

## Age, growth, and reproduction of blackspot snapper *Lutjanus fulviflammus* (Forsskal 1775) around Yaeyama Islands, southern Japan, between 2010 and 2014

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### Summary

Age, growth, and reproductive characteristics of blackspot snapper *Lutjanus fulviflammus* around the Yaeyama Islands (24°N, 124°E) in southern Japan were investigated between 2010 and 2014. Samples were caught by angling or purchased monthly at fish markets to cover all size ranges and seasons. Specimens consisted of 280 females (176–347 mm fork length), 177 males (193–325 mm), and 17 juveniles (42–128 mm). Spawning was confirmed from April to August by the presence of postovulatory follicles, which, based on the occurrence of yolked oocytes possibly also occurred in March and September. Maximum fork length and age in the specimens around Yaeyama Islands were 347 mm and 23 years for females and 325 mm and 21 years for males. These results were compared to those reported previously for the species in other regions by standardized criteria. Possible spawning duration of 7 months in the population around Yaeyama Islands is similar to that in New Caledonia (22°S, 5 months) and Okinawa Island (26°N, 6 months), but shorter than that in Tanzania (8°S) and the southern Arabian Gulf (25°N) (~12 months). The maximum body sizes and ages around Yaeyama Islands are also similar to the populations in New Caledonia and Okinawa Island (>300 mm FL, >20 years old), but larger/older than those in Tanzania and the southern Arabian Gulf (<300 mm FL, <20 years old). These differences are thought to reflect water temperature, i.e. spawning duration is shorter in lower temperature regions (annual mean <26°C, New Caledonia, Okinawa Island, Yaeyama Islands) than in higher temperature regions (annual mean >27°C, Tanzania, southern Arabian Gulf). Subsequently, a shorter spawning duration extends the life-span as well as the maximum body size. Longevity of blackspot snapper is thought to be negatively correlated with the duration of the spawning season.

### Introduction

Blackspot snapper *Lutjanus fulviflammus* is a commercially exploited fish species widely distributed in the Indo-Pacific Ocean (Allen, 1985). Due to its commercial importance, the age, growth, and reproductive biology of the species have been studied in several regions. Loubens (1978, 1980a,b) estimated age, growth, and spawning season of the species along

with many other coastal fishes in New Caledonia (ca. 22–23°S, 166–167°E). Kamukuru and Mgya (2004), Kamukuru et al. (2005), Shimose and Tachihara (2005a, 2006) and Grandcourt et al. (2006) studied age, growth and reproductive biology of the species in Tanzania (ca. 8°S, 39–40°E), Okinawa Island, southern Japan (ca. 26°N, 128°E), and in the southern Arabian Gulf (ca. 24–27°N, 52–56°E), respectively. These four study sites are geographically distant from each other and located in the northern and southern hemispheres and in the Indian and Pacific oceans (Fig. 1). The more recent studies were published within 2 years of each other; hence, comparisons were drawn only to Loubens (1978, 1980a,b) work but they provide little discussion on geographical differences and similarities.

The present study investigated the age, growth, and reproductive biology of blackspot snapper around Yaeyama Islands (ca. 24°N, 124°E), southern Japan. The Yaeyama Islands are located ca. 2° south of Okinawa Island, where Shimose and Tachihara (2005a, 2006) also studied the species. The species composition of the genus *Lutjanus* differs greatly between the Yaeyama Islands and Okinawa Island, reflecting the different environments (Shimose and Nanami, 2013). The purpose of this study was to clarify the life history parameters of blackspot snapper around the Yaeyama Islands for comparison of the results with previously published studies, and to examine the possible reasons for the observed differences among the regions.

### Materials and methods

#### Sample collection

Adult samples of blackspot snapper ( $n = 457$ ) were purchased at the Yaeyama fish market (24°21'N, 124°09'E) from May 2010 to July 2014. These fish were captured around the Yaeyama Islands by handline and longline, with a small proportion caught by spear, gillnet, and small set net fisheries. Juveniles (<150 mm fork length) were not available at the market but were collected by angling at various sites on Ishigaki Island, a part of the Yaeyama Islands ( $n = 17$ ). Four years of data were combined for analyses to increase the sample size in each month, which was also beneficial to minimize possible annual fluctuations and to obtain rare large fish.

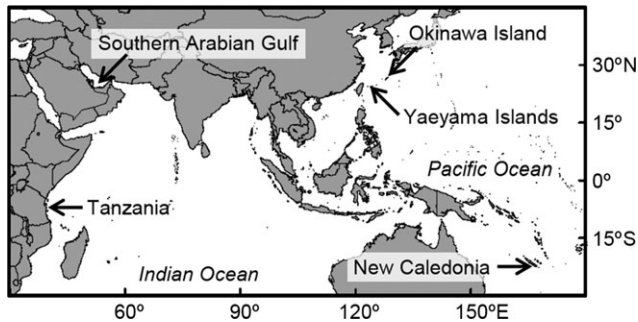


Fig. 1. Map of locations where life history of blackspot snapper *Lutjanus fulvivittatus* has been studied: New Caledonia (Loubens, 1978, 1980a,b), Tanzania (Kamukuru and Mgaya, 2004; Kamukuru et al., 2005), Okinawa Island (Shimose and Tachihara, 2005a), southern Arabian Gulf (Grandcourt et al., 2006), Yaeyama Islands (present study)

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 1 (juvenile) or 2 (adult) g. The weight of the contents in a specimen's stomach was deducted from the BW. Relationships of TL-FL and SL-FL were estimated by fitting linear functions by the least squares method for conversion purposes to compare with previous studies. The FL-BW relationship was also estimated by fitting a power function. Sex of each specimen was identified by visual inspection of the gonad morphology for fish  $\geq 150$  mm FL.

#### Observation of the gonads

Gonads of 277 females and 173 males were observed to estimate the spawning season and the size and age at sexual maturity. Sexual maturity first occurs at age-2 for both sexes (see Results), and the spawning season was estimated using  $\geq 2$ -year-old specimens. Gonad weight (GW) of both females and males was measured to the nearest 0.01 g, and the gonadosomatic index (GSI) was calculated for individual fish as  $GSI = GW \times 100/BW$ . The gonadosomatic index is the relative size of gonads and is commonly used to evaluate the reproductive activity of fishes. Gonads of females and males were histologically examined by standard methods (Shimose and Nanami, 2014). Histological observation is more accurate to estimate the spawning season and individual sexual maturity.

Ovarian developmental phases were divided into four phases based on the most advanced stage of oocytes, abundance of alpha stage atresia, and also the existence of postovulatory follicles (Ebisawa, 1999; Shimose and Nanami, 2014). The least developed phase of the ovary was 'inactive' (Fig. 2a), containing only peri-nucleolus and/or yolk vesicle oocytes. The second development phase was 'mature' (Fig. 2b): late yolk globule stage oocytes were present, and indicated the possible occurrence of spawning. Ovaries with early yolk globule ( $n = 4$ ) and migratory nucleus oocytes ( $n = 3$ ) were also included in this phase because of their infrequent occurrence. The third development phase was

'spawned' (Fig. 2c): postovulatory follicles were observed, and indicated the evidence of spawning. The last phase was 'atresia' (Fig. 2d): the alpha stage of atresia was observed with  $>70\%$  proportion, and indicated cessation of spawning.

Testicular developmental phases were divided into four phases based on the area of spermatozoa occupied in the section and frequency of areas showing active spermatogenesis (Ebisawa, 1999; Shimose and Nanami, 2014). The least developed phase was 'inactive' (Fig. 2e), mostly containing spermatogonia and few areas in spermatogenesis. The second development phase was 'maturing' (Fig. 2f), occurrence of spermatogenesis but only a small amount of spermatozoa ( $<40\%$ ) not sufficient for spawning. The third development phase was 'mature' (Fig. 2g), active spermatogenesis occurred and a large amount of spermatozoa ( $40\text{--}70\%$ ) observed. The fourth development phase was 'spent' (Fig. 2h), where a portion of spermatozoa had been released and the amount of spermatogenesis had decreased, but a large amount of spermatozoa ( $>70\%$ ) was still present.

#### Age determination and growth analysis

Right and left sagittal otoliths were removed from 444 individuals (111–347 mm FL), and preserved in a dry condition for age determination. Otoliths were transversely sectioned including the core and placed on glass slides. The sections were approximately 0.3 mm thick. 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. Otolith edge condition was classified into three types (Shimose and Nanami, 2014): opaque, narrow translucent (less than half the width of previous translucent zone), or wide translucent (more than half the width of previous translucent zone). The month when yearly age increases was assumed as 1 April, because spawning in the study area was confirmed from April (see Results). Following Shimose and Nanami (2014), 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, and 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. This age estimation was conducted twice by a single reader 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. 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 ( $n = 6$ , 42–124 mm FL) were not observed; these sizes were considered to be 0-year-old, based on the growth rate estimated by modal progression analysis in Okinawa Island (Shimose and Tachihara, 2005a).

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



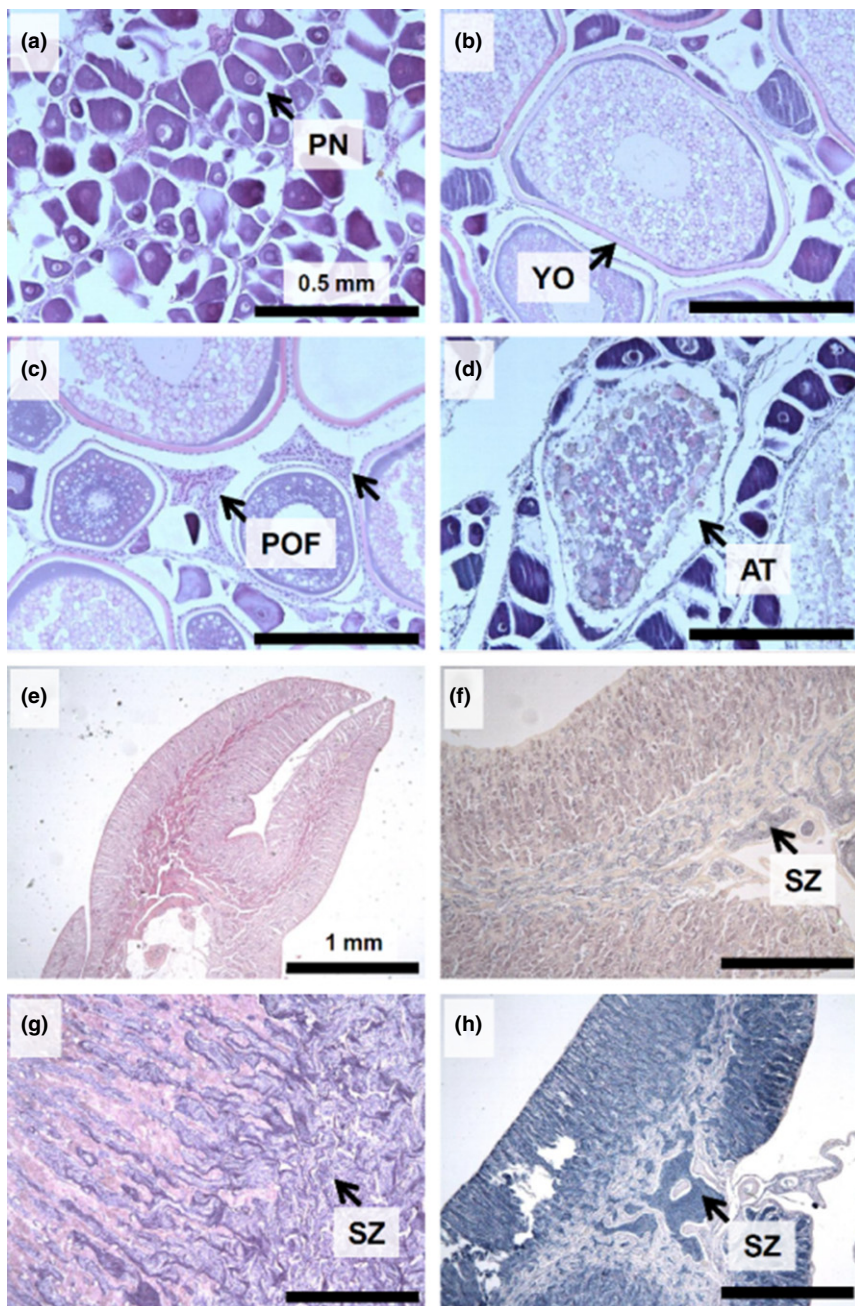


Fig. 2. Photomicrographs of histological slides for four ovarian and four testicular developmental phases of blackspot snapper *Lutjanus fulvivittatus*. (a) Inactive phase ovary with only peri-nucleolus oocytes (PN); (b) Mature phase ovary with yolk globule stage oocytes (YO); (c) Spawned phase ovary with postovulatory follicles (POF); (d) Atresia phase ovary with abundant alpha stage atresia (AT); (e) Inactive phase testis mostly containing spermatogonia; (f) Maturing phase testis with a small amount of spermatozoa (SZ) and inactive spermatogenesis; (g) Mature phase testis with large amounts of spermatozoa (SZ) and active spermatogenesis; (h) Spent phase testis with decreased levels of spermatogenesis but with large amounts of spermatozoa (SZ). Scale bar = 500  $\mu\text{m}$  in a–d; 1 mm in e–h

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

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 at 1 month (=1/12 years) intervals with the assumption of hatch month = April. Sex combined and sex-specific growth parameters were estimated. Juvenile data ( $n = 17$ , 42–128 mm FL) for which the 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

### Sizes of juveniles, females, and males

Fork lengths of 280 females purchased at the fish market were from 176 to 347 mm, and dominated by the 220–310 mm classes (90%). Fork lengths of 177 males were from 193 to 325 mm, dominated by the 220–290 mm classes (85%). Mean ( $\pm$ SD) FL of females was 265 ( $\pm$ 29) mm and

significantly larger than that of males 255 ( $\pm 25$ ) mm (Welch's *t*-test; *t* = 3.91, *df* = 413.7, *P* < 0.001).

Relationships between TL-FL, SL-FL and FL-BW, ranging from 43 to 377 mm TL, 42–347 mm FL, 35–300 mm SL, and 1–968 g BW, were expressed by the equations:

$$FL = 0.93 \times TL + 0.4; n = 474, R^2 = 0.99$$

$$FL = 1.17 \times SL + 4.7; n = 437, R^2 = 0.99$$

$$BW = 21.14 \times 10^{-6} \times FL^{2.98}; n = 474, R^2 = 0.99$$

#### Spawning season

The smallest sexually mature female and male were 212 and 193 mm FL, respectively. Gonadosomatic indices showed similar seasonal trends for females and males (Fig. 3). Mean GSI values for females and males began to increase in April (female: 2.70, male: 3.10), reached a peak in May (4.00, 4.09) and then decreased from June (3.69, 3.69) through to August (1.35, 1.40). From September to March GSI values for females and males were small (<1.0).

Females in the mature and the spawned phases were observed from March to September and indicating possible spawning, with higher frequency in May (94%) and June (86%) (Fig. 4). Females in the spawned phase were observed from April to August (5–36%) and indicating the evidence of spawning. Males in mature phase were observed from March to December, and in high frequency from March to August (71–93%). Females in the spawned phase were observed at all lunar phases.

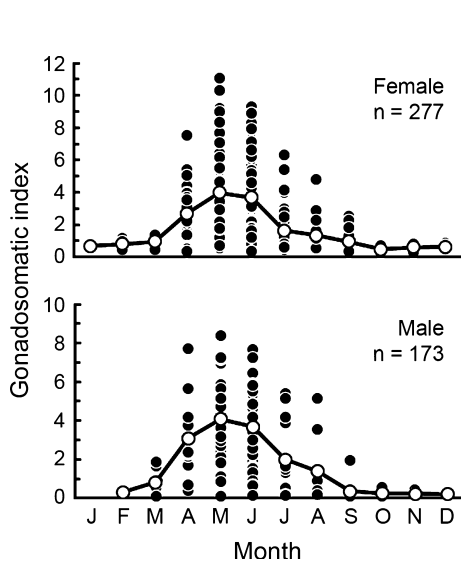


Fig. 3. Monthly changes in the gonadosomatic index, female and male blackspot snapper *Lutjanus fulvivflammas*, around the Yaeyama Islands. Open circles = monthly plotted mean values and connected by a solid line

#### Age and growth

The sectioned otoliths had distinct opaque and translucent zones alternately formed from the core to the edge (Fig. 5). Opaque zones appeared on the edge of the otolith from February to August and October, with a high frequency from April to June (66–80%) (Fig. 6). A single peak in a year and nearly 100% switch between an opaque edge (80% in June) and translucent edge (100% from November to January) indicated that the opaque zone was formed annually. Of 444 otoliths, two small individuals were aged to be less than 1 year old. In the two age determinations of 442 otoliths, 413 (93%) showed complete agreement between results. Mean APE and CV were quite low, with values of 0.72 and 1.02, respectively.

Ages of unsexed juveniles (<150 mm) were estimated to be 0–1 years old (Table 1). Ages of females were estimated to be from 1 to 23 years old, and dominated by the 2–17 years old classes (96%). Male ages were estimated to be from 2 to 21 years old, dominated by the 2–15 year old classes (94%). The oldest female (23 years) was 291 mm FL and not the largest in size; the largest female (347 mm FL) was 22 years old. The oldest male (21 years) was the largest fish (325 mm FL).

Mean ( $\pm$ SE) values of von Bertalanffy growth parameters were  $L_{\infty}$  = 287 ( $\pm 2$ ) mm,  $k$  = 0.44 ( $\pm 0.02$ ), and  $t_0$  =  $-0.36$  ( $\pm 0.08$ ) years for females, 266 ( $\pm 2$ ) mm, 0.52 ( $\pm 0.03$ ), and  $-0.22$  ( $\pm 0.08$ ) years for males, and 279 ( $\pm 1$ ) mm, 0.45 ( $\pm 0.02$ ), and  $-0.42$  ( $\pm 0.09$ ) 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 2–3 years and the fish attained a size of about 185 mm at age 2 and about 220 mm at age 3 (Fig. 7). Sexual difference in growth rate appeared from age 4 (*P* < 0.05), and females grew to be larger than

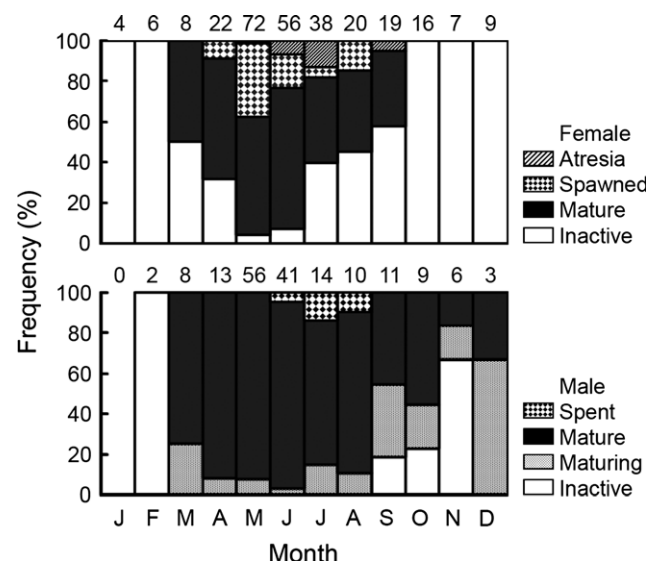


Fig. 4. Monthly changes in frequency of ovarian and testicular developmental phases, blackspot snapper *Lutjanus fulvivflammas*, around Yaeyama Islands. Numbers above bars = numbers of samples

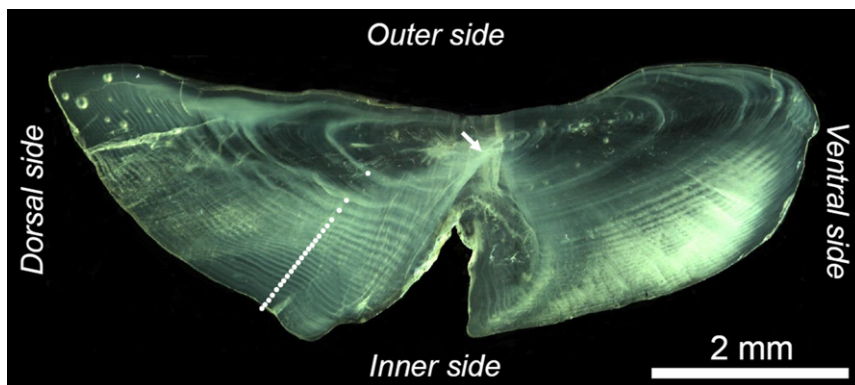


Fig. 5. Photograph of sectioned otolith of oldest female blackspot snapper *Lutjanus fulviflammus*, 291 mm fork length and estimated at 23 years of age. Arrow and dots = core and opaque zones, respectively

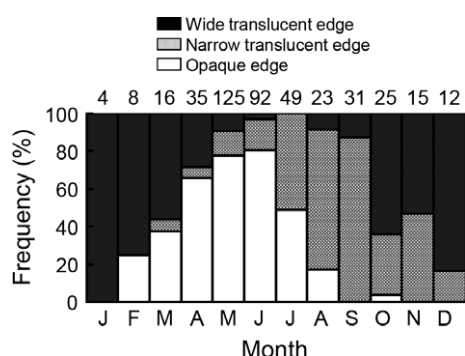


Fig. 6. Monthly changes in frequency of occurrence for opaque, narrow translucent, or wide translucent zones on otolith edge of blackspot snapper *Lutjanus fulviflammus* around Yaeyama Islands. Numbers above bars = number of samples

males. Likelihood ratio tests revealed significant differences between sexes for  $L_{\infty}$  ( $P < 0.001$ ) and  $k$  ( $P < 0.05$ ), but not for  $t_0$  ( $P = 0.288$ ), because the same juvenile data were used for both females and males.

The estimated ages of the smallest sexually mature female (212 mm) and male (193 mm) were 2 years; >50% were mature at age 3 for females and age 2 for males.

## Discussion

Spawning seasonality of blackspot snapper around Yaeyama Islands was confirmed from April to August by the observation of postovulatory follicles (spawned phase females). Mean monthly GSI data for both sexes and a higher frequency of occurrence of mature/spawned phase females indicated that the period May to June was the peak spawning season. The occurrence of yolked oocytes (mature phase) in the ovarian sections, which is normally a good indicator of spawning (Shimose and Tachihara, 2005a,b), suggests that spawning most likely also occurred in March and September. On the other hand, males in the mature phase were found over a more protracted period (March to December), implying that testicular developmental phases are not a precise indicator of spawning.

Mean FL and  $L_{\infty}$  of blackspot snapper around Yaeyama Islands were significantly larger in females than males. Simi-

lar observations were made in all other regions (Kamukuru et al., 2005; Shimose and Tachihara, 2005a; Grandcourt et al., 2006). The reason for this sexual dimorphism in body size has not yet been fully elucidated for *Lutjanus* snappers (Shimose and Tachihara, 2005a; Shimose and Nanami, 2014). Growth rate decreased from age 3 and sexual dimorphism in length-at-age started from age 4, probably because of maturation. Observed maximum ages between sexes (females, 23 years; males, 21 years) were not much different, and sexual difference in maximum age is also not reported in other regions (females 22 years vs males 23 years, Loubens, 1980b; 18 vs 14, Kamukuru et al., 2005; 24 vs 24, Shimose and Tachihara, 2005a; 14.3 vs 12.8, Grandcourt et al., 2006) (Table 2).

Spawning season around Okinawa Island is confirmed from April to July with possible spawning in August and September (Shimose and Tachihara, 2005a), which is very similar to that around Yaeyama Islands. Geographical difference of  $2^{\circ}$  in latitude (and therefore temperature) might cause slight differences in spawning duration between the two regions. Although the sample size is not large ( $n = 68$ ), the spawning season of blackspot snapper in New Caledonia is estimated to be at least 5 months from October to February (Loubens, 1980a). Spawning season in the southern Arabian Gulf is estimated to be 4 months from April to July, from the observations of 'hyaline eggs free running (ripe stage)' (Grandcourt et al., 2006), which is similar to the observations around Okinawa and Yaeyama Islands. However, 'hyaline eggs not free running (mature stage)' and 'cream colored eggs (maturing stage)' are found in the remaining 8 months in the southern Arabian Gulf (Figure 6 in Grandcourt et al., 2006), and implies that intermittent spawning possibly occurs throughout the year. The spawning season in Tanzania is estimated to be 7 months, from September to March with a peak in December (Kamukuru and Mgaya, 2004). Although the result is based on sex-combined data, 'active' stage gonads are found in all months in Tanzania (Figure 5 in Kamukuru and Mgaya, 2004), and spawning possibly occurs throughout the year. Annual mean water temperature is higher in Tanzania ( $7-8^{\circ}\text{S}$ ,  $40-41^{\circ}\text{E}$ ,  $27.2^{\circ}\text{C}$ ) and the southern Arabian Gulf ( $25-26^{\circ}\text{N}$ ,  $54-55^{\circ}\text{E}$ ,  $27.4^{\circ}\text{C}$ ), and lower in New Caledonia ( $22-23^{\circ}\text{S}$ ,  $166-167^{\circ}\text{E}$ ,  $23.9^{\circ}\text{C}$ ), Okinawa Island ( $26-27^{\circ}\text{N}$ ,  $127-128^{\circ}\text{E}$ ,  $24.8^{\circ}\text{C}$ ) and the Yaeyama Islands ( $24-25^{\circ}\text{N}$ ,  $124-125^{\circ}\text{E}$ ,  $25.8^{\circ}\text{C}$ ) (Japan Oceanographic Data Center,



Table 1  
Mean fork length (FL, mm) per age class for female and male blackspot snapper, *Lutjanus fulvivflammus*, around Yaeyama Islands between 2010 and 2014

Age class (years)	Sex unknown			Female			Male			t-test P
	n	Mean	SD	n	Mean	SD	n	Mean	SD	
0	8	84.0	36.5							
1	9	112.9	11.7	1	176.0					
2				15	220.2	10.9	11	212.5	10.6	0.085
3				36	231.2	8.9	14	230.1	9.6	0.708
4				22	246.2	9.7	12	235.7	13.3	0.027*
5				20	253.6	10.7	13	241.6	11.4	0.006**
6				26	263.2	14.6	14	246.9	11.4	<0.001***
7				23	263.3	13.8	9	249.3	17.4	0.051
8				13	271.5	14.7	16	259.5	11.1	0.024*
9				19	276.7	13.0	21	254.6	14.0	<0.001***
10				23	281.6	14.0	12	257.4	20.7	0.002**
11				7	284.3	22.7	8	257.7	13.8	0.023*
12				11	282.0	13.6	8	275.3	16.8	0.364
13				3	314.0	22.3	7	276.1	24.2	0.071
14				12	291.3	25.4	6	280.2	17.9	0.303
15				7	300.4	23.0	4	280.1	2.8	0.059
16				12	296.6	15.6	2	274.5	0.7	<0.001***
17				7	311.9	23.8	2	292.0	17.0	0.300
18				4	291.9	22.1	3	302.0	8.7	0.451
19				1	322.0		1	307.0		
20				3	290.8	13.9	1	268.0		
21							1	324.5		
22				2	313.5	47.4				
23				1	291.0					

Mean lengths are compared between sexes by *t*-test \* $<0.05$ , \*\* $<0.01$ , \*\*\* $<0.001$ . n = sample size, SD = standard deviation, P = probability value.

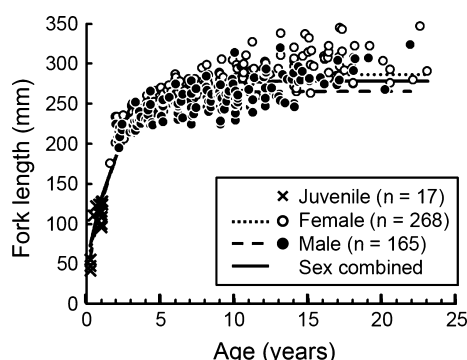


Fig. 7. Fork length at age and fitted von Bertalanffy growth curves, female and male blackspot snapper *Lutjanus fulvivflammus* around Yaeyama Islands. Sexes combined curve also shown. Juvenile data used to estimate all three growth curves

[http://www.jodc.go.jp/index\\_j.html](http://www.jodc.go.jp/index_j.html)). Thus considered, possible spawning duration tends to be shorter in lower temperature regions (5 months in New Caledonia, 6 months in Okinawa Island, 7 months in the Yaeyama Islands) and longer in higher temperature regions (12 months in the southern Arabian Gulf and in Tanzania) (Fig. 8).

Maximum FL in New Caledonia [(females, 339 mm; males, 307 mm, converted from SL (Loubens, 1980a)] and Okinawa Island [(females, 361 mm; males 321 mm, converted from SL (Shimose and Tachihara, 2005a)] are similar to those around the Yaeyama Islands [(females, 347 mm; males, 325 mm)], all exceeding 300 mm FL. Maximum age in these three areas also exceeds 20 years for both sexes (Loubens, 1980a; Shimose and Tachihara, 2005a; present

study). On the other hand, the maximum FL of the fish in Tanzania [(sexes combined: 277 mm, converted from TL (Kamukuru et al., 2005)] and in the southern Arabian Gulf [(females, 287 mm; males, 258 mm (Grandcourt et al., 2006)] are smaller than those in New Caledonia, Okinawa Island, and the Yaeyama Islands. Maximum ages in Tanzania [(sexes combined: 18 years) (Kamukuru et al., 2005)] and the southern Arabian Gulf [(females, 14.3 years; males, 12.8 years (Grandcourt et al., 2006)] are also less than those observed in the other three regions, even for the greater number of specimens observed (Table 2). This may suggest that populations of blackspot snapper in lower temperature regions tend to grow larger and live longer than in higher temperature regions (Fig. 8). Differences in body size and longevity may be explained by latitude or water temperature. A larger body size in higher latitudes is reported for John's snapper *Lutjanus johnii* (Cappo et al., 2013), and a shorter life-span in higher temperature regions is known in surgeonfishes *Acanthurus bahianus* (Robertson et al., 2005) and *Ctenochaetus striatus* (Trip et al., 2008). A smaller maximum body size and shorter life-span is found in higher latitudes and higher temperature regions (25–26°N, 27.4°C, southern Arabian Gulf), indicating that the current results of length and longevity of blackspot snapper correlate more closely with temperature rather than with latitude (Fig. 8).

The five populations of blackspot snapper with known life history parameters were divided into two groups (Table 2): those with a longer life-span and a bigger maximum size (New Caledonia, Okinawa Island, Yaeyama Islands), and those with a shorter life-span and a smaller maximum size (Tanzania, southern Arabian Gulf). Lower

Table 2

Comparison in life history parameters of blackspot snapper *Lutjanus fulvivflammmus* among five geographically separate regions. Fork length (FL) is used for body size and converted from standard length or total length, when necessary. Mean water temperature (WT) data is from Japan Oceanographic Data Center (see text)

Region (latitude) (Reference)	Sex	Mean WT (°C)	Number observed	Max. FL (mm)	Max. age (years)	$L_{\infty}$ (mm)	$k$ (year <sup>-1</sup> )	$t_0$ (years) *	First maturity		50% maturity	
									mm FL	Years	mm FL	Years
New Caledonia (22°S) (Loubens, 1980a,b)	Combined	23.88	68	339	23	295	0.30					
	Female		36	339	22	302			206	4**	—	—
	Male		32	307	23	284			221	6**	—	—
Tanzania (8°S) (Kamukuru and Mgaya, 2004; Kamukuru et al., 2005)	Combined	27.24	2,344	277	18	271	0.15	-2.7			182–202	6**
Okinawa I. Japan (26°N) (Shimose and Tachihara, 2005a)	Combined	24.84	901	361	24							
	Female		230	361	24	328	0.144	-5.22	209	2	—	3
	Male		307	321	24	294	0.227	-3.18	208	2	—	—
Southern Arabian Gulf (25°N) (Grandcourt et al., 2006)	Combined	27.35	690	287	14.3	232	1.0	-0.06				
	Female		444	287	14.3	236	1.0	-0.06	—	—	187	1.9
	Male		246	258	12.8	223	0.9	-0.14	—	—	167	1.6
Yaeyama Island, Japan (24°N) (Present study)	Combined	25.83	474	347	23	279	0.45	-0.42				
	Female		280	347	23	287	0.44	-0.36	212	2	—	3
	Male		177	325	21	266	0.52	-0.22	193	2	—	2

\* $t_0$  not adjusted in length conversion

\*\*Converted from FL using a growth function in the area.

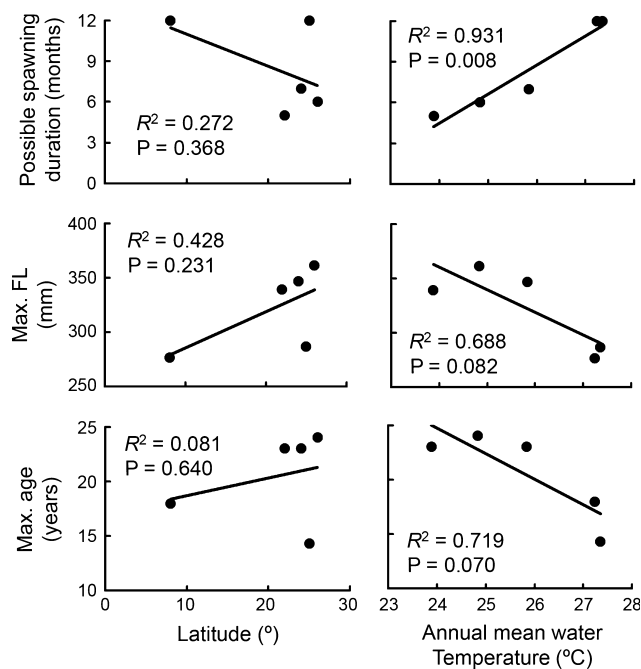


Fig. 8. Relationships between latitude/annual mean water temperature and possible spawning duration/maximum fork length/maximum age of blackspot snapper *Lutjanus fulvivflammmus* in five different regions. Data source is in Table 2 and in the text

water temperatures shorten the spawning duration, and subsequently extending the longevity and also leading to larger maximum body sizes (Robertson et al., 2005). Life history parameters are pliable through the effects of temperature, and longevity is negatively correlated with the duration of the spawning season. To discuss this theory, quantitative

comparison with more detailed information (e.g. batch fecundity, spawning frequency in each month and age) and standardized methodology to estimate reproductive output are required.

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