Transitions in the morphological features, habitat use, and diet of young-of-the-year goosefish (*Lophius americanus*)

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Abstract—This study was designed to improve our understanding of transitions in the early life history and the distribution, habitat use, and diets for young-of-the-year (YOY) goosefish (*Lophius americanus*) and, as a result, their role in northeastern U.S. continental shelf ecosystems. Pelagic juveniles (>12 to ca. 50 mm total length [TL]) were distributed over most portions of the continental shelf in the Middle Atlantic Bight, Georges Bank, and into the Gulf of Maine. Most individuals settled by 50–85 mm TL and reached approximately 60–120 mm TL by one year of age. Pelagic YOY fed on chaetognaths, hyperiid amphipods, calanoid copepods, and ostracods, and benthic YOY had a varied diet of fishes and benthic crustaceans. Goosefish are widely scattered on the continental shelf in the Middle Atlantic Bight during their early life history and once settled, are habitat generalists, and thus play a role in many continental shelf habitats.

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Our understanding of the life history and ecology of the goosefish (*Lophius americanus*) is incomplete. Much of what we believe to be true is drawn by analogy from European congeners (Caruso, 2002). This lack of knowledge is especially relevant given the development of an important fishery for goosefish since the 1980s (Caruso, 2002) and given the evidence that goosefish were overexploited in the 1990s (Almeida et al., 1995). Goosefish are found in the western North Atlantic from the Grand Banks off Newfoundland to the east coast of Florida (Wood, 1982; Caruso, 1983). Larval development, from hatching to completion of fin rays (up to 12 mm total length [TL]) has been described in detail (Everly, 2002). Little is known about pelagic and settled young-of-the-year (YOY) life stages and thus their role in continental shelf ecosystems. The smallest benthic individuals reported by Caruso (2002) were 76–114 mm TL (n=3).

Information on ages of YOY goosefish appears to be contradictory, but does indicate that sizes attained by the end of age 1 can be quite variable. Size of YOY goosefish by their first fall has been variously reported as 64–76 mm TL (Steimle et al., 1999) and as 59 mm TL (Scott and Scott, 1988). However, larger sizes have been reported by Armstrong et al. (1992) for goosefish from southern New England–Mid-Atlantic Bight (average of 123–126 mm TL at age 1 for females and males) and by Hartley (1995) for goosefish from the Gulf of Maine (120–139 mm TL). Scott and Scott (1988) reported fish of 100–114 mm TL to be 2 years of age.

A portion of the National Marine Fisheries Service (NMFS) groundfish survey data and associated collections along the northeast coast of North America have been examined to determine some aspects of the life history and food habits for large juveniles and adult goosefish (Armstrong et al., 1992, 1996; Almeida et al., 1995; Hartley, 1995; Martinez, 1999). These studies focused on reproduction, age, and growth over short time periods and relied on data collected from geographically disparate sources. Recently, goosefish distribution and abundance in relation to depth and temperature were summarized from a large portion of the NMFS database for groundfish surveys in the Gulf of Maine and the Middle Atlantic Bight (Steimle et al. 1999). Steimle et al. (1999) grouped all fish <43 cm TL into the juvenile category. As a result, several age classes were combined and there was no resolution for habitat of YOY goosefish. Prior descriptions of other aspects of the life history and ecology of YOY goosefish include associations of fish with depth and substrate type for Canadian waters (Jean, 1965; Scott, 1982), and with food habits for juveniles and adults (Sedberry, 1983; Armstrong et al., 1996).

The gaps in our knowledge about YOY goosefish, as articulated by Steimle et al. (1999), motivated the efforts reported here. Our objectives were 1) to describe more fully the morphological development of goosefish during the transition from pelagic larvae to benthic juveniles, 2) to estimate the timing, sizes, and ages of early life history events, and the growth rates of YOY goosefish, 3) to determine the distribution of pelagic and benthic juveniles in time and space, and 4) to identify the food habits and habitats of settled YOY goosefish.

Materials and methods

Two species of *Lophius* are found in the waters of the northwestern Atlantic, goosefish (*L. americanus* Valenciennes) and blackfin goosefish (*L. gastrophysus* Miranda-Ribeiro) (Caruso, 2002), and thus correct taxonomic identification is essential. Previously, *L. gastrophysus* was considered to be distributed from Brazil to Florida, and *L. americanus* was considered to range from Nova Scotia to Cape Hatteras (Bigelow and Schroeder, 1953; Scott and Scott, 1988) and to overlap occasionally between Florida and Cape Hatteras (Caruso, 1983). Preliminary data from the NMFS Commercial Cooperative Research goosefish survey indicate that *L. gastrophysus* has a much broader range, which is believed to extend into the Gulf of Maine (Richards[1]). To ensure proper identification of our specimens, we used the diagnostic characters reported for these congeners (Caruso, 1983).

Morphological development

For some species of fish, ontogenetic state of an individual has proven to be a better metric of early life history events than has age (Policansky, 1983; Fuiman et al., 1998). For this reason, we used morphological and meristic data from pelagic and benthic individuals of *L. americanus* as a basis for describing early life history stages and for estimating size and age at settlement. We define planktonic juveniles as those individuals that have completed fin ray formation (>12 mm TL; Everly, 2002), but have not yet settled. Benthic juveniles include all postsettlement YOY and juveniles of older age classes. A total of 88 fish (9.8–188 mm TL) were collected and examined (three fish per 5-mm size class) from a variety of sources (Table 1). These specimens were either collected and frozen, preserved in a solution of 70–95% ethanol or 5% formalin onboard the sampling vessel, or were obtained from museum collections. Shrinkage was determined by measuring fish upon capture and after preservation in ethanol or formalin. In total, 28 morphometric and meristic characters were examined (Table 2). These characters were based largely on those general character definitions provided by Hubbs and Lagler (1958). Modifications to these definitions in our study were due to the unique features possessed by *L. americanus*. Head length was measured from the anterior tip of the premaxillary bone to the gill opening. The length of the first dorsal spine, or illicium, was measured from its base to the base of the esca, the fleshy distal pendant of the illicium. The length of the esca was measured from its base to its distal end. An ocular micrometer was used for lengths ≤10 mm and a dial caliper was used for lengths >10 mm; all measurements were taken to 0.1-mm resolution.

Changes in body proportions that occurred during the pelagic-benthic transition were determined by examining the relation between each morphological character and total length. Such changes in allometry were detected by alteration in the slope of the line relating a focal character and total length (or any other reference character) on a log-log scale. When a fish is growing but not changing shape (i.e., exhibits isometric growth), the slope of this relationship is unity. When an individual or, as used here, an ontogenetic series of individuals, exhibits changes in shape with increasing total length, this means that the character(s) defining shape have changed in relation to total length. This transition in the degree of allometry will be reflected by a systematic deviation of the slope in the bivariate character plot. The magnitude of the slope before and after the transition, as well as the total length at which the transition occurred, were estimated by using piecewise regression (Toms and Lesperance, 2003).

Unlike measures of body proportions, other characters that change during the larval- juvenile-adult states are difficult to quantify. For example, the degree of pigmentation and the development of tubercles (Wiley and Collette, 1970) and cirri (fleshy flaps or tags, see Caruso, 2002) change gradually and in multiple dimensions during the progression from larval to juvenile phenotypes. These types of characters were scored as 0 or 1 for the larval state and juvenile-adult state, respectively. The juvenile-adult state was assumed to be represented by the largest size class that we examined (185–190 mm TL). For each of these characters, the median and standard error (SE) of size at transition to the juvenile/adult state were identified by fitting a cumulative normal distribution to the 0–1 scores by using a probit regression model. Because these estimates are based on data at the population level, our estimate of the mean size at transition was actually the size

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at which 50% of individuals expressed the juvenile-adult state of the character. The standard error of the median was converted to a 95% confidence interval, which indicates the sizes at which 5% to 95% of individuals express the adult state of the character.

Size and age at early life history events

Events during the early life history of goosefish were assessed by examination of sizes of fish at capture and by determination of ages and past events in the life of the fish as reflected in its otolith microstructure. Pelagic and benthic specimens (51–128 mm TL) used for daily otolith increment analysis were collected from a variety of sources (Table 1). An additional set of larvae hatched in the laboratory from egg veils collected in coastal waters off Long Beach Island, New Jersey, were examined for evidence of otolith microstructure that reflected hatching and the absorption of yolk. Preliminary examination of all three otoliths indicated that the lapilli were the easiest to interpret because of the clarity of increments and the lack of secondary growth structures. Hislop et al. (2001) came to a similar conclusion for *L. piscatorius*. Before otolith removal, individual fish were measured to the nearest 1 mm TL. Lapilli were removed, cleaned in bleach, and dried in 95% ethanol before they were mounted on glass slides by using a thermoplastic adhesive (Crystal Bond, Electron Microscopy Sciences, Hatfield, PA). Lapilli from fish >70 mm TL were ground and polished to the primordia on both surfaces with 1500 grit wet-dry sand paper with water as a lubricant, then finely polished with a 0.3-micron micropolish on a Buehler micropolishing cloth. Lapilli from fish <70 mm TL were polished to the primordia with the same materials but on the surface of the sulcus. Lapilli were cleaned with distilled water before they were immersed in oil for viewing. An analysis of

Table 1

Sources of data and specimens from field surveys used to determine aspects of the life history transitions, distribution, and diet of young-of-the-year goosefish (*Lophius americanus*). MAB = Middle Atlantic Bight (Cape Hatteras to Cape Cod); GB = Georges Bank; GOM = Gulf of Maine. NMFS = National Marine Fisheries Service; Mass DEP = Massachusetts Department of Environmental Protection; NJDEP = New Jersey Department of Environmental Protection; ACE = Army Corps of Engineers; VIMS = Virginia Institute of Marine Science.

Source	MAB	GB	GOM	Sampling gear	Sampling period	Sampling frequency	Range of sample depths (m)	Number of specimens (*n*)	Size range of specimens (mm total length)
NMFS	X	X	X	Bongo plankton net (1 m)	1977–87	6–8 cruises per year	11–1400	827	2.9–54.6
NMFS	X	X	X	Otter trawl (24 m)	1982–present	One cruise during fall, winter, and spring	9–365	3551	50–300
Michaels (2001)			X	Frame net	2000–2001	One cruise/year, generally in fall	35.5–818	66	20–210
NMFS	X	X	X	Commercial otter trawl	2001	Two simultaneous cruises	20–600	1093	25–300
NMFS	X	X	X	Scallop dredge	1982–2001	One cruise per year	21–144	9541	20–300
Mass DEP	X		X	Otter trawl (15 m)	1978–2001	Semi-annual sampling; spring and fall	6–82	490	40–300
NJDEP	X			Otter trawl (30 m)	1989–2000	Winter, spring, summer, fall	5–30	118	30–290
ACE	X			Bongo plankton net (1m)	1995–99	Bimonthly during summer	0–7	787	3.6–15.61
VIMS	X			Otter trawl (13.5 m)	1973–76	One cruise per year	35–818	587	53.37–299.37
NMFS	X			Otter trawl	2000	One cruise	20–330	98	180–300
Steves et al. (1999)	X			Beam trawl (2 m)	1996–97	Monthly cruises summer and fall; bimonthly winter and spring	20–90	19	72–233

Table 2

Summary of changes for 18 morphological characters in relation to total length of young-of-the-year goosefish (*Lophius americanus*). All estimates are derived from a linear piecewise regression. "Slope" refers to the estimate of the slope in the allometric equations applied to characters before and after the shift from juvenile to adult state. "Size" refers to the estimated size at which the shift occurs. Back-calculated lower and upper 95% confidence limits (L95 and U95, respectively) pertain to the estimated size at shift. R^2 (coefficient of what?) values and significance levels are for the entire piecewise regression model. ($^{*}P<0.05$, $^{**}P<0.001$, $^{***}P<0.0001$, ^{ns} not significant.)

	Slope						
Character	Pre-shift	Post-shift	Size (mm)	L95	U95	R^2	
Second dorsal ray (Illicium)	2.98	1.06	27.39	24.51	30.75	0.97	***
Esca length	1.61	0.8	84.10	50.91	138.38	0.80	*
Dorsal base length	1.41	0.95	20.11	14.44	28.50	0.98	**
Pectoral fin length	1.24	0.82	46.99	36.23	60.34	0.97	***
Snout length	1.2	0.95	42.56	24.05	75.19	0.97	**
Caudal peduncle depth	1.06	0.59	39.41	26.31	58.56	0.91	***
Head width	1	1.39	39.25	26.58	58.56	0.98	***
Pelvic fin length	0.93	0.24	48.42	41.26	57.40	0.92	***
Standard length	0.84	1.05	26.05	20.49	33.12	0.99	***
Orbit diameter	0.72	0.96	61.19	38.09	98.49	0.95	**
Head depth	0.49	1.1	60.95	34.81	107.77	0.79	***
Second dorsal ray length	0.45	1.06	84.10	67.36	104.58	0.86	***
Predorsal length	0.12	0.79	53.52	40.85	70.11	0.73	***
Caudal peduncle length	0.10	0.90	27.66	20.70	37.34	0.88	***
Head length	1.44	0.45	12.94	2.94	56.26	0.99	ns
Upper jaw length	1.23	1.33	39.25	7.88	197.16	0.98	ns
Third dorsal ray length	0.53	0.36	38.09	3.22	454.86	0.56	ns
Otolith size	0.33	0.71	17.97	10.5	30.91	0.97	**

evidence of allometric shifts in otolith dimensions for pelagic and settled YOY goosefish (8.6–285 mm TL, n=60) was conducted in the same manner as described above for body proportions.

Lapilli were viewed by transmitted light with an Olympus BH-2 compound microscope and Optimus 6.2 video imaging software (OPTIMUS Corp., Fort Collins, CO) at a magnification of 1250×. Distances from the primordium to each of multiple distinct marks (checks) on the otolith (e.g., at hatching, yolksac absorption, settlement, annulus formation) were taken along an axis to the dorsal edge. Increments (which are believed to be formed daily) were counted along the axis that exhibited the least ambiguous sequence of increments and greatest distance from the primordium to the outer edge. Increment counts and location of checks were determined twice on each otolith by a single observer.

Although we were reasonably confident of the age estimates derived with the above approach, we attempted to evaluate the precision and accuracy of our daily increment counts. A subset of otoliths (n=20) from fish (11–251 mm TL) were compared between the primary reader (PJC) and a second reader (K. Lang, NMFS, Woods Hole). The differences between readers in increment counts were small but increased with the size of the otolith from 6.5% (the interval from the hatching check) to 8.8% (focus to yolk absorption), to 10.6% (focus to otolith edge).

Distribution and abundance

Pelagic and benthic goosefish were collected on the continental shelf in waters from the Gulf of Maine, Georges Bank, and the Middle Atlantic Bight (Table 1, Fig. 1A). Major sources of data for pelagic juveniles were the NMFS Hydroacoustic Survey 2000 to 2001, collections from the Harvard Museum of Comparative Zoology (MCZ), and the NMFS Marine Resources Monitoring, Assessment and Prediction Program (MARMAP) Survey spanning from 1977 to 1987 (Morse et al., 1987), as well as miscellaneous collections from throughout the study area. The primary source for recently settled benthic individuals (n=6731; 20–200 mm TL) was the historical scallop survey conducted by NMFS (Serchuk and Wigley, 1986).

Food habits and habitat

Fish used for analysis of food habitats in relation to settlement were collected from a variety of sources (Table 1). Immediately after capture, whole fish were either flash

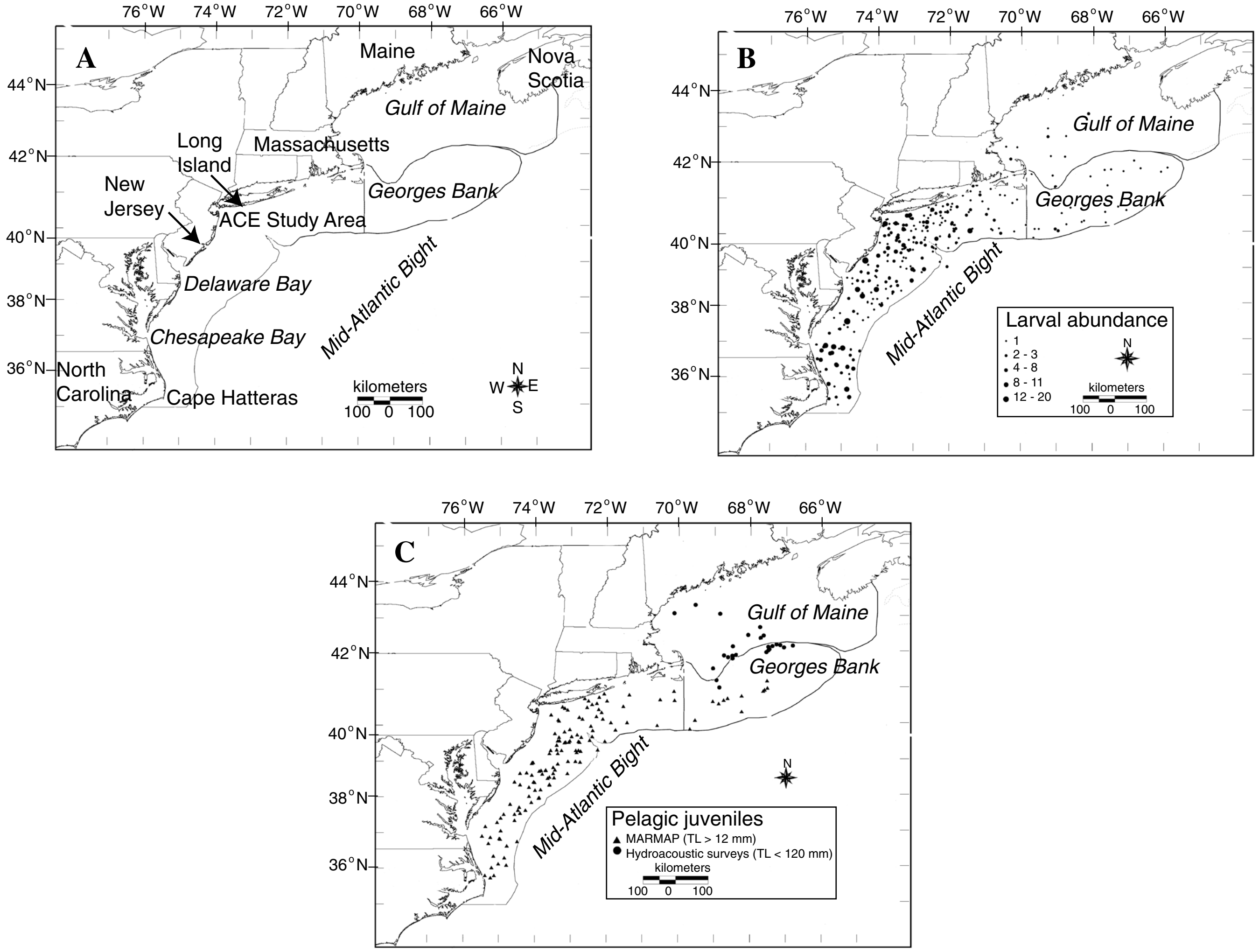

Figure 1

(**A**) Study area, including the Middle Atlantic Bight, Georges Bank, and Gulf of Maine. Study area boundaries are indicated by the light gray lines, which in most instances approximate the 200-m isobath. ACE = Army Corps of Engineers. (**B**) Distribution of larval (≤12 mm total length [TL]) goosefish *(Lophius americanus)* in the study area based on National Marine Fisheries Service and Marine Resources Monitoring, Assessment and Prediction sampling programs during the period from 1977 to 1987. Size of the symbol at each location is in proportion to the composite abundance (number of fish per location). (**C**) The distribution and abundance of pelagic juvenile (>12 to 130 mm TL) goosefish in the study area based on composite collections (Table 1).

frozen or preserved in ethanol to preserve stomach contents. In the laboratory, frozen fish were thawed, fish lengths (TL mm) were recorded, and stomachs were extracted and placed in 95% ethanol. A solution of rose bengal was later added to the stomach contents to aid in the identification of the contents. Upon examination, the proportion (by weight) of each prey category was determined according to the sieve-fractionation method of Carr and Adams (1972), by using sieves of three sizes (2000, 850, and 75 μ). All prey were identified to the lowest taxonomic level practical.

General inferences about the habitats of YOY goosefish were based on the location and depth of collection and the known habitat of items found in the stomach contents of goosefish specimens. Special attention was given to whether the prey was of pelagic or benthic origin, if known, to help us identify presettlement (pelagic) and postsettlement (benthic) goosefish. This method was effective in identifying size at settlement in haddock (*Melanogrammus aeglefinus*) for Mahon and Neilson (1987).

Results and discussion

Morphological development

Goosefish undergo changes in morphological features and pigmentation during the transition from pelagic

Table 3

Summary of changes in seven qualitative characters of goosefish (*Lophius americanus*). Size at shift represents the total length (TL) at which 50% of the individuals in the sample achieved an adult state in the character. SE = standard error. Back-calculated lower (CL [lower]) and upper (CL [upper]) 95% confidence limits are shown.

Character	Size at shift (TL, mm, mean ±SE)	CL (lower)	CL (upper)
Body pigmentation	68.64 ±11.46	46.18	91.10
Fin pigmentation	129.97 ±57.95	16.38	243.56
Tubercle development	78.77 ±20.11	39.35	118.20
Esca pigmentation	64.74 ±18.97	27.55	101.92
Illicium pigmentation	64.74 ±9.76	45.60	83.87
Lateral line pigmentation	71.67 ±16.13	40.06	103.28
Cirri	70.55 ±17.27	36.72	104.39

larvae to settled juveniles. The size range examined here (10–188 mm TL) brackets the interval from late larvae to juveniles. All but four of the 18 morphological characters displayed significant shifts in their relations to total length during the transition from pelagic juveniles (Table 2). These shifts occurred between 20.1 mm TL (dorsal base length) and 84.1 mm TL (esca length) resulting in a transformation from a laterally compressed, pelagic shape to a dorso-ventrally compressed, benthic shape. Eleven of the 14 morphological characters shifted from an allometric (body proportions changing) to isometric (body proportions not changing) growth pattern. Many of the allometric changes in characters that occurred during the pelagic phase were related to the flattening of the head and the reorganization of the dorsal fin, particularly the illicium. Five characters exhibited rapid growth (in relation to total length) during the pelagic phase. These characters were lengths of the dorsal fin base, the second dorsal ray (resulting in the development of the illicium and the esca), the snout (to accommodate the illicium), the esca, and the pectoral fin. Six characters exhibited slow growth (in relation to total length) during the pelagic phase to near isometric growth. These included a decrease in head depth, in orbit diameter, in caudal peduncle length, and in the length of the second dorsal ray. A dramatic reduction also occurred in the predorsal length as the anterior dorsal rays migrate towards the snout.

For the characters changes, better described as qualitative transitions (i.e., for changes in pigment, in the development of tubercle and cirri) and scored either as representing a larval (0) or juvenile-adult (1) state (Table 3), the start of such changes began at about 30 mm TL and ended at about 120 mm TL. The most dramatic changes occurred between 60 and 80 mm TL. The size range over which changes in fin pigmentation occurred was broader (16–243 mm TL). Although the timing of fin pigmentation may be intrinsically more variable than the other qualitative characters that were scored, the variability in fin pigmentation can also be an artifact of preservation technique.

As a result of these procedures, the changes in morphometric and character state traits (i.e., the changes in the shape from a lateral compressed pelagic larvae with long trailing pelvic fins to a dorsoventrally compressed head and body with much shorter pelvic fins as represented in some published illustrations) were quantified (Fahay, 1983; Caruso, 2002). These general changes in body proportions were found to be similar to those of *L. piscatorius* (Tåning, 1923; Dahlgreen, 1928) and *L. budegassa* (Stiasny, 1911; Bowman, 1919).

Several of the specimens evaluated for size-specific character transitions appeared to be at the pelagic juvenile stage (i.e., they were 21.6, 30.7, and 32.3 mm TL), although they were reportedly collected with benthic sampling gear. We suspect that these individuals were inadvertently collected in the water column because 1) they shared the same morphological and pigmentation characters as other pelagic individuals, 2) they were collected with gear that lacked opening and closing capability and thus the specimens could have been collected anywhere in the water column, and 3) the collection data indicated that in each instance the sampling gear spent more time in the water column than it did on the bottom. We therefore treated these individuals, in subsequent analyses, as pelagic juveniles.

Size and age at early life history events

The distribution of YOY goosefish was affected to a large degree by the timing and location of reproduction. Along much of the northeast coast of the United States, spawning occurs from spring through early fall (Wood, 1982; Hartley, 1995; Caruso, 2002), although exact details of spawning locations are lacking (Steimle et al., 1999). Collections during May through July 1996–99 in the surf zone (0–2 m, mean=0.66 individuals/100 m^3) and nearshore (6–7 m, mean=0.68 individuals/100 m^3) off northern New Jersey between Long Branch and Manasquan Inlet (Army Corps of Engineers [ACE] study area, Fig. 1A) showed densities of larval (3.6–15.6 mm TL, mean 7.6 mm) goosefish to be large in June (peak)

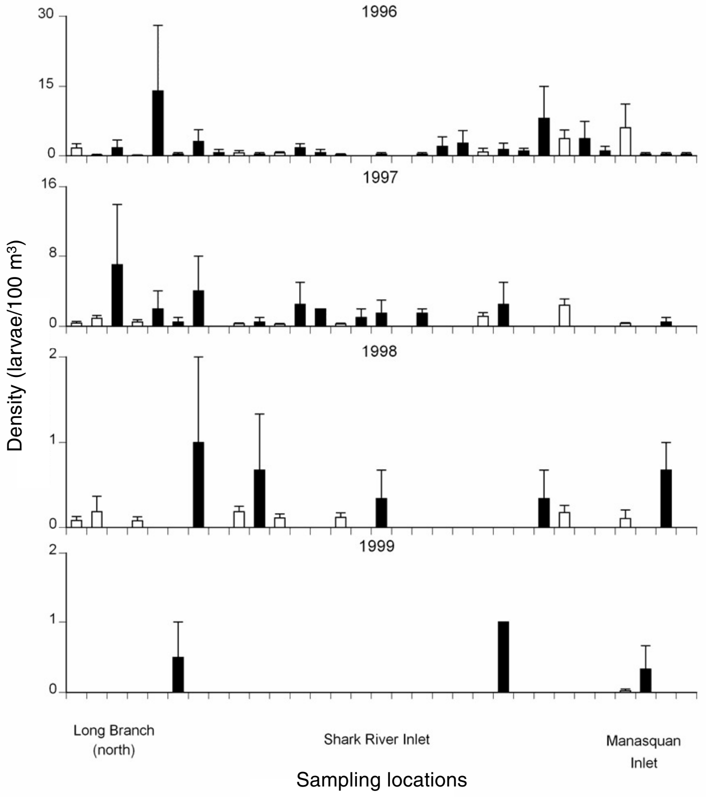

Figure 2

Composite spatial distribution and density (vertical lines above bars=mean standard error) of larval goosefish *(Lophius americanus)* sampled along the northern New Jersey coast (Fig. 1, Army Corps of Engineers) based on nearly equally spaced sampling locations between Long Branch and Manasquan Inlet, NJ, from 1996 through 1999. Samples were collected in the surf zone (0 to 2 m, closed bars, n=22 sampling stations) and in nearshore waters (6 to 7 m, open bars, n=9 sampling stations).

and July (Fig. 2). These collections of goosefish larvae were consistent with a May–June reproductive period estimated from gonadal condition of specimens collected in the area from Cape Hatteras to southern New England (Armstrong et al., 1992).

Our examination of lapillar otoliths provided estimates of the timing of several early life history events. There was good correspondence between the release of just-hatched larvae from the veil and the formation of a hatching check on the lapilli of laboratory-reared individuals. There were multiple microincrements before hatching (mean=5, range: 0–8). The variable number of microincrements prior to a "hatching check" on the lapillar otoliths may reflect the completion of hatching from the chorion and subsequent release of larvae from the egg veil. The completion of the yolk absorption appeared to correspond with a second check. The hatching and yolk absorption checks corresponded to similar checks in the otoliths of *L. piscatorius* (Hislop et al., 2001). Further, examination of otoliths from juvenile goosefish caught in the Middle Atlantic Bight indicated good correspondence between the hatching check and back-calculated mean size at hatching (4.5 mm TL, Fig. 3) and hatching sizes (2.5–4.5 mm TL) (Caruso, 2002). Back-calculations to a hatching check in lapilli (see below) indicated that hatching in specimens collected in the Middle Atlantic Bight occurred from June to October and peaked around July. This prolonged period of spawning and hatching was in agreement with several other spawning and hatching estimates for goosefish in the area (Caruso, 2002). The check on lapillar otoliths corresponding to yolk absorption occurred after 9–26 (mean=18) increments (days) at reported sizes of 6–8 mm TL (Caruso, 2002; Everly, 2002).

A third check (Fig. 3), which we believe corresponded with settlement, occurred in 57% of the lapilli examined. Back-calculated lengths at this check resulted in estimates of sizes at settlement from 52–83 (mean=68) mm TL and at ages 34–71 days after hatching. Individuals at these sizes were undergoing rapid changes in

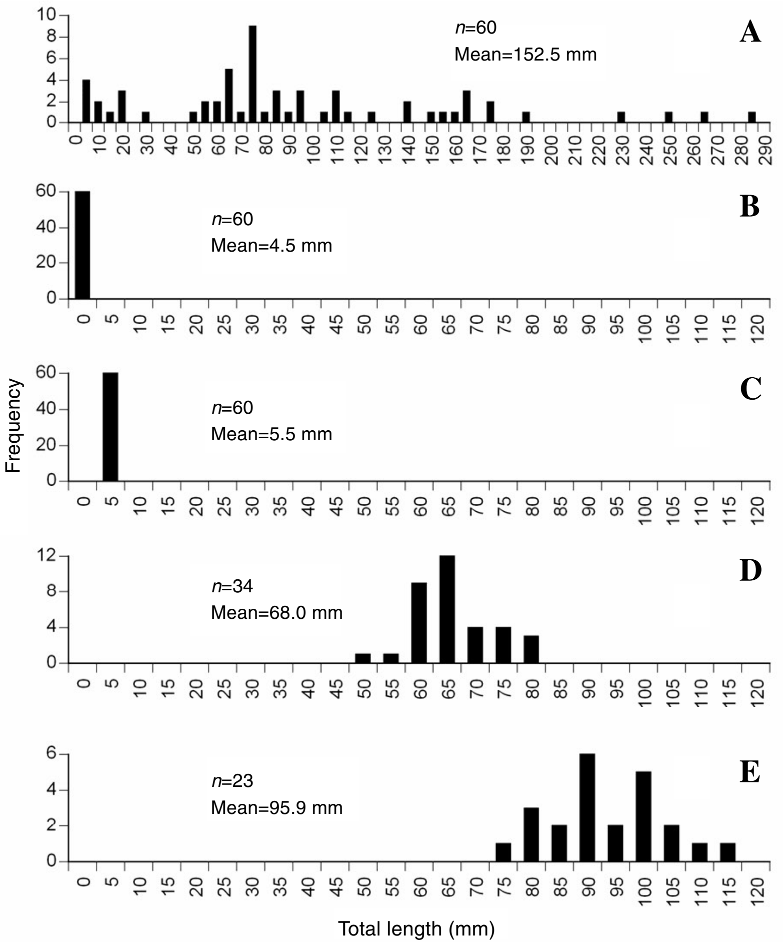

Figure 3

Sizes (total length mm) of goosefish *(Lophius americanus)* during the first year of life. (**A**) Size of goosefish at collection. All other sizes are based on back-calculated sizes from lapillar otoliths. (**B**) Size at formation of hatching check. (**C**) Size at absorption of yolk. (**D**) Size at settlement check. (**E**) Size at formation of first annulus.

relative body proportions as they approached or equaled the juvenile-adult condition (Table 2). Most of these changes occurred between 30 and 120 mm TL and were especially prominent in individuals of 60–80 mm TL. Settlement, as indicated by the length frequency of pelagic and benthic individuals, occurred over a relatively large range of sizes (Figs. 3 and 4). This interpretation may have been influenced by gear biases, the seasonal nature of the collections, and the ability of *Lophius* spp. to re-enter the water column, as occurs for *L. americanus* (Bigelow and Schroeder, 1953) and *L. piscatorius* (Hislop et al., 2000). The overlap in the magnitude of the size range of pelagic and benthic specimens was approximately 30–120 mm depending on the sampling technique (Figs. 3 and 4). Most of the individuals larger than 60 mm TL collected from May to November in the pelagic zone were collected with a mid-water trawl. The smallest benthic individuals (<60 mm TL) were collected in June, July, and August as incidental captures in scallop dredges. Benthic individuals were also collected, at low levels, from September to November. Together, these observations suggest that settlement occurs at sizes of 30–83 mm TL and extends from June into November. The two smallest settled individuals previously reported were 64 and 76 mm (Connolly, 1921). Similarly small-size settled individuals were reported for individuals of *L. piscatorius* (Bowman, 1919).

The growth of YOY goosefish appears to be fast compared to that of other north temperate marine fishes. Using size at capture, as well as estimates of age, size, and life history event checks deduced from otoliths, we estimated growth rates of 1.4 and 1.3 mm/day for the pelagic and benthic YOY life stages, respectively. A marginal increment analysis of lapilli indicated that the first annulus forms at sizes of 70–119 (mean=95.8) mm TL (Fig. 2). This estimate of size at first annulus forma-

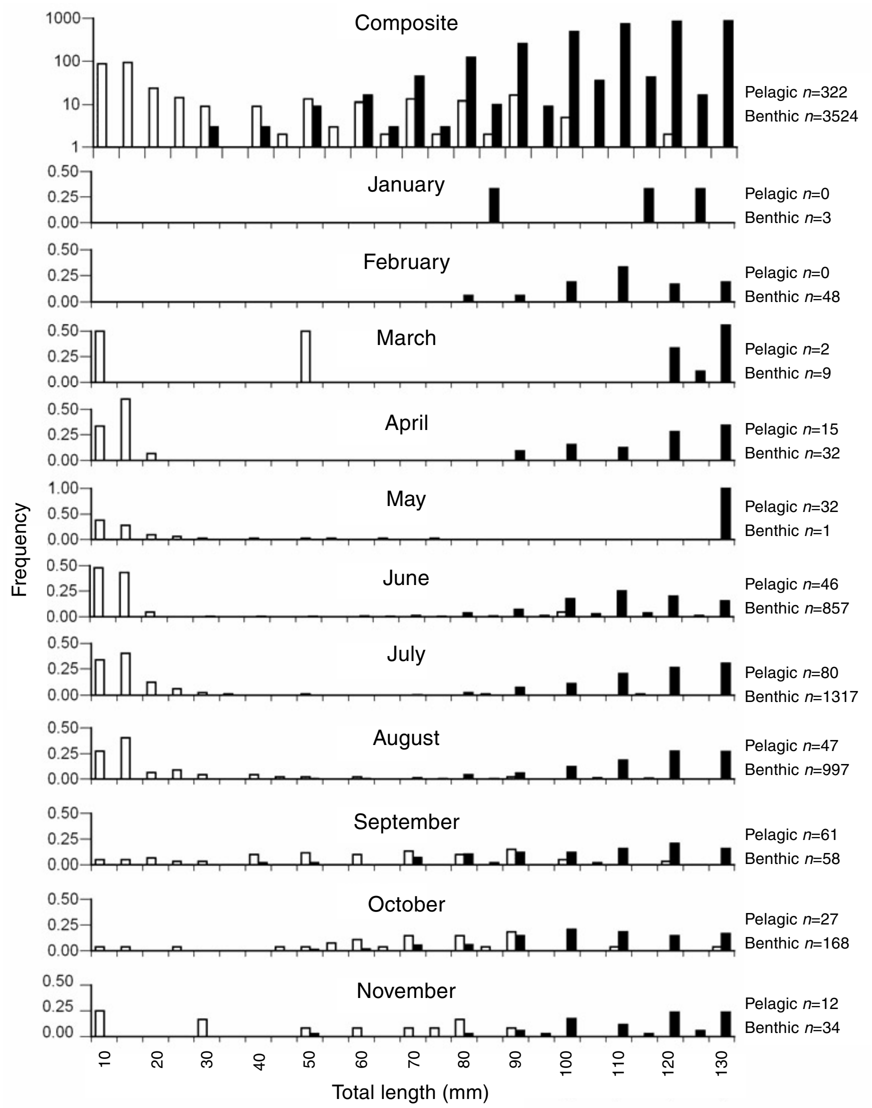

Figure 4

Composite and monthly length-frequency distributions of pelagic (open bars) and benthic (closed bars) goosefish (*Lophius americanus*) based on collections from the Middle Atlantic Bight, Georges Bank, and Gulf of Maine (Table 1; Fig. 1).

tion was consistent with estimates from whole goosefish otoliths made by resource scientists (Lang[2]).

Distribution and abundance

Spawning of goosefish, as inferred from the distribution of larvae (≤12 mm TL) is centered in the Middle Atlantic Bight (Fig. 1B). Far fewer larvae have been collected on Georges Bank and in the Gulf of Maine relative to the Middle Atlantic Bight, although sampling effort was comparable between regions (Steimle et al., 1999). Local collections of goosefish larvae (range: 1.7–10.8 mm notochord length [NL]) along the northern New Jersey coast from 1996 to 1999 reveal their densities to be similar between the surf (mean=0.68 [±0.19] individuals/100 m^3) and nearshore (mean=0.66 [±0.11] individuals/100 m^3) habitats (Fig. 2). The abundance of larvae along the northern New Jersey coast was variable and there were no consistent patterns between years (Fig. 2). These local, inshore data show that the larvae inhabit waters shallower than those surveyed in the NMFS MARMAP program.

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[2] Lang, K. 2004. Personal commun. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026.

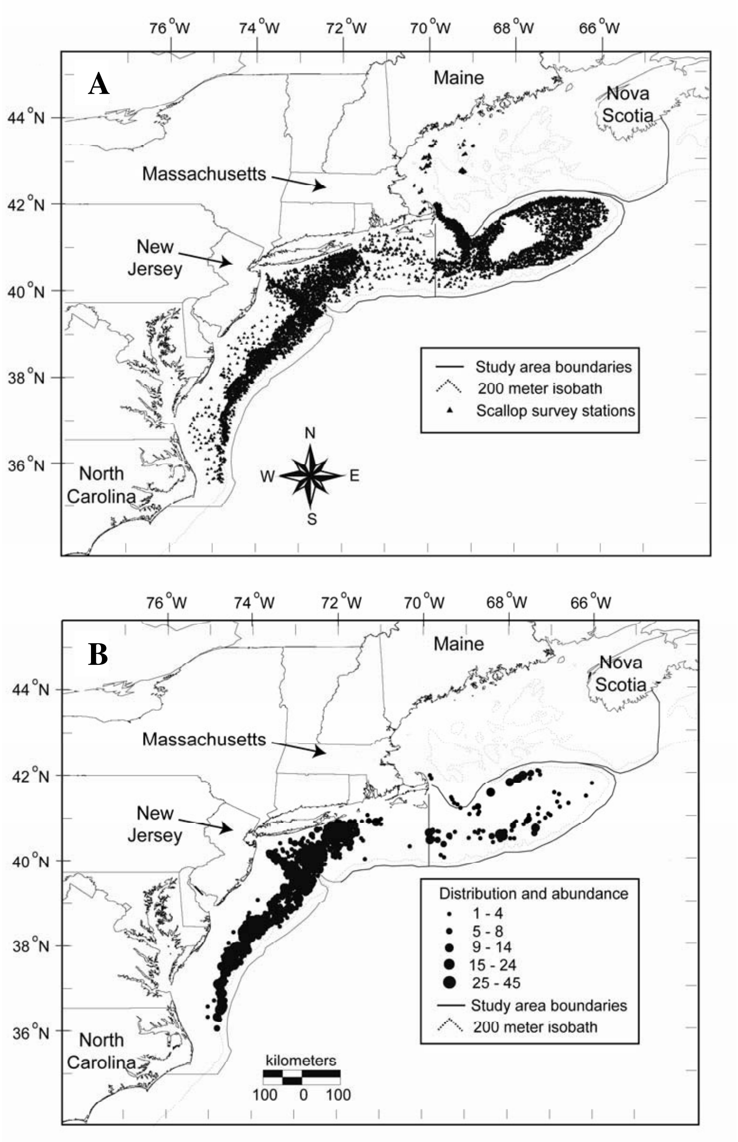

Figure 5

Distribution of (**A**) scallop dredge survey stations in the study area during 1982–2001 and (**B**) collections of benthic young-of-the-year (20–130 mm total length) goosefish *(Lophius americanus)* from these same surveys during the same period.

In the Middle Atlantic Bight, settlement may occur in a smaller area than that over which larvae are distributed. Even though the larvae (≤12 mm TL) were generally evenly distributed over the continental shelf up to and including the surf zone (Fig. 1B), pelagic juveniles (>12–120 mm TL) were concentrated in the middle and outer portion of the shelf (Fig. 1C). An exception to this pattern was the collection of some pelagic juveniles in waters close to the coast of Long Island, NY. Although goosefish larvae were not abundant on Georges Bank and in the Gulf of Maine (Fig. 1B), pelagic juveniles were captured there in relatively large numbers along the northern edge of Georges Bank and the adjacent portion of the Gulf of Maine (Fig. 1C). In these latter collections during NMFS hydroacoustic cruises from September through October 2000 and 2001, frame trawls were used to verify fish species. This sampling gear captured pelagic juveniles (50–130 mm TL) at depths ranging from the surface to 95 m within water depths of 65–191 m.

Most of the data and the majority (76%) of the benthic YOY (20–120 mm TL) goosefish specimens were collected from the NMFS scallop assessment surveys in the Middle Atlantic Bight and on Georges Bank during 1982 to 2001 (Fig. 5). The distribution of YOY goosefish reflects the boundaries of this survey. In the Middle Atlantic Bight, benthic YOY goosefish were collected on the central portion of the continental shelf from approximately the Virginia–North Carolina state line north to eastern Long Island, NY, where they were found in shallow nearshore waters. The benthic YOY goosefish also were present up the Hudson Canyon shelf valley. Few benthic YOY goosefish were collected in waters off Rhode Island and southern Massachusetts—likely the result of lower sampling effort (Fig. 5). On Georges Bank, the benthic YOY goosefish were distributed around the perimeter of the bank but were not collected as frequently on the eastern end of the bank, even though these areas were well sampled. YOY goosefish were occasionally collected off the "elbow" of Cape Cod, but were found infrequently in the Gulf of Maine.

Benthic juveniles are probably more widely distributed over the continental shelf and on the upper slope than indicated by the sea scallop survey. The best evidence for their distribution in deeper waters has been from four seasonal cruises centered on the continental shelf and slope off Virginia covering depths to 3080 m (Wenner, 1978; Wenner[3]). Many juveniles were collected at depths from 75–900 m and the greatest density was found at 200–399 m depths. A large number of these individuals (30%) were <120 mm TL and the smallest specimen was 53.4 mm TL.

Food habits and habitats

The stomach contents of YOY goosefish in the Middle Atlantic Bight were diverse (Table 4). The dominant prey group in the stomach contents comprised fish (45.1% frequency of occurrence [FO]) and crustaceans (17.6% FO). The most numerous prey fish were gadids, *Ammodytes*, and bothid and pleuronectid flatfishes. Invertebrates were also consumed, including mollusks, chaetognaths, nematodes, nemerteans, trematodes, polychaetes, and crustaceans. This diversity of prey has been frequently reported for juveniles and adults of *L. americanus* (Sedberry, 1983; Armstrong et al., 1996; Bowman et al., 2000; Caruso, 2002) and other congeners, including *L. piscatorius* (Tsimenidis, 1980; Crozier, 1985, Laurenson and Priede, 2005) and *L. budegassa* (Tsimenidis, 1980). The greater occurrence of invertebrates in the stomachs of *L. americanus* in our study (67.2% FO, Table 4) than in prior studies (Sedberry, 1983; Armstrong et al., 1996) was probably due to our emphasis on examining smaller YOY fish.

The food habits of YOY goosefish varied with fish size; a shift to a larger proportion of fish in the diet occurred at larger sizes (Fig. 6, A and B). Although invertebrates were common in the diet of all YOY examined, they occurred in 100% of the stomach contents at sizes smaller than approximately 50 mm TL and to a variable extent in most larger YOY fish. The vast majority of stomach contents, on the basis of weight (Table 4), were composed of fish in larger goosefish. Prior studies are equivocal on ontogenetic change in diet. Armstrong et al. (1996) reported smaller (<200 mm TL) individuals to have a higher proportion of invertebrates in their diet than we observed. Sedberry (1983) found the diets of all size classes of goosefish, including the two smallest (<100 and 101–200 mm), were dominated by fishes. Our results clarify the sizes at which this change to piscivory occurs (i.e., >50 mm TL).

Table 4

Prey items of young-of-the-year and small juvenile (age 1+) goosefish (*Lophius americanus*). Gut contents were expressed by percentage frequency of occurrence (% FO) across all specimens examined and average percent total weight in individual stomachs. Determination of prey habitat (P=pelagic, B=benthic, I=indeterminate, potentially both benthic and pelagic habitat) was based on knowledge of the life history of prey.

Prey	Habitat	% FO	% Total weight
Osteichthyes	B, I	79.4	86
Invertebrates		67.2	8.8
Molluska	I, B	1.6	7.2
Chaetognatha	P	3.1	<0.1
Nematoda			
(free-living)	B	3.1	<0.1
(unspecified)	I	1.5	<0.1
Nemertea	B	4.6	<0.1
Trematoda	I	7.6	<0.1
Polychaeta	B	3.8	<0.1
Hirudinea	I	0.8	<0.1
Crustacea	B, P	17.6	0.3
Other	I	58	5.2

The food habits also changed as a result of the transition from presettlement (pelagic) to postsettlement (benthic) habitats (Fig. 6, C and D). Individuals that were captured in the water column (<50 mm TL) had pelagic taxa such as chaetognaths, hyperiid amphipods, calanoid copepods, and ostracods in their stomachs. The dominance of pelagic prey was apparent whether prey were quantified as percent weight or percent frequency of occurrence. The stomach contents of larger individuals (60–280 mm TL, YOY, and small juveniles) were dominated by benthic prey when expressed as percent frequency of occurrence. The shift to benthic prey was not as obvious, however, when prey were expressed as percent weight. This was due to a large percentage of prey items that could not be assigned unequivocally to either benthic or pelagic habitats. The benthic prey comprised a variety of fishes and crustaceans including amphipods, cumaceans, mysids, shrimps, nematodes, nemerteans, and polychaetes (Table 4). The location of capture of some prey, such as that of small gadids and squid, was considered indeterminate because these prey could have been consumed by goosefish in either pelagic or benthic habitats.

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[3] Wenner, C. 2004. Personal commun. Marine Resources Research Institute South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

Conclusions

It appears that goosefish in the Middle Atlantic Bight spend ~5–10 weeks in the plankton as larvae and pelagic juveniles. As they change from pelagic larvae and juveniles to benthic juveniles (ca. 30–85 mm TL from June to November), they undergo major changes in body shape, pigmentation, and diet. Some of these life history changes are reflected in the microstructure of lapillar otoliths. Overall, changes in these suites of characteristics are most evident before and during settlement. Most of the events in the early life history of goosefish appear to occur without dependency on water depth or location across the continental shelf. Larvae, pelagic juveniles, and benthic juveniles tend to be most abundant on the mid to outer continental shelf, but they are also widely distributed inshore, indicating that they are habitat generalists.

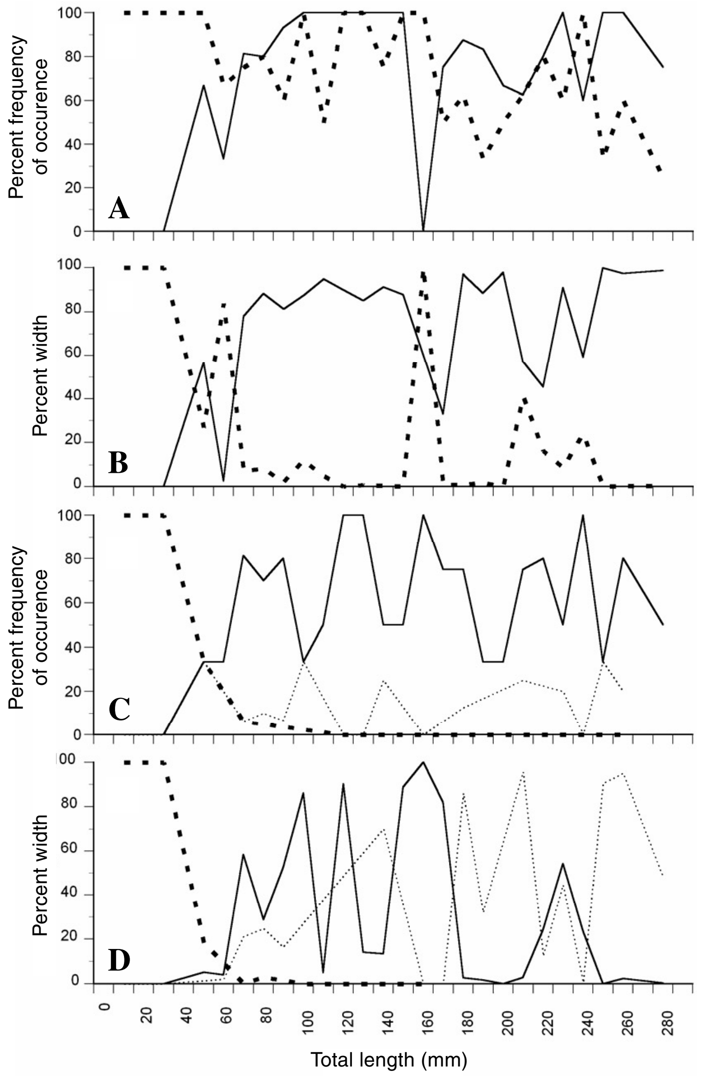

Figure 6

Change in diet (**A, B**) and habitat (**C, D**) of young-of-the-year goosefish *(Lophius americanus)* with increasing total length (TL). Diet changed from mostly invertebrates (dotted line) to mostly fish (solid line), whether expressed as percent frequency of occurrence (A) or percent weight in stomach contents (B). Habitat, determined from stomach contents, changed as a function of goosefish sizes (TL). Prey in stomach was expressed as frequency of occurrence (C) and percent weight (D). Prey habitats, based on knowledge of prey life history, were classified as either benthic (solid line), pelagic (large dotted line), or indeterminate (small dotted line).

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Literature cited

Almeida, F. P., D. L. Hartley, and J. Burnett.
1995. Length-weight relationships and sexual maturity of goosefish off the northeast coast of the United States. N. Am. J. Fish. Manag. 15:14–25.

Armstrong, M. P., J. A. Musick, and J. A. Colvocoresses.
1992. Age, growth, and reproduction of the goosefish *Lophius americanus* (Pisces: Lophiiformes). Fish. Bull. 90:217–230.
1996. Food and ontogenetic shifts in feeding of the goosefish, *Lophius americanus*. J. Northwest Atl. Fish. Sci. 18:99–103.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull 53, 577 p.

Bowman, A.
1919. The eggs and larvae of the angler (*Lophius piscatorius*) in Scottish waters. Fish Board Scotland Rep. Sci. Invest. 1919:(2):21–23.

Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein.
2000. Food of Northwest Atlantic fishes and two common species of squid. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NE-155, 138 p.

Carr, W. E., and C. A. Adams.
1972. Food habits of juvenile marine fishes: evidence of the cleaning habit in the leath-

erjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. Fish. Bull. 70:1111–1120.

Caruso, J. H.
1983. The systematics and distribution of the lophiid anglerfishes: II. Revisions of the genera *Lophiomus* and *Lophius*. Copeia 1983:11–30.
2002. The goosefishes or monkfishes. Family Lophidae. *In* Bigelow and Schroeder's Fishes of the Gulf of Maine (B. B. Collette, and G. Klein-MacPhee, eds.), 561 p. Smithsonian Institution Press, Washington, D.C.

Connolly, C. J.
1921. On the development of the angler (*Lophius piscatorius L.*). Contrib. Can. Biol. 7:115–124.

Crozier, W. W.
1985. Observations on the food and feeding of the angler-fish, *Lophius piscatorius L.*, in the northern Irish Sea. J. Fish Biol. 27:655–665.

Dahlgreen, U.
1928. The habits and life history of *Lophius*, the angler fish. Nat. Hist. 28:18–32.

Everly, A. W.
2002. Stages of development of the goosefish, *Lophius americanus*, and comments on the phylogenetic significance of the development of the luring apparatus in Lophiiformes. Environ. Biol. Fishes 64:393–417.

Fahay, M. P.
1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. 4:1–423.

Fuiman L., K. R. Poling, and D. M. Higgs.
1998. Quantifying developmental progress for comparative studies of larval fishes. Copeia 3:602–611.

Hartley, D. L.
1995. The population biology of the goosefish, *Lophius americanus*, in the Gulf of Maine. M.S. thesis, 142 p. Univ. of Mass., Amherst, MA.

Hislop, J. R., A. Gallego, M. R. Heath, F. M. Kennedy, S. A. Reeves, and P. J. Wright.
2001. A synthesis of the early life history of the anglerfish, *Lophius piscatorius* (Linnaeus, 1758) in northern British waters. ICES J. Mar. Sci. 58:70–86.

Hislop, J. R. G., J. C. Holst, and D. Skagen.
2000. Near-surface captures of post-juvenile anglerfish in the North-east Atlantic–an unsolved mystery. J. Fish Biol. 57:1083–1087.

Hubbs, C. L., and K. F. Lagler.
1958. Fishes of the Great Lakes region, 332 p. Univ. Michigan Press, Ann Arbor, MI.

Jean, Y.
1965. Seasonal distribution of monkfish along the Canadian Atlantic mainland. J. Fish. Res. Board Can. 22:621–624.

Laurenson, C. H., and I. G. Priede.
2005. The diet and trophic ecology of anglerfish *Lophius piscatorius* at the Shetland Islands, U.K. J. Mar. Biol. Assn. U.K. 85:419–424.

Mahon, R., and J. D. Neilson.
1987. Diet changes in Scotian Shelf haddock during the pelagic and demersal phases of the first year of life. Mar. Ecol. Prog. Ser. 37:123–130.

Martinez, C. M.
1999. The reproductive biology of goosefish, *Lophius americanus*. M.S. thesis, 78 p. Univ. Rhode Island, Naragansett, RI.

Michaels, W. L. (ed.)
2001. Report on the third Northwest Atlantic herring acoustic workshop, Univ. Maine, Darling Marine Center, Walpole, ME, March 13–14, 2001. U.S. Dep. Commer., NOAA Tech. Memo.NMFS-NE-166, 18 p.

Morse, W. W., M. P. Fahay, and W. G. Smith.
1987. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia (1977–1984). Atlas no. 2: Annual distribution patterns of fish larvae. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NEFSC, 215 p.

Policansky, D.
1983. Size, age and demography of metamorphosis and sexual maturation in fishes. Amer. Zool. 23:57.63.

Scott, J. S.
1982. Selection of bottom type by groundfishes of the Scotian Shelf. Can. J. Fish. Aquat. Sci. 39:943–947.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Sedberry, G. R.
1983. Food habits and trophic relationships of a community of fishes on the outer continental shelf. NOAA Tech. Rep. NMFS-SSRF-773, 56 p.

Serchuk, F. M., and S. E. Wigley.
1986. Evaluation of USA and Canadian research vessel surveys for sea scallops (*Placopecten magellanicus*) on Georges Bank. J. Northwest Atl. Fish. Sci. 7:1–13.

Steimle, F. W., W. W. Morse, and D. L. Johnson.
1999. Essential fish habitat source document: Goosefish, *Lophius americanus*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-127, 31 p.

Steves, B. P., R. K. Cowen, and M. H. Malchoff.
1999. Settlement and nursery habits for demersal fishes on the continental shelf of the New York Bight. Fish. Bull. 98: 167–188.

Stiasny, G.
1911. Regarding certain postlarval development stages of *Lophius piscatorius* L. Arbeit. Zool. Inst. Vienna 19:54–74. [In German.]

Tåning, Å. V.
1923. *Lophius*. Danish Oceanogr. Exped., 1908–10, Rep. no. 7, vol. 2 (Biol.), A 10, 30 p.

Toms, J. D., and M. L. Lesperance
2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology 84:2034–2041.

Tsimenidis, N. H.
1980. Contribution to the study of the angler-fishes *Lophius budegassa* Spinola, 1807 and *L. piscatorius* L. 1758 in Greek seas. Spec. Publ. Inst. Oceanogr. Fish. Res. Athens 4, 190 p. [In Greek.]

Wenner, C. A.
1978. Making a living on the continental slope and in the deep-sea: life history of some dominant fishes of the Norfolk Canyon area. Ph.D. diss., 294 p. College of William and Mary, Williamsburg, VA.

Wiley, M. L., and B. B. Collette.
1970. Breeding tubercles and contact organs in fishes: their occurrence, structure, and significance. Bull. Am. Mus. Nat. Hist. 143(3):145–216.

Wood, P. W., Jr.
1982. Goosefish, *Lophius americanus*. *In* Fish distribution (M. D. Grosslein, and T. R. Azarovitz, eds.), p. 67–70. MESA New York Bight Atlas Monograph 15. N.Y. Sea Grant Institute, Albany, NY.