Age, growth, and reproduction of jewfish *Epinephelus itajara* in the eastern Gulf of Mexico

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Abstract.– We sampled jewfish from recreational and commercial catches in the eastern Gulf of Mexico from November 1977 to January 1990 to obtain life history information. A single annual minimum in mean marginal increment ratios during May–August supported the hypothesis that jewfish up to at least age 10 can be aged by counting the opaque marks observed on otolith sections. Annual opaque mark formation was observed for a 3- and a 4-year-old jewfish using oxytetracycline (OTC) reference marks on otoliths (sagittae). Male jewfish (*N* 41) ranged 3–26 years old; females, 0–37 years (*N* 85). Growth was similar for males and females, averaging >100 mm/year through age 6, then slowing to about 30 mm/year by age 15, and finally declining to <10 mm/year after age 25. Observed total length and age data were described well by the following von Bertalanffy growth model: total length (mm) = 2006 $(1 - e^{(-0.126(\mathrm{age(yrs)}+0.49))})$. Jewfish spawned from June through December, with peak activity from July through September. Male jewfish matured at about 1100–1150 mm when 4–6 years old; females matured at 1200–1350 mm when 6 or 7 years old. The extensive overlap of length and age distributions of males and females, and the slight differences between their sizes and ages at maturity, prevent us from designating jewfish as a protogynous hermaphrodite. No transitional individuals were found. Their relatively slow growth, longevity, and behavioral characteristics, such as the tendency to form spawning aggregations, make jewfish populations highly susceptible to overfishing.

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The jewfish *Epinephelus itajara*, largest of the western North Atlantic groupers (possibly reaching 455 kg; Robins et al. 1986), ranges from the east coast of Florida throughout the Gulf of Mexico, Caribbean Sea, and south to Brazil (Smith 1971), and also in the Pacific Ocean from Costa Rica to Peru. Jewfish occur at depths ranging from several meters (shallow estuarine areas) to about 50 m. Juveniles can be found in holes and below undercut ledges in swift tidal creeks draining mangrove swamps. Large adults occur both inshore around structures such as piers and bridges, and offshore around ledges and wrecks (Bullock and Smith 1991).

Jewfish have recently been granted protected status, eliminating harvest in both the U.S. Exclusive Economic Zone (NMFS 1990a, b) and Florida's territorial waters (Florida Marine Fisheries Commission 1990). Prior to this designation, jewfish were captured by hook-and-line, speargun, shark and grouper/snapper longlines, and as a bycatch of shrimp trawling. Historically, the majority of the U.S. commercial catch has been landed along the Florida Gulf coast, where landings reached a high of approximately 61,700 kg in 1988 (Fla. Dep. Nat. Resour. Annual Landings Summ., Fla. Mar. Res. Inst., St. Petersburg, unpubl. data).

A comprehensive study of jewfish life history does not exist. Smith (1971) discussed their systematics, distribution, and ecology. Randall (1967) described food habits from nine individuals. Other researchers have contributed incidental observations on diet (Beebe and Tee-Van 1928, Tabb and Manning 1961, Odum 1971), habitat (Smith 1976, Odum et al. 1982), spawning (Schroeder 1924, Colin 1990), and parasites/pseudoparasites (Breder and Nigrelli 1934, Pearse 1934 and 1952, Manter 1947, Olsen 1952). Bullock and Smith (1991) provided basic life-history information on jewfish in the eastern Gulf of Mexico, but did not discuss age and growth or size/age-at-maturity. In this paper, we describe age and growth, spawning seasonality, and approximate size- and age-at-maturity for jewfish in the eastern Gulf of Mexico. We also briefly discuss the implications of these life-history characteristics as they relate to the jewfish's susceptibility to overfishing.

Methods and materials

Jewfish were sampled aperiodically from recreational and commercial catches from the eastern Gulf of Mexico, November 1977 through January 1990. Fifty-six percent (269/481) of the sampled jewfish were captured using spearguns, 27% by hook-and-line, 8% by bottom longline (either grouper/snapper or shark fisheries), and the remaining 9% by shrimp trawl, trap, or unrecorded methods. We attempted to determine sex, whole (WW) and/or gutted (GW) weight (kg), and total length (mm TL) for each specimen, although we could not determine whole weight and sex when fish had been eviscerated (*N* 271). Although eviscerated, unsexed fish could not be included in our study of reproduction, they were used in the age and growth analyses. If sagittae could be located, they were removed from the otic capsule (*N* 384) and stored dry. A portion of the gonad, if available (*N* 173), was preserved in 10% formalin and later transferred to 70% ethanol.

Otolith sections were examined for evidence of age marks. Transverse sections, approximately 0.5 mm thick, were cut from each sagitta with a Buehler Isomet low-speed saw. Sections were mounted on microscope slides with Histomount mounting media and examined for age marks under a dissecting microscope using reflected light. Age marks were counted independently by two readers. Later, a joint reading was conducted in an attempt to resolve differences between counts.

Monthly mean marginal increment ratios were calculated for fish with 1–10 annuli to determine the periodicity of mark formation. Marginal increment was standardized for differences in growth among age-classes by dividing the marginal increment for each fish by the distance between its penultimate and outermost annuli. We called this calculated value the 'marginal increment ratio' (*sensu* percentage of marginal increment; Hood et al. Unpubl. manuscr.). Fish were assigned ages based on the number of annuli and a biologically realistic hatching date of 1 September (time of peak spawning; see Results). All fish were assigned an age equal to their annulus count, except for fish collected prior to 1 September and that had already deposited an annulus during the most recent period of mark deposition (April–August; see Results). The assigned age for these fish was one less than their number of annuli.

Observations to determine the validity of age marks were made from two jewfish (290 mm TL, 509 g; and 375 mm TL, 934 g) that were injected intramuscularly with 50 mg oxytetracycline (OTC) per kg body weight on 3 November 1990 and 21 October 1989, respectively. These fish were maintained at ambient light and temperature in flow-through 1038-gallon seawater tanks located at the Keys Marine Laboratory in the Florida Keys. The smaller specimen survived 11 months after OTC treatment; the larger fish was sacrificed after 22 months.

Nonlinear regression of all available age and length data (using FSAS; Saila et al. 1988) was used to estimate parameters of the von Bertalanffy growth equation,

$$l_t = L_\infty(1 - e^{(-K(t-t_0))}),$$

where l_t is total length (mm), t is age (years), L_∞ is asymptotic length, K is the Brody growth coefficient, and t_0 is the age at zero length (von Bertalanffy 1957). Likelihood ratio tests were used to compare male and female von Bertalanffy parameter estimates (Kimura 1980, Cerrato 1990). Nonlinear regression was used to fit the exponential equation, WW or GW $= aTL^b$, to whole- or gutted-weight and total-length data.

Histological preparations of gonads were made to determine gonad developmental class, following the criteria presented by Moe (1969) for red grouper *Epinephelus morio*. Initially, gonad samples were embedded in paraffin, but beginning with fish sampled in 1988, gonads were embedded in plastic (glycol methacrylate) because of its superior tissue-infiltrating abilities. Gonad samples were sectioned to a thickness of 3.5 μm and stained with Weigert's hematoxylin and eosin Y for microscopic examination. Spawning was inferred from seasonal changes in the relative abundance of fish having ovaries containing vitellogenic oocytes or testes containing sperm in their efferent ducts. Sizes or ages at maturity were determined from changes in the proportion of mature fish over the entire age range or across 50 mm size-classes.

Results

Age and growth

Opaque bands can be recognized and counted on thin-sectioned jewfish sagittae. Initial counts of opaque bands by two independent readers agreed on 62% (237/384 fish) of sections analyzed, with 91% (348/384) of all counts either in agreement or differing by one. After a second, joint reading, agreement was reached on opaque-band counts for all but two sections, leaving 382 specimens for analysis of age and growth.

The annual pattern of monthly mean marginal increment ratios and observations from two OTC-marked jewfish support the hypothesis that annuli form once each year. Mean marginal increment ratios were greater than 70% during November–April and declined to a minimum of 20% in June. The mean marginal increment ratio remained less than 30% through August (Fig. 1). For a large number of specimens captured

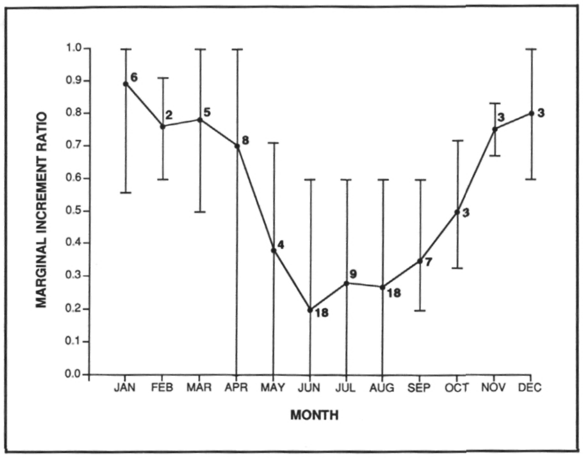

Figure 1

Monthly mean marginal increment ratios for jewfish with 1–10 opaque marks on otolith sections. Vertical lines indicate range of observations; sample size indicated by the number adjacent to the mean (*N* 86).

Table 1

Number of aged jewfish *Epinephelus itajara* from the eastern Gulf of Mexico, and average observed and predicted total lengths for age groups 0–37 years old. Predicted lengths are based on the von Bertalanffy growth equation mm TL = 2006 $(1 - e^{(-0.126\,(\text{age (yr)} + 0.49))})$.

	Average observed total length (mm)						Predicted total length (mm)		
Age	*N*	Male	*N*	Female	*N*	Unknown	Male	Female	Pooled*
0	0	—	1	338	4	170			—
1	0	—	3	517	0	—	434	382	344
2	0	—	5	717	1	711	605	563	541
3	2	863	4	708	4	751	759	725	714
4	1	1184	3	924	4	913	897	871	867
5	2	1080	1	1218	8	1067	1021	1002	1002
6	4	1078	0	—	5	1161	1132	1119	1121
7	5	1318	0	—	4	1423	1232	1225	1226
8	2	1476	2	1333	8	1437	1322	1319	1318
9	2	1400	2	1399	12	1368	1403	1404	1400
10	2	1398	6	1515	12	1516	1475	1481	1471
11	1	1660	6	1632	23	1544	1540	1549	1535
12	1	1690	7	1647	31	1612	1598	1611	1590
13	5	1620	10	1653	26	1644	1651	1666	1640
14	2	1849	7	1762	15	1723	1698	1715	1683
15	4	1828	4	1913	12	1737	1740	1760	1721
16	3	1909	4	1860	8	1735	1778	1800	1755
17	1	1770	2	1878	6	1879	1812	1836	1785
18	0	—	4	1820	8	1750	1843	1868	1811
19	0	—	0	—	6	1833	1870	1897	1834
20	0	—	2	1990	11	1842	1895	1923	1854
21	0	—	4	2023	8	1818	1917	1946	1872
22	0	—	2	2011	9	1820	1937	1967	1888
23	0	—	0	—	4	1938	1955	1986	1902
24	1	1905	1	1950	7	1936	1971	2003	1914
25	2	1955	0	—	4	1821	1985	2018	1925
26	1	1930	0	—	5	1891	1998	2032	1935
27	0	—	2	2065	3	1853	2010	2044	1943
28	0	—	1	1935	2	2006	2020	2055	1951
29	0	—	0	—	1	2090	2030	2065	1957
30	0	—	0	—	1	2040	2038	2073	1963
33	0	—	1	2015	2	1820	2058	2095	1977
34	0	—	0	—	1	2032	2064	2101	1980
36	0	—	0	—	1	1908	2073	2110	1986
37	0	—	1	1970	0	—	2077	2115	1988

* Including fish of unknown sex

during April–August, we observed an opaque band at the outer edge of the otolith section and interpreted this as the deposition of a new annulus. After August, the mean marginal increment ratio increased until reaching a maximum during November–April. The observed annual minimum in monthly mean marginal increment ratios suggests that opaque bands form once each year in the otoliths of jewfish ≤10 years of age. The validity of age marks was confirmed for two OTC-marked jewfish. The OTC reference mark was clearly evident on otoliths of each of the two specimens. The otolith of the 3-year-old jewfish that had survived for 11 months in captivity contained a single annulus distal to the OTC mark. This fish, injected with OTC in November 1990, had apparently deposited an annulus prior to its death in October 1991. Its total length and weight were 505 mm TL and 2.7 kg. The 4-year-old specimen, injected with OTC in October 1989 and sacrificed in August 1991 after 22 months in captivity (total length and weight of ~735 mm TL and 9 kg), had deposited two annuli distal to the OTC reference mark.

A total of 481 jewfish were sampled for life-history data. Age data were determined for 382 individuals. Age range was 3–26 years for males (*N* 41), 0–37 for females (*N* 85), and 0–36 for fish of undetermined sex (*N* 256). Total lengths of jewfish sampled were 795–2057 mm for males (*N* 75), 338–2155 mm for females (*N* 131), and 75–2160 mm for fish of undetermined sex (*N* 275).

Jewfish grow slowly relative to their potential maximum size. Annual growth was most rapid (averaging >100 mm/year) through age 6, then declined to about 30 mm/year by age 15, and to less than 10 mm/year after age 25 (Table 1,

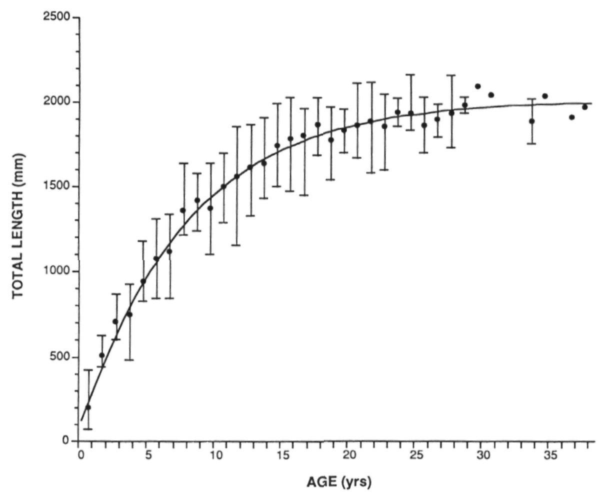

Figure 2
Observed ages (years) and total lengths (mm), and predicted growth modeled for jewfish collected from the eastern Gulf of Mexico. Parameters for the von Bertalanffy growth model are $L_\infty = 2006$ mm TL, K=0.126/year, and $t_0 = -0.49$ year (*N* 382).

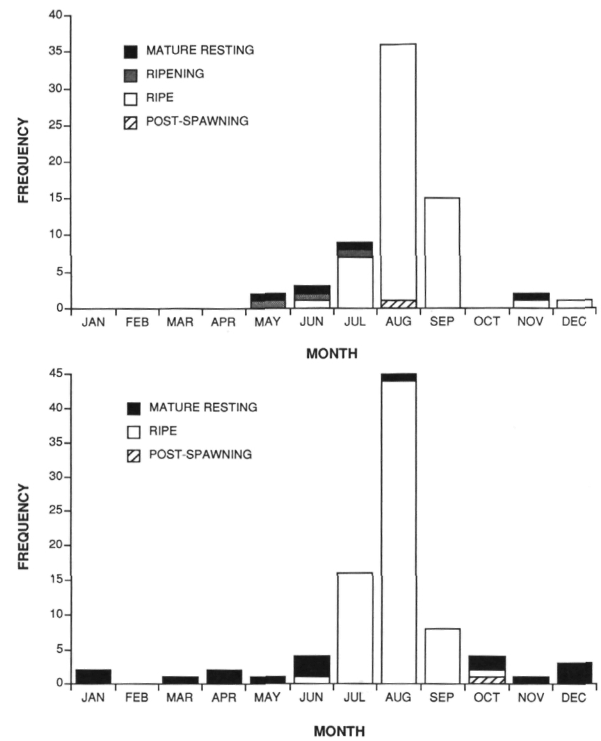

Figure 3
Monthly distribution of gonad classes for mature (upper) male (*N* 66) and (lower) female (*N* 86) jewfish collected from the eastern Gulf of Mexico. Histological criteria for gonad classes correspond to Moe's (1969) descriptions for red grouper.

Fig. 2). Average observed and predicted (von Bertalanffy equation) sizes-at-age were similar between sexes (Table 1). Results of likelihood ratio tests indicated no significant differences between sex-specific estimates of L_∞ (χ^2 0.136, df 1, $P>0.70$), K (χ^2 4.0×10^{-5}, df 1, $P>0.90$), or t_0 (χ^2 0.138, df 1, $P>0.70$). Estimates of the growth equation parameters (asymptotic standard error) for pooled length and age data were $L_\infty = 2006$ mm TL (23.3), K=0.126/year (0.0057), and $t_0 = -0.49$ years (0.200).

The relationships of whole and gutted weight (kg) to total length (mm) were

$$WW = 1.31 \times 10^{-8} TL^{3.056} \quad (N\ 66,\ r^2\ 0.964)$$
$$GW = 2.94 \times 10^{-8} TL^{2.941} \quad (N\ 402,\ r^2\ 0.941).$$

Gutted and whole weights were linearly related (*N* 50, r^2 0.995) as follows:

$$WW = -0.717 + 1.1039\,GW$$
$$GW = 1.001 + 0.9018\,WW.$$

Reproduction

Jewfish spawn during June–December in the eastern Gulf of Mexico, with peak activity during July–September (Fig. 3). Ripe males and females first appeared in our collections during June. Nearly all gonads collected from mature fish in July, August, and September were classified as ripe. Most spawning appears to end by October, although a ripe male was collected in November and another in December. Spent fish were collected in August (one male) and October (one female). No transitional fish were found.

Male jewfish become sexually mature at a slightly smaller size and younger age than females. Male jewfish were first mature when about 1100–1150 mm TL at 4–6 years of age. All males <1150 mm TL (*N* 6, 795–1100 mm) were immature, whereas all larger males in our samples (*N* 55, 1155–2057 mm) were mature. Both 3-year-old males sampled were immature, whereas one large (1184 mm TL) 4-year-old male was mature. Fifty percent of males 5 or 6 years old (3 of 6 individuals) and all males age 7 or older (*N* 31) were mature. Female jewfish first mature when about 1200–1350 mm TL at age 6 or 7. All females <1225 mm (*N* 21, 338–1218 mm) and <6 years old (*N* 17, 0–5 yr) were immature. All larger (*N* 90, 1350–2155 mm) and older (*N* 68, 8–37 yr) females sampled were mature.

Discussion

Age and growth

The spring–summer period of annulus formation in jewfish seems somewhat protracted. However, there appears to be a considerable range for the duration of annulus deposition in grouper populations: 2 or 3 months for *Epinephelus morio*, *E. nigritis*, *E. drummondhayi*, and *E. niveatus* (Moe 1969, Matheson and Huntsman 1984, Moore and Labisky 1984, Manooch and Mason 1987) to 5–7 months for *Mycteroperca phenax* and *M. microlepis* (Matheson et al. 1986, Hood and Schlieder 1992). Moe (1969) discussed factors affecting annulus formation and concluded that spawning and its associated physiological processes probably caused annulus formation in red grouper. However, annulus formation does not always occur in phase with spawning in epinephelines. For example, Matheson et al. (1986) found *M. phenax* to spawn during April–August in the South Atlantic Bight, but annulus formation occurred during December–April.

The annual deposition of opaque bands, seen in 3- and 4-year old OTC-marked jewfish, needs to be validated for fish older than 10 years. Due to the difficulty in sampling large numbers of these older fish year-round, it is probably not feasible to utilize indirect validation techniques (i.e., marginal increment analysis). Validation will probably require direct observations of individuals that have been injected with OTC and recaptured after annulus deposition.

The growth rate of jewfish (i.e., *K* 0.13/year) falls within or near the range observed for some of its congeners in the South Atlantic Bight and Gulf of Mexico: speckled hind, 0.13/year (Matheson and Huntsman 1984) and red grouper, 0.11–0.18/year (Moe 1969, Muhlia-Melo 1975). However, jewfish growth is somewhat faster than that of the deepwater snowy grouper *E. niveatus* (*K* 0.07–0.09/year; Matheson and Huntsman 1984, Moore and Labisky 1984) and considerably greater than that of the second-largest grouper in the western North Atlantic Ocean, the warsaw grouper *E. nigritis* (*K* 0.05/year; Manooch and Mason 1987), which may reach weights >200 kg.

Reproduction

We found jewfish to be in peak spawning condition during July–September in the eastern Gulf of Mexico. This agrees with Schroeder's (1924) finding that jewfish spawned during July–August, when heavily exploited aggregations of jewfish appeared off the Florida Keys. Furthermore, Colin (1990) observed what he interpreted as courtship behavior in jewfish off southwest Florida during the full moons of August and September.

When compared with that of females, the slightly smaller size and younger age of males at first maturity is unexpected, given that jewfish are assumed to be protogynous hermaphrodites (Smith 1971). Furthermore, whereas the youngest fish in our sample was female, as would be expected for a protogynous fish, so was the oldest. However, Sadovy and Shapiro (1987) point out several factors that may obscure differences in length, age, and maturity between males and females of a protogynous fish: (1) Some females may never change sex for lack of genetic or environmental cues and therefore may attain sizes (ages) equal to or greater than males, (2) a fraction of the population may initiate female development but change to males prior to sexual maturation, and (3) size at sex-reversal may differ among subpopulations of the same species and thus may obscure differences in length or age distribution between the sexes. Conclusive evidence for protogynous hermaphroditism in jewfish (i.e., the presence of transitional individuals) was not found in this study. Transitional individuals in confirmed protogynous hermaphrodites, such as *E. morio* (Moe 1969) and *M. microlepis* (Collins et al. 1987, Hood and Schlieder 1992), never represent a large percentage of the population; therefore, more extensive collections than ours may be needed to detect the presence of these individuals.

Fisheries implications

The life-history characteristics that we describe imply that jewfish are highly vulnerable to overfishing. Their slow growth, longevity, and presumed low natural mortality specify a population composed of cohorts that reach their maximum biomass at relatively old ages (Alverson and Carney 1975). Thus the greatest yield from a cohort of jewfish would be attained at either low rates of fishing or when only large fish are harvested. If jewfish are indeed protogynous hermaphrodites, fishing may also disrupt their spawning and recruitment by limiting the number of older males available for spawning (Smith 1982, Bannerot et al. 1987, Huntsman and Waters 1987). In addition, behavioral traits exhibited by large jewfish, such as their general unwariness of spearfishermen and apparent site-specific spawning aggregations (Shroeder 1924, Colin 1990), make them readily available for capture. Fisheries managers of Florida territorial and U.S. Exclusive Economic Zone waters have recognized the jewfish's susceptibility to overfishing and have recently banned all harvest of jewfish from waters under their jurisdictions.

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