Some aspects of reproduction and sexuality in the spotcheek emperor, *Lethrinus rubrioperculatus*, in waters off the Ryukyu Islands

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Abstract The reproductive cycle and sexuality of *Lethrinus rubrioperculatus* in waters off Okinawa and Yaeyama were studied. The spawning period extended from April to December off Okinawa, but only until August off Yaeyama. Sexual maturation in the species started at about 20 cm FL, being completed in females at 26 cm FL. Spawning intervals were estimated as between 1.0 and 1.52 days from May to October. FL-batch fecundity relationships were also estimated. The species exhibited protogynous hermaphroditism. The smallest male and largest female were 26.4 cm and 41.9 cm FL, respectively, off Okinawa, and 29.2 cm and 32.8 cm FL, respectively, off Yaeyama.

Key words. — Lethrinidae; reproduction; hermaphroditism; batch fecundity.

The spotcheek emperor, *Lethrinus rubrioperculatus*, is an important target species of the line fishery off Okinawa, being included with other lethrinid species found in the Okinawa market (drab emperor [*L.* sp.2 in Carpenter and Allen, 1989], *L. semicinctus*, *L. genivittatus*, *L. harak*, *L. obsoletus*, *L. xanthochilus* and *L. amboinensis*) under the local name "muru." The total landing of muru in 1993 was about 70 t (catch statistics of Okinawa Pref. Fish. Exp. Stn.), some 50% comprising *L. rubrioperculatus* and *L.* sp.2. The former is more abundant than *L.* sp.2 in about 50% of the local fishing grounds around Okinawa Island (Ebisawa, 1996), the length range of individuals caught by the line fishery being between 18 and 43 cm FL. *L. rubrioperculatus* is seldom caught by other methods.

Biological information on *L. rubrioperculatus* is limited (Young and Martin, 1982), since the species has often been confused with the adult form of *L. variegatus* (Sato, 1978; Carpenter and Allen, 1989). A number of literature accounts of, purportedly, *L. variegatus* in fact correspond to *L. rubrioperculatus* (Loubens, 1978, 1980a, b; Nzioka, 1979). Some aspects, including growth, spawning season and sex-related age composition of the species have been reported for a New Caledonian population (Loubens, 1980a, b). The spawning season of *L. rubrioperculatus* has also been reported from east Africa, from 2–10°S (Nzioka, 1979). Evidence of protogynous hermaphroditism of lethrinid fishes, including *L. rubrioperculatus*, has been reported from northwestern Australia (Young and Martin, 1982).

Total population fertility, an indicator of the reproductive strength of a population, defined as the number of eggs spawned in one year by the population, is controlled by several factors, such as length of the spawning period, spawning frequency during that period, batch fecundity of individuals, number of females in the population and length or age composition of the female.

Many species have undergone changes in some of these factors as the population fertility has stabilized following decreases in stock numbers (Rijnsdorp, 1991; Koslow et al., 1995). A comparison between two populations, under different exploitation pressures, indicates how the species has adapted to lower stock numbers. The Yaeyama *L. rubrioperculatus* population underwent lower exploitation than the Okinawa population during the years of this study, although catch statistics were limited. The spawning season, batch fecundity and sexuality are reported for and compared between the Okinawa and Yaeyama populations.

Materials and Methods

Specimens were collected during the period from 1984 to 1988, mainly by purchase from commercial fishermen (Itoman Fishery Cooperative) conducting a bottom long line fishery and partly by capture on R/V *Kuroshio* and R/V *Tonan*. A total of 753 specimens were thus collected from waters around Okinawa and adjacent islands and 156 from Yaeyama waters. Fork length, body length, body weight, sex and gonad weight of each specimen were recorded. Gonads were kept in formalin or Bouin's solution. Ovaries obtained from Okinawan specimens were embedded in either paraffin or celoidin for histological observations. Gonad somatic index (GSI) is expressed as the percentage of gonad weight against body weight. Stages of oocyte development were determined from the histological preparations. Following Yamamoto (1956), the stages were classified into early peri-nucleolus, late peri-nucleolus, yolk vesicle, primary yolk globule, secondary yolk globule, tertiary yolk globule, migratory nucleus, pre-maturation, maturation and ripe egg stages. However, some of these were combined and re-named as follows in the analysis: Peri-nucleolus stage for the early and late peri-nucleolus stages; yolk globule stage for the primary to tertiary yolk globule stages; and hydrated stage for the migratory nucleus to ripe egg stages. The maturity stage of each ovary was determined according to the most advanced oocytes. An atretic ovary was defined as one in which atresia was observed in more than 70% of oocytes in the most advanced stage. Batch fecundity was determined from ovaries belonging to either pre-maturation or maturation stages for Okinawan specimen. Batch fecundity of Yaeyama specimens, for which histological preparations were not available, was determined from ovaries in pre-maturation/maturation stages judged from their external appearance (hydrated oocytes visible and scattered uniformly throughout entire ovary with no sign of ovulation). Oocytes in both pre-maturation and maturation stages were collected by filtering the sample through either 400 μm or 450 μm nylon mesh and counted. The batch fecundity was calculated using the following equation.

$$Bf = (gw/sw) \times fn$$

where Bf is batch fecundity; gw, gonad weight with the ovarian wall removed; sw, sample weight of the gonad; and fn, the number of pre-maturation or maturation stage oocytes in the sample. The procedure for oocyte isolation followed Ebisawa (1990). Analysis of covariance (ANCOVA, Snedecor and Cochran, 1980) was applied to compare FL-batch fecundity relationships. Spawning intervals were calculated by dividing the total number of mature ovaries, which included tertiary yolk globule to ripe egg stages, by the number of ovaries bearing post-ovulatory follicles (POF) in each month (Hunter et al., 1986). Monthly group maturation ratios were calculated by dividing the number of females with mature ovaries by the total number of females. Condition factor was calculated by BW/FL^3 (g/cm^3). Water temperatures of the Okinawan area were reproduced from the average data at St. 9, depth 0 m and 50 m, from 1984 to 1987 of the so-called "Okinawa Nanbu Engan Teisen," oceanographic observations carried out in southern waters off Okinawa Island (Motonaga et al., 1986, 1987; Motonaga and Kyan, 1988; Motonaga and Kanashiro, 1989). Typical habitat and depth ranges of *Lethrinus rubrioperculatus* extend beyond 50 meters. Water temperatures in the Yaeyama area were reproduced from the average surface water temperatures inside the reef of Kabira Bay from 1981 to 1985 (Murakoshi et al., 1987). Names of the lethrinid species in this paper follow Carpenter and Allen (1989).

Results

Monthly changes of maturation

Transitions in GSI from both Okinawa and Yaeyama are shown in Figure 1. Yaeyama specimens were collected only from June to September. Monthly changes in ovarian maturity stages in Okinawan specimens are shown in Figure 2. In the Okinawan specimens, the GSI's of females began to increase from mid April and remained high until late October, before suddenly decreasing and remaining low until March. The GSI's of males were high from mid May to late July and low in the remaining months. The magnitude of changes in male GSI was considerably less than that in females. In the transition between maturity stages in females, ovaries at the peri-nucleolus stage appeared from October to January, but at a low frequency. Ovaries at the yolk vesicle stage appeared from October to May (and July), the frequency being greater than 50% in February and March. Ovaries at the yolk globule stage

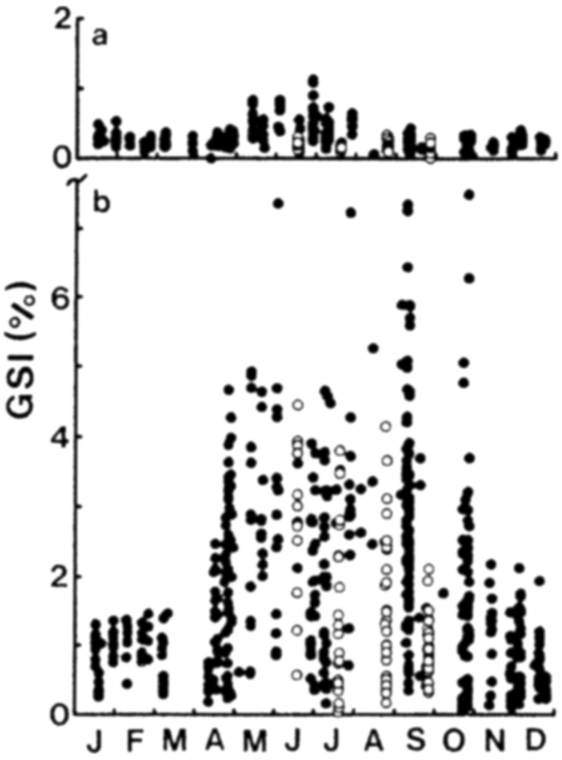

Fig. 1. Monthly changes in GSI of a) male and b) female from Okinawa (solid dots) and Yaeyama (open dots) waters.

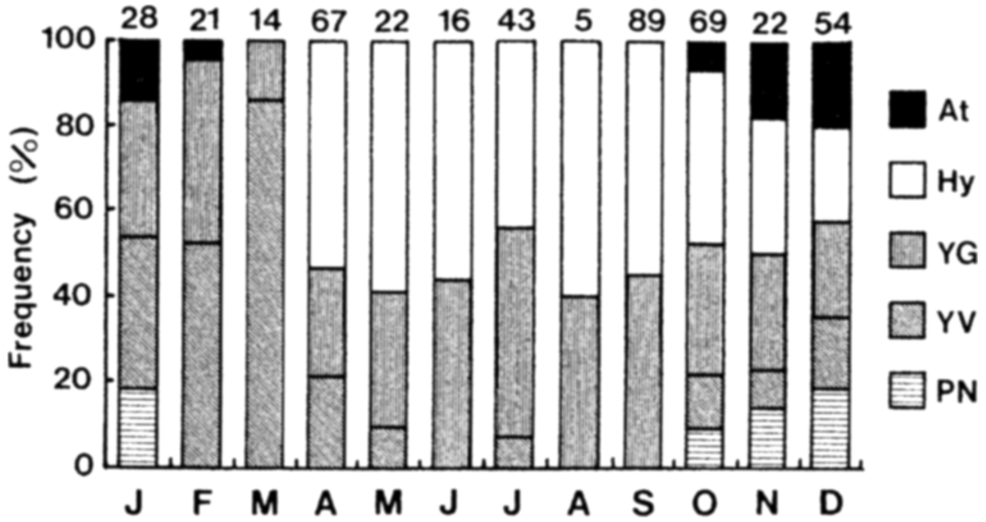

Fig. 2. Monthly changes in maturity stages of ovaries. *PN*—peri-nucleolus stage; *YV*—yolk vesicle stage; *YG*—yolk globule stage; *Hy*—hydrated stage; *At*—atresia. Number of samples given above each column.

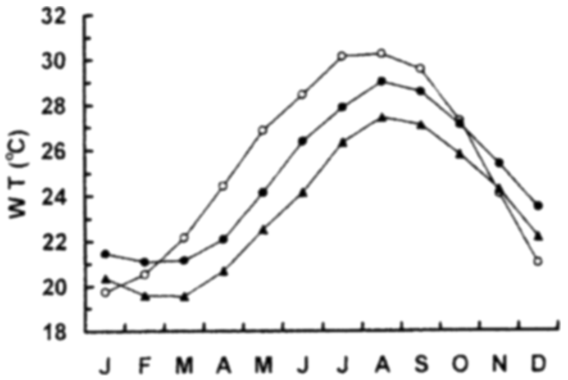

Fig. 3. Monthly changes in surface (solid dots) and 50 m depth (triangles) water temperature at Okinawa (from Motonaga et al., 1986, 1987; Motonaga and Kyan, 1988; Motonaga and Kanashiro, 1989) and surface water temperatures (open dots) at Yaeyama (from Murakoshi et al., 1987).

appeared every month and at the hydrated stage from April to December. Atretic ovaries appeared from October to February. In Yaeyama specimens, GSI's of females were high from June to August and decreased in September. GSI's of males were lower in July than in the other three months, although the magnitude of the change was small.

Spawning intervals and group maturation ratios of the Okinawa population in each month are given in Table 1. Intervals were not calculated from January to March and in December, since POF was not observed in any ovaries at those times. However, the occurrence of hydrated stage ovaries in December indicated that some proportion of the females spawned in December. Thus, spawning of the population in Okinawan waters started in April and was fully active from May to September, becaming gradually less active toward December and being inactive from January to March, although yolked oocytes existed during the last-mentioned period.

Monthly changes in water temperatures are shown in Figure 3. Water temperatures at 50 m depth off Okinawa began to rise after March (lowest temperatures recorded), peaking in August. The surface water temperatures off Yaeyama peaked in August, after their minimum levels in January. The decreases in water temperature off Yaeyama were more drastic than the surface temperature changes off Okinawa, because the former were measured inside the reef while the latter were taken offshore. Trends in temperature changes seemed similar in both areas, although temperatures off Yaeyama were slightly higher and dropped to their lowest level one month earlier. The beginning of the spawning period at Okinawa coincided with the beginning of an increase in water temperature, the latter being near its lowest during the period of no spawning from January to March. Water temper-

Table 1. Spawning intervals based on POF method and group maturation rate in each month

Month	spawning intervals (days)	Group maturation ratio
January	—	0.00
February	—	0.00
March	—	0.00
April	4.67	0.75
May	1.19	0.86
June	1.15	0.88
July	1.27	0.93
August	1.00	1.00
September	1.49	0.99
October	1.52	0.68
November	6.00	0.59
December	—	0.35

Table 2. Number of ovaries with or without POF in each three lunar day period

Lunar days	Number of ovaries bearing POF	Number of ovaries without POF
1–3	14	14
4–6	8	11
7–9	0	4
10–12	5	2
13–15	8	3
16–18	2	11
19–21	21	12
22–24	11	11
25–27	55	18
28–30	2	0

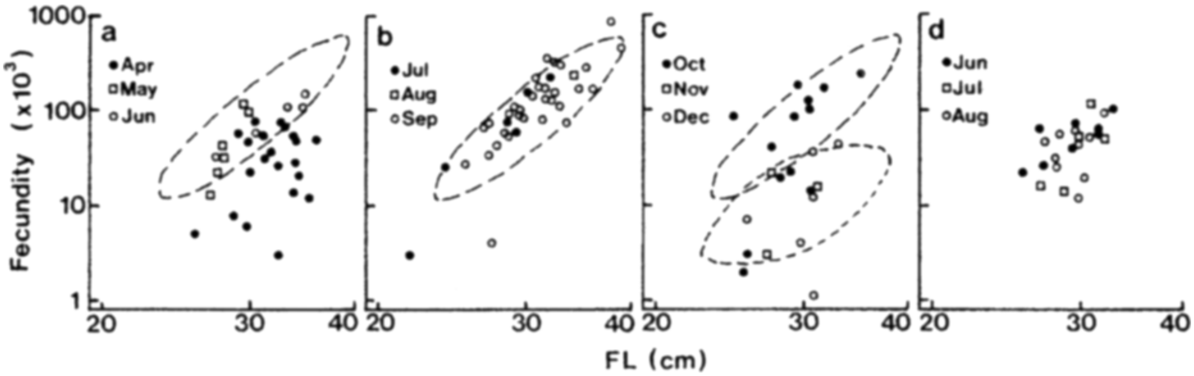

Fig. 4. Fork length-batch fecundity relationships in a) April to June; b) July to September; c) October to December in Okinawa; d) June to August in Yaeyama. For explanation of encircled groups, see text.

atures had just started to decrease in September when rapid GSI decreases were observed in the Yaeyama population.

Spawning with respect to lunar periodicity

The number of ovaries with and without POF obtained in each three lunar day period (shown in Table 2) were counted so as to determine whether or not a relationship between spawning and the lunar cycle existed. Although no sign of spawning was found in the interval including the 7th to 9th lunar day, one hydrated ovary was apparent. Thus, spawning of *Lethrinus rubrioperculatus* had no obvious relationship with the lunar cycle.

Length at sexual maturation

Among females obtained in Okinawan waters, the lengths of immature specimens belonging to the peri-nucleolus stage were between 19 cm and 26 cm FL, while those of matured specimens at the yolk vesicle stage were greater than 20 cm FL, at the yolk globule stage, greater than 22 cm FL, and at the hydrated stage, greater than 21 cm FL (Table 3). No specimens smaller than 18 cm FL were obtained, since fish of this length are rarely caught by the bottom long line fishery. Therefore, beginning at around 20 cm FL, sexual maturation in *L. rubrioperculatus* female was completed by 26 cm FL.

Table 3. Number of individuals at different maturity stages

FL (cm)	Peri-nucleolus	Yolk vesicle	Yolk globule	Hydrated
19.0–19.9	2	0	0	0
20.0–20.9	0	2	0	0
21.0–21.9	5	1	0	1
22.0–22.9	4	1	3	0
23.0–23.9	5	7	0	1
24.0–24.9	4	4	2	2
25.0–25.9	1	11	5	7
26.0–26.9	3	8	4	6
27.0–27.9	0	8	9	15
28.0–28.9	0	4	14	17
29.0–29.9	0	1	13	28
30.0–	0	25	73	90

Batch fecundity

FL-batch fecundity relationships from April to December (Okinawan samples) and from June to August (Yaeyama samples) are plotted in Figure 4. Batch fecundity was lower and the variance in the relationships greater in April than in later months. Most of the plots from May to September (and a portion of those in October) are located in a confined range. The remaining October samples, which had lower fecundity, were confined within a limited range together with those for November and December. The Yaeyama plots were also limited to a narrow range. ANCOVA comparisons applied to Okinawan monthly data from May to September indicated that the slopes and adjusted means were not significantly different, unlike the variances (Table 4). The slopes, adjusted means and variances were not significantly different between either the November and December Okinawan samples or the June to August Yaeyama samples. ANCOVA comparisons between Okinawan (May–September) and Yaeyama (June–August) samples showed the adjusted mean of the former to be significantly higher, although slopes and variances did not differ. Parameters for the FL-batch fecundity relationships grouped after the ANCOVA results are listed in Table 5. The regressions for April and November/December for the Okinawan samples were insignificant.

Sexuality

L. rubrioperculatus exhibited protogynous hermaphroditism. Although the length distributions of both sexes had a relatively wide overlap in the specimens from Okinawa, a distinctive difference in modal lengths was observed (Table 6). The smallest male specimen was 26.4 cm FL,

Table 4. F values in comparisons of fork length - batch fecundity relationships; numbers in parentheses indicate degrees of freedom (d.f.), first number in parentheses incicates d.f. of mean square in numerator

	Variance	Equality of slopes	Equality of adjusted means
Okinawa			
May through September	*9.13 (3) **2	2.188 (3, 42) ns	1.629 (3, 45) ns
November vs. December	1.23 (4, 1) ns	0.00076 (1, 5) ns	0.153 (1, 6) ns
Yaeyama			
June through August	*2.47 (2) ns	1.108 (2, 18) ns	1.166 (2, 20) ns
May to September in Okinawa vs. June to August in Yaeyama	1.13 (49, 22) ns	2.782 (1, 71) ns	8.919 (1, 72) **1

* Bartlett's chi-square test; **1 at 1%, **2 at 5% significance level.

Table 5. Parameters determining fork length (cm) - batch fecundity (eggs) relationships (batch fecundity=$a\times FL^{b}$)

	a	b	r^2	*n*
Okinawa				
April	1.243×10^{-1}	3.535	0.0874 ns	21
May–September	3.828×10^{-7}	7.652	0.684 *1	51
October	9.642×10^{-11}	10.01	0.403 *2	13
November–December	2.253×10^{-3}	4.495	0.089 ns	9
Yaeyama				
June–August	1.290×10^{-2}	4.44	0.235 *2	24

*1 at 1%, *2 at 5% in significance level with (n-2) degree of freedom.

which was larger than the range of maturing females. The largest female was 41.9 cm FL, which was slightly smaller than the largest male. Sexually transitional specimens were obtained in the area of overlap, the latter being narrower for specimens from Yaeyama. The smallest male and the largest female from Yaeyama were 29.2 cm FL and 32.8 cm FL, respectively. Thus, sexual transition in *L. rubrioperculatus* was post-maturational.

Sexual transition of the gonads of *L. rubrioperculatus* is categorized as "Undelimited type-II", according to Sadovy and Shapiro (1987). During the transition from ovary (Fig. 5a) to testis, the latter possessing a cavity derived from the ovarian lumen (Fig. 5b), testicular cells were observed among the decaying oocytes (Fig. 5c, d). The transition started with the absorption of the oocytes. Concurrently or successively spermatogenesis began in the ex-ovarian lamellae. The gonadal wall contracted and thickened due to the decrease in mass of gonadal tissue. Testis, just after the completion of the transition, were characterized by a thick gonadal wall (Fig. 5e), undeveloped lamellae and numerous brown bodies (Fig. 5f).

Sexually transitional gonads were obtained all year round. Nine transitional gonads were obtained in all, one specimen each in February, March, April, July and October, and two each in September and December. Nine males just after sexual transition were obtained, one in April, three in September and five in December. Since two specimens out of the 18 were obtained during the inactive spawning period, from January to March, and the remaining 16 during the active spawning period, sexual transition in the species apparently occurs irrespective of the spawning cycle.

Other biological parameters and comparison of maturity factors

The relationships of both FL (cm) -BL (cm) and FL (cm) -BW (g) were obtained as follows.

$$BL=-0.287\times 0.899\times FL \quad (r^2=0.997)$$

$$BW=0.01768\times FL^{3.028} \quad (r^2=0.988)$$

Condition factors in both Okinawan and Yaeyama samples showed no significant difference between those areas in the same month (June: $t=2.9541$, d.f.$=85$, $p>0.05$; July: $t=1.8829$, d.f.$=116$, $p>0.05$; August: $t=0.0949$, d.f.$=60$, $p>0.05$; September: $t=0.0583$, d.f.$=175$, $p>0.05$).

Table 6. Number of individuals examined by sex

FL (cm)	Okinawa			Yaeyama	
	female	transitional	male	female	male
18–19.9	3	0	0	1	0
20–21.9	11	0	0	3	0
22–23.9	35	0	0	10	0
24–25.9	53	0	0	17	0
26–27.9	72	0	2	23	0
28–29.9	98	3	17	20	3
30–31.9	98	0	24	12	19
32–33.9	85	3	46	6	15
34–35.9	37	2	75	0	20
36–37.9	14	1	52	0	6
38–39.9	3	0	13	0	1
40–41.9	3	0	2	0	0
42–43.9	0	0	1	0	0
Total	512	9	232	92	64

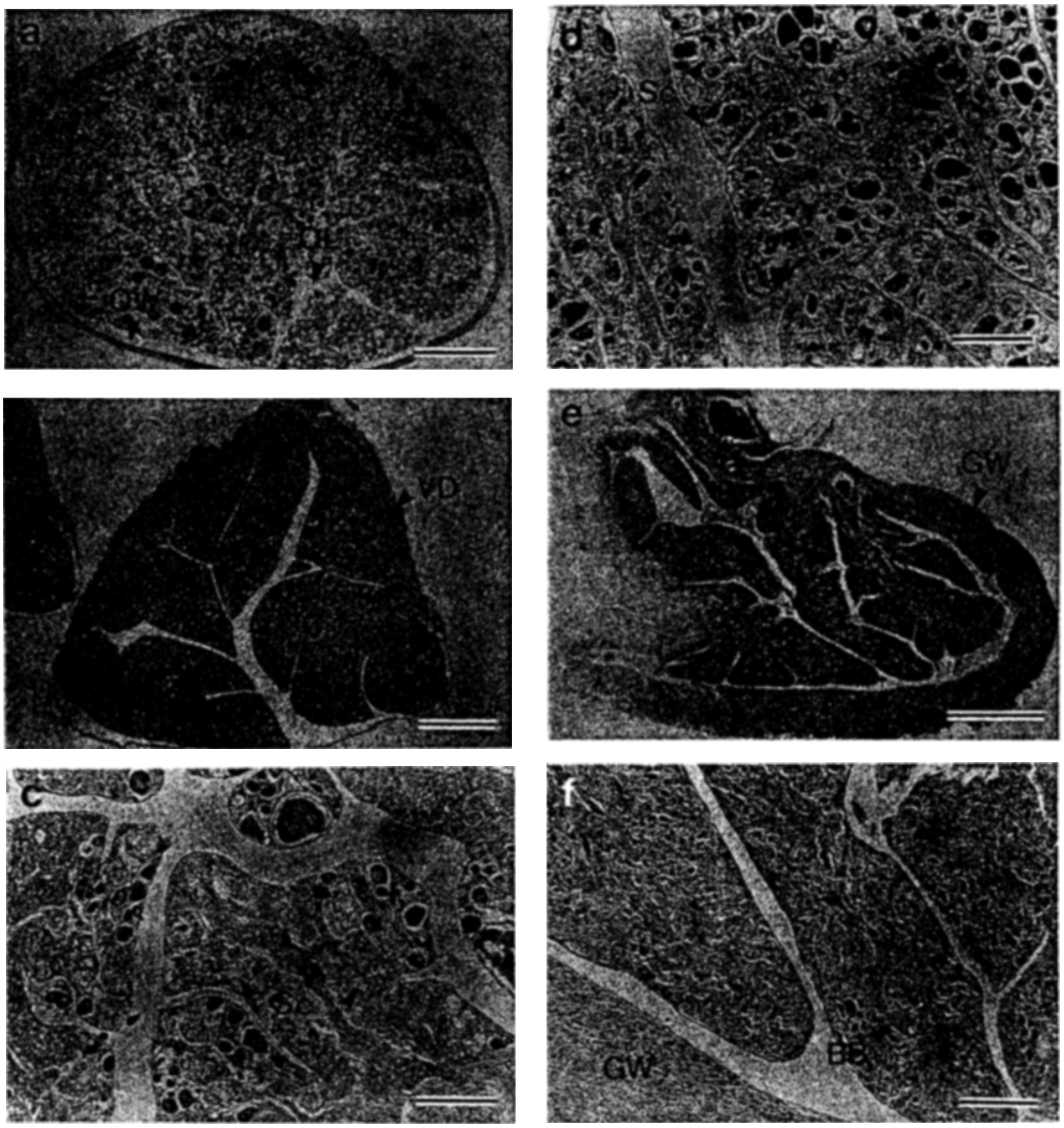

Fig. 5. Histological appearance of gonads. a) Transverse section of late peri-nucleolus stage ovary, 24.8 cm FL, February 10, 1987; b) transverse section of testis, 29.1 cm FL, July 8, 1986; c) transitional gonad with residual oocytes and spermatogenetic cells, 28.0 cm FL, July 12, 1984; d) transitional gonad with spermatocytes and numerous residual oocytes, 33.2 cm FL, March 6, 1987; e) transverse section of testis just after completion of sexual transition, showing thickened gonadal wall and undeveloped lamellae, 31.5 cm FL, April 16, 1985; f) higher magnification of e) visualizing brown bodies. a), b) and e) scale bar=1 mm; c), d) and f) scale bar=200 μm. *BB*—brown body; *CC*—central cavity; *GW*—gonadal wall; *OL*—ovarian lumen; *OW*—ovarian wall; *Sc*—spermatocytes; *VD*—vas deferens.

Discussion

The differences in spawning periods between the Okinawan and Yaeyama populations were probably caused not by differences in the water temperature but by other factors. Although the onset of spawning at Yaeyama could not be determined from the present data, it probably occurred in April, since some other co-existing lethrinid species start to spawn from late March–April (Ebisawa, in prep.). The decrease in GSI to around 1%, observed in September at Yaeyama, corresponded to that in November at Okinawa. Thus the end of the spawning period at Yaeyama is two months earlier than at Okinawa. The differences in water temperatures between the two areas included: 1) maximum temperature slightly higher at Yaeyama, and 2) lowest temperature attained possibly one month earlier at Yaeyama. These differences are not sufficient to explain the differences in the spawning periods, although other factors could not be determined.

Lethrinus rubrioperculatus in New Caledonia spawns from October to March (Loubens, 1980 a), one month longer than the Yaeyama population. Environmental changes, such as water temperature and photoperiod transition, from October to March in the southern hemisphere correspond to those from April to September in the northern hemisphere. Ripe specimens have been obtained in January, February, August and October in east Africa, from between 2–8°S in latitude (Nzioka, 1979). Although the water temperatures and other environmental conditions were not given for these areas, the spawning period of *L. rubrioperculatus* seems to be relatively long.

The genus *Lethrinus* is either protogynous (Lebeau and Cueff, 1975; Loubens, 1980a; Young and Martin, 1982) or exhibits juvenile hermaphroditism (Ebisawa, 1990). *L. rubrioperculatus* exhibits protogynous hermaphroditism. In New Caledonia, a small number of males were included in the length class 180–219 mm SL (smallest 202 mm SL) (Loubens, 1980a), corresponding to 20.3–24.8 cm FL and 22.8 cm FL, respectively. The minimum length of matured females recorded was 175 mm SL (19.8 cm FL), that is, smaller than the smallest male; hence the species is protogynous in New Caledonia. However, some discrepancies, such as length of the smallest male and maximum length of both male and female, between Okinawa and New Caledonia were found and are indicated in Table 7.

L. rubrioperculatus is likely to spawn in pairs. The GSI's of males were considerably lower than that of females in both Okinawa and New Caledonia (Loubens, 1980 a). In some other lethrinid species known to form large spawning aggregations, such as *L. nebulosus* and *L. atkinsonii*, the GSI's of males were as high as that of females (Ebisawa, 1990; Ebisawa, in prep.). In other families, such as Scaridae and Labridae, the size of the testicular mass is closely related to their mating system, equal male and female GSI's indicating a group spawning habit, wheras lower male GSI's indicate a pair spawning habit (Robertson and Choat, 1974; Robertson and Warner, 1978; Warner and Robertson, 1978; Nemtzov, 1985). Unlike species inhabiting shallow waters, where their reproductive activities are observable, the activities of deeper water species are unknown. The testicular mass in protogynous hermaphrodites is generally smaller than that of the ovary in females (Nagelkerken, 1979; Loubens, 1980a; Ross and Merriner, 1983). Male mating success would be determined by the energy balance between production of sperm and body growth, more sperm and larger body size being advantageous. In some species body size is emphasised so as to defend a territory, the lower sperm production being offset by more efficient spawning. Other species are characterized by high sperm production and group spawning. *L. rubrioperculatus* probably belongs to the former, although territoriality and spawning behavior have not yet been observed.

Spawning intervals can be calculated from the

Table 7. Ranges of fork length (cm) for each sex in different areas

	Okinawa	Yaeyama	New Caledonia*
Smallest male	26.4	29.2	22.8
Largest male	42.4	38.6	39.0
Smallest matured female	21.9	23.8	19.8
Largest female	41.9	32.8	40.1

* Loubens (1980b).

proportion of hydrated versus matured ovaries (Demartini and Fountain, 1981), the method being inapplicable in the present study for the following reason. *L. rubrioperculatus* are more or less equally catchable in daytime and at night (Ebisawa, 1988). For most of the specimens obtained from commercial fishermen for this study, the time of catch was unable to be specified. Specimens obtained between spawning and the start of the maturation phase show no sign of spawning, even if such would have occurred in the following 24 hours (Hourigan and Kelley, 1985; Matsuyama et al., 1988). Thus any estimation of spawning interval would be positively biased. On the other hand, POF estimates also include a possible bias when the longevity of POF is less than 24 hours. Preliminary observations indicated that decaying POF often occurred in the maturation stage ovary, with one female (in September) possessing simultaneously newly-formed and decaying POF. Therefore it was concluded that the longevity of POF is about 24 hours, thus excluding any possible bias when estimating the spawning interval.

Spawning intervals determined in this study included one contradiction. The intervals from May to October, calculated as one day, seemed reasonable. The intervals calculated were longer in April and November, although relatively high numbers of hydrated ovaries were recorded. No signs of spawning were evident in December by the POF estimate, although some hydrated ovaries were found. This is probably explained by the catchability of maturation phase females being higher than that of other females. The latter could result from the species forming spawning aggregations, resulting in more intensive fishing and a greater likelihood of capture. However, this contradicts the likelihood of the species reproducing by "pair spawning within a territory" (see above). Further information on reproductive behavior is necessary.

Fecundity-FL relationships are often different in different areas and in different years (Rijnsdorp, 1991; Wright, 1992; Koslow et al., 1995; Milton et al., 1995), one of the reasons being thought to be differences in food availability. High food availability increased fecundity in *Melanogrammus aeglefinus* in an experimental study (Hislop et al., 1978). In *Hoplostethus atlanticus*, fecundity adjusted by standard length increased by about 20%, corresponding to stock decreases of about 50% owing to fishery pressures (Koslow et al., 1995). In addition, the proportion of non-spawners (i.e. adult fish with undeveloped gonads) in that species declined, corresponding to the stock decreases. These results were probably due to increased food availability, since a positive correlation between condition factor and fecundity was found. In the case of lethrinid species, the cumulative effects of high food availability led to improve body condition and prolonged spawning period in captive *L. nebulosus*, although changes in batch fecundity adjusted for size were unknown (Ebisawa, 1990). The condition factors of both the Okinawan and Yaeyama populations of *L. rubrioperculatus* were not significantly different, indicating similar food availability in both areas. Therefore, other factors, which caused the difference in batch fecundity, may exist.

Many tropical species are known to spawn in conjunction with the lunar cycle, including some lethrinids, such as *L. miniatus*, *L. microdon* and *L. harak* (Johannes, 1978; Carpenter and Allen, 1989). On the contrary, *L. rubrioperculatus* (present study) and *L. nebulosus* (Ebisawa, 1990) at Okinawa are non-lunar spawners. Generally, lunar or semi-lunar spawning species inhabit shallow waters (Ross, 1983; Taylor, 1984). Because transportation of eggs and hatched larvae is greatly affected by tidal currents, many species inhabiting shallow waters spawn outside their usual habitat, such as on outer reef slopes and reef edges (Randall and Randall, 1963; Johannes, 1978; Robertson and Warnaer, 1978). Thus eggs and larvae are transported offshore, where predators of both are less abundant (Johannes, 1978; Lobel, 1978). Because the usual habitat and spawning sites of *L. rubrioperculatus* are in deep areas, where predators of eggs and larva are fewer than in shallow areas, tidal effects are less important, as is the lunar cycle by implication.

Sex ratios, length of the spawning periods and batch fecundity adjusted for size differed between the Okinawan and Yaeyama populations of *L. rubrioperculatus*. However, further research is necessary for an understanding of the mechanism by which stock changes of such tropical hermaphroditic species are compensated.

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