



# The reproductive biology of female crimson sea bream *Evynnis tumifrons* off the southwestern coast of Kyushu, Japan

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Received: 23 April 2019 / Accepted: 23 October 2019 / Published online: 11 November 2019  
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## Abstract

Ovarian maturation, size at sexual maturity and the annual reproductive cycle of female crimson sea bream *Evynnis tumifrons* were studied using samples collected from April 2012 to June 2014 off the southwestern coast of Kyushu, Japan. A total of 801 ovaries were examined histologically to estimate the degree of ovarian maturation. *E. tumifrons* showed an asynchronous ovary signifying multiple spawning in a single reproductive season. Ovarian maturity stages were classified into six categories based on the appearance of the most advanced oocytes, post-ovulatory follicles and atretic oocytes in the ovary as follows: immature, maturing, mature, spawned, spent and resting. Females with ovaries at maturing, mature, spawned or spent stages were defined as sexually mature individuals, and the size at sexual maturity was estimated to be 179-mm fork length based on 50% maturity size. Monthly changes in the gonadosomatic index and the occurrence of mature or spawned maturity stages showed that the spawning season lasts from November to May with an intermission in March 2013. The factor responsible for this intermission was considered to be the low water temperature that occurred in the preceding month.

**Keywords** Condition factor · *Evynnis tumifrons* · Gonadosomatic index · Ovarian maturation · Sexual maturity size · Spawning season

## Introduction

The crimson sea bream *Evynnis tumifrons* (Sparidae) is distributed in the coastal waters of China, Hong Kong, Japan, South Korea and Taiwan (Akazaki 1962, 1984; Youn 2002; Iwatsuki et al. 2007, 2014). This species inhabits rocky reefs, gravel and sandy bottoms on continental shelves (Hayashi 2002). Its bathymetrical distribution is determined by its ontogenetic development where juveniles are commonly found at shallow depths (~ 10 m) and adult stages mostly in deeper waters (50–100 m) (Iwatsuki et al. 2014).

*Evynnis tumifrons* is a commercially important fish species in the coastal waters of Japan (Kudoh and Yamaoka

2004), and its population biology has been studied in various localities (prefectures). Mio (1961, 1962) reported the age and growth, and spawning season and fecundity, of this species off Fukuoka. Toriyama et al. (1975) estimated the distribution and spawning season of *E. tumifrons*, and Toriyama and Kudo (1976) determined its age and growth off Kochi and Miyazaki. Yamahora (1983) compared the life history of *E. tumifrons* and *Pagrus major* off Yamagata. In addition, Shibuya (1985) studied the age and growth of *E. tumifrons* off Akita, while Anzawa et al. (1987) examined its spawning season and age and growth off Niigata.

Among these biological studies, those on the reproductive biology of the species are important for the estimation of the reproductive potential of stock and for the construction of appropriate management models for sustainable harvesting (Farley et al. 2015). The reproductive strategies of a fish also play a major role in its geographical distribution and population dynamics. Therefore, reliable information and sufficient understanding of a fish's reproduction are essential. In previous studies, however, the spawning season of *E. tumifrons* was estimated mainly from monthly changes in its gonadosomatic index (GSI), and its size at sexual maturity has only

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been examined in Niigata Prefecture (Anzawa et al. 1987). Some studies have suggested that the estimation of the reproductive characteristics of a fish can be improved through histological observation of its ovaries (West 1990; Tyler and Sumpter 1996; Blazer 2002; Alejo-Plata et al. 2011). Histological techniques have been used successfully in other related species, e.g. *Pagrus major*, to determine the diurnal rhythm of oocyte development during the spawning season (Matsuyama et al. 1988), and e.g. in *Dentex hypselosomus*, to clarify gonadal development and the annual and/or diurnal reproductive cycle (Oki and Tabeta 1998; Tominaga et al. 2005; Yoda and Yoneda 2009), but up to now histological techniques have been infrequently used to determine the fecundity *E. tumifrons* (Mio 1962).

Furthermore, the localities of previous studies range widely from the northern to southern regions of Japan, but did not include the southwestern region, where *E. tumifrons* is targeted by a variety of commercial fisheries, e.g. using gillnets, surrounding seine nets and angling. In addition to these limitations, the duration of the spawning season, the percentage of females spawning per day (spawning frequency) and the number of oocytes per spawning (batch fecundity), which are essential for the estimation of the annual fecundity of a multi-spawning fish with indeterminate fecundity (Yoda and Yoneda 2009), should be determined so that appropriate and timely management approaches can be established to protect sexually mature populations of *E. tumifrons* and to allow a sufficient proportion of sexually mature fish to spawn.

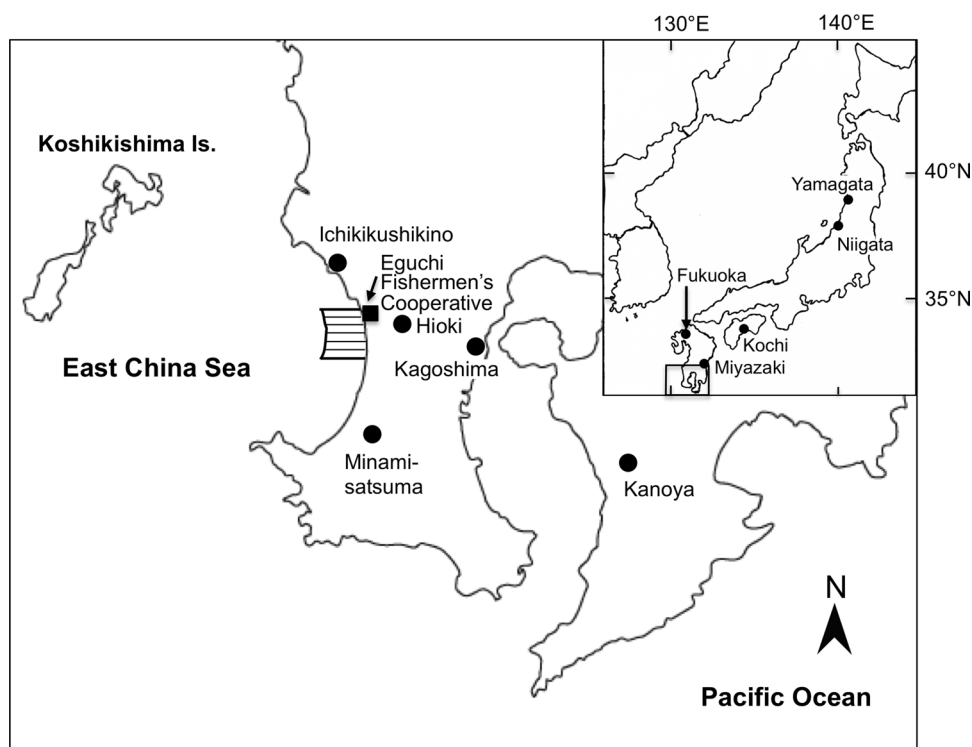
The focus of the present study is on the elucidation of the spawning season of *E. tumifrons*. Hence, the objectives of this study were to describe ovarian maturation, size at sexual maturity and the annual reproductive cycle of female *E. tumifrons* off the southwestern coast of Kyushu, Japan using an histological approach. The obtained results are indispensable for the estimation of the reproductive potential of this species and for the development of appropriate management measures.

## Materials and methods

### Sampling and measurement

Monthly sampling of *E. tumifrons* was conducted at Eguchi Fishermen's Cooperative, Hioki City, Kagoshima Prefecture, southern Japan from April 2012 to June 2014. Fishers belonging to this cooperative caught *E. tumifrons* using gillnets and surrounding seine nets from 31°33' to 31°39'N and from 130°13' to 130°20'E off Hioki City, on the southwestern coast of Kyushu, Japan (Fig. 1). After landing, fish were sorted into eight categories according to their weight by the cooperative's staff. We sampled specimens of various size from these categories once a month; a total of 1101 females were collected. Fish specimens were immediately chilled on ice and taken to the Laboratory of Fisheries Biology of Faculty of Fisheries, Kagoshima University.

**Fig. 1** Map of the sampling site (shaded area) of *Evynnis tumifrons* off the southwestern coast of Kyushu, Japan



For each specimen, fork length (FL) was measured on a measuring board to the nearest 1 mm, body weight (BW) on an electronic balance (UX6200H; Shimadzu) to the nearest 0.01 g and ovarian weight (OW) on an electronic balance (UX620H; Shimadzu) to the nearest 0.001 g. Ovaries were fixed in 10% formalin until they were histologically examined. The GSI was calculated as:

$$\text{GSI} = 100 \times \text{OW}/(\text{BW} - \text{OW}).$$

### Histological analysis

A total of 801 ovaries were examined histologically to estimate the degree of ovarian maturation. A small piece of tissue was taken from the middle part of a female's gonad, embedded in paraffin, sectioned into 6- $\mu\text{m}$  thickness, and stained with Mayer's haematoxylin and eosin. The developmental stages of oocytes were classified according to Yamamoto (1956) and Granada et al. (2004) with a few modification for this species, and the histological classification of atretic oocytes and post-ovulatory follicles followed Hunter and Macewicz (1985). Ovarian maturity stages were estimated from the appearance of the most advanced oocytes, post-ovulatory follicles and atretic oocytes (Granada et al. 2004; Alejo-Plata et al. 2011; Sun et al. 2015; Okochi et al. 2016).

### Size at sexual maturity

In the present study, the FL at which 50% of females are sexually mature ( $\text{FL}_{50}$ ) was estimated as the mean length at sexual maturity (King 2007). Sexually mature individuals were defined as females with ovaries at maturing, mature, spawned or spent stages which had yolked oocytes. The percentage of sexually mature females (PMF) was plotted against FL and size at 50% maturity was estimated by fitting a logistic function based on the least-squares method using the software DeltaGraph 7 (Red Rock Software, Salt Lake City, UT). The logistic equation was expressed as:

$$\text{PMF} = 100/[1 + \text{Exp}(-r(\text{FL}_m - \text{FL}_{50}))],$$

where  $r$  is slope of the curve and  $\text{FL}_m$  is the median value of each FL class.

### Annual reproductive cycle

Annual reproductive cycle was analysed from the monthly changes in the GSI and the occurrence of each ovarian maturity stage. Fish smaller than the minimum size of the sexually mature females were excluded from this analysis.

### Condition factor

The monthly change in condition factor (CF) was analysed to examine the seasonal change of the body condition of the fish throughout the year. The formula used was based on Zhu et al. (1989):

$$\text{CF} = (\text{BW} - \text{OW}) \times 1000/\text{FL}^3.$$

where BW is in grams, OW is in grams and FL is in millimetres.

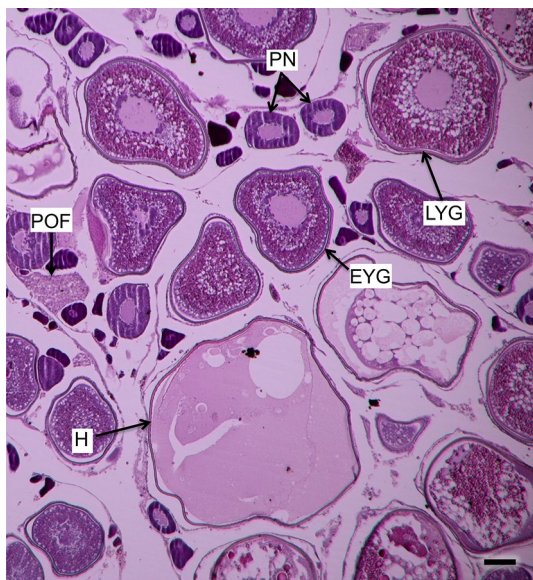
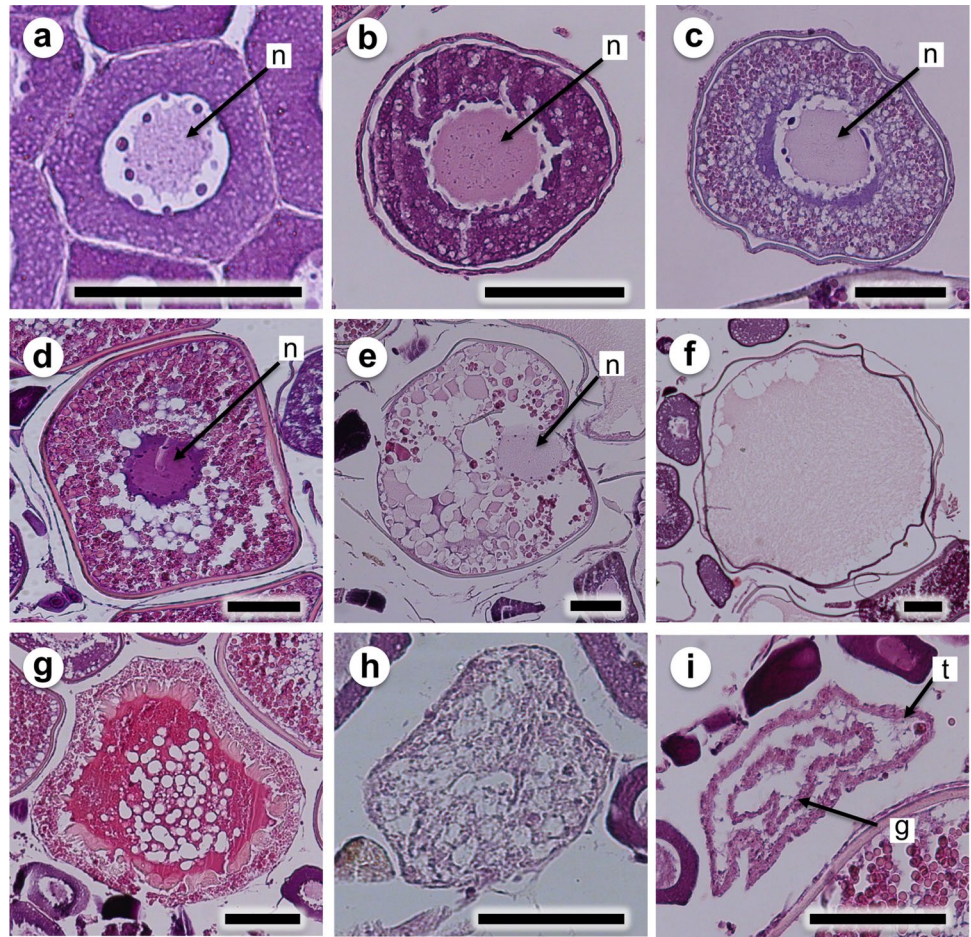
## Results

### Developmental stages of oocytes

The following developmental stages of the oocytes were observed. Peri-nucleolus stage (Fig. 2a): the nucleus is relatively large and multiple nucleoli can be seen around its periphery. The cytoplasm is basophilic and stained dark blue by hematoxylin. Oocyte diameter ranges from 60 to 120  $\mu\text{m}$ . Pre-vitellogenic stage (Fig. 2b): yolk vesicle- or oil droplet-like granules appear in the cytoplasm and gradually increase in number and size. The cytoplasm is basophilic and oocyte diameter ranges from 90 to 275  $\mu\text{m}$ . Early yolk globule stage (Fig. 2c): small acidophilic yolk globules start to appear in the cytoplasm. Oocyte diameter ranges from 195 to 310  $\mu\text{m}$ . Late yolk globule stage (Fig. 2d): yolk globules increase in size and cover the whole cytoplasm. Oil droplets around the nucleus increase in size. Oocyte diameter ranges from 295 to 450  $\mu\text{m}$ . Migratory nucleus stage (Fig. 2e): the nucleus migrates towards the animal pole where smaller yolk globules occur and the yolk globules begin to coalesce. Oocyte diameter ranges from 370 to 485  $\mu\text{m}$ . Hydrated stage (Fig. 2f): yolk globules completely undergo coalescence and form a single translucent yolk mass. Oocyte diameter ranges from 385 to 650  $\mu\text{m}$ . Early atretic stage (Fig. 2g): the nucleus and yolk globules disintegrate and are reabsorbed, leaving only the follicular layers. This stage corresponds with alpha stage atresia described by Hunter and Macewicz (1985). Late atretic stage (Fig. 2h): the follicle decreases in size and is characterized by numerous disorganized granulosa cells and intracellular vacuoles. This stage corresponds with beta stage atresia described by Hunter and Macewicz (1985). In addition, the post-ovulatory follicle (Fig. 2i), which is characterised by a granulosa cell layer, coils up within a less irregular thecal cell layer covering, and is frequently observed during the spawning season.



**Fig. 2** Oocyte developmental stages and post-ovulatory follicle of female *E. tumifrons*: **a** peri-nucleolus, **b** pre-vitellogenic, **c** early yolk globule, **d** late yolk globule, **e** migratory nucleus, **f** hydrated follicle, **g** early atretic follicle, **h** late atretic follicle, and **i** post-ovulatory follicle. *n* Nucleus, *g* granulosa cell layer, *t* thecal cell layer. Scale bars 100  $\mu$ m



**Fig. 3** Asynchronous oocyte development in the ovary of female *E. tumifrons*. *PN* Peri-nucleus, *EYG* early yolk globule, *LYG* late yolk globule, *H* hydrated, *POF* post-ovulatory follicle. Scale bars 100  $\mu$ m

### Ovarian maturity stages

*Evynnis tumifrons* has an asynchronous ovary containing oocytes at various stages of development (Fig. 3). Based on the appearance of the most advanced oocytes, post-ovulatory follicles and atretic oocytes, the ovaries were classified into six ovarian maturity stages: immature (I), maturing (II), mature (III), spawned (IV), spent (V) and resting (VI). The development of oocytes at each stage is shown in Table 1.

### Size at sexual maturity

The size at sexual maturity was estimated from the 177 females collected in the spawning months from November 2013 to May 2014. The minimum size of the mature females was 161 mm FL. The estimated logistic function was as follows:

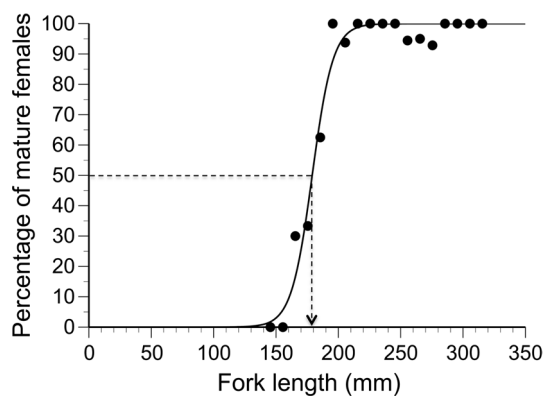
$$PMF = 100/[1 + \text{Exp}(-0.119(\text{FL}_m - 179))](n = 18, r^2 = 0.975).$$

$\text{FL}_{50}$  was estimated to be 179 mm FL (Fig. 4).

**Table 1** Six ovarian maturity stages of female *Evynnis tumifrons* off the southwestern coast of Kyushu, Japan

Ovarian maturity stage	Developmental stage of oocytes
Stage I (immature)	Only unyolked oocytes, such as PN and PV, were present. Oocytes ranged from 60 to 275 $\mu\text{m}$ in diameter
Stage II (maturing)	Most advanced oocyte was in EYG or LYG. Oocytes were 195–450 $\mu\text{m}$ in diameter
Stage III (mature)	Most advanced oocyte was in MN or H. Oocytes were 370–650 $\mu\text{m}$ in diameter
Stage IV (spawned)	Yolked oocytes and POF were present
Stage V (spent)	More than 50% of yolked oocytes were in EA. POF was absent
Stage VI (resting)	Unyolked oocytes and LA oocytes were present

PN Peri-nucleolus stage, PV pre-vitellogenic stage, EY early yolk globule stage, LYG late yolk globule stage, MN migratory nucleus stage, H hydrated stage, EA early atretic stage, LA late atretic stage, POF post-ovulatory follicle



**Fig. 4** Percentage of sexually mature females at 10-mm fork length (FL) intervals. A logistic curve was fitted to the data and the dotted arrow shows the FL at 50% maturity

### Annual reproductive cycle

According to the results shown in Fig. 5a, the GSI had two yearly peaks, a higher one in November to December (late autumn–winter 2012, 2013), and a lower one around April (spring 2012, 2013, 2014). The monthly occurrences of the six ovarian maturity stages from April 2012 to June 2014 are shown in Fig. 5b. Though *E. tumifrons* had an asynchronous ovary, which suggested multiple spawning during its reproductive season (Fig. 3), we noticed a general trend in which females tended to be mostly immature from June to September (early summer–early autumn 2012, 2013, 2014), and mature or spawned from November to May (late autumn–late spring 2012–2013, 2013–2014), though in March 2013 mature or spawned females could not be detected within our samples.

### Annual condition factor cycle

The condition factor of fish tended to be high from June to October (summer–autumn 2012, 2013), decreased in November (late autumn 2012, 2013) and was lowest in

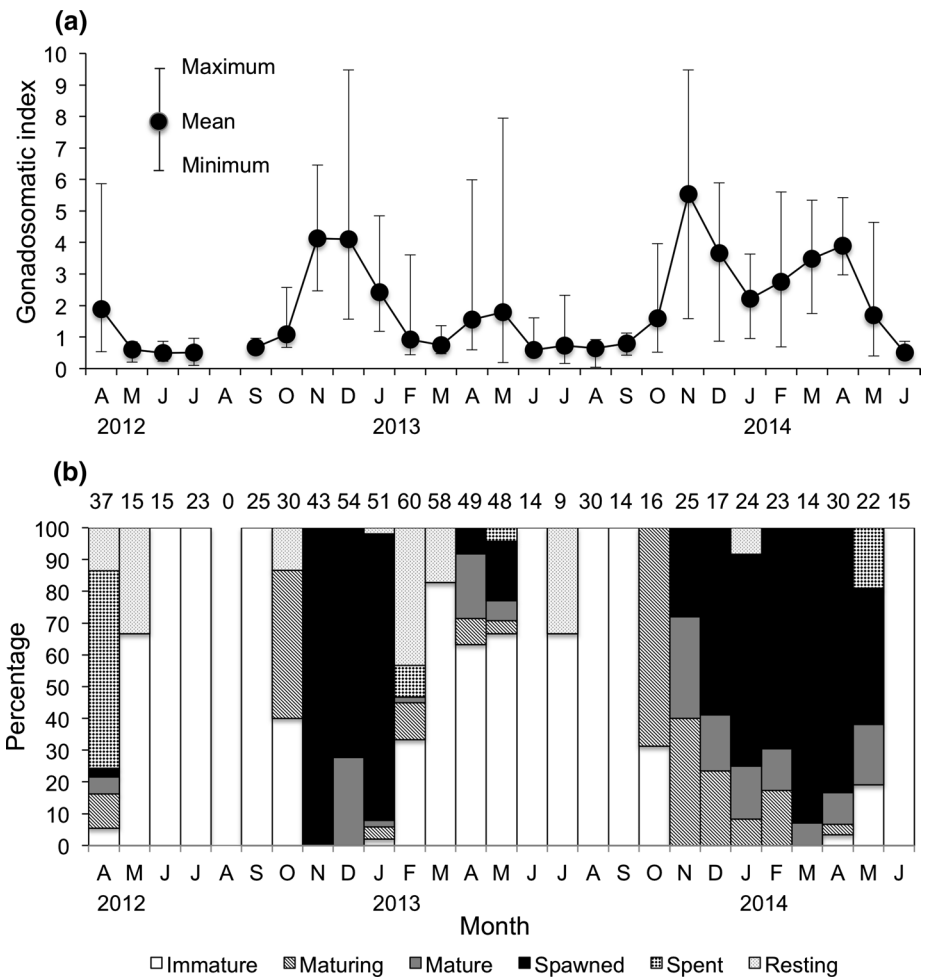
December or January (winter 2012, 2014) (Fig. 6). However, there seemed to be variation in the increase after the periods of lowest condition factor until May (spring 2013, 2014) within the 2 years of study. From January 2013 to May 2013, the increase was sharp compared to that from February 2014 to May 2014.

### Discussion

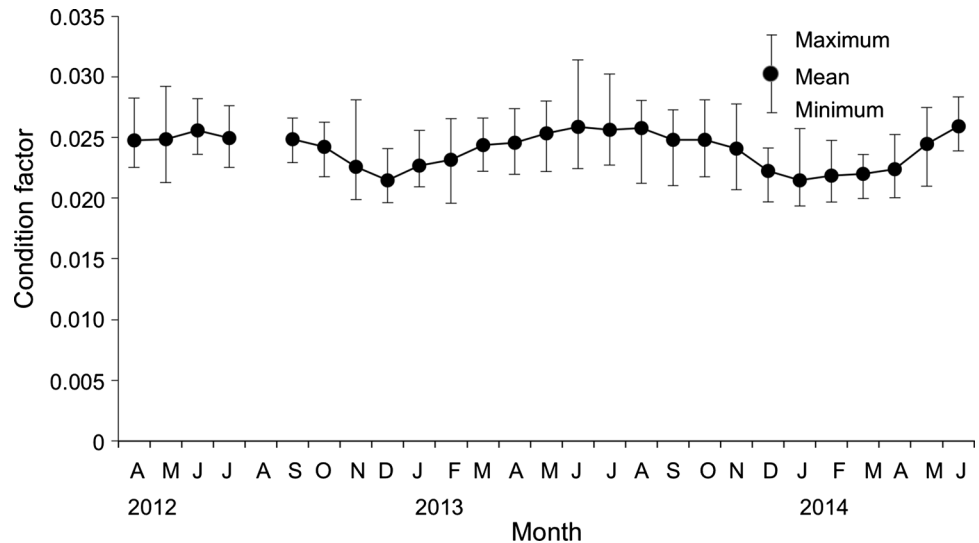
Ovarian maturity stages of female *E. tumifrons* were classified into six categories based on the appearance of the most advanced oocytes, post-ovulatory follicle and atretic oocytes. Stage III was regarded as mature because a migratory nucleus or hydrated oocytes occurred in the ovary. In the present study, the time course of the maturation process was not clarified, but in the related species *P. major* and *D. hypselosomus*, nucleus migration starts at around 24 h before spawning, and the subsequent hydration of the oocyte starts at around 12 h before spawning (Matsuyama et al. 1988; Yoda and Yoneda 2009). Stage IV (spawned) could be determined from the occurrence of post-ovulatory follicles (evacuated follicles) in the ovary. Post-ovulatory follicles occurring at ovulation are believed to be reabsorbed within 24 h (Matsuyama et al. 1988; Yoda and Yoneda 2009). Thus, stage III (mature) and stage IV (spawned) *E. tumifrons* were assumed to appear within a few days of spawning. It is also important to note that the time course of the maturation process is temperature dependent (Kurita et al. 2011). However, according to Hunter and Macewicz (1985), a migratory nucleus and hydrated oocytes indicate imminent spawning, while post-ovulatory follicles are histological evidence of very recent spawning (Hunter et al. 1992).

Size at sexual maturity is an important reference point for decision-making in fisheries management (Zhu et al. 2011). However, some previous related research (e.g. Mio 1962; Toriyama et al. 1975; Yamahora 1983) did not estimate this vital biological parameter. Anzawa et al. (1987), however, did estimate the minimum size of mature female

**Fig. 5** Monthly changes in the gonadosomatic index (a) and percentage occurrence of the six ovarian maturity stages (b) of female *E. tumifrons* off the southwestern coast of Kyushu, Japan. Samples could not be collected in August 2012. Fish smaller than the minimum size of mature females (< 161 mm) were excluded from this analysis. Numbers of females examined shown above the bars



**Fig. 6** Monthly changes in the condition factor of female *E. tumifrons* off the southwestern coast of Kyushu, Japan. Samples could not be collected in August 2012. Fish smaller than the minimum size of mature females (< 161 mm) were excluded from this analysis



*E. tumifrons*, i.e. 170 mm FL, from its GSI. In the present study, we estimated the minimum size of mature females as 161 mm FL and their size at  $FL_{50}$  as 179 mm FL (Fig. 4), based on the histological technique used. Thus, the minimum

size of mature females differed slightly between the current study and Anzawa et al.'s (1987). According to DeMartini et al. (2000) and Alejo-Plata et al. (2011), a histological approach has been proven to have greater precision for the



estimation of size at maturity, so the difference in minimum size estimated in our and Anzawa et al.'s (1987) might be due to the different methodologies used. On the other hand, the locality and date on which these two studies were conducted were very different; this may be another factor contributing to the different estimated minimum size of females at sexual maturity. In future studies, histological techniques should be used to examine samples collected at the same time from different localities.

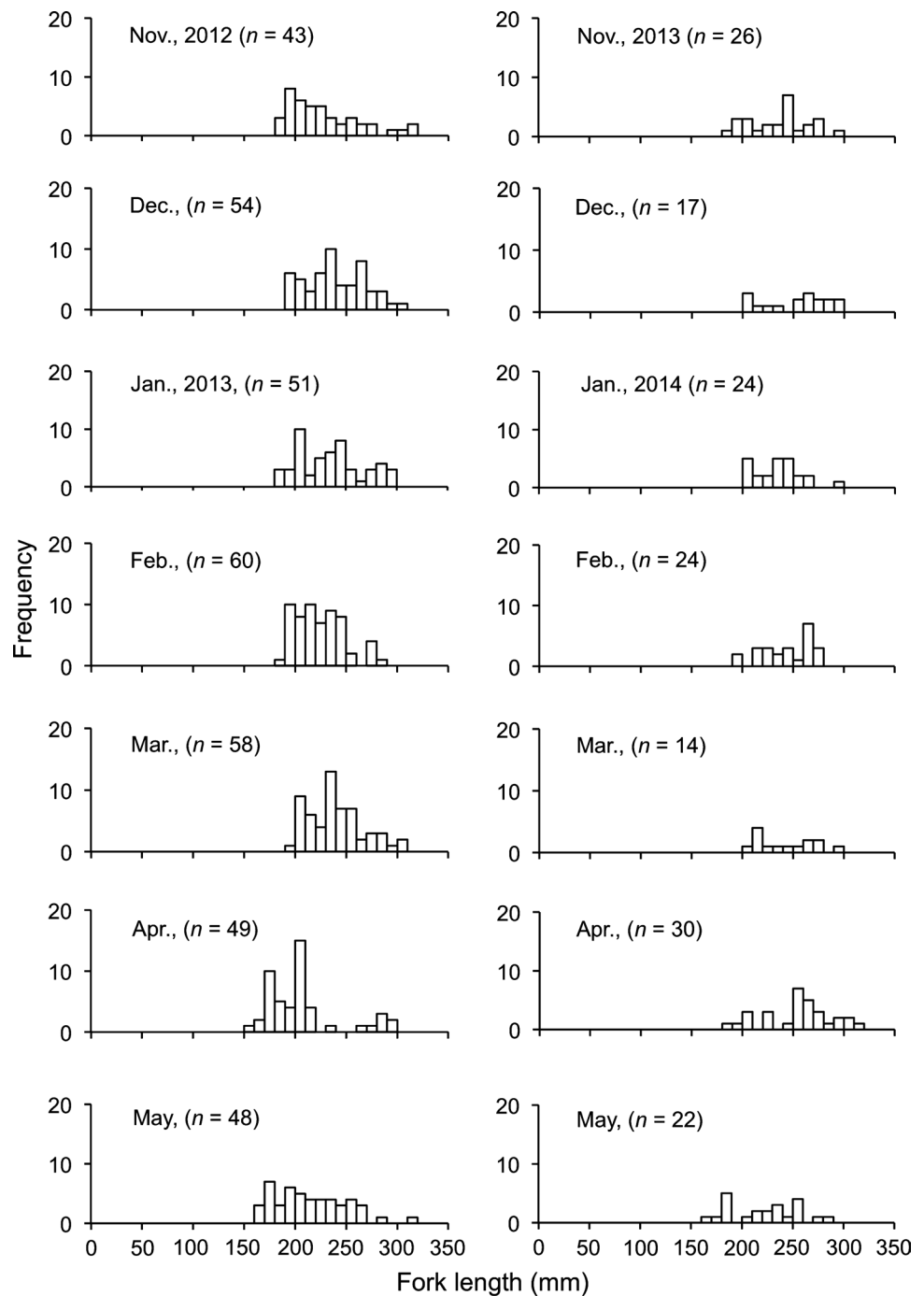
The simultaneous occurrence of a high GSI and mature or spawned maturity stages, which were considered to show the spawning season, lasted from November to May (7 months). The onset of the spawning season was clearly marked by the sharp increase in GSI and the occurrence of the mature or spawned stage in November. The preceding ovarian maturity stage II (maturing), which also occurred during the spawning season, may subsequently shift to ovarian stages III (mature) and IV (spawned), so that most fish were considered to undergo spawning judging from the transition of the six ovarian maturity stages (Fig. 5b). The end of the spawning season around May and June was clearly marked by the subsequent precipitous decline in the monthly change in GSI and the occurrence of fish with spent ovaries at stage V. This spent stage indicates that the cessation of spawning is imminent (Hunter and Macewicz 1985; Yoneda et al. 1998; Granada et al. 2004). However, in 2013 (Fig. 5b), the spent stage occurred in February and in the subsequent month, no mature or spawned females were detected. This suggests that there was an intermission in spawning in March 2013. In some fish species, skipped spawning is observed, which is mostly attributed to a deficient diet and poor nutritional condition (Rideout et al. 2005; Rideout and Tomkiewicz 2011). However, in the present study, the mean condition factors of the individuals collected in February and March 2013 were higher than those of individuals collected in February and March 2014 (Fig. 6). Figure 7 shows the monthly size composition during the spawning season (November–May) of the two study years. Small individuals were collected in April and May 2013 and May 2014, but not in March 2013. Thus the intermission in spawning in March 2013 may have not been due to individual status such as poor body condition and small body size. Figure 8 shows the water temperature from April 2012 to June 2014 off Ichikikushikino City, which is located near the study area. A similar trend in temperature fluctuations occurred throughout each year, but it should be noted that the minimum temperature in February 2013 was only 15.4 °C and in the following month (March) spawning was interrupted. On the other hand, in January 2014 the minimum temperature was 1 °C higher (16.4 °C), and this might have made conditions favourable for continuous spawning until May of that year. Although these temperature data were measured at a different depths to those of the species' distribution, it should be noted that 5 m is below

the water surface. Moreover, these temperatures were measured at a consistent depth throughout the study. Hence, the monthly temperature change observed should be sufficient to explain the change in spawning behaviour. Furthermore, the co-occurrence of sexually mature and immature individuals in April and May 2013 (Fig. 5b) following the intermission in spawning in March 2013 is an interesting phenomenon. According to Lowerre-Barbieri et al. (2011), larger, older individuals exhibited an extended spawning season compared to younger, mature individuals. However, our investigation revealed that nearly half or all larger individuals were immature during this extended spawning season (Fig. 9a). There was no significant difference ( $P > 0.05$ ) in the condition factors of the immature and sexually mature individuals either (Fig. 9b). Therefore, we could not determine the reason for the co-occurrence of sexually mature and immature individuals in April and May 2013.

The spawning season of *E. tumifrons* in the coastal waters of Japan varied according to locality (see Table 2; localities at the top of the table are located further north). In northern Japan (Yamagata and Niigata Prefectures), it tended to occur from mid-summer to mid-autumn, whereas in southern Japan (Fukuoka, Kochi and Miyazaki Prefectures), it occurred from early autumn to early winter. In the present study, which was conducted off the southwestern coast of Kyushu (the southernmost limit of *E. tumifrons*' distribution in Japanese coastal waters), it occurs from late autumn to late spring. This trend shows that in the north *E. tumifrons* spawns during the warmer months of the year, but shifts its spawning season closer to the colder months in southern areas, while at its southernmost limit, it spawns throughout the cold season. In addition, there seems to be a trend in the duration of spawning according to locality: at the southernmost location of *E. tumifrons* (present study), the spawning season lasts longer than at higher latitudes. This phenomenon was also observed in *Plectropomus areolatus* and *Epinephelus fuscoguttatus*, in which spawning season appeared longer nearer to the equator in the northern hemisphere (Sanchez-Cardenas and Arregui-Sanchez 2012).

To elucidate why the spawning season varied depending on latitude, three localities were selected to investigate the effect of water temperature and day length on spawning season because these two factors are generally thought to be the most important triggers in the timing of gametogenesis and termination of spawning in temperate fish (Lam 1983; Hanyu 1991; Tominaga et al. 2005). In Fig. 10 we illustrate the mean water temperatures during *E. tumifrons*' spawning season in Niigata (northern location) and Fukuoka (southern location), which had similar high water temperatures at spawning that overlapped. On the other hand, off the southwestern coast of Kyushu (southernmost location, present study), the trigger seemed to change to colder rather than warmer water; spawning in this species probably also has

**Fig. 7** Monthly lengths of female *E. tumifrons* collected during the spawning season of the 2 years of the study. Fish smaller than the minimum size of mature females (< 161 mm) were excluded from this analysis



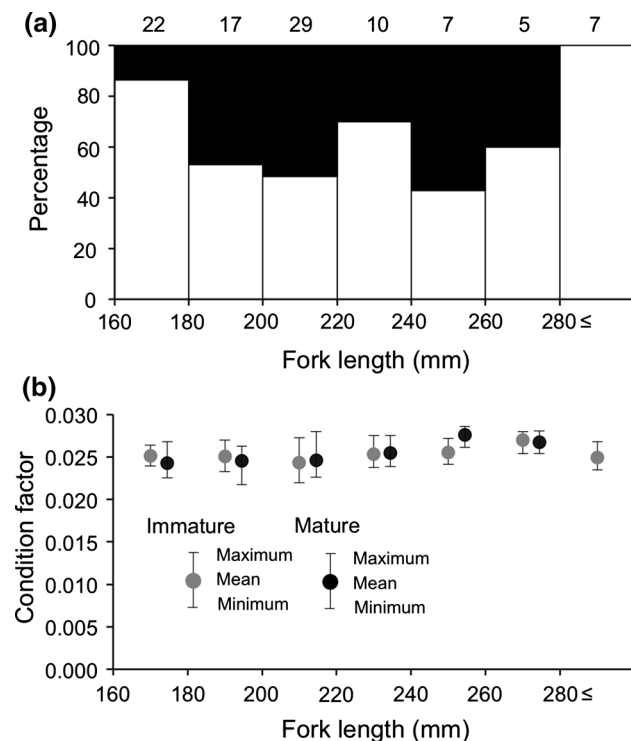
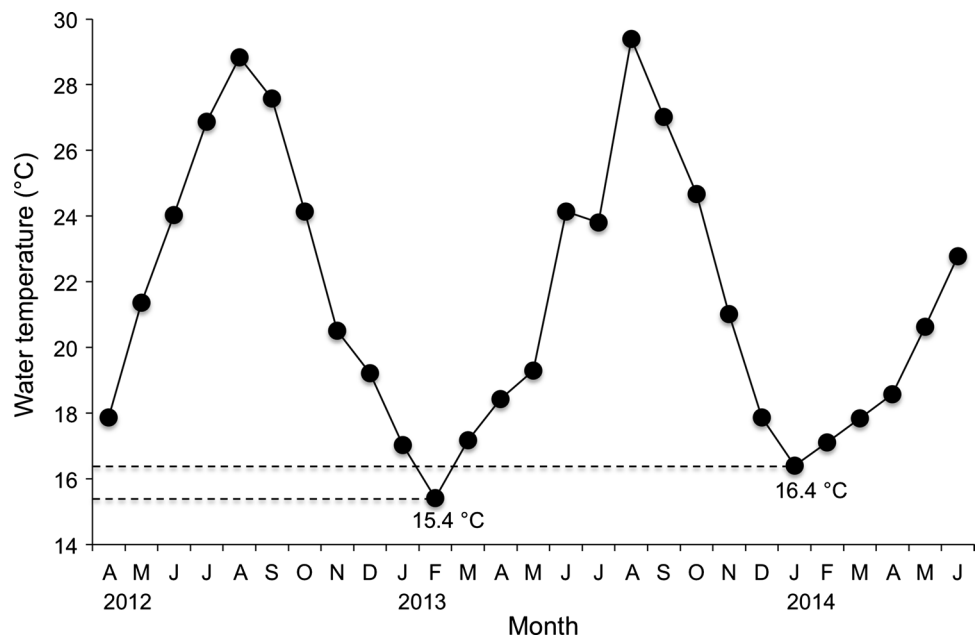
a lower threshold of water temperature beyond which the spawning process may stop.

Regarding the effect of day length (Fig. 10), spawning in northern Niigata was favoured when conditions combined warmer water with longer days, while to the south in Fukuoka a combination of warmer water conditions but with shorter days was preferred; finally in the southernmost location off the southwestern coast of Kyushu (present study), day length did not seem to have much effect. Thus, the range as well as the transition of water

temperature and day length during the spawning season differed between these three localities, which might have influenced the timing of gametogenesis and termination of spawning in different ways. Moreover, the following factors should be considered: firstly, each population of *E. tumifrons* distributed in the coastal waters of Japan may have evolved an intrinsic spawning behaviour to ensure a match between emergent larvae and their food source; secondly, each population might have evolved to suit the characteristics of the environment they are distributed in.



**Fig. 8** Monthly changes in mean water temperature off the southwestern coast of Kyushu, Japan. Data were recorded daily off Ichikikushikino City near the study area by a temperature sensor at 5 m below the water surface attached to the hull of a ferry. Data are cited from the database of Kagoshima Prefectural Fisheries Technology and Development Centre (<http://kagoshima.suigi.jp>)



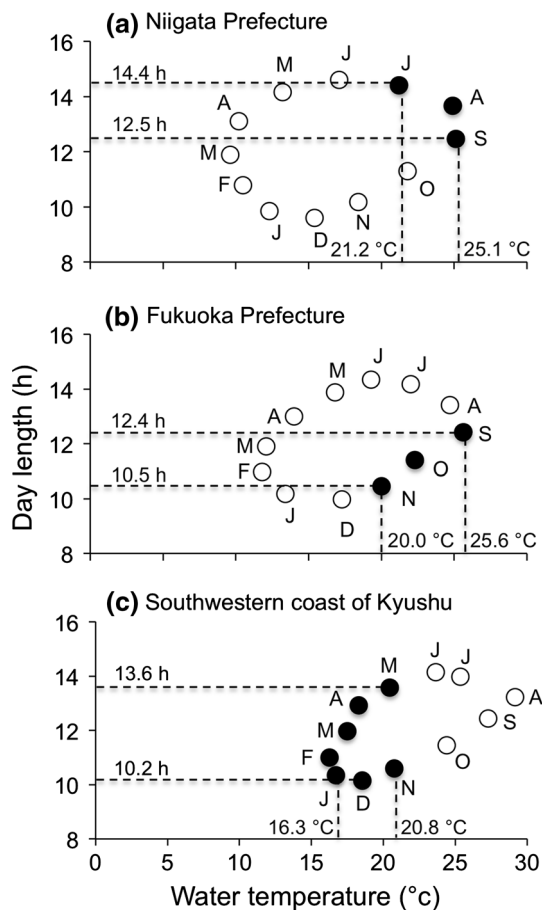
**Fig. 9** Percentage occurrence (a) and condition factor (b) at 20-mm FL intervals of immature and mature female *E. tumifrons* collected in April and May 2013 off the southwestern coast of Kyushu, Japan. Fish smaller than the minimum size of mature females (<161 mm) were excluded from this analysis. Non-shaded bars indicate immature females, shaded bars indicate mature females. Numbers of females shown above the bars

Because the coastal waters of Niigata (northern Japan) are part of the Sea of Japan, those of Fukuoka (southern Japan) are part of the Tsushima Strait, and those off the southwestern coast of Kyushu (further south) are part of the East China Sea, they differ greatly from one another. Hence, *E. tumifrons* may have evolved over time to contend with the conditions of the habitat they are distributed in. To elucidate this assertion, future experimental studies on each population are needed, as this will help to achieve an understanding of their behavioural characteristics, especially the degree at which genetic variation and/or thermal or light plasticity contribute towards the variation in their spawning seasons.

The present study was conducted to promote an understanding of the reproductive biology of *E. tumifrons* off the southwestern coast of Kyushu, Japan, and is the first to provide detailed information on this species’ ovarian maturation using an histological technique. The minimum size of mature females was estimated to be 161 mm FL and the FL<sub>50</sub> 179 mm FL. The spawning season was estimated to last from November to May. These findings and those of previous studies evidence regional differences in the reproductive biology of *E. tumifrons* that may have important implications for the appropriate management of this species. It is therefore paramount that current management measures targeting this species are scrutinized and updated so that the biological variability of each geographical population is taken into account and incorporated into future management policies.

**Table 2** Comparison of spawning season of *E. tumifrons* according to latitude in the coastal waters of Japan

Locality	Latitude	Spawning season	Author
Yamagata Prefecture	38°55'N	July–October	Yamahora (1983)
Niigata Prefecture	37°50'N	July–September	Anzawa et al. (1987)
Fukuoka Prefecture	33°50'N	September–November	Mio (1962)
Kochi and Miyazaki Prefectures	33°16'N and 32°10'N	October–December	Toriyama et al. (1975)
Southwestern coast of Kyushu	31°39'–31°33'N	November–May	Present study



**Fig. 10** Mean water temperature and day length when spawning occurred: **a** Niigata Prefecture, **b** Fukuoka Prefecture and **c** southwestern coast of Kyushu. Solid circles indicate spawning months and open circles indicate non-spawning months of *E. tumifrons*. Water temperature data in Niigata and Fukuoka Prefectures were obtained from serial station data between 1906 and 2003 at 10-m depth and are cited from the database of the Japan Oceanographic Data Centre (<http://www.jodc.go.jp/jodcweb/>). Water temperature data off the southwestern coast of Kyushu are pooled mean data from Fig. 8. Day length data are records for 1987 in Niigata, 1962 in Fukuoka and April 2012–June 2014 off the southwestern coast of Kyushu, and are cited from the database of the National Oceanic and Atmospheric Administration (<https://www.esrl.noaa.gov/gmd/grad/solcalc/>)

**Acknowledgements** We would like to acknowledge the tireless cooperation of the commercial fishers of the Eguchi Fishermen's Cooperative and the students of the Fisheries Biology Lab, Faculty of Fisheries, Kagoshima University for data sampling and measurement. We would also like to express our sincere gratitude to Mr Shugo Matsuo and Ms Yuki Katsuha for their assistance in preparing the histological sections of the ovaries.

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