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Spring feeding of Atlantic wolffish (*Anarhichas lupus*) on Stellwagen Bank, Massachusetts

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Abstract—Full life history information is lacking for Atlantic wolffish (*Anarhichas lupus*), a species of concern in U.S. waters. Scientific studies indicate that Atlantic wolffish are found in low densities—either solitary or, during spawning season, paired. Groundfish surveys show wolffish abundance in U.S. waters is highest in the Gulf of Maine–Georges Bank region, especially in the southwestern portion at depths of 80–120 m. Contrary to these data, commercial fishermen have reported, and we have validated, that high concentrations of Atlantic wolffish are found in specific shallow locations and at specific times on the Stellwagen Bank National Marine Sanctuary (SBNMS) in Massachusetts Bay. From 53 tows conducted during May–June 2011, 395 Atlantic wolffish were captured on the SBNMS. Average daily catch per unit of effort ranged from 0.6 to 37.8 fish h^{-1} in an area characterized by shallow (depths: 27–46 m), cold (5–7°C) water, and a sand and gravel substrate. At this site, wolffish were mature (mean age: 20 years; range: 7–33 years) and in prespawning condition, both sexes were equally represented, and 99% of the fish were feeding actively. Total mortality (Z) estimated from the age frequency was 0.35. Considering the observed wolffish abundance and their feeding intensity, it appears that this area of the SBNMS is a foraging area used collectively by a large group of wolffish during May–June.

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Atlantic wolffish (*Anarhichas lupus*), 1 of 3 wolffish species found in the northwest Atlantic, is classified as a data-poor species (NDPSWG1) and is listed as a species of concern under the Endangered Species Act. Complete life history information, including biology, migration patterns, and seasonal movements, is lacking for Atlantic wolffish populations, especially in U.S. waters (NDPSWG[1], Keith[2]). There has not been much of a directed fishery for Atlantic wolffish; it is thought that they are typically solitary fish or, at most, paired during the spawning season (Scott and Scott, 1988; Le Francois et al., 2010), and it has been challenging to obtain large sample sizes for thorough biological analyses. To confound matters, these demersal fishes are often associated with complex habitat, such as rocky burrows and crevices (Keats et al., 1985), making them difficult to survey with trawl gear.

Atlantic wolffish range from Greenland to Cape Cod, occasionally as far south as New Jersey (Rountree, 2002; Keats et al., 1986), and inhabit waters from 5 to 240 m depending on fish size, age, and season (Nelson and Ross, 1992). According to trawl surveys in U.S. waters, abundance south of Canada is highest (<1.5 kg [3.3 lb]/tow) in the Gulf of Maine–Georges Bank (GOM–GB) region, especially in the southwestern portion at depths of 80–120 m (AW-

[1] NDPSWG (Northeast Data Poor Stocks Working Group). 2009. The Northeast Data Poor Stocks Working Group report, December 8–12, 2008 meeting. Part A: Skate species complex, deep sea red crab, Atlantic wolffish, scup, and black sea bass. Northeast Fish. Sci. Cent. Ref. Doc. 09-02, 496 p. [Available from http://www.nefsc.noaa.gov/publications/crd/.]

[2] Keith, C. 2006. Status of fishery resources off the northeastern US: Atlantic wolffish, 6 p. Resource Evaluation and Assessment Division, Northeast Fish. Sci. Cent., Woods Hole, MA. [Available from http://www.nefsc.noaa.gov/sos/spsyn/og/wolf/.]

BRT[3]. As with many other species, abundance and biomass of Atlantic wolffish have declined since the 1980s (Sosebee and Cadrin[4]). In the U.S. GOM–GB region, biomass estimates for this species, according to 2007 models, range from 89,000 to 384,000 adult fish (AWBRT[3]) and have not significantly changed in the subsequent 3 years (Keith and Nitschke[5]). Depending on the model parameters, current spawning stock biomass is low (371–505 metric tons in 2010; Sosebee and Cadrin[4]).

Little is known of the spawning behavior and spawning habitat of Atlantic wolffish; most information is derived from dive surveys or hatchery studies. An estimated 4–5 months before spawning, these typically solitary fish begin courting and form bonded pairs (Johannessen et al., 1993); inshore migrations into shallower water may occur at this time (Nelson and Ross, 1992). Spawning is believed to occur from September through October in the GOM, but there is no conclusive proof of this spawning period (Pavlov and Moksness, 1994; Rountree, 2002). Spawning events of captive fish have been documented by Johannessen et al. (1993) and Rountree (2002). A few days before spawning, eggs are fertilized internally and extruded within 1 day after copulation and before cell cleavage. Atlantic wolffish are determinate spawners (Johannessen et al., 1993); the female deposits all eggs in one batch and then curls around the sticky, demersal eggs, shaping them into a cluster. The eggs are hidden under rocks and boulders in nests and guarded exclusively by the male for 9–10 months until the eggs hatch (Keats et al., 1985; Moksness and Pavlov, 1996). During this time, the male ceases feeding (Keats et al., 1985). Tagging studies indicate that Atlantic wolffish movements are short (AWBRT[3]).

Although not often targeted by fishermen, Atlantic wolffish from U.S. waters were landed in both recreational and commercial fisheries and marketed as ocean catfish. In May 2010, a moratorium on Atlantic wolffish went into effect in U.S. waters for both commercial and recreational fisheries to protect stock biomass (Amendment 16 to the New England multispecies Fisheries Management Plan; NEFMC, 2009). Contrary to what is documented in the scientific literature (Scott and Scott, 1988; Le Francois et al., 2010), commercial fishermen have reported that Atlantic wolffish are not always dispersed in U.S. waters but are seasonally aggregated in shallow areas at the edge of the Stellwagen Bank National Marine Sanctuary (SBNMS) in Massachusetts Bay (statistical area 514). At this location, catch rates of tows targeted toward Atlantic wolffish habitat were higher than those from scientific surveys. In early June, during 2007–2009, average catch rates were 91–136 kg/h (200–300 lb/h; Ford[6]), corresponding to commercial landings reported by Keith and Nitschke[5]. One fisherman reported 6350 kg (14,000 lb) of Atlantic wolffish was landed in June 2009 (Ford[6]). By the end of June, these fishermen turned their efforts elsewhere.

To characterize the Atlantic wolffish observed by the fishing industry, a study was conducted on the SBNMS in Massachusetts Bay in an area where fishermen have reported large catches of Atlantic wolffish, to determine whether Atlantic wolffish occur in dense concentrations seasonally, and, if so, to determine why. Our objectives were 1) to sample the Atlantic wolffish population in the selected study area during May–June to quantify abundance and 2) to use a proportion of the wolffish catch to calculate age and growth and total mortality (Z), determine sex ratio and reproductive status, and analyze food habits.

Materials and methods

Capture and disposition of catch

Atlantic wolffish were sampled on the western edge of the SBNMS in Massachusetts Bay (statistical area 514; Fig. 1) by trawl during dedicated sampling trips from 23 May to 21 June 2011. This 40-km^2 area was selected because it is the only place that has been identified by fishermen as one where Atlantic wolffish are highly abundant in the southern GOM and because it is where wolffish historically have been targeted by fishermen. The area ranges in depth from 27 to 40 m, the majority of it is 33-m deep, and the substrate, as described by fishermen, is characterized by a hard bottom of sand littered with shells. Sampling was undertaken throughout the area where it was possible to use trawl gear, including the specific location where Atlantic wolffish were reported to congregate. All Atlantic wolffish were captured with standard legal groundfish nets (15.24-cm body, 16.51-cm codend mesh size) and placed in flowing seawater tanks onboard the vessel. All bycatch was identified according to the methods of Collette and Klein-MacPhee (2002), enumerated, and immediately released alive. Atlantic wolffish were measured (total length [TL]) to the nearest centimeter and weighed (W) to the nearest 0.1 kg. They were either euthanized for collection of life history information or tagged and released alive for a separate study. Fish were euthanized

[3] AWBRT (Atlantic Wolffish Biological Review Team). 2009. Status review of Atlantic wolffish (*Anarhichas lupus*). Report to Natl. Mar. Fish. Serv., Northeast Reg. Off., 149 p. [Available from http://www.nmfs.noaa.gov/pr/species/Status%20Reviews/atlantic_wolffish_sr_2009.pdf.]

[4] Sosebee, K. A., and S. X. Cadrin. 2006. A historical perspective on the abundance and biomass of Northeast demersal complex stocks from NMFS and Massachusetts inshore bottom trawl surveys, 1963–2002. Northeast Fish. Sci. Cent. Ref. Doc. 06-05, 200 p. [Available from http://www.nefsc.noaa.gov/publications/crd/.]

[5] Keith, C., and P. Nitschke. 2012. Atlantic wolffish—2012 groundfish update. *In* Assessment or data updates of 13 northeast groundfish stocks through 2010. Northeast Fish. Sci. Cent. Ref. Doc. 12-06, p. 650–721. [Available from http://www.nefsc.noaa.gov/publications/crd/.]

[6] Ford, J. 2009. Personal commun. FV *Lisa Ann II,* Kingston, NH.

by an overdose of tricaine methanesulfonate (MS-222), and then heads, gonads, and entire gastrointestinal tracts were removed, bagged separately, and frozen until further analyses.

Age

Otoliths were processed at the Massachusetts Division of Marine Fisheries Age and Growth Laboratory, located at the Annisquam River Marine Fisheries Station in Gloucester, Massachusetts. The sagittal otoliths removed from each wolffish head were cleaned, embedded in 2 part epoxy, and sectioned transversely through the core. A low-speed Isomet[7] saw (Buehler, Lake Bluff, IL), with 2 diamond blades separated by a 0.4-mm spacer, was used to take sections. Otolith sections were affixed to microscope slides with Flo-Texx mounting medium (Thermo Fisher Scientific Inc., Waltham, MA) and then viewed through a compound microscope at 100–400× magnification for the enumeration of annuli. If the annuli were not clearly visible, the section was polished on a Buehler Ecomet 3000 variable-speed grinder-polisher until it was thin enough for easy enumeration. Annuli were defined as the thin hyaline zones described by Jonsson (1982) and were counted along the ventral side of the sulcal groove. Age was determined by 3 independent readers. When discrepancies occurred, all 3 readers reviewed the otoliths together and ages were decided by the majority. Coefficient of variation (Chang, 1982) was calculated between each reader combination. A birth date of 1 January was used.

Total mortality

From the age frequency of the pooled samples (n=303), Z was estimated by the method of Chapman and Robson (1960) with bias correction (Seber, 1982) for Z and a correction for over-dispersion for the standard error of Z (Smith et al., 2012). According to Murphy (1997) and Smith et al. (2012), the Chapman-Robson estimator performs better and is less biased than other available estimators (e.g. linear regression). Calculations were performed with R statistical software, vers. 2.15.1 (R Core Team, 2012) with the function agesurv in the R package fishmethods, vers. 1.3-0 (Nelson, 2012). The starting point was the age of full recruitment (age at maximum catch) plus 1 year (Smith et al., 2012). Sensitivity of the estimate to the starting point was examined by running the same analysis but starting 1 year before and 1 year after the initial starting point.

Sex and reproductive maturity

Whole, paired gonads were thawed, identified as testes or ovaries, and weighed to the nearest 0.1 g. For females, smallest and largest oocytes were measured (diameter to the nearest 0.1 mm), overall color was recorded, and, if possible, gross morphology of oocyte stages was noted. Maturity guidelines published by Templeman (1986a) and Gunnarsson et al. (2006) and based on egg size and color were used to classify maturity. In mature prespawning Atlantic wolffish, 3 generations of oocytes are present in the ovary: primary oocytes, which will advance to the cortical alveolus (CA) stage in the following year (<0.5 mm, whitish); oocytes in the CA stage to be spawned next year (0.5–1.8 mm, yellow and orange); and oocytes to be spawned in the current year (spawning stage 3; 2.5–4.8 mm, deeper yellow and orange; Gunnarsson et al., 2006). Atlantic wolffish with oocytes in the CA stage (>0.5 mm) are deemed mature (Gunnarsson et al., 2006). To assess reproductive state, the gonadosomatic index (GSI) was calculated as $GSI = W_{Gonads}/(W_{Body} - W_{Gonads})$.

Feeding ecology

Gastrointestinal tracts were thawed, weighed to the nearest 0.1 g, and dissected, and all prey items were identified to the lowest possible taxon and weighed as a group to the nearest 0.1 g. Frequency of occurrence, volume of dietary items, feeding index, and Fulton's condition factor (K) were calculated with the following equations

$$\textit{Frequency of occurrence} = [\textit{number of stomachs containing prey item i} / \textit{total number of examined stomachs}] \times 100.$$

$$\textit{Volume by species} = [W_{\text{prey item } i} \ / \ W_{\text{stomach}}] \times 100.$$

$$\textit{Feeding index} = [W_{\text{total stomach contents}} \ / \ W_{\text{fish}}] \times 100.$$

$$K = W\ (\text{g})/TL^3\ (\text{mm}) \times 105.$$

Because Atlantic wolffish crush their prey and because of the prevalence of hard-shelled invertebrates like mollusks, crustaceans, and echinoderms, no attempts were made to quantify numerical abundance of prey.

Statistical analyses

A chi-square test of independence was used to determine whether the sex ratio deviated from a 1:1 female-to-male ratio. Spearman rank order correlation tests were used to determine relationships between gonad size, GSI, and K and sex, age, TL, and W of Atlantic wolffish, and Mann-Whitney rank sum tests were used to compare TL, W, age, and K between male and female wolffish with SigmaPlot (vers. 11.0, Systat Sofware Inc., San Jose, CA).

Results

In the study area, 53 tows were completed, resulting in the capture of 395 Atlantic wolffish (Table 1, Fig. 1). The first 4 days of sampling yielded 304 wolffish, all of which, except for 1, were euthanized for life his-

[7] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Summary of data from trips dedicated to sampling of Atlantic wolffish (*Anarhichas lupus)* from 23 May to 21 June 2011 on Stellwagen Bank National Marine Sanctuary, Massachusetts. Catch per unit of effort (CPUE) was measured as the number of Atlantic wolffish captured per hour. Mean tow durations and bottom temperatures are given with standard errors in parentheses. Substrate types were identified by fishing captains: G=gravel, HS=hard sand, SS=soft sand, S=sand, SG=sandy gravel, euth=euthanized.

Trip	Date	Total tows	Total wolffish caught	CPUE	Number of wolffish euth.	Number of wolffish tagged	Fishing period	Mean tow duration (min)	SD Tow duration (min)	Speed range (knots)	Depth (m)	Mean bottom temp (°C)	SD bottom temp (°C)	Substrate
1	23 May	3	107	22.8	107	0	5:35–10:55	95.33	6.81	2.7–3.1	28	6.06	0.79	G
2	26 May	4	187	37.8	187	0	4:22–10:35	73.00	9.06	–	31–40	6.40	0.03	HS, G
3	7 June	6	7	1.8	7	0	8:30–13:33	35.50	9.44	2.5–3.0	29–39	–	–	HS, G
4	8 June	4	3	1.2	2	1	8:18–13:05	55.25	13.96	2.8–3.2	29–35	5.00	0.00	HS, SS, G
5	10 June	5	2	0.6	0	2	6:44–12:15	41.80	15.37	2.6–2.7	29–36	5.75	0.71	HS, SS, G
6	13 June	7	9	2.4	0	9	7:15–12:58	34.14	7.38	2.5–2.9	28–46	5.53	0.39	S, SG, G
7	16 June	8	6	1.2	0	6	7:30–13:12	26.88	11.28	2.5–2.9	27–38	6.51	0.29	G, S, SG
8	17 June	5	29	10.8	0	26	7:49–12:54	32.33	3.08	2.6–2.7	28–38	6.70	0.33	SG
9	20 June	5	5	1.8	0	5	8:50–13:35	39.40	7.64	2.7–2.8	29–37	–	–	SG
10	21 June	6	40	18.6	0	37	7:37–12:57	33.00	15.11	2.8–2.9	27–38	6.00	0.28	SG

tory analyses. The remaining sampling days yielded 85 wolffish that were tagged and released for a separate study, and 6 wolffish were released untagged because of poor condition. As a result of damaged caudal fins, 13 euthanized fish (7 females and 6 males) were excluded from analyses of size and growth.

Age, growth, and sex

Annuli in otolith sections were easily discernible as thin hyaline zones. As growth slows in older fishes, the annuli form closer together, requiring a higher magnification and thinner sections to enumerate them accurately. Coefficients of variation between each of the 3 readers were 2.93%, 2.60%, and 2.57%. Atlantic wolffish captured from late May to early June 2011 ranged in age from 7 to 33 years old with a mean (1 standard deviation [SD]) age of 20.1 years (SD 4.5; Fig. 2A), with equal numbers of males and females caught (χ^2=0.1617, P=0.69). Sexual dimorphism was evident in this group with males being longer (Mann-Whitney U statistic (U)=8147.5, P<0.001; Fig. 2B) and slightly heavier (U=9586.5, P=0.014), although some of these differences may be attributed to the males also being older than the females (U=8313.0, P<0.001; Table 2).

Total mortality

The age at full recruitment to the trawl gear was 21 years (Fig. 2A); therefore, age 22 was used as the starting point for the Chapman-Robson calculation. With that calculation we estimated that Z was 0.35 (standard error 0.034). We explored the sensitivity of this estimate to the choice of starting age by running the analysis with starting points of 21 and 23 years. The starting age had little effect on the estimate; results for Z were 0.36 and 0.38 for starting ages 21 and 23, respectively.

Reproductive status

Gonad size (weight) increased with increasing fish size (female W: coefficient of correlation (r) 0.665, P<0.05; male W: r=0.408, P<0.05; female TL: r=0.632, P<0.05; male TL: r=0.781; P<0.05) and age (females: r=0.590, P<0.05; males: r=0.408, P<0.05) in both male and female Atlantic wolffish. In females, GSI was correlated positively with age (r=0.463, P<0.05) but not in males (r=0.097, P=0.258; Fig. 3). Mean GSI values ranged from 0.0003 (SD 0.0) at age 16 to 0.0008 (SD 0.0002) at age 27 in males, whereas, in females, they ranged from 0.003 (SD 0.0) at age 7 to 0.029 (SD 0.016) at age 26.

Female reproductive state was not easy to classify because ovaries were frozen and then thawed instead of inspected fresh or preserved in a fixative; as a result, only 146 samples were usable, and, even so, interpretation was difficult. The majority of oocytes ranged from yellow to orange in color (Fig. 4), and all inspected oocytes were >0.5 mm (Table 3), indicating that all females were mature and most of them were in prespawning stages (Gunnarsson et al., 2006).

Feeding ecology

Atlantic wolffish sampled (n=286) were actively feeding; only 2 stomachs were empty. The feeding index

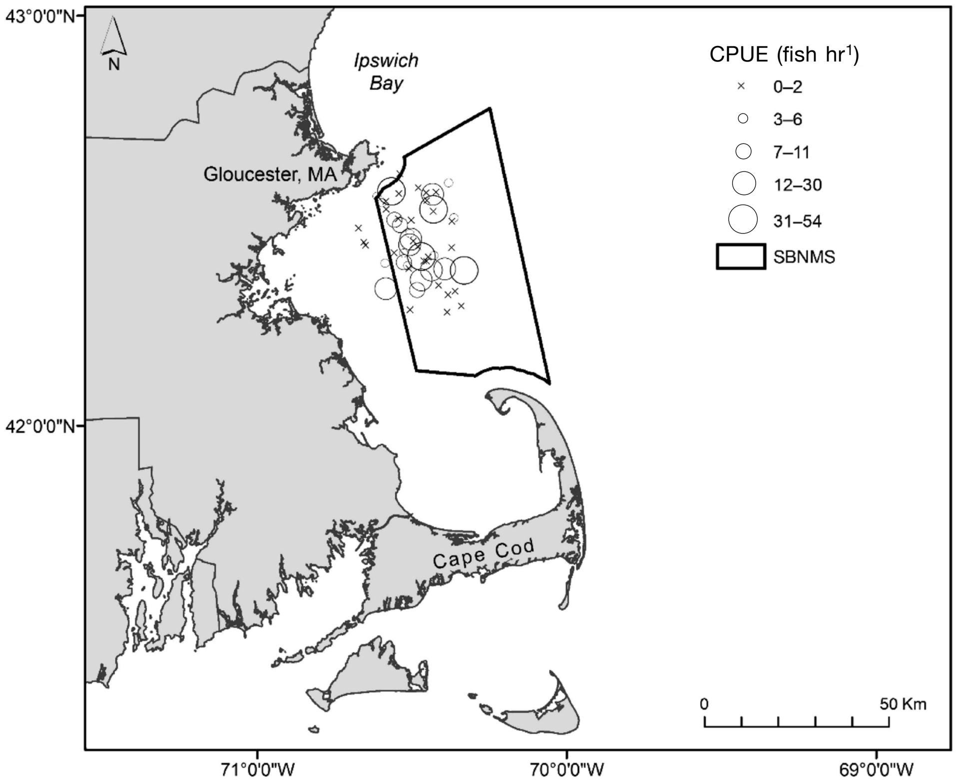

Figure 1

Map of the study area on the Stellwagen Bank National Marine Sanctuary (SBNMS) in Massachusetts Bay and catch per unit of effort (CPUE), measured as the number of Atlantic wolffish (*Anarhichas lupus*) caught per hour by bottom trawl gear.

(1 SD), a measure of feeding intensity, for all Atlantic wolffish sampled was 7.77 (SD 5.58), indicating that this population of wolffish was feeding heartily in late May and early June on the SBNMS.

Including nonprey items such as rocks and, in one instance, a metal fishing hook (Table 4), 18 items were identified in stomachs of Atlantic wolffish. In addition, 2 Atlantic wolffish contained whole undigested longhorn sculpin (*Myoxocephalus octodecemspinosus*) that likely were ingested during the tow because of an abundance of longhorn sculpin in the study area. As expected, the most frequently occurring prey items were bivalves, decapod crustaceans, gastropods, and echinoderms. Bivalves, decapod crustaceans, and echinoderms were the most volumetrically important prey items because of the prevalence of indigestible shells and exoskeletons. The sea scallop (*Placopecten magellanicus*) was the most dominant prey taxon both in frequency of occurrence and overall weight.

In both females and males, K was correlated positively with age (males: r=0.198, P=0.02; females: r=0.283, P<0.05; Fig. 5). Overall, there was no difference in K between sexes (U=9349.5; P=0.179). Mean K was 0.99 (SD 0.19) for females and 1.03 (SD 0.24) for males.

Discussion

Atlantic wolffish abundance

It is clear that high concentrations of Atlantic wolffish occurred on the SBNMS, especially in late May and to a lesser degree in early June 2011 (Table 1, Fig. 1), thereby confirming the accounts of fishermen. On the basis of published literature reviews, this degree of density of Atlantic wolffish is not well documented. Although references to Atlantic wolffish distribution "hotspots" can be found in agency reports (i.e., AWBRT[3], Kulka et al.[8]), we were able to find only one published account of dense wolffish aggregations. This account documented spotted wolffish (*A. minor*) caught on the northwest slope of the Grand Banks from August to early September in 1972 by Newfoundland trawlers (Templeman, 1986a). Captains estimated in their logbooks that they caught as much as 59,000 kg (130,073 lb) of spotted

[8] Kulka, D. W., M. R. Simpson, and R. G. Hooper. 2004. Changes in distribution and habitat associations of wolffish (Anarhichidae) in the Grand Banks and Labrador Shelf. Can. Sci. Advis. Secr. Res. Doc. 2004/113, 44 p. [Available from http://www.dfo-mpo.gc.ca/csas.]

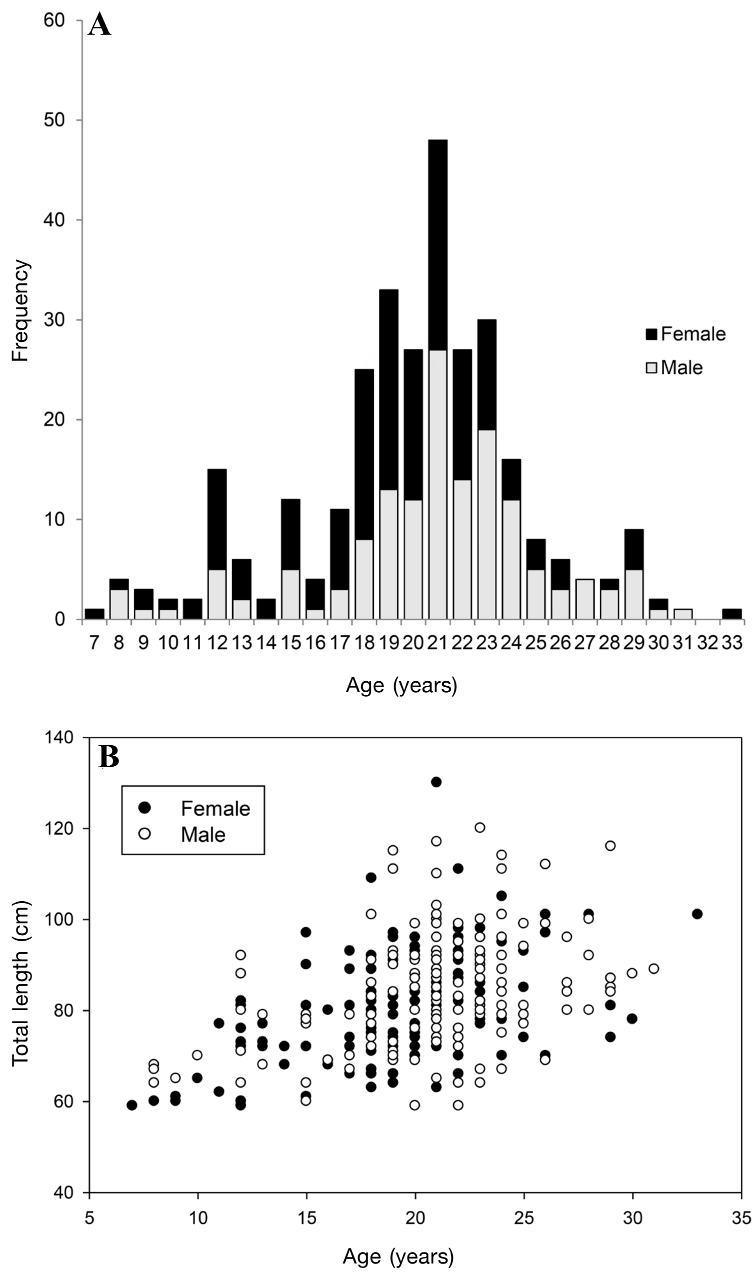

Figure 2

Population characteristics of 303 Atlantic wolffish (*Anarhichas lupus*) captured on the Stellwagen Bank National Marine Sanctuary, Massachusetts, from 23 May to 8 June 2011: (**A**) age by sex and (**B**) length at age.

wolffish per day at depths of 146–192 m. Templeman (1986a) surmised that these unusually large landings of spotted wolffish may have coincided with spawning behavior because their time of capture was close to the likely spawning season (summer).

Atlantic wolffish in the SBNMS group were mature (Fig. 2) and likely in prespawning condition (Fig. 4), but this group was not a spawning aggregation. During the spawning season, mature Atlantic wolffish cease feeding and undergo tooth replacement (Liao and Lucas, 2000a, 2000b). For females, this pause in feeding occurs mostly within the month before ovulation (Pavlov and Moksness, 1996). For males, tooth shedding and replacement and fasting occur with nest guarding (Keats et al., 1985). One tooth was found in a female fish's stomach (Table 4), but it likely broke off and was ingested during fishing operations. None of the 395 captured Atlantic wolffish showed signs of teeth shedding, and 99% of fish sampled were feeding actively.

We used traditional ecological knowledge of fishermen to identify an area where Atlantic wolffish were known to occur in spring to ensure that sufficient numbers of fish could be studied for biological analyses. As such, sampling for Atlantic wolffish on the SBNMS was selective, both temporally and spatially (in area and depth). In addition, tows were not standardized by duration. As a result of these limitations, we were able to verify only the presence of a large wolffish group but not its distribution. We observed a decrease in catch of Atlantic wolffish on the SBNMS from May to early June (Table 1); it remains unknown whether this decline was a result of reduction in biomass or the effects of dispersion. We were unable to sample the population during the first week of June, sampling that would have helped clarify this matter. When we resumed sampling on 7 June, we found Atlantic wolffish in a slightly different location on the SBNMS; however, by this time, Atlantic cod (*Gadus morhua*) were also present. In an effort to reduce cod bycatch mortality, we chose to avoid these mixed populations. Therefore, potential catch per unit of effort (CPUE) for Atlantic wolffish probably was much higher than the documented CPUE. A study of tagged and released Atlantic wolffish will help elucidate movements of this SBNMS population.

In the GOM–GB region, there is some evidence of size-segregated, seasonal movements of Atlantic wolffish, likely linked to spawning, from shallow (<10 m) to deep (274 m) waters in fall and then the reverse in spring (Albikovskaya, 1982; Nelson and Ross, 1992; AWBRT[3]). For instance, in spring in the GOM, predominantly larger fish have been found at depths of 5–40 m, and the largest fish was 98 cm TL and 22

Table 2

Size and age, by sex, of Atlantic wolffish (*Anarhichas lupus*) sampled from 23 May to 8 June 2011 on Stellwagen Bank National Marine Sanctuary, Massachusetts. *P*-values denote results of Mann-Whitney rank sum tests between sexes for each category. Atlantic wolffish with damage to caudal fins were not included in analyses of total lengths. SD=standard deviation of the mean.

	Total Length (cm)			Weight (kg)			Age (year)		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Females	80.49	11.91	148	5.79	2.85	155	19.20	4.48	155
Males	85.19	12.71	142	6.52	2.93	148	20.97	4.39	148
P-value		<0.001			0.014			<0.001	

years old, supporting the theory that Atlantic wolffish occupy deeper, warmer waters until they are sexually mature (Keats et al., 1986; Nelson and Ross, 1992). In this study of shallow (27–46 m) SBNMS waters, Atlantic wolffish ranged from 59 cm TL (age 7) to 130 cm TL (Fig. 2)—a finding that corroborates a seasonal separation of fish size by water depth in the GOM.

This movement pattern also has been found in Icelandic waters and the White Sea where Atlantic wolffish move into colder (3°C) waters before spawning (Jonsson, 1982; Pavlov and Novikov, 1993). However, spring and summer surveys at similar depths and temperatures throughout the period 1971–1980 in Newfoundland yielded no Atlantic wolffish (Albikovskaya, 1982) and indicated that concentrations of wolffish may occur at other depths elsewhere or be very discrete. During the study period, bottom temperatures on the SBNMS where wolffish concentrations occurred ranged from 5°C to 7°C (Table 1). From hatchery studies, it is known that Atlantic wolffish egg survival decreases if oocyte maturation and ovulation occur at temperatures >8°C (Tveiten et al., 2001). Therefore, it follows that this spring in-shore movement of prespawning, mature Atlantic wolffish into shallower, colder water likely is linked to the maintenance of thermal homeostasis as fish prepare for the fall spawning season.

Age, growth, and sex

In the GOM–GB region, Atlantic wolffish may attain TLs of 150 cm and weights of 18 kg (40 lb) (Rountree, 2002), yet scant age and growth data are available for larger sized (>100 cm TL) fish. Although we were fortunate enough to capture many large individuals, including a 130-cm-TL fish, we were prevented from calculating meaningful growth equations because no individuals <7 years old were collected. Our age data for older fish may be more accurate than data from previous studies. Nelson and Ross (1992) aged whole, polished otoliths, which can be difficult to read because they grow thicker in older fish; whereas, we aged sectioned otoliths. It is possible that slightly younger fish were present in the SBNMS group but, because of gear selectivity, were excluded from the catch. In spring surveys conducted in shallow depths (<40 m) over a span of 26 years, Atlantic wolffish always were >50 cm TL (Nelson and Ross, 1992).

On the SBNMS during May–June, male Atlantic wolffish are larger (heavier and longer; Table 2) than

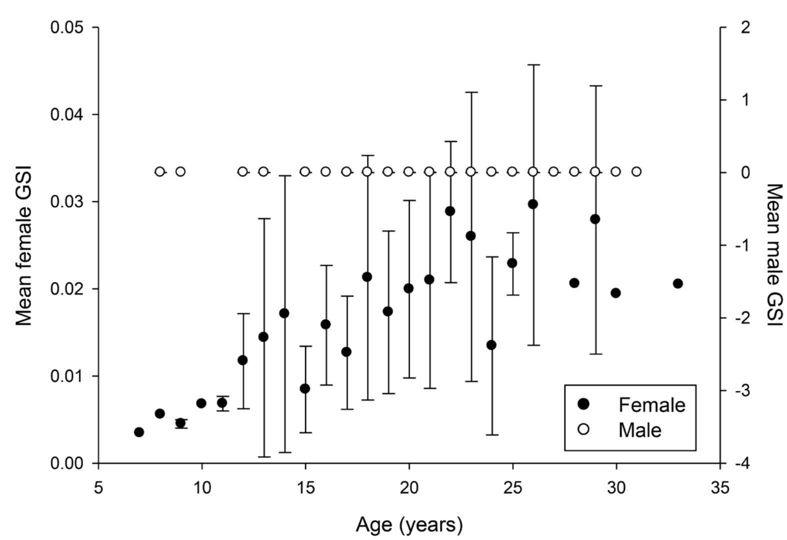

Figure 3

Mean gonadosomatic indices (GSIs) by age for female and male Atlantic wolffish (*Anarhichas lupus*) captured on the Stellwagen Bank National Marine Sanctuary, Massachusetts, from 23 May to 8 June 2011. Error bars indicate 1 standard deviation.

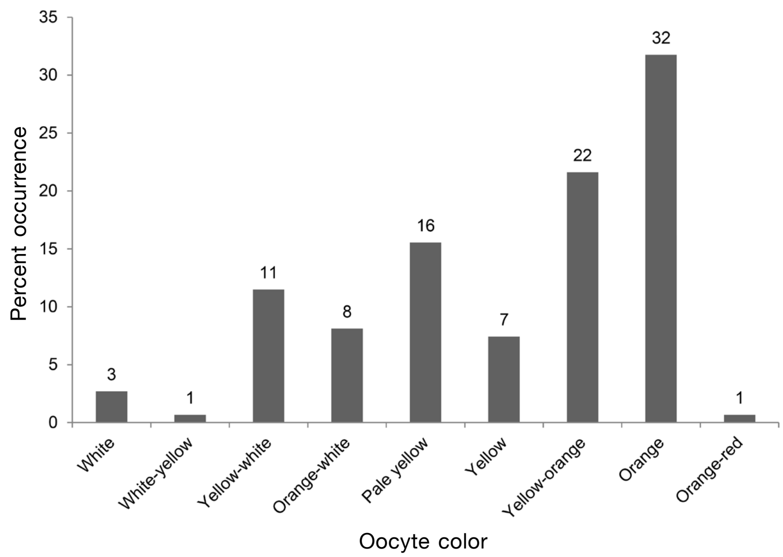

Figure 4

Percent occurrence of oocyte colors seen in 146 female Atlantic wolffish (*Anarhichas lupus*) captured on the Stellwagen Bank National Marine Sanctuary, Massachusetts, from 23 May to 8 June 2011. Color range represents degree of oocyte development from white (least) to orange-red (most). Colors were classified by the same individual by gross visual inspection of frozen, then thawed ovaries. Only one color was assigned to each ovary.

females. Although sexual dimorphism of Atlantic wolffish has not been evident in captivity, other than swollen "pot-bellied" females in the 4–5 months before spawning (Johannessen et al., 1993), historically, males tend to be heavier than females throughout the year in the wild (Templeman, 1986a). The largest fish captured in Templeman's (1986a) study were a 127-cm-TL male and 121-cm-TL female from the Grand Banks in 1966. However, more recently, Nelson and Ross (1992) did not find any differences in length between males and females (n=132), and they attributed this lack of differences to small sample sizes.

Total mortality

If natural mortality (M) is assumed to be 0.15 (Keith and Nitschke[5]), then fishing-induced mortality (F) is 0.20. The latest stock assessment for Atlantic wolffish in the GOM estimated F at 0.07 in 2010 and a mean F of 0.29 for the period 2006–2010 (Keith and Nitschke[5]). The differences in methods used make it difficult to compare these values, but the fact that the estimate from our study lies within the range found in the stock assessment increases our confidence in that stock assessment. An F of 0.20 for fully recruited Atlantic wolffish is relatively low and consistent with the findings of the latest stock assessment that overfishing is not occurring ($F<F_{msy}$ Proxy(0.33)).

Reproductive status

In the U.S. GOM–GB region, Atlantic wolffish reach sexual maturity at 40–47 cm TL, or about 5–6 years of age (Templeman, 1986b; Nelson and Ross, 1992; McBride[9]). Because the smallest fish in this study was 59 cm TL and eggs were >0.5 mm in diameter in all females (Table 4), it is clear that the SBNMS fish were mature. Less clear, because of the lack of proper gonad

[9] McBride, R. 2012. Personal commun. Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 166 Water St., Woods Hole, MA 02543.

Table 3

Numbers of Atlantic wolffish (*Anarhichas lupus; n*=146) with oocytes within the following ranges of size (min. to max). Oocytes were collected from ovaries of individuals captured from 23 May to 8 June 2011 on Stellwagen Bank National Marine Sanctuary, Massachusetts.

Minimum oocyte diameter (mm)	Maximum oocyte diameter (mm)							
	0.5–0.9	1.0–1.4	1.5–1.9	2.0–2.4	2.5–2.9	3.0–3.4	3.5–4.0	>6.1
0.5–0.9	1	6						2
1.0–1.4		8	17	1		4		
1.5–1.9			18	25	2	2		4
2.0–2.4				4	11	8		2
2.5–2.9					1	16	2	
3.0–3.4						6	4	1
3.5–4.0							1	
Total	1	14	35	30	14	36	7	9

Table 4

Relative frequency of occurrence and weight, by species, of items found in the stomachs of 286 Atlantic wolffish (*Anarhichas lupus*) from 23 May to 8 June 2011 on Stellwagen Bank National Marine Sanctuary, Massachusetts.

Prey item	Frequency (%)	Weight (g)
Sea scallop (*Placopecten magellanicus*)	87.8	25.4
Hermit crab (*Pagurus* sp.)	51.0	1.8
Ocean quahog (*Arctica islandica*)	46.6	7.7
Gastropods, unidentified to species	46.3	1.6
Green sea urchin (*Strongylocentrotus droebachiensis)*	43.9	4.9
Rocks	34.5	0.3
Jonah crab (*Cancer borealis*)	25.3	5.3
Sand dollar (*Echinarachnius parma*)	2.7	0.4
Sea star, unidentified to species	1.4	<0.1
American lobster (*Homarus americanus*)	1.4	0.2
Spider crab (*Libinia* sp.)	1.4	<0.1
Longhorn sculpin (*Myoxocephalus octodecemspinosus*)	0.7	0.3
Algae (green), unidentified to species	0.7	<0.1
Common sun star (*Crossaster papposus*)	0.3	<0.1
Mussel, unidentified to species	0.3	<0.1
Polychaete, unidentified	0.3	<0.1
Tooth, Atlantic wolffish	0.3	<0.1
Hook	0.3	<0.1

preservation, was their reproductive status. Egg color is helpful for identifying stages of oocytes. Templeman (1986b) found that Atlantic wolffish eggs that had not developed beyond a "whitish condition" were indicative of mature females who had not spawned yet and that yellowish eggs were "newly-maturing" eggs. From gross visual inspection of the ovaries of these SBNMS fish, only a small proportion of females was spawning for the first time (3–4%, Fig. 4). The majority of females had yellow-orange oocytes, indicating that these fish likely were in prespawning condition (Fig. 4). Further studies with proper gonad preservation and histology would be helpful in differentiating these stages more accurately.

Worth noting, Atlantic wolffish eggs were not present in any guts. After spawning, males remove eggs stuck to the exterior of the female's body by sucking and spitting them out (Johannessen et al., 1993); it is reasonable to suspect that some eggs are ingested incidentally. In addition, in intensive culture, Atlantic wolffish have been observed eating eggs from other pairs, and females have been seen destroying their own unfertilized eggs (Johannessen et al., 1993). When Atlantic wolffish guts were excised from the fish in our study, they immediately were frozen on ice until analysis; we are confident that if eggs had been in the guts, they still would have been present during processing. The absence of wolffish eggs in the guts provides additional evidence that this population had not spawned in the recent past.

In Atlantic wolffish, fecundity increases exponentially with increasing size (Gunnarsson et al., 2006; Templeman, 1986b; Falk-Petersen and Hansen[10]), and because size is positively correlated to age, it is not surprising that older females generally had higher GSI than younger females (Fig. 3). In contrast, male Atlantic wolffish have relatively small testes and produce only a small amount of sperm, as would be expected for a species with internal fertilization; male GSI does not increase with age or TL. Even within the year, there is low variation in GSI for males >3 kg (6.6 lb) (Johannessen et al., 1993; Moksness and Pavlov, 1996; Pavlov and Moksness, 1996), whereas females show pronounced GSI peaks leading up to spawning (Hansen, 1992 as cited by Tveiten and Johnsen, 1999).

Feeding ecology

Often known for their unusual tooth structure, wolffishes have highly specialized teeth for capturing and grinding hard-bodied prey. Adults feed almost exclusively on hard-shelled benthic invertebrates. Past studies in the GOM–GB region revealed that economically important bivalves (sea scallop, Iceland scallop [*Chlamys islandica*], ocean quahog [*Arctica islandica*], arks clam [Family Aricidea], and Atlantic surfclam [*Spisula solidissima*]) were the most predominant prey group in stomachs of Atlantic wolffish (13–108 cm TL) collected in spring (Nelson and Ross, 1992), followed by echino-

[10] Falk-Petersen, I.-B., and T. K. Hansen. 1991. Reproductive biology of wolffish *Anarhichas lupus* from north-Norwegian waters. ICES Council Meeting (C.M.) Documents 1991/G.14, 17 p.

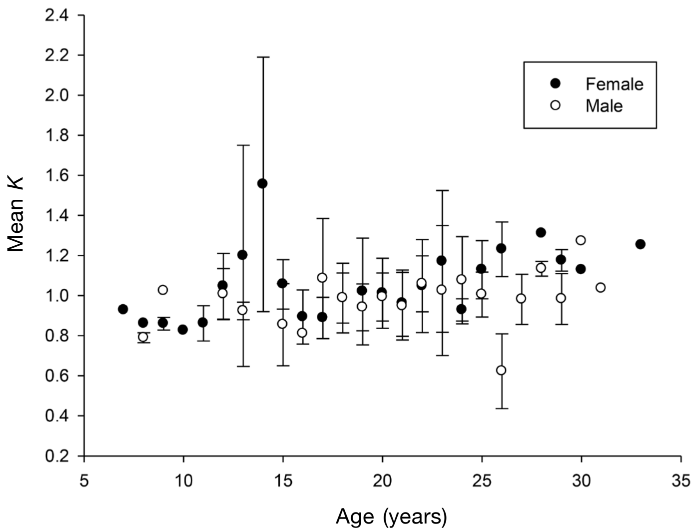

Figure 5

Mean Fulton's condition factor (K) by age for female and male Atlantic wolffish (*Anarhichas lupus*) captured on the Stellwagen Bank National Marine Sanctuary, Massachusetts, from 23 May to 8 June 2011. Error bars indicate 1 standard deviation.

derms, gastropods, and decapod crustaceans. By frequency of individual species, sea and Iceland scallops were most common, followed by whelks (Buccinum sp.), green sea urchin (*Strongylocentrotus droebachiensis*), hermit crabs (*Pagurus* sp.), and ocean quahogs (Nelson and Ross, 1992). We found similar dietary groups but a different order of rankings. Although the sea scallop still ranked first in frequency and volume, hermit crabs were more predominant in the diet of wolffish sampled during spring 2011, followed by ocean quahogs, gastropods, green sea urchin, and Jonah crab (*Cancer borealis*). Dietary differences may be a reflection of spatial differences in prey availability or ecological changes in the benthic community in the SBNMS area over the past 4 decades.

Some scientists believe communal Atlantic wolffish foraging areas (or locations that are used by large groups) may exist (Auster and Lindholm, 2005). This particular area on the SBNMS appears not to be complex habitat that is normally associated with essential wolffish habitat, but rather an assemblage of sand and gravel substrates (Table 1) containing scallop beds (Hart and Chute, 2004). Considering the density of Atlantic wolffish present during May–June, as well as their feeding intensity, it is likely that this area of the SBNMS is a foraging area for large aggregations of Atlantic wolffish.

We have validated fishermen accounts of high density of Atlantic wolffish on the SBNMS, at least for a brief period in spring, and these large, mature fish appear to use this area as a communal foraging ground. Future field studies that use a randomized sampling design inside and outside of the SBNMS at varying depths from early spring through summer would help clarify wolffish distribution. In particular, it is not known if Atlantic wolffish aggregate on the SBNMS in spring or if this area contains a biomass hotspot subject to annual variability in wolffish densities. For low biomass species like Atlantic wolffish (Sosebee and Cadrin[4]), traditional surveys coupled with alternative means of sampling are required for accurate assessments. Comprehensive tagging studies, video monitoring, and targeted cooperative industry surveys would provide more information on the movements, ecology, and population structure of this data-poor species.

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