

7-12-2006

Anguilliform larvae collected off North Carolina

Steve W. Ross

Center for Marine Science, University of North Carolina, ross@uncw.edu

Tara L. Casazza

Center for Marine Science, University of North Carolina

Andrea M. Quattrini

Florida Integrated Science Center, Center for Aquatic Resource Studies, United States Geological Survey,

Kenneth J. Sulak

Florida Integrated Science Center, Center for Aquatic Resource Studies, United States Geological Survey

Follow this and additional works at: <http://digitalcommons.unl.edu/usgsstaffpub>

 Part of the [Geology Commons](#), [Oceanography and Atmospheric Sciences and Meteorology Commons](#), [Other Earth Sciences Commons](#), and the [Other Environmental Sciences Commons](#)

Ross, Steve W.; Casazza, Tara L.; Quattrini, Andrea M.; and Sulak, Kenneth J., "Anguilliform larvae collected off North Carolina" (2006). *USGS Staff -- Published Research*. 1063.

<http://digitalcommons.unl.edu/usgsstaffpub/1063>

This Article is brought to you for free and open access by the US Geological Survey at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USGS Staff -- Published Research by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Anguilliform larvae collected off North Carolina

Steve W. Ross · Tara L. Casazza ·
Andrea M. Quattrini · Kenneth J. Sulak

Received: 17 February 2006 / Accepted: 18 May 2006 / Published online: 12 July 2006
© Springer-Verlag 2006

This document is a U.S. government work and is not subject to copyright in the United States.

Abstract The distinctive larval stage of eels (leptocephalus) facilitates dispersal through prolonged life in the open ocean. Leptocephali are abundant and diverse off North Carolina, yet data on distributions and biology are lacking. The water column (from surface to 1,293 m) was sampled in or near the Gulf Stream off Cape Hatteras, Cape Lookout, and Cape Fear, North Carolina during summer through fall of 1999–2005, and leptocephali were collected by neuston net, plankton net, Tucker trawl, and dip net. Additional samples were collected nearly monthly from a transect across southern Onslow Bay, North Carolina (from surface to 91 m) from April 2000 to December 2001 by bongo and neuston nets, Methot frame trawl, and Tucker trawl. Overall, 584 tows were completed, and 224 of these yielded larval eels. The 1,295 eel leptocephali collected (combining all methods and areas) represented at least 63 species (nine families). Thirteen species were not known previously from the area. Dominant families for all areas were Congridae (44% of individuals, 11 species), Ophichthidae (30% of individuals, 27 species), and Muraenidae (22% of

individuals, ten species). Nine taxa accounted for 70% of the overall leptocephalus catches (in order of decreasing abundance): *Paraconger caudilimbatus* (Poey), *Gymnothorax ocellatus* Agassiz complex, *Ariosoma balearicum* (Delaroche), *Ophichthus gomesii* (Castelnau), *Callechelys muraena* Jordan and Evermann, *Letharchus aliculatus* McCosker, *Rhynchoconger flavus* (Goode and Bean), *Ophichthus cruentifer* (Goode and Bean), *Rhynchoconger gracilior* (Ginsburg). The top three species represented 52% of the total eel larvae collected. Most leptocephali were collected at night (79%) and at depths > 45 m. Eighty percent of the eels collected in discrete depth Tucker trawls at night ranged from mean depths of 59–353 m. A substantial number (38% of discrete depth sample total) of larval eels were also collected at the surface (neuston net) at night. Daytime leptocephalus distributions were less clear partly due to low catches and lower Tucker trawl sampling effort. While net avoidance may account for some of the low daytime catches, an alternative explanation is that many species of larval eels occur during the day at depths > 350 m. Larvae of 21 taxa of typically shallow water eels were collected at depths > 350 m, but additional discrete depth diel sampling is needed to resolve leptocephalus vertical distributions. The North Carolina adult eel fauna (estuary to at least 2,000 m) consists of 51 species, 41% of which were represented in these collections. Many species of leptocephali collected are not yet known to have juveniles or adults established in the South Atlantic Bight or north of Cape Hatteras. Despite Gulf Stream transport and a prolonged larval stage, many of these eel leptocephali may not contribute to their respective populations.

Communicated by J.P. Grassle, New Brunswick

S. W. Ross (✉) · T. L. Casazza · A. M. Quattrini
Center for Marine Science, University of North Carolina
Wilmington, 5600 Marvin K. Moss Lane, Wilmington
NC 28409, USA
e-mail: ross@uncw.edu

K. J. Sulak · S. W. Ross
Florida Integrated Science Center, Center for Aquatic
Resource Studies, United States Geological Survey,
7920 Northwest 71st Street, Gainesville, FL 32653, USA

Introduction

The larval stage of Anguilliformes, the leptocephalus, is among the most morphologically and physiologically distinct of all larval fishes. The most striking features of leptocephali are laterally compressed, transparent bodies, fang-like teeth, well developed eyes, and large sizes (50–100 mm total lengths common). All Anguilliformes spawn in oceanic waters and exhibit a prolonged larval period, lasting several months to years (Smith 1989a). Although eel leptocephali are unlike adult eels, they can be readily identified to species with the exceptions of very small (< 10 mm TL) and metamorphic specimens. Even so, many leptocephali await taxonomic treatment, several described larval types cannot yet be matched to adults, and their biology and ecology remain poorly known (Smith 1989a).

Leptocephali are often transported great distances from spawning sites to habitats suitable for recruitment of juveniles. These movements are difficult to track, partly because exact spawning localities of most eel species are unknown. Eleven mesopelagic and coastal benthic anguilliform species may spawn in the Sargasso Sea (Schmidt 1922; Kleckner and McCleave 1982; Wipfelhauser et al. 1985; McCleave 1993; McCleave and Miller 1994; Miller and McCleave 1994; Miller 1995, 2002). Other species (e.g., ophichthids) may spawn at the surface over the continental shelf off the southeastern United States (Ross and Rohde 2003). Leptocephali can also be transported to areas where recruitment is apparently unsuccessful, as evidenced by the lack of adult populations (Richardson and Cowen 2004). Regardless of future recruitment success, the combination of an extended larval period and the northward flow of the Gulf Stream facilitates dispersal of leptocephali along the East Coast of the United States and beyond.

Eel populations are extensive and diverse in coastal and offshore waters of North Carolina. Fifty-one species of adult eels from 12 families occupy a wide range of habitats from rivers to the continental slope in this area (S.W. Ross, unpublished data), and 15 of these species are restricted to depths > 200 m as adults (Table 1). Although eel leptocephali have been collected frequently in ocean waters off North Carolina and/or in the South Atlantic Bight (SAB) (Powles and Stender 1976; Powell and Robbins 1994, 1998; Govoni and Spach 1999; Powell et al. 2000; Quattrini et al. 2005), they were often not identified to species. Data on vertical distributions and distributions relative to water masses (e.g., Gulf Stream) are also lacking for larval eels in this area or have been noted only at the family level (Govoni and Spach 1999; Quattrini et al.

2005). The lack of species level identifications and detailed distribution data hamper assessments of the complete life history of most eel species, including the role of leptocephali in the oceanic plankton.

During recent cruises off North Carolina, we collected a large diversity of anguilliform larvae. Our objectives were to: (1) describe the taxonomic composition of anguilliform larvae collected off North Carolina, (2) document their relative abundances, size structures, and depth distributions, and (3) compare the taxonomic composition of the oceanic larval pool in this region to that of the known adult eel populations.

Materials and methods

The water column in or near the Gulf Stream off Cape Hatteras, Cape Lookout, and Cape Fear, North Carolina (Fig. 1 and Table 2) was sampled during annual summer or fall cruises (August 1999, July 2000, August 2001, September 2001, August 2002, August 2003, June 2004, and October 2005). As part of a larger study, an overall objective was to sample diverse fish and invertebrate taxa in many habitats; thus, eel leptocephali were opportunistically collected during daylight and at night using a variety of nets targeting depths from the surface to 1,293 m (Table 2). We also incorporated leptocephalus data from a separate study which sampled an inshore to offshore transect across southern Onslow Bay, April 2000–December 2001 (Quattrini et al. 2005). Generally, all gears were towed against the current at approximately 3.7 km h⁻¹ ground speed.

Several methods were used to sample surface waters. Frequent occurrences of *Sargassum* spp. in surface waters interfered with flow meters, preventing accurate measures of water volume sampled and catch density calculations. A 1 × 3-m neuston net (6.4-mm mesh body, 3.2-mm mesh tailbag), NN1, was towed in the upper meter of the water column for 30 min in 1999 and 15 min during all other years. This gear effectively collected larger leptocephali, but the mesh size of this net eliminated smaller leptocephali (< 25 mm). To determine the extent to which smaller leptocephali may be missed in surface waters, we conducted limited sampling off Cape Lookout during October 2005 using the NN1 frame fitted with a Tucker trawl net (1.59-mm mesh net), designated NN3. A 1-m diameter plankton net (505- μ m mesh), PN, was towed for 30 min on the surface during 2002–2004 cruises. One metamorphic specimen was collected at the surface by dip net during night lighting collections.

Table 1 Anguilliformes known off North Carolina as adults or leptocephali

Taxa (≤ 200 m)	Adults	Larvae
Anguillidae		
<i>Anguilla rostrata</i>	T	x
Moringuidae		
<i>Moringua edwardsi</i>	T	x
* <i>Neoconger mucronatus</i>		x
Chlopsidae		
<i>Chlopsis bicolor</i>	T	x
<i>Chlopsis dentatus</i> ^a		x
<i>Chlopsis</i> sp. ^a		x
<i>Kaupichthys nuchalis</i>		+
Muraenidae		
* <i>Anarchias similis</i>		x
<i>Gymnothorax conspersus</i>	T	
<i>Gymnothorax hubbsi</i>	T	
<i>Gymnothorax kolpos</i>	T	
<i>Gymnothorax maderensis</i>	T	
<i>Gymnothorax miliaris</i> ^a		x
<i>Gymnothorax moringa</i>	T	x
<i>Gymnothorax polygonius</i>	T	
<i>Gymnothorax saxicola</i> ^b	T	x
<i>Gymnothorax vicinus</i>	T	x
<i>Gymnothorax</i> sp. C		x
* <i>Gymnothorax</i> sp. D		x
* <i>Gymnothorax</i> sp. E		x
<i>Monopenchelys acuta</i>		x
<i>Muraena retifer</i>	T	
<i>Muraena robusta</i>	T	
* <i>Uropterygius macularius</i>		x
Ophichthidae		
<i>Ahlia egmontis</i>	T	x
* <i>Aprognathodon platyventris</i>		x
<i>Apterichthys ansp</i>	T	x
<i>Apterichthys kendalli</i>	T	x
<i>Bascanichthys bascanium</i>	T	+
<i>Bascanichthys scuticaris</i>	T	x
* <i>Callechelys guineensis</i>		x
<i>Callechelys muraena</i>	T	x
<i>Callechelyini</i> sp.		x
<i>Echiophis intertinctus</i>	T	+
<i>Echiophis punctifer</i>	T	+
<i>Gordiichthys ergodes</i> ^a		x
* <i>Gordiichthys leiby</i>		x
* <i>Ichthyapus ophioneus</i>		x
<i>Letharchus aliculatus</i> ^a		x
<i>Letharchus velifer</i>	T	x
<i>Myrichthys breviceps</i>	T	x
<i>Myrichthys ocellatus</i>	T	
<i>Myrophis platyrhynchus</i>		x
<i>Myrophis punctatus</i>	T	x
<i>Ophichthini</i> sp. 3		x
<i>Ophichthini</i> sp. 7		x
<i>Ophichthus cruentifer</i>	T	x
<i>Ophichthus gomesii</i>	T	x
<i>Ophichthus melanoporus</i>	T	x
* <i>Ophichthus menezesi</i>		x
<i>Ophichthus puncticeps</i>	T	x
* <i>Pseudomyrophis fugesae</i>		x
<i>Pseudomyrophis nimius</i>		x

Table 1 continued

<i>Pseudomyrophis</i> sp.		x
* <i>Quassiremus ascensionis</i> ^a		x
Congridae		
<i>Ariosoma balearicum</i>	T	x
<i>Bathycongrus dubius</i>		x
<i>Bathycongrus</i> sp. A		x
<i>Conger esculentus</i>		x
<i>Conger oceanicus</i>	T	x
<i>Conger triporiceps</i>		+
<i>Gnathophis bathytopos</i> ^c	T	x
<i>Gnathophis bracheatopos</i> ^c	T	x
<i>Heteroconger luteolus</i>		x
<i>Paraconger caudilimbatus</i>	T	x
<i>Rhynchoconger flavus</i>	T	x
* <i>Rhynchoconger gracilior</i>		x
<i>Uroconger syringinus</i>		x
Nettastomatidae		
<i>Nettastoma syntresis</i>		+
<i>Saurenhelys cognita</i>	T	x
<i>Saurenhelys stylura</i>		x
Taxa (> 200 m)	Adults	Larvae
Synaphobranchidae		
<i>Dysomma anguillare</i> ^a		x
<i>Dysommia rugosa</i>	T	
<i>Histiobranchus bathybius</i>	T	
<i>Ilyophis brunneus</i>	T	
<i>Simenchelys parasitica</i>	T	
<i>Synaphobranchus affinis</i>	T	
<i>Synaphobranchus brevidorsalis</i>	T	
<i>Synaphobranchus kaupii</i> ^a	T	+
Derichthyidae		
<i>Derichthys serpentinus</i>	T	
<i>Nessorhamphus ingolfianus</i>	T	+
Nemichthyidae		
<i>Labichthys carinatus</i>		+
<i>Nemichthys curvirostris</i>	T	
<i>Nemichthys scolopaceus</i>	T	x
Congridae		
<i>Conger oceanicus</i>	T	
Nettastomatidae		
<i>Hoplunnis diomediana</i>	T	x
<i>Hoplunnis macrura</i>		x
<i>Hoplunnis similis</i>		x
<i>Hoplunnis tenuis</i>		x
<i>Nettenchelys exoria</i>	T	
<i>Nettenchelys inion/exoria</i> ^c		x
<i>Venefica procera</i>	T	
Serrivomeridae		
<i>Serrivomer beanii</i>	T	

Adult records (T) compiled from the senior author's unpublished checklist. x = collected in this study, * = not previously collected off North Carolina as larvae or adults, + = other collections (Böhlke 1989b)

^aLarvae tentatively identified to species as in Böhlke (1989b)

^bLarvae as *Gymnothorax ocellatus* complex (see the text)

^cLarvae cannot be differentiated at species level (Böhlke 1989b)

Discrete depth sampling was accomplished using Tucker trawls. The intent was to sample as much of the water column as practical in the range of about 20–1,200 m, with individual tows covering no more than 50 m of depth. In 1999, a 3.7 × 1.8-m Tucker trawl (6-mm mesh), TT1, was towed for 28–64 min (mean ± SE 44 ± 6 min) at different depths. A clock timer release triggered this net to open and close at depth. For all other years, a 2 × 2-m Tucker trawl (1.59-mm mesh), TT2, rigged with a double-release mechanism was towed for 18–73 min (mean ± SE 35 ± 1 min) at discrete depths. TT2 fished two nets sequentially in 2000 and in one deployment in 2001, but it fished one net for all other collections. In most cases, the bottom net (or only net when single rigged) was lowered in the open position. Because of the rapid lowering, steep wire angle, and minimal forward movement, we assumed there was little fishing as the net was deployed. When double nets were used, Tucker trawls were deployed to a target depth, fished for approximately 30 min, when a messenger triggered the first net to close, which opened the second net. The second net then fished for 30 min, was triggered by a second messenger to close and was retrieved. Plankton nets (0.5-m diameter, 333- μ m mesh), PN-TT, were suspended in the mouth of the Tucker trawl frame in 1999, 2000, and at two stations in 2001. All Tucker trawls were fitted with a Sea-Bird SBE39 data logger to

record time, depth, and temperature during the tow at ≤ 30 -s intervals. Mean depths where Tucker trawls fished were calculated by averaging all Sea-Bird data from the time the net opened until the time it closed.

A number of nets were towed obliquely, covering a range of depths that included the surface. A 1-m diameter plankton net (505- μ m mesh) was towed for 29–80 min in 1999 and 30 min in 2003 and 2004. Most plankton nets were fitted with a Sea-Bird SBE39 data logger to record depth and temperature where the nets fished. Tucker trawls (see above methods), did not always close, resulting in a water column sample that included the surface. While these oblique tows provided valuable species occurrence data, we did not use them to determine depth distributions.

Additional samples were collected approximately monthly, during daylight, across southern Onslow Bay, North Carolina (surface to 91 m) (Fig. 1 and Table 2). A 60-cm diameter bongo net (335- μ m mesh), BN, was fished in a stepped oblique or oblique pattern for 5–10 min, and a 1 × 2-m neuston net (950- μ m mesh), NN2, was fished at the surface for 10 min. From April 2000 to January 2001, the above two nets were deployed once per station on each sample trip, and from April to December 2001, they were deployed three times per station per trip. For details on these methods, see Quattrini et al. (2005). In April–June 2000, a 5-m² Methot frame trawl (2-cm mesh), MT, was deployed

Fig. 1 Collection sites of anguilliform larvae from four areas off North Carolina, 1999–2005. CH Cape Hatteras, CL Cape Lookout, CF Cape Fear, SOB southern Onslow Bay. Dotted line in SOB area separates inshore from offshore samples. See Table 2 for details

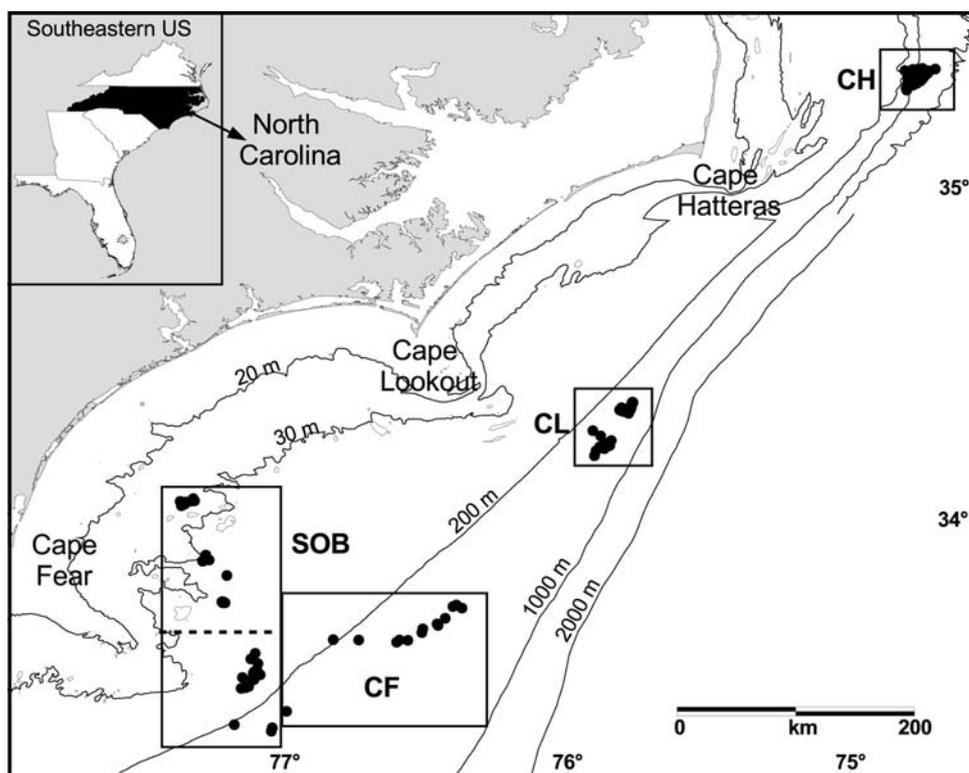


Table 2 Collection data for leptocephali off North Carolina, 1999–2005

Sample dates	Net	Depth range (m)	Area	Day		Night		Offshore		Inshore		Total leptocephali
				SC (ST)	#	SC (ST)	#	SC (ST)	#	SC (ST)	#	
2–7 Aug 1999	NN1	S	CH	2 (7)	12	8 (9)	110	10 (16)	122	–	–	122
2–7 Aug 1999	TT1	75–585	CH	1 (1)	2	3 (5)	25	4 (6)	27	–	–	27
2–7 Aug 1999	PN-TT	76–320	CH	–	–	2 (2)	2	2 (2)	2	–	–	2
2–7 Aug 1999	PN	0–133	CH	0 (1)	0	1 (1)	3	1 (2)	3	–	–	3
20–27 Jul 2000	NN1	S	CH	0 (12)	0	6 (15)	40	6 (27)	40	–	–	40
20–27 Jul 2000	TT2	0–938	CH	14 (20)	74	22 (30)	320	36 (50)	394	–	–	394
20–27 Jul 2000	PN-TT	0–938	CH	5 (20)	11	15 (29)	53	20 (49)	64	–	–	64
22–29 Aug 2001	NN1	S	CH	2 (22)	2	6 (15)	23	8 (37)	25	–	–	25
22–29 Aug 2001	TT2	0–1060	CH, CL	3 (3)	11	21 (23)	187	24 (26)	198	–	–	198
22–29 Aug 2001	PN-TT	0–326	CH	–	–	0 (2)	0	0 (2)	0	–	–	0
20–24 Sep 2001	NN1	S	CH, CL	0 (6)	0	7 (16)	12	7 (22)	12	–	–	12
20–24 Sep 2001	TT2	0–1293	CH, CL	4 (5)	4	16 (17)	104	20 (22)	108	–	–	108
6–15 Aug 2002	NN1	S	CL, CF	0 (23)	0	0 (9)	0	0 (32)	0	–	–	0
6–15 Aug 2002	PN	S	CL, CF	0 (4)	0	–	–	0 (4)	0	–	–	0
19–26 Aug 2003	NN1	S	CF	1 (3)	1	0 (2)	0	1 (5)	1	–	–	1
19–26 Aug 2003	TT2	0–365	CF	1 (1)	2	8 (12)	56	9 (13)	58	–	–	58
19–26 Aug 2003	PN	S, 0–60	CF	–	–	3 (7)	4	3 (7)	4	–	–	4
14–16 Jun 2004	NN1	S	CL	–	–	0 (2)	0	0 (2)	0	–	–	0
14–16 Jun 2004	PN	S, 0–57	CL, CF	0 (1)	0	5 (6)	34	5 (7)	34	–	–	34
16–20 Oct 2005	NN3	S	CL, CF	0 (14)	0	14 (28)	54	14 (42)	54	–	–	54
12–14 Jun 2000	TT3	0–89	SOB	5 (8)	23	–	–	3 (4)	21	2 (4)	2	23
Apr–Jun 2000	MT	0–76	SOB	3 (11)	3	–	–	1 (5)	1	2 (6)	2	3
Apr 2000–Jan 2001 ^a	NN2	S	SOB	2 (27)	2	–	–	1 (12)	1	1 (15)	1	2
Apr 2000–Jan 2001 ^a	BN	0–84	SOB	11 (27)	27	–	–	6 (12)	20	5 (15)	7	27
Apr–Dec 2001 ^a	NN2	S	SOB	4 (69)	6	–	–	0 (27)	0	4 (42)	6	6
Apr–Dec 2001 ^a	BN	0–91	SOB	29 (69)	87	–	–	17 (27)	32	12 (42)	55	87
Total				87 (354)	267	137 (230)	1,027	198 (460)	1,221	26 (124)	73	1,294

Area: *CH* Cape Hatteras, *CL* Cape Lookout, *CF* Cape Fear, *SOB* southern Onslow Bay. *SC* number of stations where leptocephali were collected, *ST* total number of stations sampled, # total number of leptocephali collected, *S* surface only, inshore = bottom depths < 40 m, offshore = bottom depths > 40 m. Net: NN1 = 1 × 3-m neuston net, NN2 = 1 × 2-m neuston net, NN3 = 1 × 3-m neuston net, TT1 = 3.7 × 1.8-m Tucker trawl, TT2 = 2 × 2-m Tucker trawl, TT3 = 2 × 2-m Tucker trawl, PN = 1-m plankton net, PN-TT = 0.5-m plankton net inside Tucker trawl net, BN = 60-cm bongo net, MT = 5-m² Methot frame trawl. Single specimen collected by dip net is not included

^aApproximate monthly sampling

about 10 m from the bottom and towed for 30 min at 5.6–7.4 km h⁻¹ in a stepped oblique pattern. In June 2000, a 2 × 2-m Tucker trawl (950- μ m mesh), TT3, fitted with two nets and a double-release mechanism was deployed (nets closed) to approximately 10 m from the bottom. After reaching target depth, a messenger opened the bottom net, which was towed in a stepped oblique pattern for 10 min through the lower half of the water column. A second messenger closed this net and opened the upper net, which then fished the upper half of the water column to the surface in a stepped oblique pattern for 10 min. All subsurface nets were fitted with Sea-Bird SBE37 Microcat data loggers to record time, temperature, salinity, and depth at 5-s intervals.

Size and depth distributions were examined for the dominant species. Depth intervals selected for analysis were based on the temperature data (not shown) and Adams et al. (1993) and divided Gulf Stream waters into an upper, warm layer subject to some seasonal

variation (surface to 275 m), a lower, colder layer (276–1,016 m), and a transition layer straddling these zones (75–450 m, since some Tucker trawls fished depths ranging from deeper Gulf Stream waters into cooler waters below). A Kolmogorov–Smirnov test (Statistica 6.0) was used to compare length frequency distributions among the three depth intervals.

Most specimens were preserved in the field in 10% formalin seawater solution and later stored in 40% isopropanol. Specimens collected along the southern Onslow Bay transect were preserved and stored in 95% ethanol. All specimens were identified to the lowest possible taxon, measured to the nearest 0.5 mm standard length (SL), and deposited in the ichthyology collection of the North Carolina Museum of Natural Sciences. Because *Ariosoma balearicum* may be represented by several populations in our area that exhibit different myomere count patterns (Smith 1989b; Miller 2002), we report those counts in a discussion of that species.

Results

In all areas and using diverse methods, we sampled 584 stations, 224 (38%) of which yielded eel leptocephali (Table 2). Thirty-nine percent of the stations were at night, with nearly equal effort split between surface neuston tows and deeper Tucker trawls. The more numerous daytime samples were heavily weighted toward surface neuston stations. Of the total 125 Tucker trawl tows (53 with embedded plankton nets), 90 (39 with embedded plankton nets) fished at discrete depths, and the remainder fished mostly at depth but also obliquely as they were hauled open to the surface. Most of the sampling effort (79%) was in offshore (> 40 m bottom depth) Gulf Stream waters, and this produced 94% of the larval eels (Fig. 1 and Table 2).

During the October 2005 cruise, the smaller mesh TT2 net was used on the surface neuston frame. No eel leptocephali were collected from the 14 day stations, and the 28 night stations produced 54 eel larvae of five species (14–102 mm SL, Table 3). These data were too limited for extensive comparisons; however, somewhat smaller eels were collected by this gear compared to previous years' neuston (NN1) samples. Lack of eels in the day surface tows suggested that we did not miss small eels during past day sampling because of gear bias, but rather that they were absent or rare in surface waters during the day.

Eel leptocephali were unevenly distributed by depth and time of day. Most larval eels were collected at night (79%, Table 2) and at depths > 45 m (Fig. 2). Discrete depth samples (neuston and Tucker trawl samples) from offshore waters contained 634 eel leptocephali. The 126 daytime offshore surface neuston tows yielded 16 leptocephali, compared with 239 individuals collected at night (96 tows) (Table 2). Nighttime offshore Tucker trawls that fished discrete depths (62 tows, 45–1,060 m) collected 329 larval eels, most (80%) occurring over a mean depth range of 59–353 m (Fig. 2). In contrast, daytime discrete depth Tucker trawl tows (24 tows, 103–1,293 m) yielded 50 specimens. Also, no eels were captured in six daytime Tucker trawls that fished obliquely over a depth range of 625 m to the surface (mean depth range 48–405 m). Species from three families that typically occupy only deep water as adults (Nemichthyidae, Nettastomidae, Synphobranchidae) were poorly represented and generally caught at depths > 43 m (Table 3). Three species from these families were only caught in oblique Tucker trawls, resulting in unknown capture depths, but probably they were caught where the nets spent most of the fishing time (109–268 m mean depths). Twenty-one taxa (107 individuals) of typically shallow

water families were collected in > 350 m (Table 4). Of the 29 discrete depth tows deeper than 350 m, 19 nighttime tows yielded 80% of these specimens (Table 4).

A total of 1,295 leptocephali (14 specimens identifiable only to Anguilliformes) were represented by 63 eel species in nine families (Table 3). Ninety-six percent of the specimens belonged to three families which were collected by most methods (Table 3). Most individuals (44%) were in the family Congridae, with at least 11 species collected, but the second most abundant family, Ophichthidae (30% of total individuals), contained more species (at least 27). Ten species represented the third most abundant family, Muraenidae (22%). Nine taxa accounted for 70% of the overall leptocephalus catches (in order of decreasing abundance): *Paraconger caudilimbatus*, *Gymnothorax ocellatus* complex, *A. balearicum*, *Ophichthus gomesii*, *Callechelys muraena*, *Letharchus aliculatus*, *Rhynchconger flavus*, *Ophichthus cruentifer*, and *Rhynchconger gracilior*. The top three species represented 52% of the total eel larvae collected and are discussed below.

The only offshore samples collected in colder months (November–May) were from the southern Onslow Bay stations. Few eel larvae (34 specimens) of ten taxa (*Anarchias similis*, *Apterichtus ansp*, *Gnathophipis* sp., *G. ocellatus* complex, *Hoplunnis diomediana*, *Myrophis punctatus*, *Ophichthini* sp., *O. cruentifer*, *O. gomesii*, *O. puncticeps*) were collected from November to May, and none were collected in January. Most (32 individuals, nine taxa) were collected in 11 (of 18) oblique bongo net tows. No taxa were unique to these samples.

Inshore Southern Onslow Bay collections

Leptocephalus collections from inshore waters (< 40 m) resulted from 124 daytime tows with small mesh nets in southern Onslow Bay (Fig. 1). These samples produced 73 larval eels of nine species in three families (Table 2). Most specimens were < 10 mm SL and/or were damaged and could not be identified to species. Ophichthidae was the dominant (66% of total) and most diverse (seven species) family collected from May to December. Only ophichthids were collected inshore from November to December, and the majority (63%) of small ophichthids (< 10 mm) were collected in October and November. In December, three *M. punctatus* (55–58 mm SL), one *A. ansp* (16 mm), and one unidentified ophichthid (damaged) were collected. Two other families, Congridae (8–34 mm) and Muraenidae (12–57 mm), were collected at inshore

Table 3 Numbers of anguilliform leptocephali followed by standard length ranges in parentheses collected off North Carolina by method. Depth ranges are based on all collections. Number of stations yielding leptocephali is in parentheses under gear type

Taxa	Depth range (m)	NN1 (32)	NN2 (6)	NN3 (14)	PN (9)	PN-TT (22)	TT1 (4)	TT2 (89)	TT3 (5)	BN (40)	Total, n
Anguillidae											
<i>Anguilla rostrata</i>	93–795	–	–	–	–	1 (16)	–	6 (18–50)	–	–	7
Moringuidae											
<i>Moringua edwardsi</i>	750–870	–	–	–	–	–	–	1 (42)	–	–	1
<i>Neocoinger mucronatus</i>	S	–	–	1 (33)	–	–	–	–	–	–	1
Chlopsidae											
<i>Chlopsis bicolor</i>	0–179	–	–	–	–	–	–	2 (13.5–17)	–	–	2
<i>Chlopsis dentatus</i> ^a	45–89	–	–	–	–	–	–	1 (19)	1 (25)	–	2
<i>Chlopsis</i> sp. ^a	312–389	–	–	–	–	–	–	1 (26.5)	–	–	1
Muraenidae											
<i>Anarchias similis</i>	90–113	–	–	–	–	–	–	1 (38.5)	–	1 (15)	2
<i>Gymnothorax miliaris</i> ^a	90–113	–	–	–	–	–	–	2 (26–29)	–	–	2
<i>Gymnothorax moringa</i>	97–611	–	–	–	–	–	–	10 (21–60)	–	–	10
<i>G. ocellatus</i> complex	S, 62–1,016	132 (28.5–87)	1 (26)	–	8 (12–36)	3 (18–45)	4 (39–56.5)	70 (17–68.5)	1 (21)	7 (12–31)	226
<i>Gymnothorax</i> sp. C	0–410	–	–	–	–	–	–	1 (45.5)	–	–	1
<i>Gymnothorax</i> sp. D	S, 90–383	2 (45–51.5)	–	–	–	–	1 (N/A)	9 (23–52)	–	–	12
<i>Gymnothorax</i> sp. E	0–629	–	–	–	–	–	–	1 (29)	–	–	1
<i>Gymnothorax vicinus</i>	90–113	–	–	–	1 (17)	–	–	5 (22–48)	–	–	6
<i>Gymnothorax</i> spp.	S, 45–1,293	2 (84–91)	–	–	1 (14)	2 (15–16)	–	7 (22–86.5)	–	1 (13)	13
<i>Monopenchelys acuta</i>	0–36	–	–	–	–	–	–	1 (17)	–	–	1
<i>Uropterygius macularius</i>	87–128	–	–	–	–	–	–	4 (29–31)	–	–	4
Undetermined	236–251	–	–	–	–	–	–	2 (44.5–53)	–	1 (9.5)	3
Synphobranchidae											
<i>Dysomma anguillare</i> ^a	0–268	–	–	–	–	–	–	1 (33)	–	–	1
Ophichthidae											
<i>Ahlia egmontis</i>	S, 62–68	1 (82)	–	–	1 (15.5)	–	–	5 (39–77)	–	–	7
<i>Apronathodon platyventris</i>	S	1 (76.5)	–	–	–	–	–	–	–	–	1
<i>Apterichthys ansip</i>	91–673	–	–	–	–	1 (52)	1 (53.5)	9 (22–50)	–	7 (12–64)	18
<i>Apterichthys kendalli</i>	93–336	–	–	–	–	–	–	1 (39)	–	–	1
<i>Bascanichthys scuticaris</i>	S, 215–938	1 (82)	–	–	–	1 (73.5)	–	4 (28–38)	–	–	6
<i>Callechelyini</i> sp. ^a	S, 45–320	1 (61.5)	–	–	–	–	1 (72.5)	2 (31–44.5)	–	–	4
<i>Callechelys guineensis</i>	113–335	–	–	–	–	–	–	1 (30)	–	–	3
<i>Callechelys muraena</i>	S, 45–938	6 (52–60)	–	–	1 (6)	4 (19.5–57.5)	–	45 (13–62)	–	2 (13–40)	60
<i>Callechelys</i> sp.	113–335	–	–	–	1 (7.5)	–	–	–	–	–	1
<i>Gordichthys ergodes</i> ^a	231–406	–	–	–	1 (28)	–	–	1 (78)	–	1 (63)	2
<i>Gordichthys leiiby</i>	500–673	–	–	–	–	2 (34–39)	–	2 (46–67.5)	–	–	5
<i>Gordichthys</i> sp.	0–77	–	–	–	–	–	–	–	–	1 (13)	1
<i>Ichthyapus ophioneus</i>	0–129	–	–	–	–	–	–	–	–	–	1
<i>Letharchus aliculatus</i> ^a	S, 45–938	2 (67–78.5)	–	–	3 (9–34.5)	1 (66)	1 (60)	23 (16–72.5)	–	1 (61)	31
<i>Letharchus velifer</i>	S, 105–401	1 (47)	–	–	–	1 (49)	–	1 (28)	–	–	3
<i>Myrichthys breviceps</i>	105–223	–	–	–	–	–	–	3 (28–52)	–	–	3
<i>Myrophis platyrhynchus</i>	S, 87–128	–	–	2 (14–20.5)	–	–	–	4 (15–49.5)	–	1 (9)	7
<i>Myrophis punctatus</i>	62–68	–	3 (55–58)	–	–	–	–	1 (61)	–	3 (14.5–28)	7

Table 3 continued

Taxa	Depth range (m)	NN1 (32)	NN2 (6)	NN3 (14)	PN (9)	PN-TT (22)	TT1 (4)	TT2 (89)	TT3 (5)	BN (40)	Total, n
<i>Myrophis</i> sp.	0–18	–	–	–	–	–	–	–	–	1 (36)	1
<i>Ophichthini</i> spp.	628–812	–	–	–	–	–	–	1 (71)	–	2 (11.5–17.5)	3
<i>Ophichthini</i> sp. 3	0–142	–	–	–	1 (12)	–	–	1 (56.5)	–	–	2
<i>Ophichthini</i> sp. 7	7–9	–	–	–	–	–	–	1 (45)	–	–	1
<i>Ophichthus cruentifer</i>	S, 121–938	1 (77)	–	–	–	3 (8–85)	–	19 (16–68)	–	1 (9)	24
<i>Ophichthus gomesii</i>	S, 83–938	7 (44.5–90)	–	1 (54)	4 (11–25)	5 (19.5–34)	–	41 (19–76)	–	11 (7.5–40)	69
<i>Ophichthus melanopus</i>	484–938	–	–	–	–	3 (18–40)	1 (23)	12 (17–84)	–	1 (15)	17
<i>Ophichthus menezesi</i>	0–139	–	–	–	–	–	–	2 (27–48)	–	–	2
<i>Ophichthus puncticeps</i>	99–320	–	–	–	–	–	1 (72.5)	4 (31–42.5)	1 (24)	3 (24.5–65)	9
<i>Ophichthus</i> sp.	0–53	–	–	–	–	–	–	–	–	1 (13)	1
<i>Pseudomyrophis fugesae</i>	0–116	–	–	–	–	–	–	1 (63)	–	–	1
<i>Pseudomyrophis nimius</i>	506–938	–	–	–	–	–	–	1 (74)	–	–	1
<i>Pseudomyrophis</i> sp. ^a	91–878	–	–	–	1 (54.5)	–	–	10 (29–58)	2 (18–53)	–	13
<i>Quassiremus ascensionis</i> ^a	0–84	–	–	–	–	–	–	–	–	1 (23)	1
Undetermined	S, 93–812	1 (N/A)	4 (5–9)	–	8 (5–11)	13 (4–10)	–	1 (36)	1 (12)	44 (4–18)	72
Nemichthyidae											
<i>Nemichthys scolopacea</i>	445–808	–	–	–	–	–	–	1 (181)	–	–	1
Congridae											
<i>Ariosoma balearicum</i>	S, 45–938	35 (62.5–155)	–	48 (44–102)	2 (86–95.5)	2 (71.5–99)	5 (56–102.5)	118 (20–139)	1 (10.5)	–	211
<i>Bathycongrus dubius</i>	59–448	–	–	–	–	–	–	5 (18–47)	–	–	5
<i>Bathycongrus</i> sp. A	0–54	–	–	–	1 (28)	–	–	–	–	–	1
<i>Bathycongrus</i> sp.	76–258	–	–	–	–	–	1 (105)	–	–	–	1
<i>Conger esculentus</i>	0–629	–	–	–	–	1 (17)	–	–	–	–	1
<i>Conger oceanicus</i>	99–320	–	–	–	–	–	1 (76.5)	–	–	–	1
<i>Conger</i> sp.	500–673	–	–	–	–	–	–	–	–	–	1
<i>Gnathophis</i> sp. ^a	0–629	–	–	–	1 (16)	–	–	1 (38)	–	–	1
<i>Heteroconger luteolus</i>	S, 45–799	4 (43–59.5)	–	–	1 (10)	–	–	3 (29.5–77)	–	1 (73)	6
<i>Paraconger caudilimbatus</i>	S, 45–938	2 (53–54)	–	2 (40.5–47)	2 (31–33)	14 (10.5–28)	3 (70.5–78.5)	5 (29.5–57.5)	–	–	11
<i>Paraconger</i> spp.	97–1,060	–	–	–	–	4 (9–14.5)	–	216 (10–84)	–	2 (12–34)	241
<i>Rhynchoconger flavus</i>	S, 45–370	1 (49.5)	–	–	1 (34.5)	1 (28)	1 (62)	11 (16–66.5)	1 (8.5)	1 (11)	17
<i>Rhynchoconger gracilior</i>	62–645	–	–	–	–	1 (68)	1 (109)	23 (34–63.5)	–	–	27
<i>Uroconger syringinus</i>	99–408	–	–	–	–	–	1 (106)	21 (38–91)	–	–	23
Undetermined	S, 57–74	–	–	–	–	–	–	1 (123)	–	–	2
Nettastomatidae											
<i>Hoplunnis diomediana</i>	105–223	–	–	–	–	1 (73)	–	4 (39–60)	–	1 (46)	6
<i>Hoplunnis macrura</i>	45–812	–	–	–	–	–	2 (91)	15 (58–99)	–	–	17
<i>Hoplunnis similis</i>	43–86	–	–	–	–	–	–	–	1 (23)	–	1
<i>Hoplunnis tenuis</i>	97–264	–	–	–	–	–	–	1 (N/A)	–	–	1
<i>Hoplunnis</i> spp.	43–86	–	–	–	–	–	–	–	2 (11–16)	–	2
<i>Nettenchelys inion/exoria</i> ^b	0–139	–	–	–	–	1 (8)	–	–	–	–	1
<i>Saurenchelys cognita</i>	97–878	–	–	–	–	–	1 (38)	6 (41–74)	–	–	7
<i>Saurenchelys stylura</i>	0–502	–	–	–	–	–	–	1 (62)	–	–	1

Table 3 continued

Taxa	Depth range (m)	NN1 (32)	NN2 (6)	NN3 (14)	PN (9)	PN-TT (22)	TT1 (4)	TT2 (89)	TT3 (5)	BN (40)	Total, <i>n</i>
<i>Saurenhelys</i> sp.	43–86	–	–	–	–	–	–	–	1 (12)	–	1
Undetermined	43–89	–	–	–	–	–	–	–	3 (15–28)	–	3
Total <i>n</i>		200	8	54	39	66	27	758	20	105	1,277

NN1 = 1 × 3-m neuston net, NN2 = 1 × 2-m neuston net, NN3 = 1 × 3-m neuston net, PN = 1-m plankton net inside Tucker trawl net, TT1 = 3.7 × 1.8-m Tucker trawl, TT2 = 2 × 2-m Tucker trawl, TT3 = 2 × 2-m Tucker trawl, BN = 60-cm bongo net, Total *n* = total number of leptocephali collected, S = surface. Specimens collected by dip net (*n* = 1) and Method frame trawl (*n* = 3) are not included. Unidentified (Anguilliformes, *n* = 14) specimens are not included

^aLarvae tentatively identified as in Böhlke (1989b)

^bLarvae cannot be differentiated at species level (Böhlke 1989b)

stations from May to August. Except for one *G. ocellatus* complex (57 mm), congrid and muraenids were collected inshore only when Gulf Stream waters moved onto the shelf (see Quattrini et al. 2005). No taxa were unique to the inshore stations.

Dominant species

The congrid, *P. caudilimbatus*, was the most abundant (19% of total) species collected. *Paraconger caudilimbatus* ranged from 10 to 84 mm SL (Table 3), but most (74%) specimens were small (< 40 mm, Fig. 3). They exhibited no significant size differences with depth zone (Kolmogorov–Smirnov test, $P > 0.05$). Only two specimens (12 and 34 mm) were collected at inshore southern Onslow Bay stations in oblique bongo net tows (0–20 m) in July and August. Discrete depth sampling yielded 77 *P. caudilimbatus* collected from the surface to a maximum mean depth of 764 m (Fig. 3). During the day, no *P. caudilimbatus* were collected at the surface (neuston net), and only nine were collected between 170 and 679 m. Four individuals were collected at the surface at night, but the majority (72%) was caught at night at mean depths of 67–353 m. There was a noticeable absence of *P. caudilimbatus* deeper than 400 m at sizes > 35 mm (Fig. 3).

The second most abundant taxon, *G. ocellatus* complex, could include up to three species (*G. ocellatus*, *G. nigromarginatus*, *G. saxicola*) whose larvae cannot be distinguished (Smith 1989c). Although we conservatively use the term *G. ocellatus* complex for these larvae, they are likely *G. saxicola* (see Discussion). This taxon composed 18% of the total individuals collected. Sizes ranged from 12 to 87 mm SL (Table 3), but the majority (66%) of specimens were large (42–72 mm, Fig. 4). There were no significant differences in sizes of *G. ocellatus* complex leptocephali collected by depth (Kolmogorov–Smirnov test, $P > 0.05$). Nine specimens (12–57 mm) were collected at inshore southern Onslow Bay stations between the surface and 22 m in May–August. Discrete depth collections produced 152 individuals from the surface to a mean depth of 977 m (Fig. 4). The majority (74%) of the *G. ocellatus* complex was collected on the surface at night, but a few (6%) were collected on the surface during the day. Below surface daytime discrete depth tows (275–977 m) resulted in 2% of the catch, while 18% were collected during discrete depth tows at night (67–569 m). This species was lacking from mean sample depths > 569 m at all sizes, except for one individual (Fig. 4).

Ariosoma balearicum composed 16% of the total leptocephali collected. This species was represented by

Fig. 2 Diel distribution by mean collection depths of all eel leptocephali collected off North Carolina, 1999–2005, by discrete depth Tucker trawl tows ($n = 86$) and surface neuston tows ($n = 222$). Each bar represents total numbers caught. Daytime bars to right of zero and nighttime bars to left represent Tucker trawl effort resulting in no eel captures. Number of surface neuston stations where no eels were caught are in center boxes at top for day (left) and night (right)

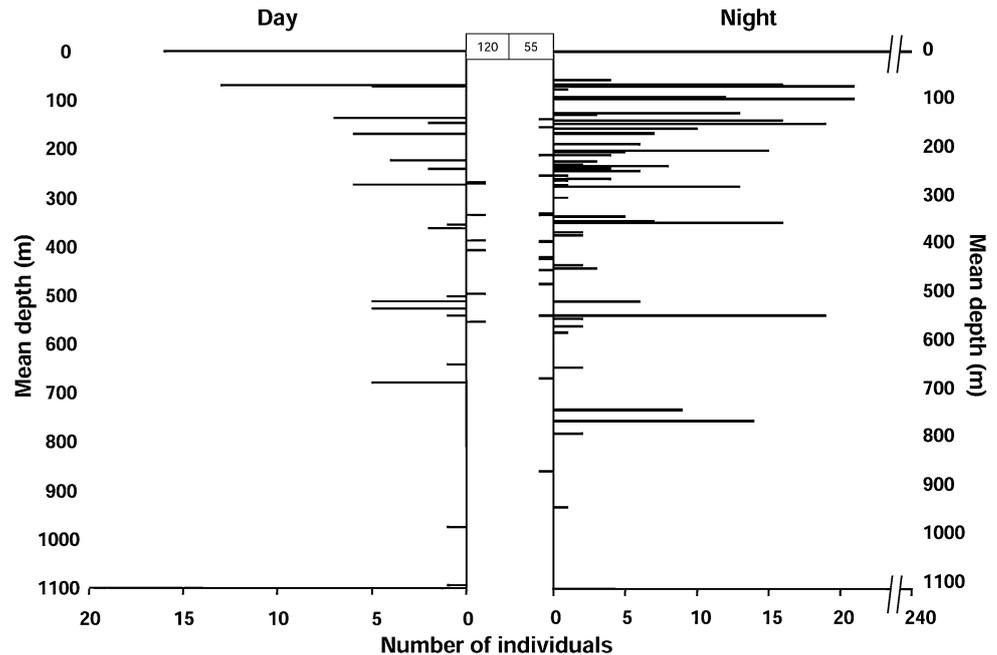


Table 4 Numbers of larvae of shallow water anguilliform species collected in 29 discrete depth tows ≥ 350 m off North Carolina, 1999–2005

Taxa	Day	Night
Anguillidae		
<i>Anguilla rostrata</i>		2
Moringiidae		
<i>Moringua edwardsi</i>		1
Chlopsidae		
<i>Chlopsis</i> sp. ^a		1
Muraenidae		
<i>Gymnothorax moringa</i>	1	
<i>Gymnothorax ocellatus</i> complex	2	9
<i>Gymnothorax</i> sp. D		1
<i>Gymnothorax</i> spp.	1	3
Ophichthidae		
<i>Apterichtus ansip</i>		1
<i>Bascanichthys scuticaris</i>		2
<i>Callechelys muraena</i>	3	3
<i>Gordüchthys leiby</i>		1
<i>Letharchus aliculatus</i> ^a	2	2
Ophichthini sp.	1	
<i>Ophichthus cruentifer</i>	1	7
<i>Ophichthus gomesii</i>	1	4
<i>Ophichthus melanoporus</i>		7
<i>Pseudomyrophis nimius</i>		1
<i>Pseudomyrophis</i> sp.		1
Undetermined	1	1
Congridae		
<i>Ariosoma balearicum</i>		17
<i>Conger</i> sp.		1
<i>Heteroconger luteolus</i>	1	1
<i>Paraconger caudilimbatus</i>	5	13
<i>Paraconger</i> sp.		2
<i>Rhynchoconger gracilior</i>	2	5
Total	21	86

^aLarvae tentatively identified as in Böhlke (1989b)

a large size range (10.5–155 mm SL, Table 3) and displayed no significant differences in sizes collected by depth (Kolmogorov–Smirnov test, $P > 0.05$). Most of these eels were between 30 and 65 mm SL, but there appeared to be a second group with SL ~ 70 –105 mm (Fig. 5). The smallest specimen collected (10.5 mm), perhaps recently hatched, was collected offshore in the upper 45 m in June. One glass eel stage specimen (98 mm) was observed actively swimming on the surface at night (August inshore station at a water depth of 39 m) and was subsequently collected by dipnet. A bimodal distribution of myomere counts was exhibited by *A. balearicum* with a dominant low count group (139 individuals, 10.5–155 mm), ranging from 122 to 130 (mean = 125.4), and a high count group (16 individuals, 21–30.5 mm), having a myomere count range of 133–136 (mean = 134.3). The majority (98%) of *A. balearicum* were collected at night (Fig. 5), with 77 of these from surface collections and 62 from a mean depth range of 67–764 m. The three specimens collected during the day were split between two surface tows (two individuals) and one Tucker trawl tow (one individual) from a mean depth of 148 m. This species was uncommon at depths > 400 m, especially at sizes > 80 mm (Fig. 5).

Discussion

The assemblage of anguilliform larvae that is transported along the coast of the southeastern United States via the Gulf Stream is diverse. However, this

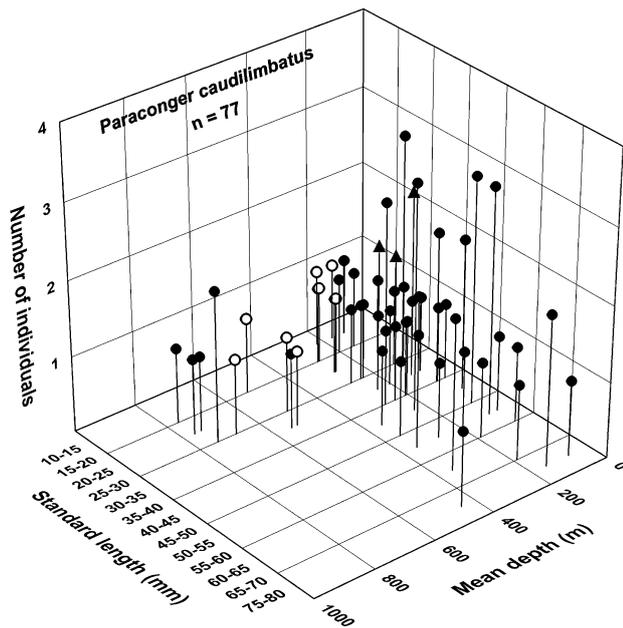


Fig. 3 *Paraconger caudilimbatus*. Length frequency distributions by mean collection depth for leptocephali collected off North Carolina (1999–2005). Discrete depth Tucker trawl tows (circles) and surface neuston tows (triangles) separated by day (open symbols) and night (closed symbols)

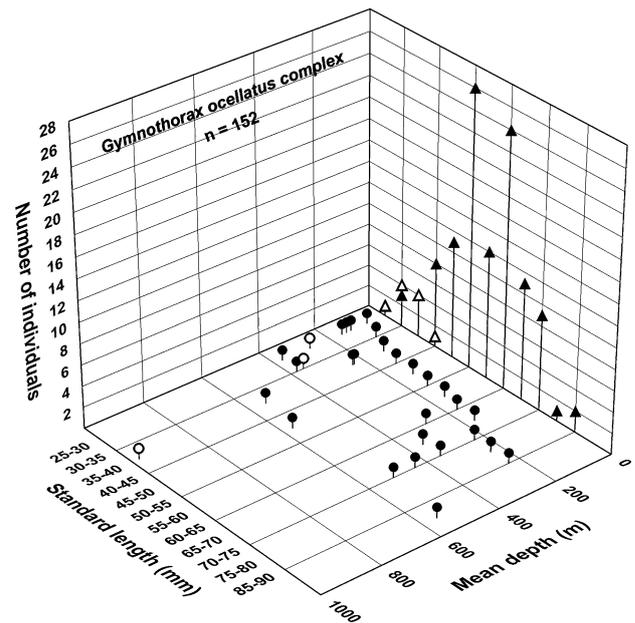


Fig. 4 *Gymnothorax ocellatus* complex. Length frequency distributions by mean collection depth for leptocephali collected off North Carolina (1999–2005). Discrete depth Tucker trawl tows (circles) and surface neuston tows (triangles) separated by day (open symbols) and night (closed symbols)

diversity was not reflected in previous larval fish studies in this area (Fahay 1975; Powles and Stender 1976; Powell et al. 2000; Marancik et al. 2005; Quattrini et al. 2005). Explanations for lower numbers of individuals and species in these studies compared with our study may be: (1) relatively more sampling effort at inshore stations in previous studies, (2) sampling at shallower depths even when offshore, (3) relatively more daytime sampling in some previous studies, (4) their use of smaller nets, (5) lack of identification of specimens beyond order or family levels, (6) eels omitted from analyses (Grothues et al. 2002). Despite some spatial and temporal limitations, our June to October Gulf Stream collections off North Carolina yielded a substantial proportion (63 species) of the 152 described anguilliform species (14 families) known from the western central Atlantic Ocean (Carpenter 2002). Thirteen species of these anguilliform larvae were not reported previously off North Carolina at any life history stage. Of eight possible shallow water families in the region, only two poorly known families (Heterenchelyidae and Muraenesocidae), occurring from the southern Caribbean to South America (Smith 2002a, b), were not represented in the North Carolina samples.

Other eel larvae were also notably rare or absent in our collections. Deep-water anguilliforms were poorly represented with only nine (three families) of a possi-

ble 37 (six families) western central Atlantic Ocean species collected. Lack of deep-water species may be partially explained by life history traits (e.g., spawning location, shorter larval duration) that facilitate

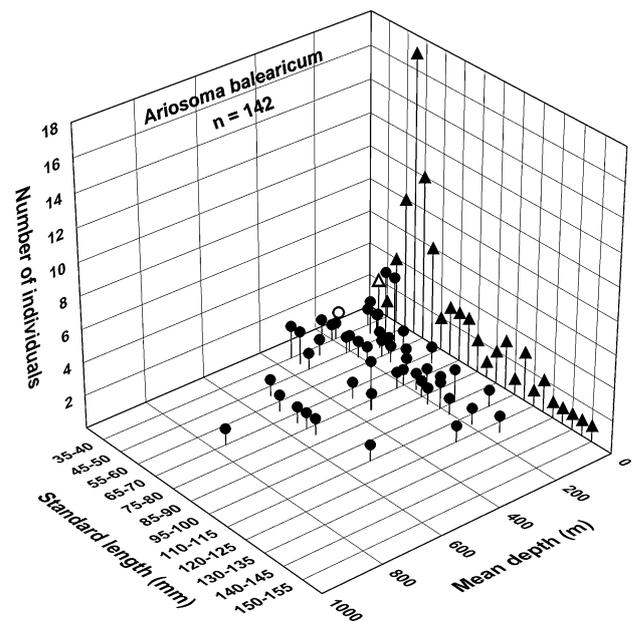


Fig. 5 *Ariosoma balearicum*. Length frequency distributions by mean collection depth for leptocephali collected off North Carolina (1999–2005). Discrete depth Tucker trawl tows (circles) and surface neuston tows (triangles) separated by day (open symbols) and night (closed symbols)

retention in Sargasso Sea (or other) waters (McCleave 1993), thus minimizing Gulf Stream entrainment. In addition, we may have missed some of these species because they spawn in the winter (Böhlke 1989a; McCleave 1993) or we did not sample deep enough. Except for the abundant *A. balearicum*, we only collected a few individuals of coastal or shelf eel species (*Anguilla rostrata*, *Conger oceanicus*, *Anarchias similis*) suspected of spawning in or near the Sargasso Sea (McCleave 1993). In addition, ophichthids (primarily *Ahlia egmontis*) that may spawn over the shelf edge off the Carolinas (Ross and Rohde 2003) were poorly represented in our samples. Lack of the Sargasso Sea and shelf edge spawning coastal species is curious, especially as *A. rostrata* and *C. oceanicus* have large populations along the Atlantic coast, and *A. rostrata* was abundant in previous July–August collections between Cape Romain and Cape Hatteras (Kleckner and McCleave 1982). Probably *C. oceanicus* was poorly represented in our samples because it spawns in the Sargasso Sea from late fall through early winter (McCleave and Miller 1994). Despite multiple gears and a range of temporal and spatial sampling, we may have under sampled some species because of the variable and patchy nature of larval fish distributions, and because we did not sample the same months or locations in all years.

The June to October species richness of larval eels off North Carolina was nearly equally represented by species with adult populations in this area and those for which juveniles or adults are not known. Including the *G. ocellatus* complex (see below), the leptocephali of 26 species (41% of the total species captured) correspond with juvenile or adult records of the 51 eel species known off North Carolina from the estuary to 2,300 m (S.W. Ross, unpublished data; Table 1). These 26 species accounted for 75% of the leptocephali collected, while other species were usually represented by few individuals. Adults or juveniles of most of the eel species we collected are also not known north of Cape Hatteras, where the adult eel fauna is relatively depauperate. Although at least 85 species of larval Anguilliformes are known north of Cape Hatteras (M. Fahay, personal communication), adults of only 25 species (18 restricted to > 200 m) are recorded from the Middle Atlantic Bight (MAB) through the Gulf of Maine (Collette and Klein-MacPhee 2002; Moore et al. 2003). More northern benthic habitats may be unsuitable (e.g., lack of coral reefs, low salinities, cooler temperatures) for juvenile or adult eels, most of which are warm water shelf species. Post larval stages of many eel species may not be known from the SAB or north of Cape Hatteras because: (1) their cryptic

nature hampers discovery, (2) they occupy unexplored habitats (Smith 2002c), or (3) their larvae never settle in this area. Although eels are difficult to collect at all stages, the estuaries and much of the continental shelf of the SAB, the MAB, and Gulf of Maine are well sampled. New records of adult or juvenile eels have been added from the SAB shelf (Burgess et al. 1979; Ross et al. 1981; Quattrini et al. 2004), and more are possible in this warm temperate region, but only one (*R. gracilior*) was recently discovered in shelf waters north of Cape Hatteras (Moore et al. 2003). It seems most likely that the absence of many tropical shelf species along the US East Coast is because they do not settle successfully.

Eel larvae that do not settle in the SAB or MAB face several potential fates. They may ultimately not contribute to their respective populations, or they may successfully recruit to their populations via several migratory pathways. Eel larvae could exit the Gulf Stream to the east or southeast (Schultz and Cowen 1994) and settle around Bermuda or be recirculated south toward the Bahamas (Miller 1995). We collected larvae of 20 of the 35 eel species known from Bermuda (Smith-Vaniz et al. 1999), seven of which are not recorded from the SAB as adults. Leptocephali could also avoid expatriation from the western Atlantic by completing a circuit around the North Atlantic, perhaps facilitated by the North Atlantic subtropical gyre (Sy 1988; McCleave 1993; Bourles et al. 1999). The long larval phase of many shelf eel species (from months to years) (Thresher 1984; Miller and Tsukamoto 2004) could facilitate long distance migrations such as in *Anguilla anguilla*. Supporting this hypothesis, Strang (1996) documented larvae of seven western Atlantic species in the eastern Atlantic whose adults are not known in the eastern Atlantic. She also noted that larvae of several ampho-Atlantic species occurred in the eastern Atlantic at moderate to large (e.g., *Chlopsis bicolor*) sizes. These could have been western Atlantic larvae continuing a full circuit migration of the North Atlantic basin.

Vertical distributions and diel migrations

Many eel larvae appear to undertake diel vertical movements (Keller 1976; Castonguay and McCleave 1987; Smith 1989a). Leptocephali are reported to be most common in the upper 250 m (Castonguay and McCleave 1987; Smith 1989a; Miller 1995; Miller and Tsukamoto 2004; Wouthuyzen et al. 2005); however, discrete depth sampling > 350 m is limited. While we also collected most eel larvae at depths < 350 m, substantial numbers were collected deeper. Beebe (1934)

observed eel leptocephali off Bermuda during daytime at depths of 230–700 m, and in the same region Keller (1976) collected larvae of six eel species at > 300 m. Leptocephali of 15 species were collected in the eastern and central Atlantic from 400–2,000 m depths (Strang 1996). Shelf species occurring deeper than 350 m may not return to shallower depths, thus being lost to their populations. Alternatively, depths > 350 m may be part of the normal diel or ontogenetic migrations of larval eels. Some leptocephali use increasingly greater depth ranges as they age (e.g., *Anguilla* spp., Castonguay and McCleave 1987). Eel leptocephali seem to be good swimmers (Beebe 1934; Smith 1989a; Tomoda and Uematsu 1996; Miller and Tsukamoto 2004) and are capable of moving significant vertical distances, assuming that thermoclines (Kajihara et al. 1988) or mesopelagic habitats are not restrictive. Additional deep discrete depth sampling is needed, especially during the day and at > 300 m.

In agreement with other studies, the majority of larval eels off North Carolina were collected at night in the upper 300 m. Daytime distributions were less clear, due to low catches and lack of discrete depth sampling. Low daytime catches of leptocephali are often attributed to net avoidance (Keller 1976; Schoth and Tesch 1984; Castonguay and McCleave 1987). The daytime net avoidance argument ignores that these large nets are probably visible at all depths, especially at night due to high densities of bioluminescent organisms in the Gulf Stream (Wiebe et al. 1982). Larval eels, with great visual acuity and optic systems enhanced for night vision (Tomoda and Uematsu 1996), should be as likely to avoid the nets at night. Pressure waves preceding these small mesh nets may also cause catch inefficiency (Fleminger and Clutter 1965), but this would have the same effect regardless of time of day or depth. Even allowing for substantial net avoidance during the day (Barkley 1972; Ianson et al. 2004) and the patchiness of plankton, if larval eels were abundant in the daytime depths we sampled, it seems that they should have been more abundant in our day catches (Wiebe et al. 1982). For example, 98% of *A. balearicum* were collected at night, but it seems unlikely that nearly the whole population avoided our daytime tows. However, our low daytime catches could be accounted for if eel larvae had moved to depths that were poorly sampled (> 350 m). This seems reasonable in that: (1) eel larvae > 20 mm should be capable of swimming over at least a 500–600 m range in 3–4 h, and (2) numerous leptocephali have been collected at depths > 400 m. Both explanations (net avoidance and deeper daytime distributions) should be examined in more detail, including more sampling over a broader daytime

depth range to at least 800 m (Wiebe et al. 1982; Ianson et al. 2004).

Dominant species

All three dominant eel species reach the northern end of their adult distributions off North Carolina, but little is known of their biology or ecology. Adult *P. caudilimbatus*, occurring in Bermuda (rare) and south through the Gulf of Mexico, Bahamas, Cuba, Caribbean coast of Mexico, and eastern Colombia, seem to be most common on shelf edge hardgrounds in the SAB, but inhabit soft substrate bottoms in other areas (Ross et al. 1981; Smith 1989d). All of the larval specimens we collected were much smaller than the 110 mm SL maximum size at metamorphosis (Smith 1989b), suggesting that they were likely to spend more time in the plankton. Identification of *Paraconger* sp. larvae can be difficult as vertebral counts of several species overlap (Smith 1989b, d). Identifications of *P. caudilimbatus* in the present study are believed to be correct because: (1) all had myomere counts < 126.2) other *Paraconger* species are unknown from the area, (3) a recognized expert (D.G. Smith, Smithsonian Inst.) confirmed identifications of subsamples.

Although the three species in the abundant *G. ocellatus* complex cannot be resolved, it is likely that most of our specimens were *G. saxicola*. *Gymnothorax saxicola* is well established along the southeastern US coast and is one of the most abundant eels on and near shelf hardgrounds, while *G. ocellatus* has no adult populations north of the Greater Antilles and *G. nigromarginatus* adults seem to be restricted to the Gulf of Mexico (Böhlke et al. 1989). Our length data suggested that spawning had occurred some months prior to collection off North Carolina. Since larvae in this group probably metamorphose around 80–90 mm SL (Smith 1989c) and most of our specimens were 25–70 mm, these larvae were probably not near settlement. The most common eel larva collected off Barbados during April–June was *G. ocellatus* (Richardson and Cowen 2004). We assume that Richardson and Cowen (2004) considered these to be *G. ocellatus*, rather than the complex of three species, because their collections were close to the adult distribution of *G. ocellatus* and were upstream of the adult distributions of the other two *Gymnothorax* species.

Despite its abundance in leptocephalus collections (Castle 1970; Keller 1976; Miller 1995, 2002), little is known of later stages of *A. balearicum*. It occurs on soft substrates from North Carolina to Brazil, including the Gulf of Mexico and the Caribbean, and adults may not migrate far to spawn (Smith 1989d). *A. balearicum*

larvae metamorphose at 105–200 mm SL (Smith 1989b; Miller 2002), and most of our collections were well below these sizes. Miller (2002) consistently collected 70–100 mm *A. balearicum* in the Sargasso Sea during February–April. We also collected a small number in this size range, but most of our collections were 40–65 mm SL, which matched those reported by Miller (2002) from Bermuda and various Gulf Stream collections in September–November. Populations of *A. balearicum* identified by high and low myomere/vertebral counts mix in the Florida Current and Gulf Stream (Smith 1989b, d; Miller 2002), and we collected both groups off North Carolina. Our collections were dominated by the low count form which is believed to represent populations from the Gulf of Mexico and Bahamas/Caribbean region (Miller 1995). Higher vertebral numbers supposedly characterize a southeastern US population (represented in our samples by the less abundant, small sized *A. balearicum* larvae) (Smith 1989b, d); however, the sample size of adults for these counts was low and few of these were from north of Florida (Smith 1989d). It seems likely that low count *A. balearicum* would settle along the southeastern US coast, and they may spawn there or nearby (the smallest one we collected, 10.5 mm SL, was low count), thus the mechanisms isolating these groups are unclear and require further investigation.

Data from off North Carolina are especially valuable as this is the ecological/zoogeographical terminus for many species within the SAB region and is the area where the Gulf Stream changes direction eastward. It is important to note that we sampled a moving fauna within a huge system, the Gulf Stream. For that reason these North Carolina data likely represent a larger area as well (e.g., Florida to South Carolina).

Acknowledgments This research was partially funded by grants from the NOAA Office of Ocean Exploration (grants NA16RP2696, NA030AR4600090, NA040AR4600056, NA050AR4601065 to S.W. Ross, lead Principle Investigator). The 1999 and 2000 cruises were partially supported by the North Carolina Legislature (to S.W. Ross). The August 2001 RV Cape Hatteras mission was sponsored by the Duke/UNC Oceanographic Consortium (to S.W. Ross). We thank the UNC-Wilmington Coastal Ocean Research and Monitoring Program (funded by NOAA grants NA16RP1460 and NA96RU0259) for the 2000–2001 southern Onslow Bay study. United States Geological Survey (USGS), Florida Integrated Science Center (through K.J. Sulak) provided personnel and logistics support. Jennifer McClain provided valuable assistance in sorting leptocephali from numerous plankton samples. We thank David G. Smith (Smithsonian Inst.) for his generous donations of time to help identify several eel leptocephali. We thank Michael Fahay (NOAA Fisheries Service) for encouraging this study and providing us with a preliminary list of eel larvae collected in the Middle Atlantic Bight. We thank Jose Torres (Univ. of South Florida) for loan of Tucker trawls for the 1999 cruise.

References

- Adams CE, Jr, Berger TJ, Boicourt WC, Churchill JH, Earle MD, Hamilton P, Vukovich FM, Wayland RJ, Watts DR (1993) A review of the physical oceanography of the Cape Hatteras, North Carolina region, vol 1. Literature synthesis. OCS Study MMS 93/0031, US Dept Int, Minerals Management Serv
- Barkley RA (1972) Selectivity of towed-net samplers. Fish Bull 70:799–820
- Beebe W (1934) Half mile down. Duell, Sloan and Pearce, New York
- Böhlke EB (eds) (1989a) Fishes of the western North Atlantic: anguilliformes and saccopharyngiformes. Mem Sears Found Mar Res, New Haven
- Böhlke EB (ed) (1989b) Fishes of the western North Atlantic: leptocephali, Part 9, vol 2. Mem Sears Fdn Mar Res, New Haven
- Böhlke EB, McCosker JE, Böhlke JE (1989) Family Muraenidae. In: Böhlke EB (ed) Fishes of the western North Atlantic: anguilliformes and saccopharyngiformes, Part 9, vol 1. Mem Sears Fdn Mar Res, New Haven, pp 104–206
- Bourles B, Molinari RL, Johns E, Wilson WD, Leaman KD (1999) Upper layer currents in the western tropical North Atlantic. J Geophys Res 104:1661–1375
- Burgess GH, Link GW, Jr., Ross SW (1979) Additional marine fishes new or rare to Carolina waters. Northeast Gulf Sci 3:74–87
- Carpenter KE (ed) (2002) The living marine resources of the Western Central Atlantic, vol 2: Bony fishes part 1 (Acipenseridae to Grammatidae). FAO Species Identification Guide for Fishery Purposes and Amer Soc Ichthyol and Herpetol. Spec publ no. 5, Rome
- Castle PHJ (1970) Results of the research cruises of FRS 'Walther Herwig' to South America. XI. The leptocephali. Arch Fischereiwiss 21:1–21
- Castonguay M, McCleave JD (1987) Vertical distributions, diel and ontogenetic vertical migrations and net avoidance of leptocephali of *Anguilla* and other common species in the Sargasso Sea. J Plankton Res 9:195–214
- Collette BB, Klein-MacPhee G (eds) (2002) Bigelow and Schroeder's fishes of the Gulf of Maine. Smithsonian Institution Press, Washington
- Fahay MP (1975) An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV Dolphin cruises between May 1967 and February 1968. NMFS Tech Rep SSRF 685
- Fleminger A, Clutter RI (1965) Avoidance of towed nets by zooplankton. Limnol Oceanogr 10:96–104
- Govoni JJ, Spach HL (1999) Exchange and flux of larval fishes across the western Gulf Stream front south of Cape Hatteras, USA, in winter. Fish Oceanogr 8:77–92
- Grothues TM, Cowen RK, Pietrafesa LJ, Bignami F, Weatherly GL, Flagg CN (2002) Flux of larval fish around Cape Hatteras. Limnol Oceanogr 47:65–175
- Ianson D, Jackson GA, Angel MV, Lampitt RS, Burd AB (2004) Effect of net avoidance on estimates of diel vertical migration. Limnol Oceanogr 49:2297–2303
- Kajihara T, Tsukamoto K, Otake T, Mochioka N, Hasumoto H, Oya M, Tabeta O (1988) Sampling leptocephali with reference to the diel vertical migration and the gears. Bull Jap Soc Sci Fish 54:941–946
- Keller AA (1976) Systematics, vertical distribution, and life history of anguilliform leptocephali in the Bermuda Ocean Acre. MSc thesis, University of Rhode Island

- Kleckner RC, McCleave JD (1982) Entry of migrating American eel leptocephali into the Gulf Stream system. *Helgol Meeresunters* 35:329–339
- Marancik KE, Clough LM, Hare JA (2005) Cross-shelf and seasonal variation in larval fish assemblages on the southeast United States continental shelf off the coast of Georgia. *Fish Bull* 103:108–129
- McCleave JD (1993) Physical and behavioural controls on the oceanic distribution and migration of leptocephali. *J Fish Biol* 43:243–273
- McCleave JD, Miller MJ (1994) Spawning of *Conger oceanicus* and *Conger triporiceps* (Congridae) in the Sargasso Sea and subsequent distribution of leptocephali. *Environ Biol Fish* 39:339–355
- Miller MJ (1995) Species assemblages of leptocephali in the Sargasso Sea and Florida Current. *Mar Ecol Prog Ser* 121:11–26
- Miller MJ (2002) The distribution and ecology of *Ariosoma balaericum* (Congridae) leptocephali in the western North Atlantic. *Environ Biol Fish* 63:235–252
- Miller MJ, McCleave JD (1994) Species assemblages of leptocephali in the Subtropical Convergence Zone of the Sargasso Sea. *J Mar Res* 52:743–772
- Miller MJ, Tsukamoto K (2004) An introduction to Leptocephali: biology and identification. Ocean Research Inst, University of Tokyo, Tokyo
- Moore JA, Hartel KE, Craddock JE, Galbraith JK (2003) An annotated list of deepwater fishes from off the New England region, with new area records. *Northeast Nat* 10:159–248
- Powell AB, Robbins RE (1994) Abundance and distribution of ichthyoplankton along an inshore–offshore transect in Onslow Bay, North Carolina. NOAA Tech Rep NMFS 120
- Powell AB, Robbins RE (1998) Ichthyoplankton adjacent to live-bottom habitats in Onslow Bay, North Carolina. NOAA Tech Rep NMFS 133
- Powell AB, Lindquist DG, Hare JA (2000) Larval and pelagic juvenile fishes collected with three types of gear in Gulf Stream and shelf waters in Onslow Bay, North Carolina and comments on ichthyoplankton distribution and hydrography. *Fish Bull* 98:427–438
- Powles H, Stender W (1976) Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. Tech Rep S.C. Mar Resour Cent no. 11, Charleston
- Quattrini AM, Ross SW, Sulak KJ, Necaie AM, Casazza TL, Dennis GD (2004) Marine fishes new to continental United States waters, North Carolina, and the Gulf of Mexico. *Southeast Nat* 3:55–172
- Quattrini AM, Lindquist DG, Bingham FM, Lankford TE, Govoni JJ (2005) Distribution of larval fishes among water masses in Onslow Bay, North Carolina: implications for cross-shelf exchange. *Fish Oceanogr* 14:413–431
- Richardson DE, Cowen RK (2004) Diversity of leptocephalus larvae around the Island of Barbados: relevance to regional distributions. *Mar Ecol Prog Ser* 282:271–284
- Ross SW, Rohde FC (2003) Collections of ophichthid eels on the surface at night off North Carolina. *Bull Mar Sci* 72:241–246
- Ross SW, Link GW Jr, MacPherson KA (1981) New records of marine fishes from the Carolinas, with notes on additional species. *Brimleyana* 6:61–72
- Schmidt J (1922) The breeding places of the eel. *Philos Trans R Soc Lond B* 211:179–208
- Schoth M, Tesch FW (1984) The vertical distribution of small 0-group *Anguilla* larvae in the Sargasso Sea with reference to other anguilliform leptocephali. *Meeresforschung/Rep Mar Res* 30:188–195
- Schultz ET, Cowen RK (1994) Recruitment of coral-reef fishes to Bermuda: Local retention or long-distance transport? *Mar Ecol Prog Ser* 109:15–28
- Smith DG (1989a) Introduction to leptocephali. In: Böhlke EB (ed) *Fishes of the western North Atlantic, Part 9, vol 2*. Mem Sears Fdn Mar Res, New Haven, pp 657–668
- Smith DG (1989b) Family Congridae: Leptocephali. In: Böhlke EB (ed) *Fishes of the western North Atlantic, Part 9, vol 2*. Mem Sears Fdn Mar Res, New Haven, pp 723–763
- Smith DG (1989c) Family Muraenidae: Leptocephali. In: Böhlke EB (ed) *Fishes of the western North Atlantic, Part 9, vol 2*. Mem Sears Fdn Mar Res, New Haven, pp 900–916
- Smith DG (1989d) Family Congridae. In: Böhlke EB (ed) *Fishes of the western North Atlantic, Part 9, vol 1*. Mem Sears Fdn Mar Res, New Haven, pp 460–567
- Smith DG (2002a) Larvae of the garden eel genus *Gorgasia* (Congridae, Heterocongrinae) from the western Caribbean Sea. *Bull Mar Sci* 70:831–836
- Smith DG (2002b) Family Heterenchelyidae. In: *The living marine resources of the Western Central Atlantic, vol 2. Bony fishes part 1 (Acipenseridae to Grammatidae)*. FAO Species Identification Guide for Fishery Purposes and Amer Soc Ichthyol Herpetol, Spec publ no. 5. Rome, p 694
- Smith DG (2002c) Family Muraenesocidae. In: *The living marine resources of the Western Central Atlantic, vol 2. Bony fishes part 1 (Acipenseridae to Grammatidae)*. FAO Species Identification Guide for Fishery Purposes and Amer Soc Ichthyol Herpetol, Spec publ no. 5. Rome, pp 738–739
- Smith-Vaniz WF, Collette BB, Luckhurst BE (1999) *Fishes of Bermuda: history, zoogeography, annotated checklist, and identification keys*. Amer Soc Ichthyol Herpetol, Spec publ no. 4. Lawrence
- Strang PM (1996) On the identity and distribution of eel leptocephalus larvae in the eastern North Atlantic. PhD, Queen Mary and Westfield College, University of London
- Sy A (1988) Investigation of large-scale circulation patterns in the central North-Atlantic - the North-Atlantic Current, the Azores Current, and the Mediterranean Water plume in the area of the mid-Atlantic ridge. *Deep-Sea Res* 35:383–413
- Thresher RE (1984) *Reproduction in reef fishes*. T.F.H. Publ, Neptune City
- Tomoda H, Uematsu K (1996) Morphogenesis of the brain in larval and juvenile Japanese eels, *Anguilla japonica*. *Brain Behav Evol* 47:33–41
- Wiebe PH, Boyd SH, Davis BM, Cox JL (1982) Avoidance of towed nets by the euphasiid *Nematoscelis megalops*. *Fish Bull* 80:75–91
- Wippelhauser GS, McCleave JD, Kleckner RC (1985) *Anguilla rostrata* leptocephali in the Sargasso Sea during February and March 1981. *Dana* 4:93–98
- Wouthuyzen S, Miller MJ, Aoyama J, Minagawa G, Sugeha HY, Suharti SR, Inagaki T, Tsukamoto K (2005) Biodiversity of anguilliform leptocephali in the central Indonesian Seas. *Bull Mar Sci* 77:209–223