

Life history and morphology of Eel Larvae in the Gulf of Guinea of western Africa: revisiting Jacques Blache's research (1960–1977) 40 years later

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Abstract Eel larvae (leptocephali) are rarely studied extensively both spatially and temporally, and detailed illustrations of most species are limited. This study uses the unique research reported in the monograph of Blache (*Leptocéphales des poissons anguilliformes dans la zone sud du golfe de Guinée*. ORSTOM Faune Tropicale 10:1–381, 1977, in French) to describe and evaluate the species composition, abundance, life history characteristics and morphology of 10,284 anguilliform leptocephali collected throughout the year during 15 ichthyoplankton surveys (1960–1971) in relation to regional oceanography. Leptocephali of 70 species of 7 families were described, with Ophichthidae (26 species), Muraenidae (13), and Congridae (13) being the most diverse, and local spawning indicated by ≥ 34 species. Larvae of

biogeographically restricted Heterencheylidae eels (mud eels) were abundant along the continental shelf and 5 species comprised 35% of total catches. Their larval distributions may reflect adult depth-segregation from nearshore/estuaries to the outer shelf and slope and larval retention. Nettastomatid leptocephali of *Hoplunnis punctata* were the most abundant species, and *Rhynchoconger* sp., *Uroconger syringinus*, *Chlopsis olokun*, and *Dalophis boulengeri* were also abundant. Small leptocephali distributions indicated spawning occurred over or near the continental shelf, and length-frequency data indicated most spawning was during the November–May warm-water season. Detailed morphology illustrations showed the characteristics of all stages of larvae. The Gulf of Guinea eel fauna is not diverse compared to the Indo-Pacific possibly due to phylogeography and a lack of coral reef habitats and the unusual low-latitude seasonal influx of cold surface waters, but is unique in being the worldwide center of distribution of the burrowing eels of the Heterencheylidae.

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Introduction

The eels of the Anguilliformes are a diverse group of fishes comprising about 900 species worldwide (Eschmeyer and Fong 2017) that includes some fisheries species, but the faunas of eels in many parts of the world have not been carefully studied. Catadromous eels of the family Anguillidae are commercially harvested in some regions where they live in freshwater and estuarine habitats (Jacoby et al. 2015), and several marine eel species are also harvested, such as eels of the genus *Conger* (Congridae) and the Muraesocidae. In contrast, most marine eels living in a wide range of habitats from shallow water to the mesopelagic zone are not fisheries species and their adults and larvae have not been extensively studied.

One unique aspect of both freshwater and marine eels is that they have a type of larvae called leptocephali. These unusual larvae are only found in eels and their close relatives (Albuliformes and Elopiformes), and they differ from other fish larvae in having extreme transparency, large maximum sizes before metamorphosis, interesting morphological and behavioral features (Castle 1984; Smith 1989a; Miller 2009; Miller et al. 2013a), unique physiology and growth strategy (Bishop et al. 2000), and a feeding ecology based on consuming marine snow (see Liénart et al. 2016).

Leptocephali have only been intensively studied in a few regions of the world, partly due to the difficulty in collecting them in small plankton nets typically used in ichthyoplankton and oceanography research, and also because they are difficult to identify and match with adult species (Smith 1989a; Miller and Tsukamoto 2006; Miller et al. 2013b). One of the first regions where major progress was made in understanding the morphology and species identifications of leptocephali and their seasonal occurrence was in the Gulf of Guinea of the eastern equatorial Atlantic along western Africa during the study by Blache (1977). That unique study resulted from 10 years of ichthyoplankton sampling that was designed to study the population dynamics of fisheries species, which also collected about 10,000 leptocephali from 1960–1971 in surveys spread out over most months of the year. The 381-page Blache (1977) monograph entitled “Leptocéphales des poissons Anguilliformes dans la zone sud du golfe de Guinée”, which translates to “Leptocephali of Anguilliformes fishes in the southern

zone of the Gulf of Guinea”, presented detailed identification information, morphological/meristic data, monthly size data, and illustrations of the leptocephali at various sizes. It also presented maps of catch locations of different size ranges and abundance information of some species of leptocephali. The present study overviews and analyzes the unique and valuable information in this monograph, in relation to what is presently known about Gulf of Guinea oceanography and the ecology and life history of leptocephali and marine eels in other parts of the world.

The other region of the world where intensive efforts were made to study leptocephali and marine eels is the western North Atlantic (WNA). Decades of research on eels and leptocephali was assembled into separate volumes about all the families of adult species (Böhlke 1989a) and their larvae (Böhlke 1989b). Earlier (Smith 1979) and later (Fahay 2007) identification guides for leptocephali were also published. The research on the species identifications of leptocephali in the WNA then facilitated studies on the species compositions (Richardson and Cowen 2004; Ross et al. 2007), depth distributions (Castonguay and McCleave 1987; Miller 2015) and assemblage structures of leptocephali (Miller and McCleave 1994, 2007; Miller 1995).

A different situation exists in the Indo-Pacific because most leptocephalus larvae have not been matched with their adult species, in part because of the greater number of eel species there compared to in the Atlantic Ocean (Miller and Tsukamoto 2004, 2006). Various early efforts were made to evaluate the species compositions in some regions of the Indo-Pacific (e.g., Castle 1964, 1965a, b). Species-types have been distinguished without knowing what adult species they correspond to (Mochioka and Tabeta 2014; Miller et al. 2013c), but most species of leptocephali can still only be distinguished at family or genus levels. A main cause of this limited progress is that pre-metamorphosing leptocephali do not resemble the juvenile and adult eels, so morphological and meristic information and transitional larvae are required to match the larval and adult forms (Smith 1989a; Miller and Tsukamoto 2006). Genetic sequence-matching for identification has been useful in cases where both larval and adult sequences can be obtained (Ma et al. 2007, 2008; Tawa et al.

2013, 2014; Anibaldi et al. 2016; Kurogi et al. 2016) and this likely will be used more in the future.

Despite these limitations various studies in the Indo-Pacific have progressed the understanding of biodiversity of eels and species assemblages of leptocephali through collections of their larvae during surveys usually designed to study the spawning areas of anguillid eels. Most leptocephali in those studies could be separated into species-types within each family or genus, which provided approximate species richness and some basic life history information (Miller et al. 2006, 2015, 2016; Minagawa et al. 2004; Wouthuyzen et al. 2005). In general, those studies had limited ability to link adult species that are present in each area with the larval types found in the same areas, and the data from one or a few sampling surveys could only provide limited life history information.

This makes the wide range of information in the Blache (1977) monograph unique in its details and ecological implications. It was preceded by at least 17 papers that Blache wrote or coauthored on adult eels or leptocephali of the Muraenidae and Ophichthidae and various other anguilliform families in the Gulf of Guinea and West Africa (e.g., Blache 1968, 1971, 1972; see Online Resource 1). It was difficult to identify eels to the species level in the region before his work, so they were studied systematically by recording the total number of vertebrae (TV) and abdominal vertebrae of adults to compare to the total number of myomeres (TM) and the number of myomeres of the last vertical blood vessel (behind kidney) of leptocephali. Blache (1977) described that there were 95 types of identified leptocephali and 41 unidentified types in the Atlantic Ocean and Mediterranean Sea at that time, with 22 of the identified types being reported before 1950 and 73 after 1950. Using existing information and new data gathered from both the adults and leptocephali in the region, the monograph describes how to identify each family of larvae and the various genera within families and describes the variations of catches of the leptocephali in the sampling surveys.

40 years after this monograph, our objective was to evaluate eel biodiversity and life histories in the Gulf of Guinea by analyzing the species composition, distributions, size, and morphology of the leptocephali reported on in the Blache (1977) monograph in relation to the oceanographic conditions of the region and knowledge about leptocephali and eels in other

parts of the world. We reproduce some of the data contained in catch and meristic tables in the monograph, plot examples of catch maps, present graphs of monthly length-frequency data, and show some of the monograph's remarkable illustrations of leptocephali. The Gulf of Guinea has a unique combination of geographic and oceanographic features that may provide clues about factors affecting eel life histories. Therefore, this paper provides a new view of the implications of the unique dataset in the monograph in relation to the present state of understanding about eel life history and leptocephali worldwide and how these species may interact with oceanographic conditions.

Characteristics of the Gulf of Guinea

The Gulf of Guinea is an interesting region of the world's oceans due to a combination of several geographic and oceanographic features. The only offshore Islands are the larger Bioko Island closer to the coast, São Tomé and Príncipe Island and the smaller Annobón Island farthest offshore, that extend out from the northeastern corner of the Gulf of Guinea. The near-surface currents of the Equatorial Atlantic region include 4 branches of the westward flowing South Equatorial Current (northern, 1–3°N, equatorial, 3–5°S, central, 7°S, and southern, > 15°S), and the eastward flows of the South Equatorial Counter-current, Equatorial Undercurrent, and South Equatorial Undercurrent (Fig. 1; Stramma and England 1999). The nearshore Guinea Current flows eastward along the southern shore of West Africa. There also is an eastward flowing undercurrent located below the Guinea Current (Guinea UnderCurrent) that is stronger in spring, which reverses to be westward in August–September (Herbert et al. 2016).

The Equatorial Undercurrent transports water from the western Equatorial Atlantic into the Gulf of Guinea at depths of about 25–150 m and has maximum flows in January and from June to September (Bourlès et al. 2002; Kolodziejczyk et al. 2009). It originates from recirculation of the North Brazil Current, the North Brazil Undercurrent and the South Equatorial Current on the western side of the basin (Schott et al. 1998; Bourlès et al. 1999). The nearshore eastward Guinea Current flowing along the southern coast of West Africa to the north is an important fisheries area and is considered as being part of one of the world's five most productive “large marine ecosystems” (Ukwe

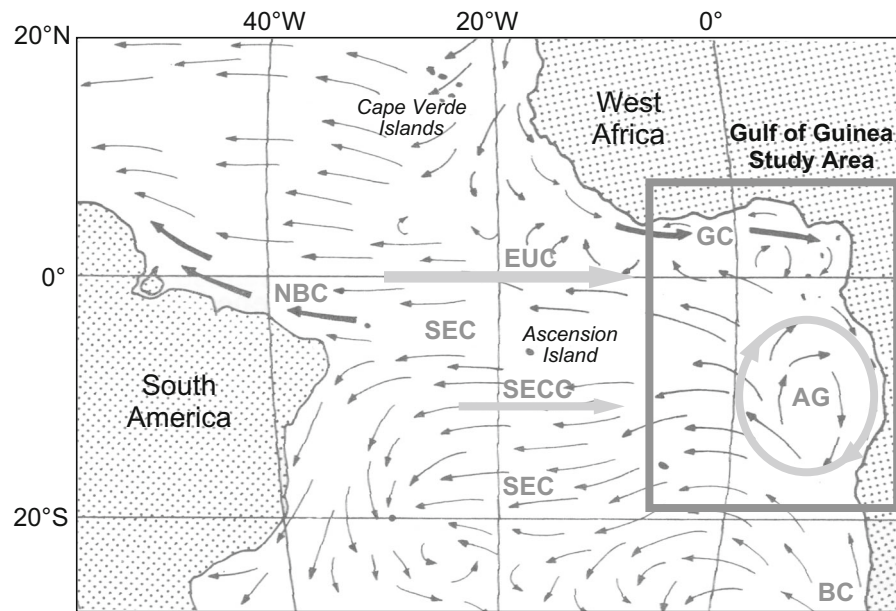


Fig. 1 Map of the equatorial Atlantic modified from Blache (1977) showing ocean currents and the study area (rectangle). The black arrows from the original map show the Guinea Current (GC) in the northern Gulf of Guinea (right side) and the North Brazil Current (NBC) along northeastern South America

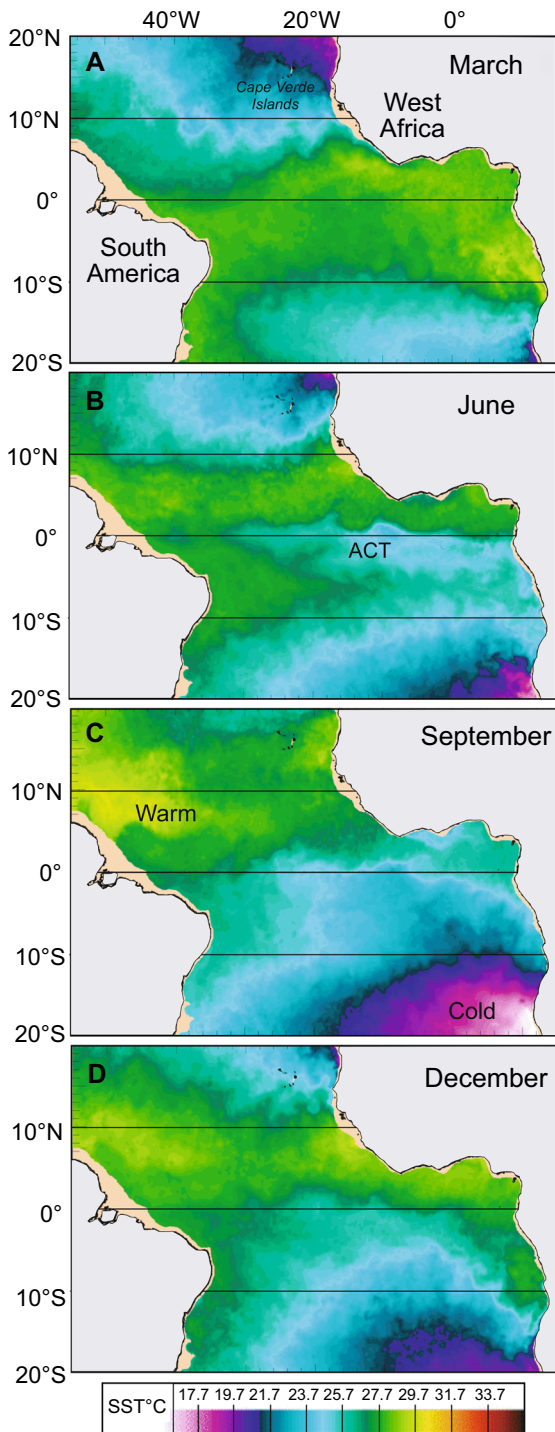
et al. 2006; Chukwuone et al. 2009; Ukwe and Ibe 2010). The Angola Current flows southward along the coast, and the more-nearshore Benguela Coastal Current flows to the north (Hopkins et al. 2013) (Fig. 1). A front forms at 15°S, which is a hydrographic boundary between warmer northern and colder southern (Benguela Current) water masses (Hopkins et al. 2013). Offshore to the north, currents form the cyclonic Angola Gyre (Stramma and England 1999).

The Gulf of Guinea region has a strong seasonal cycle that includes cold water moving northeast from the southwestern African coast (Fig. 2; Online Resource 2). Cold water of the Atlantic cold tongue extends northwestward to the Equator in the upper 50 m during May–September and that changes surface temperatures by about 5–7 °C (Caniaux et al. 2011; Da-Allada et al. 2017). The eastward movement of surface water in the cold tongue was seen clearly in 2012 (Fig. 2B; Online Resource 2). Upwelling occurs in several other Gulf of Guinea coastline areas (Lutjeharms and Meeuwis 1987). Eddies can form inshore of the Guinea Current and may contribute to upwelling (Bakun 1978; Djakourè et al. 2014). The

(left side), and grey arrows and labels show general latitudes of the westward flowing South Equatorial Current (SEC), and the eastward flows of the offshore South Equatorial Countercurrent (SECC), Equatorial Undercurrent (EUC), Benguela Current (BC), and the Angola Gyre (AG) (Stramma and England 1999)

changes in ocean surface temperatures resulting from upwelling and the Atlantic Cold Tongue also appear to influence climatic factors in the region such as the monsoon cycle (Ali et al. 2011; Caniaux et al. 2011; Okumura and Xie 2004).

Another unusual feature of the region is the large influx of freshwater from the Congo River at 6°S in the south and the Niger River in the northeastern corner of the Gulf of Guinea (Fig. 3B, Online Resource 3). The Congo River has the second highest river outflow in the world after the Amazon River (Dai and Trenberth 2002). The continental shelf throughout the Gulf of Guinea is narrow and drops off steeply to depths of 3000–4000 m, so the Congo River water reaches areas over deep water (Sibuet and Vangriesheim 2009; Denamiel et al. 2013). Its outflow can influence surface salinity and temperature, and high outflow causes a water-column barrier layer to form that reduces vertical mixing into the upper 15–20 m (Materia et al. 2012; Denamiel et al. 2013; Hopkins et al. 2013; White and Toumi 2014; Vic et al. 2014). Phytoplankton productivity can increase in the river plume areas (Signorini et al. 1999) as a result of organic matter inputs, with river discharge being



◀ **Fig. 2** Maps of sea surface temperature (SST) in the Equatorial Atlantic region on the 15th day of March, June, September, and December in 2012 that show the presence of warm water along the coastal areas of the sampling area from January to May and areas of upwelling of cold water south of 10°S from May to January in that year. The Atlantic cold tongue (ACT) extended up to the equator mostly during May–September 2012 (**B**). Maps were modified using imagery from the data assimilative 1/32° global ocean nowcast/forecast system of the US Naval Research Laboratory (see Shriver et al. 2007 and Online Resource 2)

world for amount of outflow (Dai and Trenberth 2002). The sediment and organic matter from these rivers and the seasonal influx of cold water may be why there are very few coral or seagrass habitats in the Gulf of Guinea (Laborel 1974; Spalding et al. 2001; Short et al. 2007). The possible areas of influence of the river outflows can be seen throughout much of the year in Online Resource 3.

Methods of sampling surveys and this paper

The leptocephali in Blache (1977) subsequently also referred to as the monograph were collected by 15 surveys made in 1960–1971 during at least a few days of every month of the year except October, which varied in their regional coverage within the Gulf of Guinea (Fig. 3). The surveys were conducted by the “Laboratory d’Océanographie biologique” at Pointe-Noire (from the former ORSTOM organization; now the IRD-Institute of Research for Development) adjacent to countries such as Gabon, Republic of Congo, and Angola. The primary net used was the 1-m Calcofi Net (see Wiebe and Benfield 2003) with 0.57 mm mesh, although other unspecified nets were apparently used. The Calcofi net was equipped with a flow meter and depth recorder and was towed obliquely from the surface to near the bottom in coastal waters and from the surface to 70 m at stations over deeper water (up to 1500 m depth). Horizontal towing steps were made during net deployments to result in each tow having 15 min durations, with a target of 1000–1500 cubic meters of water volume filtered. Larval yields were calculated per surface unit using the number of larvae/volume (Online Resource 1, Fig. S1).

highest from about October–February (Spencer et al. 2012). The Niger River is the third longest river in Africa after the Congo and Nile and is 27th in the

The exact station locations of each survey were not shown, but can be partly inferred from sampling region outlines (Fig. 3) and collection locations of

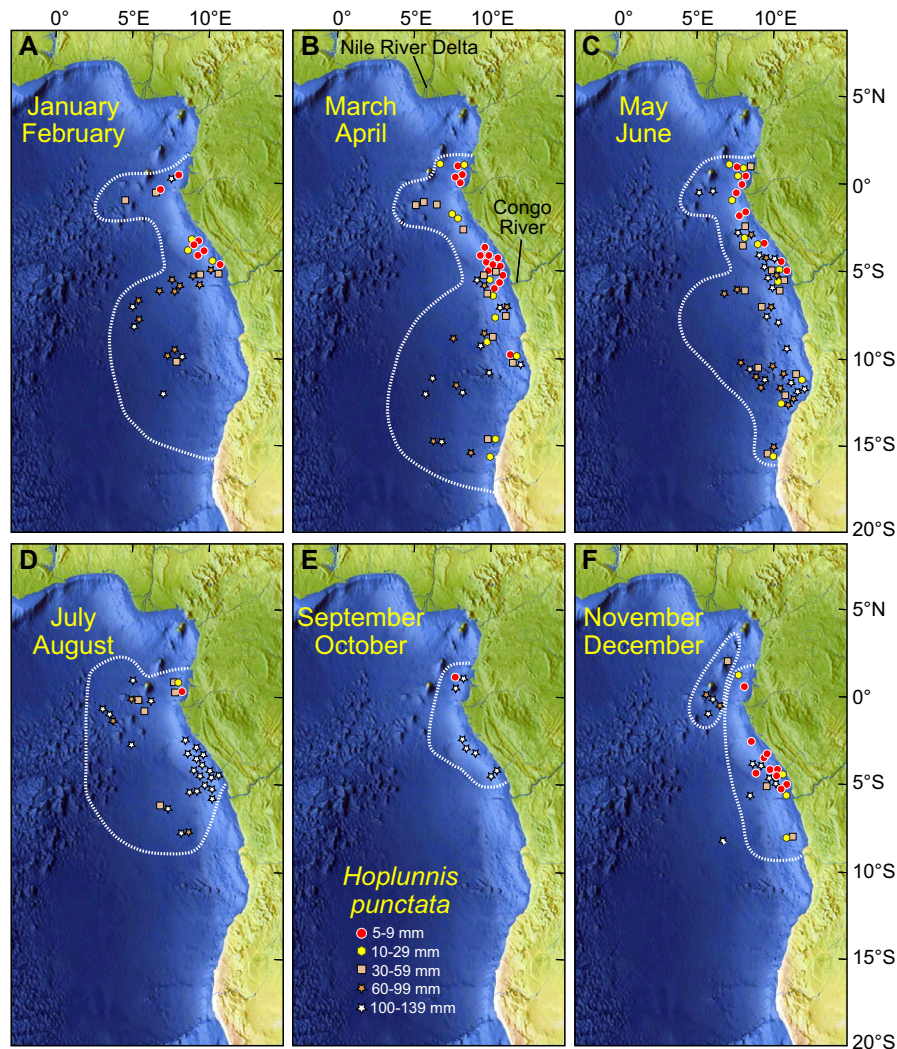


Fig. 3 Locations where different sizes of *Hoplunnis punctata* leptocephali (Nettastomatidae) were collected in 2-month periods (1960–1971) in the Gulf of Guinea from Blache

(1977) replotted over a bathymetric map (light blue: shallow; dark blue: deep). Regions where sampling occurred during each period of the year are shown by white lines

leptocephali (Figs. 3, 4; Blache 1977). The surveys were described as being in the 3 habitat areas of (1) shelf and slope, (2) offshore, and (3) the “archipelago” area in the north (near the islands of São Tomé and Príncipe). The 15 surveys listed by time of the year were: NIZ01-71: 19–20 January 1971 (around Annobón Island, southern archipelago); OM40: 25 January–9 February 1969; OM14: 24 February–12 April 1961 (including offshore); CAP01-71: 13 February–7 March 1971 (offshore); OM41: 20 March–2 April 1969; OM36: 6–21 May 1968; OM42: 16–31 May 1969 (Angola coast in south); NIZ01-70: 30 May–9

June 1970 (offshore Angola in south); OM43: 8–23 July 1969; OM37: 24 July–16 August 1968; NIZ02-70: 7–19 July 1970 (north of Congo River offshore up to Príncipe); OM38: 17–28 Sept 1968; OM44: 7–8 November 1969 (archipelago); OM39: 18 November–3 December 1968; NIZ15-71: 12–15 December 1971 (along archipelago) (also see literature in Online Resource 1).

All specimens were preserved in neutralized and glycerined 5% formalin-seawater and were deposited in the French National Museum of Natural History in Paris (MNHN). Illustrations of the leptocephali were

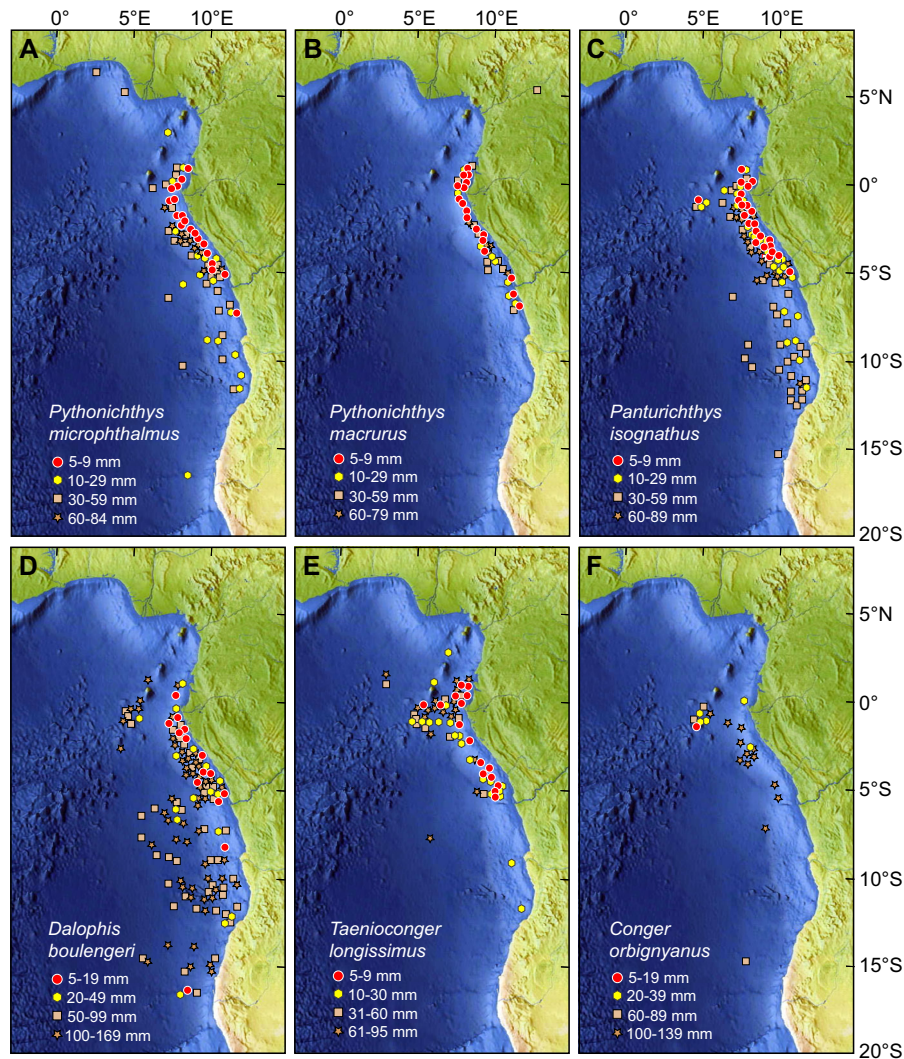


Fig. 4 Locations where different sizes of leptocephali were collected of *Pythonichthys microphthalmus* (A), *Pythonichthys macrurus* (B), *Panturichthys isognathus* (C) (Heterenchelyidae), *Dalophis boulengeri* (Ophichthidae) (D), *Heteroconger*

longissimus (E), and *Conger orbignyanus* (F) (Congridae) during net sampling from 1960 to 1971 in the Gulf of Guinea from Blache (1977) that are replotted over a bathymetric map (light blue: shallow; dark blue: deep)

made with a camera lucida. Leptocephali of mesopelagic eels of Serrivomeridae, Nemichthyidae, and Cyematidae were excluded from the study because they are not linked to the continental shelf ecosystem that was the focus of the sampling surveys. Adult eels of two species of Muraenidae (*Echidna peli* and *Channomuraena vittata*), one Congridae (*Japonoconger africanus*) and a Muraenesocidae (*Cynoponticus ferox*), and some species of the Synphobranchidae (Synphobranchinae), Simemchylidae, Myrocongridae, and Colocongridae were present in the Gulf of Guinea, but their larvae were not collected. The

families Anguillidae, Derichthyidae (*Derichthys* and *Nessorhamphus*), and Moringuidae were absent at all life history stages in the southeastern Atlantic (Blache 1977). The leptocephali of tarpon, ladyfish and bonefish are known from Angolan waters (Richards 1969), but were not mentioned in the monograph, either due to not being members of the Anguilliformes, or because they were not collected. The monograph provided dichotomous keys for identifying the species of the Muraenidae, Heterenchelyidae, Congridae, and Ophichthidae.

Common names have not been clearly established yet for most eel species or even some families, so we will not attempt to use either consistently, but will include a few common names. Some scientific names of the eel species have been changed since the monograph was published, so we will use the new names with the original names being shown in Table 1. Scientific name updates primarily follow Froese and Pauly (2017). This paper contains a mixture of information translated from the monograph, and our assessments of its data, which for convenience, are not always distinguished.

Taxonomic composition of leptocephali

A total of 10,284 leptocephali of 7 anguilliform families (Table 1) were collected during the 15 1960–1971 surveys reported on by Blache (1977). The collections included 26 species of Ophichthidae of 15 genera (at the time) (N = 1763 larvae), 13 species of Muraenidae of 6 genera (N = 270), 13 species of Congridae of 12 genera (N = 1908), 5 species of Heterenchelyidae of 2 genera (N = 3662), 2 species of Chlopsidae (*Chlopsis*) (N = 649), 5 species of Nettastomatidae of 4 genera (N = 2027), and 2 species of Synphobranchidae (Illyophinae, *Dysomma*) (N = 5). The 2 species of Muraenesocidae listed in the monograph, *Xenomystax congroides* (Congridae) and *Hoplunnis punctata* (Nettastomatidae) have been moved out of that family.

There were 7 species of abundant leptocephali with more than 500 individuals collected (Table 1). The nettastomatid *Hoplunnis punctata* (N = 1791) was the most abundant species. Two species of heterenchelyiids were the next most abundant (*Pythonichthys macrurus*, N = 1603; *Panturichthys isognathus*, N = 1239), followed by *Pythonichthys microphthalmus* (N = 771), the congrid *Rhynchoconger* sp. (N = 601) and *Uroconger syringinus* (N = 528), and the chlopsid, *Chlopsis olokun* (N = 634). The Heterenchelyidae was the most abundant family of leptocephali, which comprised 35.6% of the total leptocephali. The ophichthids *Echelus pachyrhynchus* (N = 343), *Dalophis boulengeri* (N = 474) and *Myrophis plumbeus* (N = 247) were also abundant, along with 3 congrids, 2 ophichthids, and 1 nettastomatid species that had more than 100 specimens collected (Table 1).

Distribution, abundance and size of leptocephali

General factors affecting larval distributions

Some species were clearly spawning in the sampling area because small leptocephali were collected that must have been spawned near where they were collected. Small larvae < 10 mm were collected for 35 species indicating they were spawning in the Gulf of Guinea (Table 1). However, Blache (1977) pointed out that leptocephali can grow to large sizes, so some larvae can be transported into the sampling area from other regions and that some of the species of leptocephali collected were not representative of the adult eel species known to be present in the Gulf of Guinea. Eight species of 3 families (Congridae, Muraenidae, Ophichthidae) were only collected at sizes of 48–206 mm, so they could have been spawned in other areas (Table 1).

Blache (1977) also discussed how the distributions and sizes of leptocephali were linked to the two different seasons and the transition periods that were distinguished by water temperatures as described in more detail later. In the north, the spawning period can be all year long in the warm water, but in the south the spawning peak is in March–April and then stops from June until September when cold water flows up. Where the different types of eels spawn in relation to water depth can also affect how their larvae are distributed due to their long larval durations and offshore transport by currents (Blache 1977). The larvae of adults spawning in deep habitats would be rapidly transported offshore after hatching. No evidence was found that particular types of larvae were linked to types of ocean conditions or water types nearshore or offshore. However, the timing and location of spawning and hatching and seasonal changes in ocean currents (see Online Resource 2) may influence larval distributions. Plots of the geographic distributions of the abundance of leptocephali in the monograph illustrated the seasonal patterns of spawning and offshore transport of larvae, with abundances being higher in the March–May period (Online Resource 1, Fig. S1, S2).

Heterenchelyidae eels and leptocephali

One of the most interesting aspects of the monograph was the detailed information it provided about the

Table 1 Species, size ranges (total length: TL range), and meristic information (total number of myomeres: TM; myomere number of last vertical blood vessel: LVBV) of the leptocephali collected in the Gulf of Guinea during the study by Blache (1977), showing the months of spawning (when < 10 mm larvae were collected; using numbers for months, or a “x” when the month is not known) and the size ranges of metamorphosing larvae (meta range)

Family/species	N	TL range	Meta range	TM	Mean TM	LVBV	Months of spawning
Heterenchelyidae (N = 3662)							
<i>Pythonichthys macrurus</i>	1603	4.5–79	50–69	124–136	130.2 ± 2.4	42–49	1,3,5,7,11
<i>Pythonichthys microphthalmus</i>	771	4.3–81		110–131	115.0 ± 2.1	47–55	1,2,3,4,5,9,10
<i>Pythonichthys</i> sp.	18	7.6–62		111–119	115.7 ± 2.0	39–44	12
<i>Panturichthys isognathus</i>	1239	4.6–84	70–84	149–167	157.7 ± 3.8	50–60	3,4,5,11
<i>Panturichthys longus</i>	31	7.5–88		205–230	214.6 ± 7.1	61–71	3
Congridae (N = 1908)							
<i>Ariosoma balearicum</i>	175	8.0–216	145–194	126–138	130.4 ± 2.2	63–71	1,5,11
<i>Ariosoma melissi</i>	40	5.4–275	225–269	141–151	145.8 ± 2.1	66–74	11
<i>Parabathymyrus</i> sp.	10	38.0–260	~ 177	146–154	150.0 ± 2.4	91–99	
<i>Paraconger notialis</i>	191	8.1–157	115–144	132–144	138.2 ± 2.7	51–66	2,3,7
<i>Conger orbignianus</i>	22	14.0–133	~ 117	160–170	164.7 ± 2.8	57–62	
<i>Uroconger syringinus</i>	528	8.0–140	115–139	212–229	218.9 ± 3.8	63–73	3,5
<i>Rhynchoconger</i> (<i>Hildebrandia</i> sp.)	601	5.5–104	80–99	161–172	165.7 ± 2.3	41–49	1,2,3,4,5,7,11
<i>Bathycongrus bertini</i> (<i>Rechias bertini</i>)	45	10.0–199		167–177	172.1 ± 2.1	49–56	
<i>Gnathophis</i> sp.	34	6.0–133		130–140	135.5 ± 3.1	42–47	1,2,3
<i>Bathyuroconger vicinus</i>	6	65.0–206		176–187	180.3 ± 3.9	59–64	
<i>Gorgasia inferomaculata</i> (<i>Leptocephalus inferomaculatus</i>)	12	15.0–75		166–171	168.9 ± 1.8	70–74	
<i>Heteroconger longissimus</i> (<i>Taenoconger longissimus</i>)	198	6.0–95		162–175	167.5 ± 2.8	61–69	1,2,3,5,11
<i>Heteroconger</i> sp. (<i>Taenoconger</i> sp.)	20	6.5–82		191–199	194.5 ± 3.1	72–78	x
<i>Xenomystax congroides</i> (<i>Paraxenomystax bidentatus</i>)	26	9.0–253	228,235	213–219	216.2 ± 1.8	63–67	11
Chlopsidae (N = 649)							
<i>Chlopsis olokun</i>	634	9.0–89	60–89	125–139	132.0 ± 2.6	43–53	2
<i>Chlopsis dentatus</i>	15	24.0–59	50–59	118–126	121.3 ± 2.6	40–47	
Muraenidae (N = 270)							
<i>Anarchias similis</i>	75	7.3–81	70–81	103–111	107.6 ± 2.1	51–54	2
<i>Anarchias yoshaei</i>							
<i>Anarchias euryurus</i>	5	75–67		111–117	114.4 ± 2.1	50–56	
<i>Uropterygius wheeleri</i>	3	26–69		127–135	132.0 ± 4.4	60–67	
<i>Muraena melanotis</i>	23	22–63		122–129	125.8 ± 2.0	57–62	
<i>Muraena robusta</i>	9	9.3–100		153–159	156.3 ± 1.8	73–79	x
<i>Gymnothorax maderensis</i>	4	24–107	50–104	157–160	158.7 ± 1.5	79–84	
<i>Gymnothorax</i> sp.	7	60–67		124–128	126.0 ± 1.4	54–59	
<i>Gymnothorax vicinus</i>	36	17.0–78		128–134	131.1 ± 1.7	59–64	
<i>Gymnothorax afer</i>	38	7.8–79		142–148	145.1 ± 1.7	66–70	2

Table 1 continued

Family/species	N	TL range	Meta range	TM	Mean TM	LVBV	Months of spawning
<i>Gymnothorax unicolor</i>	21	13.0–82		135–143	185.0 ± 1.9	60–65	
<i>Enchelycore anatina</i> (<i>Gymnothorax anatinus</i>)	1	30		154		68	
<i>Gymnothorax mareei</i>	46	35.0–89	80–89	131–139	136.2 ± 2.0	60–68	
<i>Enchelycore nigricans</i>	2	17.0–53		140–147		68–70	
Ophichthidae (N = 1763)							
<i>Myrophis plumbeus</i>	247	5.1–103	75–94	145–156	149.6 ± 2.3	56–62	2,3,5,7,11
<i>Pseudomyrophis atlanticus</i>	99	7.0–83	70–74	168–181	174.1 ± 2.4	65–70	5
<i>Pseudomyrophis nimius</i>	1	95		214		73	
<i>L. mononucleus</i> sp. nov.*	15	8.2–104		141–148	144.9 ± 2.6	58–62	x
<i>Echelus myrus</i>	109	6.0–93		149–160	154.0 ± 2.7	55–61	1,3,4
<i>Echelus pachyrhynchus</i>	343	5.0–114		153–162	157.6 ± 2.0	64–70	1,2,3,4,5,7,8,11
<i>Bascanichthys paulensis</i> (<i>Bascanichthys congoensis</i>)	23	6.9–127		185–195	190.5 ± 3.4	105–110	x
<i>Bascanichthys</i> sp.	8	8.0–82		230–241	234.3 ± 4.2	146–154	x
<i>Callechelys leucoptera</i>	7	8.8–87		164–171	167.7 ± 2.9	89–92	x
<i>Callechelys</i> sp.	65	7.0–80		131–142	135.2 ± 2.8	70–79	2,3,12
<i>Myrichthys pardalis</i>	17	7.5–119		160–163	161.3 ± 1.6	64–68	1,3,11
<i>Dalophis boulengeri</i>	474	5.0–168	95–154	143–165	153.2 ± 4.2	60–74	1,2,3,5,11
<i>Dalophis</i> sp 1	112	6.6–145	110–144	128–145	137.5 ± 4.0	58–70	1,5
<i>Dalophis</i> sp 2	67	48–129	100–119	167–178	171.8 ± 2.8	73–81	
<i>Dalophis cephalopeltis</i>	69	12.2–141	105–129	181–197	187.0 ± 3.0	76–86	
<i>Brachysomophis atlanticus</i>	23	6.3–81	60–84	113–119	117.1 ± 1.8	55–61	1,3,11
<i>Ophisurus serpens</i>	11	7.0–122		204–212	209.2 ± 3.1	84–87	x
<i>Ophichthus ophis</i>	23	16.0–131		162–172	167.4 ± 2.9	80–86	
<i>Ophichthus leonensis</i>	3	11.0–78		144		70–74	
<i>Ophichthus</i> sp.	13	8.5–94		156–161	158.8 ± 2.3	64–67	x
<i>Pisodonophis cruentifer</i>	4	100–139		148–152	149.5 ± 1.7	66–69	
<i>Phaenomonas longissima</i> (<i>Microrhynchus</i> sp. aff. <i>Foresti</i>)	4	61–99		191–195	193	131–135	
<i>Apterichthys caecus</i>	18	12.0–93	~ 77	132–141	137.0 ± 2.4	57–62	
<i>Callechelys</i> sp. (<i>Verma kendalli</i>)	4	50–64		139–144	141.5 ± 2.1	83–86	
<i>Apterichthys monodi</i> (<i>Verma monodi</i>)	2	92,134		149,151		76–79	
Unknown* (<i>Verma</i> sp.)	2	99,110		187,192		119–24	
Nettastomatidae (N = 2027)							
<i>Hoplunnis punctata</i> (<i>Hoplunnis schmidti</i>)	1791	5.5–141	110–139	233–250	242.3 ± 3.4	47–56	1,2,3,4,5,6,7,9,11
<i>Nettastoma melanurum</i>	1	47		206		59	
<i>Facciolella oxyrhyncha</i>	1	Damaged				48	

Table 1 continued

Family/species	N	TL range	Meta range	TM	Mean TM	LVBV	Months of spawning
<i>(Facciolella physonema)</i>							
<i>Saurenchelys cancrivora</i>	190	5.6–117		192–210	201.0 ± 4.9	47–54	1,2,3,5,7
<i>Saurenchelys stylura</i>	44	11.0–128	115–128	216–228	222.8 ± 3.8	56–60	
<i>(Leptocephalus stylurus)</i>							
Synphobranchidae (N = 5)							
<i>Dysomma brevirostre</i>	1	29		195		67	
<i>(Nettodarus brevirostris)</i>							
<i>Dysomma</i> sp.	4	21.0–59	~ 57	153–157	154.5 ± 1.9	70–77	
<i>(Nettodarus</i> sp.)							

Species names that were changed are shown in parentheses below the currently valid name. The present identity of a few species is not known (*)

adults and larvae of the mud eels of the Heterenchelyidae (Online Resource 1), whose juveniles and adults burrow in sediment. In the Gulf of Guinea there are 2 coastal/littoral species (*Pythonichthys macrurus* and *Panturichthys longus*) and 2 deeper-water species (*Pythonichthys microphthalmus* and *Panturichthys isognathus*) that live at depths of about 40–150 m (Blache 1977) and their larvae were abundant in the study area.

The 1603 *Pythonichthys macrurus* leptocephali were collected at sizes of 4.5–79.0 mm. The peak spawning was in March–May during the warm-season with small larvae being mostly absent during the cold season from June to October (Fig. 5A). Most of the metamorphosing larvae were collected in September at 55–79 mm, with no large larvae being collected after September, which suggested a larval duration of 5–7 months. Although many larvae were collected in March and May, the data table in the monograph showed an absence of larvae in April. The smallest larvae (5–9 mm) were mostly collected over depths of 12–52 m all along the shelf. Most larvae were in water < 100 m and no larvae were found over > 250 m depths. The small leptocephali and larvae were collected from just south of the Congo River to just north of the Equator (Fig. 4B). Compared to the larval distributions of other species of this family, this species appears to spawn very near the coast and the leptocephali have greater larval retention (Fig. 4).

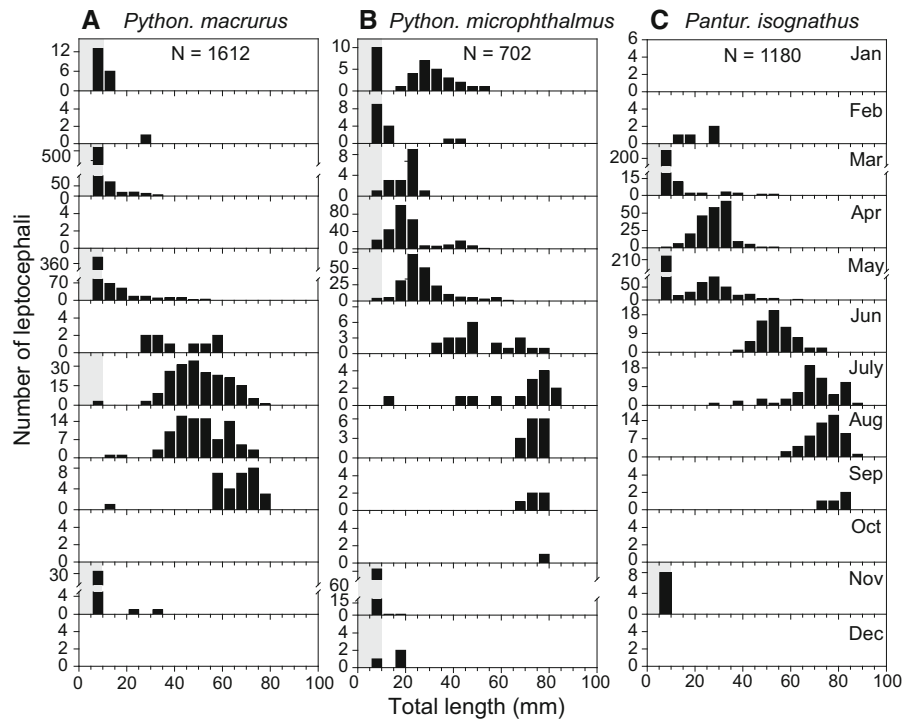
The 771 *Pythonichthys microphthalmus* were collected at a similar size range of 4.3–81.0 mm, with smallest larvae being present from November–May (Nov, Apr peaks; Fig. 5B). Spawning occurred at

6–10°S (Fig. 4A) during the warm season along the continental shelf. Larvae reached > 55 mm in May and 65–81 mm in August–November, suggesting a larval duration of 7–9 months. Blache (1977) indicated that they spawn near estuaries and near the Congo River and their larvae are all over the shelf. Only a few 40–44 mm larvae were caught over deep water and none were at stations over > 2000 m water depths, although some larvae were far from shore (Fig. 4A).

The leptocephali of *Panturichthys isognathus* were also abundant (N = 1239) and were collected at sizes reaching higher maximum lengths (4.6–89.0 mm). The 5–9 mm larvae were present in November and March–May all along continental shelf (Figs. 4, 5C) indicating spawning during the warm season. One small larva was collected offshore along with some larger larvae. They start metamorphosing in July and continue into August and September at sizes of 70–84 mm. They had a more concentrated spawning time compared to the other species and had a larval duration of 5–8 months. All larvae > 52 mm were over > 1500 m depths, but most were between 100 and 1500 m, indicating they have a wider larval dispersal. During the warm period the larvae go north to south with Guinean Current water. From July the water moves north and distributes larvae along the slope. Some larvae are distributed offshore due to the Angola Gyre.

The length-frequency distribution plots of the 3 abundant Heterenchelyidae species (Fig. 5) and the catch locations of different sizes of their larvae showed some interesting differences among the

Fig. 5 Length-frequency distributions during each month of the Heterenchelyidae leptocephali of *Pythonichthys macrurus* (A), *Pythonichthys microphthalmus* (B), *Panturichthys isognathus* (C) collected during net sampling from 1960 to 1971 in the Gulf of Guinea plotted from data in tables in Blache (1977)



species (Fig. 4). The gradient of habitats described by Blache (1977) appeared to be reflected by a high degree of larval retention of the shallow species and greater larval dispersal by the deeper species (Fig. 4A–C). Collectively the larvae of this family contributed 53.1% of the assemblage of leptocephali over the shelf and slope, 11.2% offshore, and 1.5% to the archipelago area.

Congridae leptocephali

The distributions and life history characteristics of Congridae leptocephali (18.5% of total larvae) were different than those of the Heterenchelyidae. Most congrid eels live at depths of 150–1000 m and spawning probably occurs in deep water, with some species possibly migrating offshore to spawn (Blache 1977). For example, even though the adults of *Coloconger* (now considered a separate family) and *Japonoconger* were common, their leptocephali were never caught in the study area. All species of congrid leptocephali reached larger sizes of about 100–275 mm and probably have a longer larval life, except for the garden eels of *Gorgasia* and *Heteroconger* (75–95 mm) (Table 1). The length-frequency

data indicated that congrid eels had a similar pattern of spawning during the warm water season as the heterenchelyiids, with the sizes of *Rhynchoconger* (N = 601; Fig. 6A) and *Paraconger notialis* (N = 191; Fig. 7A) progressing during the year. The small larvae < 10 mm of the congrids *Uroconger syringinus* and *Rhynchoconger* sp. were caught along the continental shelf where they live. There were wide size ranges of *Rhynchoconger* leptocephali from February–May, possibly suggesting some larger larvae were transported into the sampling area by the eastward Guinean Current, but the smallest larvae were collected in the same areas as the small heterenchelyiids.

The leptocephali of *Ariosoma balearicum* (N = 175) were collected at sizes of 8.0–216 mm and were metamorphosing at 145–194 mm. Small larvae were collected in January, May and November over 50–2000 m depths, and large larvae were only over deep waters. The adults live at 20–70 m depths and the larval duration was estimated to be 20–22 months by Blache (1977). *Uroconger syringinus* was another abundant congrid leptocephalus (N = 528) that was caught at 8.0–140.0 mm, with 347 larvae collected in April. *Heteroconger*

Fig. 6 Length-frequency distributions during each month of the leptocephali of *Rhynchoconger* sp. (Congridae) (A), *Echelus pachyrhynchus* (B), *Myrophis plumbeus* (Ophichthidae) (C) collected during net sampling from 1960 to 1971 in the Gulf of Guinea plotted from data in tables in Blache (1977)

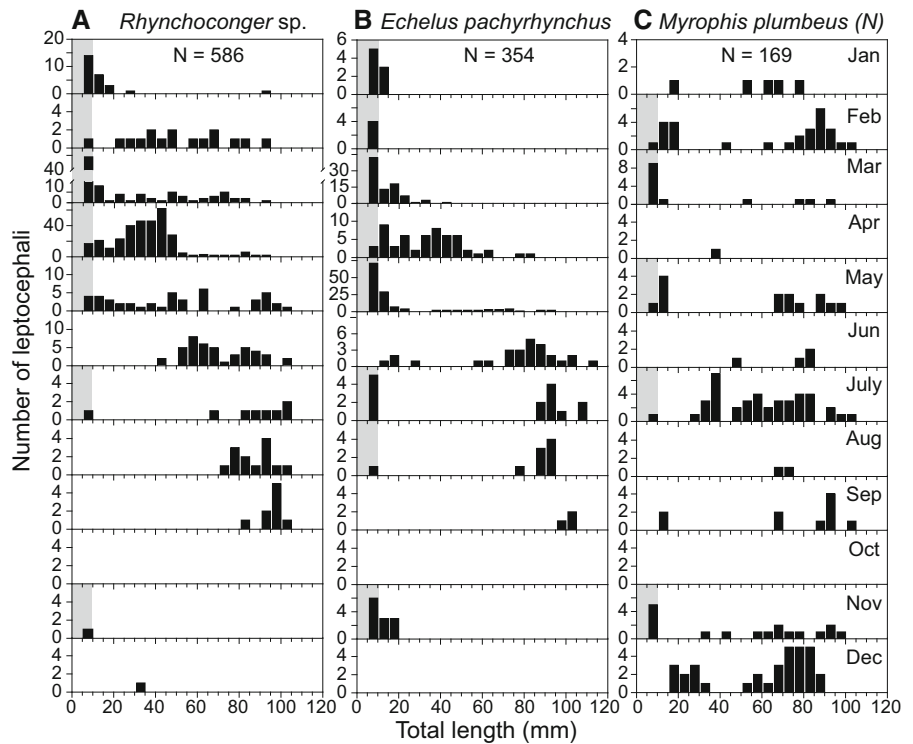
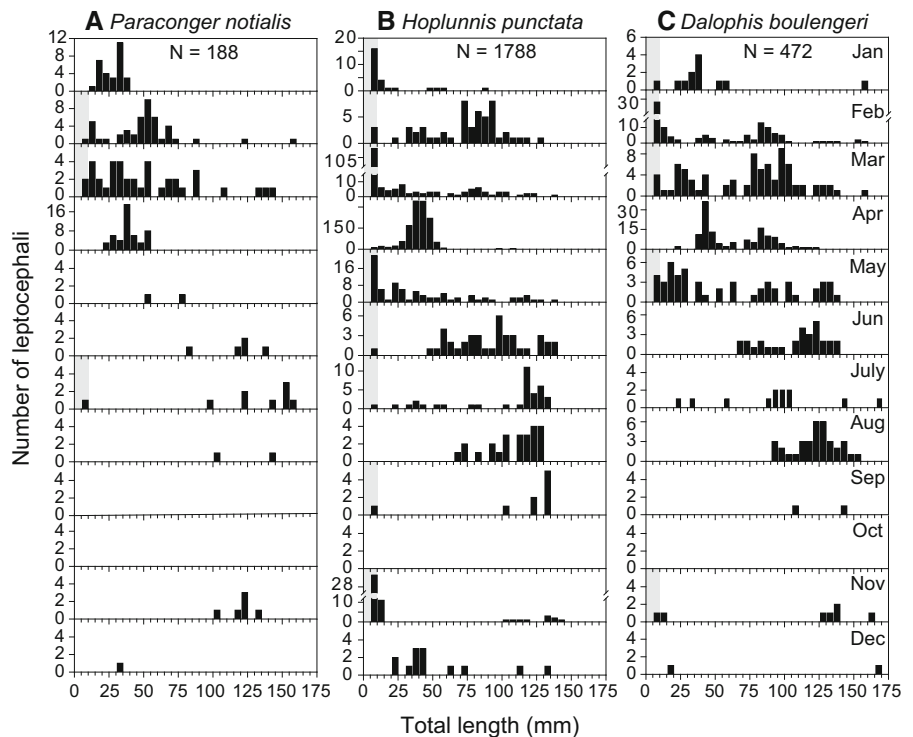


Fig. 7 Length-frequency distributions during each month of the leptocephali of *Paraconger notialis* (A) (Congridae), *Hoplunnis punctata* (B) (Nettastomatidae), *Dalophis boulengeri* (C) (Ophichthidae) collected during net sampling from 1960 to 1971 in the Gulf of Guinea plotted from data in tables in Blache (1977)



longissimus (N = 198) was collected at sizes of 6.0–95.0 mm and appeared to be spawning between the Congo River and the archipelago area (Fig. 4E). *Conger orbignianus* (5–19 mm) larvae were mostly collected in the archipelago area (Fig. 4F). In contrast to heterenchelyiids, the center of abundance of congrid leptocephali was in the archipelago area. Their leptocephali contributed 31.4% to the assemblage of the archipelago area, 22.9% offshore, and only 11.6% over the shelf and slope. Although thought to be in the Muraenesocidae at the time, so not included in those calculations (now included in the Congridae), a few *Xenomystax congroides* leptocephali were collected (N = 26, 9.0–253 mm).

Ophichthidae leptocephali

A significant proportion of the collected leptocephali (17.1%) were of the family Ophichthidae but they were distributed among at least 26 species (Table 1). The most abundant ophichthid species was *Dalophis boulengeri* (N = 474, 5.0–168 mm). The adults of that species live in shallow sand and silt areas, including in estuaries and lagoons (Blache 1977). Their small leptocephali were mostly caught in the region north of the Congo River (Fig. 4D), and the smallest specimens indicate they spawn throughout the warm season (Fig. 7C). Larger larvae were widespread including offshore and were present during most of the year, suggesting a larval life of 12–14 months after metamorphosing at sizes of 95–154 mm. Their juveniles and adults appear to be rare south of the Congo River (John and Zettler 2005). The other abundant ophichthid species *Echelus pachyrhynchus* (N = 343, 5.0–114 mm), *Myrophis plumbeus* (N = 247, 5.1–103 mm) and other ophichthid larvae do not appear to reach as large of a maximum size as *D. boulengeri* or other species of that genus, but they also appeared to mostly spawn in the warm season and had a wide size range of larvae collected in some months (Figs. 6, 7C). *Echelus pachyrhynchus* appeared to be spawning in the same areas as the heterenchelyiid eels (Blache 1977). There were also 13 other species of ophichthids collected at small sizes, indicating spawning in the study area (Table 1). Fewer than 10 specimens were collected for 9 ophichthid species, many of which were large. Those species may not be abundant in the study area, and the

catch maps suggest they live in northern areas outside the sampling zone (Blache 1977).

Nettastomatid and other leptocephali

The most abundant species in the Gulf of Guinea collections, *Hoplunnis punctata* (N = 1791), was listed in the family Muraenesocidae in the monograph, but is now in the Nettastomatidae. They comprised 17% of all leptocephali and were collected at a wide size range (5.5–141 mm). Its smallest leptocephali were distributed differently than the similarly abundant heterenchelyiid species by having small larvae mostly in two different areas (north of the Congo and near the archipelago area; Fig. 3) rather than in a wide-continuous area over the shelf (Fig. 4A–C). Their small larvae were distinctly most abundant in March (N = 115, < 10 mm), but at least a few were also collected during 8 other months (Table 1; Fig. 7B). In April, 1269 leptocephali of a wide size range were collected. This resulted in April being the month with the overall highest catch of all leptocephali (Online Resource 1, Fig. S2). Their larger larvae were collected far offshore during months when sampling occurred there. Blache (1977) noted that the adults are common on the shelf and slope at depths of 80–200 m in the Gulf of Guinea and on the Brazilian side of the South Atlantic and that they have a warm season (November–June) spawning period with a larval duration of < 1 year, probably about 6–8 months, before they metamorphose at sizes of 110–139 mm. The contribution of this species to the assemblages of leptocephali was shelf and slope 7.2%, offshore 21.8%, and archipelago 2.6%. Two other species of nettastomatid leptocephali were collected in modest numbers in the study area, including at small sizes, that were *Saurenehelys cancrivora* (N = 190, 5.6–117 mm) and *Saurenehelys stylura* (N = 44, 11.0–128 mm). Only single specimens were collected of 2 other nettastomatid species (Table 1).

Only 2 species of the family Chlopsidae were collected, with the leptocephali of *Chlopsis olokun* (N = 634, 9.0–89.0 mm) being abundant. Smallest larvae were collected near shore, but only two 9 mm larvae were caught during the warm season. The monograph pointed out that this species is endemic to the west coast of Africa, and Blache (1972) analyzed the distribution of *C. olokun* leptocephali in greater detail, and showed that larvae < 20 mm were caught both

over 30 and 1000–1500 m depths. Many larvae of *C. olokun* were collected in February and March (~ 40–59 mm) and August (60–74 mm), and they appeared to have a 6–10 month larval duration, with 60–89 mm metamorphosing larvae. None of the 15 *Chlopsis dentatus* (24.0–59 mm) were small enough to indicate where they were spawned.

Interestingly, relatively few Muraenidae species were collected at small sizes (Table 1). More than 20 specimens were collected for only 6 of the 13 species (N = 21–75), so compared to some other taxa, muraenid leptocephali were not abundant in the study area. *Anarchias similis*, *Muraena melanotis*, and 3 species of *Gymnothorax* were collected most frequently, but only 2 of those species had larvae < 10 mm in size. The contribution of this family to the assemblages were greatest around the archipelago (22.0%) and were low over the shelf (1.4%) and offshore (2.5%). Blache (1972) analyzed the distribution Muraenidae leptocephali and compared their meristic data among species.

The remaining family reported on was the Synphobranchidae (5 specimens of 2 species of *Dysomma* 21–59 mm). The monograph listed those as the Dysommatidae, which has been changed to be the subfamily Illyophinae (Synphobranchidae) (Böhlke 1989a). Some leptocephali of the Serrivomeridae, Nemichthyidae, and Cyematidae were apparently collected, but were not included in the study as mentioned above.

Morphological characteristics of leptocephali

Small leptocephali

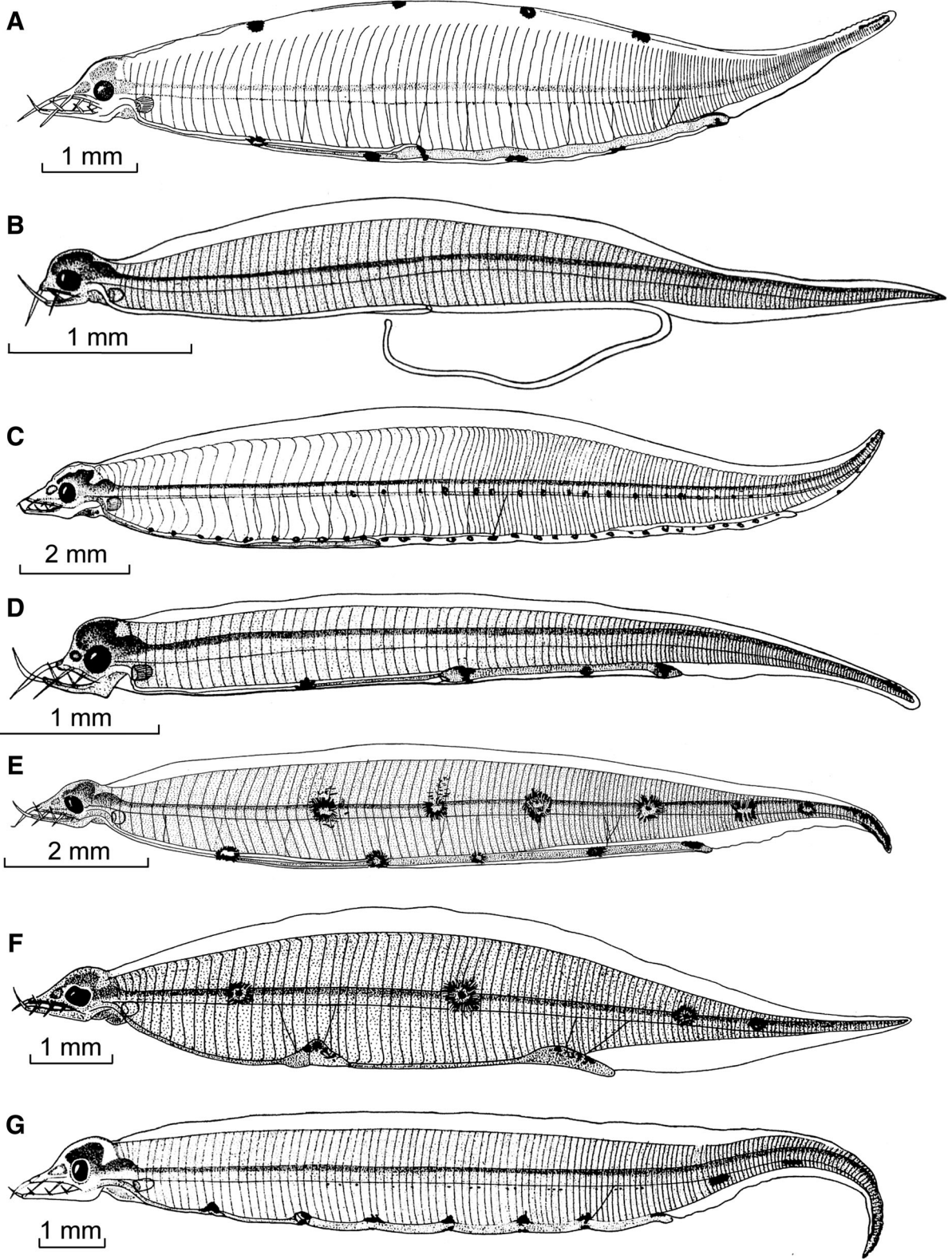
The illustrations of small leptocephali are a valuable aspect of the monograph that can be compared to the body shapes of larger leptocephali (Fig. 8; Online Resource 1). A particularly interesting drawing was of a 5.4 mm *Ariosoma mellissi* that shows the exterillum gut of that species has already formed shortly after hatching (Fig. 8B). The function of that type of intestine extending outside the body is not known, and it frequently breaks off during collection. Also interesting was a 9.5 mm *Ariosoma balearicum* larva (a species with no exterillum gut) that had 4 prominent spots at that small size (Fig. 8A), which are not present in larger leptocephali that have very small and numerous spots. A 11 mm larva of that

species from the Gulf of Mexico had 7 smaller dorsal spots (Smith 1989b). The 16.2 mm *Rhynchoconger* sp. (Fig. 8C) looks the same as the 15 mm *Rhynchoconger flavus* of Smith (1989b).

The illustrations of the 12 mm *Xenomystax congroides*, 11 mm *Saurenchelys stylurus*, and *Saurenchelys cancrivora* (Fig. 8E, F) may be unique for those taxa and show pigmentation patterns that are different than in larger leptocephali. The monograph also includes drawings of some small ophichthid larvae that have less developed gut swellings and lateral pigmentation than the larger leptocephali (Fig. 8G; Online Resource 1), as also seen in small WNA ophichthid leptocephali (Leiby 1989). The illustrations of small *Pythonichthys* leptocephali show no lateral pigment in a 5.5 mm larva (Fig. 8D), but it has started to form in a 7.6 mm larva and extends all along the body in large leptocephali (Online Resource 1).

Large leptocephali

The detailed illustrations of large leptocephali in the monograph (see Online Resource 1 for illustrations of specimens referred to below) were also interesting in relation to the morphology of leptocephali in the WNA (Böhlke 1989b; Smith 1989b) or elsewhere. The drawings of Heterenchelyidae leptocephali are unique and show resemblances with the lateral pigment spots and spots on the gut in some congrid larvae. Several unusual pigment patterns were seen in the drawings, such as a large pigment patch in a 150 mm *Parabathymyrus* sp. *Parabathymyrus oregoni* in the WNA has not been reported to have that kind of pigment patch. Indo-Pacific *Ariosoma*-type sp. 3 larvae have a patch like that (Mochioka and Tabeta 2014), although their adult species is not known (Miller et al. 2013c). Similarly, the anteroventral spots in the 255 mm *Xenomystax congroides* seem not to have been reported, and that genus is absent in the Indo-Pacific. The lateral spots in a 97 mm *Gnathophipis* sp. 2 may not be seen in WNA species, but lateral spots can form in larger larvae of some congrid even if absent in smaller individuals (Ma et al. 2007). The large spots shown for a 39 mm *Hoplunnis punctata* seem enlarged compared to other species of that genus (Smith and Castle 1982), but that could partly be related to its relatively small size.



◀ **Fig. 8** Illustrations of small leptocephali of a 9.5 mm *Ariosoma balearicum* (A), 5.4 mm *Ariosoma mellissi* (B), 16.2 mm *Rhynchoconger* sp. (C), 5.5 mm *Pythonichthys microphthalmus* (D), 12 mm *Xenomystax congroides* (E), 11 mm *Saurenchelys stylura* (F), 14 mm *Echelus pachyrhynchus* (G) of the Congridae, Heterenchelyidae, Nettastomatidae, and Ophichthidae, respectively, that were adapted from Blache (1977)

The morphology of most of the leptocephali shown from the Gulf of Guinea have the same morphological features as in other regions. The Muraenidae leptocephali showed typical muraenid features, and the two genera of garden eel leptocephali, *Heteroconger* and *Gorgasia* also seem the same as other species (Smith 2002; Castle 1997; Miller and Tsukamoto 2004). The 3 rows of lateral pigment of *Bathydroconger vicinus* are like those of *Bathycongrus* leptocephali in the eastern Pacific and Indo-Pacific (Raju 1985; Castle and Smith 1999), and *Chlopsis dentatus*, and *Dysomma brevirostre* leptocephali appear the same as in the WNA.

Ophichthidae leptocephali have diverse variations in the shapes of their guts and in several types of internal and external pigmentation (Leiby 1989; Miller and Tsukamoto 2004), so the numerous illustrations of leptocephali of this family in Blache (1977) are interesting. These variations include the height of gut curvatures, which range from low to high. The number and size of internal postanal pigment spots also vary, and many species have rows of small spots on the myosepta between the myomeres (muscle segments).

There are also many close-up illustrations of the head regions of leptocephali from the Gulf of Guinea in the monograph with 28 examples shown in Online Resource 1. They show the same head shapes and pigmentation patterns as those taxa in other regions for congrids, *Dysomma brevirostre*, *Nettastoma melanurum*, muraenids, and ophichthids and many species. The head shapes of the Heterenchelyidae leptocephali are unique though, compared to other families. They are most similar to the shapes of Muraenidae leptocephali heads, but are even more rounded in front or elevated on top.

Metamorphosing leptocephali

Illustrations of metamorphosing larvae (postlarvae) were also shown, such as of *Chlopsis olokun* (64 and

85 mm), *Pythonichthys macrurus* (67 mm), and a much larger 235 mm *Xenomystax congroides* (See Online Resource 1) that seem to be unique in the literature. Leptocephali usually lose their larval teeth and the end of their gut and dorsal fin position move forward (Raju 1985; Smith 1989a; Miller 2009), as was seen in some of the illustrations. Other changes can occur, such as the formation of nostrils or enlarged olfactory organs that were also seen. Some metamorphosing larvae in the illustrations have very small teeth or new teeth that will probably remain during the juvenile and adult stage as seen in a 131 mm *Hoplunnis punctata* postlarva. Three sizes of *Pythonichthys macrurus* showed the anterior movements of the gut and dorsal fin during metamorphosis.

Discussion

The study of Blache (1977) that we have overviewed here provided types of unique and detailed information about marine eels that has not yet been obtained anywhere in the world, even 40 years later. It provides the most complete view of regional marine eel biodiversity and early life history that was made possible by the extensive year-round larval sampling that collected more than 10,000 leptocephali on the continental shelf and offshore in the Gulf of Guinea and by other research on adult eels living there (Blache 1968, Online Resource 1). The distributions of small leptocephali showed when and where spawning occurred in relation to the seasonal cycle of oceanographic conditions, and the seasonal growth-progression of the larvae could be seen in ways that have not been documented in other areas of the world for marine eels, except to some degree in the Gulf of Mexico (Smith 1989a). The illustrations of the different sizes of the species of leptocephali in the Gulf of Guinea are mostly unparalleled in their detail and diversity. In addition, the information obtained about the spawning locations and different patterns of larval dispersal for the species of the Heterenchelyidae is the only information about that family of eels anywhere worldwide. As overviewed below, the information provided in the monograph and presented here adds valuable information to the understanding of the interactions of marine eels with the environmental conditions where they live in a unique way due to the unusual oceanography of the Gulf of Guinea.

Gulf of Guinea eel biodiversity

Compared to knowledge about eels that has emerged after the monograph was published, it is apparent that fauna of benthic eels living continental shelf habitats and over the slope within the sampling region in the Gulf of Guinea is not particularly diverse for most families as discussed below, because evidence of recent spawning (< 10 mm larvae) was only found for 34 of the 70 species of collected leptocephali (~ 45 species < 20 mm). Mesopelagic eel leptocephali were not included in the monograph as was explained, and some of those larvae apparently were caught in deep waters. Those families (Serrivomeridae, Nemichthyidae, and Cyematidae) are not diverse in number of species anywhere in the world (e.g., Böhlke 1989a), so they would only include a few species in the Gulf of Guinea. Including some mesopelagic species, and a few species of the Simemchylidae, Myrocongridae, and Colocongridae not collected as larvae, it is possible that about 55 species of marine eels were living in the Gulf of Guinea region at that time period, which is a low number compared to the Indo-Pacific.

One factor possibly causing a low diversity of eels there is that the Gulf of Guinea coastal waters or islands do not have many corals, as reflected by the reef fish fauna not being diverse, with 50% or more of the fish species possibly being endemic (Jones 1994). The Gulf of Guinea was ranked third in the world for its level of endemism as a marine biodiversity hotspot for some types of species (Roberts et al. 2002). True coral reefs are not present anywhere, but some types of corals live in a few areas (Laborel 1974; Spalding et al. 2001). Seagrass habitats are also absent except at São Tomé Island (Short et al. 2007). There are some mangrove habitats in the region though, such as in northern areas and the Niger River Delta estuary (Feka and Ajonina 2011). The large inflows of river water containing sediment and organic material and the frequent upwelling of cold water may cause the limited Gulf of Guinea coral and seagrass fauna (Jones 1994; Spalding et al. 2001). This suggests that the habitats available for eels in the Gulf of Guinea are limited compared to regions that have many coral reefs or seagrass beds. This also appears to have been the case throughout the geological history of the South Atlantic that is the most recent ocean basin to emerge due to continental drift, and the eastern South Atlantic appears to have never had high marine biodiversity

compared to other ocean regions due to a lack of shallow shelf areas with coral reefs (Leprieur et al. 2016).

Interestingly, the most abundant Gulf of Guinea family of leptocephali was the Heterenchelyidae, with 3 abundant species and 2 other species. They are called mud eels because they burrow in soft sediments, so estuaries and habitats near large rivers with heavy sediment loads are probably good habitats for them. Heterenchelyiid eels are head-first burrowers (Online Resource 1, Fig. S3; Smith 1989c; Smith et al. 2012; Eagderi and Adriaens 2010) that live on sandy or silty bottoms and feed on worms, crustaceans and mollusks (Blache 1968). They appear to be phylogenetically closely related to the Muraenidae, one of the most ancestral anguilliform families (Inoue et al. 2010).

The Gulf of Guinea and West Africa region appears to be the center of distribution of this family because only 3 other species are known elsewhere worldwide. Those species are *Panturichthys fowleri* in the eastern Mediterranean (Levantine and Aegean seas), *Pythonichthys sanguineus* (western central Atlantic, Cuba, Puerto Rico, Suriname), and *Pythonichthys asodes* (eastern central Pacific, Mexico and Panama) (Smith et al. 2012; Froese and Pauly 2017). The remaining species is *Panturichthys mauritanicus*, found from Morocco to Guinea to the north of the study area. It is unclear if this is the same species as *Pythonichthys* sp. leptocephali (Table 1; Blache 1977), that was somehow misidentified. Either way, the Gulf of Guinea seems to be the only region where there are so many species of mud eels.

The circumtropical snake and worm eels of the Ophichthidae also burrow in sediments (De Schepper et al. 2007) and were the most diverse family of leptocephali (26 species). Small leptocephali of 15 ophichthid species (11 spp. < 10 mm, 4 spp. ≤ 16 mm) were collected, with 7 species only being caught at larger sizes ≥ 48 mm (Table 1). Four species, *Pseudomyrophis nimius*, *Pisodonophis cruentifer*, *Apterichtus monodi*, and *Apterichtus* sp., with fewer than 5 larvae collected (all > 90 mm) may have come from outside the study area. This suggests about 20 species of ophichthids were living in the Gulf of Guinea region.

The abundance and presence of small leptocephali of other species such as *Hoplunnis punctata*, *Chlopsis olokun*, and several species of congrid (7 spp. < 10 mm, 3 spp. ≤ 15 mm) indicated those

adult species must also be present in the study area. Fewer small muraenids were collected (3 spp. < 10 mm, 3 spp. \leq 17 mm), mostly in the northern sampling area. No muraenids were among the most abundant taxa, so moray eels may have low biodiversity in the region, possibly due to the lack of coral reefs or other habitats. Only 6 species of moray and ophichthid eels were detected at São Tomé Island (Afonso et al. 1999). The few small *Chlopsis olokun* < 10 mm were only caught at 2 station locations, which provides few clues about where this endemic species (Robins and Robins 1966) lives and spawns in the area. The Guinean conger, *Paraconger notialis* is also endemic to the region, as are the garden eel *Gorgasia inferomaculata* and the ophichthid *Dalophis boulengeri* (Froese and Pauly 2017). Other abundant species of leptocephali in the region were the larvae of widespread species, such as the congrid *Uroconger syringinus*, the brown garden eel, *Heteroconger longissimus*, and the balearic conger, *Ariosoma balearicum* (Smith 1989b).

The Blache (1977) monograph is suggestive of which species of eels live in the Gulf of Guinea area or are only present in the wider region, but those numbers of species are low compared to some other tropical regions. The 70 species of leptocephali collected in the Gulf of Guinea (or \sim 55 eel species living in the area) is similar to the 63–77 species of leptocephali collected in surveys in the WNA (Richardson and Cowen 2004; Ross et al. 2007; Miller and McCleave 2007), but is lower than the \sim 90 species collected in both the western South Pacific (Miller et al. 2006) and the western Indian Ocean near the Mascarene Plateau (Miller et al. 2015). The highest number of species of leptocephali found so far was in the central Indonesian Seas in the center of the Coral Triangle where more than 130 species have been collected (Wouthuyzen et al. 2005; Miller et al. 2016). Due to the diversity of habitats including coral reefs there, it is not surprising that geological history and phylogeography (Leprieur et al. 2016) and other factors has resulted in the apparent number of eel species in the Gulf of Guinea region being considerably lower than in the Coral Triangle where marine biodiversity is highest (Hoeksema 2007), including for marine fishes (Randall 1998; Carpenter and Springer 2005). The number of leptocephali species collected at higher latitudes is lower (< 30) than the Gulf of Guinea however, such as in coastal Japan (Kimura et al. 2006) and the western

South Atlantic (Fortuño and Olivar 1986; Figueroa and Ehrlich 2006; De Castro and Bonecker 2005).

Gulf of Guinea leptocephalus morphology

In addition to the highly-detailed information about the species composition of leptocephali in the Gulf of Guinea, another unique and valuable aspect of the monograph was the many illustrations of leptocephali. The drawings of small larvae can facilitate future studies, because small larvae are hard to identify when they usually have different pigmentation patterns and body proportions than larger leptocephali, and most identification guides focus on larger leptocephali (Smith 1979; Böhlke 1989b; Miller and Tsukamoto 2004; Fahay 2007; Mochioka and Tabeta 2014). An exception is the small leptocephali, including recently hatched pre-feeding larvae (3–7 mm), included in the Leiby (1989) identification guide, which covers all WNA Ophichthidae species.

The present paper includes 64 illustration examples of the of Gulf of Guinea leptocephali. The level of detail of the drawings and other monograph data should enable future evaluations of the species identifications that were used, which in a few cases may have been tentative. For example, the species referred to as “*Verma kendalli*”, which has now have been changed to *Apterichtus kendalli* (McCosker and Hibino 2015), is not the same as that species in the WNA and is thought to be a species of *Callechelys* (Leiby 1989). Similarly, “*Verma* sp.” looks different than *Apterichtus* leptocephali, but “*Verma monodi*”, now *Apterichtus monodi* (Table 1), looks like a larva of that genus. Evaluating how many ophichthid or other larvae match up among different studies is beyond the scope of this paper, but the detailed drawings of Blache (1977) will enable future comparisons among leptocephali in the Gulf of Guinea and other areas.

Spawning ecology and early life history

The sampling campaign conducted at all times of year in the Gulf of Guinea provided a unique opportunity to examine spawning activity and larval growth. Larger leptocephali may have been under-sampled due to net avoidance (Miller et al. 2013b), but many larvae of all sizes were collected. Water clarity might be low along the shelf in those areas, and many tows were made that

resulted in the documentation of some interesting patterns of spawning locations and larval growth.

The catch locations of small leptocephali indicated that most species were spawning over or along the edge of the continental shelf. The clearest example of this were the Heterenchelyidae eels that were spawning nearshore over the shelf, apparently at 3 different depth zones ranging from very nearshore to farther out over the shelf or slope (Blache 1977). Their larval distributions suggest that depth of spawning and possibly larval behaviors may result in different levels of larval retention. The distribution patterns seem to show that *Pythonichthys macrurus* spawns very nearshore and has very little larval dispersal. The small *Pythonichthys microphthalmus* were caught in similar areas, but their larvae were much more widely distributed over deeper water and in the south. Small larvae of *Panturichthys isognathus* were also caught farther out over the shelf and were more abundant in the south. This suggests different spawning locations, the larvae being influenced by different currents, or differences in larval behavior could possibly occur.

Taxonomically-linked differences in larval dispersal seem to exist based on differences in the larval distribution patterns of eels (Miller 2009; Miller et al. 2011). Garden eels and ophichthid eels have far fewer larvae collected offshore than species that may spawn in similar locations such as muraenids, moringuids, and chlopsids, which are commonly collected offshore (Miller and McCleave 1994, 2007; Miller et al. 2006). Garden eels appear to spawn within their colonies (Kakazaki et al. 2015) and moray eels may also spawn in the habitats where they live (Moyer and Zaiser 1982; Thresher 1984; Ferraris 1985). Ophichthid eels also appear to spawn over the continental shelf based on collections of their larvae (Fahay and Obenchain 1978; Miller 2009). These types of marine eel spawning locations have also been supported by collections of leptocephali near the Bahamas in the WNA (Miller 1995; Miller and McCleave 2007), at the edge of the East China Sea Kuroshio Current (Miller et al. 2002; Miller 2009), along coastal Japan (Kimura et al. 2006), and near the shallow banks of the Mascarene Plateau in the western Indian Ocean (Miller et al. 2015). But despite similar spawning habitats, far fewer garden eel and ophichthid larvae seem to get transported offshore than moray eels and other marine eels spawning along continental shelves.

Interestingly, the small garden eel larvae of *Heteroconger longissimus* in the Gulf of Guinea had a similar distribution as the small larvae of the ophichthid *Dalophis boulengeri*, the heterenchelyiids, and *Hoplunnis punctata*, but the larger larvae of *H. longissimus* and *Pythonichthys macrurus* were much less widely distributed offshore and in the south than the ophichthid, the other heterenchelyiids or *Hoplunnis punctata* (Figs. 3,4). This suggests that *H. longissimus* and *P. macrurus* have some kind of larval retention strategy.

Most species of congrid, muraenids and chlopsids did not show distributions centered along the coast like the Heterenchelyidae, ophichthids, and garden eels. Therefore, the data of Blache (1977) seem to support the hypothesis that there are taxa-specific levels of larval retention or dispersal that are based on spawning location and active larval behavior by some species, presumably mediated by swimming or position in the water column to reduce offshore transport. Other types of fish larvae appear to use active swimming to mediate their distributions and recruitment (Leis 2002, 2006), so it is possible that some leptocephali do as well.

What is clearly unique about the implications of the findings of Blache (1977) is that the seasonal and spatial distribution of spawning seems to be clearly linked to the distribution and timing of the presence of cold water as discussed more in the next section. The majority of small larvae were collected from November to May for all the families. The size of the collected larvae then increased from June to September for most species as seen in the plots shown here (Figs. 5, 6, 7) and the data shown for other species such as *Panturichthys longus*, *Ariosoma balaricum*, and *Chlopsis olokun* in the monograph tables. These data show a unique view of seasonal spawning by shallow water marine eels and growth of their leptocephali.

In comparison, there are only limited data available about the seasonality of eel spawning in other areas. Available data suggests possible year-round spawning in tropical regions, and summer to fall spawning in subtropical to southern temperate areas (Miller 2009). Monthly length frequency data of *Moringua edwardsi* plotted by Castle (1979) from various WNA collections showed no clear seasonal spawning or growth pattern. A north–south transect was sampled during almost every month of the year in the eastern Indian

Ocean off western Australia and south of Indonesia and some evidence of seasonal spawning was found (Castle 1969). Sampling during several times of year in the tropical Indonesian Seas suggest many eels may spawn year-round based on the wide size ranges of leptocephali (Wouthuyzen et al. 2005; Miller et al. 2016). Catches of small *Gnathophis* leptocephali off western Australia suggested year-round spawning, however seasonal spawning was implicated along New Zealand, eastern Australia, and South Africa (Castle 1968; Castle and Robertson 1974). Sampling during 4 seasonal periods of the year in the Gulf of Mexico showed evidence of fall spawning followed by a larval size progression for *Rhynchoconger flavus* and *Xenomystax congroides* (Smith 1989a, b). Comparisons of larval sizes in late-spring and late-autumn in the subtropical East China Sea and southern temperate coastal Japan along with other information indicated most eels were spawning in the summer or fall (Minagawa et al. 2007). Therefore, it is possible that most tropical eels spawn throughout the year, but eels at higher latitudes spawn seasonally due to colder winter temperatures. The Gulf of Guinea maybe a unique example of seasonal spawning in a tropical area near the equator, which has resulted from the unique oceanographic and geographic conditions found there.

Geography, oceanography and Gulf of Guinea eels

One of the most interesting aspects of the catch data is how the presence of small leptocephali in the Gulf of Guinea collections corresponded to the seasonal cycle of warm water along the coast (Fig. 2). During about November–May the warm water extends southward past 10°S, and small leptocephali were collected in warm water areas from about the Congo River at 6°S up to the northern sampling area edge (Figs. 3,4). There was no evidence of much spawning occurring farther south than the Congo River, where warm water may only be present for about 6–7 months based on the pattern in 2012 (Online Resource 2). It is possible that less sampling occurred, or smaller areas were sampled during the cold season, such as in September and October, so the catch data may not fully reflect the size distributions of leptocephali present throughout the year. Spawning may also occur outside of the sampling area along the northern margin of the Gulf of Guinea where warm water is usually present. Larvae

from that region might sometimes be transported into the study area after eastward transport by the Guinea Current.

In addition, eastward transport by the Equatorial Undercurrent (Bourlès et al. 2002; Kolodziejczyk et al. 2009) could bring larger leptocephali into the northern study area. The circulation of the Angola Gyre might be an important influence on the distributions of larger sizes of leptocephali in the southern study area. Larger larvae of many species were collected there, so it is possible that the gyre can function as a larval retention area after spawning occurs along the coastline to the north of the Congo River. Some larvae could be transported offshore to the west by the Atlantic Cold Tongue when it forms (Fig. 2B; Online Resource 2) and by the South Equatorial Current.

It is also interesting to evaluate why the Gulf of Guinea and West Africa region is the center of distribution of mud eels of the Heterenchelyidae. Four species (*Pythonichthys marcurus*, *Pythonichthys microphthalmus*, *Panturichthys isognathus*, and *Panturichthys longus*) and apparently a fifth (*Pythonichthys* sp., or *Panturichthys mauritanicus*, Guinea to Morocco) were collected there as larvae or adults. The 3 other single heterenchelyid species are known from regions relatively close to the equatorial Atlantic (Mediterranean, western Central Atlantic, across the isthmus of Panama in the eastern central Pacific; Smith et al. 2012; Froese and Pauly 2017), which is suggestive of species radiation out from the Gulf of Guinea to the northwest and eastward into the Mediterranean. Smith et al. (2012) points out that the family could have been more widespread in the past, but it may also be possible that the Gulf of Guinea is especially favorable for mud eels compared to other types of eels, and the family may have radiated out from there.

The major changes in ocean temperatures at tropical latitudes near the equator may prevent the formation of extensive coral reefs or seagrass beds (Labrel 1974; Jones 1994; Short et al. 2007; Spalding et al. 2001) as already mentioned. This may also be related to the other unique aspect of the Gulf of Guinea, which is the presence of inflow of two large rivers, and especially the Congo River, which is the second largest in the world (Dai and Trenberth 2002). The inflows of these 2 rivers can be seen in Online Resource 3. The Congo River transports sediment into

the ocean (Sibuet and Vangriesheim 2009; Spencer et al. 2012) and coastal currents could transport sediment throughout the region where the burrowing eels of the Heterenchelyidae and Ophichthidae appear to live and spawn. It is impossible to know though, if the presence of the Congo and Niger rivers and their sediment input into the Gulf of Guinea in combination with seasonal cooling of water temperatures may be related to the presence of 3–4 species of Heterenchelyidae eels there, compared to only one species being present in any other part of their range.

It is clear though that the sampling effort conducted in the Gulf of Guinea and the remarkable work of Blache (1977) provide a unique and valuable insight into the life histories of marine eels in an oceanographically dynamic place in the world, which can be used to help guide future research in other parts of the world. Research on the species compositions and distributions of eels and the characteristics of leptocephali in other areas that also use spatially and temporally diverse sampling strategies will provide new information about the biodiversity and life history of eels that will lead to greater understanding of the ecology of marine eels in marine ecosystems worldwide.

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