# Life-history traits of a widely distributed coral reef fish, *Mulloidichthys flavolineatus* (Mullidae), Okinawa Island, southern Japan

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**Abstract** Yellowstripe goatfish, *Mulloidichthys flavolineatus*, is a widely distributed commercial fish in the Indo-Pacific. However, there have been few comprehensive studies on its life history, which is important for resource management. In this study, we examined age, growth, sexual maturity, and spawning season of *M. flavolineatus* near Okinawa Island, southern Japan, based on sectioned otolith and gonadal histology. These fish have short life spans, with a maximum age of 5 + years and reach maturation within the first year of life. Monthly changes in the appearance of an opaque edge indicate annual production of otolith bands. This fish shows sexual size dimorphism due to the faster growth of females compared to males. The von Bertalanffy growth functions were $L_t = 31.5\{1\text{-exp}[-0.61(t + 0.44)]\}$ for females and $L_t = 24.8\{1\text{-exp}[-0.75(t + 0.48)]\}$ for males. Observed fork lengths at 50% maturity were 17.0 cm for female and 14.5 cm for male. The spawning season occurs from May to September, and the peak is from May to July. Histological observations and fish market surveys indicate that the peak spawning and catching seasons overlap substantially. The development pattern of oocytes in the Okinawan fish showed group synchronous spawning, which indicates a different spawning strategy than that of this species with genetic continuity in other regions.

**Keywords** *Mulloidichthys flavolineatus* · Spawning · Age · Growth · Sectioned otolith

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## Introduction

Global decline in fishery resources and degradation of ecosystem functions have increased the need for sustainable fisheries and to understand the impacts to marine biodiversity (Worm et al. 2006; Bonaldo et al. 2014). Life history is strongly correlated to life cycle, migration, and feeding habits, so it provides basic knowledge for understanding biology, the role of ecosystems, and evolution. In addition, a comparison of life-history characteristics between regions contributes to the relationship between environmental conditions and ecology (Trip et al. 2008). In particular, detailed information, such as longevity, maturity size, and spawning periodicity, is indispensable for resource management.

Goatfishes (Mullidae) are widely distributed in temperate and tropical oceans, with more than 80 species in six genera reported (Nelson et al. 2016). They possess a large pair of barbels extending downward from their lower jaw, which they use to probe substrate materials in search of prey. Their vigorous foraging behavior with flexible barbels and mouth are responsible for mixing sediments that were recently produced by the action of boring bivalves and coral-cropping parrotfishes (McCormick 1995). As nuclear species are followed by many other species, goatfishes play a key role in the formation of multi-species foraging associations (Uiblein 2007; Sazima et al. 2006). Many species of Mullidae are commercially important and are a significant food resource for coastal communities (Holland et al. 1993; Reñones et al. 1995; Santana et al. 2006). Despite the importance of these fish to fisheries and ecosystems, little information is available on otolith-based age assessment and basic reproductive biology based on gonadal histology, compared to other coral reef fishes such as Scaridae and Lutjanidae.

Yellowstripe goatfish, *Mulloidichthys flavolineatus*, has a particularly wide geographic distribution among coral reef fishes. They are distributed across half of the tropical oceans, from the Red Sea and the eastern coast of Africa to the central Pacific region (Lessios and Robertson 2013). This wide distribution may be correlated with their large size attained by the postlarvae at settlement, approximately 10 cm and long pelagic larval duration of over 2 months (Kamikawa et al. 2019).

Because of its wide distribution area, life-history characteristics for this fish have been reported in the Red Sea and some Pacific regions. Age determination from scales and reproduction estimates by the gonadosomatic index (GSI) and larval survey were conducted in the Red Sea (Wahbeh 1992; Abu El-Regal 2018; Abu El-Regal et al. 2019), and an age assessment based on otoliths and reproductive traits based on the GSI and histological observation were performed in Saipan (Reed and Taylor 2020). A report from Hawaii estimated the spawning period and mature size with a small sample size (Cole 2009). Recently, Fernandez-Silva et al. (2015) investigated the genetic population structure of *M. flavolineatus* from the Red Sea, and the Indo-Pacific and showed that populations differed in the Northwest Indian Ocean (the Red Sea to the Arabian Sea), Indo-Pacific

(excluding Hawaii), and Hawaii. Fish for which genetic population differences were identified in such widely distributed species require basic ecological studies on a regional basis and at a broader scale. Furthermore, opportunities exist to explore correlations between life history and genetics, including variations in life-history traits based on genetic continuity.

Approximately 20 species of Mullidae (three genera: *Mulloidichthys*, *Parupeneus*, *Upeneus*) inhabit waters surrounding Okinawa Island, southern Japan. Of these, eight species of two genera, *Parupeneus* and *Mulloidichthys*, account for the majority of the catch, and these fish are caught by gill nets, set nets, and spearfishing and are used for food. Of the 69 categories of littoral fish and shellfish targeted for catch around Okinawa Island, the family Mullidae ranks 20th in terms of catch. Fish catch of Mullidae in Okinawa Prefecture from 1989 to 2015 was the highest, approximately 47 t/year, in 1989, and then gradually decreased each year. In the 2010s, the catch was approximately 12 t/year, and the stock declined (Ohta et al. 2017). In this report, groups of coastal fish are evaluated as "high, middle, or low" for the stock status and "increase, constant, or decrease" for the stock trends, compared with the past stock status. The Mullidae is positioned as "low" and "decrease." *M. flavolineatus* is one of the most common goatfish in waters around Okinawa Island and are often observed in groups of several to dozens in coastal areas during daylight hours. Although this species is the most commonly caught and consumed species of the genus *Mulloidichthys* on Okinawa Island and are used for food, there are no detailed reports on the life history around Okinawa Island. In the present study, we investigate age assessments based on sectioned otoliths and reproductive characteristics based on histological observations as part of a comprehensive study on *M. flavolineatus* of Okinawa Island. We also compare the life-history traits of this species from other regions to understand their similarities and differences.

## Materials and methods

### Sampling site and fish collection

Specimens of *Mulloidichthys flavolineatus* ($n=329$) were obtained almost every month between

December 2009 and March 2014. We purchased 313 specimens at local fish markets (Awase, Henza, Katsuren, and Nago) and collected 16 specimens from the coastal areas on Okinawa Island (26° 04′–26° 53′ N, 127° 37′–128° 31′ E). All samples were transported to the laboratory on ice. The following parameters were recorded for each specimen: total length (TL; to the nearest 1 mm), fork length (FL; to the nearest 1 mm), body weight (BW; to the nearest 1 g), and gonad weight (GW; to the nearest 0.01 g). This study converted previous data to FL using a TL-FL relational expression for comparison with a previous work (Wahbeh 1992; Mehanna et al. 2017; Abu El-Regal 2018). Fish sex was determined by histological observation. Specimens with very small gonads that could not be removed were recorded as sex unknown. Gonads were fixed in Bouin's solution and stored in 70% ethanol for histological examination. Paired sagittae otoliths were removed and kept dry throughout the research.

We investigated the catches of *M. flavolineatus* at the Henza fish market, which was the main sampling site of this study. There are five main fishing methods in the Henza fish market: gillnet and bottom longline fishing, which operate from dusk to dawn; spearfishing, which operates at night; Pole-and-line fishing, which operates during the day; and set net, which operates from a fixed location. Fishing gear and numbers of *M. flavolineatus* were recorded 4 to 11 times a month (average 6.0) from January 2010 to July 2012. The market auctions are held about 24 times a month; thus, the rate of sampling corresponds to 16.7–45.8% (average 25.0%). We estimated the number of fish landed per month based on the number of market surveys and the number of fish landed per fishing gear.

## Age determination

After embedding in epoxy resin, the right sagittae otolith, which was cut through the nucleus into 0.5 to 0.6 mm sections with a low-speed saw (ISOMET™, Microstructural Analysis Div., Buehler, Lake Bluff, IL, USA). The sectioned otolith was observed under incident light using a binocular stereomicroscope (M10, LEICA, Germany). Opaque rings of sectioned otoliths from the focus to the edge were counted three times during separate periods by the first author. If two or all three counts

were the same, that number was designated as the number of opaque zones on the otolith. The first growth ring was determined to be the innermost opaque band outside of the central opaque area (Ebisawa et al. 2010). The average percent error (APE; Beamish and Fournier 1981) and coefficient of variance (CV; Campana 2001) were calculated to estimate aging precision, as follows:

$$\text{APE}_j = \frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \times 100$$

$$\text{CV}_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \times 100$$

where $X_{ij}$ is the $i$th age determination of the $j$th fish; $X_j$ is the mean age estimate of the $j$th fish; and $R$ is the age determination for each fish.

Otolith edges were determined to be translucent or opaque, which validated the periodicity of growth ring formation at the time of counting. Monthly percentages of the opaque edge were calculated for age validation. Individuals with no opaque ring were less than 1-year-old, so they were excluded from this analysis. With reference to Granada et al. (2004), we assigned each individual an age of $-0.33$, 0.00, or 0.33 years, depending on the month in which the sample was taken and the number of opaque rings. The spawning season of this species is from May, but the peak of ring formation is from January to April (see the "Results" section); thus, ring formation occurred less than 1 year after birth. Therefore, the age of the fish collected from January to April was defined as the number of opaque rings minus 0.33 years. For example, an individual with two opaque rings collected in March was 1.67 years old. Individuals collected from May to August did not add age because the ring had already been formed (0.00). Individuals collected from September to December added 0.33, but new opaque ring found on fish otoliths caught during this period were not considered as an annulus in age assignment. The von Bertalanffy growth formula (VBGF) was fitted to FL and age data using nonlinear least squares, as follows:

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

where $L_t$ is the FL of fish at age $t$, $L_\infty$ the asymptote of the growth curve, $K$ the growth coefficient (rate at which growth curve approaches asymptote), $t$ the age of fish in years, and $t_0$ is the age at which FL = 0.

Six individuals of unknown sex were used in admixture with males or females to estimate VBGF for each female and male. VBGF parameters for each sex were compared using a likelihood ratio test (Kimura 1980) using the "fishmethods" package (http://cran.r-proje ct.org) of the R program (R Core Team 2019).

Gonad observations

The GSI of individuals was calculated for females and males as follows.

$$GSI = GW/BW \times 100$$

Pieces of gonads were dehydrated with a series of ethanol dilutions and then were embedded in paraffin. Afterward, the tissues were sectioned transversely at 6 to 8 μm and then stained with Mayer's hematoxylin and counterstained with eosin. We histologically determined the cellular stage and reproductive phase of the oocytes based on observation of the sectioned gonads under light microscopy (Eclipse 90i, NIKON, Japan). Progression of oocyte growth and development were classified into eight stages based on definition reported by Lowerre-Barbieri et al. (2011) as primary growth (PG), cortical alveolar (CA), primary vitellogenesis (Vtg1), secondary vitellogenesis (Vtg2), tertiary vitellogenesis (Vtg3), germinal

vesicle migration (GVM), germinal vesicle breakdown (GVBD), and hydration (H). The reproductive phase was categorized based on the modified schema of Brown-Peterson et al. (2011) using the following categorizations: immature (Im), developing (De), spawning-capable (SC), actively spawning (AS; only females), regressing (Rg), and regenerating (Re). The presence or absence of postovulatory follicles (POF) and atretic oocytes was also recorded (Table 1, Fig. 1). The spawning season was determined based on the appearance of SC and AS phases. Additionally, appearance of postovulatory follicles (POF) and average GSI value were considered.

The size of females at maturity was estimated by examining specimens obtained during the peak of the spawning period (May to July). In males, estimation was performed on individuals from April to September (SC phase is 50% or more). Specimens were scored based on the maturity status (immature, 0, representing Im phase; mature, 1, De, SC, AS, Rg, and Re phases). Length at maturity was estimated for both females and males using a logistic function:

$$L_{FL} = 100/\{1 + \exp[-a(FL - b)]\}$$

Length at 50% maturity ($L_{50}$) was defined as the size at which 50% of individuals matured and was estimated using a generalized linear model (GLM) with a logit link function and binomial error. The

**Table 1** Reproductive phase of *Mulloidichthys flavolineatus* showing histological features modified from classifications provided by Brown-Peterson et al. (2011). *PG* primary growth, *CA* cortical alveolar, *Vtg1* primary vitellogenic, *Vtg2* secondary vitellogenic, *Vtg3* tertiary vitellogenic, *GVM* germinal vesicle migration, *GVBD* germinal vesicle breakdown, *POF* postovulatory follicles, *Sg* spermatogonia, *Sc* spermatocyte, *St* Spermatid, *Sz* spermatozoa

| Reproductive phase | Female | Male |
|---|---|---|
| Immature | Small ovaries. Only PG oocytes present. No atresia or muscle bundles. Thin ovarian wall | Small testes. Only Sg present. No lumen in lobules |
| Developing | Enlarging ovaries. Only PG and CA or PG to Vtg2 oocytes present. No POFs and Vtg3 oocytes | Small testes. All stages of spermatogenesis (Sg to Sz) present. But Sz not present in lumen of lobules or in sperm ducts |
| Spawning capable | Large ovaries. Vtg3 oocytes dominate | Large testes. All stages of spermatogenesis (Sg to Sz) present. Sz in lumen of lobules and sperm ducts |
| Actively spawning | Large ovaries. Oocytes undergoing late GVM, GVBD, and hydration | - |
| Regressing | Flaccid ovaries. Atretic oocytes and POFs present. Some PG and CA oocytes present | Small testes. Residual Sz present in lumen of lobules and in sperm ducts |
| Regenerating | Small ovaries. Only PG oocytes present. Muscle bundles, enlarged blood vessels present. Thick ovarian wall | Small testes. Proliferation of spermatogonia throughout tests. Small amount of residual Sz present in lumen of lobules and in sperm duct |
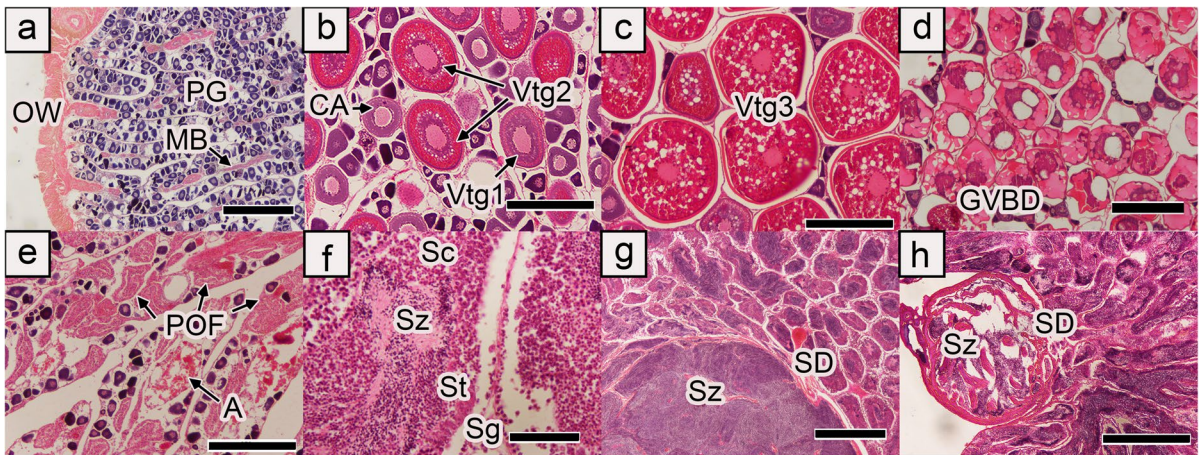
**Fig. 1** Photomicrographs of gonad sections of *Mulloidichthys flavolineatus*. **a** Regenerating phase of a female with thick ovarian wall and muscle bundles, **b** developing phase of a female, **c** spawning-capable phase of a female (primary growth oocyte and tertiary vitellogenic oocytes occupy most of the whole, and some early vitellogenic oocytes can be confirmed), **d** actively spawning phase of a female (consists of two groups of oocytes, primary growth oocytes, and hydrated oocytes), **e** regressing phase of a female (showing many postovulatory follicles and primary growth oocytes in ovaries, with some atretic oocytes scattered), **f** development process of testicular cells in lobules, **g** spawning-capable phase of a male, **h** regressing phase of a male. Scale bar indicated 500 μm (**a**, **g**); 250 μm (**b**, **c**, **d**, **e**, **h**); 50 μm (**f**). OW, ovarian wall; MB, muscle bundle; PG, primary growth oocyte; CA, cortical alveolar oocytes; Vtg1, primary vitellogenic oocyte; Vtg2, secondary vitellogenic oocyte; Vtg3, tertiary vitellogenic oocyte; GVBD, germinal vesicle breakdown; A, atretic oocyte; POF, postovulatory follicle; Sg, spermatogonia; Sc, spermatocyte; St, spermatid; Sz, spermatozoa; SD, sperm duct

corresponding 95% confidence intervals (CI) for $L_{50}$ were derived by bootstrap resampling with 1,000 iterations using the "FSA" package (http://cran.r-project.org) of the R program (R Core Team 2019).

Mature ovaries collected between the Vtg3 and hydrated stages (GVBD and H) during the spawning season (collected 2011 and 2012) were examined to estimate the total and batch fecundity. Ovaries with POF were excluded because only pre-spawning ripe females in the late vitellogenic maturity stages should be used to estimate fecundity. Fecundity was estimated using the gravimetric method (Hunter et al. 1985; Murua et al. 2003). A portion of fixed ovarian tissue was removed and weighed as a subsample (weight of subsample: $w$). After the tissue was well-stirred on a petri dish, the number of oocytes larger than 0.3 mm in diameter and the number of hydrated oocytes were counted (the number of oocytes in the subsample: $No$) under a profile projector. This procedure was replicated three times, and all counts were averaged to estimate the fecundity ($F$) as:

$$F = \frac{[\sum_{i=1}^{n} \frac{No_i}{w_i}]}{n} \times \text{GW}$$

where $No$ is the number of eggs counted in the subsample ($w$) and $n$ is the number of times the eggs were counted.

We analyzed the total fecundity and batch fecundity together. Histological observation before and after spawning of ovaries and developmental ovary type suggested that the total fecundity could be correlated with the total number of eggs spawned during a single spawning period. In addition, two hundred oocytes were randomly selected from subsamples collected during the AS phase, which were measured under a profile projector to estimate the oocyte development types.

## Results

Length composition, sex ratio, and fishing gear

*M. flavolineatus* specimens included 227 females (12.1–32.7 cm FL, mean ± SD: 22.1 ± 4.8 cm FL), 96 males (10.6–28.1 cm FL, 18.1 ± 3.4 cm FL), and 6 sex unknown (8.4–11.5 cm FL, 9.7 ± 0.9 cm FL). All fish larger than 29 cm FL were female (Fig. 2).The sex ratio of specimens was female: male = 2.3:1. The monthly distribution of females and males showed that the sex ratio was significantly skewed toward females in some months (May, June, July, September, and December; binominal test, $p < 0.05$; Table 2). The relationship between TL and FL for both sexes was calculated using the following equation:

$$FL = 0.86 \times TL - 0.194 (n = 329; r^2 = 0.99; p < 0.001)$$

In a survey conducted at the Henza fish market from January 2010 to July 2012, *M. flavolineatus* were mainly caught by four types of methods: set net,
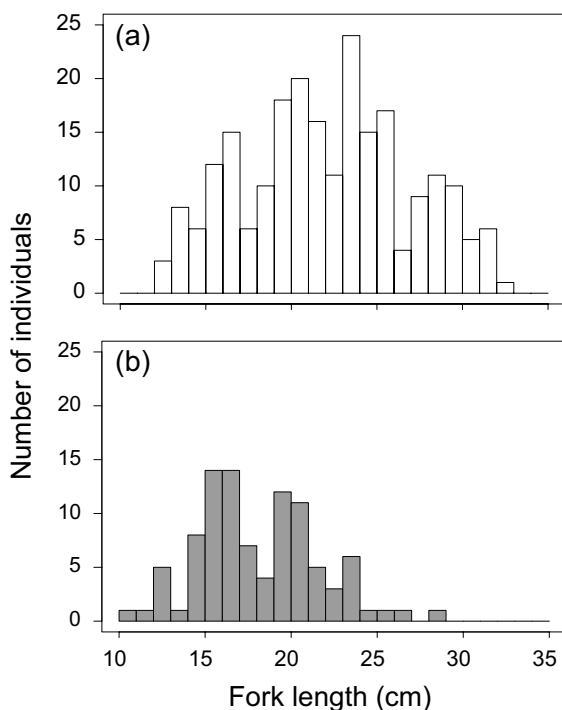
**Table 2** Monthly distribution of females and males of *Mulloidichthys flavolineatus* and results of binomial tests

| Month | Female | Male | Total | *p* value |
|-------|--------|------|-------|-----------|
| Jan | 18 | 14 | 32 | 0.59 |
| Feb | 21 | 11 | 32 | 0.11 |
| Mar | 5 | 5 | 10 | 1.00 |
| Apr | 13 | 6 | 21 | 0.11 |
| May | 16 | 4 | 20 | < 0.05 |
| Jun | 42 | 15 | 57 | < 0.001 |
| Jul | 33 | 7 | 40 | < 0.001 |
| Aug | 4 | 1 | 5 | 0.37 |
| Sep | 13 | 2 | 15 | < 0.05 |
| Oct | 13 | 8 | 21 | 0.38 |
| Nov | 35 | 22 | 57 | 0.11 |
| Dec | 14 | 1 | 15 | < 0.001 |
| total | 227 | 96 | 323 | < 0.001 |

gill net, spearfishing, and bottom longline (Table 3). The set net catches tended to be higher in all years compared to other fishing gears (2010, 65%; 2011, 39%; 2012, 84%). The gill nets were the second largest catch after set nets and were often fished together with the families Scaridae and Siganidae. The spearfishing catches varied from month to month, with annual catches lower than gillnets and set nets. The bottom longline catches were low and rare throughout the year. The catches were particularly high in May and June, and much of the annual catch was concentrated during these months (2010, 46.4%; 2011, 34.0%; 2012, 74.8%).

Age and growth

The otoliths of 11 individuals were excluded because they could not be removed entirely (six individuals), or the otolith bands were cloudy and unreadable (five individuals). Therefore, a total 318 (96.6%) otoliths were observed. The first growth ring was confirmed based on the individual without the opaque band (Fig. 3a). In the sectioned otoliths, opaque and translucent bands alternated (Fig. 3b). The frequency of otoliths with an opaque edge in specimens increased rapidly from November to June, peaked from January to April (> 50%), and then began decrease in May and beyond. No individuals with opaque edges were observed from June to September (Fig. 4).



**Fig. 2** Fork length frequency of *Mulloidichthys flavolineatus* collected between December 2009 and March 2014. **a** Female (*n* = 227); **b** male (*n* = 96)

**Table 3** Estimated monthly catch numbers of *Mulloidichthys flavolineatus* for each fishing gear in the Henza fish market from January 2010 to July 2012. *BL* bottom longline, *GN* gill net, *S* spearfishing, *SN* set net, *SR* survey rate

| Month | 2010 | | | | | 2011 | | | | | 2012 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | BL | GN | SN | *SR* (%) | S | BL | GN | SN | *SR* (%) | S | BL | GN | SN | *SR* (%) |
| Jan | 0.0 | 0.0 | 0.0 | 0.0 | 20.8 | 0.0 | 0.0 | 0.0 | 0.0 | 20.8 | 3.7 | 0.0 | 3.7 | 3.7 | 29.2 |
| Feb | 0.0 | 0.0 | 0.0 | 2.9 | 37.5 | 0.0 | 0.0 | 0.0 | 0.0 | 16.7 | 0.0 | 0.0 | 55.7 | 59.4 | 29.2 |
| Mar | 0.0 | 0.0 | 2.9 | 20.2 | 37.5 | 0.0 | 0.0 | 26.0 | 0.0 | 16.7 | 3.7 | 0.0 | 18.6 | 29.7 | 29.2 |
| Apr | 0.0 | 0.0 | 2.4 | 26.0 | 45.8 | 0.0 | 0.0 | 0.0 | 0.0 | 16.7 | 0.0 | 3.7 | 22.3 | 3.7 | 29.2 |
| **May** | 0.0 | 0.0 | 0.0 | 190.7 | 37.5 | 6.5 | 0.0 | 13.0 | 45.5 | 16.7 | 36.4 | 0.0 | 5.2 | 5.2 | 20.8 |
| **Jun** | 3.3 | 3.3 | 136.5 | 175.5 | 33.3 | 4.3 | 0.0 | 0.0 | 65.0 | 25.0 | 0.0 | 0.0 | 0.0 | 754.0 | 16.7 |
| **Jul** | 0.0 | 0.0 | 45.5 | 91.0 | 16.7 | 9.8 | 3.3 | 3.3 | 0.0 | 33.3 | 0.0 | 0.0 | 6.5 | 0.0 | 16.7 |
| Aug | 0.0 | 0.0 | 0.0 | 0.0 | 16.7 | 13.0 | 0.0 | 0.0 | 0.0 | 25.0 | - | - | - | - | - |
| Sep | 11.1 | 11.1 | 3.7 | 7.4 | 29.2 | 0.0 | 0.0 | 0.0 | 0.0 | 25.0 | - | - | - | - | - |
| Oct | 6.5 | 0.0 | 11.1 | 0.0 | 16.7 | 17.3 | 4.3 | 39.0 | 0.0 | 25.0 | - | - | - | - | - |
| Nov | 6.5 | 0.0 | 26.0 | 0.0 | 16.7 | 0.0 | 0.0 | 22.3 | 0.0 | 29.2 | - | - | - | - | - |
| Dec | 0.0 | 0.0 | 4.3 | 0.0 | 25.0 | 20.8 | 0.0 | 15.6 | 15.6 | 20.8 | - | - | - | - | - |
| total | 27.4 | 14.4 | 232.4 | 513.7 | - | 71.7 | 7.6 | 119.1 | 126.1 | - | 43.8 | 3.7 | 112.0 | 855.8 | - |

*Bold indicates the main spawning season of Mulloidichthys flavolineatus. In 2012, the annual catch was calculated from January to July. SR was calculated based on the number of surveys per month and the number of days the market was open*

**Fig. 3** Photomicrographs of transverse sections of sagittal otolith of *Mulloidichthys flavolineatus*. **a** Otolith with no opaque zone collected in September 2011 (10.3 cm FL sex unknown). **b** A translucent edge otolith with three opaque zones (indicated by black lines) collected in November 2011 (26.5 cm FL male). Scale bar indicated 1 mm
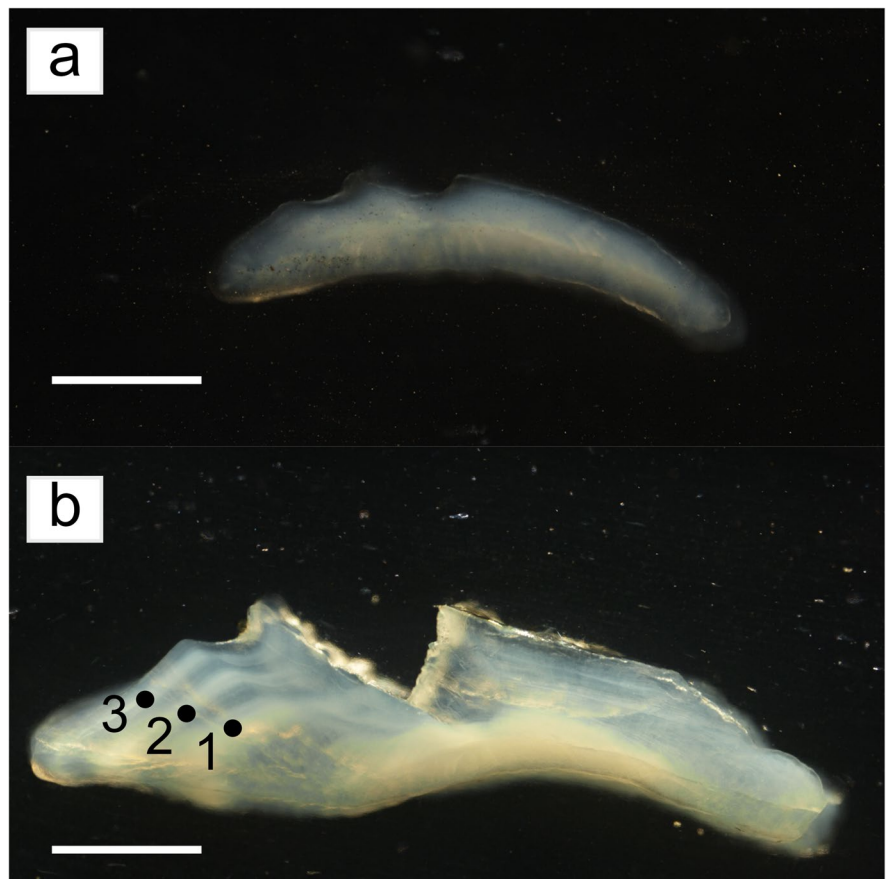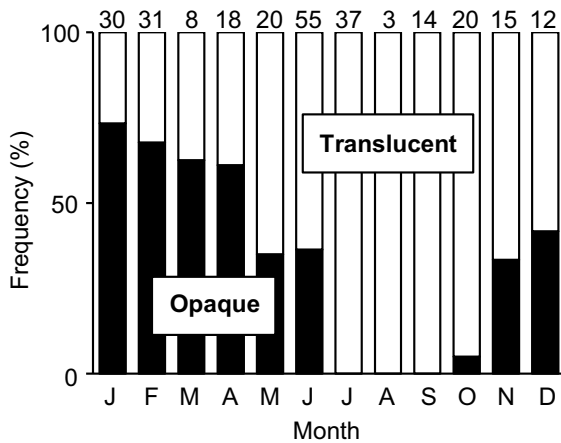
**Fig. 4** Monthly changes in the frequency of the otolith edge condition for *Mulloidichthys flavolineatus*. Numbers on bars indicate sample size

The age range in *M. flavolineatus* was 0.33 (12.1 cm FL) to 5.33 years (32.0 cm FL) for females, 0.33 (12.8 cm FL) to 4.33 years (26.5 cm FL) for males, and 0.33 year for sex unknown. One- and 2-year-old fish accounted for 60.3% of the sampled population. Mean APE and CV were comparatively low at 3.3 and 4.4, respectively. The VBGF of females and males were as follows, and von Bertalanffy growth curves were fitted to the length based on age data for both sexes (Fig. 5).
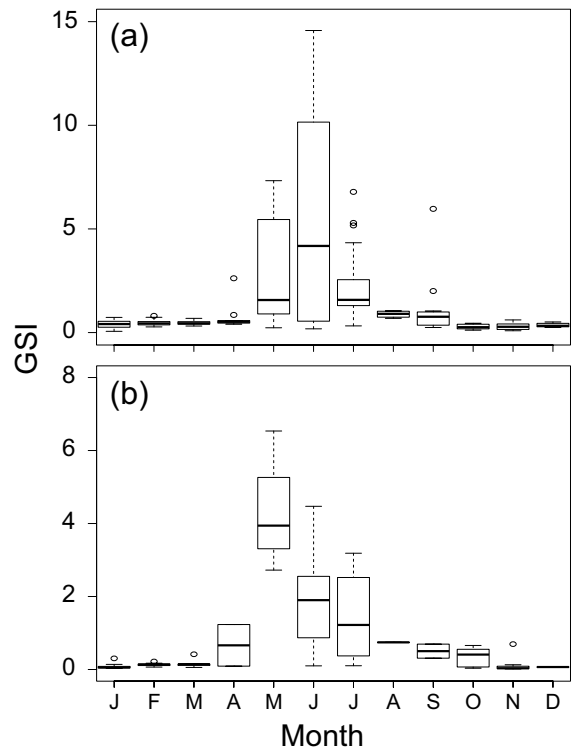


**Fig. 6** Monthly changes in the gonadosomatic index (GSI) of *Mulloidichthys flavolineatus* above the minimum mature size collected between December 2009 and March 2014. **a** Female ($n = 192$), **b** male ($n = 73$). Boxes, central lines, interval lines above and below each box, and circles indicate 25th–75th quartiles, median, max and min distribution values, and outlier values. Note the two different *Y*-axis scales

$$\text{Females}; L_t = 31.5\{1 - \exp[-0.61(t + 0.44)]\}(n = 224)$$
$$\text{Males}; L_t = 24.8\{1 - \exp[-0.75(t + 0.48)]\}(n = 101)$$
$$\text{Sexes combined}; L_t = 30.9\{1 - \exp[-0.55(t + 0.57)]\}(n = 318)$$

A likelihood ratio test showed a significant difference between the von Bertalanffy growth equations for females and males ($\chi 2 = 126.0$, df $= 3$, $p < 0.001$), with females reaching larger size than males. The growth rates were rapid during the first 3 years for females and rapid during the first 2 years for males. In females, growth continued gradually after 3 years. In contrast, growth was stagnant in males after 2 years. At 1-year-old, females tended to be larger than males.

Reproductive biology

GSI values of both sexes increased rapidly from May to July with a peak in June (Fig. 6). In females, the



**Fig. 5** Sex-specific and combined von Bertalanffy growth curves of *Mulloidichthys flavolineatus*

SC, AS, and Rg phases were predominant (>50%) from May to July, and ovaries bearing POF were observed during the same period (May to July). In addition, De phase individuals appeared in August, and a small number of SC phase individuals appeared in September. In contrast, SC phase males appeared over a longer period (April to October) than females (Fig. 7). The mean GSI of females in the SC and AS phases were 4.4 and 10.1, respectively; the average GSI of the male SC phase during May to July was 2.5.

Two distinct oocyte development groups were observed during the SC and AS phases. Ovaries in which the POF was observed were dominated by PG stage oocytes in addition to numerous POFs (Fig. 1e). We measured the oocyte diameter in the AS phase and found two different size distributions that were discontinuous; one was a PG of $120.8 \pm 49.4$ µm (mean ± SD) and the other was a hydrated oocytes of $612.2 \pm 66.7$ µm. In addition, 12 of the 14 females

caught in set nets at the Henza fish market on June 8, 2012, were caught during the AS phase (the remaining two were caught during the SC phase), and the oocyte development stages were synchronized.

The range of length and age of immature and mature females ranged from 14.8 to 19.4 cm FL (1 year old) and 16.1 to 29.6 cm FL (1 to 4 years old), respectively. In males, the ranges were 11.7 to 17.1 cm FL (0.67 to 1 year old) and 15.5 to 28.1 cm FL (1 to 4 years old). The $L_{50}$ of females and males were estimated to be 17.0 (CI: 15.5–18.1) cm FL and 14.5 (CI: 13.6–15.3) cm FL, respectively, and the logistic equations were (Fig. 8):

$$\text{Female}: L_{50} = 100/\{1 + \exp[-16.20(FL - 0.95)]\}(n = 91)$$
$$\text{Male}: L_{50} = 100/\{1 + \exp[-19.22(FL - 1.32)]\}(n = 35)$$

Fecundity based on pre-spawning ovaries (n = 29) was estimated to range from 57,000 to 475,000 (18.2 to 31.8 cm FL). A significant linear relationship between the FL and fecundity was observed (Fig. 9; fecundity = 27,442 FL (cm)—456,239; $r^2 = 0.79$; $p < 0.001$).

## Discussion

### Age validation, longevities, and sex-specific growth patterns

Many reports of age assessment of Mullidae are used scales and whole otolith methods, and few reports of age validation have been published. However, the otolith section method is more accurate than scale and whole otolith methods for many fish (Lowerre-Barbieri et al. 1994; Beamish and McFarlane 1995). Also, the most important aspect of age and growth studies is age validation (Campana 2001). We estimated the ages using sectioned otoliths and found that the periodicity of opaque zones in the otoliths of *M. flavolineatus* is annual (Fig. 4). Opaque zones on sectioned otoliths were evident in a high percentage of readable otoliths (96.6%). This study is the first to report of age validation of the *M. flavolineatus* by using the sectioned otolith method. In addition, the APE and CV of this fish were low and were comparable to other commercial fish, such as Lutjanidae, Scaridae, and Serranidae (Barnett et al. 2020; Burton et al. 2016; Gordo et al. 2016; Pottos
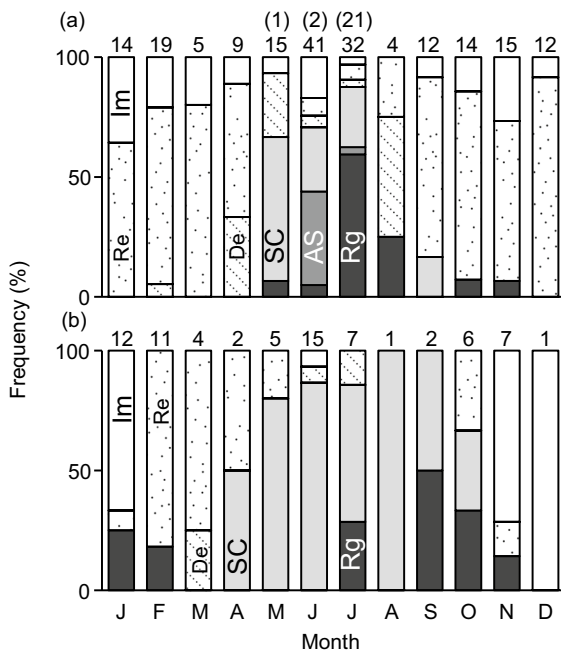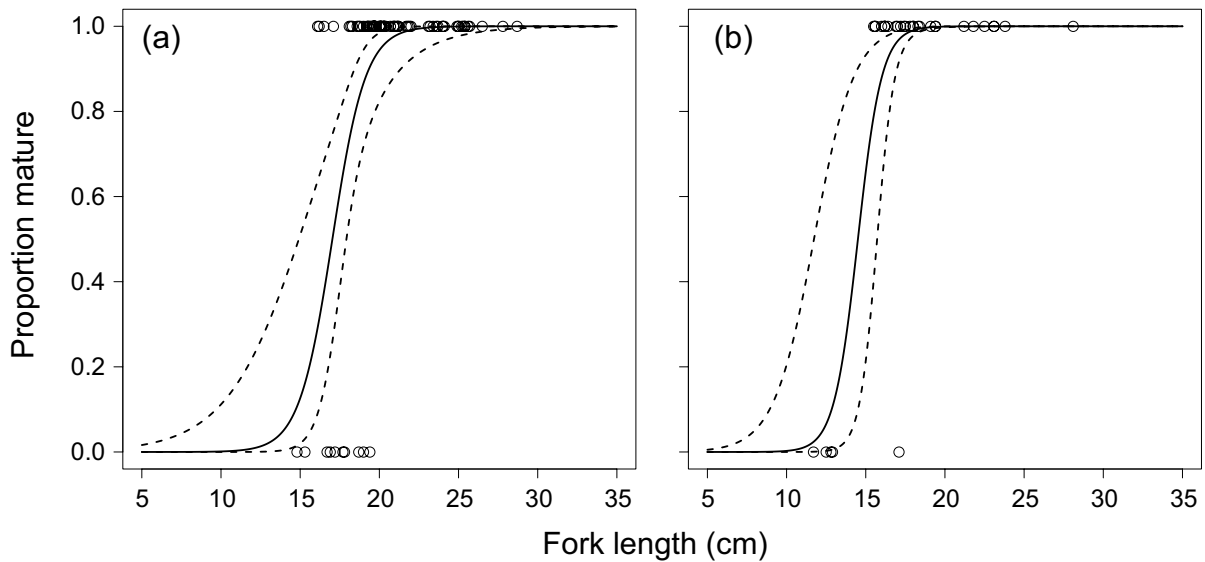


**Fig. 7** Monthly changes in the reproductive phase of *Mulloidichthys flavolineatus* above the minimum mature size collected between December 2009 and March 2014. **a** Female (*n* = 192), **b** male (*n* = 73). Numbers on bars indicate sample size, and numbers in parentheses indicate the number of ovaries with postovulatory follicles. Im, immature; De, developing; SC, spawning-capable; AS, actively spawning; Rg, regressing; Re, regenerating

**Fig. 8** Maturation schedules by fork length fitted to maturity status data for *Mulloidichthys flavolineatus*. **a** Female ($n=91$), **b** male ($n=35$). Solid lines represent logistic models; dotted lines represent the associated 95% confidence intervals

et al. 2016). Collectively, our data show that the sectioned otolith age assessment method is suitable for *M. flavolineatus*.
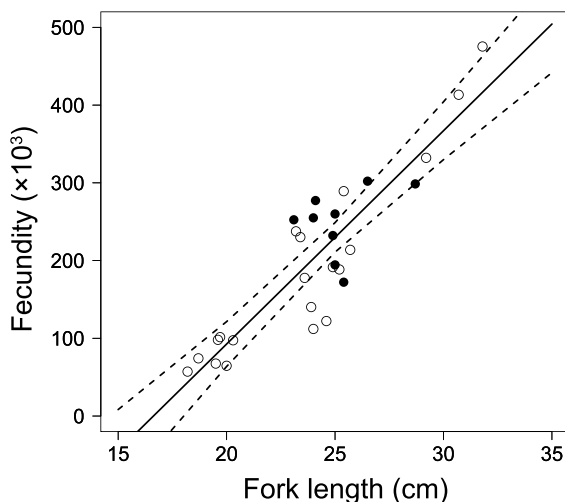


**Fig. 9** Relationship between the fork length and fecundity of *Mulloidichthys flavolineatus* collected during the main spawning season of 2011 and 2012. Open and closed circles indicate total and batch fecundity, respectively. The linear regression line includes both total and batch fecundity data ($n=29$). Solid line represents linear model; dotted lines represent the associated 95% confidence intervals

A significant difference was observed between von Bertalanffy growth equations calculated for both sexes, and females are larger than males (Fig. 5). This observation was also reported in *M. flavolineatus* and *M. vanicolensis* (Table 4). Sexual size dimorphism (SSD) is associated with mating systems in many fish. For example, males are larger than females in a pair spawning species due to competition among males. Species that display sperm competition show high GSI values (Stockley et al. 1997; Schütz et al. 2010; Pyron et al. 2013). Mullidae display genus-specific female and male growth patterns: males are larger or similar to females in *Parupeneus* (Wahbeh and Ajiad 1985; Pavlov et al. 2011; Reed and Taylor 2020) and smaller than females in *Upeneus* (İşmen 2005, 2006; Ozvarol et al. 2010), *Mullus* (Reñones et al. 1995; Arslan and İşmen 2013), and *Mulloidichthys* (Wahbeh 1992; Reed and Taylor 2020). The genus *Parupeneus* has a matching system, and testes size trends are consistent with the SSD (female smaller than male). For example, *Pa. bifasciatus* and *Pa. multifasciatus* display male territories and spawn in pairs (Sancho et al. 2000). In addition, *Pa. multifasciatus* has a small testes (Emel'yanova et al. 2013), and males of *Pa. barberinus* show a low GSI value (0.3 or less) during the spawning season (Reed and Taylor 2020). No report of *M. flavolineatus* spawning behavior is available, and whether this fish spawns in groups or

**Table 4** Summary of the length, age, growth parameters, and maturity size of genus *Mulloidichthys flavolineatus* based on previous studies. The genetic group of this table followed Fernandez-Silva et al. (2015). *NWI* Northwest Indian Ocean, *IP* Indo-Pacific Ocean (excluding Hawaii), *H* Hawaii, *S* scale, *SO* sectioned otolith, *WO* whole otolith, *TL* total length, *FL* fork length, *F* female, *M* male, *C* sex combined

| Locality | Genetic group | Aging method | Length | Sex | Maximum | | VBGF parameters | | | Maturity | Literature |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Size | Age | $L_\infty$ | $K$ | $t_0$ | $L_{50}$ | |
| Aqaba | NWI | S | TL | F | - | 7 | 35.0 | 0.16 | −0.97 | - | 1 |
| | | | | M | - | 6 | 31.7 | 0.21 | −0.78 | - | |
| Hurghada | NWI | - | TL | F | 31.0 | - | - | - | - | 14.5 | 2 |
| | | | | M | 26.0 | - | - | - | - | 12.5 | |
| Hurghada | NWI | WO | TL | C | 33.4 | 6 | 38.0 | 0.27 | −1.15 | - | 3 |
| Okinawa | IP | SO | FL | F | 32.7 | 5 | 31.5 | 0.61 | −0.44 | 17.0 | 4 |
| | | | | M | 28.1 | 4 | 24.8 | 0.75 | −0.48 | 14.5 | |
| Saipan | IP | SO | FL | F | 30.5 | 5 | 25.5 | 1.24 | - | 15.8 | 5 |
| | | | | M | 27.7 | 4 | 21.8 | 1.69 | - | 16.1 | |
| Hawaii | H | - | FL | F | - | - | - | - | - | 18.2 | 6 |

(1)Wahbeh 1992; (2)Abu El-Regal 2018; (3)Mehanna et al. 2017; (4) present study; (5)Reed and Taylor 2020; (6)Cole 2009

exhibits parasitic spawners is unclear. However, we do not consider the Okinawan *M. flavolineatus* to be simple pair spawners, since the species exhibits the following two characteristics. First, the male GSI is much higher during the spawning season (average 2.5, maximum 6.5) than the GSI of *Parupeneus* species, which is considered pair spawning. Second, males show a smaller maximum and mature sizes (Figs. 1, 5, 9). In the future, greater investigation into the on SSD, testis and sperm size, and reproductive behavior of Mullidae would clarify these unknowns.

Conversely, according to age and growth reports of Mullidae, maximum age is typically 4 to 8 years (Arslan and İşmen 2013; İşmen 2006; Ozvarol et al. 2010; Reñones et al. 1995; Wahbeh and Ajiad 1985), and no studies report a long life span species, such as Lutjanidae (Taylor et al. 2018), Lethrinidae (Ebisawa and Ozawa 2009), and Acanthuridae (Choat and Axe 1996), which are found in common commercial coral reef fishes. However, regional differences in growth parameters of *M. flavolineatus* were found. The $K$ value of VBGF of the Red Sea population (Table 4; $K = 0.16$ to 0.27; Wahbeh 1992; Mehanna et al. 2017) was lower than the Northwestern Pacific population ($K = 0.61$ to 1.69; present study; Reed and Taylor 2020).

### Reproductive seasonality and style

We showed reproductive seasonality of *M. flavolineatus* in waters surrounding Okinawa Island based on the GSI and histological evidence (Figs. 6 and 7). Monthly changes in the GSI and spawning phase (i.e., SC and AS) in females indicated that the main spawning season of *M. flavolineatus* of Okinawan populations occurs from May–July or May–September. Spawning was inactive from October to April, which is due to decreases in the water temperature and duration of the photoperiod (Japan Meteorological Agency; https://www.jma.go.jp). This finding supports a previous study of *M. flavolineatus,* which showed that spawning occurred during high water temperature periods in the Gulf of Aqaba, Hurghada, and Hawaii (April to August), and the GSI value decreased as the water temperature decreased (Wahbeh 1992; Abu El-Regal 2018; Cole 2009) and fish larval survey in the Red Sea and Hawaii (Abu El-Regal et al. 2019; Kamikawa et al. 2019). In Okinawa Island, a few SC phase females appeared in September, but no individuals with POF have been confirmed, so it is unclear whether the spawning will actually continue until September. However, some reports of *M. flavolineatus* show high GSI values in the fall as well as in the spring–summer (Saeed et al 2016; Reed and Taylor 2020). Most Mullidae that live in the northern hemisphere spawn from spring

to autumn (İşmen 2005, 2006; Kaya et al. 1999; Reñones et al. 1995). Thus, the main spawning period of *M. flavolineatus* is a high water temperature period, like that of other Mullidae; however, it may extend into autumn. Males in the SC phase appeared from April to October, which was 1 month longer before and after than the appearance of females in the SC phase (Fig. 7). This may provide data to reinforce that the spawning season continues until around autumn. Alternatively, males may arrive to spawning grounds before females and remain after most females have left, as seen in some fish (Rhodes and Sadovy 2002; Nanami et al. 2013).

Some coral reef fish form large spawning aggregations (Sadvy et al. 1994; Chort 2012; Ohta and Ebisawa 2015). Among the Mullidae, *M. vanicolensis* and *Pseudupeneus maculatus* exhibit confirmed spawning aggregations (Colin and Clavijo 1978; Robinson et al. 2008). No detailed research reports on spawning aggregations for *M. flavolineatus*. However, the catch of *M. flavolineatus* at the Henza fish market is concentrated during the set net fishing season from May to June (Table 3), which is based on information collected from the Henza fish market, surveyed from 2009 to 2011. Therefore, the main spawning and catching seasons of this fish greatly overlap (Figs. 6, 7; Table 3). We hypothesized that *M. flavolineatus* would be caught in set nets when fish gathered or migrated during spawning. The sex ratio of the samples collected during the spawning period was skewed toward females, which may be related to the special spawning behavior of this species (Table 2). Holland et al. (1993), who tracked individuals of *M. flavolineatus*, suggested that apart from daily short-distance movements within and among foraging and resting sites, the fish show seasonal migrations, in particular during the reproductive period. Abu El-Regal (2018) also suggested the possibility that *M. flavolineatus* migrate during the spawning season, and therefore, the catch varies from season to season. The fish from the spawning aggregations are more susceptible to fishing because they gather in large numbers to spawn at predictable locations and times (Sadovy and Domeler 2005; Ohta and Ebisawa 2015). Detailed reproductive information could be used for resource management and understanding the biology of the target fish. We hope that our research data will be utilized in the future.

The following dynamic types of oocyte developments have been defined (Marza 1938; Murua and Sborido-Ray 2003). (1) Synchronous: all oocytes develop and ovulate at the same time. The oocyte diameter frequency distribution is represented by a single bell curve. (2) Group synchronous: at least two groups of oocytes (synchronous group of larger oocytes and a heterogeneous group of smaller oocytes) are recognized. (3) Asynchronous: oocytes of all stages of development are present without dominant groups. This classification of female reproductive patterns in *M. flavolineatus* of the Okinawan population indicates the oocyte development of group synchronous batch spawners. After the SC phase, females developed oocytes synchronously to form bimodal populations of mature and immature oocytes (Fig. 1c, d). Furthermore, in ovaries of individuals with many POFs, most oocytes were in the PG stage, with few atretic oocytes (Fig. 1e). However, *M. flavolineatus* of the Jeddah coast (Red Sea) and northern Mariana Island (Saipan) displayed asynchronous ovaries (Saeed et al 2016; Reed and Taylor 2020), which indicated a different type of oocyte development from Okinawa. At present, the spawning type found in *M. flavolineatus* in the Okinawan population is specific within Mullidae, because the oocyte development of *Pa. cyclostomus* and *Pa. heptacanthus* in the Red Sea (Saeed et al. 2018), *Pa. barberinus* near Saipan (Reed and Taylor 2020), *Ps. grandisquamis* along coastal Mexico (Lucano-Ramírez et al. 2006), and *Upeneus margarethae* in Vietnamese waters (Pavlov and Emel'yanova 2016) were asynchronous. In addition to the group synchronous oocyte development, the catch is increased by the set net during the spawning season, and the characteristic of synchronous timing of maturation with other individuals may imply that Okinawan *M. flavolineatus* spawns at a specific location and timing. Further research is needed to clearly show why the reproductive characteristics of *M. flavolineatus* are as described above and when and how they spawn. Probably, it may be a life-history strategy to promote egg dispersal and recruitment of juvenile at a time favorable for survival. However, if these fish had such a life-history strategy, intensive fishing during the spawning season could deprive them of the opportunity to reproduce.

The reproductive characteristics of male *M. flavolineatus* may differ in the Gulf of Aqaba, Saipan, and Okinawa. The average male GSI value at the peak of

the spawning period was 2.5 in Okinawa and approximately 0.5 in the Gulf of Aqaba and Saipan (Wahbeh 1992; Reed and Taylor 2020). As mentioned earlier, the testis size was closely related to matching systems and sperm competition (Stockley et al. 1997). In other words, *M. flavolineatus* on Okinawa Island may have more intense sperm competition than the Gulf of Aqaba and Saipan.

The $L_{50}$ value for females was estimated to be 17.0 cm FL, which was 51.9% of the maximum length (32.7 cm FL) in this study. In comparing the $L_{50}$ for females of other reports, the $L_{50}$ value is 14.5 cm TL (converted to 12.3 cm FL) in Hurghada (Abu El-Regal 2018), 15.8 cm FL in Saipan (Reed and Taylor 2020), and 18.2 cm FL in Hawaii (Cole 2009). Regional differences were found in the maturity size of females, especially in the Gulf of Aqaba, where it is smaller (Table 4). The difference in maturity size was related to the maximum length recorded in Okinawa (32.7 cm FL), Saipan (30.5 cm FL), and Hurghada (31.0 cm TL; converted to 26.6 cm FL). In summary, 50% of the mature size of females falls within 46 to 52% of the maximum size reported for any location. The spawning frequency and intervals between spawning periods are unclear, as no study has yet to determine the precise values and correlation between them. However, we expect that the amount and frequency of spawning at one time differ depending on the region.

Relationship between ecological characteristics and region

We described the age, growth, and reproductive biology of *M. flavolineatus* in waters surrounding Okinawa Island. This species matures in a year and spawns multiple times from spring to summer or autumn. Oocytes are group-synchronized, and we predicted that their reproductive strategy involves substantial amounts of eggs spawned at one time, with a low frequency of spawning activity. We also found that the lifespan and spawning season tend to be common to the family Mullidae, based on the results of this study in comparison with the results of previous studies. However, *M. flavolineatus* showed differences in growth, mature size, and spawning style for each region. Recent advances in molecular phylogenetic analysis demonstrate the population structure of fish. *M. flavolineatus* in the Red Sea, Pacific (Okinawa,

Saipan), and Hawaii have genetically different populations, according to Fernandez-Silva et al. (2015). These authors found that the genetic continuity of the Indo-Pacific supports the high dispersal ability of *M. flavolineatus*. Furthermore, based on morphological and genetic differences, Fernandez-Silva et al. (2016) reported that *M. flavolineatus* from the Red Sea to the Arabian Sea is a new subspecies (*M. flavolineatus flavicaudus*). Naturally, environmental factors may be involved, but the difference in mature size and growth between Okinawa and Hawaii and between Okinawa and the Red Sea can be explained by the more recent split with Hawaii compared to the split between the Red Sea and Indo-Pacific lineages and that the population of the Okinawa and Red Sea have a species-subspecies relationship (Fernandez-Silva et al. 2015, 2016).

The timing of fish maturity and spawning is a complex integration of various environmental and habitat conditions (Servili et al. 2020). Age structure and growth vary greatly depending on the local environment (water temperature, salinity, fishing pressure) and the inner or outer shelf of reef crests (Gust et al. 2002; Gust 2004; Trip et al. 2008). Therefore, these characteristics (mature size and growth) may be sensitive to the physical environment. Conversely, differences in oocyte development (asynchronous or group synchronous) and testes size were observed in regions with genetic continuity (i.e., Okinawa and Saipan). In other words, factors that underlie these differences are not limited to genetic variation and include environmental conditions. These findings suggest that the environment can greatly change the ecology and spawning strategies of *M. flavolineatus*. However, it is difficult to identify causal factors of differences in ecological characteristics, since various factors, such as environmental conditions, fishing pressures, and population density, are intricately related (Anderson et al. 2008; Lowerre-Barbieri et al. 2011; Servili et al. 2020). Therefore, future research is needed to investigate the effects of various environments on the life history of the species though a comparisons of its characteristics at the Indo-Pacific, where there is genetic continuity. In addition to its importance in fisheries, the family Mullidae is a potentially useful indicator species for tropical and temperate coastal habitats (Uiblein 2007). We trust that the results of the present study will facilitate resource management

and lead to greater understanding of the relationship between fishes and their habitats.

**Author contribution**   All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Shota Samejima and Masato Uehara. The first draft of the manuscript was written by Shota Samejima, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data availability**   Data sharing is not applicable to this article as no datasets was generated during the current study.

**Code availability**   Not applicable

**Declarations**

**Ethics approval**   Not applicable

**Consent to participate**   Not applicable

**Consent for publication**   Not applicable

**Conflict of interest**   The authors declare no competing interest.

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