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EVIDENCE OF DISPLACEMENT OF LANTERNFISH LARVAE ASSOCIATED WITH SURFACE WATER MOVEMENT: CASE STUDIES FROM SOUTHERN AFRICA

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The paper is based on larval distribution data from five lanternfish species outside the spawning grounds of the adult populations. Using hydrographic information collected with the larvae, the effect of surface currents on the observed patterns of distribution is discussed. In the South-East Atlantic, adjacent to the Benguela upwelling system, larvae of the pseudoceanic *Lampanyctodes hectoris* were found farther offshore (250 – 450 km) than usual. The general flow of the current is parallel to the coast, but upwelling filaments extend offshore. The size distributions of the *L. hectoris* larvae found, together with the rather low temperature at two of the oceanic stations sampled, indicate that they had been displaced by a filament. In the South-West Indian Ocean, the distribution of larvae of highly oceanic species of lanternfish over the shelf is related to onshore intrusions of the Agulhas Current. The size distributions of *Hygophum hygomii* and *Scopelopsis multipunctatus* indicate southward transport of larvae. The presence of larvae of *Myctophum selenops* and *Benthosema pterotum*, which have not been documented as adults in the region, indicates not only transport to the area, but also that spawning could be taking place closer to the area than previously reported.

Distributions of marine organisms have often been used as indicators of water masses and currents (e.g. Olson and Backus 1985, Soule and Kleppel 1988, Fedoryako 1993). Such indicators become increasingly useful when no direct observations of temperature, salinity or currents are available, and they are specially relevant to studies of physico-biological interactions. However, examination of the literature that has used marine organisms as indicators, or those in which such organisms have been used to compile world biogeographic maps (e.g. Van der Spoel and Heyman 1983), indicates that interpretation may differ, depending on the selected taxa. Lanternfish distributions have been widely used. For instance, Hulley and Lutjeharms (1995) analysed the distribution of adult and juvenile myctophids of Indo-West Pacific origin in the eastern South Atlantic. Although adults may be good indicators of currents or water masses, they are not as suitable for the purpose as are their planktonic larval stages. The poor mobility of early larvae permits their consideration as temporary passive tracers, and their relatively short time of residence in the plankton allows them to be related to recent hydrographic events.

Distributions of adult lanternfish around the coast of southern Africa are well documented (Hulley 1981, 1984, 1986), and several papers have reported on the distribution of their larvae (Shelton 1986, Olivar 1988, Olivar and Fortuño 1991, Olivar and Beckley 1994). These studies showed the larvae of several species to be remote from the known distribution ranges of the adults, and indicated a close relationship with the prevailing currents. In order to obtain additional evidence of larval transport, the distribution ranges and size frequency distributions of the larvae of five myctophid species in two regions off southern Africa, the open ocean off Namibia adjacent to the Benguela upwelling system, and the eastern coast of South Africa, adjacent to the Agulhas Current, are analysed.

For the Benguela, the investigation centred on the presence of larvae of the pseudoceanic lanternfish *Lampanyctodes hectoris* farther offshore than their usual range of distribution. The typical picture of the Benguela upwelling system is a series of upwelling cells along the coast (Shannon 1985, Fig. 1). The main flow is parallel to the coast, but upwelling filaments extend offshore (Lutjeharms *et al*. 1991). Olivar and Fortuño (1991) mentioned the presence offshore of *L. hectoris* larvae, but the lack of CTD data for the cruise those authors analysed precluded further interpretation. The publication of a study by Lutjeharms *et al*. (1991), showing the presence of an "extreme" upwelling filament extending more than 1 300 km offshore, some weeks after the survey reported on by Olivar and Fortuño (1991) prompted a detailed reanalysis of all the data available from that survey.

For the Agulhas Current region, the presence in shelf and offshore waters of larvae of two highly oceanic species *Hygophum hygomii* and *Scopelopsis*

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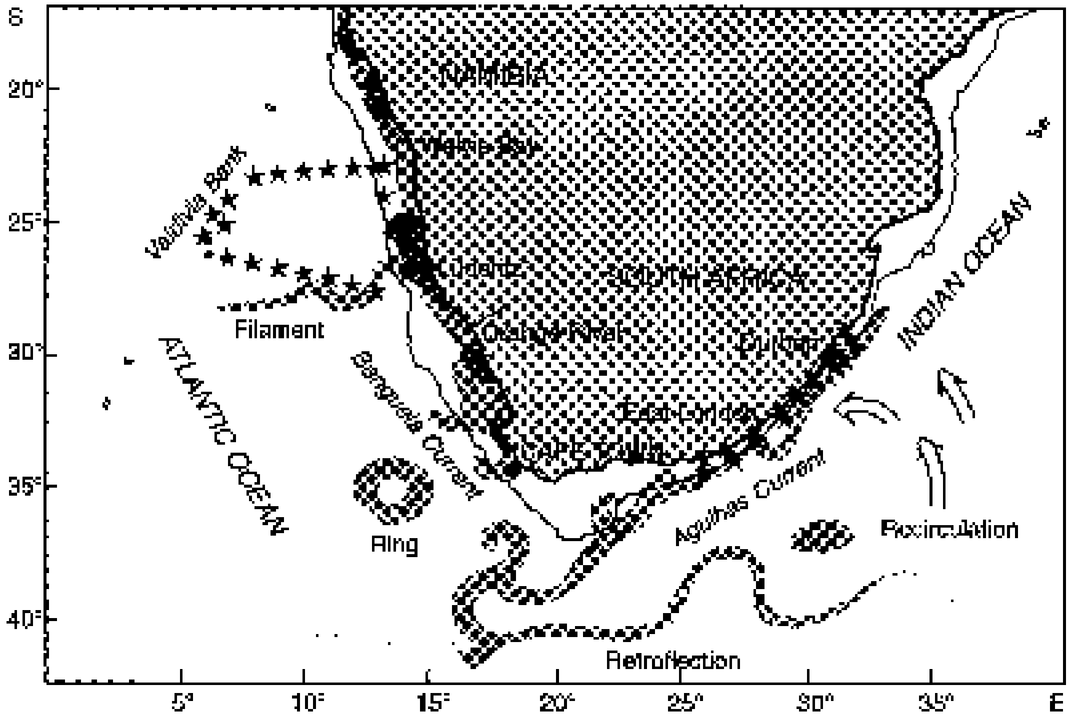

Fig. 1: Study area, showing the main hydrographic features of the South-East Atlantic and South-West Indian oceans and the position of the stations sampled in both areas. Dark areas off the West Coast indicate main upwelling centres

multipunctatus (Hulley 1986) and the occurrence of larvae of *Myctophum selenops* and *Benthosema pterotum,* whose adults have not been reported in the area (Hulley 1984, 1986), are analysed. The large-scale oceanographic feature that dominates the South-West Indian Ocean is the Agulhas Current (Fig. 1). The study was centred at latitudes where the Current reaches its full stature as regards velocity and volume flux (Lutjeharms 1981), between Durban (30°S) and East London (33°S). The axis of the Agulhas Current follows the continental margin and approaches the coast in the central part of the study area; it then moves farther away where the shelf widens to the south (Gründlingh 1978). Most of its water returns to the Indian Ocean through the Agulhas Retroflection (Harris and Van Foreest 1978).

MATERIAL AND METHODS

The areas of study were the open ocean off Namibia in the South-East Atlantic (cruise of May 1982) and the eastern coast of South Africa in the South-West Indian Ocean (cruise of May/June 1990).

In both areas, ichthyoplankton hauls were performed following the standard procedures described by Smith and Richardson (1977). The larvae were collected by means of oblique hauls made with a Bongo gear fitted with nets of 0.3 and 0.5 mm mesh size in the SE Atlantic and SW Indian Ocean respectively. Flow of water was determined by means of a flow-meter mounted centrally in the mouth of the net. Towing speed was 2 knots in attempting to maintain a wire angle of 45°. In the SE Atlantic Ocean, tows were made from 200 m to the surface, whereas in the SW Indian Ocean, tows were from 80 m to the surface. The depth of each haul was estimated from the length of wire let out. For the SW Indian Ocean survey, the net was also equipped with a recording diving depth gauge. Both total abundance of fish larvae and abundances of the different size-classes were standardized to the number of larvae under 10 m^2 of sea surface. For those species selected, the standard length *SL* of all

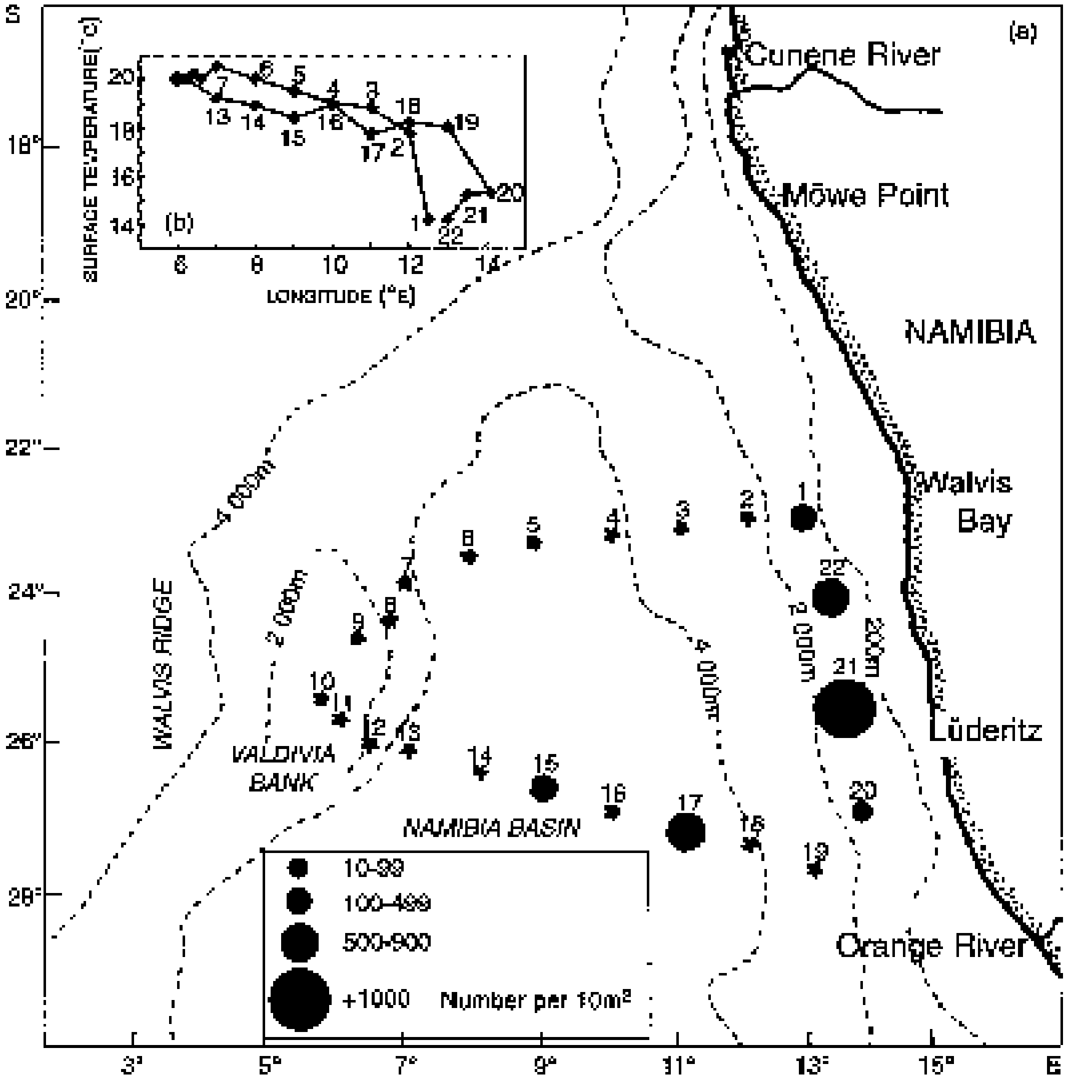

Fig. 2: (a) Abundance (number per 10 m^2) of *Lampanyctodes hectoris* larvae at the stations sampled during the May 1982 survey in the South-East Atlantic Ocean. (b) Sea surface temperatures at various longitudes, at the sampled stations (numbers correspond to the stations shown in Fig. 2a)

larvae collected at each station was measured using an ocular micrometer, with a precision of 0.1 mm.

From the SE Atlantic Ocean, the distribution of *Lampanyctodes hectoris* larvae collected at four stations located over the continental slope (500 – 1 000 m) and along two transects between the Benguela upwelling system and the Valdivia Bank (located 400 miles offshore, Fig. 2a) was analysed. The only hydrographic information available during that cruise was the sea surface temperature obtained at each station (Fig. 2b). One satellite image, a thermograph for 31 May 1982 (the last day of the cruise), and one CZCS composite image for April 1982, combining 12 satellite observations, plus the METEOSAT II image of 5 July 1982, analysed in detail by Lutjeharms *et al*. (1991), were examined.

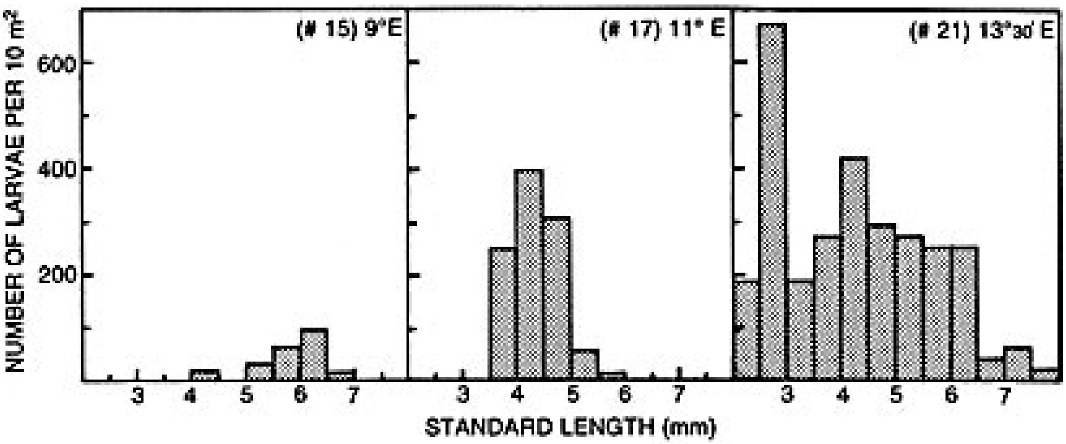

Fig. 3: Size frequency distributions for *Lampanyctodes hectoris* larvae at the slope station with highest abundance (#21) and at the two offshore stations of the southern line (#17, #15). Location of the stations is shown in Figure 2a

From the SW Indian Ocean, the size distributions of *Hygophum hygomii*, *Scopelopsis multipunctatus*, *Myctophum selenops* and *Benthosema pterotum* larvae collected during the survey carried out in May/June 1990 were analysed. Nine transects of stations from Algoa Bay to the mouth of the Tugela River were sampled. Each transect had two inshore stations, at 50 and 100 m bottom depth, and two "Agulhas Current" stations, offshore of the continental shelf-break (at 500 and 2 000 m). Measurements of temperature were made at all stations with a CTD profiler to a depth of 200 m; its accuracy was 0.01°C (Beckley and Van Ballegooyen 1992).

RESULTS

South-East Atlantic Ocean

Sea surface temperature recorded in May 1982 was lower over the slope stations than at the stations located along the two transects out to the Valdivia Bank (Fig. 2b). In the northern transect (from Walvis Bay to the Valdivia Bank), sea surface temperatures offshore were typically oceanic (>19°C, Boyd and Agenbag 1985), with a continuous upward trend. Sea surface temperatures along the southern line (off Lüderitz) showed a similar trend, though temperatures were slightly lower than along the northern transect. However, at two stations (15 and 17) along the southern transect there were anomalous sea surface temperatures, more than 1°C below the general trend (Fig. 2b). Examination of the satellite images showed cold water extending far offshore (at least 450 km) off Lüderitz on 31 May 1982, and high concentrations of chlorophyll extending even farther offshore (at least 550 km) at 29°S in April 1982. In July 1982, six weeks after the survey during which the larvae were collected, an unusually long upwelling filament was reported at 26°S by Lutjeharms *et al*. (1991).

Analysis of the species composition of ichthyoplankton samples showed that *Lampanyctodes hectoris* larvae appeared at all the slope stations, but only at the two offshore stations with anomalous temperatures (Fig. 2a). The size frequency distribution of *L. hectoris* larvae (Fig. 3) at the slope station with the highest abundance (#21, 13°30′E) showed a wide size range, from 2.0 to 7.5 mm *SL*, with two modal size-classes at 2.5 and 4.0 mm. At the next station offshore where the larvae were present (#17, 11°E), specimens measured between 3.5 and 5.5 mm *SL*, with a modal size-class of 4.0 mm. The farthest offshore these larvae were found (#15, 9°E), their *SL*s were 4.0–6.5 mm and the modal size-class had shifted to 6.0 mm.

South-West Indian Ocean

Hydrographic features observed during the May/June 1990 survey were described and discussed by Beckley and Van Ballegooyen (1992). Waters of the

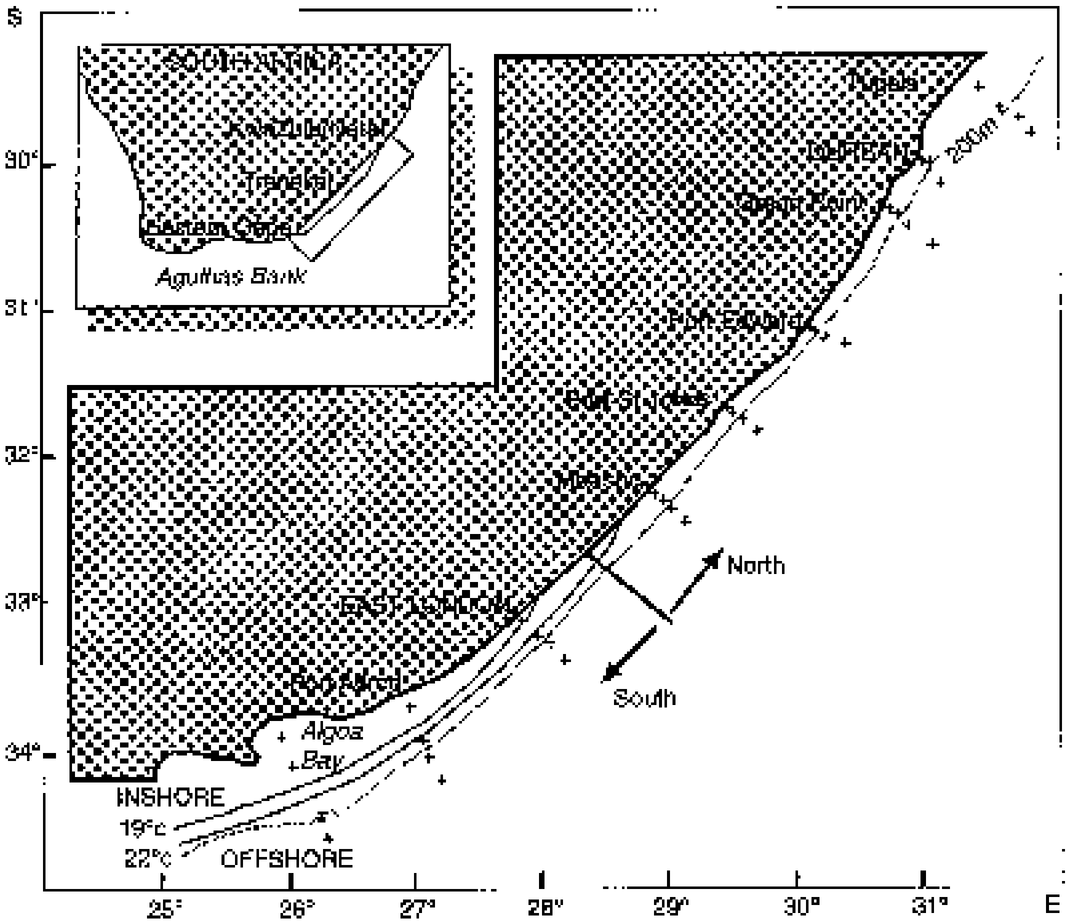

Fig. 4: Stations sampled during the May/June 1990 survey in the South-West Indian Ocean, sea surface isotherms and the 200 m isobath (redrawn from Beckley and Van Ballegooyen 1992). The four sectors into which the area was divided are shown

south-flowing Agulhas Current were detected offshore, with temperatures >22°C and salinities of 35.4×10^{-3} extending down to >50 m. There was a marked penetration of warm Agulhas Current water onto the shelf at all the northern 50 and 100 m stations, except at the 50 m station off the Tugela River. Evidence of small-scale meandering was apparent at the 500 m station off Durban. A temperature front was detected between Mbashe and East London. Sea surface temperatures at the inshore stations south of that front were markedly lower (<19°C), indicative of deep water upwelling onto the shelf along the shoreward edge of the Agulhas Current south of Mbashe (Beckley and Van Ballegooyen 1992). According to the bottom topography and water characteristics, the region could be divided into four sectors (Fig. 4): inshore and offshore of the 200 m isobath and north and south of the thermal front between East London and Mbashe.

From the large number of species of lanternfish larvae collected during the May/June 1990 cruise (Olivar and Beckley 1994), four highly oceanic species were selected for this paper: *Hygophum hygomii*, *Scopelopsis multipunctatus*, *Myctophum selenops* and *Benthosema pterotum*. *Hygophum hygomii* and *Scopelopsis multipunctatus* were selected as repre-

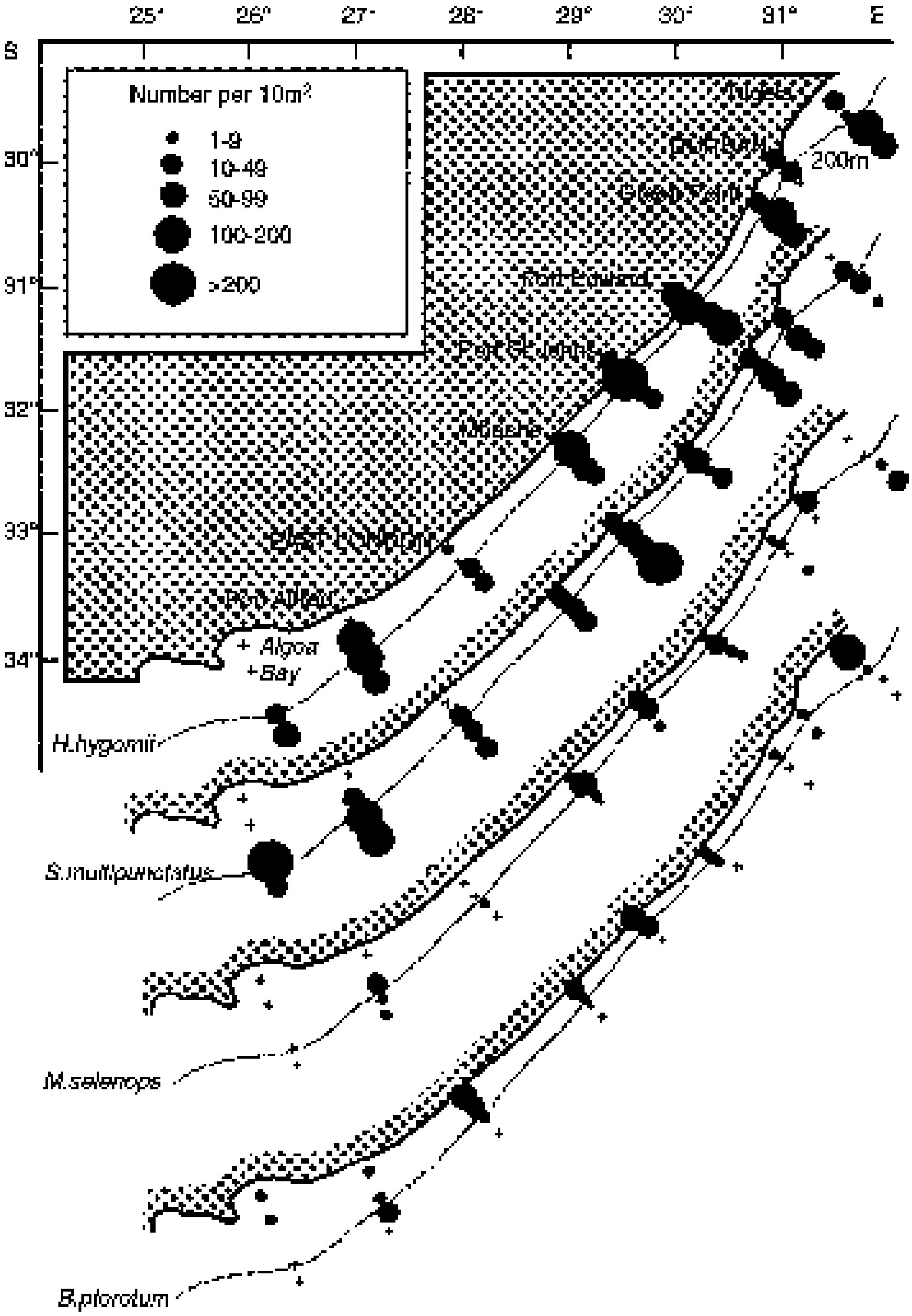

Fig. 5: Distribution and abundance of *Hygophum hygomii*, *Scopelopsis multipunctatus*, *Myctophum selenops* and *Benthosema pterotum* larvae during the May/June 1990 survey in the South-West Indian Ocean

sentative of autochthonous species because of the common presence of adults in the region (Hulley 1984) and the fact that their larvae were the most abundant lanternfish in plankton samples of the region during that cruise (Olivar and Beckley 1994). Among the species whose larvae appeared in the plankton samples, but which could be considered as allochthonous, because their adults have not been reported in the region (Hulley 1984, 1986), were *Myctophum selenops* and *Benthosema pterotum* (Olivar and Beckley 1994).

Larvae of the two autochthonous species, *Hygophum hygomii* and *Scopelopsis multipunctatus*, appeared at many of the shelf stations, except in the southern stations at 50 m (Olivar and Beckley 1994, Fig. 5). Size frequency distributions of *H. hygomii* (Fig. 6) revealed a wide range of sizes in the northern inshore and southern offshore sectors, with the absence of larvae >5.5 mm noticeable at the southern inshore stations. The proportion of larvae of the smaller size-classes (<3.5 mm) was higher in the northern inshore sector than in the other sectors. The modal size-classes (4.0 mm) were not clearly defined in the two northern sectors, but in the south they were better defined and slightly larger (4.5 mm inshore and 5.0 mm offshore). There was a wider size range of *S. multipunctatus* offshore than inshore, larvae >5.0 mm being absent at the southern inshore stations. The proportion of larvae <3.5 mm was higher in the northern inshore sector, whereas larvae larger than 4.0 mm were more abundant in the southern offshore sector. Modal size-classes in the two offshore sectors (4.0 mm) were slightly higher than at the inshore ones (3.0 mm for northern inshore and 3.5 mm for southern inshore).

Larvae of the two allochthonous species showed different distribution patterns (Fig. 5). *Myctophum selenops* larvae were more related to the presence of warm Agulhas Current water than those of *Benthosema pterotum*, which occurred in most of the stations with lower temperatures (Olivar and Beckley 1994). *M. selenops* larvae were more common in the northern sectors, where they seemed to be distributed both inshore and offshore, except at 500 m off Durban and Green Point. In the southern sectors they were patchily present. The smaller size-classes (<3.5 mm) of *Myctophum selenops* larvae predominated (60%) inshore (Fig. 6), and there was a general decrease in abundance with increasing length. Offshore, no particular size-class was dominant.

Larvae of *Benthosema pterotum* were more abundant inshore (Fig. 5). The size ranges of the larvae collected in the northern and southern inshore sectors were similar, but the size structure was quite different (Fig. 6). In the northern inshore sector, 60% of the larvae were <3.5 mm, with a modal size-class of 2.5 mm, but in the southern inshore sector the proportion of larvae <3.5 mm was only 11% and the modal size-class was higher, at 4.5 mm. Only 7% of larvae from the northern inshore sector were >5.5 mm, whereas in the southern inshore sector these larvae constituted 30% of the *B. pterotum* larvae collected. Offshore, both size range and abundance were noticeably lower.

DISCUSSION

Adult *Lampanyctodes hectoris* have a pseudoceanic distribution pattern (Hulley 1981). Whereas the species occurs over bottom depths to about 3 000 m, they are most abundant at depths shallower than 800 m (Hulley and Lutjeharms 1989). No adults of this species were collected at any of the offshore stations in the transects to the Valdivia Bank, whereas they were abundant at all the slope stations sampled (Rubiés 1985). During winter and spring, the species' main spawning season, their eggs and larvae are commonly found from the 150 m isobath to the slope (around 1 000 m, Olivar and Shelton 1993). During the study reported on here, concentrations were not as high as those recorded in the area during the main spawning season, when maximum densities of c. 10 000 larvae per 10 m^2 and mean abundances of 2 366 larvae per 10 m^2 have been reported (Olivar *et al.* 1992). The presence of larvae at the two offshore stations with anomalous sea surface temperature, so far from the usual area of distribution of the species, and the absence of larvae <3.5 mm at those offshore stations, indicates that there was no spawning there, but it does suggest that larvae had been advected from the slope area.

Among the offshore transport mechanisms, upwelling filaments are common features of the Benguela and other upwelling areas, such as off California and Peru (Flament *et al.* 1985, Lutjeharms and Stockton 1987, Brink 1992). Currents within filaments are energetic and fast (typical velocities of 40–60 $cm\cdot s^{-1}$). The associated offshore transport may be 1 Sv greater than Ekman transport (Kosro and Huyer 1986) and is responsible for the transport of suspended particles, pollutants, planktonic organisms and even pre-recruiting fish out of their usual distribution areas (Shillington *et al.* 1990, 1992, Duncombe Rae *et al.* 1992). Filaments of cold water generated from the Lüderitz upwelling cell have been reported on many times (Shillington *et al.* 1992). Filaments can persist for several weeks, are usually narrow (50 km wide) and extend from the surface to a depth of at least 100 m. The length of these filaments is usually limited to 250–300 km offshore, but occasionally they can

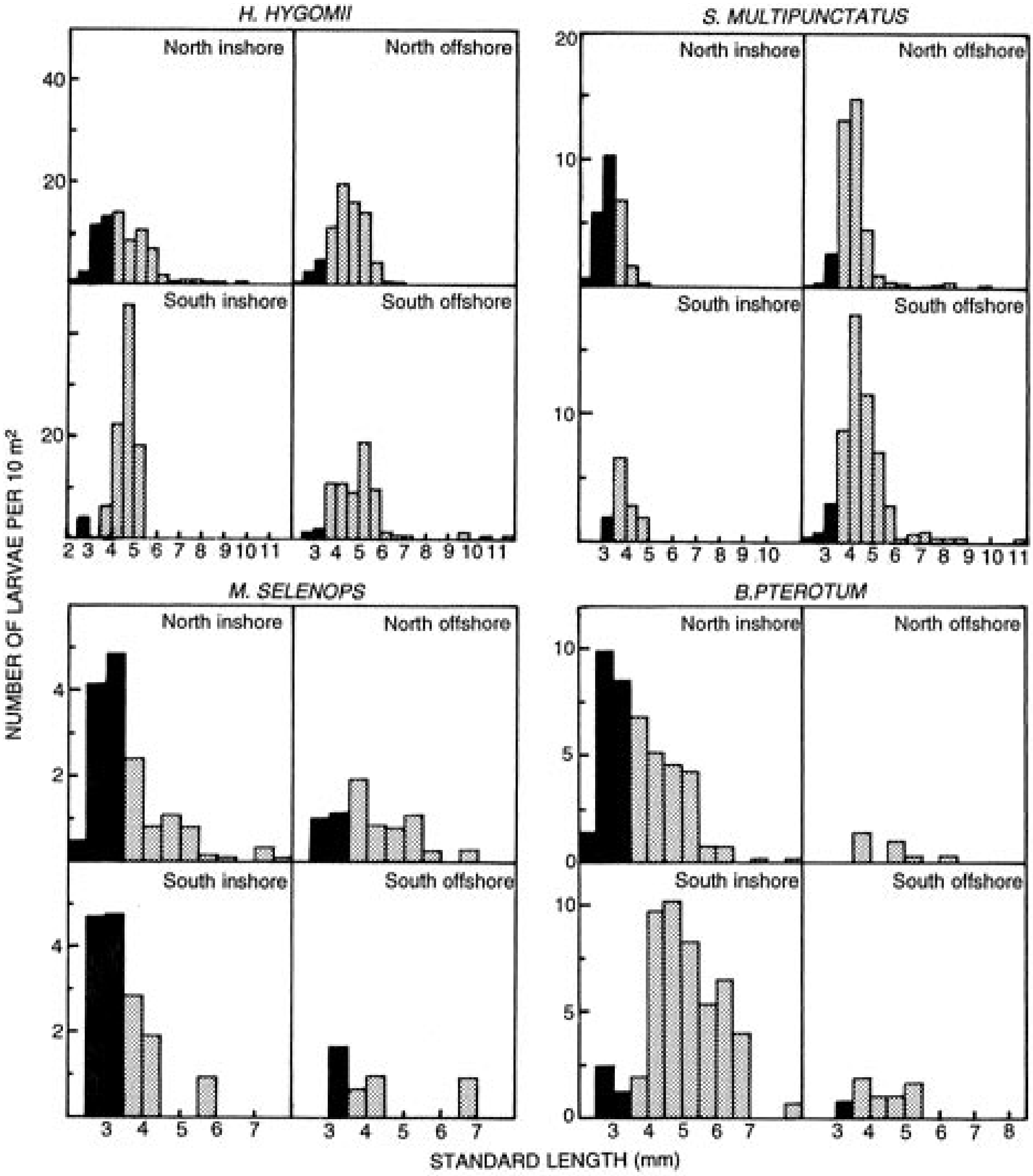

Fig. 6: Size frequency distributions of *Hygophum hygomii*, *Scopelopsis multipunctatus*, *Myctophum selenops* and *Benthosema pterotum* larvae during the May/June 1990 survey in the South-West Indian Ocean, averaged over each of the four sectors shown in Figure 4

reach to more than 1 000 km (Lutjeharms *et al.* 1991). In the case of such long filaments, water has been found entrained by other mesoscale features, such as Agulhas eddies, which helps in the offshore expansion, meandering shape and persistence of the filament (Duncombe Rae *et al.* 1992).

Whether the sea surface temperature anomalies measured in the survey of May 1982 correspond to the long filament observed in July 1982 by Lutjeharms *et al.* (1991) cannot be proven with the available data. However, the typical characteristics of filaments, together with the temperature anomaly observed offshore and the presence and size distribution of *Lampanyctodes hectoris* larvae found, are consistent with those of a long Benguela upwelling filament.

The position of *Lampanyctodes hectoris* larvae in the water column, and the vertical extension of upwelling filaments, allow them to be subject to transport by upwelling filaments. More than 70% of *L. hectoris* eggs and larvae (from early stages to 8.0 mm) are located in the upper 100 m (Olivar *et al.* 1992), within the vertical range of filaments. The typical velocities within a filament are 40–60 cm·s^{-1} and, considering a non-rectilinear trajectory (Lutjeharms *et al.* 1991), a minimum time of 5–8 days would be required for water to move between the two offshore stations with anomalous temperature. Regarding the larval size structure of the samples found at those stations, the observed shift of the modal size-class (2 mm) should be consistent with such a time interval. All the available information on size at age for this species corresponds to later developmental stages than those studied here. Cruickshank (1983) and Young *et al.* (1988) reported growth rates of *L. hectoris* juveniles of 0.2–0.33 mm·day^{-1}. Bearing in mind that the growth rate of animals tends to decay exponentially with increasing age (Laird *et al.* 1965), the growth rates of larvae must be higher than those given for juveniles. Using a minimum growth rate of 0.33 mm·day^{-1}, larvae may have increased from 1.7 to 2.6 mm in 5–8 days, which is within the range of the observations made here.

The general flow of the Agulhas Current in the SW Indian Ocean follows the continental margin. It is mostly confined inshore of the 2 000 m isobath, approaching the coast in the central part of the study area and then moving away where the shelf is wider to the south (Gründlingh 1978). Typical surface velocities are from 90 to 119 cm·s^{-1}, with a vertical extension of 600 – 1 500 m (Gordon *et al.* 1987). The hydrographic characteristics of the area observed in the present study show typical surface intrusions of warm Agulhas water onto the shelf in the central area between Durban and Mbashe (Beckley and Van Ballegooyen 1992). Whereas records of adults of oceanic lanternfish over depths <300 m are infrequent (Hulley and Lutjeharms 1989, 1995), the intrusions of the Agulhas Current to the shelf region have been found to be responsible for the appearance of larvae of many truly oceanic lanternfish inshore (Olivar and Beckley 1994).

The observed size structure of the two autochthonous species, *Hygophum hygomii* and *Scopelopsis multipunctatus*, reflects the Agulhas Current intrusions. The higher modal size-classes, i.e. the greater contribution by larger larvae at the southern offshore stations and the low concentrations of larvae <3.5 mm at the southern inshore stations, indicate both the remoteness of the spawning area from the study area and southward transport. The low concentrations of small larvae inshore in the south are justified by the absence of direct transport from the oceanic region in the same latitudes. Therefore, only larvae that were spawned some way to the north could have been transported by the Agulhas Current to the study area.

Myctophum selenops is a species that has been recorded in equatorial waters (Bekker 1983), but the presence of adults has also been reported west of the Cape Peninsula (35°S), associated with pockets of Agulhas Current water (Hulley 1981, 1986). The presence of small larvae (<3.5 mm) at the 100 m station off Port Alfred (southern inshore sector) indicates that spawning had to be closer to the studied region than the latitudes of equatorial waters. There are three possibilities:

(i) the distribution of equatorial adults extended southwards;
(ii) the population from Agulhas water pockets are also present in the retroflection area;
(iii) larvae spawned from adults in Agulhas water pockets had been introduced via the counter flows that form at the edge of the current above the 200 m isobath on the eastern Agulhas Bank (Lutjeharms *et al.* 1989, Boyd *et al.* 1992, Boyd and Shillington 1994).

The proving of any of the above three possibilities would indicate that the species may not be allochthonous, in spite of the lack of adult records from the region (Hulley 1986). The observed size distributions of *M. selenops* larvae did not show a southward displacement of the modal size-class, as in the two species discussed above. Although adults could have a more southerly distribution than so far reported, this does seem to counter Possibility (i) above. Possibility (iii) does not appear very feasible, because if larvae were introduced via the counter-flows, they should appear inshore in the south. However, larvae were found only at one station. The most likely possibility is therefore (ii), because of the presence of adults in Agulhas water pockets, the similar characteristics of the water of these pockets and that of the retroflection, and its proximity to the study area.

In the Indian Ocean, adult *Benthosema pterotum* are distributed from the Arabian Sea to about 25°S (off Moçambique, Hulley 1986, Dalpadado 1988). The only available information on length-at-age for larvae of *B. pterotum* was given by Gjøsaeter and Tilseth (1988), and that indicated that larvae of 2.4 mm are 3–5 days old (in water 21–25°C). Using this information, the typical surface flows of the Agulhas Current and the presence in the study area of larvae of 2.5 mm, these larvae could only come from a spawning site at latitudes 26–27°S, which is slightly south of the closest record of adults off Moçambique**.**

Contrary to the results obtained for the three other species, larvae of *Benthosema pterotum* were common in all southern inshore stations. Moreover, the concentrations of larvae >5.0 mm at the southern inshore stations were higher than those of the smaller sizes. One way to explain this difference would be on the basis of the marked drop in surface temperature inshore south of Mbashe. Such an observation has been associated with topographically induced upwelling of Indian Ocean central water from below the warm shelf-edge flow (Bang 1970, Harris and Van Foreest 1978, Gill and Schumann 1979). According to the temperature distribution, water inshore in the south has been upwelled from depths of at least 100 m from the core of the Agulhas Current, as can be seen by comparing the transects at Mbashe and Algoa Bay (Beckley and Van Ballegooyen 1992, Fig. 2). On the other hand, the vertical size distribution of larvae of *B. pterotum* given by Röpke (1993) showed that small larvae (<3.4 mm) rarely reach depths >60 m in the water column, whereas larger specimens (>4.4 mm) are widely distributed up to a depth of 120 m. Therefore, the presence of large specimens (>5.0 mm) of this species in that area is an indication that they could have been transported there when water from the offshore deeper layers upwelled to the shelf. The absence of larger larvae of the three other species in this southern sector, compared to their presence in the rest of the area, suggests a lower rate of survival. Taking into account the fact that productivity levels in the southern area are high as a result of the intense shelf-edge upwelling (Hutchings 1994, Probyn *et al*. 1994, 1995), food concentrations should not be *a priori* a cause of larval mortality. However, the type of prey in this inshore zone is probably different from that offshore, so it may not be adequate. Furthermore, Hutchings (1994) indicated that euphausids, siphonophores, salps and doliolids are abundant on the eastern Agulhas Bank, which may imply that predation pressure is important there. Temperature is another important factor. The lower temperatures in this area than in the common areas of distribution of these species could also be a negative factor influencing larval survival.

The results of the present study show that surface currents can play an important role in determining the extent of lanternfish larval distribution, and contribute to the establishment of wider distribution areas of larvae than of adults. However, the actual survival potential of such larvae is a subject which requires more investigation. Aspects such as food requirements and the distribution and abundance of the zooplankton components in the different areas where larvae are found need to be investigated.

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