE I**

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<th>Benguela I</th>
<th>Benguela II</th>
<th>Benguela III</th>
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<th>Benguela IV</th>
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**Note:** The table entries indicate the presence (+) or absence (-) of each species in the respective cruises.
MATERIALS AND METHODS

Plankton samples were collected (table II) between 1979 and 1986 in the waters of the Benguela upwelling region. The present study include both systematic aspects and larval distribution and abundance.

Table II also sets out the study area and the season for each of the surveys, together with the types of nets employed. Generally speaking, hauls made with bongo nets were oblique from a depth of 200 m to the surface; those made with multiple RMT 1 x 6 nets were also oblique between 200 m and the surface, but in this case depth intervals were selected according to the hydrographic profile, covering the regions above the thermocline, in the thermocline, about 30 m below the thermocline, and between 200 m and this latter depth.

Identification of eggs and larvae species was based on the descriptions available in the literature. For those species for which no previous descriptions were available, discussions of the characters leading to identification have been included.

Morphometric examination mainly took the following measurements into account: standard length (SL), the distance between the tip of the upper jaw and the end of the urostyle; preanal distance (PA), the distance between the tip of the upper jaw and the anus; body depth (BD), the perpendicular depth of the trunk at the anus; head length (HL), the distance between the tip of the upper jaw and the cleithrum; and dorsal origin distance (DD), the

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<th>Cruise</th>
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distance between the tip of the upper jaw and the onset of the dorsal fin. The indicated abbreviations will be used through the Systematic Account whenever these characters are referred to. Any unspecified larval length always means SL. Classification of the species was based on the criteria used by HULLEY (1981).

**SYSTEMATIC ACCOUNT**

**Subfamily MYCTOPHINAEE**

*Protomyctophum (Hierops)? chilensis* (LÖNNBERG, 1905)

Adults of the genus *Protomyctophum (Hierops)* reported in the Southeast Atlantic include *P. (Hierops) subparallellum* (TÄNING, 1932) and *P. (Hierops) parallellum* (LÖNNBERG, 1905) (HULLEY, 1972, 1981). No adults of this genus were taken either (RUBIÉS, 1985), but the bongo net hauls did yield some larvae attributable to the genus *Protomyctophum (Hierops)*, though not to either of the two above-mentioned species, the larvae of which have been described by PERTSEVA-OSTROUMOVA (1967), MOSER and AHLSTROM (1974) and BELYANINA and KOVALEVSKAYA (1979). Our specimens were assigned to the genus *Protomyctophum* because of their similarity with previous descriptions of some larvae belonging to this genus, and to the subgenus *Hierops* because of their narrow eyes (PERTSEVA-OSTROUMOVA, 1967; MOSER and AHLSTROM, 1974), which differentiates the subgenus *Hierops* within *Protomyctophum* (MOSER and AHLSTROM, op. cit.).

**DESCRIPTION OF THE LARVAE OF Protomyctophum (H.)? chilensis**

Figure 1 presents the larval series for this species at lengths between 3.1 and 13 mm. The morphological data are given in table III.

The body is slender, especially in the smallest larvae, with body depth at the level of the anus less than 10% of SL in larvae smaller than 6 mm. Allometry of BD in relation to SL is significantly positive (fig. 2A), i.e., the body grows thicker as size increases.

The gut has the characteristic form common to the genus *Protomyctophum*, matching the description provided by MOSER and AHLSTROM (1974). It is conical in shape, having a broad anterior portion tapering down to a narrow terminal portion, the end detached and diverging ventrally, and the characteristic spirals of the myctophid gut clearly visible. The gut is between 40 and 52% of SL in the larger larvae between 8 and 15 mm long, though the ratio is somewhat lower in smaller larvae (fig. 2B). A certain space of from 1.2 to 0.3 mm separates the anus from the anal fin in larvae up to 13 mm in length, decreasing to 0.16 m by 15 mm SL. According to MOSER and AHLSTROM op. cit., the length of the gut increases greatly in the larvae of this
Fig. 1 — Larval series for *Protomyctophum* (Hierops) *chilensis*: A) 31 mm; B) 37 mm; C) 49 mm; D) 66 mm; E) 77 mm; F) 13 mm

genus in the later stages of larval development, filling the space between the anus and the anal fin.

The head is triangular. HL makes up a rather substantial proportion of SL as compared with other members of this genus. Of the known *Protomyctophum* larvae, only an 11 mm-long specimen of *P. (Hierops) chilensis* described by Moser and Ahlstrom (*op. cit.*) displayed a comparable HL. Allometry of HL in relation to SL is positive for larvae between 2.5 and 15 mm (fig. 2C). HD is also positively allometric with respect to SL (fig. 2D).
### TABLE III

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The eyes are narrow and elongate, and hence these specimens were assigned to the subgenus Hierops. The eye is placed transversally in the head, which has been recorded only in the larvae of P. (H.) chilensis. Each eye is surrounded by transparent tissue that is more conspicuous at the base of the eye. This character is distinguishable from the earliest stages of development onwards, but no choroid tissue is present at any time.

Pigmentation is present on the tip of the snout from the smallest to the largest larval stages collected. At first this pigmentation consists of a melanophore at the tip of the lower jaw, with another developing later on the tip of the upper jaw at a length of 6 mm.

The base of the pectoral fin bears pigmentation from the earliest to the largest stages (15 mm) found. The 11 mm-long larva described by MOSER and AHLSTROM (1974) lacked such pigmentation. Slight pigmentation is also observable on the pectoral fin rays in some specimens at lengths between 5 and 7 mm.

Spots consisting of small melanophores begin to appear laterally on the upper part of the head, on the base of the cleithrum, and in the region of the isthmus at 6.6 mm. Such pigmentation becomes darker with growth. On some specimens a faint, stellate melanophore is visible in the centre of the caudal tip.

Abundant pigmentation develops over the swim bladder at 7 mm.

The fin ray complement in adults is D11-13, A21-23, P15-17 (WISNER, 1976).

The caudal fin is the first to ossify. Using TAYLOR’s (1967) method of
clearing and staining, it was found that the anal fin rays do not start to ossify until 10 mm SL and that the dorsal fin rays do not ossify until 11 mm. The pectoral fin also begins to calcify at a length of around 10 mm (table III). The pelvic fins start to become visible at a length of 10 mm as well.

Photophore B13, the only one present on the larval stages becomes visible at a length of around 6.5 mm and is well-developed by about 7.5 mm.

Notochordal flexion commences at a length of around 6.5 mm and is complete by 7.5 mm.

There are 36 vertebrae plus the urostyle. Calcification of all the vertebrae is observable only in the 15 mm-long specimen (table III).

The complement of gill rakers in adult Protomyctophum (Hierops) chilenensis is 5 + 1 + 16 – 18 (Wisner, 1976) or 4 – 5 + 1 + 15 – 16 (Bekker, 1983).

After staining of larger specimens using Taylor's method (1967), the gill rakers on the first branchial arch became countable through the now-transparent outer tissues, and the following counts were obtained: 5 + 1 + 15 – 16 in the 13.8 and 14 mm-long specimens, 5 + 1 + 17 in the 15 mm-long specimen.
DISCUSSION

The exceptionally close morphological and pigmental similarity between the 11 mm-long *Protomyctophum (Hierops) chilensis* (Wisner, 1971) larva described by Moser and Ahlstrom (1974) and our specimens as described above suggests that the larvae in our samples belong to this genus and this species. In addition, the gill raker counts in the larger larvae match the formula for this species and are, moreover, too high for any other *Protomyctophum (Hierops)* species. Adults attain a length of only 38 mm (Wisner, 1976), and their small size together with the high-oceanic character of this genus (Hulley, 1981) may explain why they have yet to be reported from this area. On the other hand, since no adults of this species have hitherto been reported in the Atlantic, these larvae cannot be assigned with absolute certainty to the species *chilensis*, their strong similarity notwithstanding, and there remains the possibility that they are in fact the larvae of another *Protomyctophum (Hierops)* species whose adult form is still undescribed at this time.

It is likely that the larvae reported by Pertseva-Ostroumova (1967) south of the Cape of Good Hope, described as *Protomyctophum (Hierops)* sp., belonged to the same species as the larvae in our samples from the Benguela upwelling region, inasmuch as the morphological characters of the smaller larvae described by that author are quite similar to those of the larvae just described above, and the gill raker counts for her larger specimens (15-19 mm) also match those for *chilensis*.

LARVAL DISTRIBUTION OF P. (HIEROPS) *CHILENSIS*

Larvae were caught off Namibia on cruises conducted in November, August, May, July and January. The largest concentration of such larvae was located some 90 miles from the coast at around 20° S latitude on the Benguela II cruise (August). On the Valdivia cruise larvae of this species were caught at two stations on one of the lines between the Valdivia Bank and the Namibian shelf, more than 200 miles offshore. They were present off South Africa only in samples taken in the Austral summer, chiefly off Saldanha Bay.

According to Pertseva-Ostroumova (*op. cit*), species of the genus *Protomyctophum* spawn in spring-summer in the Southern Hemisphere. Our results indicate that in the Southeast Atlantic spawning is also intense in the Austral winter and that it takes place over the greater part of the year (table I), with autumn the least propitious season. Spawning was found to occur over the entire range sampled in waters beyond the 200 m isobath (fig. 3).
Fig. 3. — Larval distribution of *Protonyxctophum (Hierops) chilensis* in the Southeast Atlantic.

**Diogenichthys atlanticus** (TANING, 1928)

The adults of this species have a wide distribution in the Atlantic (Nafpaktitis *et al.*, 1977), but only one specimen was found in our samples of adults (Rubiès, 1985), this may have been due to their small size, of around 22 mm (Karnella, 1987).

Some larvae of this species were caught off Namibia, off South Africa, and on the Valdivia Bank transects (fig. 4A, table I). Larvae were present in several months and did not display a clear preference for any single season (table I). Spawning of this species off Bermuda has also been reported to take place throughout the year (Karnella, *op. cit.*).
Fig. 4. — A) Location of samples yielding *Diogennichthys atlanticus* larvae  B) Location of samples yielding *Hygophum? proximum* larvae  C) Location of samples yielding *Hygophum? bruuni* larvae  D) Location of samples yielding *Lampanyctus? isaaci* larvae
At those stations where sampling of various layers was carried out, larvae of this species were always caught at depths above 100 m. This agrees with the findings reported off Northwest Africa (John, 1985), in the California Current (Loeb et al., 1983), and off Bermuda (Karrella, op. cit.).

Genus Hygophum

According to Moser and Ahlstrom (1974), three types of larvae belong to the genus Hygophum. The first type consists of extremely elongate larvae, including those of *H. reinhardtii* (Lutken, 1892) and *H. atratum* (Garman, 1899). The second comprises moderately elongate larvae, i.e., *H. proximum* Bekker, 1965, *H. bruuni* Wisner, 1971, *H. benoiti* Cocco, 1838, and *H. hansenii* (Taning, 1932). The third type consists of relatively deep-bodied larvae, i.e., *H. macrochtir* (Günther, 1864) and *H. taaningi* Bekker, 1965. All three types were taken off northern Namibia, and one transformation stage of *H. hygomii* (Lutken, 1892).

A) Extremely elongate *Hygophum* larvae

Our larvae of this first type were differentiated from *H. atratum* larvae, which has never been reported from the Atlantic and whose larval development is known (Moser and Ahlstrom, 1970).

*Hygophum reinhardtii* (Lutken, 1892)

*H. reinhardtii* larvae were taken on the Valdivia Bank, some 400 miles off the coast of Namibia. The adults are widely distributed in the Atlantic, although they are found quite far offshore off South Africa (Bekker, 1983).

B) Moderately elongate *Hygophum* larvae

Larvae of this type show great diversity. Some have morphological characters and pigmentation exactly like those of larval *H. bruuni*, while others matched the larvae of *H. proximum* both described by Moser and Ahlstrom (op. cit.). To date no adults of either species have been reported in the Atlantic, and an extremely small number of such larvae were collected. This, and identification problems qualify our results as tentative.

Despite the large number of descriptions of larvae of this second type, some difficulties are still encountered when trying to differentiate larvae of *H. benoiti*, *H. hansenii*, *H. proximum* and *H. hygomii*, given the discrepancies in the descriptions of various authors. The following descriptions were used in the present study: Taning (1918) for *H. benoiti*, Moser and Ahlstrom (1974) and Pertseva-Ostrooumov (1974) for *H. proximum*; Shiganova (1977) for *H. hansenii*, Moser and Ahlstrom (op. cit.) and Balbontín and
ORELLANA (1983) for *H. brauni*; and TÂNING (1918), MOSER and AHLSTROM (op. cit.), and PERTSEVA-OSTROUMOVA (1974) for *H. hygornii*.

**Hygophum? proximum**

The larvae assigned to this species were taken in the samples collected on the Valdivia survey and the West Coast Hake Biomass survey in June 1983 (fig. 4B, table I).

*Hygophum proximum* is one member of the *macrochir* complex, which includes the species *H. macrochir*, *H. taningi Beker*, *H. proximum Beker*, possibly *H. atratum* (Garman), and perhaps a further two species (Hulley, 1981). This species has been reported in the Indian and Pacific Oceans in both Hemispheres (Beker, 1983), but it has not been recorded in the Atlantic. Larval identification was made on the basis of an 8.9 mm-long specimen described by MOSER and AHLSTROM (1974). Figure 5A shows one of our specimens from the Southeast Atlantic.

*H. proximum* larvae are very similar to *H. hygornii* larvae. The characters used to differentiate the two were the presence of dark choroid tissue at the base of the eye in *H. proximum*, compared with transparent choroid tissue in *H. hygornii* (Moser and Ahlstrom, op. cit.), and the presence of photophore Br₂ in larvae smaller than 11 mm, the length at which this photophore appears in *H. hygornii* larvae (Tâning, 1918).

The larvae of *H. proximum* (Moser and Ahlstrom, op. cit.; Pertseva-Ostroumova, 1974) and *H. hanseni* (Shigano, 1977) also exhibit great similarity with respect to pigmentation patterns and even morphological characters. They are differentiated by photophore Br₂ which appears earlier in *H. proximum*. All the specimens caught measured between 7 and 8 mm, and all possessed photophore Br₂ and thus could not be *H. hanseni*, even though the latter is abundant in the Subtropical Convergence (Hulley, 1981).

![A] Hygophum proximum larva of 7.8 mm SL caught in the Southeast Atlantic

![B] Hygophum brauni larva of 8.9 mm SL caught in the Southeast Atlantic

**Fig 5** — A) *Hygophum? proximum* larva of 7.8 mm SL caught in the Southeast Atlantic

**B) Hygophum? brauni** larva of 8.9 mm SL caught in the Southeast Atlantic
Finally, the larvae in our samples are distinguishable from those of *H. benoiti* (which has not been recorded in the region) in that they lack the melanophores on the tips of the jaws present in *H. benoiti*.

**Hygophum hygomii** (Lütken, 1892)

One transformation stage was caught on the Benguela II survey (21°00' S, 12°15' E). It was assigned to this species on the basis of the description by Nafpaktitis et al. (1977). The species is widely distributed in the study area (Bekker, 1983; Rubíes, 1985).

**Hygophum? brunii**

According to Bekker (1983), *H. brunii* is found off the coast of Chile. The larvae assigned to this species matched the description of a 9.7 mm-long larva described by Moser and Ahlstrom (1974) and the larval series between 3.8 and 13.7 mm presented by Balbontín and Orellana (1983). Figure 5B shows a larva from the Southeast Atlantic, and figure 4C depicts the locations where larvae of this species were caught, all situated in the southern part of the Benguela region. In his paper on the spawning strategies of the fishes in the southern Benguela region, Shelton (1986) referred to the presence of larvae of an *Hygophum* species which he termed *Hygophum? brunii*.

C) Relatively deep-bodied *Hygophum* larvae

**Hygophum macrochir** (Gunther, 1864)

The larvae of this species were identified based on their similarity with a 7.3 mm-long larva of this species previously described by Moser and Ahlstrom (1974).

*H. macrochir* is a member of the *macrochir* complex. Differentiation of the adults and juveniles of these species is difficult; in contrast, the larvae are clearly distinct and readily identifiable.

Because adults of this species have not hitherto been recorded so far south, a thorough description of the larvae and juveniles collected off Namibia was prepared, and it was found to match completely the description made by Moser and Ahlstrom (1974). This species has not been recorded among adult myctophids from the Southeast Atlantic (Hulley, 1981; Rubíes, 1985), and Bekker (1965) suggested that its southern limit might be placed at 11°28' S. Nevertheless, the presence of *H. macrochir* larvae off northern Namibia had been reported earlier by O'Toole (1976).

Figure 6 illustrates the larval series along with a juvenile of this species. Table IV gives their morphometric and meristic characters.
Fig 6. — Larval series for *Hygophum macrorchir*. A) 3.5 mm; B) 5.4 mm; C) 7.6 mm; D) 11.0 mm; E) 14.4 mm

The smallest specimen in our samples is 3.5 mm long. The bodies of the smallest larvae are rather elongate, but with development the body grows thicker. The allometric relationships between BD and SL and HD and SL are significantly positive (figs. 7A and 7B). In MOSER and AHLSTROM’s (1974) description of *Hygophum macrorchir*, the larvae were considered relatively deep-bodied. Head depth represents 15% of SL at 3 mm, increasing to 27% at 16.5 mm, while body depth increases from 15% to 34% of SL.

Head length also has a significant positive allometric relation with SL during larval growth, increasing from 20% of SL in 3 mm-long larvae to 31% in 16 mm-long larvae (fig. 7C).

The gut extends somewhat beyond the midpoint of the body in all stages of larval development and is equal to between 59 and 61% of SL. The relationship between PA and SL is isometric (fig. 7D). The foregut consists of a narrow tube; the hindgut is thicker and displays the spiral musculature typical of the larval myctophid gut.

The position of the dorsal fin shifts forward during larval development, and the allometry of predorsal distance with respect to SL is thus significantly negative.
TABLE IV

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Though elongate eyes are a character of the larvae of Myctophinae, they are hardly discernible in *H. macrochir* larvae. The eyes are most elongate in the smallest larvae. Significantly negative allometry can be observed during development between depth of eye (DE) and eye diameter (ED). Eye diameter, in turn, is positively allometric with respect to SL, while the relationship between ED and HL is nearly isometric. No choroid tissue is visible in the eyes of the larvae examined in this study, thus agreeing with the findings of MOSER and AHILSTROM (1974) for the specimen they described.

Onset of notochordal flexion takes place in the larvae at a length of around 5.5 mm and is complete at 6 mm.

In the smallest larvae only the primordial fin, surrounding the body from the occipital region to the anus, is visible. The primordial fin remains present on the dorsal region even in the largest larvae caught, in which the dorsal fin rays had already ossified.

The adipose fin becomes barely visible in larvae, at around 8 mm.

Caudal fin development precedes formation of the other fins. Subsequentially, the pectoral, anal and dorsal fin rays become discernible. From 7 to 10 pectoral fin rays were visible in some specimens at about 6 mm. Dorsal and anal fin rays were counted systematically in all the specimens examined (table IV). The dorsal fin rays do not begin to form until about 7.5 or 8 mm, and the final complement is not complete until 10 or 11 mm. The anal fin rays start to become countable at around 6 mm, and the smallest size at which the adult complement was found was 11 mm.
Pelvic fins are not present in any of the larvae examined and have been observed only in juveniles.

The most characteristic feature of the pigmentation pattern on these larvae is the cluster of melanophores in the region around the end of the gut. In the smallest larvae the pigmentation in this region consists of a single dark melanophore located dorsally above the anus. In front of this melanophore there is a group of small, stellate melanophores extending along the gut and over the ventral region of the body, sometimes reaching the midpoint of the body. With growth this pigmentation is gradually lost, and only that on the posterior half of the gut remains.

Moser and Ahlstrom (1974) indicated that H. macrochir larvae lacked postanal pigmentation. However, the smaller larvae caught in the Southeast Atlantic (between 3 and 4.5 mm, sometimes even up to 5 mm) exhibit one, two or three small melanophores in the immediate vicinity of the anus. Even in the very smallest larvae there are sometimes two or three small melanophores in this same region, but on the primordial fin, shown in figure 6A. None of the larvae larger than 5 mm have postanal pigmentation.
The smallest larvae also exhibit a diffuse melanophore at the base of the cleithrum that expands with growth towards the base of the head and the distal end of the foregut.

One or two melanophores are distinguishable towards the margin of the operculum in larvae larger than 6 mm. These melanophores are not mentioned in the larval description by Moser and AHLSTROM (op. cit.). On the other hand, the pigmentation on the hindbrain shown in their 7.3 mm-long larva is not discernible in any of our specimens.

The tip of the lower jaw is pigmented in all the larvae examined. In specimens larger than 5.5 mm the tip of the upper jaw is also pigmented.

Photophore Br3 appears at a length of around 8 mm, and it is still the only photophore in the largest larvae (16 mm SL) taken. The pattern of photophores on the juveniles examined matches that on the adults of this species (fig. 6D).

**Larval distribution and abundance of Hygophum macrochir**

*Hygophum macrochir* larvae were found off the northernmost part of Namibia on cruises carried out in autumn and winter (table I). The distribution area was outside the 1000 m isobath north of 24° S (fig. 8). The larvae of this species were concentrated in the uppermost layers of the water column, above the thermocline.

**Genus Symbolophorus**

Larvae of *Symbolophorus boops* (Richardson, 1845) and another, not yet identified *Symbolophorus* species were found in the Benguela upwelling region. The *S. boops* larvae from this region were described by Olivar and RUBIES (1986), who reported that the larval distribution of this species extended up to the mouth of the Cunene River. However, examination of additional larvae from this latter area has brought to light certain differences in pigmentation, which suggests that these larvae might in fact belong to another *Symbolophorus* species. According to the location of the larvae, this species could probably be *S. barnardi*, whose adults have been found in the same area (Rubies, 1985). Still more material is needed for a specific identification.

Spawning of *S. boops* seems to extend over the greater part of the year, with the largest concentrations located beyond the 500 m isobath (Olivar and Rubies, 1986).

In their vertical distribution the larvae displayed a preference for the uppermost layers of the water column, although individuals were captured throughout the upper 100 m.
Subfamily LAMPANYCTINAE

**Diaphus hudsoni** Zubrige & Scott, 1976

*Diaphus hudsoni* larvae were described by Olivari (1987). The distribution area of these larvae extended from 19° S latitude to Cape Point, with maximum concentrations located outside the 400 m isobath. Spawning appears to take place throughout most of the year (Olivari, *op. cit.*).

**Lobianchia dolleini** (Zugmayer, 1911)

One larva of this species, measuring 9 mm SL, was taken off the mouth of the Orange River (29°20' S, 14°12' E), in an area outside the 1000 m isobath.
Another two individuals measuring between 4 and 5 mm were caught at stations in the vicinity of the Valdivia Bank (23°08′ S, 10°01′ E and 23°14′ S, 09°00′ E).

Identification was based on an 8.2 mm-long larva described by Moser and Ahlstrom (1974). Sampling yielded no adult specimens off Namibia but did yield adults in the deepest part of one of the transects lines out to the Valdivia Bank (Rubies, 1985).

**Loweina rara** (Lutken, 1892)

Adults of this species were found by Rubies *(op. cit.*.) on the Valdivia Bank, but not in the vicinity of upwelling. According to Hulley (1981), the distribution of adults of this species can be regarded as circumglobal between 20° N and 20° S. One larva measuring 23.2 mm SL was caught at a station located at 26°00′ S, 13°34′ E where bottom depth was 686 m. The specimen was taken using an RMT 1 × 6 net at a depth between 150 and 200 m. Identification was based on the description of *Loweina rara* larvae provided by Moser and Ahlstrom (1970).

Genus *Lampanycus*

For some time *Lampanycus* species in which adults have extremely small pectoral fins were regarded as belonging to a distinct genus, *Nannobrachium* (Gunther, 1887), but in recent studies on this group (Paxton, 1979; Moser et al., 1984) they have been reclassified under the genus *Lampanycus*. The larvae of this group of species are quite characteristic because of the specialization of their jaws (Moser et al., *op. cit.*).

*Lampanycus* species present in our samples are discussed below. The larvae of this genus have been divided into two groups:

a) larvae with pointed jaws and prominent teeth, belonging to species in which adults are characterized by extremely short pectoral fins;

b) larvae with less prominent jaws, belonging to species in which adults have pectoral fins of normal size.

The larvae of species in the former group included *L. ater* and others not previously described which we feel may belong to *L. isaacsi*. Larvae in the latter group included *L. pusillus* and others referred to as *Lampanycus* sp. I which could not be classified because their characters do not conform to any previous descriptions of larvae of this genus and because of the lack of transformation stages.

Genus *Lampanycus* (with short pectoral fins)

**Lampanycus ater** Tanning, 1928

The larvae of this species were described by Zadovetsky (personal communication), who kindly furnished information on the larval series
before publication of her paper. The most characteristic morphological features of the larvae taken in the Southeast Atlantic are: the presence of spines on the operculum; the extremely long jaws with prominent teeth, even in the smallest larvae; and the rather long pectoral fins.

Pigmentation consists basically of a large dorsal melanophore located a little behind the anus; a melanophore located dorsally over the terminal portion of the gut; and a melanophore at the tip of each jaw, of the lower jaw only in larvae smaller than 6 mm.

The following fin ray counts were obtained in a 14.5 mm-long specimen stained using Taylor’s method (1967): D14, A18, Plv7, P13. Vertebrae have not yet ossified at that length.

L. ater larvae, like the adults of the species, were not present near the continental shelf (Rubiés, 1985) but were collected on the Valdivia survey at 23°30' S, 09°00' E.

Genus Lampanyctus (with short pectoral fins)

* Lampanyctus? isaacsi *

**DESCRIPTION OF Lampanyctus? isaacsi larvae**

Figure 9 presents the larval series between 4.1 and 10.6 mm.

The body is laterally compressed in all stages of development. Head size is quite large in relation to the body (22-32%) and no opercular spines were present. The gut extends beyond the midpoint of the body (58-67%) and displays the spiral musculature as in other myctophids.

Jaws are prominent, though rather less so than in *L. ater* larvae. Teeth are visible at the tips of both jaws, even in the smallest larvae.

Teeth are distinguishable even in the smallest of the larval specimens collected (4.1 mm), and develop earlier on the upper jaw. Teeth are easily discernible on the lower jaw as well in the 6.9 mm-long larva.

There is a melanophore at the tip of each jaw, that of the lower jaw appearing first. This species also bears a melanophore between the eyes, present from the earliest stages, and another at the level of the isthmus. Larvae larger than 4.6 mm have a melanophore on the hindbrain and a series of melanophores along the base of the lower jaw.

There is a band of pigmentation on the cleithrum, at the level of the base of the pectoral fin.

The smallest of our specimens has a melanophore on the dorsal portion of the body and another on the end of the gut. These become more conspicuous with growth.

Larvae between 4.6 and 6.7 mm have three melanophores on the dorsal part of the primordial fin. When ossification of the dorsal fin begins, these melanophores migrate onto the dorsum.
In larvae larger than 4.6 mm, a ventral melanophore can also be distinguished below the large dorsal melanophore, at first smaller but rapidly attaining the same size.

There is a small pigmented area over the swim bladder at lengths greater than 4.6 mm, and a row of small melanophores below the gut.

The larva measuring 10.4 mm shows another pigmented area on the dorsal part of the body, situated more caudally than the dorsal melanophores mentioned above. There is also a row of melanophores on the primordial fin anterior to the dorsal fin.

Notochordal flexion is not observable in larvae smaller than 6.9 mm in length.
The specimen 10.4 mm in length has 15 dorsal fin rays and 18 anal fin rays. Formation of both these fins is complete. There are 14 rays in the pectoral fin.

In the 10.4 mm-long specimen 4 + 1 gill rakers are countable along with 6-7 buds, with room for no more than around 10 in all.

No photophores are distinguishable on any of the specimens collected.

DISCUSSION

To classify these specimens, potential Lampanyctus species with short pectoral fins were selected, and those species whose meristic characters did not match those of our specimens or whose larval development was known to differ from that in our specimens were then eliminated.

The potential Lampanyctus species with short pectoral fins selected were:

Lampanyctus achirus ANDIASHEV, 1962
Lampanyctus ? achirus
Lampanyctus ater TÂNING, 1928
Lampanyctus cuprarius TÂNING, 1928
Lampanyctus isaaci WISNER, 1974
Lampanyctus lineatus TÂNING, 1928
Lampanyctus ritteri GILBERT, 1915
Lampanyctus fernae WERNER, 1971
Lampanyctus regalis (GilBERT, 1892)
Lampanyctus idostigma PARR, 1931
Lampanyctus niger (GÜNTHER, 1887)

The following species were eliminated on the basis of the meristic characteristics of the largest of our specimens: L. cuprarius, L. fernae, L. idostigma, and L. niger. MOSER and AHLSTRÖM (1974) tentatively classified a larva as L. achirus. Its appearance did not match that of the specimens described above; and, furthermore, the origin of the adipose fin in L. achirus is located at the level of the end of the anal fin, whereas in larvae, here referred to as Lampanyctus ? isaaci, the origin of the adipose fin is considerably anterior to the end of the anal fin.

Descriptions exist for L. ritteri, L. regalis, and L. idostigma (MOSER et al., 1984) larvae. The larvae of L. ater and L. lineatus have also been described (ZADOVETSKY, personal communication) The morphological characters and pigmentation of the larvae of these species differ from those in the specimens described here.

The meristic characters of Lampanyctus isaaci match those of our 10.4 mm-long specimen. This species is endemic off Northwest Africa, although NAPPAKITTIS et al. (1977) indicated that it could be found down to 16° S and RUBIES (1985) reported its presence in the Southeast Atlantic.
LARVAL DISTRIBUTION OF *Lampanyctus ? isaacsi*

Larvae of this species were taken off northern Namibia and off South Africa (fig. 4D, table I), although only in small numbers. It may be interesting to note that larvae similar to those described here were also collected on the British Antarctic (Terra Nova) Expedition 1910 (REGAN, 1916).

Genus *Lampanyctus* (with pectoral fins of normal size)

*Lampanyctus pusillus* (JOHNSON, 1890)

Larvae of this species were found only twice, in the vicinity of the Valdivia Bank and at the deepest (> 500 m) station on the West Coast Hake Biomass survey in January 1984 (fig. 10A, table I). Adults of the species were reported by RUBIES (1985) from the Valdivia Bank; they have never been reported from Namibia.

Classification of these larvae was made on the basis of the description provided by TĀNING (1918), which they matched fully. These are short, deep-bodied larvae with a much blunter snout than other members of the genus. The most important pigmental characters for identification are the melanophores on the margin of the operculum and the dorsolateral row of melanophores on the body.

Genus *Lampanyctus* (with pectoral fins of normal size)

*Lampanyctus* sp. 1

Some *Lampanyctus* larvae were taken on the cruises along the edge of the continental shelf off Namibia. From their morphological characters and pigmentation, they would all appear to belong to a single species. However, they can not be assigned to any *Lampanyctus* species whose larval development is known; and, since the largest of these larvae measured just 7 mm, no meristic characters useful in identification to species level could be determined.

DESCRIPTION OF *Lampanyctus* sp. 1 LARVAE

Figure 11 depicts *Lampanyctus* sp. 1 larvae between 3 and 6.9 mm in length. Table V presents the morphometric data.

The body of these larvae is elongate up to 5 mm SL. From that size to the largest length collected, the body becomes deeper.

The head is quite large. Head depth and head length are positively allometric with respect to SL (fig. 12). The eyes are large and rounded, ranging from 36 to 38% of head length.
Fig. 10. — A) Location of samples yielding *Lampanyctus pusillus* larvae  B) Location of samples yielding *Lampanyctus* sp 1 larvae  C) Location of samples yielding *Notothenia* sp. larvae

The size of the gut is less than 30% of standard length in the larvae smaller than 3 mm, but it is positively allometric with respect to SL, so that in larvae 6.9 mm it extends past the midpoint of the body (fig. 12). In the smaller larvae the gut is broad, except for the posterior portion, which tapers to form an intestinal loop pointing at a right angle downwards. This hindgut runs almost straight in larvae larger than 5 mm.

Some teeth are already discernible in the larvae measuring 4.9 mm.

Pigmentation is restricted to the head in larvae 3 mm long. There is a small melanophore at the tip of the lower jaw, and two more, one on the frontal region and the other on the occipital region. An additional melanophore is located on the isthmus.

### TABLE V

<table>
<thead>
<tr>
<th>SL</th>
<th>PA</th>
<th>HL</th>
<th>HD</th>
<th>BD</th>
<th>ED</th>
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<td>1.65</td>
<td>1.18</td>
<td>0.68</td>
</tr>
<tr>
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<td>4.08</td>
<td>2.25</td>
<td>2.02</td>
<td>1.64</td>
<td>0.86</td>
</tr>
</tbody>
</table>
In addition to these four melanophores, at lengths exceeding 4 mm there is a melanophore at the tip of the upper jaw and another at the level of the hindbrain. Some small melanophores are discernible on the ventral margin of the gut, and there is some pigmentation near the intestinal loop. Some small melanophores develop on the pectoral fin rays at a length of about 5 mm.

The same pigmentation pattern is present in larvae larger than 5 mm, but the pigmentation is darker, especially on the pectoral fin rays. In addition, there are some chromatophores at the base of the pectoral fin in larvae longer than 6 mm.

The onset of ossification of the dorsal and anal fins is visible in the 5.5 mm-long specimen. Ossification of the pectoral and caudal fins occurs earlier.
MYCTOPHIDS IN THE BENGUELA UPWELLING

Fig. 12 — Lampanyctus sp. I Ratio between standard length and: A) head depth; B) head length; C) preanal distance.

Notochordal flexion takes place at a standard length of around 5 mm SL. Photophore Br₂ is the only one that forms in the larval stages of the genus Lampanyctus (Moser and Ahlstrom, 1972). In these specimens it is already present at a length of 5.5 mm.

DISCUSSION

Among the Lampanyctus species whose larvae have been described in the literature, the most similar in appearance to the ones described here are those of L. crocodilus (Risso, 1810). However, our specimens do not belong to that species, in which photophore Br₂ has not yet formed at the length at which it has already appeared in our larvae.

L. australis Tåning, 1932, is one of the most abundant lanternfish species in the Benguela region, thus their larvae should be common in the plankton of the area. On the other hand L. intricarius Tåning, 1928, species close taxonomically to L. crocodilus, also appears regularly in the area (Rubies, 1985). Thus the Lampanyctus sp. I larvae described here could belong to one of these species.

LARVAL DISTRIBUTION OF Lampanyctus sp. I

Lampanyctus sp. I larvae were found off Namibia, off South Africa, and at two stations located on lines between the Valdivia Bank and the Namibian continental shelf (fig. 10B, table I).

Scopelopsis multipunctatus Brauer, 1906

Larvae of this species were identified with the aid of Moser and Ahlstrom (1972). They were found at two stations beyond the 400 m isobath at 34°30' S, 17°55' E and 34°45' S, 18°15' E.

The adult distribution range is known to extend over the southern subtropical waters of all oceans (Nafpaktitis and Nafpaktitis, 1969; McGinnis, 1982; Hulley, 1981).
In the context of the cruises considered here, adults of this species appeared only in the samples collected on the Valdivia Bank (Rubiés, 1985).

*Lampanyctodes hectoris* (Gunther, 1876)

The first description of *L. hectoris* larvae was by Robertson (1973), presenting three larval stages taken off New Zealand. Ahlstrom et al. (1976) provided a detailed description of *L. hectoris* larvae from South Africa; the eggs have been described by Robertson (1977).

Of the myctophid larvae normally present in the Benguela upwelling region, only those of *Diaphus hudsoni* can be confused with those of *Lampanyctodes hectoris*. In her description of *Diaphus hudsoni* larvae, Olivar (1987) included a discussion of the characters useful in differentiating these two types of larvae.

**Egg and larval distribution and abundance of *L. hectoris***

During the spawning season of this species, its eggs and larvae generally contribute a large percentage to the ichthyoplankton in the region (O'Toole, 1977; Olivar, 1985; Shelton, 1986).

*Lampanyctodes hectoris* eggs and larvae are found from the area around the mouth of the Cunene River to the southern Cape of Good Hope. They are typically located more inshore than the rest of lanternfish larvae of the region. The main spawning area seems to lie some 30 miles offshore. The concentration of *Lampanyctodes hectoris* eggs and larvae is considerably higher off southern Namibia than further north (Olivar, 1985). The eggs and larvae of this species are also quite abundant off the west coast of South Africa. St. Helena Bay, despite its shallow waters, has a relatively high abundance of *L. hectoris* eggs, and the greatest densities of adults of this species have, on occasion, also been found in this same area (Centurier-Harris, 1974).

Adult *L. hectoris* have not been caught in samples taken beyond the continental slope (Rubiés, 1985), and neither eggs nor larvae of this species have been collected on the Valdivia Bank. On the other hand, the western limit for the larvae of this species in the samples is around 07° E longitude (fig. 13). The appearance of *L. hectoris* larvae collected at a station on the transect leading to the Valdivia Bank (26°45' S, 09°01' E), although it matched the description of the larvae of this species, showed certain peculiarities, in that, even though the specimens caught all measured between 6 and 8 mm, they all showed the dorsal pigmentation typical of *L. hectoris* larvae larger than 11 mm. In their description of *L. hectoris* larvae, Ahlstrom et al. (1976) referred to two individuals exhibiting this same characteristics which they assigned to this species, and consequently the same assignment was made here. The present case is noteworthy in that this phenomenon typically occurs...
sporadically, in a few individuals, but not in all the specimens taken in a single haul, as in this instance.

The eggs and larvae of this species are most abundant in the upper 60 m, but are also found in large quantities down to 200 m (OLIVAR and RUBÍES, 1987).

**SPAWNING AREA AND SEASON OF Lampanyctodes hectoris**

*L. hectoris* spawns throughout the area investigated. Of all the myctophids in the region, it is the species whose egg and larval distribution pene-
trates furthest into shallow waters. Off Namibia *L. hectoris* spawning is vigorous during the months of maximum upwelling, becoming slight or non-existent in autumn, when upwelling is less intense. Moreover, abundance of larvae of this species is extremely high near the upwelling centres around LUDERITZ and WAlVIS BAY but much lower in the waters of the Angola Current. Larval concentrations off the west coast of South Africa have also been reported to be lower than off Namibia, and they decrease still further in the waters affected by the Agulhas Current (OLIVAR, 1985, 1988; SHELTON, 1986).

Until now the eggs and larvae of this species have not been detected in the plankton before the month of August. According to our findings, however, spawning probably commences sometime around May and ends around December (table I); this coincides with the conclusion obtained by HULLEY and PROSCH (1987) from gonad examination.

In view of its distribution area, *Lampamyctodes hectoris* can be considered pseudo-oceanic (HULLEY, 1986a), whereas the rest of the myctophids mentioned here tend to dwell in a more oceanic habitat. The spawning behaviour of *L. hectoris*, which is also pseudo-oceanic, is probably responsible for the success of this species in the region, since its eggs and larvae develop in the area enriched by upwelling and hence find much higher nutrient levels than the rest of the species, which spawn over the continental slope.

**Notoscoelus sp.**

In the early stages of development *Notoscoelus* larvae are quite similar to *Lampamyctus* larvae, the main differentiating features being the pigmentation on the peritoneum of the swim bladder and the larger snout (MOSER, personal communication). Moreover, photophore PO₅ forms early in *Notoscoelus* larvae, while the only photophore that forms in *Lampamyctus* larvae is Br₂ (MOSER and AHLSTROM, 1972).

Figure 14 depicts three of the larval stages of *Notoscoelus sp.*

The adults of this genus caught during these surveys include *N. resplendens* (RICHARDSON, 1844), and *N. caudispinosus* (JOHNSON, 1983), both found in the Valdivia Bank, but not in the Benguela region (RUBIÉS, 1985), although they have been reported near the Cape of Good Hope by HULLEY (1986a and b). One stage of *N. caudispinosus* larvae have been described by BELYANINA (1982) and the complete larval development of *N. resplendens* have been described by BADCOK and MERRETT (1976) and MOSER and AHLSTROM (1972). Our largest specimen (6.2 mm) shows good agreement with the descriptions of *N. resplendens*; however, it lacks the lateral pigmentation mentioned in the descriptions of *N. resplendens* larvae of the same size.

The other *Notoscoelus* larvae collected were about 4 mm long, and, due to the absence of larger individuals, could not be identified to species level. Figure 10C and table I contain information concerning the location and presence of *Notoscoelus sp.* larvae on the surveys carried out in the study area.
Fig. 14 — Larval series for *Notoscopelus* sp: A) 3.9 mm; B) 4.5 mm; C) 6.2 mm.

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