

Reproductive Biology of *Johnius taiwanensis* (Perciformes: Sciaenidae) in Fujian Waters, Southern China

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Received 26 August 2019 / Accepted 12 November 2019 / Published 12 December 2019

Communicated by Hin-Kiu Mok

Johnius taiwanensis is a newly described species from the Family Sciaenidae (Perciformes). The species is commonly found in shallow coastal waters along both sides of the Taiwan Strait, on the west sides of Zhejiang, Fujian, Guangdong and Hong Kong and east side of Taiwan, and has been misidentified for decades. We studied the reproductive biology of *J. taiwanensis* from Fujian coastal waters, southern China, using gonadosomatic index (GSI) and gonad histology analyses. Monthly sampling from July 2016 to October 2017 was conducted and a total of 638 specimens were collected, ranging from 7.3 to 19.0 cm standard length (SL). Gonad histology suggested that the spawning activity of *J. taiwanensis* females and males lasted from April to October, and the peak spawning months for females was July to September. Mature females and males were 12.5 and 11.8 cm SL, respectively, while the estimated sizes at 50% maturity were 12.0 cm and 10.9 cm SL, respectively. Vitellogenic stage oocytes (O3) and post-ovulatory follicles (POF) or hydrated oocytes (HO) were observed, and POF and O3 in ovaries indicated that *J. taiwanensis* spawns multiple times each spawning season. HO or both HO and POF were observed in ovaries collected from one same location in May 2017 and August 2016.

Key words: Gonad histology, Gonadosomatic index, *Johnius taiwanensis*, Sciaenidae, Spawning season.

BACKGROUND

The Family Sciaenidae consists of approximately 300 species from 70 genera throughout Atlantic, Indian and Pacific Oceans, in coastal marine, brackish and freshwater; many associate with muddy or sandy bottoms (Chao et al. 2015; Lin et al. 2019). Sciaenids are important food fishes with global capture fishery production of approximate 1.7 million tons annually over the past decade (<http://www.fao.org/fishery/statistics/global-capture-production/en>, accessed on 23 August 2019). Some sciaenids form large aggregations for spawning, feeding and over-wintering, which makes them vulnerable to overfishing (Liu and Sadovy de

Mitcheson 2008). In recent years, small- and medium-sized croakers enter fisheries and become predominate in Chinese and adjacent waters, e.g., the genera *Collichthys*, *Johnius* and *Pennahia* (Yamaguchi et al. 2006; Li 2010; Tuuli et al. 2011; Wang et al. 2011; Xie et al. 2012).

The genus *Johnius* is endemic to Indo-West Pacific, with about 35 species, mainly occurring in shallow tropical and subtropical coastal waters, and *Johnius* species usually have small- to medium-sized bodies and a small mouth, sub-terminal to inferior positioned (Trewavas 1977; Sasaki 1989 2001). Eight *Johnius* species are confirmed in Chinese waters, including the most recently described species, *J.*

taiwanensis (Chao et al. 2019). *Johnius taiwanensis* inhabits shallow coastal waters of southeast China, along both sides of the Taiwan Strait, on the west sides of Zhejiang, Fujian, Guangdong and Hong Kong and east side of Taiwan (Chao et al. 2019) (Fig. 1). It is a common species but has been misidentified for years as *J. belangerii*, *J. macrorhynchus*, *J. sina* or *Wak sina* (Chu et al. 1963; Yu and Shen 1987; Shen 1993; Lin et al. 2007). *Johnius taiwanensis* can be caught by trawler and hook-and-line almost year-round and is an important local food fish.

As a newly described species, no studies have been conducted on the biology or ecology of *J. taiwanensis*. The present study examines the reproductive cycle of *J. taiwanensis* in Fujian waters, southern China, using the gonadosomatic index (GSI) and gonad histology analyses, to evaluate its spawning seasonality and sizes at maturity, and to discuss the results in the context of fisheries.

MATERIALS AND METHODS

Fish sampling

Johnius taiwanensis was collected by hook-and-

line in Zhangzhou waters (117°33'50"E, 23°41'20"N), and by trawler in Quanzhou (118°57'42"E, 24°51'10"N), Fuzhou (119°46'12"E, 26°07'16"N) and Ningde (119°50'25"E, 26°36'50"N) waters, Fujian Province, southern China (Fig. 1). Specimens were randomly collected monthly from July 2016 to October 2017 with a continuous. Measurements of total length (TL 0.1 cm), standard length (SL 0.1 cm), whole body weight (BW 0.1 g) and gonad weight (GW 0.1 g) were conducted in the laboratory.

Gonad histology

Middle portions of paired gonad lobes from males and females were fixed in Dietrich's fixative for at least one week. Gonad tissue was transferred to 70% alcohol prior to histological procedures. The gonad tissue was dehydrated in a series of alcohols (from 75 to 100%), cleared in toluene, and embedded in paraffin wax. Gonad tissue were sectioned at 6-7 μm, stained with haematoxylin and eosin, and mounted on slides.

Sexual maturation stages

Gonad sections were examined under microscopy. Maturity stages of ovaries were determined based

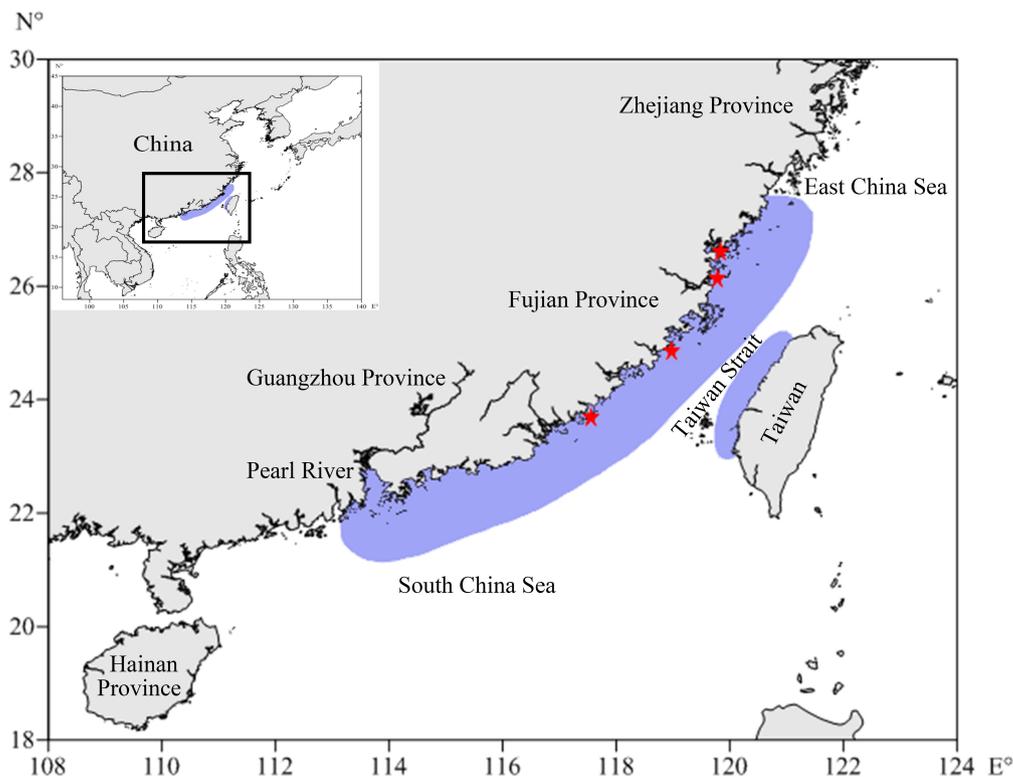


Fig. 1. Distribution of *Johnius taiwanensis* (light purple areas) in Chinese waters. Red stars: the sampling sites from north to south, Ningde, Fuzhou, Quanzhou and Zhangzhou in Fujian waters.

on the most advanced oocytes, and the occurrence of hydrated oocytes (HO), post-ovulatory follicles (POF) and/or atretic oocytes. The relative proportion of primary and secondary spermatocytes (1SC/2SC) and spermatids (ST) in testes, and the appearance of sperm (SP) in sperm duct were used to determine the maturity stages of testes. Each gonad was allocated to one of the five maturity stages: immature/resting female (F1) and immature/resting male (M1), developing female (F2) and developing male (M2), maturing female (F3) and maturing male (M3), ripe female (F4) and ripe male (M4), and spent female (F5) and spent male (M5) (Grier 1981; Wallace and Selman 1981; Yamaguchi et al. 2006; Tuuli et al. 2011) (Table 1).

Spawning seasonality

The spawning months were determined using both the average monthly GSI and gonad histology analyses. The GSI was calculated using the formula: $GSI (\%) = GW / (BW - GW) \times 100$. The GSI is an easy, cheap and quick method to evaluate the spawning seasonality by identifying the peak month(s) on GSI value. Evaluating spawning seasonality through gonad histological examination gives a more detailed description of gonad developmental stages and sexual maturation stages with a time consume.

Size at maturity

The minimum body sizes for female and male maturity were estimated based on GSI data and gonadal histological results. The GSI values of mature females (F3, F4 and F5) and mature males (M3, M4 and M5),

determined by gonadal histology, were plotted against their body sizes (SL); the SL with the largest and most persistent increase in GSI% was considered to be the minimum sizes for female and male maturity.

To determine the body sizes at 50% sexual maturation for females and males, all individuals collected over the spawning months were assigned to body size classes (SL) of 1.0 cm, and the percentage of mature females and males in each size class were calculated. A maturity curve was plotted against SL classes to estimate the size at 50% sexual maturation.

Statistical analysis

Differences in body sizes of females and males were analyzed by statistical significance, set to < 0.05 .

RESULTS

Biological parameters

A total of 638 individuals were collected in July 2016–October 2017; at least 30 individuals for most of the months. Body sizes ranged from 7.3 to 18.5 cm SL (14.9 ± 1.9 , mean \pm S.D., $n = 340$) for females and from 8.0 to 19.0 cm SL (14.8 ± 1.9 , $n = 298$) for males; there was no significant difference in SL between females and males ($p = 0.313$) (Fig. 2). Sex ratio of female: male showed monthly variation between 0.69:1.00 in September and 2.50:1.00 in June, but there was no significant difference ($p = 0.569$). The relationship of TL (cm) to SL (cm) and BW (g) to SL (cm) were: $TL = 1.1366 \times SL + 0.9558$ ($R^2 = 0.9432$, $n = 638$) (Fig. 3a)

Table 1. Descriptions of sexual maturation stages for females and males of *Johnius taiwanensis*

Sexual maturation stages	Gonadal characters
Females	
Immature/resting (F1)	The most advanced oocytes are primary growth stage oocytes (O1). O1 closely packed and predominate.
Developing (F2)	The most advanced oocytes are at cortical alveolar stage oocytes (O2), together with O1.
Maturing (F3)	The most advanced oocytes are at vitellogenic stage oocytes (O3), but prior to the nucleus migratory stage. Zona radiata is thicker than those of O1 and O2. Yolk globules begin to fuse.
Ripe (F4)	The most advanced oocytes are O3 with the nucleus migratory or a single yolk mass originated from the yolk globules. Hydrated oocytes (HO) or post-ovulatory follicles (POF) may be present in some ovaries.
Spent (F5)	O1 dominate together with the occurrence of atretic O3 (AO3).
Males	
Immature/resting (M1)	Only spermatogonia (SG), primary and secondary spermatocytes (1SC/2SC) are present. No sperm in sperm duct.
Developing (M2)	Large amount of 1SC/2SC with the appearance of spermatids (ST). No sperm in sperm duct.
Maturing (M3)	Large amount of ST at the peripheral and central tubules. Sperm duct has sperm, but not full.
Ripe (M4)	Large amount of SP at the central tubules. Sperm duct is full of sperm with large amount of ST.
Spent (M5)	The lumen of tubules and sperm duct are empty or with residual sperms. SG and 1SC/2SC can be observed at the peripheral tubules.

and $BW = 0.02 \times SL^{3.0198}$ ($R^2 = 0.9533$, $n = 638$) (Fig. 3b), respectively.

Sexual maturation stages

All five sexual maturation stages for females were observed: immature/resting (F1), developing (F2), maturing (F3), ripe (F4) and spent (F5) (Table 1; Fig. 4). In males, developing (M2), maturing (M3), ripe (M4) and spent (M5) males were determined; no immature/resting males (M1) were found in the present study (Table 1; Fig. 5).

Ovaries with evidence of HO or both HO and POF were found in May (2017) and August (2016), collected in Dongshan Bay (117°33'50"E, 23°41'20"N) of Zhangzhou waters, indicating very recent spawning activity. Ovaries had O3 and POF or O3, HO and POF, confirming that *J. taiwanensis* is a multiple spawner.

Spawning seasonality

The monthly average GSI% of females and males showed similar and distinct seasonal variation patterns, with females generally having higher GSI values than males (Fig. 6). In females, the average GSI peaks were in July and August, with GSI over 5.5%, indicating that these were the peak spawning months for females.

From November to April, the average GSI% of females were low, less than 1.5%. In males, the average GSI peaks were in May and August with GSI over 1.3%, indicating that this was the peak spawning season for males. Similar to females, the average GSI% of males were low from November to next April, less than 0.6%.

Based on gonadal histology, the spawning seasons for females and males were revealed to last longer than those determined by GSI values above. In females, F1 and F2 were found from November to June, dominating from November to next April (Fig. 4a b; Fig. 7a). The proportion of F2 increased in March and April, followed by the appearance of F3 in April and the increase of F3 in May–August, indicating that this was the ovary development phase of female sexual maturation (Fig. 4c; Fig. 7a). The proportions of F3 and F4 remained high between May and October, indicating the female spawning season in May–October. In July–September, the proportions of F4 were more than 50%, indicating the peak spawning season (Fig. 4d e; Fig. 7a). The proportion of F5 and F1 were high after October, indicating the end of the spawning season (Fig. 4f; Fig. 7a).

M1 was not found in males. M2 was only found in July (Fig. 5a; Fig. 7b). M3 was absolutely dominant in March (100%), and decreased with the dramatic increase of M4 proportions in April and May (Fig. 5b c;

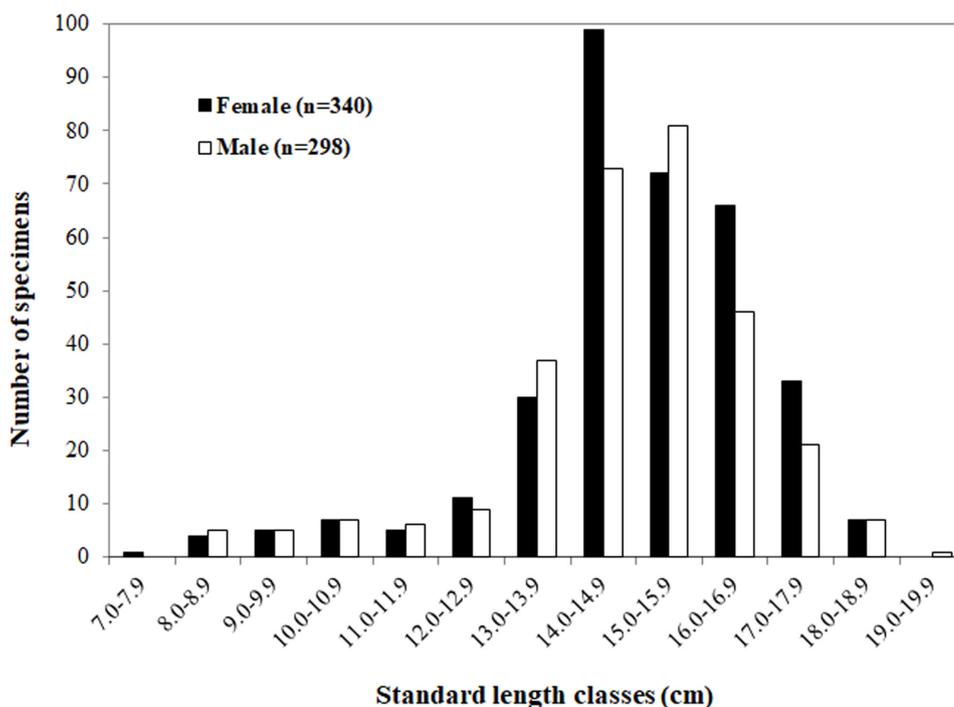


Fig. 2. Body size (standard length in cm) distributions for females ($n = 340$) and males ($n = 298$) of *Johnius taiwanensis* collected between July 2016 to October 2017 in Fujian waters, China.

Fig. 7b). M4 remained high between April and October, indicating that the male spawning season was April–October, longer than that of females. High proportions of M4 (> 50%) in April–September indicated the peak spawning season. M5 were dominant from October to next February, indicating the end of the spawning season (Fig. 5d; Fig. 7b).

Size at maturity

The estimated minimum body sizes for female and male maturity were 12.5 and 11.8 cm SL, respectively (Fig. 8a b). The estimated body sizes at 50% sexual maturation for females and males were 12.0 and 10.9 cm SL, respectively, based on all females and males collected during the spawning months from April

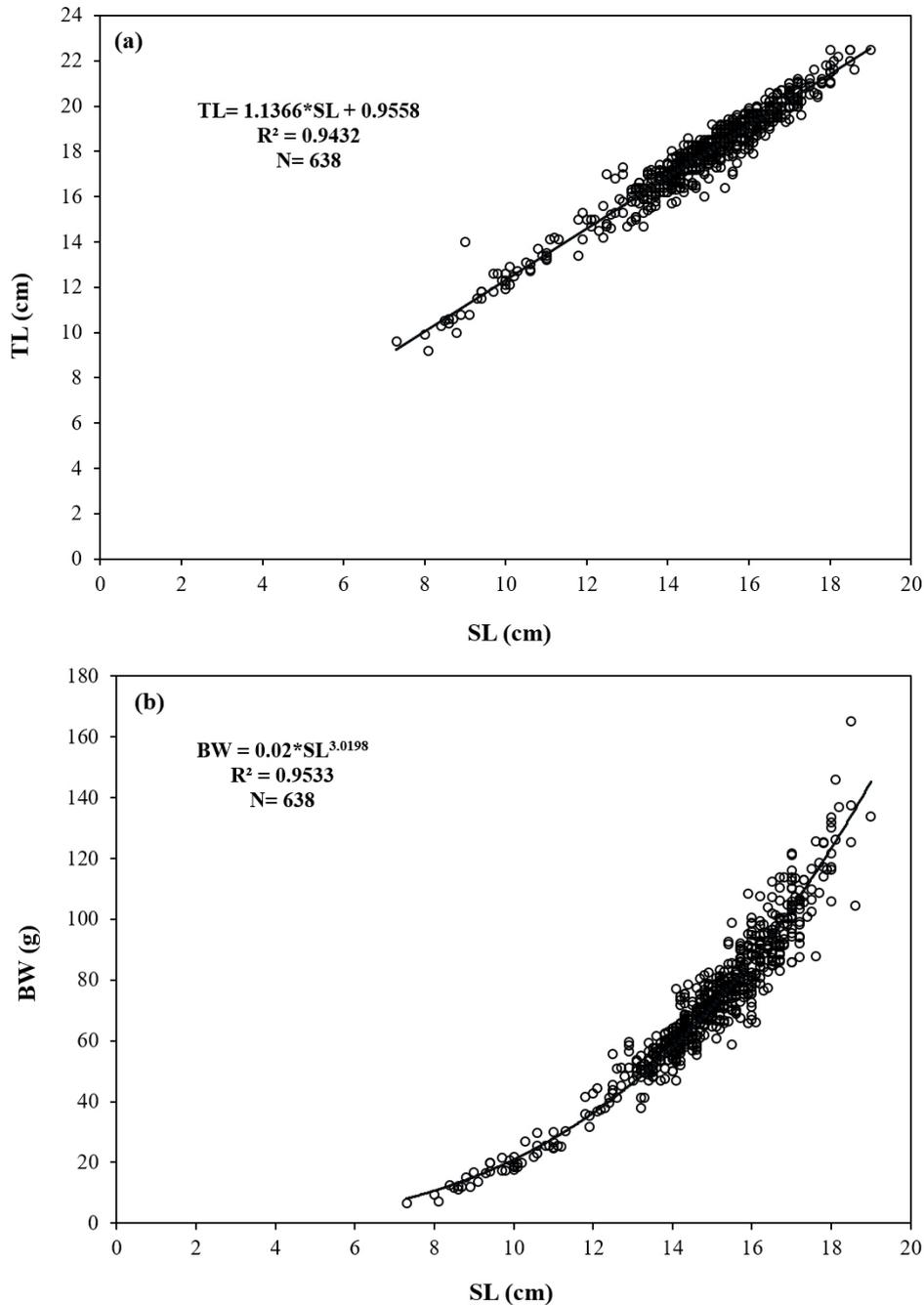


Fig. 3. Relationships of (a) total length (TL in cm) to standard length (SL in cm) and (b) body weight (BW in g) to standard length (SL in cm) of *Johnius taiwanensis* collected between July 2016 and October 2017 in Fujian waters, China.

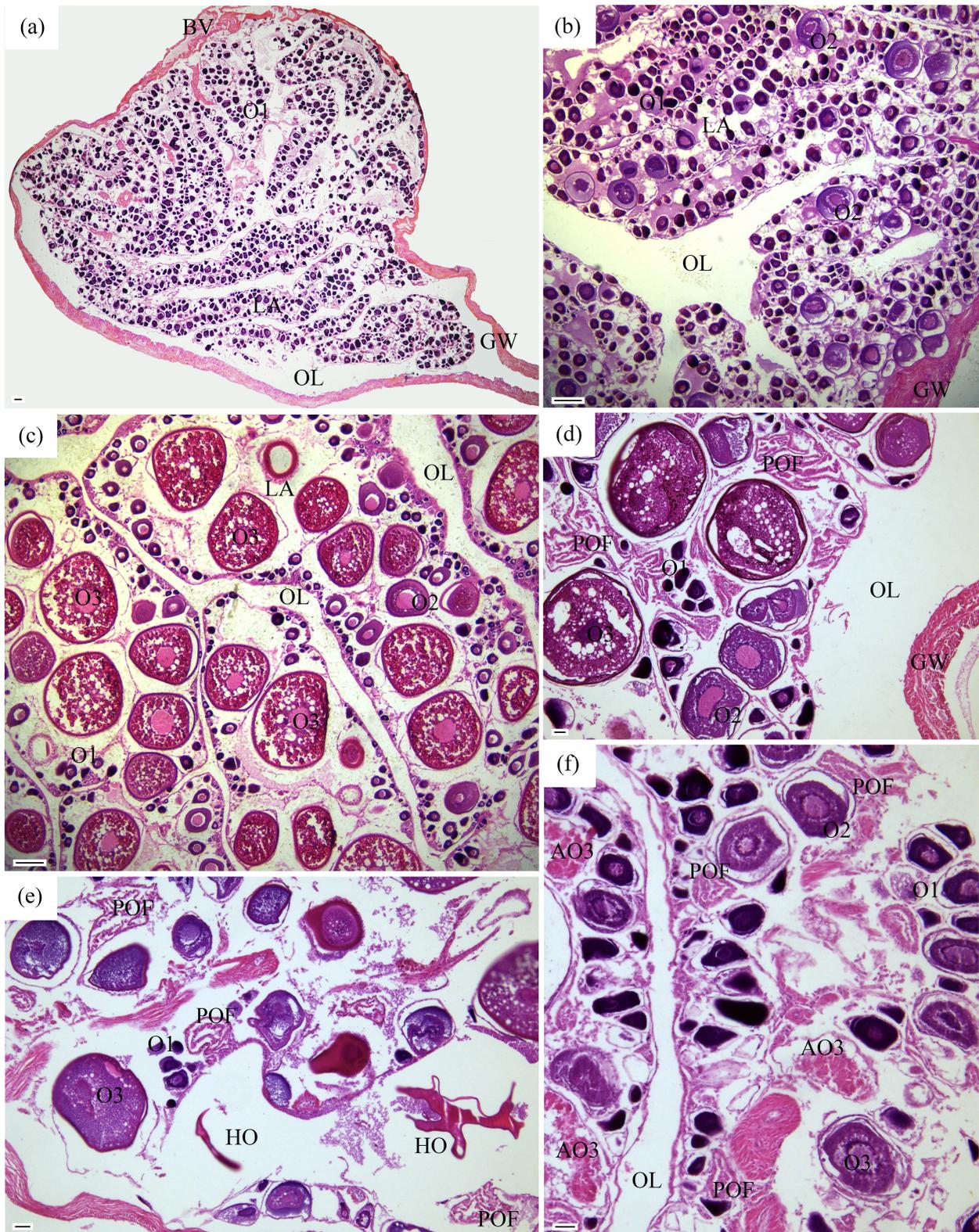


Fig. 4. Sexual maturation stages in females of *Johnius taiwanensis*. (a) Immature/resting (F1) (17.2 cm SL, November 2016); (b) developing (F2) (15.2 cm SL, April 2017); (c) maturing (F3) (16.6 cm SL, September 2016); (d) ripe (F4) (16.8 cm SL, July 2016); (e) ripe (F4) (16.5 cm SL, August 2016); (f) spent (F5) (14.2 cm SL, July 2016). AO3, atretic vitellogenic stage oocyte; BV, blood vessels; GW, gonadal wall; HO, hydrated oocyte; LA, lamellae; O1, primary growth stage oocyte; O2, cortical-alveolar stage oocyte; O3, vitellogenic stage oocyte; OL, ovarian lumen; POF, post-ovulatory follicle. Scale bars: a-c = 200 μ m; d-f = 50 μ m.

to October (Fig. 9).

DISCUSSION

In Chinese waters, 27 sciaenid species are confirmed from 14 genera (*Argyrosomus*, *Atrubucca*, *Bahaba*, *Chrysochir*, *Collichthys*, *Dendrophysa*, *Johnius*, *Larimichthys*, *Megalonibea*, *Miichthys*, *Nibea*, *Otolithes*, *Pennahia*, *Sciaenops*), including *S. ocellatus*, which was introduced from the USA for aquaculture purposes in the 1990s and has invaded Chinese waters (Liao et al. 2009; Chao et al. 2019). Most of these sciaenid species are small- and medium-sized, with only domestic and local commercial importance. The maximum size of *J. taiwanensis* in the present study was a male of 19.0 cm SL, collected in Zhangzhou

waters (Fig. 1; Fig. 2). It is confirmed to be the largest individual recorded to date because the maximum size among holotype and paratype specimens was 18.6 cm SL (Chao et al. 2019).

In Chinese and adjacent waters, the spawning seasonality of sciaenids has been examined in a few species based on either gonad external morphology only, or GSI% and/or gonad histology analyses (Chu 1960; Chu and Wu 1985; Kakuda and Nakai 1981; Li et al. 2000; Li 2010; Lin et al. 2008; Ni 2018; Tuuli et al. 2011; Wang et al. 2011 2012; Wu 1981; Xu 2014; Yamaguchi et al. 2006). The results showed that the spawning activity of most species examined lasted 3–8 months, e.g., *Chrysochir*, *Collichthys*, *Dendrophysa*, *Johnius*, *Larimichthys*, *Nibea*, *Otolithes* and *Pennahia* species (Table 2). To the north, the spawning season in the East China Sea was mainly dominant in Spring (April

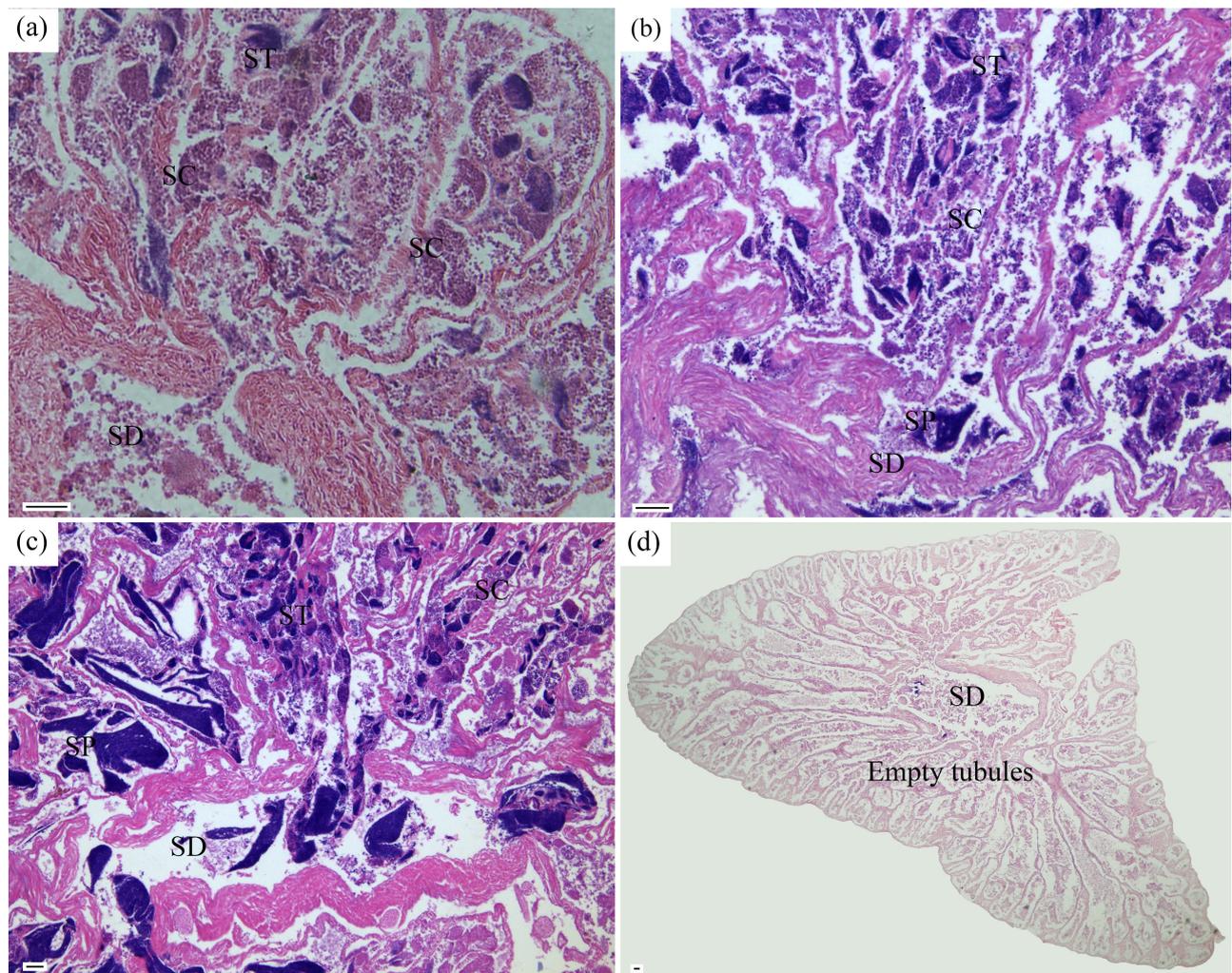


Fig. 5. Sexual maturation stages in males of *Johnius taiwanensis*. (a) Developing (M2) (13.1 cm SL, July 2016); (b) maturing (M3) (14.4 cm SL, September 2017); (c) ripe (M4) (17.8 cm SL, September 2017); (d) spent (M5) (15.1 cm SL, November 2016). GW, gonadal wall; SC, spermatocytes; SD, sperm duct; SP, sperm; ST, spermatids. Scale bars = 50 μ m.

and May), e.g., for *L. crocea* and *L. polyactis*, while to the south in the Taiwan Strait and northern South China Sea, the spawning seasons lasted longer, from Spring to Autumn, mainly dominant in May–October, e.g., for *C. aureus*, *C. lucidus*, *D. russelii*, *J. belangerii*, *J. taiwanensis*, *L. crocea* and *P. macrocephalus*. In the present study, the spawning period of *J. taiwanensis* lasted from April to October in Fujian waters, China, with the peak in July–September for females, based on gonadal histology analyses.

The minimum sizes at maturity or the sizes at 50% maturity for females and males are the two criteria commonly used for evaluating the maturity sizes of the fish. For most studies on sciaenid species, mature females are generally larger than mature males. For instance, the estimated minimum sizes of mature females and males of *P. anea* are 12.5 cm and 11.9 cm SL, respectively, and the size at 50% maturity for females was 12.3 cm SL (Tuuli et al. 2011). For *P. macrocephalus*, the sizes at 50% maturity for females and males are 15.9 cm and 14.8 cm SL, respectively (Li 2010). For *C. aureus*, the sizes at 50% maturity for females and males are 26.3 cm and 21.0 cm SL, respectively (Ni 2018). For *O. ruber*, the sizes at 50% maturity for females and males were 21.8 cm and 19.9 cm SL, respectively (Ni 2018). In a few species, mature females were smaller than mature males. For instance, in *J. belangerii*, the sizes at 50% maturity for females and males were 12.5 cm and 13.6 cm SL, respectively (Wang et al. 2012). In the present study, the

estimated minimum sizes for female and male maturity of *J. taiwanensis* were 12.5 cm and 11.8 cm SL, respectively, mature females larger than mature males. The estimated body sizes at 50% sexual maturation for females and males of *J. taiwanensis* were 12.0 cm and 10.9 cm SL, respectively, smaller than the minimum sizes for female and male maturity.

Johnius taiwanensis is a multiple spawners in a spawning season based on gonadal histology, just like other sciaenid species reported. The evidence includes the appearance of different developmental stages of oocytes from primary growth to vitellogenic in ovaries and sometimes beyond vitellogenic such as HO and POF (Kakuda and Nakai 1981; Li 2010; Ni 2018; Tuuli et al. 2011; Wu 1981; Xu 2014; Yamaguchi et al. 2006; the present study).

Spawning grounds of some sciaenid species in Chinese waters were associated with estuaries. For *B. taipingensis*, the spawning grounds were associated with the Yangtze River, the Min River and the Pearl River Estuaries (Sadovy and Cheung 2003). For *L. crocea*, the spawning grounds were also associated with the river mouths along the Chinese coast (Liu and Sadovy de Mitcheson 2008). The appearance of HO or both HO and POF in ovaries of *J. taiwanensis* was confirmed based on gonadal histology, indicating the samples were from its spawning ground. The spawning ground was subsequently confirmed in Dongshan Bay (117°33'50"E, 23°41'20"N) of Zhangzhou waters, associated with the Zhangjiang River Estuary.

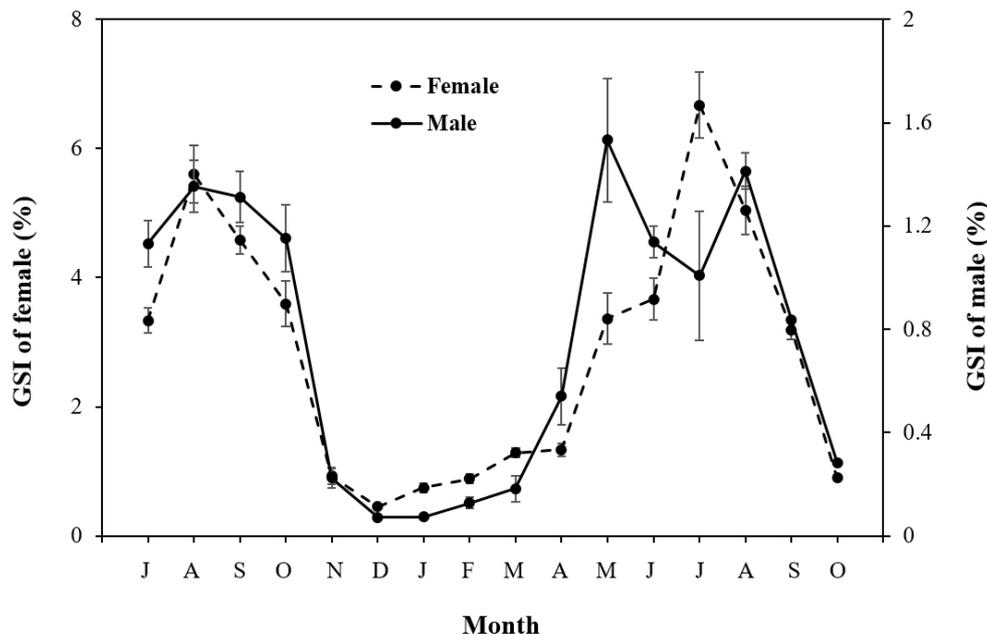


Fig. 6. Monthly gonadosomatic index (GSI%, mean ± S.D.) in females and males of *Johnius taiwanensis* collected between July 2016 and October 2017.

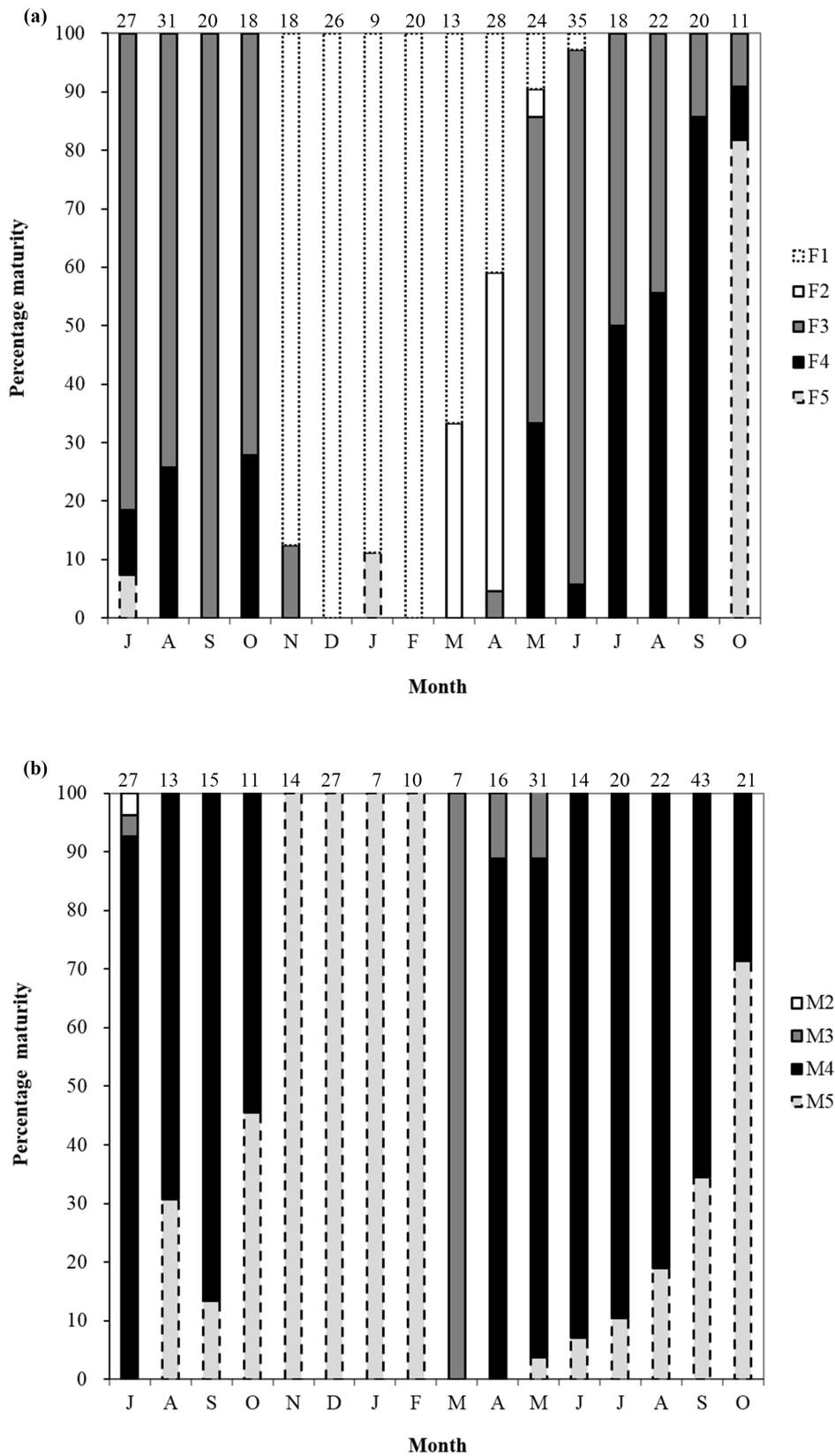


Fig. 7. Monthly female (a) and male (b) sexual maturation stages of *Johnius taiwanensis* based on gonad histology. F1, immature/resting female; F2, developing female; F3, maturing female; F4, ripe female; F5, spent female; M2, developing male; M3, maturing male; M4, ripe male; M5, spent male. The criteria for sexual maturation stages were described in tables 1 and 2. Numbers on the top of bars represent sample sizes.

CONCLUSIONS

Johnius taiwanensis is one of the few remaining wild-caught croakers commonly found in the Taiwan Strait. In the present study, the spawning seasonality, the minimum sizes for female and male maturity and the sizes at 50% maturity of *J. taiwanensis* were determined. The spawning season of *J. taiwanensis*

lasted from April to October, peaking in July-September for females. Currently, the nationwide management for domestic marine fisheries has a fishing moratorium in May-August, adjusting slightly for fishing gears. Therefore, *J. taiwanensis* can be partly protected under the current management measures. Future studies should further investigate the locations of *J. taiwanensis* spawning grounds.

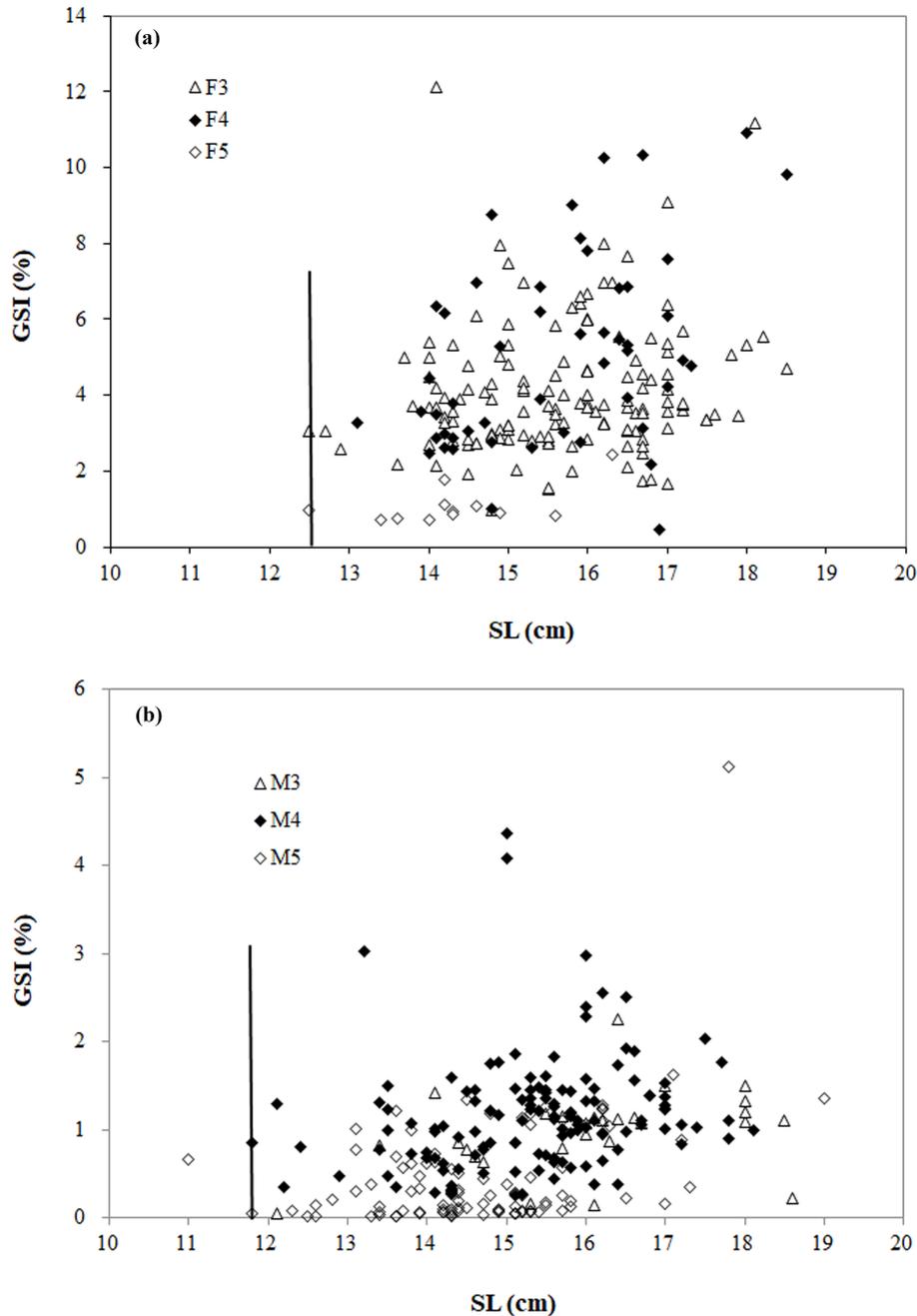


Fig. 8. Relationship of the gonadosomatic index (GSI%) and standard length (SL) for (a) mature females ($n = 204$) and (b) mature males ($n = 260$) of *Johnius taiwanensis*. F3, maturing female; F4, ripe female; F5, spent female; M3, maturing male; M4, ripe male; M5, spent male. Vertical lines represent the minimum sizes with large increase in GSI%: 12.5 cm SL in (a) and 11.8 cm SL in (b).

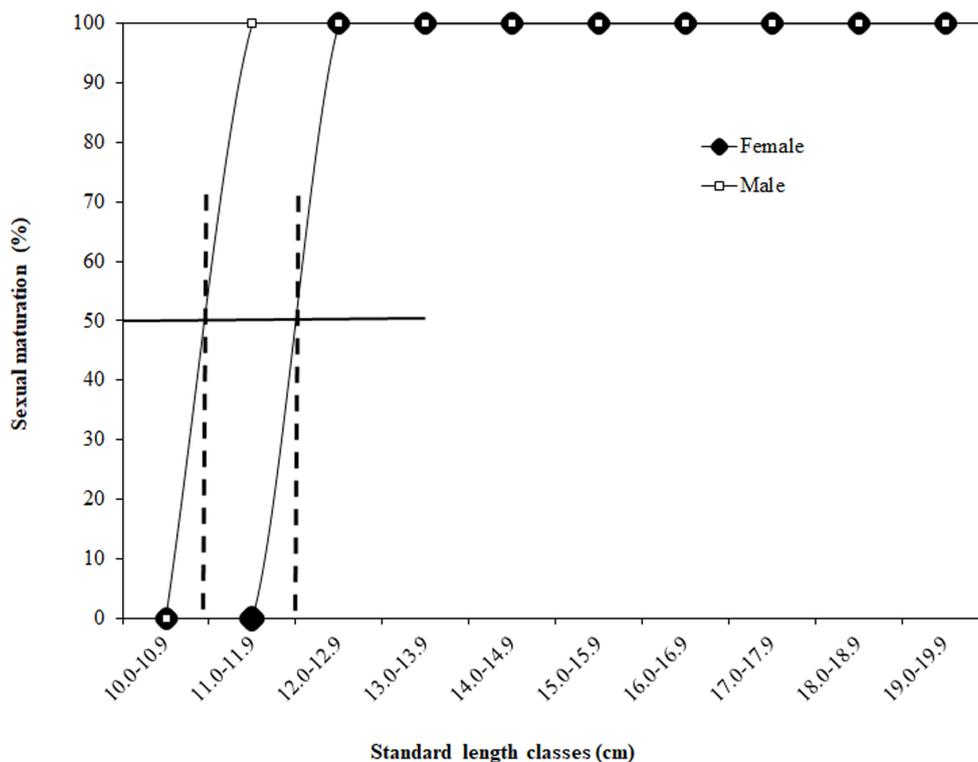


Fig. 9. Sizes at 50% sexual maturation for females and males of *Johnius taiwanensis*, based on all females ($n = 204$) and males ($n = 198$) collected during the spawning months from April to October. 12.0 cm and 10.9 cm SL were extrapolated directly for females and males, respectively.

Table 2. Spawning seasons of sciaenid species in Chinese and adjacent waters

Species	Spawning season (peak season)	Methodology	Area	Reference
<i>Chrysochir aureus</i>	June to December (July to September)	GSI and gonadal histology	Southwestern waters of Taiwan	Ni 2018
<i>Collichthys lucidus</i>	January and April	Gonad external morphology	Fujian waters, China	Wang et al. 2011
	March to December	Gonad external morphology	Pear River Estuary of Guangdong, China	Li et al. 2000
<i>Dendrophysa russelii</i>	March to September (March to May)	GSI and gonadal histology	Liusha Bay of Guangdong, China	Xu 2014
<i>Johnius belangerii</i>	June to September (July and August)	Gonad external morphology	Zhoushan waters of Zhejiang, China	Wang et al. 2012
	Year-round (April and August)	Gonad external morphology	Fujian waters, China	Wang et al. 2011
	May to July	Gonad external morphology	Pear River Estuary of Guangdong, China	Li et al. 2000
	March to October (March)	GSI and gonadal histology	Liusha Bay of Guangdong, China	Xu 2014
<i>J. taiwanensis</i>	April to October (July to September)	GSI and gonadal histology	Fujian waters, China	The present study
<i>Larimichthys crocea</i>	October to December	Gonad external morphology	Hong Kong waters	Chu 1960
	October to December	Gonad external morphology	Liusha Bay of Guangdong, China	Li et al. 2000
<i>L. polyactis</i>	April to June	-	East China Sea	Chu and Wu 1985
	April to June	GSI and gonad histology	Bohai and the northern yellow Sea	Wu 1981
	April and May	Gonad external morphology	Southern Yellow Sea	Lin et al. 2008
	March to May	Gonad external morphology	East China Sea	Lin et al. 2008
<i>Nibea albiflora</i>	May to August (June and July)	GSI and gonadal histology	Seto Inland Sea, Japan	Kakuda and Nakai 1981
<i>Otolithes ruber</i>	April to July (April to July)	GSI and gonadal histology	Southwestern waters of Taiwan	Ni 2018
<i>Pennahia anea</i>	March to June (May)	GSI and gonadal histology	Hong Kong waters, China	Tuuli et al. 2011
<i>P. argentata</i>	April to September (May to August)	GSI and gonadal histology	Ariake Sound waters, Japan	Yamaguchi et al. 2006
<i>P. macrocephalus</i>	May to October (July to September)	GSI and gonadal histology	Southwestern waters of Taiwan	Li 2010
	April and August	Gonad external morphology	Fujian waters, China	Wang et al. 2011

-: no data.

Acknowledgements: The present study was supported by the National Programme on Global Change and Air-Sea Interaction (GASI-02-PAC-YDaut), and Fundamental Research Funds for Central Universities from Xiamen University (grant no. 20720170077). The authors would like to thank Nian-Ping Cai, Wei-Di Yang, Ying Su, Yuyan Jia, Baian Lin, Xiao-Bing Jiang and Yan Jiang for field and laboratory support. We also thank Prof. Ning Labbish Chao for specimen identification and Dr. Claire Gorman for providing the distribution map.

Authors' contributions: LLZ and ML designed the study. LLZ wrote the first draft of the manuscript and performed data analyses. LLZ, LPF and JLL conducted the field collection. LLZ and QX conducted laboratory measurement, dissection and gonadal histology. ML and LPF revised the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: All the data and materials are provided within the manuscript.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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