

Abstract.—Percentages of mature male and female vermilion snapper, *Rhomboplites aurorubens*, based on total length (TL) and age were calculated for five three-year periods during 1979–93. Males and females collected during 1982–87 became sexually mature at a smaller size and younger age than individuals collected during 1979–81. The median TL at maturity for females decreased from 160 mm in 1979–81 to 151 mm in 1985–87. The median TL at maturity for males was 145 mm during 1979–81. During 1985–87 all males were mature at 140 mm. The temporal shift toward a smaller size at maturity was more pronounced in males than in females. The percentage of mature males at age 1 significantly increased from 63.6% in 1979–81 to 100% in 1985–87 and afterwards. More than twice as many females at age 1 were mature in 1985–87 (48.6%) as in 1979–81. The decline in size and age at maturity may have been caused by fishing pressure that gradually increased during the 1980's.

The sex ratio of vermilion snapper was dependent upon latitude and gear type but was generally independent of water depth, fish length, and sampling years. Although the sex ratios were significantly different among latitudes, there were no trends among latitudes 31°N, 32°N, and 33°N. The percentage of females was 72.1%, 68.0%, and 59.9% for vermilion snapper caught by trap, hook-and-line, and trawl, respectively. Reasons for the difference in sex ratio among gear types are unclear, suggesting that caution must be used when interpreting sex ratios estimated for any fish species collected by various gear types.

Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens*, in the South Atlantic Bight*

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The spawning potential ratio (SPR) has been widely used by U.S. fishery management councils to define overfishing of a fish stock (Goodyear, 1993; Rosenberg et al., 1994; SAFMC¹). To estimate SPR, life history characteristics (e.g. growth and reproduction) are required and are generally assumed constant among years (Gabriel et al., 1989). However, these parameters, particularly maturity schedules, are not static. They can change in response to fishing pressure, predator and prey abundance, stock composition, and other biotic and abiotic environmental factors (Wootton, 1990). Ignorance of temporal changes in life history parameters may result in the use of incorrect data by fishery managers and therefore may be a reason why fish stocks fail to be protected from overfishing (Rosenberg et al., 1994).

Vermilion snapper, *Rhomboplites aurorubens*, from the South Atlantic Bight (SAB) occur in shelf and upper-slope waters between depths of 26 and 183 m (Grimes, 1978). This species spawns multiple times during a prolonged spawning season (April through September: Grimes and Huntsman, 1980; Cuellar et al., 1996). Vermilion snapper have been of extreme commercial and recreational importance along southeast-

ern states since the early 1980's. Total landings in this region have increased over the years with a peak in 1991 (Zhao and McGovern²). However, recent studies have suggested that vermilion snapper are overfished. The stock abundance estimated by virtual population analysis (VPA) has declined since 1984 (Zhao and McGovern²). The relative abundance represented by catch per unit of effort (CPUE) markedly declined during 1988–93. There has also been a significant decrease in mean length of vermilion snapper caught by fishery-independent surveys and by the headboat and commercial fishery (Zhao and McGovern²). Changes in life history characteristics induced by intense harvesting have been reported for vermilion snapper. Zhao et al. (1997) validated the ageing

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¹ SAFMC (South Atlantic Fishery Management Council). 1993. Amendment 6, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the snapper grouper fishery of the south Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 155 p.

² Zhao, B., and J. C. McGovern. 1996. Population characteristics of the vermilion snapper from the southeastern United States. In preparation

method of otolith sections and demonstrated that size-at-age decreased with time. Collins and Pinckney (1988) reported preliminary evidence that vermilion snapper caught in 1978–80 from SAB became reproductively mature earlier in life than those caught in 1972–74. Grimes and Huntsman (1980) determined that vermilion snapper were gonochorists, females (62.5%) significantly outnumbered males, and the sex ratio was dependent on fish length. However, Nelson (1988) reported that the sex ratio of vermilion snapper from the Gulf of Mexico differed from 1:1 in favor of males (54.5%). He also reported that area and season had a significant effect on this ratio. Although what may have caused the difference in sex ratios of two studies was unknown, limited sample sizes made their comparisons among areas, lengths, or seasons less convincing (Grimes and Huntsman, 1980: $n=874$; Nelson, 1988: $n=881$).

In this paper, we investigated the percentage of mature vermilion snapper at each length class and age for each sex and examined the temporal change in maturity schedules during 1979–93. We also determined the sex ratio of vermilion snapper according to depth and latitude of sampling sites, fish length, sampling period, and types of fishing gear used.

Materials and methods

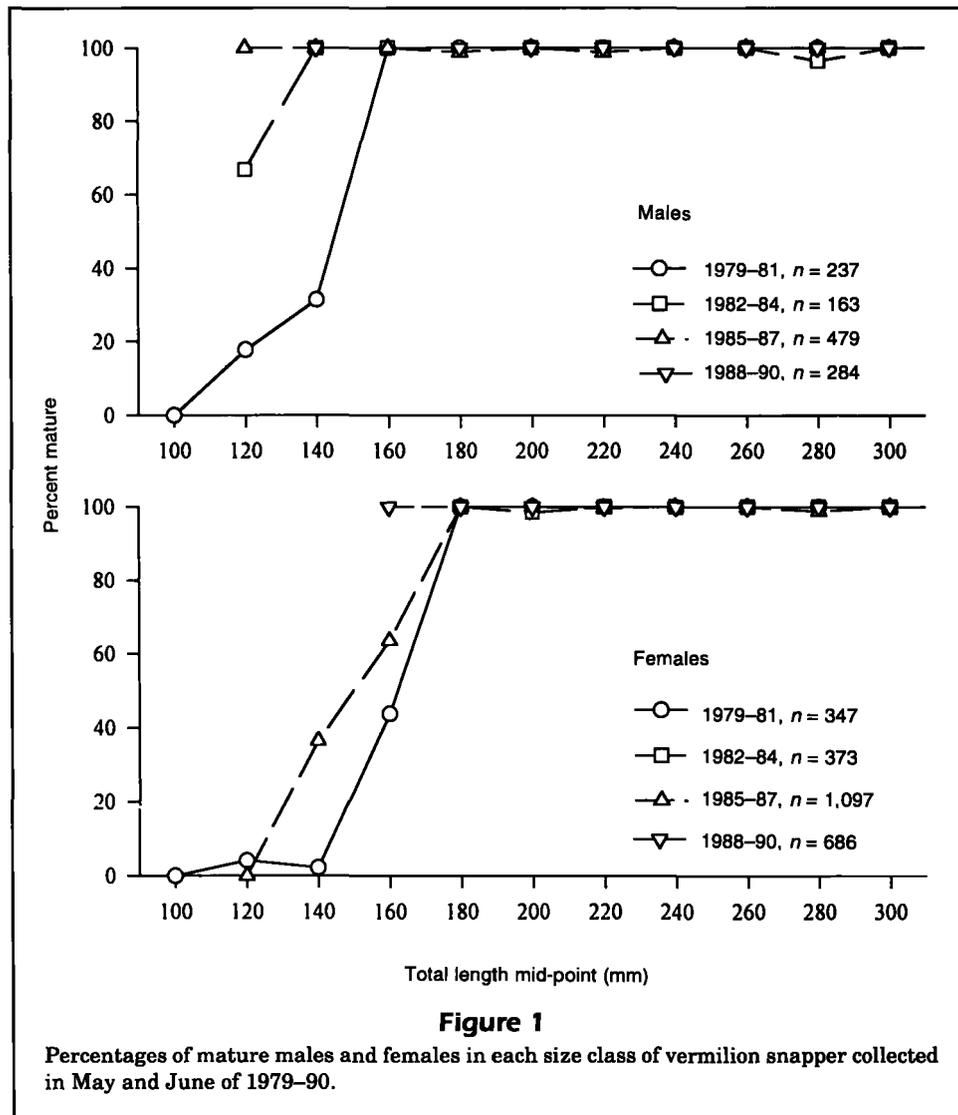
Data were collected from the SAB during 1979–93 by reef fish surveys of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program. Most vermilion snapper were captured by standardized hook-and-line and trapping gear during the spring and summer of 1979–93 (Collins, 1990; Collins and Sedberry, 1991). In addition, many vermilion snapper were obtained from the MARMAP trawling program that was terminated in 1988. In the field, fish were measured to the nearest mm (TL and FL) and weighed to the nearest gram (whole body weight). Water depth, latitude, and longitude of sampling sites were recorded. The posterior portion of the gonad was removed and preserved in 10% formalin buffered with seawater. In the laboratory, sex and maturity stages were determined by examining the stained gonad sections according to standard MARMAP histological criteria (Cuellar et al., 1996). All gonad samples taken in 1987–93 were examined with histological methods. During 1979–86, sex of specimens was determined and a reproductive condition was assigned in the field by using clearly defined visual staging criteria. The definitions of maturity stages by gross visual inspection were confirmed to be accurate by histological examination during 1978–80 (Collins and

Pinckney, 1988). The codes used for defining maturity stages were consistent between histological and macroscopic methods. Seven reproductive stages were used: 1) immature, 2) developing, 3) running ripe, 4) spent, 5) resting, 6) developing with evidence of spawning in the previous week, and 7) mature, but stage-unknown. Mature fish included those in stages 2–7.

Percentages of mature males and females based on total length (TL) and age were calculated for five periods, each corresponding to a three-year interval, i.e. 1979–81, 1982–84, 1985–87, 1988–90, and 1991–93. Because the monthly distribution of samples was not necessarily similar among periods, it was essential to define a standard month(s) if comparison of maturity schedules among years was to be meaningful. In addition, the reproductive condition was most discernible and the sizes and ages at first maturity could be determined during and immediately prior to the spawning season. Therefore, we used the data only from May and June that corresponded to the time of slow somatic growth. Age assignments of vermilion snapper were based on the number of annuli on otolith sections (Zhao et al., 1997). We took into consideration knowledge of the time of annulus formation, the relative growth of the otolith margin, the date of sampling, and used a January 1 hatching date. Because only a part of the samples was aged, some sexed and maturity-determined samples did not have age information.

Although the variation in gear type, latitude, and depth of sampling sites should have been included in the maturity analysis before the data were pooled, limited sample sizes of small (TL < 170 mm) and young (age-1) vermilion snapper prevented us from comparing maturity schedules by area (latitude) or by gear type. However, 97% of the males and females smaller than 170 mm were collected by trawl in consistent depth ranges during 1979–90. A majority of these small fish were collected from similar areas, with 88% males and 82% females from latitude 31°N, and 12% males and 18% females from 32°N. Thus, gear selectivity and geographical distribution can be disregarded as sources of bias in comparison of maturity schedules among periods.

As recommended by Trippel and Harvey (1991), the *G*-test was used to compare maturity schedules of each sex among periods with the same length class or the same age (e.g. age 1). Maturity schedules between sexes at age 1 were compared for the periods of 1979–81 and 1985–87 respectively, when sample sizes of both sexes were sufficient. When conditions of the *G*-test were not met, Fisher's exact test was used (Zar, 1984). When the percentages of mature fish of each sex in 20 mm TL intervals exhibited a successive increase with length, the median length



at sexual maturity (TL_{50}) was calculated by probit analysis following the recommendation of Tripple and Harvey (1991). The likelihood ratio test at a significance level of 0.10 was used to determine if the probit model could be fitted to the observations of maturity-at-length (SAS Institute, 1990).

Because sex ratio may change with water depth and latitude of sampling sites, fish length, sampling year, gear, or season (Grimes and Huntsman, 1980; Nelson, 1988), all sexed samples, including mature and immature individuals between 1979 and 1993, were split into the same five periods as described above for maturity analysis. The time frame was increased to May through August to increase the sample size. We compared the percentages of females among varying water depths (midpoints: 25, 35, 45, and 55 m), latitudes (31°N, 32°N, and 33°N), length classes (TL=100 – 450 mm, with 50-mm intervals),

periods, and gear types (traps, hook-and-line, and trawl). Latitudes of 31°N, 32°N, and 33°N refer to 31°00'–31°59'N, 32°00'–32°59'N, and 33°00'–33°59'N, respectively. When the independence between sex ratio and one of above factors was tested, other factors were kept consistent. The chi-square test and Fisher's exact test were used to decide the independence. As a reference, Bonferroni's method was used to adjust the significance level, i.e. $\alpha' = 0.05/m$, where m = the number of cases (Sokal and Rohlf, 1995). First, we compared the percentage of female vermilion snapper taken from varying depths with the same length classes (TL=200–249 mm and TL=250–299 mm respectively), same latitude (32°N), same periods, and same gear type. Seventy-three percent of the vermilion snapper were collected from latitude 32°N during 1979–93, and eighty percent of them were between 200 and 299 mm TL. If the hypothesis

of independence between sex ratio and depth was not rejected, the data from all depth classes were pooled to compare further the percentage of females among latitudes, other factors (length, period, and gear) being consistent. If the hypothesis was rejected, data from a certain depth class were chosen for further comparison. In a similar fashion, we compared the percentage of females among length classes, periods, and gear types.

The statistical methods available in SAS were used to analyze data of maturity and sex ratio (SAS Institute, 1990). Rejection of the null hypothesis was based on a significance level of 0.05, unless otherwise noted.

Results

Maturity schedules

Males and females collected in 1982–84 and 1985–87 became sexually mature at a smaller size than individuals collected in 1979–81 (Fig. 1). For instance, 31% of male vermilion snapper collected in 1979–81 were mature at 140 mm. However, 100% of males taken at the same size during 1982–90 were mature. All fish taken in May and June of 1991–93 were larger than 180 mm and mature, and therefore were not included in our analysis. There was a significant temporal increase in the percentage of mature males among 1979–81, 1982–84, and 1985–87 at 120 mm (Fisher's exact test: two-tailed $P < 0.01$), and at 140 mm (two-tailed $P < 0.005$). The percentage of mature females also showed a significant in-

crease with time for 140-mm individuals collected between 1979–81 and 1985–87 (two-tailed $P < 0.005$). The observed differences in the percentage of mature females at 160 mm collected during 1979–81, 1985–87, and 1988–90 were not statistically significant (Fig. 1). Males larger than 140 mm and females larger than 160 mm were not tested because all fish were mature.

The likelihood ratio tests indicated that the probit model could be used to describe the maturity at length during 1979–81 for both males (likelihood ratio $\chi^2 = 2.721$, $P > 0.10$) and females (likelihood ratio $\chi^2 = 1.407$, $P > 0.10$), and for females during 1985–87 (likelihood ratio $\chi^2 = 4.647$, $P > 0.10$). The median TL at maturity of males was 145 mm (95% limits: 135–203 mm) during 1979–81. The TL_{50} of females was 160 mm (95% limits: 155–164 mm) in 1979–81 and 151 mm (95% limits: 143–156 mm) in 1985–87.

There was a significant increase in the percentage of mature age-1 males with time between 1979–81, 1982–84, and 1985–87 (Fisher's exact test: two-tailed $P = 0.013$) (Table 1). The percentage of mature age-1 females increased ($G = 5.318$, $P = 0.021$) between 1979–81 and 1985–87. More than twice as many age-1 females were mature in 1985–87 (48.6%) as in 1979–81 (23.1%). The median age at sexual maturity could not be calculated because of the abrupt transition from immature to mature.

Males matured at a smaller size and younger age than females (Fig. 1; Table 1). During 1979–81, TL_{50} for males (145 mm) was smaller than that for females ($TL_{50} = 160$ mm). Although TL_{50} for males in 1985–87 could not be calculated, it was observed that the TL_{50} of males declined with time faster than that of fe-

Table 1

Percentages of sexually mature vermilion snapper caught in May and June of 1979–93. Numbers of fish in each category are given in parentheses. Blanks indicate no data available for that category. There were significant ($P < 0.05$) differences in percent mature of age-1 fish among periods for each sex.

| Period | Age 1 | Age 2 | Age 3 | Ages 4+ |
|----------------|------------|------------|------------|-------------|
| Males | | | | |
| 1979–81 | 63.6 (11) | 100.0 (15) | 100.0 (12) | 100.0 (13) |
| 1982–84 | 85.7 (7) | | | 100.0 (28) |
| 1985–87 | 100.0 (19) | 100.0 (12) | 100.0 (10) | 100.0 (55) |
| 1988–90 | 100.0 (2) | 100.0 (4) | 100.0 (4) | 100.0 (47) |
| 1991–93 | | | 100.0 (1) | 100.0 (32) |
| Females | | | | |
| 1979–81 | 23.1 (39) | 91.3 (23) | 100.0 (9) | 100.0 (9) |
| 1982–84 | | 100.0 (4) | 100.0 (6) | 100.0 (67) |
| 1985–87 | 48.6 (35) | 95.8 (24) | 100.0 (18) | 100.0 (135) |
| 1988–90 | 100.0 (2) | 100.0 (8) | 100.0 (10) | 100.0 (104) |
| 1991–93 | | | 100.0 (3) | 100.0 (86) |

males (Fig. 1). During 1979–81 and 1985–87, the percentage of mature males at age 1 was significantly larger than that of females at the same age (Table 1; 1979–81: Fisher’s exact test, two-tailed $P=0.024$; 1985–87: $G=20.252$, $P<0.001$).

Sex ratios

More vermilion snapper were caught by traps and hook-and-line in the depth range of 40–49 m than in other depth classes (Table 2). The trawl was generally deployed in shallower water (20–39 m) than were

traps and hook-and-line. These three gear types were deployed most often in latitude 32°N than in other areas (Table 2). To exclude the effects on sex ratios from varying latitude, fish length, years, and gear types, we used the data collected from the same latitude (32°N), length (200–249 mm or 250–299 mm TL), period, and gear when the independence between sex ratio and depth was tested. Sample sizes in all categories were not always sufficient for a chi-square test. If the expected frequency of a depth-class was unacceptably low, that data was discarded from the contingency table. When sample sizes of depth

Table 2

Numbers of sexed vermilion snapper collected from May through August during 1979–93 by depth and latitude of sampling sites. Blanks indicate that no samples were available for that category.

| Period | Depth midpoint (m) | Traps | | | | | Total | Hook-and-line | | | | Trawl | | |
|---------|--------------------|-------|------|------|------|------|-------|---------------|------|------|-------|-------|------|-------|
| | | 30°N | 31°N | 32°N | 33°N | 34°N | | 31°N | 32°N | 33°N | Total | 31°N | 32°N | Total |
| 1979–81 | 15 | | | | | | | | | | | | 3 | 3 |
| | 25 | | 26 | | | | 26 | 27 | 10 | | 37 | 5 | 97 | 102 |
| | 35 | | | 1 | | | 1 | 5 | 10 | 27 | 42 | 242 | 120 | 362 |
| | 45 | | | 8 | | | 8 | | 326 | | 326 | | | |
| | 55 | | | | | | | | | | | | | |
| | 65 | | | | | | | | | | | | | |
| | Total | | 26 | 9 | | | 35 | 32 | 346 | 27 | 405 | 247 | 220 | 467 |
| 1982–84 | 15 | | | | | | | | | | | | | |
| | 25 | | | 21 | | | 21 | 6 | 42 | | 48 | 29 | 217 | 236 |
| | 35 | | | 50 | | | 50 | | 31 | | 31 | | 28 | 28 |
| | 45 | | | 298 | | | 298 | | 214 | | 214 | | | |
| | 55 | | | 100 | | | 100 | | 27 | | 27 | | | |
| | 65 | | | | | | | | 7 | | 7 | | | |
| | Total | | | 469 | | | 469 | 6 | 321 | | 327 | 19 | 245 | 264 |
| 1985–87 | 15 | | 129 | | | | 129 | | | | | | | |
| | 25 | | | | | | | 13 | | | 13 | 283 | 22 | 305 |
| | 35 | | | | | | | | 1 | | 1 | | 173 | 173 |
| | 45 | | 20 | 367 | | | 387 | | 145 | | 145 | | | |
| | 55 | | | 95 | | | 95 | 17 | 114 | | 131 | | | |
| | 65 | | | | | | | | | | | | | |
| | Total | | 149 | 462 | | | 611 | 30 | 260 | | 290 | 283 | 195 | 478 |
| 1988–90 | 15 | | | | | | | | | | | | | |
| | 25 | | 44 | 111 | 80 | | 235 | 50 | 53 | 27 | 130 | | | |
| | 35 | 3 | 13 | 70 | | | 86 | 22 | 12 | | 34 | | | |
| | 45 | | | 406 | 23 | | 429 | | 226 | | 226 | | | |
| | 55 | 2 | | 153 | | | 155 | | 118 | | 118 | | | |
| | 65 | | | 1 | | | 1 | | | | | | | |
| | Total | 5 | 57 | 741 | 103 | | 906 | 72 | 409 | 27 | 508 | | | |
| 1991–93 | 15 | | | 9 | | | 9 | | | | | | | |
| | 25 | | 155 | 69 | 81 | 10 | 315 | 1 | | | 1 | | | |
| | 35 | | 104 | 84 | 155 | 6 | 349 | | 10 | 4 | 14 | | | |
| | 45 | 3 | | 124 | | | 127 | | 35 | | 35 | | | |
| | 55 | 18 | | 286 | | | 304 | | 14 | | 14 | | | |
| | 65 | | | 4 | | | 4 | | | | | | | |
| | Total | 21 | 259 | 576 | 236 | 16 | 1,108 | 1 | 59 | 4 | 64 | | | |

classes were similar to one another and were small relative to the size of a contingency table, Fisher's exact test was used instead of a chi-square test (Zar, 1984). All tested cases supported the null hypothesis of independence between sex ratio and depth, except for the samples of 200–249 mm TL fish caught

with traps during 1982–84 (Table 3). After allowance for multiple-testing ($\alpha' = 0.05/18 = 0.0028$), none of the cases was statistically significant.

Since there were no significant differences among depth classes, we pooled the data from all depth classes to compare the percentage of females among

Table 3

Comparison of percentages of females among water depth-classes with the same latitude (32°00'–32°59' N), length ranges (TL=200–249 mm and 250–299 mm), period, and gear type. % = female percent. *n* = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of depth. Blanks indicate no or few samples available for comparison. df = degrees of freedom.

| Period | Depth midpoint (m) | Traps | | | | Hook-and-line | | | | Trawl | | | |
|---------|--------------------|------------|----------|------------|-----------------|-----------------------|----------|-----------------------|----------|------------|----------|------------|----------|
| | | TL=200–249 | | TL=250–299 | | TL=200–249 | | TL=250–299 | | TL=150–199 | | TL=200–249 | |
| | | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> |
| 1979–81 | 25 | | | | | | | | | 54.6 | 55 | 53.9 | 39 |
| | 35 | | | | | | | | | 66.7 | 48 | 59.7 | 62 |
| | chi-square | | | | | | | | | 1.572 | | 0.333 | |
| | <i>P</i> | | | | | | | | | 0.210 | | 0.564 | |
| | df | | | | | | | | | 1 | | 1 | |
| | Reject H_0 | | | | | | | | | No | | No | |
| 1982–84 | 25 | 83.3 | 18 | 100.0 | 2 ¹ | 66.7 | 15 | 57.7 | 26 | | | 58.9 | 112 |
| | 35 | 91.7 | 36 | 84.6 | 13 | 64.7 | 17 | 80.0 | 10 | | | 65.2 | 23 |
| | 45 | 67.1 | 152 | 69.1 | 97 | 74.4 | 43 | 71.6 | 109 | | | | |
| | 55 | 80.0 | 45 | 75.6 | 41 | 75.0 | 8 | 40.0 | 15 | | | | |
| | chi-square | 11.28 | | 1.708 | | Fisher's ² | | Fisher's ² | | | | 0.314 | |
| | <i>P</i> | 0.010 | | 0.426 | | 0.859 | | 0.056 | | | | 0.575 | |
| | df | 3 | | 2 | | | | | | | | 1 | |
| | Reject H_0 | Yes | | No | | No | | No | | | | No | |
| 1985–87 | 25 | | | | | | | | | | | 57.9 | 19 |
| | 35 | | | | | | | | | | | 62.2 | 135 |
| | 45 | 86.9 | 206 | 72.4 | 134 | 68.6 | 51 | 63.9 | 72 | | | | |
| | 55 | 76.7 | 60 | 82.4 | 34 | 61.4 | 44 | 71.2 | 59 | | | | |
| | chi-square | 3.727 | | 1.414 | | 0.550 | | 0.783 | | | | 0.132 | |
| | <i>P</i> | 0.054 | | 0.234 | | 0.458 | | 0.376 | | | | 0.716 | |
| | df | 1 | | 1 | | 1 | | 1 | | | | 1 | |
| | Reject H_0 | No | | No | | No | | No | | | | No | |
| 1988–90 | 25 | 82.7 | 81 | 73.7 | 19 | 61.8 | 34 | | | | | | |
| | 35 | 77.1 | 48 | 79.0 | 19 | | | | | | | | |
| | 45 | 72.5 | 189 | 67.1 | 176 | 65.1 | 126 | 60.0 | 45 | | | | |
| | 55 | 64.9 | 74 | 75.0 | 76 | 70.0 | 60 | 71.8 | 39 | | | | |
| | chi-square | 6.808 | | 2.484 | | 0.745 | | 1.286 | | | | | |
| | <i>P</i> | 0.078 | | 0.478 | | 0.689 | | 0.257 | | | | | |
| | df | 3 | | 3 | | 2 | | 1 | | | | | |
| | Reject H_0 | No | | No | | No | | No | | | | | |
| 1991–93 | 25 | 80.0 | 30 | 84.6 | 13 ¹ | | | | | | | | |
| | 35 | 74.5 | 47 | 80 | 20 | | | | | | | | |
| | 45 | 70.0 | 30 | 77.9 | 68 | | | | | | | | |
| | 55 | 64.4 | 160 | 73.5 | 102 | | | | | | | | |
| | chi-square | 3.910 | | 0.649 | | | | | | | | | |
| | <i>P</i> | 0.271 | | 0.723 | | | | | | | | | |
| | df | 3 | | 2 | | | | | | | | | |
| | Reject H_0 | No | | No | | | | | | | | | |

¹ The row was discarded from the contingency table because of its excessively low expected frequency.

² When conditions for a chi-square test were not met, Fisher's exact test was used.

latitudes with other factors (length, period, and gear) remaining consistent. Six of the 14 tested cases indicated that sex ratio was dependent on latitude (Table 4). Even after allowance for multiple-testing ($\alpha'=0.05/14=0.0036$), there were still two cases indicating significant difference (1979–81, trawl, 150–199 TL and 1988–90, traps, 200–249 TL). Because the latitudinal distribution of samples was not similar among periods for any gear type (Table 2), we used only data from the latitude of 32°N in subsequent analyses.

There were no significant differences in percentage of females caught by traps among length classes 200–249, 250–299, and 300–349 mm during 1982–84, 1988–90, or 1991–93 (Table 5). During 1979–81, the hypothesis of independence between sex ratio and

length was rejected for fish caught by hook-and-line within the length range of 150–449 mm. However, it was not rejected within 200–299 mm (Table 5). Thus, the common TL range of vermilion snapper caught by hook-and-line was 200–299 mm, within which the sex ratio was independent of length during 1979–93. There were no significant differences in percentages of females caught by trawl within 150–249 mm during 1979–81 and 1985–87 (Table 5). After allowance for multiple-testing ($\alpha'=0.05/12=0.004$), none of the 12 cases showed significant difference.

We compared the percentage of females among periods by pooling data for each gear type within the common TL range and periods when the sex ratio was independent of length. There were no signifi-

Table 4

Comparison of percentages of females among latitudes with the same length ranges (TL=200–249 mm and TL=250–299 mm), period, and gear type. All data were pooled from various water depth classes. % = female percent. *n* = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of latitude. Blanks indicate no or few samples available for comparison.

| Period | Latitude (°N) | Traps | | | | Hook-and-line | | | | Trawl | | | |
|--------------|---------------|------------|----------|------------|----------------|-----------------------|----------|-----------------------|----------|------------|----------|------------|----------|
| | | TL=200–249 | | TL=250–299 | | TL=200–249 | | TL=250–299 | | TL=150–199 | | TL=200–249 | |
| | | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> | % | <i>n</i> |
| 1979–81 | 31 | | | | | 57.1 | 14 | 87.5 | 8 | 36.5 | 115 | 57.1 | 14 |
| | 32 | | | | | 73.6 | 106 | 67.6 | 105 | 60.2 | 103 | 57.4 | 101 |
| | 33 | | | | | 87.5 | 16 | 50.0 | 4 | | | | |
| | chi-square | | | | | Fisher's ² | | Fisher's ² | | 12.205 | | 0 | |
| | <i>P</i> | | | | | 0.178 | | 0.352 | | <0.001 | | 0.984 | |
| | df | | | | | | | | | 1 | | 1 | |
| Reject H_0 | | | | | No | | No | | Yes | | No | | |
| 1985–87 | 31 | 82.6 | 115 | 50.0 | 20 | 72.7 | 11 | 93.3 | 15 | 39.4 | 221 | 52.3 | 44 |
| | 32 | 84.6 | 266 | 74.4 | 168 | 65.6 | 96 | 67.2 | 131 | 58.3 | 36 | 61.7 | 154 |
| | chi-square | 0.234 | | 5.258 | | Fisher's ² | | Fisher's ² | | 4.571 | | 1.260 | |
| | <i>P</i> | 0.629 | | 0.022 | | 0.747 | | 0.039 | | 0.033 | | 0.262 | |
| | df | 1 | | 1 | | | | | | 1 | | 1 | |
| | Reject H_0 | No | | Yes | | No | | Yes | | Yes | | No | |
| 1988–90 | 31 | 63.9 | 36 | 100.0 | 4 ¹ | | | | | | | | |
| | 32 | 73.7 | 392 | 70.5 | 291 | | | | | | | | |
| | 33 | 91.8 | 61 | 76.7 | 30 | | | | | | | | |
| | chi-square | 11.96 | | 0.511 | | | | | | | | | |
| | <i>P</i> | 0.003 | | 0.475 | | | | | | | | | |
| | df | 2 | | 1 | | | | | | | | | |
| Reject H_0 | Yes | | No | | | | | | | | | | |
| 1991–93 | 31 | 80.0 | 235 | 57.1 | 7 | | | | | | | | |
| | 32 | 68.8 | 276 | 76.8 | 207 | | | | | | | | |
| | 33 | 77.7 | 206 | 60.0 | 20 | | | | | | | | |
| | chi-square | 9.509 | | 3.925 | | | | | | | | | |
| | <i>P</i> | 0.009 | | 0.141 | | | | | | | | | |
| | df | 2 | | 2 | | | | | | | | | |
| Reject H_0 | Yes | | No | | | | | | | | | | |

¹ The row was discarded from the contingency table because of its excessively low expected frequency.

² When conditions for a chi-square test were not met, Fisher's exact test was used.

Table 6

Comparison of percentages of females among periods with the same latitude (32°00'–32°59' N) and gear type. All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of period. Blanks indicate few samples available for comparison or the null hypothesis of independence between sex ratio and length was rejected in Table 5. df = degrees of freedom.

| Period | Traps (TL=200–349) | | Hook-and-line (TL=200–299) | | Trawl (TL=150–249) | |
|--------------|-----------------------|-----|-------------------------------|-----|-----------------------|-----|
| | % | n | % | n | % | n |
| 1979–81 | | | 70.6 | 211 | 58.8 | 204 |
| 1982–84 | 72.6 | 453 | 68.4 | 244 | | |
| 1985–87 | | | 66.5 | 227 | 61.1 | 190 |
| 1988–90 | 72.5 | 727 | 67.6 | 321 | | |
| 1991–93 | 71.1 | 554 | 64.4 | 45 | | |
| chi-square | 0.382 | | 1.199 | | 0.204 | |
| P | 0.826 | | 0.878 | | 0.652 | |
| df | 2 | | 4 | | 1 | |
| Reject H_0 | No | | No | | No | |

Table 7

Comparison of percentages of females among gear types with the same latitude (32°00'–32°59' N). All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of gear type. Data were pooled from periods that were used in Table 6. Data with different length ranges were used in A, B, and C. (A) TL ranges were the same as used in Table 6 for each gear; (B) TL = 200–249 mm for all gear types; (C) TL = 186–540 mm, mean TL = 254 mm for traps, TL = 142–560 mm, mean TL = 261 mm for hook-and-line, and TL = 112–256 mm, mean TL = 203 mm for trawl.

| Gear | A | | B | | C | |
|---------------|--------|------|--------|-----|--------|------|
| | % | n | % | n | % | n |
| Traps | 72.1 | 1734 | 72.4 | 919 | 72.1 | 1786 |
| Hook-and-line | 68.0 | 1048 | 68.6 | 544 | 66.2 | 1395 |
| Trawl | 59.9 | 394 | 60.0 | 255 | 61.0 | 415 |
| chi-square | 23.460 | | 14.558 | | 24.938 | |
| P | <0.001 | | 0.001 | | <0.001 | |
| df | 2 | | 2 | | 2 | |
| Reject H_0 | Yes | | Yes | | Yes | |

ranges (Table 7B: a single TL range for all gear types; Table 7C: all data available were used with full TL ranges). Vermilion snapper caught by all gear types had an unequal sex ratio that was female-biased (traps and hook-and-line: $P < 0.001$, trawl: $P < 0.005$).

Discussion

Maturity schedules

Although data used for maturity analysis were limited to those collected in the same season (May and June) of each period, growth may occur, and stages of maturity may change, within two months. An immature fish in May may become mature in June. If more fish were collected in June of recent years than in 1979–81, the percent mature at a certain age would be overestimated for recent years. The monthly distribution of observations, however, was similar among periods with more than 80% of the fish smaller than 170 mm being collected in May. Relative differences in maturity schedules among periods remained valid throughout the study.

The essential underlying assumption of the maturity analysis is that length, age, and reproduction conditions are correctly measured or determined. In 1985, 1986, 1987, and 1988, only fork lengths (FL) were measured. These FL were converted to TL with TL (mm) = $1.115FL - 0.254$ (Zhao et al., 1997). For

other years, observed TL was available. Because the method for ageing vermilion snapper by means of otolith sections has been validated by Zhao et al. (1997) and because the persons who read otoliths in Zhao et al.'s study also read otoliths in our study, incorrect ageing of vermilion snapper is not considered a source of bias. During 1979–86, gonads were examined macroscopically by experienced biologists by means of clearly defined gross morphological staging criteria. These criteria were confirmed to be accurate by histological examination during 1978–80. All gonads, since 1987, were examined by using reliable histological techniques (Cuellar et al., 1996). Therefore, it is believed that sex and maturation were correctly determined. In general, sex and maturity stages can be more reliably determined during the spawning season than in off-seasons. Data used for maturity analysis were only from May and June, the first part of the spawning season, during which errors in maturity determination were not expected. Furthermore, in the present study, all maturity stages of mature fish were pooled in only one maturity state, i.e. mature. As long as immature and mature fish could be distinguished, inaccurate classification of mature substage would not introduce a bias in estimates of age and size at maturity.

This study indicated that both age and length at sexual maturity of vermilion snapper declined over time. This decline may have resulted from increased fishing pressure, because the total landings consis-

tently increased during the 1980's (Zhao and McGovern²). The demonstration that the harvest of a fish stock can lead to declines in length or age at maturity has been reported for many fishes, including northeast Arctic cod (Jørgensen, 1990), Pacific salmon (Ricker, 1981), and California halibut (Love and Brooks, 1990). Changes in size or age at maturity may be the result of a density-dependent response to decreased stock abundance, selective removal and incomplete replacement of later-maturing fish by the fishery, or genetic change within a population (Nelson and Soulé, 1987). Jørgensen (1990) attributed a decline in median age-at-maturity in northeast Arctic cod to an increase in length-at-age (i.e. faster growth) coincident with declining stock density, an idea that implicitly assumes a minimum threshold for size-at-maturity. If the scenario of Jørgensen (1990) is correct, declines in length and age should not occur concurrently. Furthermore, Zhao et al. (1997) indicated that the size-at-age of vermilion snapper has decreased with time. Therefore, changes in maturity schedules of vermilion snapper are not part of a density-dependent compensatory response to harvesting, but quite likely a result of the selective removal and incomplete replacement of faster-growing, later-maturing fish by the fishery. If intensive fishing pressure continues, and the early-maturing trait is heritable, length and age at maturity in the population will decrease with time. Life history theory predicts that genetic changes in life history characteristics will occur following increased mortality (Roff, 1992). Harvesting can reverse the relative fitness of genotypes, because an inferior genotype (e.g. slow-growing and early-maturing) in an unexploited population may be more fit under increased fishing pressure (Bergh and Getz, 1989). Early-maturing genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger sizes or older ages tend to be removed before reproduction. This process would explain the decreasing abundance of larger, immature fish with time and would account for declines in both size and age at maturity. The long-term impacts of size-selective fish harvests may have caused the decline in size-at-age of vermilion snapper through disproportionate harvesting of fast-growing individuals (Zhao et al., 1997). Similarly, it may be that late-maturing genotypes were removed from the vermilion snapper population in the 1980's when fishing pressure was intensive.

Maturity schedules of vermilion snapper collected during 1972–74, prior to heavy exploitation, were investigated by Grimes and Huntsman (1980). They used a gonadosomatic index and indicated that "most fish attain sexual maturity during their third or

fourth years of life (186–256 and 256–324 mm TL), but a few precocious individuals may mature in their second year (100–186 mm TL) at about 150 mm TL." It is not rigorous to compare the percent mature, based on age, between Grimes and Huntsman (1990) and the present study because an obvious discrepancy in size-at-age exists between Grimes (1978) and Zhao et al. (1997). It is meaningful, however, to compare maturity schedules based on length between these two studies. The maximum-likelihood estimates from the probit analysis of data from the present study predicted that 50% of males and 15% of females matured by 150 mm during 1979–81 and that 50% females at 150 mm matured during 1985–87. All males and females at 180 mm were mature in the present study. Differences between previous (Grimes and Huntsman, 1980) and present results could be partially due to differences in methods used to determine maturity (Collins and Pinckney, 1988) or may truly reflect the changes in maturity that occurred in the 1970's. The increase in percentage of mature females at 150 mm was faster during the 1980's than during the 1970's (i.e. an increase of 35% in six years from 1979–81 to 1985–87, versus an increase of less than 15% in seven years from 1972–74 to 1979–81). The degree of exploitation may account for the differing rates of change in maturity while the fishery for vermilion snapper was initiated in the 1970's, but heavy exploitation did not occur until the 1980's.

Sex ratios

The chi-square analysis did not suggest significant differences in percentages of females among months (May–August) for any gear type. This information supported the notion that pooling data between May through August would not bias the comparison of sex ratios. Seasonal comparisons of sex ratios could not be done because little sampling was done in fall or winter.

This study showed that the sex ratio of vermilion snapper was dependent on area (latitude) and gear type, but independent of depth of sampling sites, fish length, or sampling years. The reason for the significant differences among latitudes is unknown. However, only 2 of the 14 cases showed a significant difference according to Bonferroni's method (Table 4), and no trend was observed between latitudes. In addition, relatively small sample sizes collected from latitudes other than 32°N may have induced errors in comparison. Therefore, we attribute the difference in sex ratio between latitudes to chance.

Although significantly different, the percentages of females of vermilion snapper collected by traps

and hook-and-line were similar to each other (traps: 72.1%; hook-and-line: 68.0%) but differed from that for trawl capture (59.9%). Trawls caught smaller fish from shallower waters when compared with traps and hook-and-line (Tables 2 and 7C). However, present results indicated that sex ratios were not affected by water depth or fish length. With traps and hook-and-line gear, baits were used to attract fish. If female vermilion snapper were more aggressive in pursuing bait than males, the percentage of females in the catch of traps and hook-and-line could be higher than that in the population. In contrast, no baits were used for trawling, and therefore males and females might be caught with the same probability. If the difference in feeding behavior between sexes can account for the difference in sex ratio between gear, then the sex ratio of vermilion snapper in the population may be correctly represented by the trawl catch. Watanuki et al. (1993) reported that basket traps caught the greatest ratio of female cuttlefish among three types of gear (basket traps, jigs, and trammel nets). More females may be attracted to traps for spawning, but Watanuki et al. indicated that there are probably other unknown factors governing the entry of cuttlefish into traps. Because information on spawning behavior of vermilion snapper is unavailable, we cannot evaluate how the spawning activity of vermilion snapper may affect its vulnerability to different gear types.

We pooled data from all gear types and calculated the overall sex ratio by period. The percentage of females gradually increased from 62% in 1979–81 to 70% in 1991–93. The temporal increase in the percentage of females proved to be an artifact of unequal distribution of catch by gear among periods. Reasons for the difference in sex ratios among gear types are unknown. Caution must be used when evaluating the sex ratios of any fish species collected by various gear types.

Our conclusion of independence between sex ratios and lengths differs from previous studies. Grimes and Huntsman (1980) concluded that the sex ratio of vermilion snapper was dependent on fish length, with the percentage of females increasing in larger size classes. However, the percentage of females within the range of 551–600 mm TL (89.3%, $n=32$) was obviously higher than those for other length ranges. Thus, it is suspected that the significant chi-square calculated by Grimes and Huntsman (1980) was probably due to this length range. We used the original data published in Table 4 of Grimes and Huntsman (1980) but excluded the data with length greater than 550 mm TL ($n=32$). We found that sex ratio was independent of length ($\chi^2=13.105$, $P=0.108$, $n=841$, $df=8$, TL=101–550 mm) and thus was in

agreement with the conclusion of the present study. A further 2×2 contingency table analysis formed by the TL range of 551–600 mm versus all other length ranges rejected the null hypothesis of independence between sex ratio and length ($\chi^2=11.732$, $P=0.001$, $n=873$, $df=1$). Thus, we confirmed that the sex ratio within 551–600 mm TL is significantly different from those of other length ranges. Because our data had relatively few vermilion snapper larger than 450 mm TL, the conclusion of independence between sex ratio and length may be limited to 450 mm TL or less. However, the similar size-at-age and the same longevity of male and female vermilion snapper do not suggest the percentage of females would increase with length even beyond 450 mm TL (Zhao et al., 1997).

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