



**Abstract**—Specimens of the spotted moray (*Gymnothorax moringa*) were obtained from fishery-dependent and fishery-independent sources off the Atlantic coast of the southeastern United States from May 2005 through April 2007. A total of 491 individuals, ranging in total length (TL) from 556 to 1267 mm, were collected; age estimates ranged from 4 to 23 years, with a mean of 12.3 years. Females attained greater ages and had a significantly greater mean age than males. Length at age of males was greater than that of females at all ages but was significantly greater only at ages 9, 10, 12, and 17. In size classes with lengths greater than 900 mm TL, males were significantly heavier than females. The overall male-to-female sex ratio of 1:1.09 did not significantly differ from 1:1. All specimens were examined histologically, and none were immature. Spawning females were collected from late April through February, and estimates of spawning periodicity (24–31 d) indicate that a female could spawn up to 12 times during a spawning season. Males were in spawning condition throughout the year, with the exception of March, when all individuals were in regressing condition. Two individuals had both testicular and ovarian tissue; however, histological evidence indicates that this species is likely gonochoristic.

Manuscript submitted 24 January 2022.  
Manuscript accepted 3 June 2022.  
Fish. Bull. 120:195–204 (2022).  
Online publication date: 17 June 2022.  
doi: 10.7755/FB.120.3-4.1

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

## Life history of the spotted moray (*Gymnothorax moringa*) off the Atlantic coast of the southeastern United States: age, growth, and reproduction

Marcus A. Zokan (contact author)<sup>1</sup>

David M. Wyanski<sup>1,2</sup>

D. Byron White<sup>2</sup>

George R. Sedberry<sup>1,2</sup>

Email address for contact author: [marcus.zokan@myfwc.com](mailto:marcus.zokan@myfwc.com)

<sup>1</sup> Grice Marine Lab

College of Charleston  
205 Fort Johnson Road  
Charleston, South Carolina 29412

Present address for contact author: Division of Freshwater Fisheries Management  
Florida Fish and Wildlife Conservation Commission  
1239 SW 10th Street  
Ocala, Florida 34471

<sup>2</sup> Marine Resources Research Institute

South Carolina Department of Natural Resources  
217 Fort Johnson Road  
Charleston, South Carolina 29412

The spotted moray (*Gymnothorax moringa*) is one of the most abundant moray species in the western Atlantic Ocean (Böhlke et al., 1989). It ranges from North Carolina south through the West Indies to Brazil, including the Gulf of Mexico and the islands of Bermuda, St. Helena, and Ascension (Smith, 1976; Böhlke et al., 1989). Within this range, it inhabits a variety of habitats, including coral and rock reefs, seagrass beds, and jetties, at depths ranging from less than 1 m to greater than 90 m (Böhlke et al., 1989). It is a moderately large moray species, reaching at least 1025 mm in total length (TL) (Böhlke et al., 1989).

Hiding in holes and crevices in the reef structure by day and actively hunting prey in the surrounding area at night, the spotted moray is primarily nocturnal (Bardach et al., 1959; Young and Winn, 2003), although diurnal feeding may occur opportunistically (Michael,

1998). The spotted moray feeds largely on reef fish, decapod crustacean, and cephalopod species, with the proportion of fish in the diet increasing with size (Randall, 1967; Young and Winn, 2003). Because of its large size and abundance, the spotted moray is believed to be an important predator within reef ecosystems of the western Atlantic Ocean (Carr and Hixon, 1995).

Morays are caught in trawl, trap, and line fisheries in many tropical and subtropical areas of the world (Böhlke et al., 1989; Böhlke, 2002) and are consumed in Asia and many island regions, despite the possibility of ciguatera fish poisoning (Böhlke and Chaplin, 1968; Yip, 1971). Off the southeastern United States, spotted moray are often captured by using hook-and-line gear in the snapper and grouper fishery and are abundant enough in some areas to be considered a nuisance by fishermen

(Smith, 1976). Although not eaten in the southeastern United States, spotted moray are occasionally landed as bycatch there and sold to Asian markets in Canada (Marhefka<sup>1</sup>).

Few studies have investigated the basic biology of the spotted moray. Previous studies have examined activity patterns, movements, diet, and sensory biology (Bardach et al., 1959; Bardach and Lowenthal, 1961; Randall, 1967; Abrams et al., 1983; Abrams and Schein, 1986; Young and Winn, 2003), but to date no studies have examined age, growth, or reproduction. To bridge this gap, the purpose of our study was to provide baseline life history characteristics for a population of spotted moray inhabiting the waters of the Atlantic Ocean off the southeastern United States, information that should prove useful to further studies of this species. The primary objectives of this study included the examination of age and growth, length–weight relationships, and aspects of reproductive biology for spotted moray in this region.

## Materials and methods

### Sample collection

Specimens for this study (sample size [ $n$ ]=491) were obtained from commercial fishing vessels and research vessels between Cape Lookout, North Carolina (34°11'N, 76°8'W), and northeastern Florida (30°1'N, 80°17'W), with most specimens collected off South Carolina. Fishery-independent samples ( $n=102$ ) were collected between May 2005 and October 2006 during research cruises of the South Carolina Department of Natural Resources as part of the Marine Resources Monitoring Assessment and Prediction (MARMAP) Program, primarily by using baited chevron traps (Collins, 1990) deployed at depths of 14–94 m. Other gears in which spotted moray were captured during surveys conducted for the MARMAP Program included baited Florida traps (Collins, 1990), hook and line, and bottom longlines (Harris et al., 2004). Baited wire-mesh minnow traps were used in 2006 in an attempt to sample small individuals (<500 mm TL), but no spotted moray were captured. Fishery-dependent samples of spotted moray ( $n=389$ ) were obtained from commercial catches in the snapper and grouper fishery from July 2005 through April 2007.

The method of capture used by commercial fishermen was a vertical hook-and-line gear called a *bandit reel* (see Wyanski et al., 2000). Commercial fishermen reported location, date of capture, and depth in feet for 47% of the specimens they provided. For an additional 12% of commercially caught specimens, only general trip data were provided; in such cases, the median date of the trip was used as the date of capture, the center of the reported fishing area was used for location, and the average of the reported depth range was used for depth. The remaining specimens

had only trip dates and were treated as described previously. All specimens were assigned a month of capture on the basis of the exact collection date or median trip date. Depth of capture was compared between sexes by using a *t*-test; specimens for which depth data were lacking were omitted from this analysis.

Total length in millimeters and total body weight ( $W$ ) in grams were measured for all retained specimens of the spotted moray. All stomach contents were removed, weighed, and subtracted from the original weight of the specimen because many individuals consumed large pieces of bait (up to 515 g). Differences between sexes in length and weight were examined by using Welch's analysis of variance (ANOVA) for unequal variances, and weight was compared between sexes by 100-mm-TL size classes with Wilcoxon rank sum tests because of violations of normality in some comparisons. The weight–length relationship was modeled with the equation  $W=aTL^b$ , where  $a$  and  $b$  are constants (Le Cren, 1951). This equation was log-transformed as  $\log W = \log a + b \log TL$ , and parameters were estimated by using linear regression. Akaike information criterion (AIC) scores were used to assess whether sexes were best separated or pooled in weight–length models.

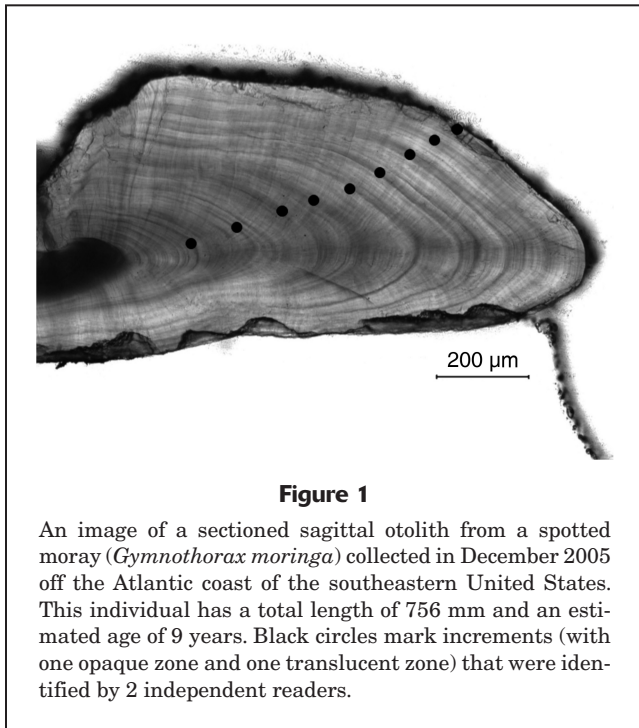
### Age and growth

Right and left sagittal otoliths were removed and placed in microcentrifuge tubes filled with 95% ethanol for 3–5 d and then transferred to dry vials for storage. For aging, the left sagitta was marked at the core and embedded in epoxy resin. In cases of missing or damaged otoliths, the right sagitta was substituted. A single transverse, 0.7-mm-thick section was made through the core by using an IsoMet 1000<sup>2</sup> high-speed saw (Buehler, Lake Bluff, IL). Sections were mounted on glass slides with Cytoseal XYL mounting medium (Thermo Fisher Scientific, Waltham, MA) and viewed with transmitted light under a Nikon SMZ-U dissecting microscope (Nikon Corp., Tokyo, Japan).

Otolith increments (with one translucent zone and one opaque zone) were independently counted by 2 readers without knowledge of specimen size, location, or date of capture. The readers agreed that the first increment was the first distinct ring outside the opaque core (Fig. 1). If increment counts differed between readers, both readers reexamined the otolith simultaneously. Marginal increment analysis was not attempted because edges were frequently narrow or chipped. Differences between sexes in age were compared by using Kolmogorov–Smirnov tests and Welch's ANOVA for unequal variances, and length was compared between sexes by age classes with Wilcoxon rank sum tests because of violations of normality in some comparisons. A von Bertalanffy growth curve was then fitted to the age and length data (von Bertalanffy, 1938). Akaike information criterion scores were used to assess

<sup>1</sup> Marhefka, M. 2006. Personal commun. Abundant Seafood, 4731 Mixon Ave., North Charleston, SC 29412.

<sup>2</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



**Figure 1**

An image of a sectioned sagittal otolith from a spotted moray (*Gymnothorax moringa*) collected in December 2005 off the Atlantic coast of the southeastern United States. This individual has a total length of 756 mm and an estimated age of 9 years. Black circles mark increments (with one opaque zone and one translucent zone) that were identified by 2 independent readers.

whether sexes were best separated or pooled in the von Bertalanffy growth functions.

### Reproduction

Whole gonads from each specimen were removed and weighed (to the nearest 0.1 g). A modified gonadosomatic index (GSI) was calculated for females with this equation:  $GSI = 100(\text{gonad weight} / \text{total body weight without stomach contents})$ . For gonads  $\leq 4$  mm in diameter, a sample 2.5–3.0 cm in length was excised from the posterior end of both gonads, placed in a Tissue-Tek Uni-Cassette tissue cassette system (Sakura Finetek USA, Inc., Torrance, CA), and fixed in a solution of 11% formalin in seawater buffered with marble chips. For gonads  $> 4$  mm in diameter, a transverse section approximately 4 mm thick was removed from near the posterior end of the gonad and treated with the same procedure used for sections from those with diameters  $\leq 4$  mm.

Gonad samples were processed for histological examination following the methods of Harris et al. (2004). These samples were vacuum-infiltrated with paraffin by using an automated tissue processor. Samples from gonads with diameters  $\leq 4$  mm were cut into 3 portions, and all portions were embedded in paraffin. Three transverse sections that were 7  $\mu\text{m}$  thick, with an interval of 350  $\mu\text{m}$  between sections, were made by using a Leica RM2255 rotary microtome (Leica Biosystems, Wetzlar, Germany). The sections from each sample were placed on one glass slide, stained with double-strength Gill's hematoxylin, and counterstained with eosin Y. Sections were viewed with a Nikon 55i compound microscope (Nikon Corp.) at magnification of 40–400 $\times$ . Sex and reproductive phase were assessed by

2 readers independently without knowledge of size, age, location, and date of capture.

Histological sections were used to assign sex and reproductive phase microscopically by following the criteria of Harris et al. (2004), and postovulatory follicle complexes (POCs) were evaluated by using the methods of Hunter et al. (1986). Reproductive terminology follows that proposed by Brown-Peterson et al. (2011). Specimens with developing, spawning capable, regressing, or regenerating gonads were considered sexually mature; immature specimens were defined as having no active gonad development and no indication that spawning had previously occurred.

The length of the spawning season was estimated as the number of days from the first day to the last day that spawning indicators (oocytes undergoing yolk coalescence and germinal vesicle migration [GVM], hydrated oocytes, or POCs) were observed. Spawning interval was estimated by using 2 methods: 1) the number of reproductively active females (presence of vitellogenic oocytes, oocyte maturation, or POCs) divided by the number of females with oocytes in GVM or with hydrated oocytes and 2) the number of reproductively active females divided by the number of females with POCs less than 24 h old. These methods of estimating spawning interval follow those of Hunter and Goldberg (1980). The number of spawning events per season was estimated by dividing the number of days in the spawning season by the spawning interval.

Sex ratios were evaluated with a chi-square goodness-of-fit test to determine if the ratios differed from 1:1 for the population as a whole. Ratios were compared by length class and age class to examine differences between sexes in population size and age structure.

All statistical tests were performed with R, vers. 3.6.3 (Dalggaard, 2002; R Core Team, 2020). The results of all tests were considered significant if  $P < 0.05$ .

### Results

The specimens of spotted moray examined in this study ( $n=491$ ) had lengths of 556–1267 mm TL (sample mean: 912.1 mm TL [standard error of the mean (SE) 5.6]) and had weights of 308–4410 g (sample mean: 1435.5 g [SE 31.3]). Sex was assigned to 490 specimens: 234 specimens were male, 254 eels were female, and 2 specimens had both testicular and ovarian tissue. All specimens examined were sexually mature. The smallest male was 556 mm TL, and the smallest female was 611 mm TL. Specimens ( $n=332$ ) were collected from depths of 30–79 m (sample mean: 48.8 m [SE 0.4]), with males ( $n=172$ ; sample mean: 49.1 m [SE 0.6]; range: 30–79 m) and females ( $n=159$ ; sample mean: 48.5 m [SE 0.5]; range: 30–69 m) occupying the same depths ( $t$ -test:  $t=-0.76$ ,  $P=0.45$ ,  $df=328$ ).

There were no significant differences between sexes in mean TL (ANOVA:  $F=1.4$ ,  $P=0.24$ ,  $df=449$ ); however, males were significantly heavier than females in mean weight (ANOVA:  $F=13.6$ ,  $P<0.001$ ,  $df=398$ ). When examined by 100-mm-TL length classes, males were significantly heavier than females at lengths  $\geq 900$  mm TL ( $P<0.01$ ) (Table 1A).

**Table 1**

Comparisons (**A**) of weight by length class and (**B**) of total length (TL) by age class between sexes with Wilcoxon rank sum tests for spotted moray (*Gymnothorax moringa*) collected off the Atlantic coast of the southeastern United States from May 2005 through April 2007. Sample size ( $n$ ) and mean weight and length of the sample are given by sex for each length and age class. Tests were run only when expected frequencies were  $>5$  individuals. Test results were considered significant if  $P < 0.05$ .  $w$  = test statistic.

<b>A</b>						
Length class (mm TL)	Males		Females		$w$	$P$
	$n$	Mean weight (g)	$n$	Mean weight (g)		
500–599	2	325.0	–	–	–	–
600–699	9	524.0	5	437.2	35	0.11
700–799	36	697.6	44	726.9	697	0.36
800–899	64	1110.3	68	1052.6	2551	0.09
900–999	52	1611.0	84	1455.9	2916	$<0.01$
1000–1099	48	2218.8	44	1941.8	1497	$<0.001$
1100–1199	19	2990.9	8	2499.0	129	$<0.01$
1200–1299	4	3985.8	1	3203.0	–	–

<b>B</b>						
Age class (years)	Males		Females		$w$	$P$
	$n$	Mean length (mm TL)	$n$	Mean length (mm TL)		
4	2	674.5	–	–	–	–
5	2	697.5	1	665.0	–	–
6	13	759.2	4	751.0	21	0.57
7	14	820.8	8	796.1	67	0.48
8	33	843.0	10	818.0	189	0.51
9	17	907.9	11	812.9	139	0.03
10	26	939.4	31	871.5	561	0.01
11	14	899.4	21	897.9	152	0.88
12	22	954.6	20	883.2	303	0.04
13	15	948.5	25	932.7	206	0.62
14	10	1018.1	13	958.4	91	0.12
15	11	1009.3	18	951.6	123	0.30
16	10	1044.4	15	972.3	105	0.10
17	11	1093.0	14	932.1	143	$<0.001$
18	7	990.7	15	923.7	69	0.27
19	2	1043.0	8	1030.4	–	–
20	–	–	9	958.2	–	–
21	–	–	5	995.2	–	–
22	2	1057.0	2	953.0	–	–
23	–	–	2	947.0	–	–

The weight–length relationship for all specimens was  $W = (2.36 \times 10^{-7}) TL^{3.29}$ , and the coefficient of determination ( $r^2$ ) was 0.89. The weight–length parameters,  $a$  and  $b$ , were  $1.22 \times 10^{-7}$  and 3.40 for males, respectively ( $r^2 = 0.93$ ), and were  $6.94 \times 10^{-7}$  and 3.13 for females, respectively ( $r^2 = 0.86$ ). The AIC scores favor the weight–length model with sex as an independent variable (AIC:  $-441.53$ ) over the model with sexes pooled (AIC:  $-412.09$ ), indicating that the sexes had different weight–length relationships.

Intact sagittal otoliths were removed from 480 specimens (Fig. 1). Initial agreement on ages by both readers was only 38%; however, agreement within 1 year was 80%.

If agreement was not reached when the slide was viewed simultaneously by both readers, the specimen was omitted from analyses. The primary discrepancy in increment number was due to differences in the designation of the first increment. Otoliths from 34 individuals were deemed unreadable and were excluded from further analysis.

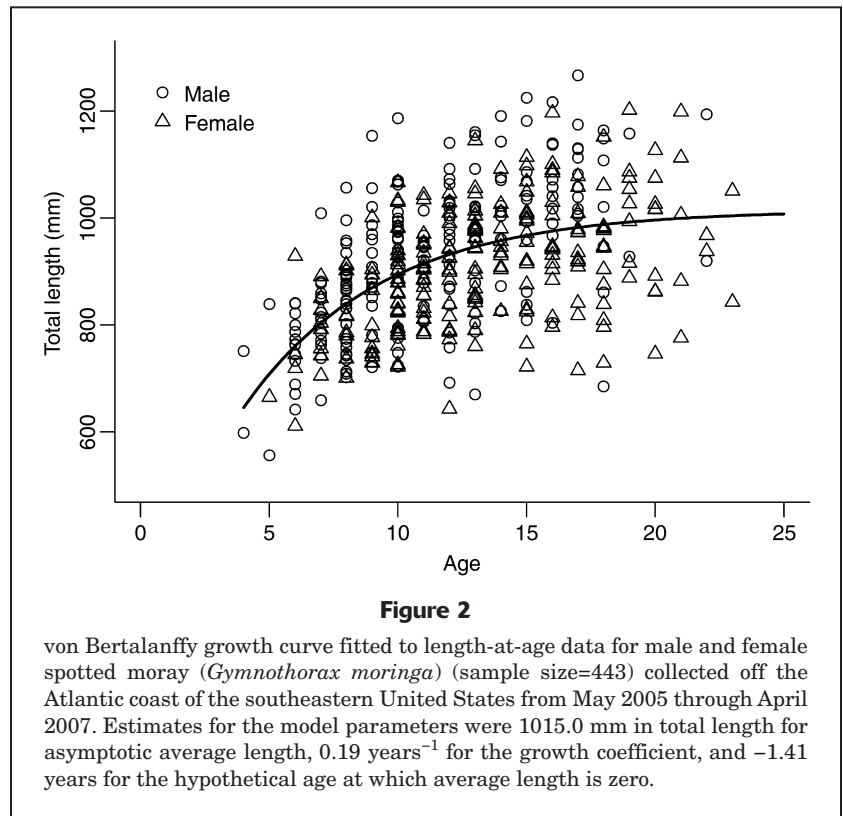
Age estimates ranged between 4 and 23 years, with a mean of 12.3 years (SE 0.2) ( $n = 443$ ). The mean age for females ( $n = 232$ ) of 13.4 years (SE 0.3) is significantly greater than that for males ( $n = 211$ ) of 11.1 years (SE 0.3) (ANOVA:  $F = 38.6$ ,  $P < 0.001$ ,  $df = 440$ ), and females also had an older age distribution (Kolmogorov–Smirnov test:



$D=0.24, P<0.001$ ). Length at age of males was greater than that of females at all ages, but was significantly greater only at ages 9, 10, 12, and 17 ( $P<0.05$ ) (Table 1B). Estimates of the von Bertalanffy growth parameters for sexes combined are as follows: the asymptotic average length ( $L_{\infty}$ ) is 1015.0 mm TL (SE 21.5), the growth coefficient ( $k$ ) is 0.19 years<sup>-1</sup> (SE 0.04), and the hypothetical age at which average length is zero ( $t_0$ ) is -1.41 years (SE 1.45) (Fig. 2). The growth parameters differed between males and females, with males having a greater  $L_{\infty}$  and lower  $k$ , indicating that they have a greater mean length at age (Table 2). The AIC scores favor the growth model with sex as an independent variable (AIC: 5360.71) over the model with sexes pooled (AIC: 5387.52), signifying that sexes had different growth characteristics.

The overall male-to-female sex ratio was 1:1.09 and did not significantly differ from 1:1 (Table 3A). Females were more abundant than males in the length classes between 700 and 999 mm TL, but this trend was significant only at lengths of 900–999 mm TL (Table 3A). In contrast, there were significantly more males than females at lengths  $\geq 1100$  mm TL. Among age classes, males were more abundant than females at ages  $\leq 9$  years, with this trend being significant at ages  $\leq 6$  years and at age 8 (Table 3B). In contrast, females were more abundant at ages  $\geq 13$  years, but this trend was significant only at ages  $\geq 19$  years.

The spawning season, based on the presence of hydrated oocytes and POCs in ovaries, spanned at least 278 d from late May through February. In addition, an individual with oocytes in GVM was collected in late April, leaving



**Figure 2**  
von Bertalanffy growth curve fitted to length-at-age data for male and female spotted moray (*Gymnothorax moringa*) (sample size=443) collected off the Atlantic coast of the southeastern United States from May 2005 through April 2007. Estimates for the model parameters were 1015.0 mm in total length for asymptotic average length, 0.19 years<sup>-1</sup> for the growth coefficient, and -1.41 years for the hypothetical age at which average length is zero.

January and March as the only months in which females that were spawning capable or that had recently spawned were not collected. Females with developing oocytes were collected in all months of the year, whereas the greatest proportions of specimens that were females in the regenerating phase occurred from December through March (Fig. 3A). Mean female GSI values climbed rapidly from a low in March to a peak in June and then declined through the remainder of the year, remaining low from December through March; the results of comparisons of mean TL by month indicate that changes in GSI values were not influenced by changes in size between months (Fig. 4).

Histology revealed that oocytes in reproductively active specimens were typically in multiple developmental stages in a single ovary (Fig. 5A) and that individuals that recently spawned had both POCs and vitellogenic oocytes, both of which indicate that the spotted moray is a batch spawner. Estimates of spawning interval ranged from 24 d, based on the proportion of specimens with POCs <24 h old (218/9=24.2 d), to 31 d, based on the proportion of specimens that had oocytes in GVM or hydrated oocytes (218/7=31.1 d). Given these spawning interval calculations and a spawning season that lasts approximately 278 d, a female could spawn between 9 and 12 times during the spawning season. The single female with hydrated oocytes was captured at a depth of 49–64 m and had oocytes approximately 2 mm in diameter. Females near spawning condition or postspawning (those with oocytes undergoing GVM and postovulatory follicles <24 h old) were all collected off South Carolina at depths of 33–62 m. The estimated dates

**Table 2**

Estimates of von Bertalanffy growth parameters for male, female, and all specimens (sample size=443) of spotted moray (*Gymnothorax moringa*) collected off the Atlantic coast of the southeastern United States from May 2005 through April 2007. The parameters include the asymptotic average total length (TL) ( $L_{\infty}$ ), the growth coefficient ( $k$ ), and the hypothetical age at which average length is zero ( $t_0$ ). Standard errors of the mean are given in parentheses.

Sex	$L_{\infty}$ (mm TL)	$k$ (years <sup>-1</sup> )	$t_0$ (years)
Male	1112 (60)	0.14 (0.05)	-2.47 (2.21)
Female	990 (27)	0.19 (0.06)	-1.36 (2.35)
All	1015 (22)	0.19 (0.04)	-1.41 (1.45)

**Table 3**

Comparisons of sex ratios by (A) length class and (B) age class with chi-square tests for spotted moray (*Gymnothorax moringa*) collected off the Atlantic coast of the southeastern United States from May 2005 through April 2007. Sample size ( $n$ ) is given for males (M) and females (F). Some length and age classes with low sample sizes were combined to allow for statistical comparisons. Tests were considered significant if  $P > 0.05$ . TL = total length.

<b>A</b>					
Length class (mm TL)	$n$		M:F ratio	$\chi^2$	$P$
	M	F			
≤699	11	5	1:0.45	2.25	0.13
700–799	36	44	1:1.22	0.80	0.37
800–899	64	68	1:1.06	0.12	0.73
900–999	52	84	1:1.62	7.53	<0.01
1000–1099	48	44	1:0.92	0.17	0.68
≥1100	23	9	1:0.39	6.13	0.01
Total	234	254	1:1.09	0.82	0.37

<b>B</b>					
Age class (years)	$n$		M:F ratio	$\chi^2$	$P$
	M	F			
≤6	17	5	1:0.29	6.55	0.01
7	14	8	1:0.57	1.64	0.20
8	33	10	1:0.30	12.30	<0.001
9	17	11	1:0.65	1.29	0.26
10	26	31	1:1.19	0.44	0.51
11	14	21	1:1.50	1.40	0.24
12	22	20	1:0.90	0.10	0.76
13	15	25	1:1.67	2.50	0.11
14	10	13	1:1.30	0.39	0.53
15	11	18	1:1.64	1.69	0.19
16	10	15	1:1.50	1.00	0.32
17	11	14	1:1.27	0.36	0.55
18	7	15	1:2.14	2.91	0.09
≥19	4	26	1:6.50	16.13	<0.001
Total	211	232	1:1.10	1.00	0.32

of spawning for females with POCs <24 h old ( $n=8$ ) did not correspond to any particular lunar phase; the exact date of capture of the female with hydrated oocytes, and therefore the lunar phase, was unknown.

Males capable of spawning were collected in all months of the year, with the exception of March, and were proportionally most frequently caught from August through February (Fig. 3B). The highest percentages of developing males occurred from May through July; regressing individuals appeared in most months of the year but predominated in December, March, and April.

Two specimens had both testicular and ovarian tissue within their gonads. One individual, which had a length of 881 mm TL and an age of 12 years, had developing testicular tissue with inactive ovarian tissue at the periphery of each testis (Fig. 5B); the ovarian tissue was present along the entire lateral surface and approximately 50%

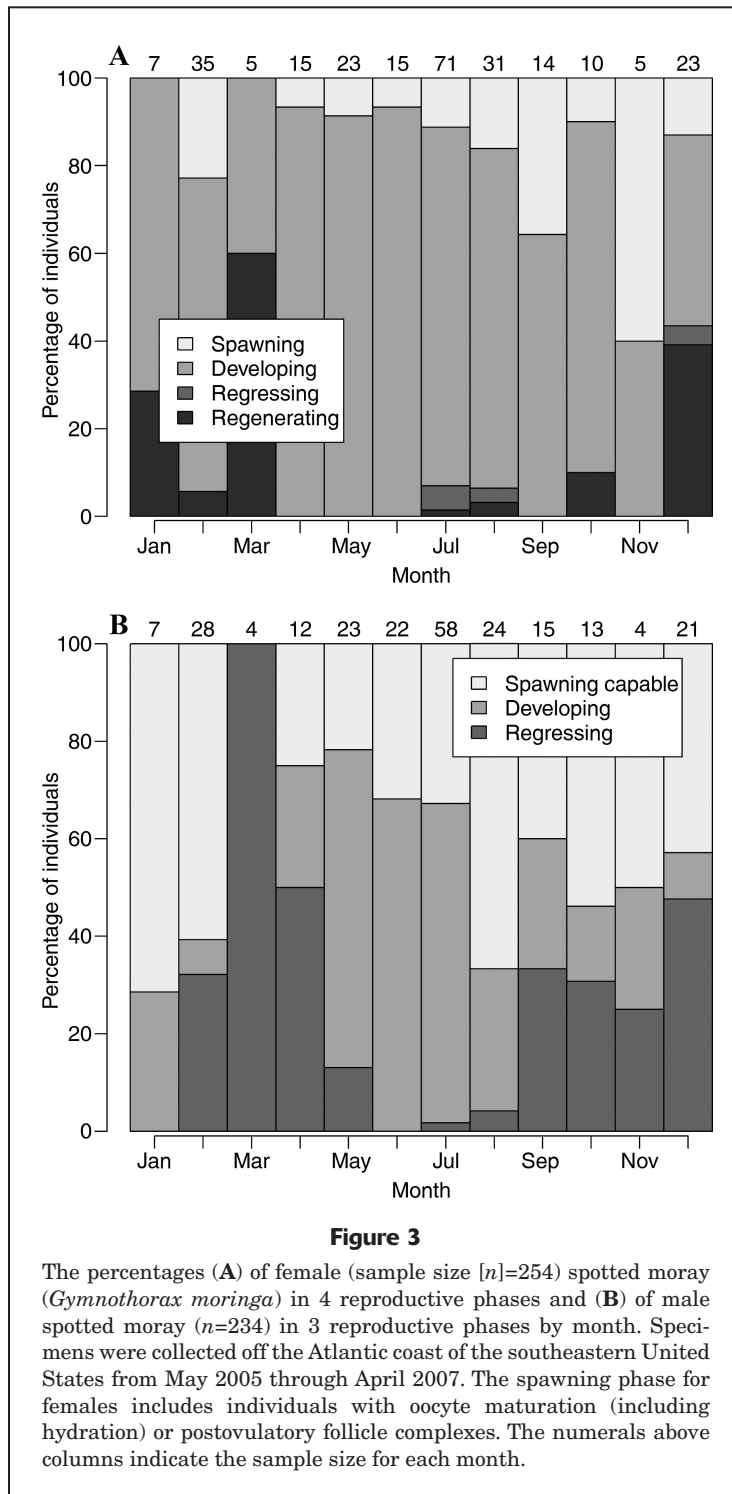
of the medial surface. Most histological sections from the second individual, which had a length of 1032 mm TL and an age of 18 years, had early developing testicular tissue with 10–15 oocytes, at development stages ranging from the primary growth stage to the mid-to-late vitellogenic stage, scattered throughout (Fig. 5C).

## Discussion

The TLs of 91 specimens collected for this study exceeded the maximum recorded size of 1025 mm TL (Böhlke et al., 1989) by up to 242 mm, indicating that this species attains a considerably greater size than has been previously reported. More interesting, however, was the difference in size between sexes. Males attained lengths over 1100 mm TL more frequently than females and were significantly heavier in all length classes  $\geq 900$  mm TL. The greater mass at length for males indicates sexual dimorphism in this species. Although not quantified beyond overall mass, males over ~1000 mm TL could be distinguished from females externally because the head of the males had a bulkier, more muscular appearance. In studies of another moray species, the Mediterranean moray (*Muraena helena*), males of that species also were heavier at length than females, indicating this difference between sexes may be common among moray species (Matić-Skoko et al., 2011; Sallami et al., 2016). The larger size of the males could be related to aggressive behavior between males during spawning events as has been observed in 2 species of *Gymnothorax* (Loh and Chen, 2018).

The weight–length relationship of the spotted moray in our study had a greater weight increase per unit of length than that for a population off the coast of Brazil ( $b=3.07$ ) (Macieira and Joyeux, 2009), but this difference is likely due to the smaller size of the specimens examined (90–641 mm TL) in comparison to the specimens in our study. Overall, the weight–length relationships of other moray species, the green moray (*G. funebris*), purple-mouth moray (*G. vicinus*), *M. augusti*, and Mediterranean moray, are similar to that of the spotted moray, with values of the  $b$  parameter for sexes combined ranging from 2.78 to 3.31 (Jiménez et al., 2007; Macieira and Joyeux, 2009; Matić-Skoko et al., 2011; Sallami et al., 2016).

The finding that males attained greater lengths overall and at age than females is supported by results of studies of growth in the Mediterranean moray: Matić-Skoko et al. (2011) and Sallami et al. (2016) found that males had greater  $L_{\infty}$  and  $k$  than females. Although males attained a greater length more frequently than females, they tended to have shorter lifespans. Only 11 of the 52 individuals with ages of 18 years or older were male. Conversely, males numerically dominated the younger age classes: only 23 of the 87 individuals with ages  $\leq 8$  years were female. This result indicates that most females with ages of 8 years or less were too small to be readily caught by the fishing gear used in this study. In general, the younger age (<7 years) and smaller length (<700 mm TL) classes of both sexes were undersampled because of gear selectivity. As a result of the



lack of small specimens, the age and size at maturity for the spotted moray remain unknown. In the studies of 2 moray species similar in size to the spotted moray, the Mediterranean moray and *M. augusti*, 50% maturity was found to have been attained at lengths and ages within the ranges sampled in our study, indicating that the spotted moray may reach maturity earlier than these species; however,

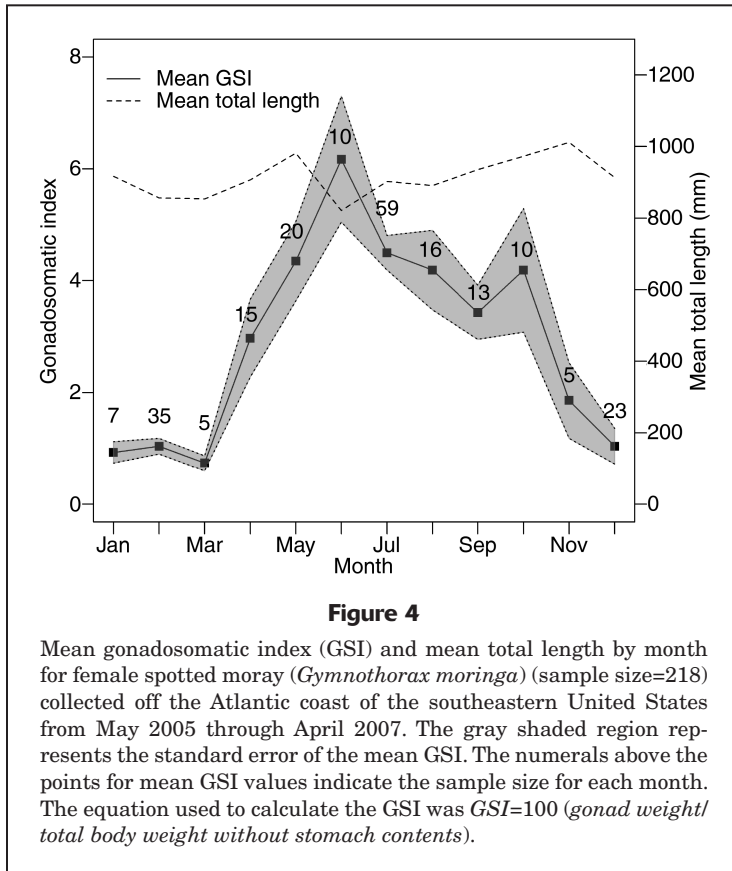
macroscopic examinations largely were used in these studies (Jiménez et al., 2007; Matic-Skoko et al., 2011).

The otoliths were difficult to age because increments often varied in width and occasionally consisted of 2 or more closely spaced increments that were treated as 1 increment, similar to those described in Harris et al. (2004). In addition, the designation of the first increment was problematic. However, it is believed that relatively accurate results were obtained given the high degree of agreement on age (only a difference of 0–1 increments for 80% of specimens) between readers. Although annual formation of otolith increments was not validated in this study, it has been reported for 3 other moray species at similar latitudes (Matic-Skoko et al., 2011; Sallami et al., 2016; Higgins et al., 2017) and is likely true for the spotted moray.

Ages have been estimated for 3 moray species, including the California moray (*G. mordax*) (Higgins et al., 2017), *M. augusti* (Jiménez et al., 2007), and Mediterranean moray (Jiménez et al., 2007; Matic-Skoko et al., 2011; Sallami et al., 2016). The maximum ages determined in these studies were 12 years for *M. augusti*, 15 years for the Mediterranean moray, and 22 years for the California moray. In addition, an individual California moray at the Steinhart Aquarium, in San Francisco, California, lived for 29 years in captivity (Tucker<sup>3</sup>), indicating that the maximum age of 23 years for the spotted moray estimated in our study is reasonable. No other studies have noted a difference between sexes in maximum age or age distribution.

The spotted moray appears capable of spawning throughout the year with reproductive activity lowest during winter and early spring. Histological and GSI data indicate that most females begin spawning between April and June and continue to spawn in batches through the summer into fall. Estimates of spawning intervals indicate that females were capable of spawning approximately once per month. Michael (1998) reported that a captive specimen of the spotted moray expelled eggs “several times” over a 6-month period. Although this observation is not precise, it indicates that the estimates of spawning frequency obtained in our study are reasonable. Results from studies in which the spawning seasonality of moray species has been examined by using GSIs indicate that timing varies by species; however, the length of the period of elevated GSI values (~6 months) appears consistent across studies, including the study described herein (Jiménez et al., 2007; Lucano-Ramírez et al., 2008; Matic-Skoko et al., 2011; Sallami et al., 2016).

<sup>3</sup> Tucker, T. 2005. Personal commun. Steinhart Aquarium, 55 Music Concourse Dr., San Francisco, CA 94118.



**Figure 4**

Mean gonadosomatic index (GSI) and mean total length by month for female spotted moray (*Gymnothorax moringa*) (sample size=218) collected off the Atlantic coast of the southeastern United States from May 2005 through April 2007. The gray shaded region represents the standard error of the mean GSI. The numerals above the points for mean GSI values indicate the sample size for each month. The equation used to calculate the GSI was  $GSI=100 \text{ (gonad weight/total body weight without stomach contents)}$ .

The complete lack of early POCs (<12 h old) indicates that the spotted moray probably spawns in the early evening, given that all fishery-independent and most fishery-dependent sampling occurred between sunrise and sunset. This notion is supported by the limited observations of moray spawning behavior, which has been reported to occur around sunset (Moyer and Zaiser, 1982; Ferraris, 1985). Both group spawning and pair spawning have been noted for species of *Gymnothorax* (Moyer and Zaiser, 1982; Ferraris, 1985; Loh and Chen, 2018). Our data provide no evidence for spawning aggregations because individuals in different reproductive phases occurred in the same catch; therefore, pair spawning is the more likely behavior for the spotted moray. Individuals capable of spawning (imminent or recently spawned) were captured over a range of depths and geographical locations, indicating that they likely do not migrate to spawning sites but instead spawn on the reefs they inhabit, a theory that is also supported by limited observations of moray reproductive behavior (Moyer and Zaiser, 1982; Thresher, 1984; Ferraris, 1985). In addition, there is no evidence from our study that sexes segregated by depth, and both sexes were frequently caught at the same locations and even within the same trap.

The occurrence of 2 intersex individuals in this study raises the question of whether the spotted moray is a hermaphroditic species. Both sequential and simultaneous hermaphroditism has been noted within the family Muraenidae, with some examples of protogyny noted within the genus

*Gymnothorax* (Fishelson, 1992). However, the gonad morphology of the 2 intersex individuals differed substantially from one another, with one having primary growth oocytes on the periphery of testicular tissue and the other having scattered individual oocytes of various stages embedded within testicular tissue. This difference in gonad morphology as well as the rarity of intersex specimens indicates that these 2 spotted moray may represent aberrant individuals (Sadovy and Shapiro, 1987). Until further evidence is available, the spotted moray should be considered functionally gonochoristic.

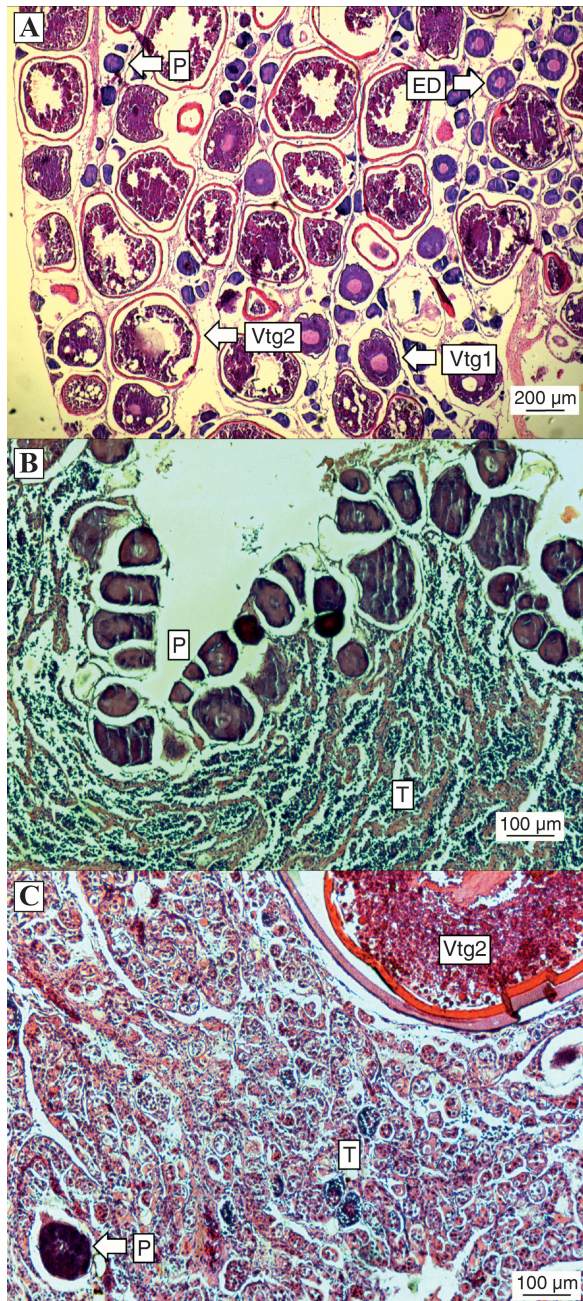
## Conclusions

The results of this study indicate that spotted moray living off the Atlantic coast of the southeastern United States can reach at least 23 years of age, with females living longer on average than males. They also display sexual dimorphism in size, with males reaching greater lengths more frequently and having greater mass at a given length than females at sizes >900 mm TL. Results indicate that the spotted moray is gonochoristic and capable of spawning throughout the year off the southeastern United States. Females reach peak reproductive activity during the summer, and both sexes experience a lull in reproductive activity in March. The spotted moray appears to be a batch spawner, with females spawning approximately monthly. Two intersex specimens were collected, but they appear to be aberrant individuals and not indicative of hermaphroditism. This study has resulted in the first published results on several aspects of the life history of the spotted moray, information that may aid in understanding the role of this species in reef ecosystems of the western Atlantic Ocean. Additionally, in no other studies have both age and reproduction of a *Gymnothorax* species been examined; therefore, the data from this study can be used for further comparisons among other moray species.

## Resumen

Entre mayo de 2005 y abril de 2007 se obtuvieron especímenes de morena manchada (*Gymnothorax moringa*) de fuentes dependientes e independientes de la pesca en la costa atlántica del sureste de Estados Unidos. Se colectaron un total de 491 individuos, cuya longitud total (LT) oscilaba entre 556 y 1267 mm; las estimaciones de edad oscilaban entre 4 y 23 años, con una media de 12.3 años. Las hembras alcanzaron mayores edades y tuvieron una edad media significativamente mayor que los machos. La longitud de los machos fue mayor que la de las hembras en todas las edades, pero sólo fue significativamente mayor en las edades de 9, 10, 12 y 17 años. En las clases de longitudes mayores a 900 mm LT, los machos fueron significativamente más pesados que las hembras. La proporción sexual entre





**Figure 5**

Images of histological sections of gonad tissues of spotted moray (*Gymnothorax moringa*) collected off the Atlantic coast of the southeastern United States. (A) This section from an 11-year-old female (886 mm in total length [TL]) collected in April 2006 shows oocytes in multiple stages of development. (B) In this section from a 12-year-old specimen (881 mm TL) sampled in August 2005, inactive ovarian tissue is visible at the periphery of an otherwise normal testis. (C) This section from an 18-year-old spotted moray (1032 mm TL) collected in July 2006 shows oocytes in 2 stages scattered within an early developing testis. P=primary growth oocyte; ED=early developing oocyte with cortical alveoli; Vtg1=oocyte in primary vitellogenesis; Vtg2=oocyte in secondary vitellogenesis; T=testicular tissue.

machos y hembras de 1:1.09 no difiere significativamente de 1:1. Todos los especímenes fueron examinados histológicamente y ninguno era inmaduro. Las hembras reproductoras se colectaron desde finales de abril hasta febrero, y las estimaciones de la periodicidad de desove (24–31 d) indican que una hembra podría desovar hasta 12 veces durante una temporada de desove. Los machos estaban en condición reproductiva durante todo el año, con la excepción de marzo, cuando todos los individuos estaban en condición regresiva. Dos individuos tenían tanto tejido testicular como ovárico; sin embargo, las pruebas histológicas indican que esta especie es ciertamente gonocórica.

### Acknowledgments

We thank A. Williams and the late O. Pashuk for assistance with gonad histology, the crew of the RV *Palmetto* for assistance in fishery-independent sample collection, and the crews of the commercial FVs *Amy Marie*, *Ken R. Hair*, *Lady Madeline*, *Malachi III*, and *Searider* for fishery-dependent collection of samples. This research was funded through MARMAP Program contract 50WCNF106007. This paper is contribution no. 582 of the Grice Marine Lab, College of Charleston, and contribution no. 856 of the South Carolina Marine Resources Center.

### Literature cited

- Abrams, R. W., and M. W. Schein.  
1986. Individual movements and population density estimates for moray eels on a Caribbean coral reef. *Coral Reefs* 5:161–163. [Crossref](#)
- Abrams, R. W., M. D. Abrams, and M. W. Schein.  
1983. Diurnal observations on the behavioral ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean coral reef. *Coral Reefs* 1:185–192. [Crossref](#)
- Bardach, J. E., and L. A. Lowenthal.  
1961. Touch receptors in fishes with special reference to the moray eels (*Gymnothorax moringa* and *G. vicinus*). *Copeia* 1961:42–46. [Crossref](#)
- Bardach, J. E., H. E. Winn, and D. W. Menzel.  
1959. The role of the senses in the feeding of the nocturnal reef predators *Gymnothorax moringa* and *G. vicinus*. *Copeia* 1959:133–139. [Crossref](#)
- Böhlke, E. B.  
2002. Muraenidae. In *The living marine resources of the Western Central Atlantic*. Vol. 2: Bony fishes part 1 (Acipenseridae to Grammatidae). FAO species identification guide for fishery purposes and Am. Soc. Ichthyol. Herpetol. Spec. Publ. 5. (K. E. Carpenter, ed.), p. 700–718. FAO, Rome.
- Böhlke, J. E., and C. G. G. Chaplin.  
1968. Fishes of the Bahamas and adjacent tropical waters, 771 p. Livingstone Publ., Wynnewood, PA.
- Böhlke, E. B., J. E. McCosker, and J. E. Böhlke.  
1989. Family Muraenidae. In *Fishes of the western North Atlantic*. Part 9, Vol. 1: orders Anguilliformes and Saccopharyngiformes, p. 104–206. Mem. Sears Found. Mar. Res., Yale Univ., New Haven, CT.
- Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri.  
2011. A standardized terminology for describing reproductive development in fishes. *Mar. Coast. Fish.* 3:52–70. [Crossref](#)

- Carr, M. H., and M. A. Hixon.  
1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar. Ecol. Prog. Ser.* 124:31–42. [Crossref](#)
- Collins, M. R.  
1990. A comparison of three fish trap designs. *Fish. Res.* 9:325–332. [Crossref](#)
- Dalgaard, P.  
2002. *Introductory statistics with R*, 267 p. Springer-Verlag, New York.
- Ferraris, C. J., Jr.  
1985. Redescription and spawning behavior of the muraenid eel *Gymnothorax herrei*. *Copeia* 1985:518–520. [Crossref](#)
- Fishelson, L.  
1992. Comparative gonad morphology and sexuality of the Muraenidae (Pisces, Teleostei). *Copeia* 1992:197–209. [Crossref](#)
- Harris, P. J., D. M. Wyanski, and P. T. P. Mikell.  
2004. Age, growth, and reproductive biology of blueline tilefish along the southeastern coast of the United States, 1982–1999. *Trans. Am. Fish. Soc.* 133:1190–1204. [Crossref](#)
- Higgins, B. A., D. Pearson, and R. S. Mehta.  
2017. El Niño episodes coincide with California moray *Gymnothorax mordax* settlement around Santa Catalina Island, California. *J. Fish Biol.* 90:1570–1583. [Crossref](#)
- Hunter, J. R., and S. R. Goldberg.  
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. *Fish. Bull.* 77:641–652.
- Hunter, J. R., B. J. Macewicz, and J. R. Sibert.  
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. *Fish. Bull.* 84:895–903.
- Jiménez, S., S. Schönhuth, I. J. Lozano, J. A. González, R. G. Sevilla, A. Diez, and J. M. Bautista.  
2007. Morphological, ecological, and molecular analyses separate *Muraena augusti* from *Muraena helena* as a valid species. *Copeia* 2007:101–113.
- Le Cren, E. D.  
1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20:201–219. [Crossref](#)
- Loh, K.-H., and H.-M. Chen.  
2018. Pre-spawning snout-gripping behaviors of *Gymnothorax pictus* and *Gymnothorax thyrsoideus* (Muraenidae) in captivity. *J. Mar. Sci. Technol.* 26:111–116. [Crossref](#)
- Lucano-Ramírez, G., S. Ruiz-Ramírez, J. A. Rojo-Vázquez, and G. González-Sansón.  
2008. Reproducción de la morena, *Gymnothorax equatorialis* (Pisces: Muraenidae) en Jalisco y Colima, México. *Rev. Biol. Trop.* 56:153–163.
- Macieira, R. M., and J.-C. Joyeux.  
2009. Length-weight relationships for rockpool fishes in Brazil. *J. Appl. Ichthyol.* 25:358–359. [Crossref](#)
- Matić-Skoko, S., P. Tutman, M. Petrić, D. Skaramuca, D. Đikić, D. Lisičić, and B. Skaramuca.  
2011. Mediterranean moray eel *Muraena helena* (Pisces: Muraenidae): biological indices for life history. *Aquat. Biol.* 13:275–284. [Crossref](#)
- Michael, S. W.  
1998. *Reef fishes: a guide to their identification, behavior, and captive care*, vol. 1, 624 p. Microcosm Ltd., Shelburne, VT.
- Moyer, J. T., and M. J. Zaiser.  
1982. Reproductive behavior of moray eels at Miyake-jima, Japan. *Jpn. J. Ichthyol.* 28:466–468. [Crossref](#)
- R Core Team.  
2020. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. [Available from [website](#), accessed March 2020.]
- Randall, J. E.  
1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5:665–847.
- Sadovy, Y., and D. Y. Shapiro.  
1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* 1987:136–156. [Crossref](#)
- Sallami, B., P. Béarez, and M. Ben Salem.  
2016. Age and growth of *Muraena helena* (Muraenidae) from the north coast of Tunisia. *Cybiurn* 40:155–161. [Crossref](#)
- Smith, G. B.  
1976. Ecology and distribution of eastern Gulf of Mexico reef fishes. *Fla. Dep. Nat. Resour., Mar. Res. Lab., Fla. Mar. Res. Publ.* 19, 78 p.
- Thresher, R. E.  
1984. Eels (Anguilliformes). In *Reproduction in reef fishes*, p. 12–20. T. F. H. Publ., Neptune City, NJ.
- Wyanski, D. M., D. B. White, and C. A. Barans.  
2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. *Fish. Bull.* 98:199–218.
- von Bertalanffy, L.  
1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.* 10:181–213.
- Yip, L.-L.  
1971. Toxicity of moray eels (*Gymnothorax*) in Hong Kong. *Copeia* 1971:175. [Crossref](#)
- Young, R. F., and H. E. Winn.  
2003. Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. *Copeia* 2003:44–55.