Preliminary Observations on the Reproductive Biology of Wahoo, *Acanthocybium solandri*, from the Northern Gulf of Mexico and Bimini, Bahamas

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ABSTRACT

Wahoo, *Acanthocybium solandri*, are important in the recreational fishery throughout the Gulf of Mexico and Caribbean. However, there is limited information on the basic biology of this species. We obtained gonadal samples from 70 wahoo captured during fishing tournaments in the northern Gulf of Mexico during June - September of 1997 and May - June of 1998 and from 32 wahoo captured in November 1997 at Bimini, Bahamas. Mean GSI values of females were elevated from May to August and peaked in June. Histological analysis and oocyte frequency distributions revealed that wahoo are multiple spawners with asynchronous oocyte development throughout the spawning season. Ovaries in the late developing stage occurred in all months but September. However, 10% of the females captured in June had regressed ovaries, suggesting there may be a group of wahoo that do not spawn during the summer. Females from Bimini were either regressed (85%) or beginning early ovarian development (15%). Three Gulf females with hydrated oocytes were analyzed for estimates of batch fecundity; the mean relative batch fecundity was 57.7 ± 5.4 eggs/g ovary-free body weight. Spawning frequency estimates for June, determined from the percentage of fish with either hydrated oocytes, oocytes undergoing final oocyte maturation or post ovulatory follicles in the ovary, indicate wahoo may spawn once every 2 - 6 days. The estimated size at 50% maturity for female wahoo is 1,020 mm FL, corresponding to an estimated age of two years. In contrast, all male wahoo captured were sexually mature, suggesting size at 50% maturity for males is < 935 mm FL. Males have an extended reproductive season compared to females; the majority of males captured from June - September were running ripe and all males captured in November from Bimini had testis containing spermatozoa. Although the data available provide preliminary information on the reproduction of wahoo, many questions remain. The most intriguing concerns the possibility of two temporally different spawning groups of female wahoo.

KEY WORDS: Wahoo, reproductive biology, Scombridae

INTRODUCTION

Wahoo, *Acanthocybium solandri*, a large pelagic fish of the family Scombridae, has a worldwide circumtropical distribution that extends northward to the mid-Atlantic bight of the United States (Fritzsche 1978). Wahoo are a prized recreational species in the Gulf of Mexico and Caribbean and are incidental in the commercial longline fishery of the Indo-Pacific region (Collette and Nauen 1983). However, there is little current information on the life history of this species (see Franks et al. (1999) for review). The reproductive biology of wahoo remains virtually undescribed. Iversen and Yoshido (1957) reported wahoo in the Pacific appeared to have an extended spawning season and high fecundity. Hogarth (1976) confirmed these observations for wahoo caught in the western North Atlantic off Cape Hatteras and provided limited information on gonadal maturation in that region. The objective of this study was to provide a preliminary, but more complete, description of the reproductive biology of wahoo captured in the northern Gulf of Mexico. Aspects of the reproductive biology described include spawning season, gonadal maturation and oocyte frequency distribution, size and age at sexual maturity, and estimates of batch fecundity and spawning frequency.

MATERIALS AND METHODS

Wahoo samples were obtained from recreational anglers participating in fishing tournaments in the northern Gulf of Mexico and Bimini, Bahamas. Wahoo from the Gulf of Mexico were captured in waters off Florida, Alabama, Mississippi and Louisiana (north of latitude 29° and between longitudes 86°W and 98°W) ranging from 100 to 600 m deep from June through September 1997 and from May through June 1998. Specimens sampled from Bimini were caught in nearby Atlantic waters in November 1997. All fish were measured (mm FL) and weighed (0.1 lb, later converted to kg) at the dock and sex was determined. Gonads and dorsal spines were removed from each fish, placed in a labeled bag and stored in ice no more than 24 hours prior to laboratory processing. In the laboratory, gonads were weighed (0.1 g) and assigned to a macroscopic maturity stage. The gonadosomatic index (GSI) was calculated for each fish as GSI=[gonad weight/ovary-free body weight] x 100. A portion of the gonad (2 - 15 g) was removed and preserved in 10% neutral buffered formalin for a minimum of two weeks. Spines were prepared and aged following Franks et al. (1999).

A small (< 2 cm^2) portion of the preserved gonadal tissue was placed in individually labeled cassettes for histological processing. Following an overnight rinse in running tap water, gonadal tissue was dehydrated in a series of graded ethanol solutions and embedded in paraffin following standard histological techniques. Tissues were sectioned at 2 - 3 µm, placed on slides and stained

with hematoxylin and eosin for histological evaluation. Gonads were assigned to developmental stages based on microscopic appearance following Brown-Peterson et al. (1988). Post-ovulatory follicles and atresia were classified following Hunter et al. (1986) and Hunter and Macewicz (1985) and spawning frequency was determined histologically following procedures in Hunter et al. (1986) and Brown-Peterson et al. (1988).

The remaining preserved ovarian tissue was used for oocyte size-frequency distributions and batch fecundity estimates. Approximately 1 g of preserved tissue was weighed to the nearest 0.0001 g and all oocytes > 60 μm were teased from the tissue. The oocytes were suspended in a known volume of water, stirred to a uniform distribution and three to five 1 ml subsamples were removed. All the oocytes in each subsample were counted and measured using a stereo dissecting microscope and a computerized image analysis system. Oocyte size-frequency distributions were constructed using all the oocytes measured. Mean batch fecundity was determined by multiplying the number of hydrated oocytes in each subsample by the dilution factor.

RESULTS

Spawning Season and Gonadal Maturation

GSI values of female wahoo were elevated during June-August 1997 and in May-June 1998 (Figure 1). Male GSI values were elevated during the same time periods (Figure 1), suggesting that the spawning season for wahoo in the northern Gulf of Mexico probably extends from May through August. Mean GSI values for females were lowest in September and were slightly elevated in November in female wahoo from Bimini. Overall, GSI values of both male and female wahoo were low. The highest GSI value recorded was 9.5 for a female captured in June with hydrated oocytes. Male GSI values rarely exceeded 1.0.

Histological assessment of testicular tissue from 19 male wahoo captured from the northern Gulf of Mexico during the spawning season showed that the majority of males were in spawning condition during the entire spawning season, as most testis were ripe or running ripe and none were spent (Table 1). There was a noticeable progression in spermatogenic stages in the testis during the course of the spawning season. Males in June had testis containing spematocytes and occasionally spermatogonia throughout the entire gonad, while fish captured in August and September exhibited greatly reduced spermatogenic activity, with testis generally containing only spermatids and spermatozoa. In contrast, the 19 male wahoo captured from Bimini during November showed a greater range of testicular maturity stages (Table 1). While over half of the males were in the final stage of gonadal development (running ripe testis with no spermatogenic activity and only partially filled with spermatozoa) or spent, a large percentage (47%) appeared to be undergoing testicular development

typically found one to three months prior to spawning.

Table 1. Monthly histological testicular developmental stages of wahoo from the north-central Gulf of Mexico and Bimini, Bahamas. All values are expressed as percentages. November data represent wahoo from Bimini.

Month	N	Early Dev.	Mid Dev.	Late Dev.	Ripe	Run-ning Ripe	Spent
June 97	7	0	0	14	0	86	0
July 97	0	0	0	0	0	0	0
Aug. 97	2	0	0	0	0	100	0
Sept. 97	1	0	0	0	0	100	0
Nov. 97	19	10	22	16	0	47	5
May 98	0	0	0	0	0	0	0
June 98	9	0	0	12	22	66	0

Histological assessment of ovarian tissue from 52 wahoo captured from the northern Gulf of Mexico during the spawning season revealed that June was the only month in which females were in all stages of gonadal developmental (Table 2). A high percentage of females were in the early developing maturation stage (Figure 2A) during May and June. Sample sizes from the remainder of the reproductive season were low, but revealed the expected progression of all females in the late developing stage (Figure 2B) in July to all females in the regressed stage by September. Many females in the late developing stage had oocytes undergoing atresia. Females in the ripe stage (ovaries containing hydrated oocytes or oocytes undergoing final oocyte maturation [FOM, Figure 2C]) were only captured in June. Additionally, a small percentage of large females captured in June had regressed ovaries, suggesting these fish would not spawn during the summer. In a related finding, 15% of the 13 females captured in Bimini in November were in the early developing stage, suggesting they would have been capable of spawning within the next two to three months (Table 2). Wahoo are a multiple spawning species with asynchronous oocyte development as shown in oocyte size-frequency diagrams (Figure 3). Females in the mid and late developing ovarian stages show continuous recruitment with no

distinct modes of oocytes (Figure 3). A distinct mode of large hydrated oocytes is apparent in females in the ripe ovarian stage (Figure 3) although females in this stage continued to show large numbers of developing oocytes, suggesting multiple batches of oocytes would be spawned during the reproductive season. Histological analysis provides further evidence of asynchronous oocyte development; oocytes in a variety of stages were found in the ovaries of late developing wahoo (Figure 2B). Stronger histological evidence for multiple spawning is the presence of developing oocytes in ovaries that are undergoing FOM (Figure 2C). Finally, the presence of postovulatory follicles (POF, Figure 2D), indicative of spawning during the prior 24 hour period, shows that wahoo have the ability to spawn more than once during the reproductive season.

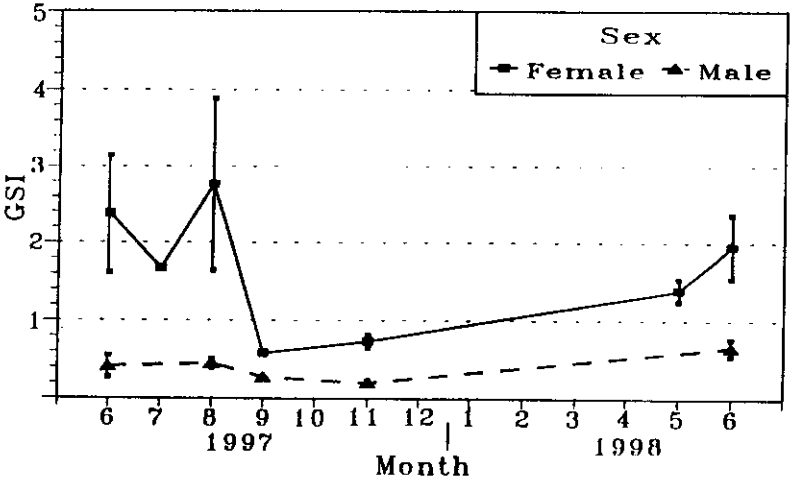

Figure 1. GSI values of female and male wahoo. Data points represent 0 ± 1 S.E. All data are from wahoo captured in the northern Gulf of Mexico with the exception of the November data, which represent wahoo captured in Bimini.

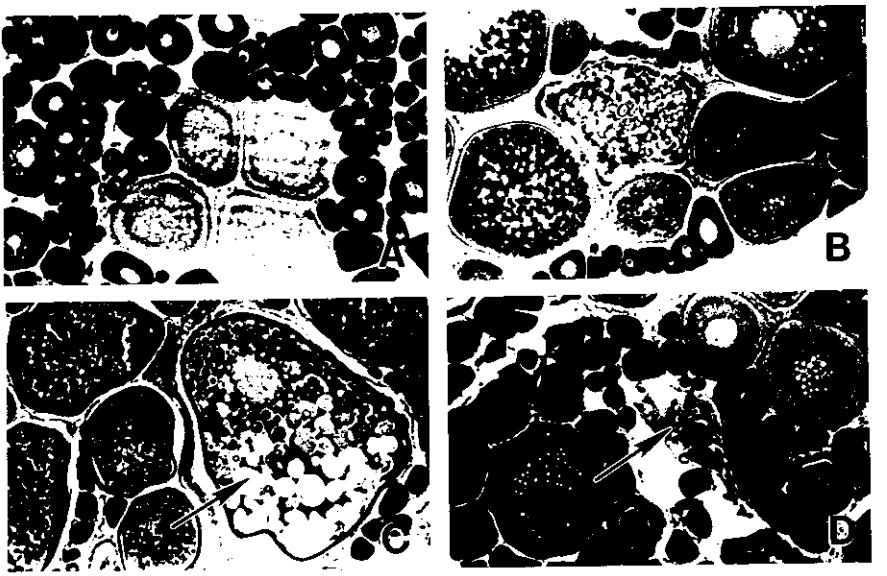

Figure 2. Histological sections of ovaries from wahoo captured in the northern Gulf of Mexico. A. Ovary from a wahoo captured in June in the early developing stage. Magnification = 50X. B. Ovary from a wahoo captured in June in the late developing stage. Note oocytes in all stages of development as well as oocytes in a-stage atresia (a). Magnification = 45X. C. Ovary from a wahoo captured in June undergoing final oocyte maturation (arrow). Note the presence of other, less mature oocytes in the section. Magnification = 43X. D. Ovary from a wahoo captured in June with a 24-h post ovulatory follicle (arrow). Magnification= 45X.

Size and Age at Sexual Maturity

Size and age at sexual maturity were determined for male and female wahoo collected from the northern Gulf of Mexico. All male wahoo sampled during this study were sexually mature with spermatogenic activity in the testis. The smallest male captured was 935 mm FL, corresponding to an estimated age of 2. Thus, preliminary data indicates that 50% sexual maturity for male wahoo is reached at a length < 935 mm FL and, most likely, at one year of age.

Overall, 17% of female wahoo collected from the northern Gulf of Mexico were sexually immature, with only primary oocytes in the ovary. Figure 4

shows the percentage of sexually mature females by 25 mm FL intervals. With the exception of one 875 mm FL individual in the early developing ovarian stage, ovarian maturation did not begin until 975 mm FL in females. All females > 1050 mm FL were sexually mature. Size at 50% maturity is approximately 1020 mm FL (Figure 4), which corresponds to an estimated age of 2.

Table 2. Monthly histological ovarian developmental stages of wahoo from the northern Gulf of Mexico and Bimini, Bahamas. All values are expressed as percentages. November data represent wahoo from Bimini.

Month	N	Early Dev.	Mid Dev.	Late Dev.	Ripe	Reg.	Imm.
June 97	29	31	14	3	14	10	28
July 97	2	0	0	100	0	0	0
Aug. 97	4	0	0	50	0	50	0
Sept. 97	1	0	0	0	0	100	0
Nov. 97	13	15	0	0	0	85	0
May 98	4	75	0	25	0	0	0
June 98	12	25	8	17	17	8	2

Batch Fecundity and Spawning Frequency

Preliminary estimates of batch fecundity were determined for three wahoo with hydrated oocytes that were captured in June from the northern Gulf of Mexico. Batch fecundity values (mean of five subsamples with standard error), FL, the estimated age of each fish and the relative batch fecundity expressed as the number of eggs per gram of ovary-free body weight are presented in Table 3. The mean batch fecundity estimate for wahoo is 1,146,395 ± 291,210 eggs/female. However, batch fecundity appears to be related to fish length and age in wahoo (Table 3). Estimated mean batch fecundity for five year old wahoo is 1,496,756 ± 81,782 eggs/female. Relative batch fecundity does not appear to increase with increasing fish size. The mean relative batch fecundity for all three fish is 57.7 ± 5.42 eggs/g ovary-free body weight.

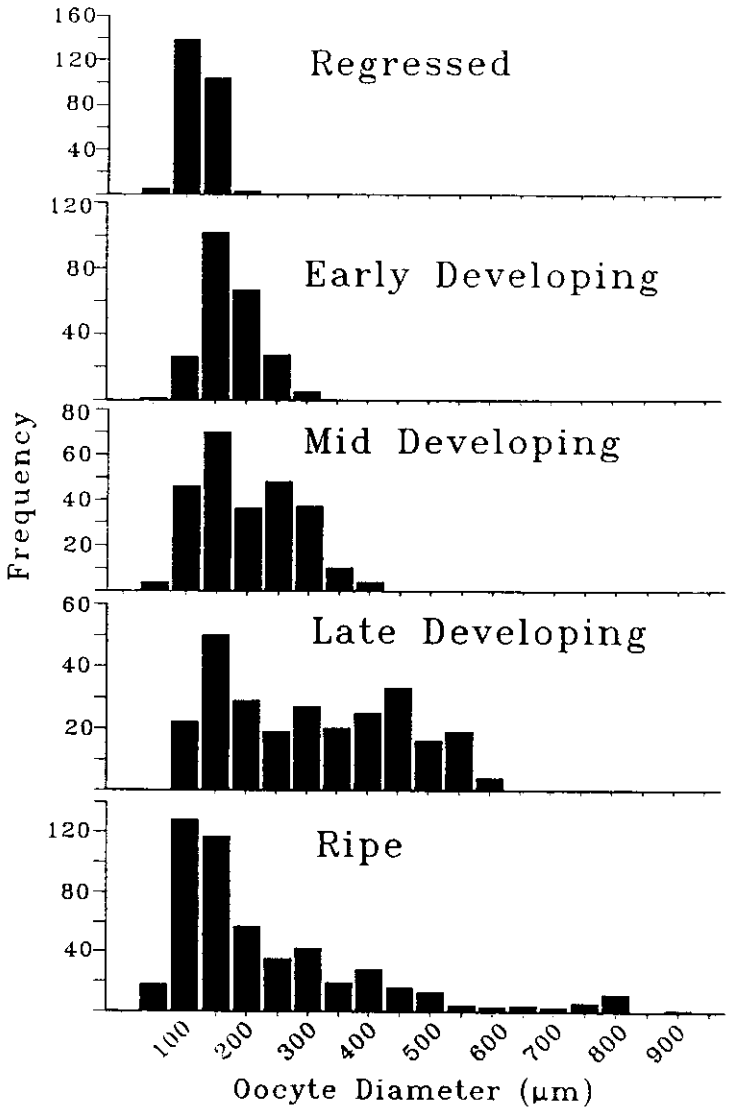

Figure 3. Oocyte size-frequency distribution of female wahoo. Frequency refers to the number of oocytes counted in each 50 mm oocyte diameter interval. Each graph represents data from a single fish at a different reproductive stage. The regressed fish was captured in Bimini. All other fish were captured in the northern Gulf of Mexico.

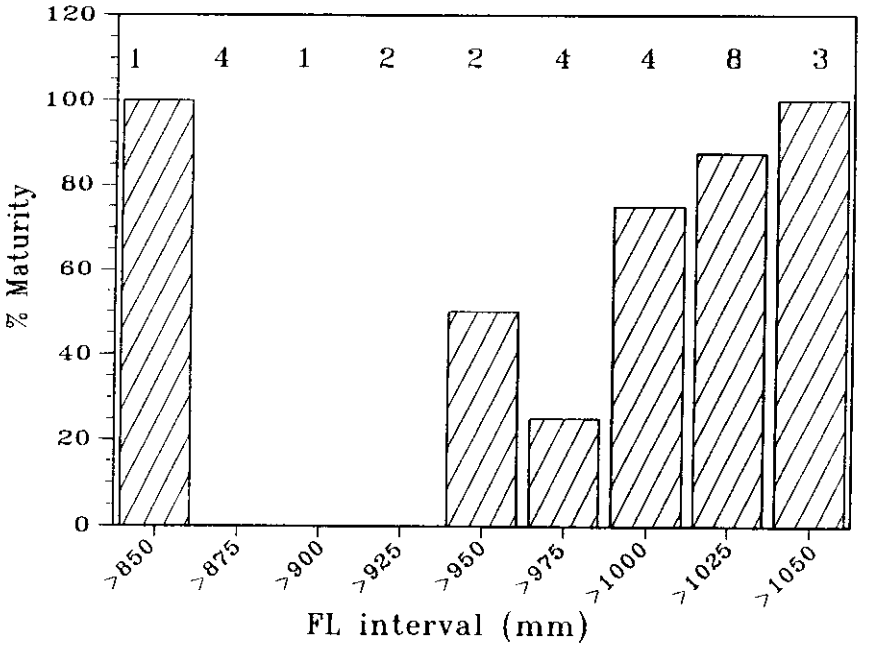

Figure 4. Size at maturity for female wahoo from the northern Gulf of Mexico by 25 mm FL intervals. The number of fish in each length interval is above each bar.

Table 3. Estimated batch fecundity for three wahoo containing ripe oocytes captured in June from the northern Gulf of Mexico. Batch fecundity is expressed as the mean of five subsamples ±1 standard error (S.E.).

FL (mm)	Estimated Age	Batch Fecundity ($\bar{x}$ ± 1 S.E.)	Relative Batch Fecundity (eggs/g)
1030	2	445,672 ± 75,369	70.4
1628	5	1,381,100 ± 426,227	47.9
1630	5	1,612,413 ± 245,277	54.8
Mean		1,146,395 ± 291,210	57.7 ± 5.4

Spawning frequency of female wahoo in the late developing or ripe ovarian stages in June was estimated using three methods; the percentage of ovaries containing hydrated oocytes, the percentage of ovaries containing oocytes undergoing FOM and the percentage of ovaries containing POF. Although the data are limited, Table 4 shows that in June 1997 spawning frequency estimates ranged from once every six days using the FOM and POF methods to once every three days using the hydrated oocyte method. Estimated spawning frequencies in June 1998 were comparable, ranging from once every four days using the FOM method to every other day using the hydrated oocyte method. These data suggest that female wahoo appear to spawn once every two to six days in the northern Gulf of Mexico. Assuming a four month spawning season (May through August), these estimates suggest that an individual female wahoo could spawn between 20 and 62 times during the spawning season, resulting in a total annual fecundity for a 5-year-old fish of 30,000,000 to 92,800,000 eggs.

Table 4. Spawning frequency estimates for female wahoo captured in the northern Gulf of Mexico. Values are the percentage of fish in each oocyte stage. FOM = final oocyte maturation; POF = postovulatory follicle.

Date	N	Hydrated	FOM	POF
June 1997	6	33	17	17
June 1998	4	50	25	0

DISCUSSION

Data from this preliminary study show that wahoo from the northern Gulf of Mexico are capable of producing multiple batches of oocytes during a spawning season extending from May through August. Additional collections of wahoo at the beginning and ending of the reproductive season would provide more definitive information on the initiation and cessation of spawning activity. The duration of the spawning season is similar to previous reports of wahoo reproduction in similar latitudes. Hogarth (1976) reported the spawning season extended from late June through August off North Carolina, while Wollam (1969) reported that wahoo spawned from May through October in the Straits of Yucatan and Florida, based on larval collections. In the sub-tropical Pacific Ocean, the wahoo spawning season extends for five months (Iversen and Yoshida 1957, Matsumoto 1967), although in equatorial regions of the Pacific, larval wahoo have been found year-round (Matsumoto 1967), suggesting a more protracted spawning season. An increase in the length of the spawning season in equatorial waters has also been reported for other scombrids (Farley and Davis 1998).

The gonadal maturation of wahoo is similar to that of most other multiple spawning species although mean GSI values during the spawning season are low when compared to other multiple spawners such as sciaenids (Brown-Peterson et al. 1988). However, Hogarth (1976) reported similar low mean GSI values for male and female wahoo from North Carolina. Other scombrids, such as yellowfin tuna (*Thunnus albacares*) and European horse mackerel (*Trachurus trachurus*) have similarly low GSI values during the spawning season (McPherson 1991; Karlou-Riga and Econmidis 1996), indicating that pelagic fish such as scombrids may expend less energy for the production of large gonads than inshore or estuarine species.

Male wahoo appear to reach sexual maturity at a smaller size and possibly younger age than females. Hogarth (1976) reported a similar occurrence in wahoo from North Carolina. Indeed, Hogarth's (1976) estimated size at maturity for female wahoo (1010 mm TL) is close to our estimated size at 50% maturity (1020 mm FL) for female wahoo in the northern Gulf of Mexico. Although we could not estimate a size at 50% sexual maturity for male wahoo since the smallest male we caught (935 mm FL) had reached sexual maturity, Hogarth (1976) estimated male wahoo from North Carolina reached sexual maturity at 860 mm TL. These lengths correspond to ages of 1 or 2 years (Franks et al. 1999), indicating wahoo reach sexual maturity at a young age as do other scombrids in the southeastern United States (Finucane et al. 1986; Schmidt et al. 1993).

This study represents the first attempt to estimate batch fecundity and spawning frequency for wahoo. Previous fecundity estimates of 6.1 million eggs (Iverson and Yoshida 1957) and 0.6 - 45.3 million eggs (Hogarth 1976) represent estimates of the total number of yolked oocytes in the ovary, an inaccurate measure of fecundity in a multiple spawning species with continual oocyte recruitment such as wahoo. Although the fecundity measurements presented here are preliminary due to small sample sizes, they are similar to batch fecundities reported for other scombrids. The relative batch fecundity of 57.7 oocytes/g calculated for wahoo is comparable to the relative batch fecundity of 57 oocytes/g calculated for bluefin tuna (*Thunnus maccoyii*; Farley and Davis 1998) and 68 oocytes/g for yellowfin tuna (Schaefer 1996), large pelagic species that have a similar life history to wahoo. However, although batch fecundity is similar among the large scombrids, the interval between spawns appears to be greater for wahoo. Based on a very limited sample size, we estimated wahoo spawning frequency to be once every two to six days. In contrast, yellowfin tuna have been found to spawn every one to two days (Schaefer 1995), with a mean spawning frequency of 1.54 days (McPherson 1991). Similarly, bluefin tuna are reported to be daily spawners (Farley and Davis 1998). Larger sample sizes would improve both the batch fecundity and spawning frequency estimates

for wahoo. However, there was no evidence of 12 to 24 hour POFs in any ovary containing hydrated oocytes or oocytes undergoing FOM (n=7), suggesting that wahoo may not be capable of daily spawning.

An intriguing aspect of this study was the presence of large (> 1,370 mm FL) female wahoo from the Gulf of Mexico with regressed ovaries during June, the height of the spawning season. There was no histological evidence that these females had recently spawned, although they did not have virgin ovaries. Equally intriguing is the presence of female wahoo in the early developing ovarian stage in Bimini during November, after the cessation of the spawning season. These two anomalies taken together suggest that there may be a group of wahoo in the subtropical Atlantic and Gulf of Mexico that spawn during early spring in an as-yet-to-be-discovered location. There is little published information on wahoo occurrence, abundance or reproductive development in the Gulf and Caribbean areas during winter and early spring (December through March). Although wahoo reportedly are abundant in these regions during November through March, the possibility of an early spring spawning season for wahoo remains speculative. Future work on wahoo in the northern Gulf of Mexico should include efforts to obtain samples during the winter and spring as well as to increase the sample size of spawning fish to obtain more accurate estimates of batch fecundity and spawning frequency.

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