Age, growth, and spawning season of red bream (Beryx decadactylus) off the southeastern United States

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Abstract—Red bream (*Beryx decadactylus*) is a commercially important deep-sea benthopelagic fish with a circumglobal distribution on insular and continental slopes and seamounts. In the United States, small numbers are caught incidentally in the wreckfish (*Polyprion americanus*) fishery which operates off the southeastern coast, but no biological information exists for the management of the U.S. red bream population. For this study, otoliths (n=163) and gonads (n=161) were collected from commercially caught red bream between 2003 and 2008 to determine life history parameters. Specimens ranged in size from 410 to 630 mm fork length and were all determined to be mature by histological examination of the gonads. Females in spawning condition were observed from June through September, and reproductively active males were found year-round. Sectioned otoliths were difficult to interpret, but maximum age estimates were much higher than the 15 years previously reported for this species from the eastern North Atlantic based on whole-otolith analysis. Estimated ages ranged from 8 to 69 years, and a minimum lifespan of 49 years was validated by using bomb radiocarbon dating. Natural mortality was estimated at 0.06/yr. This study shows that red bream are longer lived and more vulnerable to overfishing than previously assumed and should be managed carefully to prevent overexploitation.

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Red bream (*Beryx decadactylus*, Cuvier, 1829) is one of three species in the genus *Beryx* (Beryciformes: Berycidae). Similar to its congener, the splendid alfonsino (*B. splendens*), red bream have a circumglobal distribution in temperate to tropical waters and are commonly found on continental shelves and slopes, seamounts, and oceanic ridges at depths of at least 1240 m (Busakhin, 1982). The third species, *B. mollis*, is restricted to the western North Pacific region and is not further discussed in this article.[1] Red bream and splendid alfonsino are commercially exploited wherever they occur in abundance, particularly in the eastern North Atlantic around the Macaronesian Islands (Large et al., 2003); in the Pacific around New Caledonia (Lehodey et al., 1997), New Zealand (Massey and Horn, 1990) and Japan (Adachi et al., 2000); and in the Indian Ocean on Saya de Malha Bank and around the Kerguelen Islands. In the eastern North Atlantic, both alfonsino species are currently caught in a multispecies, multigear fishery that targets mainly blackspot seabream (*Pagellus bogaraveo*) at depths of 200–600 m (ICES[2]). In European waters alfonsinos are managed collectively because species-specific landings data rarely exist. The status of the European stocks is currently unknown owing to short catch time series, the lack of fishery-independent data, and unreliable estimates of mortality rates, but there are reports of serial depletion of alfonsino populations during the early years of the rapidly expanding deep-sea fisheries on and around seamounts in the eastern North Atlantic (Vinnichenko, 1997; ICES[2]).

In the western North Atlantic, alfonsinos are caught incidentally off the southeastern coast of the United States in the wreckfish (*Polyprion americanus*) fishery. The fishery operates in an area of high topographic relief known as the Charleston Bump, located on the Blake Plateau south-

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[1] Because of the confusion created by regional differences in the use of common names for the *Beryx* species, the following nomenclature will be used throughout the rest of this article: *B. decadactylus* will be referred to by its American Fisheries Society (AFS) common name "red bream" (Nelson et al., 2004; FAO common name "alfonsino"), *B. splendens* by its FAO common name "splendid alfonsino" (Froese and Pauly, 2008; AFS common name "alfonsino"), and the two collectively will be called "alfonsinos."

[2] ICES (International Council for the Exploration of the Sea). 2008. Report of the working group on the biology and assessment of deep-sea fisheries resources, 3–10 March 2008, ICES Headquarters, Copenhagen. ICES CM 2008/ACOM:14., 531 p.

east of Charleston, South Carolina. The Charleston Bump is characterized by carbonate outcrops, scarps, scour depressions, and overhangs that are essential hard-bottom habitat for demersal fishes (Sedberry et al., 2001). In most global fisheries, splendid alfonsino is the most abundant *Beryx* species in the catch, but in the U.S. wreckfish fishery, red bream composes more than 95% of the alfonsino landings (senior author, personal observ.). Alfonsino landings in the United States are currently not monitored.

Life history data for red bream are sparse because research on alfonsinos has focused almost exclusively on the economically more important splendid alfonsino. A few studies have addressed both species, and it was concluded that distribution, feeding habits, reproductive parameters, age and growth, and larval development are similar (Busakhin, 1982; Mundy, 1990; Isidro, 1996; Dürr and Gonzalez, 2002). Alfonsinos are gonochoristic batch spawners (Isidro, 1996), their eggs and larvae are epipelagic, and juveniles are pelagic for several months (Mundy, 1990) before moving into deeper waters and assuming the adult benthopelagic lifestyle (Busakhin, 1982; Lehodey et al., 1994). In the eastern North Atlantic, female red bream reach sexual maturity at 276 mm fork length. The maximum age estimate for the Azores red bream population is 15 years, although ages for this species have never been validated (Isidro, 1996).

Basic biological information has not been published for the western North Atlantic red bream population. Many other deep-sea fishes have life history patterns characterized by slow growth, high longevity, and late maturity, all of which results in low productivity, high susceptibility to overfishing, and low resiliency (Merrett and Haedrich, 1997; Koslow et al., 2000; Cheung et al., 2007). Knowledge of red bream life history traits is essential for establishing the biological reference points needed for management and, in the absence of traditional stock assessments, for conducting risk assessments to evaluate vulnerability and prevent overfishing (Patrick et al., 2010).

The purpose of this study was to investigate the age, growth, and reproductive biology of red bream caught off the southeastern United States. We hypothesized that red bream attain a much higher maximum age than previously assumed, more similar to other deep-water fishes that occur on the Charleston Bump, such as barrelfish (*Hyperoglyphe perciformis*) and blackbelly rosefish (*Helicolenus dactylopterus*), which have estimated longevities of 85 and 30 years, respectively (White et al., 1998; Filer and Sedberry, 2008). Another goal of the study was to validate high red bream age estimates obtained through the interpretation of thin-sectioned otoliths. We used bomb radiocarbon dating, a method that has previously been successfully applied to validate ages for other long-lived fishes (Kalish et al., 1997; Kerr et al., 2005; Piner et al., 2005). We used age estimates to determine growth parameters and estimate natural mortality rate. The life history parameters presented here provide critical inputs for stock assessments, risk analyses, and for determining biological reference points. This information is needed if red bream become a target for the fishery and need to be included in a fishery management plan in the future.

Materials and methods

Collection of samples

Red bream landed by the commercial wreckfish fishery operating on the Charleston Bump (approximately 31°30′N, 79°W) were sampled from April 2003 to January 2008. All specimens were caught by vertical line fishing in depths of 450–600 m (Sedberry et al., 1999) and iced on the vessel until arrival at port. Every red bream caught on a fishing trip was sampled during a port sampling trip. For each specimen, total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter, and total body weight (TBW) was recorded in grams. Sagittal otoliths were extracted and stored dry in envelopes for age and growth analysis, and the entire gonad was removed and placed in 10% buffered formalin for histological analysis. In addition, otoliths and fork lengths from 22 small ($FL \leq 400$ mm) specimens collected from the Azores were provided by Gui Menezes of the Departamento de Oceanografia e Pescas (DOP), University of the Azores. These otoliths were examined to aid with aging technique development because initial counts of age increments for Charleston Bump otoliths were much higher than ages previously reported for eastern North Atlantic red bream.

Age and growth

Sagittal otoliths were weighed to the nearest milligram, and either the right or left otolith (depending on the condition of the otolith) was embedded in epoxy resin. A Buehler Isomet low-speed saw (Buehler Ltd., Lake Bluff, IL) with a diamond wheel was used to cut transverse sections of approximately 0.6–0.7 mm thickness through the focus. Sections were mounted on glass slides with Cytoseal mounting medium and viewed under a Nikon SMZ-U dissecting scope (Nikon Instruments Inc., Melville, NY) with transmitted and reflected light.

Exploratory readings were conducted along ventral and dorsal axes toward the proximal edge of the otolith. Increments were counted independently by two readers, without knowledge of fish length or sex, and both readers rated the readability of otoliths. After the exploratory readings, the first reader made two counts (readings) over the period of several weeks to assess within-reader precision, and the second reader made one count. When ages were compared between readings and readers, both readers decided to jointly recount all otoliths because of the large variation in assigned ages for some otoliths between the two readers. During the joint count, both readers agreed that there had been an error in the second reader's interpretation of the first growth bands and, therefore, the joint count was substituted for the second reader's count in all subsequent analyses and will be referred to as “reading 3” throughout the rest of this article.

Thin sections from two otoliths were polished to the core and presumed daily growth rings were counted under 40× magnification to help with the interpretation of what was thought to be the first annulus. Presumed daily growth rings were not validated. In addition to thin section interpretation, some of the uncut second otoliths were randomly selected and viewed whole under the dissecting microscope to qualitatively evaluate the ease of determining growth bands on the whole otolith surface.

To validate ages, eighteen of the uncut, second otoliths were selected for bomb radiocarbon analysis. These otoliths were chosen for readability and to span the range of observed ages that were based on thin section growth band counts, including otoliths from specimens with estimated birth years spanning the prebomb to postbomb period. The selected otoliths were embedded in epoxy resin and sectioned transversely through the core to 1 mm thickness. The sections were then taped to plates, and the cores were isolated by using a Dremel model 221 variable speed rotary tool (Robert Bosch Tool Corporation, Mt. Prospect, IL). Core isolation was visually aided because the central opaque area of the first year of growth in red bream otoliths is clearly visible on whole and sectioned otoliths.

The extracted cores were rinsed in 10% HNO_3 for 15–30 s, ultrasonically cleaned with a Branson ultrasonic cleaner B-22-4 (Branson Ultrasonics Corporation, Danbury, CT) with distilled water, air-dried, and weighed to the nearest 0.1 mg (Baker and Wilson, 2001). Each core was placed in a glass vial that had been cleaned with 10% HNO_3, and the samples were sent to the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) laboratory at Woods Hole Oceanographic Institution. NOSAMS provided values of delta Carbon-14 ($\Delta^{14}C$) for each sample that were then plotted against otolith-derived birth years and compared to a reference chronology of validated ages for haddock (*Melanogrammus aeglefinus*) collected from Newfoundland (Campana, 1997). The timing of initial radiocarbon increase and mean year of increase were calculated with the deterministic model developed by Hamel et al. (2008) which models the pulse of radiocarbon from nuclear testing as a Gaussian curve over time and couples it with a continuous exponential decay process to describe radiocarbon dispersion and dilution.

Aging precision and bias between paired readings were examined graphically with age bias plots, and the coefficient of variation (CV) was calculated as a measure of the relative ease of aging red bream otoliths (Campana et al., 1995). Age frequencies were computed, and a standard linear regression relating increment count to otolith weight was also conducted. The von Bertalanffy growth function (VBGF; von Bertalanffy, 1938) was fitted to unweighted length-at-age data by using a random effects (RE) model with gamma population distribution likelihood as implemented in the program IGOR+, a Microsoft Excel®-based application developed by Cope and Punt (2007). The random effects model is based on a likelihood function that takes into account multiple reads for each otolith and thus incorporates both process and interpretation error into growth parameter estimations (Cope and Punt, 2007). Age and length information from all three readings could therefore be included in the estimation of the VBGF. The standard von Bertalanffy growth parameters k (the Brody coefficient), L_∞ (the theoretical mean maximum length), and t_0 (the theoretical age at length zero) were calculated with IGOR+ program. The model was run separately for males and females and for both sexes combined. The resulting sex-specific growth functions were compared by using likelihood tests (Kimura, 1980). An additional run was made including the age and length data for the 22 specimens from the Azores to assess how much the model parameters would change by including the smaller fish.

Natural mortality was estimated by using the equations developed by Hoenig (1983) and Pauly (1980) and by using the IGOR+ program. Hoenig’s longevity-based estimator, $\ln Z=1.46–1.01 \ln^*(t_{max})$, uses maximum age ($t_{max}$), and Pauly’s equation, $\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} k + 0.463 \log_{10} T$, uses von Bertalanffy growth parameters and water temperature, T, which in this case was the average annual water temperature for *Beryx* habitat from the literature. IGOR+ calculates total mortality by using the catch curve of the gamma-distributed “true ages” estimated in the RE model.

Reproductive biology

Gonads were weighed and processed according to the standard procedure used by the Marine Resources Monitoring Assessment and Prediction (MARMAP) Program at the Marine Resources Research Institute of the South Carolina Department of Natural Resources (White et al., 1998). A portion of the posterior gonad was removed, fixed in 10% formalin for 7–14 days, and transferred to 50% isopropanol for an additional 1–2 weeks. Tissues were then dehydrated, cleared, and blocked in paraffin under vacuum infiltration by using a Leica ASP300 tissue processor (Leica Microsystems Inc., Bannockburn, IL). Blocks were allowed to cool in a freezer, and three 7-µm cross sections were cut with a Leica RM2255 rotary microtome (Leica Microsystems Inc., Bannockburn, IL). These sections were then transferred to a microscope slide and allowed to dry overnight before they were stained with hematoxylin and eosin. The sections were viewed and interpreted under a Nikon Eclipse 55i compound microscope (Nikon Instruments Inc., Melville, NY), and reproductive stages were assigned independently by two readers without knowledge of specimen age, length, or collection date, according to criteria described by Harris et al. (2004). Females in spawning condition were identified by the presence of hydrated oocytes and postovulatory follicles. Specimens, for which interpretation between readers differed, were re-examined jointly, and a consensus was reached. Spawning seasonality was determined by plotting monthly frequencies of reproductive stages.

Results

Data from samples

Of the 165 red bream sampled from the commercial fishery between April 2003 and January 2008, otoliths were collected from 163 specimens, gonads from 161, and fork length was measured for 164 fish (one specimen had a damaged tail). Otolith weights were obtained for 130 otoliths. No specimens could be sampled from the fishery in February and March in any year over the sample collection period because the wreckfish fishery is closed from January 15 through April 15. Sample sizes were highest for the months of July, August, September, and December (n=23–30) and lowest for April, October, and November (n=4–8). Because of low sample sizes, samples were pooled across years.

Fork lengths ranged from 410 to 630 mm and were not normally distributed (Shapiro-Wilk test; $P<0.001$; Fig. 1). Thus, the median FL more accurately describes the central tendency of the data set. Male FLs ranged from 410 to 601 mm (n=61), and female FLs ranged from 420 to 630 mm FL (n=98) (Fig. 1). The median FL for males (538 mm FL, standard error [SE]=7) was significantly different from that of females (550 mm FL, SE=5; 2-tailed Wilcoxon rank sum test, $P=0.017$). Strong linear relationships for both sexes were detected between FL and TL (males: $TL=1.05FL+63.79$, $r^2=0.983$; females: $TL=1.03FL+73.32$, $r^2=0.973$), FL and SL (males: $SL=0.91FL+0.25$, $r^2=0.983$; females: $SL=0.91FL-5.44$, $r^2=0.970$), and FL and TBW (males: $TBW=17.52FL-5588.2$, $r^2=0.952$; females: $TBW=20.74FL-7323.1$, $r^2=0.949$). The otoliths provided from the Azores corresponded to fork lengths ranging from 190 to 400 mm.

Age and growth

On whole otoliths, growth increments were best visible on the anterior edge of the antisulcal surface close to a large, central opaque area but became virtually indistinguishable closer to the otolith margin, especially in older specimens. Age determinations based on whole otoliths were therefore not attempted. In a few cases, one of the two otoliths collected from a specimen was misshapen, and crystals were clearly visible as lumps on the otolith surface. The second otolith would look normal and was used for aging.

Thin transverse sections of red bream otoliths contained a large central opaque area, and the count of assumed daily growth rings indicated that the translucent zone outside the central opaque area marks the first annulus (first otolith: 389 daily rings, second otolith: 371 daily rings). Thin sections of red bream otoliths contained a transition zone where increment width notably decreased and otoliths started increasing in thickness on the proximal surface rather than growing along the dorsoventral and anterioposterior axes (Fig. 2, A and B).

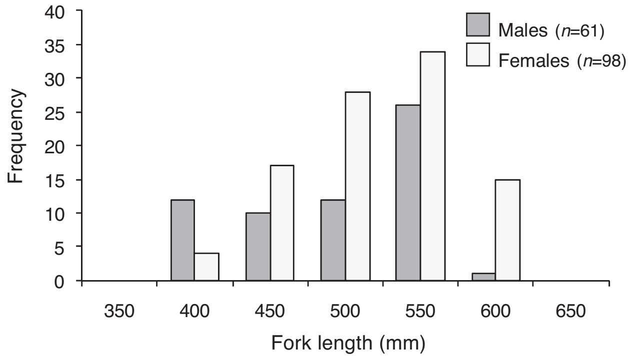

Figure 1

Length distribution of male and female red bream (*Beryx decadactylus*) sampled from the commercial wreckfish fishery off the southeastern United States from 2003 to 2008.

Thin sections of red bream otoliths had poor clarity and were difficult to interpret. Bands were often unclear, split, or irregularly spaced, and increments became thinner and harder to see toward the edge of the otolith. The dorsal axis next to the sulcus acousticus was chosen as the preferred axis for aging because the banding pattern was most distinct there. In many otoliths readability decreased at various points along the chosen axis, and counting had to be shifted away from the sulcus and toward the dorsal tip by following an increment over to the new axis. Often, increments, both close to the core and toward the edge of the otolith, were difficult to interpret in older as well as younger specimens because they were so poorly defined. In addition, semicrystalline fields were apparent in a number of thin sections, which added to difficulty in interpretation.

Even though red bream otoliths were overall difficult to age, there were no otoliths in the sample that were identified as unreadable by both readers and, therefore, all otoliths were aged and used in the analysis. Estimated ages ranged from 8 to 64 years for reading 1, 10 to 71 years for reading 2, and 9 to 69 years for reading 3. The age variation for individual otoliths between readings was high and ranged from 0 to 23 years, with a mean difference of 4 years. The age bias plots revealed that increment counts from reading 1 tended to underestimate age with respect to reading 2, increasingly so at ages 30 and higher (Fig. 3A). Reading 3 tended to underestimate ages 36 and higher with respect to reading 2 (Fig 3B), and reading 1 underestimated ages compared to reading 3, particularly ages up to 40 (Fig. 3C). Pairwise comparisons of CVs were highly variable across ages but tended to decrease with increasing age (Fig. 3, D–F). The mean pairwise CV was lowest between readings 2 and 3 at 8.6%, and highest between readings 1 and 2 at 12.2%. The mean CV across all three readings was 12.1%. Low aging precision was mostly due to overall poor clarity of otoliths and poorly defined bands. In addition, interpretation of growth bands close to the core was often particularly difficult, leading to high CVs, especially for younger fish. Bands towards otolith margins were also often difficult to distinguish.

Bomb radiocarbon analysis resulted in negative Δ^{14}C values ranging from −42.6‰ to −67.8‰ for fish estimated to have hatched before the mid-1960s, followed by rapid accumulation of Δ^{14}C over the period of atmospheric radiocarbon increase, to a peak of 93.4‰ in 1974 and a subsequent decline of Δ^{14}C levels in recent years (Table 1). The red bream Δ^{14}C chronology followed a similar pattern to that of the reference chronology for haddock from Newfoundland but was shifted by about five years to later years (Fig. 4). The year of initial radiocarbon increase was 1963, which is about five years later than that for haddock. Similarly, the mean year of radiocarbon increase for red bream was 1968, which is six years later than that for haddock (Table 2). Overall, bomb radiocarbon results supported the interpretation of growth increments as annual growth rings. In addition, a strong linear relationship was detected between otolith weight and age (r^2=0.845; n=130), which further supports otolith interpretation.

The von Bertalanffy growth curve fitted to males differed slightly from that fitted to females, and likelihood ratio tests indicated that growth functions were significantly different (χ^2=19.56, df=3, P<0.001; Fig. 5A), even though individual growth parameters were not. Sex-specific VBGFs were: $L_t=573.5(1-e^{-0.0.079(t-(-6.11))})$ for males, and $L_t=597.8(1-e^{-0.080(t-(-6.51))})$ for females. The combined VBGF for western North Atlantic red bream was: $L_t=583.1(1-e-^{-0.094(t-(-3.69))})$. The growth coefficient was almost identical between males (k=0.079/yr, standard deviation [SD]=0.014) and females (k=0.080/yr, SD=0.017), but was higher for the combined sexes (k=0.094/yr, SD=0.013). In addition, females attained larger maximum theoretical lengths than did males (females: L_∞=597.8 mm, SD=10.310; males: L_∞=573.5 mm, SD=7.551). All three growth curves are depicted in Figure 5A and show that red bream growth is rapid in the first years of life, then slows down until asymptotic length is reached at about 580 mm FL or age 35 (Fig. 5A). The addition of the 22 specimens from the Azores (mean ages ranged from 1.5 to 10.5 years) did not have an appreciable effect on VBGF parameters; it merely increased k slightly to 0.100/yr.

The age-frequency distribution based on reading 3 was multimodal for both sexes. Most males caught on the Charleston Bump fell into the age groups between 11 and 20 years and 36 and 50 years and another slight peak occurred in the highest age group, 66–70 years. The females were most abundant in the age groups from 11 to 30 years and showed another slight increase in abundance from 41 to 50 years (Fig. 5B).

Mortality estimates were calculated for the combined sexes by using the maximum age estimate from reading 3 and von Bertalanffy growth parameters for the combined-sex growth curve. Total mortality (Z) based on Hoenig's equation was calculated as Z=0.06/yr by using 69 years, the maximum age estimate from growth band count, as t_{max}. With IGOR+ program, we also es-

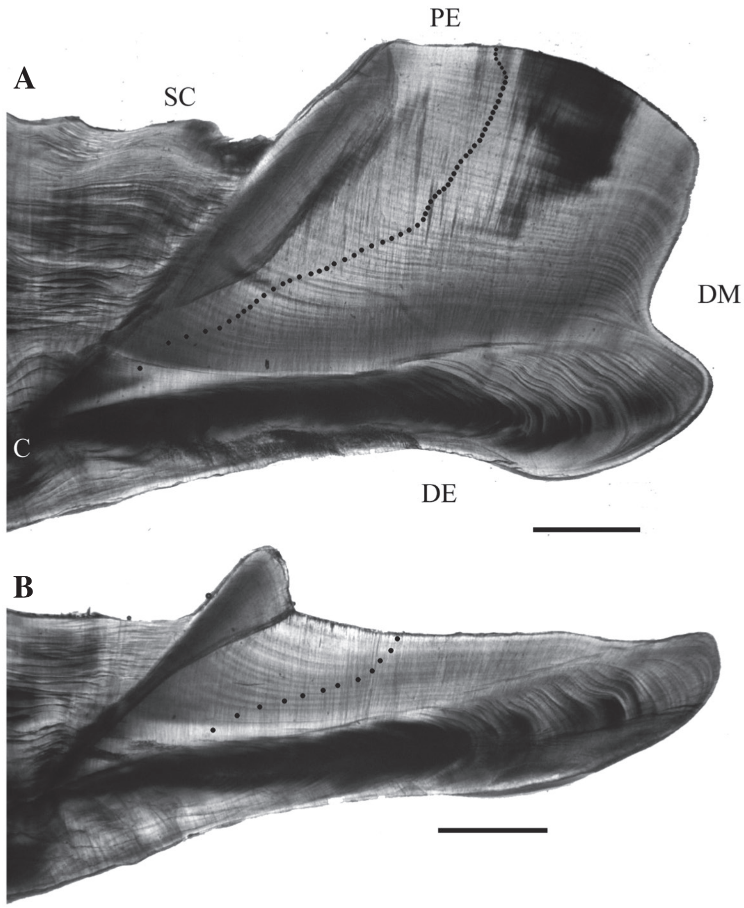

Figure 2

Transverse sections of sagittal otoliths under transmitted light showing (**A**) a male red bream (*Beryx decadactylus*) (fork length=567 mm) estimated to be 61 years old; C=core, SC=sulcus acousticus, DM=dorsal margin, PE=proximal edge, DE=distal edge; (**B**) a female specimen (fork length=502 mm) estimated to be 12 years old. Each dot represents a growth band (scale bar=1 mm).

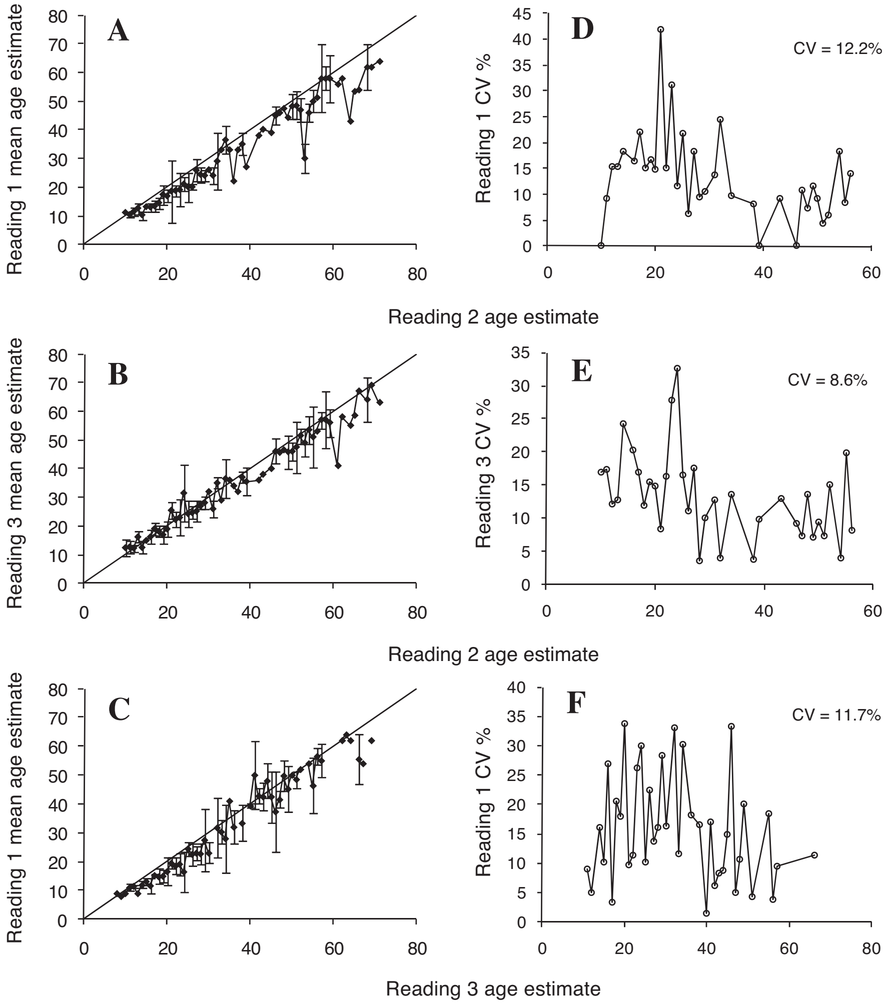

Figure 3

Pairwise comparisons of aging precision between readings of red bream (*Beryx decadactylus*) otoliths. (**A**) Mean age estimated in reading 1 for all fish assigned a given age in reading 2; (**B**) mean age estimated in reading 3 for all fish assigned a given age in reading 2; and (**C**) mean age estimated in reading 1 for all fish assigned a given age in reading 3. Error bars represent 95% confidence intervals and the solid line is the 1:1 relationship. (**D**) Coefficient of variation (CV) of reading 1 with respect to ages estimated in reading 2; (**E**) CV of reading 3 with respect to ages estimated in reading 2; and (**F**) CV of reading 1 with respect to ages estimated in reading 3. Mean CVs for pairwise readings are indicated on the individual panels.

timated a total mortality value of 0.06/yr. Estimates of *M* based on Pauly's equation were strongly influenced by the choice of mean water temperature value and ranged from 0.097 to 0.124/yr (Table 3).

Reproductive biology

Histological samples were obtained from 161 fish, of which 98 were female, 62 were male, and the sex of one specimen could not be determined. The overall sex ratio was 1:1.58 (M:F). All specimens sampled in this study were mature, and, therefore, a size and age at 50% maturity could not be established for the Charleston Bump red bream population.

Ovaries of resting females clearly showed characteristic thick, muscular walls, elongate lamellae with well-developed fibromuscular cords, and wide spaces between lamellae (Fig. 6A). Ripe females were often difficult to distinguish from individuals in the late developing stage because hydrated oocytes were few and always accompanied by oocytes in all stages of development (Fig. 6B). Female red bream in spawn-

Table 1

Summary of radiocarbon ($\Delta^{14}C$) results from red bream (*Beryx decadactylus*) otoliths collected off the southeast coast of the United States. NOSAMS accession no.= identification number assigned by the Woods Hole National Ocean Sciences Accelerator Mass Spectrometry Facility.

NOSAMS accession no.	Collection year	Birth year	Sample weight (mg)	Reading 1 age (yr)	Reading 2 age (yr)	Reading 3 (joint) age (yr)	$\Delta^{14}C$ (‰) (±error)
OS-67042	2007	1945	81.1	62	62	62	–61.5 (3.2)
OS-66866	2007	1951	40.6	58	59	56	–54.1 (4.0)
OS-66870	2006	1952	52	54	62	54	–62.1 (3.6)
OS-67041	2006	1958	56.5	48	50	48	–52.3 (2.9)
OS-66869	2007	1959	48.4	54	55	48	–67.7 (3.6)
OS-68036	2004	1959	74	38	43	45	–42.6 (3.3)
OS-68037	2005	1963	56.9	41	47	42	–67.8 (2.8)
OS-66868	2005	1964	86.6	44	50	41	–65.7 (3.2)
OS-68041	2004	1966	85.1	37	38	38	–18.7 (3.1)
OS-68142	2006	1966	152.3	40	43	40	–25.3 (3.7)
OS-68035	2003	1967	75.3	24	32	36	–14.4 (3.2)
OS-66867	2005	1969	42.7	33	38	36	–48.6 (3.6)
OS-68038	2006	1970	99	38	42	36	–34.3 (3.2)
OS-66998	2004	1974	39.6	23	29	30	–93.4 (4.1)
OS-68034	2005	1982	75.5	18	27	23	–67.0 (3.6)
OS-67038	2004	1989	35.6	11	11	15	–89.8 (4.1)
OS-68040	2003	1989	77.2	14	19	14	–85.7 (5.1)
OS-67040	2005	1991	70.6	10	11	14	–82.6 (3.4)

ing condition, based on the presence of hydrated oocytes and postovulatory follicles (Fig. 6C), were observed from June through September (Fig. 7A). There was one female for which reproductive stage could not be assigned because of poor quality of the histological sample.

There were five males that were determined to be mature, but reproductive stages could not be assigned even though spermatozoa were detected because the samples were mostly duct tissue. Consequently, those five males could not be included in the analysis of spawning seasonality. For one additional male there was not enough tissue to determine either a reproductive or maturity state, but it is unlikely that this male was immature, because it was neither one of the smallest nor one of the youngest males in the sample. Males in spawning condition, as indicated by the predominance of spermatozoa in ducts and lobules, were observed in all months for which male reproductive stages could be assigned. No resting males were present in the sample, but spent males were observed in July, August, November, December, and January (Fig. 7B).

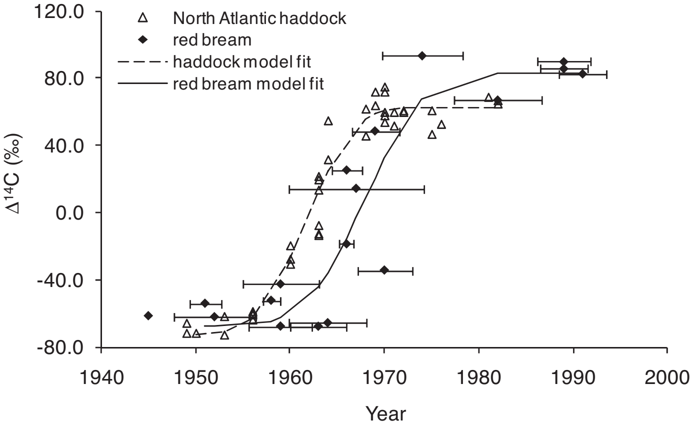

Figure 4

Radiocarbon ($\Delta^{14}C$) values plotted against otolith-derived estimates of birth year for red bream (*Beryx decadactylus*) from reading 3. Horizontal bars represent the CV of the age estimate for each sample. The reference chronology is shown for haddock (*Melanogrammus aeglefinus*) from Newfoundland (Campana, 1997). The best fit of Hamel et al.'s coupled-functions model to the otolith radiocarbon data is represented by the solid line for red bream and by the dashed line for haddock.

Table 2

Estimated parameters and derived quantities from a deterministic coupled-functions model fitted to otolith radiocarbon series for red bream (*Beryx decadactylus*) and haddock (*Melanogrammus aeglefinus*) from the North Atlantic (Campana, 1997). Parameters are total inputted radiocarbon (k), mean year of increase (μ), standard deviation of the cumulative normal (σ), estimated timing of initial radiocarbon increase (μ–σ), exponential rate of decay (r), minimum radiocarbon level observed (y_{min}), and maximum radiocarbon level that would occur in the absence of r (y_{asym}). Standard deviations (SD) are giving in parentheses, y_{min} has no SD because it is an observed point, and y_{asym} and k have the same SD.

Species	k (‰)	μ (year)	σ	μ–σ (year)	r	y_{min} (‰)	y_{asym} (‰)
Red bream	150.97 (8.64)	1967.94 (0.75)	4.87 (1..13)	1963.07 (1.59)	0	–67.8	83.17
Haddock	136.94 (6.24)	1961.81 (0.26)	3.93 (0.36)	1957.88 (0.49)	0.001 (0.004)	–72.8	64.14

Table 3

Estimates of natural mortality rates for red bream (*Beryx decadactylus*). Maximum ages used for Hoenig's estimator are 69 years based on otolith section interpretation and 49 years based on highest validated age in this study. L_∞ and k used for Pauly's equation were 583.1 mm and 0.094/yr, respectively, from the combined-sex von Bertalanffy growth function. The IGOR+ estimate is based on the random effects model with gamma-distributed population likelihood for all three readings and for both sexes combined.

Model		M (1/yr)
Hoenig (1983)	t_{max}=69 years	0.060
	t_{max}=49 years	0.085
Pauly (1980)	T=8.85°C [*]	0.097
	T=12.3°C [†]	0.113
	T=15.0°C [‡]	0.124
IGOR+		0.060

[*] Average of the range (5.4–12.3°C) reported by Ross (2007) for southeastern U.S. deep-water coral habitat.

[†] Mean bottom temperature recorded on *Beryx* fishing habitat during submersible dives in August 2003 and 2004 (G. Sedberry, unpubl. data).

[‡] Mean temperature recorded during submersible dives when red bream were present at site (G. Sedberry, unpubl. data).

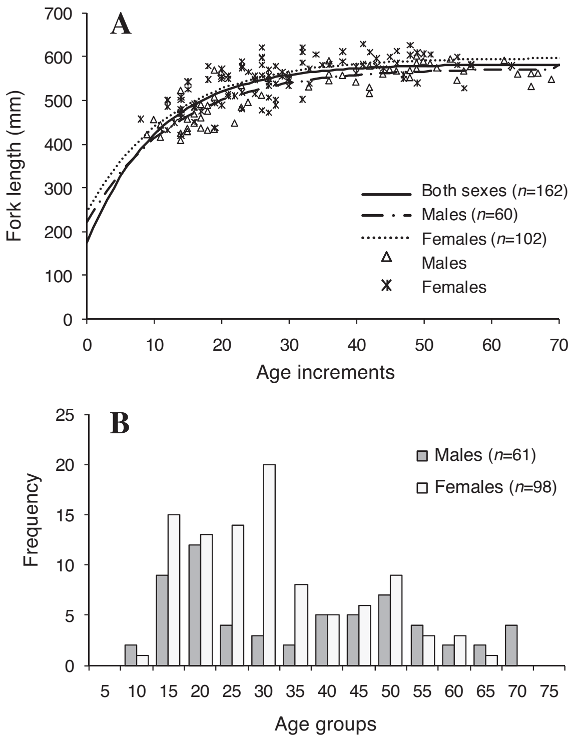

Figure 5

(**A**) Von Bertalanffy growth curves estimated from length-at-age data for Charleston Bump red bream (*Beryx decadactylus*), for males, females, and both sexes combined, and (**B**) age-frequency distribution of male and female red bream sampled from the commercial wreckfish fishery off the southeastern United States from 2003 to 2008.

Discussion

Age and growth

The presence of semicrystalline fields in a number of red bream otoliths is indicative of a partial replacement of the normal aragonite crystalline structure by vaterite, a calcium carbonate isomorph that has optical properties different from aragonite. The presence of vaterite in fish otoliths gives them a glassy and more translucent appearance and can mask usual growth banding patterns (Tomas et al., 2004; Solomon et al., 2006). Vaterite in red bream otoliths likely contributed to the aforementioned difficulties in aging that led to age estimation bias and lower aging precision than the average for otolith-derived age estimates reported by Campana (2001). The level of aging precision reported here for red bream was more similar to that achieved in other deep-sea teleost aging studies (Francis et al., 1998; Harris et al., 2004; Filer and Sedberry, 2008).

Even though interpretation error in the current study was present and significant, bomb radiocarbon

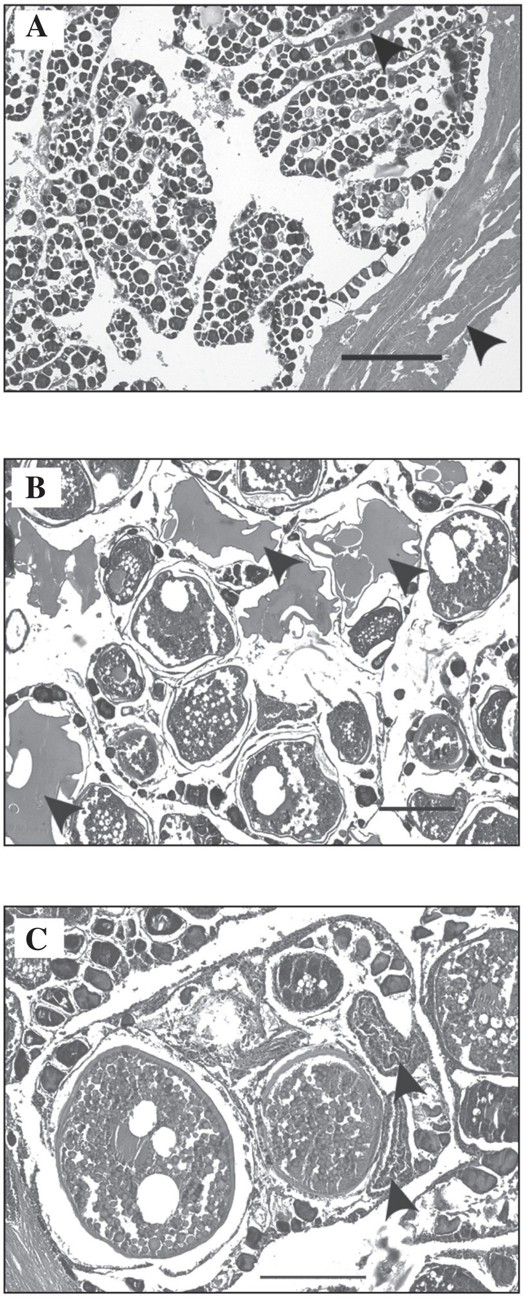

Figure 6

Transverse sections of red bream (*Beryx decadactylus*) ovarian tissue. (**A**) Ovary of resting female containing primary growth oocytes. The top arrow indicates the thickened fibromuscular cord inside long lamellae and wide spaces between lamellae; the bottom arrow indicates the thick ovary wall (bar=500 µm). (**B**) Ovary of a ripe female containing hydrated oocytes (indicated by arrows; bar=300 µm), and (**C**) ovary of a ripe female depicting 12–24 h old postovulatory follicles (indicated by arrows; bar=200 µm).

dating supported maximum ages much higher than previously reported for this species. The Δ^{14}C data also indicate that red bream in this study have been underaged by about 5 years. This is evidenced by the observed phase shift of the red bream chronology compared to the haddock reference and by the discrepancy between the two chronologies in initial and mean year of radiocarbon increase (Table 2). It is unlikely that this observed lag is due to depth-related differences in the ^{14}C signal for several reasons. First, red bream have a long pelagic juvenile stage (Mundy, 1990) which indicates that red bream and haddock experience similar environments in North Atlantic surface waters during otolith core formation. Second, the central opaque area of the first annulus in red bream otoliths is quite large and thus facilitated core extraction and reduced the likelihood that inaccurate coring was responsible for the observed phase shift. All core weights were less than the weight that was obtained for an otolith from the Azores aged to be one year old, which further indicates that coring was accurate. The bias between red bream and haddock Δ^{14}C chronologies is therefore likely due to aging error. Nevertheless, we were able to validate a minimum estimate of 49 years for red bream maximum age through bomb radiocarbon dating. In spite of the underaging indicated by the Δ^{14}C chronology shift, the bomb radiocarbon results support the annual nature of observed growth bands and, therefore, empirical age estimates of up to 69 years derived from the count of growth bands on sectioned otoliths are plausible. The positive linear relationship with a high coefficient of variation between otolith weight and estimated fish age lends additional support to maximum age estimates of 60+ years. It seems likely that red bream longevity exceeds the maximum age that can be validated with bomb radiocarbon dating. A different validation method, such as lead-radium dating which is more suitable to extremely long-lived fishes would, therefore, be more appropriate for estimating red bream lifespan (Andrews et al., 2009).

The maximum estimated age for red bream reported here is more than three times greater than previous estimates from the eastern North Atlantic (Isidro, 1996). This discrepancy could be due to underaging in previous studies, sampling bias, or it could be a reflection of a true difference in population age structure on opposite sides of the North Atlantic. Aging error is likely a contributing factor. Previous investigations of red bream age and growth from the eastern North Atlantic are based on whole otolith analysis and have not been validated. Isidro (1996) mentioned the limitations of aging larger and older red bream through whole otolith analysis and stated that his reported maximum age of 15 years should be considered a minimum estimate of longevity for this species because otoliths from larger specimens often had to be removed from the analysis due to reading difficulties. Isidro used marginal increment analysis to validate the periodicity of growth increment formation, but this method is

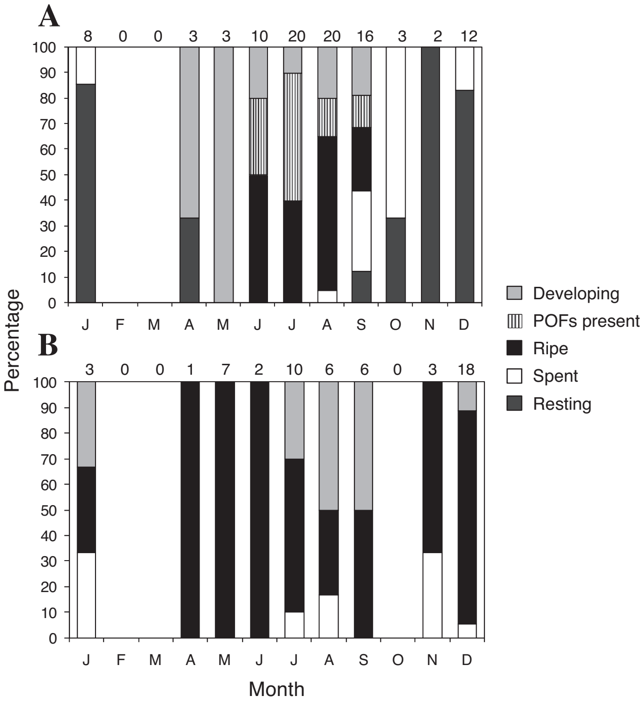

Figure 7

Percentages of reproductive stages observed for (**A**) female (n=97) and (**B**) male (n=56) red bream (*Beryx decadactylus*) collected from the commercial fishery operating around the Charleston Bump from 2003 to 2008. Sample sizes for each month are indicated above the bars. POF=postovulatory follicle.

limited to young, fast-growing fish and can lead to serious aging error if used incorrectly (Campana, 2001). Beamish (1979) showed that ages determined from the surface of otoliths tend to underestimate true ages when compared to age estimates derived from transverse sections, and there are several examples in the literature of deep-sea fishes for which ages have been severely underestimated by whole otolith analysis in the past. Orange roughy (*Hoplostethus atlanticus*) for example, was once thought to live up to 20 years, but a centenarian life span has since been validated for this species through lead-radium dating (Andrews et al., 2009). Bennett et al. (1982), also using lead-radium dating, showed that ages estimated from sectioned otoliths greatly exceeded those from whole otoliths for the rockfish genus *Sebastes*.

Although underaging of older fish was likely a factor contributing to the discrepancy in longevity estimates reported here, there was little overlap in observed fish lengths between this and previous studies, which limits our ability to make direct comparisons. Seventy-three percent of the fish sampled in this study had fork lengths of 500 mm or more, and none measured less than 410 mm FL. Conversely, fish from the Azores aged by Isidro (1996) were as small as 200 mm FL, but none reached 500 mm FL (Isidro, 1996). It is beyond the scope of this article to fully investigate the reason for this pattern in size differences, but evidence indicates that sampling bias may not be the primary explanation. In a recent study published by Menezes et al. (2009) sampling was undertaken at seamounts in the eastern North Atlantic with longlines at depths of up to 2000 m, but red bream were caught at a similar depth range to that in which the Charleston Bump fishery operates, roughly 450–600 m. The largest red bream caught in the study by Menezes measured 47 cm, which is still much less than the average length reported in our study. The observed size difference on opposite sides of the North Atlantic could thus be indicative of a true difference in population age and size structure.

The parameters of the red bream VBGF reported here for the combined sexes vary slightly from those reported by Isidro (1996) for the Azores. Isidro's L_∞ of 56 cm is 20 cm less than what was found in this study, a reflection of the smaller sizes of specimens observed in the eastern North Atlantic. Isidro estimated a k of 0.107/yr, which is slightly higher than the 0.094/yr reported here. In addition, the t_0 of –3.69 reported here is more negative than the –2.83 years reported for Azores red bream, and this is probably due to a lack of specimens younger than 8 years in the present study, resulting in a less accurate estimation of the initial slope of the VBGF. We cannot say with certainty whether the observed differences of growth parameters are driven by differences in population dynamics or missing age groups in the analysis.

We found that male red bream were more abundant than females at smaller sizes but females predominated in the higher size classes. In previous studies on splendid alfonsino from the eastern North Atlantic, similar size distribution differences between the sexes were reported. This differential size and sex relationship was attributed to findings of slower growth in males and a distribution shift to greater depths with increasing size for this species which would result in skewed sex ratios when sampling over small depth ranges (Massey and Horn, 1990; Lehodey et al., 1994; Lehodey et al., 1997). We did not detect a difference in growth rates between male and female red bream, but the observed size frequency pattern and the lack of significance in growth rate differences from this study could be due to small sample sizes and low aging precision.

Spawning seasonality

All red bream specimens sampled from the Charleston Bump between 2003 and 2008 were sexually mature. These findings are in sharp contrast to maturity stages observed in the eastern North Atlantic, where the vast majority of specimens were immature, resting, or developing (Isidro, 1996). This is not surprising, given the observed differences in red bream size ranges between the eastern and western North Atlantic. Isidro (1996) reported a length at 50% maturity of 276 mm FL for females, which is well below the size of the smallest female observed in this study (420 mm FL). Isidro did not detect population-level spawning aggregations around the Azores and observed only very few females in spawning condition. In addition, he reported that the ovaries of the few spawning females that he observed contained only small numbers of hydrated oocytes, whereas all other oocytes were in previtellogenic condition, and therefore he concluded that only one batch of oocytes developed at a time. The ovaries of Charleston Bump females, however, contained oocytes in nearly all stages of development during the spawning season, indicating that several clutches of oocytes develop simultaneously. Male red bream on the Charleston Bump seem to be spawning year-round, but sample sizes for males were very low for some months in our study, and no data were available for February, March, or October. More samples need to be collected before any conclusive statements about the seasonality of male spawning activity on the Charleston Bump can be made.

Implications for fishery management

Red bream landings in the southeastern United States are presently not monitored, and the species is not under federal management because it is currently caught only in very small numbers as bycatch in the wreckfish fishery. In 2007, the Charleston Bump was the only area with reported wreckfish landings in the southeastern United States, and only one vessel participated in the fishery (J. McGovern, personal commun.[2]). U.S. red bream landings are so few that the population can probably be considered to be at near-virgin biomass levels. This means that natural mortality (M) can be directly estimated from Hoenig's total mortality equation and the algorithm in IGOR+, because Z approximates M in unfished populations. Natural mortality estimates are important input parameters for stock assessment models and are also commonly used in calculating reference points for fishery management, such as minimum stock size threshold (the biomass level below which a stock would be considered overfished) and proxies for fishing mortality rates that would produce maximum sustainable yield.

Underestimating the maximum age of a species, and thereby M, can bias stock assessment results and productivity estimates of a fish stock. Hoenig's estimate of natural mortality for red bream is 0.06/yr when the highest estimated age from band counts of sectioned otoliths, 69 years, is used as t_{max}. This value is in perfect agreement with the IGOR+ catch-curve–based estimate of Z. If the bomb radiocarbon-validated minimum longevity estimate of 49 years is used for t_{max}, M becomes 0.094/yr, which is still less than half the value one would obtain by using the previous t_{max} estimate of 15 years (M=0.279). Estimates of natural mortality based on life history parameters according to the equation of Pauly tended to be higher (0.097–0.124/yr) than longevity-based estimates of M but were very sensitive to the choice of mean annual temperature, which can be quite variable on bottom habitat of the Charleston Bump. It has been suggested that Pauly's equation overestimates the natural mortality of long-lived fishes because relatively few representatives with high longevity were included in the data set used by Pauly to derive the empirical equation (Newman et al., 2000). In contrast, Hoenig's data set included a wide range of long-lived species, and estimates based on Hoenig's equation have been shown to result in natural mortality rates similar to those derived from catch curves. This was indeed the case for red bream, where IGOR+ estimated the same M as Hoenig's equation based on a t_{max} of 69 years. We therefore suggest that 0.06/yr should be regarded as the current best estimate of natural mortality for the southeastern U.S. red bream population.

This study has shown that red bream are slow growing and exhibit an exceptional life-span, resulting in a very low natural mortality rate. Therefore, fisheries targeting this stock may be sustainable only at low exploitation rates. Other slow-growing, long-lived deep-water species that have been targeted by fisheries in the southeastern United States have already

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[2] McGovern, Jack. 2008. NOAA Fisheries Southeast Regional Office, Saint Petersburg, FL 33701.

been showing signs of overexploitation; examples include snowy grouper (*Epinephelus niveatus*) (Wyanski et al., 2000) and blueline tilefish (*Caulolatilus microps*) (Harris et al., 2004). Even though red bream are currently not a target for commercial fisheries operating on the Charleston Bump, landings ought to be monitored closely, and red bream may need to be considered for inclusion in a fishery management plan as a stock in the fishery. Red bream that are caught are generally retained for sale, and if fishing effort increases, the stock could become subject to overfishing in the absence of management because of life history characteristics indicative of a highly vulnerable species. Management measures that would ensure the future sustainability of a fishery for red bream are likely similar to the ones that are already in place for wreckfish. They include individual transferrable quotas, closures of spawning areas, and gear restrictions.

The above comparison of life history parameters of the red bream populations from the eastern and western North Atlantic raises questions about stock structure for this species. Red bream sampled from the U.S. commercial fishery were generally larger and older than those observed in fishery-dependent and fishery-independent surveys from the Azores (Isidro, 1996; Menezes et al., 2009). Moreover, population-level spawning events have been documented in this study on the Charleston Bump, but not in the eastern North Atlantic (Isidro, 1996). These observed patterns could be due to gear selectivity and sampling bias or they could be an accurate reflection of geographic differences—perhaps even of a complex life cycle similar to that of the co-occurring wreckfish. Juvenile wreckfish are found mainly in the eastern North Atlantic, whereas spawning adults have so far been documented only on the Charleston Bump (Sedberry et al., 1999). Moreover, wreckfish have been captured off the southeastern United States with corroded hooks in their mouths that are of the same type as those used around the Azores, but not in the U.S. fishery. This finding indicates a trans-Atlantic migration of adults. In addition, population genetic analysis supports a panmictic population structure for wreckfish in the North Atlantic (Sedberry et al., 1996).

The long pelagic juvenile stage of alfonsinos would allow sufficient time for long-distance dispersal, and some authors have suggested different juvenile and adult habitat for alfonsinos in the eastern North Atlantic (Isidro, 1996; Lehodey et al., 1997). Isidro (1996) even speculated that recruitment to the Azores fishery may occur mainly through the drift of eggs and larvae from spawning areas located north or northwest of the Azores. Spawning aggregations in the Azores have since been confirmed for splendid alfonsino, but not for red bream (Menezes et al., 2009). The Charleston Bump may be an area that supplies red bream recruits to the Azores fishery by means of the Gulf Stream. Although purely speculative at this point, this hypothesis warrants further investigation. Mitochondrial DNA (mtDNA) studies to date have shown an absence of genetic structure between red bream populations from the Azores and the Charleston Bump (Friess and Sedberry, in press), but there is mtDNA evidence for localized genetically distinct populations within the eastern North Atlantic (Aboim, 2005). More extensive genetic studies that include red bream samples from throughout their range in the North Atlantic and perhaps use a different genetic marker are needed to examine red bream population structure in the North Atlantic more closely. It would be particularly important for fishery management and conservation purposes to know whether there are self-sustaining populations on individual seamounts and hard bottom habitats that serve as a source of recruits to other areas. If there was a single red bream stock in the North Atlantic, it would have to be managed carefully across international borders.

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