

# Age-based demography and sexual pattern of the white-streaked grouper, *Epinephelus ongus* in Okinawa

Itaru Ohta  · Akihiko Ebisawa

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**Abstract** The demography and sexual pattern of the white-streaked grouper, *Epinephelus ongus* (Serranidae), in the Yaeyama Islands, Okinawa, were examined based on age assessment using otoliths and gonadal histology. The von Bertalanffy growth parameters were estimated as follows:  $L_{\infty} = 34.35$  cm total length (TL);  $K = 0.187 \text{ yr}^{-1}$ ; and  $t_0 = -0.975 \text{ yr}$ . The maximum age was 20 yrs. The smallest mature female was 18.9 cm TL, and the age of females at 50 % maturity was estimated to be 3.3 yrs. There were significant differences between sexes in size and age, with males (mean  $\pm$  SD:  $29.2 \pm 3.3$  cm TL,  $9.0 \pm 2.7$  yr) being larger- and older than females ( $23.5 \pm 3.4$  cm TL,  $5.9 \pm 1.8$  yr). Inactive bisexuals appeared in intermediate size and age between both sexes, suggesting that bisexuals were essentially recognized as being in a transitional phase from functional female to male. These facts indicated a monandric protogynous hermaphrodite of the species. Furthermore, transitionals were found only in the non-reproductive period that precedes the

spawning aggregation period, indicating that the timing of the sex change has seasonality.

**Keywords** Growth · Maturity · Sex change · Monandric protogynous hermaphrodite · Sex ratio · Serranidae

## Introduction

Groupers (family Serranidae) are one of the most heavily exploited fishes on coral reefs in the world, because of their commercial importance (Heemstra and Randall 1993). There are growing concerns about the overexploitation of groupers, with all of 163 species of groupers listed on the International Union for the Conservation of Nature (IUCN) Red List ([www.iucnredlist.org](http://www.iucnredlist.org)). The Red List assessment shows that 20 grouper species (12 %) are at risk of extinction, and an additional 22 species (13 %) are considered to be Near Threatened (Sadovy de Mitcheson et al. 2013).

Three aspects of the ecological characteristics of groupers increase their vulnerability to overfishing. Firstly, groupers are generally known to be long-lived, slow-growing, have relatively low rates of natural mortality, and take many years to mature sexually (Manooch 1987; de Sadovy Mitcheson et al. 2013). Secondly, many groupers are known to exhibit protogynous hermaphroditism (de Sadovy Mitcheson and Liu 2008). Thirdly, many groupers have the habit of forming spawning aggregations at specific times and places that are often associated with the lunar cycle (Johannes 1978; Domeier and Colin 1997; Hamilton et al. 2005; Sadovy de Mitcheson and

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I. Ohta (✉) · A. Ebisawa  
Okinawa Prefectural Fisheries Research and Extension Center,  
Kyan 1528, Itoman, Okinawa 901-0354, Japan  
e-mail: ootaitar@pref.okinawa.lg.jp

*Present Address:*  
A. Ebisawa  
Okinawa Prefectural Fisheries Research and Extension  
Center, Ishigaki Branch, Kabira 828-2, Ishigaki,  
Okinawa 907-0453, Japan

Colin 2012). The spawning aggregations are highly predictable and thus are often targeted by artisanal and commercial fisheries. Such aggregations could be very vulnerable because many individuals can be efficiently caught in their reproductive season prior to spawning (Sadovy and Domeier 2005; Sadovy de Mitcheson et al. 2008; Sadovy de Mitcheson 2016). Furthermore, size-selective fisheries including aggregation fishing often target larger males and thus impact the stock dynamics of protogynous species (Huntsman and Schaaf 1994; Coleman et al. 2000; Armsworth 2001; Alonzo and Mangel 2004, 2005).

The white-streaked grouper *Epinephelus ongus* is widely distributed in the Indo-Pacific region from the east coast of Africa (northern Mozambique to Kenya) to the Ryukyu and Marshall Islands and south to Fiji, New Caledonia and northern Australia (Heemstra and Randall 1993). The species occurs in shallow water on coral reefs and rocky substrata (Heemstra and Randall 1993), especially in association with *Acropora* spp. (Nanami et al. 2013a). The maximum size of the species is 40 cm in standard length (Heemstra and Randall 1993). *E. ongus* is known to form spawning aggregations and are important fishery targeted species at some locations (Daw 2004; Hamilton et al. 2005). Particularly, *E. ongus* is one of the most common species in coral reef fish fisheries in the Yaeyama Islands, Okinawa, Japan, catches of the species ranked only below the leopard coral grouper *Plectropomus leopardus* among 42 species of groupers landed (Ohta 2008).

Some recent studies conducted in the Yaeyama Islands revealed reproductive biology of *E. ongus*. They form the transient spawning aggregations in at least five spawning sites in the region during the main spawning season from April to June (Ohta and Nanami 2009; Nanami et al. 2014; Ohta and Ebisawa 2015). There are two spawning periods associated with the specific lunar cycle, the spawning events are concentrated within a few days after the last quarter moon in two consecutive months (Nanami et al. 2013b, 2014; Ohta and Ebisawa 2015). The spawning migration distance to the major spawning site is estimated to be 2.2 to 8.8 km based on the tag and recapture method (Nanami et al. 2015). Furthermore, an investigation using acoustic telemetry showed that several individuals of the species migrated to the major spawning site and returned to the home reefs (Nanami et al. 2014). Thus, the spawning

aggregations of the species show distinct seasonality, lunar periodicity, and site fidelity, therefore, the spawning aggregations have been traditional targets in the region. Consequently, the catches during the two spawning months accounted for about 40 % of the annual total catches (Ohta and Ebisawa 2015), and annual total catches of *E. ongus* in the Yaeyama Islands have declined by about one-half over the past two decades, indicating depletion of the stock (Ohta et al. 2007; Ohta 2008). Although the species is listed as a species of “Least Concern” on the IUCN Red List (Russell et al. 2008), some aggregations have also been described as decreasing as well as in the Yaeyama Islands (SCRFA Global Database 2010). Therefore, biological information is urgently needed to aid in fisheries management.

However, the understanding of the demographic biology and sexual patterns of the species is limited to preliminary researches conducted in Okinawa (Craig 2007) and the Great Barrier Reef (Maplestone et al. 2009). Because of the diversity of sexual patterns, confirmation of the functional sexual pattern of hermaphrodites requires histological examination over a wide size range of adults and juveniles (Sadovy de Mitcheson and Liu 2008). Additionally, age-based analysis of sex distribution provides strong evidence of sexual pattern (Sadovy and Shapiro 1987; Pears et al. 2006; Rhodes et al. 2011). Protogyny has been confirmed in five genera of epinephelines, *Alphistes*, *Cephalopholis*, *Epinephelus*, *Mycteroperca*, and *Plectropomus* (Sadovy de Mitcheson and Liu 2008; Marques and Ferreira 2011). Most species appear to be monandrous (Sadovy de Mitcheson and Liu 2008), though some species were also confirmed to be diandrous (Siau 1994; Fennessy and Sadovy 2002; Adams 2003; Liu and Sadovy 2004; Marques and Ferreira 2011); however, some species were demonstrated to be gonochoristic (Sadovy and Colin 1995; Rhodes et al. 2011). A previous study suggested that *E. ongus* is a monandric protogynous hermaphrodite (Maplestone et al. 2009); however, the details of its sexual pattern and sex-change are not reported.

The objective of this study was to determine the characteristics of the reproduction and demography of *E. ongus* in the Yaeyama Islands by a combination of sectioned otolith analysis and histological assessment of the gonads, particularly to determine the (1) growth and longevity, (2) size and age at maturity, (3) sexual pattern for the purpose of fishery management.

## Materials and methods

### Sampling and study localities

A total of 885 specimens of *E. ongus* ranging from 13 to 39 cm in total length (TL) were examined. The specimens were collected in the Yaeyama Islands (24°20'N, 124°03'E), Okinawa, located in the most southwestern part of the Ryukyu archipelago, Japan (Fig. 1). Most of the fishes caught around the Yaeyama Islands are traded through one of just two markets, the local fish market of the Yaeyama Fishery Cooperative on Ishigaki Island, which is the only wholesale market in the Yaeyama Islands, or the central market at Tomari on Okinawa Island, which is 400 km northeast of the Yaeyama Islands (Ohta and Ebisawa 2015). Of the 885 specimens collected by haphazardly samplings, 160 fish were obtained at the Tomari fish market in May and June 2004 and 2005, and 492 fish were obtained at the fish market of the Yaeyama Fishery Cooperative from June 2007 to October 2009. These samples were caught mainly using spears ( $n = 567$ ), and additionally using lines, gill nets, set nets and trap cages. The remaining 233 specimens were collected by the authors using spears or by underwater line fishing; these include 135 fish taken from the spawning aggregation in the Yonara Channel, which is the largest aggregation site in the Yaeyama Islands (Ohta and Nanami 2009; Nanami et al. 2013b, 2014). For all specimens, TL and body weight (BW) were measured to the nearest 0.1 cm and 0.001 kg, respectively.

### Age and growth

Sagittal otoliths were removed from 859 *Epinephelus ongus*, cleaned and stored dry. Each pair of intact otoliths was weighed to the nearest 0.001 g. Because the otoliths were often broken by spears, the sagittal weight was given as the average of a pair of intact otoliths or as the values from a single intact otolith.

One of each pair of the otoliths was embedded in epoxy resin and sectioned transversely through the core at a thickness of about 0.5 mm using an EXAKT micro cutting machine with a diamond saw. Each section was mounted on a glass slide with a medium (Eukitt: O. Kinder) and glass coverslip. Sectioned otoliths were examined under a microscope with reflected light. Alternating opaque and translucent zones were visible, so it was assumed that one pair of opaque and translucent zones was laid down each year as one annulus. The

number of opaque zones was counted along a consistent axis near the sulcus, where the zones were most visible, on at least two occasions with an interval of over two weeks between counts and without knowledge of the length of the fish. If the two counts coincided, that reading was accepted, but if they differed, the otolith was read once more, and any two coinciding counts were accepted. The precision of these counts was quantified by the coefficient of variance (CV; Campana 2001).

Edge type analysis was conducted to test the assumption that the increments were annuli. The edge of each otolith section was judged to be opaque or translucent. The monthly frequency of opaque edges was compared to a uniform distribution using a  $\chi^2$  goodness-of-fit test for circular distributions (Zar 1984). If it was difficult to determine the edge type, it was excluded from the analysis. On the assumption that opaque zones were annual rings, the age for each individual was the number of opaque zones counted. However, the age was the number of opaque zones counted +1 for individuals with relatively wide translucent edges collected in the zone formation period, because it was considered that terminal zone formation would begin in the near future (Shimose and Nanami 2014). In addition to the age, 1/12 yr. from birth month to sampling month was given as the monthly age. The birth month was defined as May considering the spawning season of the species in this area runs from April to June (Ohta and Ebisawa 2015). A von Bertalanffy growth function (VBGF) was fitted to TL at the presumed age by the non-linear least square method to estimate the growth characteristics of this species. The VBGF is represented by

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

where  $L_t$  is the TL of a fish at age  $t$ ,  $L_\infty$  is the mean asymptotic TL,  $K$  is the growth coefficient, and  $t_0$  is the theoretical age at which TL = 0.

### Histological sex determination and sexual pattern

Gonads from 854 *E. ongus* were weighed to the nearest 0.01 g and were fixed in Bouin's fixative (15 saturated picric acid: five formaldehyde, one glacial acetic acid). Within 24 h after fixation, the samples were transferred to 90 % ethanol for long-term preservation and histological sectioning. The tissues for sectioning were embedded in paraffin, sectioned at 6  $\mu$ m, and stained with

Mayer's hematoxylin solution and 0.5 % eosin aqueous solution. Based on the observations of the sectioned gonads, the sex and the developmental stage of each gonad were determined histologically. Five developmental stages as follows perinucleolus stage, cortical alveolus stage, vitellogenic stage, hydrated stage, and post-spawning stage were used (Ohta and Ebisawa 2015). Careful observations were conducted to examine if they had male germ cells for ovaries or remnant ovarian structures for testes, such as residual oocytes, central lumen, and gonadal lamella.

The term inactive bisexual was defined for individual, which had bisexual gonad with developing testicular tissues and scattered previtellogenic oocytes (Fennessy and Sadovy 2002; Sadovy de Mitcheson and Liu 2008).

Differences of the size and age structure between sexes in the samples were determined by Kolmogorov-Smirnov test. TL and age at 50 % maturity for females based on the specimens in the spawning season were estimated by each logistic equation as:  $y = 1/[1 + \exp.(-a-bx)]$ . Parameters  $a$  and  $b$  were estimated by the non-linear least square method for each relationship. A mature female in this study was defined as an individual having more advanced oocytes than cortical alveolus stage in the spawning season (Brown-Peterson et al. 2011). TL and age at a 50 % sex ratio were also estimated by logistic equations. To estimate actual sex ratio of catches, the logistic equation for TL was applied for observed size distribution data ( $n = 1328$ ) of landings

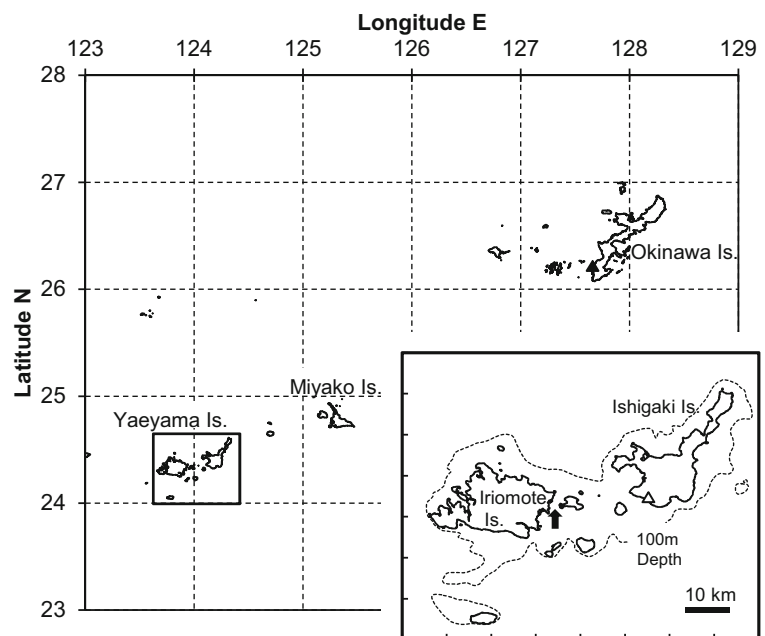
around the spawning season (from 3rd to 6th month in the lunar calendar) in the Yaeyama Islands (Fig. 15 in Ohta and Ebisawa 2015).

## Results

### Age and growth

Of the 859 otolith specimens of *E. ongus*, 781 (91 %) showed distinctive increments when sectioned (Fig. 2). In the two counts of 781 otoliths, 701 (90 %) showed complete agreement between counts. Mean CV was quite low with value of 0.85. Edge type analysis revealed an annual periodicity of increment formation with significant differences among the monthly frequencies of opaque edges ( $\chi^2 = 1370$ ,  $p < 0.001$ ). The monthly frequency of otoliths with opaque margins increased from April to July and was over 80 % from May to June (Fig. 3). There was a significant positive correlation between otolith weight and the presumed age of the fish ( $r^2 = 0.79$ ,  $p < 0.001$ ) (Fig. 4). These findings strongly indicated that the age determination done in this study was effective. The growth parameters calculated by fitting the VBGF to the length at age data for sexes combined ( $n = 747$ ) were as follows:  $L_\infty = 34.35$  cm TL, the coefficient of growth  $K = 0.187 \text{ yr.}^{-1}$ , and the theoretical age at zero length  $t_0 = -0.975 \text{ yr.}$  (Fig. 5). The youngest fish examined were 1 yr. The maximum age

**Fig. 1** Map of Okinawa and the Yaeyama Islands, indicating the locations of the two fish markets where the specimens were collected, at the Tomari market on Okinawa Island (closed triangle) and at a local fish market on Ishigaki Island (open triangles). The major spawning site “Yonara Channel” is indicated by a black arrow





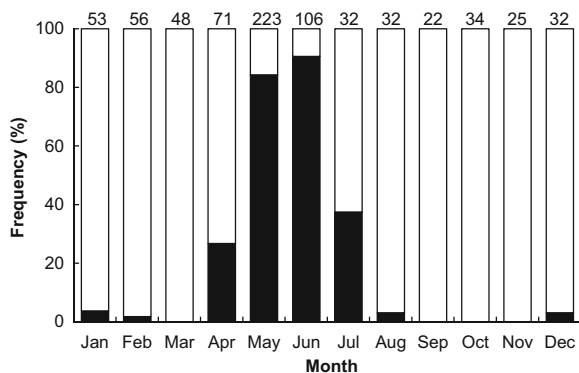
**Fig. 2** Transverse section of a sagittal otolith with annuli indicated by dots for a male (20 yr. old, 37.4 cm TL) collected in July, 2007. Scale bar =0.5 mm

$t_{\max}$  was 20 years, 80 % of  $L_{\infty}$  will be attained at 7.63 yr., i.e. 38.2 % of  $t_{\max}$ .

### Maturity and sexual pattern

Females ranged from 13.0 to 32.5 cm TL (mean  $\pm$  SD:  $23.5 \pm 3.4$  cm TL,  $n = 365$ ) and from 1 to 17 yr. ( $5.9 \pm 1.8$  yr), while 95 % were less than 8 yr. of age (Fig. 6). A central lumen and gonadal lamellae were found in all ovaries. The smallest mature female was 18.9 cm TL having a hydrated ovary, but the size at 50 % maturity could not be estimated because of a lack of smaller specimen (Fig. 7). The youngest mature female was 3 yr., and the age at 50 % maturity was estimated to be 3.3 yr. using the logistic equations (parameters  $a = -5.208$ ,  $b = 1.598$ ,  $r^2 = 0.91$ ) (Fig. 7).

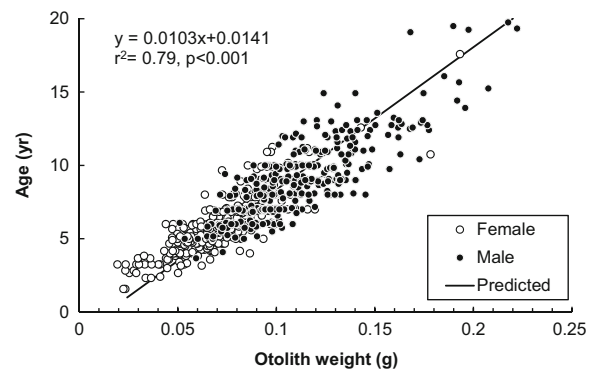
Males ranged from 20.0 to 39.3 cm in TL ( $29.2 \pm 3.3$  cm TL,  $n = 361$ ) and from 3 to 20 yr. ( $9.0 \pm 2.7$  yr) in age, with 94 % of them older than 6 yr. (Fig. 6). All gonads of males were clearly distinguishable



**Fig. 3** Edge -type analysis for sectioned otoliths, showing the percentage of otoliths with an opaque margin. Numbers above bars indicate sample sizes

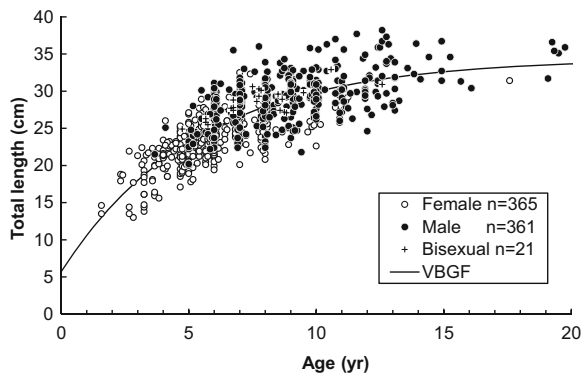
as testes in contrast with the ovaries of females based on the dominance of testicular cells at some developmental stages. A central lumen was also found in all testes (Fig. 8). In ripe testes, spermatozoa were present in the seminal lobules and the sperm sinus, but not in the central lumen (Fig. 8), indicating that the lumen is not used for sperm transport.

Twenty-one inactive bisexuals having gonads with many previtellogenic oocytes and developing testicular cells were found in samples with sizes and ages that were intermediate between those of females and males (Fig. 9). Inactive bisexuals ranged from 24.9 to 32.9 cm in TL ( $28.4 \pm 2.0$  cm TL,  $n = 21$ ) and from 4 to 12 yr. ( $7.8 \pm 1.8$  yr) in age (Fig. 6). Previtellogenic oocytes were scattered, but were biased in some parts of the gonad with developing testicular cells. A central lumen was also found in all bisexual gonads (Fig. 9). Bisexual gonads could be distinguished from nine testes with a few residual previtellogenic oocytes. The inactive bisexuals occurred in the non-spawning season from



**Fig. 4** Relationship between otolith weight and presumed age with a linear regression line for both sexes combined

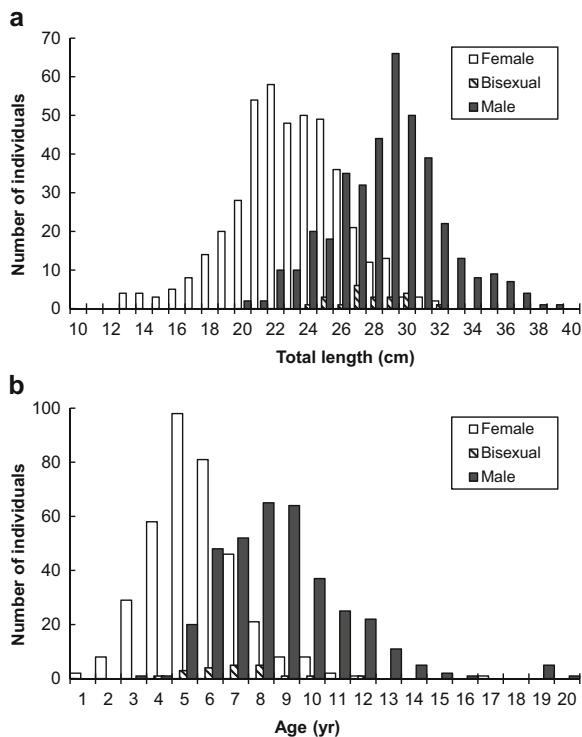




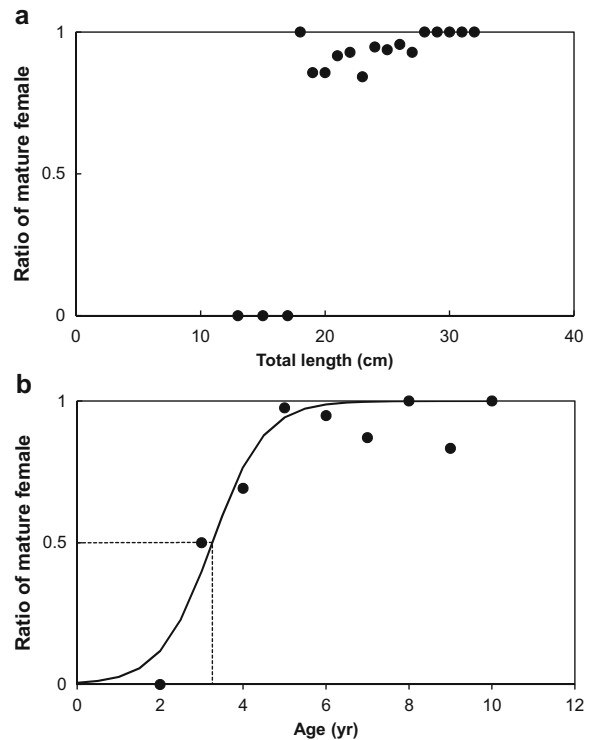
**Fig. 5** Growth curve of *Epinephelus ongus*. Von Bertalanffy growth function fitted to size-at age data for all sexual phases combined

November to March before the spawning season from April to June (Ohta and Ebisawa 2015), with the monthly percentage of inactive bisexuals among the samples ranging from about 4 to 11 % (Fig. 10).

Although the size and age ranges overlapped considerably between the sexes, the modes of their compositions were distinctly separated (Fig. 6). Significant differences between the sexes were found in both size ( $D = 0.652$ ,  $p < 0.001$ ) and age ( $D = 0.566$ ,  $p < 0.001$ ),

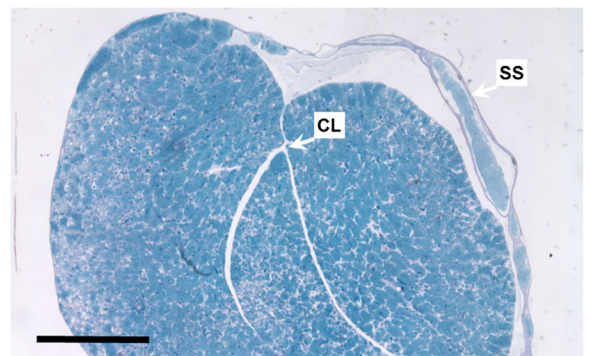


**Fig. 6** Sex-specific **a** length frequency and **b** age frequency distributions for the samples examined



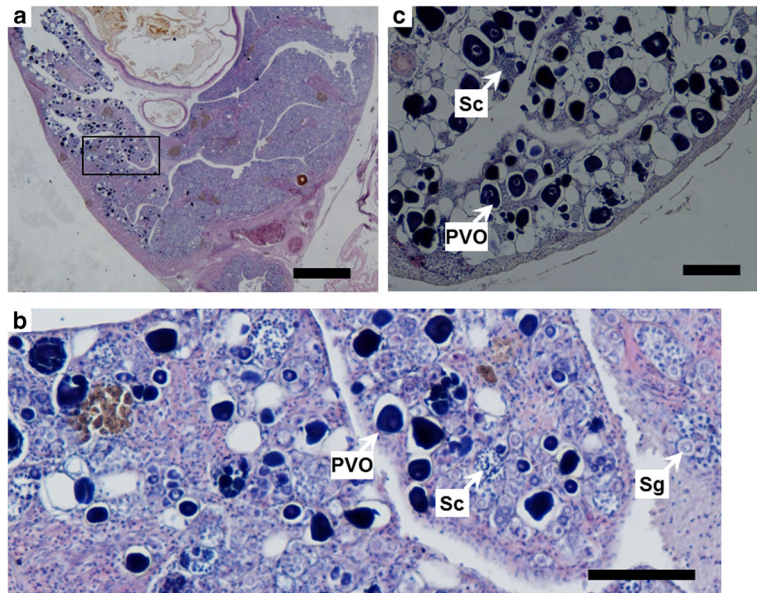
**Fig. 7** Ratio of mature females to all females during spawning months by **a** size and **b** age. Solid line indicates logistic equation fitted to the data. Dashed line indicates 50 % maturity estimate by size

with males being larger and older than females. Excluding bisexual individuals, the size at a 50 % sex ratio was estimated to be 26.1 cm TL using the logistic equations ( $a = 14.472$ ,  $b = -0.555$ ,  $r^2 = 0.99$ ) (Fig. 11). The age at a 50 % sex ratio was estimated to be 6.8 yr. using the logistic equations ( $a = 5.629$ ,  $b = -0.824$ ,  $r^2 = 0.69$ ) (Fig. 11). Based on the former logistic equation



**Fig. 8** Transverse section of testis at functional maturation stage with central lumen (CL) and sperm sinus (SS) filled with spermatozoa for a male (29.9 cm TL) collected in June, 2004. Scale bar = 0.5 mm

**Fig. 9** **a** Transverse sections of inactive bisexual gonad for an individual (30.6 cm TL) collected in November 2007 (scale bar=0.5 mm); **b** detail from (a) (scale bar=0.1 mm); and **c** transverse section of inactive bisexual gonad for an individual (27.7 cm TL) collected in January 2008 (scale bar=0.1 mm), showing previtellogenic oocyte (PVO), spermatogonium (Sg), and spermatocyte (Sc)



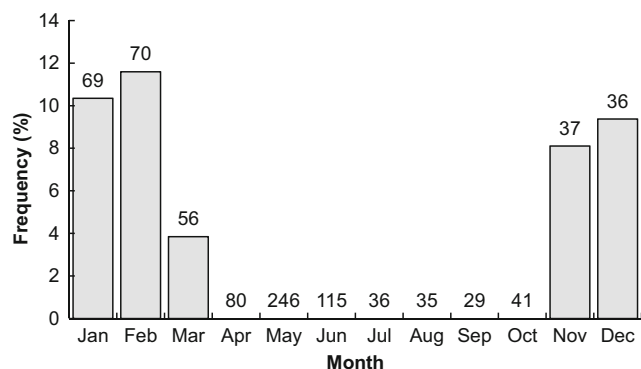
and observed size distribution of catches around the spawning season, sex ratio of mature female (more than 18 cm TL) to male was estimated to be 1.0 (Fig. 12).

## Discussion

This study demonstrated the age-based demography of *E. ongus* in the Yaeyama Islands. Opaque zones on sectioned otoliths were annuli, as in many other groupers (Matheson and Huntsman 1984; Sadovy et al. 1992; Grandcourt et al. 2005; Fennessy 2006; Pears et al. 2006; Williams et al. 2009; Rhodes et al. 2011). Groupers have generally been thought to be long-lived fishes (e.g., Manooch 1987; Pears et al. 2006), but a previous study has argued that the longevity of groupers varies greatly from <10 yr. to >40 yr. (Williams et al. 2009). This study confirmed that the maximum age of

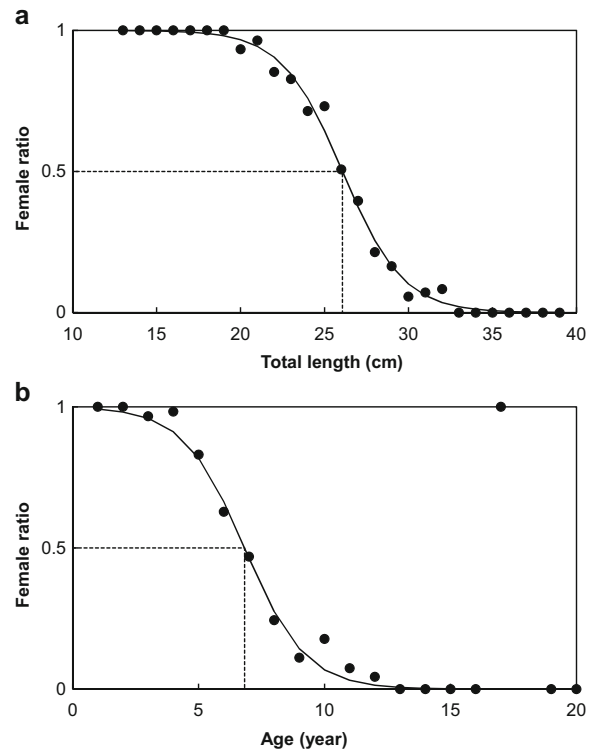
*E. ongus* in the Yaeyama Islands was 20 yr. This finding was consistent with the results of a preliminary study in Okinawa (Craig 2007), but was lower than the result in the Great Barrier Reef ( $t_{\max} = 30$  yr) (Maplestone et al. 2009). The growth pattern in this study was different from those found in previous studies that reported the VBGF parameters in Okinawa ( $L_{\infty} = 48.33$  cm TL,  $K = 0.043$  yr.<sup>-1</sup>,  $t_0 = -8.752$  yr.; converted using the standard length- TL relationship) (Craig 2007) and in the Great Barrier Reef ( $L_{\infty} = 32.63$  cm TL,  $K = 0.175$  yr.<sup>-1</sup>,  $t_0 = -3.906$  yr) (Maplestone et al. 2009). Particularly, the difference in the initial growth pattern up to 6 yr. of age between this study and others may be due the scarcity of older samples in the former (Craig 2007) and the scarcity of younger samples in the latter (Maplestone et al. 2009), respectively. However, the growth pattern of older age classes (> 7 yr) in this study was similar to that in the Great Barrier Reef

**Fig. 10** Monthly frequency of inactive bisexuals. Numbers indicate sample sizes



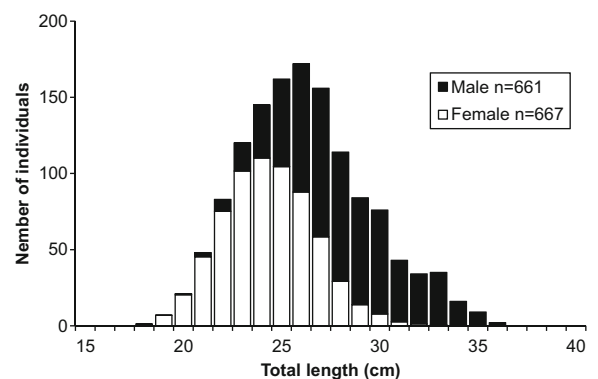
(Maplestone et al. 2009). Previous report indicated that larvae of experimentally cultured *E. ongus* grew to 10.9 cm TL on average at 1 yr. after hatching in the land tank (Yamamoto et al. 1994). This result was equivalent to 10.6 cm TL at 1 yr. of age estimated using the VBGF parameters in the present study rather than others. Therefore, the growth parameters in this study would apply well to the population in the Yaeyama Islands.

The present study demonstrated that *E. ongus* exhibited several characteristics indicative of protogynous hermaphroditism (Sadovy and Shapiro 1987). The size/age differences between sexes and the fact that the size/age of most males was beyond the first maturity of females suggested monandric protogynous hermaphroditism (Fennessy 2006; Pears et al. 2006; Williams et al. 2009). The inactive bisexual gonads observed in this study were essentially recognized as being in a transitional phase, namely as changing sex from female to male, considering that inactive bisexuals occurred at an intermediate size/age between females and males. However, they were not consistent with the general definition that transitional gonads show clear evidence of both testicular and ovarian tissues and show degeneration of one sexually mature tissue, such as the breakdown of vitellogenic or later-stage oocytes of females in protogyny, and a proliferation of the tissue of the other sex (Sadovy and Shapiro 1987; Sadovy de Mitcheson and Liu 2008). This inconsistency was due to the seasonality of sex change in the species. This study demonstrated that inactive bisexuals occurred in the non-spawning season before the spawning season. The spawning season in the Yaeyama Islands is from April to June, and mature individuals of *E. ongus* aggregate at some spawning sites in the two spawning periods associated with the lunar cycle (Ohta and Ebisawa 2015). Females change sex in the inactive reproductive period spanning from after complete degeneration of the ovary to the previtellogenic oocytes stage. On the other hands, the occurrence of younger (small) mature males suggests the potential existence of primary males that have not been functional females. However, in some groupers showing diandric hermaphroditism, quite a lot of bisexual individual or small primary males were found in samples (Fennessy and Sadovy 2002; Liu and Sadovy 2004; Marques and Ferreira 2011), unlike in the results of the present study. Therefore, it was considered that the majority of individuals of *E. ongus* in the Yaeyama Islands have been through a sex change from functional female to male.



**Fig. 11** Ratio of females to males by **a** size and **b** age. Solid lines indicate logistic equations fitted to the data. Dashed lines indicate 50 % sex ratio estimates by size and age

The present study demonstrated a seasonal occurrence of the transitional phase in this species, indicating the seasonality of sex change in the species. A previous study hypothesized that individuals assess the best time to change sex within the spawning aggregation and actually initiate their sex change shortly thereafter, leading to the prediction that transitional individuals should predominantly occur soon after the aggregation



**Fig. 12** Size distribution of landings around the spawning season and allocation of sex ratio in each size class estimated with the logistic equation



(Shapiro et al. 1993). But previous studies have not supported this hypothesis, and instead have reported that transitional individuals of groupers occurred throughout the year (Moe 1969; Shapiro 1987; Shapiro et al. 1993; Fennessy and Sadovy 2002). The results of the present study were also not consistent with this hypothesis; on the contrary, they indicated that the critical time for changing sex in *E. ongus* was in the non-aggregation periods before the spawning season. Previous studies suggest that sex change of some groupers was socially controlled and was induced by the removal of the dominant male from a social group (Nakai 2002; Mackie 2003). Further study is needed to clarify the social structure and the mechanism of sex change of the species.

The age-based demography and sexual pattern of *E. ongus* demonstrated in the present study is fundamental information for stock assessment and fisheries management. Since the response to fisheries impacts by populations is affected by sexual pattern, effective management is dependent on understanding the sexual pattern (Huntsman and Schaaf 1994; Armsworth 2001; Alonzo and Mangel 2004, 2005). Additionally, spawning aggregation fishing will impact populations substantially by the three aspects. Firstly, aggregation fishing can rapidly remove a significant proportion of assembled individuals due to the predictability in time and space (Sadovy and Domeier 2005; Sadovy de Mitcheson et al. 2008). In the Yaeyama Islands, *E. ongus* forms spawning aggregation in at least 5 spawning sites with peak at the last quarter moon in the two consecutive spawning months, and the catch during the two months accounts for approximately 40 % of the annual catch (Ohta and Ebisawa 2015). Secondly, aggregation fishing will reduce a critical reproductive opportunity, that is concentrated within a few days in a year and that may be once-yearly event for individual female (Nanami et al. 2013b, 2014; Ohta and Ebisawa 2015). Thirdly, aggregation fishing tends to be size-selective, that often targets larger males and impacts the stock dynamics of protogynous species (Huntsman and Schaaf 1994; Coleman et al. 2000; Armsworth 2001; Alonzo and Mangel 2004, 2005). The spawning aggregations may comprise mature and relatively larger (older) individuals as in *E. polyphekadion* (Rhodes et al. 2011). Furthermore, males stay in a spawning aggregation longer than females in some groupers including *E. ongus* (Nanami et al. 2014; Ohta and Ebisawa 2015). Consequently, such size-selective fishing would

cause male-biased landings, which might ultimately change the sex ratio in the natural condition. The present study also demonstrated that sex ratio of catches in the spawning season was estimated to be 1:1, contrary to the general trend that monandric protogynous hermaphrodites are characteristically biased in favor of females (Shapiro 1987; Sadovy and Shapiro 1987).

Thus, fish spawning aggregation are especially vulnerable because of both increase of catchability (lethal effects) and decrease of reproductive output (nonlethal effects) (Sadovy de Mitcheson 2016). There is a great deal of historical evidence that aggregation-fisheries have caused serious declines or local extirpations of fish spawning aggregations throughout the world (Sadovy and Domeier 2005; Sadovy de Mitcheson et al. 2008; de Sadovy 2016). For the sake of the recovery and management of the stock of *E. ongus*, protection during the period that form spawning aggregation are critically important (Ohta and Ebisawa 2015). In the Yaeyama Islands, a temporally closure in the main spawning site for the species has been established since 2010 (Ohta and Ebisawa 2015). The demography and sexual pattern of *E. ongus* demonstrated in the present study will contribute to evaluation and improvement for the management of the species.

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