Population biology of monkfish *Lophius americanus*

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This paper provides an overview of the biology of monkfish in US waters of the Northwest Atlantic Ocean using data from resource surveys spanning the period 1948–2007. Monkfish exhibited seasonal onshore–offshore shifts in distribution, migrated out of the southern Mid-Atlantic Bight (MAB) in mid-spring, and re-appeared there in autumn. Sex ratios at length for fish 40–65-cm long were skewed towards males in the southern MAB, but approximated unity elsewhere, suggesting that a portion of the population resides outside sampled areas. Growth was linear at 9.9 cm year^{-1} and did not differ by region or sex. Maximum observed size was 138 cm for females and 85 cm for males. Length at 50% maturity for males was 35.6 cm (4.1 years old) in the north and 37.9 cm (4.3 years old) in the south; for females 38.8 cm (4.6 years old) in the north and 43.8 cm (4.9 years old) in the south. Ripe females were found in shallow (<50 m) and deep (>200 m) water in the south, and in shallow water (<50 m) in the north.

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Introduction

The American monkfish (or goosefish, *Lophius americanus*) supports one of the most lucrative fisheries in US waters of the Northwest Atlantic Ocean. The fishery developed during the 1980s, and by the mid-1990s monkfish surpassed traditional groundfish species (cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, flounders) and became the highest valued finfish in the northeastern US (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html). However, monkfish biology has been poorly understood, in part because monkfish are not well sampled by the gear used in long-standing annual resource surveys of the US continental shelf.

Monkfish are distributed in the Northwest Atlantic from the Grand Banks and northern Gulf of St Lawrence south to Cape Hatteras, NC (Caruso, 2002), from just below the tide line (Bigelow and Schroeder, 1953) to depths of at least 900 m (Markle and Musick, 1974; Wenner, 1978; NEFSC, 2002). Stock structure is not clearly understood. No genetic divergence was found among goosefish collected between North Carolina and Maine in depths up to 300 m (Chikarmane *et al.*, 2000), but growth patterns and recruitment differed in northern and southern areas (Armstrong *et al.*, 1992; Hartley, 1995). Two management areas [Northern Management Area (NMA)—Gulf of Maine and northern Georges Bank; Southern Management Area (SMA)—southern Georges Bank and Mid-Atlantic Bight, MAB; Figure 1] were established for monkfish in 1999. The basis for establishing two management regions was perceived differences in biology and substantial differences in how fisheries are prosecuted in the two regions (Haring and Maguire, 2008).

Commercial fisheries for monkfish in US Northwest Atlantic waters operate year-round using gillnets, trawls, and scallop dredges. Total reported annual landings increased from ∼100 t in the mid-1960s to a peak of 28 000 t in 1997 (Figure 2), but subsequently declined to 14 000 t in 2006 as a result of fishery restrictions (days-at-sea and trip limits; Haring and Maguire, 2008). Trends in autumn trawl survey catches show relatively high biomass in both management areas before the mid-1980s, followed by a decline through the 1990s (Northeast Data Poor Stocks Working Group, 2007; Figure 3). In the NMA, biomass increased in the late 1990s, but then declined. In the SMA, biomass has fluctuated around relatively low levels since the mid-1980s.

Seminal studies on monkfish population biology were conducted by Armstrong *et al.* (1992) and Hartley (1995). Armstrong *et al.* (1992) developed methods for determining the age of monkfish using vertebrae, and applied the method to estimate length- and age-based population parameters for monkfish collected from the SMA. Hartley (1995) applied the methods of Armstrong *et al.* (1992) to monkfish collected in the NMA. Here, we build on this foundation using information from resource surveys conducted annually since 1963 by the Northeast Fisheries Science Center (NEFSC) in US waters of the Northwest Atlantic Ocean, and from industry-based monkfish surveys (IBMS) conducted in the same region.

Methods

Annual fishery-independent surveys conducted by the NEFSC and two IBMS in 2001 and 2004 were our primary sources of biological information on monkfish. The NEFSC surveys have been conducted in offshore waters (depth range ∼27–365 m) in autumn since 1963 (bottom trawl survey), in spring since 1968 (bottom trawl survey), in summer since 1984 (sea scallop dredge survey), and in winter since 1992 (flatfish bottom trawl survey; Table 1).
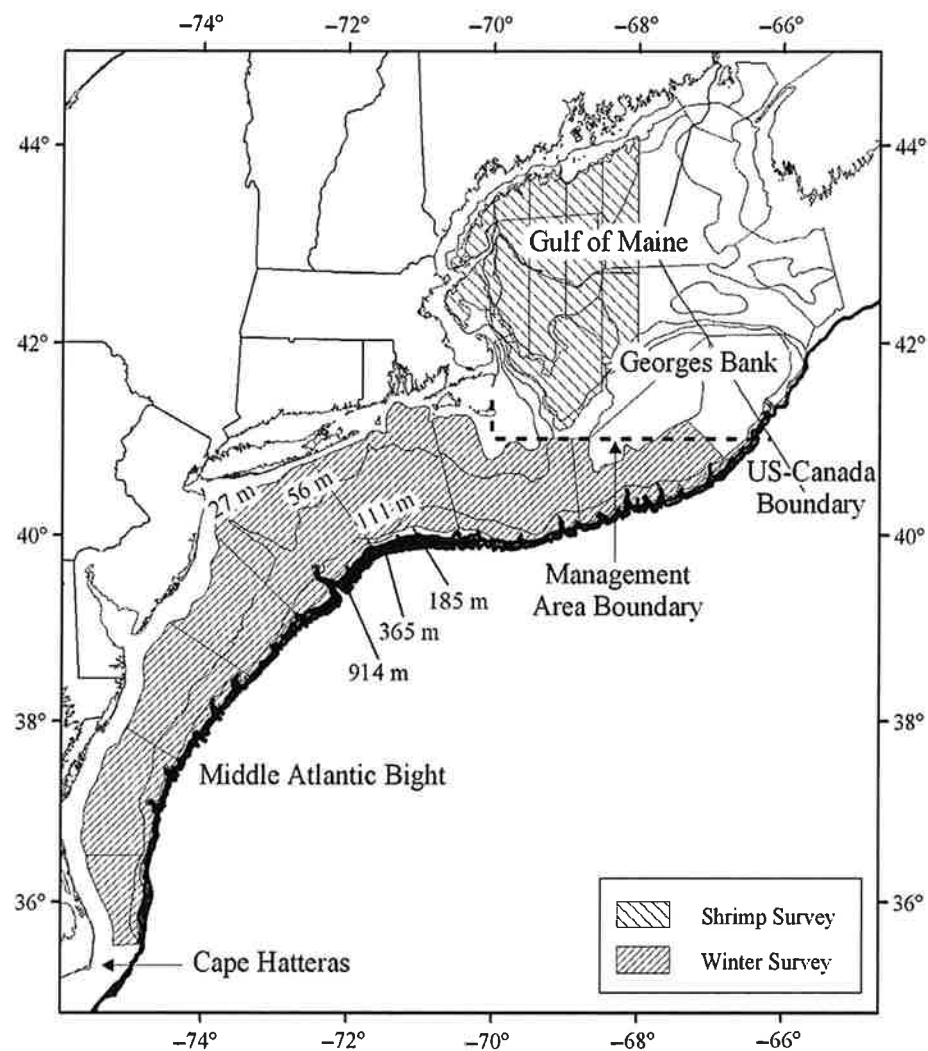
Figure 1. Survey stratification scheme for NEFSC trawl surveys. The entire area is sampled during NEFSC spring and autumn trawl surveys. Hatched areas show strata sampled during NEFSC winter trawl surveys and shrimp surveys. Additional deep-water strata sampled during IBMS are indicated in black.
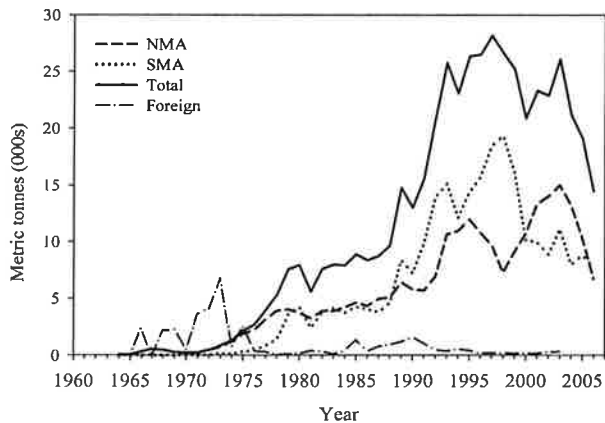
Figure 2. Reported commercial fishery landings ('000 t) of monkfish in US waters, 1964–2006. Foreign landings are from NAFO areas 5 and 6 (http://www.nafo.int/).
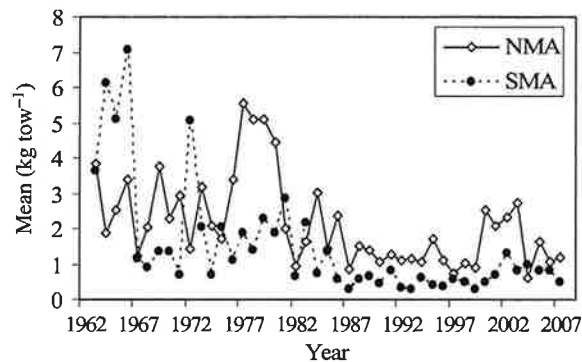
Figure 3. Biomass trends for monkfish (stratified delta distribution mean kg tow^{-1}) from NEFSC autumn trawl surveys in the NMA and SMA.

Table 1. Surveys used in the analysis of monkfish biology.

	NEFSC Winter Trawl	IBMS[a]	NEFSC Spring Trawl	NEFSC Summer Trawl	Shrimp	NEFSC Sea Scallop	NEFSC Autumn Trawl
Season	Winter	Winter/Spring	Spring	Summer	Summer	Summer	Autumn
Gear	Flatfish Bottom Trawl	Commercial Bottom Trawl	Survey Bottom Trawl	Survey Bottom Trawl	Shrimp Trawl	Scallop Dredge	Survey Bottom Trawl
Geographic coverage	Southern Georges Bank to Cape Hatteras, NC	Gulf of Maine to Cape Hatteras, NC	Gulf of Maine to Cape Hatteras, NC	Northern Georges Bank and Gulf of Maine	Western Gulf of Maine	Southern Georges Bank to Cape Hatteras, NC	Gulf of Maine to Cape Hatteras, NC
Depth range (m)							
NMA	–	26–256	22–337	21–298	85–263	–	25–331
SMA	16–314	24–430	9–325	9–272	–	31–102	9–329
Management area	SMA[b]	NMA[c], SMA	NMA, SMA	NMA	NMA	SMA	NMA, SMA
Years	1964–1966, 1972, 1978, 1981, 1992–2007	2001, 2004	1968–2007	1948/1949, 1963–1965, 1969, 1977–1981, 1991, 1993–1995	1984–1987, 1989–2007	1975, 1978, 1981–2006	1963–2006
Number of tows							
NMA	–	236	3 902	972	936	–	4 427
SMA	2 467	417	8 628	1 410	–	4 492	8 981
Total	2 467	659	13 071	2 464	936	4 492	14 070
Number of tows with monkfish (%)							
NMA	–	215 (91)	1 151 (29)	289 (30)	697 (74)	–	1 470 (33)
SMA	1 499 (61)	396 (95)	1 812 (21)	184 (13)	–	1 805 (40)	1 595 (18)
Total	1 499 (61)	617 (94)	3 057 (23)	485 (19)	697 (74)	1 805 (40)	3 206 (23)
Number of monkfish caught (average)							
NMA	–	4 208 (2 104)	2 302 (58)	555 (37)	3 677 (160)	–	2 801 (64)
SMA	10 067 (458)	12 847 (6 424)	4 676 (117)	309 (21)	–	5 400 (193)	4 337 (99)
Total	10 067 (458)	17 396 (8 698)	7 193 (180)	881 (59)	3 677 (160)	5 400 (193)	7 358 (167)

Totals may include additional stations not assigned to management area. Depth ranges are 1–99 percentiles of station average depth.
[a]Industry-based monkfish survey.
[b]Southern Management Area.
[c]Northern Management Area.

Additional survey data were available for monkfish from shrimp trawl surveys conducted by the Atlantic States Marine Fisheries Commission during the years 1992–2007. Details of the sampling designs and operating procedures can be found in Azarovitz (1981; NEFSC trawl surveys), Serchuk and Wigley (1986; sea scallop dredge survey), and Clark *et al.* (2000; shrimp trawl survey). In brief, the surveys were conducted using a stratified random sampling design, with sample allocation proportional to stratum area. NEFSC trawl survey strata are defined by depth zones of 27–55, 56–110, 111–185, and 186–365 m, which are further subdivided to create smaller sampling units (Figure 1). During the period 1963–1966, southern geographic coverage in the NEFSC autumn trawl surveys was limited to the northern MAB, but thereafter the sampling area (in both NEFSC autumn and NEFSC spring trawl surveys) extended south to Cape Hatteras, NC. Inshore strata (9–27 m) were added in 1972 (MAB) and 1979 (Gulf of Maine). The NEFSC winter trawl and summer sea scallop surveys cover the area between Georges Bank and Cape Hatteras, and the shrimp survey covers the western Gulf of Maine (Figure 1). Biological sampling of monkfish for age and growth, maturity, and food habits began in autumn 1992.

The IBMS were conducted using a stratified random sampling design with sample allocation proportional to fishing effort during the years 1995–1999. Additional non-random station locations were chosen by fishers (~30% of all stations). Stratum boundaries were the same as for the NEFSC trawl surveys, but a further set of strata was included in depths ranging from 366 to 914 m (Figure 1). The IBMS were conducted during 2001 and 2004 using commercial trawlers equipped with nets with codends of mesh size 15.2 cm (6 inches; NEFSC, 2002, 2005). Standard protocols for tow speed, tow time, scope ratios, and biological sampling were followed in each survey. The IBMS were conducted between 26 February and 6 April 2001 and between 1 March and 16 June 2004.

The age of monkfish was determined using vertebrae, following the methods developed by Armstrong *et al.* (1992). Vertebra number 8 was extracted from the vertebral column, cleaned of soft tissue, and baked in a drying oven at 230°C for 1–1.5 h to enhance the visibility of zonation. Presumed annuli on the centrum of the vertebra were counted under ×60 magnification. Known-age specimens of monkfish were not available for validation studies, but minimum criteria for the use of vertebrae for ageing were met (Armstrong *et al.*, 1992), and quality-control studies indicated high levels of precision of age estimates in blind tests (~94% agreement; Fishery Biology Branch, Northeast Fisheries Science Center, unpublished data). Seasonal patterns in growth were estimated using NEFSC winter, spring, and autumn trawl survey data, summer shrimp survey data, NEFSC summer sea scallop survey data (1993–2007), and IBMS data (2001 and 2004). Effects of management area and sex of monkfish on the age–length relationship were tested using ANCOVA of age sample data for age 2–6 males and females collected in winter and spring surveys during 2001 and 2004 (NEFSC winter trawl survey and IBMS).

Gonad stage was assigned by gross visual inspection of gonads using a 5-stage classification system based on gonad size, colour, texture, and presence or absence of ova or milt (Armstrong *et al.*, 1992). We subsequently combined spent and resting stages (post-spawning), and ripe and running ripe (ripe). Monkfish smaller than ~20 cm were difficult to assign to gender, but the sex of larger monkfish was easily determined. For analysis of

spawning patterns, the SMA was subdivided into two areas: Northern Mid-Atlantic (Cape Cod to Delaware Bay, 39–41.5°N) and Southern Mid-Atlantic (Delaware Bay to North Carolina, 35–39°N). Stations north of 41.5°N latitude were considered to be in the NMA.

Maturation rates were estimated for males and females using data on length, age, and maturity stage collected during the 2001 and 2004 IBMS. The proportion mature at length and age was estimated using the logistic regression

$$P = \frac{1}{1 + e^{-(\alpha + \beta x)}} ,$$

where *p* is the proportion mature at length or age, *x* the length or age, and α and β the model parameters to be estimated. The model was fitted using maximum likelihood methods (SAS version 9.1; SAS Institute, Cary, NC, USA).

Seasonal length–weight relationships were determined for males and females using measurements taken during NEFSC winter, spring, and autumn trawl surveys, summer shrimp and NEFSC sea scallop surveys (1993–2007), and IBMS (2001 and 2004). The regression model used was $\log W = \log a + b \log L$, where *W* is the weight (kg), *L* the total length (cm), *a* the *y*-intercept, and *b* the slope. Tests for the effects of sex and season on the length–weight relationship excluded fish >70 cm because males >70 cm were scarce.

Sex ratios were estimated by 3-cm length interval for each management area using samples of monkfish (≥ 20 cm) from NEFSC winter, spring, and autumn trawl surveys, summer shrimp and NEFSC sea scallop surveys (1993–2007), and IBMS (2001 and 2004). Stratified mean number at length (3-cm intervals) by sex was derived using stratum area as the weighting factor. To examine detailed spatial patterns in sex ratio at length, only NEFSC winter and spring trawl survey and IBMS data were used, because sample sizes in the other surveys were too small. For the spatial analysis, survey strata were grouped into four regional sets (Gulf of Maine, Georges Bank, Northern Mid-Atlantic, and Southern Mid-Atlantic), and three depth zones (21–110, 111–185, and >185 m). This grouping of strata resulted in a similar north–south split of the MAB as used in the spawning pattern analysis.

Results

Distribution patterns

Monkfish in the SMA were distributed across the MAB and southern flank of Georges Bank in February, but had largely disappeared from the southern MAB by April (Figure 4). Concentrations re-appeared along the outer shelf of the southern MAB in September and October. Few monkfish were present on the northwest part of Georges Bank in any season, but they were distributed throughout the Gulf of Maine in all months. The abundance-weighted depth distribution of monkfish in the Gulf of Maine was shallowest in summer (Figure 5).

Monkfish occupied a broad range of depths in all seasons (Figure 5). Overall, 90% of the monkfish caught in NEFSC winter, spring, summer, and autumn trawl surveys were in depths of 32–339 m, similar to the overall range of depths sampled (90% within 24–346 m). During winter and spring, monkfish were associated with relatively deep water (compared with the depth distribution of all stations), but in summer they more closely matched the sampled depth distribution.
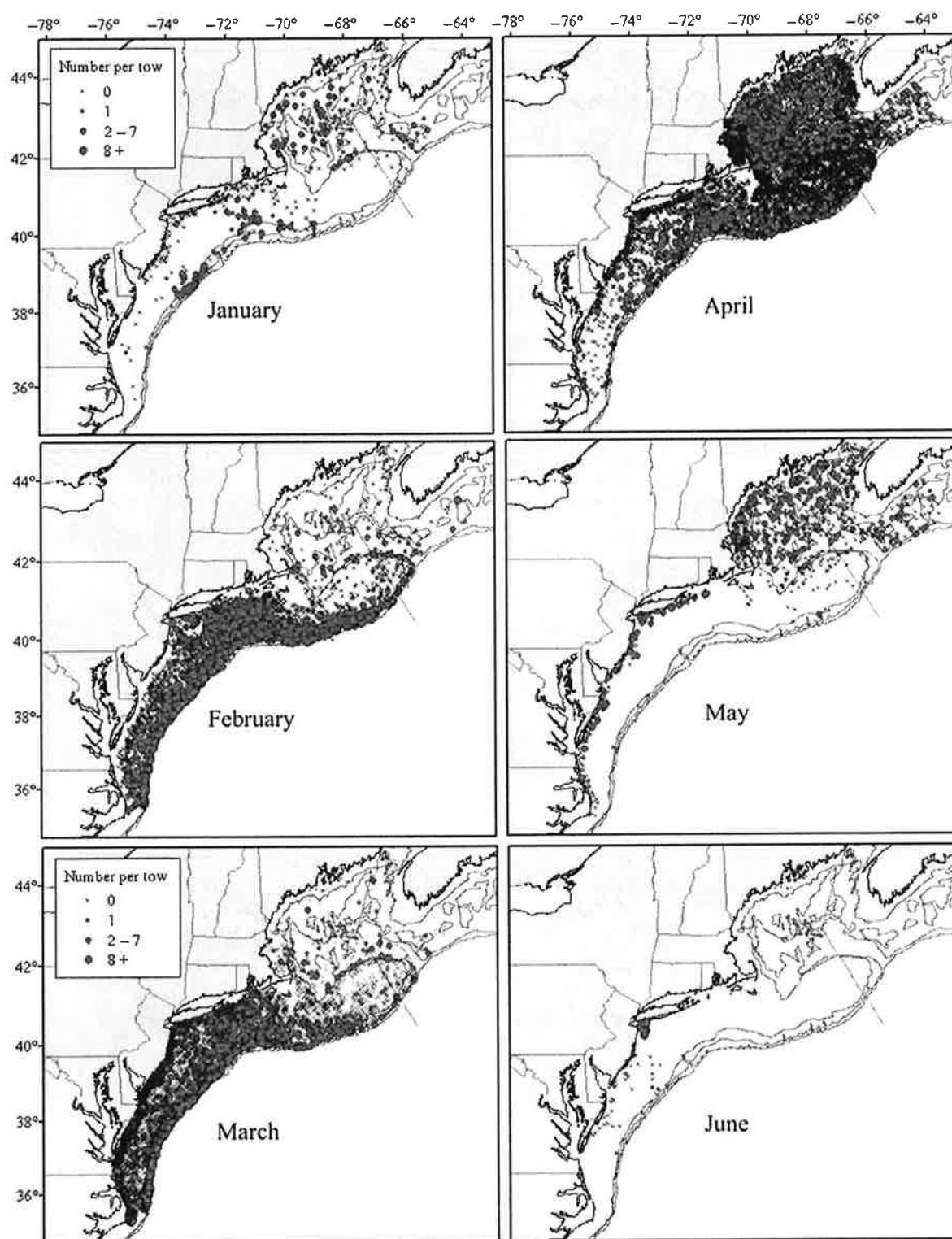
Figure 4. Monthly distribution (number per tow) of monkfish caught in NEFSC winter, spring, summer, and autumn bottom trawl surveys, 1948/1949 and 1963–2007 (continued on next page).

In autumn, monkfish distribution was similar to the sampled depths in the NMA, but was relatively deep in the SMA. Monkfish distribution with respect to temperature was more restricted than the depth distribution. Overall, 90% of monkfish were caught at bottom temperatures of 4.5–13.0°C, and 90% of

the stations encompassed the range 3.8–19.3°C. In the NMA, temperatures occupied by monkfish mirrored the distribution of bottom temperature of the stations (Figure 6). In the SMA, monkfish were associated with relatively warm temperature in winter and spring, and cool temperature in summer and autumn (Figure 6).
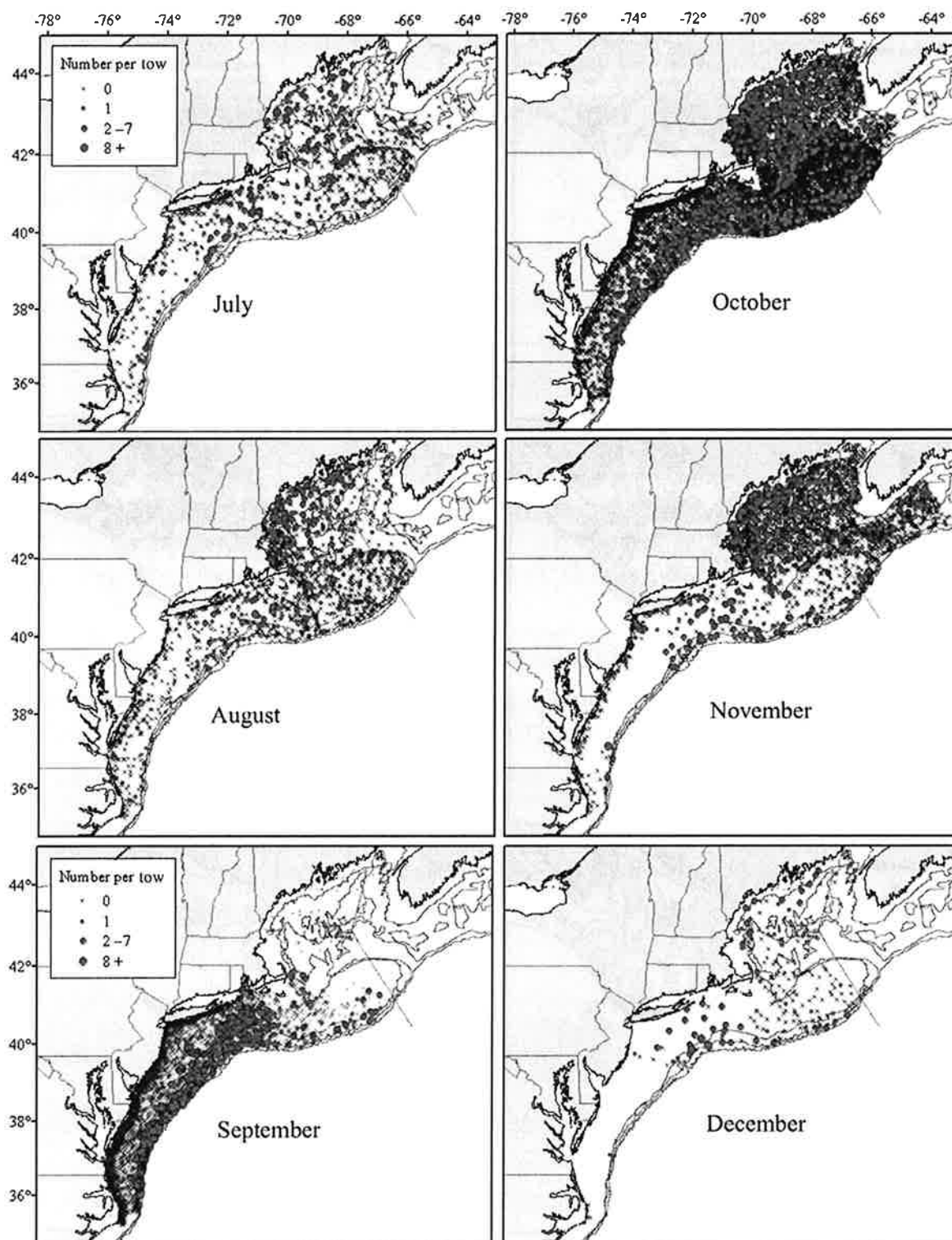
Figure 4. Continued.

Temporal and spatial patterns in sex ratio at length are shown in Figures 7 and 8. In the NMA, sex ratios approximated unity in fish up to ~55 cm, then increased steadily to 100% female by ~70 cm (Figure 7). In the SMA, sex ratios of 40–65 cm monkfish were strongly skewed towards males (Figure 7). The skewing in the SMA was more pronounced in deeper water and farther south (Figure 8). In shallow waters of the northern MAB, sex ratios at length resembled those in the Gulf of Maine, where sex ratios did not become skewed towards males. On Georges Bank, the skewed pattern was not apparent in shallow (27–100 m) water,
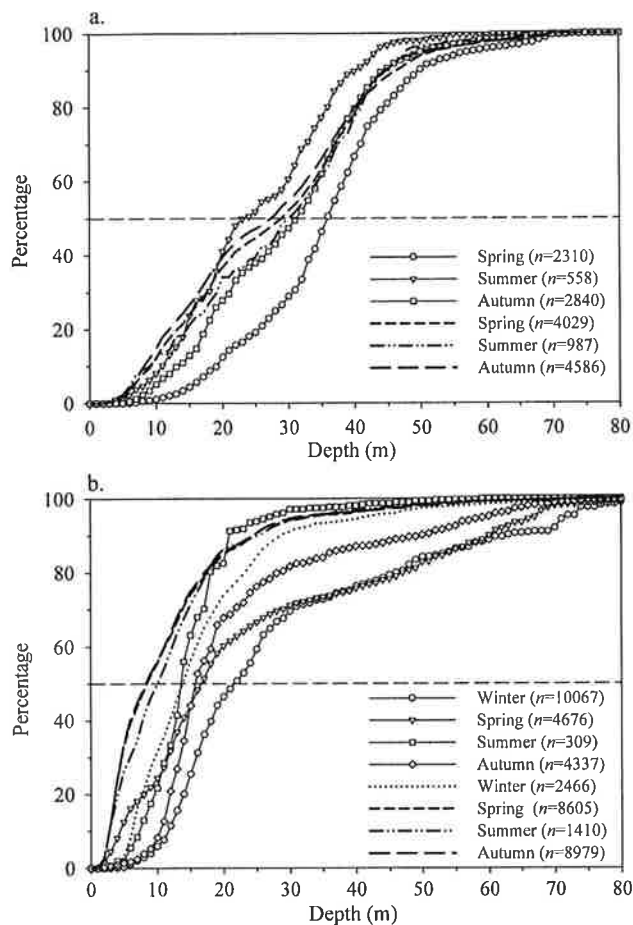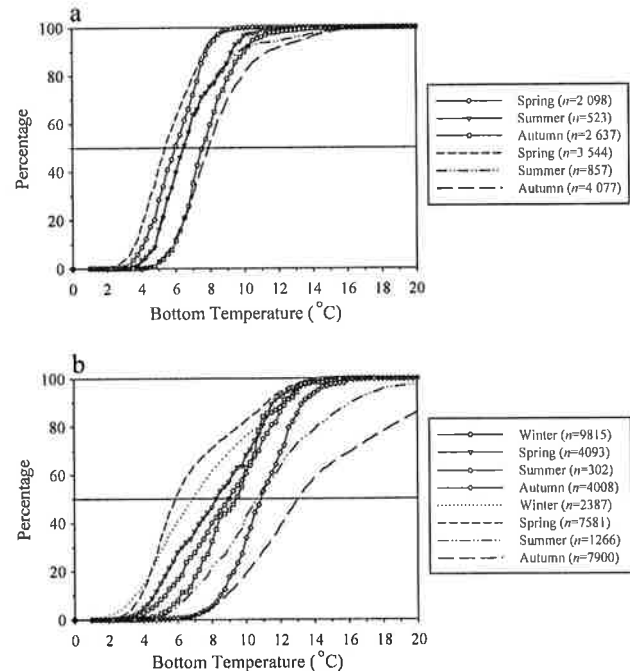
Figure 5. Cumulative frequency distributions of sampled depth in NEFSC winter, spring, summer and autumn trawl surveys (unweighted), and abundance-weighted depth, 1948/1949 and 1963–2007. (a) NMA, and (b) SMA. Dashed lines unweighted, symbols abundance-weighted.

but appeared in deeper (111–185 m) water. In the Gulf of Maine, sex ratios were ∼ unity in monkfish up to ∼60-cm long in all depths. Figure 9 shows the spatial distribution of sex ratios of 40–65 cm monkfish in winter and spring surveys. Strata in the southern MAB and deep strata in the northern MAB and on the southern flank of Georges Bank were dominated (>60%) by males. Few strata were dominated by females, and there were no strata with >80% females.

Age and growth

The largest monkfish recorded from NEFSC survey sampling was 138 cm, collected in 1978. Longevity of males appears to be less than for females, because few males >70 cm and older than 7 years have been collected. The largest male was 85 cm (9 years old) and the 99th percentile for male length was 66 cm. The largest aged female was 110 cm (10 years old) and the 99th percentile was 88 cm.

Growth of monkfish up to age 10 was linear, with annual increments averaging 9.9 cm for ages 2–9 (Figure 10, Table 2). Length-at-age did not differ significantly between management areas or by sex (ANCOVA, $p > 0.05$), but significant seasonal differences were detected (ANCOVA, $p < 0.001$). Most growth

Figure 6. Cumulative frequency distributions of bottom temperature at stations sampled in NEFSC winter, spring, summer, and autumn trawl surveys (unweighted) and abundance-weighted temperature, 1948/1949 and 1963–2007. (a) NMA, and (b) SMA. Dashed lines unweighted, symbols abundance-weighted.

was in late spring and early summer, during the period between spring and summer surveys (Table 2). Year effects were also significant in the two age–length datasets (1993–2007, all seasons; 2001 and 2004, winter–spring surveys). However, year accounted for ≤0.1% of the total sums of squares in each analysis and was therefore ignored.

Length–weight relationships differed significantly ($p < 0.001$) by sex and season. The allometric growth parameter (b) ranged between 2.76 (males in spring) and 3.12 (females in spring). The length–weight relationship had a lower r^2 during spring (Table 3) when many fish were in developing or spawning condition (Figure 11).

Reproduction

Parameter estimates for maturity ogives for females and males are given in Table 4. Estimated median length (L_{50}) and age (A_{50}) at maturity for females was 39 cm (4.6 years) in the NMA and 44 cm (4.9 years) in the SMA. For males, L_{50} was 36 cm (4.1 years) in the NMA and 38 cm (4.3 years) in the SMA. Differences between the two management regions in L_{50} and A_{50} were significant ($p < 0.05$) for both sexes.

Samples of reproductive state were not available for all months of the year, but the available data suggest earlier spawning in the MAB than in the Gulf of Maine (Figure 11). Few ripe females were found in autumn, but ripe males were found in all seasons and all months sampled except January. Ripe females were found mainly in shallow water (<50 m) or >200 m (Figure 12). Ripe males were distributed across all depths, except in the Gulf of Maine, where they were found mainly in depths <50 or >300 m (Figure 12).
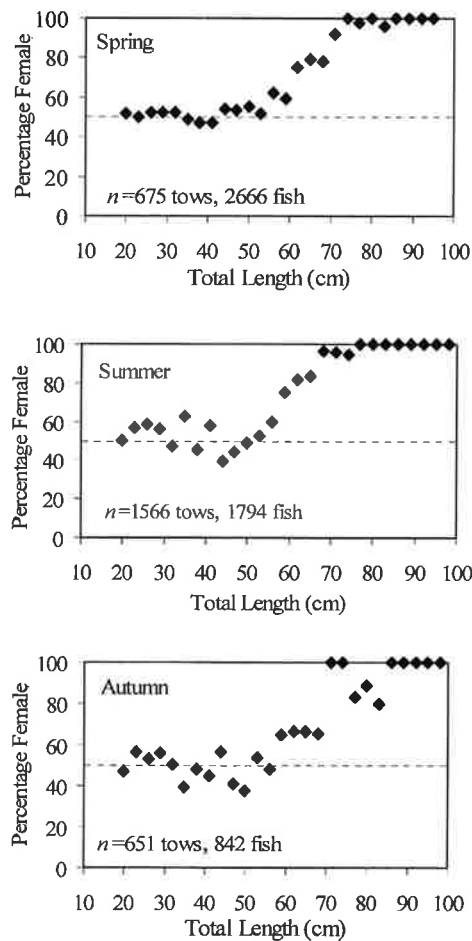
Northern Management Area   Southern Management Area
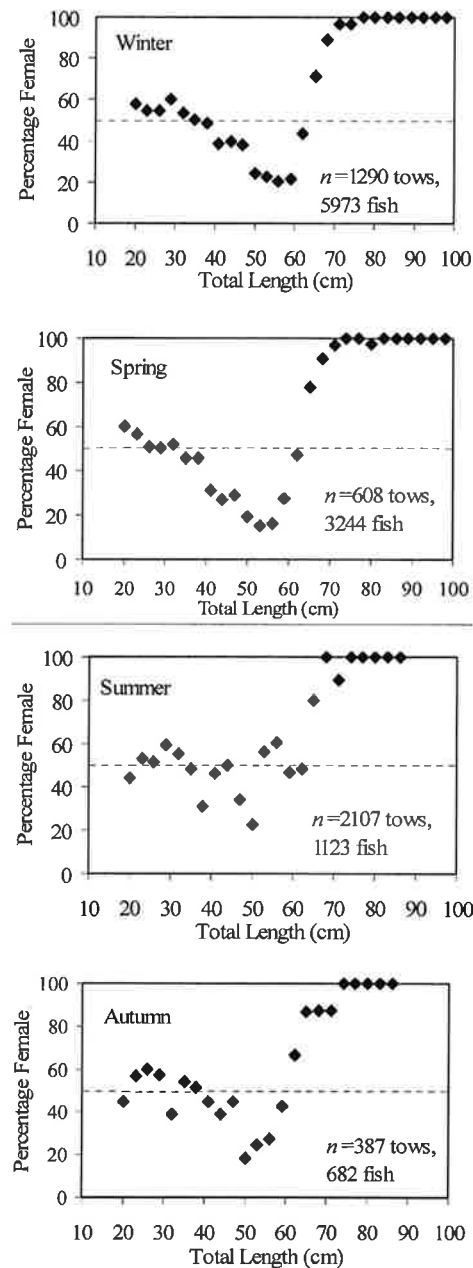
Figure 7. Sex ratio at length estimated from NEFSC winter, spring, and autumn trawl surveys, NEFSC scallop surveys, ASMFC shrimp trawl surveys (1993–2007), and IBMS (2001 and 2004). Estimates are derived from stratified mean number per tow at length, by sex (3-cm bins, lower bound shown).

Discussion

Monkfish are broadly distributed across the US continental shelf, except the shallows of Georges Bank. Seasonal distribution patterns suggest onshore–offshore movement, particularly in the southern MAB (Figures 4 and 5), and an apparent northward or deep-water (>365 m) excursion from the southern MAB in mid-spring. Onshore–offshore seasonal migrations have been noted previously for *L. americanus* (Jean, 1965; Almeida *et al.*, 1995; Steimle *et al.*, 1999); but a mid-spring movement of monkfish out of the southern MAB has not been reported previously.

Plotting the distributions by decade and season did not reveal obvious changes in distribution patterns over time, but during the 1970s (before escalation of fishing effort), monkfish may have been more broadly distributed across the continental shelf in the southern MAB.

Persistent features of monkfish distribution are their general absence on the northwest part of Georges Bank and their continuous presence in the area bounded by 70–72°W and 40–41°N (dubbed "The Mudhole" by fishers; Figure 4). These two regions have habitat characteristics which differ from the surrounding
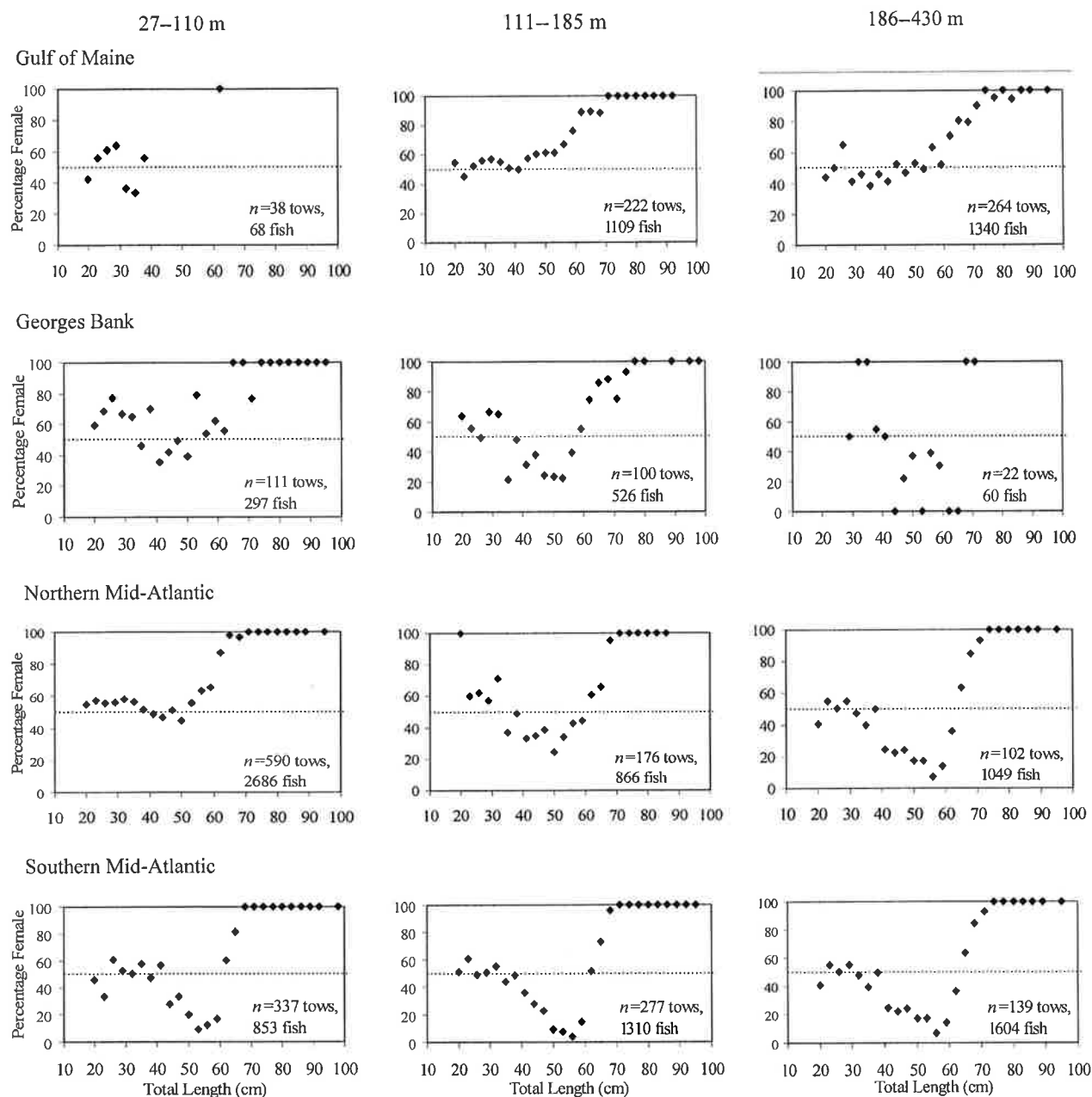
Figure 8. Sex ratio at length from NEFSC winter and spring trawl surveys (1993–2007) and IBMS (2001 and 2004) in three depth zones and four regions (Gulf of Maine, Georges Bank, Northern Mid-Atlantic, Southern Mid-Atlantic). Estimates are derived from stratified mean number per tow at length by gender (3-cm bins, lower bound shown).

areas. The Mudhole contains clayey and silty sand (Poppe *et al.*, 2005), whereas the rest of the MAB is primarily sand with sandy silt along the edge of the continental shelf. The northwest part of Georges Bank has large areas of coarse sediment (sand and gravel) because of strong tidal action (Backus, 1987; Poppe *et al.*, 2005). In a study of habitat associations of groundfish on the Scotian shelf, Scott (1982) found that *L. americanus* was more abundant in fine sediments and less abundant on coarse sediments. The same pattern seems to hold in US waters of the Northwest Atlantic.

Despite seasonal shifts in distribution, monkfish inhabit a wide range of depths throughout the year (Figure 5). However, the distribution probably extends much deeper than the areas sampled.

Monkfish have been caught at ~900 m (Markle and Musick, 1974; NEFSC, 2002), and deep-water studies in two regions in the SMA found that monkfish catch rates did not decline until depths greater than ~700 m (Wenner, 1978; Balcom, 1997). The amount of habitat represented by these depths is relatively small owing to the steepness of the continental slope, but the portion of the monkfish population residing outside sampled areas is unknown and could be significant, particularly during late autumn and winter, when the distribution shifts offshore.

Monkfish in the SMA were associated with relatively warm temperature in winter and spring, and relatively cool temperature in summer and autumn, but little selection for temperature was evident in any season in the NMA (Figure 6). This suggests that
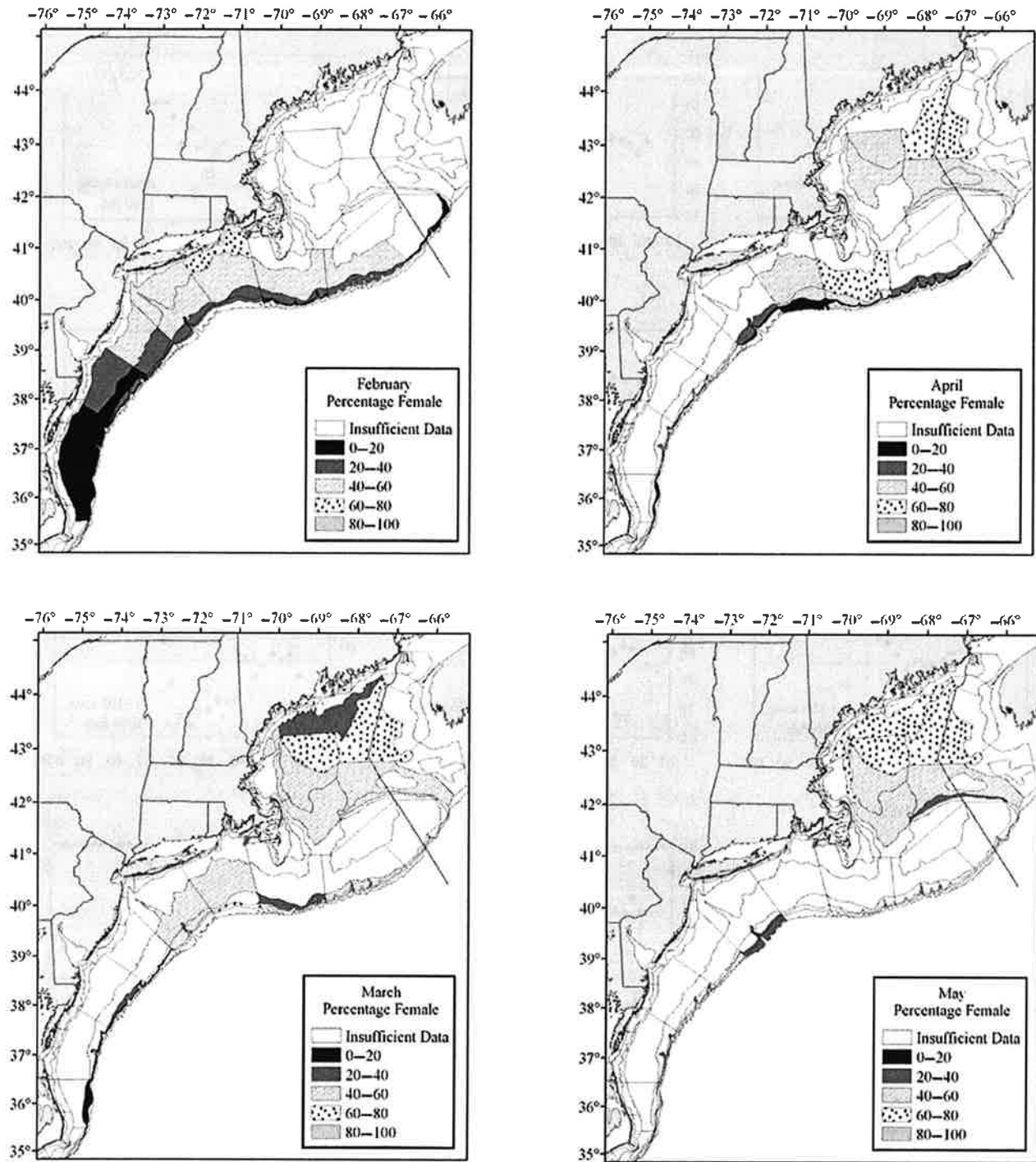
Figure 9. Spatial distribution of sex ratios for monkfish 40–65-cm long from NEFSC winter and spring trawl surveys (1993–2007) and IBMS (2001 and 2004), February–May. The number of fish sampled was 6284, and strata with fewer than 20 fish sampled in the 40–65 cm size range are not included.

temperatures in the NMA are within the preferred range for the species and that monkfish distribution shifts away from warm waters in the SMA (Figures 5 and 6). Shifts in the distribution of *Lophius* associated with changes in temperature have been reported for *L. americanus* in the Northwest Atlantic (Murawski, 1993), *Lophius piscatorius* in the North Sea (Perry *et al.*, 2005), and *L. piscatorius* in the North Atlantic (Solmundsson *et al.*,

2007). In Icelandic waters, *L. piscatorius* has expanded its range and increased in abundance concurrent with a doubling of the volume of warm water (bottom temperatures >5°C) since the mid-1980s (Solmundsson *et al.*, 2007). These observations suggest that changes in thermal environment can affect monkfish distribution, and therefore availability of monkfish to fisheries. In light of recent warming trends in the Northwest Atlantic

(Mountain, 2004), a closer examination of monkfish responses to thermal habitat is warranted.

Skewed sex ratios have been reported for other populations of *Lophius* (*L. piscatorius*—Ofstad and Laurenson, 2007; *L. piscatorius* and *Lophius budegassa*—Duarte *et al.*, 2001). Always, the ratios approximate unity in small fish, but become skewed towards
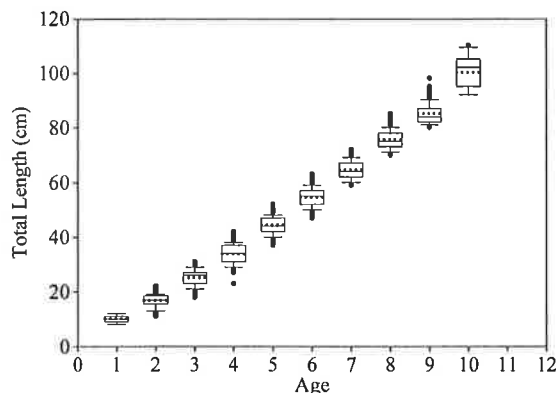
Figure 10. Box and whisker plots of monkfish length-at-age from NEFSC winter and spring trawl surveys (1993–2007) and IBMS (2001 and 2004); *n* = 4630. The box encloses the 25–75th percentile with median (solid line) and mean (dashed line), the whiskers indicate tenth and 90th percentiles, and the dots are values lying outside the tenth and 90th percentiles.

males in larger fish, before eventually becoming 100% female in the largest fish. Several explanations can be invoked to explain this pattern. The most obvious is that male growth slows or stops, so that male numbers accumulate near the maximum size, skewing the sex ratio. This was the explanation invoked for *L. piscatorius* and *L. budegassa* (Duarte *et al.*, 2001; Ofstad and Laurenson, 2007), but it does not seem to fit for *L. americanus*. We found no difference in the growth rates of male and female *L. americanus*, nor any evidence of a broad range in age at size in large *L. americanus* (Figure 10), which would be expected if male growth slowed significantly. Another explanation is differential mortality of males and females in the 40–65-cm size range, possibly resulting from a selectivity factor in fisheries (such as recorded for spiny dogfish by Rago *et al.*, 1998). This, however, would seem to be an unlikely explanation, because there is no apparent sexual dimorphism in *L. americanus*. Finally, there could be behavioural differences such as sex-specific movement patterns that lead to skewed sex ratios. The spatial and temporal distribution of sex ratios suggests that this may be the case in *L. americanus*. In the SMA, the magnitude of the skewed pattern differed with season and location, with stronger skewing in winter and spring (Figure 7) and in deep water (Figure 8). The skewed pattern or its inverse (skewing towards females) was not generally detected in the NMA (Figure 7). However, there were survey strata in the Gulf of Maine and on Georges Bank where sex ratios in spring were skewed towards females (Figure 9). These sex ratio patterns suggest that mature female monkfish in

Table 2. Mean length (cm, and standard error, s.e.) at age by season for monkfish samples from NEFSC winter, spring, and autumn trawl surveys, NEFSC sea scallop surveys, shrimp surveys, and IBMS.

Age	Mean length (s.e.)				
	Winter	Spring	Summer	Autumn	*n*
1	10.4 (0.27)	11.0 (0.32)	15.1 (0.19)	14.7 (0.15)	474
2	16.1 (0.29)	17.1 (0.14)	22.7 (0.19)	23.4 (0.17)	948
3	25.5 (0.11)	25.0 (0.12)	32.6 (0.17)	33.5 (0.19)	1 812
4	34.0 (0.10)	34.0 (0.11)	42.9 (0.23)	44.0 (0.20)	2 458
5	44.1 (0.09)	44.9 (0.11)	53.5 (0.34)	54.1 (0.22)	2 462
6	54.2 (0.09)	54.6 (0.12)	64.4 (0.20)	64.0 (0.32)	2 329
7	63.7 (0.17)	64.7 (0.14)	71.1 (0.42)	74.3 (0.64)	1 114
8	74.6 (0.34)	75.7 (0.18)	80.8 (0.98)	85.4 (0.86)	536
9	85.7 (0.79)	85.4 (0.32)	91.5 (3.80)	92.8 (0.63)	174
10	90.7 (2.91)	100.2 (1.63)	87.1 (19.1)	–	18
n	4 765	4 470	1 378	1 712	12 325

Table 3. Parameter estimates for length–weight relationships for male and female monkfish from NEFSC winter, spring, and autumn trawl surveys, NEFSC sea scallop surveys, shrimp surveys, and IBMS.

Season	Sex	Length range (cm)	*n*	log(*a*)	s(*a*)	*b*	s(*b*)	r^2
Winter	Male	10–74	3 110	−1.4932	0.01581	2.8153	0.00971	0.96
	Female	11–101	2 679	−1.7120	0.01575	2.9615	0.00978	0.97
Spring	Male	40–85	2 913	−1.4165	0.04645	2.7604	0.02715	0.85
	Female	40–110	3 229	−2.0180	0.03393	3.1228	0.01904	0.93
Summer	Male	12–75	915	−1.5540	0.02343	2.8548	0.01527	0.97
	Female	11–111	1 314	−1.6355	0.01812	2.9179	0.01113	0.98
Autumn	Male	8–83	852	−1.5841	0.01969	2.8748	0.01282	0.98
	Female	10–98	852	−1.6527	0.02182	2.9260	0.01383	0.98

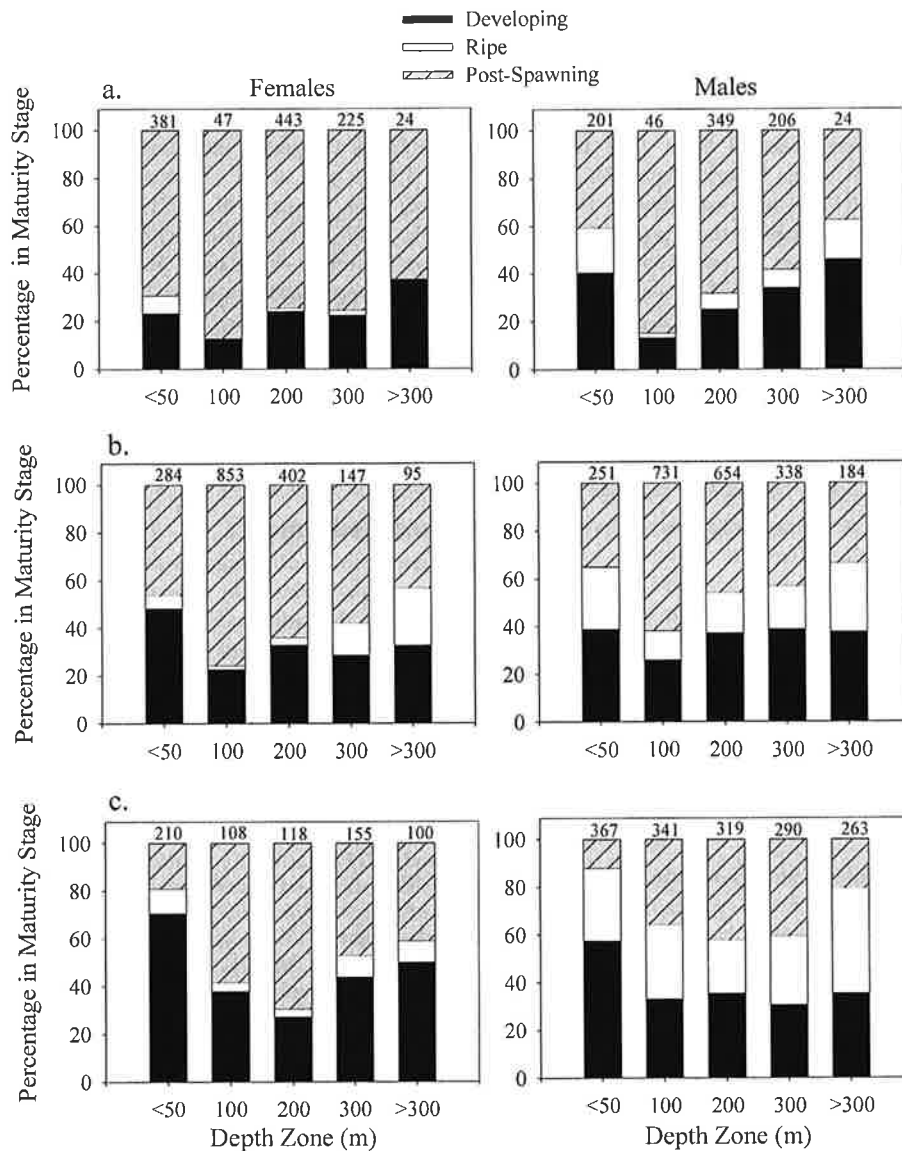Length is total length (cm), weight in g.
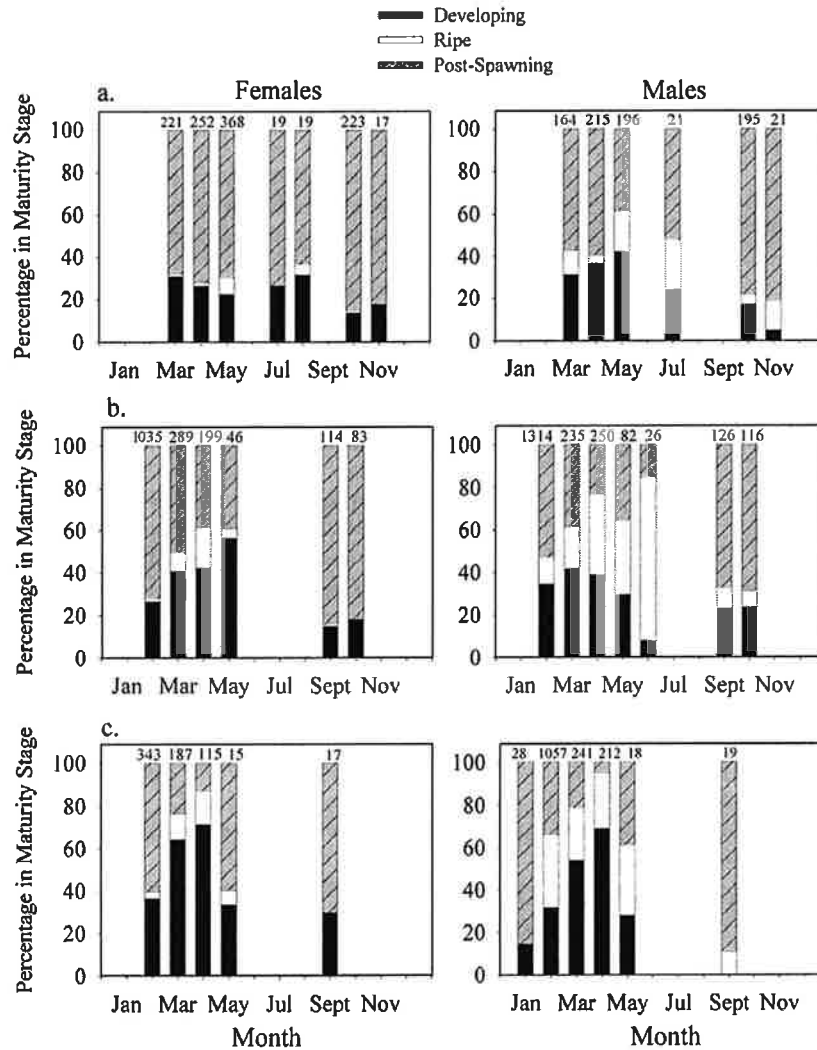
Figure 11. Percentage of mature monkfish females and males in developing, ripe, and post-spawning condition by month in samples from NEFSC winter, spring, summer, and autumn trawl surveys (1992–2007) and IBMS (2001 and 2004). (a) Gulf of Maine, (b) northern MAB, and (c) southern MAB. The sample size is given above the bars.

Table 4. Parameter estimates (a, b) from logistic regression of (top panel) length and (bottom panel) age on maturity, standard error (s.e.) of regression estimates, median length at maturity ($L_{50} = -a/b$), and the number of fish sampled (n).

Region	Sex	n	a	s.e.(a)	b	s.e.(b)	L_{50}
NMA	Female	1 159	−9.765	0.647	0.252	0.016	38.8
SMA	Female	1 304	−9.029	0.533	0.206	0.012	43.8
NMA + SMA	Female	2 463	−9.056	0.404	0.221	0.010	41.0
NMA	Male	792	−11.571	0.904	0.325	0.025	35.6
SMA	Male	1 364	−12.123	0.750	0.320	0.019	37.9
NMA + SMA	Male	2 156	−11.486	0.556	0.312	0.015	36.8

Region	Sex	n	a	s.e.(a)	b	s.e.(b)	A_{50}
NMA	Female	826	−10.354	0.778	2.273	0.168	4.6
SMA	Female	888	−9.647	0.700	1.956	0.141	4.9
NMA + SMA	Female	1 714	−9.791	0.520	2.078	0.109	4.7
NMA	Male	519	−12.233	1.168	2.951	0.279	4.1
SMA	Male	812	−15.798	1.234	3.665	0.283	4.3
NMA + SMA	Male	1 331	−13.870	0.849	3.274	0.198	4.2

Data are from IBMS.

Figure 12. Percentage of mature monkfish females and males in developing, ripe, and post-spawning condition by depth zone in samples from NEFSC winter, spring, summer, and autumn trawl surveys (1992–2007) and IBMS (2001 and 2004). (a) Gulf of Maine, (b) northern MAB, and (c) southern MAB. The sample size is shown above the bars, and the x-axis label is the upper bound of non-overlapping depth zones.

the SMA move into deep water (outside the sampling area) or to the north in late spring, perhaps to spawn again. Monkfish have been assumed to spawn only once per year because of the presumed large energetic investment in producing egg veils. However, Martinez (1999) found evidence from histochemical studies that *L. americanus* may spawn more than once per year, and Yoneda *et al.* (2001) have suggested the same possibility for *Lophius litulon*.

The location of monkfish spawning is not clearly understood. Bigelow and Schroeder (1953) concluded that monkfish are indifferent to the depth at which they spawn because egg veils have been found close to shore and over deep water (~2000 m). Our observations of the depth distribution of ripe females (Figure 12) suggest that in the Gulf of Maine, monkfish spawn in shallow (<50 m) water, but that in the SMA they may spawn in both shallow (<50 m) and deep (>200 m) water. Monkfish larvae in the MAB are found almost exclusively in deep water along the

shelf–slope break in April, but across the shelf from May to July, the distribution moving progressively northwards with time (Steimle *et al.*, 1999). Water temperatures in the MAB are colder on the mid- and outer continental shelf than over the slope during the early part of the year (Houghton *et al.*, 1982), so the distribution of larvae may reflect the seasonal availability of suitable thermal habitat. Steimle *et al.* (1999) reported that larvae were most abundant at 10–16°C, and peak catches were obtained at 11–15°C, regardless of month or area.

Basic life-history parameters for *L. americanus* (growth, maturity, and longevity) have been estimated in the past using samples from surveys and commercial fisheries (Armstrong *et al.*, 1992; Almeida *et al.*, 1995; Hartley, 1995). Our results are similar in many ways, but they include some important differences. Previous studies indicated faster growth in the SMA (Armstrong *et al.*, 1992) than in the NMA (Hartley, 1995), and these growth differences were part of the justification for establishing two

management areas. However, we found no differences in growth between the NMA and the SMA. This discrepancy in growth between studies may be due partly to the exploitation history of the stock at the time of each of the studies. The 610 samples of Armstrong et al. (1992) were collected from 1982 to 1985, before the rapid development of the fishery (Figure 2), whereas the 671 samples of Hartley (1995) were collected in 1992 and 1993, when landings were approaching their peak (Figure 2). Observed mean lengths-at-ages 2–9 in our study (Figure 10) were similar to those of Hartley (1995), but ~6 cm lower on average than the back-calculated mean lengths-at-age and 11 cm less than the observed mean lengths-at-age documented by Armstrong et al. (1992).

Previously published rates of maturation for L. americanus are variable, L_{50} ranging from 32.0 to 43.4 cm for males and from 36.1 to 48.5 cm for females (Armstrong et al., 1992; Almeida et al., 1995; Hartley, 1995). Our results fall in the middle of these ranges, but it is inappropriate to compare the results of these studies directly because of the differences in seasons and years sampled. The estimate by Armstrong et al. (1992) for the SMA combined spring and autumn samples for the sampling years 1982–1985, Hartley's (1995) estimate for the NMA was based on samples collected during summer a decade later (in 1992 and 1993), and Almeida et al. (1995) estimated L_{50} by season and area using samples collected from 1975 to 1993. Our study cannot resolve these discrepancies, but it does provide estimates (Table 4) based on large samples collected in both areas during winter and spring, when the advanced reproductive state is most apparent.

Important aspects of monkfish biology remain poorly understood and will require new approaches to resolve. Our conceptual framework for monkfish biology in the Northwest Atlantic has assumed that surveys sample a representative portion of the population and that exchange between management regions is limited. However, the observation of relatively high densities of monkfish at depths far exceeding the limits of sampling (Wenner, 1978; Balcom, 1997) and the unbalanced sex ratios across the continental shelf (Figures 7–9) suggest that a segment of the population is poorly represented in survey sampling. Further studies to examine the density and size and sex composition of monkfish outside regularly sampled areas need to be conducted to evaluate the importance of this segment of the overall population.

The assumption that exchange between management regions is relatively limited underlies monkfish fishery management in the USA. However, movement between regions may prove more important than previously thought. Tagging studies with other species of Lophius have demonstrated extensive movements by some fish (e.g. 876 km by L. piscatorius; Laurenson et al., 2005), and it is likely that L. americanus has similar dispersal capability. The buoyant egg veils and wing-like pectoral fins of late-stage larvae (Martin and Drewry, 1978), juveniles, and adult monkfish suggest a capacity for transport by currents. Selective tidal stream transport is suggested by the spring off-bottom behaviour of an archival-tagged L. americanus (Rountree et al., 2006), and the same mechanism has been proposed for migration in L. piscatorius (Hislop et al., 2000; Laurenson et al., 2005). The dispersal of monkfish out of the southern MAB in spring (Figure 4) indicates that L. americanus can and do move substantial distances. These pieces of evidence paint an incomplete picture, but suggest that monkfish patterns of movement and distribution may be more dynamic than previously thought. A better understanding of the

spatial and temporal dynamics of monkfish distribution in the Northwest Atlantic, including Canadian waters, is therefore crucial to fishery management.

Lophius americanus shares life-history traits with other members of the genus, including apparently linear growth rates over a large part of the observed life history (e.g. Griffiths and Hecht, 1986; Landa et al., 2001, 2008; García-Rodríguez et al., 2005), shifts in sex ratios with length (Duarte et al., 2001; García-Rodríguez et al., 2005; Maartens and Booth, 2005; Ofstad and Laurenson, 2007), shorter longevity of males than females (Duarte et al., 2001; García-Rodríguez et al., 2005; Ofstad and Laurenson, 2007), and some degree of spatial segregation by sex (Yoneda et al., 2001; García-Rodríguez et al., 2005). Such commonalities are intriguing and suggest that advances in understanding the biology of one species could help in developing new perspectives for understanding the dynamics of related species.

Acknowledgements

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