S. Afr. J. mar. Sci. 14: 349–359
1994

INVESTIGATIONS ON THE OCCURRENCE OF LARVAE OF *SYMBOLOPHORUS* SPECIES (MYCTOPHIDAE) OFF SOUTHERN AFRICA

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Adults of three species of lanternfish of the genus *Symbolophorus* occur along the west and south-east coasts of southern Africa: *Symbolophorus boops* from the Benguela system and *S. barnardi* and *S. evermanni* from the Agulhas Current. Information on the distribution and morphometric features of these three species is provided from ichthyoplankton collections taken from Namibian and South African waters. The distribution of a fourth species, *S. kreffti*, which appears to be associated with the intrusions of warm Angolan waters into the northern Benguela, is also described.

Die volwassenes van drie spesies lanternvis van die genus *Symbolophorus* kom langs die wes- en suidweskus van suider-Afrika voor: *Symbolophorus boops* in die Benguelastelsel en *S. barnardi* en *S. evermanni* in die Agulhasstroom. Inligting oor die verspreiding en morfometriese kenmerke van hierdie drie spesies word verskaf uit igtioplanktonversamelings in Namibiese en Suid-Afrikaanse waters. Die verspreiding van 'n vierde spesie, *S. kreffti*, wat blykbaar met die instroming van warm Angolese water na die noordelike Benguela in verband staan, word ook beskryf.

Midwater fish of the family Myctophidae are distributed worldwide. The genus *Symbolophorus* is found in both the northern and southern hemispheres (Hulley 1981, Bekker 1983) and only *S. boops* and *S. barnardi* are restricted to the southern hemisphere, where they occur in the Atlantic, Indian and Pacific oceans. These species and *S. evermanni* occur off southern Africa. Although another species of the genus, *S. rufinus*, has not been found off southern Africa, its southern limit is just north of those of the other three species (16°S in the Atlantic Ocean and 10°S in the Indian Ocean; Nafpaktitis and Nafpaktitis 1969, Hulley 1981). Ichthyoplankton collections off northern Namibia indicated the presence of a different species (Olivar 1990), which is proved herein to belong to *S. kreffti*, a species whose adult distribution has been reported to be between c. 20°N and 3°30′S (Hulley 1981). Of the aforementioned species, only *S. boops* belongs to the "Cold Water group", whereas the others relate to the "Warm Water group" (*sensu* Hulley 1981).

Studies which include information on the distribution and systematics of adults of the genus *Symbolophorus* are substantial (Nafpaktitis and Nafpaktitis 1969, Wisner 1976, Hulley 1981, 1984, 1986a, b, McGinnis 1982, Bekker 1983, Rubiés 1985), but the taxonomy of the genus remains unresolved. Recent work by Gago (1993), using otolith morphology, attempted to describe the genus more definitively. Studies on the larvae of the family Myctophidae by Moser and Ahlstrom (1970, 1972, 1974) and Moser *et al.* (1984) demonstrated that larval characteristics can be important taxonomic tools and aids in defining their evolutionary lineages. At present, larval characteristics of *Symbolophorus* species differentiate the same two groups of species as were distinguished by Hulley (1981) on the basis of adult characteristics (Zelck *et al.* 1993).

There is information on the early life history stages of the genus *Symbolophorus* for *S. californiense*, *S. veranyi*, *S. boops*, *S. evermanni*, *S. kreffti* and *S. rufinus* (Tåning 1918, Pertseva-Ostroumova 1964, 1974, Dekhnik and Sinyukova 1966, Moser and Ahlstrom 1970, 1974, Moser *et al.* 1984, Olivar and Rubiés 1986, Zelck 1991, Zelck *et al.* 1993). The present study is an investigation of early larval characteristics and distinguishes the larvae of the four species of *Symbolophorus* that occur in waters off southern Africa. *S. barnardi* is described for the first time. Information is provided on the distribution of these larvae in relation to local hydrographic features.

MATERIAL AND METHODS

Larvae of *S. barnardi* and *S. evermanni* were collected along the east coast of South Africa during three cruises conducted in May/June 1990, October 1990 and February 1991. The survey grid extended from Algoa Bay (34°S, 26°E) to the Tugela River

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Manuscript received: February 1994

Table I: Morphometric measurements as a proportion of body length *BL* for larvae of *Symbolophorus barnardi*, *S. boops* and *S. evermanni* (abbreviations beneath)

Species or parameter	Body length (mm)	Morphometric measurements as a proportion of body length (%)							
		PA	*HL*	*BDP*	*Ede*	*Edi*	*LP*	*OW*	*DD*
Symbolophorus barnardi	3,5	47	24	10	7	4	–	–	–
	4,0	49	25	11	8	5	–	28	–
	4,5	51	26	12	8	5	12	28	–
	5,0	53	26	12	8	5	12	28	–
	5,5	55	27	12	8	5	12	28	–
	6,0	57	27	13	9	6	13	28	–
	6,5	58	28	13	9	6	13	28	–
	7,0*	60	28	14	9	6	13	28	–
	7,5*	61	29	14	9	6	14	28	–
	8,0*	63	29	15	10	6	14	28	–
	8,5	64	29	15	10	6	14	28	–
Number of fish examined	51	32	31	36	11	11	15	9	–
CIE_y (%)		12,5	16,8	31,1	24,5	33.7	12,5	22,2	–
Symbolophorus boops	5,0	57	28	13	–	–	14	24	–
	5,5	57	29	14	–	–	13	24	–
	6,0	58	29	14	–	–	13	24	–
	6,5*	58	29	15	–	–	13	24	–
	7,0*	58	29	15	–	–	13	24	–
	7,5*	59	29	15	–	–	13	23	–
	8,0	59	29	16	–	–	13	23	–
	8,5	59	29	16	–	–	13	23	–
	9,0	59	29	17	–	–	13	23	49
	9,5	60	29	17	–	–	13	23	49
	10,0	60	29	17	–	–	13	23	49
	10,5	60	30	18	–	–	13	23	49
	11,0	60	30	18	–	–	13	23	49
Number of fish examined	17	14	15	13	–	–	16	8	3
CIE_y (%)		9,3	15,4	31,0	–	–	14,9	27,8	8,9
Symbolophorus evermanni	3,5	62	–	10	–	–	–	–	–
	4,0	62	28	11	–	–	9	–	–
	4,5	62	28	11	–	–	10	32	–
	5,0	63	29	12	–	–	11	31	–
	5,5*	63	29	13	–	–	12	30	–
	6,0*	63	29	13	–	–	13	29	51
	6,5*	63	29	14	–	–	14	28	51
	7,0	63	30	15	–	–	15	27	51
	7,5	63	30	15	–	–	15	27	51
	8,0	63	30	16	–	–	16	26	51
	8,5	63	30	16	–	–	17	25	50
	9,0	64	30	17	–	–	–	25	50
Number of fish examined	32	30	19	18	–	–	14	12	5
CIE_y (%)		5,9	18,9	16,1	–	–	32,8	18,9	12,8

* Specimens undergoing notochord flexion

PA = preanal length; *HL* = head length; *BDP* = body depth at pectoral fin; *Ede* = eye depth; *Edi* = eye diameter; *LP* = length of pectoral fin bases; *OW* = orbital width; *DD* = dorsal distance; CIE_y = confidence interval for *y* estimates

(29°S, 31°E), from the shallow continental shelf into the Agulhas Current offshore (Beckley and Van Ballegooyen 1992). Ichthyoplankton samples were collected with Bongo nets of mesh size 500 μm, towed obliquely from 80 m (depth permitting) to the surface. Samples were preserved in buffered 5% formalin. Larvae of *S. boops* and *S. kreffti* were obtained from several surveys (November 1979, August 1980, April 1981, July 1983, January and July 1984, September 1985 and April 1986) conducted in the Benguela system, using a Bongo net until 1984 and an RMT 1×6 in 1985 and 1986 (Olivar and Rubiés 1986, Olivar and Fortuño 1991). Type specimens of larvae of *S. evermanni*, *S. boops* and *S. barnardi* from the Australian Museum (collected in the Pacific Ocean), and larvae of *S. kreffti* from the Museum of Zoology in Hamburg (collected in the tropical North-East Atlantic) were also examined.

Morphometric measurements of the larvae (±0,1 mm) were made at least one year after collection. Measurements recorded were body length *BL* (the distance along the midline of the body from the tip of the snout to the end of the urostyle in preflexion larvae, and to the posterior margin of the hypural elements in postflexion stages), preanal length *PA* (distance along the midline of the body from the tip of the snout to the vent), head length *HL* (distance from the tip of the snout to the posterior margin of the cleithrum), body depth at pectoral *BDP* (body depth measured at the level of the pectoral fin bases), eye diameter *Edi*, eye depth *Ede*, length of pectoral fin bases *LP* (longest distance between the cleithrum and the distal margin of the pectoral fin bases), dorsal distance *DD* (distance from the tip of the snout to the origin of the developing dorsal fin), orbital width *OW* (distance between both distal surfaces of the orbit, with eye stalks aligned perpendicular to the body axis).

In order to ascertain if there is allometric growth, the relationships between the various body measurements and body length were calculated from the equation $y = ax^b$, where x is *BL*, y the variable measurement, b the allometric factor and a the expected value of y at $x = 1$ (Gould 1966). Tables of morphometric characteristics were constructed from the results obtained using the allometric equations. Confidence intervals for the y estimates (CIE_y) from the fitted equations give the maximum relative error between the real measure of a specimen and the value calculated from the equation given in Table I.

RESULTS

Larvae of four species of *Symbolophorus* were found off the coast of southern Africa: *S. kreffti* off northern Namibia, *S. boops* off the entire Namibian coast and the west coast of South Africa, and *S. barnardi* and *S. evermanni* off the east coast of South Africa. Larvae of *S. kreffti* were described by Zelck (1991), *S. boops* larvae by Pertseva-Ostroumova (1964) and Olivar and Rubiés (1986) and *S. evermanni* larvae by Pertseva-Ostroumova (1964) and Ozawa (1986).

Morphological features of *Symbolophorus barnardi* larvae

The developmental series for this species is illustrated in Figure 1. Larvae are slender and flattened, especially in the early stages. *BDP* progressively increases from preflexion to postflexion stages (Table I), showing a significant positive allometric relationship with body length (b = 1,4021 ± 0,1921). The gut is straight, reaching the midpoint of the body in small larvae, and slightly more than 60% of *BL* in flexion and postflexion stages. The relationship between *PA* and *BL* is also significantly positively allometric (b = 1,3547 ± 0,0727). *HL* increases with development (b = 1,2166 ± 0,1205, Table I). Eyes are narrow and stalked in all larval stages, having a transparent scleral envelope protruding from the ventral surface of the eye in larvae c. 4 mm long and an opaque mass of choroid tissue appearing within this envelope in later stages. *OW* is 28% of *BL* and teeth become visible from 5 mm onwards. Notochordal flexion begins at 7 mm and is completed by 8,8 mm.

The pectoral fin base is wing-shaped, increasing from 12% in preflexion larvae to 14% in a larva of 8,8 mm (the largest specimen examined). Pectoral fin rays develop early, and in two larvae 4,8 mm long, 10 rays were observed, in four larvae of c. 6 mm, ray counts ranged from 11 to 14, and in two larvae of 8 and 8,8 mm, 14 rays were recorded (the two lowest rays were still very short). Although the length of the pectoral fin rays cannot be measured accurately because they are damaged in most larvae, it is noteworthy that, in larvae >5 mm, the longest rays appear to reach the anus. The caudal fin is the second fin to ossify. In the largest larva examined (8,8 mm), 17 pterygiophores were observed in the anal fin bases. The dorsal fin bases were still not visible in that larva, but very small pelvic fin buds were apparent.

No photophores were developed in any of the *S. barnardi* larvae examined. The number of myomeres was quite difficult to count in small larvae, but in three flexion and postflexion larvae, myomere counts ranged from 39 to 41.

Pigmentation of *S. barnardi* larvae

Pigmentation on the isthmus, lateral cleithral region and between the eyes was a general feature in all

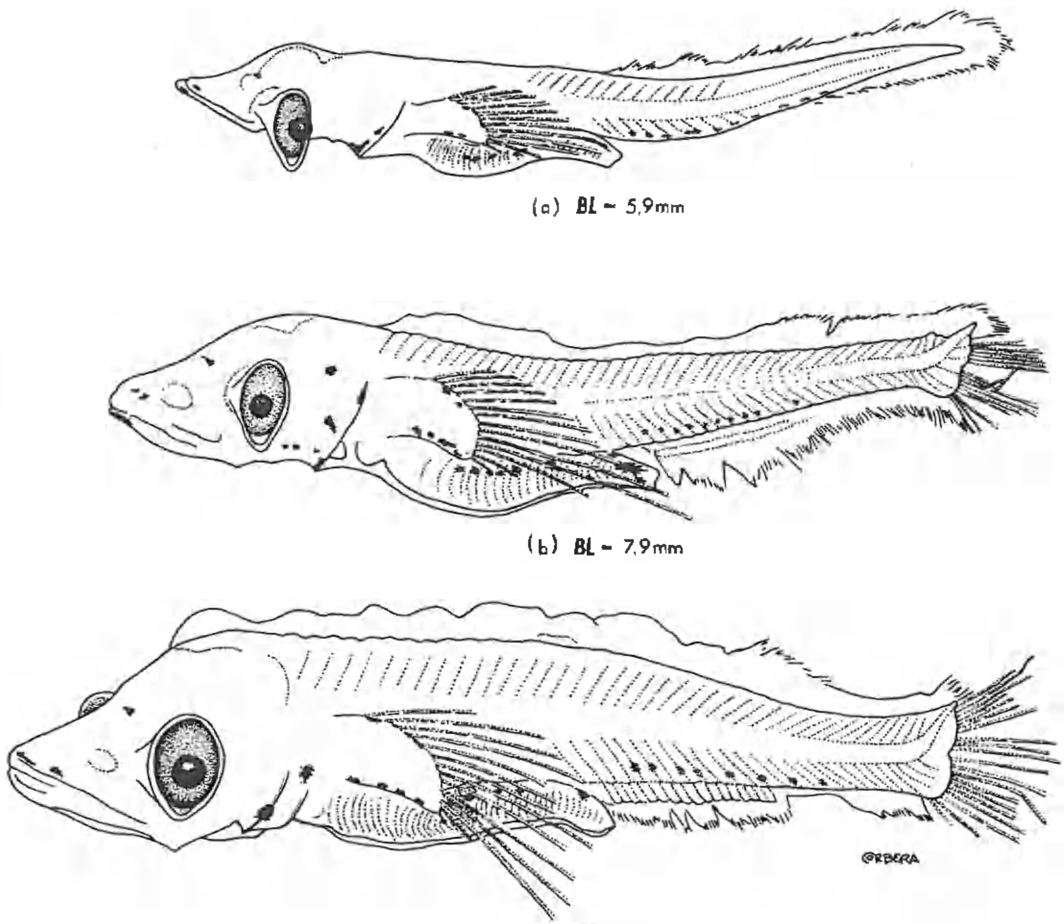

Fig. 1: Larvae of *Symbolophorus barnardi* from the Agulhas Current

specimens examined. Although not very distinct, pigmentation was visible also inside the head, in the otic zone. All larvae had pigmentation on the snout and, except for the largest larva, on the tip of the lower jaw. In larvae >4 mm, the pectoral fin bases were outlined by melanophores, which were scattered over the pectoral fin rays. A pigment series of between 5 and 8 closely spaced melanophores was present laterally on the gut. A melanophore was present on the free terminal section of the gut. In early developing larvae (<4 mm), a row of 11–15 melanophores was present on the postanal midventral line of the body, decreasing to 8–10 melanophores in larger larvae of 5–8 mm. In flexion and postflexion stages, melanophores were embedded in the body, located at the level of the anal fin bases and extending thereafter for about 2 or 4 myomeres.

Comparisons

Larval specimens of *S. kreffti*, described by Zelck (1991) from the tropical North-East Atlantic, were used to identify this species from the northern Benguela collections. A diagnostic feature specific to *S. kreffti* larvae was the conspicuous series of midventral tail melanophores which extended to the end of the caudal peduncle. Figure 2 illustrates the larval development

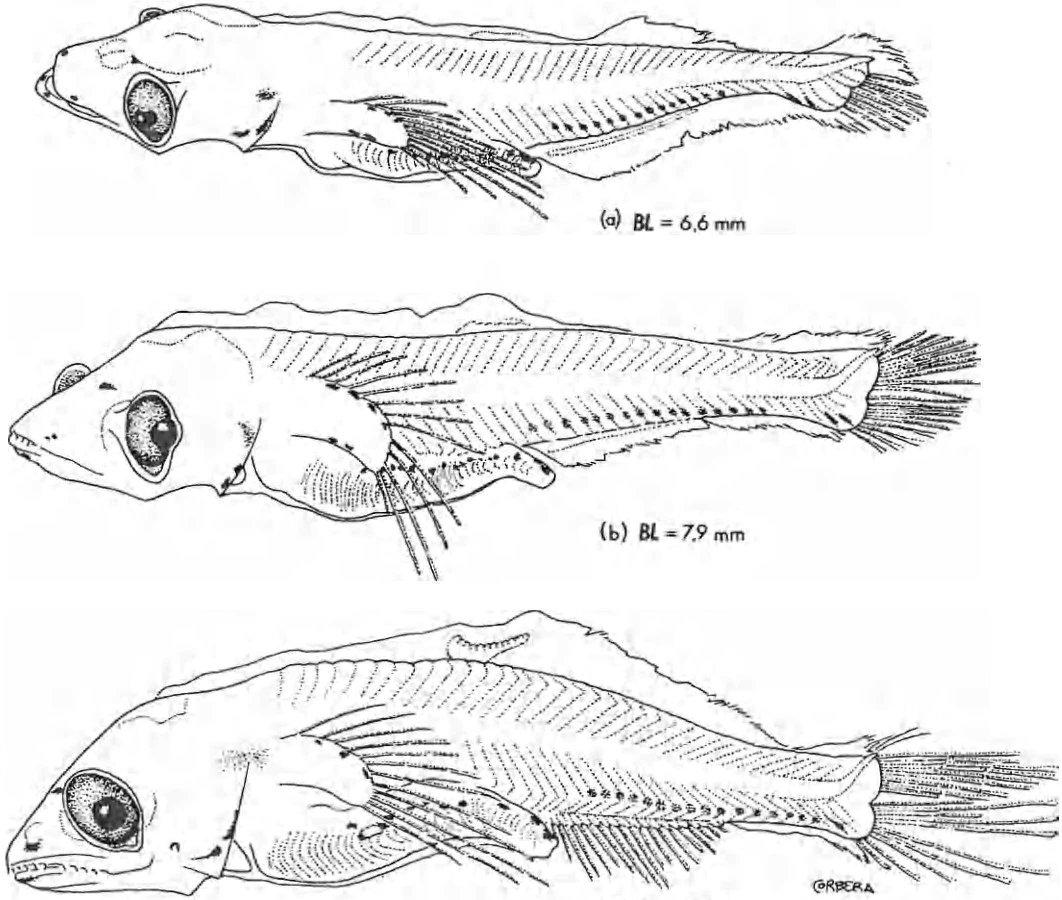

Fig. 2: Larvae of *Symbolophorus kreffti* from the northern Benguela system

of specimens collected off northern Namibia.

S. boops larvae were selected solely from stations within the central Benguela, an area where only this species of *Symbolophorus* has been recorded (Hulley 1981, Rubiés 1985). As upwelling occurs throughout most of the year there (Shannon 1985), water temperatures would probably be too cold for the other "Warm Water group" of *Symbolophorus* species (Hulley 1981). Figure 3 illustrates three larval stages of *S. boops*. From Table I, it is clear that their morphological measurements are similar to those of *S. barnardi* larvae, especially in the preflexion stages. The main morphometric difference is the smaller *PA* ratio in flexion and postflexion larvae in *S. boops* (PA/BL = 0,589, SD = 0,024, n = 14) than in *S. barnardi* (PA/BL = 0,619, SD = 0,019, n = 4). The pigmentation pattern was also quite similar between the two species, but the pigmentation of *S. boops* larvae from the Benguela was lighter, especially at the embedded postanal midventral tail, which was visible in the larvae described by Olivar and Rubiés (1986). The larvae from the Benguela were collected between 1984 and 1985, whereas those from the Agulhas Current were taken in 1990 and 1991.

The most notable difference between the two species was the presence of a small Br_2 photophore (the second photophore in the branchiostegal membrane) in *S. boops* larvae of c. 9 mm and its absence from the *S. barnardi* larvae of 8,8 mm. The only previous record of *S. barnardi* larvae is that of Crossland (1982) from off north-

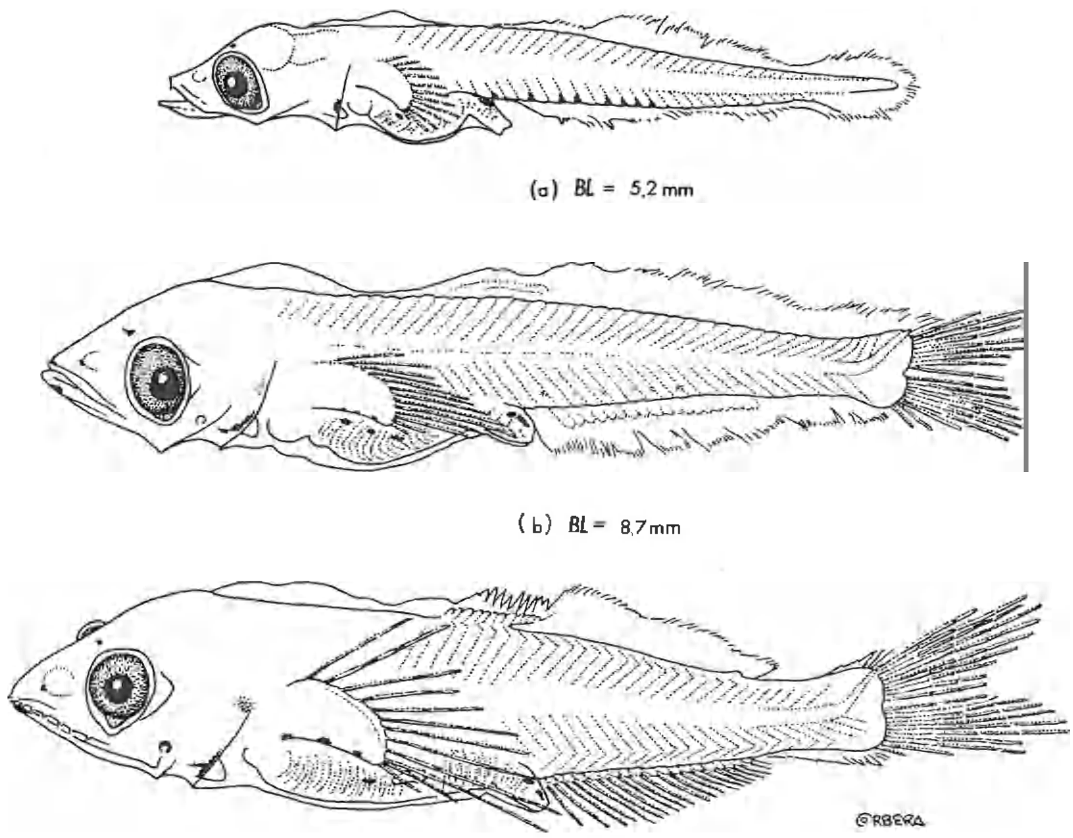

Fig. 3: Larvae of *Symbolophorus boops* from the central Benguela system

eastern New Zealand, but their presence was tentatively based on the fact that adults of the same species were present in the same area. The large *Symbolophorus* specimen in Crossland's study, which measured 10,7 mm and had no Br_2 melanophore, is probably *S. barnardi*.

S. evermanni larvae collected from the Agulhas Current were identified using the descriptions of Pertseva-Ostroumova (1974) and Ozawa (1986) and are illustrated in Figure 4. Their morphometric data are also presented in Table I. The larvae of *S. barnardi* and *S. evermanni* were easily distinguishable, *S. evermanni* larvae being less pigmented than *S. barnardi*, pigment being located on the lateral walls in three places: the anus, foregut and midway between these regions. Postflexion larvae had less pigmentation along the gut and sometimes no melanophores. The row of midventral tail melanophores was present in preflexion larvae only. The pectoral fin was also less pigmented in *S. evermanni* than in *S. barnardi*, melanophores being concentrated at the lower part of the bases, and no melanophores were present at the rays. In preflexion stages, *PA* was longer in *S. evermanni*. For the same length of larva, the *LP* (bases and rays) was always shorter in *S. evermanni* than in *S. barnardi*. Fins develop earlier and the Br_2 photophore appears earlier (at c. 6,5–7,0 mm) in *S. evermanni* than in *S. barnardi*. The number of myomeres in *S. evermanni* larvae ranged between 35 and 38.

None of the larvae collected from Namibian and South African waters could belong to the neighbouring species *S. rufinus*. Larvae of this species were described by Zelck *et al.* (1993), and they are distin-

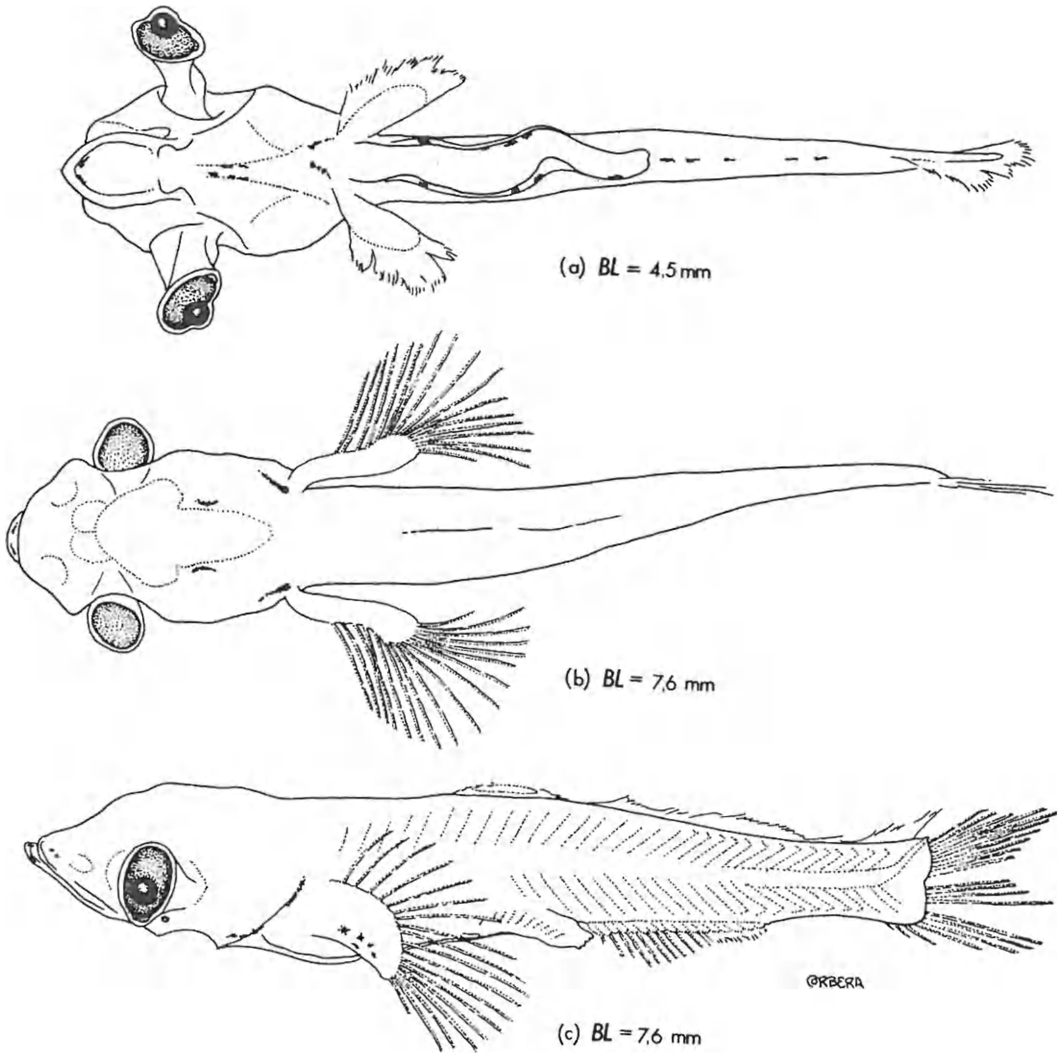

Fig. 4: Larvae of *Symbolophorus evermanni* from the Agulhas Current — (a) ventral view, (b) dorsal view, (c) lateral view

uished by the conspicuously long eyestalks (39,4% f *BL*) in preflexion and flexion larvae and the long igestive tract (70,6% of *BL*) in larvae between 5 and 3 mm long (Zelck *et al.* 1993).

istribution

S. kreffti occurs mainly in the tropical North-East tlantic and adults have not been found off southern Africa (Hulley 1986a, b). However, larvae of this species were found along the continental slope in the northern Benguela during three cruises, August 1980, March/April 1981 and April 1986, only where Angolan water was present. Using a multiple opening/closing plankton net at a fixed 48-h station during the April 1986 cruise, Olivar (1990) demonstrated that *S. kreffti* larvae remained above the thermocline. Larvae of *S. boops* occur throughout the Benguela in offshore waters (>500 m) and are present during most of the year (Olivar

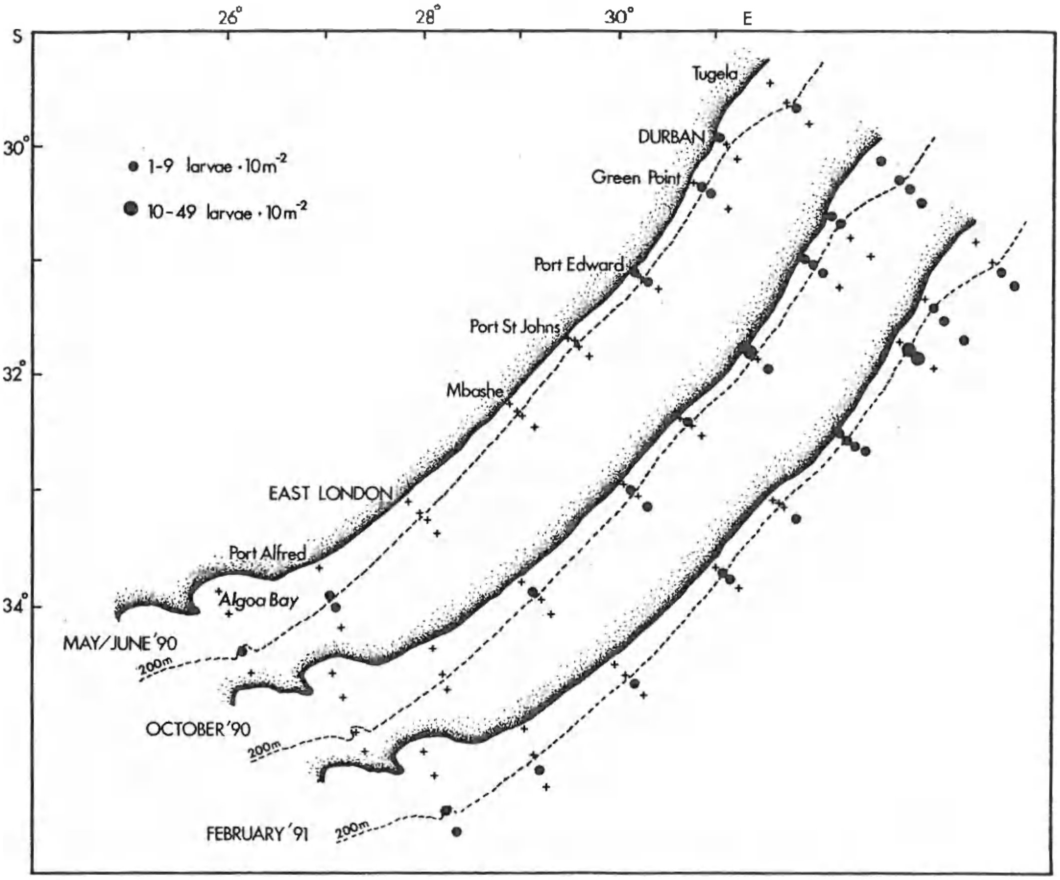

Fig. 5: The study area along the east coast of South Africa, showing the sampling stations and the distribution of *Symbolophorus barnardi* larvae during three cruises in 1990 and 1991

and Fortuño 1991).

S. barnardi larvae were present during all three cruises conducted in the Agulhas Current, being more abundant during spring and summer than in winter. The larvae were more concentrated in the northern sector of the study area, occurring at both inshore (50 m) and offshore (500–2 000 m) stations (Fig. 5). *S. barnardi* larvae did not occur at the shallow stations of the southern sector of the study area. Lowest temperatures were observed in this region, *SST* being <19°C in winter and spring and <22°C in summer, whereas temperatures in the upper 100 m ranged from 16 to 19°C in winter, from 13 to 19°C in spring and from 13 to 22°C in summer. *S. evermanni* larvae were also present during all three cruises, but they were not as abundant as those of *S. barnardi*. The distribution of both species were quite similar, but *S. evermann* larvae were less frequent at the innermost coastal station (Fig. 6).

DISCUSSION

Adult *S. barnardi* and *S evermanni* occur in th warm Agulhas Current off the east coast of South Afric (Hulley 1984, 1986b). Off the west coast of souther Africa, *S. boops* are found in the cold Benguela wate and *S. barnardi* in the northern and southern war water boundaries of the Benguela system (Hulle

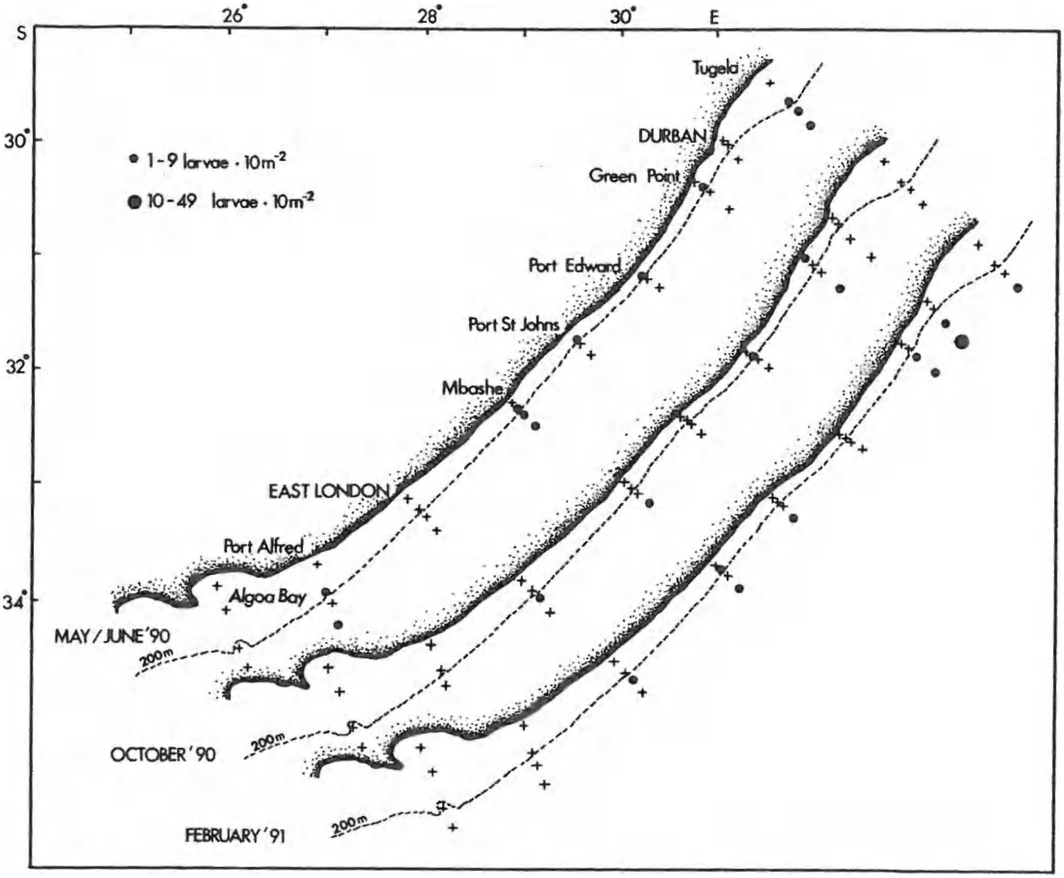

Fig. 6: Distribution of *Symbolophorus evermanni* larvae in the study area during three cruises in 1990 and 1991

1981, 1986b, Rubiés 1985). Although *S. boops* have not been recorded off the east coast of South Africa, the large number of adults of two typical subantarctic or semi-subantarctic species, *Metelectrona ventralis* and *Diaphus hudsoni* (Hulley 1986b), that were found south-east of Mossel Bay, suggests that *S. boops* may also occur on the East Coast (P. A. Hulley, South African Museum, pers. comm.). If *S. boops* larvae drifted from the Benguela system to the Agulhas Current, larval abundance should be higher in the south, decreasing to the north-east. This pattern contrasts with that observed for *S. barnardi* larvae, which were present during the winter, spring and summer surveys, predominantly in the northern sector of the study area. This finding suggests that these larvae are not *S. boops*. Furthermore, the high temperatures recorded during the three cruises were outside the thermal range assumed for *S. boops*. Hulley (1981) reported that the distribution of adult *S. boops* may be confined to temperatures ranging between 10 and 15°C, whereas *S. barnardi* appear to prefer temperatures between 15 and 20°C in the upper 100 m.

In addition to the presence of *S. boops* and *S. barnardi* in Namibian waters (Rubiés 1985), the present results show that *S. kreffti* larvae may penetrate from the north into the northern Benguela by the intrusion southwards of warm Angolan waters.

The similar distributions observed between the larvae of *S. barnardi* and *S. evermanni* is of interest because of the difference in their adult distributions. *S. barnardi* has a southern tropical distribution, whereas *S. evermanni* has a tropical-subtropical distribution (Hulley

1981). Although adults of both species have also been found in the Agulhas Current (Hulley 1984), they were considered by that author as being individuals that may have been actively transported as expatriates into that region. The presence of their larvae in the study area could be the result of their transport from the north, or alternatively, the larvae may be a product of spawning by residential adult populations. Larvae of many other possible expatriate lanternfish species were also found in the same collections, which suggests that transport, aided by the strong Agulhas Current, plays an important role in the extent of myctophid larval distributions off the east coast of South Africa.

ACKNOWLEDGEMENTS

We are especially grateful to Drs C. Zelck and H-Ch. John (both Zoologisches Institut und Museum, Hamburg) for providing help and information during the preparation of the manuscript. Dr P. A. Hulley (South African Museum, Cape Town) and Mr P. Rubiés (Instituto de Ciencias del Mar, Barcelona) are thanked for their useful comments. We are grateful to Dr T. A. Shiganova (Institute for Oceanology, Moscow) for making available additional larvae from the Benguela system and to Drs J. M. Leis and T. Trnski (Australian Museum, Sydney) for the loan of larval type specimens. Finally, we express our gratitude to Mr J. Corbera who drew the larvae.

LITERATURE CITED

BECKLEY, L. E. and R. C. VAN BALLEGOOYEN 1992 — Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 83–93.

BEKKER, V. E. 1983 — *Myctophidae of the World Ocean*. Moscow; Nauka: 248 pp. (In Russian).

CROSSLAND, J. 1982 — Distribution and abundance of fish eggs and larvae from the spring and summer plankton of northeast New Zealand, 1976–78. *Fish. Res. Bull., N.Z.* **24**: 59 pp.

DEKHNIK, T. V. and V. I. SINYUKOVA 1966 — Distribution of pelagic fish eggs and larvae in the Mediterranean Sea. 2. On the reproduction and ecology of larvae of Mediterranean Myctophidae. In *Studies on the Plankton of Southern Seas*. Moscow; Nauka: 82–108 (In Russian).

GAGO, F. J. 1993 — Morphology of the saccular otoliths of six species of lanternfishes of the genus *Symbolophorus* (Pisces: Myctophidae). *Bull. mar. Sci.* **52**(3): 949–960.

GOULD, S. J. 1966 — Allometry and size in ontogeny and phylogeny. *Biol. Rev.* **41**(4): 587–640.

HULLEY, P. A. 1981 — Results of the research cruises of FRV "Walther Herwig" to South America. 58. Family Myctophidae (Osteichthyes, Myctophiformes). *Arch. FischWiss.* **31**(Suppl. 1): 300 pp. + 3 pp. of Index.

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. 1986a — Lanternfishes of the southern Benguela region. 1. Faunal complexity and distribution. *Ann. S. Afr. Mus.* **97**(7): 227–249.

HULLEY, P. A. 1986b — Order Myctophiformes. In *Smiths' Sea Fishes*. Smith, M. M. and P. C. Heemstra (Eds). Johannesburg; Macmillan: 282–322.

McGINNIS, R. F. 1982 — Biogeography of lanternfishes (Myctophidae) south of 30°S. In *Biology of the Antarctic Seas* **12**. Pawson, D. L. (Ed.). *Antarct. Res. Ser., Am. geophys. Un.* **35**: 110 pp.

MOSER, H. G. and E. H. AHLSTROM 1970 — Development of lanternfishes (family Myctophidae) in the California Current. 1. Species with narrow-eyed larvae. *Sci. Bull. nat. Hist. Mus. Los Angeles* **7**: 1–145.

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 Myctophidae and its role in a proposed mechanism for the evolution of photophore patterns in lanternfishes. *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. Ichthyol. Herpetol.* **1**: 218–238 (Proceedings of an International Symposium in La Jolla, California, August 1983).

NAFPAKTITIS, B. G. and M. NAFPAKTITIS 1969 — Lanternfishes (family Myctophidae) collected during Cruises 3 and 6 of the R/V *Anton Bruun* in the Indian Ocean. *Sci. Bull. nat. Hist. Mus. Los Angeles* **5**: 1–79.

OLIVAR, M-P. 1990 — Spatial patterns of ichthyoplankton distribution in relation to hydrographic features in the northern Benguela region. *Mar. Biol.* **106**: 39–48.

OLIVAR, M-P. and J-M. FORTUÑO 1991 — Guide to ichthyoplankton of the Southeast Atlantic (Benguela Current region). *Scientia Mar., Barcelona* **55**(1): 383 pp.

OLIVAR, M-P. and P. RUBIÉS 1986 — Distribución y abundancia de larvas de *Symbolophorus boops* (Osteichthyes, Myctophidae) en el Atlántico sudoriental, y descripción de su desarrollo larvario. *Investicagión pesq., Barcelona* **50**(3): 437–447.

OZAWA, T. 1986 — The larvae of three Japanese species of the gonostomatid genus *Gonostoma*. In *Studies on the Oceanic Ichthyoplankton in the Western North Pacific*. Ozawa, T. (Ed.). Fukuoka, Japan; Kyushu University Press: 68–73.

PERTSEVA-OSTROUMOVA, T. A. 1964 — On some morphological peculiarities of myctophid larvae (Myctophidae, Pisces). In *Biology and Distribution of the Fishes of the Pacific and Indian Oceans*. Rass, T. S. (Ed.). *Trudy Inst. Okeanol.* **73**: 79–92 (In Russian).

PERTSEVA-OSTROUMOVA, T. A. 1974 — New data on lanternfish larvae (Myctophidae, Pisces) with oval eyes from the Indian and Pacific oceans. *Trudy Inst. Okeanol.* **96**: 77–142 (In Russian).

RUBIÉS, P. 1985 — Zoogeography of the lanternfishes (Osteichthyes, Myctophidae) of Southwest Africa. In *International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Namibia)*[, *Barcelona, November 1983*] **1**. Bas, C., Margalef, R. and P. Rubiés (Eds). Barcelona; Instituto de Investigaciones Pesqueras: 573–586.

SHANNON, L. V. 1985 — The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. In *Oceanography and Marine Biology. An Annual Review* **23**. Barnes, M. (Ed.). Aberdeen; University Press: 105–182.

TÅNING, A. V. 1918 — Mediterranean Scopelidae (*Saurus*, *Aulopus*, *Chlorophthalmus* and *Myctophum*). Schmidt, J. (Ed.). *Rep. Dan. oceanogr. Exped. Mediterr.* **2**(A.7): 154 pp.

WISNER, R. L. 1976 — *The Taxonomy and Distribution of Lanternfishes (family Myctophidae) of the Eastern Pacific Ocean*. Washington, D.C.; U.S. Government Printing Office: 229 pp.

ZELCK, C. 1991 — The larval development of *Symbolophorus kreffti* Hulley, 1981 (Teleostei, Myctophidae). *Mitt. Hamb. zool. Mus. Inst.* **88**: 221–226.

ZELCK, C., JOHN, H-Ch. and M-P. OLIVAR 1993 — The larval development of *Symbolophorus rufinus* (Tåning, 1928) (Teleostei, Myctophidae). *Mitt. Hamb. zool. Mus. Inst.* **90**: 313–320.