Spawning and development of *Lesueurigobius sanzoi* off northern Namibia

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The presence of the gobiid *Lesueurigobius sanzoi* in the Benguela upwelling region was recorded for the first time from the capture of five adult specimens in 1980. This paper presents evidence that this region can be included in the species distribution range. It also presents the first description of the larval series and juveniles, together with a morphometric study of the larval stages and a comparative study of the characters differentiating larvae of this species from those of *Nematogobius bibarbatus*, the dominant gobiid in the region. The smallest stages of the larvae of these two species are distinguished by their pigmentation patterns, the larger stages by the number of fin rays. Information on the geographical and depth distribution of *Lesueurigobius sanzoi* larvae is also included. This species spawns on the northernmost part of the Namibian continental shelf in autumm. The larval distribution area is associated with the warmer waters of the Angola Current.

Die teenwoordigheid van *Lesueurigobius sanzoi* (Gobiidae) in die Benguela-opwelgebied is vir die eerste keer aangeteken toe daar vyf eksemplare in 1980 daar versamel is. In hierdie artikel word inligting verskaf wat bevestig dat bogenoemde gebied ingesluit kan word as deel van die verspreidingsgebied van hierdie visspesie. Hierbenewens word die eerste beskrywing van die larvaalstadiums en onvolwasse stadiums verskaf wat ook morfometriese inligting van die larvaalstadiums insluit. Verder is daar ook 'n vergelykende studie uitgevoer van die differensiële kenmerke van die larvaalstadiums van dié spesie ten einde te bepaal hoe dit van die larvaalstadium van *Nematogobius bibarbatus* verskil. Laasgenoemde is die dominante spesie van die familie in hierdie gebied. Hierdie studie het aangetoon dat die jong larvaalstadiums van die twee spesies onderskei kan word op grond van hul pigmentasiepatrone, terwyl die latere larvaalstadiums verskillende getalle vinstrale het. Inligting met betrekking tot die geografiese en diepteverspreidingspatrone word ook verskaf. *L. sanzoi* broei in die gebied teenoor die mees noordelike deel van die Namibiese kontinentalebank gedurende die herfs terwyl die larvaalstadiums in die warmer water van die Angola-stroom aangetref word.

The presence of *Lesueurigobius sanzoi* (de Buen, 1918) on the continental shelf off northern Namibia was recorded for the first time in 1982. The distribution range of this species extends from Portugal to Mauritania in the eastern Atlantic and into the Alboran sea in the western Mediterranean (Miller 1986). The first record of *Lesueurigobius sanzoi* in the south-east Atlantic consisted of five adults caught opposite the mouth of the Cunene River (17°30'S / 11°32'E) at a depth of 117 m (Lloris 1982).

When the species was detected off Namibia for the first time, it was postulated that the region might be an expatriation area in which the species evinced survival but not reproductive capability (Lloris, Rucabado & Gomes 1984). However, the presence of larvae of this species in plankton from the region constitutes evidence that northern Namibia can in fact be considered within its normal distribution range. There is no previous information in the literature on the spawning areas and spawning seasons for this species or on the geographical and depth distributions of its larvae.

The early developmental stages of *Lesueurigobius sanzoi* larvae and juveniles are described here for the first time, together with a discussion on the identity of this species. The characters that bring us to the conclusion that the larvae belong to this species and not to the other species present in nearby areas are also specified.

The gobiid *Nematogobius bibarbatus* (von Bonde, 1923) is quite abundant in the pelagic zone and is endemic to the Benguela upwelling region. Its larvae are the major component of the neritic plankton in the northern Benguela region during the greater part of the year (O'Toole 1978; Olivar 1985).

The present paper contains, in addition to the first description of the larvae and juveniles of *Lesueurigobius sanzoi,* a comparison of the characters differentiating this species from *Nematogobius bibarbatus.* This is important because the distribution of these two species overlaps on the continental shelf off northern Namibia.

Material and methods

The specimens examined in this study were taken in plankton hauls carried out in the northern Benguela region in August 1980, March – April 1981, and April 1986 (Table 1). In the first two surveys larvae were collected using Bongo nets with mesh sizes of 300 and 500 μm. Tows were oblique from 200 m, or from 10 m above the bottom at shallower stations, to the surface. In April 1986 a multiple RMT (rectangular midwater trawl) 1 × 6 net with a 200 μm mesh size was used. Again, hauls were effected from 200 m, bottom depth permitting, or from 10 m above the bottom. Oblique tows were carried out from 200 to 60 m, from 60 to 40 m, and from 40 to 0 m.

Observed larval abundance is expressed as the number of individuals under 10 m^2 of sea surface for Bongo net hauls and as the number of individuals per 1000 m^3 for RMT 1 × 6 net hauls.

Specimens on which the description was based were measured using an ocular micrometer accurate to 0,1 mm and drawn with the aid of a camera lucida. Morphometric analysis was also performed, and the following measurements were taken: standard length

Table 1 Location and dates of surveys on which *Lesueurigobius sanzoi* larvae were caught

Cruise	Date	Sampling area
Benguela II	August 1980	17°30'S – 23°00'S
Benguela III	March – April 1981	17°30'S – 23°00'S
SNEC II	April 1986	17°30'S – 26°30'S

(SL), the distance along the midline of the body from the tip of the snout to the end of the urostyle; preanal length (PA), the distance along the midline of the body from the tip of the snout to the vent; head length (HL), the distance from the tip of the snout to the posterior margin of the cleithrum; head depth (HD), maximun depth of the head; and body depth (BD), maximum depth of the body. Allometric relationships were established between the other body measurements and standard length. The equation $y = ax^b$ was applied, where x is standard length, y the other measurement being related, b the allometric factor, and a the expected value of y at $x = 1$ (Gould 1966). Confidence intervals were calculated at the 95% level of significance.

Taylor's (1967) method of clearing and staining was applied to some of the larger larvae, after which counts of fin rays and vertebrae were made.

Description of larvae of *Lesueurigobius sanzoi*

The larval series is illustrated in Figure 1, and morphometric characters are presented in Table 2. The most important morphological aspects are discussed below, followed by a consideration of the characters differentiating the larvae and juveniles of this species from those of *Nematogobius bibarbatus*.

Juveniles of *Lesueurigobius sanzoi* can be identified by the dorsal and anal fin ray counts and by the presence of rows of papillae on the head. Larger larvae can be identified by the number of dorsal and anal fin rays and by comparing the morphological characters and the ventral pigmentation pattern with those of juveniles. Smaller larvae were identified by tracing pigmentation backwards from the larvae through a graded series of specimens (Moser & Ahlstrom 1970).

Morphology and morphometry

The body is slender and elongate in all the developmental stages. The gut is straight, reaching a little beyond the midpoint of the body, 62% of SL in 2-mm long larvae, 55% in 7,5 and 9-mm long larvae, 53% in 14,5-mm long larvae, and 52% in juveniles. The allometry of preanal length with respect to SL is slightly negative through development, and the relationship is, therefore, practically isometric (b = 0,9207 ± 0,0396, 62 data points, r = 0,9864) (Figure 2A).

Head length is isometric with respect to standard length and amounts to between 26 and 28% of SL (b = 1,0413 ± 0,0482, 62 data points, r = 0,9843) (Figure 2B). In juveniles it reaches 30% of SL.

Both head depth and body depth are slightly

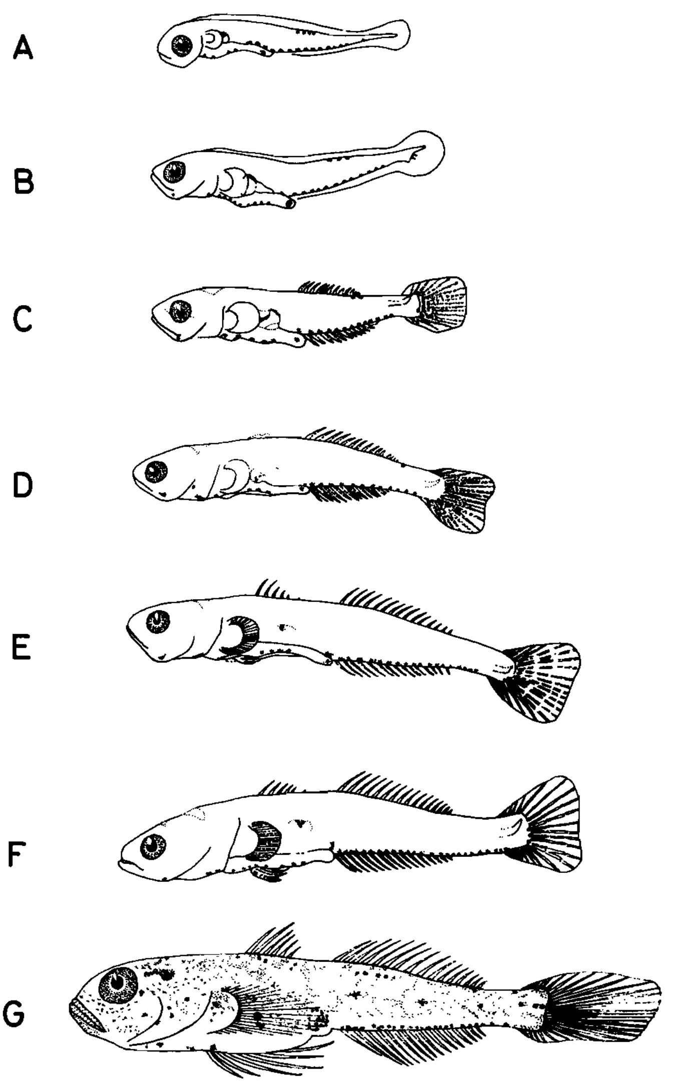

Figure 1 Larval series for *Lesueurigobius sanzoi*: (A) 2,0 mm; (B) 3,7 mm; (C) 5,4 mm; (D) 7,0 mm; (E) 9,6 mm; (F) 11,9 mm; (G) 21,00 mm.

negatively allometric with respect to SL. Head depth is between 15 and 18% of SL (b = 0,9064 ± 0,0683, 57 data points, r = 0,9633) (Figure 2C). Body depth ranges between 16 and 18% of SL (b = 0,9333 ± 0,0665, 57 data points, r = 0,9669) (Figure 2D). Both HD and BD are 17% of SL in juveniles.

Juveniles have the g and h rows of dorsal papillae connected forming one unique and long row, and the cheek row b reaches the edge of the pre-opercle. No such papillae were observed in any of the larval stages examined.

Pigmentation

The eyes were pigmented even in the smallest larvae (2 mm) present in the samples.

The pattern of pigmentation on the ventral portion in the smallest larvae comprises one series of melanophores running from the angular region of the lower jaw to the end of the gut and another series from behind the anus to the caudal tip. Pigmentation on the anterior portion

Table 2 Meristic and morphometric (mm) characters of *Lesueurigobius sanzoi* larvae and juveniles

SL	PA	HL	BD	HD	Notochordal flexion	Pelvic fin present	Anal fin	Number of fin rays: 2nd dorsal fin	Number of fin rays: 1st dorsal fin
2,00	1,23	0,52	0,36	0,36	–	–	–	–	–
2,50	1,51	0,66	0,45	0,44	–	–	–	–	–
3,00	1,79	0,80	0,53	0,52	–	–	–	–	–
3,50	2,06	0,94	0,61	0,59	–	–	–	–	–
4,00	2,33	1,08	0,70	0,67	+–	–	3–4	3–6	–
4,50	2,60	1,22	0,78	0,75	+–	-	4–10	6-10	–
5,00	2,86	1,36	0,86	0,82	+–	–	11–13	9–13	–
5,50	3,13	1,50	0,94	0,90	+	–	11–13	10–13	–
6,00	3,39	1,64	1,02	0,97	+	–	11–14	11–13	–
6,50	3,65	1,79	1,09	1,04	+	–	14–15	13–14	–
7,00	3,90	1,93	1,17	1,11	+	–	14–15	14–15	–
7,50	4,16	2,07	1,25	1,19	+	–	14–15	14–15	–
8,00	4,41	2,22	1,33	1,26	+	+	14–15	14–15	–
8,50	4,67	2,36	1,41	1,33	+	+	14–16	14–16	2
9,00	4,92	2,51	1,48	1,40	+	+	15–16	15–16	2–5
9,50	5,17	2,65	1,56	1,47	+	+	16	16	5–6
10,00	5,42	2,80	1,64	1,54	+	+	16	16	6
10,50	5,67	2,95	1,71	1,61	+	+	16	16	6
11,00	5,92	3,09	1,79	1,68	+	+	16	16	6
11,50	6,16	3,24	1,86	1,75	+	+	16	16	6
12,00	6,41	3,38	1,94	1,82	+	+	16	16	6
12,50	6,66	3,53	2,02	1,89	+	+	16	16	6
13,00	6,90	3,68	2,09	1,95	+	+	16	16	6
13,50	7,15	3,83	2,17	2,02	+	+	16–17	16–17	6
14,00	7,39	3,97	2,24	2,09	+	+	16–17	16–17	6
14,50	7,63	4,12	–	2,16	+	+	16–17	16–17	6
21,00	10,97	6,23	3,49	3,40	+	+	16–17	16–17	6
23,05	11,05	7,05	–	4,00	+	+	16–17	16–17	6

consists of from five to ten melanophores and does not undergo significant variation during larval development. In juveniles, in contrast, the anterior portion is practically unpigmented. There is a melanophore at the end of the gut from the smallest stages up to around 9 mm SL; more conspicuous in the smaller larvae. Ventrally behind the anus is a single row of 10 to 20 pigment spots, fewer than 15 in larvae smaller than 8 mm and around 20 in juveniles. With onset of anal fin development (at around 4 mm), this row of melanophores splits in two around the base of the fin.

Dorsal pigmentation can be observed in newly hatched larvae and in larvae up to 6,5 mm SL. The smaller sizes have a row of three or four melanophores towards the end of the trunk. These melanophores decrease in number with growth, disappearing by a larval length of over 6,5 mm.

The postanal and dorsal pigmentation patterns differentiate *Lesueurigobius sanzoi* larvae from *Nematogobius bibarbatus* larvae. The latter have fewer (8 – 10) postanal melanophores, and the ventral chromatophores below the row of dorsal melanophores are fused. Dorsal pigmentation on the trunk in *Nematogobius bibarbatus* larvae consists of a continuous band of pigment which disappears during notochordal flexion (4,5 mm) and is shorter than that on *Lesueurigobius sanzoi* larvae.

A melanophore is discernible ventrally at the base of the caudal fin in all stages of development, with up to three melanophores distinguishable in larvae longer than 9 mm SL.

There is a patch of light pigmentation in the region of the swim bladder that lasts throughout larval development.

No pigmentation is discernible on the head, except for a small melanophore located on the lower jaw at its junction with the upper in the larvae at around 4 mm. On the other hand, in *Nematogobius bibarbatus* larvae this melanophore does not make its appearance until 7,5 mm SL. Furthermore, there are two patches of pigmentation on the occipital region of the head in *Nematogobius bibarbatus* larvae longer than 10 mm SL; in contrast, pigmented patches like these are absent in *Lesueurigobius sanzoi* larvae.

Postanal pigmentation in juveniles is similar to that in the larvae, but pigmentation is much more pronounced on the rest of the body, which is completely covered with small melanophores. There are five clusters of melanophores along the lateral line. These small melanophores

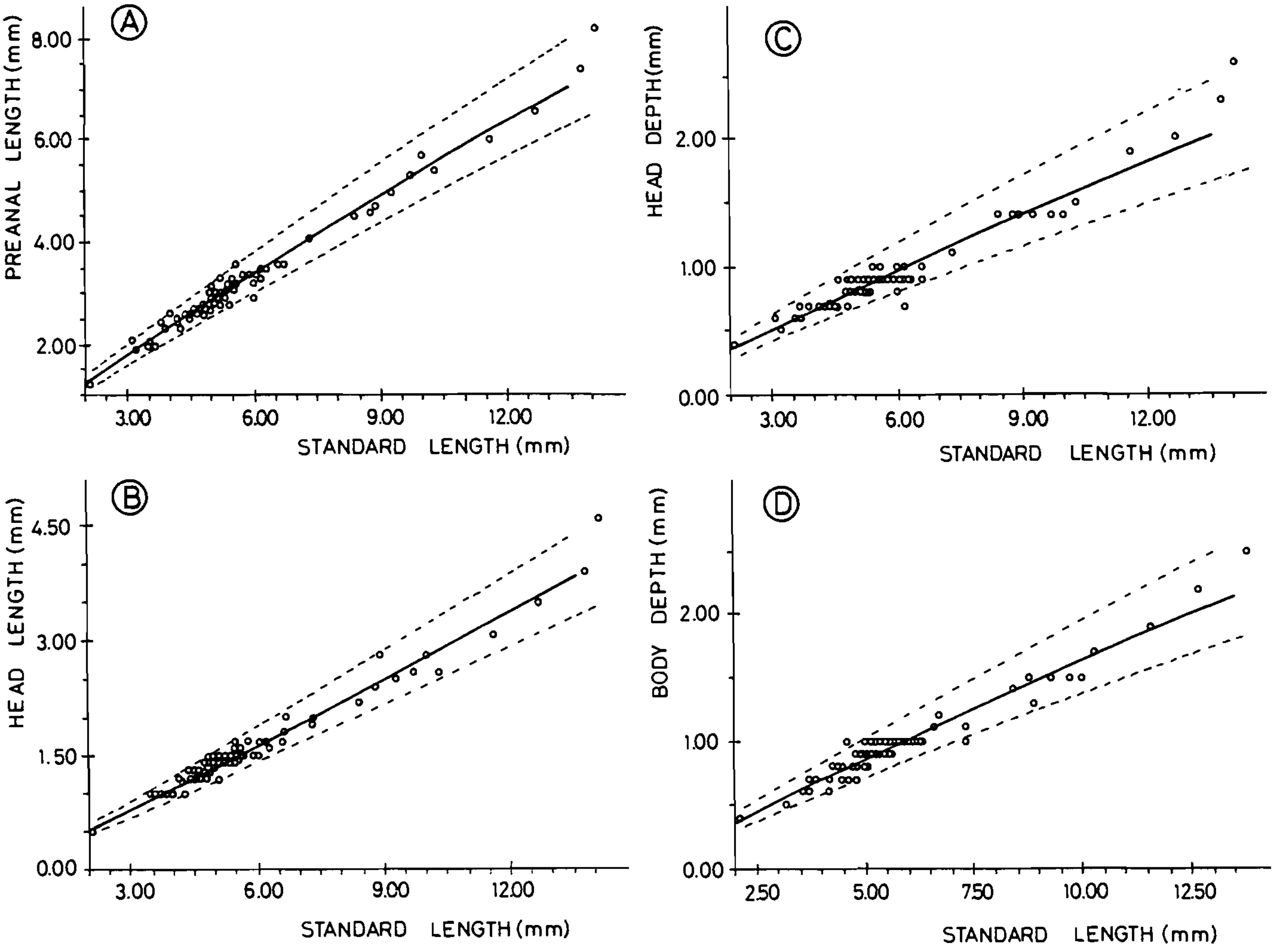

Figure 2 Relationship between standard length and: (A) preanal length; (B) head length; (C) head depth; and (D) body depth.

are somewhat more densely packed on the occipital region, the snout, and above the gut. There is a more darkly pigmented cluster at the base of the pelvic fin that is practically the sole pigmentation on the ventral region of the gut.

Notochordal flexion

Notochordal flexion commences at a larval length of about 4 mm and is usually complete by a larval length of around 5,5 mm.

Fin development

The caudal fin is the first fin to ossify, with the number of rays countable from 8 mm SL. The pectoral fin is the last fin to ossify, at around 14 mm SL. Anal and second dorsal fin development occurs more or less at the same time. The number of rays in these fins in the different transformation stages is shown in Table 2. By 10 mm the number of rays has attained the full complement of 16 in both the second dorsal fin and the anal fin. The first dorsal spine is not distinguishable from the dorsal fin rays even in the largest larvae or juveniles and has therefore been included as one of the rays in our counts. Ossification of the rays in the first dorsal fin commences at 9 mm SL, with the adult complement of six rays first discernible at 10 mm. The length of these rays is much shorter than in adults, even in the juveniles examined. The first pelvic fin buds appear at a larval length of 8 mm SL. Length of the pelvic fins increases dramatically in juveniles, in which the rays may overreach the origin of the anal fin. The same is true of the pectoral fin rays.

The length of the pectoral fins in juveniles is longer in *Lesueurigobius sanzoi* than in *Nematogobius bibarbatus* as is the length of the pelvic fins, which are much more developed in *Lesueurigobius sanzoi*. The two species are clearly differentiated by the meristic characters of the second dorsal fin and the anal fin, since *Nematogobius bibarbatus* presents I13 for both fins (O'Toole 1978), as opposed to I15–I16 for these fins in *Lesueurigobius sanzoi* (Lloris *et al.* 1984). However, the number of vertebrae (26) is the same in both species.

Distribution

Lesueurigobius sanzoi larvae were taken on three surveys conducted off northern Namibia in August 1980, March – April 1981, and April 1986. The number of larvae captured on the first survey was quite small, and larvae were present only in the northernmost part of the sampling area.

On the March – April 1981 survey, larvae were

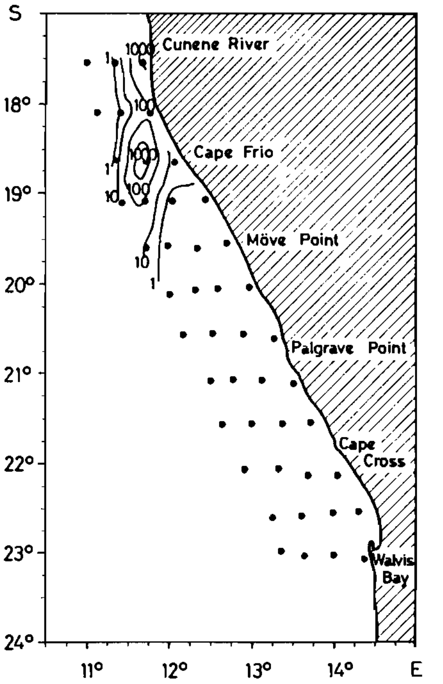

Figure 3 Distribution and abundance of *Lesueurigobius sanzoi* larvae on the Benguela III survey (No. larva / $10m^2$).

present north of parallel 19°30'S (Figure 3). The northern boundary of the sampling area was opposite the mouth of the Cunene River, where larval density was extremely high, and it therefore seems reasonable to expect that the spawning products extend further north, towards Angola. The largest larval concentrations were found in waters with a bottom depth ranging from 60 to 300 m; higher than that recorded for adults in the region (Lloris *et al.* 1984). In order to establish possible larval drift, larvae were divided into two size classes, less than 4 mm and greater than or equal to 4 mm. The resulting distributions were quite similar for both size classes. Most of the larvae collected in the samples on this survey measured between 2,5 and 3 mm. The largest size present was 11,9 mm (Figure 4A). The length frequency distribution for the station with the highest larval abundance (located 30 miles offshore) shows a clear predominance of small sizes (Figure 4B). The distribution was smoother at the station with the next highest larval abundance (located 10 miles offshore), where lengths between 3 and 4 mm were most frequent (Figure 4C).

In April 1986 larvae of this species were found at the stations closest to the coast (less than 30 miles offshore) north of latitude 20°S. The larval length range on this survey was broader, from 2 to 14,5 mm, although larvae between 2 and 5 mm accounted for the largest share. Some juveniles between 20 and 23 mm were also collected. Nearly all the larvae were obtained between surface and 60 m, although some were captured even at the lowest sampling depths (between 100 and 200 m). There were no significant differences in the vertical distribution of larvae of different lengths (Figure 5).

Discussion

The presence of interorbital papillae is a generic character for *Lesueurigobius* (Miller, 1981), which allowed us to identify our juveniles to a generic level. The identifi-

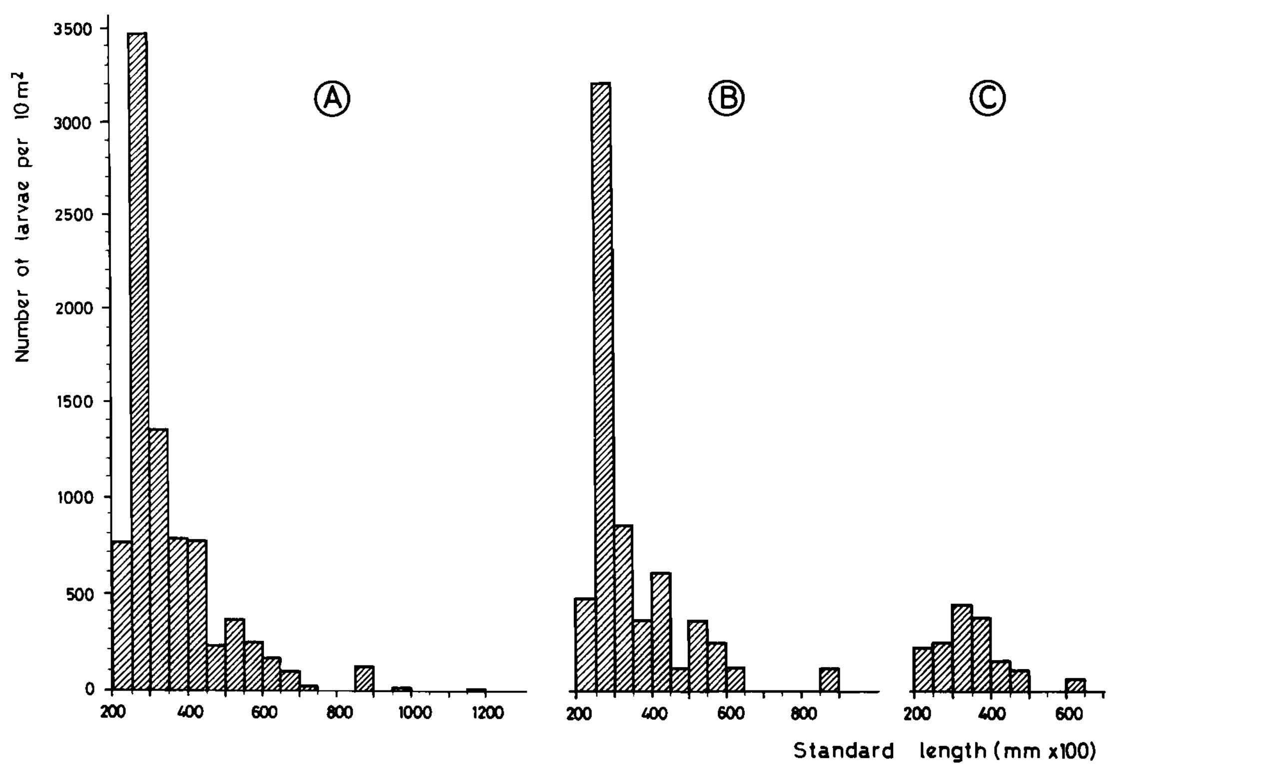

Figure 4 Length frequency distribution for *Lesueurigobius sanzoi* larvae caught: (A) on the Benguela III survey; (B) at the station of highest larval abundance; (C) at the station of next highest larval abundance.

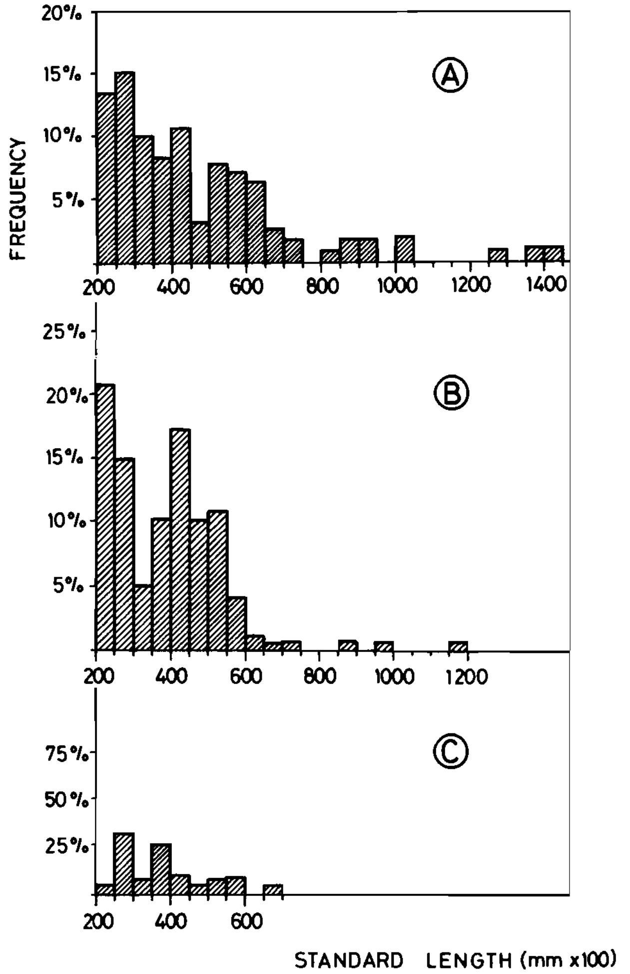

Figure 5 Length frequency distribution for *Lesueurigobius sanzoi* larvae caught: (A) between 40 and 0 m; (B) between 60 and 40 m; (C) below 60 m.

cation to species level was mainly based on the presence and pattern of rows of dorsal papillae, and on the number of dorsal and anal fin rays.

Off Namibia and South Africa the only reference to the presence of the genera *Lesueurigobius* is that given by Lloris (1982) and Lloris *et al.* (1984). On the other hand, in the Eastern Central Atlantic the following species of *Lesueurigobius* are present: *L. heterofasciatus* Maul, 1971; *L. koumansi* (Norman, 1935); *L. sanzoi* (de Buen, 1918); and *L. suerii* (Risso, 1810) (Miller 1981). Of these, only *L. sanzoi* fits the number of both the second dorsal and anal fins, although *L. koumansi* has very close fin ray counts (Table 3) (Norman 1935). This latter species, which was first identified by Norman (1935) as *Acentrogobius koumansi,* can be clearly differentiated from the adults and juveniles found off Namibia because they only have the anterior row of papillae (*g*), while in *L.sanzoi* the two dorsal rows of papillae (*g* and *h*) are connected forming a unique and longer row. The pattern of papillae serves as well as the fin ray counts to separate the other species from *L.sanzoi.* This information is given in Table 3, constructed after the papers of De Buen (1923, 1930), Norman (1935), Maul (1971), and Miller (1986).

The presence and the abundance of the larvae of this species in the samples confirms that it is not an expatriate species and that the continental shelf off northern Namibia can be included among its spawning areas.

Although sampling covered the oceanic region from Lüderitz (26°30′S) to the mouth of the Cunene River (17°30′S), the spawning area of *Lesueurigobius sanzoi* extended southwards only to 19°30′S. No larvae or juveniles of this species were collected in samples taken off the west coast of South Africa (Olivar 1985; Shelton 1986).

The larval distribution coincided rather well with that of the warmer waters of the Angola Current detected during the two cruises carried out in autumm (Salat 1982; Boyd, Salat & Masó 1987; Masó 1987). The surface temperature in the region where the larvae occurred varied between 16 and 19°C, and the main concentrations were found at surface temperatures of 17°C. This preference for warmer waters is corroborated by the fact that the larvae of this species did not occur in the remainder of the Benguela region, where the water is colder, or during periods of active upwelling (Olivar 1985), when the waters of the Angola Current do not extend as far southwards.

On all three cruises the spawning areas of *Lesueurigobius sanzoi* and *Nematogobius bibarbatus* were found to overlap. In the area of overlap, abundance of larval *Lesueurigobius sanzoi* was lower than that of larval *Nematogobius bibarbatus* in winter, and higher in autumm (Olivar 1985). The differences in spawning area and period of maximum spawning in these two species coincided with the habitats of the adults, since *Nematogobius bibarbatus* is a species endemic to the upwelling region, while *Lesueurigobius sanzoi* is typical of warmer waters.

Table 3 Characters that differentiate the species of *Lesueurigobius* of the Eastern Atlantic

	L. heterofasciatus	*L. koumansi*	*L. sanzoi*	*L. suerii*
Dorsal papillae *g,h*	two widely separated rows *g* & *h*	only anterior row *g*	one row *g h*	two separate rows *g* & *h*
Row of papillae *b*	far from reaching edge of pre-opercle	reaching edge of pre-opercle	reaching edge of pre-opercle	reaching edge of pre-opercle
Second dorsal fin	I, 14	I, 16–17	I, 15	I, 13–14
Anal fin	I, 14–15	18–20	I, 16–17	I, 13–14

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