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The Reproductive Biology of *Pempheris schwenkii* (Pempheridae) on Okinawa Island, Southwestern Japan

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Keita Koeda, Taiki Ishihara, and Katsunori Tachihara (2012) The reproductive biology of *Pempheris schwenkii* (Pempheridae) on Okinawa Island, southwestern Japan. *Zoological Studies* **51**(7): 1086-1093. The reproductive biology of *Pempheris schwenkii*, one of the most common nocturnal fishes in Okinawan waters, was studied using a total of 1834 specimens (3.1-125.9 mm standard length, SL) collected around Okinawa I. The spawning season was estimated to occur from Jan. to June, with a peak from Feb. to May, based on monthly changes in the gonadosomatic index and histological observations of the ovaries. The relationship between the SL and the appearance of mature females, and the monthly growth of the 0^+ group suggested that maturity occurred at ca. 70 mm SL, corresponding to 1 yr after hatching. Spawning was not related to the lunar cycle. The batch fecundity of *P. schwenkii* was calculated as ca. 700-4100 eggs. *Pempheris schwenkii* appeared to spawn at night based on diurnal changes in the frequency of females exhibiting hydrated ovaries and postovulatory follicles. Such nighttime spawning seems to reduce the risk of predation of adults and eggs, which may be an adaptive characteristic of nocturnal fishes. http://zoolstud.sinica.edu.tw/Journals/51.7/1086.pdf

Key words: Nocturnal, *Pempheris schwenkii*, Reproduction, Spawning season, Spawning time.

Fishes of the genus *Pempheris* comprise one of the most abundant groups in rocky and coral areas, particularly in the Indo-West Pacific Ocean and western Atlantic Ocean. In total, 21 species are recognized in this genus (Nelson 2006), and 4 species were reported in coastal waters of Japan (Hayashi 1988, Hatooka 2002). However, considerable confusion remains regarding the classification of these species. For example, 2 new records from Japan, *P. oualensis* and *P. vanicolensis*, were collected from the Ryukyu Archipelago (Koeda et al. 2010a b). *Pempheris schwenkii* is one of the most abundant pempherid fishes in the Ryukyu Archipelago, and this species is widely distributed in the Pacific Ocean.

Fishes of the genus *Pempheris* school in caves or crevices during the day and swim out to open water at night, where they primarily prey on zooplankton (Fishelson et al. 1971, Gladfelter 1979, Golani and Diamant 1991, Fishelson and Sharon 1997, Platell and Potter 1999 2001, Annese and Kingsford 2005, Sazima et al. 2005). Golani and Diamant (1991) determined the spawning season of *P. vanicolensis* in the Mediterranean Sea and Red Sea. The early life history of *P. japonica* and *P. xanthopterus* in the Pacific Ocean was examined in 2 early Japanese studies (Uchida 1933, Kohno 1986). Specifically, Uchida (1964) reported that *Pempheris* exhibits ovoviviparity of the reproductive system. However, no subsequent reports have supported that observation. Recently, Koeda et al. (in press) clarified the reproductive characteristics of *Pempheris* sp., which is the most common pempherid fish in the tropical Pacific Ocean, and the 2nd common species at Okinawa I. The objectives of the present study were to

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describe of the reproductive biology of *P. schwenkii* in Okinawan waters and compare it to that of *Pempheris* sp.

MATERIALS AND METHODS

Samples

In total, 1834 specimens (females: n = 472, 57.3-125.9 mm standard length (SL); males: n = 383, 50.3-118.7 mm SL; sex unknown: n = 979, 3.1-86.5 mm SL) were collected in coastal waters at 5 sites (Maeda, Mizugama, Ohdo, Onna, and Ginowan; Fig. 1) around Okinawa I. (26°04'-26°52'N, 127°36'-128°20'E; Fig. 1) in May 2006 to July 2010. Specimens were caught using a trammel net (with an inside mesh size of 18 mm, and an outside mesh size of 90 mm), a spear gun, a fishing rod and line, and a small seine net (with special fish collecting license no. 21-71 from Okinawa Prefecture). Collecting times included morning (sunrise to 12:00), afternoon (12:00-15:00), and evening (15:00 to sunset); sunrise and sunset ranged from 05:37-07:18, and 17:37-19:26, respectively. In addition, some samples were purchased from the Henza and Nago Fish Markets. Fish were brought back to the laboratory in a cooler filled with ice and measured. The SL was measured to the nearest 0.1 mm, and the body weight (BW) to the nearest 0.1 mg. When possible, the sex of the specimens was determined from the shape of the gonads.

Sea surface water temperatures were obtained monthly from the Japan Meteorological Agency (2012). Day lengths and lunar day data were acquired from the National Astronomical Observatory of Japan (2012). Water temperatures and lunar days did not seem to differ greatly between the years, thus data of 2009 were used.

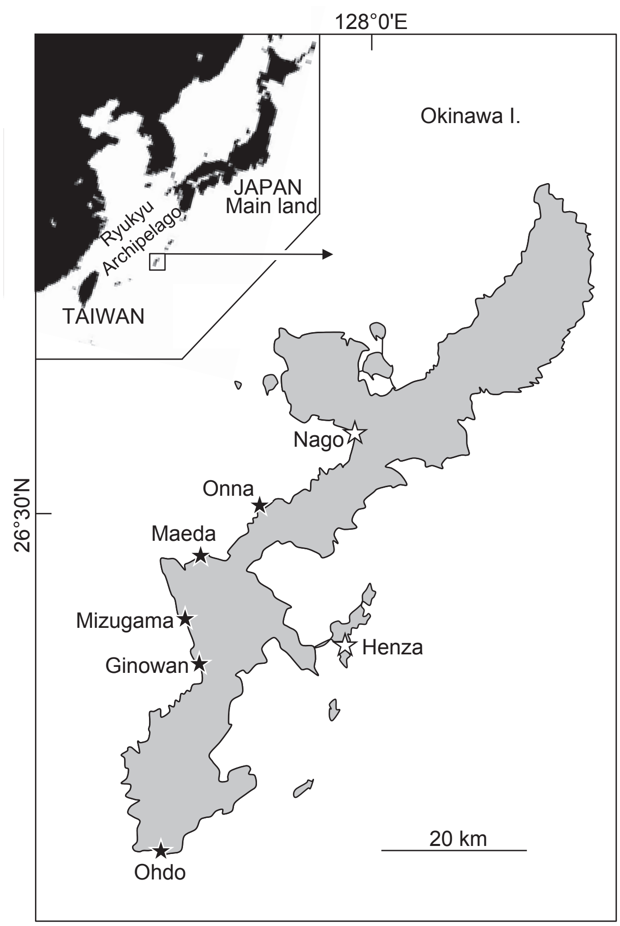

Fig. 1. Map of sampling sites around Okinawa I., southwestern Japan. Solid stars indicate underwater sampling sites; open stars indicate fish markets.

Gonadal observations

The spawning season was estimated using 833 fish specimens (464 females and 369 males) of > 70.0 mm SL. The gonad weight (GW) of each fish was recorded to the nearest 0.1 mg, and the gonado-somatic index (GSI) was calculated using the following equation: GSI = 100 × GW / (BW - GW).

For females, the ovaries were fixed using Bouin's solution or 10% buffered formalin, dehydrated through an ethanol series, and embedded in paraffin. Ovaries were dissected to slices of 6 μm using a microtome, and then stained with Mayer's hematoxylin and eosin. Oocytes in the ovaries were classified in 7 stages (perinucleolus, yolk vesicle, early yolk globule, late yolk globule, migratory nucleus, prematuration, and hydrated stage) according to Shirafuji et al. (2007). The maturity stage of each individual was determined based on the most advanced oocytes in the ovary, and the presence or absence of postovulatory follicles (POF) was also noted. Females with ovaries classified as the late yolk globule to the hydrated stage were defined as mature. To assess whether the spawning of *P. schwenkii* followed a lunar cycle, the GSIs of females were plotted against the lunar day, although sampling was random with respect to the phase of the moon.

Batch fecundity

Only hydrated-stage ovaries were used

for batch-fecundity estimates. Ovarian walls were removed, and oocytes were weighed to the nearest 0.1 mg. Then, hydrated oocytes (> 700 μm in diameter) were counted, and the batch fecundity was calculated using the following formula (samples were taken 5 times, the highest and lowest data were excluded, and an average of the remaining samples was calculated):

$$BF = GW \times NHO / SM;$$

where BF is the batch fecundity, GW is the gonad weight, SM is sample mass, and NHO is the number of hydrated oocytes in the sample.

RESULTS

Monthly changes in gonadal maturation

Monthly changes in the GSI, water temperatures, and day lengths are shown in figure 2. The GSI of females began to increase in Jan., and the average GSI value increased towards Apr.; it gradually decreased in June, and then remained near 0 until Dec. Changes in the male GSI followed a similar pattern as in females. The GSI began to increase in Jan., when the water temperature was < 23°C, and the day length began to increase. In contrast, the GSI rapidly decreased from June to July, when the water temperature increased up to 28°C, and the day length began to decrease.

Monthly changes in the ovary maturational stage are shown in figure 3. Mature females were observed from Jan. to June. The frequency of mature females increased from Feb. to May. Hydrated ovaries appeared from Jan. to June. POFs also appeared in Jan. to June, and their frequency was highest in Apr. (51.7%). Oocytes of various maturity stages coexisted in hydrated ovaries. POFs appeared only in mature females. No evidence of initiation of embryonic development was observed in this study.

Female maturity first appeared at 68.2 mm SL (with a GSI of 3.94; Fig. 4). In males, fish with GSIs > 2.00 and > 4.00 first appeared at 69.4 (GSI = 2.06) and 70.0 mm SL (GSI = 4.56), respectively.

The frequency of the females exhibiting hydrated ovaries gradually increased during the day and was highest in the evening (28%; Table 1). In contrast, the appearance of POFs was highest in the morning (33%) and decreased with the time of day. No apparent lunar periodicity was associated with the GSI (Fig. 5).

Batch fecundities were calculated as ca. 700-4100 eggs (mean ± S.D.: 2350 ± 880, 82.8-118.1 mm SL, n = 23; Fig. 6). The relationship between the SL and batch fecundity (BF) was expressed as follows: BF = 66 × SL - 4663 (r^2 = 0.50).

Growth of the 0⁺ group

Juveniles < 10.0 mm SL were observed from Mar. to Apr. at depths of < 1 m (Fig. 7). Larger juveniles (> 10 mm SL) were collected from May to July in areas near caves or artificial swell protection barriers. They grew rapidly from July to Sep. and had reached 70.0 mm SL by Nov. In the

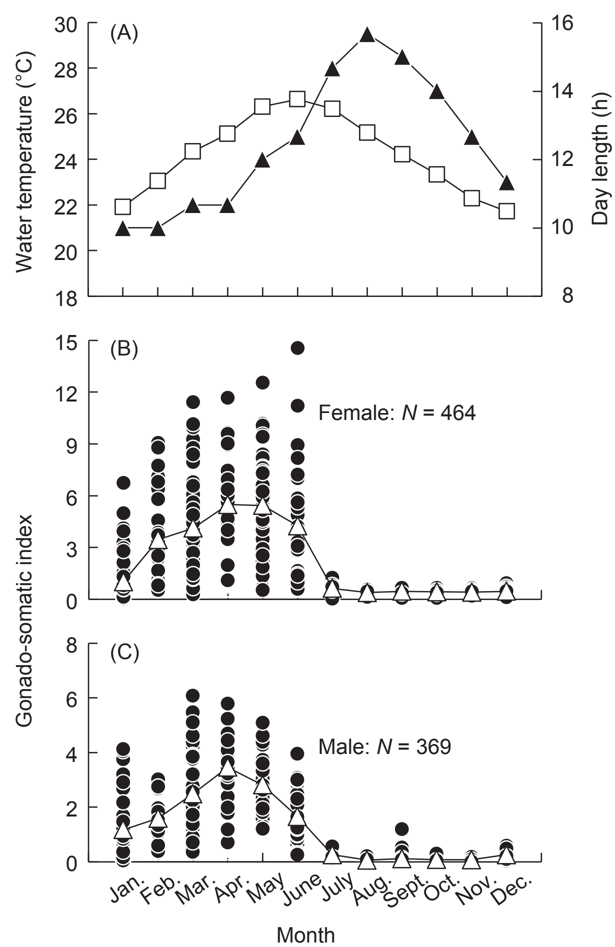

Fig. 2. (A) Monthly changes in water temperature (solid triangles) and day length (open squares) at Okinawa I. in 2009. Data were respectively obtained from the Japan Meteorological Agency (2012) and the National Astronomical Observatory of Japan (2012). (B and C) Monthly changes in the gonado-somatic index of females and males, respectively. Open triangles indicate the means in each month.

subsequent spawning season (see "Discussion"), the SL of the 0^+ group ranged 70.0-100.0 mm. Growth during the 1st year was rapid, and the SL reached up to 80% of the maximum SL.

DISCUSSION

In marine fishes, ovoviviparity is known to occur in approximately 55% (515 species) of chondrichthyan fishes, but only approximately 2%-3% (510 species) of bony fishes (Osteichthyes) such as Embiotocidae, Scorpaenidae, and Sarcopterygii (Balon 1991, Yamada and Kusakari 1991, Wourms and Demski 1993). Uchida (1964) observed ovulated eggs of pempherid fishes collected by commercial fishermen in mainland Japan, and reported that embryonic development had begun. However, the observed species was

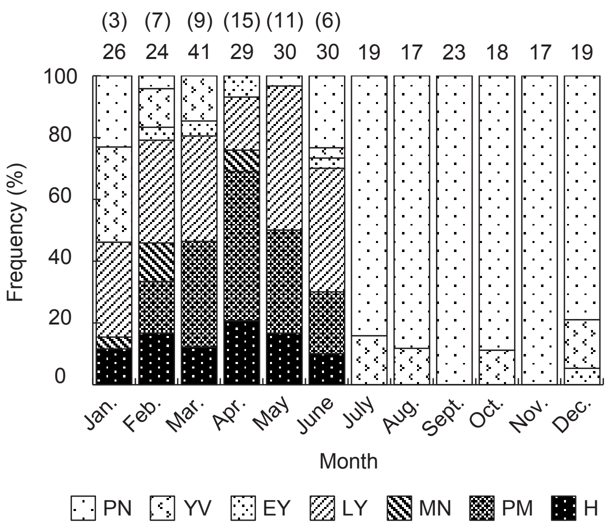

Fig. 3. Monthly changes in histologically observed maturational stages. Numbers on the bars represent sample numbers, and numbers in parentheses indicate ovaries with postovulatory follicles. H, hydrated stage; PM, prematuration stage; MN, migratory nucleus stage; LY, late yolk globule stage; EY, early yolk globule stage; YV, yolk vesicle stage; PN, perinucleolus stage.

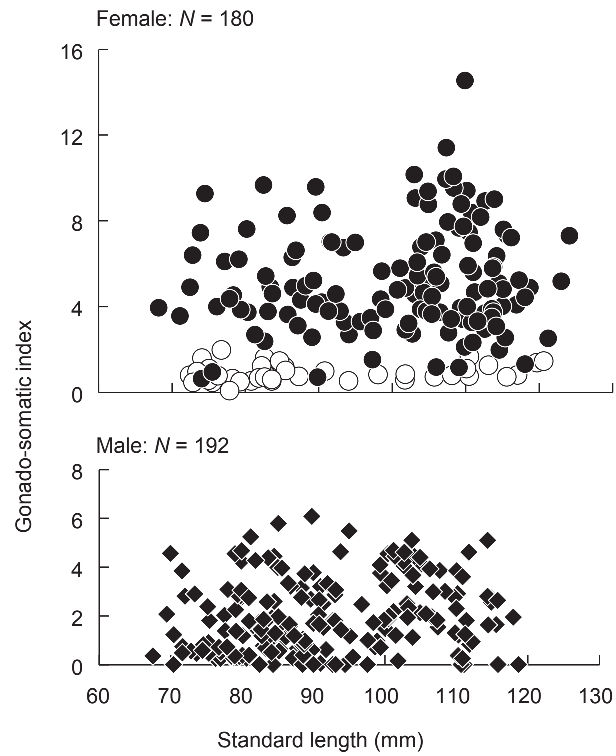

Fig. 4. Relationships between the standard length and gonadosomatic index of *Pempheris schwenkii* collected in the spawning season (Jan. to June). Solid circles indicate mature females and open circles immature females, as determined by histological observations.

Table 1. Relationships between sampling time and ovary maturity stages, and postovulatory follicles

Ovary maturity stages	Sampling time		
	Morning	Afternoon	Evening
Perinucleolus stage	10 (8%)	-	5 (10%)
Yolk vesicle stage	15 (13%)	-	3 (6%)
Early yolk globule stage	2 (2%)	-	4 (8%)
Late yolk globule stage	43 (36%)	8 (80%)	10 (20%)
Migratory nucleus stage	-	-	6 (12%)
Prematuration stage	40 (33%)	-	8 (16%)
Hydrated stage	10 (8%)	2 (20%)	14 (28%)
Total	120	10	50
Postovulatory follicles	39 (33%)	3 (30%)	9 (18%)

only noted as "*Pempheris*", which does not allow identification to species. *Pempheris schwenkii*, *P. japonica*, and *P. nyctereutes* are common in mainland Japan. In the present study, no evidence of ovoviviparity was observed in *P. schwenkii*, or *Pempheris* sp. (Koeda et al. in press). To understand the evolution of these species and the overall reproductive strategy of the genus *Pempheris*, the reproductive characteristics of other *Pempheris* species need to be verified.

Mature females, hydrated ovaries, and POF appeared only from Jan. to June, gradually increasing from Feb. to May. These observations suggest that in Okinawan waters the spawning season of *P. schwenkii* extends from Jan. to June, with a peak from Feb. to May. The spawning season begins in Jan. when the day length begins to increase, and the water temperature is < 23°C;

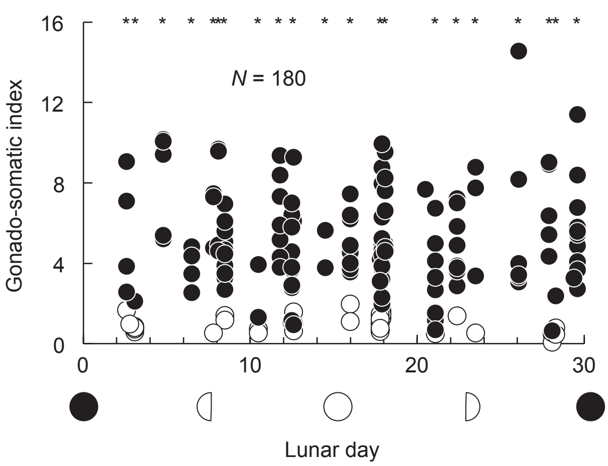

Fig. 5. Relationships between the lunar day and gonado-somatic index of mature females (solid circle) and immature females (open circle). Asterisks indicate the lunar day when postovulatory follicles were observed.

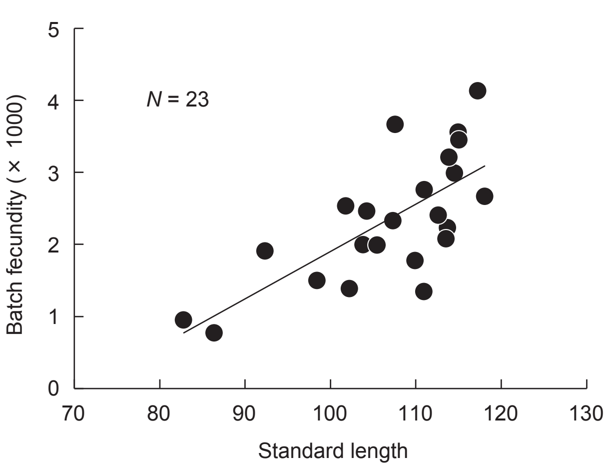

Fig. 6. Relationships between the standard length (SL) and batch fecundity (BF) of *Pempheris schwenkii*: BF = 66 × SL - 4663 (r^2 = 0.50).

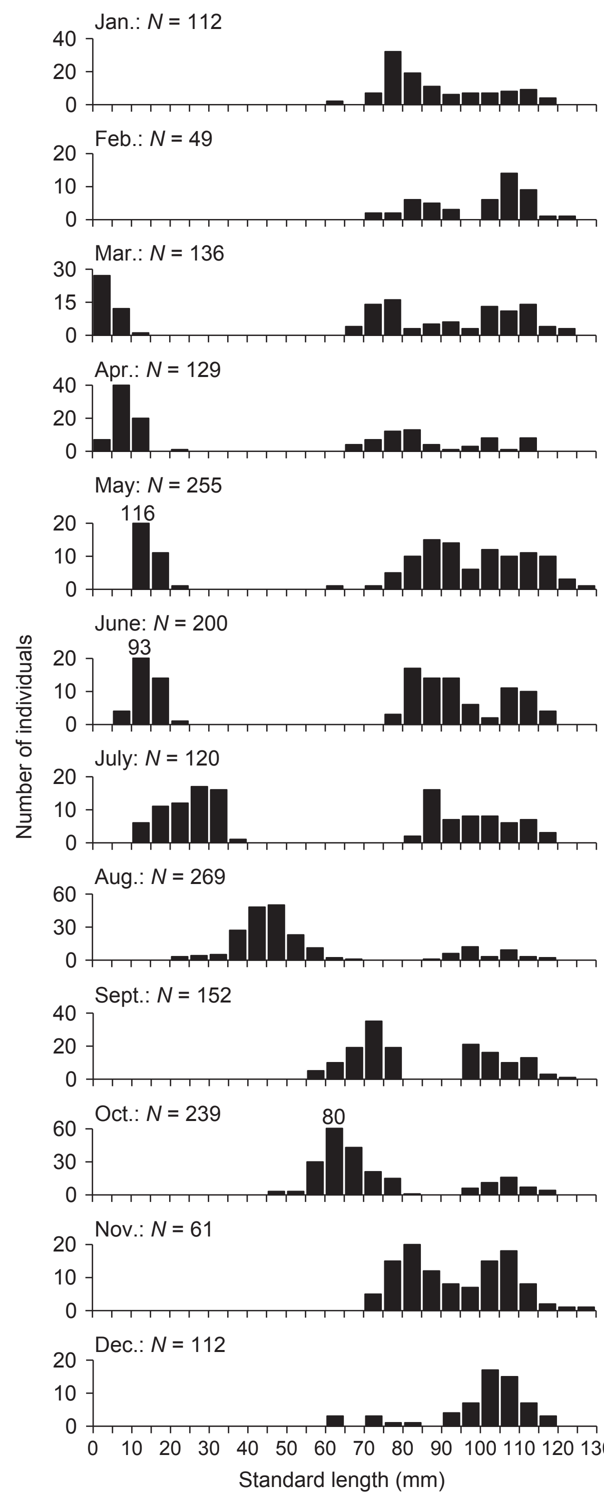

Fig. 7. Monthly changes in the standard length frequency of *Pempheris schwenkii*. Data taken in 2006 to 2011 were combined.

it then abruptly ends in June, when the day length begins to decrease, and the water temperature is > 28°C. The spawning season of *Pempheris* sp. was reported to take place throughout the year near Okinawa, but the peak corresponded to that of *P. schwenkii* (Koeda et al. in press). These observations indicate that the environment influences reproduction in this genus. However, Golani and Diamant (1991) reported a change in the reproductive period of *P. vanicolensis* when Red Sea populations immigrated to the Mediterranean Sea (throughout the year in the Red Sea vs. Apr. to Sept. in the Mediterranean). Therefore, pempherid fishes may flexibly change their reproductive characteristics in different localities and environments.

Juveniles of *P. schwenkii* appeared from Mar. to July, a period which is shorter than the spawning season. This species is estimated to recruit less than 1 mo after hatching (Koeda, Ishihara, and Tachihara unpubl. data). Therefore, the survival rate of individuals born in the beginning of the spawning season may be low. More-extensive "wasted reproduction" occurs in *Pempheris* sp. in Okinawa. For example, juvenile recruitment was only observed during 8 mo of the year, while spawning takes place every month (Koeda, Ishihara, and Tachihara unpubl. data). Moreover, only juveniles recruited from June to Aug. grew up.

Based on the relationship between body length and the GSI as well as histological observations, maturity of both sexes was reached at 70 mm SL. Given the monthly growth of the 0^+ group, almost all individuals were larger than 70 mm SL by November and had reached 70-100 mm SL by the 1st spawning season. Therefore, the fish reproduce in the 1st year after hatching, which is supported by age data determined by sectional otolith analyses (Koeda and Tachihara unpubl. data). In another study conducted at the same locality using the same methods as the present analysis, the smallest mature *Pempheris* sp. was estimated to be 120 mm SL, which corresponded to 2-yr-old fish (Koeda et al. in press). The batch fecundity also differed between the 2 species, such that *P. schwenkii* and *Pempheris* sp. respectively produced ca. 700-4100 and 1800-18600 eggs (Koeda et al. in press). Comparison of the reproductive characteristics of the 2 species in Okinawa revealed that *Pempheris* sp. appears to have much higher reproductive potential than *P. schwenkii* in having a longer spawning season, and high batch fecundity. However, *P. schwenkii* begins to reproduce at a younger age than *Pempheris* sp., which may be advantageous in reducing the risk of predation before reproducing. Therefore, these 2 closely related species that are distributed in the same region exhibit substantially different life cycle strategies.

Most coral reef fishes synchronize their spawning with the lunar cycle (Lobel 1978, Doherty 1983, Samoilys 1997, Takemura et al. 2004a b, Vagelli and Volpedo 2004, Nanami et al. 2010). However, spawning of the 2 pempherid species discussed herein was not related to the lunar cycle, and multiple spawnings occurred in a single spawning season. Spawning patterns of these species were previously compared with a few coral reef fish, such as the Chaetodontidae (Ralston 1981). In the present study, a relatively high ratio of hydrated ovaries was observed in specimens collected in the evening, and POFs mainly appeared in the morning. In addition, within *Pempheris* sp., hydrated ovaries appeared most frequently in the evening, and rapidly decreased at night (Koeda et al. in press). These results suggest that these 2 fishes spawn exclusively at night. Several studies reported long-distance feeding migration for zooplankton by pempherid fishes at night (Fishelson et al. 1971, Gladfelter 1979, Golani and Diamant 1991). In accordance with those reports, the spawning of the 2 pempherid fishes seems to be performed during their nocturnal migration. Johannes (1978) indicated that migratory spawners mostly migrate to the outer reef for spawning to reduce risk of egg predation. Nighttime spawning was observed in the Apogonidae and Serranidae under natural underwater conditions (Kuwamura 1987, Samoilys 1997) and in a nocturnally active lutjanid in an aquarium (Suzuki and Hioki 1979), but not in other coral reef fishes. For example, the Pomacanthidae and Zanclidae spawn at twilight around sunrise, the Caesionidae, Chaetodontidae, and the Mullidae spawn just before sunset, and the Scaridae, Labridae, and Acanthuridae spawn during the day, as influenced by the diurnal tide cycle (Lobel 1978, Doherty 1983, Gladstone 1986; Colin and Bell 1991). However, hatching usually takes place at night to reduce the predation risk by plankton feeders (Doherty 1983, Ochi 1986, Samoilys 1997, Okuda and Ohonishi 2001, Vagelli and Volpedo 2004). Night spawning decreases the predation risk for eggs and adults by piscivorous species (Johannes 1978). Several piscivorous species are adapted to hunt smaller fish at night, and some groupers prey upon the Pempheridae

(Hobson 1968, Shpigel and Fishelson 1989). However, compared to the number of large piscivorous predators which are active during the day, relatively few seem to be active at night (Harmelin-Vivien and Bouchon 1976). Finally, several observations indicate that the reproductive characteristics of *P. schwenkii* (and of *Pempheris* sp.), which hide during the day and migrate and spawn at night, reduce predation risks for eggs and adults, which is a specific adaptation of nocturnal fishes, and this may result in spawning which is not synchronized with the lunar cycle.

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