ISSN 2188-2037 www.scesap.org

Coastal Ecosystems

Mating system and group spawning in the wrasse *Pteragogus aurigarius* in Tateyama, central Japan

Shota Shimizu, Shuta Endo, Masahiro Sasaki, Atsunobu Murase,
Masakazu Masuko, Masayuki Miyazawa, Tomoki Sunobe

Coastal Ecosystems, 2016, vol 3, 38-49

Regular Paper

Mating system and group spawning in the wrasse *Pteragogus aurigarius* in Tateyama, central Japan

Shota Shimizu[1], Shuta Endo[1,2], Masahiro Sasaki[1,3], Atsunobu Murase[1,4], Masakazu Masuko[1], Masayuki Miyazawa[1,5], Tomoki Sunobe[1]

[1]Laboratory of Fish Behavioral Ecology, Tateyama Station, Field Science Center, Tokyo University of Marine Science and Technology, Tateyama, Chiba 294-0308, Japan
[2]Tokyo Sea Life Park, Edogawa-ku, Tokyo 134-8587, Japan
[3]Kinosaki Marine World, Toyooka, Hyogo 669-6192, Japan
[4]Department of Marine Biology and Environmental Science, Faculty of Agriculture, Miyazaki University, 1-1 Gakuen-Kibanadai-Nishi, Miyazaki 889-2192, Japan
[5]Anan International Co., Ltd., Minato-ku, Tokyo 108-0071, Japan

Corresponding author : S. Shimizu, e-mail: shimizu10shota@gmail.com

Abstract

The reproductive behaviour in the protogynous wrasse *Pteragogus aurigarius* was investigated in Tateyama, central Japan from 2007 to 2009. Three types of reproductive behaviour were recorded: pair spawning (territorial male courted and spawned with a female), streaking (streaker joined a spawning pair and released sperm), and group spawning (18–76 males aggregated at the spawning site, and one to three males followed a female to spawn). Territorial males were larger in size than streakers. Males participating in group spawning were significantly smaller than territorial males. A gonadal histological examination revealed that territorial and group spawning males consisted of secondary males. This is the first report documenting group spawning in this species. In both sexes the number of individuals increased and the body size decreased from 2007 to 2009. Territorial males were present throughout the study period, whereas streaker males appeared in 2007, and group spawning males appeared in 2008 and 2009. The possibly sex-changed males were dominant and small in 2008 and 2009, surrendered their established territories, and exhibited group spawning. These results indicate that the appearance of small males may have influenced the mating behaviour of other fish within this population.

Keywords: group spawning, Labridae, mating system, *Pteragogus aurigarius*, sex change

Introduction

Sexual dimorphism in the polygynous social system, including large body size, conspicuous colouration and showy male courtship display, is favoured by male–male competition and/or female mate choice. Competition for mates may favour behavioral polymorphisms in fish species with polygynous social systems. Under a conditional strategy in which individuals adopt alternative tactics depending on the prevailing conditions, a relatively small-sized male of low social status may adopt alternative tactics, such as streaking, in which the male releases sperm into the gamete cloud produced by a spawning pair, or sneaking, in which a male creeps into the territory of another male and spawns in a pair. In contrast, the behaviour of larger males tends to be territorial because expected reproductive success is generally greater than that of smaller males (e.g., Warner, Robertson & Leigh 1975; Taborsky 1994; Gross 1996; Gonçalves *et al*. 1996; Sunobe & Nakazono 1999; Taru, Kanda & Sunobe 2005; Takegaki, Kaneko & Matsumoto 2013).

Polymorphic reproductive behaviour and female-to-male sex change have been studied in Labridae, including parrotfishes (Warner 1984; Kuwamura & Nakashima 1998; Munday, Buston & Warner 2006; Sadovy de Mitcheson & Liu 2008). Males function either first as a male (primary male) or are derived from a female by sex change (secondary male). The coloration of small-sized primary males and females is rather drab and is defined as the initial phase (IP). IP males and females change to bright colouration (terminal phase: TP) after growth and sex change, respectively (Kuwamura & Nakashima 1998).

Labrids are classified into species comprising primary and secondary males (diandric species) or those with secondary males only (monandric species). TP males of diandric species maintain territories for mating and spawning in pairs, whereas primary IP males are non-territorial and exhibit streaking, sneaking, and/or group spawning, whereby a group of males mates simultaneously with a single female (e.g., Warner, Robertson & Leigh 1975; Nakazono 1979; Warner & Hoffman 1980; Yogo, Nakazono & Tsukahara 1980; Moyer 1991; Shibuno *et al*. 1994; Adreani & Allen 2008; Suzuki *et al*. 2008, 2010). TP males of most monandric species maintain territories and court females for spawning (e.g., Robertson & Warner 1978; Warner & Robertson 1978; Moyer & Yogo 1982; Yogo 1985; Donaldson 1995; Hubble 2003; Colin 2010; Sadovy de Mitcheson, Lui & Suharti 2010). Other than pair spawning, *Cirrhilabrus temmincki* males exhibit streaking and sneaking, those of *Sparisoma radianus* group spawn and streak, those of *S. rubripinne* group spawn, and those of *S. viride* streak (Randall & Randall 1963; Robertson & Warner 1978; Bell 1983; Marconato & Shapiro 1996; van Rooij, Kroon & Videler 1996).

The labrid fish *Pteragogus aurigarius* (Richardson 1845) inhibits coastal rocky reefs, from Aomori, northern Japan to the East China Sea (Shimada 2013). The IUCN Redlist status is “Data Deficient” (Sadovy 2010). *P.aurigarius* is a monandric protogynous species (Nakazono 1979), the reproductive behavior of which having been observed in Tsuyazaki, Fukuoka, Japan (33°47’N, 130°28’E) and Miyake Island, Japan (34°10’N, 139°37’E). Males at the Tsuyazaki site maintain territories and spawn with four or five females throughout the spawning period, suggesting that their mating system is harem polygyny (Nakazono 1979). Males at the Miyake Island location maintain territories, and females visit male territories to spawn, whereas territorial males (TMs) spawn by streaking and sneaking in addition to pair spawning (Moyer 1991).

In this study, we observed the reproductive behavior of *P. aurigarius* on a rocky reef at Banda Beach, Tateyama, Japan between 2007 and 2009. Here, we describe the first occurrence of group spawning by this species and discuss how this behavior emerged.

Materials and Methods

This study was conducted on a rocky reef at the Banda Beach, Tateyama, Japan (34° 58’ N, 139° 46’ E; Fig. 1a) between 2007 and 2009. The reef extends offshore gradually from the beach to about 200 m, where the substratum transitions to a sandy bottom. A study site of 10 × 16 m was established on the boundary between the rocky and the sandy bottom at a depth of 8 m during high tide, where *P. aurigarius* spawning was observed frequently (Fig.1b). The species spawns before sunset from early August through late September in Fukuoka, Japan (Nakazono 1979). As weather permitted, daily observations were made by SCUBA for about 2 h before sunset from 5 June to 30 September 2007, from 5 July to 25 September 2008, and from 17 June to 25 September 2009. Water temperature at the study site ranged from 15.9 to 26.1°C.

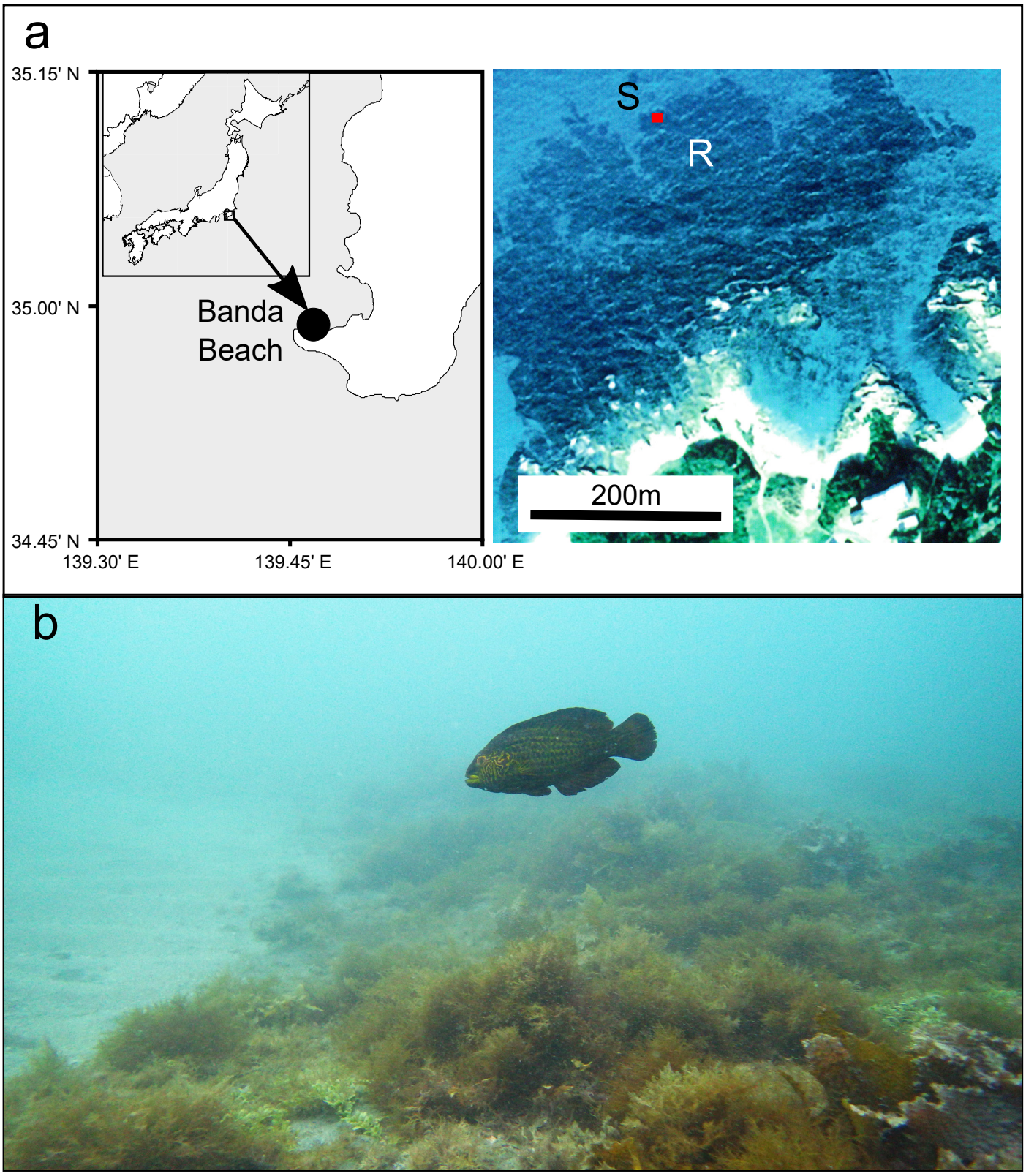

Fig. 1 (a) Map and aerial photograph of the Banda Beach, Tateyama, Japan. Red square, study site; R, rocky area; S, sandy area. (b) *Pteragogus aurigarius* at study site.

We recorded time, individual identification number, and the pattern of courtship display of tagged males on a plastic slate during the underwater observation. We also took photographs and video with a digital camera (Canon Power Shot A630; Canon Electronics Inc., Saitama, Japan). The swimming tracks of six and seven tagged TMs were recorded 3–27 times for 5 min in 2007 and 2008, respectively, to clarify territorial boundaries. As only four TMs appeared in the study area in 2009, we observed and recorded three additional TMs in an adjacent area using the same methods.

Two divers collected untagged individuals for 1 hour using hand nets and a curtain net (height 150 cm and width 300 cm) during 5, 10, and 9 dives in 2007, 2008, and 2009, respectively, to estimate the abundance of *P. aurigarius* in the study site. The abundance was expressed as mean (± SD) number of individuals collected from the study site on a yearly basis. Sex of the individuals was determined by sexual dichromatism and dimorphism. Females have a dark reddish-brown body and their abdomen is white with blue spots (Fig. 2a), while males are basically black-green with their scales being edged grass-green and display a complex pattern of yellow lines from the eye to the opercula (Fig.2b). The first and second dorsal spines are conspicuously elongated in the male (Nakazono 1979). Fish individuals were measured for total length (TL), marked with a hypodermic injection of a visible implant elastomer tag (Northwest Marine Technology, Shaw Island, WA, USA) for observing reproductive behaviour, and released where they were captured.

We observed three types of reproductive behavour in this study: pair spawning, streaking, and group spawning (see “Results” in detail). Although we did not collect any streakers, we collected eight specimens that exhibited pair and group

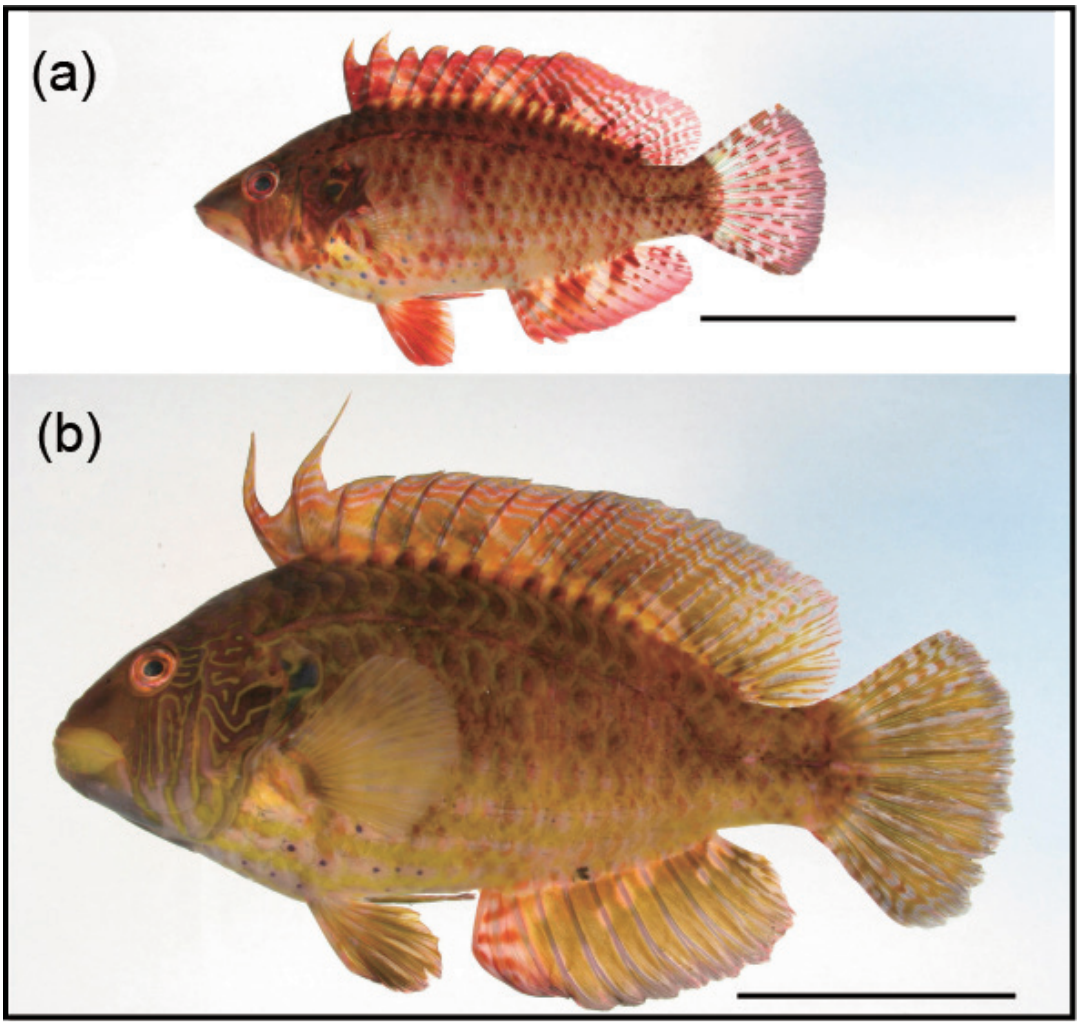

Fig. 2 Colouration of *Pteragogus aurigarius*. (a) female, (b) terminal phase (TP) male; scale bars, 50 mm.

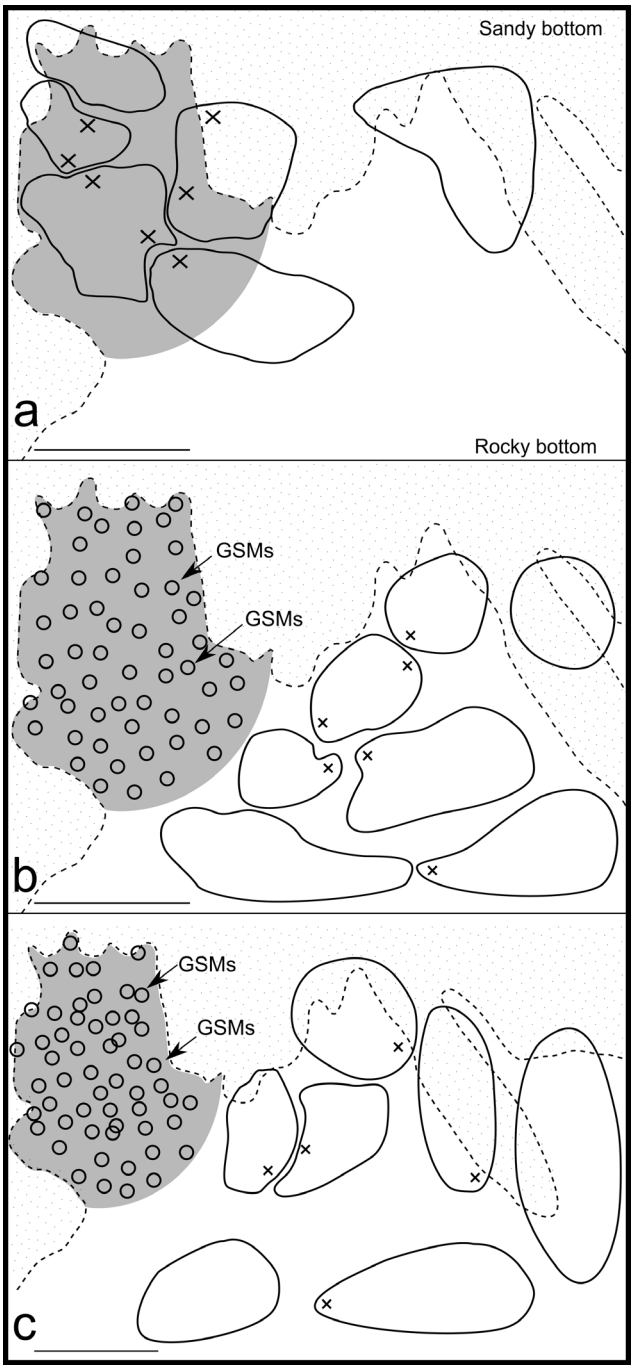

Fig. 3 Distribution of territories in (a) 2007, (b) 2008, and (c) 2009. Solid lines, territory boundaries; broken line, border between rocky and sandy area; shaded area, the bulging rock; white circles, location of GSMs; crosses, location of aggressive interactions; scale bars, 4 m.

spawning, respectively. We examined the gonadal structure of these males to distinguish primary and secondary males based on testicular structure with or without an ovarian cavity, following the methods of Nakazono (1979) and Shimizu (2016). We extracted the testes, fixed the tissue in Bouin's solution for 24 h, and preserved the samples in 70% ethanol. These samples were embedded in paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin.

Results

Spawning was observed on all days of field observation, regardless of lunar phase, from 21 June to 3 September 2007, from 22 July to 9 September 2008, and from 8 July to 6 September 2009. Spawning started at 15:00–16:00 and finished at 16:00–18:00, which was about 1 h before sunset. This species spawned in areas between the rocky reef and sandy bottom. However, the majority of spawning occurred on a rocky up-thrust we called the bulging rock, which was about 4 × 8 m in size and located 60–70 cm above the bottom (Fig. 3). Three types of reproductive behaviour were observed: pair spawning, streaking, and group spawning. However, we did not observe any sneakers. All males

and females had disappeared from the study site by 29 September 2007, 18 September 2008, and 20 September 2009 to signal the end of the reproductive season.

Pair spawning

TMs maintained territories at the bulging rock in 2007 (Fig. 3a). However in 2008 and 2009, they chose territories in areas other than the bulging rock because non-territorial males aggregated there (Fig. 3b–c). TM exhibited aggressive behavior at territorial borders to both neighboring TM and approaching non-territorial males (Fig. 3). Females visited a male's territory before spawning. When a TM courted a female (Fig. 4a), he exhibited lateral wave swimming and sway swimming above her (Fig. 4b). If the female angled her body upwards, the TM approached and touched her (Fig. 4c). Then, they rushed together rapidly and released gametes in the water column (Fig. 4d). After

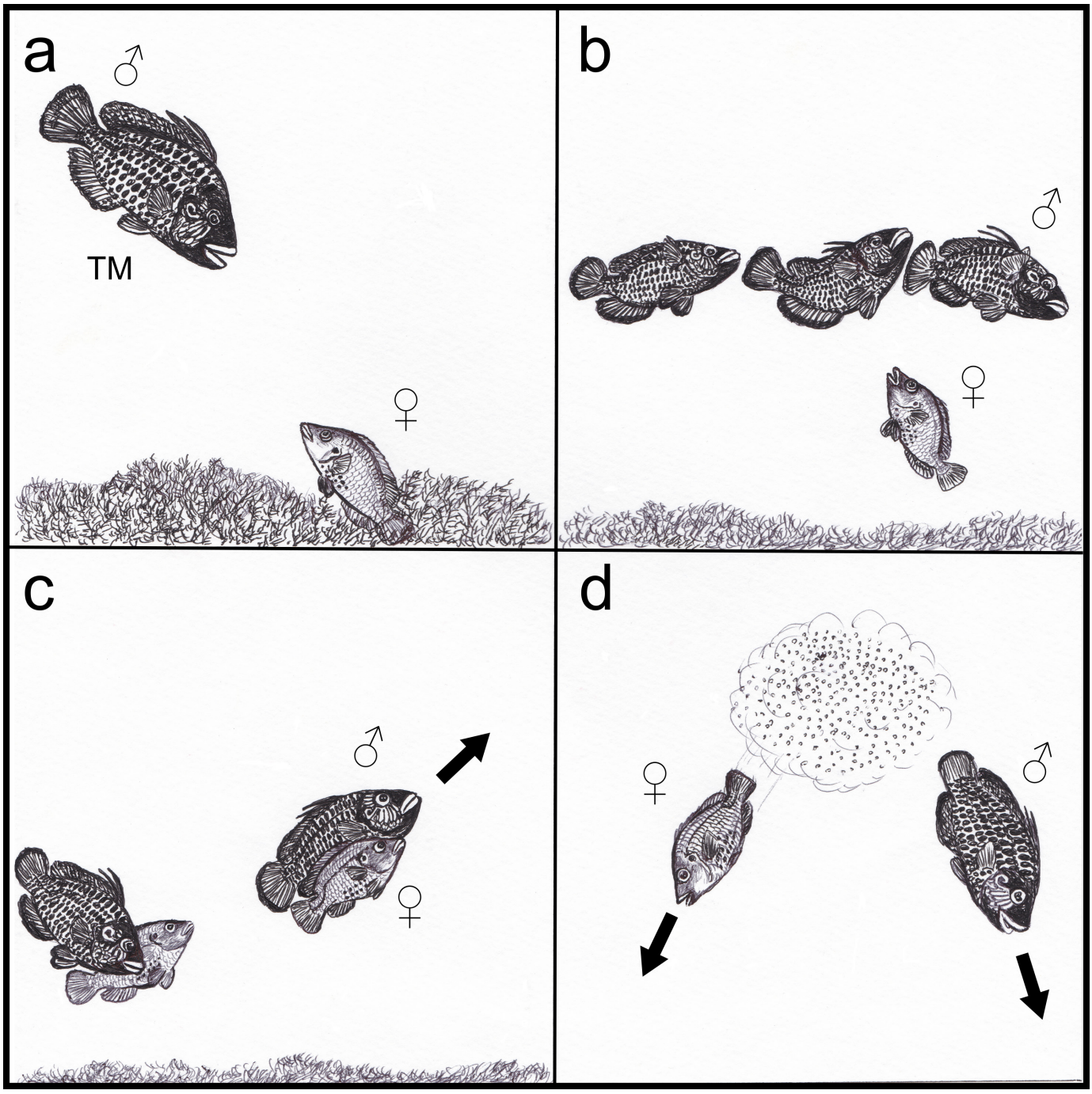

Fig. 4 Pattern of courtship display during pair spawning (illustration by Sakana-kun). (a) Approaching to female by TM, (b) sway swimming and female rising, (c) body touching, and (d) spawning. Video of behavioral sequences is registered in the Movie Archives of Animal Behavior (http://www.momo-p.com: registered number; momo150116pa01b).

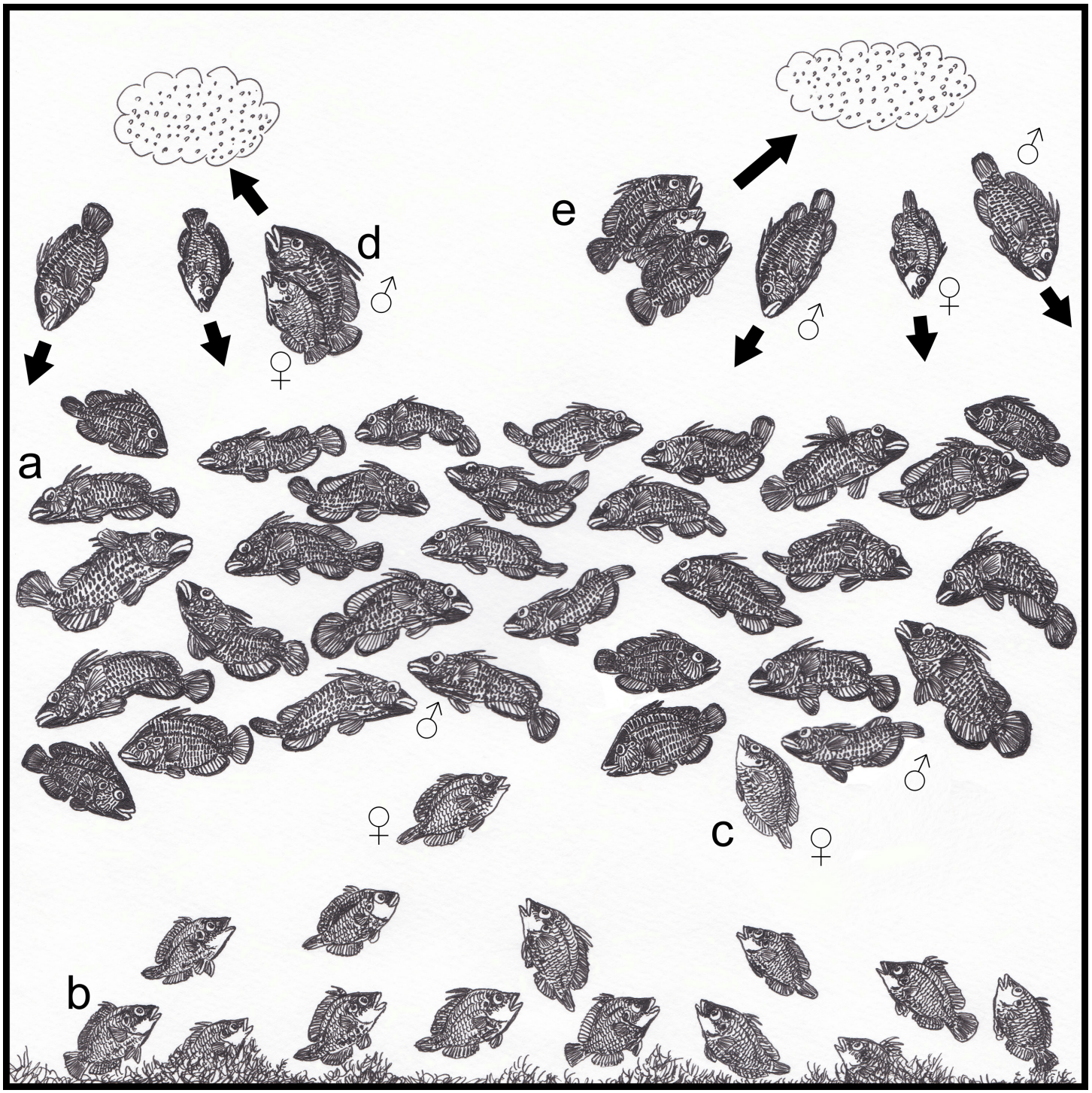

Fig. 5 Pattern of courtship display during group spawning (illustration by Sakana-kun). (a) GSMs exhibiting sway swimming, (b) females hiding among algae, (c) female rising, (d) pair spawning, and (e) spawning by a female and two males. Video of behavioral sequences is registered in the Movie Archives of Animal Behavior (http://www.momo-p.com: registered number; momo150116pa03b).

Table 1 Abundance (number of individuals in the study site) and body size (mm TL) of male and female *P. aurigarius*.

	2007	2008	2009	Size change across years (Scheffe's *F* test)		
				2007-2008	2008-2009	2007-2009
Number of sampling occasions	5	10	9			
Males						
abundance (mean ± SD)	4.4 ± 0.8	17.0 ± 11.0	21.4 ± 13.9			
size (TL, mean ± SD)	152.8 ± 18.0 (*n*=22)	140.1 ± 19.8 (*n*=170)	126.3 ± 18.6 (*n*=193)	*F* = 11.7*	*F* = 6.3 **	*F* = 13.5**
size range (TL)	120-178	91-175	84-170			
Females						
abundance (mean ± SD)	10.4 ± 1.9	26.0 ± 24.3	35.2 ± 27.6			
size (TL, mean ± SD)	94.8 ± 10.0 (*n*=52)	83.4 ± 13.6 (*n*=260)	78.2 ± 11.8 (*n*=317)	*F* = 9.1**	*F* = 4.3*	*F* = 9.0**
size range (TL)	76-117	58-137	50-111			
Size difference between sexes (Student *t* test)	*t* = 17.8**	*t* = 35.1**	*t* = 34.9**			

*$P < 0.05$ **$P < 0.01$

spawning, the female left the territory, and the TM courted another female.

Streaking

Non-territorial males wandered and lurked around established territories. Non-territorial males occasionally approached rapidly and released sperm, when pairs spawned. Three streakers appeared in 2007, but none was observed in 2008 and 2009 (Table 2). These streakers joined spawning in different territories.

Group spawning

Non-territorial males occupied the bulging rock in 2008 and 2009 (Fig. 3b–c) and exhibited group spawning. Females visited the bulging rock around spawning time and hid among the algae and rocks. If a female swam up, one to three of these males followed and rushed in to spawn (Fig. 5). Here, we define this type of male as a "group spawning male (GSM)". The number of GSMs fluctuated from 18 to 76 during the spawning season (mean ± SD = 49 ± 15 individuals, *n* = 49), and no aggressive interactions were observed among them. No male changed behavioral categories from pair spawning to group spawning (or vice versa) throughout the study period.

Abundance, body size and gonadal structure

The abundance of individuals of both sexes in the study site apparently increased from 2007 to 2009 (Table 1). Males had significantly larger body sizes than females in all years of the study (Student *t* test, $P < 0.05$). The body sizes of both sexes decreased significantly from 2007 to 2009 (Scheff's *F* test, $P < 0.05$; Table 1).

Two of the streakers were smaller than the TMs, but another was the same size as the smallest TM (Table 2). The TMs were significantly larger than the GSMs in 2008 and 2009 (Student *t* test, $P < 0.05$). The largest and the second largest GSMs (175 and 160 mm TL) in 2008 were larger than and the same size as the largest TM (160 mm TL), respectively (Table 2). Although we did not examine the

Table 2 Variation in body size (mm TL) of territorial males (TMs), streakers, and group spawning males (GSMs).

	2007	2008	2009
TMs			
n	6	7	7
size (TL, mean ± SD)	145 ± 9.0	156 ± 3.5	150 ± 6.4
size range (TL)	130-150	149-160	140-160
Streakers			
n	3		
size (TL)	110, 120, 130		
GSMs			
n		21	15
size (TL, mean ± SD)		138 ± 19.0	130 ± 18.2
size range (TL)		102-175	101-158
Student *t* test (TL between tactics)		*t* = 2.8*	*t* = 2.2*

*$P < 0.05$

gonads of any streakers, ovarian cavities were detected in the testes of eight TMs and eight GSMs (Fig. 6). Sperm was produced by both types of male.

Discussion

The pattern of *P. aurigarius* courtship display seen in Tateyama was similar to previous observations in Tsuyazaki (Nakazono 1979) and Miyake Island (Moyer 1991). Although the observations in Tsuyazaki suggested that the *P. aurigarius* mating system is harem polygyny, the

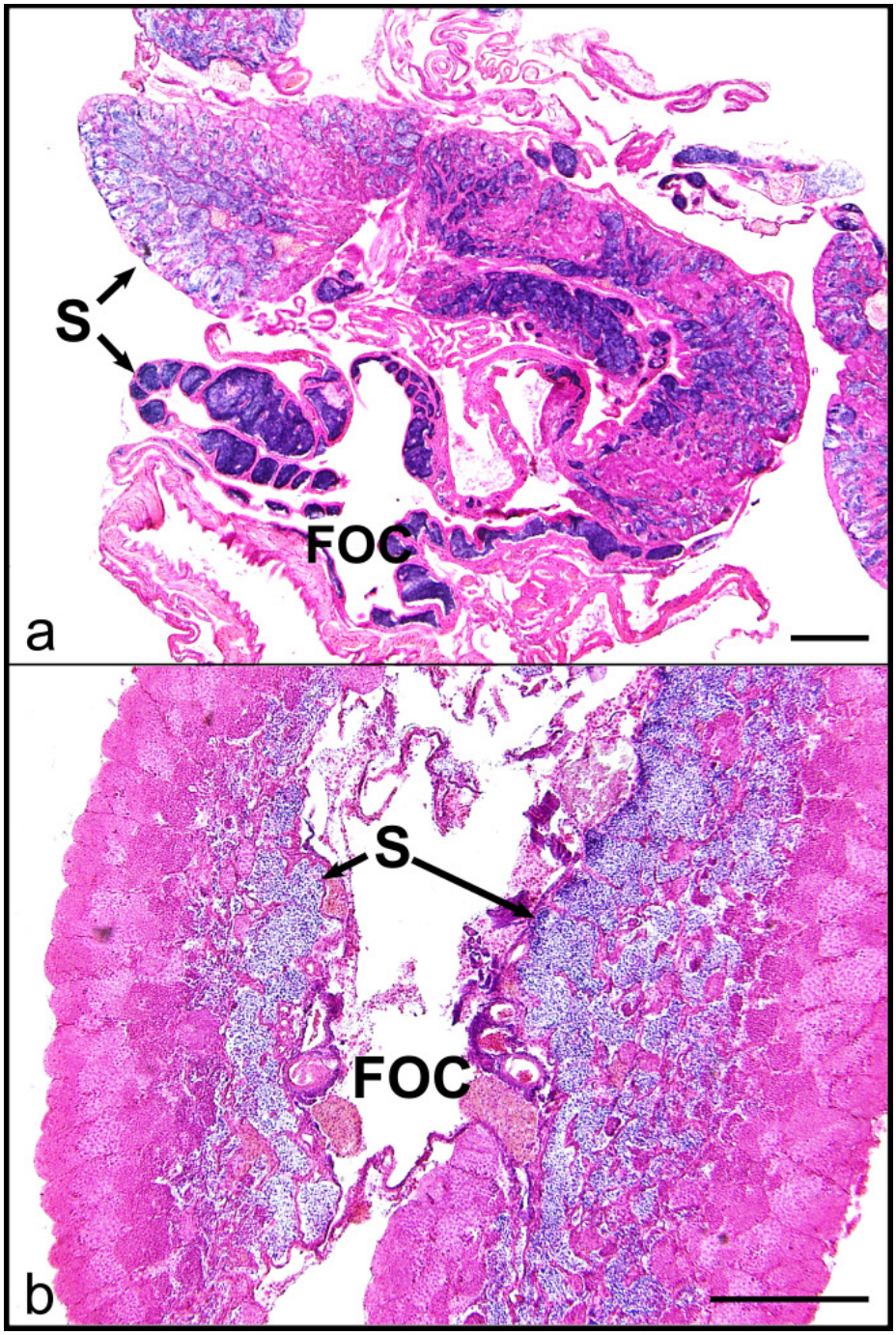

Fig. 6 Cross-section of testis from (a) a territorial male (TM; 166 mm total length [TL]) and (b) a group spawning male (GSM; 140 mm TL). S, sperm; FOC, former ovarian cavity; scale bars, 200 μm.

present study shows that females visit male territories to spawn alternatively, which is similar to the mating system on Miyake Island. Streaking, but not sneaking, was exhibited by non-territorial males in Tateyama, whereas streaking and sneaking tactics by neighboring TMs were reported from Miyake Island. The territories in Miyake ranged from 3 × 4 m to 20 × 30 m, being larger than those in Tateyama (see Fig. 3). This size difference means that TMs on Miyake Island can easily invade other territories and exhibit streaking and sneaking, whereas the smaller-sized territories in Tateyama prevented other TMs from streaking and sneaking. Thus, the mating system of *P. aurigarius* varied among the three sites.

This study is the first to report group spawning in *P. aurigarius*. Group spawning by primary IP males is common in diandric species (e.g., Nakazono 1979; Warner & Hoffman 1980; Yogo, Nakazono & Tsukahara 1980; Moyer 1991; Adreani & Allen 2008; Suzuki *et al*. 2008, 2010), whereas group spawning has been reported in secondary IP and TP males of *Sparisoma radianus* and secondary IP males of *S. rubripinne*, which are monandric species (Randall & Randall 1963; Robertson & Warner 1978; Marconato & Shapiro 1996).

Sadovy de Mitcheson & Liu (2008) concluded that the ovarian cavity is not the evidence of sex change. In our experiment involving established ten pairs of *P.aurigarius* females of different sizes, which were sexed by palpating the abdomen to release eggs, the larger female individual of all pairs changed sex to male after nine months. Gonads of these secondary males had sperm and ovarian cavities as Nakazono (1979) reported (Shimizu 2016). The *P. aurigarius* GSMs were all TP, and the gonadal histological examination showed that they were secondary males (Fig. 6). Group spawning by secondary TP *P. aurigarius* males is unique among labrid fishes and occurs infrequently in TP males of *S. radianus* (Marconato & Shapiro 1996).

Studies of wrasses and parrotfishes have shown that TP males abandon territories and join group spawns. This alternative reproductive tactic occurs when TP males cannot defend their territories against intruding IP males (Nakazono 1979; Shibuno *et al*. 1994; Kuwamura, Sagawa & Suzuki 2009; Suzuki *et al*. 2010). Large *Halichoeres trimaculatus* IP males exclusively defend against small IP males to minimize sperm competition during streaking. However, they only weakly defend against competitors and allow them to join a group spawn (Suzuki *et al*. 2008).

The body sizes of *P. aurigarius* males and females decreased while their abundances increased from 2007 to 2009 (Table 1). The largest males successfully maintained their territories during the 2007 spawning period because most TP males may have been large enough to establish territories. Small non-territorial TP males seemed to adopt a streaking tactic as a response. However, small TP males were relatively abundant in 2008 and 2009, allowing them to easily enter the bulging rock and establish a group for spawning. We also found large TP males among the GSMs (Table 2). When the number of males increased in the population, these males could not maintain territories. They gathered in the suitable site for spawning and might exhibit group spawning.

Acknowledgments

We are grateful to T. Takayama, S. Kihara, S. Sakaida, M. Watai, and M. Sakuma and all of the other members of the Laboratory of Fish Behavioral Ecology for assistance in the field and other insights that allowed this study to progress. We also thank M. Tokeshi and two anonymous reviewers for their kind reviewing of the manuscript. This study was supported by KAKENHI Grants to T. Sunobe (Nos. 19570016 and 24370006) from the Japan Society for the Promotion of Science.

References

Adreani MS & Allen LG (2008) Mating system and reproductive biology of a temperate wrasse, *Halichoeres semicinctus*. Copeia 2008, 467-475.

Bell LJ (1983) Aspects of the reproductive biology of the wrasse, *Cirrhilabrus temminckii*, at Miyake-jima, Japan. Japanese Journal of Ichthyology 30, 158-167.

Colin PL (2010) Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): general aspects of spawning behaviour. Journal of Fish Biology 76, 987-1007.

Donaldson TJ (1995) Courtship and spawning of nine species of wrasses (Labridae) from the Western Pacific. Japanese Journal of Ichthyology 42, 311-319.

Gonçalves EJ, Almada VC, Oliveira RF & Santos AJ (1996) Female mimicry as a mating tactic in males of the blenniid fish *Salaria pavo*. Journal of Marine Biological Association UK 76, 529-538.

Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11, 92-98.

Hubble M (2003) The ecological significance of body size in tropical wrasses (Pisces: Labridae). PhD thesis, James Cook University, Queensland.

Kuwamura T & Nakashima Y (1998) New aspects of sex change among reef fishes: recent studies in Japan. Environmental Biology of Fishes 52, 125-135.

Kuwamura T, Sagawa T & Suzuki S (2009) Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. Ichthyological Research 56, 357-362.

Marconato A & Shapiro DY (1996) Sperm allocation, sperm production and fertilization rates in the bucktooth parrotfish. Animal Behaviour 52, 971-980.

Moyer JT (1991) Comparative mating strategies of labrid fishes. The Watanabe Ichthyological Institute, Monograph 1, i-x + 1-90.

Moyer JT & Yogo Y (1982) The lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyake-jima, Japan. Zeitschrift für Tierpsychologie 60, 209-226.

Munday PL, Buston PM & Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends in Ecology and Evolution 21, 89–95.

Nakabo T ed (2013) Fishes of Japan with pictorial keys to the species third edition. pp. 1101. Tokai University Press. Kanagawa, Japan (In Japanese)

Nakazono A (1979) Studies on the sex reversal and spawning behavior of five species of Japanese labrid fishes. Reports of Fisheries Research Laboratory, Kyushu University 4, 1-64 (In Japanese with English abstract).

Randall JE & Randall HA (1963) The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48, 49-60.

Robertson DR & Warner RR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, II: the parrotfishes (Scaridae). Smithsonian Contribution to Zoology 255, 1-26.

Sadovy de Mitcheson Y & Liu M (2008) Functional hermaphroditism in teleosts. Fish and Fisheries 9, 1-43.

Sadovy de Mitcheson Y, Lui M & Suharti S (2010) Gonadal development in a giant threatened reef fish, the humphead wrasse *Cheilinus undulatus*, and its relationship to international trade. Journal of Fish Biology 77, 706-718.

Sadovy de Mitcheson Y (2010) *Pteragogus aurigarius*. The IUCN Red List of Threatened Species 2010: e.T187433A8534385. http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T187433A8534385.en. Downloaded on 25 May 2016.

Shibuno T, Chiba I, Hashimoto H & Gushima K (1994) Reproductive behavior of the wrasse, *Thalassoma lutescens*, at Kuchierabu-jima. Journal of Faculty of Applied Biological Science, Hiroshima University 33, 43-50 (In Japanese with English abstract).

Shimizu S (2016) Diversity of mating behaviour and sex change of *Pteragogus aurigarius* (Labridae) in Tateyama-bay, central Japan. Ph.D. thesis, Tokyo University of Marine Science and Technology, I-III + 1-74 (In Japanese).

Sunobe T & Nakazono A (1999) Alternative mating tactics in the gobiid fish, *Eviota prasina*. Ichthyological Research 46, 212-215.

Suzuki S, Toguchi K, Makino Y, Kuwamura T, Nakashima Y & Karino K (2008) Group spawning results from the streaking of small males into a sneaking pair: male alternative reproductive tactics in the threespot wrasse *Halichoeres trimaculatus*. Journal of Ethology 26, 397-404.

Suzuki S, Kuwamura T, Nakashima Y, Karino K & Kohda M (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the threespot wrasse *Halichoeres trimaculatus*. Environmental Biology of Fishes 89, 71-77.

Taborsky M (1994) Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. Advances in the Study of Behavior 23, 1-100.

Takegaki T, Kaneko T & Matsumoto Y (2013) Tactic changes in dusky frill goby sneaker males: effects of body size and nest availability. Journal of Fish Biology 82, 475-491.

Taru M, Kanda T & Sunobe T (2005) Competition for spawning sites between two gobiid fishes, *Bathygobius fuscus* and *Eviota abax*, derived by alteration of mating tactics of the former. Ichthyological Research 52, 198-201.

van Rooij JM, Kroon FJ & Videler JJ (1996) The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. Environmental Biology of Fishes 47, 353-378.

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. American Scientist 72, 128-136.

Warner RR & Hoffman SG (1980) Population density and the economics of territorial defense in a coral reef fish. Ecology 61, 772-780.

Warner RR & Robertson DR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, I: the wrasses (Labridae). Smithsonian Contribution to Zoology 254, 1-27.

Warner RR, Robertson DR & Leigh EG (1975) Sex change and sexual selection. Science 190, 633-638.

Yogo Y (1985) Studies on the sexual maturation and reproductive ecology in three protogynous fishes. Reports of Fisheries Research Laboratory, Kyushu University 7, 37–83 (In Japanese with English abstract).

Yogo Y, Nakazono A & Tsukahara H (1980) Ecological studies on the spawning of the parrotfish, *Scarus sordidus* Forsskål. Science Bulletin of Faculty of Agriculture, Kyushu University 34, 105-114 (In Japanese with English abstract).

Published: 12 December 2016