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ABSTRACT

Red snapper (*Lutjanus campechanus*) is a valuable commercial and recreational species throughout the southeastern United States and Caribbean. Recent reports of reduction in red snapper stock sizes throughout this range highlight the necessity for a better understanding of the biology of the species. Except for Florida panhandle red snapper, little is known of the reproduction of red snapper off Florida. We collected red snapper from recreational-for-hire boats in two distinct areas of Florida to examine potential regional differences in their reproductive biology. Samples were obtained from the Florida East Coast (EC—St. Augustine to Melbourne, N = 66) from June – November 2004 – 2005 and from the Dry Tortugas (DT, N = 81) during May, June, and August 2004-2005. Females from EC were spawning capable and actively spawning from June – October, with peaks in GSI values in July and September. Females from DT were spawning capable and actively spawning in June and August. Males were spawning capable from June – October in EC and in May, June and August in DT. There was a significant relationship between length and batch fecundity for red snapper from EC but not from DT. Relative fecundity estimates were low in DT fish (27 ± 11 eggs/g) relative to 235 ± 56 eggs/g in EC fish but similar to those reported from Alabama. Spawning frequency estimates varied from every 2.2 days in EC to every 4.3 days in DT. The apparent regional differences in reproductive biology among Florida red snapper may require region-specific management plans for this species.

KEY WORDS: Reproductive biology, fecundity, *Lutjanus campechanus*

Las Diferencias Regionales en la Reproducción de Huachinango del Golfo en Florida

El huachinango del Golfo (*Lutjanus campechanus*) es una especie valiosa en las pesquerías comerciales y de recreativas a través del Golfo de México y la Región Caribe. Los informes recientes de la reducción en tamaño de poblaciones de huachinango a través de la región total destacan la necesidad para una mejor comprensión de la biología de la especie. Con la excepción de los huachinangos desde la pordiosea de la Florida, hay poco información sobre su reproducción en las aguas de la Florida. Recogimos huachinango de los barcos recreativos para emplea en dos áreas distintas de Florida para examinar las diferencias regionales potenciales en su biología reproductiva. Las muestras fueron obtenidas de la costa este de Florida (EC—St. Augustine a Melbourne, N = 66) de junio a noviembre del 2004 – 2005 y de las Tortugas Secas (DT, N = 81) durante mayo, junio, y agosto de 2004-2005. Las hembras de EC eran en los fases desove capaz y desove activamente junio a octubre, con picos en valores de GSI en julio y septiembre. Las hembras de DT eran en los fases desove capaz y desove activamente en junio y agosto. Los machos eran en fase desove capaz de junio a octubre en EC y de mayo, junio y agosto en DT. Había una relación significativa entre fecundidad y longitud por el huachinango de EC pero no era relación por huachinango de DT. Las estimaciones relativas de la fecundidad fueron baja en los peces desde DT (27 ± 11 huevos/g) pero fueron 235±56 huevos/g en los peces desde EC, semejante a valores de Alabama. La estima de la frecuencia de desolve vario de cada 2,2 días en EC a cada 4,3 días en DT. Las diferencias regionales aparentes en la biología reproductiva entre huachinango de Florida pueden requerir los planes región-específicos de manejo para esta especie.

PALABRAS CLAVES: Biología reproductiva, fecundidad, *Lutjanus campechanus*

Variations Régionales des Caracteristiques de la Reproduction du Vivaneau Campeche en Floride

Le vivaneau campèche (*Lutjanus campechanus*) est une espèce à haute valeur, commerciale et récréative dans le Golfe de Mexique et la région des antilles. Le besoin d'une meilleure compréhension de la biologie du vivaneau campèche est souligné par les rapports récents d'un déclin des stocks de cette espèce dans l'ensemble de la région. A l'exception de la partie nord-ouest de la Floride, la reproduction du vivaneau campèche, en Floride est peu connue. Nous avons échantillonné des vivaneaux campèches capturés par les pêcheries récréatives dans deux secteurs de la Floride pour examiner les différences potentielles à la biologie de la reproduction. Les échantillons ont été obtenus sur la côte est de la Floride (CE—entre St. Augustine et Melbourne, N = 66) entre juin et Novembre en 2004-2005, et dans le parc national des 'Dry Tortugas' (DT, N = 81) pendant les mois de mai, juin, et août 2004-2005. Les femelles du CE est étaient frayaient activement de juin à octobre, les valeurs des RGS culminants au juillet et septembre. Les femelles du DT étaient frayaient activement aux mois de juin et août. Les mâles de EC étaient sexuellement matures juin à novembre et de mai à juin sur DT; aucun mâle n'a été capturé au mois d'août en DT. Une relation significative entre la fécondité et la longueur est observée pour les specimens capturés sur CE mais pas pour ceux capturés sur DT. Les estimateurs de la fécondité relative sont bas pour les poisson de DT (27±11 oeufs/g) mais sont de 235±56 oeufs/g chez les poisson de CE, valeurs similaire à celles rapportées au large de l'Alabama. La fréquence estimée des pontes varie de une ponte chaque 2,2 jours sur CE est à une ponte chaque 4,3 jours à DT. Les différences apparentes entre les caractéristiques de la reproduction peuvent rendre nécessaire une gestion planifiée spécifique à chaque région pour vivaneau campèche.

MOTS CLÉS: Biologie de la reproduction, fécondité, fréquence de ponte, *Lutjanus campechanus*

INTRODUCTION

The red snapper, *Lutjanus campechanus*, is a highly prized species in both commercial and recreational fisheries from the southeastern United States Atlantic Ocean, the Gulf of Mexico, and the Caribbean. Red snapper abundance in the Gulf of Mexico fishery decreased by an estimated 90% between the 1970s and the 1990s (Goodyear and Phares 1990) as a result of overexploitation by commercial and recreational fishers, high juvenile mortality due to the shrimp-trawl fishery, and habitat change (Christman 1997, Gallaway *et al*. 1998). The stock currently is considered 'overfished and undergoing overfishing,' and a rebuilding plan is in effect leading to increased regulation of the fishery (SEDAR 2005). However, an understanding of the reproductive biology of a species throughout its range is necessary for an effective rebuilding plan. Little information exists in the primary literature on the spawning and reproductive biology of red snapper with the exception of the northern Gulf of Mexico, despite the importance of the species to the commercial and recreational fisheries in the areas in which they occur. Information on spawning seasonality as well as size and age at maturity is available for the northern Gulf of Mexico (Bradley and Bryan 1975, Wilson *et al.* 1994, Collins *et al.* 1996, Woods *et al.* 2003), the southern Gulf of Mexico (Brulé *et al.* 2004), and the southeastern U.S. Atlantic Ocean (White and Palmer 2004). The only information available on the reproduction of red snapper for the southeastern U.S. Gulf of Mexico is 30 years old (Futch and Bruger 1976). Current information indicates red snapper in the northern Gulf of Mexico reach sexual maturity at age two, have a reproductive season from April or May through September, are capable of spawning multiple times during the reproductive season, and exhibit a distinct diel spawning periodicity, with peak spawning occurring in the late afternoon (Collins *et al.* 2001, Woods *et al.* 2003, Jackson *et al.* 2006). However, red snapper from the southern Gulf of Mexico (Yucatan Peninsula) were found to be reproductively active throughout the year, although the primary spawning season was from March through November with May and August-October peaks (Brulé *et al.* 2004). Fecundity estimates are limited to reports from the northern Gulf of Mexico and suggest large variations with age and size of the fish (Woods 2003; Collins *et al.* 2001). Notably, size at maturity appears to differ for red snapper from Alabama and Louisiana, with Alabama fish achieving sexual maturity at a smaller size (at the same age) than fish from Louisiana (Woods *et al.* 2003). This observation suggests that there may be geographical differences in the reproduction of the species in the northern Gulf of Mexico east and west of the Mississippi River. Similar differences may occur in red snapper reproduction from distinct areas of Florida, resulting from different fishing pressures and management. The objective of this work was to provide preliminary information on the reproductive biology of red snapper from two distinct regions of Florida (the Florida east coast and the Dry Tortugas).

MATERIALS AND METHODS

Red snapper were caught on hook and line from headboat and commercial vessels from the Florida east coast (EC; St. Augustine to Melbourne) and the Dry Tortugas (DT) during 2004 - 2005. Total length (TL, mm), fork length, (FL, mm), and gonad weight (GW, 0.1 g) were recorded for all fish. Total weight (W, 1.0 g), when not recorded, was calculated using length-weight regressions developed by Nelson and Manooch (1982) for Florida east and west coast red snapper (Table 1).

Table 1. Length-weight regression equations used to calculate total weight of red snapper from two regions in Florida. Equations from Nelson and Manooch (1982).

Region	Equation	Applied to
East Coast	$W = 0.00136 * (TL^{3.017})$	East Coast
West Coast	$W = 0.00182 * (TL^{2.966})$	Dry Tortugas

Gonadal tissue was removed from fresh specimens within eight hours of capture. Most fish were sampled immediately after the vessel had docked. Fish that were captured during longer trips were sampled immediately upon capture. After removal, gonadal tissue was weighed and fixed whole in 10% neutral buffered formalin (NBF), and shipped to The University of Southern Mississippi (USM) for subsequent processing and analysis. At USM, preserved gonadal tissue was re-weighed and a 1 cm^3 piece of tissue from the midsection of one gonad was placed in a cassette and stored in 10% NBF prior to histological processing. A 5 – 10 g piece of tissue from ovaries containing hydrated oocytes or oocytes undergoing oocyte maturation (OM) was removed, weighed (0.1g), and preserved in 10% NBF in a separate, labeled jar for fecundity analysis. Gonadal tissue for histological analysis was rinsed overnight in tap water, dehydrated in a series of graded ethanols, cleared, and embedded in paraffin following standard histological techniques. Tissues were cross-sectioned at 4µm, mounted on slides, and stained with hematoxylin and eosin. Slides of ovarian tissue were inspected at 40X and 100X, and all oocyte stages, OM stages, and postovulatory follicle (POF) stages were counted in one 100X field of view. The POF were staged following the procedure of Hunter and Macewicz (1985), and OM oocytes were staged according to Brown-Peterson *et al.* (1988). Ovarian maturity was assigned to a phase of development based on Brown-Peterson *et al*. (2007) which included immature, early developing, developing, spawning capable, actively spawning, regressing, and regenerating phases. Testicular tissue was inspected at 100X and 400X, and all stages of spermatogenesis present in the section were recorded. Testicular maturation was staged

according to criteria outlined by Brown-Peterson *et al*. (2007) and included the developing, spawning capable, regressing, and regenerating phases.

Fecundity was determined following the volumetric method (Bagenal and Braum 1971). Ovarian tissue was rinsed in tap water overnight, and all oocytes were teased from the ovarian walls and membranes with gentle scraping. The oocytes were suspended in 200 – 300 ml of water, and six replicate 1-ml sub-samples were removed for fecundity determinations. All oocytes >600 µm that represented the largest batch of oocytes (those undergoing OM and/or hydrated) were counted in each sub-sample, typically, 40-90 oocytes. Fecundity was expressed as both batch fecundity (mean number of eggs/batch) and relative fecundity (mean number of eggs/g ovary-free body weight (OFBW)).

The gonadosomatic index (GSI) was calculated for each fish as follows: GSI = (GW/OFBW) x 100. Spawning frequency was estimated for females in the spawning capable and actively spawning phases on the basis of percentage of females with oocytes undergoing OM, following procedures used by Brown-Peterson and Warren (2001).

RESULTS

Gonads from Florida east coast red snapper (n = 66) and from the Dry Tortugas (n = 81) were analyzed. Only five immature females, all from EC, were captured during the study; the smallest immature female was 129 mm TL, the largest immature female was 361 mm TL. The smallest sexually mature female captured was 312 mm TL, and the smallest female captured with hydrated oocytes was 394 mm TL; both fish were from EC. Due to the small sample size of immature fish, length at 50% maturity could not be estimated. No males in the immature phase were captured during the study; the smallest male captured was 305 mm TL and was spawning capable.

Red snapper were captured monthly from June through November along the Florida EC. Peak GSI values for both males and females were evident in July, with a secondary peak for females in September (Figure 1). Elevated GSI values from June through September in both sexes suggest that these are the prime reproductive months for red snapper along the Florida east coast. Insufficient monthly samples were available from DT for similar analysis.

Histological examination of ovarian and testicular tissues showed red snapper from EC were spawning-capable from June through October, with females captured in the spawning capable or actively spawning phases during those 5 months (Table 2). Actively spawning females had hydrated oocytes in the ovary (Figure 2a), suggesting that spawning would have occurred within 2 – 6 hours of capture. All sexually mature males and females from EC were undergoing gonadal recrudescence by June, and fish of both sexes had gonads in the regenerating phase in November (Table 2). All males from EC were spawning capable from June through September (Table 2). By October, active spermatogenesis had ceased although the lobules remained full of spermatozoa and proliferation of spermatogonia along the periphery of the testis was evident as fish were beginning preparation for the next spawning season (Figure 2b).

Red snapper from DT were captured only during May, June, and August. Ovarian recrudescence appeared to begin in May in this region since the most females were in the early developing phase in May, although 43% were still in the regenerating phase (Table 3). By June, 40% of females were spawning capable, and, in both June and August, females were in the actively spawning phase. However, female collections from DT always contained some in the regenerating phase (Table 3), suggesting some females from this region may not spawn or have a very short spawning season. The majority of males captured in DT were spawning capable each month (Table 3), but unlike in EC, some males were developing during May and June in DT. Furthermore, males in the regenerating phase were found in May and August in DT. While the data suggest that the red snapper reproductive season may be shorter in DT than in EC, the duration of the reproductive season in DT is unknown due to limited seasonal data.

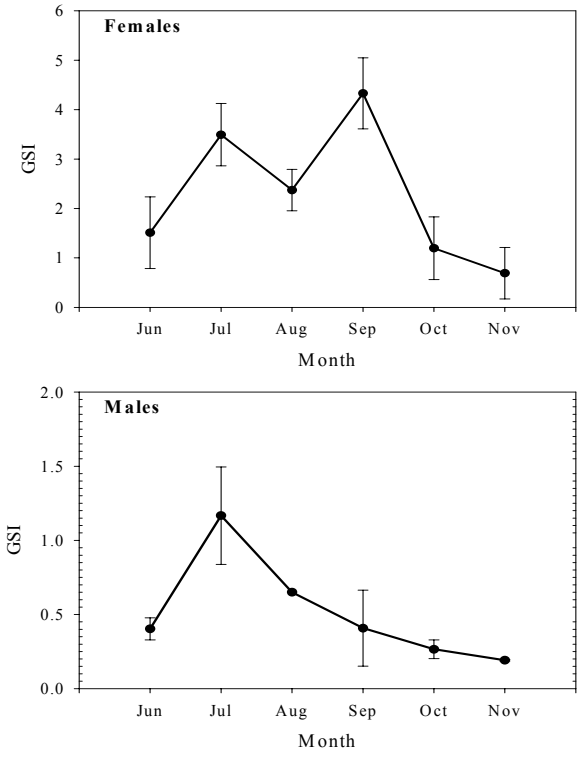

Figure 1. Mean (± SE) monthly gonadosomatic index (GSI) values for female and male red snapper captured from the east coast of Florida 2004 – 2005.

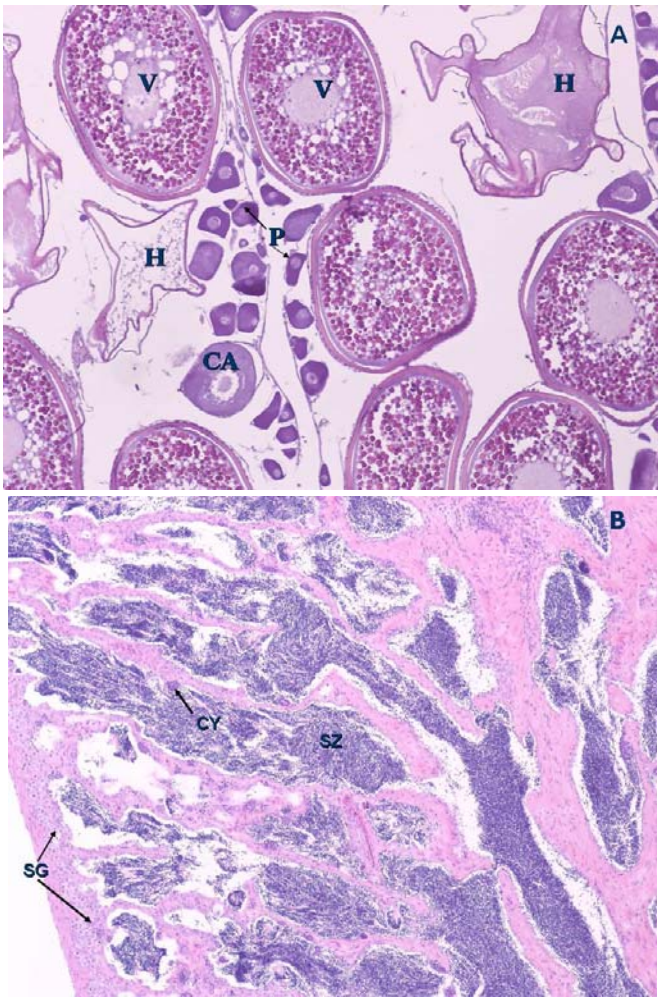

Figure 2. Histological sections of red snapper gonadal tissue. A. Ovarian section of a red snapper in the actively spawning phase showing asynchronous oocyte development and hydrated oocytes. B. Testis of red snapper at the end of the reproductive season showing abundant spermatozoa, reduced spermatogenesis, and spermatogonial proliferation at the periphery of the testis. CA—cortical alveolar oocyte; CY—spermatocyst; H—hydrated oocyte; P—primary growth oocyte; SG—spermatogonia; SZ—spermatozoa; V—vitellogenic oocyte.

Red snapper in Florida are capable of spawning multiple times during the reproductive season as indicated by asynchronous oocyte development and the presence of vitellogenic oocytes in the ovaries of spawning fish (i.e., a subsequent batch of oocytes in the same ovary with hydrated oocytes, Figure 2a). Additional evidence of multiple spawning is the presence of POFs in ovaries with mature vitellogenic oocytes. Ovaries with POFs were only occasionally observed in our samples, and those were found exclusively in fish from EC.

Spawning frequency was estimated based on the percentage of spawning capable and actively spawning fish with hydrated but non-ovulated oocytes. Spawning frequency of EC fish was estimated to be every 2.2 days based on 12 of 26 females in this group with hydrated oocytes from June through October. Red snapper spawned less frequently in DT than in EC, with an estimate of spawning every 4.3 days based on three of 13 spawning capable fish with hydrated oocytes in June and August. These estimates should be viewed with caution as they are based on a small number of fish and may not represent the entire population.

Batch fecundity was calculated for females with hydrated oocytes (n = 12, EC and n = 6, DT). There was a significant, positive relationship between TL and batch fecundity (BF) for EC females (BF = 9,548TL – 5,224,104; $r^2 = 0.67$, p = 0.002; Figure 3A). The EC fish ranged from 560 – 937 mm TL. In contrast, there was no relationship between BF and TL for DT females (p = 0.95); with the exception of one outlier, all batch fecundity values were low regardless of fish size (Figure 3B). The DT fish ranged from 632 – 750 mm TL. Relative fecundity (RF) for EC females was 235 ± 56 eggs/g OFBW; RF for DT females was a low 27 ± 11 eggs/g OFBW. Combining the BF estimates with spawning frequency for EC females suggests that an "average size female" of 2,900 g would be capable of spawning 669,750 eggs during each spawning event for a total of 46,578,068 eggs over the 6-month reproductive season (June – October). However, these estimates are based on a small sample size and may not be an accurate representation of east coast red snapper spawning abilities.

Table 3. Monthly gonadal maturation phases of male and female red snapper from Dry Tortugas. Values are expressed as percentage.

Month	Sex	N	Early Developing	Developing	Spawning Capable	Actively Spawning	Regressing	Regenerating
May	Female	7	57					43
	Male	13		31	54			15
June	Female	22	18	14	36	4		23
	Male	16		12	88			
August	Female	21	22	20	5	5		48
	Male	11			55		27	18

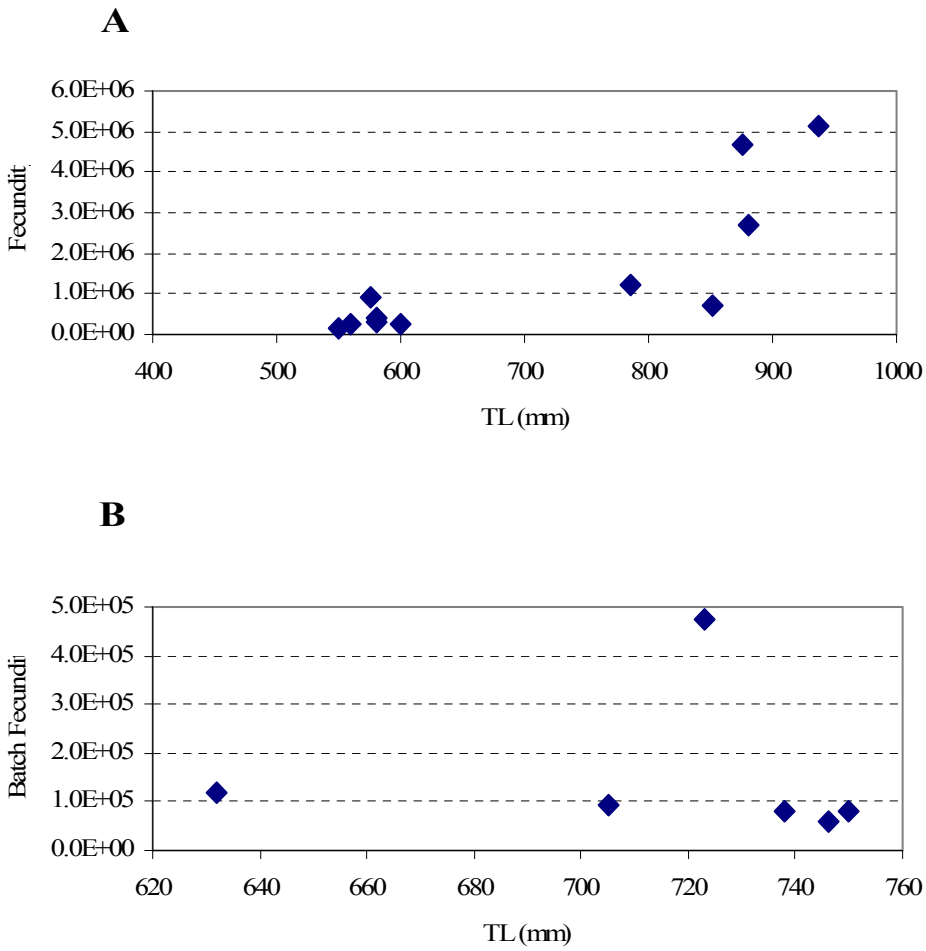

Figure 3. Batch fecundity-total length relationships for red snapper from (A) Florida east coast and (B) Dry Tortugas.

DISCUSSION

Data from this study adds to existing knowledge of red snapper reproductive biology from the Florida east coast (EC) (White and Palmer 2004) and is the first report on the reproductive biology of red snapper from the Dry Tortugas (DT). Our findings on the reproductive biology of red snapper from the Florida east coast confirm previously reported data from the region (White and Palmer 2004), despite a smaller sample size (n = 66) than the previous study (n = 1,027). Size at maturity appeared similar for both males and females and agrees with White and Palmer (2004). Sampling for our study began during the reproductive period in June, and histological evidence showed females in spawning condition from June through October with peak activity from July through September, similar to previous reports of a May through October reproductive period (White and Palmer 2004). A greater proportion of females with hydrated oocytes were observed in this study, based on the higher GSI values during the reproductive season (mean GSI range 0.69 – 4.33, this study; mean GSI range 0.35 – 2.67, White and Palmer 2004). This difference may be due to time of day when the fish were captured, as hydration occurs in mid-morning in red snapper, with ovulation occurring in early afternoon (Jackson *et al*. 2006). Finally, while White and Palmer (2004) provided histological evidence that east coast red snapper spawn several times during the reproductive season (based on presence of POFs), this study represents the first estimate of batch fecundity and spawning frequency for the region. Batch fecundity (BF) estimates are similar to those previously reported for red snapper off Alabama (Woods 2003). However, EC red snapper appear to have a higher spawning frequency (2.2 days) than that reported by Woods (2003) for fish from the northern Gulf of Mexico (3 – 4 days).

Limited data from DT precluded a complete analysis of the seasonality of red snapper reproduction from this region. However, spawning definitely occurred from June

through August in the Dry Tortugas. Additional collections during other months will most likely extend the spawning season of red snapper from that area and may more closely resemble that of fish from Mexico. Red snapper off the Yucatan Peninsula have a March through November, 9-month reproductive season (Brulé *et al.* 2004). The lack of correlation between BF and TL in DT red snapper is surprising and probably is the result of the limited data set. The extremely low BF reported (57,366 – 475,879) for DT are consistent with findings by Collins *et al.* (2001) for fish < 8 years from St. Petersburg, FL, to South Padre Island, TX; the DT fish were 4 – 5 years old (Burns *et al*. 2006). Finally, spawning frequency estimates for DT red snapper (every 4.3 days) are similar to the 3 – 4 day spawning frequency reported for northern Gulf of Mexico red snapper (Woods 2003).

The limited data available suggest there are differences in the reproductive biology of EC and DT red snapper. While the peak of the spawning season appears similar, fecundity and spawning frequency are higher in EC red snapper than in those from DT. Regional differences have been reported in size and age at maturity for red snapper from Alabama and Louisiana (Woods *et al.* 2003), and those authors suggested that mortality differences due to fishing might explain these demographic differences. Fishing pressure on red snapper, in the form of size and bag limits and seasonal closures, differed between the EC and DT regions during the time these data were collected.

Along the EC, the minimum size limit was 508 mm TL (20 inches), and there was a two fish bag limit per person; these regulations have been in force since 1991, and there has never been a seasonal closure for red snapper (R. Mahood, Southeast Fishery Management Council Pers. comm.). In contrast, regulations for red snapper in west Florida and the Gulf of Mexico, which include the Dry Tortugas, were a minimum length of 406 mm TL (16 inches) and a four fish bag limit per person per trip during 2004 - 2005. Furthermore, the recreational fishing season for red snapper was 15 April – 31 October in Florida state waters of the Gulf of Mexico, but recreational fishing for red snapper was closed when a pre-set quota of 4.47 million pounds had been reached (S. Atran, Gulf of Mexico Fishery Management Council Pers. comm.). Additionally, juvenile red snapper undergo high mortality as by-catch in shrimp trawls in the Gulf of Mexico (Galloway *et al.* 1998). These differences in fishing pressure and fishery regulations, plus possibly predation and temperature, may explain the differences observed in red snapper reproductive biology between Florida regions. Clearly, additional research is necessary to gain a better and more complete understanding of red snapper reproductive biology throughout Florida. Regional differences may require implementation of regional management strategies for red snapper similar to the existing regional management plans in Florida for spotted seatrout (VanderKooy and Muller 2003).

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