

# Life-history traits of eight *Lethrinus* species from two local populations in waters off the Ryukyu Islands

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**Abstract** The number of growth rings was counted on broken and burnt otoliths of eight *Lethrinus* spp. from two local populations: *Lethrinus atkinsoni*, *L. harak*, *L. miniatus*, *L. nebulosus*, *L. obsoletus*, *L. ornatus*, *L. ravus*, and *L. rubrioperculatus*, collected from 1985 to 1996 in waters off the Ryukyu Islands. Growth rings were revealed to be formed annually from about October to June by marginal analysis. In addition to obtaining the three parameters in von Bertalanffy growth equation and the maximum age in specimens, the relationship between age and both ovarian maturity rate and sex ratio (percentage female) was analyzed. The age at 50% of ovarian maturity was the lowest at 1–2 years old in *L. harak*, *L. ravus*, and *L. rubrioperculatus* and was the highest at approximately 4 years old in *L. nebulosus*. The age at which the sex ratio decreased to 50% due to sexual transition from female in protogynous hermaphrodite species was the lowest at 3–4 years old in the *L. atkinsoni* Okinawa population and was the highest at 7–8 years old in *L. miniatus*. The oldest maximum age for specimens was 26 years in *L. nebulosus* and the youngest maximum age was 12 years in *L. ornatus*.

**Keywords** Growth · *Lethrinus* · Otolith · Sex ratio with age · The Ryukyu Islands

## Introduction

Fish of genus *Lethrinus* have been utilized as significant food resources in areas from the western Pacific Ocean to the Indian Ocean because of their dominant catch amount [1]. The genus is a significant fish resource in the Ryukyu Islands, southwest of mainland Japan, as well. Because of their importance, the resources must be rationally utilized. For rational utilization of the fish resources, stock evaluation based on the age component in the catch is necessary. Accordingly, research to reveal the relationship between age and length, in other words “growth study,” is very important.

Growth studies of *Lethrinus* began in the mid-1960s [2] and the number has continued to increase [3–11]. During this period, many studies regarding age determination have revealed that using either a thin sectioned or broken and burnt otolith gives the best accuracy in all age groups, whereas ages determined from the whole otolith, scales, or other calcified tissues might result in a serious underestimation error, especially in older age groups [12–14]. In the case of *Lethrinus* species as well, the maximum ages determined from methods other than sectioned otoliths seem to be underestimates. For example, the oldest age determined from a sectioned otolith in *Lethrinus nebulosus* was 27 years [4], while that from a scale was 14 years [3], and those from vertebrae were 21 years [5] and 6 years [6]. Among the many growth studies in *Lethrinus*, those based on sectioned otoliths are limited [4, 8–11]. Almost all of the studies were limited to the southern hemisphere.

In Okinawa, the reproductive biology and sexual characteristics of eight commercially important *Lethrinus*

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species including two local populations were revealed based on body size [15–18]. The sexuality of the species is either protogynous hermaphroditism [16–20] or juvenile hermaphroditism [15, 17, 18], where sexual differentiation occurs before sexual maturation. As this trait is not species-dependent, the sexuality can differ among populations of the same species [17].

In the eight species, the main habitat of *Lethrinus atkinsoni*, *L. harak*, *L. obsoletus*, and *L. ornatus* is shallow coastal areas where different kinds of fishing gear are used for their capture, and that of *L. miniatus*, *L. rubrioperculatus*, and *L. ravus* is deeper offshore areas where mostly long-line fishing is utilized. The main habitat of *L. nebulosus* is wide and overlaps those of the other seven species. The abundance and the status of the stock differs from species to species [21–23]. In general, species inhabiting shallow coastal areas have suffered decline from various types of fishing gear, and species forming large schools have suffered from strong fishing pressure.

For stock management, stock analysis and stock simulation, which give us keys to choosing a management strategy, are employed [24–26]. These analyses are carried out based on age and age-related parameters, such as age at sexual maturation and sex ratio with age in the hermaphroditic species [27, 28]. Therefore, the age at sexual maturation and the age at sexual transition are to be clarified in parallel with the growth study.

According to earlier analyses [21–23], the rates of stock decreases in *L. rubrioperculatus* and in *L. ravus* in the waters of the Okinawa Island were relatively small, while the decline of *L. miniatus* in the same area was very large. The resilience of the species to fishing seems to be affected not only by the depth of the habitat, and whether or not it forms large schools, but also the species' growth rate, longevity, age at sexual maturation, presence or absence of sexual transition, fertility, main habitat at juvenile stage, length of the period at buoyant fry, and so on. To compare and contrast biological parameters among species studied by the same methods by contrasting their stock status in the same area is meaningful. In addition, to elucidate similar and different biological parameters by comparing different populations of the same species is important for understanding the standardized ecological profile of the species. Developing a species profile is important for providing fundamental knowledge to areas where the resource is rationally to be utilized.

This research, using the same sources of specimens as earlier studies [16–18], reveals the growth and the maximum age using broken and burnt otoliths from two local populations of eight *Lethrinus* species: *Lethrinus atkinsoni*, *L. harak*, *L. miniatus*, *L. nebulosus*, *L. obsoletus*, *L. ornatus*, *L. ravus*, and *L. rubrioperculatus*. The timings of sexual transition and sexual maturation were

re-analyzed based on age. By comparing the results among species within the Ryukyu Islands area, and within species among populations in the southern hemisphere, similar and different ecological profiles have been clarified.

## Materials and methods

### Sources of specimens

The scientific names in this study follow those used by Carpenter [29] and Carpenter and Randall [30]. Periods and locations of the samplings, the number of specimens of each of the eight species, and references describing reproductive and sexual characteristics using the same source of specimens are indicated in Table 1. Specimens of *L. atkinsoni* were sampled from both Okinawa and Yaeyama (Fig. 1), those of *L. nebulosus*, *L. miniatus*, *L. rubrioperculatus*, and *L. ravus* were sampled from Okinawa, and those of *L. harak*, *L. obsoletus*, and *L. ornatus* were sampled from Yaeyama. A total of 478 specimens of *L. nebulosus*, differing from those of Ebisawa [15], were newly collected from April 1994 to January 1996. Fork length ( $L_f$ ), standard length ( $L_s$ ), and body weight were measured to the nearest 0.1 cm and 1 g in each specimen. Gonads were examined histologically to determine the stage of development [15]. Otoliths were kept dry throughout this research.

### Reading procedures

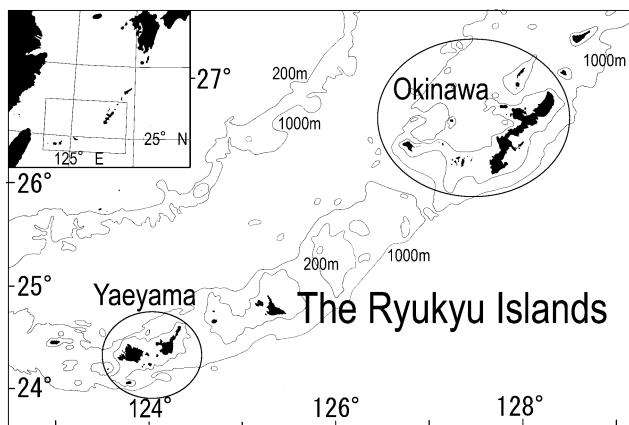
Each otolith was cut along the focus (Fig. 2a), burnt, and covered with oil [31], and then observed under reflected light with a microscope. On a sectioned burnt otolith, opaque bands and brownish translucent bands alternate (Fig. 2b). The brownish translucent band in the area of D1 is employed as the growth ring of the otolith. The number of growth rings was counted twice at separate times on the same otolith by the same reader, with the number at the first reading kept unknown at the second reading, which occurred 10–20 years after the first reading. Otoliths were digitally recorded (1,600 × 1,200 pixels, 24-bit color) at the time of the second reading with a PDMC-I.e Polaroid digital microscope camera. When the numbers of the two readings coincided, the number of growth rings on the otolith was determined. When the numbers did not coincide, two more additional readings by the same reader were carried out, with the previous numbers unknown to the reader. When the numbers of three readings among four agreed, the number of growth rings on the otolith was determined. In other cases, the otolith was excluded from the later analysis.

**Table 1** Locations, periods, and number of *Lethrinus* specimens sampled

Species	Location	Period of sampling	Number of specimens	Spawning period <sup>a</sup>	Reference
<i>Lethrinus atkinsoni</i>	Okinawa	February 1987 to March 1988	451	April to November	Ebisawa [17]
<i>Lethrinus atkinsoni</i>	Yaeyama	October 1988 to August 1992	1,522	March to June	Ebisawa [17]
<i>Lethrinus harak</i>	Yaeyama	August 1988 to March 1992	452	April to November	Ebisawa [18]
<i>Lethrinus miniatus</i>	Okinawa	February 1987 to March 1988	454	April to July	Ebisawa [18]
<i>Lethrinus nebulosus</i>	Okinawa	April 1994 to January 1996	478	March to June <sup>b</sup>	None: newly collected
<i>Lethrinus obsoletus</i>	Yaeyama	July 1988 to March 1992	523	April to October	Ebisawa [18]
<i>Lethrinus ornatus</i>	Yaeyama	April 1989 to May 1992	80	April to November	Ebisawa [18]
<i>Lethrinus ravus</i>	Okinawa	April 1985 to July 1987	241	April to October	Appeared as <i>Lethrinus</i> sp2 in Ebisawa [18]
<i>Lethrinus rubrioperculatus</i>	Okinawa	April 1985 to July 1987	652	April to December	Part of specimens in Ebisawa [16]

<sup>a</sup> The spawning periods are referenced for the determination of the birth month and ovarian maturity rate with age and are based on specimens from the source in the cited studies

<sup>b</sup> After Ebisawa [15]



**Fig. 1** Map of the Ryukyu Islands with 200-m and 1,000-m depth contours. Specimens were obtained in the circled areas of both the Okinawa Islands and Yaeyama Islands

In order to determine the period and frequency of growth-ring formation, the following measurements were carried out using the otolith pictures. The outermost zone was judged to be a growth ring or not on the D1 area of the otolith. In some otoliths, the growth ring bifurcated and the opaque zone was formed at the extension of the original brownish band near the area of D1 (Fig. 2c). In this case, the condition of the outermost zone was impossible to determine. Therefore, for this type of bifurcated and reversed growth-ring otolith, areas D2, D3, and D4 were observed to determine the growth-ring numbers and the condition of the outermost zone. Widths of both the start of the outermost growth ring to the outer edge ( $X_0$ ) and the start of the innermost growth ring to the end of the next opaque edge ( $X_1$ ) were measured in the otolith picture (Fig. 2d). The marginal index was calculated as  $X_0$  divided by  $X_1$ .

#### Determination of age for each individual

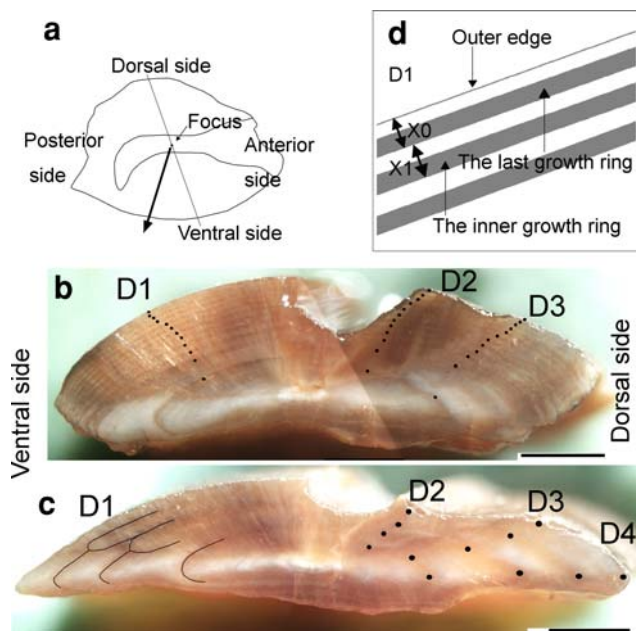
The birth month of the species was considered to be the start month of the spawning period (Table 1). The periodicity of growth-ring formation is described in the “Results” section; the growth rings are formed annually from about October to June. Hence, the birth months fall at the later period of the growth-ring formation. The integer part of the age is determined by the number of growth rings, and the order of birth and sampled months. The decimal part of the age is given by the fraction of a year from birth to sampled month.

#### Statistical analyses

Growth parameters in the von Bertalanffy growth equation are calculated using nonlinear regression (SPSS) for each age and  $L_f$  of the specimens. Growth parameters are estimated combined with sex because most of the species are protogynous hermaphrodites. However, they are also estimated separately for each sex for juvenile hermaphroditic species, i.e., *L. nebulosus* [15], *L. atkinsoni* at Yaeyama [17], and *L. obsoletus* [18], where undifferentiated individuals are included as females and hermaphroditic individuals as males. Analysis of covariance [32] was conducted to examine whether the growth curves between sexes were significantly different.

#### Correspondence of sex and ovarian maturity with age

Mean  $L_f$  and SD were calculated for each sex according to integer age group. Sex ratio ( $R_s$ ) was calculated as the number of females divided by the total number of females, hermaphrodites, and males in the same integer age group.



**Fig. 2** **a** Broken line of otolith. **b** Broken and burnt otolith of *Lethrinus atkinsoni* Yaeyama, sampled 25 April 1992, showing the 12th ring as the outermost. The specimen was female, had an  $L_f$  of 31.1 cm, and weighed 649 g. Growth rings are shown with dots. **c** Broken and burnt otolith of *Lethrinus nebulosus*, sampled 21 May 1994, showing bifurcations of growth zones indicated by lines at area D1. Extensions of the original two growth zones were changed to opaque areas. The specimen was male, had an  $L_f$  of 42.2 cm, and weighed 1,364 g. Growth rings are marked at areas D2 and D4. **d** Schematic diagram for the measurement of  $X_0$  and  $X_1$  in broken and burnt otoliths to calculate marginal index. Scale bars 1 mm

Ovarian maturity rate ( $R_{OM}$ ) was calculated for each species from the histologically examined ovarian stages as the number of ovaries from the primary yolk globule stage to the ripe stage divided by the number of whole ovaries collected during the spawning period for each integer age group.

## Results

### Periods of growth-ring formation

To reveal the timing and periodicity of growth-ring formation, monthly changes in the rates of growth-ring-edged and opaque-band-edged otoliths are shown in Fig. 3. Though there were some temporal changes, the trends for the monthly changes were approximately the same in all eight species from two local populations. That is, almost all otoliths from January to April were growth-ring-edged ones. Opaque-band-edged otoliths began to appear from about May/June, and dominated in July to September/November. Growth-ring-edged otoliths began to appear in October and gradually increased. Thus, growth rings were

determined to be formed once a year from October to June, i.e., autumn to spring.

To show the relationship between the monthly changes of both the outermost condition and the marginal index of otoliths and the determination of age in each specimen, Fig. 4 for *L. atkinsoni* at Yaeyama is drawn as a representative of all eight species. The number of growth rings for groups with one to nine rings are drawn separately and those more than ten are combined as one group in Fig. 4. The changes in outermost conditions correspond to Fig. 3b.

The changes in the marginal indices of the otolith in each ring group were similar. Marginal indices increased gradually from the lowest in October at the first emergence of growth-ring-edged otoliths with average values of about 0.3 on both one- and two-ring groups, and to about 0.8 in the larger ring groups by the following September. In the area of D1 in the otolith, the number of growth rings is usually countable because of the alternate emergence of both growth rings and opaque bands, except for the type of otolith shown in Fig. 2c. The integer part of the age is given by the number of growth rings minus one for the specimens sampled before March, and by the total number of growth rings for those sampled after March (Fig. 4). All other specimens were aged in the same manner as that used for the *L. atkinsoni* Yaeyama population.

Growth parameters, mean size at age, sex ratio, and the maximum ages in specimens

The mean  $L_f$  for each sex and the sex ratio are listed in Table 2, and plots of age and  $L_f$  for all eight species are shown in Figs. 5 and 6. The mean  $L_f$  at each age increased rapidly in the first few years, but had almost ceased by the latter half period in all eight species. The mean  $L_f$  at each age in females was larger by the latter half period than that of males in *L. atkinsoni* and in *L. harak*, and it was smaller in *L. miniatus* and in *L. ornatus*.

In the comparison of growth in juvenile hermaphroditic species, the results for both males and females were significantly different in *L. atkinsoni* Yaeyama ( $P < 0.01$ ) and *L. nebulosus* ( $P < 0.05$ ), whereas the differences were insignificant in *L. obsoletus*. All female specimens obtained were older than either zero or 1 year old, while all males were older than 2 years old except some specimens of 1-year-old males in *L. nebulosus*. The maximum ages of both males and females are summarized in Table 3. The species whose maximum ages in males or females exceeded more than 20 years of age were *L. atkinsoni*, *L. miniatus*, *L. nebulosus*, and *L. obsoletus*, and those less than 15 years of age were *L. harak*, *L. ornatus*, *L. ravus*, and *L. rubrioperculatus*.

Hermaphroditic individuals were obtained in the age range where obvious decreases in sex ratio ( $R_s$ ) were

**Fig. 3** Monthly changes in the rate of growth-ring-edged (filled square) and opaque-band-edged (open square) otoliths in **a** *Lethrinus atkinsoni* from Okinawa, **b** *Lethrinus atkinsoni* from Yaeyama, **c** *Lethrinus harak*, **d** *Lethrinus miniatus*, **e** *Lethrinus nebulosus*, **f** *Lethrinus obsoletus*, **g** *Lethrinus ornatus*, **h** *Lethrinus ravus*, and **i** *Lethrinus rubrioperculatus*

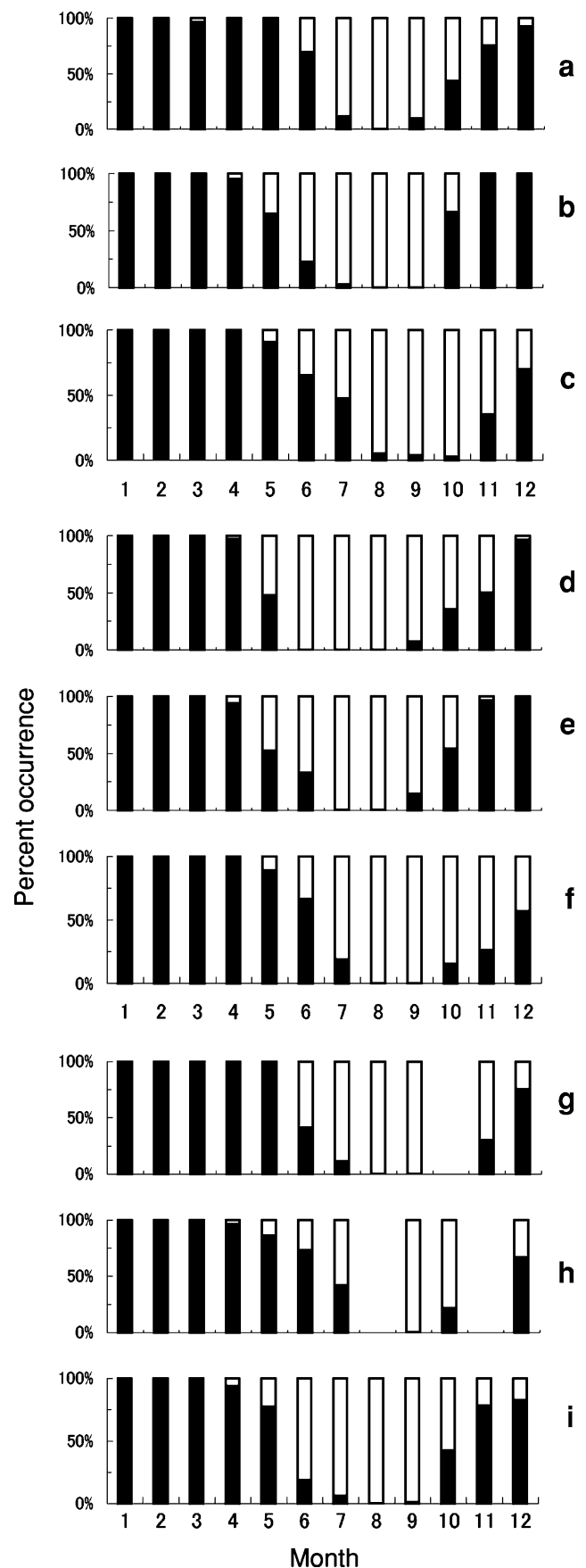
observed in most of the species. Beyond the range in which  $R_s$  is obviously decreasing—between 1 ( $R_s$ : 0.80) and 2 ( $R_s$ : 0.62) years old—hermaphroditic specimens up to 4 years old were obtained in *L. obsoletus*. They were obtained only in the latter half of the period of decreasing  $R_s$  in both *L. ornatus* and *L. ravus*, probably due to the relatively small number of specimens. Age when sex ratio had decreased to 50% ( $A_{RS50}$ ) was between 3 and 4 years old in *L. atkinsoni* Okinawa; about 4 years old in *L. harak*, *L. ornatus*, *L. ravus*, and *L. rubrioperculatus*; about 6 years old in *L. miniatus*; and 2 years old in *L. nebulosus*.  $A_{RS50}$  did not exist in *L. atkinsoni* Yaeyama or in *L. obsoletus* because sex ratios had not decreased to 50%. Growth parameters in the von Bertalanffy equations and the maximum age for specimens of the present research and those from previously reported studies are summarized in Table 3 and will be compared below.

#### Ovarian maturity rate with age

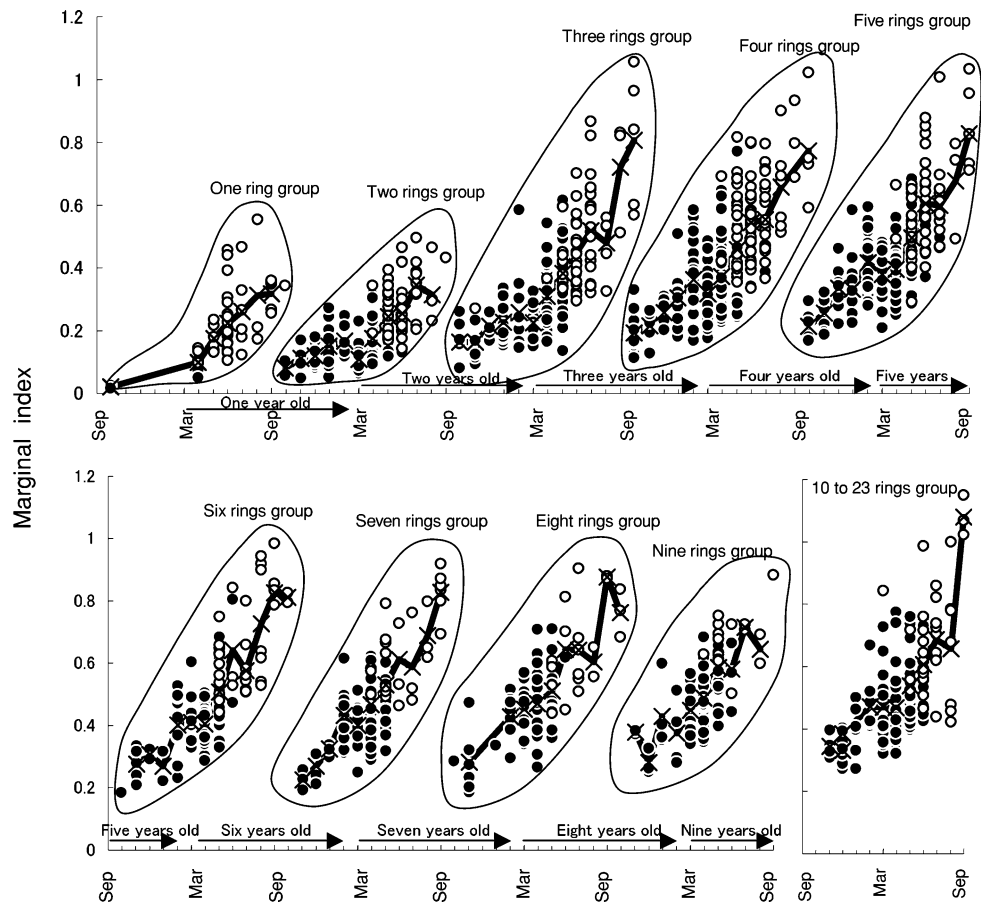
The ovarian maturity rate in each age group (Table 4) indicates that only *L. rubrioperculatus* started to mature from 1 year old; the Okinawa and Yaeyama populations of *L. atkinsoni*, *L. harak*, *L. obsoletus*, *L. ornatus*, and *L. ravus* from 2 years old; and both *L. miniatus* and *L. nebulosus* from 3 years old. Most females completed maturation in the following years. Therefore, age at 50% of ovarian maturity ( $A_{OM50}$ ) was not clear except for *L. nebulosus* (4 years old) and *L. ornatus* (2 years old).

#### Discussion

In the present study, a translucent zone was formed in the otoliths during autumn to spring. The number of translucent-margin *L. miniatus* otoliths at the Great Barrier Reef (GBR) has been shown to decrease from October to December [9]. The marginal index, taken by measuring the minimum value at the time of opaque band completion of the otolith, indicates constant growth from the minimum value in January/February to that in December in *L. miniatus* at the GBR [33]. Therefore, opaque-band formation (October to December: spring to early summer) in the GBR *L. miniatus* otolith approximately coincides with the annual cycles of the present results. Growth-ring formation of *L. nebulosus* and *L. rubrioperculatus* otoliths in



**Fig. 4** Monthly changes in marginal index and outermost condition (filled circle growth ring, open circle outside of growth ring) in each age group from 1 to 9 and for 10 to 23 together in *Lethrinus atkinsoni* from Yaeyama. The crosses and lines indicate the average marginal index in each month. Arrows indicate the correspondence of the integer part of the age to the ring-number groups



New Caledonia (NC) [34] also coincides with the present results. However, in *L. nebulosus* of the northern GBR, marginal increment analysis of the whole otolith shows opaque zone formation during the winter period [35]. In many coral-reef species, opaque and translucent zones are formed during summer and winter, respectively [36]. There are some hypotheses regarding factors affecting growth-ring formation, including physiological change, growth-rate differences, and reproductive cycles, based on water temperature changes [36]. However, it is difficult to determine what factors control the timing of the different growth-ring formations in *L. nebulosus* in the northern GBR.

Growth was outstanding in the first few years, but was extremely slow in the remaining period in all eight species (Fig. 7). The longevity of *L. miniatus* and *L. nebulosus*, who belong to the large body-size group, were the longest at about 25 years, and that of the smallest species of *L. ornatus* was the shortest, approximately 12 years. However, the longevity of the third largest species of *L. rubrioperculatus* was 13 years, and those of the smaller species *L. atkinsoni* and *L. obsoletus* were approximately 25 and 20 years, respectively. Therefore, the longevity and

the maximum body size of the species do not seem to be connected.  $A_{OM50}$  in *L. nebulosus*, the largest body-size species among juvenile hermaphrodites, was the highest, and that in *L. miniatus*, the largest body-size species among protogynous hermaphrodites was the second. Thus, larger body-size species were found to mature later in each sexual group.

In the protogynous hermaphrodite group, two types of sexual transition were observed. In one type, all females in the species changed to male; as such, no females appeared in the older age groups. In the other type, some portion of females in the species did not change sex and were present up to the oldest age group. All females in *L. miniatus* and in *L. ravus* changed to male, thus belonging to the former type. Though one female remained in the maximum age group in *L. rubrioperculatus*, that the second-oldest female was 6 years old suggests that a 13-year-old female might be the exceptional individual. Therefore, *L. rubrioperculatus* seems to belong to the former type. No female appeared in age classes older than 19 years in the Okinawa population of *L. atkinsoni*. However, considering the stable sex ratios at age classes higher than 7 years old and the small sample sizes in the higher age classes, females in the

**Table 2** Number of specimens, mean  $L_f$  (cm)  $\pm$  SD, and sex ratio [ $R_S = f/(f + m + h)$ ]

Age	<i>Lethrinus atkinsoni</i> from Okinawa				<i>Lethrinus atkinsoni</i> from Yaeyama				<i>Lethrinus harak</i>						
	n	f	m	h	$R_S$	n	f	m	h	$R_S$	n	f	m	h	$R_S$
0	0				–	4	11.9 $\pm$ 0.9			1	1	14.6			1
1	9	19.8 $\pm$ 1.4			1	88	18.1 $\pm$ 2.6		17.4 $\pm$ 1.8	0.84	14	19.2 $\pm$ 2.5			1
2	92	23.1 $\pm$ 1.3	23.2 $\pm$ 1.2	23.6 $\pm$ 0.9	0.71	186	20.9 $\pm$ 1.5	20.5 $\pm$ 1.5	20.3 $\pm$ 1.2	0.72	81	23.6 $\pm$ 1.8	24.4 $\pm$ 1.3	24.5 $\pm$ 0.8	0.86
3	34	26.1 $\pm$ 1.7	27.2 $\pm$ 1.6		0.63	253	23.3 $\pm$ 1.3	22.5 $\pm$ 1.2	23.6 $\pm$ 0.3	0.65	115	25.1 $\pm$ 1.8	25.3 $\pm$ 1.2	25.3 $\pm$ 1.9	0.67
4	61	27.3 $\pm$ 1.7	28.5 $\pm$ 1.4	29.1	0.36	274	24.6 $\pm$ 1.4	23.4 $\pm$ 1.1		0.70	66	25.8 $\pm$ 2.1	25.9 $\pm$ 1.7	26.0 $\pm$ 0.4	0.56
5	74	28.9 $\pm$ 1.6	29.6 $\pm$ 1.2	30.0	0.30	169	25.8 $\pm$ 1.6	24.7 $\pm$ 1.4		0.72	45	27.2 $\pm$ 1.4	26.5 $\pm$ 1.4	26.0	0.36
6	40	30.9 $\pm$ 2.1	30.6 $\pm$ 1.2		0.33	121	26.7 $\pm$ 1.5	25.8 $\pm$ 1.4		0.66	44	28.5 $\pm$ 1.8	27.0 $\pm$ 1.2	26.9	0.25
7	19	31.9 $\pm$ 2.3	31.3 $\pm$ 1.5		0.21	93	28.3 $\pm$ 2.0	26.5 $\pm$ 1.5		0.72	24	29.1 $\pm$ 2.6	27.6 $\pm$ 0.7		0.42
8	28	33.9 $\pm$ 1.2	32.1 $\pm$ 1.2		0.11	89	29.0 $\pm$ 2.1	27.1 $\pm$ 1.5		0.67	14	29.2 $\pm$ 0.9	27.9 $\pm$ 1.5		0.29
9	3	32.9	32.7 $\pm$ 0.3		0.33	85	29.3 $\pm$ 2.0	27.9 $\pm$ 1.4		0.75	15	30.4 $\pm$ 2.0	28.4 $\pm$ 0.7		0.27
10	18	34.0 $\pm$ 1.4	32.6 $\pm$ 0.9		0.17	37	30.2 $\pm$ 2.4	28.4 $\pm$ 1.9		0.70	8	31.0 $\pm$ 0.9	27.3 $\pm$ 0.7		0.25
11	7	35.3 $\pm$ 2.2	32.3 $\pm$ 1.9		0.29	36	30.8 $\pm$ 2.2	28.7 $\pm$ 1.3		0.86	8	31.4 $\pm$ 4.2	27.9 $\pm$ 0.9		0.25
12	8	34.1 $\pm$ 1.1	33.3 $\pm$ 0.9		0.38	24	32.0 $\pm$ 1.6	28.6 $\pm$ 1.7		0.75	8	31.1 $\pm$ 0.6	28.1 $\pm$ 0.7		0.25
13	4	32.2	33.5 $\pm$ 2.9		0.25	13	31.9 $\pm$ 2.7	30.8 $\pm$ 0.6		0.77	3		28.5 $\pm$ 1.7		0
14	24	36.4 $\pm$ 1.6	33.6 $\pm$ 1.1		0.33	10	33.6 $\pm$ 1.1	30.7 $\pm$ 1.0		0.60	2	34.1	28.6		0.50
15	3	37.7	35.9 $\pm$ 3.0		0.33	12	32.0 $\pm$ 3.3	29.9 $\pm$ 0.8		0.67					
16	4	38.3 $\pm$ 1.4	34.8 $\pm$ 2.7		0.50	5	31.9 $\pm$ 2.5	29.8		0.80					
17	3	41.6	34.2 $\pm$ 0.6		0.33	4	35.2 $\pm$ 1.9	32.7 $\pm$ 1.8		0.50					
18	2	40.2 $\pm$ 0.8			1	4	35.7 $\pm$ 1.0			1					
19	1		36.2		0	1		30.2		0					
20	0				–	0				–					
21	3		33.2 $\pm$ 0.9		0	2	31.1	27.3		0.50					
22	1		35.3		0	2	34.5	33.8		0.50					
23	2		34.6 $\pm$ 1.8		0										
24	1		37.8		0										
Total	441					1,512					448				

Age	<i>Lethrinus miniatius</i>				<i>Lethrinus nebulosus</i>				<i>Lethrinus obsoletus</i>						
	n	f	m	h	$R_S$	n	f	m	h	$R_S$	n	f	m	h	$R_S$
0	0				–	0				–	0				–
1	12	26.5 $\pm$ 1.1			1	89	22.9 $\pm$ 3.5	26.3 $\pm$ 1.8	25.2 $\pm$ 1.8	0.76	5	20.7 $\pm$ 1.5		21.0	0.80
2	157	31.9 $\pm$ 3.5	33.8 $\pm$ 1.9	34.8 $\pm$ 3.0	0.96	72	29.2 $\pm$ 4.8	29.3 $\pm$ 4.2	26.1 $\pm$ 4.1	0.47	69	24.4 $\pm$ 1.3	24.0 $\pm$ 1.3	23.4 $\pm$ 1.1	0.62
3	138	37.5 $\pm$ 2.8	41.5 $\pm$ 3.4	39.0	0.93	82	37.1 $\pm$ 3.9	39.5 $\pm$ 4.3		0.51	133	25.9 $\pm$ 1.2	25.6 $\pm$ 1.2	24.5 $\pm$ 2.2	0.65
4	12	41.4 $\pm$ 1.8	42.7 $\pm$ 0.6	44.3	0.67	60	43.1 $\pm$ 3.6	43.6 $\pm$ 2.7		0.50	112	26.9 $\pm$ 0.7	26.7 $\pm$ 1.2	27.8	0.54

Table 2 continued

Age	<i>Lethrinus miniatus</i>				<i>Lethrinus nebulosus</i>				<i>Lethrinus obsoletus</i>						
	n	f	m	h	R <sub>s</sub>	n	f	m	h	R <sub>s</sub>	n	f	m	h	R <sub>s</sub>
5	12	43.8 ± 2.4	45.4 ± 1.8		0.83	54	47.5 ± 2.8	46.5 ± 3.3		0.44	31	28.1 ± 0.9	28.1 ± 1.3		0.61
6	34	44.5 ± 2.4	47.5 ± 2.0	48.1 ± 0.4	0.56	24	48.3 ± 2.9	50.5 ± 2.5		0.38	20	28.6 ± 1.3	29.2 ± 1.3		0.60
7	16	47.1 ± 2.4	51.7 ± 0.8	50.9	0.56	17	51.0 ± 2.6	51.0 ± 3.2		0.59	22	29.0 ± 1.0	28.8 ± 0.8		0.64
8	14	47.4 ± 2.2	50.0 ± 2.2	46.4	0.43	16	54.0 ± 4.2	53.8 ± 2.2		0.44	17	29.5 ± 1.2	29.1 ± 0.9		0.65
9	6		51.4 ± 1.1		0	8	50.1 ± 0.9	53.0 ± 1.8		0.25	13	30.3 ± 0.7	30.2 ± 1.2		0.54
10	3		54.8 ± 2.2		0	6	56.0 ± 5.9	53.7 ± 1.7		0.50	26	30.1 ± 1.5	29.9 ± 1.1		0.62
11	8	49.5	53.7 ± 2.2		0.13	6	57.3 ± 3.2			1	20	30.6 ± 0.8	32.5 ± 0.6		0.85
12	5	54.0	53.4 ± 1.3		0.20	12	54.7 ± 2.6	55.7 ± 1.7		0.50	17	29.8 ± 0.9	29.9 ± 1.2		0.53
13	2		52.6 ± 3.4		0	2	55.3 ± 3.9			1	10	31.3 ± 1.1	31.8 ± 0.4		0.80
14	1		56.4		0	2	60.7	55.9		0.50	4	32.1 ± 0.8	31.8		0.75
15	2	53.6	59.2		0.50	3	55.1	54.9 ± 3.5		0.33	6	31.5 ± 0.9	32.4 ± 0.8		0.67
16	3		57.2 ± 0.7		0	1	63.1			1	4	32.9 ± 1.5	31.0 ± 0.8		0.50
17	1		56.0		0	1	59.7			1	1	31.2			1
18	1		56.8		0	1	53.9			1	1		32.1		0
19						2	60.6 ± 0.8			1	2	32.3 ± 1.6			1
20						1	65.0			1	1	33.4			1
21						0				-	1	33.1			1
22						1		59.8		0					
23						0				-					
24	1		57.7		0	2	61.4	61.6		0.50					
25		-				0				-					
26						1	61.4			1					
Total	428					463					515				

Age	<i>Lethrinus ornatus</i>				<i>Lethrinus ravus</i>				<i>Lethrinus rubrioperculatus</i>						
	n	f	m	h	R <sub>s</sub>	n	f	m	h	R <sub>s</sub>	n	f	m	h	R <sub>s</sub>
0	0				-	0				-	0				-
1	10	17.4 ± 2.3			1	3	20.8 ± 1.7			1	67	24.4 ± 1.9			1
2	16	20.1 ± 0.8	20.8 ± 1.3		0.88	20	25.2 ± 1.7	28.6		0.95	152	28.5 ± 2.7	31.0 ± 2.7	31.7 ± 2.7	0.87
3	15	21.3 ± 1.3	22.0 ± 1.2		0.73	57	27.4 ± 1.0	28.6 ± 0.7		0.79	207	30.7 ± 2.6	33.0 ± 2.1	32.3 ± 3.6	0.84
4	4	22.1 ± 1.0	22.2	22.1	0.50	74	28.5 ± 1.1	29.4 ± 1.1	28.8 ± 0.9	0.55	103	33.3 ± 2.1	33.3 ± 2.7	34.8	0.52
5	7	23.2 ± 0.9	23.5 ± 1.1		0.43	38	29.5 ± 0.8	30.3 ± 1.3	32.2	0.29	53	36.2 ± 2.3	36.1 ± 1.8	36.4	0.28
6	12	22.8 ± 0.7	24.2 ± 0.7	23.1	0.42	18		30.4 ± 1.2		0	27	37.1 ± 1.3	36.7 ± 1.0		0.15
7	5	23.1	24.0 ± 0.1		0.20	7		30.8 ± 1.1		0	9		35.2 ± 2.8		0



Table 2 continued

Age	<i>Lethrinus ornatus</i>					<i>Lethrinus ravus</i>					<i>Lethrinus rubrioperculatus</i>				
	<i>n</i>	<i>f</i>	<i>m</i>	<i>h</i>	<i>R<sub>S</sub></i>	<i>n</i>	<i>f</i>	<i>m</i>	<i>h</i>	<i>R<sub>S</sub></i>	<i>n</i>	<i>f</i>	<i>m</i>	<i>h</i>	<i>R<sub>S</sub></i>
8	4	22.9 ± 0.5	23.9 ± 1.7	0.50	3	0	30.7 ± 0.8	0	3	34.6 ± 3.0	0	0			0
9	0			–	0	–		–	4	34.7 ± 3.4	0	0			0
10	3	23.8	24.7 ± 0.1	0.33	0	–		–	3	36.6 ± 2.8	0	0			0
11	2		25.2 ± 0.2	0	1	0	29.7	0	3	38.4 ± 1.6	0	0			0
12	2		26.2 ± 0.9	0	1	0	32.1	0	3	41.1 ± 1.7	0	0			0
13					0	–		–	1		–	1	41.6		1
14					1	0	31.4	0							
Total	80				223						635				

*f* Female, *m* male, *h* hermaphrodite

population seem to present in the oldest age class. Therefore, *L. harak* and the Okinawa population of *L. atkinsoni* belong to the latter type. The body sizes of old and sex-unchanged females in the latter type have a tendency to be larger than those of males in the same age groups. Categorization of *L. ornatus* to either of the two types was not possible due to the small sample sizes for the old age classes.

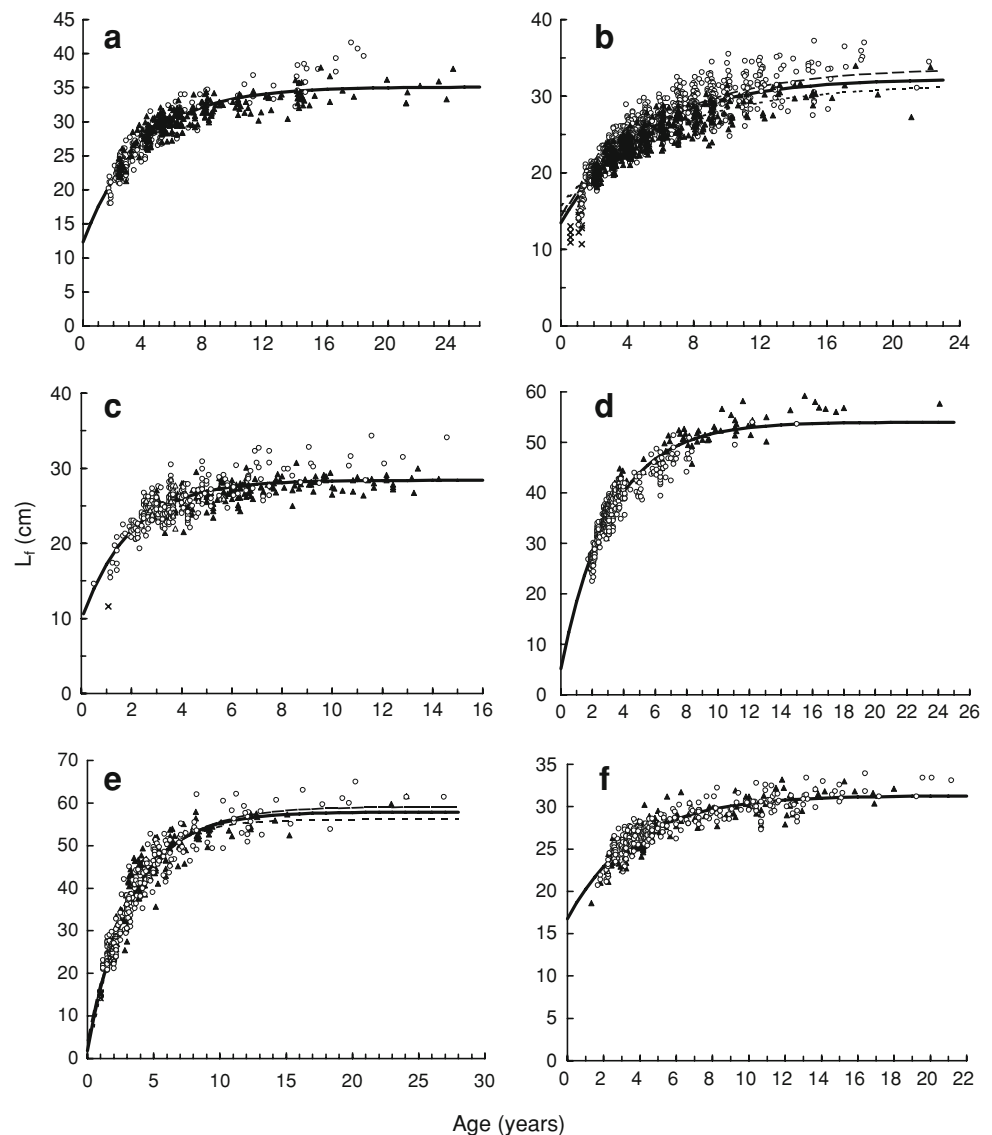
$A_{RS50}$  of *L. miniatus*, which belongs to the large body-size group, was the highest, between 7 and 8 years of age.  $A_{RS50}$  of *L. ornatus*, the smallest species, and that of *L. rubrioperculatus*, the third largest body-size species, was 4 years old.  $A_{RS50}$  of the Okinawa population of *L. atkinsoni*, the fourth largest body-size species, was between 3 and 4 years of age. Except for the largest body-size species,  $A_{RS50}$  and the maximum body size of the species seem to be unrelated. In the juvenile hermaphrodite group,  $A_{RS50}$  existed only in *L. nebulosus* and not in *L. obsoletus* and the Yaeyama population of *L. atkinsoni*. Sex ratios in juvenile hermaphrodite species were stable after the age of sexual differentiation; as such,  $A_{RS50}$  seems to be meaningless for these species.

Thus far in the comparisons of biological parameters with age among different species in the Ryukyu Islands area, the longevities of *Lethrinus* species can be categorized into two groups of approximately 20–25 years and 12–15 years; the smaller body-size species do not always belong to the latter.  $A_{OM50}$  of larger body-size species were higher than those of smaller body-size species. In the protogynous hermaphroditic group, although  $A_{RS50}$  of the large body-size species was high, those of other species showed little relation to maximum body size of the species.

From the perspective of the usual habitat of the species, the complete disappearance of females in older age classes due to sexual transition was common in the offshore deeper-water group composed of *L. miniatus*, *L. rubrioperculatus*, and *L. ravus*. Due to the small body sizes,  $A_{OM50}$  were relatively low in the coastal shallow-water group composed of *L. atkinsoni*, *L. harak*, *L. obsoletus*, and *L. ornatus*. However, when *L. nebulosus* is included, those two common characteristics disappear because the species inhabits both coastal shallow and offshore deep areas, despite showing juvenile hermaphroditism with the highest  $A_{OM50}$ . Thus, the biological characteristics related to age in the *Lethrinus* species appear to have less relation to the usual habitat of the species.

We compared our present results to the growth curves, the maximum age in specimens,  $A_{RS50}$ , and  $A_{OM50}$  in the NC *L. nebulosus*, *L. miniatus*, *L. atkinsoni*, and *L. rubrioperculatus* [4, 37] and GBR (Brown and Sampton [9], GBR-BS; Sampton and Brown [38], GBR-SB; Williams et al. [39], GBR-W) and Norfolk Island (NI) [8]

**Fig. 5** The von Bertalanffy growth curves fitted to observed fork length ( $L_t$ ) and age of male (dotted line, filled triangle), female (broken line, open circle), and combined (bold line) in **a** *Lethrinus atkinsoni* from Yaeyama, **b** *Lethrinus atkinsoni* from Okinawa, **c** *Lethrinus harak*, **d** *Lethrinus miniatus*, **e** *Lethrinus nebulosus*, and **f** *Lethrinus obsoletus*

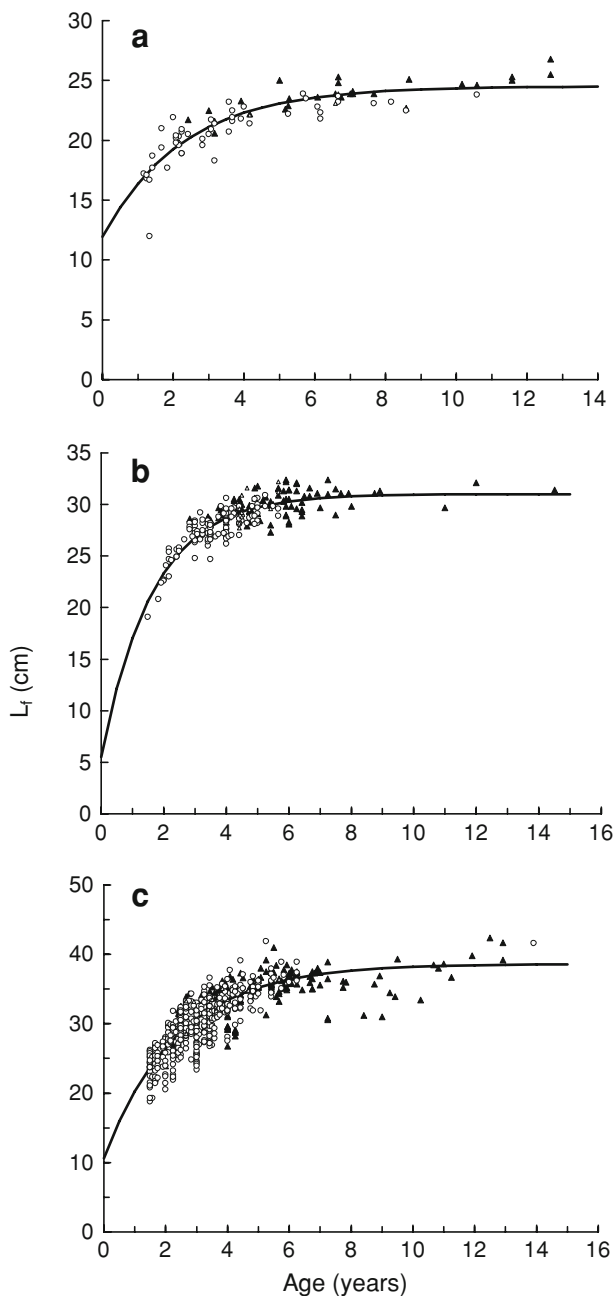


*L. miniatus* (Table 3). In *L. atkinsoni* in the NC population, although  $A_{OM50}$  was not indicated, the youngest mature female was 5 years old. Therefore, it appears that females in NC start to mature at a much later stage than do those in the two populations of the Ryukyu Islands.  $A_{RS50}$  probably does not exist because sex ratios are constant at about 80% in all length classes larger than 14 cm  $L_S$ .

Because growth parameters of *L. miniatus* in the NC population are indicated separately by sex, Table 3 includes them separately and those of other areas combined. Extremely larger  $L_\infty$  and smaller  $k$  were obtained in the NI population than those of other areas. The growth curve in the NI population shows relatively constant growth to the maximum age, whilst those of the other three areas attain near-maximum size at about age 10. However, the maximum size of about 66 cm  $L_F$  in the specimens of

NI is only slightly larger than those of the other three areas. The maximum ages in males were close to those at GBR-SB, NC, and Okinawa. The maximum ages of males were larger than those of females in all four populations, but the differences in age between males and females were large in NC and in Okinawa, but small in GBR and in NI.  $A_{RS50}$  is the largest between the 9 and 10–11 coupled age groups in NC, and is the smallest between 5 and 6 in the NI population.

$A_{OM50}$  ranges from 2.1 years old in GBR-W to about 7 years old in GBR-SB. Age or size at ovarian maturation is affected by the definition of maturity employed. Williams et al. [39] concluded that the overestimation of age at maturity [38] was caused by the inadequate treatment of the “mature resting” and “immature” ovary. However, in all four studies, except that by Church [8], who did not



**Fig. 6** The von Bertalanffy growth curves and parameters fitted to observed fork length ( $L_f$ ) and age of male (filled triangle) and female (open circle) in **a** *Lethrinus ornatus*, **b** *Lethrinus ravus*, and **c** *Lethrinus rubrioperculatus*

indicate the age at maturity, ages of ovarian maturity were determined by using specimens collected only during their spawning periods. It is not plausible that such a difference in ages at maturity is caused only by the different treatment of the “mature resting” individuals. From this perspective, determining these parameters with age by the same methods in the species applied in this research is meaningful.

The maximum age in *L. nebulosus* found by Grandcourt et al. [11] is much smaller than those found in other studies. They concluded it that it was because of underestimation due to the absence of fish close to the maximum reported sizes in the region. Therefore, their study was excluded in the present discussion. In comparisons of *L. nebulosus* in the NC population, the maximum ages were very similar to the present results, while the  $A_{OM50}$  was not. If we consider the sizes of 50% ovarian maturation in NC being 51.3 cm  $L_f$  and 39.7 cm  $L_f$  in Okinawa [15], we see that both age and size for ovarian maturation in the species were considerably different between these areas.

$L_\infty$  in *L. rubrioperculatus* in the Okinawa population were larger than those in the NC population, however, the maximum ages in the two areas were not so different.  $A_{RS50}$  and  $A_{OM50}$  in Okinawa were slightly younger than those of NC.

In the studies of other NC *Lethrinus* species, only the maximum ages in *L. harak* and *L. obsoletus* were indicated. The maximum ages of *L. harak* in the NC population and in the Okinawa population were approximately the same. However, that of *L. obsoletus* at 14 years old in NC was much younger than that the 21 years old in Okinawa. This is probably due to the sample size of each specimen. In *L. ravus* and *L. ornatus*, which are species with smaller body sizes,  $A_{RS50}$  and  $A_{OM50}$  exhibited similar values, but there is no information available about a comparison with growth in other areas.

Upon comparison of the biological parameters for a particular species among the different areas, the maximum age of the specimens, which probably indicates the longevity of the species, exhibits similar values even in widely separated areas between the northern (Okinawa) and the southern (NC, GBR, NI) hemisphere, and their exploitation rates are probably different. In contrast,  $L_\infty$  in the von Bertalanffy growth equation, or in other words “the maximum size” in the same species, differs from area to another. In addition, although  $A_{RS50}$  and  $A_{OM50}$  are often confined to a similar range, they occasionally differ considerably from area to area.

Stock status in *Lethrinus* species differs from species to species in the Ryukyu Islands area. These differences in status can be observed in severely decreased rates due to strong fishing pressures, as well as in the occurrence of different rates even in species suffering the same levels of fishing pressure in the same habitat [21–23]. For the rational use of these resources, careful evaluations of stock status and investigations of management strategy are necessary. Based on these analyses, some restrictive fisheries have been enacted for *L. nebulosus* [40] in the northwest area of Okinawa Island and for *L. atkinsoni* [41] in the Yaeyama Islands. Effective management strategies must be established through careful stock assessments and

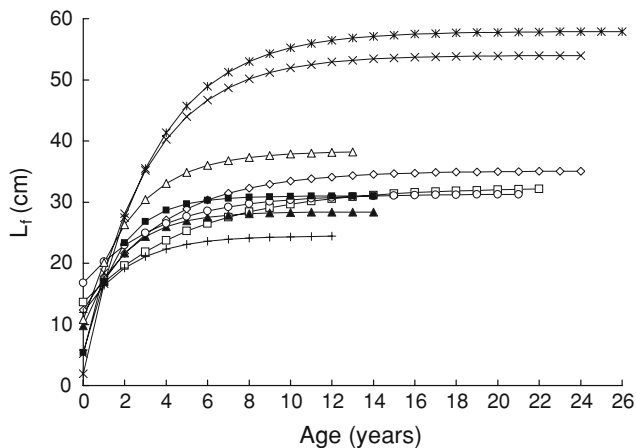
**Table 3** Growth parameters in the von Bertalanffy growth equation and the maximum age of both males and females in specimens of eight *Lethrinus* species aged from sectioned otoliths, including previously reported studies

Species	Area	Sex	$L_{\infty}$	$k$	$t_0$	Maximum age		$A_{RS50}$	$A_{OM50}$	Reference
						Male	Female			
<i>Lethrinus atkinsoni</i>	Okinawa	f + m	35.1	0.260	-1.67	24	18	3–4	2–3	Present study
	Yaeyama	f + m	32.4	0.193	-2.83	22	22	ne	2–3	Present study
		f	33.0	0.198	-2.61					Present study
		m	30.9	0.186	-3.43					Present study
NC	f + m	37.4	0.292	-0.50	23	24	ne	na	Loubens [4, 37]	
<i>Lethrinus harak</i>	Yaeyama	f + m	28.4	0.509	-0.83	14	14	4–5	1–2	Present study
	NC	f + m					15	na	na	Loubens [4, 37]
<i>Lethrinus miniatus</i>	Okinawa	f + m	54.0	0.317	-0.32	24	15	7–8	3–4	Present study
	NC	f	52.2	0.272	0.08		14	9–10/11	6	Loubens [4, 37]
		m	55.8	0.263	-0.01	22				Loubens [4, 37]
	NI	f + m	79.0	0.071	-3.65	18	15	5–6		Church [8]
<i>Lethrinus nebulosus</i>	GBR	f + m	52.1	0.229	-1.43	25	21	6	7	Brown and Sumpton [9], Sumpton and Brown [38]
						18	17	7.4	2.1	Williams et al. [39]
	Okinawa	f + m	57.9	0.305	-0.11	24	26	2	4	Present study
		f	58.9	0.283	-0.20					Present study
<i>Lethrinus obsoletus</i>	NC	m	56.5	0.344	0.05					Present study
		f	61.7	0.212	-0.08		27	<3	9	Loubens [4, 37]
	AG	m	57.9	0.220	-0.14	24				Loubens [4, 37]
		f + m	66.2	0.110	-3.00		14	ne	na	Grandcourt et al. [11]
<i>Lethrinus ornatus</i>	Yaeyama	f + m	31.3	0.276	-2.78	18	21	ne	2–3	Present study
	NC	f + m					14	na	na	Loubens [4, 37]
<i>Lethrinus ornatus</i>	Yaeyama	f + m	24.5	0.435	-1.54	12	10	4	2	Present study
<i>Lethrinus ravus</i>	Okinawa	f + m	31.0	0.601	-0.32	14	5	4–5	1–2	Present study
<i>Lethrinus rubrioperculatus</i>	Okinawa	f + m	38.3	0.415	-0.80	12	13	4	1–2	Present study
	NC	f + m	33.9	0.431	-0.38	15	9	5–6	2.5	Loubens [4, 37]

ne Nonexistent, na not available, NC New Caledonia, NI Norfolk Island, GBR Great Barrier Reef, AG Arabian Gulf,  $L_{\infty}$  asymptotic mean fork length,  $k$  growth rate,  $t_0$  hypothetical age at zero length,  $A_{RS50}$  age when sex ratio decreased to 50%,  $A_{OM50}$  age at 50% ovarian maturity

**Table 4** Ovarian maturity rate ( $R_{OM}$ ) and the number of female specimens obtained in the spawning period ( $n$ ) in each age group of eight *Lethrinus* species

Species	<i>Lethrinus atkinsoni</i> from Okinawa		<i>Lethrinus atkinsoni</i> from Yaeyama		<i>Lethrinus harak</i>		<i>Lethrinus miniatus</i>		<i>Lethrinus nebulosus</i>		<i>Lethrinus obsoletus</i>		<i>Lethrinus ornatus</i>		<i>Lethrinus ravus</i>		<i>Lethrinus rubrioperculatus</i>	
	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$	$R_{OM}$	$n$
1	–	0	0	20	0	8	–	0	0	16	–	0	0	7	–	0	0.20	49
2	0.36	45	0.30	84	0.85	39	0	42	0	36	0.18	11	0.50	12	0.67	8	0.85	105
3	0.92	13	0.95	86	0.93	61	0.38	64	0.04	26	0.72	50	0.75	8	0.81	22	0.88	141
4	1	18	0.96	124	1	26	1	1	0.50	10	0.90	41	1	2	0.97	31	0.98	44
5	0.95	20	0.99	77	1	10	1	4	0.83	12	1	13	1	1	1	8	1	11
6	1	9	1	48	1	5	1	4	1	6	1	5	1	3	–	0	1	4
Over 7	0.88	26	0.97	219	0.95	21	1	15	0.97	33	1	67	1	3	–	0	–	0



**Fig. 7** Comparisons of growth curves in eight *Lethrinus* species from two local populations obtained in this study. *Open diamonds* indicate *Lethrinus atkinsoni* from Okinawa, *open squares* *Lethrinus atkinsoni* from Yaeyama, *filled triangles* *Lethrinus harak*, *times signs* *Lethrinus miniatus*, *stars* *Lethrinus nebulosus*, *open circles* *Lethrinus obsoletus*, *plus signs* *Lethrinus ornatus*, *filled squares* *Lethrinus ravus*, *open triangles* *Lethrinus rubrioperculatus*

evaluations based on age structure for hermaphrodite species in tropical waters.

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