

## ARTICLE

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**Male morphological characteristics and mating success in a protogynous coral reef fish, *Halichoeres melanurus***

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**Abstract** Morphological sexual differences and their effects on male mating success were investigated in the tailspot wrasse, *Halichoeres melanurus*, on a subtropical coral reef of Okinawa, southern Japan. Male mating territories were established along the reef edge from late April to early October, during which time pair-spawning occurred just before sunset in the male territories. Territorial males were larger and brighter than females in this protogynous fish. The males had longer, colorful ventral fins and colorful caudal fins, both of which were used during courtship. Multiple regression analysis of the effects of male characteristics on male mating success revealed that the yellow spot at the pectoral fin base was the most effective. It is suggested that large body size is favored in male–male competition for establishing mating territories and that conspicuous body color is favored in female mate choice.

**Key words** Sexual selection · Mate choice · Mating territory · Spawning · *Halichoeres* · Labrids

**Introduction**

Secondary sexual traits may often evolve through sexual selection, conflicting with natural selection (Darwin 1871). The faster rate of gamete production in males usually results in male–male competition and female mate choice as sources of intra- and intersexual selection, respectively (Bateman 1948; Trivers 1972). Consequently, males become larger and brighter than females in many species of animals (Andersson 1994).

Males are almost always larger than females in protogynous fishes, in which female-to-male sex change occurs due to reproductive advantages in larger males (i.e., the size-advantage model: Warner 1975, 1988; Kuwamura and Nakashima 1998). The reproductive advantages in larger males may result from male–male competition or female mate choice. Sexual difference in body color is also known in many species of protogynous wrasses (Labridae) (Warner and Robertson 1978; Thresher 1984). Females are small with drab coloration (initial phase, IP), whereas large males with bright coloration (terminal phase, TP). In some species there are also small IP males, which later change to TP with growth. TP males establish mating territories and pair-spawn with females, while IP males are nonterritorial and perform streaking, sneaking, or group spawning (Warner et al. 1975; Warner and Robertson 1978).

Such reproductive behavior and polygynous mating systems have been reported from many labrid species (Robertson and Hoffman 1977; Nakazono 1979; Kuwamura 1984; Thresher 1984; Colin and Bell 1991; Moyer 1991; Shibuno et al. 1993). However, the influence of intra- and intersexual selection has been quantitatively studied only in the bluehead wrasse *Thalassoma bifasciatum* (Warner et al. 1975; Warner 1984; Warner and Schultz 1992). The multiple regression analysis on effects of male morphological characteristics upon mating success revealed that both large body size and bright body color are favored in male–male competition and the latter also in female mate choice in the bluehead wrasse (Warner and Schlutz 1992).

The purpose of the present study was to detect morphological sexual differences in the tailspot wrasse, *Halichoeres melanurus*, and to examine their effects on male mating success, as the first step to understand the process of sexual selection in this species. This wrasse inhabits coral reefs of the Western Pacific and is known to exhibit considerable sexual dichromatism (Masuda et al. 1984; Myers 1989; Randall et al. 1990). Spawning behavior has been briefly reported from Eniwetok Atoll, Marshall Islands (Colin and Bell 1991): TP males defend territories and spawning occurs during late afternoon. Factors affecting male mating success are mostly unknown.

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In this article, we describe sexual dimorphism in body color and fin length of *H. melanurus*, as well as its reproductive behavior, male territories, mating success, and mortality observed on a subtropical coral reef of Okinawa, southern Japan. We analyze effects of male morphological characteristics on mating success to discuss basic features of intra- and intersexual selection in this species.

## Materials and methods

### Color phase

Sexual dichromatism in *H. melanurus* is known to occur (Masuda et al. 1984; Myers 1989; Randall et al. 1990). Females (IP fish) have alternating narrow orange-yellow and pale-blue stripes on the body, with a blue-edged black spot at front of and in middle of the dorsal fin and at the upper base of the caudal fin. In TP males, the three black spots disappear and the alternating stripes become orange-red and blue-green. Ventral and caudal fins of females are pale, while those of TP males are blue with orange-red bands, also with a large vertically elongate dusky to black spot submarginally in the middle of the caudal fin. The most conspicuous is a large yellow spot at the pectoral fin base in TP males.

We distinguished four color phases, i.e., initial phase (IP), intermediate phase (INT), subterminal phase (sTP), and full-terminal phase (fTP), based on the presence of dorsal black spots, yellow spot at pectoral fin base, and red bands on caudal fin. In INT fish, the black spot at the front of the dorsal fin disappears, and longitudinal orange-red bands appear on caudal fin. In sTP males (Fig. 1), the black spot disappears from the middle of the dorsal fin but remains at the upper base of the caudal fin; a small yellow spot appears at the pectoral fin base. The alternating stripes on

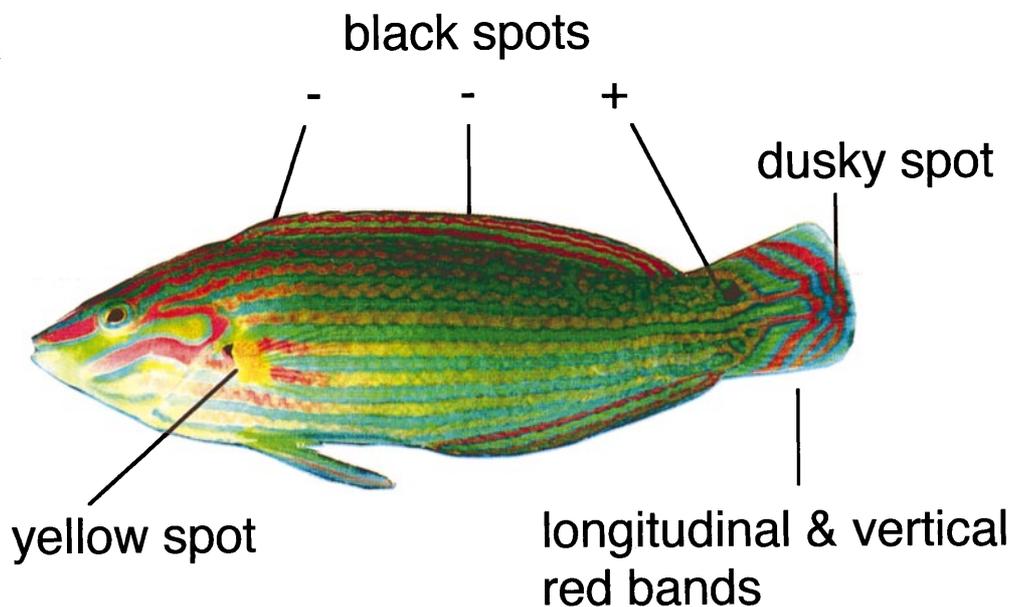
the body become orange-red and blue-green, which also appear on ventral fins, and both longitudinal and vertical red bands develop on the caudal fin. A vertically elongate dusky spot sometimes appears submarginally in the middle of the caudal fin. In fTP males, the black spot disappears from the upper base of the caudal fin, the yellow spot at the pectoral fin base becomes larger, and the dusky spot on the posterior part of the caudal fin becomes larger and darker. We hereafter use the term TP to include both sTP and fTP.

### Collection and measurement

Fieldwork was conducted using SCUBA or by snorkeling on the fringing reef of Sesoko Island (26°38' N, 127°52' E), Okinawa. Within a study area about 50 × 100m along the reef edge, we caught territorial TP males, INT fish, and the largest IP fish by screen nets and hand nets every 1–3 months from July 1993 to October 1995, except in winter when the fish were usually inactive and hiding themselves in sand. Additional collections of IP fish of various size were conducted at the beginning of the spawning season (late April to early May, spring sample) and in the middle of it (July–August, summer sample).

The fish were measured in total length (TL), standard length (SL), pectoral fin length (PF), and ventral fin length (VF); caudal fin length (CF) was calculated as TL minus SL. Sex was determined by the shape of urogenital papilla and also by pushing the abdomen to release sperm or to see eggs; all the TP and INT fish were males, as were about 5% of IP fish (primary males; see Warner and Robertson 1978). We took pictures of the fish from the side and gave subcutaneous injection of colored dye (Alcian blue) for individual discrimination. Then we released the fish at their collection sites. TP males could be distinguished by the individual variation in stripe patterns on the body even if the dye injection mark disappeared.

**Fig. 1.** Characteristics of the subterminal phase (sTP) coloration in *Halichoeres melanurus*



To examine morphological differences among the color phases, we used measurements of both spring and summer samples, because male coloration changed considerably between the two seasons (see Results). Measurements were pooled for each color phase; although some individuals were measured both in spring and summer, they grew and often changed color phase, and so were treated as different data. We analyzed differences in proportion of fin length to standard length between the color phases, calculating linear regression against SL for each fin length. We used the average values of paired structures (PF and VF) for the analysis.

#### Field observation and data analysis

Because preliminary observations at various times of day in July 1992 indicated that spawning occurred just before sunset, we observed each TP male from about 1 h before sunset until its sleeping. Both males and females hid themselves in sand during night. We observed 1–3 males during each evening, almost every day during July and August 1993, and from late April to early October 1994. We recorded the moving range, territorial behavior, courtship behavior, spawning time and site, and sleeping time and site.

We then compared daily mating success, i.e., the average number of spawnings per day, among the territorial TP males. As spawning activities tended to decrease on days around half moon (unpublished data), we tried to analyze data for each spawning period of 10–11 days around new or full moon, excluding data of 4 days around half moon. However, as the mortality of TP males was very high during the breeding season (see Results), there were only two spawning periods throughout which all the males in the study area survived and during which every male was observed more than one evening (2–4 times). Thus, we report here the results of the analysis of daily mating success in the two periods, July 15–24, 1993 ( $n = 7$  TP males) and August 1–11, 1994 ( $n = 10$ ). Because all males found in August 1994 were different individuals from those of July 1993 and the frequency of spawnings in the whole study area was similar between the two periods (see Table 1), data of the two periods were pooled in the following correlation and regression analyses of the relationship between mating success and morphological characteristics.

In addition to body size and fin lengths, we measured the area of the yellow spot at pectoral fin base (YP) as an indicator of the conspicuousness of TP males. A dusky to black spot on the posterior part of caudal fin was also conspicuous, but it was difficult to measure because its margin was ambiguous and unstable. We measured the area of YP from the pictures of males using a digitizer, and calculated actual size comparing with the ruler on the picture. We used the square root of the average area of both sides for the following analysis.

We analyzed the effect of the male morphological characteristics (SL, PF, VF, CF, and YP) on mating success, conducting simple correlation and multiple regression for the pooled data ( $n = 17$  males) of the two periods. Reduced

**Table 1.** Male size (TL mm) and daily mating success (MS, the average number of spawnings per day) in each site and period (see Fig. 4)

Site	July 15–24, 1993		August 1–11, 1994	
	TL	MS	TL	MS
Site A	98	11.0	109	11.5
	94	4.7	104	9.5
			76	3.5
			69	2.0
Subtotal		15.7		26.5
Site B	111	16.0	92	8.0
	102	4.3	88	5.0
	89	1.3	71	1.0
Subtotal		21.6		14.0
Site C	103	14.5	85	10.5
	78	5.5	72	2.0
			71	4.7
Subtotal		20.0		17.2
Total of 3 sites		57.3		57.7

models were calculated by the stepwise methods with forward selection and backward elimination (Hocking 1976). We chose the one with the largest coefficient of determination (adjusted  $r^2$ ). Multiple regressions were also run for transformed values expressed as the individual's residual in a linear regression of the character against SL to reduce collinearity (see Warner and Schultz 1992). Thus individuals with larger-than-average yellow spots, for example, would have a large positive residual value.

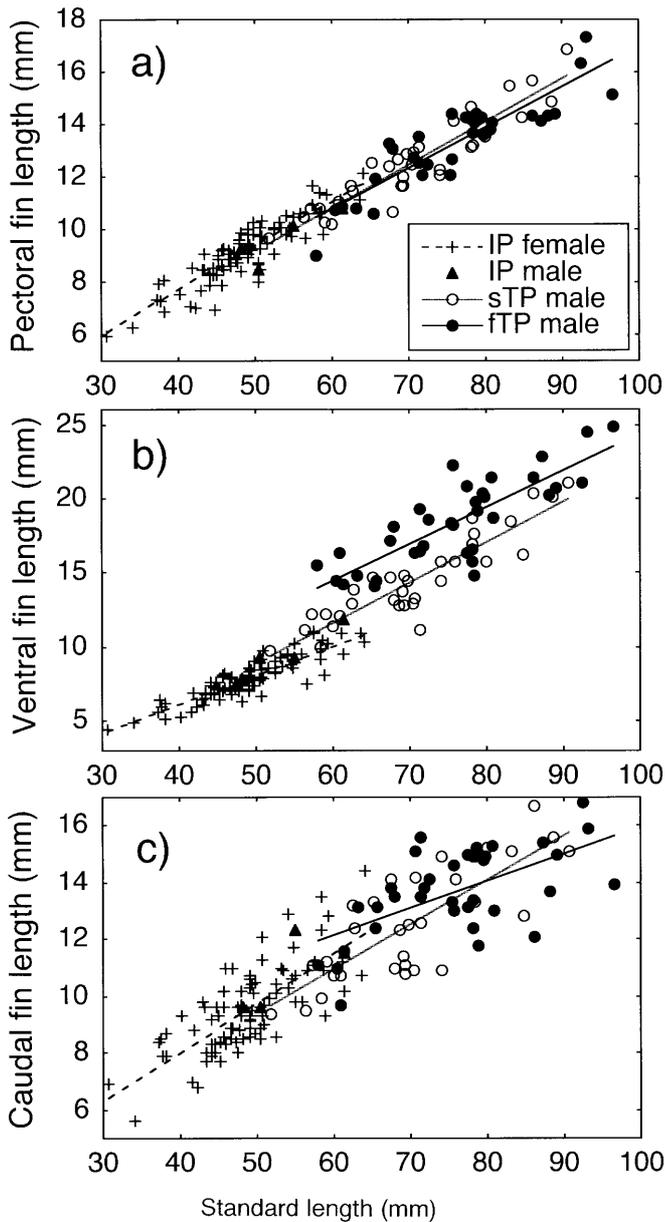
## Results

### Sexual difference in fin length

The proportions of lengths of pectoral fin (PF), ventral fin (VF), and caudal fin (CF) to body length (SL) were compared between the color phases, IP, sTP, and fTP. Most IP fish were smaller in SL than TP males, while SLs of sTP and fTP males largely overlapped (Fig. 2). INT fish were not found in the sample, and IP males ( $n = 4$ ; 4.2% of IP fish) were excluded from the following description because their sample size was small.

There was no significant difference in the slope and intercept of regression lines of PF against SL among IP females and sTP and fTP males ( $P > 0.1$ ; Fig. 2a). Also, there was no sexual difference in the coloration of pectoral fins, i.e., colorless and transparent in both IP and TP fish.

The regression line of VF against SL in IP females showed significant difference from that of sTP males both in slope ( $t = 3.61$ ,  $P < 0.001$ ) and intercept ( $t = 2.26$ ,  $P < 0.05$ ), although no significant difference was detected among others (Fig. 2b). The ratio of VF to SL became significantly larger in fTP (mean  $\pm$  SD = 24.3%  $\pm$  2.2;  $n = 35$ ) than that in sTP males (20.4%  $\pm$  1.9,  $n = 32$ ;  $t = 7.55$ ,  $P < 0.0001$ ), which was also larger than that in IP females (16.0%  $\pm$  1.4,  $n = 91$ ;  $t = 14.18$ ,  $P < 0.0001$ ). Thus, ventral fins became longer in males with progression of color phase.



**Fig. 2a-c.** Relation between standard length (SL) and pectoral fin length (PF) **a**), ventral fin length (VF) **b**), and caudal fin length (CF) **c**). Regression lines against SL for each group of initial phase (IP) females ( $n = 91$ ), subterminal phase (sTP) males ( $n = 32$ ), and full-terminal phase (fTP) males ( $n = 35$ ) are **a**)  $y = 0.170x + 0.857$ ,  $y = 0.163x + 1.036$ ,  $y = 0.156x + 1.467$ ; **b**)  $y = 0.197x - 1.764$ ,  $y = 0.272x - 4.710$ ,  $y = 0.244x - 0.088$ ; **c**)  $y = 0.175x + 1.034$ ,  $y = 0.157x + 1.563$ ,  $y = 0.096x + 6.369$ , respectively (ANOVA;  $P < 0.001$  for every regression)

The regression line of CF against SL in fTP males significantly differed from that of IP females both in slope ( $t = 3.04$ ,  $P < 0.01$ ) and intercept ( $t = 3.18$ ,  $P < 0.01$ ) and from that of sTP males in intercept ( $t = 2.09$ ,  $P < 0.05$ ; Fig. 2c). The ratio of CF to SL in fTP males ( $18.2\% \pm 1.9$  SD) did not differ from that of sTP males ( $17.9\% \pm 1.7$ ;  $t = 0.55$ ,  $P > 0.05$ ), although both were significantly smaller than that of IP females ( $19.6\% \pm 2.0$ ;  $t = 3.69$ ,  $P < 0.001$  and  $t = 4.26$ ,  $P < 0.0001$ , respectively).

## Seasonal change of male color, growth, and mortality

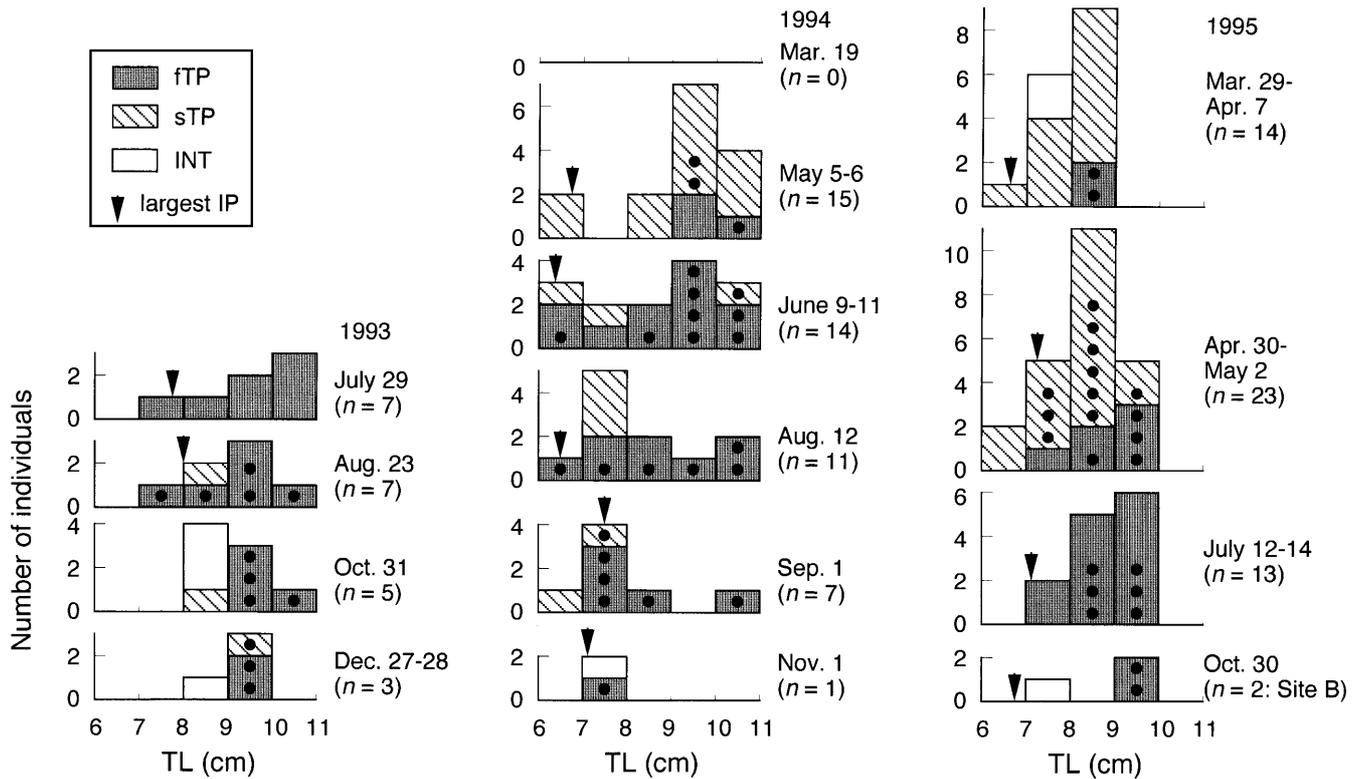
TP males established territories from late April or early May, and continued reproductive activities until early October. The number of TP males gradually decreased throughout the breeding season (Fig. 3). The TP males found at the beginning of the breeding season ( $n = 15$ , May 1994) never remained until the next year. As 11 of 38 TP males remained from May to July (1994 and 1995) and 10 of 17 TP males from July to August (1993 and 1994), the per-month remaining rate was calculated to be about 60%, suggesting only 5% per 6 months through the breeding season. By contrast, 3 of 16 TP males remained from the end of August to next May (1993–1994 and 1994–1995); i.e., 82% per month. Thus, the disappearance rate of TP males seems to be higher during the breeding season than the nonbreeding season, during which they were often hiding themselves in sand.

In late March, when the fish became active, most males were sTP (Fig. 3), except for those that had already become fTP by the end of the breeding season of the previous year. The proportion of sTP males was still large at the beginning of May, but they became fTP by July. New INT and sTP males occasionally appeared during the breeding season (Fig. 3) as a result of the sex change of IP females. The color change from sTP to fTP occurred more rapidly during the breeding season (8 of 10 sTP males changed to fTP within a month) than before the breeding season (only 2 of 10 sTP in late March changed to fTP by late April; Fisher's exact probability test,  $P < 0.05$ ). On the other hand, growth rate of sTP males was significantly higher from late March to late April ( $3.8\text{ mm} \pm 3.3$  SD per month,  $n = 10$ , original TL =  $79.4\text{ mm} \pm 7.0$ ) than in the breeding season ( $1.7\text{ mm} \pm 0.7$  SD per month,  $n = 15$ , original TL =  $85.5\text{ mm} \pm 13.0$ ; unpaired  $t$ -test for growth rate,  $t = 2.34$ ,  $P < 0.05$ ). Thus sTP males seem to have allocated to growth rather than color change until the beginning of the breeding season.

## Courtship, spawning, and male territories

Spawning occurred between 60 min before and 6 min after sunset. From about 1 h before spawning, males actively patrolled their territories to court females that were moving to the spawning sites or hiding under hard or soft corals. Major patterns of male courtship were as follows: (1) lateral displays in a head-up or head-down position just beside the female; (2) circling around the female; and (3) head-up quivering, i.e., quivering caudal fin in a head-up position, just above the head of hard or soft coral. During each type of courtship, ventral fins were usually hanging down.

During the male's head-up quivering, a female approached and swam up above the coral head, then rapidly rushed upward about for 30–60 cm, the male following her. At the apex of the rapid rush, gametes were released. After spawning, the male and female rapidly swam down to the bottom. In 26 (3.0%) of 860 spawnings observed in the 1993–1994 breeding seasons, a small IP male rushed to follow the spawning pair; i.e., streaking occurred.



**Fig. 3.** Seasonal change of size-frequency distribution of fishes with each color phase in a  $50 \times 100$  m study area. Data of October 30, 1995, were obtained only from a middle part (site B; see Fig. 4), about one-

third of the study area. Number of TP males (=sTP + fTP) is given in parentheses. Solid circles within each column indicate TP males that survived from the previous census

TP males had 1–5 spawning sites within their territories (Fig. 4), and repeated pair-spawning up to 20 times per dusk. Within 1–20 min after the last spawning, males hid themselves in the sand bottom. The sleeping sites were not always situated within the male territories (Fig. 4) and were sometimes shifted.

Several male territories were adjacently distributed at each spur of reef edge (sites A, B, and C in Fig. 4), but the three groups of male territories were separately distributed throughout the breeding season. In each group, larger males tended to have their territories offshore (Fig. 4). Males often shifted their territories within each group after some males disappeared, and sometimes moved even between the groups; e.g., a new male appeared in August 1993 (A3 in Fig. 4b), and a male found at site A in April 1994 (a5 in Fig. 4c) moved into site B in late May 1994.

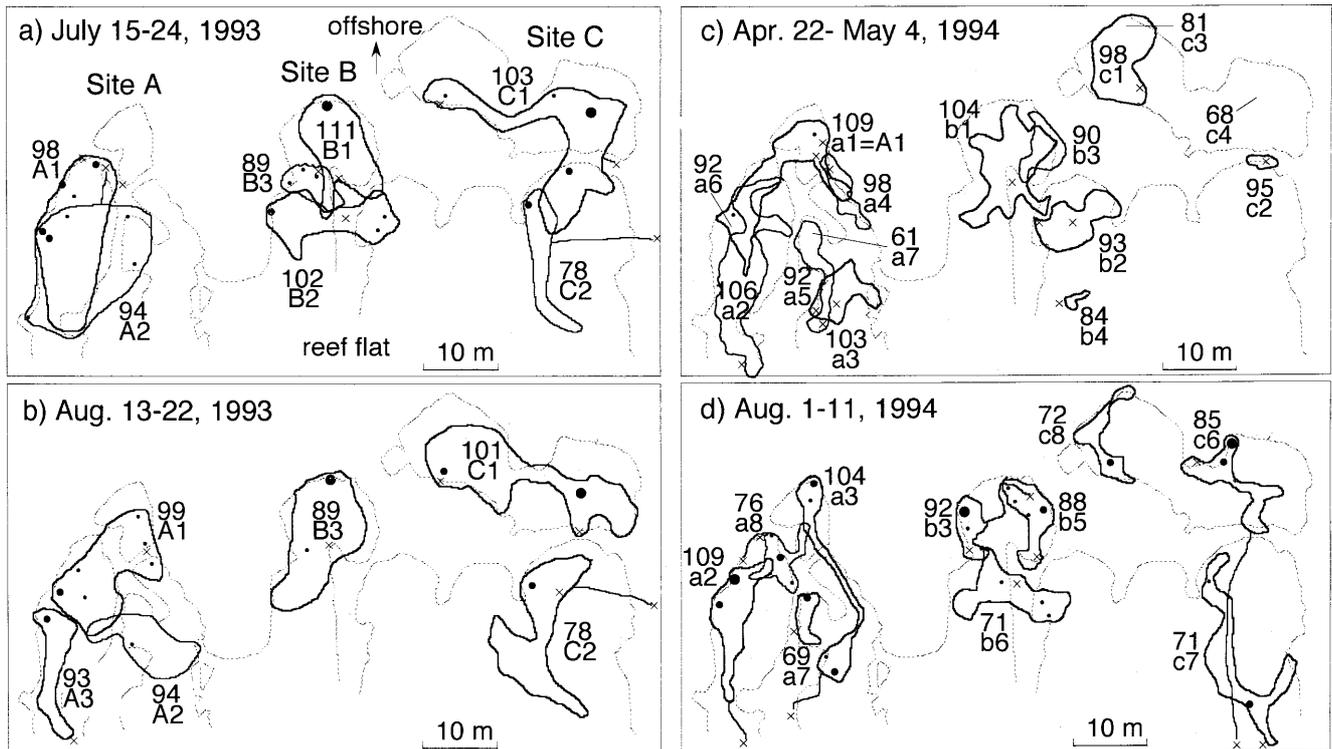
#### Effect of male morphological characteristics on mating success

In each male group, the largest male always achieved the highest mating success (Table 1). The subtotal of daily mating success at site A was the lowest among the three sites in 1993 but was the highest in 1994 (Table 1). The mating success in each territory of males in August 1994 was not significantly correlated with that observed in the same area in July 1993 ( $r = 0.38$ ,  $n = 10$ ,  $P > 0.1$ ).

Male mating success was significantly correlated with each of the five morphological characteristics (Table 2). The multiple regression analysis for the untransformed values showed a significantly positive effect of the yellow area at the pectoral fin base (YP) on daily mating success (Table 2). All four morphological characteristics were significantly correlated with body size (SL), and when the residuals in regressions against SL were used for multiple regression analysis, no significant effect was found in the morphological characteristics except SL (Table 2). There were no negative or significantly positive correlations among the transformed values ( $r = 0.10$ – $0.28$ ,  $n = 17$ ,  $P > 0.2$ ).

## Discussion

The present study confirmed that body size strongly affected male mating success in the protogynous wrasse *Halichoeres melanurus*. Male mating territories were newly established every spring because the fish were inactive during winter in the study site. TP males rarely survived until the next breeding season, and so at the beginning of the breeding season most territorial males were sTP, which should have been IP females (or IP males in a few cases) in the breeding season of the previous year. The sTP males allocated to growth rather than color change until the



**Fig. 4a-d.** Distribution of territories of TP males in four periods of 1993-1994. Territories of each male are encircled by a solid line, accompanied by TL (mm) and name code (e.g., A1). These data are based on 1-4 evening observations of about 1 h for each male in each period; no data are available for 4 males in map c, and only their positions are

shown. Spawning sites and frequencies for each male are given by solid dots; smallest, <2 matings per day, 2 ≤ middle size < 6, and largest, ≥6. Crosses indicate sleeping sites of each male. Reef edges and patch reefs are shown by dotted lines

**Table 2.** Linear effects of morphological characteristics of TP males measured in July 1993 and August 1994 on the daily mating success (MS) during each period (see Table 1)

Male characters	Untransformed values				Transformed values		
	Range	Correlation with:		Multiple regression		Multiple regression	
		MS	SL	Full	Reduced	Full	Reduced
SL (mm)	57.9-96.6	0.75***	-	0.13 (0.14)		0.75** (3.92)	0.75*** (4.38)
PF (mm)	9.0-17.4	0.72**	0.94***	-0.05 (-0.09)		-0.02 (-0.09)	
VF (mm)	11.4-24.8	0.72**	0.92***	0.16 (0.31)		0.06 (0.31)	
CF (mm)	9.7-15.9	0.68**	0.78***	0.20 (0.63)		0.13 (0.63)	
YP (mm <sup>2</sup> )	5.8-27.2	0.76***	0.97***	0.38 (0.51)	0.76*** (4.49)	0.10 (0.51)	
Adjusted $r^2$ (F)				0.42* (3.28)	0.55*** (20.15)	0.42* (3.28)	0.53*** (19.22)

Data for the two periods are pooled ( $n = 17$ ). Untransformed morphometric values and transformed values (residuals in regressions against SL) were used for the multiple regression analyses; standard partial regression coefficients (and  $t$ -values in parentheses) and adjusted  $r^2$  (and  $F$ -values in parentheses) are shown for full and reduced models

SL, standard length; PF, pectoral fin length; VF, ventral fin length; CF, caudal fin length; YP, yellow spot at pectoral fin base

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

beginning of breeding season. This result suggests that large size is more important than bright color in male-male competition for establishing territories in *H. melanurus*. By contrast, both body size and color are effective in male-male competition in another labrid, *Thalassoma bifasciatum* (Warner and Schultz 1992), in which male mating territories are established along the reef edge only temporarily during the spawning time of each day.

The male mating territories of *H. melanurus* were situated along the reef edge; larger males tended to have their territories offshore. Such sites seem to be preferred by females for spawning sites because of faster offshore dispersion of spawned eggs, as have been reported in other labrid species as well as other pelagic spawners (Johannes 1978; Warner 1984; Colin and Bell 1991). However, no significant correlation was detected in daily mating success between

years in each site, suggesting that females may have chosen not only spawning sites but also male morphological characteristics, as is the case in *T. bifasciatum* (Warner and Schultz 1992).

Morphological sexual difference was detected not only in body color but also in ventral fin length of *H. melanurus*. Males used the long ventral fins hanging down and vibrating during courtship. The effect of long ventral fins on male mating success has been reported in some other fishes (Karino 1997). However, the present results of multiple regression analysis indicated that the most important factor affecting male mating success was the yellow area at the pectoral fin base, although its residual in regression against body size showed no significant effect. The yellow spot at the pectoral fin base was the most conspicuous mark in the male coloration and seems to be most visible by females during male courtship of every kind, i.e., lateral display, circling, and head-up quivering.

Caudal fins of *H. melanurus* were pale in females, but became colorful in TP males and were used during male courtship, especially in head-up quivering. The presence of a large black spot submarginally in middle of the caudal fin may indicate that TP males are trying to show their total length honestly toward females during courtship. This possibility suggests that a longer caudal fin would be favored in sexual selection, as is known in some fish (e.g., swordtails) (Basolo 1998). However, caudal fins of TP males were proportionally shorter than those of females in *H. melanurus*. The proportion of caudal fin did not differ significantly between sTP and fTP males, and so the difference between IP and TP fish is probably not a result of sexual selection but seems to be a kind of allometry related to swimming efficiency.

Thus, the present study suggests that large body size is favored in male–male competition for establishing territories and that conspicuous body color of males may affect female mate choice in *H. melanurus*. As the yellow area at pectoral fin base was significantly correlated with body size, further studies to distinguish the effects of these two factors on female mate choice are in progress.

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