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Abstract.—Analysis of surface and subsurface plankton collections in the Middle Atlantic Bight (MAB) yielded larvae and juveniles of *Phycis chesteri* and five species of *Urophycis*. Identification was based on numbers of epibranchial gill rakers, abdominal vertebrae, and fin rays (dorsal, caudal, pelvic), patterns of pterygiophore interdigitation, and morphometric characters including body depth at the vent and a ratio between height of the pelvic-fin base and length of the mandible. *Urophycis tenuis* accounted for 99% of the *Urophycis* larvae and pelagic juveniles collected during spring off Virginia and New Jersey and was most abundant offshore. *Urophycis tenuis* larvae were smallest at offshore stations and increased in size as collections proceeded shoreward. *Urophycis chuss* was found in summer and fall collections off the coasts of New Jersey and Virginia, with abundances highest at midshelf stations. *Urophycis chuss* was the only species of hake found during August and early September, and it dominated summer ichthyoplankton collections. *Urophycis regia* was found primarily in midshelf areas off Virginia during fall, but was also collected offshore from both Virginia and New Jersey during winter. *Phycis chesteri*, also found in fall and winter collections, was restricted to offshore stations. Southern species, found exclusively in offshore winter collections, included *U. floridana* and *U. cirrata*.

Identification and distribution of *Urophycis* and *Phycis* (Pisces, Gadidae) larvae and pelagic juveniles in the U.S. Middle Atlantic Bight*

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Species of the gadid genera *Urophycis* (Gill) and *Phycis* (Artemi), collectively referred to as 'hakes', are abundant on the continental shelf and slope of the northwest Atlantic Ocean. Six species of *Urophycis* and one species of *Phycis* are found in this area (Svetovidov 1948, Wenner 1983): *U. tenuis* (Mitchill), *U. chuss* (Walbaum), *U. regia* (Walbaum), *U. floridana* (Bean and Dresel), *U. earlli* (Bean), *U. cirrata* (Goode and Bean), and *P. chesteri* (Goode and Bean). Larval hake are present at all times of the year in the Middle Atlantic Bight (MAB) and dominate summer plankton collections (Comyns 1987), but persistent taxonomic problems (Dunn & Matarese 1984) have hindered the accumulation of ecological data on these important components of offshore ichthyoplankton communities (Kendall & Naplin 1981, Hermes 1985).

Newly hatched *U. chuss* and *U. regia* of known parentage were described by Hildebrand & Cable (1938), Miller & Marak (1959), Barans & Barans (1972), and Serebryakov (1978). Although these sources describe pigmentation differences between the two species, this information alone is insufficient to positively identify field-caught larvae.

Older larvae and juveniles of *U. chuss*, *U. regia*, *U. floridana*, and a single juvenile specimen of *U. earlli* were described by Hildebrand & Cable (1938). Larvae and juveniles of *U. regia* were collected off Beaufort NC and were identified by the presence of relatively few second dorsal-fin rays and lack of dark ventral-fin pigment. A second larval morph collected off Beaufort was tentatively identified as *U. floridana* because adult *U. floridana* was the only other species of *Urophycis* commonly found in the collection area. These specimens differed from *U. regia* in having darkly-pigmented ventral fins and more second dorsal-fin rays. A single juvenile specimen (37mm) collected off Beaufort was identified as *U. earlli* because this specimen was darker than *U. regia* and *U. floridana*, and possessed smaller scales. Specimens of a fourth morph, collected off Cape Henry VA were identified as *U. chuss* because they possessed dark ventral-fin pigment, were relatively slender-bodied, and it was assumed that

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U. floridana would not be found as far north as Cape Henry.

Methven (1985) presented a size-dependent key to the identification of young *U. chuss*, *U. tenuis*, and *P. chesteri* from the Northwest Atlantic. Identifications were based on body depth, numbers of epibranchial gill rakers (Musick 1973, Wenner 1983), and numbers of caudal-fin rays. Material for Methven's study came primarily from Canadian waters, and he did not encounter *U. cirrata*, *U. earlli*, *U. floridana*, or *U. regia*. As a result, Methven's key is of limited use in more southerly locations where these species occur.

The objective of this paper is to describe additional morphometric and meristic characters that aid in the identification of *Urophycis* and *Phycis* larvae, and to describe the spatial and temporal distribution of these larvae collected 1975–77 off Virginia and New Jersey in the Middle Atlantic Bight.

Materials and methods

Sampling locations and shipboard procedures

Sampling extended from October 1975 until August 1977 and was conducted quarterly at 12 stations off Virginia and New Jersey (Fig. 1, Table 1). Neuston samples were collected with a floating sampler developed at Woods Hole Oceanographic Institution (Bartlett & Haedrich 1968, Craddock 1969). The net, constructed with 505 μm mesh Nitex, was 1 m wide and fished to a depth of 12 cm in calm seas. Tows were of 20 min duration at a ship speed of ~ 2 kn. The net was deployed from a boom and the towing course followed a widely-circular track to prevent sampling in the ship's wake. A single neuston tow was made at 3 h intervals over a 24 h period at each station, resulting in eight samples per station during each cruise. Two oblique tows between nearsurface and bottom were made at all stations with 60 cm opening-closing bongo systems (McGowan & Brown 1966), the first with paired 202 μm Nitex nets and the second with paired 505 μm nets. To prevent surface contamination, all nets were closed during passage through the surface layer (upper meter). Both bongo and neuston nets were equipped with flowmeters (General Oceanics, Inc.). The flowmeter attached to the underside of the neuston frame provided an estimate of horizontal distance relative to sea surface fished by the net. Estimates of volume filtered by the neuston sampler were determined by multiplying distance fished by net area fished (1 m \times 12 cm). In calm seas the neuston sampler consistently fished to a depth of 12 cm, but in rough seas the net opening would occa-

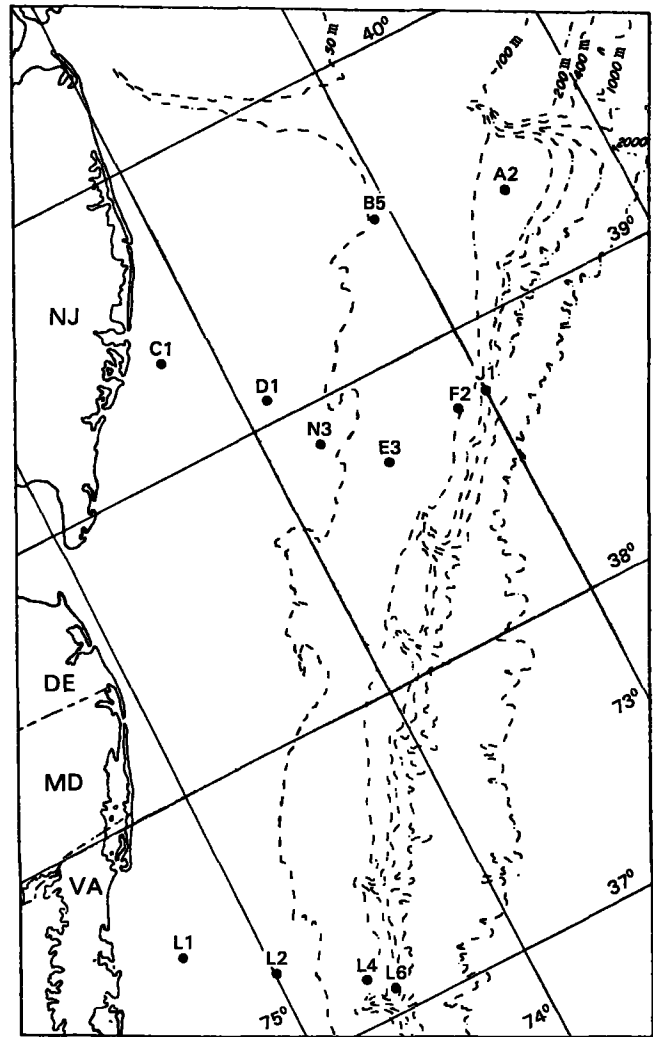


Figure 1

Ichthyoplankton sampling locations off New Jersey and Virginia. Stns. F2, J1, A2, L4, and L6 are considered offshore stations.

sionally be almost completely filled or empty (the flowmeter was always submerged). This variability decreased precision of neuston volume estimates but was not expected to bias volume estimates. Comparisons between neuston and bongo collections were performed only to emphasize the relative importance of the surface layer to larval hakes. Patterns of the spatial and temporal distribution of larvae were based only on comparisons among neuston collections because most specimens were collected with this gear type.

Laboratory procedures

Fish larvae were sorted from whole collections. All specimens of *Urophycis* and *Phycis* were cleared and stained (Dingerkus & Uhler 1977, Potthoff 1984, Tay-

Table 1

Sampling schedule for twelve stations occupied off New Jersey (NJ) and Virginia (VA), 1975-77.

Stn.	1975		1976			1977		
	Oct	Feb	Jun	Aug Sep	Nov	Feb Mar	May	Aug
C1 (NJ)	X	X	X	X	X	X	X	X
D1	X	X	X	X	X	X	X	X
N3	X	X	X	X	X	X	X	X
E3	X	X	X	X	X	X	X	X
F2	X	X	X	X	X	X	X	X
J1	X	X	X	X	X	X	X	X
B5 (NJ)					X	X	X	X
A2					X	X	X	X
L1 (VA)					X	X	X	X
L2					X	X	X	X
L4					X	X	X	X
L6					X	X	X	X

lor & Van Dyke 1985), except those occurring in collections taken during August-September 1976 ($n > 16,000$) and August 1977 ($n > 4000$). During these periods of high abundance, subsamples of over 2000 larvae from August-September 1976 and > 900 larvae from August 1977 were randomly selected and similarly processed. Herein specimens < 18 mmSL are arbitrarily termed larvae, whereas fish ≥ 18 mm are termed juveniles (Markle et al. 1982). Fish $< \sim 12$ mm were measured with an ocular micrometer, while lengths of larger specimens were measured with a dial caliper ruler. The largest pelagic juveniles found were ~ 40 mmSL.

The following morphometric criteria were used in the analysis: (1) height of pelvic fin/vertical distance from base of pelvic fin to ventral margin of body; (2) mandible length/distance from anterior tip of the dentary to posteroventral tip of the angular; and (3) body depth at anus/vertical distance from anterior end of anal-fin base to dorsal surface immediately above. Morphometric measurements were made with an ocular micrometer. The first interneural space was defined as the space anterior to the first neural spine.

Hake larvae and juveniles possessing the adult meristic complement were initially identified using published and unpublished meristic data (Table 2). Meristic observations included epibranchial gill rakers (left side examined), abdominal vertebrae, and fin rays (dorsal, caudal, pelvic). Observations were taken from both cleared and stained material and from radiographs of juvenile and adult museum specimens (App. Table 1).

Identification of smaller larvae was facilitated by using morphometric criteria, patterns of interdigitation between pterygiophores supporting the median fins and the neural or haemal spines, and by defining the size at which larvae attained various stages of fin-ray, vertebral, and gill-raker development. Unfortunately, faded pigmentation caused by specimen storage in formalin and subsequent clearing and staining prevented use and further description of larval pigmentation in the present study.

Table 2

Ranges of meristic characters in *Phycis chesteri* and six species of *Urophycis*. Numbers in parentheses indicate meristic ranges that were extended by the present study. Data sources are (1) Svetovidov 1948, (2) Hildebrand & Cable 1938, (3) Bigelow & Schroeder 1953, (4) Leim & Scott 1966, (5) Miller & Jorgenson 1973, (6) Musick 1973, (7) Hoese & Moore 1977, (8) Markle 1982, (9) Fahay 1983, (10) Wenner 1983, (11) Methven 1985, (12) J.A. Musick, pers. commun., VIMS, Gloucester Point VA 23062.

	<i>U. tenuis</i>	<i>U. chuss</i>	<i>U. regia</i>	<i>U. floridana</i>	<i>U. earlIIi</i>	<i>U. cirrata</i>	<i>P. chesteri</i>
Caudal-fin rays	33-38(40)	28-34	28-32(34)	28-32(34)	27-30(31)	28-33	28-35(36)
1st dorsal-fin rays	9-10(12)	9-11(12)	8-10	10-13	8-11	9-11(12)	8-11(12)
2nd dorsal-fin rays	50-59(62)	(52)53-64	43-51(52)	54-63	57-63(68)	54-68	50-63
Anal-fin rays	41-52(53)	45-57	41-50(52)	45-54(55)	49-56(60)	46-58	43-54
Vertebrae (total)	47-50(51)	45-50(51)	(44)45-47(48)	44-50(51)	45-47(48)	47-53	45-52
Caudal vertebrae	(32)34-35	33-36	(30)31-33(34)	30-34(35)	31-33(34)	32-37	31-37
Abdominal vertebrae	*13-17	14-17	13-15	14-17	14-15	15-17	13-16
Pelvic-fin rays ^b	3	3	3	3	3	3	3
Epibranchial gill Rakers (1st arch)	*2	3	3	2	2	3	4-5
Data source	1,3,6,8,11	1,2,4,5,6,8,11	1,2,3,4,5,8	1,7,12	1,5,12	1,12	1,10,11,12

* In our material ($n=205$) *U. tenuis* never possessed < 15 abdominal vertebrae.

^b The third pelvic-fin ray in adult *Urophycis* and *Phycis* is rudimentary.

^c *Urophycis tenuis* occasionally has three epibranchial gill rakers.

Results

Identification of *Urophycis* and *Phycis* larvae and juveniles

Meristics

Epibranchial gill rakers (Table 3) A complete size-series of all species was not available, but size (mm) at which *U. regia*, *U. chuss*, and *U. tenuis* larvae attain the adult complement of epibranchial gill rakers and other meristic elements is shown in App. Table 2. The following sections are abbreviated to avoid repeating in the text what the tables and figures succinctly show. *Phycis chesteri* does not attain the adult complement of epibranchial gill rakers until 16–18 mm (Methven 1985), but by 13 mm the third gill raker has developed and serves to separate larvae of this species from *U. tenuis*, *U. earlli*, and *U. floridana*. Occasionally *U. chuss* and *U. regia* possess two or four epibranchial gill rakers on one side, but most of these specimens have the normal complement of three gill rakers on the other side. *Urophycis tenuis* occasionally possesses a 3rd epibranchial gill raker, but only very rarely is this third gill raker found on both sides of a specimen.

Caudal-fin rays (Table 3) All but two specimens of *U. tenuis* ($n=195$) had more caudal-fin rays than all other species of *Urophycis*. Numbers of caudal-fin rays of *U. tenuis* overlapped those of *P. chesteri*, but more than half of our *U. tenuis* were distinct in having >36 rays, and over 40% of *P. chesteri* ($n=56$) differed from *U. tenuis* in having <34 rays. As few as 28 caudal-fin rays have been reported in *P. chesteri* (Wenner 1983) and *U. cirrata* (J.A. Musick, VA Inst. Mar. Sci., pers. commun.), but this may be because some of the small procurrent rays are not easily seen in radiographs of larger fish.

No *U. earlli* specimens ($n=31$) possessed >31 caudal-fin rays, while all other hake commonly have >31 rays.

Dorsal-fin rays (Table 3) Despite overlapping extremes, numbers of first dorsal-fin rays helped distinguish *U. floridana* from other species of hake. In our material, *U. regia* and *U. earlli* never possessed >10 and 11 first dorsal-fin rays, respectively, while over 80% of *U. floridana* ($n=45$) had >11 rays. One-third of *U. floridana* specimens examined possessed 13 first dorsal-fin rays, delimiting these from all other hake taxa.

The relatively low number of second dorsal-fin rays in *U. regia* separated this species from *P. chesteri* and other *Urophycis* species with little overlap. *Urophycis chuss* and *U. regia* with incomplete development of second dorsal-fin rays were delimited by numbers of pterygiophores supporting these rays at sizes as small as 6 mm (Fig. 2). Although extremes in numbers of

second dorsal-fin rays overlapped in all other taxa, many of the available specimens of *U. earlli* and *U. cirrata* were distinct in possessing >63 rays.

Abdominal vertebrae (Table 3) Numbers of abdominal vertebrae cannot be used alone to identify individual specimens because of overlapping extremes, but this meristic character is useful when identifying collections comprised entirely of *U. tenuis* or *U. chuss*. *Urophycis tenuis* larvae, identified by numbers of epibranchial gill rakers and caudal-fin rays, were found in the MAB only in spring and accounted for 99% of the *Urophycis* collected at this time (*U. regia* juveniles accounted for the other 1%). *Urophycis* larvae <10 mm ($n=154$) that were present in spring collections had not yet developed the adult complement of caudal-fin rays, but these larvae (>4 mm) had developed the adult complement of abdominal vertebrae and were identified as *U. tenuis* because their frequency-distribution of numbers of abdominal vertebrae was identical to that found in larger *U. tenuis*; 88% of the larvae had 16 abdominal vertebrae, and no specimens were found with <15. It is unlikely that any of these small larvae were *U. floridana* or *U. cirrata*, two other species with similar numbers of abdominal vertebrae, because these two southern species were found only in offshore winter collections and most specimens were pelagic juveniles.

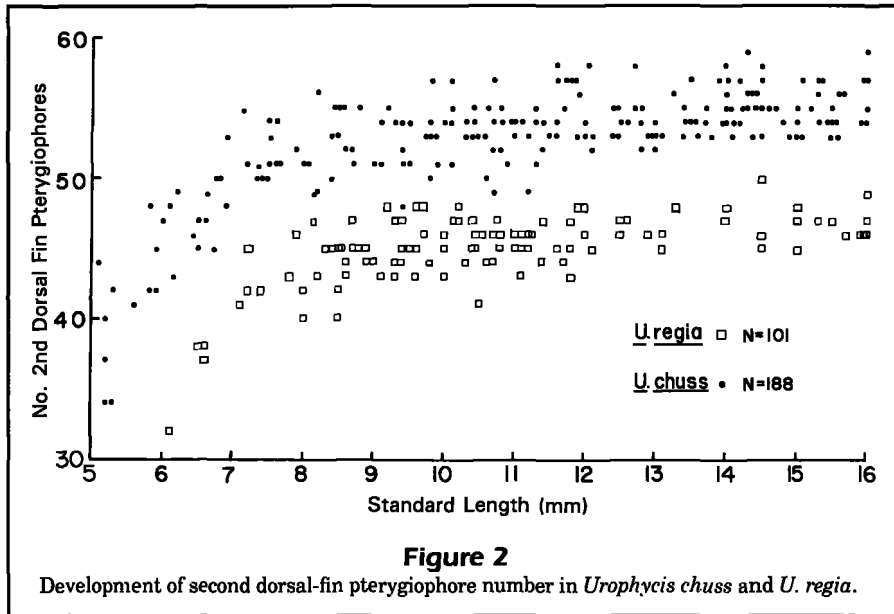
Urophycis chuss >4 mm ($n=448$) possessed 14–16 abdominal vertebrae, but the majority of specimens ($n=391$) had 15. In all other species of *Urophycis* the count of 15 occurred in <20% of the specimens; and although extremes of *U. chuss* and *P. chesteri* were similar, *P. chesteri* commonly had 14 or 16 abdominal vertebrae (17%). Consequently, in the MAB during late summer when *U. chuss* larvae are extremely abundant (and, in this study, were the only species of hake found at this time), complete meristic counts to check for species other than *U. chuss* need be performed only on those specimens that do not have 15 abdominal vertebrae. If species other than *U. chuss* are found in late-summer collections, numbers of abdominal vertebrae are no longer taxonomically useful and complete meristic counts are necessary to identify larvae.

Urophycis regia ($n=698$) had 13–15 abdominal vertebrae, but only eight specimens had 15, and seven of these specimens had an anomalous 15th abdominal vertebra. This anomalous vertebra possessed one short transverse process characteristic of abdominal vertebrae and one long transverse process typical of caudal vertebrae. Because 99.9% of *U. regia* examined had <15 normal abdominal vertebrae, it was assumed that specimens with ≥ 15 abdominal vertebrae were not *U. regia*. This meristic character aided in the separation of small (<6 mm) *U. chuss* and *U. regia* in fall collec-

Table 3

Frequency distribution of meristic values recorded in *Phycis chesteri* and six species of *Urophycis*. Asterisks denote that data from juvenile and adult specimens are included. All larvae had attained the adult meristic complement.

Epibranchial gill rakers on left first gill arch. Slash separates numbers on left and right sides.																									
	2	3/2	3	4/3	4	5																			
* <i>P. chesteri</i>					24	8																			
<i>U. chuss</i>		8	596	8	2																				
<i>U. regia</i>		4	631	4	2																				
* <i>U. cirrata</i>			19																						
<i>U. tenuis</i>	160	6	1																						
* <i>U. floridana</i>	44																								
* <i>U. earlli</i>	32																								
Number of caudal-fin rays																									
	29	30	31	32	33	34	35	36	37	38	39	40													
<i>U. tenuis</i>			1	8	15	2	28	56	65	34	9	1													
* <i>P. chesteri</i>			19	34	16	19	10	3																	
<i>U. regia</i>		1	19	34	16	1																			
<i>U. chuss</i>	1	1	22	13	10	3																			
* <i>U. cirrata</i>			3	8	2																				
* <i>U. floridana</i>		5	13	21	14	2																			
* <i>U. earlli</i>	12	13	6																						
Number of first dorsal-fin rays																									
	8	9	10	11	12	13																			
* <i>U. floridana</i>				8	22	15																			
* <i>U. cirrata</i>				2	8	3																			
<i>U. chuss</i>			2	33	51	9																			
<i>U. tenuis</i>			10	24	26	3																			
* <i>P. chesteri</i>		1	19	38	13	2																			
* <i>U. earlli</i>			6	21	5																				
<i>U. regia</i>		14	61	7																					
Number of second dorsal-fin rays																									
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
* <i>U. cirrata</i>																1	1	1	1	2	2	5		1	
* <i>U. earlli</i>														1		2	8	8	3	7	1	1			1
<i>U. floridana</i>												6	6	7	9	6	5	3	3						
* <i>P. chesteri</i>									3	8	5	14	13	5	5	3	1		1						
<i>U. chuss</i>								1	3	4	6	16	16	16	20	9	6	6	3						
<i>U. tenuis</i>							1	3	9	7	8	3	12	5	4	1	1	2							
<i>U. regia</i>	2	1	15	22	30	36	29	16	2																
Number of abdominal vertebrae																									
	13	14	15	16	17																				
<i>U. tenuis</i>			20	180	5																				
* <i>U. cirrata</i>			2	10	1																				
* <i>U. floridana</i>			1	7	38	3																			
<i>U. chuss</i>			50	391	7																				
* <i>P. chesteri</i>			8	57	4																				
* <i>U. earlli</i>			27	4																					
<i>U. regia</i>		66	624	8																					
Note: Although 8 specimens of <i>U. regia</i> had 15 abdominal vertebrae, in only one of these specimens (0.1%) was the 15 th vertebra normally developed.																									
Number of anal-fin pterygiophores anterior to first haemal spine																									
	3	4	5	6	7	8	9																		
* <i>U. earlli</i>					4	14	8	1																	
* <i>U. floridana</i>					11	23	7	1																	
<i>U. regia</i>				8	156	202	14																		
<i>U. chuss</i>				18	173	152	7																		
<i>U. tenuis</i>			3	36	25	1																			
* <i>U. cirrata</i>			1	8	2																				
* <i>P. chesteri</i>	3	28	34	5																					
Interneural space into which projects the pterygiophore supporting the first ray of the second dorsal fin																									
	7	8	9	10																					
<i>U. tenuis</i>		8	52	6																					
* <i>U. floridana</i>	1	10	25	6																					
* <i>P. chesteri</i>	3	31	20	1																					
<i>U. chuss</i>	4	203	220	4																					
<i>U. regia</i>	141	41																							
* <i>U. earlli</i>	15	12																							
Note: If pterygiophore was aligned with the tip of a neural spine, it was arbitrarily recorded as pointing into the space posterior to the spine in question.																									



tions when numbers of second dorsal-fin pterygiophores were not yet taxonomically useful.

Numbers of abdominal vertebrae may help separate *U. earlli* from *U. floridana* and *U. cirrata*, the other two southern species of *Urophycis*. Over 80% of *U. floridana* and *U. cirrata* possessed 16 or 17 abdominal vertebrae, but *U. earlli* has never been recorded with this many.

Anal-fin pterygiophores (Table 3) The number of anal-fin pterygiophores positioned anterior to the first haemal spine helps distinguish *P. chesteri*, *U. cirrata*, and *U. tenuis* from *U. earlli*, *U. floridana*, *U. regia*, and *U. chuss*. Only one specimen of *U. tenuis* ($n=65$) and no *U. cirrata* ($n=11$) or *P. chesteri* ($n=70$) were found with >7 anal-fin pterygiophores positioned anterior to the first haemal spine, but 45% of *U. chuss* ($n=350$) and over half of *U. earlli* ($n=27$), *U. floridana* ($n=42$), and *U. regia* ($n=380$) had at least 7 of these pterygiophores. More than 60% of *U. tenuis*, *U. cirrata*, and *P. chesteri* had <6 anterior anal-fin pterygiophores, whereas <2% of *U. regia* and no *U. earlli* or *U. floridana* had this few.

Second dorsal-fin pterygiophores (Table 3) The interneural space into which points the first pterygiophore of the second dorsal fin helped

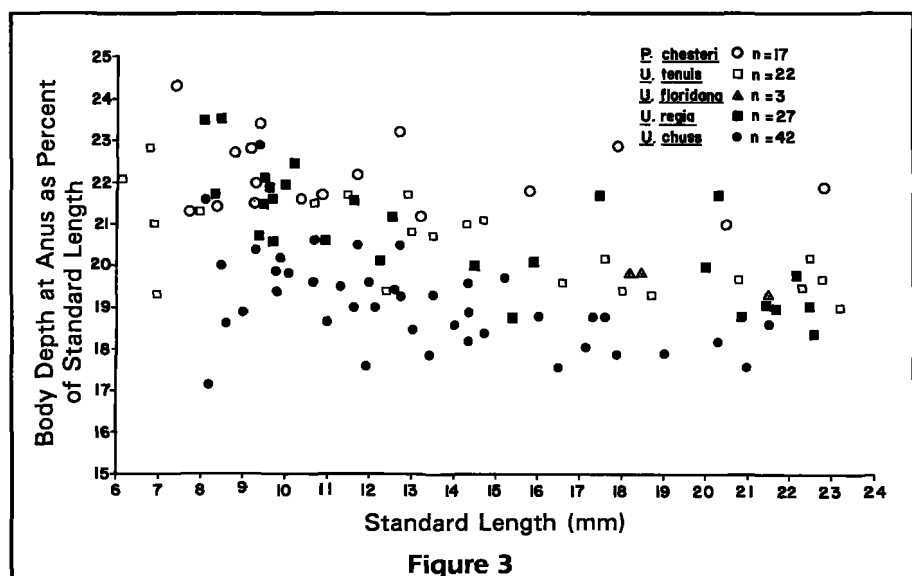
separate *U. chuss* from *U. regia*, and *U. floridana* from *U. earlli*. In over half of *U. chuss* examined ($n=431$) the first pterygiophore of the second dorsal fin pointed into the 9th or 10th interneural space, whereas in all *U. regia* examined ($n=182$) this pterygiophore pointed into the 7th or 8th interneural space. In >75% of *U. regia* this pterygiophore pointed into the 7th interneural space, whereas <1% of *U. chuss* showed this pattern.

In >70% of *U. floridana* examined ($n=42$) the first pterygiophore of the second dorsal fin pointed into the 9th or 10th interneural space, whereas in all juvenile and adult *U. earlli* examined ($n=27$) this pterygiophore pointed into the 7th or 8th interneural space. In

over half of *U. earlli* examined, the first pterygiophore of the second dorsal fin pointed into the 7th interneural space, but in only 2% of *U. floridana* did this pterygiophore project this far forward.

Morphometrics

Body depth at anus (Fig. 3) Body depth at the anus separated some species of hake larvae at sizes >12–13 mm. Extremes of body depth as percent of standard length for cleared and stained *P. chesteri*, *U. tenuis*, and *U. chuss* were 21.0–23.4, 19.0–21.1,



Body depth at anus as a percent of standard length plotted against standard length for larvae and juveniles of *Phycis chesteri* and four species of *Urophycis*.

Table 4

Ranges of pelvic-fin-base height as percent of mandible length for *Phycis chesteri* and five species of *Urophycis*. Ranges of values are given for different size-intervals of larvae. ND = no data.

		Size-interval (mm)						
		5-9	10-14	15-19	20-24	25-29	30-34	35-45
<i>U. regia</i>	(n=31)	21-30	19-33	19-25	16-28	12-17	ND	ND
<i>U. floridana</i>	(n=19)	ND	ND	29-36	23-37	23-28	24-29	ND
<i>U. chuss</i>	(n=38)	20-39	23-33	24-36	19-22	15-16	16	16
<i>U. cirrata</i>	(n=4)	ND	ND	ND	39	31	ND	19-31
<i>P. chesteri</i>	(n=29)	44-74	52-61	54-61	46-61	52-64	50-59	26-57
<i>U. tenuis</i>	(n=39)	28-42	24-42	33-40	29-37	26-30	32	ND

and 17.6-19.7, respectively. Body depth of *U. floridana*, however, was found to overlap extremes of *U. tenuis* and *U. regia*, while *U. regia* exhibited the greatest variation in this character, overlapping the extremes of *P. chesteri* and all other species of *Urophycis* studied.

Mandible length and height of pelvic fin (Table 4, Fig. 4) Height of the pelvic fin plotted against mandible length separated larval *P. chesteri* from other hake at sizes between ~6 and 35 mm. At sizes > 3 mm *P. chesteri* was similar to *Urophycis* with respect to this character because *P. chesteri* became more slender-bodied and the pelvic-fin origin moved closer to the ventral margin of the body. Ranges of pelvic-fin height as percent of mandible length in cleared and stained larvae ranging in length from 6 to 35 mm varied from 44 to 74% in *P. chesteri* (n=29), but the highest value of this ratio in five species of *Urophycis* (n=131) was only 42%.

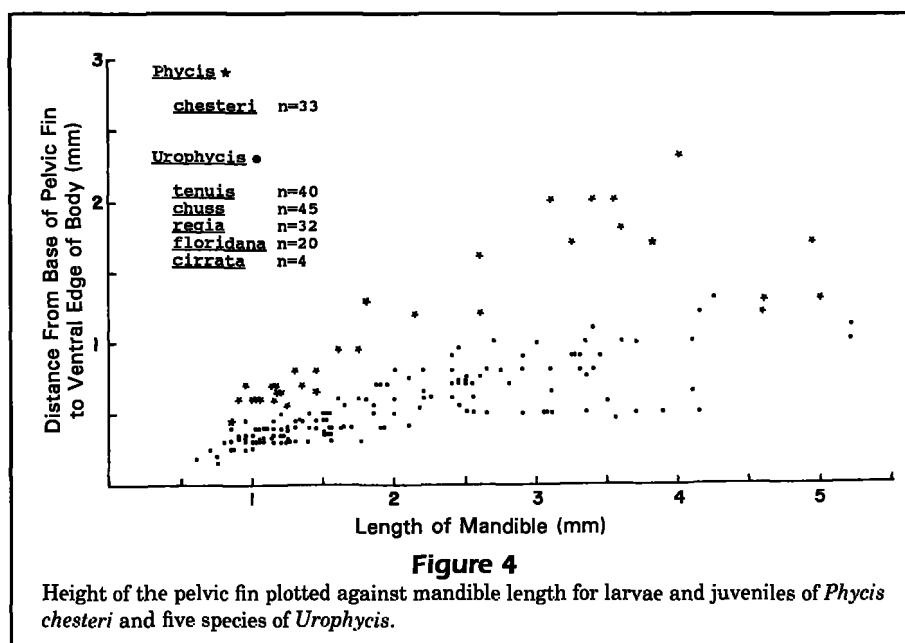
Distribution and abundance of hake larvae

Urophycis chuss *Urophycis chuss* was found only in summer and fall plankton collections from the MAB, and was the only species of larval hake found in August and early September. Densities of *U. chuss* in summer collections off the coast of New Jersey were up to two orders of magnitude greater than densities found off Virginia (Fig. 5). In October 1975 and November 1976, *U. chuss* were still present off both Virginia and New Jersey, but were far less abundant than during summer.

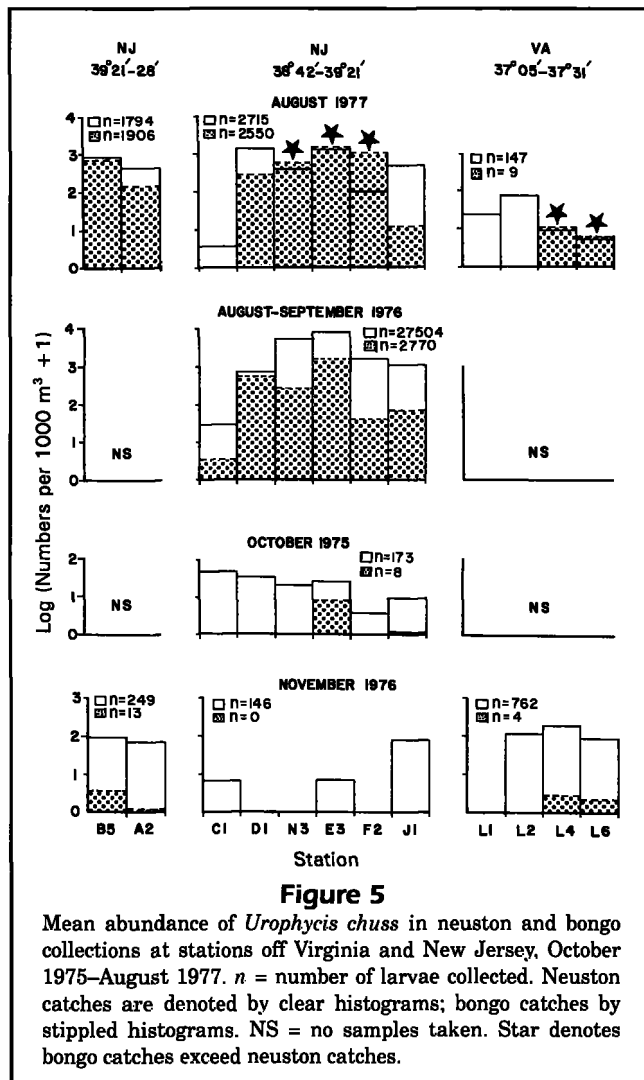
Densities of larval *U. chuss* also varied with distance from shore (Fig. 5), particularly during summer when lowest densities occurred inshore and highest densities were found in midshelf regions in water depths of 40-120 m. Variations in larval density with both latitude and water depth were not well defined in collections.

An increase in mean size of *U. chuss* was evident in fall collections (Fig. 6). As larval size increased in fall collections, the number of larvae collected with bongo nets decreased greatly. More than 1300 specimens were collected in October 1975 and November 1976, but only 25 of the larvae were collected with bongo gear. Onshore-offshore variation in size of *U. chuss* was most evident in fall collections off both Virginia and New Jersey; size tended to increase with decreasing water depth.

Urophycis regia *Urophycis regia* was collected in the MAB from October until May, with highest densities of larvae occurring in fall collections off the Vir-

**Figure 4**

Height of the pelvic fin plotted against mandible length for larvae and juveniles of *Phycis chesteri* and five species of *Urophycis*.



ginia coast at midshelf station L2 (Fig. 7). Densities of *U. regia* were much lower in collections taken in February and March, and most specimens were pelagic juveniles found at offshore stations off both Virginia and New Jersey. By May, *U. regia* was scarce; only seven neustonic juveniles were found at offshore stations.

Urophycis tenuis Apart from an occasional *U. regia* juvenile found at offshore stations, *U. tenuis* was the only species of hake present in spring plankton collections off Virginia and New Jersey. Abundance of *U. tenuis* in May 1977 was up to one order of magnitude greater than abundances in June 1976 (Fig. 8). Larvae were collected at all but inshore stations off both Virginia and New Jersey, but were most abundant at offshore stations. Larvae were smallest at offshore stations and increased in size as collections proceeded inshore (Fig. 9, page 220).

Urophycis floridana* and *U. cirrata *Urophycis floridana* ($n=41$, 13–32 mmSL) and *U. cirrata* ($n=5$, 20–42 mmSL) were found exclusively in offshore winter collections (Fig. 10, page 221). With the exception of a single juvenile *U. floridana* (23.0 mmSL) captured in a bongo tow, all specimens were found in neuston samples.

Phycis chesteri *Phycis chesteri* larvae first appeared in fall neuston collections from the Middle Atlantic Bight; 16 larvae 6–13 mm in length were collected in November 1976 at offshore stations off Virginia (Fig. 11, page 221). *Phycis chesteri* larvae and pelagic juveniles remained in surface waters during winter and were found in water deeper than ~100 m off both Virginia and New Jersey ($n=41$). All specimens were collected with the neuston net.

Discussion

Because of similarities between larvae of the seven hake species found in the MAB, a dichotomous key is not a practical tool with which to identify hake larvae in this area. However, the specific identification of larval and pelagic juvenile hake is feasible using a suite of diagnostic characters (App. Table 2). Identifications in this study were based on comparison of larval meristics with adult meristics. Further examination of larvae revealed diagnostic characters comprised not only of meristic information, but also morphometric and pterygiophore interdigitation data. Spawning season and capture location were not used as 'characters' to identify larvae in this study.

Methven (1985) had limited success using pigment characters to separate *U. chuss* and *U. tenuis* >7–8 mm. Problems will persist with the identification of small hake larvae until ontogenetic pigment patterns of all species have been described. These ontogenetic pigment patterns, when used in concert with meristic characters, will hopefully enable relatively routine identifications of these taxa.

The only species of *Urophycis* not found in the present study was *U. earlli*. Adult *U. earlli* are rare and larvae remain undescribed, but they are expected to co-occur with *U. floridana* (Hildebrand & Cable 1938). Both species are similar in having two epi-branchial gill rakers, but numbers of first dorsal-fin rays, abdominal vertebrae, and caudal-fin rays delimit most specimens of these two species.

Larval and juvenile *Urophycis* or *Phycis* were present in the MAB throughout the year, and patterns of spatial and temporal distribution of larvae were consistent during both years of this study. *Urophycis chuss* larvae were found in summer and fall collections, with greatest abundances occurring during summer in the

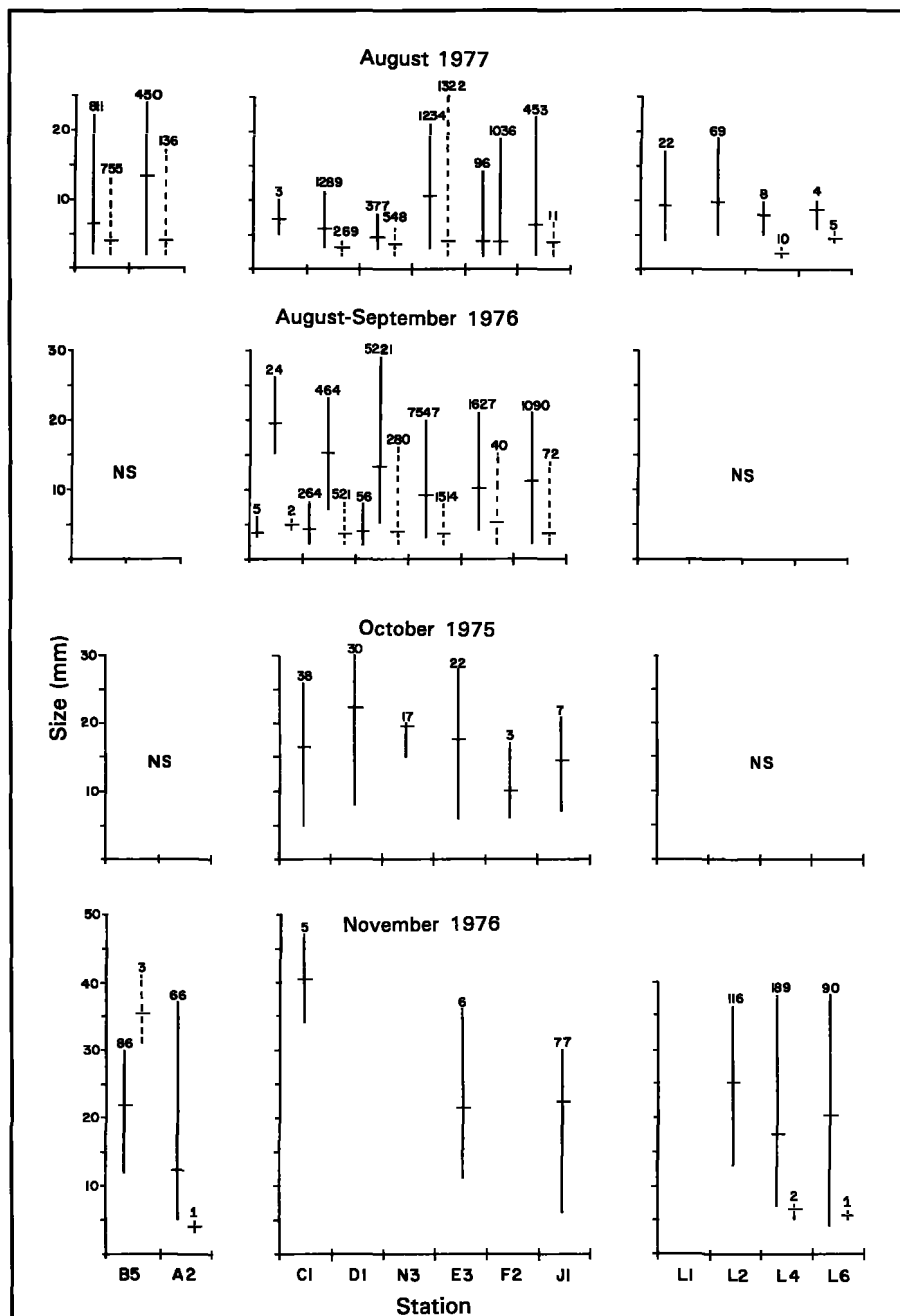


Figure 6

Range and mean size of *Urophycis chuss* in neuston and bongo collections at stations off Virginia and New Jersey. Solid and dashed lines indicate neuston and bongo collections, respectively. Horizontal lines show mean values. Two neuston ranges are shown if more than one size-mode is present. NS = no samples taken; numbers = no. larvae/1000m³.

central and northern MAB where water depth was 40–60 m. *Urophycis chuss* was the only species of larval hake found in summer collections, and accounted for 80% of all hakes collected during this 2-year study.

Most *U. regia* in the present study were collected in November, but some larvae or neustonic juveniles were

collected from October to May. *Urophycis regia* in the MAB is reported to spawn from late September through November, and possibly to February, with peak activity in October (Barans & Barans 1972). *Urophycis regia* was most abundant during fall in the southern MAB in the relatively shallow (41–43 m) midshelf area. Size range of *Urophycis regia* collected in this area was 2–34 mm, and although some of the larger specimens may have drifted from deeper water, small larvae were most likely spawned on the shallower central shelf. Evidence of *U. regia* spawning in shallow water was also found in October 1975 off New Jersey where larvae as small as 4mm were found in water as shallow as 12 m. However, not all specimens off New Jersey originated in shallow water; a second group of larvae 6–23 mm in length was found offshore.

The offshore distribution of *U. regia* became quite distinct in winter collections, with abundances being greatest at offshore stations in February 1976, February–March 1977, and May 1977. These *U. regia* were probably spawned in offshore waters of the MAB or in offshore waters of the South Atlantic Bight and transported northward. Larval *U. regia* have been found in abundance in winter collections from offshore waters off North Carolina in the South Atlantic Bight (Fahay 1975, Powles & Stender 1976).

Late-summer spawning by *U. tenuis* occurs in shallow water of the southern Gulf of St. Lawrence and the Scotian Shelf (Markle et al. 1982). Fahay & Able (1989) suggest the existence of a second stock of *U. tenuis* that spawns in deep water during early spring on the slope of Georges Bank, and probably also along the slopes of the Scotian Shelf, southern New England, and the MAB. The present study found direct evidence of spring spawn-

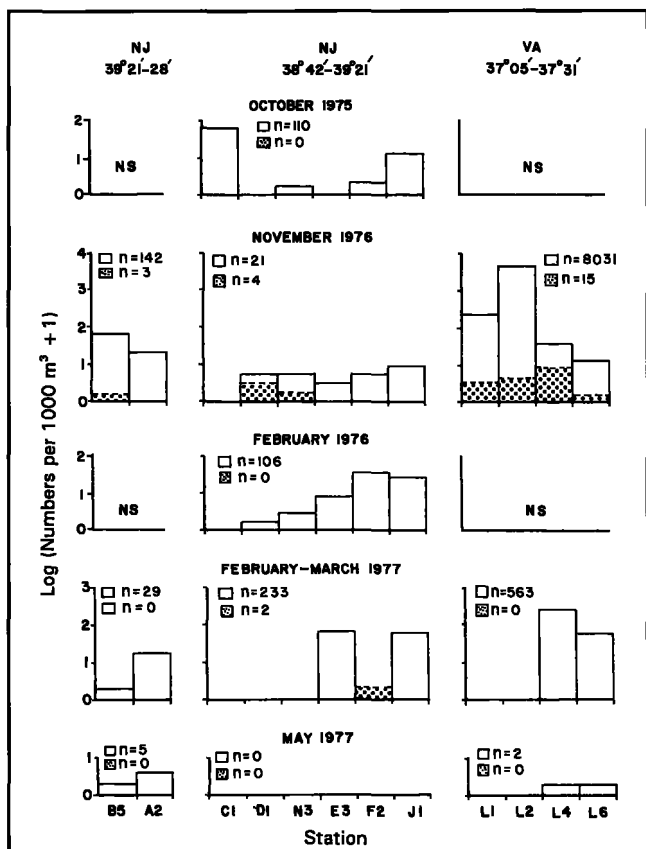


Figure 7

Mean abundance of *Urophycis regia* in neuston and bongo collections at stations off Virginia and New Jersey, October 1975–May 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

ing by *U. tenuis* in deep water of the MAB; in May 1977 *U. tenuis* larvae as small as 3–4 mm were found over the continental break and slope off both New Jersey and Virginia. In June 1976 *U. tenuis* found at offshore stations were 16–38 mm in length. Based on estimated larval and pelagic juvenile growth rates of 10–22 mm/mo (Markle et al. 1982) and demersal juvenile growth rates of ~30 mm/mo (Fahay & Able 1989), these fish were probably spawned in late April and May.

Fahay & Able (1989), studying young *U. tenuis* in the Georges Bank area, found a shoreward migration with growth. Recruitment to nearshore areas was also indicated in the present study by the increasing size of *U. tenuis* as collections proceeded shoreward. Neustonic juveniles (35–53 mm) were captured in water as shallow as 32 m off the coast of New Jersey.

Urophycis floridana and *U. cirrata*, two southern species of hake, were found off New Jersey and Virginia only in offshore winter collections. The large size

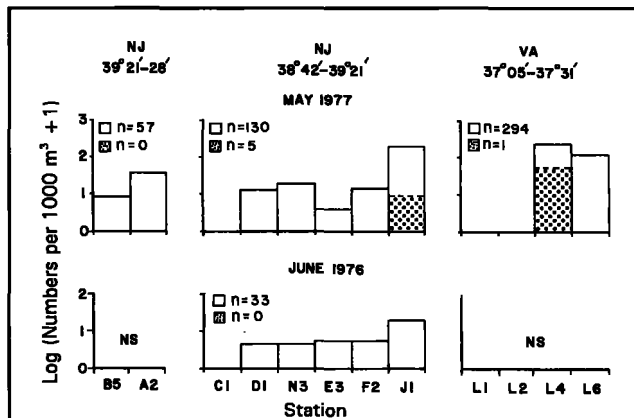


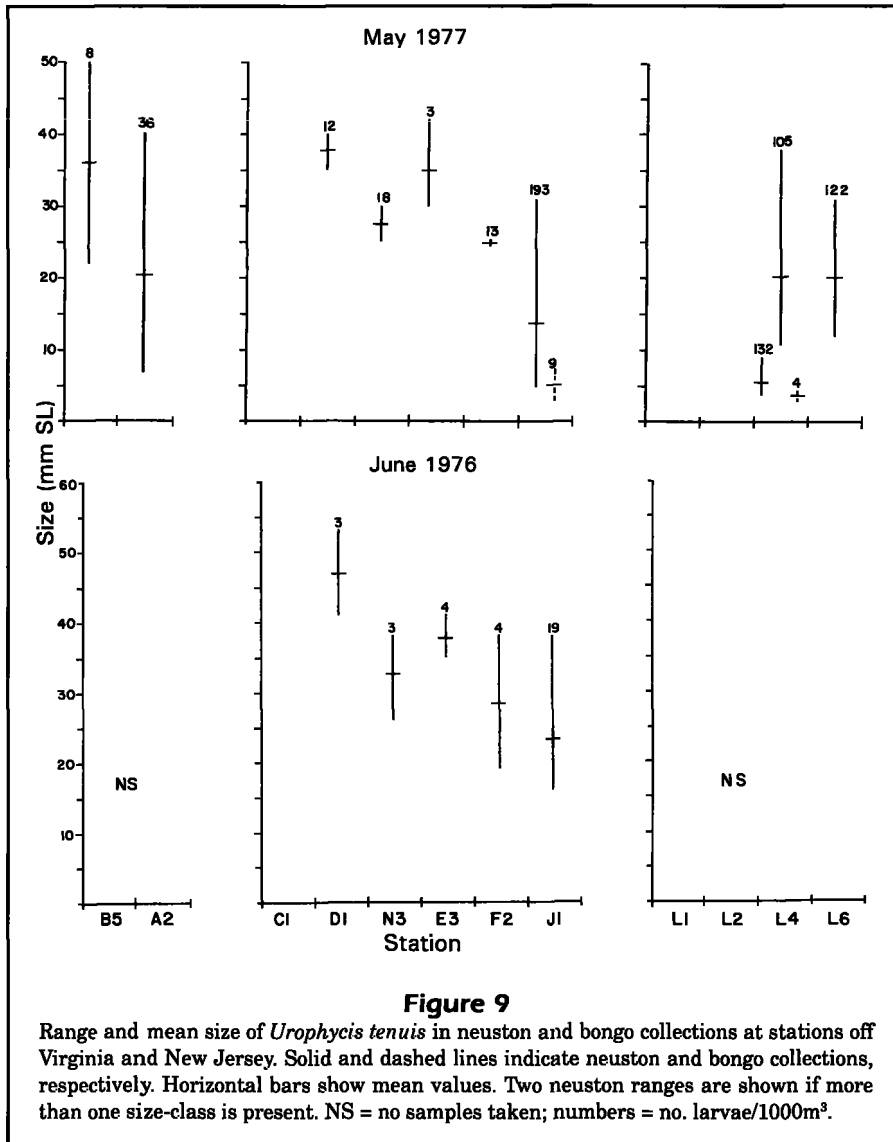
Figure 8

Mean abundance of *Urophycis tenuis* in neuston and bongo collections at stations off Virginia and New Jersey, June 1976 and May 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

and offshore distribution observed for both species suggest that these pelagic juveniles may have been transported northward into the study area. Larvae of *U. earlli*, another species found south of the MAB, are rare and remain undescribed, but this species may also occur occasionally in offshore waters of the MAB during winter. Hildebrand & Cable (1938) expected *U. earlli* to be a winter spawner after collecting three juveniles (37, 75, 103 mm) in March and April off North Carolina, and Fahay (1975) collected a few neustonic *U. earlli* in winter in the South Atlantic Bight.

Phycis chesteri larvae and pelagic juveniles appeared at offshore stations in fall and winter off Virginia and New Jersey. This larval distribution concurs with Wenner (1983) who found adult *P. chesteri* generally at depths >183 m on the continental slope from 36°N to 47°N in the western North Atlantic, and noted that spawning off Virginia took place between late September and April, with peak spawning occurring in December and January. Methven & McKelvie (1986) collected 51 *P. chesteri* larvae and pelagic juveniles along the edge of the continental shelf in the MAB, Grand Bank, and Labrador Shelf, and based on estimated growth rates suggested that most spawning occurs in October.

This study has shown the spatial and temporal distribution of hake larvae in the MAB to be more complex than previously thought. Additional taxonomic characters, particularly ontogenetic pigment patterns, are still needed in order to routinely identify small hake larvae, and more research is needed to explain the observed patterns of larval distribution. Of particular interest is an understanding of the processes that result in the northward transport of larvae and



pelagic juveniles of southern species into the MAB. Assuming that these individuals are transported northward by the Gulf Stream, it remains to be shown how they leave the influence of this current and move shoreward.

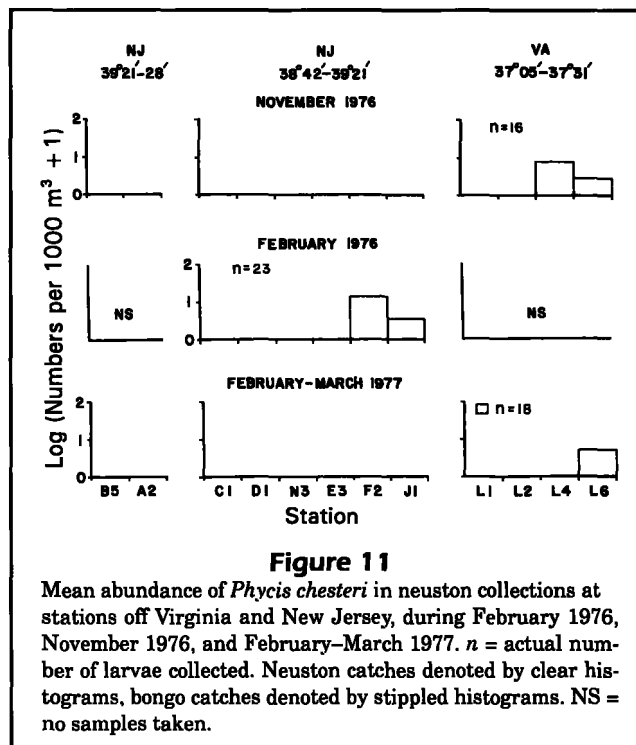
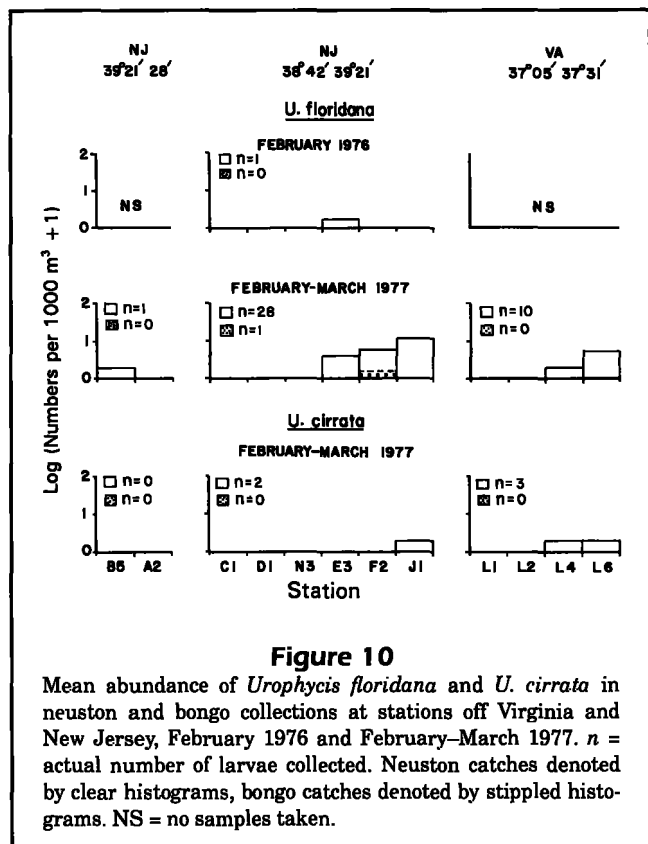
Acknowledgments

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thesis submitted as partial requirement for the MA degree at the College of William and Mary.

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Appendix Table 1

Sources of material, collection data, and lengths of hakes used in radiographic analyses of meristics and pterygiophore interdigitation. Standard acronyms for resource collections follow Leviton et al. (1985).

Species	Collection #	Location	No. specimens	SL(mm)
<i>U. earlII</i>	USNM 025295	N. Carolina	1	124
	USNM 155746	32°34'N, 79°05'W	1	55
	USNM 155747	Wilmington, NC	2	50-60
	USNM 226521	32°29'N, 79°42'W	3	88-129
	USNM 226522	32°29'N, 79°41'W	3	91-122
	USNM 226523	32°29'N, 79°41'W	1	113
	USNM 226524	33°14'N, 78°24'W	1	130
	USNM 226525	34°14'N, 78°24'W	1	82
	USNM 226526	32°28'N, 79°42'W	4	91-132
	USNM 226530	32°29'N, 79°40'W	4	96-157
	USNM 226531	32°29'N, 79°41'W	5	138-166
	USNM 226543	28°48'N, 80°38'W	1	74
	VIMS 06557	Gulf of Mexico	1	195
	<i>U. floridana</i>	USNM 073010	Key West, FL	1
USNM 116729		Beaufort, NC	16	35-49
USNM 131586		26°18'N, 83°09'W	1	59
USNM 155738		Texas	1	77
USNM 155782		Cape Canaveral, FL	1	86
USNM 155783		St. Augustine, FL	1	67
USNM 156146		Pelican-Stn. 120-5	1	94
USNM 214118		Brickhill Creek, GA	5	64-75
VIMS 03756		Silver Bay	1	165
VIMS 04142		Brunswick Sound, GA	5	78-113
VIMS 04152		Silver Bay	4	52-85
VIMS 04192		Pensacola, FL	2	81-109
VIMS 04193		Cumberland Id., GA	2	129-184
VIMS 04194		N. Cumberland R., GA	2	133-157
VIMS 04195		Santa Rosa Sound, FL	1	66
VIMS 04196		Oregon S646	1	185
<i>U. cirrata</i>	GCRL 433	29°09'N, 88°33'W	1	281
	GCRL 436	29°22'N, 87°30'W	1	290
	GCRL 525	29°11'N, 88°07'W	3	318-343
	GCRL 2783	Louisiana	4	109-130
	GCRL 17534	28°27'N, 90°38'W	1	145
	USNM 115686	22°23'N, 91°45'W	1	141
	USNM 116929	Tortugas, FL	1	140
	USNM 155642	29°04'N, 88°44'W	1	114
	USNM 218169	29°18'N, 88°51'W	1	108
	USNM 218192	28°58'N, 84°44'W	1	109
	USNM uncat.	24°32'N, 83°36'W	1	197
	USNM uncat.	28°59'N, 88°48'W	1	198
	USNM uncat.	28°35'N, 91°12'W	2	186-220
	<i>P. chesteri</i>	USNM 025903	Newport, RI	17
USNM 026081		Martha's Vineyard, MA	5	68-83
USNM 026097		No data	1	79
USNM 028732		No data	9	58-76
USNM 083821		GA, SC	12	54-65
USNM uncat.		Atlantic Arctus Exped.	6	105-147
USNM 092695		No data	1	63
VIMS 05238		36°43'N, 74°39'W	4	67-150

Appendix Table 2

A summary of key meristic, morphometric, and pterygiophore interdigitation characters used to separate *Phycis chesteri* and six species of *Urophycis*. Given for each species: length (mm) at which characters are attained (upper), morphometric or meristic value (middle), and explanatory notes (**bold** letters in parentheses). Percentages indicate proportion of a species that possesses a particular character.

	Epibranchial gill rakers	Caudal-fin rays	2nd dorsal-fin rays	1st dorsal-fin rays	Abdominal vertebrae	Anal-fin pterygiophores anterior to first haemal spine	Interdigitation of second dorsal-fin pterygiophore	Body depth at vent as %SL	Height of pelvic-fin base as percent of mandible length	
<i>U. tenuis</i>	11–13 mm 2 (95%) (A)	11 mm ≥35 (99%)	14 mm ≥53 (93%)	15 mm ≤12	4 mm ≥15 (H)	8–9 mm >6 (2%) <6 (60%)	≥9 (88%) (L)	12 mm 19.0–21.1 (M)	6–19 mm 24–42 (N)	20–34 mm 26–37
<i>U. chuss</i>	11–13 mm 3 (97%)	8–9 mm <35	14 mm ≥53 (E)	14 mm ≤12	4 mm ≥15 (87%) (I)	8–9 mm >6 (45%) <6 (5%)	12 mm ≥9 (52%)	12 mm 17.6–19.7	6–19 mm 20–39	20–34 mm 15–22
<i>U. regia</i>	11–13 mm 3 (97%)	8–9 mm <35	14 mm ≤52 (E)	13 mm <12 (G)	4 mm ≤14 (J)	8–9 mm >6 (57%) <6 (2%)	12 mm <9	12 mm 18.4–21.7	6–19 mm 19–33	20–34 mm 12–28
<i>U. floridana</i>	2	<35	≥53	13 (33%)	≥15 (98%) (K)	>6 (74%) <6 (0%)	≥9 (73%)	12 mm 17.7–19.8	15–19 mm 29–36	20–34 mm 23–37
<i>U. earlli</i>	2	<35 (C)	>53	<12 (G)	≤14 (87%) (K)	>6 (85%) <6 (0%)	<9			
<i>U. cirrata</i>	3	<35	>53 (F)	≤12	≥15 (K)	>6 (0%) <6 (82%)				20–34 mm 31–39
<i>P. chesteri</i>	16–18 mm 4–5 (B)	<35 (77%) (D)	≥53	≤12	≥15 (88%)	>6 (0%)	≥9 (38%)	12 mm 21.0–23.4	6–19 mm 44–74	20–34 mm 46–61 (O)

Notes

- (A) *U. tenuis* occasionally possessed a third gill raker, but in only one specimen ($n=167$) were three gill rakers found on both left and right sides.
- (B) Three epibranchial gill rakers had developed by 13 mmSL.
- (C) *U. earlli* has never been recorded with >31 caudal-fin rays, while all other hake commonly have >31 rays.
- (D) Although ranges in *U. tenuis* and *P. chesteri* overlapped, numbers of caudal-fin rays separated over 40% of *P. chesteri* (<34 rays) from more than half of *U. tenuis* (>36 rays).
- (E) Numbers of second dorsal-fin pterygiophores separated *U. regia* from *U. chuss* at sizes as small as 6 mmSL. Although not shown here, one specimen of *U. chuss* ($n=106$) possessed 52 second dorsal-fin rays.
- (F) Although ranges overlap, almost 70% of *U. cirrata* had at least 64 second dorsal-fin rays, while *P. chesteri* and other species of *Urophycis* (except *U. earlli*) had <64 rays.
- (G) *U. regia* and *U. earlli* have never been found with >10 and 11 first dorsal rays, respectively, while over 80% of *U. floridana* ($n=45$) possessed >11 rays.
- (H) Numbers of abdominal vertebrae helped identify *U. tenuis* larvae <10 mm, the size below which numbers of caudal-fin rays no longer afford confident identifications. See Results.
- (I) Numbers of abdominal vertebrae aided in the identification of *U. chuss* in summer collections from the MAB when this was the only species of hake found. See Results.
- (J) Only eight specimens of *U. regia* from the Middle Atlantic Bight ($n=698$) had 15 abdominal vertebrae, and seven of these specimens had an anomalous 15th vertebra.
- (K) *U. floridana* and *U. cirrata* commonly possessed 16 or 17 abdominal vertebrae, but *U. earlli* has never been recorded with this many.
- (L) Numbers refer to the interneural space into which points the pterygiophore supporting the first ray of the second dorsal fin. The first interneural space was defined as the space anterior to the first haemal spine.
- (M) Specimens of all species were cleared and stained.
- (N) Size ranges do not define size when character first became useful, but bracket the size-range over which particular morphometric values were found.
- (O) At sizes >35 mmSL, *P. chesteri* was similar to *Urophycis* with respect to this character.