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Poleward transport of equatorial fish larvae in the Atlantic Eastern Boundary Current system

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Abstract

Fish larval distributions support the hypothesis that East Atlantic "upwelling" undercurrents are interconnected, and can entrain plankton from the Equatorial Undercurrents towards temperate latitudes. This conclusion is based on historic and recently collected data on the distribution of adults and larvae of mainly two equatorial, mesopelagic fish species *Bathylagus argyrogaster* and *Hygophum macrochir* and consistent with hydrographic data. Along the continental slope these larvae occur 440 to 920 km polewards of the reproductive ranges of their adults. Larval *B. argyrogaster* occurs mainly below the thermocline and reaches farther polewards than larval *H. macrochir*, which dwells mainly at thermocline depths. At tropical latitudes the larvae of both species occur frequently, and within a generally poleward flow. Immediately polewards of the Cape Verde Frontal Zone, and Angola-Benguela Frontal Zone, respectively, the larvae become rare and more deeply distributed. At these fronts the poleward flows are thought to submerge below the equatorward flows of the Canary Current and Benguela Current, and to form the slope-undercurrents of the Northwest and Southwest African upwelling systems. Larvae in these undercurrents reach minimum latitudes of 22° N and 23°30′ S. At the poleward flanks of East Atlantic cyclonic gyres, such as the Guinea Dome, Central Mauritanian Gyre, and Angola Dome, retroflections of the poleward current systems occur, also entraining and transporting larvae offshore.

Kurzfassung

Polwärtiger Transport äquatorialer Fischlarven im atlantischen Ostrandstromsystem

Fischlarvenverbreitungen stützen die Hypothese, daß sogenannte „Auftriebsunterströme" am ostatlantischen Kontinentalabhang miteinander verbunden sind und Planktonorganismen von den äquatorialen Unterströmen polwärts bis in gemäßigte Breiten transportieren können. Diese Schlußfolgerung basiert überwiegend auf dem Abgleich der Larvenverbreitungen gegenüber dem Reproduktionsgebiet der Adulten zweier äquatorialer, mesopelagischer Fischarten, sowie hydrographischen Daten. Entlang dem Kontinentalabhang kommen die Larven von *Bathylagus argyrogaster* und *Hygophum macrochir* 440 bis 920 km polwärts der Reproduktionsgebiete vor. Die Larven von *B. argyrogaster* leben subthermoklinal und reichen weiter polwärts als die thermoklinalen Larven von *H. macrochir*. In den Tropen sind beide Arten frequent und kommen in generell polwärtigen Stromsystemen vor. Mit Erreichen der Kap Verde Frontalzone, bzw. der Angola-Benguela Frontalzone werden beide Arten seltener und zeigen tiefere Vertikalverteilungen. Vermutlich verbleiben sie innerhalb der fortbestehenden Schelfabhangs-Unterströme, welche den

äquatorwärts gerichteten Kanarenstrom bzw. Benguelastrom der Nordwest- bzw. Südwest-afrikanischen Auftriebsgebiete unterschichten. Die Larven erreichen mindestens 22° Nordbreite und 23°30' Südbreite. An den polwärtigen Flanken der zyklonischen ostatlantischen Wirbel (Guinea-Dom, Mauretanischer Zentralwirbel, Angola-Dom) kommen seewärtige Stromablen-kungen aus dem generell polwärtigen Transport vor, die ebenfalls Larven mitführen.

Introduction

Some species of fish or copepods from the subtropical and tropical East Atlantic can spread along the North-East Atlantic continental slope up to the British Isles (*e.g.* Stöhr *et al.* 1997; Quéro *et al.* 1998; John *et al.* 1998, and literature referenced there). These authors stressed that the extreme northern limits of such species contrast with more common biogeographical explanations via the temperature field, water masses, or dispersal by the North Atlantic Drift. The above mentioned authors think that such distributions are linked with poleward-flowing slope currents, entraining mesopelagic species (or mesopelagic larvae) northwards. The role of slope undercurrents as transport or recirculation vehicles in subtropical and tropical upwelling systems has already been described two decades earlier (*e.g.* Binet and Suisse de Sainte Claire 1975; Peterson *et al.* 1979; Hamann *et al.* 1981).

Poleward-flowing undercurrents along the continental slopes are typical features of Eastern Boundary Current upwelling systems. A model presented by Clarke (1989) implies that each upwelling regime creates its own undercurrent, being largely independent of adjacent systems. Voituriez and Herbland (1982) presented a conceptual model, suggesting that the undercurrents off tropical West Africa are fed by three eastward equatorial undercurrents, namely the Equatorial Undercurrent and the North and South Equatorial Undercurrents (Figure 1). Their poleward spread is caused by the continental slope, and they interconnect (among others) with the Guinea Undercurrent and Angola Current. Cyclonic domes like the Guinea Dome or Angola Dome were anticipated to cause seaward


Figure 1 (*opposite page*): A conceptual model of the surface and subthermocline currents along the western African continental slope during summer conditions (for both hemispheres). Own compilation based on the literature listed in Table 4.

Large, white arrows indicate currents reaching from the surface to 200 m at higher latitudes. Narrow white arrows show tropical surface currents which terminate at the thermocline and which are directionally less stable. Black arrows depict undercurrents generally opposite to the surface flow. The model distinguishes between undercurrents known to transport plankton polewards (continuous arrows), and such undercurrents where biological evidence is still lacking (interrupted). The wavy lines depict the Cape Verde Frontal Zone CVFZ off Mauritania and the Angola-Benguela Frontal Zone ABFZ off Angola, respectively. Crosses within cyclonic deflections of undercurrents denote the locations of the subthermoclinal cyclonic gyres Mauritanian Central Gyre (18° N), Guinea Dome (11° N) and Angola Dome (10° S).

Geographical names denote coastal regions, not political boundaries. Diagonal shading inside the coastlines depicts seasonal coastal upwelling, cross-hatching, the permanent upwelling areas.

Abbreviations for current systems: AC = Angola Current, BC = Benguela Current, CC = Canary Current, EUC = Equatorial Undercurrent, NEC = North Equatorial Current, NECC = North Equatorial Countercurrent, SEC = South Equatorial Current, SECC = South Equatorial Counter Current, SEUC = South Equatorial Undercurrent.

The NECC continues eastwards into the Guinea Current (GC), beneath that flows the Guinea Undercurrent (GUC) westwards (both unlabelled for lack of space).
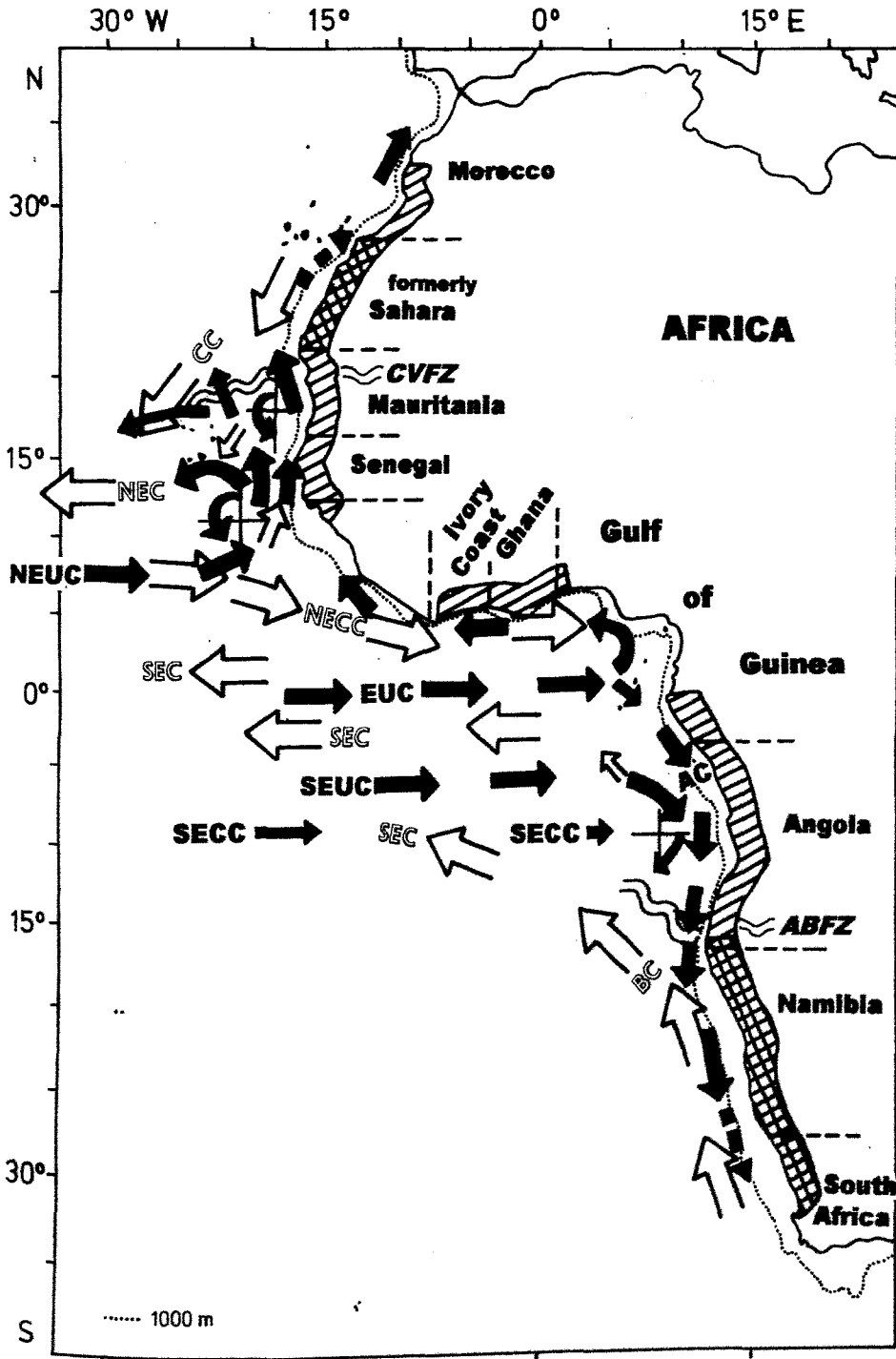
deflection of parts of the poleward currents (Voituriez and Herbland 1982). This model is presently widely accepted for the tropical eastern Atlantic between approximately 15° N to 15° S (Siedler *et al.* 1992; Wacongne and Piton 1992, and cited literature therein).

Shannon (1985) suggested that the Angola Current has a subsurface interconnection with the Namibian upwelling undercurrent, and Mittelstaedt (1989) believed that the equatorial undercurrent system also feeds the undercurrents of the North-West-African upwelling systems at higher latitudes. The poleward undercurrent would thus be a continuous and permanent feature also in non-upwelling areas and seasons, onto which the seasonal signal is superimposed. Such a current opposing the equatorward surface flow would form an important component in any physical model of Atlantic water-mass transport, or of any biological model explaining distribution patterns by plankton transport.

Barton (1989) stated that the hypothesis of a submerging, permanent and continuous poleward slope undercurrent was unproven, and that this question could not be tested by physical methods alone (today, floats provide excellent means, but have not yet been released into upwelling undercurrents; Zenk 1997). The undercurrent is narrow and changes its depth and water-mass characteristic both with latitude and, on smaller scales, with depth and distance cross-slope. Seasonal changes in intensity and location are likely. Barton (1989) suggested the inclusion of the dispersal of passive tracers like nutrients or fish larvae in studies of transport by the undercurrent.

John and Zelck (1997) described a respective three-dimensional, high-resolution ichthyoplankton study (concerning open ocean scales) off Mauritania and Senegal. The study revealed that the distribution patterns of several larval fish species coincided well with the currents or water-masses at the preference depths of the larvae (John and Zelck 1997). Larval patterns described the pathways of the slope undercurrent, as well as its offshore deflections at mesoscale oceanic gyres. Among a larger number of "undercurrent" species in the study by John and Zelck (1997), the larvae of the deep-sea smelt *Bathylagus argyrogaster* Norman, 1930 (family Bathylagidae) and lanternfish *Hygophum macrochir* (Günther, 1864; family Myctophidae) seem to be particularly suitable for a new, larger-scale study of poleward dispersal along the East Atlantic margin. The above-mentioned larvae had an equatorial origin. *Bathylagus argyrogaster* preferentially occurred in the layer 60 to 90 m deep. *Hygophum macrochir* was most abundant at 25 to 50 m, but also abundant in the stratum beneath (50 to 100 m). The larval depth range 25 to 100 m coincided with the depths of the poleward undercurrents (John and Zelck 1997).

In contrast with several other species of potential value as tracers, however, distributional information for larval *B. argyrogaster* and *H. macrochir* is available from either literature or new data covering a much wider latitudinal range, 26° N to 36° S. Besides presenting new data from the tropical Atlantic, the entire set of biological data so far available will be reviewed and compared with hydrographical knowledge to analyse whether poleward dispersal and gyral retroflection of mesopelagic, tropical fish larvae occurs in the Southeast Atlantic, too.

Materials, data bases and methods

This paper compares larval distributions of *Bathylagus argyrogaster* and *Hygophum macrochir* (by abundance, or at least frequency, data) with the respective distribution of

the adults, and the ocean currents in the larval depth range. The comparison is based on both literature, and new data for the distribution of adult fish, larval fish and hydrography. To facilitate understanding, the data base is grouped for subjects as follows.

Adult distribution of Bathylagus argyrogaster

Bathylagus argyrogaster is a mesopelagic species (Kobylyanskiy 1985) caught also in bottom trawls (Parin *et al.* 1978). It has epipelagic to shallow-mesopelagic juveniles (Ion *et al.* 1995). It is restricted to the tropical East Atlantic (unless the Pacific *B. nigrigenys* is considered as synonymous). To summarize the most recent reviews, Cohen (1990) listed a latitudinal range from 13°25' N to 18°37' S; the distribution map by Kobylyanskiy (1985) shows a range between approximately 23° N and 20° S. Adult *B. argyrogaster* was not listed for Namibia (Lloris 1986), South Africa (Cohen 1986), or north of 30° N (Cohen 1984).

The reviews cited above did not relate the occurrences of the species to sampling effort. We found it necessary to revise the existing data base either from literature or from the collection at the Zoologisches Museum Hamburg (ZMH), for coherent occurrences, stray individuals or the absence of the species, to depict the distributional range of adult and juvenile *B. argyrogaster* (Table 1). These data happened to become scant near the distributional limits. Therefore, apart from the above data we have also taken into account that there are records for the species with limited or no reference to sampling positions or overall sampling effort (Table 2). These databases have been split to subareas, when possible. We consider an occurrence to be inside the distributional range, when at least one of three adjacent stations (a combination of different surveys) yielded one specimen or more.

Distribution of adult Hygophum macrochir

As shown by Nafpaktitis *et al.* (1977), *Hygophum macrochir* is a high-oceanic species which seems to be distributed widely in the tropical Atlantic. Relyable quantitative data, however, are available only from the central equatorial Atlantic, where the distribution is narrower (17°30' N to 3° S, Nafpaktitis *et al.* 1977, Hulley 1981). The species is mesopelagic during daytime and is also caught near the surface by neuston nets at night. The most recent summary of its distribution was given by Bekker (1983) and is used as a base for the distribution map.

A lack of detailed data from the Eastern Boundary Currents does not allow a similar, effort-related, quantitative study of its adult distribution, as done for *B. argyrogaster*, in order to distinguish its true reproductive range from the occurrence of stray individuals. As mentioned by Nafpaktitis *et al.* (1977), some further bias may be involved in the southern area, due the earlier confusion between *H. macrochir* and *H. taaningi*.

Larval data

Table 3 lists the currently available information on the distribution of both larval species. In the first case, new data refer to the cruise "Atlex 89" by RV "Alexander v. Humboldt" in the summer of 1989. A station map and hydrographical results from this cruise were published by Hagen (1992). Fish larvae were analysed from 31 Bongo-net tows 0 to 200 to 0 m at a towing speed of 1.3 $m·s^{-1}$, fishing an average area of 3.7 m^2 (±0.82 m^2).

Table 1: The data basis for Figure 3: Presence/absence position data for juvenile and adult *Bathylagus argyrogaster* in the East Atlantic, compiled from literature and Zoological Museum Hamburg (ZMH) data (grouped from north to south). Stations beyond 39° of latitude or 30° W have been excluded. Replicate tows at one and the same position have been counted and plotted as one single station. The symbol § indicates a plankton net only. Abbreviations WH and AD refer to respective "Walther Herwig" and "Anton Dohrn" cruises.

Subarea Degrees Lat.	Source	Published	Stations total	positive	Specimens total
37° N - 21° S	ZMH-WH 15 Post/Kobylyanskiy	1987/unpubl.	16	6	11
37° N - 21° S	ZMH-WH 23 Post/Kobylyanskiy	1987/unpubl.	42	3	5
33° N - 39° S	ZMH-WH 36 Post/Kobylyanskiy	1987/unpubl.	50	7	47
30° N - 35° S	Norman	1930	35	7	15
26° N - 18° N	Lloris & Rucabado	1979	113	0	0
19° N - 09° N	ZMH-WH 03 Kreft diary	unpublished	11	6	11
14° N - 09° N	ZMH-AD 176 Post/Kobylyanskiy	1987/unpubl.	6	4	55
03° N - 17° S	Parin *et al.*	1978	59	9	16
01° N - 18° S	Blache	1964	46	23	60
03° S - 11° S	Fraser-Brunner	1931	8	1	2
11.5° S	Ion *et al.*	1995	21 §	1	3
17° S - 29° S	Lloris	1986	223	0	0

Table 2: Additional information to show the distributional limits of juvenile and adult *Bathylagus argyrogaster*, but lacking detailed station data. Respective occurrences of the species are depicted in Figure 3 by symbol X.

Subarea Degrees Lat.	Source	Published	Stations total	positive	Specimens total
38° N - 24° N	Maurin	1968	389	0	0
30° N - 26° N	Parin & Golovan	1976	6	0	0
29° N - 20° N	Maurin *et al.*	1977	187	1	4
26° N - 17° N	Maurin *et al.*	1970	63	0	0
23° N - 21° N	Parin & Golovan	1976	27	1	1
22° N - 19° N	Maurin	1968	20	0	0
20° N - 15° N	Maurin *et al.*	1977	64	1	4
19° N - 17° N	Maurin	1968	8	0	0
19° N - 17° N	Parin & Golovan	1976	5	0	0
12° N - 04° N	Parin & Golovan	1976	10	0	0
11° N - 08° S	Kobylyanskiy	1985	?	8	13
3.5° S	Parin & Golovan	1976	1	0	0
18° S - 22° S	Parin & Golovan	1976	14	0	0
23° S - 35° S	Parin & Golovan	1976	22	0	0

We have combined these data, together with those from other sources, adding information for the western and northwestern part of the distribution maps from the North-East Atlantic presented below.

The new data gathered from "Meteor" cruise 28 off Angola will be presented in some more detail, since that area has not been studied previously. The station grid for CTD-O_2 hydrography and plankton sampling is shown in Figure 2. Information on this cruise was
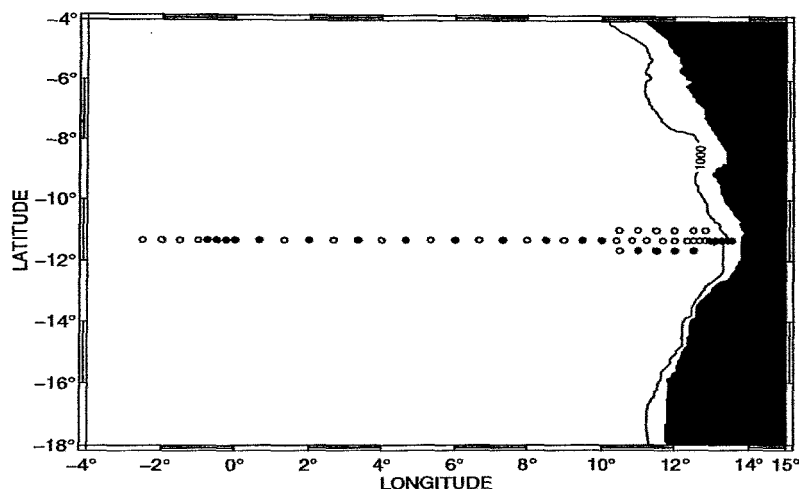
Figure 2: The location of the survey off Angola (RV "Meteor" cruise 28, ship sta. nos. 245 - 290, May 1994). Circles represent CTD-only stations. Dots depict CTD/plankton stations.

Table 3: Larval catches of *Bathylagus argyrogaster* and *Hygophum macrochir* in the East Atlantic, compiled from literature and new data (grouped from north to south). Symbols (for details see text):
* = referred to under other species name in original source,
+ = partly replicates material from other sources listed,
§ = probably underestimated,
> = subsequent additional identifications by Shiganova or minimum estimate,
not cons. = not considered.

Subarea Degrees Lat.	Source	Published	B. argyrogaster			H. macrochir		Season(s)
			Sta-tions total	positive	Speci-mens total	Sta-tions positive	Speci-mens total	
34° N - 04° N	John & Zelck	1997	178	43	175	86	366	Autumn/Winter
32° N - 10° N	"Atlex 89" cruise	new data	31	6	28	7	126	Summer
26° N - 23° N	Palomera & Rubiés	1978/82	46	0	0	0	0	Spring
24° N - 15° N	Bendixen	thesis 1977	35	9 *	54	17	138	Autumn
21° N - 17° N	John	1985	86	24 *	34	0	0	Winter
21° N - 15° N	Hermes & Olivar +	1987	?	46	147	- not cons. -		Autumn/Winter
20° N - 13° S	Shiganova +	1975	>100	- not cons. -		?50%	many	all
05° N - 13° S	Zhudova	1969	81	4*§	35 §	16(>20)	>119	all
11.5° S	"Meteor 28" cruise	new data	21	16	138	21	647	Autumn
18° S - 36° S	Olivar & Fortuño	1991	467	7	8	14	?14	all
20° S - 24° S	Hermes & Olivar +	1987	?	3	3	-not cons. -		Autumn/Winter

published by Zenk and Müller (1995); Zelck and John (1995) gave details for the plankton stations. The gross ichthyoplankton composition and abundance across the Atlantic was described by John and Zelck (1998). This paper focusses on those indicator species obtained by the 21 westernmost oblique tows with a multiple-opening-closing net ("MCN", 0.25 m^2
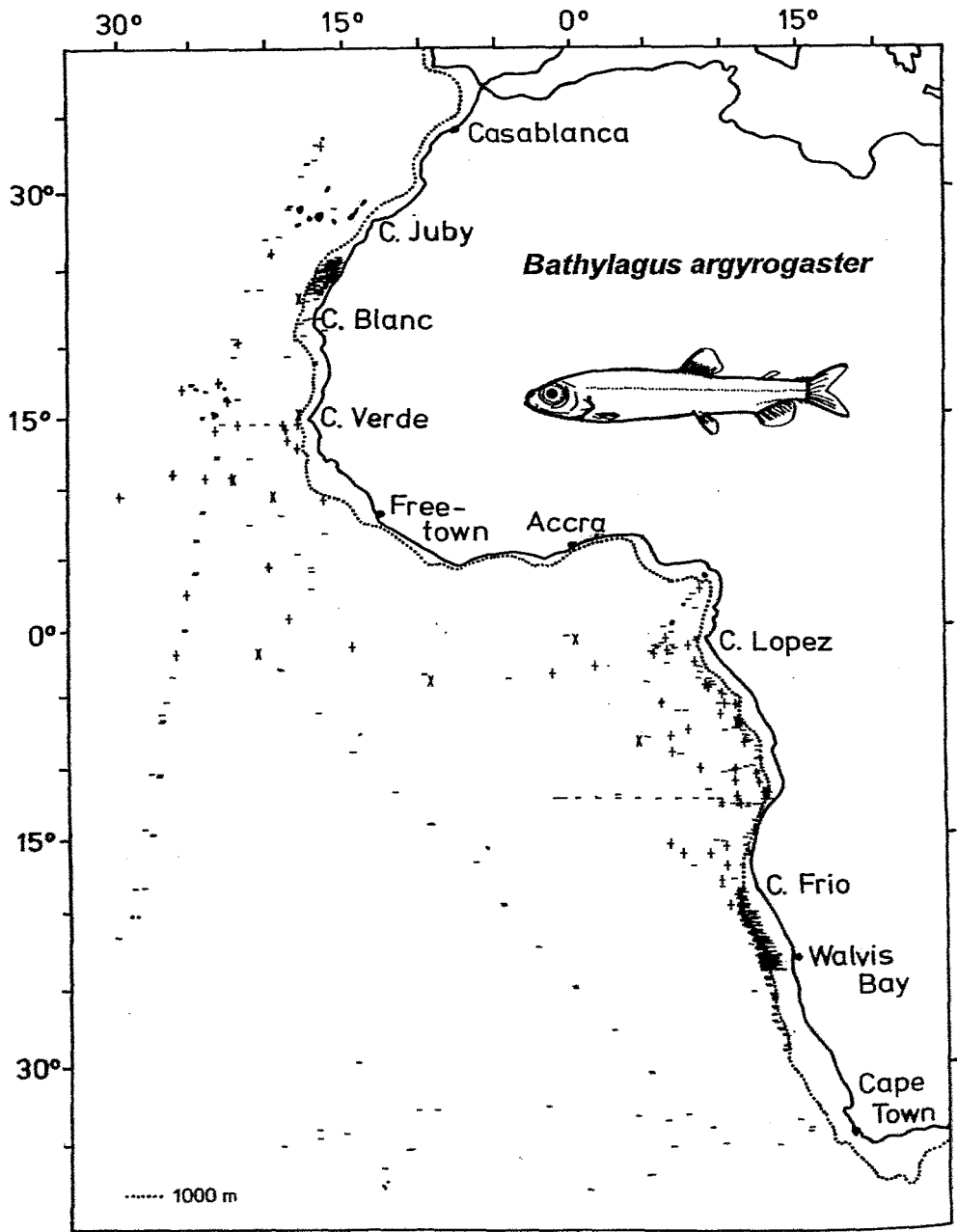
Figure 3: The distribution of adult and juvenile *Bathylagus argyrogaster* (own compilation from Table 1). Dashes indicate absence, crosses presence at documented trawling positions. Sign X depicts additional records from sources where position details on negative stations were unavailable. Note that the shelf edge between *e.g.* Cape Verde and Cape Blanc as well as off northern Morocco has been more intensely surveyed than shown here (Table 2).

mouth opening and 300 µm mesh-size) from the strata 200 to 150, 150 to 100, 100 to 50, 50 to 25 and 25 to 0 m depth. The MCN was towed at speeds of 1.0 to 1.5 m·s^{-1} and sampled on average 4.3 ± 1.4 m^2). Average vertical distributions have been calculated as mean-weighted depth MWD = $\Sigma(n_i \times d_i) \times N_i^{-1}$ with n_i being the abundance per squaremeter in stratum i, d_i the mean depth of stratum i, and $N_i = \Sigma n_i$.

No ichthyoplankton data are available for the subarea 13° S to 18° S. The coverage is poor for the continental slope areas of 14° N to 6° N and 5° S to 10° S.

The above listed samples generally cover the vertical range from 0 to 200 m. The samples by Zhudova are an exception, only reaching down to 50 or 100 m, and also probably those by Shiganova (1975), which include the grid analysed by Zhudova. Shiganova's data base was much larger, but the number of stations was not stated. Such a number cannot be counted from her station map, which became contorted and overlaid during the drawing or printing process. It was not possible to extract along-slope distribution patterns in any detail from contorted coastlines.

A shallow sampling range may underestimate frequency and abundance of both relatively deep-living larval species in the tropics, and does not yield *B. argyrogaster* larvae at subtropical latitudes. No information on abundance per station is available from Olivar and Fortuño (1991), Shiganova (1975) and Zhudova (1969); we have to use frequency data. These differences in the original data exclude any combination of the larval data into one single map.

Larval taxonomy of Bathylagus argyrogaster

A large, transforming *B. argyrogaster* was illustrated in Ahlstrom *et al.* (1984). Early larval stages were identified and described by Hermes and Olivar (1987). In previous ichthyoplankton surveys, larval *B. argyrogaster* were referred to as "*Bathylagus* spec." by Bendixen (unpublished thesis 1977, with description of the larvae; material held by us), or "?*Glossanodon leioglossus* or *Bathylagus* sp.?" by John (1985). Zhudova (1969) referred to "*Argentina sphyraena*", and provided a sketch showing the higher number of melanophores distinguishing *B. argyrogaster* from Argentina. This material is no longer available, but our assumption that Zhudova's larvae actually belonged to *B. argyrogaster* was corroborated by the AtlantNIRO staff (I. Trunov, pers. communication).

Larval taxonomy of Hygophum macrochir

It is little known that the larvae of *H. macrochir* were first identified by Zhudova in 1969 (see her Figures 15 and 16). More recent descriptions became widely known (Moser and Ahlstrom 1974; Moser *et al.* 1984; Shiganova 1975). The larvae are fairly characteristic, therefore the large international data base concerning the distribution of these larvae is relyable.

Hydrography

Figure 1 presents a conceptual model of the surface and subsurface currents along the East Atlantic margin, applying the hypothesis of continuous poleward undercurrents to the latitudinal range of our data. The model is based on the earlier work listed in Table 4, and refers to summer and autumn conditions for both hemispheres to concur with our larval data at higher latitudes.

Table 4: Sources for the conceptual model of surface and subsurface currents presented in Figure 1 (from north to south, preference given to review papers. Original data marked by $).

Region	Source
Portugal-Morocco	Stöhr *et al.* 1997
Canary-Current system	Barton 1989; Mittelstaedt 1982, 1989
Cape Verde Frontal Zone	Klein 1992
Mauritania - Senegal	John & Zelck 1997
Central Atlantic equatorial current system	Siedler *et al.* 1992
Guinea-Current system	Binet 1997
Equatorial undercurrent system	Voituriez & Herbland 1982
Northeastern Gulf of Guinea	Wacongne & Piton 1992
Angola-Current	Gordon & Bosley 1991
11.5° S	"Meteor" 28 cruise, new data $
12° S	Dias 1983 $
Angola-Benguela Frontal Zone	Meeuwis & Lutjeharms 1990 $, Shannon *et al.* 1987
Benguela-Current system	Shannon 1985
Benguela Undercurrent	Nelson 1989 $, Shannon & Nelson 1996

Results

The distribution of adult and juvenile Bathylagus argyrogaster

Figure 3 shows presence (respectively absence) data from the sources listed in Tables 1 and 2. The data are likely to describe the average distribution, since they have accumulated over more than 60 years. It became apparent that adults of the species are concentrated in the tropical East Atlantic, where their distribution is believed to be contiguous. However, data for the northern Gulf of Guinea are scant and may suggest a paucity of the species in the eastern part of the gulf. Surveys polewards of 17° N, or 17° S to 18° S did not, as a rule, record *Bathylagus argyrogaster*. The actual northern boundary seems to be south of 15° N (ZMH data, 5 adjacent stations at this boundary latitude being positive, whilst Maurin *et al.* (1977) reported only one occurrence among 4 stations at 15° N). Table 2 lists 77 negative stations for the adjacent subarea northwards. The southern boundary of contiguous distribution would be established at 15.5° S on hand of Blache's data alone (all 5 stations 14°25' S to 15°05' S positive, all 4 more southern ones (15°53' S to 17°53' S negative), or at 17° S from the total data set. To mention only those surveys with a wider latitudinal coverage in any detail, the data of Blache, Kobylyanskiy, Norman, and Parin *et al.* (with 3 exceptions discussed below) all fall within these boundaries. It was interesting to note that in the ZMH data, all oceanic stations south of 01°24' S were negative, and that there was a distributional gap at the 7 oceanic stations coinciding with the North Equatorial Counter Current (Figure 3).

In the off-slope realm of the North-East Atlantic, the range of adults extends farther northwards than along the continental slope and includes the Cape Verde Islands (ZMH data, 6 adjacent stations positive). Furthermore, Figure 3 shows four isolated North-East Atlantic occurrences within many, otherwise negative, surveys along the continental slope (Table 2). These 4 findings are from ZMH, 3 occurrences, and Parin and Golovan (1976). The identification of the northern ZMH specimens has been corroborated by D. Cohen, S. Kobylyanskiy and ourselves.

The three southernmost findings (15°55' to 18°37' S; Norman 1930; Parin *et al.* 1978) in the South-East Atlantic may also prove to be exceptional and polewards of this general equatorial range, when more data for the subarea 15° to 18° S become available.

The distribution of adult Hygophum macrochir

We generally accept the distribution map by Bekker (1983) and present it for comparative purposes in Figure 4. As Nafpaktitis *et al.* (1977) stated, the southern boundary of the species might have a bias, from *H. macrochir* being confused with the subtropical *Hygophum taaningi*. Hulley (1981) considers *H. taaningi* to be a tropical-subtropical species, overlapping the distribution of *H. macrochir* in the tropics. The actual southern boundary of *H. macrochir* off South-West Africa might lie as far northwards as 11.5° S (Hulley 1981).

Frequency and abundance data by both Nafpaktitis *et al.* (1977) and Hulley (1981) show that *H. macrochir* is concentrated in the equatorial currents. In the map by Nafpaktitis *et al.* (1977) the species distribution along the northeastern Atlantic continental slope broadens towards subtropical latitudes. The scant data for the South-East Atlantic seem to conform this (compare Nafpaktitis *et al.* 1977 with Hulley 1981).

In the northeastern subarea off Mauritania, *H. macrochir* ranked 7 in abundance in autumn samples analysed by Backus *et al.* (1977), but appeared to be restricted to the Southern Mauritanian Province. John and Zelck (1997) have made more than two hundred neuston tows off Mauritania additionally to the plankton stations listed in Table 3, all of which yielded only five adult *H. macrochir* in two hauls. This indicates that, off Mauritania, the northeastern boundary is indented, as was found similarly for *B. argyrogaster*, with possibly a seasonal shift.

Surface and subsurface currents along the East Atlantic margin

We refer to the conceptual model shown by Figure 1, and sources for this model listed in Table 4. At subtropical latitudes, the currents flow towards the equator and broadly parallel to the coast. These, the broad Canary Current in the north (designated CC in Figure 1) and the Benguela Current in the south (BC), generally include the subsurface and upper mesopelagic layer. Along the continental slope at least in the upwelling systems below the Canary Current and Benguela Current there are so-called "upwelling undercurrents". Their existence has not yet been proven for the (temporarily unaccessible) slope off Sahara, but is generally unquestioned. Upwelling undercurrents are believed to be less than 100 km wide, and to follow the upper continental slope. It is disputed whether these undercurrents are individual components of upwelling regimes, or are interconnected and permanent. Figure 1 distinguishes between undercurrents corroborated by both hydrographical measurements and biological data (solid black arrows) and such so far only known from hydrographical evidence (dotted black arrows).

At the frontal zones (depicted by wavy lines in Figure 1), the Canary and Benguela Currents, respectively, detach from the shelf edge westwards and continue as the North Equatorial Current (NEC) and South Equatorial Current (SEC in the tropical South Atlantic). The frontal zones Cape Verde Frontal Zone (CVFZ) off northern Mauritania, and Angola-Benguela Frontal Zone (ABFZ) off southern Angola displace seasonally. The positions shown in Figure 1 are for the warmer seasons, when the fronts have their most poleward positions. The mean seasonal variation is some 2° of latitude.
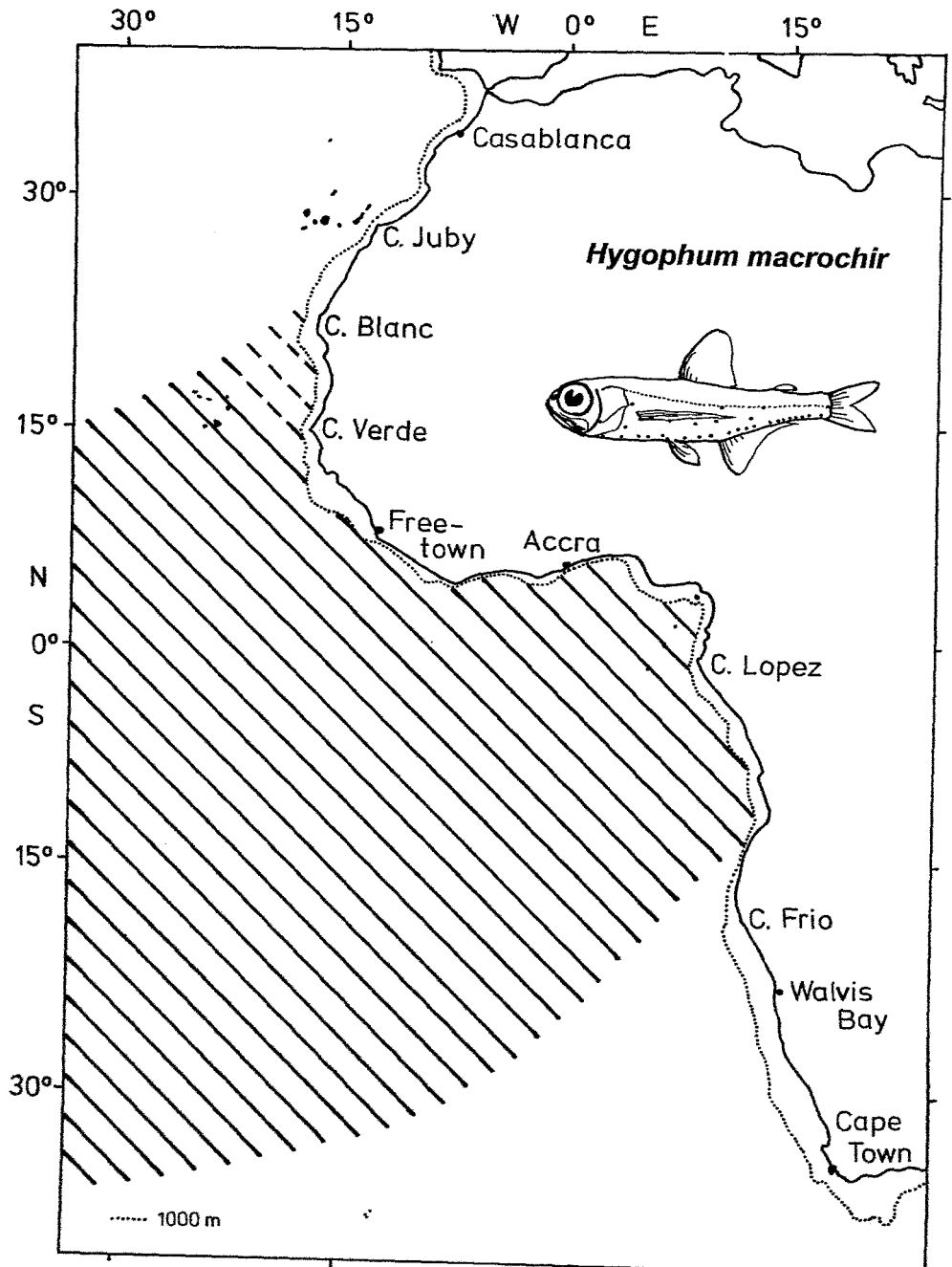
Figure 4: The distribution of adult *Hygophum macrochir* (from Bekker 1983, modified). The area north of Cape Verde (dotted hatching) is here considered not to be within the regular range of adults. The southern boundary is questionable (see text).

Equatorwards of the frontal zones, the wind-driven equatorward surface flow becomes weak, directionally unstable, and restricted to the shallow layer above the thermocline (which can be as shallow as 25 m in depth). The equatorward surface flow is weakest during the warm seasons.

Recent research in the region off Mauritania and Senegal has revealed a very complex system of subsurface currents for that region. This complexity results from converging subsurface currents at the frontal zone, and cyclonic gyres around the subthermocline domes (Guinea Dome, at about 10° N, 22° W, and Mauritanian Central Gyre off Mauritania, at about 17°30' N, 17°30' W, both marked by crosses in Figure 1). Such complexity has not been described off Angola, but might be found when more data will become available.

The equatorial current system between the frontal zones can be described as follows: At about 5° N to 8° N, the eastward flow of the North Equatorial Counter Current (NECC) enters the region (Figure 5). This surface current is strongest during summer. It bifurcates into a smaller northward branch that continues into the poleward flow off Senegal. The larger branch continues along the northern slope of the Gulf of Guinea as the Guinea Current (GC, not labelled in Figure 1, due to lack of space). Below the NECC flows the narrow North Equatorial Undercurrent (NEUC). This current does not continue into the Gulf of Guinea, but is deflected by the Guinea Dome and the continental slope off Senegal northwards, driving (at least partly) the poleward flow and the retroflection westwards into the NEC off Senegal (Figure 5).

Farther south, the South Equatorial Current (SEC) is a surface flow towards the west. Its location and latitudinal extension differs with longitude, but it does not drive the boundary currents which are of interest for this study. Below the SEC two undercurrents flow eastwards and feed the boundary current system, namely the narrow Equatorial Undercurrent at 0° latitude (EUC) and the South Equatorial Undercurrent (SEUC) at about 3° S to 6° S. A third, less intense eastward undercurrent is the South Equatorial Counter Current (SECC). It is thought to merge with the circulation west of the Angola Dome. Both the EUC and SEUC deeply penetrate into the Gulf of Guinea. The EUC hits the continental slope at Cape Lopez (Cape Lopez is shown in Figure 3) and bifurcates. Its northern branch follows the Guinean continental slope westwards and forms the westward Guinea Undercurrent (GUC). The GUC subsequently follows the West African continental margin, and contributes to the poleward flow off Senegal-Mauritania, too.

The southern branch of the EUC flows from Cape Lopez southwards along the Angolan continental slope. The SEUC is
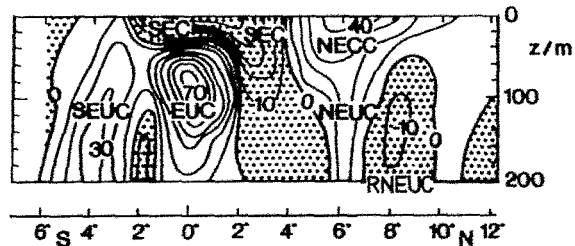

Figure 5: Zonal equatorial currents along 23.5° W (compiled by Siedler *et al.* 1992, modified). Stippled areas indicate westward flow. The currents are indicated as follows: NECC, North Equatorial Countercurrent; SEC, South Equatorial Current; NEUC, SEUC and EUC stand for the North Equatorial, South Equatorial and Equatorial Undercurrent. The westward retroflection of NEUC around the Guinea Dome is denoted RNEUC.

deflected southwards by the subthermoclinal Angola Dome (depicted in Figure 1 by the cross off Angola). Together with the southward branch of the EUC it forms the Angola Current (AC). The AC extends from the surface to a depth of at least 500 m and is permanent (Dias 1983). It is probably strongest during autumn, due to the summer relaxation of westward windstress (Shannon 1985). As anticipated in literature (Table 4), a smaller branch is retroflected westwards by the Angola Dome (new data).

On the basis of physical data Shannon *et al.* (1987) described how the AC submerges at the ABFZ and continues as a slope undercurrent off Namibia at depths of between 100
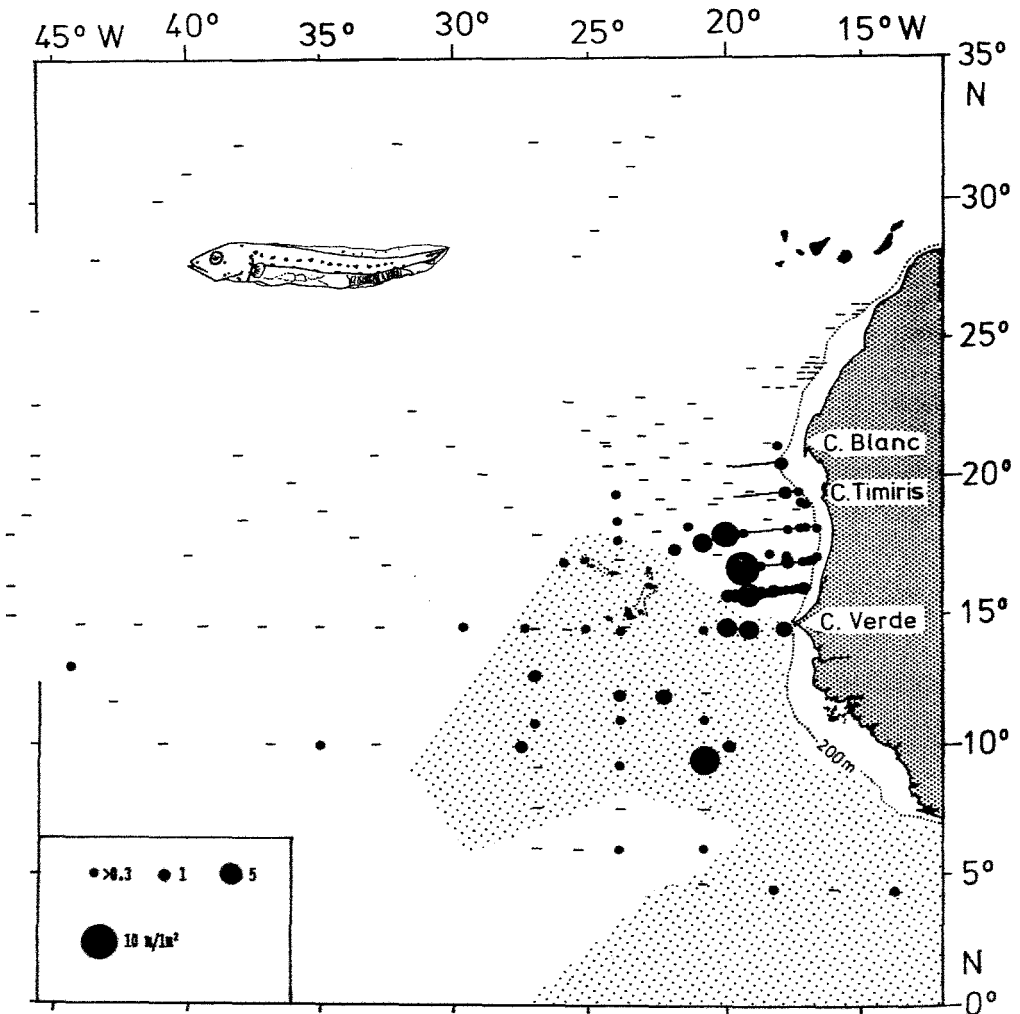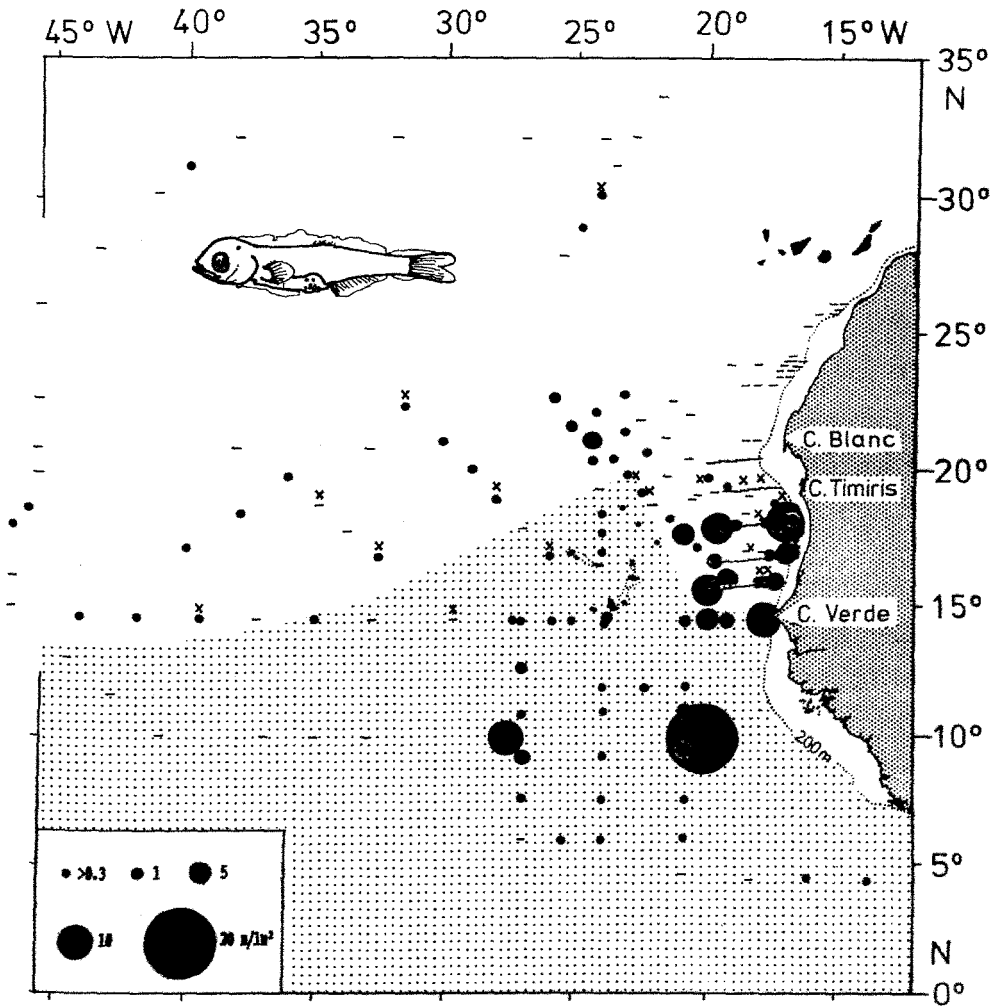

Figure 6: The quantitative distribution of larval *Bathylagus argyrogaster* in the upper 200 m of the tropical and subtropical Northeast Atlantic (for data base see text). Dashes depict negative stations, dots, occurrences and abundances (for scale see inset). The adult distribution is stippled.

and 400 m. Conditions off the Sahara are believed to be generally similar, but with an undercurrent below 200 m in depth.

Larval distribution patterns off North-West Africa

To establish possible dispersal mechanisms off North-West Africa, we present the quantitative larval distributions of *B. argyrogaster* and *H. macrochir* in Figures 6 and 7. These figures combine the station grids analysed in more detail by Bendixen (1977), Palomera and Rubiés (1978 and 1982, in particular the earlier paper) and John and Zelck (1997)

Figure 7: The quantitative distribution of larval *Hygophum macrochir* in the upper 200 m of the tropical and subtropical Northeast Atlantic (for data base see text). Dashes depict negative stations, dots occurrences and abundances (for scale see inset). Additional larval occurrences in neuston nets are indicated by x, and the adult distribution is stippled.

with new data from Atlex 89 (Table 3). Atlex 89 stations cover the northwestern and western extreme positions of Figures 6 and 7, and generally yielded only single specimens of both species. The exceptions are two stations east and west of the Guinea Dome, where high frequencies and elevated abundances were also found in the earlier data (Figures 6 and 7).

Larvae of both species revealed a fairly regular occurrence within the respective ranges of the adults. Larval *B. argyrogaster* is more restricted to the eastern area than is the high oceanic *H. macrochir*. Furthermore, *H. macrochir* larvae occur with a much higher frequency and much broader distribution in the North Equatorial Current; they even occur in low frequency in the Canary Current and the Central North Atlantic Gyre. This latter larval range is distinctly beyond the regular distribution of adults.

Larvae of both species were frequent, even abundant, in the slope undercurrent off Mauritania, discernible from its surroundings by salinity and oxygen characteristics (John and Zelck 1997). *B. argyrogaster* reached 22°30' N during autumn (Bendixen data), but rarely 20.5° N during surveys under cooler conditions (John and Zelck 1997). The species was not caught at 21°30' N under upwelling conditions (John 1985, but from a sampling range of only 0 to 150 m). *Hygophum macrochir* always became rare at 19° N. These positions conform with the seasonal location of the CVFZ near the continental slope.

The extreme occurrences of larval *B. argyrogaster*, beyond the established boundaries of adults at 14°30' N, were 770 km along the North-East Atlantic slope. Larval *Hygophum macrochir* exceeded the range of adults by 440 km. The value for *B. argyrogaster* may be an underestimate because the area off Sahara has been surveyed only in spring.

In the centre of the Mauritanian Bight both species were rare. The few occurrences correspond with the recirculation around the Central Mauritanian Gyre. Both species became frequent and abundant again farther offshore. There, a coherent pattern of higher abundances spread northwestwards from the passage between Cape Verde and the Cape Verde Archipelago. *Bathylagus argyrogaster* could be traced up to 20° N and 25° W. *Hygophum macrochir* extended beyond the station grid of higher resolution (terminating at 23° N, 27° W). Perhaps *B. argyrogaster* could not be caught beyond the above given position. It is likely that transforming larvae and juveniles live deeper than 200 m and become too rare and too motile to be caught by plankton nets. Both coherent patterns correspond with the subsurface northwestward currents depicted in Figure 1. John and Zelck (1997) showed that this pattern coincided with water-masses showing tropical sea surface temperatures, carrying South Atlantic Central Water ("SACW") and tropical, neritic, as well as oceanic, fish larvae originating from south of Cape Verde.

Larval *H. macrochir* penetrates the CVFZ northwestwards into the regime of supposedly pure North Atlantic Central Water. During summer, larvae occurred up to 1000 km beyond the front. Hagen and Schemainda (1987, non-synoptic data) described geostrophic meridional flow with admixtures of SACW, coinciding broadly with the areas of catches of larval *H. macrochir*.

The Atlex 89 data from non-closing nets do not provide any information on the vertical distribution, additional to the data presented by John and Zelck. These authors mentioned a deeper vertical distribution immediately polewards of the CVFZ. We want to specify this as a mean-weighted depth of MWD = 92.8 ± 21.5 m (34 specimens, 7 stations) for *B. argyrogaster* and MWD = 56.1 ± 23.1 m (124 specimens, 23 stations) for *H. macrochir.*

Larval distributions in the Gulf of Guinea

In the Gulf of Guinea (Figure 8), only four positive stations yielded 35 larval *B. argyrogaster*. Three of these stations were continental slope stations at the locations of the Guinea Undercurrent and Angola Current. More than 119 *H. macrochir* were found, and those mainly in oceanic, western waters. Both values are probably underestimates in frequency and abundance, due to the shallow sampling range (particularly for *B. argyrogaster*, for which, however, an adult distribution in the innermost Gulf of Guinea remains uncertain). Figure 8 includes four additional positions to where *H. macrochir* was found in Zhudova's station grid, during the subsequent study by Shiganova. No catch values are available for these 4 eastern stations. Shiganova's map suggests an actually much higher frequency of *H. macrochir* than was visible in Zhudova's data, but corroborates a higher frequency in the western Gulf of Guinea than in the east. Shiganova's map includes also occurrences at the continental slope near Freetown, where the Guinea Undercurrent veers polewards. However, the scant and unquantified data do not reveal distribution patterns attributable to dispersal by individual components of the current system.
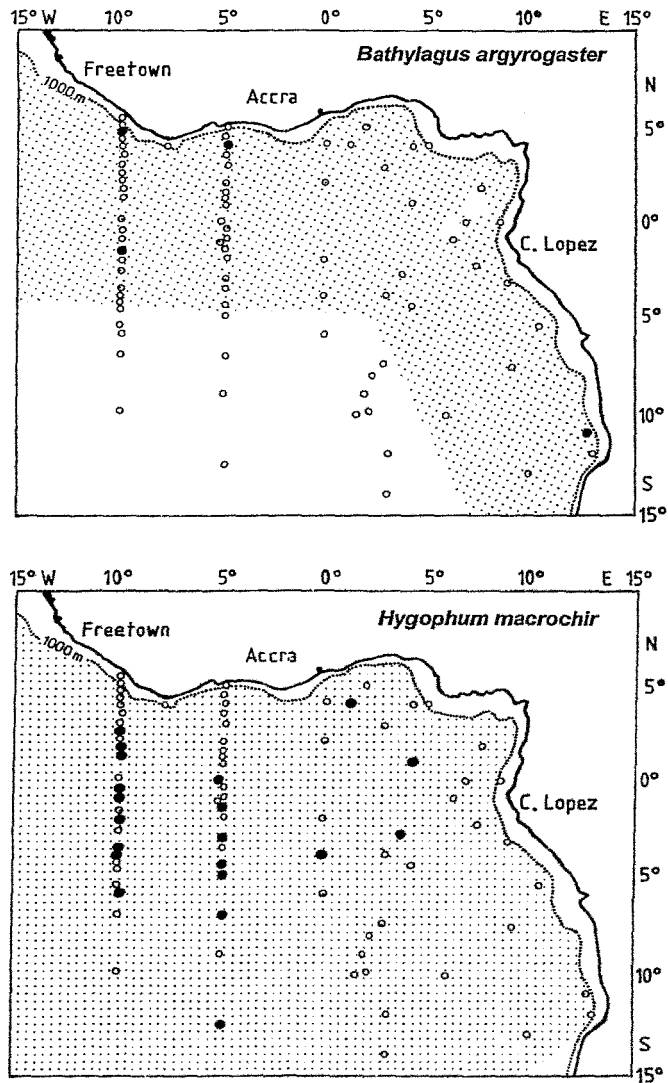

Figure 8: The frequency of larval *Bathylagus argyrogaster* and *Hygophum macrochir* in the surface waters of the Gulf of Guinea, as based on data by Zhudova (1969). Circles denote negative stations, dots, occurrences (including subsequent identifications of *H. macrochir* by Shiganova 1975). The adult distributions are stippled.
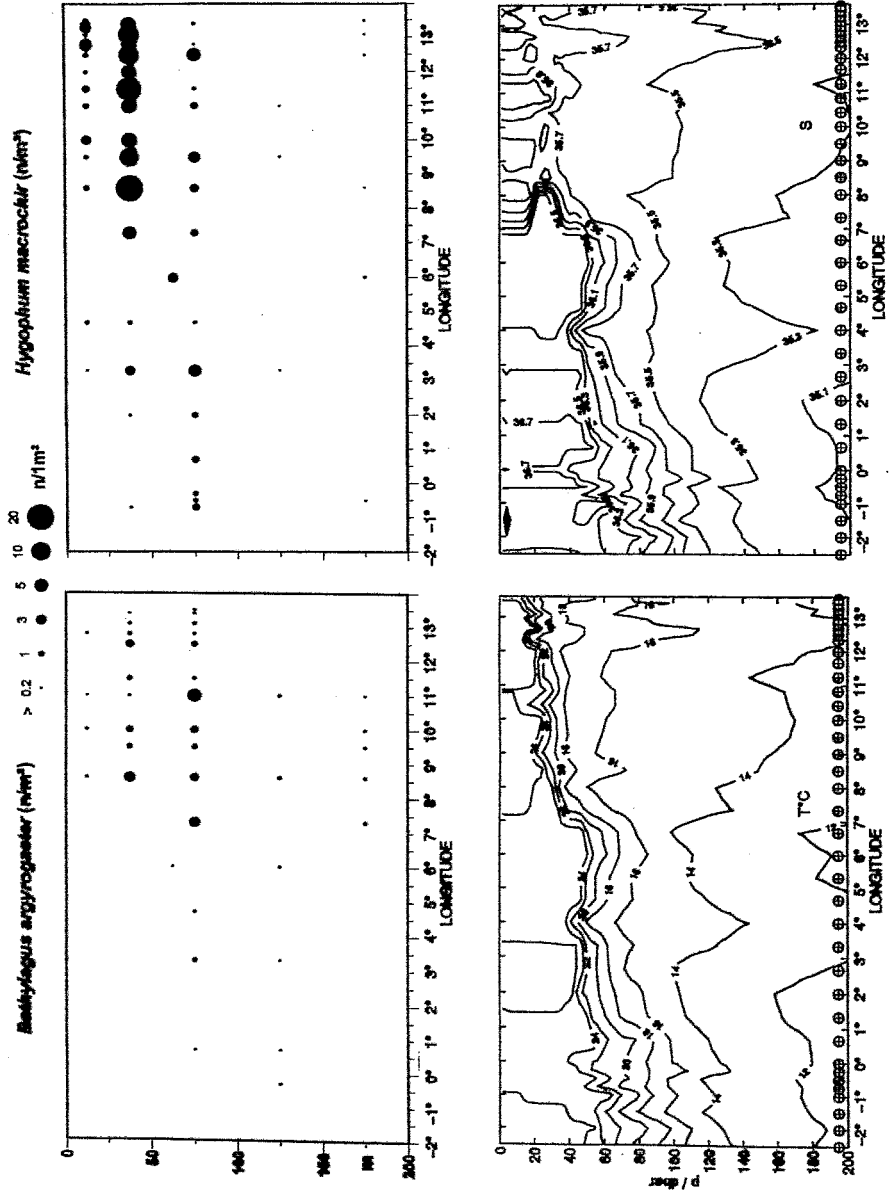
Figure 9: The cross-slope abundance and vertical distribution of larval *Bathylagus argyrogaster* (top, left), *Hygophum macrochir* (top, right), and the related temperature and salinity structure (lower panels) off Angola in May 1994. The adult distributions along this transect are believed to be confined to east of 12° E (compare oxygen undersaturations in Figure 11).

Larval distributions and hydrography off Angola (new data)

The station distribution for the survey off Angola was shown in Figure 2. Along this transect, both species revealed comparatively high frequencies and abundances at the eastern, more coastal, stations (Figure 9). However, embedded into this maximum was a narrow belt of stations with somewhat lower abundances at about 11 to 12° E. Irrespective of the high-oceanic or slope origin of both species considered, the abundances of both decreased west of 7° E. *Bathylagus argyrogaster* became rare beyond 3° E. It is worth noting that the abundance gradients of both species coincided with the decreasing percentage of neritic fishes among the total catch, but independently from the tendency in total catch, or species richness per station (Figure 10). Neritic fishes could be traced regularly up to 1400 km offshore of the Angolan continental slope. Furthermore, beyond 7° E, larvae of both species became rare in or disappeared from (*B. argyrogaster*) the upper two strata, but not so at a depth of 50 to 100 m (Figure 11).

Figure 10: The number of fish larvae per station (upper panel, unquantified), and the number of fish taxa and the percentage of neritic fish larvae among the total of each station (below) along the transect off Angola in May 1994.
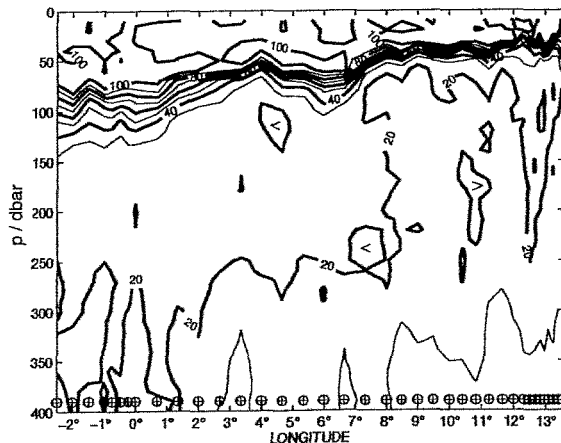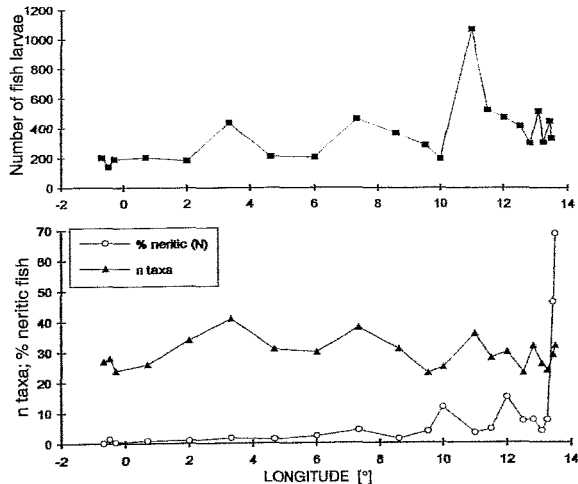

Figure 11: The cross-slope vertical structure of oxygen off Angola (in saturation percentage, otherwise as for Figure 9).

These tendencies concur well with the hydrographic stratification shown in Figure 9. This figure indicates a slight doming of the lower thermocline (*e.g.* 16 °C) between 7° E and 12° E, and, more pronounced, in the isohaline 35.7 PSU. Particularly strong is the doming of oxygen deficient water, rising from the mesopelagic realm to 60 m depth (Figure 11). The thermocline descended gradually from the coast westwards, but additionally both the thermo- and halocline revealed a pronounced ABFZ at about 7° to 8° E. The salinity front extended through the upper 50 m. The temperature front seemed to be restricted to the thermocline, but at the same position surface temperatures showed a relative minimum (John and Zelck 1998: Figure 5). Offshore of the front, the halocline followed the descent of the thermocline. Inshore of the front, temperature and salinity were only correlated at subthermocline depths.

Along this transect, the vertical distributions of both species showed significant positive correlations with the depth of the thermocline. For *H. macrochir*, MWD correlated well with the 24 °C isotherm (R = 0.8139, N = 21; the 5 deepest, low abundance datapoints representing 3 to 9 specimens each). As found off Mauritania, *B. argyrogaster* larvae lived at a greater depth than *H. macrochir*. In spite of scant data offshore, *B. argyrogaster* was also positively correlated with the depth of the 20 °C isotherm (R = 0.6441, N = 16; the 5 offshore datapoints representing 1 to 4 specimens each).

The oxycline generally coincided with the lower thermocline (Figure 11). The doming structure found in temperature and salinity was more pronounced in oxygen saturation. Oxygen-deficient waters of ≤ 20 % ascended to about 60 m depth between the front and 12° E. We interpret this doming structure as the southern periphery of the subthermoclinal Angola Dome (compare with Figure 1). Farther offshore of the front, the upper mesopelagic layer showed oxygen saturations of 40 to 60 %.

The low oxygen saturation rules out that the larvae hatched within the doming structure itself. The decline in abundance with the distance offshore of *B. argyrogaster*, *H. macrochir* and neritic fishes indicates offshore flow along the southern periphery of the Angola Dome, as suggested by Voituriez and Herbland (1982). A calculation of zonal geostrophic transport is not reasonable from our data.

Geostrophic calculations of meridional velocities (Figure 12) revealed an equatorward flow close to the coast within the Angolan Bight. This flow was characterised by having only few larvae of *B. argyrogaster* and *H. macrochir*, but abundant larvae of species
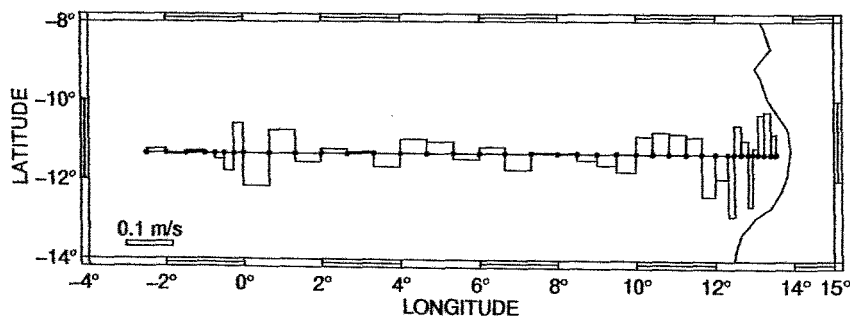

Figure 12: Mean geostrophic velocities (unsmoothed) between the thermocline (24 °C) and 200 m along the central line off Angola in May 1994 (reference level 1000 m).

having coastal origins (Figure 10). This flow might be a coastal countercurrent generated by the coastline topography farther northwards, projecting into the Angola Current. The poleward-flowing Angola Current was found between 11°45' E and 13° E (with a narrow equatorward flow in between) and had velocities of 6 to 13 cm·s⁻¹ (for the integrated depth range, core velocities may be higher). It showed slightly elevated salinities $S \geq 36.0$ near the surface. Such values are considered to be indicative for the Equatorial Undercurrent after its retroflection southwards and dilution by Congo Water (Wacongne and Piton 1992).

Only one out of three hydrographic transects covered the inshore zone (Figure 2), but otherwise the monitored features were fairly consistent among transects, irrespective of whether a smoothed or unsmoothed geostrophy was calculated. A smoothed calculation revealed weak poleward flow for the area 7° E to 12° E. An assumed equatorward transport at the western flank of the doming structure was not apparent in our data. Higher salinity values west of the Angola Dome remain ambiguous (Wacongne and Piton 1992).

Larval distributions in the South-East Atlantic

In the South-East Atlantic, larvae of both species were rare and generally restricted to a few stations off northern Namibia between the Cunene River and Walvis Bay (Figure 13). They were caught exclusively above the continental slope and the adjacent waters, but the coverage farther offshore is poor. *H. macrochir* occurred slightly more seawards than did *B. argyrogaster* (for the cross-coast zonation see Olivar and Fortuño 1991: Table 4).

Olivar (1985) summarized, from all cruises, a total catch of approximately 100 *H. macrochir* on the basis of standard catches of 10 m², which suggests that only single larvae were actually found. These larvae occurred mainly at, or above, the thermocline and did not occur south of Walvis Bay. *B. argyrogaster* reached farther southwards by about one degree of latitude, but was even more rare with a total catch of 8 larvae. The extreme occurrences of larval *B. argyrogaster* were 920 km beyond the established boundaries of adults at 15°30' S. Larval *H. macrochir* exceeded the range of adults polewards by 850 km. Describing the original data, Olivar and Fortuño (1991) emphasized that adult *H. macrochir* had never been reported so far south.

Six larval *B. argyrogaster* occurred in opening-closing nets, and exclusively in the deepest stratum sampled (100 to 200 m; Olivar, pers. communication). Both species were found during autumn and winter, under upwelling as well as non-upwelling conditions (Olivar and Fortuño 1991: Table 2). However, the individual catch localities in respect of seasons or the actual hydrographical structure are unknown. In comparison with the North-West African area, upwelling off northern Namibia is not exclusively dependent on the wind field (which does not show a strong seasonality there), but may be "primed" by coastal-trapped Kelvin waves (Shannon 1985).

Discussion

For equatorial species it is unusual that their distributions fan out at the East Atlantic margin, where the belt of tropical temperatures is narrow and commonly known currents flow towards the equator. It was shown above that such pattern applies to both the adults
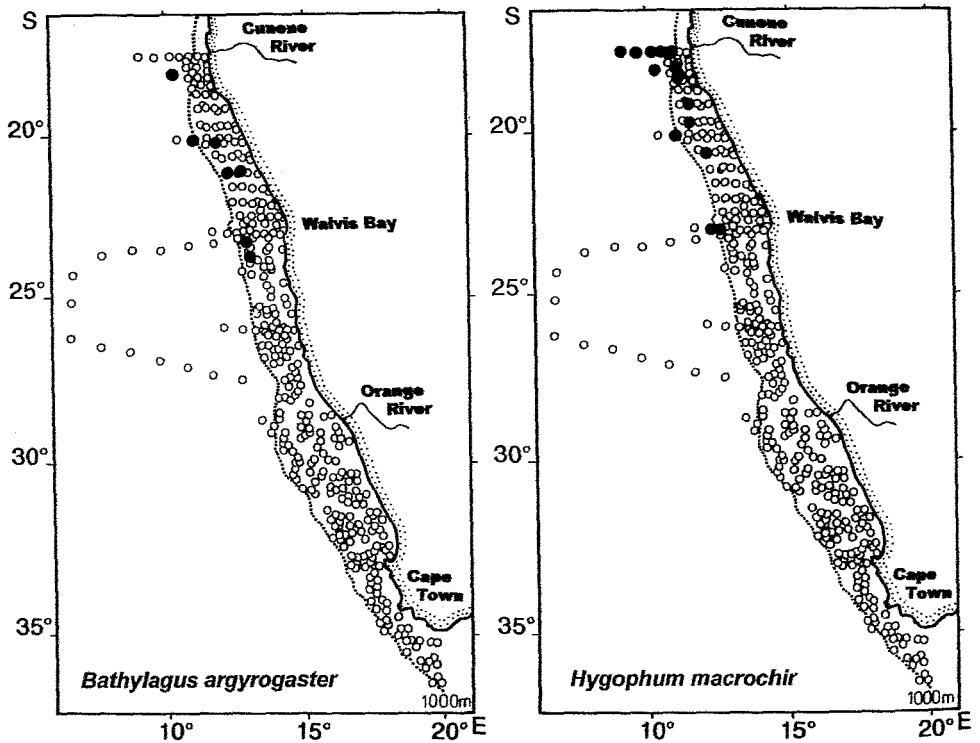
Figure 13: The frequency of larval *Bathylagus argyrogaster* and *Hygophum macrochir* in the upper 200 m of the Southeast Atlantic (after Olivar and Fortuño 1991). Circles denote negative stations, and dots, occurrences. The southernmost boundary of adults lies north of the map at 15.5° S.

and larvae of the two species investigated, and larvae spread farther polewards than adults. We postulate that such distributions are influenced by poleward flowing, mostly subsurface slope currents.

The overall wide reproductive range of *H. macrochir* includes the open ocean, whilst adult and larval *B. argyrogaster* occur closer to the coast. The more coastal occurrence of larval *B. argyrogaster* in pelagic waters, as well as the occurrence of adults in bottom trawls on the continental slope (Maurin *et al.* 1977; Parin *et al.* 1978) suggest that *B. argyrogaster* is a pseudoceanic species (Hulley 1981), reproducing mainly along the tropical West African continental slope.

Somewhat exceptional is the North Equatorial Current/Undercurrent system, where adult *B. argyrogaster* has its westernmost occurrences, and larvae occur up till at least 45° W. In contrast, adult as well as larval *B. argyrogaster* was absent (respectively scarce) in the eastward flowing North Equatorial Counter Current. Apparently the retroflections of undercurrents north of the Guinea Dome seed larvae of *B. argyrogaster* into the North Equatorial Current, which subsequently carries these larvae westwards. The retroflections and the Mauritanian Undercurrent beyond the passage between the Guinea Dome and

the continental slope are fed by the North Equatorial Undercurrent from the open ocean, and the Guinea Undercurrent from the east, advecting larval B. *argyrogaster* besides neritic fish larvae. A retroflection around the Angola Dome into the South Equatorial Current transports larvae across the ABFZ and attains similar geographical transport scales of approximately 1000 km, as in the retroflection of the NEUC. In the South-East Atlantic, the effect on the distribution of adult B. *argyrogaster* remains unknown.

The mechanisms of how larval *H. macrochir* penetrates the CVFZ northwestwards by up till 1000 km into the regime of supposedly pure North Atlantic Central Water are not yet understood. The assumption that the occurrences were linked with passive dispersal is corroborated by hydrographical data. Hagen and Schemainda (1987, non-synoptic data) described geostrophic meridional flow with admixtures of SACW, coinciding broadly with the areas of catches of larval *H. macrochir*.

Close to the reproductive ranges of adults, the larvae of *B. argyrogaster* and *H. macrochir* revealed similar distribution patterns. In station grids with high resolution, the larval distributions were clearly attributable to dispersal by subsurface currents in the larval depth range both in the North-East Atlantic and off Angola. At tropical latitudes, these subsurface currents are fed by the equatorial undercurrents which are symmetrical to the equator (whilst the symmetry-axis of the winddriven equatorial surface currents lies farther northwards). Except for the northern Gulf of Guinea, the topography of the continental slopes off North-West and South-West Africa is also somewhat symmetrical to the equator. Further symmetrical features are the hydrographical domes Guinea Dome and Angola Dome, although the Guinea Dome is permanent, with the Angola Dome being perhaps a summer feature (Siedler *et al.* 1992; Mazeika 1967; in contrast with Voituriez 1981). However, the Central Mauritanian Gyre may be a feature unique to the North-East Atlantic. It had been suggested by Hagen and Schemainda (1984, originally for the Guinea Dome) that such gyres are generated by the effect of the slope-topography on the undercurrents. Off Mauritania, the indented slope deflects a branch of the poleward undercurrent westwards at about Cape Timiris (shown in Figures 6 and 7), whilst off southern Angola the slope runs straight.

On the basis of symmetry we therefore postulate that larval transport systems corroborated for one hemisphere can also generally be transposed to those hydrographically corresponding subregions in the other hemisphere, where the insufficient larval data presently available allow one only to postulate whether they might fit with or contradict our current model. Such subregions of lacking, scant or two-dimensional data are 5° S to 10° S and 13° S to 18° S, the open South-East Atlantic and off the Sahara.

At greater distances from the reproductive ranges the distribution patterns of both species became different, and non-uniform with respect to extreme occurrences of either of the two species. Along the continental slope, larval *H. macrochir* had a narrower distribution than *B. argyrogaster*, and it is possible that the above shown poleward boundaries of larval *B. argyrogaster* are underestimates, as sampling was too shallow to catch larger larvae. In contrast with slope waters, *H. macrochir* larvae exceeded the range of *B. argyrogaster* by 6° of latitude in the Canary Current and, occasionally, 12° of latitude in the Central North Atlantic Gyre. The respective conditions in the open South-East Atlantic remain unknown.

John and Zelck (1997) underestimated the transport scale of *B. argyrogaster* as being some 630 km and 29 days. For the distances stated above, the recalculated transport

durations are 36 days for *B. argyrogaster* and 21 days for *H. macrochir* in the Mauritanian slope undercurrent (25 cm·s⁻¹). Actual data on the duration of the planktonic phase of both species are lacking. On the basis of synoptic data on the persistence and spreading of a tropical water-mass entraining both indicator species, John and Zelck suggested that the minimum time scale for the planktonic phase of *B. argyrogaster* and *H. macrochir* exceeds one month.

We have only limited knowledge concerning transport velocities along the slope of the South-East Atlantic. In the "Meteor" 28 data, integrated poleward current velocities off Angola were up to 13 cm·s⁻¹. Speer *et al.* (1996) reviewed that the Congo Undercurrent at 6° S should have a mean southward speed of 8 cm·s⁻¹ during winter, velocities at 16° S could exceed 50 cm·s⁻¹, and assumed 8 cm·s⁻¹ for 11° S. Off the Orange River (for its location, see Figure 13), at depths approximately 150 to 300 m, "typical current speeds" 6 to 12 cm·s⁻¹ polewards were found (Nelson 1989: Figure 2). The poleward undercurrent may reach Cape Town with core velocities of 15 cm·s⁻¹ (Shannon and Nelson 1996: Figure 20). Assuming a minimum core velocity of only 13 cm·s⁻¹, the time scales for the transport of *B. argyrogaster* towards their extreme latitudes would be 82 days, and 76 days for *H. macrochir*, which might be on the high side.

In tropical waters larval *H. macrochir* have a shallower vertical distribution and higher temperature preferences than *B. argyrogaster*. Immediately beyond the front the larvae live at a greater depth. With transformation, both species become mesopelagic (Nafpaktitis *et al.* 1977 for H. macrochir; Blache 1964 for *B. argyrogaster*), which limits our ability to catch them, by our methods.

At the fronts, the slope undercurrents apparently submerge below the equatorward flow of the Canary Current and Benguela Current, respectively. Deep-living larval *B. argyrogaster* cross both the ABFZ and CVFZ, remaining in the poleward undercurrent and not changing their physical environment noticeably. Juveniles probably survive in the poleward undercurrent along Sahara and Morocco, which reaches mesopelagic depths off Morocco (Barton 1989) and transports, among others, the mesopelagic diapausing stage of *Calanoides carinatus* along the Moroccan and Iberian continental slopes northwards at a mean speed of 10 cm·s⁻¹ (Stöhr *et al.* 1997, and literature therein). This may explain the findings of expatriate *B. argyrogaster* there (Figure 3).

Along-slope dispersal of the shallow living equatorial larvae like *H. macrochir* stops immediately at the CVFZ, which reaches down to 150 or 200 m in depth (Klein 1992). Such larvae will probably not survive in the cool waters north of the CVFZ either. Few larval *H. macrochir* penetrate the ABFZ, which extends only to some 50 m in depth. Larval *H. macrochir* was shown to cross both the CVFZ and ABFZ in the open ocean under summer and autumn conditions. During summer, the force from eastward flow in the equatorial current system is strongest, and surface waters of the Central North Atlantic Gyre warmer than 23 °C facilitate survival.

Besides the two species dealt with above, Zelck and John (1997) found the larval distributions of *Vinciguerria nimbaria* and *Symbolophorus kreffti* to be indicative of poleward transport. Comparative data are restricted to the South-East Atlantic. Olivar and Shelton (1993) discussed a northern larval fish complex for Namibia including (besides *B. argyrogaster* and *H. macrochir*) also the photichthyid fish *Vinciguerria nimbaria*. The latter was encountered only north of 20° S and only during autumn, when intrusions of "Angolan

waters" were said to be "intense" (Olivar and Fortuño 1991: 96). As mentioned, during summer and autumn the ABFZ is in its southernmost position (Meeuwis and Lutjeharms 1990) or may break down, leading to a penetration of Angolan waters as far south as 22° S (Shannon *et al.* 1987). Lanternfish larvae of the tropical slope species *Symbolophorus kreffii*, not yet identifiable at the time of Olivar's studies but actually found off northern Namibia (Olivar, pers. comm.), also fit into such a dispersal pattern. Future investigations might furthermore show that leptocephali of the tropical elopoid fish *Pterothrissus belloci* were indeed advected to, instead of spawned off Namibia, as previously concluded by Smith (1966).

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