# Age validation of the North Atlantic stock of wreckfish (*Polyprion americanus*), based on bomb radiocarbon ($^{14}C$), and new estimates of life history parameters

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# Age validation of the North Atlantic stock of wreckfish (*Polyprion americanus*), based on bomb radiocarbon ($^{14}C$), and new estimates of life history parameters

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**Abstract**—The wreckfish (*Polyprion americanus*), a commercially important, long-lived, demersal fish, is found in the eastern Atlantic from Norway to South Africa and in the western Atlantic from the Grand Banks, Newfoundland, to Argentina. Using bomb radiocarbon analysis, we validated the annual increment formation observed in otoliths and determined that increment counts are a good proxy for age. The maximum observed age was 80 years, more than double the previously reported maximum age of 39 years in the North Atlantic population. The updated fit of the length-at-age information to the von Bertalanffy growth model resulted in $L_\infty$, $k$, and $t_0$ estimates of 1026 mm in fork length, 0.124/year, and –4.96 years, respectively. We used these updated values for maximum age and growth parameters to estimate rates of instantaneous and age-varying natural mortality, and found that instantaneous natural mortality ranged from 0.088 to 0.091 and age-varying natural mortality reached an asymptote of 0.07–0.12 by 15 years of age. This study highlights the need for age validation in long-lived fish species to prevent inaccurate estimates of age that ultimately can lead to mismanagement of a species

Deepwater fishes (depths >400 m) are becoming increasingly important to commercial fisheries (Clarke et al., 2003). Unfortunately, the general longevity—some species such as orange roughy (*Hoplostethus atlanticus*) live up to 150 years—and slow maturation rates of many deepwater fishes make them highly susceptible to overfishing and slow to recover from an overfished state (Clark, 2001; Roberts, 2002; Clarke et al., 2003). An additional issue is that deepwater fish species are difficult to age (Fenton et al., 1991, Friess and Sedberry, 2011;). Accurate aging is critical for the estimation of several life history parameters, such as growth, mortality, and stock productivity, and is essential for any age-structured model of population dynamics.

One deepwater species whose age estimates are subject to aging error is the wreckfish (*Polyprion americanus*). This grouper-like, commercially important, long-lived, demersal fish is found in the eastern Atlantic from Norway to South Africa and in the western Atlantic from the Grand Banks, Newfoundland, to Argentina, although it is noticeably absent from tropical latitudes—an absence that indicates an antitropical distribution for this species (Sedberry et al., 1999). Using microsatellite genetic markers, Ball et al. (2000) determined that North Atlantic and South Atlantic populations are genetically distinct. Our study focused on the North Atlantic, and unless otherwise specified, *wreckfish* hereafter refers to the stock in the North Atlantic. Adult wreckfish are found concentrated around steep, rocky bottoms and deep coral reefs, occurring in lower concentrations along flat hard bottom, from depths of 40 to 800 m; however, most wreckfish occur in waters deeper than 300 m, and at a maximum reported depth of 1000 m (Sedberry et al., 1999). They grow to a size of 2 m and can approach 50 kg in weight (Sedberry et al., 1999).

Until the mid-1980s, when crews aboard pelagic longliners accidentally "discovered" the resource along the Charleston Bump, an area off the coast of South Carolina (Sedberry et al., 1999), wreckfish were unexploited commercially in the western North Atlantic. The fishery for this species developed rapidly, and the majority of effort was focused on or around the Charleston Bump, where landings peaked at 4.2 million lb whole weight (ww) in 1989 (Vaughan et al.,

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2001). The rapid expansion of the fishery for wreckfish, along with growing concern among fishermen and managers about the sustainability of this fishery, resulted in the establishment of an "individual transferable quota system" for wreckfish in 1990 by the South Atlantic Fishery Management Council (SAFMC), and several subsequent management changes have been implemented since then. Currently the total allowable catch is set at 235,000 lb ww, and the fishery for wreckfish was estimated to be worth $700,000 in 2012.

Despite the widespread distribution and commercial importance of wreckfish, there have been only 2 publications in which the age of this species has been documented and its associated life history traits have been described: one on the North Atlantic population (Vaughan et al., 2001) and another on the South Atlantic population (Peres and Haimovici, 2004). These 2 studies differed widely in their estimate of maximum age for wreckfish; Vaughan et al. (2001) suggested a maximum age of 39 years and Peres and Haimovici (2004) suggested maximum ages for males and females of 62 and 76 years, respectively. Unfortunately, neither study included attempts to validate age estimates despite the suggestion in other literature that maximum age differences of this magnitude between populations of the same species are unlikely (Collins et al., 1987; Begg and Sellin, 1998). A related species, hapuku (*Polyprion oxygeneios*), reaches ages in excess of 60 years in the South Pacific (Francis et al., 1999). Another observation that indicates potential underaging of wreckfish is the lack of decoupling of size at age in the von Bertalanffy growth model (VBGM) presented by Vaughan et al. (2001); this decoupling is often characteristic of long-lived fish species (Coulson et al., 2009; Friess and Sedberry, 2011).

Using bomb radiocarbon analysis, we validated age estimates for wreckfish caught in the North Atlantic, in particular for fish captured in the area of the Charleston Bump. We presumed that wreckfish attain a much higher maximum age than has been reported previously for the North Atlantic population. We then recalculated various life history parameters, including length at age, growth, and natural mortality on the basis of the validated age estimates.

## Materials and methods

### Collection of samples

Personnel from the National Marine Fisheries Service and South Carolina Department of Natural Resources collected otoliths from commercially landed wreckfish from 1991 through 2011 at ports in South Carolina, Florida, and North Carolina. Data recorded for most fish included fork length (FL, in millimeters), although, on some fish, measures of standard length (SL, in millimeters) and total length (TL, in millimeters) also were taken. We developed a FL-TL meristic conversion to facilitate the conversion to and from different length measurements. Fishermen generally gutted all fish at sea and kept them on ice until landed, a process that prevented sex-specific analyses. For aging purposes, port samplers removed at least the left sagittal otolith, although removal of both sagittal otoliths occurred in some cases.

### Age validation

The otoliths that were used for bomb radiocarbon analysis were collected in 1991 ($n$=323) from wreckfish that had at least a measurement of TL and both sagittal otoliths were removed. Vaughan et al. (2001) did not provide detailed information about the technique they used for processing otoliths, and we based our otolith processing on a slightly modified protocol detailed in Peres and Haimovici (2004). After an otolith was embedded in a marine grade epoxy, we cut a series of transverse sections (~0.25–0.35 mm thick) from the left sagittal otolith, ensuring that at least one section included the otolith core. Sectioning was done with an IsoMet Low Speed Saw[1] (Buehler, Lake Bluff, IL) with a diamond-coated waffering blade. We mounted (and cleared) resulting sections, typically 2 sections per otolith, on glass slides, using Cytoseal XYL medium (Thermo Fisher Scientific Inc., Waltham, MA).

Two readers independently examined otoliths for age determination, without knowledge of fish size, capture date, or the results of the other reader, with an Eclipse 55i compound microscope (Nikon, Tokyo) under transmitted light at magnifications of 40–100×. Readers prioritized reading the section that contained the core, unless there was an obvious reason, such as damage to the otolith, not to use that section. Counts of increments were determined by counting all opaque growth increments along the medial surface of the transverse otolith section ventral to the sulcus. Identification of the first growth increment was based on the protocol of Peres and Haimovici (2004), in which the first increment follows 1–3 "false" rings and exhibits a discontinuity, which is a thin crack-like structure running between a translucent and opaque increment.

After determining initial increment counts, we selected 20 specimens for analysis of bomb radiocarbon levels for age validation. We selected for analysis those specimens with a birth year between 1950 and 1980, as determined from increment count and year of capture (1991), and agreement between readers. If reader disagreement was greater than 1 year, we excluded the specimen from consideration. We embedded the right sagittal otolith of the specimen in resin and obtained a single, 1-mm-thick transverse section through the core. The resultant section was washed with deionized water and dried overnight. Extraneous otolith material surrounding the core was removed with a Dremel, model 732, rotary tool (Robert Bosch Tool Corp., Mt. Prospect, IL) with a carbide-cutting wheel.

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

To prevent cross-contamination between samples we used a new carbide cutting wheel for each otolith and removed the core under a ventilation system. We removed additional surface contaminants by rinsing the extracted otolith cores for two 30-s intervals in deionized water, followed by an acid bath in 10% $HNO_3$ for 30 s, and a final rinse with deionized water.

After the otoliths had dried overnight, we measured each otolith core to the nearest 0.01 mg to ensure that enough material (>8 mg) had been obtained for bomb radiocarbon analysis. We did not obtain enough material from a single section for several specimens; for such specimens, we removed and processed a second section from the same otolith using the same technique, adding the additional material to the original sample.

We shipped the resultant core samples in plastic 5-mL vials to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at the Woods Hole Oceanographic Institution. Preparation of the samples for bomb radiocarbon analysis followed the protocol outlined by NOSAMS for inorganic carbonate materials. First, samples underwent acid hydrolysis, with an $H_3PO_4$ solution, to form $CO_2$. The evolving $CO_2$ was then removed by using an automated system that included acidification and sparging with nitrogen, and the $CO_2$ was reduced with a catalyst (Fe or Co) in the presence of excess hydrogen to form graphite. The graphite was then loaded into the accelerator mass spectrometer for reading $^{14}$C levels. Staff of the NOSAMS subsequently compared the observed $^{14}$C concentrations for each specimen to $^{14}$C levels found in 19th century wood formed before nuclear testing, using $^{13}$C concentrations to correct for any natural or machine-generated fractionation effects. The resultant statistic ($\Delta^{14}$C, in parts per million) provides a measure of the increase in $^{14}$C due to uptake of $^{14}$C from nuclear bomb testing in the 1950s through early 1970s compared with $^{14}$C levels found in early 19th century wood.

To facilitate comparisons with other studies, we transformed the raw $\Delta^{14}$C chronologies to proportion of total bomb radiocarbon ($\%\mathrm{C}_\mathrm{i}^{14}$),

$$\%C_\mathrm{i}^{14} = \frac{C_\mathrm{min}^{14} + C_\mathrm{i}^{14}}{C_\mathrm{min}^{14} + C_\mathrm{max}^{14}}, \tag{1}$$

where $C_\mathrm{min}^{14}$ = the inverse of the lowest radiocarbon level found;
$C_\mathrm{max}^{14}$ = the highest radiocarbon value found;
$C_\mathrm{i}^{14}$ = the $^{14}$C level of the $i^\mathrm{th}$ sample; and
$\%C_\mathrm{i}^{14}$ = the percentage of total bomb radiocarbon of the $i^\mathrm{th}$ sample.

We then fitted $\%C^{14}$ values to a logistic curve,

$$\%C^{14} = \frac{\alpha}{1 + e^{\left(\beta - \text{Birth Year}/\lambda\right)}}, \tag{2}$$

where α (asymptote), β (inflection point), and λ (scaling parameter determining curve shape) are the 3 parameters of the logistic curve to be estimated by nonlinear regression.

We analyzed the accuracy of our initial increment counts as a proxy for age by comparing the wreckfish $\%\mathrm{C}_\mathrm{i}^{14}$ chronology to a reference $\%\mathrm{C}_\mathrm{i}^{14}$ chronology of validated ages for haddock (*Melanogrammus aeglefinus*) collected from Newfoundland (Campana, 1997). We used a variance ratio test to determine if there was any significant difference between the 2 chronologies. We conducted all analyses using R, vers. 3.0.2 (R Core Team, 2012).

## Age and growth analysis

Because of our desire to use more recently caught fish, which presumably would better represent recent growth patterns in the population, we excluded all specimens used in previous bomb radiocarbon analysis, instead randomly selecting 500 specimens collected from 2000 through 2011. Almost all randomly selected fish measured between 800 and 1000 mm FL because of the high availability of these size classes in the sample archive—an availability that is likely due to commercial fishing practices. To improve growth curve fit, we included all available specimens from 2000 through 2011 that were smaller than 700 mm FL ($n$=44) or larger than 1100 mm FL ($n$=24) and that were not already randomly selected in the age and growth analysis. Our intent with this selection strategy was to reduce the sensitivity of the growth curve to small sample sizes of younger and older age classes. Furthermore, inclusion of the oldest fish, under the assumption that larger fish are generally older, improves our probability of identifying the oldest fish in the fishery-dependent sample database. Because many mathematical estimators of natural mortality ($M$) make use of maximum age, proper identification of the oldest fish in the sample is vital.

For specimens used in the age and growth analysis, we processed otoliths to the same approximate thickness (0.25–0.35 mm) and mounted them as we did for the bomb radiocarbon study. We used only the left otolith for age estimates, and the 2 readers, once again, performed the readings blindly and independently. If readers disagreed on an age, the otolith was aged concurrently to reach a consensus on age. If disagreement persisted, the otolith was excluded from this study.

We fitted the length-at-age data to the VBGM,

$$L_\mathrm{t} = L_\infty\left(1 - e^{-\mathrm{k}(t - t_0)}\right), \tag{3}$$

where $L_\mathrm{t}$ (in millimeters) = length at age $t$ (in years);
$L_\infty$ (in millimeters) = the asymptotic length;
$k$ (1/year) = the Brody growth coefficient; and
$t_0$ = the theoretical age (in years) at which length is 0 (von Bertalanffy, 1938).

We fitted the VBGM and obtained estimates of growth model parameters, using a nonlinear regression in R, vers. 3.0.2.

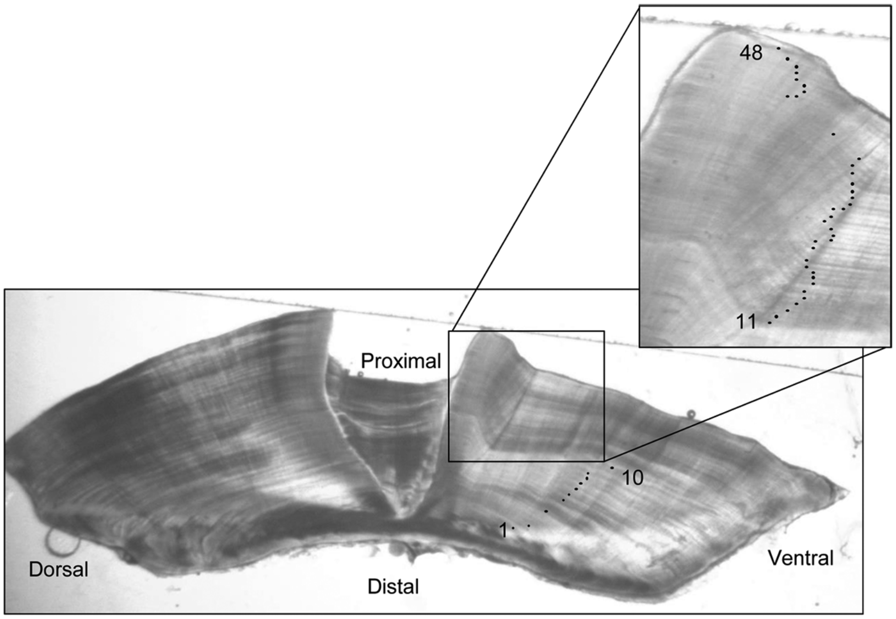

**Figure 1**

Transverse section of a sagittal otolith, taken from a wreckfish (*Polyprion americanus*) caught in the North Atlantic in 2005, that shows the typical pattern of increment formation. Each black dot (opaque growth increment) represents 1 year of growth. The fish from which this otolith was removed was estimated to be 48 years old.

### Natural mortality

We investigated 4 distinct $M$ estimators, 2 age-constant estimators from Then et al. (2015, eqs. 4 and 5),

$$M = 4.899({t_{\max}}^{-0.916}) \text{ and} \tag{4}$$

$$M = (4.118k^{0.73})\,({L_\infty}^{-0.33}), \tag{5}$$

and 2 age-varying $M$ estimators from Gislason et al. (2010, eq. 6) and Charnov et al. (2013, eq. 7),

$$M = e^{(0.55-1.61\times \mathrm{Ln}(L_t)+1.44\times \mathrm{Ln}(L_\infty)+\mathrm{Ln}(k))} \text{ and} \tag{6}$$

$$M = \left(\frac{L_t}{L_\infty}\right)^{-1.5} \times k. \tag{7}$$

Each of these estimators used either estimates for VBGM parameters ($k$ and $L_\infty$) or maximum age ($t_{\max}$) to predict $M$.

## Results

### Examination of otoliths and growth increments

External examination of 3 of the whole otoliths from wreckfish that were selected for use in the age and growth analysis revealed a misshaped translucent otolith with white crystalline lumps along the external surface. We sectioned one otolith with these characteristics to examine growth increment formation, only to discover that the otolith contained no distinguishable growth increments. We excluded these 3 specimens from further analysis.

Otolith sections exhibited a distinct opaque core, trapezoid in shape, between 5 and 6 mm in length and from 2 to 3 mm in height. Growth increments in transverse otolith sections were most visible along the medial surface ventral to the sulcus, although the first few increments were highly variable in width and spacing in any plane (Fig. 1). The first 4–6 opaque bands were broad and tended to widen or begin to bifurcate as they extended to the ventral surface of the section. Often, the first 4–6 opaque increments were followed by a distinct, crack-like structure. Thereafter, the growth bands continued to be broad and diffuse until an increment count of 10–15, after which the growth increments became noticeably more compact and regularly spaced but harder to discern.

Earlier, broader increments (<15) were read more easily at a lower magnification (40×) by bringing the increments in and out of focus and allowing the reader to focus on the more distinct increment patterns. The later and more compact opaque increments (>15) were more easily read at higher magnification (100×), which

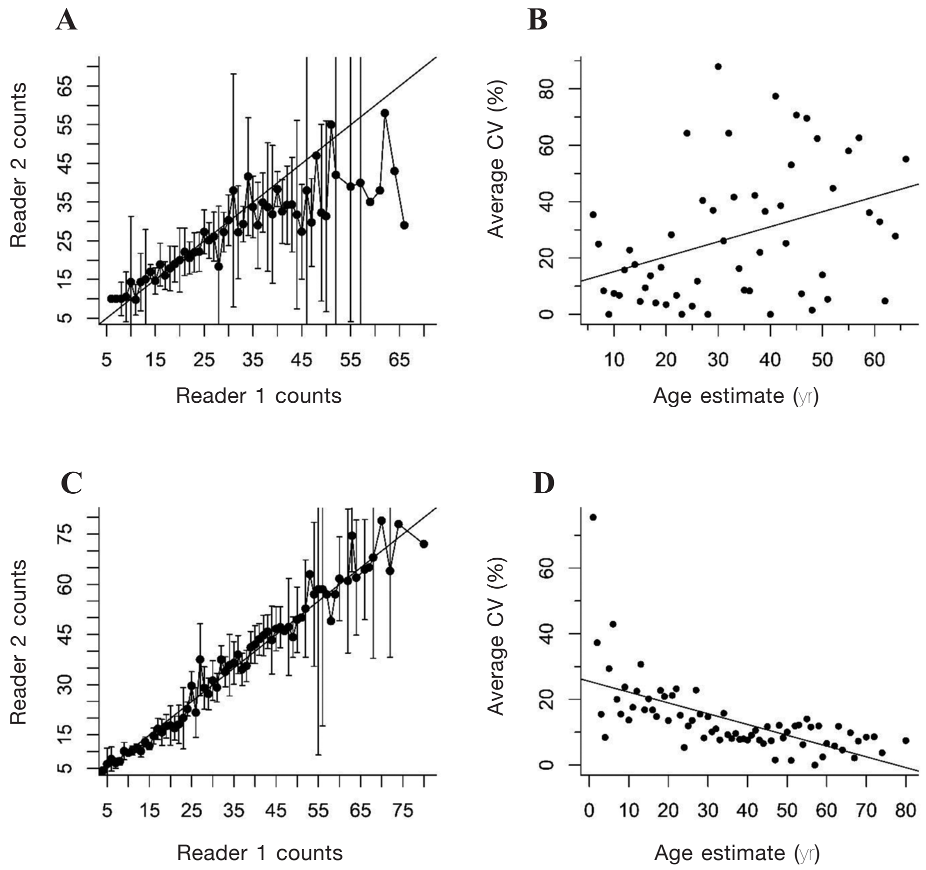

**Figure 2**

Bias plots of increment counts made by readers 1 and 2: (**A**) for identification of appropriate specimens for bomb radiocarbon analysis before identification of strict increment identification protocols, and (**C**) for growth analyses. Coefficients of variation (CV) in age estimates made by (**B**) reader 1 and (**D**) reader 2. Error bars in panels A and C represent 95% confidence intervals. Increment count-specific CVs increased ($y$=0.53$x$+9.86; coefficient of determination [$r^2$]=0.12, $P$=0.005) with increment number before identification of strict aging protocols. For specimens analyzed for growth analysis, CVs decreased with increment count ($y$=–0.33$x$+25.47; $r^2$=0.39, $P$<0.001).

allowed for better resolution between tightly compacted increments that may have otherwise been grouped together. In many of the otoliths, readability decreased at various points along the chosen reading axis, forcing readers to shift to a new reading axis by following a growth increment along a lateral plane.

## Age validation

Although increment counts for otoliths of wreckfish were relatively difficult to determine because increments could be difficult to discern, no samples were identified as unreadable and all specimens ($n$=323) were included for possible selection for bomb radiocarbon analysis. Lengths of the specimens ranged from 880 to 1070 mm TL. Initial estimated increment counts ranged from 6 to 66 increments for reader 1 and from 6 to 60 increments for reader 2. Count disagreements between readers ranged from 0 to 35 increments (average disagreement of 9 increments). Readers produced identical counts only 4.3% of the time, were within 1 increment 13.3% of the time, and were within 5 increments 45.7% of the time. Bias plots revealed that reader 2 counted fewer increments than reader 1 when reader 1 counted greater than 35 increments, indicating a bias between readers in fish of older ages (Fig. 2A). At increment counts of less than 35 for reader 1, there was no bias pattern between readers. Coefficients of variation (CV) increased significantly with age ($P$=0.005; Fig. 2B). The average CV between readers was 27.5%—a result that is likely due to the lack of validation-based aging criteria at this stage.

The wreckfish used in bomb radiocarbon analysis ($n$=20) had increment counts ranging from 11 to 43,

**Table 1**

Summary of results of the bomb radiocarbon analysis of otoliths from wreckfish (*Polyprion americanus*) that were collected in the North Atlantic in 1991. The last column provides the standard errors (SE) associated with the $\Delta^{14}$C (‰) values. An asterisk (*) indicates that 2 sections were used to meet the weight requirement for processing otoliths with accelerator mass spectrometry.

| Collection number | Number of growth increments | Birth year | Weight (mg) of otolith core | $\Delta^{14}$C (‰) | SE |
|---|---|---|---|---|---|
| 910086-18 | 43 | 1948 | 11.5 | −63.36 | 2.5 |
| 910076-15 | 40 | 1951 | 13.2 | −14.98 | 4.5 |
| 910084-5 | 40 | 1951 | 10.7 | −67.43 | 2.2 |
| 910085-14 | 40 | 1951 | 8.5 | −60.97 | 2.5 |
| 910084-11 | 36 | 1955 | 11.2 | −60.35 | 2.5 |
| 910078-11 | 34 | 1957 | 9.6 | −57.15 | 3.5 |
| 910082-32 | 29 | 1962 | 11.3* | −64.32 | 2.5 |
| 910086-2 | 27 | 1964 | 8.9 | −63.87 | 2.7 |
| 910083-46 | 26 | 1965 | 12.8 | −18.90 | 2.5 |
| 910076-5 | 25 | 1966 | 15.2 | −18.47 | 4.8 |
| 910078-17 | 23 | 1968 | 9.6 | 20.67 | 2.5 |
| 910076-2 | 22 | 1969 | 15.1* | 47.48 | 4.4 |
| 910078-28 | 22 | 1969 | 9.4 | 98.90 | 2.7 |
| 910083-13 | 22 | 1969 | 11.0 | 57.52 | 2.5 |
| 910079-10 | 20 | 1971 | 12.4 | 35.80 | 2.5 |
| 910079-16 | 18 | 1973 | 16.7* | 65.90 | 3.4 |
| 910079-14 | 17 | 1974 | 12.8* | 72.14 | 2.9 |
| 910086-1 | 16 | 1975 | 8.6 | 87.13 | 2.7 |
| 910085-6 | 15 | 1976 | 9.5 | 80.04 | 4.4 |
| 910080-19 | 11 | 1980 | 10.1 | 90.88 | 2.7 |

and birth years (based on one increment formed per year) ranging from 1948 to 1980 (Table 1). The otolith core weights ranged from 8.5 to 16.5 mg; however, 4 samples required the use of a second section to meet the requirement for the minimum material needed for analysis with accelerated mass spectrometery. Otolith core values of $\Delta^{14}$C ranged from −7.43‰ in birth year 1951 to 98.90‰ in birth year 1969, well within the range of previously published $\Delta^{14}$C levels from haddock (Campana, 1997). Levels of $\Delta^{14}$C in otolith cores from wreckfish showed a prominent increase beginning in the early 1960s, peaking around 1975 and leveling off thereafter (Fig. 3A). There was no evidence of the expected decline in $\Delta^{14}C$ levels after 1975, possibly as a result of the lack of sufficient samples past that date. Wreckfish with birth years before 1963 exhibited relatively constant low levels $\Delta^{14}$C, with the exception of one outlier fish that had an estimated birth year of 1951 ($\Delta^{14}$C= −14.98‰). Another possible outlier was a fish with a birth year of 1969 ($\Delta^{14}$C=98.90‰). Because most samples exhibited a good fit to the logistic regression curve, we believe the outliers resulted from a contamination issue during core removal rather than from aging error.

The %$^{14}$C uptake chronology for wreckfish ($\alpha$=0.87, $\beta$=1967, $\lambda$=1.31) exhibits an uptake pattern similar in shape to the published %$^{14}$C chronology for haddock ($\alpha$=0.93, $\beta$=1962, $\lambda$=2.35) (Campana, 1997; Fig. 3B). However, the fitted logistic curve for %$^{14}$C of wreckfish fell below the fitted logistic curve for %$^{14}$C of haddock for the entire time period (Fig. 3B), and there was a noticeable phase shift of 5–6 years between the models (wreckfish $\beta$=1967 and haddock $\beta$=1962). The variance ratio test confirmed that the curves were significantly different ($P$<0.001). Despite the small difference in curves, which indicates potential underaging, the similarity in uptake patterns between the 2 curves indicates annual growth increments.

### Age and growth

After completion of all otolith readings ($n$=568) for age and growth analysis, we omitted 14 otoliths because of disagreements between readers. Specimens ranged in size from 452 to 1340 mm FL (Fig. 4.). Ignoring the potential phase shift identified in the bomb radiocarbon validation study, ages of wreckfish ranged from 1 to 80 years for reader 1 and from 2 to 79 years for reader 2, with an average disagreement of 4 years. Readers produced identical counts 10.8% of the time, had agreement within 1 year 30.4% of the time, and had agreement within 5 years 72.7% of the time, a considerable improvement over the bomb radiocarbon readings. This improvement resulted from the development and use

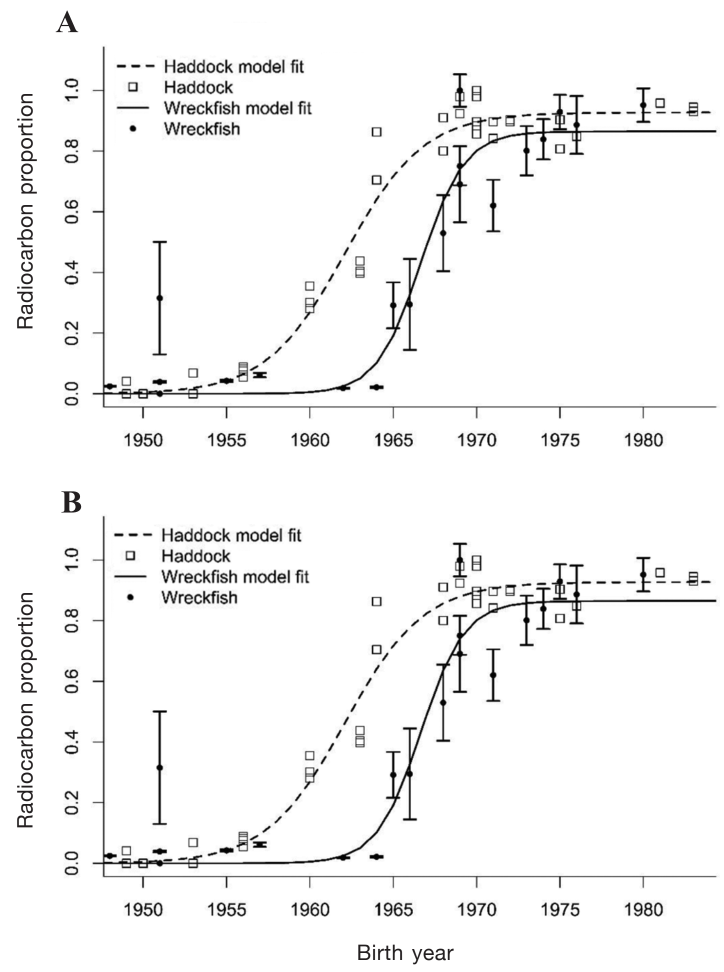

**Figure 3**

(**A**) Mean proportion of total bomb radiocarbon (%$^{14}$C) of total $\Delta^{14}$C by birth year for otolith cores from wreckfish (*Polyprion americanus*) collected in the North Atlantic in 1991. We fitted a logistical regression model (solid line) to the data. (**B**) Mean %$^{14}$C values for wreckfish from this study and for haddock (*Melanogrammus aeglefinus*) from Campana (1997). Symbols represent observed values, and lines represent fits of the logistic model for wreckfish (dotted) and haddock (solid), respectively. In both panels, error bars represent the standard errors around the means.

of a strict aging protocol for these readings, a protocol that had not been put in place before the bomb radiocarbon readings.

After completion of the consensus readings, age estimates ranged from 1 to 80 years. There was no clear pattern of bias between readers in age estimates (Fig. 2C). The CV decreased with increasing age, and the average CV for age estimates was 17.4% ($P<0.001$; Fig. 2D). The highest CV value of 75.4% occurred for fish aged as 1 year old by reader 1. When we exclude the CV for age-1 fish, because the CV is susceptible to inflation as the mean approaches 0 and only reader 1 estimated specimens to be 1 year old, the CV estimate dropped to 12.2%. The reduced CV estimates, after development of aging protocols, are in the range of CV reported by other researchers for long-lived, deepwater, difficult-to-age species (Friess and Sedberry, 2011; Harris et al., 2004).

The VBGM fit to the remaining sample of 554 wreckfish used for age and growth analysis resulted in

$$L_t = 1026(1 - e^{-0.12(t-4.96)}).$$

This result indicates that wreckfish experience rapid growth during the early years of life, attaining approximately 95% of asymptotic length, on average, by 20 years of age. After age 20, growth in length slows dramatically, and fish older than approximately 20 years in the population exhibit similar size distributions (Fig. 5).

To allow for comparison of VBGM parameters from previous age and growth studies on wreckfish, all FL measurements were converted to TL measurements and the VBGM was rerun, resulting in

$$L_t = 1071(1 - e^{-0.12(t-4.96)}). \tag{8}$$

In comparison with the 2 previous studies of wreckfish (Fig. 6, Table 2), our data indicate a more rapid growth rate at younger ages and a smaller asymptotic length.

### Natural mortality

For calculation of our $M$ estimates, we used the maximum age ($t_{ma}$=80 years) observed in the fish aged for growth curve analysis and the estimates of von Bertalanffy growth curve parameters $k$ (0.124) and $L_\infty$ (1026 mm FL). Age-constant estimates of $M$ based on the methods reported in Then et al. (2015) yielded $M$=0.088 with equation 4 and $M$=0.091 with equation 5. These 2 estimates are remarkably similar given that they are based on 2 fundamentally different estimators. The $M$ estimates from both age-varying estimators indicate a type-3 survival curve, which is common among finfish species, for North Atlantic wreckfish (Fig. 7). The Charnov et al. (2013) method yielded $M$ at age 0=0.398, and with an expected rapid decrease in $M$ values to age 15 years and a leveling off at around $M$=0.120. The Gislason et al. (2010) method (eq. 6) yielded a lower value of $M$ at age 0 ($M$=0.231), than that with the Charnov et al. (2013) method (eq. 7), but with a similar rapid decline up to age 15 years and reaching an asymptotic $M$ value of around 0.060.

For evaluation of age-varying estimators against the age-constant $M$ estimators, we compared the proportion of recruits surviving from age at full recruitment to the fishery to maximum age as estimated from each

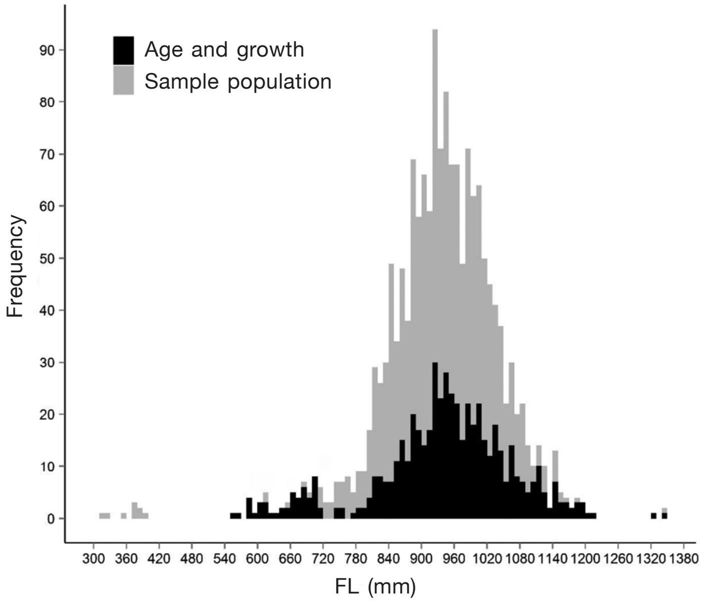

**Figure 4**

Length frequency (in 10-mm bins) of fork lengths (FLs) from the samples of wreckfish (*Polyprion americanus*) collected in the North Atlantic in 1991 and used in age and growth analysis ($n$=563; black), the data of which are overlaid on the total sample population from which these samples were randomly selected. Note that the specimens that had sizes <700 mm FL or >1100 mm FL were not randomly selected.

of the 4 methods. We defined age at full recruitment to the fishery as the age calculated for the most common (900 mm FL and 12 years old) length in the fishery-dependent samples based on our calculated VBGM. This approach resulted in 2.5%, 2.1%, 1%, and 0% recruits surviving to maximum age with Equations 4, 5, 6, and 7, respectively.

## Discussion

Age validation, here referring to confirmation of absolute age and periodicity of growth increment formation, is a crucial step for stock assessment of any fish species. Without validated age data, greater uncertainty in estimates of age-related life history parameters (e.g., growth and natural mortality) and age compositions would persist, resulting in an increase in uncertainty in stock assessment models. Particularly daunting is the task of validating the ages of long-lived fishes because few techniques are applicable to these species and most attempts have unclear results (Tracey and Horn, 1999; Harris et al., 2004). For the techniques available, Campana (2001) suggests that validation through bomb radiocarbon levels has high scientific merit and therefore is preferable to most other techniques, and only modest sample sizes (20–30 individuals) are needed.

Annual increment formation in the otoliths of wreckfish was validated by the radiocarbon dating method used in our study for wreckfish from the North Atlantic, and by the comparison with the haddock standard. As expected, with the exception of one outlier believed to have resulted from contamination, we detected no measurable radiocarbon in the otolith cores that were formed before 1958. One caveat for the use of a bomb radiocarbon technique for age validation is that it allows for validation of a maximum age only to the year of bomb radiocarbon onset (1958). Because all specimens of North Atlantic wreckfish used in this study were collected in 1991, we were able to validate a maximum age of up to 33 years with this technique. Collection and validation of age of otoliths in later years should eliminate the need for this caveat in the future. Still, the results of this study are useful today. The bomb radiocarbon technique validated the structure and annual formation of increments, indicating increment counts can successfully be used to age otoliths from wreckfish.

A distinct phase shift of approximately 5–6 years was apparent when comparing the chronology of radiocarbon levels in wreckfish with the standard chronology of haddock.

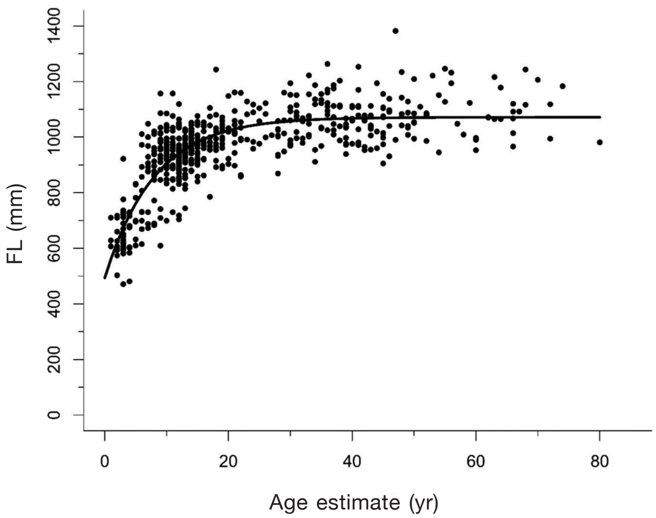

**Figure 5**

Observed length-at-age data for wreckfish (*Polyprion americanus*) collected in the North Atlantic from 2000 through 2011 used in the growth analysis. The solid line represents estimates from the fitted von Bertalanffy growth model.

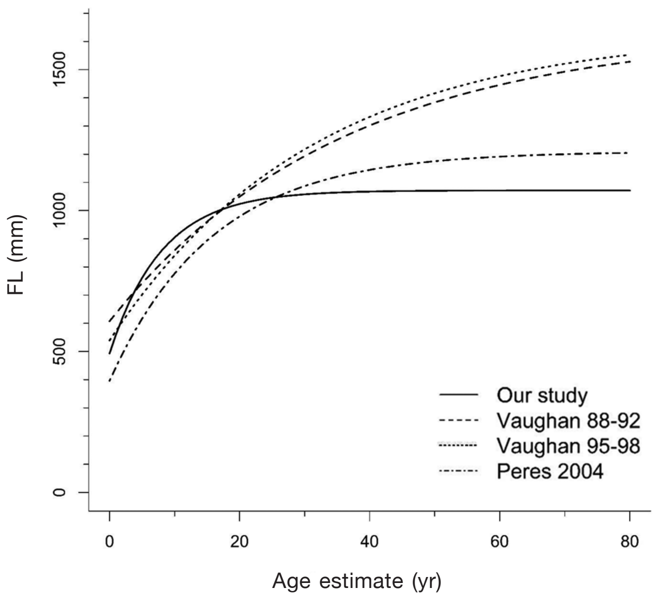

**Figure 6**

Comparison of growth curves from the fitted von Bertalanffy growth models for wreckfish (*Polyprion americanus*) from Peres and Haimovici (2004, dashed-and-dotted line), Vaughan for specimens caught in 1988–1992 (dashed line), Vaughan et al. (2001) for the specimens caught in 1995–1998 (dotted line), and the study described in this paper (solid line)

At face value, such a phase shift indicates a systematic underaging of wreckfish by 5–6 years, but Filer and Sedberry (2008) observed a similar phase shift in an age validation study performed on barrelfish (*Hyperoglyphe perciformis*) captured from the Charleston Bump. The authors hypothesized that the phase shift observed in barrelfish resulted from differences in oceanographic conditions experienced by barrelfish, compared with those experienced by haddock in the standard chronology for that species, variances caused by localized upwelling events or regional differences in onset of increases in $^{14}$C in surface waters. Because the only known spawning location for adult wreckfish in the North Atlantic is the Charleston Bump, juvenile wreckfish may also have been exposed to lower levels of radiocarbon in a given year compared with the levels to which known-age haddock captured off the eastern coast of Canada were exposed.

Researchers also have also documented a similar phase shift in bomb radiocarbon levels in the Pacific Ocean. A radiocarbon validation study performed on canary rockfish (*Sebastes pinniger*) revealed that differences in oceanographic conditions caused by upwelling caused a phase shift of 5–6 years between the radiocarbon chronologies of canary rockfish and that of a reference chronology developed from Pacific halibut (*Hippoglossus stenolepis*) (Piner et al., 2004).

Two additional sources of aging error that could explain the observed phase shift and apparent underaging in aging studies are 1) the misidentification of the first annulus and 2) the annulus overlay at older ages due to otolith section thickness. Misidentification of the first annulus could be directly related to our reliance on the aging protocol developed for the population of wreckfish in the South Atlantic by Peres and Haimovici (2004). On the basis of the daily increment counts in their study, Peres and Haimovici proposed that there were 1–3 false rings before the first annual increment. Inclusion of the false rings as annuli in our age estimates would have potentially shifted the curve to a later date, leading to a better phase agreement with the standard curve. Interestingly, such systematic underaging of wreckfish due to incorrect first annuli identification would shift the resulting growth curve along the $x$-axis and would provide a more realistic estimate of the $t_0$ parameter. Researchers have not performed

**Table 2**

Parameters from the von Bertalannfy growth model (VBGM), with associated standard errors (SE), from our study in which the converted total lengths (TLs) [see *Methods and methods* section] and from 2 previous studies on wreckfish (*Polyprion americanus*) in Atlantic ocean waters. An asterisk (*) indicates that Vaughan et al. 2001 experienced problems with convergence when trying to freely estimate VBGM parameters with data collected in 1988–1992. To alleviate this issue, they fixed $L_\infty$ to 1638 mm TL, constraining the values that the other VBGM parameters can take because of correlation among parameters.

| Source | Population | Period | Sex | $n$ | $L_\infty$ | SE | $k$ | SE | $t_0$ | SE | $t_{\max}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Our Study | North | 2000–2011 | Combined | 554 | 1071 | 6.80 | 0.124 | 0.007 | −4.96 | 0.553 | 80 |
| Vaughan et al., 2001 | North | 1988–1992 | Combined | 738 | 1638* | | 0.028 | 0.001 | −16.56 | 0.590 | 39 |
| | | 1995–1998 | Combined | 117 | 1638 | 121.92 | 0.032 | 0.006 | −12.48 | 1.760 | 30 |
| Peres and Haimovici, 2004 | South | 1986–1997 | Combined | 337 | 1210 | | 0.063 | | −6.30 | | 76 |

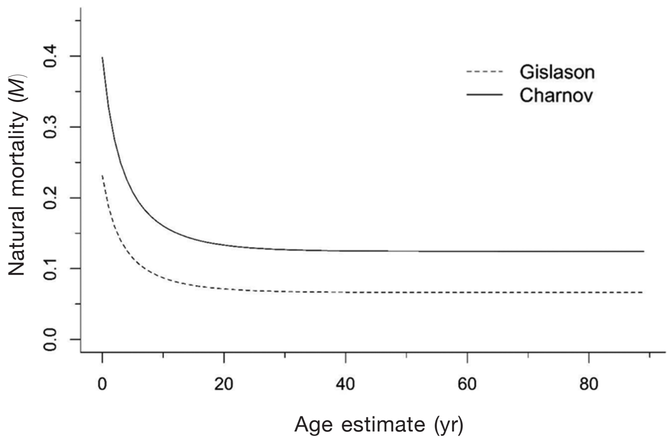

**Figure 7**

Estimates of age-varying natural mortality ($M$) for wreckfish (*Polyprion americanus*) caught in the North Atlantic from 2000 through 2011, based on the Gislason et al. (dashed line) and the Charnov et al. (solid line) methods.

daily increment analysis on North Atlantic wreckfish to validate the first annulus; therefore, no conclusion can be made as to which method is correct.

Peres and Haimovici (2004) also suggested annulus overlay could be a source of aging error in their study, with the implication being that it would cause underaging of wreckfish in a population. To investigate this possibility, Peres and Haimovici (2004) experimented with different thicknesses of otolith sections, suggesting that much thinner sections (0.11–0.15 mm for ages greater than 40 years compared with 0.2–0.25 mm for small fish [TL <75 cm]) were needed to clearly discern banding patterns in older wreckfish. Further research is warranted to determine whether the phase shift is due to regional differences in $^{14}$C concentrations, to systematic underaging of specimens that results from incorrect first annulus identification, to annulus overlay, or to other reasons.

Irrespective of the observed phase shift, we validated annual increment formation, and, having found no evidence of overaging in our bomb radiocarbon study and having identified several individuals aged over 75 years in our relatively small sample, we are confident that wreckfish are living in excess of 75 years. The maximum age observed, 80 years, is approximately twice the previously reported maximum age of 39 years (Vaughan et al., 2001). Our revised maximum age estimate is consistent with findings for the congeneric species Hapuku (63 years; Francis et al., 1999) and the South Atlantic stock of wreckfish (76 years; Peres and Haimovici, 2004). The finding that wreckfish live twice as long as previously reported by Vaughan et al. (2001) can be attributed to a difference in aging technique. We aged wreckfish using transverse otolith sections that were 0.25–0.30 mm wide, and the prior study used sections that were 0.35–0.50 mm wide (Potts[2]).

The surface of an otolith from a wreckfish is far from uniform; there are many raised bumps along the surface, and edges are often serrated. Because of the narrow width between outer increments along these irregularities, the same band may be seen along different planes when the otolith is sectioned at thicker widths. Inclusion of the same band at different planes can potentially cause a “smear,” that masks other nearby growth increments, resulting in the bands being grouped together and leading to under-estimates of ages. A similar argument was put forward to justify the use of thinner sections as reported in Peres and Haimovici (2004).

The $k$ value obtained in our study ($k$=0.124/year, sexes combined) is approximately 4 times the value previously reported for wreckfish in the North Atlantic ($k$=0.032/year and $k$=0.028/year for sexes combined for the periods 1995–1998 and 1988–1992; Vaughan et al., 2001) and double that for the South Atlantic stock ($k$=0.063/year, sexes combined; Peres and Haimovici, 2004).

All $t_0$ values reported for wreckfish are negative, and the value obtained in our study ($t_0$=−4.96 years) is similar to the values reported for the population in the South Atlantic ($t_0$=−6.30 years; Peres and Haimovici, 2004) but very different from the $t_0$ values ($t_0$=−12.48 years and $t_0$=−16.56 years for the periods 1995–1998 and 1988–1992) previously reported for North Atlantic wreckfish (Vaughan et al., 2001). The difference in $t_0$ values is most likely due to the lack of smaller, younger fish in the samples used in the Vaughan et al. (2001) study. It is expected that if samples of younger (0–3 years old) fish are available and included in an analysis, the resulting estimates of VBGM parameters would shift $t_0$ values closer to zero. As noted previously, if the phase shift observed in the bomb radiocarbon analysis is the result of systematic underaging of wreckfish by 5–6 years because of issues with first annulus identification, any such correction should result in a shift of $t_0$ toward zero.

The $L_\infty$ values obtained in our study ($L_\infty$=1071 mm TL, sexes combined) were lower than those of the population in the South Atlantic ($L_\infty$=1210 mm TL, sexes combined; Peres and Haimovici, 2004) and the stock in the North Atlantic ($L_\infty$=1638 mm TL; Vaughan et al., 2001). Note that the largest specimen (1340 mm TL) in our samples was nearly 300 mm TL smaller than the $L_\infty$ value reported by Vaughan et al. (2001), and 95% of all the specimens in our study were less than 1200 mm TL. The difference in reported $L_\infty$ values between our study and the study of the South Atlantic stock by Peres and Haimovici (2004) could simply be

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[2] Potts, J. 2014. Personal commun. NOAA Southeast Fisheries Science Center, Beaufort, NC 28516.

due to a disparity in growth between the 2 stocks. The difference in estimates between the Vaughan et al. (2001) and our study may have resulted from the lack of larger fish (>1100 mm TL) in our sample; however, the length frequency of the subsample used in age and growth analysis in our study mirrored the length frequency of our total sample population. It is more likely that the difference in $L_\infty$ values between the aforementioned study and ours was caused by incorrect age assignments, which in turn would impact the VBGM parameters. Either way, this difference in $L_\infty$ values has implications for estimating related life history parameters and highlights the importance of validation efforts, as well as the importance of the inclusion of sufficient samples from the oldest age groups when developing a VBGM.

Our samples contained only 3 specimens that were less than 500 mm FL, the proposed size at settlement for wreckfish from both the North and South Atlantic (Sedberry et al., 1998; Peres and Haimovici, 2004). The smallest specimen was 452 mm FL and was estimated to be 3 years old. The lack of smaller and younger fish (only 14 specimens <2 years old) within the sample is consistent with the notion that juvenile North Atlantic wreckfish settle at a size around 500 mm TL and at an age of 1–2 years. If juveniles are present at the same locations as adults, gear selectivity is unlikely to have excluded them from our sampling because juvenile wreckfish have relatively large mouths and would be susceptible to hook-and-line capture.

Natural mortality is a fundamental life history parameter used in stock assessments. Without a realistic estimate of $M$, fishing-induced mortality cannot be estimated from the age or size composition of commercial catches, and the effects of fishing mortality on future yields cannot be predicted. Methods used to estimate $M$ treat it either as a constant value (Pauly, 1980; Hoenig, 1983; Alagajara, 1984; Polovina and Ralston, 1987; Hewitt and Hoenig, 2005; Then et al., 2015) or as an age- or size-varying parameter (Lorenzen, 1996; Gislason et al., 2010; Charnov et al., 2013), but the latter is the generally preferred method for estimating $M$.

Although treating $M$ as a constant value has been a historically common practice, today researchers generally accept that $M$ is highest during larval stages and decreases as a fish ages, finally arriving at some steady state (Gislason et al., 2010). Assuming $M$ varies with age, managers can consider the effects of size composition when examining alternate management strategies. Data from our study indicated that age-based estimates of $M$ reached an asymptote by approximately age 15. The value of the asymptote varied according to the aging method used, ranging from 0.07 for Gislason et al. (2010) to 0.12 for Charnov et al. (2013), respectively. Most fish captured along the Charleston Bump are greater than 900 mm FL (Sedberry et al., 1999), corresponding to an age of around 10–15 years from the VBGM. If managers were to select a point estimate of $M$, because of the absence of younger age classes, it is likely that the point estimate of $M$ used to determine the allowable biological catch would fall between the asymptotic values of $M$ from the age-varying methods. This value would represent the $M$ experienced by the fished portion of the stock.

When selecting the appropriate method for estimation of $M$, researchers are faced with a daunting selection of estimation techniques, most of which involve the use of estimates of one or multiple parameters from the VBGM, $t_{\max}$, or weight-at-age data. Proper selection of a technique will first depend on the information available and then on the confidence in the accuracy of the parameter estimate being used (e.g., whether a researcher is more confident in the accuracy of the VBGM parameters or of $t_{\max}$). However, Then et al. (2015) asserts that $t_{\max}$ is the best proxy for estimating $M$ when a value is available. Because this study validated age estimates of wreckfish captured in the North Atlantic and because the $M$ estimate based on VBGM parameters ($M$=0.091) was close to the $M$ estimate that was based on $t_{\max}$ ($M$=0.088), 0.09 is an appropriate value to use for $M$ in stock assessments of wreckfish.

The new information presented here on the life history of wreckfish in the North Atlantic represents the North Atlantic stock more accurately because it is based on recent samples collected during 2000–2011, because new aging criteria and resulting estimates have been validated with bomb radiocarbon analysis, and because the new age estimates are similar to estimates for other *Polyprion* species. Several aspects of the life history of wreckfish in the North Atlantic are still in need of study. The validation of the maximum age of 80 years reported here cannot be validated by radiocarbon analysis until the year 2038. However, we have validated the aging criteria used to determine ages of wreckfish through bomb radiocarbon analysis. In addition, the structure and formation of the first annual increment needs to be elucidated and investigated because it may potentially affect age estimates by up to 3 years. Samples from the eastern Atlantic are needed to compare potential differences in life history parameters within the North Atlantic population and to investigate connectivity between populations. Finally, the determination of size and age at maturity and sex-specific differences in age and growth is essential for future stock assessments and requires samples from whole, rather than gutted, fish.

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