Comparison of life history parameters for landed and discarded fish captured off the southeastern United States

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Abstract—Commercial fisheries that are managed with minimum size limits protect small fish of all ages and may affect size-selective mortality by the differential removal of fast growing fish. This differential removal may decrease the average size at age, maturation, or sexual transition of the exploited population. When fishery-independent data are not available, a comparison of life history parameters of landed with those of discarded fish (by regulation) will indicate if differential mortality is occurring with the capture of young but large fish (fast growing phenotypes). Indications of this differential size-selective mortality would include the following: the discarded portion of the target fish would have similar age ranges but smaller sizes at age, maturation, and sexual transition as that of landed fish. We examined three species with minimum size limits but different exploitation histories. The known heavily exploited species (*Rhomboplites aurorubens* [vermilion snapper] and *Pagrus pagrus* [red porgy]) show signs of this differential mortality. Their landed catch includes many young, large fish, whereas discarded fish had a similar age range and mean ages but smaller sizes at age than the landed fish. The unknown exploited species, *Mycteroperca phenax* (scamp), showed no signs of differential mortality due to size-selective fishing. Landed catch consisted of old, large fish and discarded scamp had little overlap in age ranges, had significantly different mean ages, and only small differences in size at age when compared to comparable data for landed fish.

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Size limits are commonly used to manage commercial and recreational fisheries. Minimum size limits, which are relatively easy to enforce, have been used to restrict total harvest, prevent growth overfishing (where fish are harvested at an average size smaller than the size needed to produce maximum yield per recruit), and allow individuals at least one spawning event before removal from the fishery (Pitcher and Hart, 1982; Rothschild, 1986). One widely acknowledged disadvantage of size limits is the mortality immediately at release (release mortality) for under-size fish, but another emerging concern is that size-selective fisheries drive a phenotypic change in the life history traits of a population (Stokes and Law, 2000; Hutchings, 2005; Williams and Shertzer, 2005; Swain et al., 2007). Observed phenotypic changes can be driven by genetic and environmental influences. If the observed phenotypic change is mostly influenced by environmental changes (e.g., fishing pressure), then the observed phenotype may easily be reversed by adjusting the environmental influence, whereas if the change is largely influenced by genetic changes, it may not be readily reversed.[1] Recent studies have shown that high levels of fishing pressure can create changes in size at age, age at maturation, and size at maturation (Law, 2000; Heino and Godø, 2002; Grift et al., 2003; Olsen et al., 2005; Kuparinen and Merilä, 2007; Mollet et al., 2007; Sharpe and Hendry, 2009). In long-lived species, the decrease in individual growth rates, caused by early maturation in response to size-selective mortality, may have a severe effect on the stock. High levels of fishing pressure can not only decrease size at maturation, which results in an overall decrease in size at age, but because fecundity is correlated with size (Buckley et al., 1991; Hutchings and Meyers, 1993; Kjesbu et al., 1996; Trippel et al., 1997), high fishing pressure can also decrease reproductive potential of a population (Ratner and Lande, 2001). That these phenotypic shifts not only occur, but occur within several generations has been documented in several experimental studies (Reznick et al., 1990; Conover and Munch, 2002; Conover et al., 2005; Reznick and Ghalambor, 2005; Walsh et al., 2006).

Size limits are intended to protect fished populations by allowing young, small fish to grow larger and spawn at least once before capture, and thereby increase long-term yield (Ricker, 1945; Goodyear, 1996; Coleman et al., 2000). However, minimum size limits can increase fishing mor-

[1] Law, R. 2002. Selective fishing and phenotypic evolution: past, present, and future. ICES CM 2002/Y:11, 9 p.

tality on faster-growing phenotypes that reach the minimum size limit at a young age. Size limits protect all small fish of all ages, and over time small fish of all ages may dominate the population, because they have more opportunities to reproduce before removal from the population. Size at age and size at maturation may decrease in response to a higher proportion of slower growing phenotypes in the population (Pitcher and Hart, 1982). Such changes may result in decreased population abundance and biomass (Kuparinen and Merilä, 2007).

All current indications of phenotypic shifts for reef species off the coast of the southeastern United States have been derived solely from fishery-independent research surveys (Harris and McGovern, 1997; Zhao et al., 1997; Harris et al., 2002). Yet for many reef species in this region, there is not enough fishery-independent data to make this determination. When a lack of such data occurs, there are only fishery-dependent data sources available to determine if phenotypic shifts are occurring. To the authors' knowledge no one has used fishery-dependent data from commercial or recreational harvests to confirm whether or not the selective harvest of fast growing phenotypes is creating a phenotypic shift in fished populations. By comparing the life history parameters of landed (legal size) fish to those of regulatory (sublegal size) discards, one can determine if the minimum size limit is an appropriate management technique for a given species. If a phenotypic shift towards small, slow growing fish is occurring, then the discarded portion of the catch when compared to the landed portion should show similar age ranges, smaller size at age, smaller size at maturity, and smaller size at sexual transition for hermaphroditic species. Alternatively, if no phenotypic shift is occurring, then the discarded portion of the catch would consist almost exclusively of young, immature fish (although maturity stage would vary depending on the minimum size limit and species being investigated).

The South Atlantic Fisheries Management Council (SAFMC) is responsible for managing stocks in federal waters from North Carolina to Key West, Florida. Size limits (supplemented by seasonal closures for some species) have been the preferred regulatory control measure of the SAFMC since the development of the Fishery Management Plan for the snapper grouper fishery of the South Atlantic Region in 1983 (SAFMC, 1983). We investigated whether minimum size limits are contributing to a phenotypic shift towards small, slow growing phenotypes for three managed species of the snapper-grouper complex at different levels of exploitation: vermilion snapper (*Rhomboplites aurorubens*), currently experiencing overfishing with a fishing mortality rate (F) of 0.49 (SEDAR, 2008); red porgy (*Pagrus pagrus*), currently considered overfished, with predicted F of 0.095 (SEDAR, 2006); and scamp (*Mycteroperca phenax*), last classified as experiencing overfishing in 1998 (Manooch et al., 1998).

Table 1

The total number of days when samples of fish were collected by commercial fishermen off the coast of southeastern United States for each month within each year.

Month	2005	2006	2007	Total
January		10	5	15
February		10	10	20
March		12	8	20
April		7	8	15
May		16	14	30
June		3	8	11
July	10	8	6	24
August	9	13	4	26
September	13	14	7	34
October	11	13		24
November	6	11		17
December	8	2		10

Materials and methods

Sampling took place on a South Carolina commercial snapper-grouper fishing vessel from July 2005 through September 2007 and consisted of 52 trips (246 sampled days) across all months (Table 1). The vessel captain dedicated the last few days of each trip (trips ranged between five and nine days) to collecting samples, when he would retain all legal and sublegal size fish of vermilion snapper, red porgy, and scamp. The sampling locations were selected by the captain as part of his normal fishing routine. Fishing locations were situated from 30°16.558′N to 33°36.795′N, and most locations were along the shelf-break (Fig. 1). Sampling depths ranged between 20 and 128 m. Three bandit-reels, with terminal tackle consisting of two 4/0 J-hooks and baited with mackerel (*Sarda sarda*), were fished simultaneously by three crew members, and all fishing took place from sunrise to sunset. For each location, the captain recorded the position (latitude and longitude) and depth. Fish were tagged with a numbered t-bar tag (Floy Tag, Inc., Seattle, WA) and immediately placed on ice to preserve reproductive tissue in samples. Up to 90 sublegal and legal size fish of each species were kept from each trip, for up to 500 fish per species for each of two size categories (legal and sublegal) per year of the study. All fish were immediately collected from the captain upon returning to port and transported to the laboratory.

In the laboratory individual weight (g) and lengths (total [TL], fork [FL], and standard length [SL]; mm) were measured for each fish sampled. Both sagittal otoliths were removed and stored dry in coin envelopes. A posterior section of each gonad was removed and stored in 10% buffered seawater formalin. Although the sampling period was limited to one experienced commercial fisherman's catch over multiple

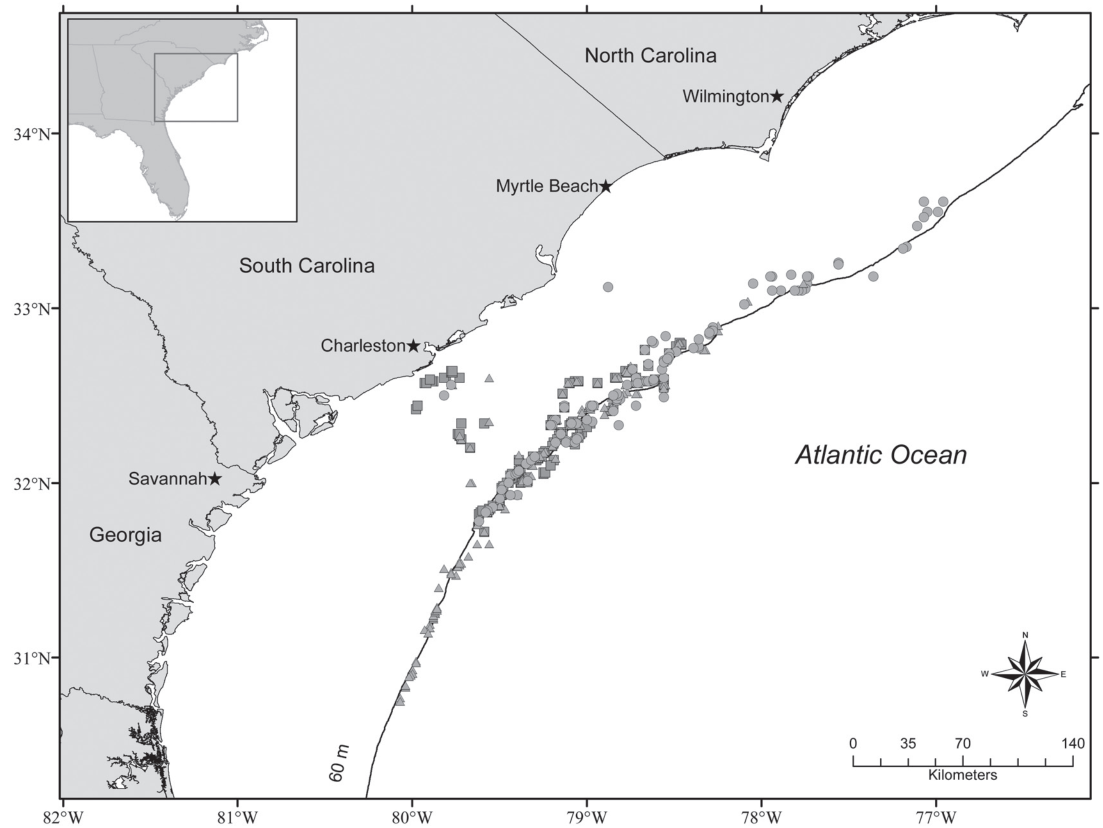

Figure 1

Fishing locations selected by the commercial fishermen for collections of vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*). General sampling locations overlapped among years (square=2005; triangle=2006; circle=2007) and were primarily on the shelf-break.

years, his catches were typical of catches for commercial snapper-grouper fishermen in this region (Stephen and Harris, 2010).

Age and growth

Vermilion snapper and scamp otoliths were embedded in epoxy resin, sectioned through the core (~0.7 mm) with a Buehler IsoMet low-speed saw (Buehler, Lake Bluff, IL), and mounted on glass slides. All red porgy otoliths were first read whole. Otoliths from fish older then 6+ years were also sectioned and read to ensure accurate determination of age. Increments, defined as one translucent and one opaque zone for all species, were counted independently by two readers. Readers had no prior knowledge of the length, weight, sex, or capture date for any fish. Readers counted increments on sectioned otoliths along the dorsal side of the sulcus acousticus, from the core to the outer edge of the otolith and qualitatively ranked the edge type and otolith quality. For whole otoliths, increments were counted along a straight line midway between the posterodorsal dome and the most posterior point on the otolith. Edge types were categorized as either 1) an opaque zone on the otolith edge; 2) a narrow translucent zone on the otolith edge; 3) a medium translucent zone on the otolith edge; or 4) a wide translucent zone on the otolith edge. Edge type and increment count were used to assign an age to each fish. For otoliths with a medium or wide translucent zone (edge type 3 or 4) in fish captured after January 1 but before the month of opaque zone formation (vermilion snapper=September [Zhao et al., 1997]; red porgy=June [Harris and McGovern, 1997]; scamp=April [Harris et al., 2002]), ages equaled the increment count plus one; for all other fish, the age equaled the increment count.

For vermilion snapper and scamp otoliths, two readers independently counted the increments for all fish. Total agreement, agreement within one increment, and average percent error (APE) were calculated for both vermilion snapper and scamp readings. For both species, readers simultaneously re-examined otoliths when increment count or edge type did not agree. If readers could not agree on a count and edge type, that otolith was not used in analyses. For red porgy otoliths, the first reader aged all otoliths, and a second reader aged a subset (n=100 otoliths). Because there was a 98% agreement within one year, all final readings were from the first reader.

Age distributions for sublegal and legal size fish were compared by using a Kolmogorov-Smirnov two sample test. Sublegal and legal mean ages were compared using a one-way ANOVA. Proportions of sublegal and legal fish within each age class were compared by using a 2x2 contingency table with a chi-square test statistic or Fisher's test statistic when cell sizes were low. Mean lengths of sublegal and legal size fish within each age class where compared by using individual one-way ANOVAs. For comparison with other studies, total lengths were converted to fork lengths based on equations generated from the 30+ year collaborative fishery-independent reef fish survey program MARMAP (Marine Resources Monitoring, Assessment, and Prediction) (M. Reichert, unpubl. data) (Table 2). All statistical analyses were done in SAS, vers. 9.2 (SAS Institute Inc., Cary, NC).

Reproduction

Reproductive tissues were stored in 10% buffered seawater formalin for 1–2 weeks, after which samples were transferred to 50% isopropanol for 1–2 weeks. Reproductive tissues were then vacuum-infiltrated in a tissue processor, blocked in paraffin, and sectioned (7 µm) on a rotary microtome. Three sections from each sample were placed on a glass slide, stained with double-strength Gill's hematoxylin, and counter-stained with eosin-Y (Schmidt et al., 1993). Each section was viewed under a compound microscope (40–400× magnification) to determine sex and reproductive state by criteria modified from Harris et al. (2001). Correct assignment of reproductive stage was confirmed through length histograms by reproductive state (immature and mature), in which there was little overlap in the tails of the distribution (Wyanski et al., 2000).

Sex ratios (male:female) were compared to 1:1 ratios by using the chi-square goodness-of-fit test. The chi-square test (large sample sizes) or Fisher's exact test (small sample sizes) were used to compare sex ratios of legal and sublegal size fish. Probability of maturation and transitions at length and age were calculated with the maximum likelihood estimates, and the Wald's chi-square test statistic was used to compare probability estimates between sublegal- and legal-size fish.

Table 2

The linear relationship (with coefficient of determination [r^2]) between total length (TL) and fork length (FL) for vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) based on lengths collected through the 30+ year fishery-independent reef fish MARMAP (Marine Resources Monitoring, Assessment and Prediction) survey off the coast of the southeastern United States. n=number of fish in samples for each species.

Species	FL–TL relationship	n	r^2
Vermilion snapper	$FL=0.8948TL+1.127$	13,249	0.9964
Red porgy	$FL=0.8700TL+0.290$	16,498	0.9924
Scamp	$FL=0.8745TL+26.903$	2910	0.9883

Results

Vermilion snapper

A total of 1739 vermilion snapper were collected, of which 845 were legal-size (>305 mm TL) and 894 sublegal-size fish. Of these, 1638 were successfully aged. Age ranges were similar between legal- (1–10 years) and sublegal-size (0–12 years) vermilion snapper, but the distributions were significantly different (Kolmogorov-Smirnov test statistic [D]=0.29, P<0.001) (Fig. 2A). As expected, the younger age classes (0–3 years) were predominantly sublegal size fish, whereas the older ages were predominately legal size. Mean age (3.5 yr) of sublegal-size fish was significantly different from the mean age (4.5 yr; F=196, P< 0.001, degrees of freedom [df]=1) of legal-size fish. Proportions within each age class were significantly different except for age four (χ^2=2.779, P=0.096, d.f.=1), where sublegal-size fish represented 46% of the catch (Fig. 2A). Sublegal vermilion snapper consistently had significantly smaller sizes at age for all comparable (n>3 per classification) age classes (F values between 7.0 and 509.7, P values between 0.0181 and <0.001, df=1; Fig. 3A).

Sex and maturity status were assigned to 1708 vermilion snapper. Vermilion snapper sex ratios (M:F) of sublegal-size fish favored males (1:0.81; χ^2=9.2, P=0.002, df=1), whereas there was no difference from a 1:1 ratio for legal-size vermilion snapper (1:0.92; χ^2=1.4, P=0.237, df=1). Sex ratios were not statistically different between legal- and sublegal-size vermilion snappers (χ^2=3.2, P=0.07, df=1). Sex ratios for legal and sublegal sizes were not statistically different within age classes, except for age three (legal-size fish=1:1.10, sublegal-size fish=1:0.55; χ^2=8.9, P=0.002, df=1).

Size at 50% maturity could not be determined for legal-size vermilion snapper because all legal-size fish were mature. In fact, all males in this study were mature, across all lengths (111–470 mm FL) and ages (0–12 years). There were 31 (3.9%) immature female sublegal vermilion snapper in our sample ranging in age from 0 to 2 years (Table 3) and in size from 99 mm to 257 mm FL (Table 4). Including all females, of legal and sublegal size, length at 50% maturity was estimated at 212 mm FL (95% confidence intervals [CI]=197–220 mm FL) and 100% maturity was reached by 258 mm FL.

Red porgy

A total of 2009 red porgy were collected, of which 1014 were legal size (>356 mm TL) and 1005 were sublegal-size fish. Of these, 2010 fish were successfully aged. Age ranges were similar between legal-size (0–14 years) and sublegal-size (0–12 years) red porgy, but the distributions were significantly different (D=0.37, P<0.001), with mean ages differing by one year (Fig. 2B). Red porgy aged seven and older represented a small portion of the catch for both legal- and sublegal-size fish, and the average age of legal-size fish was 4.5 years (±1.61 standard deviation [SD)]). Mean age at sublegal size was significantly different from mean age (F=369.68, P<0.001, df=1) at legal size and proportions within each age class were significantly different (χ^2 values between 7.35 and 123.60, P values between 0.006 and <0.001, df=1). Sublegal-size red porgy consistently had significantly smaller sizes at age for all comparable (n>3 per classification) age classes (F values between 11.85 and 1078.56, P values between 0.002 and <0.001, df=1; Fig. 3B).

Sex and maturity status were assigned to 1894 red porgy (955 males and 939 females). Sex ratios were significantly different from 1:1 (legal-size fish χ^2=15.6, P<0.001, df=1 and sublegal-size fish χ^2=29.6, P<0.001, df=1). As expected for a protogynous species, sex ratios for sublegal-size red porgy favored females (1:1.43) and for legal-size red porgy, ratios favored males (1:0.77). Sex ratios by age classes were not significantly different, except for age five (legal-size fish 1:0.64 and sublegal-size fish 1:1.24; χ^2=7.80, P=0.005, df=1). Because of the limited number of immature females (n=23; 1.1%), size at maturity estimates could not be determined. The two immature legal-size red porgy were both four years old, and the remaining immature sublegal red porgy (n=21) were between one and five years old (Table 3). Immature female lengths ranged between 150 and 346 mm FL (Table 4). Sexually transitioning red porgy (n=266) were between zero and eight years old, of which 144 were sublegal-size and 122 were legal-size fish. Eleven of the transitional fish were juveniles, that is immature females that have transitioned to male (primary male), and all were sublegal size. Age at 50% sexual transition was not significantly different (Wald's χ^2=1.02, P=0.312, df=1) between legal- and sublegal-size red porgy and occurred around age two (legal-size fish=2.17 yr and sublegal-size fish=2.23 yr). All red porgy were male by age 10. There were not enough data to conduct an analysis of length at sexual transition. Sexually transitioning red porgy were between 215 and 416 mm FL and 47% of the transitioning red porgy were at or over the legal minimum size limit.

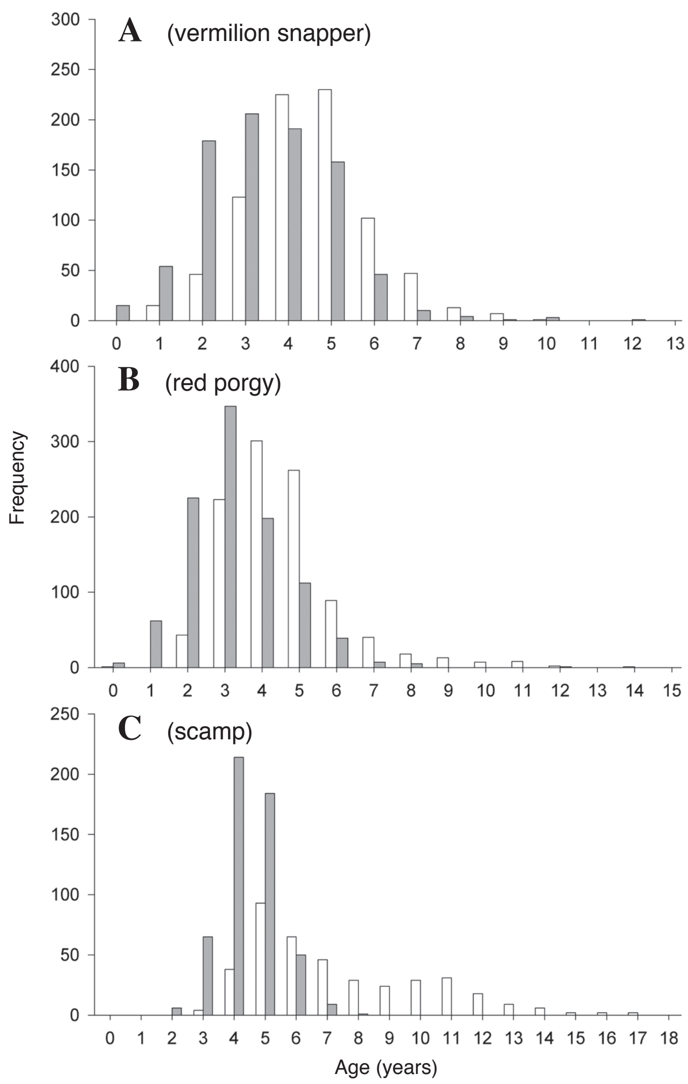

Figure 2

Age-frequency distributions for sublegal- (gray) and legal-size (white) fish by species: (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp). Fish were collected by commercial fishermen off the coast of the southeastern United States from 2005 through 2007.

Scamp

A total of 952 scamp were collected, of which 409 were legal-size (>508 mm TL) and 543 were sublegal-size fish. Of these, 927 were successfully aged. There was a narrow range of overlapping age ranges for sublegal-size (2–8 years) and legal-size (3–17 years) scamp (Fig. 2C), and the distributions were significantly different (D=0.11, P=0.006). The sublegal-size scamp distribution was narrow and peaked at ages four and five, whereas the legal size distribution was platykurtic (kurtosis=0.09) and left skewed. Mean age for sublegal-size fish was significantly different from mean age at legal sizes(F=485.1, P<0.001, df=1) and proportions of legal- and sublegal-size scamp within each age class were significantly different, except for age 6 (χ^2=1.95, P=0.162, df=1). Legal-size scamp were significantly larger at age than sublegal-size scamp for all ages (F values from 26.8 to 497.4, all P values were <0.001, df=1; Fig. 3C).

Sex and maturity status were assigned to 943 scamp (821 females and 122 males). Sex ratios of legal- and sublegal-size fish were significantly different from 1:1 (legal-size fish: χ^2=68.5, P<0.001, df=1; sublegal-size fish: χ^2=525.1, P<0.001, df=1). There were low numbers of males captured, and sex ratios favor females for both legal- and sublegal-size scamp (legal-size fish 1:2.40 and sublegal-size fish 1:134.25). Immature scamp were between two and six years old (Table 3) and 307 to 473 mm FL (Table 4). Because a limited number of immature legal females were collected (n=2), probability of maturity at size and age were calculated by using both legal- and sublegal-size fish. Length and age at 50% maturity were estimated at 331 mm FL and two years, and length and age at 100% maturation were estimated at 474 mm FL and seven years, respectively. Sexual transition occurred over a wide range of ages and lengths (3–13 years; 440–720 mm FL; n=26) and consisted entirely of adult fish. Probabilities of sexual transition were calculated from the entire data set because of the low number of sublegal-size males. Length at 50% and 100% sexual transition were 629 mm FL and 740 mm FL, respectively, whereas age at 50% sexual transition was 9.7 years and at 100% sexual transition, 14 years.

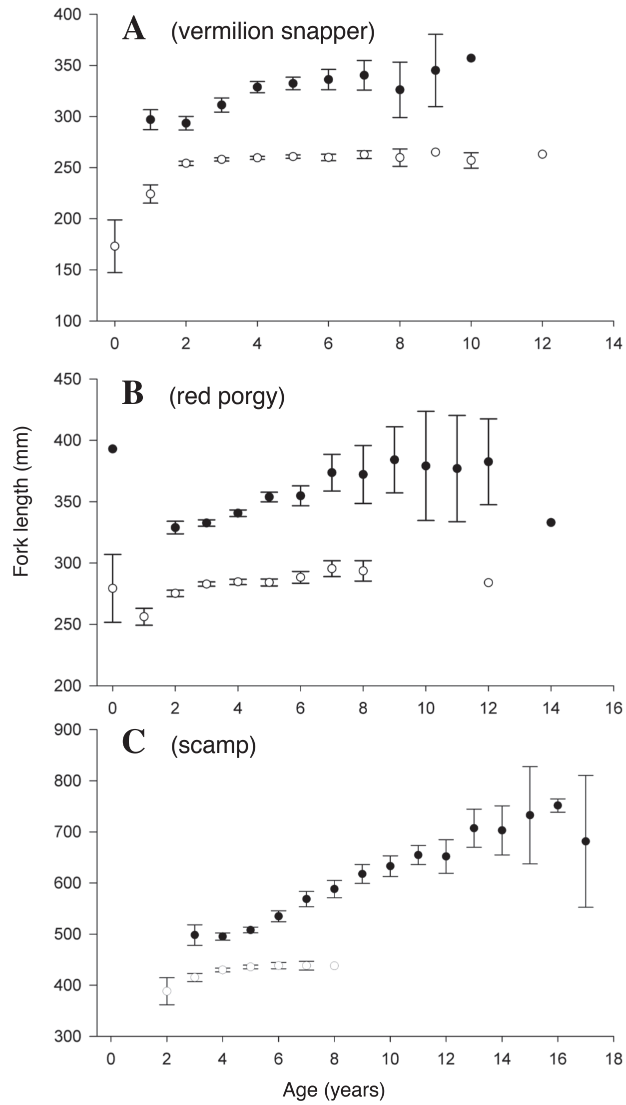

Figure 3

Mean fork length at age (±2 standard errors) for sublegal- (white) and legal-size (black) fish by species: (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp).

Discussion

Vermilion snapper

Vermilion snapper were reported in the South East Data, Assessment, and Review (SEDAR) 2008 stock assessment as experiencing overfishing, but were not overfished, with an F of 0.49 (SEDAR, 2008). This species has been managed with a 12 inch TL (274 mm FL) commercial minimum size limit since 1999. Despite the minimum size limit regulation, F has continued to increase (SEDAR, 2008). The comparison of the life history parameters of commercially caught legal- and sublegal-size vermilion snapper show that commercial fishing crews are capturing young, but large vermilion snapper—a fast growing phenotype. Comparing growth curves to previous time periods (1979–81 and 1985–93, Zhao et al., 1997), we found an increased growth rate for the current time period, particulary for the young fish (<5 yr), although asymptotic length, L_∞, values are similar to those found from 1979 to 1981 (Fig. 4A). This increased growth rate allows fish to reach the minimum size limit at an earlier age. Interestingly, the L_∞ for this study is only 25 mm greater than the minimum size limit.

Size at maturity is not a good indicator of differential fishing pressure on fast growing phenotypes for vermilion snapper because all immature fish in the collections were female and sublegal. This is not an unexpected result because vermilion snapper mature at a very small size and age. In a study on the reproductive biology of vermilion snapper, Cuellar et al. (1996) found no immature fish (n=1004, size range=165–375 mm FL). Comparison with other studies (Zhao and McGovern, 1997), shows that vermilion size and age at maturity has decreased since the 1980s, a period when maximum length decreased.

The observed sex ratios in our study favored males, in contrast to either 1:1 ratios or more females from other studies (Zhao and McGovern, 1997; Hood and Johnson, 1999; Allman, 2007; SEDAR, 2008). These differences may be attributed to location and gear selectivity. Hood and Johnson (1999) noted that the ver-

Table 3

Percentage of mature fish by age class for female vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) by sublegal- and legal-size classification. All fish were examined histologically. (*n*)=number of fish in samples.

	Vermilion snapper		Red porgy		Scamp	
Age (yr)	Sublegal size % (*n*)	Legal size % (*n*)	Sublegal size % (*n*)	Legal size % (*n*)	Sublegal size % (*n*)	Legal size % (*n*)
0	22 (9)	—	100 (1)	100 (1)	—	—
1	52 (31)	100 (9)	67 (33)	—	—	—
2	94 (94)	100 (22)	97 (119)	100 (28)	33 (3)	—
3	100 (71)	100 (64)	99 (161)	100 (107)	77 (44)	50 (2)
4	100 (74)	100 (106)	98 (91)	99 (137)	93 (178)	100 (30)
5	100 (81)	100 (109)	94 (53)	100 (98)	97 (156)	100 (73)
6	100 (17)	100 (47)	100 (15)	100 (31)	100 (44)	98 (49)
7	100 (2)	100 (13)	100 (2)	100 (10)	100 (8)	100 (36)
8	100 (2)	100 (2)	100 (2)	100 (4)	100 (1)	100 (20)
9	—	100 (4)	—	100 (2)	—	100 (11)
10	—	100 (1)	—	—	—	100 (13)
11	—	—	—	—	—	100 (13)
12	—	—	—	—	—	100 (5)

milion sex ratio (generally 1:1) in the Gulf of Mexico was different from sex ratios found off the coast of the southeastern United States. Zhao and McGovern (1997) noted that traps caught more females than hook-and-line or trawl gear. All of our catches were from hook-and-line gear that was fished about 3 m off the bottom, rather than from on-bottom gear (e.g., traps). If vermilion snapper schools segregate by sex, with males higher in the water column, it is possible that the males would encounter the baited hooks first. The difference in sex ratios is of utmost concern because it will have significant impact in fishery stock assessment models. Such a study as that performed by DeVries (2006), who looked at size- and sex-induced fish behavior bias, is needed to determine the cause of this difference and which sex ratio is more indicative of the population.

Red porgy

The 2006 SEDAR stock assessment of red porgy, a protogynous hermaphrodite, concluded that although this stock was not experiencing overfishing, it was overfished (SEDAR, 2006). A commercial 12 inch TL (307 mm FL) minimum size limit for red porgy was introduced in 1992, but fishing mortality remained high from 1992 through 1998, with F values between 0.44 and 0.75 (SEDAR, 2006). In 1999, the minimum size limit was increased to a 14 inch TL (307 mm FL), a seasonal closure (from May to December) was instituted, as well as an emergency closure from September 1999 through August 2000. In late 2000, a commercial trip limit on catch (50 lb/trip) was established, and in 2006 this was modified to 120 fish/trip or a 127,000 lb gutted yearly quota. Since 2001, F has continued to decrease (F=0.078 in 2004) and spawning stock biomass has increased (SEDAR, 2006).

Commercial fishermen are harvesting faster growing (young but large) fish. In our study the sublegal- and legal-size portions of the population had broad overlapping age ranges, and mean ages differed by only one year. The age-frequency distributions for legal red porgy were left-skewed (skewness=1.5) and had a high peak (kurtosis=4.13) that indicated high fishing mortality occurring on ages four and five. Red porgy are a relatively long-lived species with a maximum age of 18 years (Potts and Manooch, 2002), and yet red porgy 10 years and older were <1% of the catch. Interestingly, the majority of all red porgy being captured are between ages three and five, indicating that there is a lack of not just large fish, but also old fish in the population. For a species known to live 18 years, these values indicate a considerable change in the population structure because many of the older fish have been removed. Comparison of von Bertalanffy curves (Fig. 4B) with those of previous studies (Manooch and Huntsman, 1977; Harris and McGovern, 1997) show that current growth rates are greater than those in earlier time periods (1979–81 and 1988–90). Interestingly, the asymptotic length is only 20 mm higher than the minimum size limit. Maturity in red porgy in our study occurred as early as less than one year in both legal- and sublegal-size specimens, and by age one, over 60% of the sublegal-size specimens were considered mature, indicating that maturation is occurring at a young age and small size. This is consistent with the findings from Harris and McGovern (1997) and Hood and Johnson (2000) who also noted mature females at a small sizes and ages. Our age of 100% female maturation, age six, was two years older than that reported in the Hood and Johnson (2000)

Table 4

Percentage of mature fish by length interval for female vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) by sublegal and legal classification. All fish were examined histologically. *n*=number of fish in samples.

	Vermilion snapper			Red porgy			Scamp		
Fork length (mm)	Age range	Sublegal size % (*n*)	Legal size % (*n*)	Age range	Sublegal size % (*n*)	Legal size % (*n*)	Age range	Sublegal size % (*n*)	Legal size % (*n*)
101–120	0–1	0 (3)	—	—	—	—	—	—	—
121–140	0	0 (1)	—	—	—	—	—	—	—
141–160	0	0 (3)	—	1	0 (1)	—	—	—	—
161–180	0–1	0 (3)	—	—	—	—	—	—	—
181–200	0–1	100 (1)	—	1–2	0 (2)	—	—	—	—
201–220	0–2	47 (15)	—	0–1	100 (3)	—	—	—	—
221–240	1–6	81 (43)	—	1–4	63 (11)	—	—	—	—
241–260	0–10	97 (153)	—	1–6	89 (55)	—	—	—	—
261–280	0–12	100 (171)	100 (48)	0–8	97 (147)	—	—	—	—
281–300	1–9	—	100 (69)	0–12	98 (193)	—	—	—	—
301–320	1–9	—	100 (68)	0–11	100 (67)	100 (102)	—	0 (1)	—
321–340	1–9	—	100 (63)	2–14	—	99 (131)	2–4	0 (1)	—
341–360	2–10	—	100 (45)	2–11	—	99 (103)	3–5	67 (6)	—
361–380	3–8	—	100 (35)	2–12	—	100 (45)	2–5	83 (18)	—
381–400	3–7	—	100 (25)	0–12	—	100 (15)	2–6	88 (26)	—
401–420	3–9	—	100 (23)	4–11	—	100 (9)	2–7	85 (59)	—
421–440	3–8	—	100 (7)	5–9	—	100 (7)	2–8	97 (135)	—
441–460	4–7	—	100 (7)	5–9	—	100 (4)	3–7	97 (143)	—
461–480	5–7	—	100 (7)	5–8	—	100 (5)	3–6	96 (54)	94 (31)
481–500	—	—	—	11	—	100 (1)	3–17	—	100 (46)
501–520	—	—	—	—	—	—	3–8	—	100 (40)
521–540	—	—	—	—	—	—	3–12	—	100 (31)
541–560	—	—	—	—	—	—	4–12	—	100 (25)
561–580	—	—	—	—	—	—	5–11	—	100 (21)
581–600	—	—	—	—	—	—	5–14	—	100 (22)
601–620	—	—	—	—	—	—	5–17	—	100 (9)
621–640	—	—	—	—	—	—	7–13	—	100 (11)
641–660	—	—	—	—	—	—	6–13	—	100 (10)
661–680	—	—	—	—	—	—	7–11	—	100 (8)
681–700	—	—	—	—	—	—	7–15	—	100 (2)
701–720	—	—	—	—	—	—	10–12	—	100 (2)
721–740	—	—	—	—	—	—	10–14	—	100 (2)

study, showing a shift to older age at maturation. This may be a response to the reduced fishing mortality that was instituted to rebuild the stock.

Age at transition was similar for both sublegal- and legal-size red porgy, indicating that different growth rates did not affect the age of sexual transition. Instead, sexual transition may be related to other factors, particularly local social dynamics. In fact, size at transition does not appear to have changed much over time. Although age at transition in our study (two years) was younger than previously reported values of 3.5–5 years (Hood and Johnson, 2000; Daniels, 2003), mean size of transitional fish was similar (Daniels, 2003; Harris, 2003). Using Allsop and West's (2003) formulas to estimate age (2.5×age at maturity) and size at transition (80% of maximum body size), we found that the expected age at transition was similar to the observed value and the expected size at transition was within the range of the observed transitioning fish. Sex ratios at age in our study support these estimates, because by age 2 sex ratios are approximately 1:1.15, by ages 3 and 4 are close to 1:1, and by age 5 favor males. Similarly, sex ratios for red porgy smaller than 320 mm FL favored females, between 320 and 359 mm FL were close to 1:1, and favored males after 360 mm FL. Primary males (juvenile transitional fish) are often a socially mediated plastic response to high population densities or sex ratios that severely favor females (Liu and Sadovy, 2004; Munday et al., 2006a; Munday et al., 2006b). The low number of juvenile transitional fish is indicative of a stable sex ratio in the red porgy population, low to moderate local red porgy densities, or any combination thereof.

There are a variety of fishing regulations for red porgy that may act to counter differential fishing mortality on young, large fish. Red porgy currently have a commercial minimum size limit, a 120 fish/trip limit, seasonal closure, and a total gutted weight quota [SAFMC[2]]. Despite these regulations, red porgy continue to be hooked throughout the year or after a limit has been reached because of their close association with other targeted snapper-grouper species. These red porgy must be discarded, but, as a study from Stephen and Harris (2010) indicated, all sizes may experience high immediate release mortality. During the closed season or after trip limits or quotas are reached, all red porgy experience the same release mortality, and this mortality counteracts any differential fishing mortality. Furthermore, discarded sublegal-size red porgy are also experiencing a high release mortality that may remove many of the small old fish from the population.

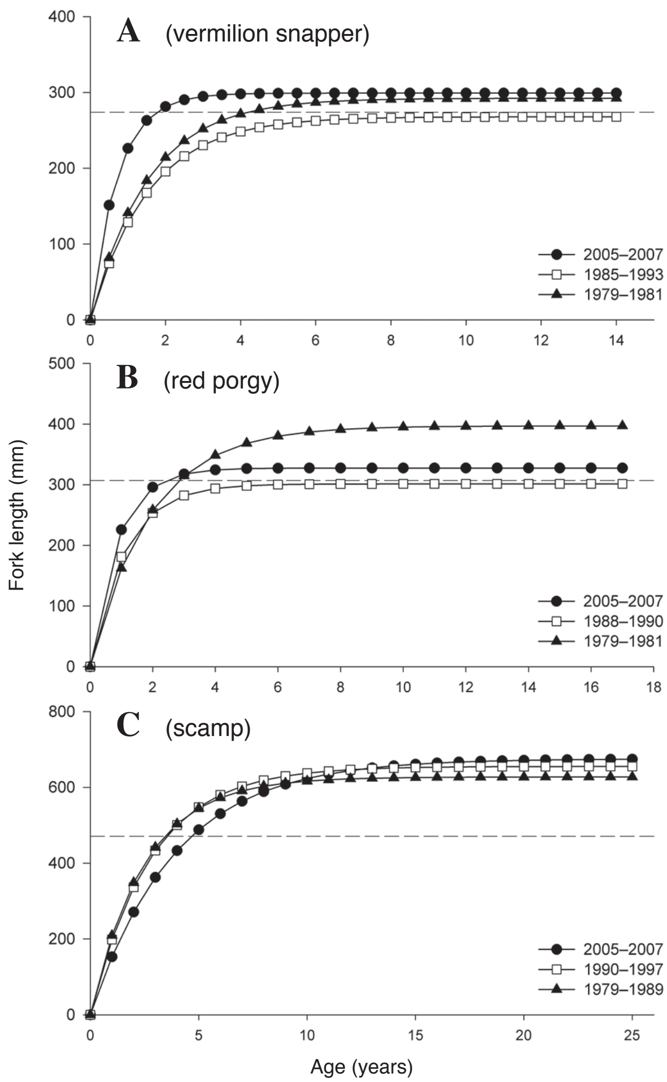

Figure 4

Comparison of von Bertalanffy growth curves from various locations in the Atlantic Ocean for (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp). All curves represent a two-parameter function, with t_0 set to 0, to allow for a comparison of growth rates between time periods. For *R. aurorubens*, the 1985–93 and 1979–81 curves are modified from Zhao et al. (1997). For *P. pagrus,* curves from 1979–81 and 1988–90 are modified from Harris and McGovern (1997), and for *M. phenax* curves from 1979–89 and 1990–97 are modified from Harris et al (2002). The dashed line in each graph represents the minimum size limit for that species.

Scamp

Scamp were classified as experiencing overfishing through a population study in 1998 (Manooch et al., 1998), and this has remained the official NMFS status (NMFS, 2010). Scamp have been managed with a commercial 20 inch TL (471 mm FL) minimum size limit since 1992. There have been no other commercial regulations for this species until recently when a seasonal closure (January through April) was implemented to protect the species during their spawning season.

In contrast to red porgy and vermilion snapper, legal-size scamp comprised almost entirely older fish. This finding indicates that the commercial catches are not retaining a high proportion of fast growing phenotypes (young, but large fish). Sublegal- and legal-size scamp had minimal overlap in age ranges with mean ages differing by more than three years. Ages 5 and under were predominately sublegal-size fish, and nearly all immature scamp were sublegal size and female (Fig. 2; Tables 3 and 4). Size and age at maturation and transition are similar to values from the 1970s through the 1990s (Harris et al., 2002), indicating that scamp are not undergoing increased fishing mortalities and that minimum size limits are an effective management tool for scamp. Comparisons of von Bertalanffy curves from previous studies (Matheson et al., 1986; Harris et al., 2002) show similar growth rates and asymptotic lengths (Fig. 4C). Furthermore, since the 1992 minimum size limit regulation, landings, although variable, have shown no in-

[2] SAFMC (South Atlantic Fishery Management Council). 2008. Final, amendment number 15B to the fishery management plan for the snapper grouper fishery of the South Atlantic region, 159 p. + appendices. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

Table 5

Summary of the commercial fishing regulations mandated by the South Atlantic Fishery Management Council that have affected the snapper-grouper complex. TL=total length, t=metric ton. Amend.=amendment.

Year	Species	Regulation
1983 (Amend. 1)	Snapper-Grouper complex	Trawls were required to have a 4-inch (10-cm) mesh size.
1992 (Amend. 4)	Snapper-Grouper complex	Trawls were banned
1998 (Amend. 8)	Vermilion snapper	12-inch (30-mm) TL minimum size limit
	Red porgy	12-inch (305-mm) TL minimum size limit
	Scamp	20-inch (508-mm) TL minimum size limit
1999 (Amend. 9)	Red porgy	14-inch (356-mm) TL minimum size limit; Mar–Apr closure
1999–2000	Red porgy	Emergency interim ruling: No landings Sep 1999–Aug 2000
2000 (Amend. 12)	Red porgy	50 lb/trip (23 kg/trip) limit May–Dec and a Jan–Apr closure
2006 (Amend. 13C)	Vermilion snapper	11,000,000 lb (5000 t) quota (gutted fish)
	Red porgy	127,000 lb (58 t) quota (gutted fish); 120 fish/trip limit from May to Dec
2009 (Amend. 16)	Vermilion snapper	Jan–Jun: 315,523 lb (143 t) quota (gutted fish); Jul–Dec: 302,523 lb (137 t) quota (gutted fish)
	Scamp	Jan–Apr closure for scamp (beginning in 2010)

creasing trend. Current size regulations (471 mm FL) restrict the removal of scamp to large mature females and males. Scamp spawn as small as 289 mm FL (Harris et al., 2002), providing ample time for both young and old females to have multiple reproductive seasons before being removed by the fishery.

One note of concern is the continual decrease in the number of males. Harris et al. (2002) noted a decrease in the number of males from 1979–89 to 1990–97, from 34% to 21%, and Coleman et al. (1996) in the Gulf of Mexico noted a decrease over 20 years from 36% to 18%. Males have continued to decline to the 12% found in our study. The limited number of transitioning and male scamp are of concern, because this may be an indication of sperm limitation. Comparing our age and size of transition to those determined by Allsop and West (2003), we found that our age of transition is much higher than expected, but the size of transition (based on the FL_{max} in this study) is similar to the expected value. The age at transition may be higher than that estimated in Allsop and West (2003) because it is thought that sexual transition in scamp is socially mediated within post-spawning aggregations (Harris et al., 2002), thereby limiting transition in both time and space. Simply increasing the minimum size limit may not reverse this trend because more females will survive but may not transition to males, thereby further skewing the sex ratio (Heppell et al., 2006). A management regime that protects males and preserves the sex ratio is needed. Year round deep water area closures or marine protected areas would work best to preserve the expected sex ratios, as these closures would protect males as shown by Heppell et al.'s model (2006). An alternative hypothesis to explain the lack of male specimens in our study is the segregation of males from females in time and space as is seen in gag (*Mycteroperca microlepis*) (Coleman and Koening, as cited in Heppell et al., 2006). Current data do not allow us to test these hypotheses, but conservative management is needed to protect males in locations where scamp is known to occur.

Conclusions

This study indicates strongly that heavily exploited fish stocks (those being overfished or in the state of having been overfished) managed by minimum size limits can create populations with many small, old fish through the disproportional removal of the large, young fish (fast growing phenotype). Which stocks are affected would depend on the selected minimum size limit and the specific life histories of that stock. The two species undergoing heavy exploitation, vermilion snapper (experiencing overfishing) and red porgy (overfished), both showed signs that the fishery was landing many young, large fish (fast growing phenotypes). For both species, growth has increased from historical periods, and asymptotic length is near the minimum size limit. Additional factors that may be influencing these changes are gear type and gear selectivity because the past fishery was primarily a trawling fishery, whereas the current fishery is a hook-and-line industry. For scamp, the species not experiencing overfishing (overfished status unknown), there were few young large fish captured, and growth rate and asymptotic length were similar to those of other time periods.

Our study shows that the hook-and-line fishery targets young, but large fish with a fast growing phenotype. These fast growing phenotypes often have an associated bold and aggressive behavior and are caught more often than their counterparts, the slow growing phenotypes (Biro and Post, 2008). Although growth rates have increased for both vermilion snapper and red porgy, it is interesting to note that asymptotic lengths are only slightly greater than the minimum size limits. Because this increased growth rate is not seen in fish larger than the minimum size limit, this finding may imply that the portion of the population that is larger than the minimum size limit consists of more slow growing phenotypes.

Conover and Baumann (2009) noted that after removing a minimum size limit regulation, even if the shift in the population's size-at-age was due solely to phenotypic plasticity, the population had not regained its previous size-at-age distribution after four generations. In fish such as snappers and groupers, which have long generation times, it could take many decades before a recovery is seen. Managers need to consider the life history characteristics of each species in light of its susceptibility to phenotypic shifts due to minimum size limits. Therefore, in a multispecies industry where species-specific minimum size limits are aiding in a shift to smaller sizes at age, an ecosystem-based management plan that includes a multispecies quota system is a good precautionary approach to maintaining a sustainable fishery.

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