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FULL PAPER

# Age, growth, and reproductive biology of blacktail snapper, *Lutjanus fulvus,* around the Yaeyama Islands, Okinawa, Japan

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**Abstract** Age, growth, and reproductive characteristics of blacktail snapper, *Lutjanus fulvus*, which is a commercial fish species, were investigated using 322 specimens (40–332 mm in fork length) caught around the Yaeyama Islands, Okinawa, Japan. Spawning season was estimated to be from April to October, and spawning was confirmed around the full moon and the last quarter moon. Age determination using sectioned otoliths revealed that ages ranged from 0 to 34 years and the majority was $\geq$ 3 years. Parameters of the von Bertalanffy growth function were estimated to be $L_\infty = 270$ mm, $k = 0.40$, and $t_0 = -0.48$ years for females, and 257 mm, 0.44, and $-0.42$ years for males. Initial growth was rapid during the first 3 years, attaining over 200 mm for both sexes, and then females grew larger than males. Sizes (ages) at the first sexual maturity were 225 mm (4 years) for females and 207 mm (3 years) for males. The wide range of age composition in catch with majority of $\geq$3 years old implied that the current fishing effort to harvest was not sufficiently large enough to collapse the stock immediately.

**Keywords** Age · Blacktail snapper · Growth · Lunar spawning · Reproduction

## Introduction

Lutjanid snappers (Perciformes; Lutjanidae) are important commercial target fishes in tropical to subtropical regions of the western Pacific (Allen 1985; Polovina and Ralston 1987). Among this family, the genus *Lutjanus* contains the largest number of species (Allen 1985), some of which are consumed in the Yaeyama Islands, Okinawa, Japan (Shimose and Nanami 2013). Blacktail snapper, *Lutjanus fulvus*, is widely distributed in the Indo-Pacific (Allen 1985), and is a valuable food fish in some regions (Randall and Brock 1960). Blacktail snapper is the fourth most abundant *Lutjanus* species in the Yaeyama fish market (Shimose and Nanami 2013), and the mean annual catch between 2008 and 2010 is estimated to be ca. 1,300 kg, caught by various fishing gears (Akita et al. 2011). Blacktail snapper is recorded with other small *Lutjanus* and *Pristipomoides* species collectively under the local name "Bitarou" in the fish market at Yaeyama (Shimose and Nanami 2013). The life history characteristics of blacktail snapper and other *Lutjanus* species comprising "Bitarou" are required for proper fisheries assessment and management of these snappers.

Maximum body size varies among *Lutjanus* species, for example, *Lutjanus biguttatus* grows up to 20 cm and *Lutjanus cyanopterus* to 160 cm in total length (Allen 1985). Blacktail snapper is a smaller sized species (up to 40 cm; Allen 1985) in the genus, and the largest individual recorded around the Yaeyama Islands is 372 mm in total length (Shimose and Nanami 2013). Sectioned sagittal otoliths have been used in age and growth studies of *Lutjanus* species, but relatively few studies have focused on small species (e.g., Newman et al. 1996, 2000; Shimose and Tachihara 2005; Grandcourt et al. 2011), and no information is available for blacktail snapper. These previous studies suggest that some small *Lutjanus* species are long lived (> 20 years) and vulnerable to fishing pressure (Newman et al. 1996). Therefore, information on growth and longevity is crucial

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for assessing the stock of *Lutjanus* species (Shimose and Tachihara 2006).

Reproductive traits such as spawning season and size (age) at maturity are also useful for fisheries management and are well studied for *Lutjanus* species (e.g., Fry et al. 2009; Nanami et al. 2010b; Fernandes et al. 2012). Some *Lutjanus* species are known to exhibit spawning aggregations with lunar periodicity (e.g., Johannes 1978; Domeier and Colin 1997; Heyman and Kjerfve 2008), and such information is important because targeting these aggregations at known times and locations could result in overexploitation. In this study, growth rate, age composition of catch, longevity, spawning season, maturation size, and maturation age of blacktail snapper were estimated to discuss the vulnerability of this species.

## Materials and methods

*Sample collection.* Adult samples of blacktail snapper ($n = 302$) were purchased at the Yaeyama fish market from May 2007 to October 2012. Yaeyama fish market is located in Ishigaki Island (24°21′N, 124°09′E), Okinawa, Japan, and the island is a part of the Yaeyama Islands in the Ryukyu Archipelago (Fig. 1). Fish market samples were caught around the Yaeyama Islands by handline, spear, longline, gillnet, and small set net fisheries (Shimose and Nanami 2013). Juveniles (< 150 mm) were not available at the market, and they were collected by angling from several coastal sites in Ishigaki Island in February ($n = 2$), May (1), June (4), July (6), and August (7).

The total length (TL), fork length (FL), and standard length (SL) of specimens were measured to the nearest 1 mm and whole body weight (BW) to the nearest 2 g. Relationships between TL–FL and SL–FL were estimated by fitting linear functions by the least squares method. FL–BW relationship was estimated by fitting a power function. The sex of each specimen was identified by visual inspection of the gonad morphology for fish ≥ 150 mm FL.

*Observation of the gonads.* Gonads of 158 females and 116 males were observed to estimate the spawning season, lunar phase, and size (age) at sexual maturity. Spawning season was estimated using specimens larger than the size at which the first sexual maturity occurred for both sexes, assuming them as adults. Gonad weight (GW) of both females and males was measured to the nearest 0.01 g, and the following gonadosomatic index (GSI) was calculated: GSI = GW × 100/BW. Gonads of females and males were preserved in 20 % buffered formalin for

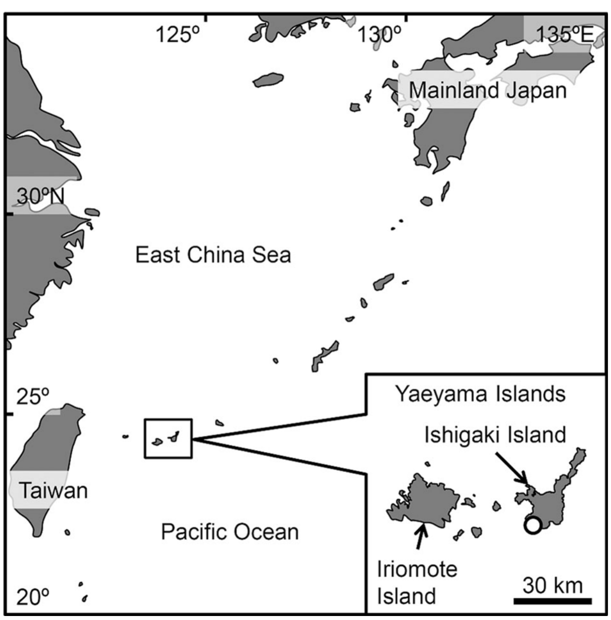


**Fig. 1** Map showing the location of Ishigaki Island and the Yaeyama fish market (*open circle*) where samples of blacktail snapper, *Lutjanus fulvus*, were collected

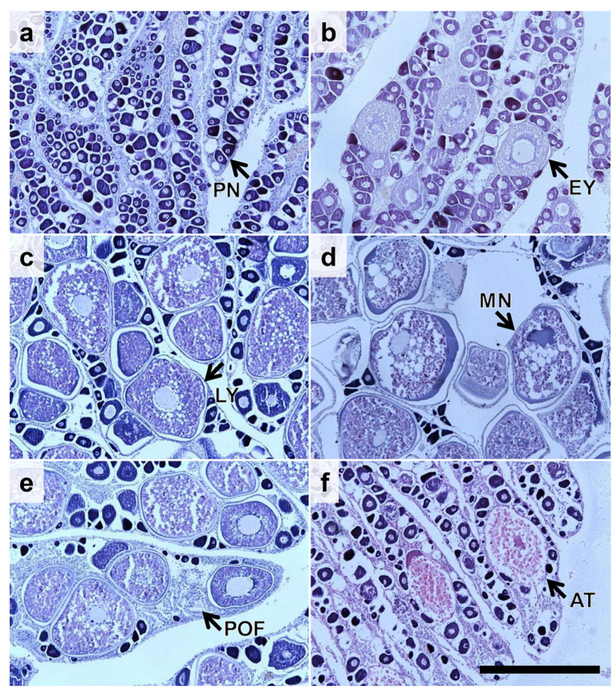


**Fig. 2** Photomicrographs of histological slides for six ovarian phases in blacktail snapper, *Lutjanus fulvus*. **a** Immature phase with perinucleolus oocytes (*PN*); **b** maturing phase with early yolked oocytes (*EY*); **c** mature phase with late yolked oocytes (*LY*); **d** ripe phase with migratory nucleus oocytes (*MN*); **e** spawned phase with postovulatory follicles (*POF*); **f** atresia phase with abundant atretic oocytes (*AT*). *Scale bar* indicates 500 μm

more than 48 hours in a refrigerator for later histological analyses. Fixed gonads were then placed in 70 % alcohol, and pieces of gonad were dehydrated and embedded in paraffin. Paraffin blocks were sectioned to 6 μm thick, and sections were attached to glass slides. Gonad sections were stained with Mayer's haematoxylin and counterstained by eosin.

Ovarian developmental phases were divided into the following six phases based on the most advanced stage of oocytes, abundance of alpha stage atresia (Ebisawa 1999; Shimose et al. 2009a), and also the existence of postovulatory follicles. The least developed phase of ovary was "immature" (Fig. 2a): containing only peri-nucleolus oocytes in the ovary. The second development phase was "maturing" (Fig. 2b): yolk globules started accumulating in the cytoplasm of oocytes (early yolk oocyte). The third development phase was "mature" (Fig. 2c): most developed oocytes were filled with yolk globules (late yolk oocyte) and ready for spawning. The fourth development phase was "ripe" (Fig. 2d): nucleus moved to the animal pole (migratory nucleus oocyte) and indicated spawning was imminent. The fifth development phase was "spawned" (Fig. 2e): postovulatory follicles were observed after ripe eggs had been released. The last phase was "atresia" (Fig. 2f): yolked oocytes did not develop further and were reabsorbed. In this study, maturing and more advanced phases were considered as sexually mature. Mature, ripe, and spawned phases were considered as reproductively active. Ripe and spawned phases were considered as evidence of spawning.

Testicular developmental phases were divided into the following four phases based on the area of spermatozoa occupied in the section and frequency of areas showing active spermatogenesis (Ebisawa 1999; Shimose et al. 2009a). The least developed phase was "immature" (Fig. 3a, b): mostly containing spermatogonia and few areas in spermatogenesis. The second development phase was "inactive" (Fig. 3c, d): with occurrence of spermatogenesis but a small amount of spermatozoa (< 40 %) not sufficient for spawning. The third development phase was "ripe" (Fig. 3e, f): in which active spermatogenesis occurred and a large amount of spermatozoa (40–70 %) was observed. The fourth development phase was "spawned" (Fig. 3g, h): in which a part of the spermatozoa was released and spermatogenesis decreased, but a large amount of spermatozoa (> 70 %) was present in the testis. In this study, inactive, ripe, and spawned phases were considered as sexually mature. Ripe and spawned phases were considered as reproductively active.

*Age determination and growth analysis.* Right and left sagittal otoliths were removed from 284 individuals (72–332 mm FL), and preserved in a dry condition for age determination. Otoliths were sectioned into ca. 0.3 mm-thick sections and attached to a glass slide. Each otolith section was photographed under an optical microscope with reflected light for observation using a PC monitor. The number of opaque zones was counted and otolith edge conditions were recorded without reference to fish length and collection date. Otolith edge condition is classified into three types: opaque, narrow translucent (less than half the width of the previous translucent zone), or wide translucent (more than half the width of the previous translucent zone).

The month when yearly age increases was assumed as April, because spawning in the study area possibly starts in April (see Discussion). For this adjustment, specimens with an opaque zone on the otolith edge collected from January to March were aged as the number of opaque zones minus 1 year, because they had a new opaque zone on the edge before they reached the assumed birth month (= April)

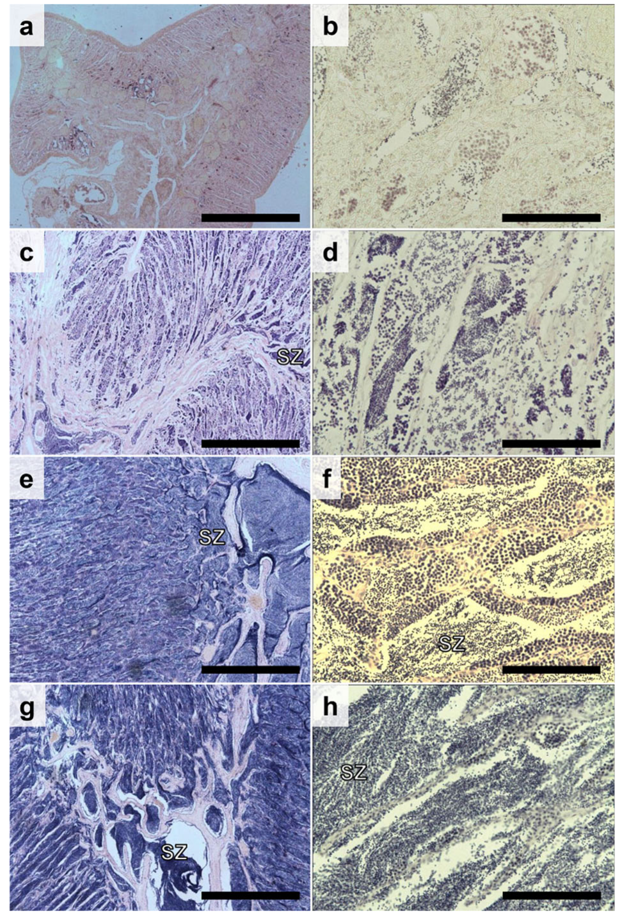


**Fig. 3** Photomicrographs of histological slides for four testicular phases in blacktail snapper, *Lutjanus fulvus*. **a**, **b** Immature phase mostly containing spermatogonia; **c**, **d** inactive phase with a small amount of spermatozoa (*SZ*) and inactive spermatogenesis; **e**, **f** ripe phase with large amounts of spermatozoa (*SZ*) and active spermatogenesis; **g**, **h** spawned phase with decreased levels of spermatogenesis, but still having large amounts of spermatozoa (*SZ*). *Scale bar* indicates 1 mm in **a**, **c**, **e**, and **g**, 0.1 mm in **b**, **d**, **f**, and **h**

(Shimose et al. 2009b). Similarly, specimens with a wide translucent zone on the otolith edge collected from April to June were aged as the number of opaque zones +1 year, because their new opaque zone was not formed despite that they had actually reached or passed the assumed birth month.

This age estimation was conducted twice with an interval of at least 1 week between reads. The precision of these two results was quantified by the average percent error (APE; Beamish and Fournier 1981) and the coefficient of variance (CV; Campana 2001) excluding results for age 0 year. The reference point of mean CV is 5% (corresponding to an APE of 3.65; Campana 2001), and CV $< 5$ % indicates higher precision in counts. If the two results were conflicting, final ages were decided by a third count with the knowledge of the previous two results. Otoliths of some small individuals ($n = 11$, 40–80 mm FL) were not observed, and these sizes are considered to be 0-year-old based on the growth rate estimated by the otolith daily increment analysis (Nakamura et al. 2008).

The von Bertalanffy growth function was employed to represent the growth of the population and fitted to length at age data using non-linear least-squares method:

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where $L_t$ is the length at age $t$, $L_\infty$ is the asymptotic FL, $k$ is the growth coefficient, and $t_0$ is the theoretical age at $L = 0$. In this estimation, ages of individual fish were assigned one month (= 1/12 years) interval with assumption of birth month = April. Both sex combined and sex-specific growth parameters were estimated. Juvenile data ($n = 20$, 40–147 mm FL) in which sex could not be determined were used to estimate growth parameters for both females and males. Growth parameters between sexes were compared by likelihood ratio tests using the R language with the package "fishmethods" (http://cran.r-project.org).

## Results

**Size of juveniles, females and males.** Fork length of 20 juveniles caught by angling ranged from 40 to 147 mm, and sex could not be determined from the gonad morphology (Fig. 4). The smallest size classes (in 10 mm intervals) 40–60 mm occurred in June, and their size increased to 47–80 mm in July and to 52–99 mm in August. Slightly larger individuals of 97–105 mm occurred in February. Even larger individuals measuring 123–147 mm occurred in May to August, which were clearly distinguished from smaller size classes (40–99 mm) in the same months, and were considered to be 1-year-old. Fork lengths of 169 females purchased at the fish market

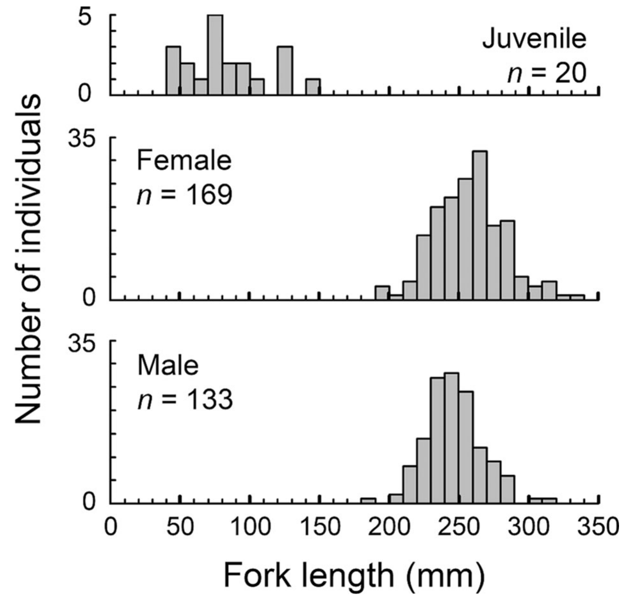


**Fig. 4** Fork length frequency distribution in 10 mm-size classes of juvenile, female, and male blacktail snapper, *Lutjanus fulvus*, caught around the Yaeyama Islands

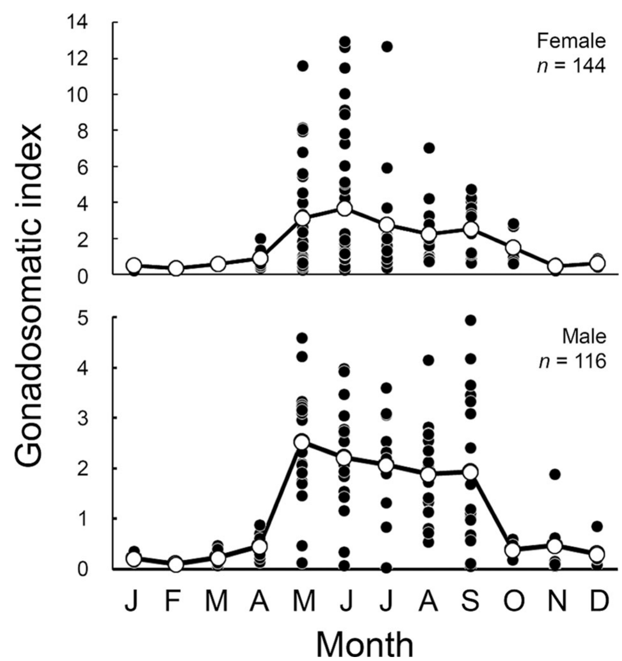


**Fig. 5** Monthly changes in the gonadosomatic index of female and male blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands. Monthly mean values are plotted as *open circles* connected by a *solid line*

were from 196 to 332 mm, and dominated by the 220 to 290 mm classes (87 %). Fork lengths of 133 males were from 189 to 314 mm, and dominated by the 210 to 280 mm classes (92 %). Mean (± SD) FL of females was 258 (± 25) mm and it was significantly larger than that of males, 247 (± 20) mm (Welch's $t$-test; $t = 4.30$, df = 299, $P < 0.001$).

Relationships between TL–FL, SL–FL, and FL–BW, which ranged 43–355 mm TL, 40–332 mm FL, 35–279 mm SL, and 2–812 g BW, were expressed by the following equations:

$$\mathrm{FL} = 0.92 \times \mathrm{TL} + 2.5;\ n = 227, R^2 = 0.99$$

$$\mathrm{FL} = 1.16 \times \mathrm{SL} + 9.0;\ n = 227, R^2 = 0.99$$

$$\mathrm{BW} = 12.09 \times 10^{-6} \times \mathrm{FL}^{3.09};\ n = 227, R^2 = 0.96$$

**Spawning season and lunar day.** The smallest size of sexually matured female and male were 225 mm and 207 mm, respectively. Spawning periodicity was estimated using those adult females (> 225 mm, $n = 144$) and males (> 207 mm, $n = 116$). Gonadosomatic index showed clear seasonal trends for both females and males (Fig. 5). Mean GSI of females slightly increased in April and had higher values (> 2.0) from May to September. Then it decreased in October and had lower values (< 1.0) from November to March. Relatively high values of GSI (> 6.0) were often observed from May to August, and some plots exceeded 10.0 from May to July. Mean GSI of males slightly increased in April and had higher values (> 1.0) from May to September. Mean GSI had lower values (< 1.0) from October to March. Relatively high values of GSI (> 2.0) were often observed from May to September, but never exceeded 5.0 unlike females.

Reproductively active females (mature, ripe, and spawned phases) were observed from April to October, with a higher frequency from May to September (73–90 %) (Fig. 6). Females in spawning condition (ripe and spawned phases) were observed from June to September with low frequencies (13–25 %). Reproductively active males (ripe and spawned phases) were observed from April to January, with higher frequency from May to October and December (> 77 %).

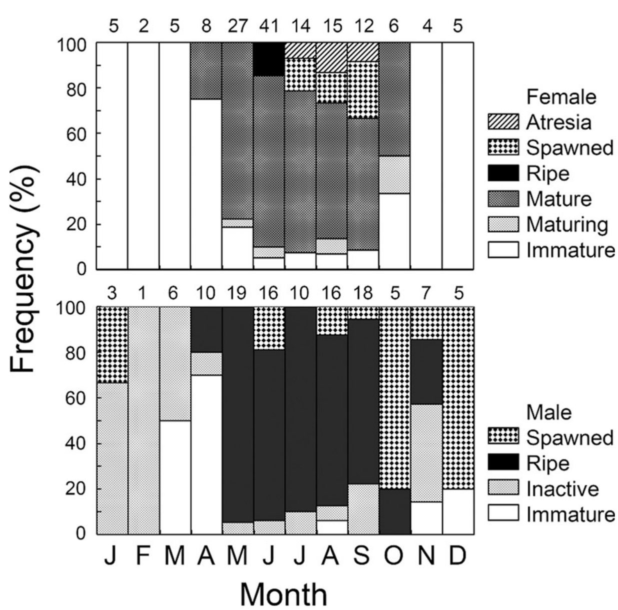


**Fig. 6** Monthly changes in the frequency of ovarian and testicular developmental phases in blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands. *Numbers* above bars indicate the numbers of samples

Lunar periodicity of spawning was estimated using 105 reproductively active adult females (> 225 mm) obtained between April and October, and those adult individuals were collected in all of 10 categorical lunar days in 3-day intervals (Table 1). Maturing females occurred from lunar day of 27.0–29.5 to 0.0–8.9 in small proportion. Mature females occurred from most lunar days with relatively high frequencies. Ripe and spawned females occurred from lunar day of 12.0–23.9, and the frequency was higher around the full moon and then decreased to the last quarter moon. Atresia females occurred from lunar day of 21.0–26.9 and 0.0–5.9. The mean GSI of females increased from the new moon to the full moon and then decreased.

**Age and growth.** Sectioned otoliths had distinct opaque and translucent zones alternatively formed from the core to the edge (Fig. 7). Otolith opaque zones appeared on the edge from January to September with a higher frequency from May to July (63–88 %) (Fig. 8). Single peak in a year and nearly 100 % switch between opaque edge (88 % in June) and translucent edge (100 % from October to December) indicated that the opaque zone was formed annually. In the observation of 284 otoliths, five small individuals (72–147 mm FL) had no opaque zones in their sectioned otoliths and were considered to be 0-year-old. In the two counts of 279 otoliths, 231 (83 %) showed complete agreement between counts. Mean APE and CV were quite low with values of 0.84 and 1.18, respectively.

Ages of juveniles (40–147 mm FL), females (196–332 mm), and males (189–314 mm) were estimated to be 0–1, 1–34, and 1–29 years old, respectively (Table 2). The small number of females and males of 1–2 years indicated that they did not recruit to fisheries. The oldest female (34 years, 315 mm) was collected in March, but not of the largest size. The age of the largest female (332 mm) was 25 years. The oldest male (29 years) was collected in May and was of the largest size (315 mm).

The mean (± SE) values of von Bertalanffy growth parameters were $L_\infty = 270$ (± 2) mm, $k = 0.40$ (± 0.02), and $t_0 = -0.48$ (± 0.08) years for females, 257 (± 2) mm, 0.44 (± 0.03), and −0.42 (± 0.07) years for males, and 265 (± 1) mm, 0.41 (± 0.02), and −0.49 (± 0.08) years for the sexes combined. Values of $L_\infty$ in all three cases were smaller than the maximum observed lengths. The growth functions indicated that growth was rapid during the first 3 years and attained a size of over 200 mm, and then the growth rate decreased (Fig. 9). Following this

**Table 1** Mean ± S.D. GSI and frequency of occurrence in each ovarian maturity phase for female blacktail snapper, *Lutjanus fulvus*, in each lunar phase (3 days interval) around Yaeyama Islands. Data from adult females (> 225 mm FL) between April and October were used

| Lunar day | *n* | GSI | | Maturity phases | | | | |
|---|---|---|---|---|---|---|---|---|
| | | mean | S.D. | maturing | mature | ripe | spawned | atresia |
| 0.0–2.9 | 11 | 1.52 | 0.86 | 2 | 8 | | | 1 |
| 3.0–5.9 | 12 | 2.23 | 0.73 | 1 | 10 | | | 1 |
| 6.0–8.9 | 14 | 3.73 | 3.22 | 1 | 13 | | | |
| 9.0–11.9 | 11 | 4.04 | 2.30 | | 11 | | | |
| 12.0–14.9 | 18 | 4.79 | 2.88 | | 17 | | 1 | |
| 15.0–17.9 | 8 | 8.23 | 4.75 | | 2 | 6 | | |
| 18.0–20.9 | 7 | 1.31 | 0.39 | | 3 | | 4 | |
| 21.0–23.9 | 16 | 1.81 | 1.60 | | 13 | | 2 | 1 |
| 24.0–26.9 | 1 | 0.64 | | | | | | 1 |
| 27.0–29.5 | 7 | 1.81 | 1.07 | 1 | 6 | | | |
| Total | 105 | 3.27 | 2.98 | 5 | 83 | 6 | 7 | 4 |

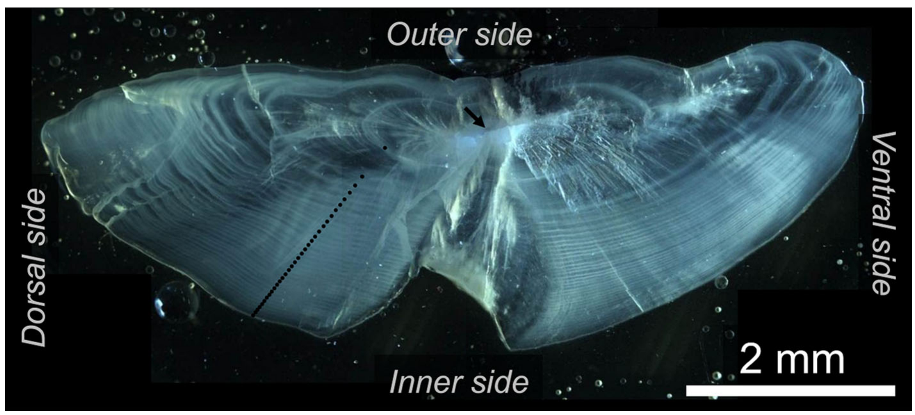


**Fig. 7** Photograph of the sectioned otoliths of the oldest female blacktail snapper, *Lutjanus fulvus*, measured 315 mm fork length and estimated to be 34 years old. *Arrow* and *dots* show core and opaque zones, respectively

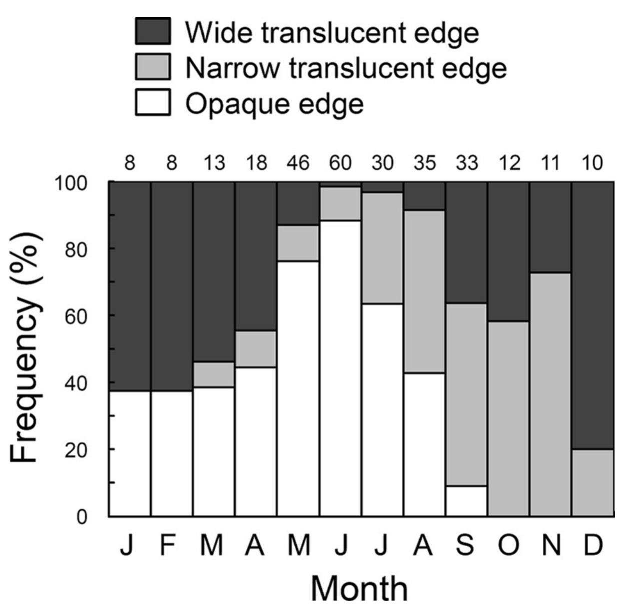


**Fig. 8** Monthly changes in the frequency of occurrence for opaque, narrow translucent, or wide translucent zones on the otolith edge of blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands. *Numbers* above bars indicate the number of samples

initial growth, females attained about 243 mm (90 % of $L_\infty$) at 6 years old, and males attained about 232 mm (90 % of $L_\infty$) at 5 years old. Likelihood ratio tests revealed a significant difference of $L_\infty$ between sexes ($P < 0.001$), but no differences were observed for $k$ ($P = 0.229$) and $t_0$ ($P = 0.624$), because the same juvenile data were used for both females and males.

The estimated ages of the smallest sexually matured females (225 mm) and males (207 mm) were 4 and 3 years old, respectively.

## Discussion

**Reproductive biology.** Spawning of blacktail snapper was confirmed from June to September by the observation of ovaries in ripe and spawned phases, but with a low frequency because of the species spawns around specific moon phases. In April, May, and October, mature phases were observed but not ripe or spawned

**Table 2** Mean ± SD fork length (mm) at each age of female and male blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands

| Age (years) | Juvenile | | | Female | | | Male | | | All combined | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | Mean | SD | *n* | Mean | SD | *n* | Mean | SD | *n* | Mean | SD |
| 0 | 16 | 72.0 | 19.2 | 0 | | | 0 | | | 16 | 72.0 | 19.2 |
| 1 | 4 | 129.9 | 11.1 | 1 | 196.0 | | 1 | 189.5 | | 6 | 150.9 | 33.6 |
| 2 | | | | 4 | 206.5 | 13.7 | 1 | 220.5 | | 5 | 209.3 | 13.4 |
| 3 | | | | 9 | 223.9 | 8.4 | 8 | 221.3 | 11.7 | 17 | 222.7 | 9.8 |
| 4 | | | | 8 | 226.4 | 7.2 | 7 | 229.4 | 8.2 | 15 | 227.8 | 7.6 |
| 5 | | | | 10 | 239.6 | 11.8 | 7 | 228.5 | 13.0 | 17 | 235.0 | 13.2 |
| 6 | | | | 8 | 246.4 | 12.3 | 6 | 244.4 | 10.8 | 14 | 245.5 | 11.3 |
| 7 | | | | 5 | 246.2 | 15.2 | 6 | 237.8 | 9.0 | 11 | 241.6 | 12.4 |
| 8 | | | | 4 | 256.9 | 11.1 | 2 | 242.5 | 9.2 | 6 | 252.1 | 12.1 |
| 9 | | | | 7 | 247.5 | 10.9 | 8 | 238.1 | 14.1 | 15 | 242.5 | 13.2 |
| 10 | | | | 9 | 255.7 | 12.4 | 5 | 250.1 | 5.7 | 14 | 253.7 | 10.6 |
| 11 | | | | 8 | 257.0 | 15.7 | 5 | 259.6 | 17.5 | 13 | 258.0 | 15.7 |
| 12 | | | | 7 | 265.5 | 12.2 | 9 | 242.9 | 9.0 | 16 | 252.8 | 15.4 |
| 13 | | | | 8 | 256.0 | 16.1 | 6 | 248.5 | 5.0 | 14 | 252.8 | 12.8 |
| 14 | | | | 15 | 263.5 | 10.8 | 3 | 252.3 | 12.4 | 18 | 261.6 | 11.5 |
| 15 | | | | 7 | 274.9 | 17.3 | 4 | 257.5 | 11.7 | 11 | 268.6 | 17.3 |
| 16 | | | | 6 | 273.7 | 8.8 | 3 | 260.2 | 9.9 | 9 | 269.2 | 10.9 |
| 17 | | | | 5 | 276.5 | 16.1 | 3 | 261.0 | 18.2 | 8 | 270.7 | 17.5 |
| 18 | | | | 2 | 293.5 | 46.7 | 2 | 261.0 | 5.7 | 4 | 277.3 | 33.0 |
| 19 | | | | 4 | 269.3 | 3.8 | 3 | 270.8 | 3.3 | 7 | 269.9 | 3.4 |
| 20 | | | | 2 | 270.3 | 15.9 | 4 | 274.5 | 11.7 | 6 | 273.1 | 11.7 |
| 21 | | | | 3 | 278.7 | 18.1 | 2 | 277.8 | 11.7 | 5 | 278.3 | 14.0 |
| 22 | | | | 3 | 295.7 | 13.4 | 2 | 266.5 | 11.3 | 5 | 284.0 | 19.4 |
| 23 | | | | 3 | 287.7 | 23.3 | 6 | 256.1 | 10.9 | 9 | 266.6 | 21.4 |
| 24 | | | | 4 | 284.4 | 15.7 | 4 | 259.9 | 18.3 | 8 | 272.1 | 20.5 |
| 25 | | | | 5 | 291.0 | 31.7 | 3 | 270.2 | 13.5 | 8 | 283.2 | 27.3 |
| 26 | | | | 3 | 265.3 | 18.9 | 1 | 256.0 | | 4 | 263.0 | 16.2 |
| 27 | | | | 2 | 267.3 | 3.2 | 2 | 287.0 | 30.4 | 4 | 277.1 | 21.0 |
| 28 | | | | 2 | 293.0 | 26.2 | 1 | 257.0 | | 3 | 281.0 | 27.8 |
| 29 | | | | 1 | 275.5 | | 2 | 299.5 | 21.2 | 3 | 291.5 | 20.4 |
| 30 | | | | 1 | 288.0 | | 0 | | | 1 | 288.0 | |
| 31 | | | | 0 | | | 0 | | | 0 | | |
| 32 | | | | 0 | | | 0 | | | 0 | | |
| 33 | | | | 2 | 280.3 | 6.0 | 0 | | | 2 | 280.3 | 6.0 |
| 34 | | | | 1 | 315.0 | | 0 | | | 1 | 315.0 | |
| Total | 20 | 83.6 | 29.6 | 159 | 258.5 | 25.2 | 116 | 248.6 | 20.7 | 295 | 242.8 | 49.4 |

phases. However, juvenile blacktail snapper were caught between June and August (40–99 mm FL). Based on the available growth rate of blacktail snapper estimated from otolith daily increments around Yaeyama Islands (Nakamura et al. 2008), 4 months (120 days) old fish is ca. 57 mm SL (= 75 mm FL). Juveniles of this size were collected in July and August implying that spawning starts in April or perhaps in March. In short, the spawning season of blacktail snapper is thought to be from April to October, with peak of June to September around the Yaeyama Islands.

Lunar-related spawning has been observed for blacktail snapper, with spawning events observed around the full moon and a few around the last quarter moon. Spawning around the full moon of this species is also reported in Tahiti (Randall and Brock 1960) and in Palau with large spawning aggregations (Sadovy de Mitcheson et al. 2012). Another common *Lutjanus* species, *Lutjanus decussatus*,

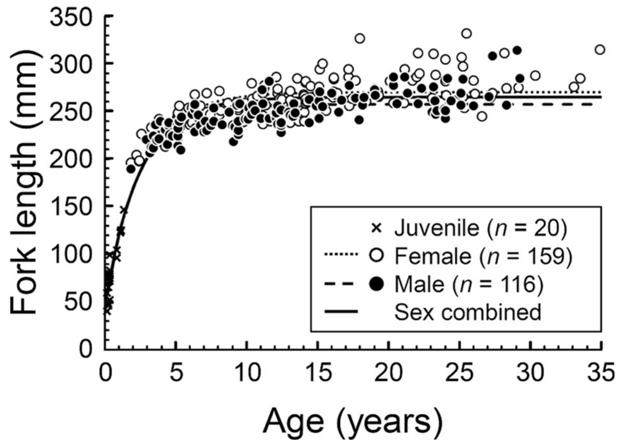


**Fig. 9** Fork length at age and the fitted von Bertalanffy growth curves for female and male blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands. Sex combined curve is also shown. Juvenile data were used to estimate all of the three growth curves

spawns only around the last quarter moon off the Yaeyama Islands (Nanami et al. 2010b). Lunar-related spawning is well known for some coastal lutjanid fishes (Grimes 1987; Davis and West 1993; D'Alessandro et al. 2010), while some other *Lutjanus* species spawn during any lunar phase (Hamamoto et al. 1992; McPherson et al. 1992). Spawning around a specific lunar phase restricts spawning frequency during a prolonged spawning season, and the potential number of total egg production becomes smaller for these species. Although spawning sites of blacktail snapper around the Yaeyama Islands have not been detected yet, the species is potentially vulnerable to fishing if the spawning sites are located and exploited.

Individual GSI of females often exceeded a value of 6.0 during the spawning season, and some females had a GSI of $>10.0$. On the other hand, GSI of males did not exceed 5.0 even in the peak spawning months. In the case of similar-sized and co-occurring *Lutjanus fulviflammus*, mean GSI of males is similar to that of females (Shimose, unpublished data) and monthly mean GSI of males over the value of females during the spawning season in the southern Arabian Gulf (Grandcourt et al. 2006). *Lutjanus fulviflammus* exhibit group spawning (Yokoyama, unpublished data) in all lunar phases (Shimose, unpublished data), and therefore large amounts of spermatozoa are beneficial. On the other hand, smaller testes of male blacktail snapper may be sufficient for short spawning days around the full moon and the last quarter moon, and males can recover their testicular size until the next spawning.

**Growth and longevity.** The present study revealed that otolith opaque zones in blacktail snapper were formed once per year around the Yaeyama Islands, and ages could be estimated accurately with a high precision. Many tropical and subtropical *Lutjanus* snappers exhibit clear seasonality of the otolith opaque zone formation, and these zones have been used for age determination (e.g., Newman et al. 1996; Cappo et al. 2000; Shimose and Tachihara 2005). Otolith opaque zones of blacktail snapper were formed between May and July, and the season agrees with the early spawning months in the area. Therefore, the number of opaque zones can be interpreted as yearly age (Shimose and Tachihara 2005; Nanami et al. 2010a). It is concluded that ages of blacktail snapper were appropriately determined by using sectioned otoliths, and this is the first study to estimate the age and growth of this species.

The maximum age of the blacktail snapper was recorded as 34 years in females caught in March indicating that this specimen was nearly 35 years old. *Lutjanus* snappers are relatively long lived, and maximum ages of some larger species ($\geq$ 50 cm TL) exceed 40 years: e.g., 56 years for *Lutjanus bohar* (see Marriott and Mapstone 2006), 52 years for *Lutjanus campechanus* (see Wilson and Nieland 2001), 48 years for *Lutjanus malabaricus*, 42 years for *Lutjanus erythropterus* (see Fry and Milton 2009), and 40 years for *Lutjanus sebae* (see Newman et al. 2010). In small *Lutjanus* species, however, the maximum ages are relatively low: e.g., 12 years for *Lutjanus vitta* (see Newman et al. 2000) and *Lutjanus ehrenbergii* (see Grandcourt et al. 2011), 19 years for *Lutjanus synagris* (see Luckhurst et al. 2000), 20 years for *Lutjanus carponotatus* (see Newman et al. 2000), 24 years for *Lutjanus adetti* (see Newman et al. 1996) and *L. fulviflammus* (see Shimose and Tachihara 2005), and rarely exceeds 30 years, e.g., 31 years for *Lutjanus quinquelineatus* (see Newman et al. 1996). Although longevity may change among areas within the same species (*L. fulviflammus*) (Shimose and Tachihara 2005; Grandcourt et al. 2006), the maximum age of blacktail snapper estimated in the present study is the oldest record for a small *Lutjanus* species.

The growth of blacktail snapper was rapid during the first 3 years of age attaining over 200 mm FL for both sexes and then became slower probably because of their maturation. Reproductive cost is often thought to be a main reason for inhibiting growth of small *Lutjanus* species (e.g., Newman et al. 2000; Shimose and Tachihara 2005). However, it is difficult to assume that there is no surplus energy for growth during their long life even after maturation (5 to 30 years of age). Decrease in growth rate after maturation may be caused by some benefits to maintain a small body size in coral reef habitats, and/or no benefit to increase their body size once they attain an appropriate size for reproduction. Decrease in growth rate and long life of this species led to a high variability of age at length. This means that the age composition of catch for this species cannot be estimated without age determination using sectioned otoliths.

Females had a slightly, but significantly larger mean FL and $L_\infty$ than male blacktail snapper. This trend is similar to some small *Lutjanus* species, *L. fulviflammus* (see Shimose and Tachihara 2005; Grandcourt et al. 2006), *L. ehrenbergii* (see Grandcourt et al. 2011), and *L. adetii* (see Newman et al. 1996), but different from *L. quinquelineatus* (see Newman et al. 1996). Some reasons of this sexual dimorphism are discussed (Newman et al. 1996; Shimose and Tachihara 2005); however, the hypotheses can not be applicable for both patterns, i.e., females > males and females < males. The size difference may be caused by the difference in timing of cost allocations to growth and reproduction.

**Implications for fisheries.** The first recruitment of blacktail snapper to the fishery was 1-year-old, but the main recruitment was $\geq$3 years old around the Yaeyama Islands. This recruitment age is almost the same as the age at sexual maturity for both sexes. Although the total and natural mortality was not determined because of the lack of market data, age composition in catch ranged widely and both mortalities were thought to be relatively low (Newman et al. 1996). The similar-sized snapper *L. carponotatus* fully recruit to the fishery at age 5 years and live for up to 20 years in the central Great Barrier Reef (Newman et al. 2000). Similarly, *L. fulviflammus* fully recruit to fisheries at age 1 year and live 24 years around Okinawa Island (Shimose and Tachihara 2006). One-year-old *L. fulviflammus* is small with a low market value at Okinawa Island, and is more marketable at 2 years of age when they are sexually mature (Shimose and Tachihara 2006). Blacktail snapper around the Yaeyama Islands have an earlier age of recruitment than *L. carponotatus*, but later than *L. fulviflammus*, and are thought as not being affected by growth overfishing. Although the current fishing effort to harvest blacktail snapper is not sufficiently large to collapse the stock immediately, monitoring the fisheries harvest is needed to keep the current level of its stock.

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