Abstract—The modern fishery for Tilefish (*Lopholatilus chamaeleonticeps*) developed during the 1970s, offshore of southern New England, in the western North Atlantic Ocean. The population quickly became over exploited, with documented declines in catch rates and changes in demographic traits. In an earlier study, median size at maturity (L_{50}) of males declined from 62.6 to 38.6 cm fork length (FL) and median age at maturity (A_{50}) of males declined from 7.1 to 4.6 years between 1978 and 1982. As part of a cooperative research effort to improve the data-limited Tilefish assessment, we updated maturity parameter estimates through the use of an otolith aging method and macroscopic and microscopic evaluations of gonads. The vital rates for this species have continued to change, particularly for males. By 2008, male L_{50} and A_{50} had largely rebounded, to 54.1 cm FL and 5.9 years. Changes in female reproductive schedules were less variable among years, but the smallest L_{50} and youngest A_{50} were recorded in 2008. Tilefish are dimorphic, where the largest fish are male, and male spawning success is postulated to be socially mediated. These traits may explain the initial rapid decline and the subsequent rebound in male L_{50} and A_{50} and less dramatic effects on females. Other factors that likely contribute to the dynamics of maturity parameter estimates are the relatively short period of overfishing and the amount of time since efforts to rebuild this fishery began, as measured in numbers of generations. This study also confirms the gonochoristic sexual pattern of the northern stock, and it reveals evidence of age truncation and relatively high proportions of immature Tilefish in the recent catch.

Changes in size and age at maturity of the northern stock of Tilefish (*Lopholatilus chamaeleonticeps*) after a period of overfishing

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As the largest malacanthid, growing to more than 1 m and 25 kg, the Tilefish (*Lopholatilus chamaeleonticeps*) is a valuable fishery species, often marketed as "golden tilefish." The Tilefish ranges from New England to the Gulf of Mexico and into the Caribbean Sea (Freeman and Turner[1]; Dooley, 1978), where 2 stocks have been identified, north or south of the Virginia and North Carolina border (Kitts et al., 2007). Northern Tilefish are morphologically and genetically distinct from southern Tilefish (Katz et al., 1983). Although individuals can range as far north as Nova Scotia, Tilefish are generally in low abundance in the Gulf of Maine (Able, 2002). Fishing on the northern stock is concentrated from Veatch Canyon, on the southern flank of Georges Bank off Massachusetts, to the Hudson Canyon off the coast of New Jersey (Grimes et al., 1980; Grimes and Turner, 1999; Kitts et al., 2007). Recent (2007–11) Tilefish landings north of the Caroli-

nas were valued at $4.2–5.6 million annually.[2]

Unlike some historic fisheries of New England (e.g., Atlantic Cod [*Gadus morhua*], American Shad [*Alosa sapidissima*]; Lear, 1998), the Tilefish fishery developed only recently, and it had a most inauspicious start. The Tilefish was described in 1879 from fishery catches off New England (Goode and Bean, 1879). Occasional catches followed, but, in 1882, Tilefish became widely known because they constituted the largest single kill of vertebrates ever recorded. Tilefish are stenothermal, occurring along a narrow band of warm water, 9–14°C, at the continental shelf-slope break (Able et al., 1982; Grimes et al., 1986; Grimes and Turner, 1999); Marsh et al. (1999) assembled the evidence that this mass mortality was caused by intrusion of the Labrador Current into these outer shelf habitats. After a decade of no reported landings and speculation that this species had become extirpated in northern waters, landings resumed in the 1890s. Specific

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[1] Freeman, B. L., and S. C. Turner. 1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean. NOAA Fisheries, Sandy Hook Lab. Tech. Ser. Rep. no. 5, 41 p. [Available from http://www.nefsc.noaa.gov/publications/series/shtsr/shltsr5.pdf, accessed October 2012.]

[2] NOAA Fisheries, Annual Commercial Landings Statistics. http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html, accessed December 2012.

efforts to popularize Tilefish as a food fish resulted in record-high landings (4500 metric tons [t]) in 1916 (Freeman and Turner, 1977; Grimes and Turner, 1999). These efforts had only modest market success, and, except when prices were high, as in the 1920s and 1950s, landings rarely exceeded 1000 t until the 1970s (Fig. 1).

Events in the 1970s proved that persistent annual landings that exceeded 1000 t were unsustainable. Beginning in 1971, landings rose rapidly from <100 t to nearly 4000 t within a decade (Fig. 1). Landings remained high in the 1980s but were accompanied by evidence of overexploitation: decreased fish density, lower catch rates, smaller maximum size, and higher mortality (Grimes et al., 1980; Turner et al., 1983; Grimes et al., 1988; Grimes and Turner, 1999). By the 1990s, only a subset of the fleet remained dedicated to fishing for Tilefish in the northeastern United States, and a 2001 fishery management plan capped annual landings at 905 t (Kitts et al., 2007).

The northern Tilefish stock is now considered largely rebuilt but uncertainty in the stock assessment hampers confidence in stock status and projections (NEFSC[3]). There is, for example, no fishery-independent index of abundance, and monitoring of biological data has been infrequent. Comparisons of assessment model results indicate that the presence of large Tilefish, and the biomass estimate in general, is dependent on periodically strong year classes, such as the 1970 and 1973 year classes and most recently the 1993 and 1999 year classes (Turner, 1986; NEFSC[3]). High levels of exploitation during the 1970s and 1980s also may have altered the demographics of the population. Vidal (2010) reports a maximum age of Tilefish of 25 years, much younger than the maximum age of 46 years reported by Turner (1986), indicating that the population has not recovered from age truncation that occurred during the period of high exploitation.

This study updates several aspects of Tilefish life history from samples collected in cooperation with the commercial fishery. We began by revisiting the question of whether Tilefish are gonochoristic at the northern extent of their range (Dooley, 1978; Grimes et al., 1988). It has been proposed but not proven that Tilefish are functional hermaphrodites (Sadovy de Mitcheson and Liu, 2008); therefore, we examined and clarified the gonochoristic sexual pattern of the northern stock with gonad histology.

Ages were estimated with an otolith method, and age and size at maturity were calculated for both sexes to reexamine sexual dimorphism and temporal dynamics of
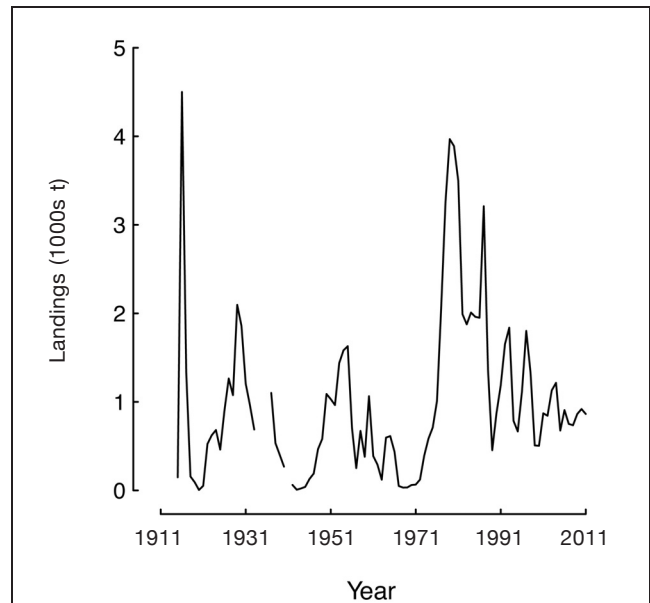
[3] NEFSC (Northeast Fisheries Science Center). 2009. Assessment of golden tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic-Southern New England region. *In* 48th northeast regional stock assessment workshop (48th SAW) assessment report, p. 11–180. Northeast Fish. Sci. Cent. Ref. Doc. 09-15 [Available from http://www.nefsc.noaa.gov/publications/crd/crd0915/pdfs/tilefish.pdf, accessed February 2013.]

Figure 1

Tilefish (*Lopholatilus chamaeleonticeps*) landings from Virginia to New England for the period of 1915–2011 in thousands of metric tons (t). Landings from 1915 to 2008 are reported in NEFSC.[3] Landing data for 2009–11 are from a NOAA Fisheries database (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html, accessed December 2012).

maturity ogives. Male Tilefish grow faster and achieve a larger maximum size than females (Turner et al., 1983). Sexual dimorphism also is observed with respect to maturity: males develop larger predorsal adipose flaps than females at maturity, and males mature at older ages and larger sizes than do females (Grimes et al., 1988). Grimes et al. (1988) made 2 other important conclusions with respect to measurement of maturity: 1) males show evidence of spermiation, as detected by gonad histology, 1–2 years earlier than macroscopic ripening of the gonad, indicating that males delay spawning for a couple of years after this initial sign of maturity, and 2), from 1978 to 1982, male age at spawning declined about 2–3 years in association with high rates of exploitation and reduced population density. The effect was so extreme that, by 1982, males matured at a younger age than females (Fig. 2).

The topic of dramatic shifts in size and age at maturity was still controversial in the 1980s (Beacham, 1987), but such dynamic metrics have now been associated with overexploitation in Tilefish (Grimes et al., 1988) and other fish stocks (Trippel, 1995; Wright et al., 2011). To continue this line of inquiry, we compared our results with the benchmark values reported by Grimes et al. (1988). Although rapid responses by maturity traits to changes in mortality can be adaptive at the

may thereby cause fishing-induced evolution can be a grave concern in terms of rebuilding fisheries to be sustainable (Conover, 2000; Heino and Dieckmann, 2008; Enberg et al., 2011).

Materials and methods

Field collections

During 2 trips by commercial fishing vessels targeting Tilefish in 2008, 688 Tilefish were sampled on 16 different days of normal longline operations. The first trip occurred in June, offshore of southern New England, where fish were collected between 70° and 72°W at depths of 104–280 m (Fig. 3). The second trip occurred in July, offshore of southern New England and farther south, where fish were collected between 70° and 74°W at depths of 119–283 m (Fig. 3). This geographic coverage overlapped all the major fishing areas by the Tilefish fishery north of the Carolinas (Turner et al., 1983; Kitts et al., 2007).

Fish were identified on the basis of taxonomic characters summarized by Able (2002). Fork length (FL) was measured to the nearest centimeter, and sex and maturity were determined macroscopically for 421 males and 267 females. Macroscopic determination of maturity followed Idelberger (1985; Table 1), which conforms to the standard maturity classifications used in the region (Burnett et al., 1989). To reduce cluster sampling in high-density areas, especially where fish from the same longline set may have had similar age or reproductive status, at least one fish of each sex was sampled for each 1-cm interval (Wigley et al., 1999; Helle and Pennington, 2004). This sampling strategy resulted in a broad range of fish sizes that was similar to the size composition in the landings, and, if anything, this strategy increased the number of larger, older fish to aid in fitting the maturity data to a model (Fig. 4).

Gonad histology

To confirm macroscopic evaluations of sex and maturity, gonad tissue was taken from 157 males and 67 females and fixed in 10% buffered formalin (Fig. 4B). Fixed tissue was prepared according to standard paraffin embedding techniques, stained with hematoxylin, and counterstained with eosin. Histological sections collected from 3 locations (anterior, medial and posterior) within the ovary lobe for 15 females were initially examined, but there was no effect of location on the most advanced stage of oocyte development, as also reported by Erickson et al. (1985); therefore, no further attention was given to the intragonad location.

The sexual pattern, meaning the functional expression of sexuality by individuals, was characterized on the basis of gonad histology. Morphological features noted were the presence of a remnant ovarian lumen
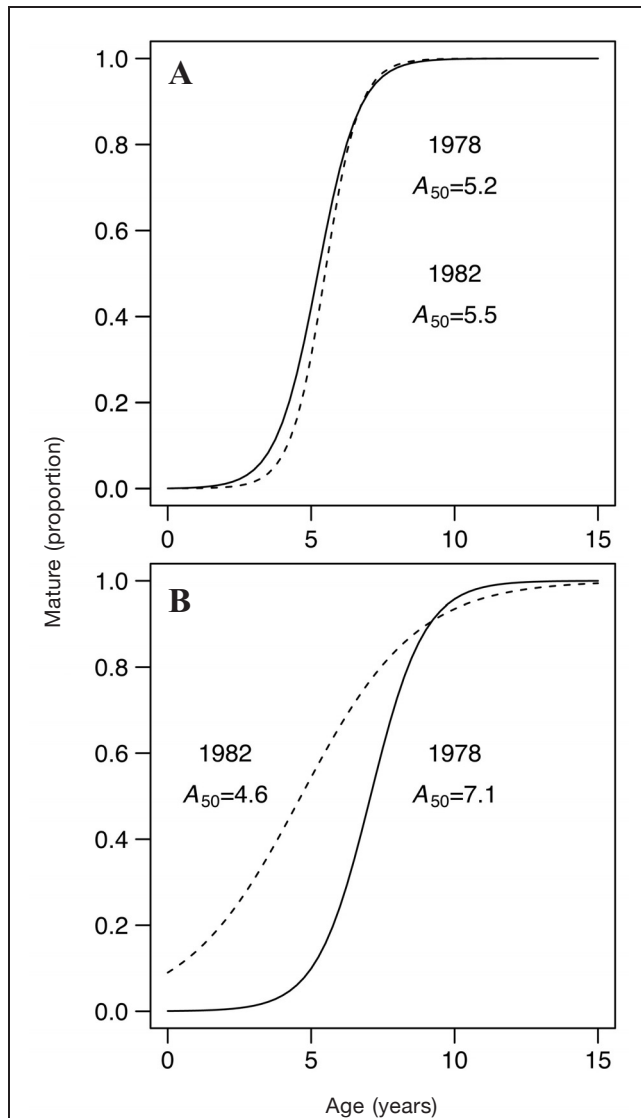

Figure 2

Maturity ogives for (**A**) female and (**B**) male Tilefish (*Lopholatilus chamaeleonticeps*) in 1978 (solid line) and 1982 (dashed line), at the height of the expansion of the modern fishery. Maturity was determined by macroscopic appearance of the gonad. Raw data were extracted from Grimes et al. (1988: tables 5 and 6). For model fitting, a generalized linear model and the logit link function in R software were used. The predicted curves together with the median age at maturity (A_{50}) are depicted by sex and year.

individual level, such responses can signal a decline in fishery yields and reproductive potential at the population level (Law, 2000; Fitzhugh et al., 2012; Cooper et al., 2013). Therefore, such data can be important to monitor and include in stock assessments (Caselle et al., 2011; Collins and McBride, 2011). In particular, the possibility that fishing selects for a certain genotype and
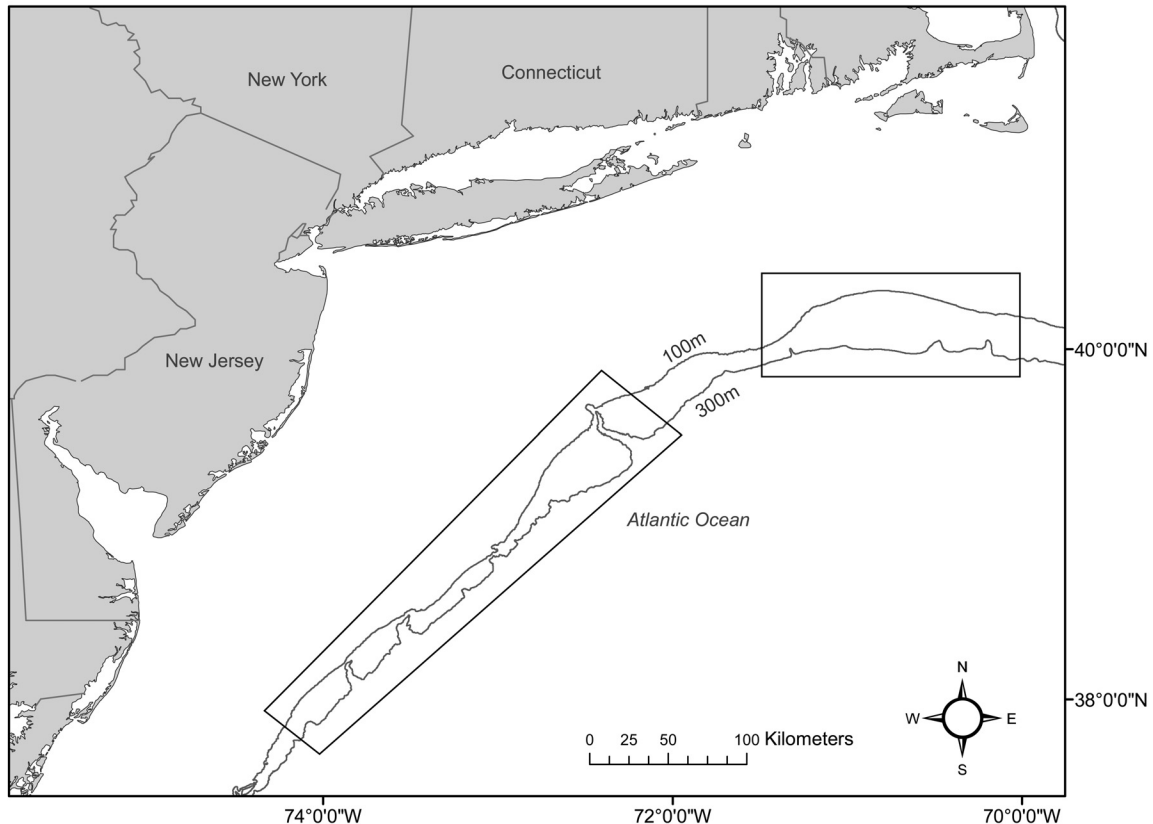
Figure 3

Map of areas where Tilefish (*Lopholatilus chamaeleonticeps*) were collected between the 100 and 300 m isobaths off southern New England in 2008 for this study to update the maturity schedules of this species. Fish were sampled during 2 trips by commercial fishing vessels targeting Tilefish: in June to the east (right polygon) and in July throughout the region (both polygons). The exact locations are not plotted to maintain confidentiality for commercial fishing operations.

in testes or a mix of ovarian and seminiferous tissue in a single gonad, the latter of which was reported by Grimes et al. (1988) and Erickson and Grossman (1986) for functional males. Although we examined morphology, our interpretation of sexual pattern was made on the basis of functionality, specifically whether gametogenesis was complete for both ovarian and seminiferous tissue during an individual's lifetime (Sadovy de Mitcheson and Liu, 2008). The existence of gonads that contained nonfunctional tissue of the opposite sex (i.e., intersex) and evidence that individuals matured and spawned as only one sex were considered to be a gonochoristic rather than a hermaphroditic trait. The infrequent presence of isolated oocytes in seminiferous tissue was not considered a bisexual condition because such oocytes also did not confer any function as a female (Sadovy and Domeier, 2005).

Because sampling occurred during the spawning season, the histological criterion for female maturity was the presence of secondary oocytes as the most advanced oocyte stage. Secondary oocytes were defined as germ cells that showed evidence of vitellogenin uptake

and transformation of lipoprotein yolk in the cytoplasm (Grier et al., 2009). Cortical alveolar-stage oocytes as the most advance stage were uncommon, and we comment on their presence and interpretation in the *Results* section. Male maturity was marked by the presence of spermatozoa in the spermatogenic lobules.

Age determination

Sagittal otoliths were extracted at sea and stored dry. These otoliths were thin-sectioned through the core according to standard methods with a low-speed, diamond-blade saw. Marginal increment analysis indicated that annuli are laid down by June of each year (Turner et al., 1983); therefore, given the timing of our collections, the number of complete bands equaled the age of the fish, in years.

Otoliths from 100 Tilefish used in Steve Turner's aging study (hereafter, called the *reference collection*) were used to train and calibrate the primary age reader (T. Vidal) in relation to the age-assignment practices reported in Turner et al. (1983) and Turner (1986).

Table 1

Macroscopic criteria for classifying maturity of Tilefish (*Lopholatilus chamaeleonticeps*), modified from Idelberger (1985: table 1), with references to new microscopic observations from gonad histology of Tilefish sampled in 2008 off southern New England for this study.

Maturity class	Description of ovary	Description of testes
Immature	Ovaries are small and transparent, becoming increasingly yellowish, rounded, and veined at the surface as fish nears maturity. Gonads compose <0.5% of body weight.	Testes consist of very narrow, transparent bands of tissue, composing <0.05% of body weight. Histological sections reveal isolated oocytes in a low percentage of young males.
Developing	Ovaries are firm, bulbous, yellow to light orange in color, and 0.5–2.0% of body weight. Vitellogenic (yolked) oocytes (0.3–0.7 mm in diameter) are visible through the gonad wall.	Gonads become opaque white, increasing modestly in size (0.03–0.12% of body weight).
Ripe	Enlarged gonads (1.0–5.0% of body weight) become lobular and have a speckled appearance. A homogenous mixture of vitellogenic and mature (hydrated; 0.7–1.0 mm) oocytes are evident through the gonad wall.	Further enlarged (0.1–0.2% of body weight) although still relatively small organs; long, flattened, and opaque milky white with phosphorescent sheen.
Running ripe	Ovaries are turgid and compose 5.0–10.0% of body weight. Gonads have a granular yellow appearance from vitellogenic oocytes in the lamellae and a transparent lumen containing hydrated oocytes, visible ventrally. Eggs (~1.2 mm) flow freely from the vent without any or only light pressure to the abdomen.	Sperm released with light abdominal pressure was diagnostic of this maturity class, although it also was observed rarely, even among the largest fish.
Spent	Gonads are reddish-orange, flaccid, and reduced to 0.5–1.0% of body weight.	Slightly flaccid and reduced to 0.04–0.07% of body weight.
Resting	Ovaries are uniformly yellow in color, becoming firm, composing 0.5–1.0% of body weight.	Indistinguishable from developing testes.

Training included testing for aging precision (i.e., repeatability of age assignment by different readers to the same otolith). Precision was first measured by percent agreement,

$$Percent\ agreement = 100 \times \frac{A}{N},\qquad(1)$$

where A = the number of replicate ages in agreement (of 2); and
N = the total number of fish aged.

Precision also was evaluated with Chang's coefficient of variation (CV; Chang, 1982):

$$CV = 100 \times \frac{1}{N} \sum_{j=1}^{N} \frac{\sqrt{\sum_{i=1}^{2} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j},\qquad(2)$$

where N = the total number of fish aged;
X_{ij} = the ith age determination (i.e., of 2) of the jth fish; and
X_j = the mean age estimate of the jth fish.

Bowker's test was used to detect departures from symmetry between the new reader and the reference collection, with the formulation of Hoenig et al. (1995):

$$\chi^2 = \sum_{i=1}^{m-1} \sum_{j=i+1}^{m} \frac{(n_{ij} - n_{ji})^2}{n_{ij} + n_{ji}},\qquad(3)$$
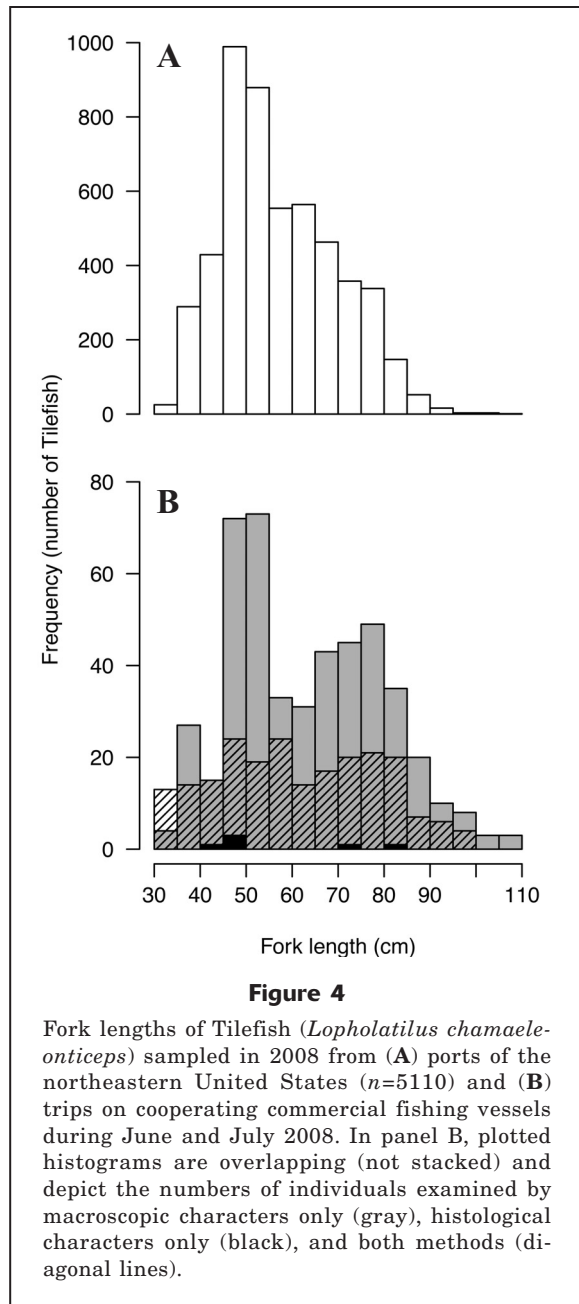
where m = the maximum age in the data set; and
n_{ij} = the number of fish in the ith row and jth column, etc.

These precision tests also were used to evaluate repeatability of multiple readings by the primary age reader. In terms of final age assignment, when the first 2 readings from each otolith collected in 2008 disagreed, a third reading was performed. The value that occurred twice was used as the final age (i.e., there were no situations in which the third reading was different from both of the first 2 readings).

Models and analysis

Generalized linear models were programmed with R, vers. 2.15.2[4] (R Core Team, 2012), to estimate parameters of maturity ogives. A full range of immature and mature fish, by size and age, was collected, making parameter estimation straightforward (Trippel and Har-

Figure 4

Fork lengths of Tilefish (*Lopholatilus chamaele-onticeps*) sampled in 2008 from (**A**) ports of the northeastern United States (*n*=5110) and (**B**) trips on cooperating commercial fishing vessels during June and July 2008. In panel B, plotted histograms are overlapping (not stacked) and depict the numbers of individuals examined by macroscopic characters only (gray), histological characters only (black), and both methods (diagonal lines).

vey, 1991). An information-theoretic approach was used to select among full and reduced models; the second-order Akaike's information criterion (AIC$_c$) was used to account for sample sizes in all comparisons.

Model selection began with evaluation of logit, probit, and complementary log-log model fits to FL or age, and histological maturity data, by sex. The logit model was selected because it consistently had a lower or a tied score (<2 ΔAIC$_c$ value) compared with the score of the probit model and a much lower score than that of the complementary log-log model.

The logit-link function was used for selection of full or reduced models (i.e., by sex [logit {mature} ~ FL +

Sex + FL:Sex], method [macroscopic, histological], or year [1978, 1982, 2008]). Model results from 2008, as presented in Tables 2 and 3, are from analyses of individuals with both size and age data. Additional fish were measured for FL only, but inclusion of these fish in the analyses did not substantially change any results. Historic data were extracted from Grimes et al. (1988). Because FLs in Grimes et al. (1988: tables 3 and 4) were pooled by 5-cm bins, when entering their data for analysis, we assigned FL values for each fish as a midpoint value. Grimes et al. (1988: tables 5 and 6) reported older fish as a plus group (i.e., 15+); therefore, we also grouped all fish ≥15 years old together as a plus group to be consistent between studies, but the use of this plus group did not alter any result.

Results

Gonad histology

No seminiferous tissue was evident in any functioning females, but morphologically intersex males, occurring in 2 morphs, were observed (Fig. 5). In the first morph, a lumen was evident but seminiferous tissue arose directly along the gonad wall and no oocytes were present (Fig. 5A). Males with a lumen were common, but their frequency was not quantified because many histological sections were incomplete across the transverse plane and the lumen was relatively small and difficult to recognize in larger testes. The other morph of intersex males appeared as rare, isolated, primary growth oocytes interspersed in continuous seminiferous tissue (Fig. 5B). This morph was observed in 4 young fish, ages 3 or 5, and at least some of the embedded oocytes were visibly degrading. In other males, remnant gaps in seminiferous tissue were evident, indicating that isolated oocytes had been present but were now fully degraded (Fig. 5C).

The immature testis was initially dominated by spermatogonia surrounded by connective tissue, with limited spermatogenesis in the form of spermatocytes and spermatids in crypts surrounded by germinal epithelia (Fig. 5C). As spermatogenesis proceeded, spermatozoa were released into lobules lined with a discontinuous germinal epithelia (i.e., spermiation), signaling physiological maturity (Fig. 5D).

The ovary of immature females was dominated by oocytes at a perinucleolar stage (Fig. 5E). In many females classified as immature, the appearance of organelles (i.e., a Balbiani body) and early formation of cortical alveoli were common in the cytoplasm of the largest primary growth oocytes (Fig. 5F); we considered these traits characteristic of a maturing state (rather than a mature one), where such individuals were only preparing to mature and would not spawn until the following year. Only a single individual had advanced cortical alveoli as the most advanced oocyte stage (Fig. 5G), and 2 other females had only begun
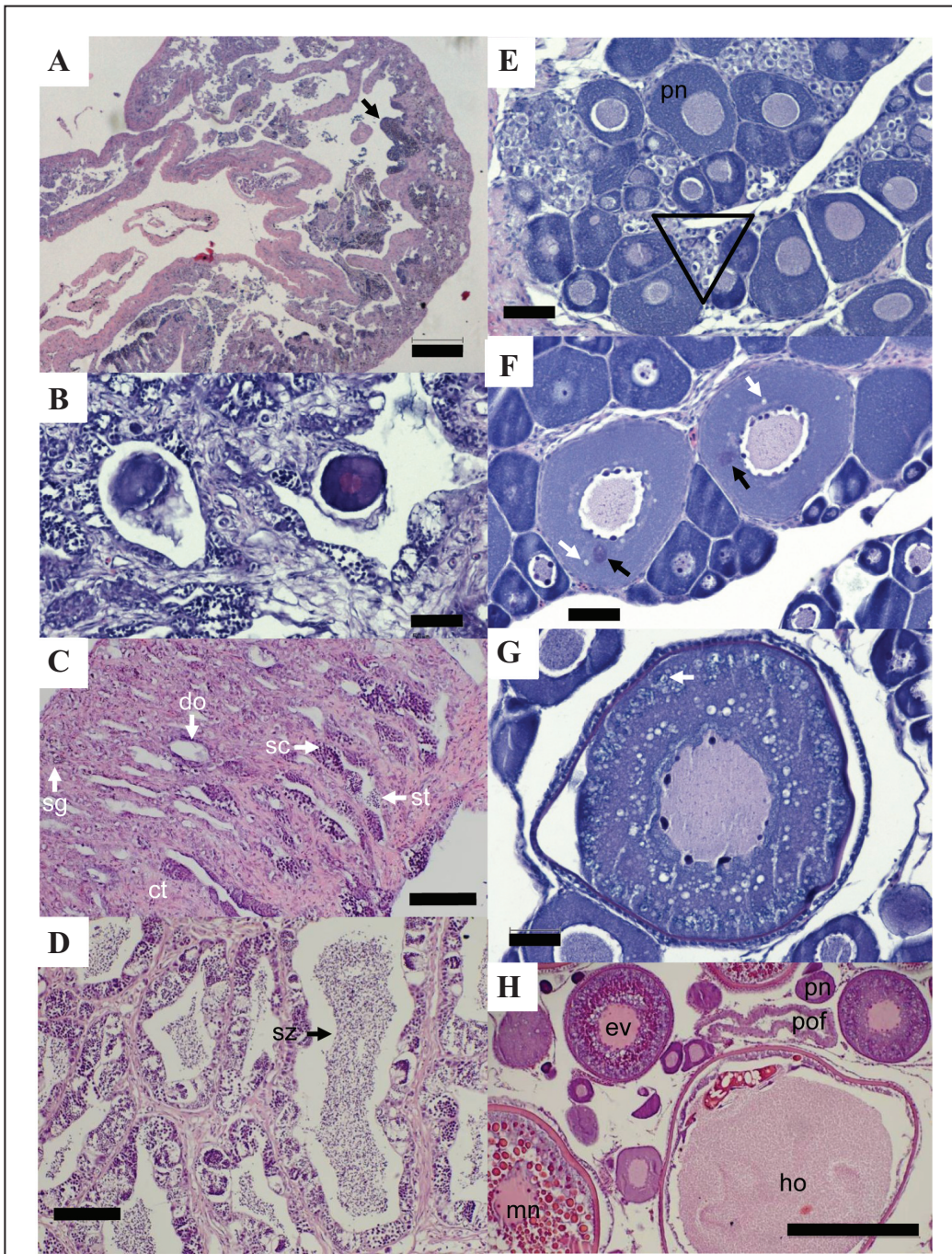
Figure 5

Microphotographs of gonadal tissue of Tilefish (*Lopholatilus chamaeleonticeps*) functional males (left) and females (right): (**A**) a functional male with seminiferous tissue developing directly along a lumen (arrow); (**B**) isolated oocytes, one partially degraded (left) and one intact (right), embedded in seminiferous tissue of a functional male; (**C**) seminiferous tissue of an immature male (ct=connective tissue, sg=spermatogonia, sc=spermatocytes, st=spermatids, do=degraded oocyte [fully degraded, no cell remaining]); (**D**) tissue of a mature (developing) male (sz=spermatozoa); (**E**) ovarian tissue of an immature female (pn=perinucleolar oocyte, triangle=oogonial nest); (**F**) primary growth oocytes, marking the Balbiani body (black arrow) and other inclusions that appear to be precursors to cortical alveoli (white arrow); (**G**) an oocyte with advanced cortical alveoli throughout the cytoplasm (arrow); and (**H**) ovarian tissue of a mature (ripe) female (ev=early vitellogenic oocyte [not fully with yolk], mn=migrating nucleus, ho=hydrated oocyte, pof=postovulatory follicle). Scale bars vary with image: 50 µm (E, F, G, B), 100 µm (C, D), 250 µm (A), and 500 µm (H).

vitellogenesis (not shown; i.e., the most advanced oo-cyte stage was only partially yolked, where the yolk inclusions did not extend from the nucleus to the cho-rion). These 3 fish were young, age 5 or 6, and, if they had been capable of spawning imminently, they evi-dently would have started spawning later than other conspecifics. In comparison, 92% of mature females were already actively spawning, with oocytes that either exhibited migrating nuclei or were in various stages of hydration; postovulatory follicles were ob-served as well (Fig. 5H).

Age determination

Tilefish otoliths are difficult to age, but good results were obtained after training the primary age reader with the reference collection. There was 62% percent agreement with the reference collection (85% and 89% agreement within 1 or 2 years, respectively), with a Chang's CV of 5.1. There was a tendency to underage fish approximately 15 years old and older; however, Bowker's test indicated this departure was not signifi-cant (χ^2=19.5; P=0.42).

Ages of Tilefish collected in 2008 ranged from 3 to 25 years for females and 3 to 23 years for males. Nearly all fish (98%; n=180) were ≤15 years old (Fig. 6). Precision, based on re-reading the 2008 otoliths, was good. Percent agreement between the first 2 read-ings was 79.6% (97% and 98% within 1 or 2 years, re-spectively), with Chang's CV of 2.2. Again, the Bowk-er's test of symmetry was not significant (χ^2=17.4; P=0.18).
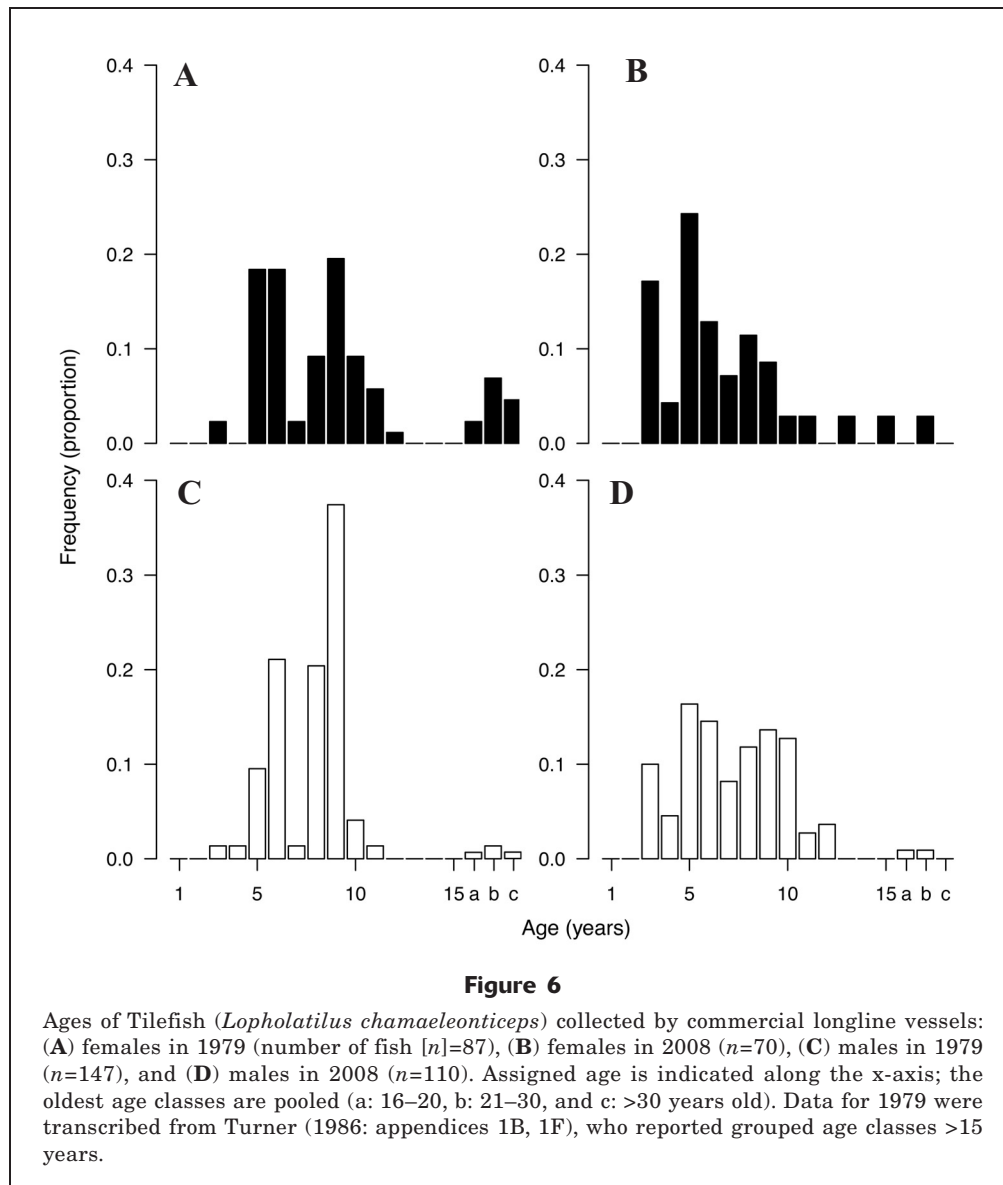

Figure 6

Ages of Tilefish (*Lopholatilus chamaeleonticeps*) collected by commercial longline vessels: (**A**) females in 1979 (number of fish [n]=87), (**B**) females in 2008 (n=70), (**C**) males in 1979 (n=147), and (**D**) males in 2008 (n=110). Assigned age is indicated along the x-axis; the oldest age classes are pooled (a: 16–20, b: 21–30, and c: >30 years old). Data for 1979 were transcribed from Turner (1986: appendices 1B, 1F), who reported grouped age classes >15 years.

Table 2

Median fork length (L_{50}, cm) and age (A_{50}, years) at maturity, standard error (SE), range, and sample size (n) of Tilefish (*Lopholatilus chamaeleonticeps*) collected in 2008 off southern New England—by year, sex, and method used to evaluate maturity. The methods used were macroscopic evaluation of the whole gonad and microscopic evaluation of gonad histology. Raw data from 1978 and 1982 are extracted from Grimes et al. (1988: tables 3–6; see text for details). Predicted ages at maturity from tabulated data in Grimes et al. (1988) also are plotted in Figure 2.

Year	Sex	Method	L_{50}	SE	Range	n	A_{50}	SE	Range[1]	n
2008	Male	Macroscopic	54.1	1.4	32–100	99	5.9	0.2	3–23	99
2008	Male	Histological	46.8	1.5	32–100	99	4.9	0.2	3–16	99
2008	Female	Macroscopic	44.1	1.1	32–90	58	4.9	0.2	3–25	58
2008	Female	Histological	46.3	1.2	32–90	58	5.2	0.2	3–21	58
1982	Male	Macroscopic	38.6	4.6	41–95	241	4.6	0.8	4–12	88
1978	Male	Macroscopic	62.6	1.0	31–115	384	7.1	0.2	4–15	246
1982	Female	Macroscopic	49.8	0.4	26–100	360	5.5	0.2	4–15	121
1978	Female	Macroscopic	45.4	1.2	31–95	393	5.2	0.1	4–15	267

[1]Ages $\geq$15 years were grouped because Grimes et al. (1988) had grouped ages at this value in their data tables.

Maturity methods compared

Before we compared maturity schedules between years, we evaluated a potentially confounding effect on estimation of maturity of Tilefish: the effect of method. There was a general agreement in maturity classification (i.e., immature versus mature) between macroscopic and microscopic (histological) methods. When both methods were used on the same fish, the agreement was higher for females (94%) than for males (84%). Mismatched females (n=4) were immature according to gonad histology but mature macroscopically.

Table 3

Comparisons of different data aggregates in testing for the effect of fish size (fork length [FL], cm) or age (years) on maturity of Tilefish (*Lopholatilus chamaeleonticeps*). The first comparison tests the effect of (**A**) method, macroscopic (macro) versus histological (histo), in evaluation of maturity status of fish collected in 2008 off southern New England for this study (controlling for factors of sex, M=male; F= female). The next comparison tests for (**B**) sexual dimorphism (by method with data from examination of fish collected in 2008). The last 2 comparisons test whether macroscopic estimates of maturity (used in all years) were different in 2008 than they were in (**C**) 1982 and (**D**) 1978, by using historic data for 1978 and 1982 from Grimes et al. (1988). See Table 2 for fitted parameter values by year, sex, and method. "Units" are modeled as a covariate, either as a main effect (+) or an interaction (*). Model sets are evaluated row-wise, with the second-order Akaike's information criterion (AIC$_c$) value. The lowest AIC$_c$ value, indicating the least uncertainty, is underlined. If ΔAIC$_c$ values are $\leq$2, indicating the effects are indistinguishable, both or all cells are underlined.

		AIC$_c$ values of full and reduced models					
		Length models			Age models		
Units compared (covariates)	Other factors	FL* units	FL+ units	FL	Age* units	Age+ units	Age
A							
Method (macro/histo)	M, 2008	<u>86.8</u>	<u>85.0</u>	97.1	<u>94.9</u>	<u>93.4</u>	104.2
Method (macro/histo)	F, 2008	<u>55.8</u>	<u>53.9</u>	<u>53.8</u>	68.5	<u>66.5</u>	<u>66.0</u>
B							
Sex (male/female)	Macro, 2008	<u>74.7</u>	<u>74.9</u>	95.8	87.3	<u>85.9</u>	93.7
Sex (male/female)	Histo, 2008	67.9	<u>66.1</u>	<u>64.2</u>	76.1	<u>74.1</u>	<u>73.8</u>
C							
Year (1982/2008)	M, Macro	<u>305.3</u>	323.9	329.4	<u>143.4</u>	153.1	151.8
Year (1982/2008)	F, Macro	<u>189.8</u>	<u>187.8</u>	208.4	<u>78.7</u>	<u>77.2</u>	<u>78.8</u>
D							
Year (1978/2008)	M, Macro	<u>353.5</u>	356.6	369.7	<u>248.9</u>	<u>249.6</u>	261.5
Year (1978/2008)	F, Macro	<u>344.8</u>	353.8	352.8	<u>230.0</u>	<u>229.8</u>	<u>229.7</u>

Mismatched males (*n*=25) were mature according to histology but immature macroscopically.

Disagreements were for fish within the size range of transition from immature to mature (females: 42–49 cm FL; males: 44–71 cm FL). Mismatches among female classifications resulted in values of median size and age at maturity (L_{50} and A_{50}, respectively) that were 2.2 cm FL larger and 0.3 years older for histology-based results than for macroscopic classifications (macroscopic: L_{50}=44.1 cm FL, A_{50}=4.9 years; histological: L_{50}=46.3 cm FL, A_{50}=5.2 years) (Table 2). Mismatches among male classifications resulted in the L_{50} and A_{50} values that were 7.3 cm FL smaller and 1.0 year younger for histological examination than for macroscopic results (macroscopic: L_{50}=54.1 cm FL, A_{50}=5.9 years; histological: L_{50}=46.8 cm FL, A_{50}=4.9 years) (Table 2). Therefore, a histological method not only shifted the median parameter estimates in opposite directions for each sex, but the magnitude of uncertainty due to method was much greater for males than for females (Table 3A).

Maturity and spawning

The fishery harvests immature fish of both sexes. Macroscopic collections indicated that 14% of females (32–49 cm FL, 3–6 years old) and 38% of males (32–71 cm FL, 3–9 years old) caught on the 2008 sampled trips were immature.

Histological classifications did not support differences in L_{50} or A_{50} between sexes; however, macroscopic observations supported sexual dimorphism in the L_{50} and A_{50} parameters (Tables 2, 3B). These results likely mean that gonad histology detects hormonal maturation, a physiological state that occurs at a similar size and age for each sex but that may not be an accurate predictor of spawning activity for males. If so, then spawning activity, which is more closely aligned to measuring spawning stock biomass, occurred when males were 10 cm FL larger and 1 year older than females, on average, in 2008 (Table 2; Fig. 7).

Discussion

This study confirms that the northern stock of Tilefish is functionally gonochoristic. Grimes et al. (1988) also concluded that this stock is gonochoristic, noting the presence of isolated oocytes in 2 of 50 testes. They did not report finding a lumen in testes, but they may have overlooked it, stating they were unsure about the sexuality of small fish with a lumen. We observed that the lumen was not always obvious in large fish, even when looking for it. The term "prematurational sex change"—where individuals express themselves as a female first but do not mature as a female before they switch to a male—does not seem to apply here. Instead, we believe that a testis containing a lumen is a common feature in Tilefish, as occurs for other fishes (e.g., Pomacentri-
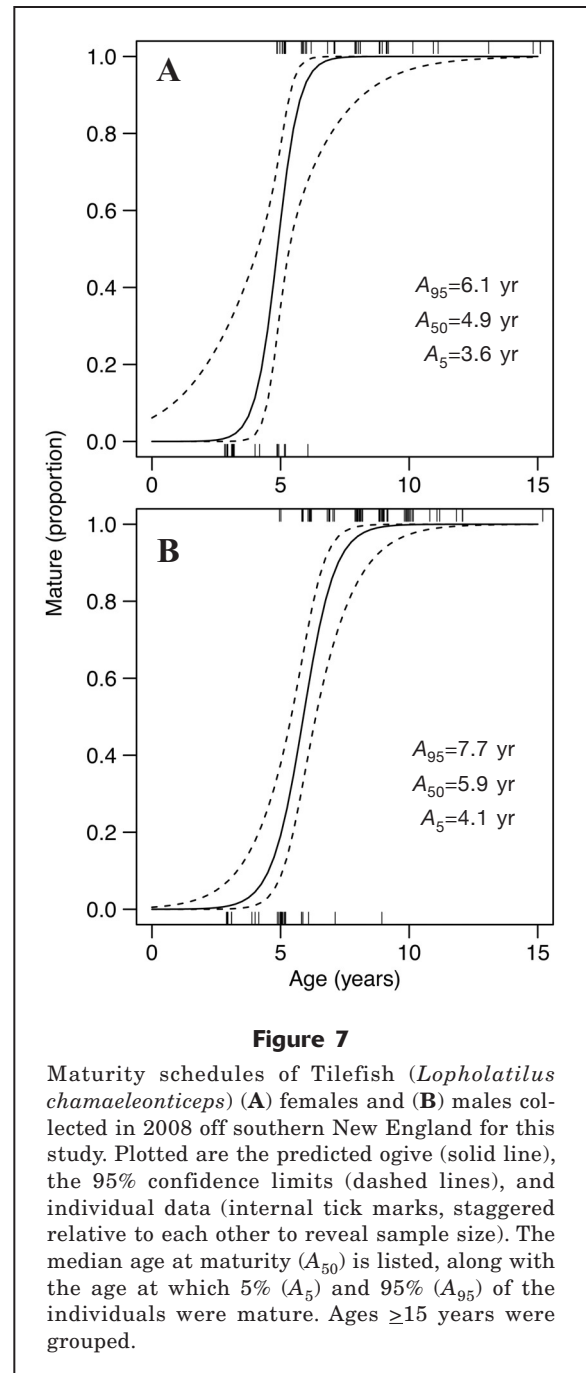

Figure 7

Maturity schedules of Tilefish (*Lopholatilus chamaeleonticeps*) (**A**) females and (**B**) males collected in 2008 off southern New England for this study. Plotted are the predicted ogive (solid line), the 95% confidence limits (dashed lines), and individual data (internal tick marks, staggered relative to each other to reveal sample size). The median age at maturity (A_{50}) is listed, along with the age at which 5% (A_5) and 95% (A_{95}) of the individuals were mature. Ages $\geq$15 years were grouped.

dae and Serranidae; Sadovy and Domeier, 2005), but is unrelated to function. We also do not categorize Tilefish as bisexual—a term that does not apply with the appearance of a lumen or the presence of isolated oocytes as described here (Sadovy and Domeier, 2005).

Our conclusion about gonochorism emphasizes function; in other words, all individuals reproduce exclusively as either male or female during their lives (Sadovy de Mitcheson and Liu, 2008). Because we sampled fish during the spawning period, and functional,

simultaneous hermaphroditism was not observed, this type of hermaphroditism is unlikely. We did not sample in winter to test for sequential sex change during the nonspawning period, but the histological evidence of similar A_{50} for both functional sexes makes this change unlikely. We predict that intersex fish would be no more common during the nonspawning season than they are reported herein for the spawning season. Also, we predict that, if collections of younger (<3 years old) fish were possible, isolated oocytes would be more commonly seen because isolated oocytes were observed to be degrading in our collections of testes. If these predictions about morphology are correct, they would confirm our conclusions that Tilefish are functionally gonochoristic. Erickson and Grossman (1986) investigated the sexual pattern of Tilefish farther south, in Atlantic waters of the Georgia Bight, and also concluded that Tilefish are functionally gonochoristic. In contrast, Lombardi-Carlson (2012) reported higher rates of intersex Tilefish in the Gulf of Mexico, evident for both functional males and females; therefore, there appears to be geographic variation in the morphological expression of intersex fish and possibly the sexual pattern by Tilefish.

Our study is the first attempt to age the northern stock of Tilefish in nearly 30 years. Turner et al. (1983) reported ages of fish collected in the longline and recreational fisheries in 1978, and Turner (1986) reported ages from the longline fisheries in 1979, 1980, and 1982. Females older than 31 years were collected in each of these sampling years, and males older than 31 years were collected in half of these years (Turner, 1986: appendix 1, A–H). The oldest fish observed was 46 years old (Turner, 1986), nearly twice as old as the oldest fish observed in 2008 in our study. Age structure during 1978–82 also appeared to be dominated by the 1970 and 1973 year classes, but dominant year classes (the most recent one being 1999; NEFSC[3]) were not obvious from the age structure measured in 2008 (Fig. 6). The reduced numbers of older fish today indicate that age truncation still exists, a finding that should not be surprising because landings >1000 t persisted well into the 1990s. We predict that fish older than 30 years will return to the population in the next decade.

The effect of method (macroscopic versus histological) in determination of maturity was more pronounced for males than for females (Tables 2, 3A). Differences in the 2008 female L_{50} and A_{50} attributable to method were minor (2.2 cm FL, 0.3 year). Our confidence in macroscopic evaluation of maturity was good at this time of year, when the main histological criterion, vitellogenic oocytes, were large enough (0.3–0.7 mm) to be seen macroscopically; hydrated oocytes were even more readily visible: 0.7–1.0 mm (as measured from histological slides by T. Vidal, unpubl. data). Data for females at other times of the year, especially during the nonspawning season, are likely to be less precise or accurate (Vitale et al., 2006; McBride et al., 2013).

That the observed differences in L_{50} and A_{50} attributed to method were larger for males (7.3 cm FL, 1.0 year) than for females was not unexpected. Grimes et al. (1988) also observed larger and older male L_{50} and A_{50} with a macroscopic method versus a histological method. We agree with Grimes et al. (1988): these differences in male maturity are not merely a methodological artifact but are of biological significance—likely the result of a physiological lag in gonad growth and the time that exists between spermiation (an indication of hormonal activity) and full ripening of the testes that precedes functional spawning by males. Such a lag may also be associated with behavioral differences. Grimes and Turner (1999) postulated that males first mature in a subordinate role and become dominate within 1–2 years.

Although such hypotheses demand further study, it is obvious that the method to determine maturity can matter in comparative analyses. The macroscopic method is likely aligned with functional spawning, and functional spawning more accurately defines spawning stock biomass. Therefore, it is the more appropriate method to use in routine measures to characterize this reference point for males. Grimes et al.'s (1988) approach emphasized the macroscopic method; therefore, our comparisons with relatively large sample sizes should be robust between all years (i.e., 1978, 1982, 2008),

The large percentage of immature Tilefish in the catch (14–38%, by sex) appears to point to violation of the principle to let fish reproduce at least once before they are harvested (Sissenwine and Shepherd, 1987). Although it is once again a topic of debate (Garcia et al., 2012), this principle prompts a re-evaluation of the effect of hook size on the proportion of immature fish landed.

Female size at maturity differed between 2008 and earlier years, but female age at maturity did not differ strongly between years (Tables 2, 3[C and D]). Female L_{50} was smaller in 2008 (44.1 cm FL) than in 1978 (45.4 cm FL) and 1982 (49.8 cm FL). The difference in A_{50} between all years was <1 year, and the low AIC_c score (i.e., <2) indicated that these differences in female A_{50} over time were similar. Nonetheless, female fitness is related to size and age (Green, 2008). In our study, the youngest A_{50} was measured in 2008. Other studies have shown that such shifts in maturity schedules are associated with reduced yield, survival, and fecundity (Law, 2000; de Roos et al., 2006; Conover et al., 2009). In particular, the mature female Tilefish that showed no immediate evidence of spawning were young (5–6 years old), indicating that newly matured females have lower spawning frequency and, therefore, a lower reproductive potential than older females. Age-specific effects on spawning frequency and batch fecundity are commonly observed in fishes and can alter stock assessment outcomes (Fitzhugh et al., 2012), and therefore continued research is warranted to clarify such

additional effects on reproductive potential of female Tilefish.

Male size and age at maturity differed between years much more dramatically than did female size and age at maturity (Tables 2, 3[C and D]). In 2008, male L_{50} was 54.1 cm FL, smaller than in 1978 (62.6 cm FL) but larger than in 1982 (38.6 cm FL). The same rebounding pattern was evident for male A_{50}, but, again, the difference in A_{50} between 1978 and 1982 (2.5 years) was not completely regained by 2008. Grimes et al. (1988) reported the initial trend, when they concluded that high fishing pressure was associated with and presumably induced a reduced size at maturity for males between 1978 and 1982. Our results indicate that this smaller size and younger age at maturity observed in 1982 did not become fixed. Because male fitness can be related strongly to size and age (Trippel, 2003), it is likely that male reproductive success is still hampered by reduced maturity parameters relative to that observed in 1978. The interpretation and predictability of these results, however, are hindered by the limited amount of data available to determine the stability of sex-specific maturity schedules between years.

Early reports that maturity schedules were flexible and could be dynamic in response to rates of fishing were treated with skepticism (Beacham, 1987), but they are becoming increasingly common and well supported (de Roos et al., 2006; Conover et al., 2009; Chuwen et al., 2011). If rates of maturation are heritable and survival rates of reproducing individuals are low, fishing will select individuals that reproduce at smaller sizes and younger ages (Reznick et al., 1990; Hutchings, 1993). If this selective pressure were to be eliminated, maturation rates would still likely require several generations to rebound (Conover et al., 2009). Tilefish have a minimum generation time of 5–7 years, according to the generation time estimated from the values of A_{50} reported here. Therefore, several generations actually have passed between 1982 and 2008. Also, the period of high exploitation (1977–87) did not extend beyond 2–3 Tilefish generations, unlike the several decades-long, chronic effects of overfishing observed in some other fisheries (Worm et al., 2009). Finally, Tilefish maturation evidently is not entirely under genetic control because males are presumed to use proximate sex and size cues to determine their reproductive potential (Grimes et al., 1988). In summary, we cannot rule out that genetic selection caused by increased fishing rates occurred 30 years ago for Tilefish, but we can point to these other factors as likely contributors to the appearance of a rebounding maturity rate among males following heavy exploitation in the 1970s and 1980s.

Conclusions

Intersex males exist, but the northern stock of Tilefish is functionally gonochoristic. Current demographics indicate age truncation and the lack of any strong year classes in the rebuilt fishery of 2008. A macroscopic method for assessment of sex-specific maturity during the spawning season was verified as a reliable and cost-effective approach to monitoring trends in Tilefish maturation. Previously published data (Grimes et al., 1988) were reanalyzed, and an information-theoretic approach revealed differences in estimates of maturity ogives attributed to methods, sexes, and years.

Once method and sex were accounted for, it was evident that male maturation rates have rebounded from an earlier decline associated with a period of overexploitation. This rebound probably occurred because the period of overexploitation did not last long, several generations have passed during a period of improved conditions for the fishery, and male maturation is socially mediated. At present, only 3 years of age and maturity data exist, but these data were available for the 2009 Tilefish assessment, and they show the value of continued cooperative biological monitoring in this data-limited fishery.

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