REPRODUCTION OF THE COMMON CORAL TROUT
PECTROPOMUS LEOPARDUS
(SERRANIDAE: EPINEPHELINAE) FROM THE
CENTRAL AND NORTHERN
GREAT BARRIER REEF, AUSTRALIA

Beatrice P. Ferreira

ABSTRACT

The reproductive biology of the serranid fish, Plectropomus leopardus, was studied from samples collected from mid shelf reefs in the central Great Barrier Reef and mid shelf reefs and waters adjacent to Lizard Island in the northern Great Barrier Reef. For the two locations, a spawning period was observed from September through November, during which multiple spawning occurred. An inverse relationship between fat and gonad weight was observed for the coral trout, indicating that these deposits of mesenteric fat are probably being used in the processing of gonad products. The mode of sexual development, monandric protogynous hermaphroditism, was confirmed through histological analyses of gonad material. The sex structure of the sampled population was analyzed based on age and size information. The size and age of first reproduction for females was 32 to 36 cm FL and 2 to 3 years of age. Size and age distribution of females overlapped with size and age distribution of males over a wide range, indicating that sex change can occur over a broad range of sizes and ages but females were significantly smaller and younger than males. While at the present point it is not clear how sex change is determined for the coral trout, the variability observed in the size and age in which sex change occurs and in the process of transition itself suggests that behavioral processes could be involved.

The common coral trout Plectropomus leopardus (Lacepede 1802) is the most commercially exploited species of Serranidae on the Great Barrier Reef, with around 1,200 tons caught annually by the commercial fishery (Trainor, 1991). In spite of its importance, the reproductive biology of the common coral trout has been studied only for a population on the southern Great Barrier Reef (Goeden, 1978). Like all epinepheline serranids that have been studied until now (Shapiro, 1987), the coral trout is a protogynous hermaphrodite (Goeden, 1978). Management of a fishery is considerably complicated by sequential hermaphroditism, as males are likely to be removed selectively (Shapiro, 1987; Bannerot et al., 1987). The responses of these populations to fishing pressure are largely unknown. Mechanisms of social induction of sex change have been suggested for epinepheline serranids as an alternative to genetically programed mechanisms, in which sex-change would occur at a certain size or age (Shapiro, 1987). For the coral trout, however, no information on population structure or behavior is available at the moment to assess these questions.

In the present work, the reproductive biology of P. leopardus was studied from data collected in two areas of the Great Barrier Reef. Gonads were analyzed to determine the mode of reproduction and spawning season. The sex, size and age structures of these populations were analyzed to determine the age and size of first reproduction, distribution of sexes and range of occurrence of sex-change.

MATERIALS AND METHODS

Samples were collected from two geographically distinct sites: mid shelf reefs off Townsville, central Great Barrier Reef (Lat. 18° to 19°30'S, Long. 146° to 147°E), and mid shelf reefs and waters adjacent to Lizard Island, northern Great Barrier Reef (Lat. 14°40'S, Long. 154°28'E), from 1990 to 1992.
Table I. Number of fish collected per month from Townsville and Lizard Island reefs from 1990 to 1992

<table>
<thead>
<tr>
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<td>--</td>
<td>--</td>
<td>52</td>
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<td>--</td>
<td>14</td>
<td>8</td>
<td>14</td>
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</tr>
<tr>
<td>Mar</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>10</td>
<td>20</td>
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<td>25</td>
<td>--</td>
<td>--</td>
<td>10</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Jul</td>
<td>21</td>
<td>10</td>
<td>5</td>
<td>61</td>
<td>20</td>
<td>--</td>
</tr>
<tr>
<td>Aug</td>
<td>5</td>
<td>--</td>
<td>35</td>
<td>5</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Sep</td>
<td>10</td>
<td>28</td>
<td>83</td>
<td>2</td>
<td>20</td>
<td>--</td>
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<td>Nov</td>
<td>16</td>
<td>--</td>
<td>--</td>
<td>6</td>
<td>161</td>
<td>--</td>
</tr>
<tr>
<td>Dec</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>161</td>
<td>73</td>
<td>24</td>
</tr>
<tr>
<td>Total</td>
<td>60</td>
<td>83</td>
<td>118</td>
<td>52</td>
<td>354</td>
<td>24</td>
</tr>
</tbody>
</table>

(Table 1). Fishes were captured using spear-fishing or line-fishing during collecting trips. Additional samples in the form of carcasses kept frozen after filleting were obtained from local commercial and recreational fishermen.

The fork length (FL) and standard length (SL) of the fish were measured in centimeters. The gonads were removed, weighed and staged macroscopically. Sex determination could be done macroscopically only if gonads were active. In this case, individuals were classified as ripe females or males and the information used to determine periodicity of spawning. The gonadosomatic index (GSI) was calculated as the ratio of gonad fresh weight to total weight of the fish. As total weight was not available for the commercial samples, estimated values were obtained through the relationship between fork length and total weight (Ferreira and Russ, 1994).

The amount of fat deposited in the mesenteries was estimated for the Lizard Island sample following a relative scale from 0 to 1, with 6 categories which indicated the proportion of fat covering the viscera (0 = no visible fat; 0.2 = thin threads of fat; 0.4; 0.6; 0.8 increasing amounts of fat, and 1.0 = fat completely covering the viscera). This scale was chosen after observing the seasonal variation in the relative amounts of mesenteric fat for a year, and estimations were always made by the same observer.

Gonads from 230 fish from Lizard Island and 131 from Townsville were preserved in F.A.A.C (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%) for later sectioning (L. Winsor, pers. comm.). Middle portions of the two gonadal lobes were embedded in paraffin and sectioned transversely at 5-μm thickness and stained with Mayer’s haematoxylin-eosin.

The age of the fishes examined histologically was determined from otolith readings following a technique described by Ferreira and Russ (1994). The periodicity of formation of annual bands was validated during the aforementioned study.

Gonadal Stages.—The nomenclature for description of the stages of oogenesis and spermiogenesis followed Yamamoto et al. (1965). Classification of males and females into ontogenetic stages (stagium) and developmental stages (stadium) followed the adaptation by Ferreira (1993) from Moe (1969). Developmental stages of ovaries were determined according to the most advanced oocyte stage present in the gonad (Ebisawa, 1990).

IMMATURE FEMALE. Ovaries that showed no evidence of prior spawning. The ovary is small in diameter and encased by a relatively thick gonadal wall. The lamellae are well packed and filled with previtellogenic oocytes in early and late perinucleolus stages. Gonia and chromatin nucleus stage oocytes are abundant.

MATURE FEMALE. Resting: the ovary is larger in diameter than those of immature females and encased by a thinner, more distended gonadal wall. The lamellae are filled with previtellogenic oocytes in early and late perinucleolus stages. Gonia and chromatin nucleus stage oocytes are present but not as abundant as observed in immature females. The presence of yellow-brown bodies is common. Ripening: oocytes in early stages of vitellogenesis, from yolk vesicle stage to primary yolk globule stage. Ripe: oocytes in late stages of vitellogenesis from tertiary yolk globule stages to hydrating stages. Spent: lamellae disrupted and disorganized, with extensive vascularization. Vitellogenic oocytes in atresia. Follicular cells, remnants of post-ovulatory follicles, present throughout the gonad. Proliferation of gonia and chromatin nucleus stage oocytes.
TRANSITIONAL. Transitional individuals were defined as having gonads that showed proliferating testicular tissue in the presence of degenerating ovarian tissue, but in which sex-transition had not yet proceeded to the point at which the dorsal sperm sinuses were formed and filled with spermatozoa (Hastings, 1981).

YOUNG MALE. Post-transitional, newly transformed testis. Ovarian tissue dominating the lamellae that had not assumed the typical lobular form of the mature testes. Sperm crypts occur in all stages of development. Dorsal sperm sinuses are formed and filled with spermatozoa.

MATURE MALE. Resting: testis dominated by stromal tissue and early stages of spermatogenesis (spermatogonia and primary spermatocytes). Ripening: later stages of spermatogenesis (secondary spermatocytes and spermatids) and spermriogenesis, spermatozoa starting to fill the dorsal sinus. Ripe: testis dominated by spermriogenesis. Most crypts containing spermatids and spermatozoa. Crypts of spermatozoa ruptured and joined within the testicular lobules, forming large intralobular or “central” sperm sinuses. Dorsal sinuses filled with spermatozoa. Spent: active development of crypts of spermatogonia and primary spermatocytes throughout the testis. Stromal tissue well developed between crypts.

To estimate the percentage of remaining female tissue in transitional and male gonads, the whole gonad was observed under low magnification (40X), the percentage of area occupied by oocytes estimated twice independently, and the results averaged.

**Size and Age Structure.**—Only individuals of age ≥2 years old were included in the comparisons between Lizard and Townsville, as younger individuals were only represented in the Lizard Island sample where fishing gear other than hook and line was employed (Ferreira and Russ, 1994).

The size and age range in which individuals changed sex was estimated from the zone in which size and age distributions of females overlapped with size and age distributions of transitional, young or mature males. The range of overlap was calculated as a percentage of the total range of sizes and ages observed. To compare if sex-change occurred at the same size and age for the two locations the distributions of size and age of individuals within the overlap range were compared using a t-test (Shapiro, 1984).

For the calculation of sex ratio, only reproductively active, i.e., mature individuals were included. The age and size of first spawning for females were determined as the age or size class in which 50% of females were mature.

**Statistics.**—One, two and three-way analyses of variance including post-hoc tests (Tukey-Kramer) were used for comparisons. Before the analyses, the assumptions of normality and homoscedasticity were examined and transformations (log (x) or arcsin square root) were used if needed. Transformed data are indicated in tables or text. Level of significance used was $P < 0.05$. Spearman-Rank correlation was used to analyze the relationship between gonad weight and fat (Lizard Island data only) and between gonad weight and age and size. A Chi-square test was used to compare sex-ratios of samples collected with line-fishing and spear-fishing. The overlap of distributions of males and females was compared by t-test.

**RESULTS**

Reproductive Biology.—The gonads of male and female *P. leopardus* were composed of two elongated lobes, usually unequal in size, which were joined posteriorly into the common duct. The gonad was formed by a germinal epithelium extending from the dorsal and lateral gonad walls into the central lumen. The gonadal wall was formed by smooth muscle and connective tissue covered by a peritoneal layer. The gonad was attached dorsally to a complex net of mesenteries, ligaments, arteries and veins. The left gonadal lobe was connected by these mesenteries to the dorsal body wall and to the right gonadal lobe, which was also attached by the same mesenteries to the intestine and other organs in the coelomic cavity. Deposition of fat occurred along the mesenteries (Fig. 1) in quantities that varied from no visible fat to a thick layer that covered all the viscera. Sex determination could be done macroscopically only if gonads were active. Resting gonads were not very reduced in length but were greatly reduced in diameter. During the resting stage, the gonads were difficult to distinguish, especially the right lobe that became covered by the viscera.

As first described by Goeden (1978), the mode of reproduction of *P. leopardus* is protogynous hermaphroditism. The germinal tissue is of the undelimited or
Figure 1 (upper left). Mesenteric fat attached to gonad of female coral trout. Scale bar = 200 μm. g = gonad; ms = mesenteries; fat = fat cells. Scale bar = 250 μm.

Figure 2 (upper right). Transverse section of a testis of a ripe mature male coral trout, showing sperm sinuses in the center of lobes joining dorsal sperm sinuses. Note remnant non-vitellogenic oocytes in the periphery of lobes. dss = dorsal sperm sinus; css = central sperm sinus. Scale bar = 250 μm.

Figure 3 (middle left). Developing sperm crypts in ovary of ripe female. Transverse section. ygs = yolk globule stage oocyte; sc = sperm crypt; str = stromal tissue. Scale bar = 125 μm.
Sex Transition.—The presence of a few precocious sperm crypts (sensu Smith, 1965) was observed in the ovaries of some resting females from the two locations. Transition was clearly indicated only when proliferation of sperm crypts was more advanced and accompanied by fragmentation and reabsorption of previtellogenic oocytes. Transitional gonads typically had a large number of germ cells, presumably spermatogonia, as chromatin nucleolus stage oocytes were rare in contrast to non-transitional resting female gonads. Proliferation of sperm crypts was concentrated in the dorsal part of the gonad, apparently in close association with the stromal tissue. Stromal cells were conspicuous during this phase and seemed to be undergoing proliferation.

During the spawning season, sperm crypts were observed in the ovaries of some mature ripe females in the Townsville region (N = 5) (Fig. 3). These sperm crypts were in all stages of development, from primary spermatocytes to spermatooza. Vitellogenic oocytes were in the final stages of development, and showed no signs of degeneration (Fig. 3) though a few fragmenting previtellogenic oocytes were observed. No sperm sinuses were formed, indicating that in spite of the presence of spermatooza, these individuals probably would not spawn simultaneously as males and females, so they were classified as mature females. Developing sperm crypts were observed in spent ovaries also (N = 3). In these gonads development of sperm crypts and degeneration of ovarian tissue occurred simultaneously with reabsorption of vitellogenic oocytes. These individuals were classified as transitionals. In two other individuals the development of sperm tissue was more advanced and the dorsal sperm sinuses were formed, so the individuals were classified as young males. A few atretic yolk oocytes were still present in these gonads indicating that the transition process had occurred over a short period (Fig. 4). Sex-transition was observed also in gonads that were characteristically immature ovaries. Figure 5 shows the gonad of a young male that apparently went through pre-maturational sex change. In this gonad, collected during the spawning season, only previtellogenic oocytes were observed.

Proliferation of sperm tissue was accompanied by degeneration and reabsorption of the ovarian tissue. The percentage of ovarian tissue in gonads of transitional, young and mature males was compared by a one-way analysis of variance. There was a significant reduction in the ovarian tissue as the gonad developed.
Table 2. Three-way ANOVA examining the effects of location, sex and month on the variation of Gonadosomatic index (GSI)* values of mature males and females

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>MS</th>
<th>F-value</th>
<th>P-value</th>
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<td>0.024</td>
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<td>0.008</td>
<td>6.544</td>
<td>0.0001</td>
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<tr>
<td>Location × sex</td>
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<td>0.001</td>
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<td>Location × date</td>
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<td>0.716</td>
<td>0.5429</td>
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<tr>
<td>Sex × date</td>
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<tr>
<td>Location × sex × date</td>
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<td>0.001</td>
<td>0.000</td>
<td>0.353</td>
<td>0.7868</td>
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<tr>
<td>Residual</td>
<td>402</td>
<td>0.493</td>
<td>0.001</td>
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<td></td>
</tr>
</tbody>
</table>

* Data arcsin square root transformed prior to analysis.

from transitional to the mature male stage (data arcsin square root transformed; \( P < 0.001 \)) (Fig. 6).

Gonads of young males were still largely ovarian, but significantly less than transitional gonads. In testes of mature males, ovarian tissue was further reduced and the presence of oocytes was usually restricted to the periphery of the testicular lobes (Fig. 2).

The presence of yellow-brown bodies was not clearly associated with sex-transition as they were common in gonads of resting and spent males and females. In mature males they were usually located in the center of the testicular lobes. Brown bodies were specially conspicuous in post-spawning individuals, and could be seen macroscopically as brown dots along the gonads.

Seasonality and Periodicity of Spawning.—For both the Lizard Island and Townsville regions, spawning was indicated for the period from September through December by gonadal stages and gonado-somatic index (GSI).

There were no significant differences between GSI values observed for Townsville and Lizard Island Reefs. GSI values of females were significantly higher than those of males, and both varied between months in the two locations (Table 2, Fig. 7). There was a significant increase from August to the peak in October, with values remaining high until November and dropping significantly by December (Tukey-Kramer, \( P < 0.05 \)). A significant interaction between sex and month indicated that differences in GSIs between males and females were dependent on

Figure 7. Monthly variations of gonadosomatic index (GSI %) values for males and females from Townsville and Lizard Island. Error bars show standard error of original data.
Figure 8. Monthly distribution of percentages of gonadal stages for females and males from Lizard Island and Townsville.

During the spawning months, the increase in the GSI values of females is up to four times greater than the increase observed for males.

Ripe females were observed from August through December at Lizard Island and from September through November at Townsville (no data for December). Ripe males were present from July through December at Lizard Island and from July through November at Townsville (no data for December) (Fig. 8).

In testes of ripe males, spermatogenesis and spermiogenesis occurred simulta-
neously, indicating continuous spawning activity (Fig. 9). Ripe females characteristically had lamellae packed with oocytes in the tertiary yolk globule stage, but oocytes in earlier stages of development were always present (Fig. 10), indicating multiple spawning throughout the season (Nagahama, 1983; Ebisawa, 1990). Oocytes in final stages of maturation (hydrated oocytes) were present in 40% of the ripe female gonads observed in the period from September through December. In those oocytes the lipid droplets and yolk globules had coalesced and the overall size of the oocyte increased due to hydration. Hydrated oocytes

Figure 9 (left). Testis of ripe male showing simultaneous occurrence of stages of spermiogenesis and spermatogenesis. sg = spermatogonia; sc1 = primary spermatocyte; sc2 = secondary spermatocyte; st = spermatid; sz = spermatozoa. Scale bar = 50 μm.

Figure 10 (right). Ovary of ripe female showing asynchronous oocyte development. eps = early perinucleus stage; lps = late perinucleus stage; yvs = yolk vesicle stage; ygs = yolk globule stage; hy = hydrated stage. Scale bar = 250 μm.

Figure 11 (center). Post-ovulatory follicle (pof) in ovary of spent female. Scale bar = 125 μm.
Histologically, the male was ripe but only a small amount of milt could be obtained.

The amount of fat deposited in the mesenteries of mature males and females from Lizard Island varied seasonally (Table 3). There were no significant differences between males and females, and both sexes showed a significant variation between months. From April onwards there was a significant increase in the amount of fat until the peak in August (Tukey-Kramer, $P < 0.05$). By October, the amount of mesenteric fat observed had dropped to almost zero in most individuals, and remained low until December, with a slight increase by February (Fig. 12).

The variation in the amount of mesenteric fat was antiphase to the variation observed in the GSI for males and females (Fig. 12), and the amount of fat was inversely correlated with gonad weight for mature females (Spearman rank $Rs = -0.361$, $P < 0.001$).

Population Structure.—The sex-ratio (mature females : mature males) of the sample collected with spear-fishing was statistically not different from the sex-ratio of the sample collected with line-fishing (Chi-square, $P = 0.133$), so the samples were pooled.

The proportion of each developmental stage for each location (Townsville and Lizard) is shown in Table 4. Sex-ratio in both locations was biased towards females. Townsville had a smaller proportion of mature males, but a higher proportion of transitional and young male stages. If transitionals and young males were considered as males, the sex-ratio would be: Lizard Island = 1.74 : 1; Townsville = 1.33 : 1.

Size distributions of mature males and females overlapped over most of the range of sizes observed (Fig. 13). The mean sizes and ages of the Lizard Island

Table 3. Two-way ANOVA examining the effects of sex and month on the amount of fat* deposited in the mesenteries of mature males and females from Lizard Island

<table>
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</table>

*Data arcsin square root transformed prior to analysis.
Table 4. Number and percentage of developmental stages and sex-ratio (mature females : mature males) for the Lizard Island and Townsville samples

<table>
<thead>
<tr>
<th></th>
<th>Imm. female</th>
<th>Mature female</th>
<th>Trans.</th>
<th>Young male</th>
<th>Mature male</th>
<th>Sex-ratio fem: male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lizard</td>
<td>8 (3.5%)</td>
<td>141 (61%)</td>
<td>10 (4%)</td>
<td>10 (4%)</td>
<td>61 (26.5%)</td>
<td>2.31:1</td>
</tr>
<tr>
<td>TSV</td>
<td>12 (10%)</td>
<td>61 (51%)</td>
<td>12 (10%)</td>
<td>12 (10%)</td>
<td>22 (19%)</td>
<td>2.77:1</td>
</tr>
</tbody>
</table>

Figure 13. Size (fork length) distribution and age distribution of developmental stages for the Lizard Island and Townsville samples.
and Townsville samples were not significantly different (Tables 5, 6). There were significant differences among ontogenetic stages (immature and mature females, transitional individuals and young and mature males), but no interaction between location and stage, indicating that the mean sizes and ages of each stage were not different for each location.

Sizes and ages of mature females, transitional and young males were not significantly different, while immature females and mature males were significantly smaller and larger respectively than all other stages. Size and age of individuals within the zone where frequency distribution of males overlapped with females were not significantly different between locations ($t$-test, size: $P = 0.192$; age: $P = 0.190$).

**Maturation**.—During the spawning season some immature females were observed undergoing limited vitellogenesis, as indicated by the presence of yolk oocytes in early stages. After the spawning season, it is possible that signs of previous vitellogenesis remained, in the form of scattered yolk globules or brown-bodies, making it difficult to separate these immature gonads from mature resting gonads. Therefore, for the calculation of size and age of first maturity, only immature individuals classified during the spawning season were included.

The size class of first reproduction (50% of individuals reproductive) for females was 32 to 36 cm FL (Fig. 13). The age of first reproduction for females was 2 to 3 years of age (Fig. 13).

Gonad weight was positively related to age and size for mature males and females ($P < 0.0001$) (Fig. 14). Some females were mature at 30 cm FL but gonad weight started to increase only after 40 cm FL.

Transitional gonads that resembled immature ovaries were observed during and outside the spawning season. Individuals observed during the spawning season ($N = 7$) were aged between 2 and 3 years (mean = 2.7, SE = 0.184) and measured between 26.9 and 36.2 cm (mean = 33.1, SE = 1.37), indicating the possibility of prematurational sex-change.

**DISCUSSION**

**Spawning Season**.—The spawning period observed for *P. leopardus* between early spring and summer in the central and northern regions of the Great Barrier
Figure 14. Relationship between gonad weight (g) and size (fork length) and age of ripe females and males of coral trout. Data from Lizard Island and Townsville regions pooled.

Reef coincides with the spawning period observed by Goeden (1978) for the southern region and with the spawning period observed by Samoilys and Squire (1994) for the Cairns region. Spawning season during this period has also been observed for the congeneric species *P. maculatus* from the Townsville region (Ferreira, 1993). The sampling design employed here did not allow for effective comparisons between locations regarding aspects such as exact time of spawning, and it is possible that latitudinal differences exist for coral trout populations of the Great Barrier Reef in terms of time of beginning and end of the spawning season. Nevertheless, it seems reasonable to infer that the spawning season for the coral trout on the Great Barrier Reef occurs generally in the same period, i.e., from early spring to early summer.

Multiple-spawning occurs during this period as was indicated by asynchronous oocyte development in females and continuous spermiogenesis in males. Males mature earlier in the season and remain active for longer and have lower GSI values than females. As males in protogynous species tend to spawn more frequently than females (Shapiro, 1984) it is likely that the strategy employed by coral trout males is a limited but continuous production of sperm throughout the season.

In fishes, oocytes in tertiary yolk globule stage are maintained within the ovary for a variable period of time, following completion of vitellogenesis, until a series
of endocrine events stimulates their final maturation and ovulation (Liley and Stacey, 1983). Hydration of oocytes is known to occur just a few hours before ovulation for some species (Clarke, 1987), however final oocyte maturation and ovulation are not always associated (Nagahama, 1983). Failure in observing hydrated oocytes in mature female gonads during the spawning season led Smith (1965) and Moe (1969) to conclude that ovulation quickly followed maturation for *Cephalopholis fulva* and *Epinephelus morio* respectively. Goeden (1978) did not observe any hydrated oocyte within the ovarian lumen of female *P. leopardus* and similarly concluded that those were rapidly ovulated. In contrast, hydrated oocytes were present in 40% of the gonads of ripe female *P. leopardus* observed during the spawning season in the Townsville and Lizard Island regions. The absence of hydrated stages within the ovarian lamellae of *P. leopardus* reported by Goeden (1978) is probably related to small sample size, as only 34 ripe females were examined.

Samoilys and Squire (1994) monitored spawning aggregations of coral trout on the northern Great Barrier Reef and observed that spawning rushes were restricted to a 22-min period around sunset. In the present study, although hydrated oocytes were observed in females caught during the morning and early afternoon, running-ripe females were only caught in the late afternoon, suggesting that hydration can occur as early as 7 to 8 h before ovulation.

Samoilys and Squire (1994) also described that fish density in the spawning aggregations peaked during the new moon. This lunar periodicity has been associated with increased egg survival, through quick dispersal by strong tidal flows (Johannes, 1978), or with the necessity to synchronize adult activity (Colin et al., 1987). Females with hydrated oocytes within the lamellae were observed during all moon phases. Hence, it seems that although spawning activity may peak at a certain moon phase (Samoilys and Squire, 1994), spawning also occurs throughout most of the spawning season.

An inverse relationship between fat and gonad weight was observed for the coral trout, indicating that these deposits of mesenteric fat are probably being used in the processing of gonad products. A similar pattern has been observed for the Baltic Herring (Rajasilta, 1992). Male GSIs were much lower than female GSIs, but no differences were observed in the amounts of fat stored. It is possible that males and females present similar energy requirements, as males remain reproductively active for longer periods in the season and probably become involved in more spawning episodes than females.

**Protogynous Hermaphroditism.**—As reviewed by Sadovy and Shapiro (1987), a series of characteristics that have been used as indicative of protogynous hermaphroditism require careful assessment before concluding on the mode of reproduction of a species. The presence of a vestigial lumen and dorsal sperm sinuses in male gonads is not necessarily an indicator of functional hermaphroditism, as their presence, as well as remnant ovarian tissue, can result from juvenile hermaphroditism or bisexuality (Sadovy and Shapiro, 1987; Ebisawa, 1990). Therefore, only the occurrence of developing sperm crypts in the presence of degenerating mature, ripe female tissue is conclusive evidence of functional protogynous hermaphroditism. Such evidence was found for coral trout, where crypts of spermatocytes, spermatids and spermatozoa were observed in spent female gonads.

In the *Epinephelus* type gonad (sensu Smith, 1965), where the female and male tissues are intermingled, the development of precocious sperm crypts in immature and mature female ovaries seems to be a widespread phenomenon (Smith, 1965;
Moe, 1969). Developing sperm crypts were observed in the ovaries of some female coral trout, but their development did not seem to interfere with the spawning process, as no degeneration of the vitellogenic oocytes was observed. Smith (1965) also observed sperm crypts in ovaries of ripe females of *Cephalopholis fulva* and *Petrometopon cruentatus* and concluded that they did not interfere with spawning.

It is not clear if the development of sperm tissue in gonads of ripe females will proceed into sex change following the spawning season. However, for several species of Serranidae, it has been suggested that sex-transition is initiated immediately after spawning (Smith, 1965; Moe, 1969; Shapiro, 1984; Sadovy and Shapiro, 1987). In fact, sex transition was observed in spent gonads of female coral trout. As the coral trout is a multiple spawner, it is possible that development of sperm tissue is initiated in a ripe female after an early spawning event, and continues while the ovary is preparing for the next. The presence of fragmenting previtellogenic oocytes, observed in the ovaries of these ripe females, also seems to confirm this hypothesis.

The process of sex-transition can apparently be completed within the same spawning season, as indicated by the presence of degenerating yolk oocytes in the gonads of young males. However, transitional individuals with gonads largely ovarian and no sperm sinuses were observed outside the spawning season. So, the sex-transition process in the coral trout can either take a variable length of time to be completed, or it can be initiated year-round. The reasons for this variability may be related to the factors influencing sex change.

**Population Structure and Mechanisms Determining Sex change.**—In theory, sex-reversal may be induced by developmental or environmental (physical or social) causes (Sadovy and Shapiro, 1987). Social induction of sex-change is known or claimed for many species of fish, but behaviorally induced sex change has not yet been successfully proven for groupers (Shapiro, 1987).

Size and age of mature females were significantly lower than those for males in both geographic samples. This expected consequence of protogynous hermaphroditism has been interpreted as an indication that sex change is a developmental process, initiated endogenously when females attain a certain size and age (Smith, 1965; Moe, 1969). Alternatively, Shapiro and Lubbock (1980) formulated a model suggesting that this characteristic population structure could equally be explained if sex change was controlled mainly by social processes, where a decline in the level of male-female interactions would cause female-to-male sex change.

The sex-ratio indicated a slightly higher proportion of females in the Townsville sample than in the Lizard Island sample. However, there were proportionally more transitional and young male stages in the Townsville sample. Development of sperm crypts in the ovaries of ripe females was observed only in the Townsville sample. It is possible that the reefs off Townsville are subject to a greater fishing pressure than the reefs around Lizard Island, due to proximity to populated areas (Craik et al., 1989). If so, it is possible that the selective removal of larger individuals (presumably mostly males) is triggering sex change as a form of compensatory mechanism.

The coral trout, like other species of groupers (Shapiro, 1987), is known to aggregate at specific sites during its spawning season (Johannes, 1978; Samoilys and Squire, 1994), and it has been suggested that social interactions occurring during these aggregations would be important for the determination of the distri-
bution of sexes in such populations (Shapiro, 1987; Gilmore and Jones, 1992; Samoilys and Squire, 1994).

Distribution of size and age of male and female coral trout overlapped over a wide range of sizes and ages. Several factors could be contributing to the occurrence of such extensive overlap. Among those are the occurrence of prematurational sex change, presence of "primary females" (Warner and Robertson, 1978) that never change sex, and variation in the size at sex change among sub-populations that have been pooled. All these alternatives are likely to apply in the case of the coral trout. Pre-maturational sex change was indicated by the occurrence of young fish in the transitional, young and mature male stages. Histological observation of gonads indicated that some of those individuals did not seem to have spawned as females before changing sex. The occurrence of females that never change sex is possible, as large and old females were observed in the samples analyzed. However, this species seems to be able to attain older ages, as observed by Loubens (1980) in New Caledonia. Collection of individuals in the upper limits of ages would be necessary to test this hypothesis. Finally, both Townsville and Lizard Island samples are likely to contain elements from different sub-populations within the two locations. In this case, if sex change is behaviorally induced and different mechanisms are operating in each sub-population, great variability in size and age at sex change would be expected in the pooled sample.

While at the present it is not clear how sex change is determined for the coral trout, the variability observed in the size and age in which sex change occurs and in the process of transition itself suggests that behavioral processes could be involved. If so, factors such as recruitment variability and fishing mortality are likely to influence the social structure of the spawning population, and therefore the distribution of sexes in coral trout populations.

A major question arises regarding the effect of fishing in relation to such social structures. Even if sex change is stimulated by social conditions assessed during spawning how fast and effectively can the population adjust if its structure is being changed continuously?

Gilmore and Jones (1992) pointed out that an undisturbed population of groupers would contain large numbers of old, sexually active and highly fecund females. Dominant males would fertilize an extraordinary number of ova passing their genotypes to entire generations of offspring. Removal of dominant males in a natural scale would be compensated by female sex change, but would this replacement be effective under constant fishing pressure?

Considering the difficulties in answering those questions, Gilmore and Jones (1992) proposed closure to fishing during the spawning season to protect grouper populations in Florida. The Plan Development Team (1990) argued for fisheries reserves, totally protected areas that would have the important advantage of protecting the genetic variability of the populations.

In conclusion, the coral trout Plectropomus leopardus is a protogynous hermaphrodite in which sex change is probably governed by both developmental and behavioral processes. Population sex structure is a result of the interaction between factors such as recruitment variability and social structure of the spawning population. More information on behavioral aspects of coral trout reproduction is still necessary to understand the precise mechanisms operating in these populations. At the present point, management decisions should include measures to preserve populations in their natural state.
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LITERATURE CITED


FERREIRA: PLECTROPOMUS LEOPARDUS REPRODUCTION


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