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# Reproductive Behavior of the Wrasse, *Halichoeres marginatus*, at Kuchierabu-jima

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**Abstract** Reproductive behavior of the wrasse, *Halichoeres marginatus*, was studied on a shallow reef at Kuchierabu-jima Island, southern Japan. Individuals foraged solitarily at a low density. The population consisted of protogynous hermaphrodites and a few (4.9%) primary males. The species is sexually dichromatic: secondary males showed the terminal phase (TP), and primary males the initial phase (IP) similar to females. In late afternoon large TP males migrated offshore to set up temporary mating territories at the prominent dead coral or rocky outcrops on the slope. They pair-spawned with single females, which migrated there. Non-territorial TP males and IP males intruded repeatedly into the mating territories which were located near the shore. They spawned by streaking, sneaking, and group spawning with females in those territories. The reproductive behavior is compared with that of other wrasses.

The labrid fishes are widely distributed in tropical and temperate seas, and are among the most abundant fishes on shallow coral and rocky reefs. In the last twenty years, the reproductive ecology of many labrid fishes has been clarified by underwater observations using SCUBA (reviewed in Thresher, 1984; Yogo, 1987). Most labrid fishes are protogynous hermaphrodites. There are two types of males: a gonochoristic male (primary male) and a male resulting from sex change from a female protogynous hermaphrodite (secondary males). In most labrid species, males differ greatly from females in color (i.e., sexual dichromatism). The structure of social and mating systems of many labrids can be broadly distinguished between lek-like and haremic. In lek-like species, males occupy traditional territorial sites only during the spawning period, mating with females which come to the sites to spawn. In haremic species, males are permanently territorial and mate almost exclusively with females included within their territories. Generally, spawning behavior can be distinguished between pair spawning, a single male mating with a single female, and group spawning, in which a number of males fertilize the eggs of one female.

The small labrid fish, *Halichoeres marginatus* Rüppell, is widely distributed in the tropical and subtropical Indo-Pacific, and is found in or around coral reefs or shallow rocky areas (Araga, 1984). It is a solitary species, feeding on benthic invertebrates (Hiatt and Strasburg, 1960; Sano et al., 1984). Choat (1969) described *H. marginatus* as a sexually monochromatic species composed of only protogynous hermaphrodites (i. e., monandric), whereas Colin and Bell (1991) reported the species as sexually dichromatic, with a haremic mating system. We studied the reproductive behavior of *H. marginatus* on a shallow reef at Kuchierabu-jima Island, southern Japan. Its pattern of sexuality, mating system and mating behavior are described and compared with other wrasses.

## Materials and Methods

The island of Kuchierabu-jima (30°28′N, 130°10′E) lies between Kyushu and the Ryukyu Islands. A study area of about 50,000 m$^2$ was selected in Nishiura Bay (see Shibuno et al., 1993). Underwater observations totalling about 500 h were made from 8:00 h to sunset, between June and November 1986.

During the observation period, each territorial male was observed continuously from 14:00 h to sunset on at least one occasion, and the location at

which each territorial male attacked other males plotted on a map. Subsequently, the maximum area in which aggressive behavior of the territorial male toward other males was observed, was regarded as the former's mating territory.

Mating behavior was observed by 1–4 observers on snorkel, from 14:00 h to sunset between 14 August and 8 September, at mating territories A, B, D and G (see Fig. 3). Equivalent to 32 days of observations were thus obtained. In each mating territory, the times and numbers of females and males appearing, spawning activities, spawning times and number of spawnings were recorded. Individuals were identified by natural marks or marking by subcutaneous injection of acrylic paints (see Thresher and Gronell, 1978).

To determine the number of spawnings per day by a female, each of 3 tagged females was observed continuously from 10:00 h to sunset on one occasion.

The population density was investigated by 1000 m line census (6 m width) on 3 occasions, at a foraging area near the shore in the morning and early afternoon on 15 and 18 June 1986.

Specimens were collected by spear gun and gill net in the inshore area in the mornings and early afternoons from 21 June to 13 November 1986. Their color phase was recorded before fixation in 10% formalin solution. In the laboratory total lengths (TL, mm) were measured, and the gonads removed and embedded in Paraplast. Serial cross sections (6–8 $\mu$m thick) were stained with haematoxylin and eosin, and examined under a microscope for confirmation of sex and gonad structure.

## Results

### Sexuality

Adults of the species conformed to either of 2 types in color phase and morphology. One type, 71–176 mm TL ($n=28$), had a dark-brown body with black ocelli on the anterior and middle parts of the dorsal fin, and a pale white caudal fin (initial phase: IP). The other type, 132–214 mm TL ($n=11$), had a deep, dark-green body with a protruding forehead, the pelvic fin prolonged and no ocelli on the dorsal fin (terminal phase: TP) (see color plate in Araga, 1984). Two specimens (136 and 150 mm TL) showed an intermediate color phase. The size ranges of IP and TP individuals overlapped extensively (Fig. 1).

Histological examination of the gonads showed that 26 out of 28 IP individuals had ovaries (Figs. 1, 2a). The remaining 2 IP fish (124 and 129 mm TL) had primary testes, characterized by the lack of a thin membrane surrounding the testis and vasa deferentia occurring between the testicular lobes (Figs. 1, 2b), indicating gonochoristic males (see Reinboth, 1970). All individuals of TP ($n=11$) and intermediate color phase ($n=2$) had secondary testes characterized by the presence of residual ovarian structures and vasa deferentia occurring within the former ovarian wall (Figs. 1, 2c), strongly indicative of their derivation from ovaries (see Reinboth, 1970; Sadovy and Shapiro, 1987). The proportion of primary males in the specimens ($n=41$) was 4.9%.

### Male mating territories

During the morning and early afternoon both males and females foraged at the bottom of rocks and dead corals about 20–50 m offshore. The density in these areas was 0.61 fish $\pm$0.14 SD per 100 m$^2$ ($n=3$).

In the late afternoon large TP males ($\geqq$200 mm TL) migrated to the spawning sites about 75–100 m offshore and 3–8 m deep. They established mating territories around prominent rocks (3–5 m in diameter, 1.5–2.5 m high) or dead corals (1.5 m in diameter, 0.5 m high). Mating territories were established at 7 sites in the study area (Fig. 3). Territory A was located at the most offshore and deepest site, B, C, D and E on the reef slope, and F and G in the near shore, shallow area. Mating territories were maintained from about 15:00 h to 30 min before sunset (Fig. 4). The average size of the mating territories was 161.5 m$^2$$\pm$7.0 SD ($n=7$). During the period of mating behavior observation, replacement of the territorial owners was not observed.

The territorial male rushed to chase non-territorial TP and IP males intruding into his territory (rushing). If the intruding TP male did not retreat, the two males oriented broadside to each other while swimming back-and-forth above the prominent rock, with fins repeatedly erecting and closing (parallel swimming). Parallel swimming was frequently followed by approaches to each other in the opposite orientation while rising in the water column, and chasing each other with head-to-tail circling, before returning to the substrate (head-to-tail circling).

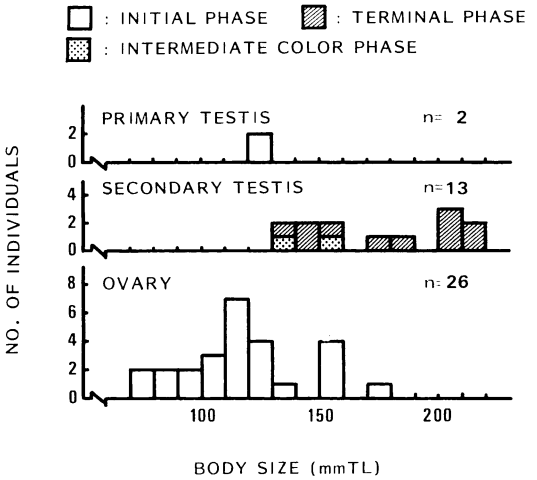



**Fig. 1.** Relationships between size, color phase and gonad condition in *Halichoeres marginatus*.

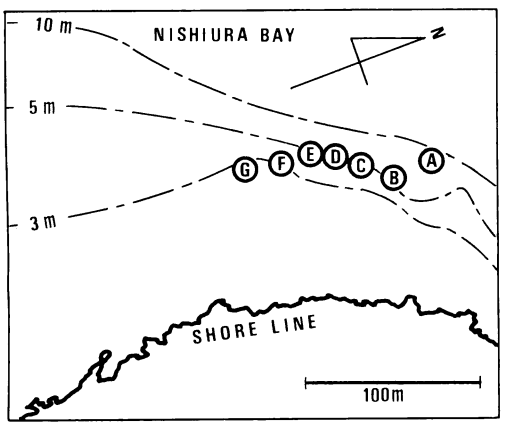



**Fig. 3.** Location of male mating territories of *Halichoeres marginatus* (A–G). Contour lines for 3, 5 and 10 m depth are given.

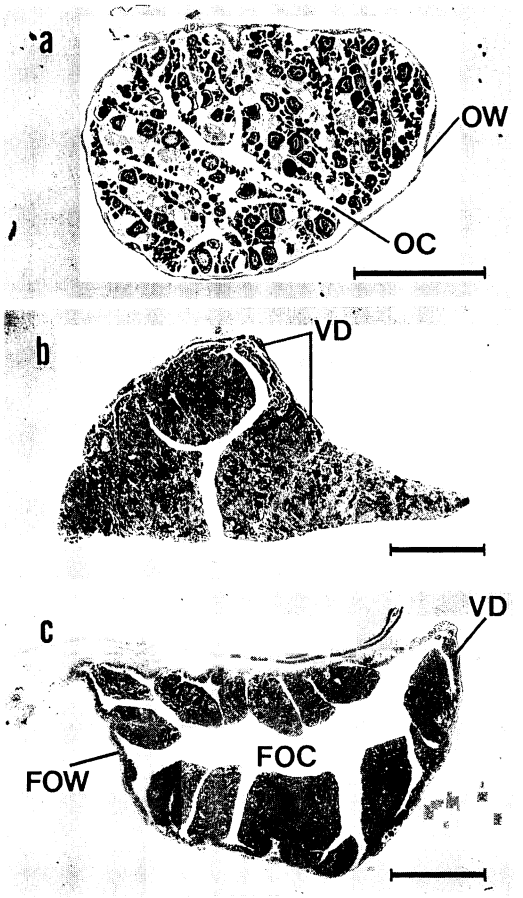



**Fig. 2.** a) Cross sections of ovary, b) primary testis and c) secondary testis of *Halichoeres marginatus*. *OC*—ovarian cavity; *OW*—ovarian wall; *FOC*—former ovarian cavity; *FOW*—former ovarian wall; *VD*—vas deferens. Each scale bar represents 1 mm.

During head-to-tail circling, sudden biting attacks were occasionally observed (biting). After the territorial male drove the intruder away, the former remained rigid at the edge of the territory, at approximately 45° from the horizontal, with the head oriented upward and fins fully extended, for 3–4 sec.

**Pair spawning**

Females began to migrate to male mating territories from about 16:00 h. They often swam along crevices with 2 or 3 other females encountered on the way, occasionally hiding in crevices or under rocks.

A territorial male, upon sighting a female, rapidly approached and circled her (rushing and circling). While the female was circled, she remained rigid with the head oriented upward and fins fully extended at approximately 45° from the horizontal (Fig. 5). After rushing and circling, the territorial male moved quickly to the water column above the prominent rock at the center of the territory, and suddenly ascended 1–2 m with rapid sculling of the caudal fin, before returning immediately to its former position (looping). During courtship the territorial male displayed 3 narrow pale bars on the posterior half of its body.

When the female hid under rocks, the male circled her again and led her to the prominent rock, all the

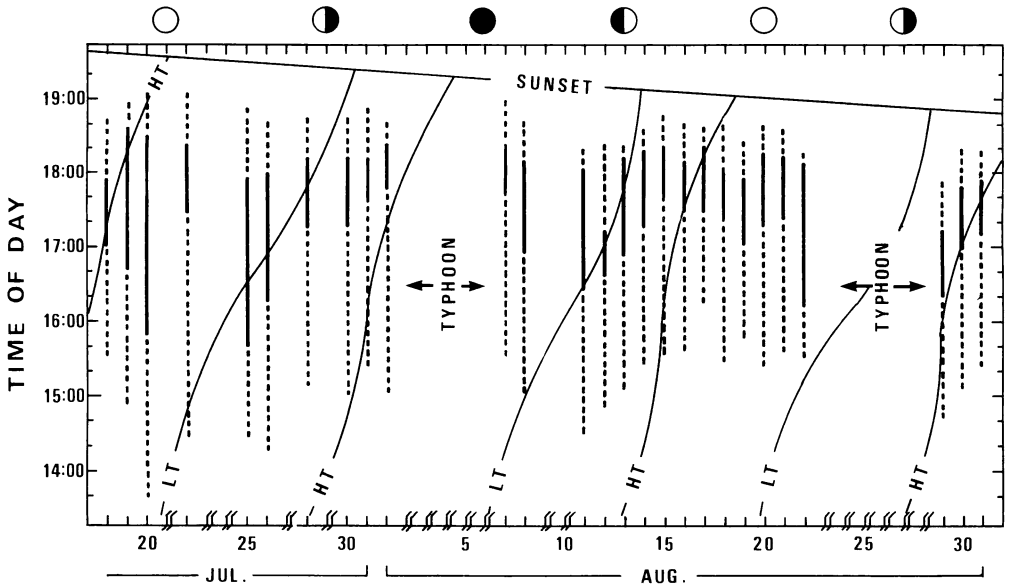
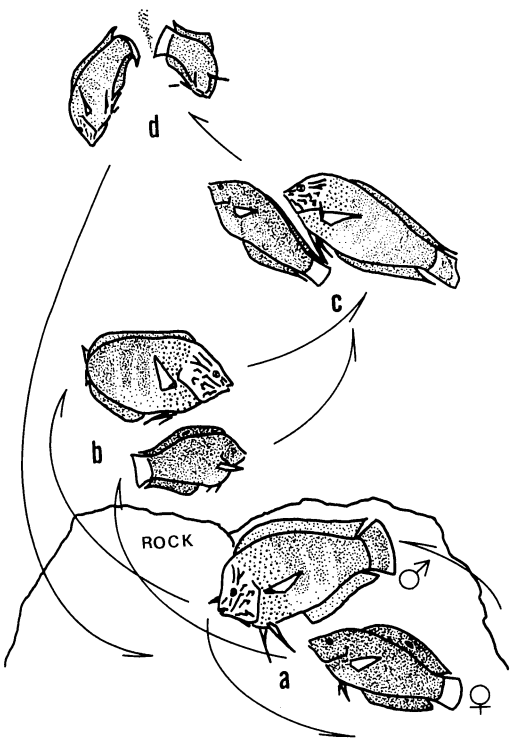



**Fig. 4.** Diurnal spawning activities of *Halichoeres marginatus* in mating territory A, observed from 18 July to 31 August, 1986. Dotted lines indicate that the territorial male was found patrolling the mating territory. Solid lines indicate the range of spawning time. Circles at top represent the lunar phase. *HT*—time of high tide; *LT*—time of low tide.




while swimming in progressively tight circles about 1 m above her. As the female rose in the water column along the rock, the male moved above her, leading her higher. When the female approached closer to the male, the latter quivered its body rapidly in lateral orientation above her with the dorsal and anal fins erect (quivering, Fig. 5). A moment later, as the female touched her snout on the male's abdomen, both fish rushed about 1 m upward (upward spawning rush) and released a cloud of gametes 1–2 m under the water surface (spawning). In this upward spawning rush, the female began to rush slightly earlier than the male. After spawning, the fish broke apart and returned rapidly to the substrate. The male approached the spent female and circled her again on the substrate (post spawning display).

The distance from the substrate of the starting point of the upward spawning rush differed between territories; about 5 m in territory A, 2.5 m in B, 1 m in D and 0.8 m in G.

The spent female subsequently left the territory

**Fig. 5.** Schematic representation of pair spawning of *Halichoeres marginatus*: a) circling; b) quivering; c) upward spawning rush; and d) spawning.

and returned to the shore. The territorial male patrolled the territory after the departure of the females, eventually returning to the shore about 30 min before sunset.

Continuous observation of 3 tagged females from 10:00 h to sunset indicated that each female spawned once a day. Most spawnings occurred between 17:00 and 18:00 h on every observation day, irrespective of the tidal cycle and the lunar cycle (Fig. 4). Spawnings were observed from the beginning of the study period (June 10) until November 1.

Out of 237 pair spawnings observed, 21 were accompanied by "streaking." In addition, 11 "sneaking" and 14 "group spawning" activities were observed (Table 1; see below).

### Sneaking and streaking

Large, non-territorial TP males, which had contended with the territorial male for the territory before the spawning period, often remained over prominent rocks or dead corals around the territory during the spawning time. They repeatedly courted females migrating to the territory, frequently following them into the latter (Table 2). Small, non-territorial TP and IP males also appeared around the territory, where females were concentrated, and also frequently followed the females into the territory. IP males were easily distinguished from females since they were attacked by the territorial male and had wounds on their bodies (evidence of previous attacks).

Both non-territorial TP and IP males pair-spawned with single females within the territory, while the territory owner left its position above the rock to pursue a intruder or court a female (sneaking; Thresher, 1984). Large, non-territorial TP males, which remained around the territory, also induced females at the periphery of the territory and attempted sneaking.

Both non-territorial TP and IP males, which remained close to the territory, also rushed to join the territorial male and a female at the climax of pair spawning, and released sperm (streaking; Thresher,

**Table 1.** Spawning behavior and number of participants in *Halichoeres marginatus*

| Mating territory | No. of days observed | Pair spawning | Streaking | | | Sneaking | | | Group spawning | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | No. | No. | IP | TP | No. | IP | TP | No. | IP | TP |
| A | 13 | 115 | 5 | 1 | 0 | 2 | 0 | 1 | 0 | — | — |
| B | 3 | 15 | 0 | — | — | 0 | — | — | 0 | — | — |
| D | 6 | 24 | 2 | 1 | 0 | 0 | — | — | 4 | 3 | 0 |
| G | 10 | 83 | 7 | 1 | 0 | 4 | 1 | 0 | 1* | 2 | 0 |
| | | | 3 | 0 | 1 | 5 | 0 | 1 | 2 | 3 | 0 |
| | | | 3 | 3 | 0 | | | | 2 | 3 | 1 |
| | | | 1 | 1 | 1 | | | | 1* | 3 | 1 |
| | | | | | | | | | 1* | 3 | 2 |
| | | | | | | | | | 1* | 4 | 0 |
| | | | | | | | | | 2 | 4 | 1 |
| Total | 32 | 237 | 21 | | | 11 | | | 14 | | |

IP: initial phase male; TP: terminal phase male; * the territorial TP male joined in group spawning.

**Table 2.** Number of spawning activities and numbers of females, IP males and TP males appearing in each territory

| Mating territory | TL of territorial male (mm) | No. of spawnings (A) | No. of individuals appearing in the territory | | | Spawning rate of females appearing in the male territory (A/B%) |
|---|---|---|---|---|---|---|
| | | | Female (B) | IP male | TP male | |
| A | 210 | 9.0±2.1 | 14.9±3.2 | 1.5±1.1 | 1.9±1.0 | 60.4 |
| B | 200 | 5.0±1.6 | 19.0±2.2 | 1.7±0.9 | 4.3±2.9 | 26.3 |
| D | 210 | 4.7±1.4 | 16.8±6.4 | 9.5±7.0 | 6.0±3.8 | 28.0 |
| G | 230 | 10.2±3.5 | 19.2±7.0 | 12.9±8.7 | 7.9±4.1 | 53.1 |

Mean±SD per day is given. For no. of days observed, see Table 1.

1984). In a few cases ($n=5$, in territory A) IP males, which had intruded surreptitiously into the territory by using their resemblance to females, attempted streaking, rising in the water column with the females induced by the territorial male. Streaking by 3 IP males and by an IP male accompanied by a non-territorial TP male were observed in territory G (Table 1).

Females left the spawning site after about 18 : 00 h, whereupon non-territorial TP and IP males also left.

### Group spawning

When 4 or 5 IP males intruded repeatedly into a territory to attempt sneaking or streaking, the territorial male was unable to drive them out. Therefore, he swam with fins erect around the prominent rock at the center of the territory, attempting to exclude all IP individuals, including females. IP males and females, however, remained within the territory and participated in group spawning. The territorial male sometimes participated in group spawning (Table 1).

After a group of 2–4 IP males had pursued a female for about 5 sec, just above the substrate, they rushed simultaneously in the water column to spawn. Group spawning also occurred when a single IP male, which quivered above a female rising in the water column, was joined by 1–3 IP males. In 6 out of 10 group spawnings observed in territory G, 1 or 2 non-territorial TP males also participated (Table 1).

In territory G tagged female was observed pair spawning with the territorial male (4 days), with a non-territorial TP male (1 day), and also participating in group spawning (1 day).

### Difference between territories

The number and patterns of sneaking, streaking and group spawning activities differed between territories (Table 1). Therefore, in each territory, the number of spawning activities, females, IP males and non-territorial TP males were compared (Table 2). Although the number of females appearing in each territory did not differ significantly between territories (Kruskal-Wallis test, $p > 0.1$), a significantly greater number of spawning activities occurred in territories A and G, compared with B and D ($p < 0.01$). The spawning rates of females appearing in territories A and G were significantly higher than those in B and D ($p < 0.01$) (i.e., more females passed through territories B and D without spawning).

The numbers of both IP or non-territorial TP males appearing in each territory differed significantly between territories ($p < 0.01$), being higher in the more inshore, shallower territories (D and G).

The territorial male, upon sighting IP and non-territorial males rushing or inducing females in attempts at sneaking, streaking or group spawning in his territory, aggressively chased them and attempted to prevent them from interfering in mating. The prevention rate [A/(A+B) %; where A=no. of males which were prevented from sneaking, streaking or group spawning, B=no. of males which participated in spawning] was 12.5% in territory A (1 out of 8 individuals), 100% in territory B (1 out of 1), 6.7% in territory D (1 out of 15), and 2.4% in territory G (2 out of 83).

## Discussion

Histological examination of *Halichoeres marginatus* indicated that females changed sex to males at 130–180 mm TL, accompanied by a color change from the dark-brownish initial phase to the dark-greenish terminal phase. As Colin and Bell (1991) found at the Marshall Islands, *H. marginatus* is a sexually dichromatic species. Although Choat (1969) stated that *H. marginatus* comprised only protogynous hermaphrodites (i.e., monandric), the present study proved that the species comprises both protogynous hermaphrodites and gonochoristic males (primary males) (i.e., diandric). The proportion of primary males in *H. marginatus* was much lower (4.9%) than in other diandric labrid fishes (e.g., 50.8% in *Halichoeres tenuispinis*, Nakazono, 1979; also see Robertson and Choat, 1974; Meyer, 1977; Warner and Robertson, 1978). No small sized or terminal phase primary males were found, but an increase in the sample size would likely reveal such, as reported in other labrid fishes (Warner et al., 1975; Meyer, 1977; Warner and Robertson, 1978; Nakazono, 1979; Yogo, 1985).

The present study indicated that the mating system of *H. marginatus* was lek-like, although a mating center (see Moyer and Yogo, 1982) was not present. In contrast, Colin and Bell (1991) described the mating system of *H. marginatus* in the Marshall Islands as haremic. Geographical variation in the mating system has also been documented in *Halichoeres maculipinna* (Thresher, 1979; Robertson,

1981). In general, females, which live in areas from which eggs can be rapidly carried off the reef, spawn with the male in whose territory they live. In locations offering an abundance of suitable spawning sites throughout the area, a haremic mating system can be established. However, if spawning sites are concentrated in specific areas, necessitating female migration for the purpose of spawning, such sites become economically defendable, with large males establishing mating territories. Consequently, a lek-like mating system is established (Robertson, 1981; Kuwamura, 1984; Fitch and Shapiro, 1990). Such a system was formed at Kuchierabu-jima, probably because spawning sites were limited.

Spawning behavior of *H. marginatus* included pair spawning, sneaking, streaking and group spawning. Pair spawning in *H. marginatus* is similar to that of *Halichoeres melanochir* (Moyer and Yogo, 1982), but differs in the absence of "pointing" and the presence of "post-spawning display." Sneaking and streaking by the IP and non-territorial TP males are similar to such activities in other diandric labrids (Warner et al., 1975; Warner and Robertson, 1978; Nakazono, 1979; Hoffman et al., 1985).

In *H. tenuispinis* and *Thalassoma bifasciatum*, living under high population densities and having a high proportion of primary males, a large number of females migrate to specific spawning areas on the offshore margin or downcurrent end of a reef, and participate mainly in group spawning with IP males, numbering from several hundred to several thousand, aggregated at such areas (Warner et al., 1975; Warner and Robertson, 1978; Nakazono, 1979). However, Warner and Hoffman (1980a, b) reported that in *T. bifasciatum* the proportion of primary males and spawning behavior varied with the local population density. On small reefs, where the density was low, primary males were almost absent from the local populations. Territorial TP males normally controlled the downcurrent spawning area, and IP and non-territorial TP males spawned by sneaking and streaking. On larger reefs with dense local populations, as mentioned above, territorial TP males could not economically defend the major downcurrent spawning area, which was therefore occupied by a spawning group of IP males.

Although *H. marginatus* had a low population density, with a low proportion of primary males, group spawning was observed. The behavioral patterns of group spawning in this species were similar to those of *H. tenuispinis* (Nakazono, 1979), but differed in the lower number of IP male participants, the participation of non-territorial TP males and the occurrence of the activity within a mating territory near the shore.

In *H. marginatus*, females seemed to choose spawning sites rather than the males occupying them (Shibuno et al., 1993; this study). Large females migrated to various spawning sites, including downcurrent sites, whereas small females migrated to the spawning sites near their home ranges in the shallower area, irrespective of the direction of water movement (Shibuno et al., 1993). The reason why a large number of females also spawned in the shallower area near the shore seemed to be related to their choice of spawning sites.

IP and non-territorial TP males concentrated in a specific part of the shallower area near the shore, among spawning sites at which a large number of females spawned. Although the territorial male's ability to defend his territory against intruding males may be related to body length (Warner and Schultz, 1992), intrusions were made most repeatedly into the largest male's territory. In the shallower area, IP and non-territorial TP males could mate near the substrate, which afforded protection from the territorial male. When such IP and non-territorial TP males intrude repeatedly into a territory and disturb the territorial male's control over the spawning site, group spawning seems to occur. Moreover, although the risk of predation upon fishes in group spawning is generally high (Colin and Bell, 1991), the distance from the substrate of the starting point of the upward spawning rush was shorter in shallower water. Consequently, the risk of predation in group spawning seems to be lower than at mating territories established in deeper water.

In *H. marginatus*, having a lek-like mating system, the proportion of primary males was low. However, IP males together with non-territorial TP males repeatedly intruded into a mating territory in the shallower area near the shore, in which a large number of females spawned, disturbing the territorial male's control over the spawning site. Consequently, IP males of *H. marginatus* probably increase their mating success by group spawning, in addition to sneaking and streaking.

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## 口永良部島におけるカノコベラの繁殖行動

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カノコベラ *Halichoeres marginatus* の雌雄性と繁殖行動について南西諸島の口永良部島の磯水域で調査した．本種の生息密度は低く，単独で摂餌していた．本種は雌性先熟の雌雄同体で，一次雄もわずかに存在した．雄には派手な体色（TP）と雌と同じ地味な体色（IP）のものがみられた．大型の TP 雄は毎日午後遅くになると，やや沖合いの岩やサンゴ岩盤の突き出た部分を中心

として一時的な繁殖縄張を形成し，そこへ移動してきた雌とペア産卵を行った．縄張をもたない TP 雄や IP 雄は岸近くの繁殖縄張に侵入を繰り返し，繁殖縄張内でストリーキング，スニーキング，グループ産卵を行った．本種の繁殖行動を他のベラ類と比較して考察した．

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