

Female Spawning Migrations of the Protogynous Wrasse, *Halichoeres marginatus*

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Abstract Spawning sites and spawning migration paths of tagged females of the protogynous wrasse, *Halichoeres marginatus*, were studied on the shallow reefs at Kuchierabu-jima Island, Japan. Males set up mating territories above prominent rocks on the offshore reef slope in the late afternoon, and pair-spawned with females, which had migrated there from their home ranges located in inshore areas. Small females migrated to the spawning sites near their home ranges, whereas large females migrated to various spawning sites located within a wide area, including downcurrent sites. Spawning at the downcurrent sites favors transport of eggs offshore, thereby increasing the female's fitness. The spawning sites where an individual had spawned as a female were subsequently used for mating after it had changed sex. It is suggested that the wide migration of females to various spawning sites, enables the storing up of information on those sites, which later helps in the acquisition of mating territories after changing sex.

Many labroid species migrate to specific spawning areas on the outer or downcurrent edges of reefs (Thresher, 1984). Such spawning areas have been suggested as giving the best opportunity for eggs to be carried rapidly off the reef and away from reef-based predators (Randall and Randall, 1963; Warner et al., 1975; Robertson and Hoffman, 1977; Johannes, 1978; Robertson, 1981; Jones, 1981; Moyer and Yogo, 1982).

Spawning sites of females shift with growth and changes in water current in *Thalassoma bifasciatum* (Warner, 1985, 1986). Warner (1985, 1986) suggested that the shift of spawning sites is related to the acquisition of mating territories after changing sex, but this has not yet been confirmed by observation of mating behavior after sex change.

In this paper, the spawning sites and paths of spawning migration in small and large females of *Halichoeres marginatus* are described and the relation of female spawning migrations to mating behavior after changing sex is discussed.

Materials and Methods

The Island of Kuchierabu-jima ($30^{\circ}28'N$, $130^{\circ}10'E$) lies between Kyushu and the Ryukyu Islands (Fig. 1). The reef fish fauna of the island shows predominantly tropical characteristics (Gushima and Murakami, 1977). A study area of about $100,000\text{ m}^2$ was selected in Nishiura Bay, where

spawning sites of *H. marginatus* were concentrated. The substrate consisted of rocks and boulders at the spawning sites from about 10 to 75 m offshore, 1 to 3 m deep, and of rocks and dead corals at those from about 75 to 100 m offshore, 3 to 8 m deep. The substratum sloped steeply about 90 to 120 m offshore, to depths of 5 to 12 m. Sampling and field observations were mainly made by snorkeling.

Halichoeres marginatus is a sexually dichromatic species composed of both protogynous hermaphrodites and primary males (i.e., diandric). General characteristics of its reproductive ecology in the study area are summarized as follows (Shibuno et al. in prep.). Both females and males fed alone on the

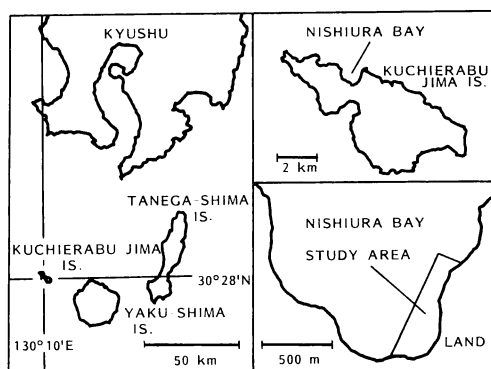


Fig. 1. Maps of Kuchierabu-jima Island and the study area.

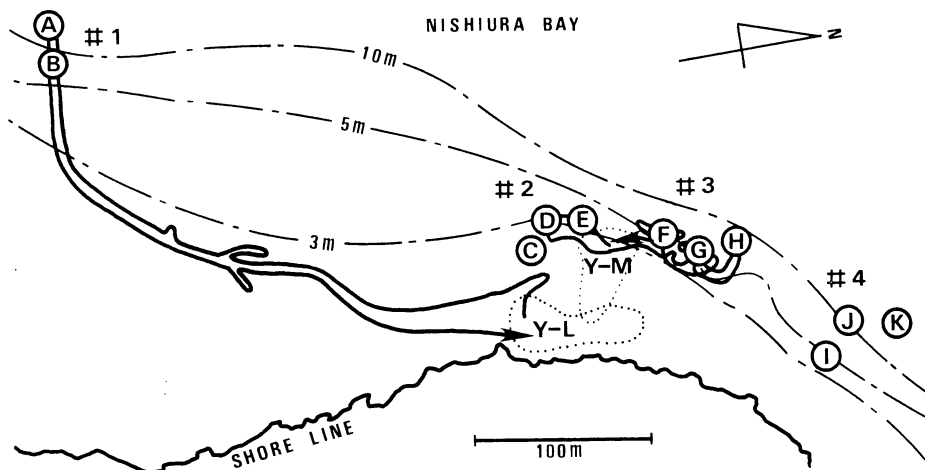


Fig. 2. Location of spawning sites of *H. marginatus* (A to K encircled). Spawning migration paths of two females are also illustrated from the observation during 17:10–17:58 on 21 July (Y–L) and 17:25–18:05 on 16 August (Y–M) 1990. Dotted lines indicate the home ranges of Y–L and Y–M. Contour lines of 3, 5 and 10 m depth are given.

hard substrate in the inshore area in the morning and early afternoon. Large terminal phase (TP) males (≥ 200 mm TL) set up mating territories around the prominent rocks on the reef slope from 15:00 to 18:30. Females began to migrate to the mating territories from about 16:00. Territorial males pair-spawned with females from about 17:00 to 18:00 everyday. Non-territorial TP males or initial phase males spawned by sneaking and group spawning. Females spawned once each day. The spawning season was from early May to early November.

In the present study underwater observations were made on tagged females. Twenty females were captured by gill net in the inshore area near spawning sites C and D (see Fig. 2) from 16 May to 7 August 1990. The total length (TL) was measured, and the fishes were marked with lettered, colored plastic tags (see Moyer and Yogo, 1982). Most females retained their tags for more than 3 months and some for more than 6 months. Observations on the mating behavior of individuals which changed sex and color phase during the observation period, were continued throughout.

Each female was tracked for 1 to 2 hours before its spawning migration on at least 2 days, and the area including all the observed locations of each female was regarded as its home range (foraging area).

Six tagged females were tracked from about 2 hours before their spawning migration until their return to their foraging areas, on 15 occasions in

total. Their location, behavior and swimming paths were recorded throughout. When other tagged females were observed spawning during tracking of a focal fish, the spawning sites of those females were also recorded. These data were collected during the peak spawning season, between 14 July and 13 September 1990. At two spawning sites (C and D in Fig. 2) observations were made during the spawning period on 9 days from 13 to 23 August 1990.

Each territorial male in the spawning site was observed for 10 to 15 minutes during the spawning period on at least 8 occasions, from 14 July to 13 September 1990. Each male was identified by individual differences in color and size, and the position of each territory recorded on a map.

Water movements in the study area were observed by releasing fluorescein dye at the time of spawning on 43 days.

Results

Spawning sites of females in relation to water movement. Large TP males established their mating territories at 11 sites (Fig. 2). On the basis of their location the 11 spawning sites were grouped into four spawning areas: area #1 included spawning sites A and B, #2 C, D and E, #3 F, G and H, and #4 I, J and K.

Out of 20 tagged females, three were not seen subsequently. The home ranges of 14 tagged females

were located in the inshore area near spawning sites C, D and E (adjacent to the home ranges of Y-L and Y-M shown in Fig. 2). The home ranges of the remaining three females (O-D, O-H and O-L) were located about 300 m south of this area (left side of the map in Fig. 2).

The spawning sites of the former 14 tagged females were analyzed. Small females (<130 mm) spawned only at spawning sites C and D near their home ranges, whereas large (>130 mm) females spawned at several, widely distributed spawning sites (3.1 ± 1.0 SD, $n=9$) (Table 1). The average distance from the center of each female's home range to its spawning sites was positively correlated with the total length of the fish (Kendall's $\tau=0.508$, $n=14$, $p<0.05$, two-sided test). The number of spawning sites and areas where each female spawned was also positively correlated with the total length ($\tau=0.688$, $p<0.01$; $\tau=0.545$, $p<0.05$, respectively).

Females spawned at an average of 2.6 (± 1.1 SD, $n=14$) spawning sites, with an average of 3.6 (± 1.7 SD) TP males; that is, females spawned with more than one male at a single spawning site. Females seemed to choose the spawning sites rather than the males, since the sites did not change even with a change of territorial male.

In the study area the direction of water movement varied day by day, but did not differ between the spawning areas. Out of 43 observation days, the direction of water movement during the spawning period was to the northeast on 27 days (62.8%), to

the southwest on 9 days (20.9%), and there was little or no water movement on 7 days (16.3%).

The relationship between spawning site selection and water movement were analysed for both small and large females. Small females (<130 mm) spawned irrespective of the direction and strength of water movement at spawning sites C and D, although they sometimes left the sites without spawning (Table 2). Large females (>130 mm) used spawning areas #1 and #4, which were distant from their home ranges, almost only when these areas were downcurrent (southwest in #1; northeast in #4; Table 3). When water movement was absent or weak, large females spawned only at spawning areas #2 and #3, near their home ranges.

Female spawning migrations. The patterns of spawning migrations in small and large females were compared. During migration to spawning sites near their home ranges, small females (<130 mm) often hid in crevices or under rocks. They often followed large females, which they encountered at a shelter, for a short distance to the next shelter. In 15 spawning migrations observed, small females followed large females on 44 occasions out of 65 encounters.

Large females (>130 mm) employed either of two spawning migration types, related to distance to the spawning areas. When large females migrated to spawning areas #2 and #3 near their home ranges, they visited several spawning sites (e.g., Y-M in Fig. 2). They often swam with other females encountered on the way, occasionally hiding at shel-

Table 1. Spawning sites of each female *H. marginatus*, observed during 14 July to 13 September 1990

Individual code	TL (mm)	Total no. of spawning	Spawning area and site												Average distance from the center of home range to the spawning site $\bar{x} \pm \text{SD}$ (m)
			#1		#2			#3			#4				
			A	B	C	D	E	F	G	H	I	J	K		
B-E	100	3	0	0	0	3	0	0	0	0	0	0	0	36.7 \pm 0	
Y-7	105	6	0	0	1	5	0	0	0	0	0	0	0	29.1 \pm 4.5	
C-3	113	5	0	0	1	4	0	0	0	0	0	0	0	18.9 \pm 3.0	
B-C	115	3	0	0	0	3	0	0	0	0	0	0	0	74.1 \pm 0	
Y-O	128	5	0	0	2	3	0	0	0	0	0	0	0	43.8 \pm 0.7	
B-H	133	5	0	0	0	1	0	0	1	3	0	0	0	152.0 \pm 53.1	
O-B	135	2	0	0	0	1	0	0	0	1	0	0	0	108.2 \pm 51.9	
O-C	135	2	0	0	0	0	1	0	1	0	0	0	0	55.8 \pm 18.4	
G-X	145	2	0	0	0	0	0	1	0	0	0	1	0	98.8 \pm 62.4	
Y-M	148	5	1	0	0	0	0	2	0	0	1	1	0	165.6 \pm 107.9	
Y-K	151	19	0	0	6	12	1	0	0	0	0	0	0	43.6 \pm 7.1	
O-K	155	4	0	0	0	0	0	1	1	2	0	0	0	77.0 \pm 19.1	
B-I	162	7	1	0	0	0	1	1	0	3	0	1	0	139.5 \pm 96.9	
Y-L	178	7	1	0	0	1	1	0	0	0	0	0	4	193.2 \pm 100.5	

ters. After spawning, they returned to their home ranges without hiding. When large females migrated to spawning areas #1 and #4, distant from their home ranges, they did not pass through other spawning areas (e.g., Y-L in Fig. 2). They moved quickly along crevices with other females encountered on the

Table 2. Frequency of spawning at spawning area #2 in relation to water movements, for 5 small females (<130 mm TL, see Table 1) during 13 to 23 August 1990. Numerals in parentheses show the number of individuals which appeared, but did not spawn

Water movement	No. of days observed	Total no. of spawnings	No. of spawning per day*
Northeast	5	12 (5)	2.4
Southwest	2	5 (2)	2.5
Weak or absent	1	2 (1)	2.0

* Kruskal-Wallis test, $p > 0.05$

Table 3. Frequency of spawning at each spawning area in relation to water movements, for 9 large females (>130 mm TL, see Table 1) during 14 July to 13 September 1990

Water movement	Spawning area				Total
	#1	#2	#3	#4	
Northeast	0	16	8	7	31
Southwest	3	3	3	1	10
Weak or absent	0	6	6	0	12

Table 4. Relationship between spawning sites visited as a female and those as a male after changing sex in *H. marginatus*

Individual code	TL (mm)	Date of last spawning as a female	No. of spawning sites visited as a female before changing sex	No. of spawning sites visited as a male after changing sex	No. of spawning sites visited both as a female and as a male	Fisher's exact probability test* (one-tailed)
B-H	133	30 Aug.	4	2	2	$p = 0.109$
B-I	162	3 Sept.	10	3	3	$p = 0.727$
O-D	162	23 July	7	8	7	$p = 0.024$
Y-L	178	1 Aug.	8	7	7	$p = 0.024$

* The null hypothesis is that the spawning sites visited as a male after changing sex present a random draw from the available 11 spawning sites, with no influence of past visits as a female; e.g., a contingency table for B-H is as follows:

	Spawning sites as ♂	
	visited	not visited
as ♀ visited	2	2
not visited	0	7

way. After spawning, they returned individually to their home ranges without passing through other spawning sites. The migration route of Y-L depicted in Fig. 2 was also used by the other two large females that spawned at area #1. Large females migrated with an average of $9.3 (\pm 7.4 \text{ SD}, n = 15)$ individuals, including an average of $3.1 (\pm 3.2 \text{ SD})$ small females and $6.1 (\pm 7.1 \text{ SD})$ large females.

Mating sites after changing sex. Five large, tagged females changed sex between July and September 1990. Except for an individual (Y-K), which changed sex in late September, four of them (B-H, O-D, B-I and Y-L) were observed to intrude repeatedly into the mating territories of other males after changing sex. All except one of the spawning site into which they intruded after changing sex, had been used by them while they were females (Table 4). Two of the four sex-changers (O-D and Y-L) showed a significant preference for the spawning sites which they had previously visited as females.

The above individuals, Y-L and O-D, mated as males within about 3 or 4 weeks of their last spawning as females, and possessed mating territories at spawning sites B and E, respectively, about 3 or 4 weeks later. Sex-changers B-H and B-I were not observed to successfully mate as males during the same spawning season.

Discussion

Females of *H. marginatus* spawned with new

males after replacement of former territorial owners, and did not follow males to new territories. They also spawned with non-territorial males at the spawning sites. These results suggest that *H. marginatus* females choose spawning sites rather than the males occupying them, as reported for other wrasses, *Pseudolabrus celidotus*, *Thalassoma duperrey* and *T. bifasciatum* (Jones, 1981; Ross, 1986; Warner, 1987, 1990).

Small females of *H. marginatus* migrated short distances to the spawning sites near their home ranges, irrespective of the direction of water movement. As they grew larger, females began to migrate to various spawning sites located within a wide area. Large females migrated long distances to down-current spawning areas. The possible advantages of spawning in a downcurrent spawning area have been suggested for many labroids (Randall and Randall, 1963; Warner et al., 1975; Robertson and Hoffman, 1977; Johannes, 1978; Robertson, 1981). Thus it appears that when females of *H. marginatus* become large, they migrate by daily assessment to spawning sites that favor the transport of their eggs offshore, thereby increasing fitness. The reason why small females did not migrate long distances to spawn seems to have been due to high predation pressure, as has been suggested for many small reef fishes (Hobson, 1974; Helfman, 1978; Johannes, 1978; Jones, 1981). The hiding behavior observed, even during short migration, for small females of *H. marginatus* suggested high predation pressure upon them in the study area.

Sex-changed individuals intruded repeatedly for mating purposes, into the spawning sites which they had previously visited for spawning as females, and later established mating territories in one of those spawning sites. This observation supports Warner's (1985, 1986) suggestion that *T. bifasciatum* females stored information on spawning sites by migrating widely to various sites, such later helping in the acquisition of a mating territory after changing sex.

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Literature Cited

- Gushima, K. and Y. Murakami. 1977. Species composition of the reef fishes at Honmura Bay of Kuchierabu Island. J. Fac. Fish. Anim. Husb., Hiroshima Univ., 16: 107–114. (In Japanese with English summary.)
- Helfman, G. S. 1978. Patterns of community structure in fishes: summary and overview. Env. Biol. Fish., 3: 129–148.
- Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., 72: 915–1031.
- Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish., 3: 65–84.
- Jones, G. P. 1981. Spawning-site choice by female *Pseudolabrus celidotus* (Pisces: Labridae) and its influence on the mating system. Behav. Ecol. Sociobiol., 8: 129–142.
- Moyer, J. T. and Y. Yogo. 1982. The lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyakejima, Japan. Z. Tierpsychol., 60: 209–226.
- Randall, J. E. and H. A. Randall. 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, D. R. 1981. The social and mating systems of two labrid fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean coast of Panama. Mar. Biol., 64: 327–340.
- Robertson, D. R. and S. G. Hoffman. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z. Tierpsychol., 45: 298–320.
- Ross, R. M. 1986. Social organization and mating system of the Hawaiian reef fish *Thalassoma duperrey* (Labridae). Pages 794–802 in T. Uyeno, R. Arai, T. Taniguchi and K. Matsuura, eds. Indo-Pacific Fish Biology. Ichthyol. Soc. Japan, Tokyo.
- Thresher, R. E. 1984. Reproduction in reef fishes. T.F.H. Publ., Neptune City, New Jersey, 399 pp.
- Warner, R. R. 1985. Alternative mating behavior in a coral reef fish: a life-history analysis. Proceedings of the Fifth International Coral Reef Congress, Tahiti, 4: 145–150.
- Warner, R. R. 1986. The environmental correlates of female infidelity in a coral reef fish. Pages 803–810 in T. Uyeno, R. Arai, T. Taniguchi and K. Matsuura, eds. Indo-Pacific Fish Biology. Ichthyol. Soc. Japan, Tokyo.
- Warner, R. R. 1987. Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. Anim. Behav., 35: 1470–1478.
- Warner, R. R. 1990. Male versus female influences on mating-site determination in a coral reef fish. Anim. Behav., 39: 540–548.
- Warner, R. R., D. R. Robertson and E. G. Leigh, Jr. 1975.

Sex change and sexual selection. Science, 190: 633-638.

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雌性先熟のカノコベラにおける雌の産卵移動

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雌性先熟のベラ類の一種であるカノコベラ *Halichoeres marginatus* の雌の産卵場所とそこへの移動経路を、個体識別して、口永良部島の磯水域で調査した。雄は毎日午後遅くに、沖合いの斜面上の突出した岩を中心に繁殖縄張を形成し、岸近くの摂餌域

から縄張内へと移動して来た雌とペア産卵を行なった。小型の雌個体は摂餌域の近くで産卵した。一方、大型の雌個体は、より広い範囲の産卵場所へ移動した。これらには潮流の下側の産卵場所も含まれていた。雌は大型になると、産み出された卵の沖合いへの移送に適した産卵場所へ移動することで適応度を高めているものと推察される。さらに、雌として産卵した場所は性転換後も引き続き繁殖のために使用された。このことは、雌個体は広い範囲を移動しながら産卵場所の情報を蓄積し、性転換後の縄張獲得のために利用していることを示唆するものである。

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