# Growth, reproduction, and feeding of large monkfish, *Lophius americanus*

A. K. Johnson, R. Anne Richards, Daniel W. Cullen, and Sandra J. Sutherland

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The American monkfish, *Lophius americanus*, supports important commercial fisheries in the Northwest Atlantic. Although life history information is available for smaller *L. americanus*, the biology of large monkfish (>70 cm) is poorly understood because relatively few large fish are caught in standard resource surveys. Between 2006 and 2008, 699 *L. americanus* of 71–118 cm total length were collected from commercial gillnet fishers operating in the mid-Atlantic Bight ($n = 689$) and in the Gulf of Maine ($n = 10$) to investigate growth rates, reproductive biology, and feeding habits of large monkfish. All those collected were mature females ranging in age from 7 to 13 years. Growth was linear at an average annual rate of 7.6 cm. Hepatosomatic indices peaked in February and gonadosomatic indices between February and April. Postovulatory follicles and vitellogenic oocytes were observed in the same ovaries, evidence that monkfish spawn over a protracted period and possibly more than once annually. Food habits were similar to those reported for smaller benthic phase monkfish, but cannibalism was more prevalent in large fish (5.6% frequency of occurrence). Frequencies of feeding and cannibalism were greatest in females in the final stage of oocyte maturation.

**Keywords:** anglerfish, cannibalism, feeding, gonadosomatic indices, goosefish, growth, hepatosomatic indices, *Lophius americanus*, life history, monkfish, reproduction.

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*A. K. Johnson and D. W. Cullen: Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, MD 21853, USA. R. A. Richards and S. J. Sutherland: NOAA Northeast Fisheries Science Center, Woods Hole, MA 02543, USA. Correspondence to A. K. Johnson: tel: +1 410 6518447; fax: +1 410 651 7739; e-mail: akjohnson@umes.edu.*

## Introduction

The American goosefish or monkfish (*Lophius americanus*) is a fast-growing anglerfish widely distributed in the Northwest Atlantic from the Grand Banks and northern Gulf of St Lawrence, Canada, to the east coast of Florida (Caruso, 2002). It supports important commercial fisheries in US waters, with landings that approached 30 000 t in the late 1990s (Haring and Maguire, 2008). US monkfish fisheries are managed separately in two regions. The northern management area (NMA) consists of the Gulf of Maine (GOM) and northern Georges Bank, and the southern management area (SMA) includes southern Georges Bank to waters off Cape Hatteras, NC (Figure 1). The two management areas were defined based on temporal patterns of recruitment, differences in growth patterns (Armstrong *et al.*, 1992; Hartley, 1995) and differences in the types of fishing gear used (NEFSC, 2002). Landings and value of *L. americanus* in both areas increased during the 1980s and 1990s, whereas the abundance of traditional groundfish species dwindled (Haring and Maguire, 2008). As landings increased during the mid-1980s, the maximum size of monkfish in the population declined (Figure 2), so fewer large monkfish are now found in commercial landings or during Northeast Fisheries Science Center (NEFSC) annual bottom-trawl surveys (NEFSC, 2005).

Several authors have described aspects of *L. americanus* life history (Armstrong *et al.*, 1992; Hartley, 1995; Martinez, 1999; Richards *et al.*, 2008), but large fish, here defined as >70 cm, were generally poorly represented. Most studies relied primarily on fish caught during NEFSC bottom-trawl surveys, which catch relatively few large monkfish (NEFSC, 2005). Growth curves estimated for both management areas were linear and did not reach an asymptote, presumably because of the absence of large fish. Large fish are also poorly represented in diet studies, though Armstrong *et al.* (1996) provided intriguing evidence of higher rates of cannibalism in larger fish. Monkfish >70 cm are usually mature females (Armstrong *et al.*, 1992) and are assumed to spawn annually (NEFSC, 2002), but little is actually known of spawning frequency in monkfish. The purpose of this study, therefore, was to obtain large monkfish to estimate growth rates, investigate reproductive biology, and examine food habits.

## Methods

Study sites were located within the two management areas (NMA and SMA). The NMA included areas north of 41°30′N (Figure 1), with all samples collected in the western GOM (WGOM). The SMA was subdivided into the northern mid-Atlantic Bight (NMAB) and the southern mid-Atlantic Bight (SMAB), based on latitude. The NMAB included the area between latitudes 39°30 and 41°30′N, and the SMAB between 35 and 39°30′N (Figure 1). In all, 699 *L. americanus* ranging in size from 71 to 118 cm total length (TL) were collected by commercial gillnetters ($n = 12$) using nets of 30.5 cm mesh between Cape Ann, MA, and Chincoteague, VA, from January 2006 to April 2008 (Table 1; Figure 1).

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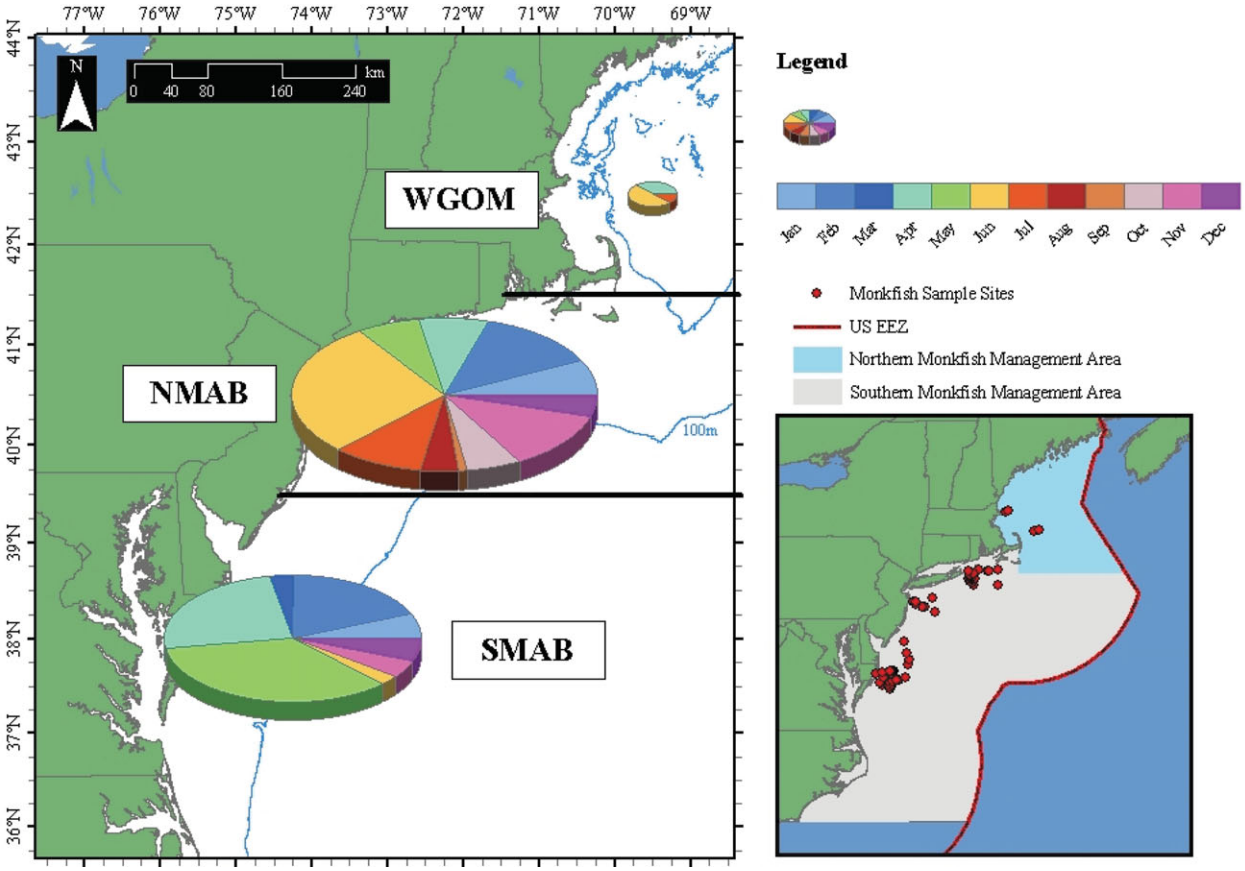


**Figure 1.** Sampling locations of large *L. americanus* collected by commercial gillnetters between January 2006 and April 2008 in the Northwest Atlantic Ocean. The size of the pie charts is proportional to the number of monkfish samples per site (Table 1).

Some 99% of the fish came from the SMA (Figure 1) and 73% were collected during the first half of the year (Table 1). *Lophius americanus* were shipped from the port of landing to the University of Maryland Eastern Shore, where most were processed in a fresh (unpreserved) state within 1–2 d of capture. Each fish was weighed to the nearest 0.1 kg and measured (TL) to the nearest 0.5 cm. Samples were collected for studies of growth, food habits, and reproductive biology, as described below.

## Age and growth

Vertebrae ($n = 661$) were used for age determination, following the procedures of Armstrong *et al.* (1992) and Hartley (1995). Armstrong *et al.* (1992) established that vertebrae meet the minimum criteria for the use of structures for age determination (Van Oosten, 1929), but the method has not been validated directly. From each fish, vertebrae numbers 3–11 were excised and vertebra number 8 (or number 9, if number 8 was damaged) was cleaned and stored frozen for 1–2 months before baking. Vertebra number 8 was baked in a drying oven for 1–1.5 h at 230°C to enhance the contrast in presumed annual rings before counts were made using a dissecting microscope at ×60 magnification. Most vertebrae ($n = 523$) were read by two independent readers, and the balance ($n = 138$) by one reader. If age readings differed by 1 year ($n = 110$), the estimate from the most experienced reader was used. If readings differed by 2 years ($n = 24$), the average age was used. Vertebrae were classified as "unreadable" and removed from the sample set if readings disagreed by 3 years or more ($n = 2$).

## Reproduction

All monkfish collected were female, and gonad samples for histological examination were taken from 630 of them. Samples were fixed in 10% neutral buffered formalin, dehydrated, embedded in paraffin, sectioned at 5 μm, and stained with haematoxylin and eosin (H&E). Histological sections were examined by light microscopy and assigned maturity stages following the criteria of Wallace and Selman (1981), Armstrong *et al.* (1992), and Martinez (1999). Ovarian stages [perinucleolar, cortical alveoli, vitellogenic, and final stage of oocyte maturation (FOM, hydrated)] were classified based on the stage of maturity of the most advanced stage oocytes.

Ovaries and livers were weighed, and the gonadosomatic index ($I_G$) and hepatosomatic index ($I_H$) calculated as:

$$I_G = 100\, W_G(W - W_G)^{-1} \quad \text{and } I_H = 100 W_H(W - W_H)^{-1},$$

where $W_G$ is the gonad weight, $W_H$ the liver weight, and $W$ the body weight.

Analysis of variance (ANOVA, SAS version 9.1; SAS Institute Inc., Cary, NC, USA) was used to test the influence of month and gonad stage on $\log_e$-transformed $I_G$ and $I_H$. Significant ANOVAs ($p < 0.05$) were followed by Tukey's multiple comparison tests (Neter *et al.*, 1996).

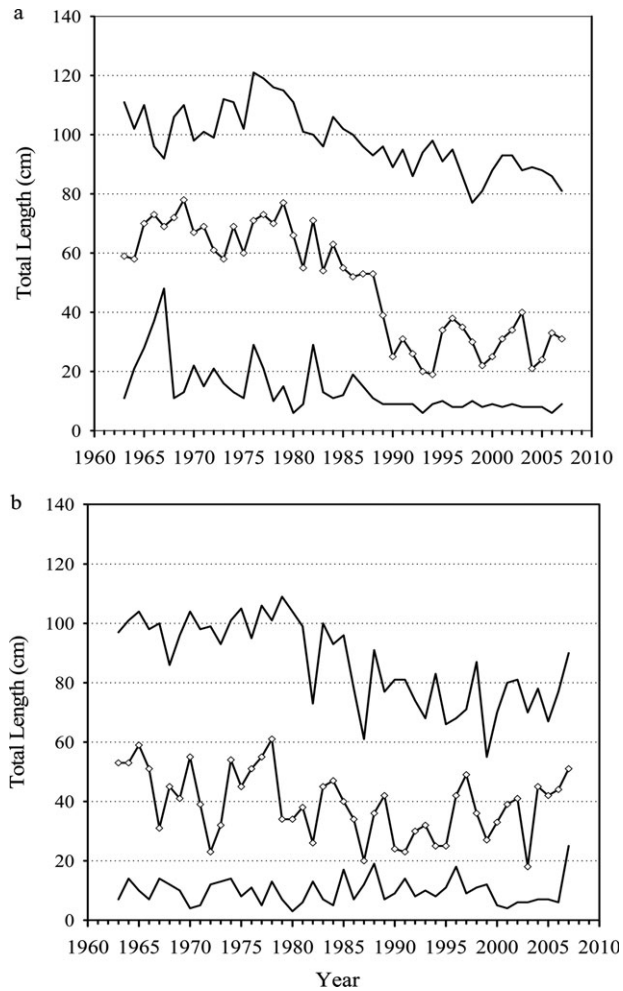


**Figure 2.** Minimum, median, and maximum size of monkfish collected during NEFSC autumn surveys in (a) the NMA and (b) the SMA, 1963–2007.

## Food habits

*Lophius americanus* stomachs were removed and the contents weighed to the nearest gramme. Prey items were sorted, identified to the lowest taxon possible, enumerated, weighed individually and by prey category, and measured if possible. Intact *L. americanus* prey ($n = 4$) were measured, weighed, and dissected to determine gender. The relative abundance of prey species were calculated as percentage frequency by number (%$N$) and weight (%$W$), and as an index of relative importance (%IRI) for major taxonomic prey groups (Armstrong *et al.*, 1996). The incidence of cannibalism was determined for *L. americanus* at each microscopic gonad stage.

## Results

The size range of the monkfish sample ($n = 699$) was 71–118 cm, and the mode was 90 cm TL (Figure 3). Most (67%) were collected during February and from April to June, very few being collected during the rest of the year (Table 1) because of the seasonality of fishing effort. The SMA collection accounted for 99% of the total ($n = 689$; Figure 1), because fishery regulations in the NMA made it more difficult to obtain collaborators there. In the SMA, 58% of the samples came from the NMAB and 42% from the SMAB (Figure 1).

**Table 1.** Monthly collection of female *L. americanus* from three regions of the Northwest Atlantic, 2006–2008.

| Month | Location | | | |
|---|---|---|---|---|
| | GOM | NMAB | SMAB | All areas |
| January | – | 23 | 12 | 35 |
| February | – | 53 | 57 | 110 |
| March | – | – | 12 | 12 |
| April | 4 | 31 | 77 | 112 |
| May | – | 33 | 107 | 140 |
| June | 5 | 95 | 4 | 104 |
| July | 1 | 46 | – | 47 |
| August | – | 23 | – | 23 |
| September | – | 5 | – | 5 |
| October | – | 32 | – | 32 |
| November | – | 44 | 10 | 54 |
| December | – | 13 | 12 | 25 |
| All months | 10 | 398 | 291 | 699 |

## Age and growth

Age was successfully estimated for 659 fish across the whole size range of the sample. Agreement between readers was 74%, and most readings that disagreed varied by just 1 year (81%). Ages ranged from 7 to 13 years, but most fish were aged 8–11. Growth increased linearly with age (Figure 4), with an average annual increment of 7.6 cm (based on quarter 2 samples, which were represented by all ages; $n = 336$). Length increased most between the second and third quarters of the year (Figure 4).

## Reproduction

All the monkfish examined were mature (Figures 3 and 5); immature ovaries containing perinucleolar oocytes as the most advanced stage were not observed. Ovaries at each stage (except FOM) contained primary oogonia, chromatin nucleolar and perinucleolar stage oocytes (Figure 5). Of the four ovarian stages, ovaries with atretic oocytes were most common (56%),

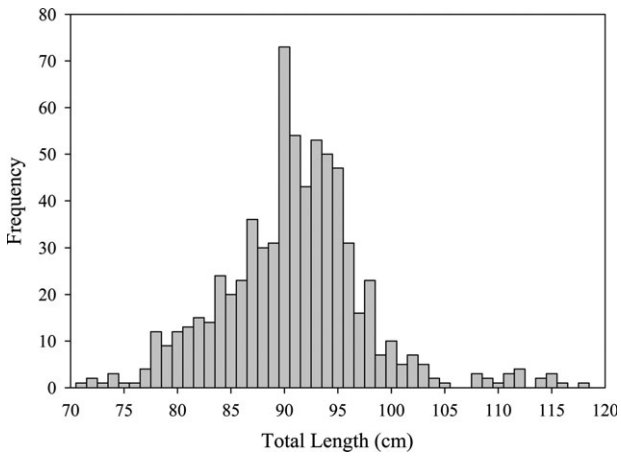


**Figure 3.** Length composition of large *L. americanus* collected between January 2006 and April 2008. Modal length = 90 cm TL ($n = 699$).

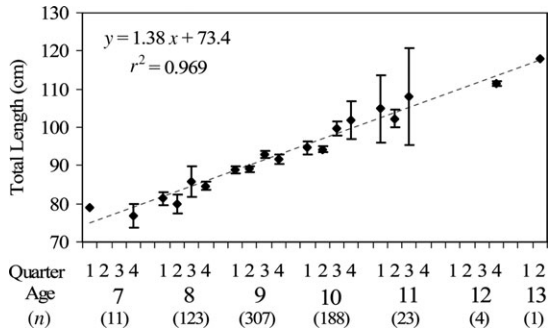


**Figure 4.** Age–length relationship for *L. americanus* by quarter of the year. Error bars are 95% confidence intervals.

followed by hydrated (18%) and vitellogenic oocytes (18%). Ovaries with cortical alveoli as the most advanced stage oocytes were least common (8%). Females with cortical alveoli stage oocytes were found mainly during winter (Figure 6). Vitellogenic oocytes were found during all months except July–September in the NMAB and November in the SMAB. No fish were collected between July and October in the SMAB (Figure 6). Hydrated oocytes were found from January to August in the NMAB, and from February to May in the SMAB (Figure 6). Atretic oocytes were found in almost every month (except January in the SMAB). Atretic postovulatory follicles (POF) were found in ovaries with both pre-vitellogenic and vitellogenic oocytes (Figure 5).

Large female *L. americanus* spawned between January and August (Figures 6 and 7). Mean $I_G$ values were significantly higher for February and March than all other months (ANOVA, d.f. = 11; $p < 0.05$; Figure 7). Mean $I_G$ values for females caught in April, May, and June did not differ significantly from those of other months (except October and November; Figure 7), because of the many post-spawning females undergoing atresia (low $I_G$; Figure 6). Mean $I_H$ was significantly higher in February than all other months (ANOVA, d.f. = 11; $p < 0.005$) except January and December (Figure 7). As a result of the small number of samples collected from the NMA, latitudinal differences in spawning of *L. americanus* could not be determined. Within the MAB, there were no differences between NMAB and SMAB.

Comparisons of $I_G$ and $I_H$ with female gonad histology showed that the mean $I_G$ peaked during FOM and that $I_H$ was highest in females with vitellogenic oocytes (Figure 8). Mean $I_G$ values were significantly different at each stage of gonad development (ANOVA, d.f. = 3; $p < 0.0001$), whereas mean $I_H$ values were significantly higher in females with vitellogenic oocytes than those at all other stages of gonad development (ANOVA, d.f. = 3; $p < 0.0001$; Figure 8).

## Food habits

Of the 699 stomachs examined, 34.9% contained prey remains. Incidence of feeding was 30% ($n = 10$) for GOM, 33.4% ($n = 398$) for NMAB, and 35.4% ($n = 291$) for SMAB. In all, 17 prey species were identified, including pelagic and benthic species belonging to four major taxonomic groups: Cephalopoda, Decapoda, Elasmobranchii, and Teleostei, of which the last was most important in both the NMAB (%IRI = 93.9) and the SMAB (%IRI = 57.8). The diet of *L. americanus* in the GOM consisted of bony fish (%$N$ = 75.0; %$W$ = 90.2) and one decapod (*Cancer borealis*; %$N$ = 25.0; %$W$ = 9.8). Bony fish, elasmobranchs, and longfin squid (*Loligo pealeii*) made up the greatest proportions by number and weight of prey of *L. americanus* from both the NMAB (%$N$ = 96; %$W$ = 99) and the SMAB (%$N$ = 99; %$W$ = 99; Figure 9). Prey items belonging to the "other" category (%$N < 1$; %$W < 1$; Figure 9) included conger eel, spiny dogfish, winter flounder, and an unidentified decapod for the NMAB, and Atlantic herring, Gulf Stream flounder, northern sea robin, and spiny dogfish for SMAB. Atlantic mackerel, skate, northern stargazer, and monkfish were the most commonly identified prey items (Figure 9). The smallest identifiable prey species was a Gulf Stream flounder (9.5 cm), and the largest a female Atlantic cod (82 cm) taken from a 97-cm *L. americanus*. There was no relationship between predator length and prey length within the size range of fish examined (Figure 10).

The overall frequency of cannibalism was 5.6%. Evidence of cannibalism ranged from jaw bones (NMAB, $n = 2$; SMAB $n = 4$) to partially digested monkfish (NMAB, $n = 21$; SMAB, $n = 11$). One incidence of a partially digested *L. americanus* was found in the GOM. The gender of *L. americanus* prey was identifiable in four specimens, one female (36.5 cm TL) and three males (36, 48, and 53 cm TL) taken from specimens >90 cm TL. The incidence of prey items was highest in hydrated (FOM) females (50.4%) and lowest in post-spawning (atretic) females (32.4%; Figure 11). The frequency of *L. americanus* in the diet was greatest in females undergoing FOM (9.6%) and lowest in those with cortical alveoli (4.3%; Figure 11).

## Discussion

A primary goal of this study was to increase the maximum observed age to extend the growth curve for *L. americanus*. Fish up to 138 cm were collected in NEFSC surveys before the development of age determination methods (Richards *et al.*, 2008), but in this study, fish >118 cm (13 years of age) were not obtained, and just 7% were >100 cm TL. The lack of large specimens is likely the result of high fishing mortality in recent years (Haring and Maguire, 2008; Figure 2). The location of our sampling may have been a factor too. The geographic distribution of large monkfish caught in NEFSC resource surveys indicates that the largest monkfish were more common in the NMA (Figure 12).

The absence of large males in this study confirms observations made by other authors. The reported maximum size of male *L. americanus* is 85–90 cm, but very few males >70 cm have been found (Armstrong *et al.*, 1992; Richards *et al.*, 2008). The pattern of smaller maximum size for males has been seen in other *Lophius* species as well. According to Afonso-Dias and Hislop (1996), the maximum size of male and female *Lophius piscatorius* is 89 cm and 129 cm, respectively, and Yoneda *et al.* (2001) reported the maximum length of male and female *Lophius litulon* to be 69 and 101 cm, respectively. A similar size difference was observed for female and male *Lophius vomerinus* off Namibia, females attaining a maximum length of 95 cm and males 67 cm (Maartens and Booth, 2005). Behavioural or distributional differences and/or early senescence have been suggested by Armstrong *et al.* (1992) for the lack of large males. The high rate of cannibalism by large monkfish, as observed here, may also impact the male population.

The gonad histology and temporal patterns in $I_G$ and $I_H$ values indicated a protracted reproductive season for large *L. americanus*, from January to August, with most spawning between February and April. We observed no differences in reproductive season

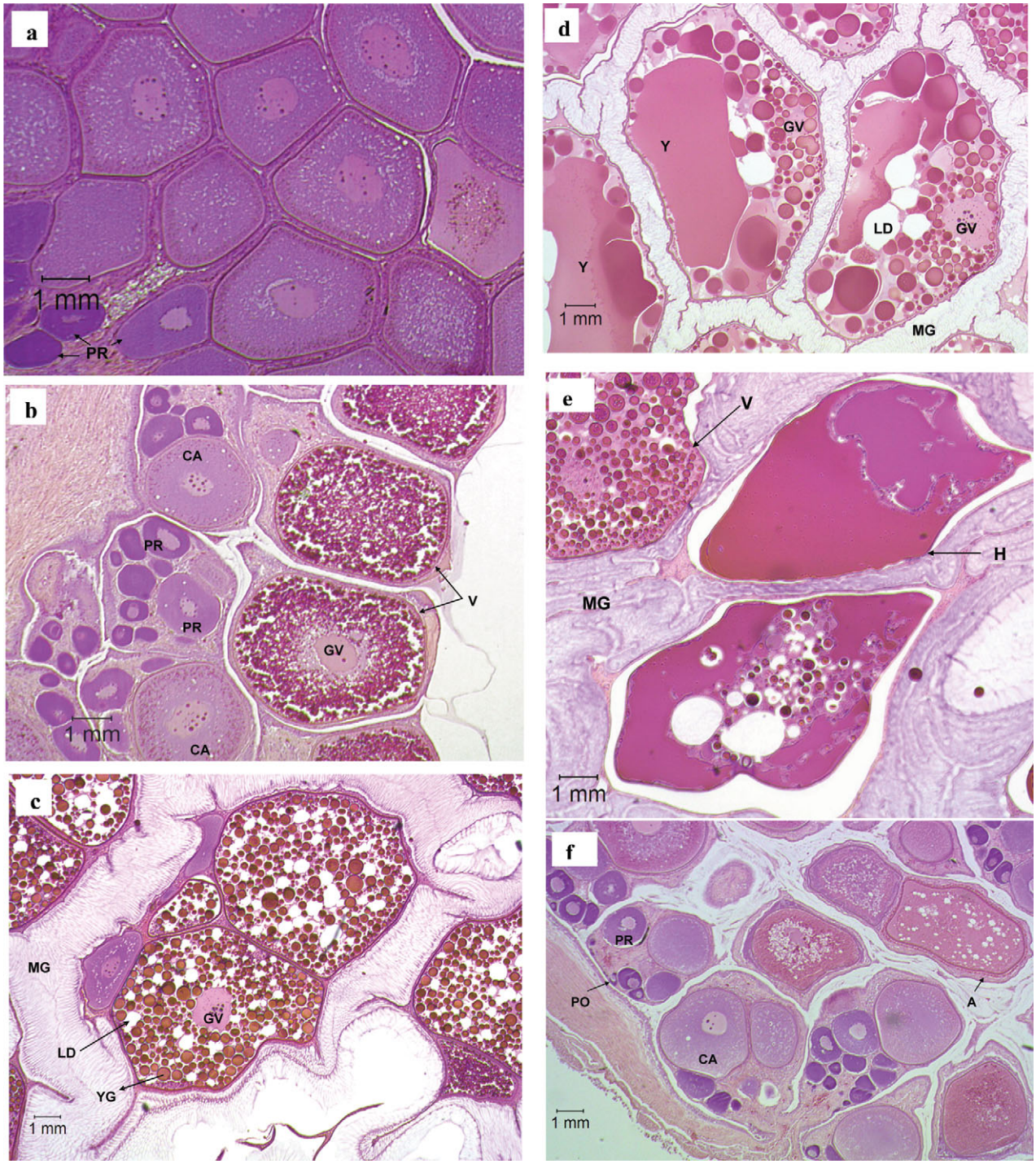


**Figure 5.** Photomicrographs of transverse sections of the ovaries of *L. americanus* stained with H&E. (a) Female caught in January with mainly cortical alveoli stage oocytes. A few perinucleolar stage oocytes were also observed in the ovary. (b) Female caught in January showing oocytes at different stages of maturation (perinucleolar, cortical alveoli and vitellogenic). (c) Vitellogenic oocytes from a female caught in February. Mucogelatinous material can be found outside the germinal compartment of the developing oocytes. (d) A female caught in May showing germinal vesicle migration, fusion of lipid droplets, and coalesced yolk globules (protein yolk) forming a homogeneous mass of yolk. (e) Ripe female with hydrated and vitellogenic oocytes. (f) Degeneration of vitellogenic oocytes and an increase in primary chromatin nucleolar and perinucleolar stage oocytes in a female caught in May. PO, primary chromatin nucleolar; PR, perinucleolar; CA, cortical alveoli; V, vitellogenic; H, hydrated; A, atretic; GV, germinal vesicle; LD, lipid droplet; YG, yolk globule; MG, mucogelatinous material; Y, yolk.

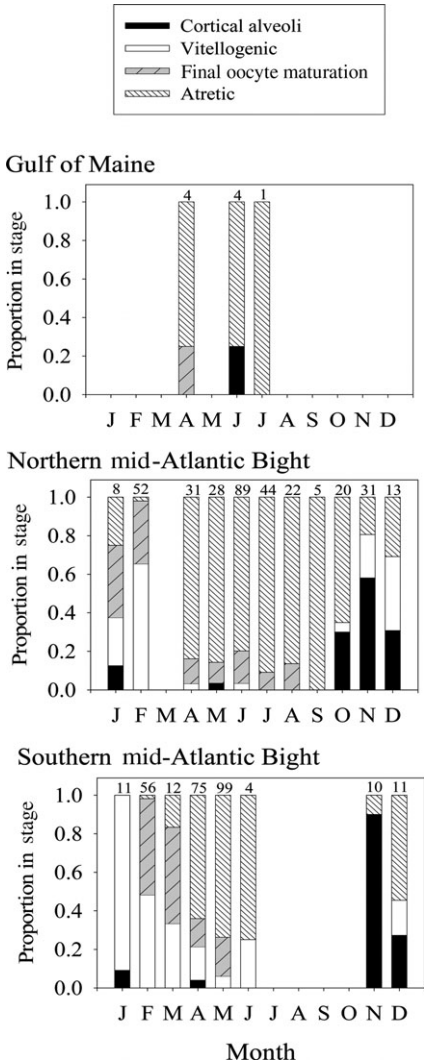


**Figure 6.** Proportion of mature female *L. americanus* at different ovarian stages (cortical alveoli, vitellogenic, FOM, and atretic) collected by month in the WGOM, NMAB, and SMAB. The numbers above each bar represent the number of fish sampled per month.

between the NMAB and the SMAB. Protracted spawning periods, as long as 4–12 months, have been reported for anglerfish around the world. The spawning season for *Lophiomus setigerus* extends over 7 months from May to November (Yoneda *et al.*, 1997) and for *L. litulon* in the East China Sea over 4 months (February–May; Yoneda *et al.*, 2001). In Scottish waters, ripe female *L. piscatorius* have been found between November and May and ripe males throughout the year (Afonso-Dias and Hislop, 1996). Also, extended spawning seasons have been recorded for *L. piscatorius* in the Bay of Biscay (May–August; Quincoces *et al.*, 1998) and the Portuguese and Spanish Atlantic coasts (January–June; Duarte *et al.*, 2001). Maartens and Booth (2005) reported spawning of *L. vomerinus* in Namibian waters throughout the year. Protracted spawning was also identified for *Lophius budegassa*, namely November–February (Duarte *et al.*, 2001) and October–March (Azevedo, 1996) off the Portuguese and Spanish coasts, respectively, although a shorter spawning period (May–July) was recorded for the Bay of Biscay (Quincoces *et al.*, 1998). In contrast, Armstrong *et al.* (1992)

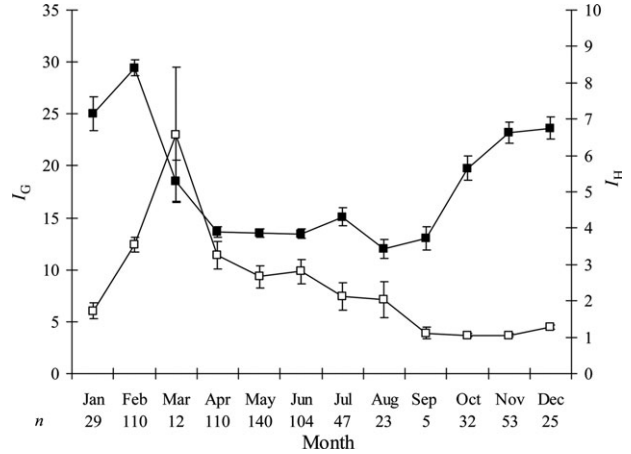


**Figure 7.** Monthly variations in mean values of GSI ($I_G$, white boxes) and HSI ($I_H$, black boxes) for female *L. americanus* caught off the east coast of the US between January 2006 and April 2008. The numbers below the months are sample size (*n*).

reported a shorter spawning period (May–June) for *L. americanus* collected from the mid-Atlantic Bight than that observed during this study, but "near-spawning" gonads were found in March and April and again in July and August. The truncated spawning season observed by Armstrong *et al.* (1992) may reflect the small number of ripe females they caught ($n = 13$), the lack of mature females collected between January and February, and the use of trawlnets to sample fish. Other recent studies on *L. americanus* (Martinez, 1999; Richards *et al.*, 2008) reported protracted spawning, consistent with this study.

The presence of oocytes at different stages of development in mature females caught during the breeding season could be taken as evidence that *L. americanus* is a multiple spawner, releasing several batches of oocytes over a protracted spawning period. The presence of POF in females with vitellogenic oocytes throughout the spawning season further supports this suggestion. Multiple spawning has been recorded for captive *L. litulon* (Yoneda *et al.*, 2001) and *L. setigerus* (Yoneda *et al.*, 1997), and atretic oocytes have been found in ovaries of *L. litulon* with vitellogenic oocytes (Yoneda *et al.*, 2001). Martinez (1999) reported the presence of developing vitellogenic oocytes in 100% of post-spawning *L. americanus* ovaries collected in summer and in 25% collected

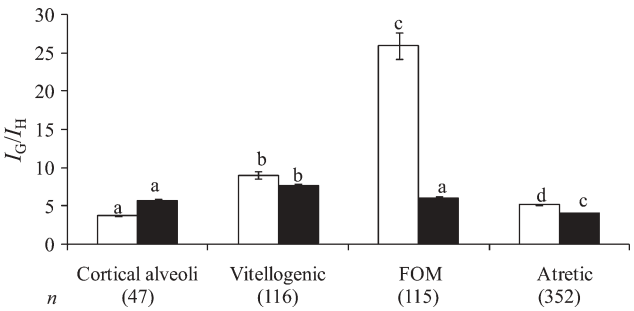


**Figure 8.** Variation in mean GSI ($I_G$, white bars) and HSI ($I_H$, black bars) values among females in successional stages of gonad development. Identical letters indicate mean values of HSI and GSI that are statistically non-significant. Numbers below gonad stages are sample sizes.

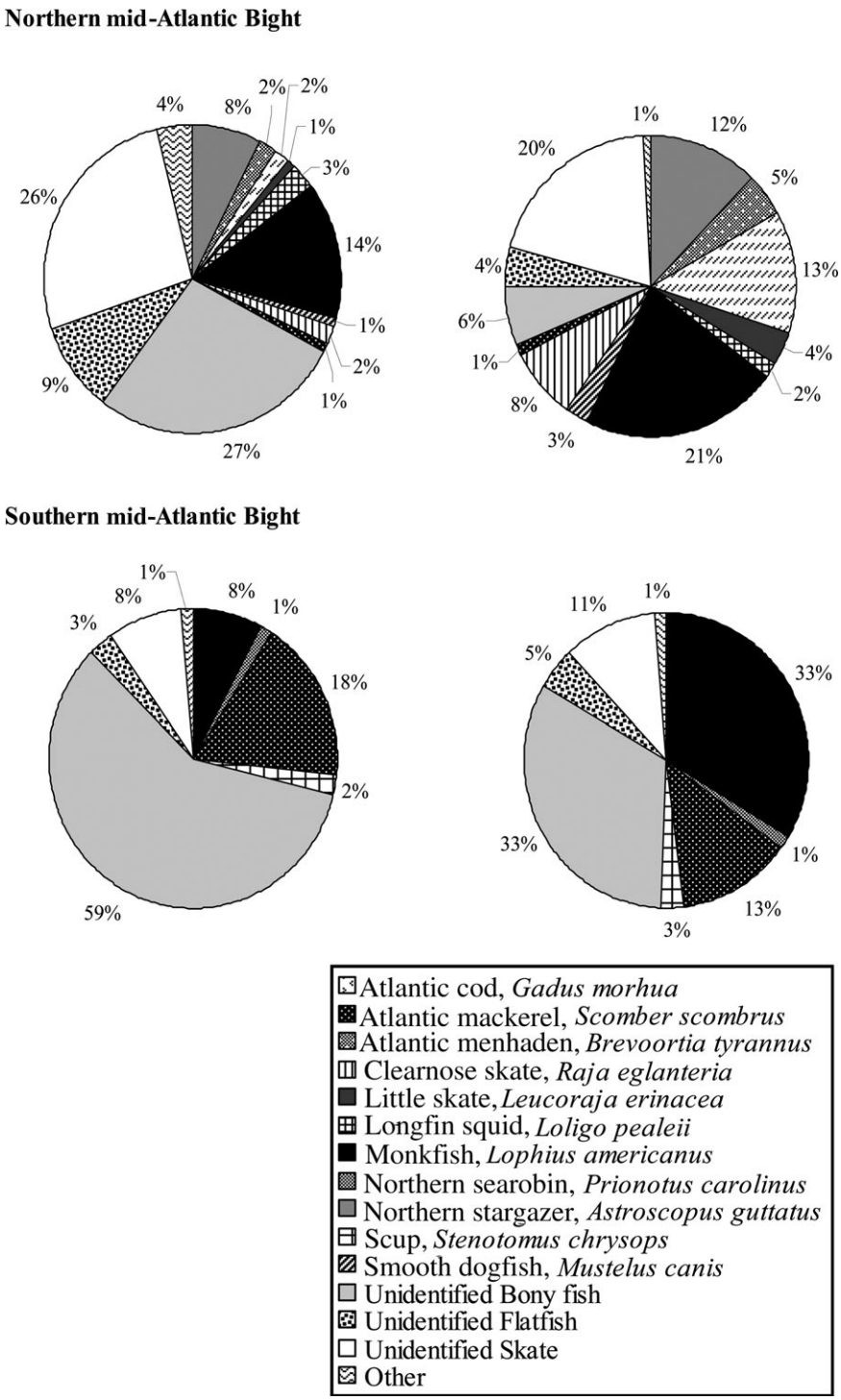


**Figure 9.** Percentage number (left) and weight (right) of prey items in *L. americanus* stomachs. Prey species were placed in the "other" category if their frequency of occurrence was $<1\%$. $n = 103$ (NMAB), $n = 134$ (SMAB).

in autumn. In contrast, atresia was not found in vitellogenic *L. piscatorius* caught off the coast of Scotland (Afonso-Dias and Hislop, 1996), and atretic oocytes were not reported by Armstrong *et al.* (1992). The latitudinal differences in timing of spawning reported for *L. americanus* (Armstrong *et al.*, 1992), *L. piscatorius* (Afonso-Dias and Hislop, 1996), and *L. litulon* (Yoneda *et al.*, 2001) were not observed in this study. However, our study had just a few samples from the NMA and no summer samples from the SMAB for comparison.

The inverse relationship between $I_H$ and $I_G$ was expected. High $I_H$ was observed in autumn and winter in females with cortical alveolar stage oocytes and vitellogenic oocytes as the most advanced stage oocytes, whereas $I_G$ was highest in spring and summer in females undergoing FOM. This increase in $I_H$ during

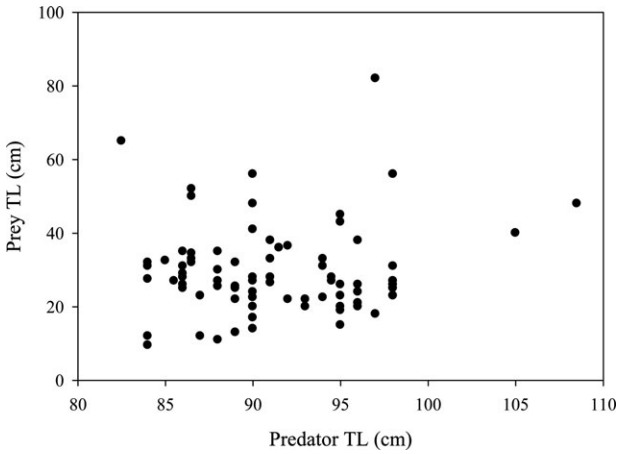


**Figure 10.** Relationship between prey length and predator (*L. americanus*) length. $n = 88$ prey items.

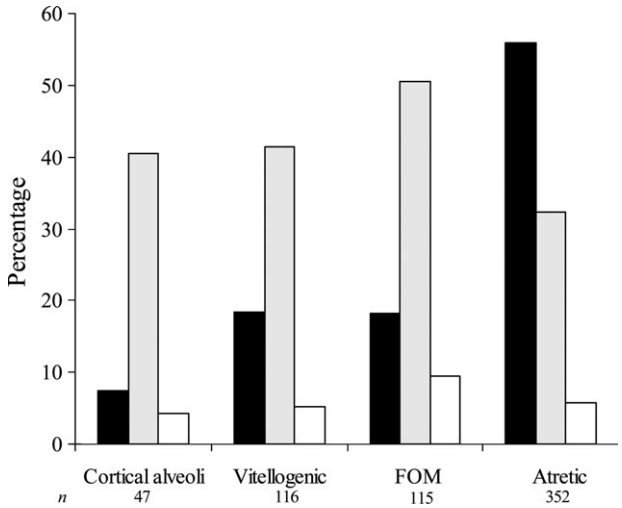


**Figure 11.** Relative frequency of feeding by microscopic gonad stage of development ($n = 630$). Percentage of all fish collected (black bars), percentage of fish with prey in their stomachs (grey bars), and percentage of fish with stomachs containing *L. americanus* (white bars). Numbers below gonad stages are sample size ($n$).

autumn and winter suggests that the production of vitellogenin (precursor to yolk protein) by the liver takes place during the development of cortical alveoli stage oocytes, before vitellogenic oocyte growth.

The predominance of fish in the diet of adult *L. americanus* has been seen in other studies (Armstrong *et al.*, 1996; Link and Garrison, 2002). Studies by Connolly (1920), Bigelow and Schroeder (1953), and Leim and Scott (1966) noted that monkfish fed on bony fish and longfin squid in the GOM and adjacent Canadian waters. The results of those studies showed that

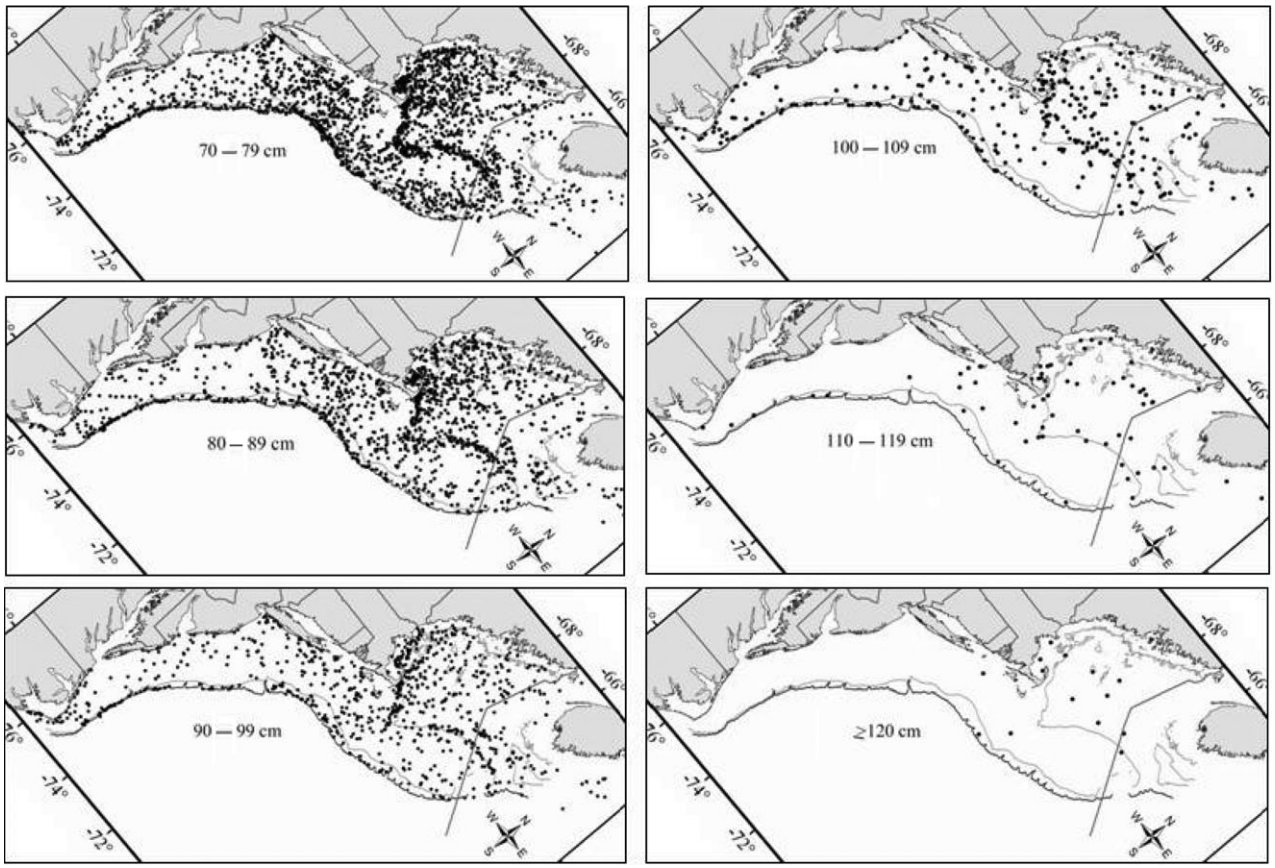


**Figure 12.** Distribution of monkfish ≥70 cm TL taken throughout the year in NEFSC survey sampling using trawls and dredges, 1963–2008. Each dot represents one fish. Depth contours shown are 100 and 400 m, and the dividing line is the US–Canada boundary. See Richards *et al.* (2008) for a description of sampling procedures.

*L. americanus* from the northern regions fed mostly on fish, whereas those from more southern areas fed on a mixed diet of fish and squid. Sedberry (1983) found that the diet of *L. americanus* along the outer continental shelf of the northwest mid-Atlantic was dominated by bony fish and invertebrates, including longfin squid, *L. pealeii*, and red shrimp, *Dichelopandalus leptocerus*. Similarly, Armstrong *et al.* (1996) found that larger *L. americanus* (>600 mm TL) fed mostly on large teleosts and less on elasmobranchs and longfin squid. Armstrong *et al.* (1996) suggested that *L. pealeii* was an important invertebrate prey item for larger monkfish because it had the ability to grow to a relatively large size. Pareda and Olaso (1990) reported both fish and cephalopods as the main species found in the stomachs of *L. piscatorius*.

The high percentage of *L. americanus* with empty stomachs suggests that feeding is sporadic or possibly that *L. americanus* regurgitate when captured. Laurenson and Priede (2005) attributed large proportions of empty stomachs in large *L. piscatorius* to infrequent feeding. The large proportions of unidentified bony fish and skates found within stomachs from all seasons could be an indication that the digestion process is slow, especially for larger prey items (Valentim *et al.*, 2008). However, estimates of daily ration and rates of gastric evacuation are not available for *L. americanus*.

Infrequent feeding by *L. americanus* may also indicate a reduced energy demand in large monkfish. During their study on the feeding ecology of *L. budegassa*, Preciado *et al.* (2006) observed that feeding intensity varied by season and predator size. Feeding intensity was greatest for smaller *L. budegassa* and during summer. Larger *L. budegassa* fed most intensively during winter and least so in autumn. As a result of a higher energy demand, Preciado *et al.* (2006) hypothesized that smaller *L. budegassa* fed more frequently than larger fish. Armstrong *et al.* (1996) briefly noted a greater frequency of feeding in younger *L. americanus*, but little was mentioned about variations in feeding intensity for larger fish. In our study, *L. americanus* fed most intensively during winter and spring, and least in autumn.

We observed a relatively high rate of cannibalism in our samples (5.6% overall). In contrast, the rate of cannibalism was only 0.13% in >10 000 *L. americanus* stomachs collected in NEFSC resource surveys during the period 1977–2007 (NEFSC, unpublished data), but the median TL of *L. americanus* sampled during those surveys was 42 cm compared with 91 cm in the current study. Armstrong *et al.* (1996) found that the frequency of cannibalism was 10.2% in *L. americanus* >60 cm ($n = 38$), but found no evidence of cannibalism in smaller *L. americanus* ($n = 221$). These results suggest that cannibalism is more common in large females. A speculative hypothesis is that ripe females produce a pheromone to attract males, some of which may end up as food rather than mates. Fishers commonly observe males "tending" females that have been caught in gillnets, presumably following a pheromone trail. Our finding that the highest rate of cannibalism (10%) was in ripe (FOM) females lends credence to this hypothesis.

Our study revealed intriguing aspects of the life history of the American monkfish, some of which have not been evident through the study of younger fish. In particular, we found that size continued to increase linearly with age, and although the annual increment was somewhat smaller than for younger monkfish, we found no indication that growth rates had reached an asymptote. Further, cannibalism was more prevalent in large female monkfish than in the population as a whole, which begs the question of what impact this may have on the productivity of the population if age structure is allowed to rebuild. Inferences from reproductive histology suggested the possibility that large female monkfish may spawn more than once per year, which also has important implications for stock productivity. These aspects of monkfish life history warrant further investigation and application to modelling studies.

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