

## Population Structure, Reproductive Behavior and Protogynous Hermaphroditism in the Angelfish *Centropyge interruptus* at Miyake-jima, Japan

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**Abstract.** Population structure, reproductive behavior and protogynous sex inversion of the angelfish *Centropyge interruptus* was studied in the waters of Miyake-jima, Japan. A single male dominates a harem of from one to four females, with the size of the harem being dependent upon the nature of the substrate. Females are controlled by aggressive herding by the single male. Six action patterns associated with maintenance of dominance by the male and with courtship are described. These include (1) rushing, (2) circling, (3) soaring, (4) mutual soaring, (5) nuzzling, and (6) spawning. Spawning usually takes place almost every day at approximately sunset during the period from May to October.

Removal of the male resulted in sex change by the ranking female. Histological examination of the gonads confirmed field observations of protogynous sex inversion. The histology of the gonads of females, males and intermediate individuals is described.

Studies of reproductive strategies and population structures of pomacanthid fishes are scarce. Lobel (1975), Shen and Liu (1976) and Suzuki et al. (1977) have reported on various aspects of reproduction in the genera *Centropyge* and *Genicanthus*. Most of these studies have been based mainly on aquarium observations and do not cover all aspects of reproductive behavior. Population structure remains unknown for any of the Pomacanthidae (Ehrlich, 1975).

Since the taxonomic revision of the angelfishes by Fraser-Brunner (1933), considerable controversy has appeared in the literature concerning the classification of angelfishes. Yasuda and Tominaga (1970) united *Genicanthus* with *Holacanthus*; however, Randall (1975) preferred to follow Fraser-Brunner (1933) in separating them into two genera. *Centropyge interruptus* (Tanaka) was long erroneously identified as *C. fisheri* Snyder. *Holacanthus interruptus* was resurrected by Tominaga and Yasuda (1973); however, Randall and Wass (1974) placed the species in *Centropyge*, partly on the basis of feeding habits. We have followed Randall and Wass (1974) as a result of observations reported in this paper. Detailed studies of both the reproductive units and courtship behavioral patterns of

representatives of the various angelfish genera may eventually provide useful tools for classification of this difficult family.

The population structure and reproductive behavior of *Centropyge interruptus* were studied near the Tatsuo Tanaka Memorial Biological Station (TMBS) at Miyake-jima (34°05'N, 139°30'E), one of the Izu Islands, from early July, 1976, to the end of the spawning season in October, 1977. Histological studies of gonads were made at the Fishery Research Laboratory of Kyushu University. This paper reports the results of these investigations.

### Methods and materials

The social behavior of *Centropyge interruptus* was investigated daily from July to September, 1976~77. Observations were limited to 2~3 dives per week from September to June in both years. More than 300 hours of observations in nature were made using SCUBA. Social interactions were recorded while lying on the bottom within the territory of the social group under study. Individual fish were not marked, but could be identified by location, individual variations in color patterns, and individual behavior. Water temperatures were read from commercial diving gauges. Forty specimens ranging from 86 to

150 mm in standard length were taken with screen nets and multi-pronged spears. They were fixed in 10% formalin and measured. The gonads of all specimens were removed

and embedded in paraffin. They were cut at  $7\mu$  in cross section and stained with haematoxylin and eosin. Their structure and sex were examined under a microscope. All

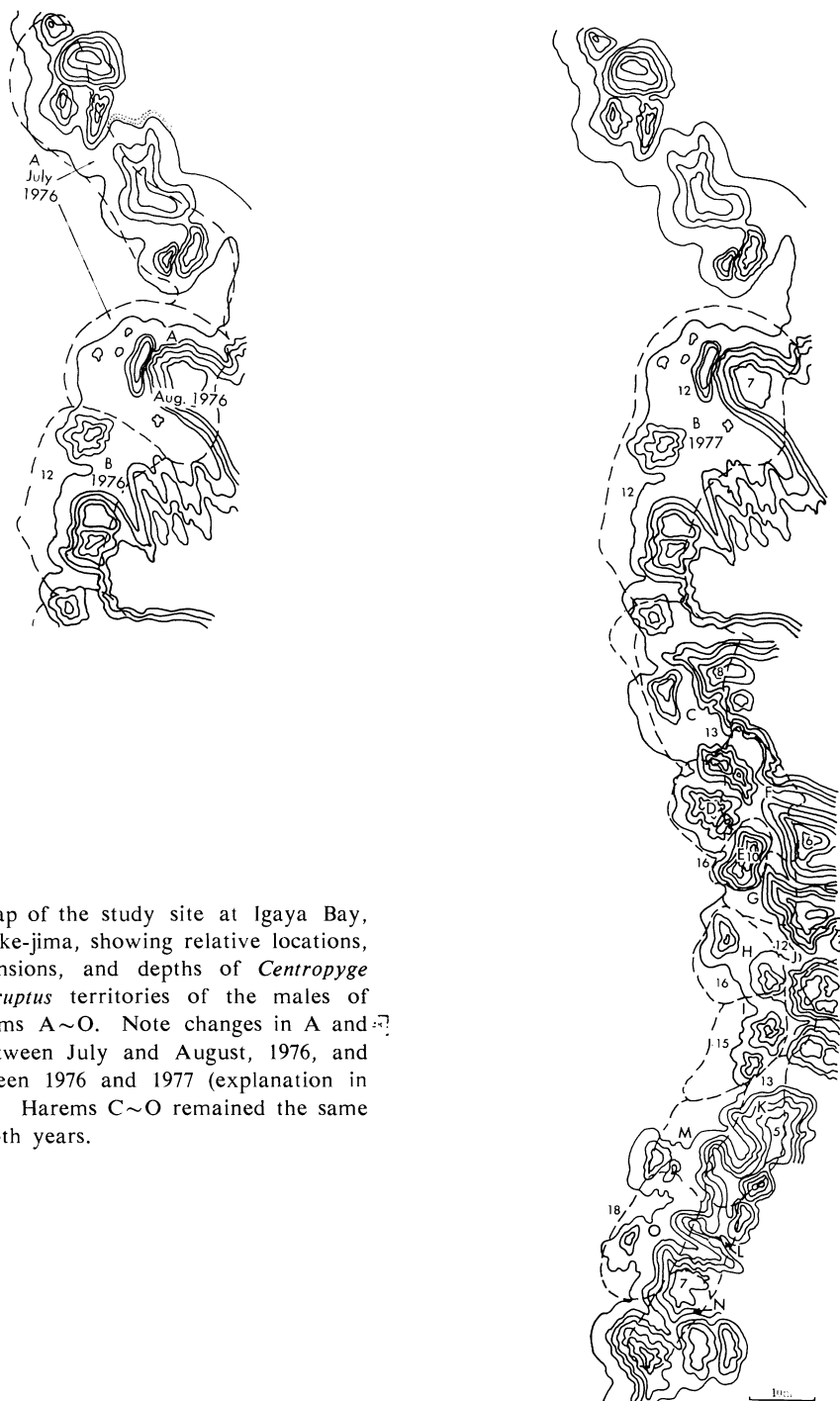


Fig. 1. Map of the study site at Igaya Bay, Miyake-jima, showing relative locations, dimensions, and depths of *Centropyge interruptus* territories of the males of Harems A~O. Note changes in A and B between July and August, 1976, and between 1976 and 1977 (explanation in text). Harems C~O remained the same in both years.

fish specimens are deposited at the Tanaka Memorial Biological Station (TMBS) and gonad specimens are at the Fishery Research Laboratory, Kyushu University.

### Results

*Centropyge interruptus* is a protogynous hermaphrodite that lives in a harem social structure with one dominant male and from 1 to 4 females per reproductive unit. The size of the harem and the intensity of territorial defense is directly influenced by the habitat.

**Habitat and population structure.** *Centropyge interruptus* occurs in a variety of habitats at Miyake-jima. All habitats are dominated by boulders and/or lava cliffs. Although there are often outcroppings of corals within a particular angelfish's territory, *C. interruptus*, unlike other members of the genus, is not a coral reef fish. In fact, in areas of extensive *Acropora* corals, the species is scarce or lacking altogether.

Three distinct habitat types were noted, i.e. (a) tunnels and arches, (b) volcanic cliffs, and (c) large boulders. The density of populations of *Centropyge interruptus* appears to be directly influenced by the nature of the habitat. Crevices, cracks, and holes along the ceiling and walls of tunnels and arches provide maximum shelter, and population densities are greatest at such locations. The main center of activity of one male and his harem of four females at the Abe Tunnel was restricted to an area of about 5 m × 3 m, directly below the ceiling of the tunnel, which consisted of a complicated network of crevices and cracks. This tunnel, a dark cavern 21 m × 5 m × 14 m and ranging in depth from 16 to 20 m, contained five harems totaling 22 fish (5 males, 17 females). Volcanic cliffs are also heavily eroded into crevices, holes, and caverns, and, like arches and tunnels, support dense populations of *C. interruptus*. Boulder habitats provide less cover and display the lowest population densities, with the reproductive unit usually a monogamous, but unstable pair.

Our chief study site was situated along an eroded volcanic cliff, running seaward for 190 m outside the fishing port of Igaya (Fig. 1). Depths at the foot of the cliff gradually

Table 1. Population structure of *Centropyge interruptus* at Igaya study site, Miyake-jima, Japan, 1976 and 1977.

Harem	1976		1977	
	Male	Female	Male	Female
A	1 (2)*	4	0	0
B	1	2	1	2**
C	1	3	1	3
D	1	1	1	2***
E	1	4	1	4(5)***
F	1	2	1	2
G	1	3	1	2
H	1	1	1	1
I	1	2	1	2
J	1	2	1	2
K	1	3	1	3
L	1	4	1	4
M	1	1	1	1
N	1	4	1	4
O	1	3	1	3
Total	15(16)	39	14	34

\* In July, 1976, two males shared this harem for several days. One was eventually driven away.

\*\* Former females at Harem A. See text for details.

\*\*\* Although male D usually mated with both females in his harem, the smaller female sometimes mated with male E.

increased from 9 to 18 m, with shallow points at the cliff-top varying considerably between 5 and 12 m (Fig. 1). Including in this area were a maximum of 15 harems in 1976 and 14 harems in 1977. The population structure within each harem is shown in Table 1, with territorial sizes and respective locations appearing in Fig. 1.

**Sexual dichromatism.** Previously undescribed sexual dichromatism in this species makes sexual discrimination obvious at distances up to 10 m or more, even by the human observer (Figs. 2, 5). The opercular region of females is primarily orange, flecked with small blue dots. The posterior soft dorsal and anal fins are dark blue. Males have heavy blue lines in the opercular area, making the head appear blue from a distance of several meters. The posterior soft dorsal and anal fins are streaked with broad, irregular bright blue bands on a black background,

easily visible from 10 m or more.

**Territoriality.** Males vigorously defend their territorial boundaries against neighboring males. Boundaries are easily defined by a particular boulder, crevice, or lava pinnacle, and are seldom violated. However, occasionally during courtship, a male will enter another male's territory to rush (Fig. 4A) a female from the neighboring harem. Such intrusions are met by aggressive chasing by the defending male. Visiting females from neighboring harems are rushed and circled (Fig. 4B) but are rarely driven from the territory.

Sex-distinguishing colors play an important role in courtship behavior; but, in addition, they appear to elicit aggression between neighboring males. Encounters between rival males at territorial borders often result in broadside posturing, head to tail, fins extended to clearly show sex-distinguishing color patterns.

Females respond somewhat agonistically toward outside females, but no more so than toward other female members of their own harem. Encounters with females from neighboring territories are relatively rare, and occur only when feeding brings them into close proximity to each other. Then the home female rushes and circles the visitor, invariably causing the outsider to flee to the safety of familiar shelter holes. This cannot be interpreted as territorial defense by the home female, due to the fact that identical behavior is displayed by dominant (larger) females against subdominant (smaller) females within the same harem.

Interspecific agonism seems to be directed only at the pomacentrid, *Eupomacentrus altus* Okada et Ikeda. Aggressive chasing of the damselfish by the male angelfish is common, and often interrupts spawning. Although the pomacentrid is forced to seek cover from attacks by male *C. interruptus*, the situation is often reversed when the damselfish chases a female member of the angelfish harem, especially if the female is small. Every *C. interruptus* male under observation shared part of his territory with at least one *E. altus*. Whether the aggressive nature of this relationship is related to food habits, competition for shelter, or both, is not yet known.

Fish species with colors resembling *C. interruptus* were often momentarily rushed. Such encounters apparently resulted from mistaken identity, suggested by the fact that the rushing male would suddenly stop several meters from the object of his attack and return to feeding. Presumably, the rushing male mistook the other blue species as a member of his harem. Rather than territorial defense, rushing of this nature is related to the establishment and maintenance of dominance, and will be discussed below. Species rushed in this manner included the damselfish *Pomacentrus coelestis* Jordan et Starks, adults of the wrasse *Coris gaimardi* (Quoy et Gaimard), and the angelfish *Centropyge bispinosus* (Günther).

With the exception of *C. bispinosus*, which appears a velvet blue at depths of 10 m or more, other congeners were tolerated. Various male *C. interruptus* in the study site shared their territories with *C. tibicen* (Cuvier), *C. ferrugatus* Randall et Burgess, and *C. vrolicki* (Bleeker).

**Establishment of dominance and sex inversion.** Observations in the field revealed the relationship between sex inversion and the social system of this species. On Oct. 10, 1976, aquarium hobbyists collected the male and one of four females from Harem A and both females from Harem B (Fig. 1, Table 1). By Oct. 17, the largest of the remaining three females at Harem A was aggressively rushing and circling the smaller females. Blue flecks on the operculum were changing into lines. By Oct. 22, the soft dorsal and anal fins were in typical male color pattern, and the opercular region was distinctly more blue. This fish was collected on Oct. 23, and the gonads were removed for histological examination. Twenty-four hours later, the largest of the remaining two females had begun to rush and circle the smaller female. However, by Oct. 29, the male from Harem B, who had lost his entire harem, had extended his territory to include most of A, establishing dominance over the remaining females in the A harem.

Histological examination indicated that the gonads of the dominant A female observed in male courtship behavior were transitional

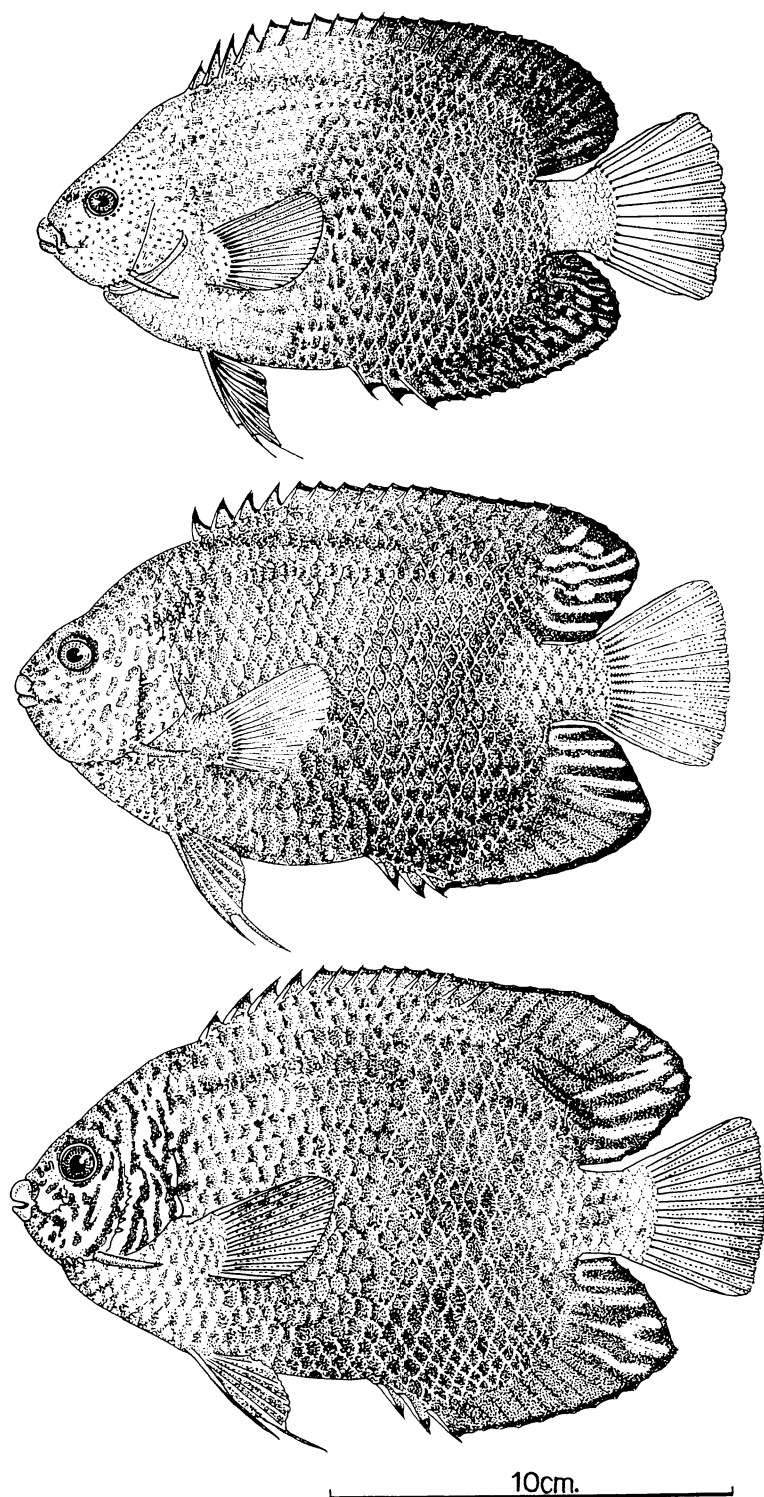


Fig. 2. Sexual dichromatism in *Centropyge interruptus*. Top: Functional female. Center: Transitional male. Bottom: Functional male.

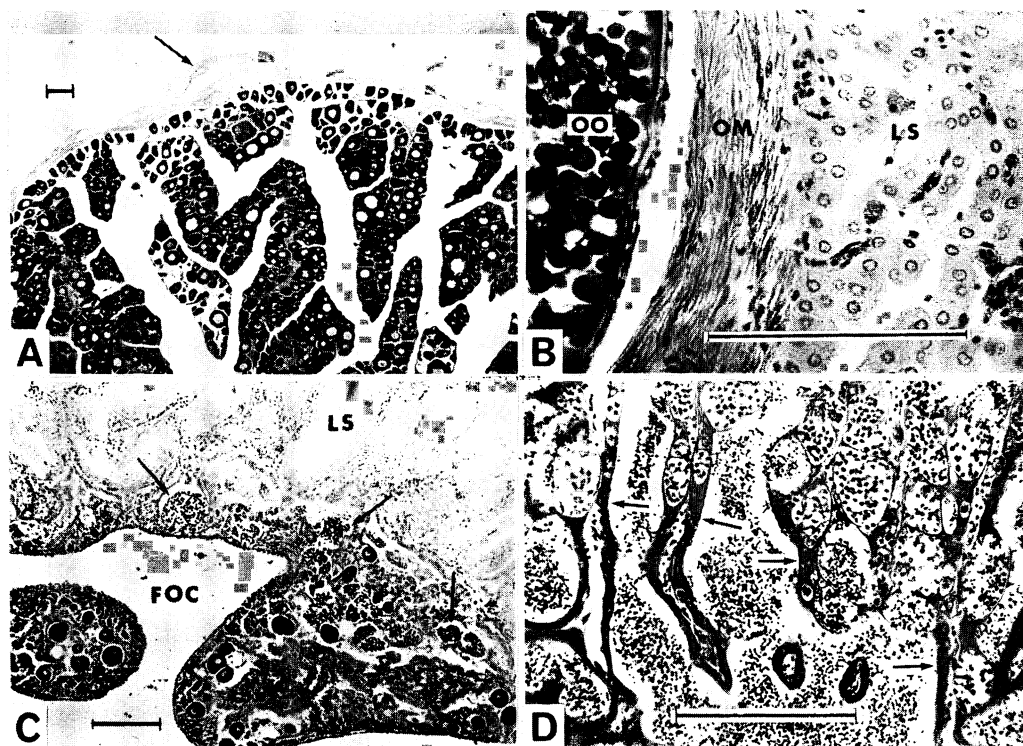


Fig. 3. Photomicrographs of the gonads of *Centropyge interruptus*. Scales show 100 $\mu$ . A: Ovary (TMBS 770509-10). Arrow shows the thickened part of the ovarian membrane. B: Higher magnification of a thickened part of ovarian membrane (TMBS 761016-2). OO, oocyte; OM, ovarian membrane; LS, labyrinth-like structure. C: Ambosexual gonad (TMBS 761023-1). Notice spermatogenic cells (arrows), scattered oocytes and the large area of the labyrinth-like structure (LS). FOC, former ovarian cavity. D: Arrows showing the occurrence of the same cells as those of the labyrinth-like structure in a mature testis (TMBS 770706-1).

(Fig. 3C). In this case, the breeding season had been over for about three weeks.

Two fish that had formerly been females were collected on July 6, 1977, in the peak of the breeding season. One of them, a male (TMBS 770706-1, Table 2, Fig. 3D), had been the ranking female in the harem of the male, TMBS 770528-2 (Table 2) that had been collected 39 days previously. Similarly, TMBS 770706-2 (Table 2) was found to be a perfect male only 20 days after the death of the former male, a large fish of 145~150 mm in standard length that was speared and lost, badly wounded, never to be seen again.

Another possible example of sex-inversion caused by collection of the dominant male is TMBS 770509-9 (Table 2), a small male of 112 mm in standard length, collected in May, 1977, from the same location that four fish

(TMBS 760926-9~760926-12) were taken the previous September.

That sex change is socially controlled, with the highest ranking fish changing from a functional female to a male is obvious from the above observations. Dominance competition continues within the harem throughout the year, especially if the sizes of the male and the ranking female are similar. Harem E displayed such a situation, with agonistic encounters, including aggressive chasing by the male, often delaying spawning by the ranking female until several minutes after the other females had spawned.

After the breeding season, open wounds can often be seen directly below the dorsal fin of both the male and the ranking female, indicating a continuing struggle for dominance. Fighting behavior was only rarely observed,

Table 2. Body length and sex of specimens of *C. interruptus* arranged in size order. The sex of all specimens were examined histologically. ♀, female; F/M, ambosexual (defined by Reinboth, 1970); ♂, male.

Specimen No.		S. L. in mm	Sex	Specimen No.		S. L. in mm	Sex
1	770509-17	86	♀	21	770509-13	115	♀
2	760926-11	87	♀	22	770509- 4	118	♀
3	770509- 6	87	♀	23	770509-11	120	♂
4	770509-15	92	♀	24	770312- 2	123	♀
5	760926-12	94	♀	25	770509- 2	126	♀
6	770509-14	99	♀	26	770509- 3	128	♂
7	760926-10	100	♀	27	770528- 1	129	♀
8	770728- 1	100	♀	28	770529- 2	130	♀
9	770509-16	104	♀	29	770706- 2	131	♂
10	770716- 4	104	♀	30	760926- 9	132	♂
11	770509-12	107	♀	31	770509- 8	132	♂
12	761023- 1	108	F/M	32	770616- 1	132	♀
13	770509- 1	109	♀	33	770716- 2	132	♂
14	770509- 7	109	♀	34	770529- 4	133	♀
15	770511- 1	109	♀	35	770312- 1	135	♂
16	770509- 5	110	♀	36	770716- 3	135	♂
17	770509-10	111	♀	37	770706- 1	139	♂
18	770509- 9	112	♂	38	770528- 2	141	♂
19	770529- 3	113	♀	39	770529- 1	148	♂
20	761016- 2	115	♀	40	770716- 1	150	♂

and although biting below the dorsal fin was noted, it is not known whether such wounds were inflicted by biting or by use of the opercular spines.

An unusual situation existed in Harem A in July, 1976 (Fig. 1). Two males shared the same harem, although usually only the larger of the two was able to spawn. Spawning by both males on the same evening was observed only once, and frequently one or the other was interrupted during courtship display by the aggressive chasing of his rival. It is possible that collecting by hobbyists at the shallow end of the territory, which shrunk greatly after the disappearance of the smaller male, accounted for this rare situation. The smaller fish disappeared after a few days.

**Histology.** The relationship between body length and sex in 40 specimens of *C. interruptus* is further evidence of sex inversion in this species (Table 2). Smaller fish were all females with the largest measuring 133 mm in standard length. On the other hand,

males were found only in larger size ranges, the smallest measuring 112 mm in standard length. Histological investigations of the gonads of these specimens indicated sex inversion in this species. The ovarian membrane of *C. interruptus* is thickened in several places and these thick parts have an inner cavity (Fig. 3A). In this cavity, cells abound in the cytoplasm forming a labyrinth-like structure (Fig. 3B). Spermatogenic cells are usually not seen when the ovarian part is functional. However, upon sex inversion, the number of cells in this structure increases and the spermatogenic cells appear among these tissues (Fig. 3C). The cells in the labyrinth-like structure were observed even in a mature testis as walls of vasa deferentia and also as supporting tissues for testicular lobules (Fig. 3D). The above mentioned histological results show that individuals of *C. interruptus* are protogynous hermaphrodites, in which the ovarian part matures initially, with undeveloped testicular parts on the

periphery, and when the ovarian parts disappear, the testicular parts begin to mature.

**Maintenance of dominance and courtship behavior.** As noted above, females are not bound by territorial borders, although familiarity with the home territory tends to limit their centers of activity. During the reproductive season, females may sometimes be attracted into neighboring territories by the courtship of the neighboring male. For example, in 1977, the No. 2 female from Harem D occasionally moved into Harem E to spawn with the E male (Table 1). Therefore, in addition to his own survival, reproductive success of a particular male is dependent to a great extent upon his ability to maintain dominance over his females and to keep them within his territory.

Six easily distinguishable action patterns are involved in the spawning sequence: (a) rushing, (b) circling, (c) soaring, (d) mutual soaring, (e) nuzzling, and (f) spawning (Figs. 4, 5). The first two of these, i.e., rushing and circling, are aggressive in nature, and therefore cannot be considered as true "courtship behavior". However, because these actions maintain the male's dominance over his harem in addition to controlling the centers of activity of his females, they are essential prerequisites to courtship and must be included in the spawning sequence.

Although both rushing and circling have been occasionally observed from morning to mid-day, normally the male spends most of his time early in the day feeding with his females on algae from the volcanic boulders at the base of the cliff or moving 3~4 m into the water column with his harem to join heterotypic aggregates that include *Chromis flavomaculata* Kamohara, *C. weberi* Fowler, *C. miyakeensis* Moyer et Ida, and *Franzia squamipinnis* (Peters). At such times, the angelfish feed on the feces of the numerous damselfishes and anthiids.

Rushing and circling of females by the male increases in frequency and intensity in the early afternoon, reaching a peak in most harems 2.5 hrs~30 min before sunset. During this time, the male stops feeding and swims rather rapidly around the borders of his territory, rushing each female as he sees her,

circling her once, and then moving rapidly on. Rushing (Fig. 4A) seems to be elicited by the blue and orange coloring of the female (see "Territoriality"). When the patrolling male sees a female, he rushes directly at her, swimming at a high speed. They circle each other, head-to-tail, abdomens facing each other (Circling: Fig. 4B). The male then swims rapidly away in search of another female, while the female continues to feed.

Actual courtship begins in most harems about 30 min before sunset with "soaring" by the male (Fig. 4C, 5A). Soaring continues until about 10 min before sunset, when mutual soaring, nuzzling, and spawning follow in sequence.

During the soaring phase, the male extends all of his fins, leans  $45^{\circ}$ ~ $90^{\circ}$  to one side, fully displaying his sex-identifying fin and opercular markings. The soft dorsal and anal fin color pattern is especially clear at such times (Fig. 5A). The male remains motionless during soaring, except for occasional stabilizing movements of his pectoral and caudal fins. The behavior of specific male is consistent. Some males, e.g. C and G, soar very high in the water column, often several meters above their mates. Others, such as D, consistently soar within 1~2 m of the substrate, directly above the female. After soaring for a few minutes over a particular female, the male may depart to search for another.

In the average harem, spawning activities start about 10 min before sunset when females begin to seek out their male, who in turn may be searching for a receptive female. Attracted by the conspicuous soaring by the male, a female approaches him and soars in front or beside him (Fig. 4D, "mutual soaring"). This elicits nuzzling (Figs. 4E, 5B) by the male, who attempts to move under his mate and place his snout against her vent. Usually nuzzling does not immediately follow mutual soaring, but is preceded often by several minutes of "positioning". Females are obviously disturbed by the body contact associated with nuzzling, and frequently move away, again and again. Finally the pair reaches the nuzzling position, which may be held from 2 to 18 sec. At a particular mo-



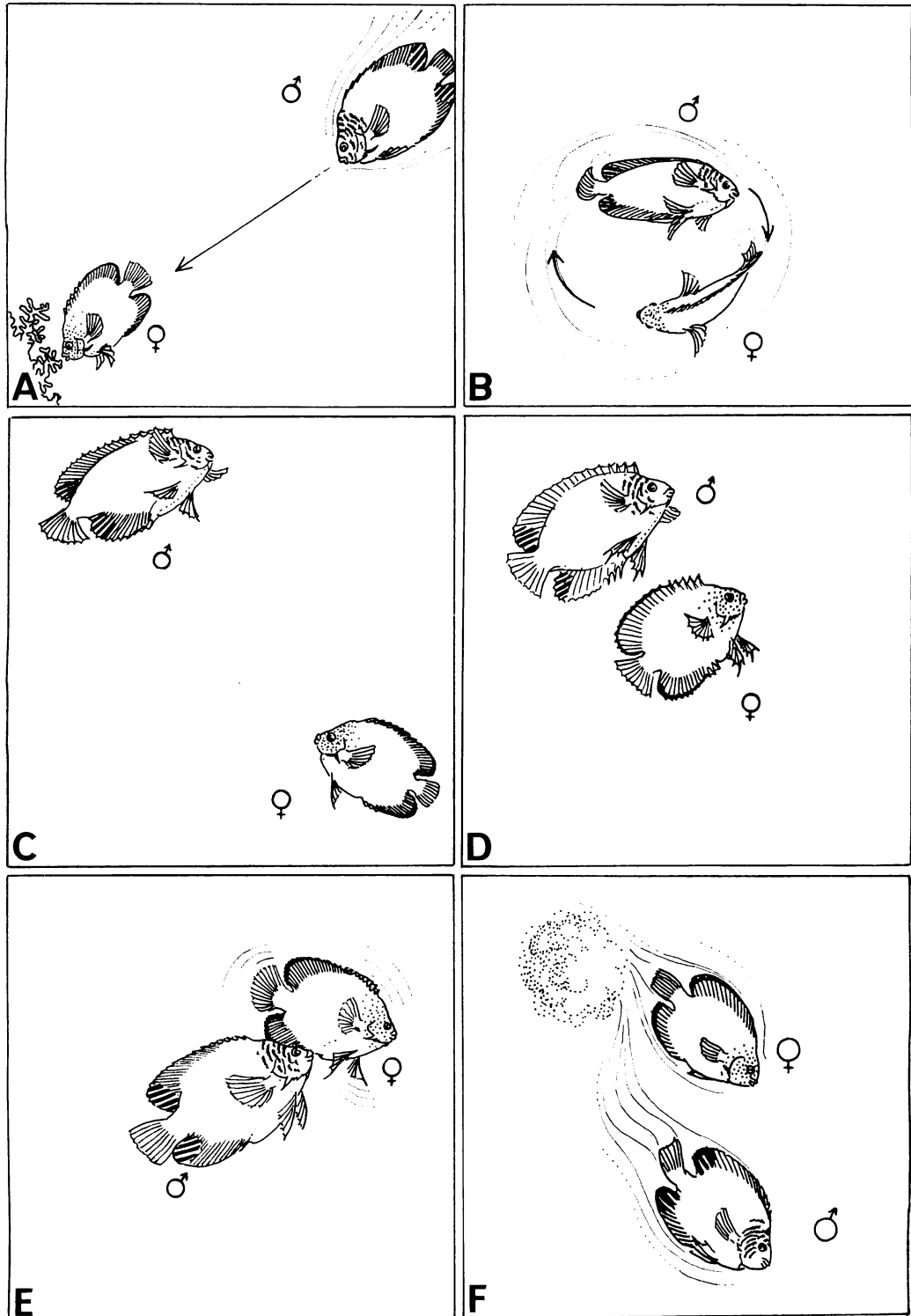


Fig. 4. Action patterns of *Centropyge interruptus* during the spawning sequence. A: Rushing. B: Circling. C: Soaring. D: Mutual soaring. E: Nuzzling. F: Spawning.

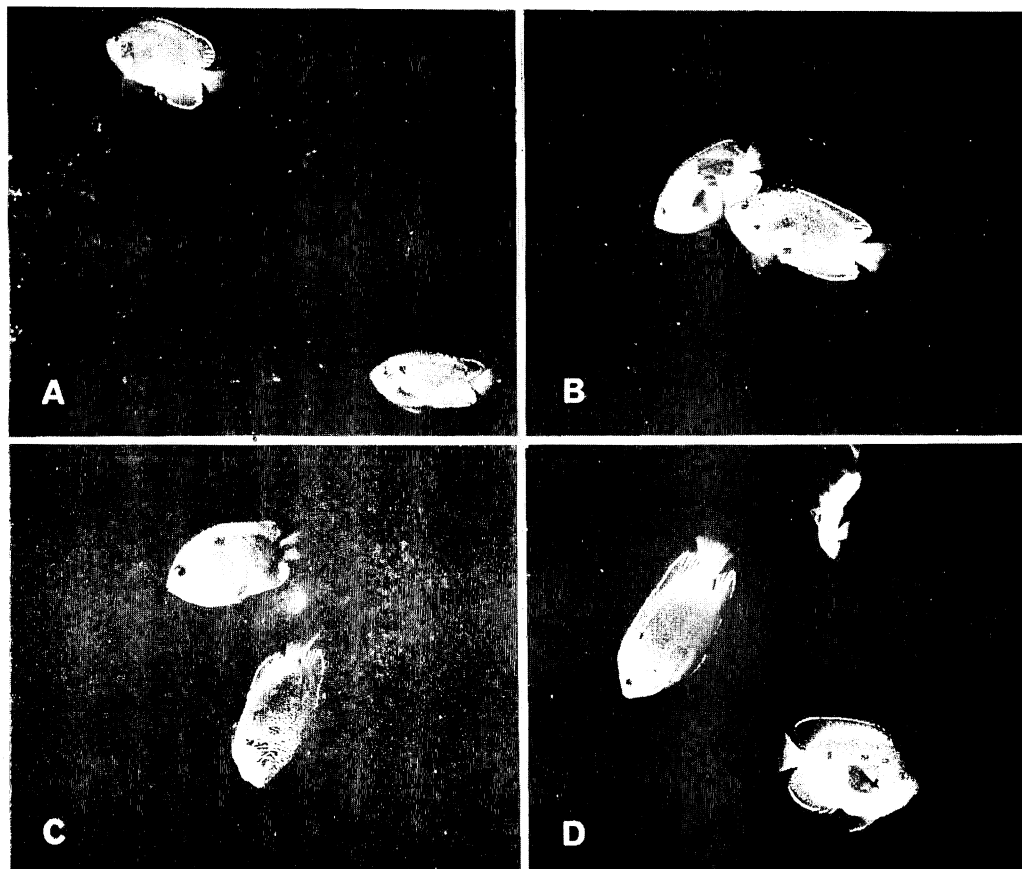


Fig. 5. Various stages of the spawning sequence of *Centropyge interruptus*. A: Male at Harem O soaring above a female. B: Male at Harem E (below) nuzzling just prior to spawning. C: Spawning. Note cloud of gametes. D: The E male spawns with one female while the next female soars. Note sex distinguishing color patterns in each photo.

ment, the male rapidly opens and closes his mouth, accompanied by a quick fluttering of the pectoral fins. Spawning follows quickly. The male dashes toward the substrate immediately after release of gametes, followed closely by the female (Figs. 4F, 5C, 5D). A short "after-chase" follows, with the male swimming in rapid pursuit of the female, occasionally soaring momentarily again.

**Spawning time and sites.** Females do not spawn in a fixed order, dependent upon dominance. The highest ranking female may or may not spawn first, dependent upon chance locations of individual harem members as the short spawning period begins. Frequently dominance competition between the male and the ranking female may delay their spawning until after lower ranking

females have spawned.

Of 175 spawnings observed, most occurred between 10 min before and 5 min after sunset on clear evenings with good visibility. On dark, overcast or rainy evenings, or when water visibility was poor, spawning times were much earlier, indicating a definite relationship between spawning and light intensity (Table 3). Individual harems were consistent in their spawning times (Table 3).

Spawnings usually occurred in rapid succession within a harem. For example, on July 13, 1977, all four Harem E females spawned with their male within 8 min. The following evening, the four E females and the second-ranking D female all spawned with the E male within six minutes. On July 15, the same five females spawned with the

Table 3. Spawning times in relation to time of sunset.

Harem	No. of spawnings observed	Range of times before (-) and after (+) sunset	Average min/sec before sunset	No. spawnings before sunset	No. spawnings after sunset
(Clear sky: water visibility $\geq 30$ m)					
B	11	-63/-38	53 min	11 (100%)	0 (0%)
E	50	- 6/+ 8	0 min, 0.6 sec	22 (44%)	28 (56%)
F	11	-12/+ 6	1 min, 2 sec	9 (82%)	2 (18%)
G	12	-11/+ 3	2 min, 4 sec	9 (75%)	3 (25%)
(Heavy cloud cover; rain; or water visibility $\leq 15$ m)					
E	23	-43/-28	34 min	23 (100%)	0 (0%)
F	3	-38/-33	35 min	3 (100%)	0 (0%)

E male over a period of eight minutes. Other harems behaved similarly.

Like spawning times, spawning sites were also consistent. For example, the A harem usually spawned about 20 m away from the cliff and high in the water column. The C, D, and I harems also moved 10~20 m from the cliff, but spawned fairly close to the substrate. C and G spawned high in the water column and close to the cliff, while E spawned within 1~2 m of the top of the lava pinnacle that made up that territory (Fig. 1).

**Frequency of spawning.** Although courtship began with intensive rushing, circling, and soaring by the male when water temperatures reached 21°C in late April, 1977, no spawning was observed until May 28, when waters rose to 22°C. Except for April 24, when the temperature reached 22°C, temperatures of 20°C or less inhibited courtship until May 21, when soaring was observed again at 21°C. A week of varying temperatures in late July, 1977, indicated that spawning was inhibited when temperatures plunged below 22°C and that no courtship occurred in waters colder than 21°C. Spawning ended in the first week of October in both 1976 and 1977, although soaring by males continued for another two weeks. Water temperatures did not drop below 22°C until December in both seasons.

Water clarity seems to be crucial to maximum spawning. All fish, male and females, remain close to shelter in cloudy water, and quickly flee for cover at the approach of harmless fishes, such as large schools of the surgeonfishes *Naso lopezi* Herre and *Prionurus*

*microlepidotus* Lacepède, both species being ignored under normal circumstances. Spawning is hindered under such conditions for two reasons: (1) Since the male remains close to the substrate, his soaring is not clearly visible to the females in his harem; and, (2) females are easily disturbed during the nuzzling stage, even under the best of conditions. The added caution caused by cloudy water means that frequently spawnings are interrupted in the nuzzling stage by the close approach of harmless schooling fishes. Darkness comes rapidly on such occasions, and females will retreat to cover for the night before spawning.

The possibility was considered that females, inhibited from spawning due to interruptions by potential predators, might spawn at the following dawn. On two occasions, females from Harem E were purposely frightened and prevented from spawning during the usual evening hour. Observations beginning before sunrise the following morning revealed that, although *Centropyge interruptus* is one of the last diurnal fish to take cover in the evening, its morning activities begin relatively late, i.e. after *Franzia squamipinnis* and various *Chromis* spp., and consist of individual feeding with no social interaction.

The moon is a factor in the spawning of many fishes (Allen, 1972; Moyer, 1975; and others). Spawning of all females within individual harems and the total number of spawnings observed were analysed in relation to moon phases. Our results showed that spawning occurs in equal intensities at all phases of the moon.

## Discussion

**Habitat and population density.** The importance of shelter and an intimate knowledge of the bottom topography within their territories has been stressed for members of the genus *Centropyge* (Ehrlich, 1975). Our observations suggest that the more fractured and eroded the substrate, the greater the density of populations of *C. interruptus*.

Food does not seem to be a major limiting factor in population densities. There appears to be sufficient algae to provide for crowded populations. The fact that *C. interruptus* territories are frequently inhabited by grazing *Eupomacentrus altus* and often by other species of *Centropyge* in addition to the *C. interruptus* harem is evidence that there is ample food for dense populations. Lobel's (1975) observations of *Centropyge potteri* (Jordan et Metz) are similar with respect to sufficiency of food supply. Fecal materials from plankton-eating pomacentrids and anthiids seem to provide an important percentage of the diet of *C. interruptus*, and may contribute in a minor way to increasing population densities along cliffs where upwelling currents attract enormous heterotypic aggregates of such plankton-feeders. However, our observations indicate that relative abundance of shelter holes seems to be more crucial to population densities in this species than food supply.

**Dominance, sex inversion and territoriality.** Territory itself seems to be entirely the result of a male's attempt to maintain dominance over, and therefore spawning rights with the females in his harem. By rushing and circling each of his females from the perimeter of his territory, he tends to herd them back into the center of the territory. This both prevents females from moving within visual range of the neighboring male's courtship display and forces all members of his harem into a relatively small area, allowing for a better chance of all females and the single male finding each other during the short spawning period.

The selective advantages of such a reproductive strategy can be explained as follows: An individual *C. interruptus* that is able to

dominate all other members of its species within its range of activity, changes from a female that spawns only once in a given evening into a male that spawns with each of his females. By changing sex, it has demonstrated a level of genetic fitness above the average member of the population, because it is contributing more to the gene pool of the population than are any of the fish it dominates (see Emlin and Oring, 1977, for definition of "fitness"). If this fish can dominate and therefore spawn with more females than can neighboring males, it has demonstrated an even higher level of fitness by contributing more than its rivals to the total gene pool. In order to maintain dominance and therefore spawning rights over the females in its range of activities, it patrols the perimeter of this area, keeping out neighboring males, permitting entrance by any neighboring females, and forcing its own females to remain within its center of activities, which therefore become, by definition, a territory. Though differing in some respects, e.g. synchrony of female spawnings, the harem social structure of *C. interruptus* serves as an example in a marine environment of "female defense polygyny" as defined by Emlen and Oring (1977), with the availability of adequate shelter being an unevenly distributed critical resource that provides the "environmental potential for polygamy".

We have observed similar harem social structures in *Centropyge vrolicki*, *C. heraldi*, *C. flavissimus*, *C. ferrugatus*, *C. sp.*, and *C. tibicen*, although we as yet have no histological evidence of sex inversion (Table 4). A nearly identical reproductive system has been described by Robertson and Choat (1974) in the labrid fish *Labroides dimidiatus* (Valeniennes). In this species, harems are established and a strict hierarchy is maintained based on the dominance of a single male over a group of females. Removal of the dominant male results in sex change by the ranking female.

## Population structure, reproductive behavior, and the problem of phylogenetic relationships.

Fricke (1973, 1976) suggests monogamy for most Chaetodontidae, within which he includes the pomacanthids. In his only direct reference to population structure of a po-

Table 4. Harem reproductive units in six species of the genus *Centropyge*.

Species	Location	Composition of reproductive unit	
		Males	Females
<i>Centropyge vrolicki</i>	Miyake-jima	1	3
" "	Miyake-jima	1	2
" "	Miyake-jima	1	2
" "	Okinawa	1	3
" "	Kuroshima, Yaeyama I.	1	3
<i>C. ferrugatus</i>	Kuroshima, Yaeyama I.	1	2
<i>C. heraldi</i>	Guam	1	3
" "	Guam	1	3
" "	Guam	1	2
" "	Guam	1	2
<i>C. flavissimus</i>	Guam	1	2
<i>C. tibicen</i>	Miyake-jima	1	2
<i>C. sp.*</i>	Guam	1	4
" "	Guam	1	3
" "	Guam	1	3
" "	Guam	1	3
" "	Guam	1	2
" "	Guam	1	2

\* The identity of this species is currently under investigation by Dr. John E. Randall and Dr. Fujio Yasuda.

macanthid species, he reports that the Caribbean angelfish *Pomacanthus paru* (Bloch) usually lives in pairs (Fricke, 1976). Our observations of *Pomacanthus imperator* (Bloch) in the Bonin Islands and *P. semicirculatus* (Cuvier) in the Yaeyama Islands are in agreement with Fricke and suggest that the reproductive unit within the large angelfishes of the genus *Pomacanthus* may be monogamous pairs. That harems do in fact occur from time to time cannot be ruled out at this time. Yasuda (personal communication) reports a harem-like social structure in the genus *Chaetodontoplus*.

Lobel (1975 and in press) reports that *Centropyge potteri* lives in pairs or in small groups in Hawaiian waters, and that the population structure appears to be related to the habitat. Although he refers to "...one or two males and several females" (Lobel, 1975) and to "harem spawnings" (Lobel, in press), the nature of *C. potteri*'s social structure remains unclear. As noted above, we have observed harems dominated by single males in *Centropyge vrolicki*, *C. ferrugatus*, *C. heraldi*, *C. flavissimus*, *C. sp.*, and *C. tibicen* (Table 4). Shepard (person communi-

cation) reports a harem social structure in *Holacanthus trimaculatus* Lacepède at Guam.

Randall (1975) suggested sex inversion within the genus *Genicanthus*, and this was later demonstrated in aquarium studies by Shen and Liu (1976) for *Genicanthus semifasciatus* (Kamohara) and by Suzuki et al. (1977 and in press) for *G. lamarck* (Lacepède). Our limited field observations of *G. semifasciatus* in the Yaeyama Islands and at Miyake-jima suggest a harem social structure similar to *C. interruptus*.

Knowledge of sequential behavioral patterns during courtship and spawning among the pomacanthids awaits further research; however, there is some evidence to support a high degree of similarity between species within the family. In addition to our observations of *C. interruptus*, we have observed rushing and circling in *C. vrolicki*, *C. ferrugatus*, *C. tibicen*, *C. sp.*, and *Pygoplites diacanthus* (Boddaert).

A photograph appearing both in Hiyama and Yasuda (1971) and in Burgess and Axelrod (1972) shows a male *Genicanthus lamarck* displaying above his mate in a posture identical to soaring in *Centropyge interruptus*,

and Randall (personal communication) reports a similar display by *G. caudovittatus* (Günther) in the Red Sea. A posture apparently identical to nuzzling in *C. interruptus* has been described for *Centropyge bispinosus*, *C. fisheri*, and *C. flavissimus* by Lobel (1975 and in press), by Hioki (personal communication) for *Genicanthus lamarck*, and by Suzuki, et al. (in press) for *G. semifasciatus*.

Such limited data make comparative analysis of behavioral patterns impossible. However, some observations seem significant. *Centropyge interruptus*, *C. ferrugatus*, and *C. sp.* all display identical sex-distinguishing blue and black stripes on the soft dorsal and anal fins, unlike sex-identifying features of other angel-fishes, suggesting close relationships between these species (personal observation). Sexual dichromatism was previously known in pomacanthids only in the genus *Genicanthus* (Randall, 1975), and differs in pattern from the *Centropyge* spp. mentioned above. Unfortunately, behavioral studies are still unavailable for most angelfishes.

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- 三宅島におけるレンテンヤッコの社会構造, 産卵行動と雌性先熟性転換
- Jack T. Moyer・中園明信
- 東京都下三宅島において, レンテンヤッコの社会構造, 産卵行動を潜水観察するとともに, 性転換について調べた. 本種の雄は, 普通雌数尾よりなるハレムを持っているが, 雌の尾数は生息基盤の性質によって異なり, 1~5 尾の範囲にあった. 本種の産卵は, 5月~10 月にかけてほぼ毎日日没前後に行なわれたが, 雄の雌に対する優位性の維持と求婚に関して (1) rushing, (2) circling, (3) soaring, (4) mutual soaring, (5) nuzzling, (6) spawning の 6 型の行動型を認めた.
- 本種のハレムより雄を取り除くと, 次の順位にある雌が性転換して雄へと変った. さらに, 組織学的に本種の雌性先熟性転換を確認するとともに, 雌, 雄および移行型の個体の生殖腺構造を記載した.
- (Moyer: 100-12 東京都三宅島阿古 富賀農園 田中達男記念生物実験所; 中園: 811-33 福岡県宗像郡津屋崎町 九州大学農学部附属水産実験所)