

EARLY DEVELOPMENT OF DIAPHUS SPP. (PISCES: MYCTOPHIDAE) OF THE AGULHAS CURRENT

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#### Abstract

The genus Diaphus is taxonomically one of the most difficult in the family Myctophidae. In the South-West Indian Ocean, at least 18 species of the genus are found hut larval development is known for only two. Larvae and juveniles collected in or near the Agulhas Cutrent provide sufficient data to describe larvae or transforming stages of three species of the genus. Postflexion and transforming specimens of $D$. diadematus, larvae and transforming stages of another species, either D. brachycephalus or D. richardsoni, and the complete larval development and transforming stages of D. mollis are described. The pigmentation pattern and photophore development of the larvae and juveniles of these three species, and the postanal pigmentation and presence or absence of suborbital photophores for juveniles of nine additional species, allowed them to be placed in two divergent groups of Diaphus, as suggested by previous authors.


Die geslag Diaphus is taksonomies een van die mneilikste in die familie Myctophidae. Ten minste 18 spesies van die geslag word in die Suidwestelike Indiese Oseaan aangetref, maar die larvale ontwikkeling van slegs twee is bekend. Larwes en jongvis wat in of naby die Agulhasstroom versamel is, lewer voldoende gegewens om die larwes of transformerende stadia van drie spesies van die geslag te beskryf. Postfleksie- en transformerende eksemplare van $D$. diadematus, larwes en transformerende stadia van nog 'n spesie, of $D$. brarhycephalus of $D$. richardsoni, en die volledige larvale ontwikkeling en transformerende stadia van $D$. mollis word beskryf. Die pigmentasiepatroon en fotofoorontwikkeling van die larwes en jongvis van hierdie drie spesies en die postanale pigmentasie en aan- of afwesigheid van suborbitale fotofore by jongvis van nege bykomende spesies het dit moontlik gemaak orn hulle in twee utteenlopende groepe van Diaphus te plaas, soos deur vorige skrywers voorgestel.

Lanternfish (Myctophidae) are a group of fish characteristic of the open ocean, but which may also be found over continental shelves. Their abundance, diversity and worldwide distribution, together with the important role they play in food wehs, have justified numerous studies dealing with their biology, systematics and abundance (Paxton 1979, Gjøsaeter and Kawaguchi 1980, Bekker 1983, Moser et al. 1984).

In the South-West Indian Ocean the genus Diaphus is represented by 18 species (Hulley 1984, 1986), of which the larval stages of only two are known (Table I). The systematics of adults of this genus have been extensively studied (Nafpaktitis et al. 1977, Nafpaktitis 1978, McGinnis 1982), but they are still not completely resolved. Nafpaktitis (1978) suggested that studies of larval development would elucidate intrageneric relationships that he postulated from adult characters.

Larvae of Diaphus species are among the most difficult to identify to species level. Studies on lanternfish larvae by Moser and Ahlstrom $(1972,1974)$ and Moser et al. (1984) have indicated the existence of two larval morphotypes ("moderately slender" and "moderately deep body"), recognized both by morphology and pigmentation. The slender morphotype
combines a moderately slender body and numerous melanophores in a postanal ventral midline series. The deep-hody morphotype is characterized by a moderately deep body together with one or a few melanophores on the postanal ventral midline. Larvae of the species that develop a suborbital photophore as adults belong to the moderately slender morphotype (Moser and Ahlstrom 1974, Moser et al. 1984).

The present study is based on a large number of Diaphus larvae collected in the region of the Agulhas Current in the South-West Indian Ocean (Olivar and Beckley 1994). This material allowed a study of the different morphotypes of Diaphus larvae to be undertaken with the aim of ascertaining larval development for some of the species in the region.

## MATERIAL AND METHODS

Diaphus material was collected off the east coast of South Africa in the region of the Agulhas Current during a pilot study carried out in 1989 and three cruises conducted in May/June 1990. October 1990 and February 1991. A locator map and some of the

[^0]Table I: Meristic characters of Diaphus species recorded in the Agulhas Current (Hulley 1986)

| Species | Adult maximum length (mm) | Number of dorsal fin rays | Number of anal fin rays | Gill rakers | Larval morplotype | Larval description |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| D. mollis Tåning, 1928 | $66^{6}$ | 12-14 | 12-14 | $(4-6)+(10-13)$ | slender | - |
| D. parri Tåning, 1923 | 65 | 12-14 | 12-13 | $(5-6)+(10-13)$ | slender | - |
| D. brachycephatus Tanning. 1928 | 57 | 12-14 | 12-14 | $(5-7)+(11-14)$ | slender | - |
| D. aliciae Fowler, 1934 | 60 | 13-14 | 12-13 | $(5-6)+(12-14)$ | slender | - |
| D. richardsoni Tåning, 1932 | 60 | 12-14 | 12-14 | $(6-7)+(13-1.5)$ | slender | - |
| D. hudsoni Zubrigg and Scott, 1976 | 84 | 13-15 | 12-14 | $(7-9)+(15-19)$ | slender | Olivar 1987 |
| D. probiematicus Parr, 1928 | 105 | 15-17 | 16-18 | (4) $+(9-11)$ | deep | - |
| D. diademanus Tanning, 1932 | 42 | 13-14 | 13-15 | $(4-5)+(1)-12)$ | deep | - |
| D. Iucidus (Goode \& Bean. 1896) | 118 | 16-18 | 17-19 | $(4-6)+(11-14)$ | deep | - |
| D. splendidus (Brauer, 1904) | 90 | 14-15 | 16-17 | (5) $+(12-14)$ | deep | - |
| D. effulgens (Goode \& Bean, 1896) | + 150 | 15-17 | 15-16 | $(5-6)+(12-14)$ | deep | - |
| D. garmani Gibert, 1906 | 60 | 15-16 | 16-17 | $(6-8)+(12-14)$ | deep | - |
| D. jenseni Tăning, 1932 | 50 | 14-15 | 13-15 | (6) + (13-15) | deep | - |
| D. Wetkeni (Brauer, 1904) | 60 | 15-17 | 14-16 | $(6-7)+(13-15)$ | deep | - |
| D. metapoclampus (Cocco. 1829) | 75 | 14-16 | 14-16 | $(7--9)+(14-15)$ | deep | Spanà 1952 |
| D. nielseni Nafpaktitis. 1978 | 40 | 13-15 | 13-15 | $(6-7)+(14-16)$ | deep | - |
| D. perspicillatus (Ogilby, 1898) | 71 | 15-17 | 14-16 | $(8-10)+(16-19)$ | deep | - |

basic hydrography of the region are given in Olivar and Beckley (1994). Ichthyoplankton samples were obtained with a Bongo net with mesh $0,5 \mathrm{~mm}$ that was hauled obliquely from 80 m to the surface, where bottom depth permitted. The sampling grid consisted of a series of nine transects perpendicular to the coastline on which the stations were located in water depths of 50, 100, 500 and 2000 m (Beckley and Van Ballegooyen 1992).

Larvae were preserved in 5\% formalin and measurements were taken at least six months after collection and fixation at sea. Measurements were performed to an accuracy of $0,1 \mathrm{~mm}$.

The larvae described here are deposited in the Ichthyoplankton Collection of the Instituto de Ciencias del Mar de Barcelona (ICICMB). Measurements were taken from a selection of lavvae, covering the complete size range of specimens. The following measurements were recorded: body length ( $B L$ ), the distance along the midline of the body from the tip of the snout to the tip of the notochord in preflexion larvae, and to the posterior margin of the hypural elements in postflexion stages; preanal length (PAL), the distance along the midline of the body from the tip of the snout to the vent; body depth at pectoral (BDP), depth of the body at the base of the pectoral fin; predorsal fin length ( $P D L$ ), the distance along the midline of the body from the tip of the snout to the origin of the dorsal fin; eye diameter (Edi) and eye depth (Ede). The allometric relationships between the various body measurements and $B L$ were calculated by use of the equation $y=a x^{\mathrm{b}}$, where $x$ is $B L, y$ the other measurement being related, b the allometric factor, and a the expected value of $y$ at $x=1$ (Gould
1966). Confidence intervals (Cl) were calculated at the $95 \%$ level of significance. Photophore nomenclature follows that of Hulley (1986). Taylor's (1967) enzyme method of clearing and staining was applied to make vertebral counts.

Definitions of photophore abbreviations used in the paper are as follows: Br , photophores located on the branchiostegal membranes; Vn , luminous organ beneath the level of the dorsal margin of the nasal apparatus; Dn. orbital organ located above the nasal apparatus; SAO, 1-3 photophores located between the lateral line and the anus; VO, ventral series of photophores situated between the pelvic fin bases and the origin of the anal fin; AOa , ventral series of photophores located on the bases of the anal fin; AOp, ventral series of photophores posterior to the end of the anal fin; Pol, any photophore between the AOa and AOp series; PO , ventral series of photophores situated between the opercle and the bases of the pelvic fin; PVO, photophores located between the opercle and the pectoral fin; VLO, photophore located somewhere between the lateral line and the pelvic fin; PLO, photophore located above the pectoral fin.

## RESULTS AND DISCUSSION

Among the large number of Diaphus larvae collected in the study, at least seven different species were evident (Olivar and Beckley 1994), but transformation specimens were available for only three species.

Examination of juveniles of several species of this genus that were collected in the pilot survey and


Fig. 1: Developmental stages of Diaphus diadematus - (a) $7,9 \mathrm{~mm}$ postlexion larva, (b) $8,8 \mathrm{~mm}$ juvenile, (c) $9,4 \mathrm{~mm}$ juvenile
entified by P. A. Hulley (South African Museum, :rs. comm.) permitted investigation of the remnants larval pigmentation. Those species that develop a borbital (So) photophore had the pigmentation ttem of the moderately slender morphotype of Moser d Ahlstrom (1972), i.e. numerous melanophores a postanal ventral midline series. The juveniles amined that conform with these characters were: aliciae and D. mollis. Diaphus species that do not velop a So photophore had the pigmentation patn of the moderately deep-bodied morphotype of

Moser and Ahlstrom (1972), i.e. one melanophore on the postanal ventral midline. The juveniles examined that conform with these characters were $D$. diadematus, D. garmani, D. jenseni, D. perspicillatus, Diaphus species A, Diaphus species B and D. splendidus.

## Diaphus diadematus

The larva of this species has a moderately deep body and a single postanal midventral tail melanophore.


Fig. 2: Developmental stages of Diaphus brachycephalus/richardsonii- (a) $3,5 \mathrm{~mm}$ larva, (b) $4,0 \mathrm{~mm}$ larva, (c) $4,5 \mathrm{~mm}$ larva, (d) $5,1 \mathrm{~mm}$ larva, (e) $5,3 \mathrm{~mm}$ larva, (f) $5,3 \mathrm{~mm}$ larva, (g) $6,3 \mathrm{~mm}$ larva, (h) $8,1 \mathrm{~mm}$ larva, (i) $10,4 \mathrm{~mm}$ juvenile, (j) $11,1 \mathrm{~mm}$ juvenile

One juvenile of $10,7 \mathrm{~mm} B L$, and three transformation specimens of $8,5,8,8$ and $9,4 \mathrm{~mm}$ were identified with the adult key of Nafpaktitis (1978). One postflexion larva ( $7,9 \mathrm{~mm} B L$ ) with several photophores already developed was identified by comparison with the transformation specimens. Early stages of development of this species could not be separated confidently from those of other Diaphus species with moderately deep-bodied larvae.

The identification of the juvenile and the transforming specimens was based on the following characteristics: absence of suborbital photophore; Vn along anterioventral orbital margin in contact with Dn; Dn much larger than the nasal rosette; $\mathrm{SAO}_{1}$ at same level as $\mathrm{VO}_{5} ; \mathrm{Vn}$ greatly elongated and its dorsal margin without projections; $\mathrm{SA}_{3}$ and Pol more than a photophore diameter below the lateral line; $\mathrm{AOa}_{1}$ not abruptly elevated; ventral fin not reaching origin of anal fin. Gill-raker counts in the $8,8 \mathrm{~mm}$ specimen were $4+11$.

The transforming specimens and the postflexion larva of $7,9 \mathrm{~mm}$ showed a peculiar morphology, with a prominent foregut region and a relatively slender tail (Fig. 1). Relative body depth at the pectoral level decreased from $28,5 \%$ of $B L$ in the larva of $7,9 \mathrm{~mm}$ to $24 \%$ in the $9,4 \mathrm{~mm}$ transforming specimen. The gut extended beyond the midpoint of the body, representing $59 \%$ of $B L$. The origin of the dorsal fin was located near the midpoint of the body $(48,6-51 \%$ for the size range examined). Eyes were nearly round in the late larva as well as in the transforming specimens (c. $8 \%$ of $B L$ ).

The typical pigmentation described by Moser et al. (1984) for "moderately deep bodied" larvae was evident in the specimens examined (Fig. 1). There was a single postanal midventral tail melanophore, another one on the free terminal section of the gut, and one on the anterioventral surface of the liver. Several melanophores were scattered in the anterior part of the trunk at the level of the cleithrum and over the gas bladder. The base of the caudal rays was outlined by melanophores.

The number of rays in the dorsal fin was $13(n=4)$ and in the anal fin $14(n=4)$.

Identification of the juvenile of $10,7 \mathrm{~mm}$, as well as that of the transforming specimens, was based on the key of Nafpaktitis (1978). The characters of the current specimens matched those of the juvenile of $10,5 \mathrm{~mm}$ illustrated by Nafpaktitis (1978). Identification of the postflexion larva is reliable because it is based on its similarity in morphology, pigmentation and photophore pattern with the late stages of devel-


Fig. 3: Morphology of Diaphus brachycephalus/richardsoni larvae. Relationship between body length ( $B L$ ) and (a) body depth at pectoral (BDP), (b) eye diameter (Edi) and (c) eye depth (Ede). Continuous lines are titted curves, dotted lines indicate the confidence intervals at the $95 \%$ level of significance, and $C l_{b}$ is the confidence interval of the b parameter
opment. However, early larval stages are considerably more difficult to identify, because among larvae with fairly similar morphology and pigmentation characteristics collected on the same cruises, several specimens with fin-ray counts or photophore pattern that did not fit those of $D$. diadematus were found. These facts suggest that smaller stages of $D$. diadematus and those belonging to other Diaphus species could be similar.

Table II: Morphometric measurements for larvae of Diaphus brachycephalus/richardsoni

| Body length (mm) | Preanal fin length (mm) | Body depth at pectoral (mm) | Predorsal fin length (mm) | Eye depth (mm) | Eye diameter (ma) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 3,00 | 1,46 | 0.38 | - | 0,24 | 0,20 |
| 3.50 | 1,78 | 0,50 | - | 0,30 | 0,25 |
| 4,00 | 2,12 | 0.63 | 1.85 | 0.35 | 0.31 |
| 4,50 | 2,47 | 0.78 | 2,09 | 0,41 | 0,36 |
| 5,00 | 2,8.3 | 0,94 | 2,32 | 0.46 | 0,42 |
| 5,50 | 3,20 | 1.11 | 2.56 | 0,52 | 0,48 |
| 6,00 | 3,59 | 1.29 | 2,79 | 0,58 | 0,55 |
| 6,50 | 3,98 | 1.48 | 3.03 | 0,65 | 0,61 |
| 7,00 | 4,38 | 1.69 | 3,27 | 0,71 | 0,68 |
| 7,50 | 4,79 | 1.91 | 3,50 | 0,77 | 0,75 |
| 8,00 | 5.21 | 2,14 | 3.74 | 0.84 | 0.83 |
| 8,50 | 5,64 | 2,38 | 3,98 | 0.90 | 0,90 |
| Number of fish examined |  |  |  |  |  |
| 48 | 45 | 44 | 27 | 39 | 41 |
| $\mathrm{Cl}_{y}(\%){ }^{*}$ | 7.3 | 20.9 | 10.3 | 19.0 | 25,3 |

* Confidence interval of y estimates


## Diaphus brachycephalus/richardsoni

These larvae belonged to a moderately slender type of Diaphus that appeared in the samples during all three seasons, mainly in winter. A total of 261 larvae was examined. Figure 2 shows the series of development, and Figure 3 and Table Il indicate the relationship between the main body measurements and $B L$.
The larvae were slender and had early notochordal flexion and early fin development. They were characterized by midventral tail pigmentation during postflexion stages which consisted of large, embedded anterior melanophores independent of each other. and posterior melanophores which were superficial, darker and fused.

The larvae were especially slender during the first stages of development. A significant positive allometric relationship existed between $B D P$ and $B L$ during larval development (Fig. 3a, Table II), body depth representing $<13-14 \%$ of $B L$ in preflexion and $<28 \%$ of $B L$ in $8,5 \mathrm{~mm}$ larvae. Preanal length also showed a positive allometric relationship with $B L$ during development $(b=1,2993 \pm 0,0496)$, increasing from $49 \%$ of $B L$ at 3 mm to $66 \%$ at $8,5 \mathrm{~mm}$ (Table II). The origin of the dorsal fin did not change during development $(\mathrm{b}=1,0148 \pm 0,1150)$, being located at $46-47 \%$ of $B L$ (Table II). Eyes were nearly round. Eye diameter increased during development from $7 \%$ of $B L$ in preflexion larvae to $11 \%$ of $B L$ in larvae 8.5 mm long (Table II, Fig. 3b, c). Notochordal flexion took place from 4 to $4,5 \mathrm{~mm} B L$.

Larvae had one melanophore on the anterioventral
surface of the liver, one or two in the midgut region, one on the free terminal section of the gut and one on the ventral lobe of the caudal fin. There were numerous postanal midventral melanophores along the tail.

In preflexion and flexion stages, tail pigmentation consisted of a row of melanophores spaced evenly (from c. 15 in the smallest larvae to 10 in flexion larvae). In postflexion stages ( $B L>4,5 \mathrm{~mm}$ ), the number of midventral lail melanophores decreased to about seven. Four large embedded melanophores, which were independent of each other, were located behind the anus. On the posterior part of the midventral tail the melanophores were superficial and darker and were fused. In the transforming specimens the caudal fin was pigmented both on the upper and lower lobe.

The $\mathrm{Br}_{2}$ photophore (the second photophore in the branchiostegal membrane) appeared at c. $6 \mathrm{~mm} B L$. $\mathrm{Br}_{2}, \mathrm{PO}_{5}$ and $\mathrm{PO}_{1}$ were present in larvae of about $8 \mathrm{~mm} B L$. The smallest transformation specimen measured $10,4 \mathrm{~mm} B L$. The So photophore was present and located behind the posterior margin of the pupil. The Vn photophore was elongated.

The first fin to ossify was the caudal, followed by the anal, dorsal, pectoral and pelvic fins. Pelvic fin buds appeared at c. $5,5 \mathrm{~mm}$. In the largest larvae in the series (c. 8 mm ) there were 12 dorsal fin rays and I2 anal fin rays, but this last fin appeared to be incompletely formed. The counts for the two juvenile specimens were 13 rays for the dorsal fin and 13 and 14 rays for the anal fin.

Myomere counts ranged from 28 to 31 . No ossification of any vertebrae or fin rays was evident in the larva of $6,1 \mathrm{~mm} B L$. In this larva there were 31 verte-


Fig. 4: Developmental stages of Diaphus mollis - (a) $2,8 \mathrm{~mm}$ larva, (b) $3,6 \mathrm{~mm}$ larva, (c) $4,6 \mathrm{~mm}$ larva, (d) $6,2 \mathrm{~mm}$ larva, (e) $6,9 \mathrm{~mm}$ larva, (f) $9,2 \mathrm{~mm}$ larva, (g) $9,3 \mathrm{~mm}$ larva, (h) $10,5 \mathrm{~mm}$ early juvenile


Fig. 5: Morphology of Diaphus moffis larvae. Relationship between body length ( $B L$ ) and (a) body depth at pectoral (BDP), (b) eye diameter (Edf) and (c) eye depth (Ede). Continuous lines are fitted curves, dotted lines indicate the confidence intervals at the $95 \%$ level of significance, and $C l_{b}$ is the confidence interval of the $b$ parameter
brae plus the urostyle.
The number of gill rakers was counted in two transformation specimens: $10,4 \mathrm{~mm}(6+13)$ and $11,1 \mathrm{~mm}$ $(6+12)$.

Among species with larvae that have a moderately slender morphotype, only those of D. hudsoni are known (Olivar 1987). They may be differentiated from those described above by later notochordal flexion, and by the later fin-ray and photophore development of D. hudsoni. Furthermore, in D. hudsoni larvae the melanophores in the midventral line are not fused.

Identification of larvae allocated as D. brachycephalus/richardsoni was based on their similarity to juveniles (pigmentation pattern, morphology, number of rays). The identification key for adults of Nafpaktitis (1978) was used to identify the two juveniles. The last dichotomic point gave two options for these specimens, namely $D$. brachycephalus and D. richardsoni, but they depend on small differences in adult body proportions that could differ between adults and juveniles. The number of gill rakers in the $11,1 \mathrm{~mm}$ specimen indicated that they were $D$. brachycephalus (Table I). No information is available concerning the size at which the full complement of gill rakers is attained. If the gill-raker count of the $11,1 \mathrm{~mm}$ individual is the final one, this would indicate that the larval series corresponds to D. brachycephalus.

## Diaphus mollis

These moderately slender Diaphus larvae appeared in Agulhas Current samples during the three seasons of sampling. In all, 158 larvae and five juveniles were examined. Figure 4 depicts the early stages of development, and Figure 5 and Table III represent the relationships between the main body measurements and $B L$ during larval development.

The following characters were used to distinguish Diaphus mollis larvae from those of D. brachycephalus. The midventral tail melanophores were closer to each other (sometimes forming a line) and the development of fins and photophores occurred later. The fitted curves for $B D P, E d i$ and Ede in relation to $B L$ (Fig. 5) indicate that the body is more slender and the eyes smaller in D. mollis. Because of the overlapping confidence intervals, these characters on their own will not conclusively identify individual specimens.

The body of $D$. mollis was slender during all stages of development, but $B D P$ increased from $12 \%$ of $B L$ at 3 mm BL to $23,5 \%$ at $10,5 \mathrm{~mm}$ BL (Fig. 5a, Table III). The gut was shorter in preflexion stages than later, increasing from $49 \%$ of $B L$ at $3 \mathrm{~mm} B L$ to $66 \%$ at $10,5 \mathrm{~mm} B L$ (Table III). The relationship between body length and preanal length during development showed a significant positive allometry ( $b=1,2252$ $\pm 0,0614$ ). The origin of the dorsal fin was located at $45 \%$ of body length during all the larval stages examined ( $b=1,0 \pm 0,0675$, Table III). The eyes were small, relative eye diameter increasing slightly during development from $6 \%$ of $B L$ at 3 mm to $8 \%$ of $B L$ at $10,5 \mathrm{~mm}$ BL (Table III, Fig. 5b). Eye depth represented $8 \%$ of $B L$ in all stages examined (Table III, Fig. 5c). Notochordal flexion took place between 4,5 and $5 \mathrm{~mm} B L$.

Table III: Morphometric measurements for larvae of Diaphus mollis

| Body length (mm) | Preanal fin length ( mm ) | Body depth at pectoral ( mm ) | Predorsal fin length ( mm ) | Eye depth (mm) | Eye diameter (mm) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 2,50 | 1.19 | 0.28 | - | 0.20 | 0,15 |
| 3,00 | 1.48 | 0,37 | - | 0,24 | 0,19 |
| 3,50 | I,79 | 0.47 | - | 0,28 | 0,23 |
| 4.00 | 2,11 | 0,57 | - | 0,32 | 0,26 |
| 4,50 | 2,44 | 0,68 | 2,01 | 0,37 | 0.30 |
| 5,00 | 2.77 | 0.80 | 2,24 | 0.45 | 0.34 |
| 5,50 | 3.12 | 0,92 | 2,46 | 0.45 | 0.38 |
| 6,00 | 3,47 | 1,05 | 2,69 | 0,49 | 0,42 |
| 6.50 | 3,82 | 1,18 | 2,91 | 0.53 | 0.46 |
| 7,00 | 4,19 | 1,32 | 3,13 | 0.57 | 0,51 |
| 7.50 | 4.56 | 1,46 | 3.36 | 0.61 | 0.55 |
| 8,00 | 4,93 | 1.61 | 3,58 | 0.65 | 0.59 |
| 8.50 | 5.31 | 1.77 | 3,80 | 0.69 | 0,6.3 |
| 9.00 | 5.70 | 1.92 | 4,03 | 0.73 | 0.68 |
| 9,50 | 6,09 | 2,08 | 4,25 | 0.78 | 0.72 |
| 10.00 | 6.48 | 2,25 | 4.48 | 0.82 | 0,77 |
| 10.50 | 6,88 | 2,42 | 4,70 | 0,86 | 0.81 |
| 11,00 | 7.29 | 2,59 | 4,92 | 0.90 | 0.86 |
| Number of fish examined |  |  |  |  |  |
| 46 | 43 | 43 | 28 | 29 | 33 |
| $\mathrm{Cl}_{3}(\%)^{*}$ | 12,8 | 30.7 | 9.3 | 18,8 | 21,8 |

* Confidence interval of y estimares

Melanophores were present on the anterioventral surface of the liver, in the midgut region, on the free terminal section of the gut and at the ventral corner of the caudal fin. A row of several melanophores was present along the postanal. midventral line of the tail. These melanophores were very close to each other, and they sometimes formed a line. Their number decreased from 11-15 in preflexion and flexion stages to $8-10$ in postflexion stages.

The $\mathrm{Br}_{2}$ photophore appeared between 8 and 9 mm $B L$. In one specimen of $9.2 \mathrm{~mm}, \mathrm{Br}_{2}, \mathrm{PO}_{5}$ and $\mathrm{PO}_{1}$ were visible. In two specimens of $9,3 \mathrm{~mm}, \mathrm{Br}_{2}, \mathrm{PO}_{5}$ and PO , were present, and $\mathrm{PVO}_{2}, \mathrm{PO}_{3}, \mathrm{PO}_{4}$ and $\mathrm{AOa}_{2,3,4,5}$ were visible but still developing. Photophore development was more advanced in the largest larva collected, although many photophores were scantily visible and photophore pattern was still not complete (Fig. 4h). The largest specimens examined were five juvenites (two of 10,0 and $11,5 \mathrm{~mm} B L$ in transformation state, and the other three of $11,5,11,5$ and $15,5 \mathrm{~mm} B L$ ). Complete photophore development was only observed for the $15,5 \mathrm{~mm}$ specimen. The rest showed all the photophores except So.

At 6 mm . the bases of the anal and dorsal fins began to form, whereas in $D$. brachycephalus/richardsoni of the same size most of the rays in those fins were already present. The number of rays counted in several larvae of $>8,2 \mathrm{~mm}$ were from $13(n=6)$ to
$14(n=1)$ in the dorsal fin, and $12(n=1), 13(n=5)$ and $14(n=1)$ in the anal fin.

Number of myomeres ranged from 31 to 33. There were 33 vertebrae (still not ossified in two larvae of $8.5 \mathrm{~mm} B L$ ) plus the urostyle.

The number of gill rakers counted in one specimen of $10,53 \mathrm{~mm}$ was $6+13$.

Five juveniles were collected in the pilot study in the vicinity of the Agulhas Current. The pigmentation pattern shown in the largest larva was stitl visible on these juveniles. A description of some larvae attributed to D mollis by Shiganova (1977) has not been considered in the present paper, because larvae depicted in that paper were deep-bodied with a single postanal melanophore.

Apart from the similarity of the larger larvae of the current study to the juveniles of $D$. mollis, the rest of the species that should have moderately slender larvae have also been considered. Among the other possible species, $D$. hudsoni may be disregarded because of its postanal pigmentation. which consists of isolated melanophores (Olivar 1987). The gill-raker count of the transforming specimen ( $10,5 \mathrm{~mm}$ ) was too low for $D$. hudsoni. Furthermore, although D hudsoni could be present in the area. its presence is associated with the northward advection of pockets of cooler water (Hulley 1984), which was not the situation in surveys from which samples were collected (Beckley
and Van Ballegooyen 1992). D. aliciae is not a good candidate because adults of this species are small. Only sizes up to 39 mm have been reported in the Indian Ocean (Nafpaktitis 1978, Table I). The larvae examined for this study should belong to a species larger than D. brachycephalus or D. richardsoni. Adult morphology of D.parri, a robust, deep-bodied myctophid (Nafpaktitis 1978, p. 67 and Fig. 67) does not agree with that of the largest specimen described here, which is slender. Finally, D. mollis is the most common Diaphus species of its type in the region of the Agulhas Current (Hulley 1984). Photophore pattern in the largest larva examined herein $(10,5 \mathrm{~mm}$ $B L$, Fig. 4h) conformed with that of adults and juveniles of $D$. mollis. PLO was nearer to the base of the pectoral fin than to the lateral line and VLO was midway hetween the lateral line and the ventral fin. In both $D$. brachycephalus and D. richardsoni, the VLO photophore is located twice as near to the hase of the ventral fin as to the lateral line. Although not shown in Figure 4h, a very small AOa, photophore was visible on the other side of the body of this specimen, and was slightly elevated.

## CONCLUSIONS

Postanal pigmentation and the presence or absence of suborbital photophores of juveniles and larvae of species of the genus Diaphus collected in the vicinity of the Agulhas Current allowed them to be placed in two divergent groups, as suggested for this genus (Moser and Ahlstrom 1974, Moser et al. 1984):
(i) D. aliciae, D. brachycephalus/richardsoni and D. mollis, which are species that develop the So photophore as adults, and show numerous melanophores in a postanal ventral midline series.
(ii) D. diadematus, D. garmani, D. jenseni, D. perspicillatus, D. splendidus and Diaphus species A and B, which are species that do not develop the suborbital photophores as adults, and that show only one melanophore on the postanal ventral midline.
Whereas identification to species level of juveniles and transforming stages of Diaphus is reliable because it is based mostly on adult characters, the present assignment of larvae to species may become a subject for discussion in future. In the light of all available information on larval stages of Diaphus species, it is evident that larval differentiation within each of these two groups is still not clear because it depends on slight morphological and pigmentation differences.

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## LITERATURE CITED

BECKLEY, I. E. and R. C. VAN BALLEGOOYEN 1992 Oceanographic condinions during three ichthyoplankion surveys of the Agulhas Cursent in 1990/91. In Benguela Trophic Functioning. Payne, A. 1. L., Rrink, K. H.. Mann, K. H. and R. Hilbom (Eds). S. Afr. J. mar: Sci. 12: 83-93.

BEKKER, V. E. 1983 - Myctophidae of the World Ocean. Moscow; Nauka: 248 pp. (in Russian).
GJøSAETER, J. and K. KAWAGUCHI 1980 - A review of the world resources of mesopelagic fish. F.A.O. Fish. rech. Pap. 193: 151 pp .
GOULD, S. J. 1966 - Allometry and size in ontogeny and phylogeny. Biol. Rev 41(4): 587-640.
HULLEY, P. A. 1984 _ The South African Museum's Meiring Naude cruises. 14. Family Myctophidae (Osteichthyes, Myctophiformes). Ann. S. Afr. Mus. 93 (2): 53-96.
Hulley, P. A. 1986 - Order Myctophiformes. In Smiths' Sea Fishes. Smith, M. M. and P. C. Heemstra (Eds). Johannesburg; Macmillan: 282-322.
McGINNIS, R. F. 1982 - Biogeopraphy of lanternfishes (Myctophidae) south of $30^{\circ} \mathrm{S}$. In Biology of the Antarctic Seas 12. Pawson, D. L. (Fd.). Antarct. Res. Ser:, Am. geophys. Un. 35: 110 pp .
MOSER, H. G. and E. H. AHLSTROM 1972 - Development of lanternfish, Scopelopsis multipunctatus Brauer 1906, with a discussion of its phylogenetic position in the family Mycrophidae and its role in a proposed mechanism for the evolution of photophore pattems in lantemfishes. Fishery Bull., Wash. 70 (3): 541-564.
MOSER, H. G. and E. H. AHLSTROM 1974 - Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, a case study. Fishery Bull., Wash. 72\{2): 391-413.
MOSER, H. G., AHLSTROM, E. H. and J. R. PAXTON 1984 Myctophidae: development. In Ontogeny and Systematics of Fishes. Moser, H. G., Richards, W. J., Cohen. D. M., Fahay, M. P., Kendall, A. W. and S. L. Richardson (Eds). Spec. Publ. Am. Soc. Ichhyol. Herpesol. 1: 218-238 (Proceedings of an International Symposium in La Jolla, Califomia, August 1983).
NAFPAKTITIS, B. G. 1978 - Systematics and distribution of lanternfishes of the genera Lobianchia and Diaphus (Myctophidae) in the Indian Ocean. Sci. Bull. nat. Hist. Mus. Los Angeles Cty 30: 92 pp.
NAFPAKTITIS, B. G., BACKUS, R. H., CRADDOCK, I. E., HAEDRICH, R. L., ROBISON, B. H. and C. KARNELLA

1977 - Family Myctophidae. Mem. Sears Fdn mar: Res. 1(7): 13-265.
OLIVAR, M-P. 1987 - Larval development and spawning of Diaphus hudsoni in the Benguela Current region. Mar: Biol. 94(4): 605-611.
OLIVAR, M-P. and L. E. BECKLEY 1994 - Influence of the Agulhas Current on the distribution of lanternfish larvae off the southeast coast of Africa. J. Plankt. Res. 16 (12): 1759-1780.
PAXTON, J. R. 1979 - Nominal genera and species of lantern-
fishes (family Myctophidae). Contr. Sci. 322: I-28.
SHIGANOVA, T. A. 1977 - Larvae and juveniles of the lanternfishes (Myciophidae, Pisces) of the Atlantic Ocean. Trud $\ddagger$ Inst. Okeanol. 109: 42-112 (in Russian).
SPARTA, A. 1952 - Contributo alla conoscenza dello sviluppo larvale di Myctophum melopoclampum Cocco. Boll. Pesca Piscic. Idrobiol. (new series) 7(1): 5-10 + I Plate.
TAYLOR, W. R. 1967 - An enzyme method of clearing and staining small vertebrates. Proc. U.S. natn. Mus. $\mathbf{1 2 2}$ (3596): 17 pp .


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