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Demographic Differences in Northern Gulf of Mexico Red Snapper Reproductive Maturation: Implications for the Unit Stock Hypothesis

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Abstract.—Red snapper, *Lutjanus campechanus*, has been fished for over a century, with management beginning in the Gulf of Mexico (Gulf) in the early 1990s when perceptions of a declining population size surfaced. Red snapper are managed as a unit stock and the fishery management plan is based upon minimal data regarding reproductive output, and size and age at sexual maturation is not certain. Differences in size and age at sexual maturity of red snapper between the northeast and north-central Gulf were evaluated to test whether the population conforms to the unit stock hypothesis. Red snapper were collected during the spawning season in 1999, 2000, and 2001 from the Gulf off Alabama and Louisiana and were used to describe maturation schedules. Progression of oocyte maturation to vitellogenesis was used to define and identify sexually mature females. Combined data showed the smallest mature red snapper was 267 mm fork length (FL) and was two years old. The smallest with hydrated oocytes, indicative of imminent spawning, or postovulatory follicles, indicative of recent spawning, were 285 mm and 297 mm FL respectively, and both were two years old. Red snapper off Alabama reached maturation at smaller sizes and younger ages than those sampled off Louisiana. Growth rates did not differ between the regions. Such differences in maturation schedules may document an important stock response to reductions in population size.

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Introduction

Over decades of exploitation, strong size-selective fishing mortality has resulted in the removal of the largest, most fecund females (Trippel 1995) and in decreases of age- and/or size-at-sexual maturity in a number of fish populations worldwide (Haug and Tjemsland 1986; Jørgensen 1990, Bowering and Brodie 1991; Rijnsdorp 1991, Harris and McGovern 1997; Zhao and McGovern 1997, McGovern et al. 1998, see Sadovy 2001). Such changes in maturation schedules may evidence an important stock response to reductions in population size (Trippel 1995). Although flexibilities in life history traits such as age-at-maturation may help both to increase egg production and to compensate for reduced population numbers, it has been demonstrated that younger fish of some species produce eggs and larvae that are less likely to survive than those produced by older conspecifics (Knutsen and Tilseth 1985; Hislop 1988, Zastrow et al. 1989). This, in addition to reduced population egg production attributable to removal of large females, engenders concerns about whether young females are sufficient in their reproductive capacity to maintain population numbers at sustainable levels while fishing mortality remains high. Thus, effective management of fish populations depends in part upon an understanding of the age and size at which a species becomes sexually mature.

The red snapper *Lutjanus campechanus* has supported important recreational and commercial fisheries in the Gulf of Mexico (Gulf) for over a century. The Gulf red snapper fishery has been intensely managed since the early 1990s under the assumption of a unit stock, which implies that age- and size-at-maturity and maturation rates should vary little Gulf-wide. Despite management efforts, red snapper in the Gulf remain overfished (Goodyear 1995; Schirripa and Legault 1999).

The red snapper is a long-lived reef fish that can exceed 900 mm total length (TL) and can live more than 50 years (Wilson and Nieland 2001). The species is restricted to the South Atlantic Bight and the Gulf, including Mexican waters but not the Caribbean Sea (Hoese and Moore 1977). This gonochoristic species spawns multiple times during a prolonged season. Though much "gray" literature on red snapper exists, little addressing spawning and reproductive biology of the species in the wild has been published in the peer-reviewed literature. Camber (1955), Moseley (1966), and Futch and Bruger (1976) all presented limited data on red snapper length- or age-at-maturity and the duration of the spawning season in the Gulf. Length-at-maturity has been reported to be 320 mm fork length (FL; Camber 1955) and between 190 and 300 mm standard length (SL; Moseley 1966). Wilson et al. (1994) presented preliminary estimates of maturation at 290 mm FL. Age-at-maturity has been reported as greater than 2 years old (Futch and Bruger 1976).

Ovary analyses have also varied among studies. While authors prior to 1976 (Camber 1955; Moseley 1966, Bradley and Bryan 1975) used macro-assessment of gonad condition and maturation, later authors (Futch and Bruger 1976; Wilson and Nieland 1994; Collins et al. 1996) used histological techniques to determine stages of oocyte maturation. Histology is a more effective method for staging oocytes because it allows a detailed view of cross-sectioned and stained oocytes and thus, precise descriptions of oocyte maturation stages can be defined more clearly (West 1990). Despite this precision, problems still exist in the histological approach due to differences in terminology among authors, as well as subtle differences in the progress of oocyte maturation among species.

The purpose of this research was to gain a better understanding of red snapper population dynamics for management purposes. The objectives were to provide data on age- and

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size-at-reproductive maturity of red snapper in the northern Gulf and to determine if differences in these reproductive variables existed east and west of the Mississippi River over a time span of three years. Our goal was to sample over greater spatial and longer temporal scale than previous studies of red snapper reproductive biology.

Methods

During the recreational fishing seasons (April–October) of 1999, 2000, and 2001, red snapper were sampled by hook and line and from charter boat docks from the Gulf west of the Mississippi River off Fourchon, Louisiana, and east of the Mississippi River off Dauphin Island, Alabama (Figure 1). A minimum total of 600 males and females were annually targeted per region in 1999 and again in 2000, and 300 males and females per region were targeted in 2001. The minimum size of individuals for recreational harvest was initially 381 mm TL, but was increased to 457 mm TL for the last half of the 1999 season. The minimum size was 406 mm TL during the 2000 and 2001 seasons. In addition to these targeted fish from the recreational fishery, a National Marine Fisheries Service (NMFS) permit allowed us to collect undersized red snapper; however, we were able to exert more effort in collecting undersized fish off Alabama than Louisiana. In this study only female individuals are considered.

Fork length (mm) and total weight (TW; to the nearest 0.01 kg) were recorded for each fish sampled. Sagittal otoliths were removed and processed for age analysis following Cowan et al. (1995). Gonads were excised, placed in individually labeled plastic resealable bags, and transported on ice to the laboratory. After the gonads were weighed (nearest 0.1 g), the ovaries were stored in 10% formalin until further analysis.

Red snapper ovaries were examined microscopically to determine age- and size-at-maturity. Oocyte maturation stages were determined using histological analysis. The

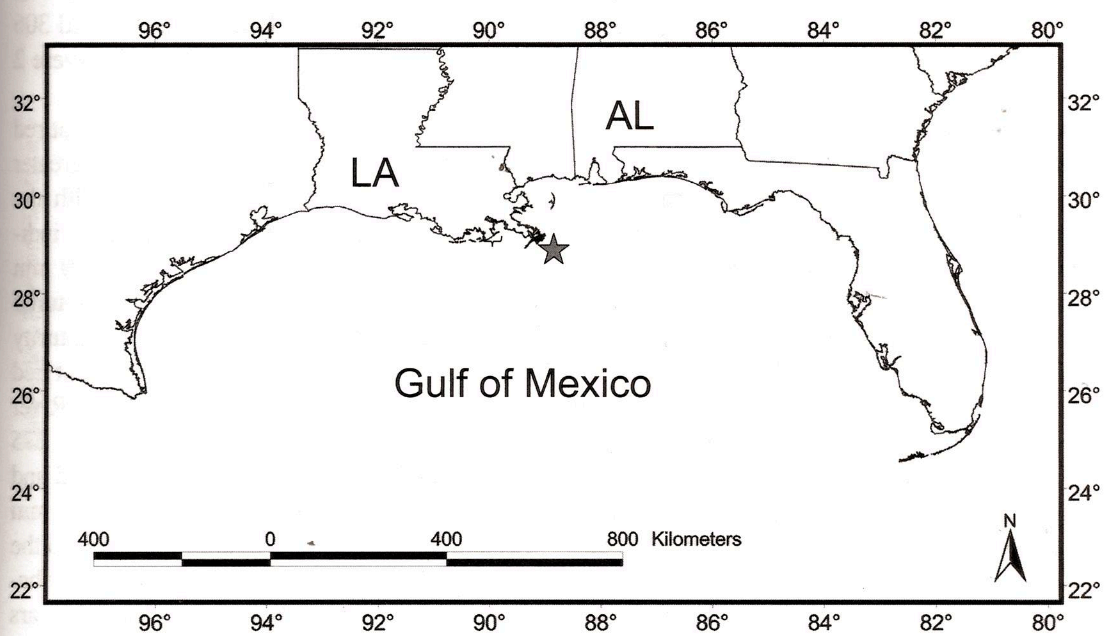

Figure 1. Red snapper *Lutjanus campechanus* were collected east of the Mississippi River outflow (star) plume off Alabama (AL) and west of the river off southeast Louisiana (LA).

lobes of red snapper ovaries are symmetrical (Collins et al. 1996); therefore, a subsample of formalin-fixed ovarian tissue (30–50 g) was dissected from one randomly chosen region of the two lobes (three regions per lobe: anterior, medial and posterior). Each subsample was embedded in Paraplast (Sherwood Medical Industries) and sectioned to 3 μm thickness. Sections were mounted on microscope slides, stained in Gill hematoxylin, and counter-stained in eosin Y.

Oocytes were categorized into one of four oocyte stages by microscopic examination of the prepared histology slides at 40x to 100x magnification. The four stages of oocyte maturation described by Wallace and Selman (1981) are primary growth (PG), cortical alveoli (CA), vitellogenic (V), and hydrated (H). Progression of oocyte maturation to vitellogenesis was used to define and identify mature females (Hunter and Goldberg 1980; Brown-Peterson et al. 1988; Nieland and Wilson 1993). Immature ovaries contained only PG and CA oocytes. Each histological section was also scanned for the presence of post-ovulatory follicles (POF), indicative of recent spawning activity.

Elevated gonadosomatic indices, or the gonad weight as the percentage of ovary free body weight, indicated that spawning began in May and ended by late September; the peak months of the spawning season appeared to be May, June, and July and spawning continued through September (Woods 2003). Thus, maturity analyses were restricted to fish collected in June, July, and August to minimize errors in differentiating between immature and resting or spent ovaries.

Females were classified as mature by size and age. Females were grouped into size classes of 50 mm FL, and into age classes. Statistical Analysis System (SAS Institute 1999) was used for statistical tests. Differences in defined reproductive characteristics between regions were tested by chisquare analysis. The Bonferroni technique was used reduce type I error.

Results

A total of 1,682 female red snapper was collected from the northern Gulf between June and early August from 1999 to 2001; 1,029 were from Alabama, 169 of those were under the legal size limit and collected with permission through a NMFS permit; 653 were from Louisiana, 111 of those were under the size limit and collected through a permit. Alabama females ranged from 237 to 916 mm FL, Louisiana females ranged from 292 to 910 mm FL. Ages of Alabama and Louisiana females ranged from 1 to 34 years and from 2 to 37 years, respectively. A total sample size of 903 females less than 625 mm FL was used for comparisons of length-at-maturity, and 806 females less than 7.5 years for comparisons of age-at-maturity.

The smallest mature Alabama red snapper was 267 mm FL; the smallest with hydrated oocytes, indicative of imminent spawning, and POF were 285 mm and 297 mm FL, respectively. The smallest mature Louisiana red snapper was 292 mm FL; the smallest with hydrated oocytes and POF were 304 and 306 mm FL, respectively. All of these fish were 2 years old.

Combined data generally showed that red snapper greater than 575 mm FL and greater than 5.5 years were 100% mature, with the exception of a 590 mm FL immature individual captured off Louisiana and a 720 mm FL, 7 year old immature individual captured off Alabama. A comparison of the maturity schedules for each region indicates that red snapper captured east of the Mississippi River off Alabama reached 50% maturity before 275 mm FL and before they are 2.5 years old and raw data showed 100% maturity by 575 mm FL and 4.5 years old. Females captured to the west, off Louisiana, reached 50% maturity before 325 mm FL and before they are 2.5 years old and raw data showed 100% maturity by 625 mm FL and 6.5 years old (Figures 2 and 3). Compared to Alabama, Louisiana female

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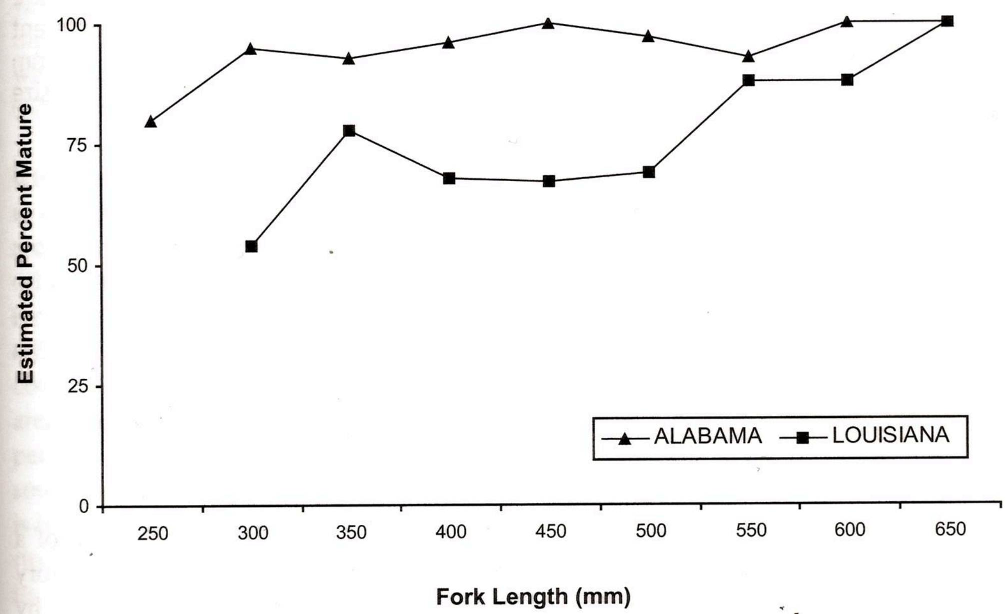

Figure 2. Percent of mature female red snapper *Lutjanus campechanus* sampled off the coasts of Alabama and Louisiana by fork length (mm).

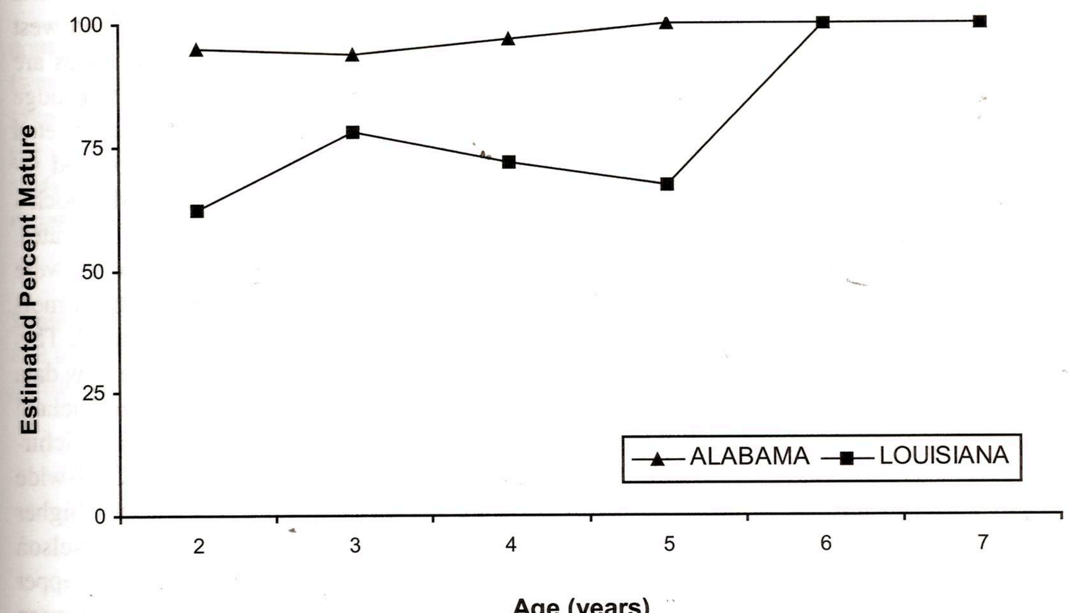

Figure 3. Percent of mature female red snapper *Lutjanus campechanus* sampled off the coasts of Alabama and Louisiana by age (years).

Table 1. Percent of mature female red snapper *Lutjanus campechanus* and sample size (*N*) by size class in 50 mm increments for Alabama and Louisiana. Size classes having significantly different proportions of mature females between states are indicated by (*). For Alabama, the 250 mm size class' smallest fish is 237; the size class is from 237–274. For Louisiana, the 300 mm size class' smallest fish is 292; the size class is from 292–324.

Size Class	Alabama		Louisiana	
FL (mm)	% Mature	*N*	% Mature	*N*
250	77	13		0
300*	89	64	54	13
350*	93	75	75	36
400*	97	133	66	56
450*	100	151	62	89
500*	98	96	63	46
550	94	64	88	17
600	100	39	88	8

red snapper progressed to 100% maturity over size- and age-classes more slowly. Chi-square analyses indicated that Alabama size classes between 300 and 500 mm FL and age classes between 3 and 5 years had significantly more mature females than those Louisiana classes (Tables 1 and 2).

Discussion

While estimates of size- and age-at-50% maturity fall within the broad range of estimates of past studies in different Gulf locations (Camber 1955; Moseley 1966; Futch and Bruger 1976; Wilson and Nieland 1994), only one other study has reported a maturation schedule to 100% maturity. Wilson and Nieland (1994) reported that females sampled from Louisiana reached 100% maturity by 420 mm FL, which differs from results reported here.

Regional differences in red snapper age- and size-at-maturation, as well as the rates at which they approach 100% maturity, could represent a real difference in population demographics of the red snapper east and west of the Mississippi River. Maturity schedules for a species generally are not static and it is rare for all individuals in a fish population to mature at the same age. However, a decrease in age-at-maturity can be an indication of a stressed population caused by compensatory responses to waning population size, or by genetic selection (Trippel 1995). More specifically, such a compensatory response may be due to fishing pressure, predator and prey abundance, stock composition and other biotic and abiotic environmental factors (Wootton 1990).

Although fishing mortality and natural mortality have been estimated east and west of the Mississippi River, these estimates are few and are based upon out-dated knowledge of longevity, and thus must be interpreted with caution. Goodyear (1995) provided revised estimates of Nelson and Manooch's (1982) red snapper natural mortality rates, concluding that both regional estimates were too high to be accurate and that natural mortality is probably less than 0.18 $years^{-1}$. This estimate also may be too high given new data on red snapper longevity (Wilson and Nieland 2001). In regards to fishing mortality, Schirripa and Legault (1999) estimated Gulf-wide fishing mortality to be 2.5–4.5 times higher than that believed to be sustainable. Nelson and Manooch (1982) estimated red snapper fishing mortality off Louisiana to be between 0.58 and 0.74 $year^{-1}$ and for west Florida, between 0.23 and 0.25 $year^{-1}$. More than 10 years later, Watterson (1998) estimated fishing mortality to be 1.14 $year^{-1}$ off Alabama when natural mortality was assumed to be 0.20 $year^{-1}$.

Maturity schedules of red snapper populations may vary by region due to differences in compensatory responses. If mortality rates are different, or if the environments in areas off the Alabama and Louisiana coastlines differ, then population demographics could also differ. Greater fishing pressure off Alabama could decrease the density of fish per unit area, thereby decreasing intra-specific competition and allowing for an increase in resource availability. However, the red snapper is believed to be overfished Gulf-wide (Schirripa and Legault 1999) and may have reached its compensatory maximum physiological growth potential, resulting in no observed difference in growth between the regions. As such, increased available energy in Alabama waters may be allocated to reproduction (Wootton 1990; Roff 1992). This would allow fish to reproduce at a smaller size and a younger age in Alabama waters.

Environmental differences also could contribute to demographic dissimilarity between regions. While both regions have a great number of artificial reefs that red snapper are known to inhabit, Alabama's artificial reefs are predominantly small, low vertical relief structures. In contrast, most of Louisiana's artificial reefs are oil and gas platforms that extend vertically to the surface, perhaps increasing their value as habitat. To date, no direct comparisons of oil rigs and lower relief artificial reefs as red snapper habitat have been made. Perhaps more importantly there is a large amount of natural low relief hard bottom off each of the coastlines (Gore 1992) and differences in the amount of structural habitat provided by either type of artificial reef is likely to be negligible.

There also may be differences in the amount of primary and secondary production available to higher trophic levels between the two regions. While coastal waters of both regions are production enhanced by river-dominated estuaries (Mobile Bay and the Mississippi-Atchafalaya Rivers for Alabama and Louisiana, respectively), the Mississippi River system drains 41% of the contiguous United States, discharging a great amount of nutrient-enriched freshwater and sediment into the Gulf (Milliman and Meade 1983); thus, the area of the continental shelf between the Mississippi River and the Yucatan Peninsula is known historically to be extremely high in primary and secondary production due to comparatively high amounts of nutrients discharged by the Mississippi River. Whether higher secondary production off Louisiana acts to affect the maturation schedule of red snapper is

Table 2. Percent of mature female red snapper *Lutjanus campechanus* and sample size (*N*) by age classes for Alabama and Louisiana. Age classes having significantly different proportions of mature females between states are indicated by (*).

Age Class	Alabama		Louisiana	
years	% Mature	*N*	% Mature	*N*
1	0	8		
2	87	55	63	16
3*	93	75	77	117
4*	97	200	65	99
5*	100	86	65	54
6	100	29	97	34
7	96	25	100	8

unknown. However, experiments with other species have shown that differences in food supply can alter the age at which fish become mature. In Pacific herring *Clupea pallasii*, brown trout *Salmo trutta*, and threespine sticklebacks *Gasterosteus aculeatus*, fish receiving higher rations of food matured earlier (Bagenal 1969; Wootton 1973; Hay et al. 1988). It may or may not be the case that red snapper off Louisiana receive greater dietary nutrients due to influence of the Mississippi River. Regardless of their high nutrient environment, they do not appear to be benefiting in a manner that allows them to reproduce at a younger age as do other fishes receiving higher rations of food. Furthermore, recent studies show that over a ten year period, size-at-age of Louisiana red snapper is decreasing (Nieland et al. 2007, this volume).

Shifts in maturation schedules in red snapper may be attributable to genetic selection coincident with increased mortality (Roff 1992). Tagging studies have inferred that red snapper movement may be sufficient to facilitate stock mixing in the northern Gulf (Patterson et al. 2001), but most movement of red snapper off Alabama is to the east and very little movement and mixing occurs west of the Mississippi River (Patterson et al. 2001). Furthermore, genetic studies of red snapper stock in the northern Gulf have not strongly supported genetic differences among regions (Camper et al. 1993; Gold et al. 1997, Heist and Gold 2000; but see Chapman et al. 1995). However, these genetic tests would not indicate differences in a maturity genotype. A genotype for smaller size and younger age-at-maturity can be selected for in some species (Trippel 1995). Early maturing genotypes reproduce before being fully recruited to the fishery. Genotypes that mature at larger sizes or older ages are more likely to be removed before reproduction. In contrast, fish that mature early may participate in one or more spawning seasons before being captured. The progeny for later maturing fish would be selected out of the population over time. Therefore, it may be that the late-maturing genotypes have been removed from the Alabama population due to high fishing pressure along this small coastline in the 1980s and 1990s; this still may be occurring today. This process also may account for differences in size- and age-at-maturity.

Other fish populations have evidenced changes in maturity schedules in response to reductions in population size. Zhao and McGovern (1997) identified changes through time in age- and length-at-maturity, and in growth rate of vermilion snapper *Rhomboplites aurorubens* in the South Atlantic Bight; these changes were probably due to gradual fishing pressure increases that ultimately resulted in growth overfishing. A preliminary study indicated that, compared to specimens sampled from the region five years earlier (Grimes and Huntsman 1980), vermilion snapper decreased in size- and age-at-maturation; however, length-at-age for one and two year old fish changed little (Collins and Pinckney 1988). A temporal comparison of the stock in 1979–1980 to the stock in 1985–1987 also concluded that vermilion snapper declined in size- and age-at-maturity through time (Zhao and McGovern 1997) and that growth rate decreased through time (Zhao et al. 1997). Because vermillion snapper growth rates decreased with time, Zhao and McGovern (1997) suggested that the decrease in size-at-maturity probably was not part of a density-dependent compensatory response to harvesting. More likely, it was a response to growth overfishing caused by the selective removal and incomplete replacement of faster-growing, later-maturing individuals (Zhao and McGovern 1997).

In contrast, Jørgensen (1990) suggested that changes through time in age-at-maturity and growth rate of Atlantic cod *Gadus morhua* were a density-dependent compensatory response to harvesting. The cod population has been intensely exploited for more than 50 years and cod stocks have undergone severe population declines. Jørgensen (1990) determined that despite high fishing pressures, it was the age distribution—and not the size distribution—of the population that changed. It is likely that in response to increased mortality, fish grow faster and mature at a younger age; implicitly, there is a minimum threshold for size-at-maturity (Jørgensen 1990). If this idea is correct, then declines in size- and in age-at-maturity should not necessarily occur simultaneously.

Reznick et al. (2001) presented a case in which populations of guppies, *Poecilia reticulata*, experiencing high and low predation pressures had different population demographics. Guppies experiencing high predation had a smaller size-and younger age-at-maturity, and a faster growth rate than fish experiencing low predation pressure because higher levels of resource availability existed as an indirect consequence of high predation. The populations experienced different mortality, lived in different environments, and due to mortality and environmental differences, food availability differed. Guppies at sites of low-predation did not have a greater density per unit area but had more large, old fish and fewer small, young fish, and, thus, greater biomass.

Although a difference in mortality due to fishing is likely to be the cause of differences in size- and age-at-maturity in regions east of the Mississippi River off Alabama and west of the River off Louisiana, no definitive conclusion can be made at this time. It is evident that differences in population demographics do exist between the two regions based upon maturation schedules. Furthermore, studies off the Louisiana coast over a 10 year time span show a decrease in total length of red snapper at ages 4, 5, and 6 years (Nieland et al. 2007). Implications of these differences in future stock assessments should be considered, along with other characteristics of red snapper growth and reproductive biology. To prevent regional overfishing, and to learn more about stock dynamics, an adaptive management approach should be considered.

For example, if red snapper reproductive characteristics differ east and west of the Mississippi River due to unsustainable fishing mortality rates off Alabama and northwest Florida, then an adaptive management approach decreasing fishing mortality off coastal Alabama should be enforced to prevent regional overfishing. Moreover, if red snapper reproductive characteristics respond to become more like those of the females off Louisiana through time, then much can be learned about how fish stocks respond to changes in fishing pressure. In contrast, if reproductive characteristics remain unchanged, then the environment may be driving differences in inherent reproductive capacity. Should this be true, a more environmental-based ecosystem approach to management could be indicated. Either way, our understanding of population dynamics would be enormously improved.

Acknowledgments

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