

Social and Reproductive Behavior of *Chaetodontoplus mesoleucus* (Pomacanthidae) at Bantayan Island, Philippines, with Notes on Pomacanthid Relationships

Jack T. Moyer

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Abstract *Chaetodontoplus mesoleucus* occurs at Bantayan Island in a habitat of small patches of mixed scleractinian and alcyonacean corals of low diversity and simple structure. Male-female pairs were predominant, and the sex-ratio showed only a slight skew towards females. However, the presence of single male, two-female social groups demonstrates that the species is polygamous. Small size of social groups is attributed to a preference for a habitat lacking structural complexity. The species did not occur on complex coral reefs. Social and spawning behavior are nearly identical to that of most pomacanthids for which data are available, and although sex-change was not demonstrated, size-related dominance hierarchies and close phylogenetic relationships to sex-changing pomacanthids suggest protogynous hermaphroditism in this species. Behaviorally, *C. mesoleucus* appears quite similar to a large group of species proposed herein to represent a generalized pomacanthid behavioral type. Divergences from this generalized type by members of *Genicanthus*, eastern Pacific *Holacanthus*, and western Atlantic *Pomacanthus* are discussed. Evidence is given to suggest the phylogenetic derivation of the subgenus *Centropyge* (genus *Centropyge*) from an ancestor of the subgenus *Xiphipops* type. Color dimorphism and "rendezvous sites" are briefly discussed.

Marine angelfishes (Pomacanthidae) are among the most colorful and popular fishes in the international marine aquarium trade, yet as late as 1975 virtually nothing was known about their social organization and reproductive behavior (Burgess and Axelrod, 1972; Ehrlich, 1975). The past decade has brought a wealth of data on pomacanthid social and reproductive biology, and by 1987 information had been published on 30 pomacanthid species representing five genera (Table 2) (reviewed by Moyer, 1987). Social organization in the remaining genera in the family, *Chaetodontoplus* and *Apolemichthys*, is known only from passing references (e.g., Moyer and Nakazono, 1978) and spawning behavior remains unreported.

Protogynous hermaphroditism has been reported in three genera: *Centropyge*, *Genicanthus*, and *Holacanthus* (Table 2). Close similarities in documented pomacanthid reproductive biology and in phylogenetic relationships have led some authors to assume protogynous hermaphroditism to be universal in the family (e.g., Neudecker and Lobel, 1982). Although increasing knowledge of the reproductive ecology of a variety of pomacanthid species seems to support this assumption

(reviewed by Moyer, 1987), it is essential to examine representatives from *Chaetodontoplus* and *Apolemichthys* before serious attempts can be made to unravel the complex interrelationships within the family and thus better comprehend the evolutionary biology of pomacanthid reproduction. In this paper I provide information on social organization and spawning behavior of *Chaetodontoplus mesoleucus* (Bloch) as a preliminary attempt to fill in the remaining gaps. This is followed by a discussion of pomacanthid relationships.

Methods and materials

The study site. The site selected for this study was located near Suwangan Point, at the southwestern tip of Bantayan Island (11°09'N, 123°44'E), in the central Visayan Islands, Philippines. The substratum at the study site consisted of a gradual sand slope which extended from the shore for about 1,000 m southward to a depth of about 40 m before dropping in a steep slope to depths over 100 m. About 400 m of this slope are exposed to the atmosphere during spring neap tides. Areas of coral rubble and pavement and

patches of living scleractinian and alcyonacean corals are scattered sporadically over the sand subtidally, however the paucity of coral reef fishes was conspicuous.

Methods of observations. Observations were made by snorkeling at depths of 2–10 m (approximate neap tide depths). Approximately 1,500 m of slope at such depths were surveyed, from Suwangan Point eastward. Due to logistical problems, daily observations were impossible, however, attempts were made to survey study populations at different times of day during a variety of lunar and tidal conditions during the period from November 1987 to January 1988. Emphasis was placed on the crepuscular spawning time. Logistics also prohibited the collection of gonads for histological examination. Consequently, the information reported herein must be considered as preliminary. Scientific nomenclature follows Allen (1979).

Results

Social organization, sex ratio, and territoriality.

The dominant pomacanthid species at the study site was *Chaetodontoplus mesoleucus*. Nearly every relatively diverse patch of living corals supported a small population of this species. In contrast, only one individual of the normally ubiquitous pomacanthid genus *Centropyge* was

observed in 28 h of observations, a single *C. vrolicki*.

Social groups consisted of a single territorial male and one to two females, with the sex ratio only slightly skewed towards females (15 males, 20 females) (Table 1). Of fifteen social groups under observation, ten were composed of male/female pairs (Table 1). Multifemale groups were found only in relatively large patches of corals (Table 1: Groups 2, 5, 6), in situations where two small coral patches were in close proximity (Group 7), or when large and small coral patches were in close proximity (Group 12). In all social groups the single male was larger than any females in the group. A size difference between females in two-female groups was also detected in all examples.

The sizes of male territories were influenced by the amount of coral substratum available. Male No. 12 (Table 1) defended a particularly large territory that encompassed two patches of corals and an isolated boulder where spawnings were initiated. This territory covered an area of approximately 30 m × 25 m. In contrast, the territory of Male No. 4 was limited to one small coral patch of about 6 m × 10 m (Table 1).

A major effort was made to determine whether or not "bachelor males" moved between social groups or remained cryptically within or near particular groups (see Moyer and Zaiser, 1984; Moyer, 1987). No bachelor males were identified; however, on one occasion Male No. 12 was observed invading the territory of Male No. 13.

Aggressive interactions. Male-male aggression: Intraspecific aggression between males of *C. mesoleucus* was minimal. Male No. 5 chased Male No. 6 from the periphery of his territory on two occasions. In both cases, the smaller Male No. 6 fled immediately to the interior of his territory and was not pursued. On one occasion, just prior to the crepuscular spawning time, Male No. 12 invaded about 5 m into the territory of Male No. 13, where he encountered the home male. A long, broadside chase followed. The two individuals, with Male No. 13 about a head-length in front, raced nearly side-by-side, two meters apart, dorsal, anal, and pelvic fins extended, for about 30 m over bare sand and away from their respective territories. Simultaneously, both fish abandoned the chase and swam rapidly back to their territories.

Table 1. Social group composition of *Chaetodontoplus mesoleucus* at Bantayan Island, Philippines.

Group	Males	Females	Approx. size of male territories
1	1	1	10 m × 8 m
2	1	2	15 m × 25 m
3	1	1	12 m × 8 m
4	1	1	6 m × 10 m
5	1	2	20 m × 25 m
6	1	2	18 m × 25 m
7	1	2	20 m × 20 m
8	1	1	10 m × 12 m
9	1	1	11 m × 15 m
10	1	1	9 m × 14 m
11	1	1	8 m × 10 m
12	1	2	30 m × 25 m
13	1	1	9 m × 12 m
14	1	1	10 m × 14 m
15	1	1	12 m × 12 m

Female-female aggression: Aggressive interactions between females were even less common than between males. My only observation of such competition was on 4 February, when the largest female in the two female Group 12 rushed and circled (see "Motor Patterns," below) the smaller female near the spawning rock shortly after sunset. The smaller female fled, but soon returned to spawn.

Male-female aggression: Males invariably rushed and circled females when their paths crossed while foraging throughout the day. On three occasions females fled such encounters and were chased by males. Aggression was never observed during intervals when the male and female foraged together in midday. However, rushing and circling of females by males commenced and increased dramatically in frequency as sunset neared (see "Motor Patterns," below).

Interspecific aggression: Males of *C. mesoleucus* were frequently observed chasing the following four species of reef fishes during the crepuscular spawning period: *Choerodon anchorago* (Labridae), *Halichoeres trimaculatus* (Labridae), *Abudefduf vaigiensis* (Pomacentridae) and *Amblyglyphidodon curacao* (Pomacentridae). These four species were never observed being chased prior to the crepuscular spawning period, and it is assumed that they represent potential gamete predators.

Courtship and spawning. Males and females forage either solitarily or in male-female pairs throughout most of the day, with a minimum of social interaction. As sunset approaches, the male begins to interact more frequently with the female(s) in his group. Intensive courtship first begins about one hour before sunset in the form of the "soaring" display (see below). Females continue to forage, showing little interest in male courtship activities until they are ready to spawn, at which time they swim directly and rapidly to a "rendezvous site" (see below) where they initiate spawning by responding to the male with "mutual soaring." Eleven spawnings were observed ranging from 9 min before to 7 min after sunset.

Motor patterns associated with spawning. Motor patterns used in the spawning behavior of *Chaetodontoplus mesoleucus* are nearly identical to those described and illustrated by Moyer and Nakazono (1978) for *Centropyge interruptus*. The following six motor patterns are described

briefly below: rushing and circling, soaring, mutual soaring, nuzzling, spawning, and after-chase.

a. **Rushing and circling:** This action is displayed by a dominant fish to a subordinate, usually directed by the male towards a female in the group. Occasionally a dominant female will rush and circle the smaller female. Rushing and circling in *Chaetodontoplus mesoleucus* is identical in function and form to that illustrated for *Centropyge interruptus* by Moyer and Nakazono (1978). It is displayed whenever the paths of dominant and subordinate fish cross throughout the day, but increases dramatically in frequency in male-female interactions as the spawning time nears. It is thus considered a component of the spawning sequence.

b. **Soaring:** Performed by the male with all fins extended, this conspicuous display is used only during the spawning period and in close proximity to a female. It is never seen prior to the crepuscular spawning time. In *C. mesoleucus*, the male performs this display in an upright position.

c. **Mutual soaring:** The female ceases foraging at the approach of the male, rises 1.5–2 m in the water column in an upright position with all fins fully extended. Spawning follows within a few minutes.

d. **Nuzzling:** The male places his snout against the abdomen of the female, near the vent. Both fish rise vertically in this position for about two meters, suddenly spawning.

e. **Spawning:** The male rotates his body 90° to the right on the long axis, ejects sperm simultaneously with the spawning of the female, and leads his mate in a vertical dash to the substratum.

f. **After-chase:** Directly after the post-spawning downward dash, the male chases the departing female for 2–3 m before foraging, searching for another female, or taking shelter.

Rendezvous sites. In five social groups where courtship was witnessed three times or more, males and females commenced courtship activities at the same specific topographical feature on all occasions. These "rendezvous sites" (Moyer and Zaiser, 1981) included a conspicuous *Acropora* colony (Table 1: Group 1), a large boulder of dead coral (Groups 2, 5, and 12), and a large soft coral (Group 4). In all cases, males and females began courtship at the rendezvous site, but moved

elsewhere to spawn. For example, the spawning site for Group 12 was at a boulder some 30 m from the dead coral rendezvous site, across a patch of bare sand.

Discussion

Social organization, sex ratio, and habitat. *Chaetodontoplus mesoleucus* at Bantayan Island most frequently occurs in male-female pairs. The fact that single male social groups of three individuals also occur regularly, though less frequently than pairs, indicates that *C. mesoleucus* is polygamous and that male-female pairs should be considered as "facultative monogamy." The habitat at the study site consisted of a flat, monotonous substratum of predominantly soft sand with sporadically scattered patches of mixed stony and soft corals; however, coral cover was not extensive and lacked complexity. Shelter sites were scarce and fish populations were not large. The small size and simplicity of coral patches apparently restrict the size of *C. mesoleucus* social groups to pairs and small groups of three. Multi-female groups were found only within the comparatively larger coral patches. Moyer and Nakazono (1978) reported a similar situation for the pomacanthid *Centropyge interruptus* at Miyakejima, Japan. That species was found to occur in pairs over a flat, monotonous substratum of relative simplicity. However, in fractured, complex habitats, single male social groups of from 3–6 individuals were the norm. Although details are lacking, Lobel's (1978) study of *Centropyge potteri* at Hawaii suggests a similar situation. Thus, the sex ratio of *C. mesoleucus* at Bantayan Island, where only a slight skew towards females was recognized, appears to result from habitat restrictions on population size. It is noteworthy that the species was never observed in careful censuses on complex, rich, diverse coral reefs at the island where scleractinians were dominant.

Species within the genus *Centropyge* normally occur in complex habitats where polygamous groups predominate. Most *Centropyge* spp. are either permanently or temporarily sexually dichromatic. One might suggest, based on the work of Selander (1972), that the scarcity of sexual dichromatism in the genus *Chaetodontoplus* may result from a predominance of male-female pairs and/or very small social groups, as was the case

with *C. mesoleucus* at Bantayan Island. This is tempting speculation, because *C. mesoleucus* was not found to occur in a complex coral environment, seeming to prefer a habitat of low diversity and simple structure, with the resulting low population density and only a slight female bias in sex ratio. However, this may not always be the case. My brief observations of the monochromatic *Chaetodontoplus personifer* at Wistari Reef, on the Great Barrier Reef, Australia, suggested a situation very similar to *Centropyge* spp., i.e. a habitat of complex coral structure and the presence of single male social groups with 3–4 females. Sufficient data are not yet available on the social organization of the monochromatic *C. mesoleucus* to permit broad generalizations; however, at Bantayan Island, *C. mesoleucus* social groups appear to exist with only minimal male-male competition, i.e. selective pressures for sexual dichromatism appear minimal.

Is *Chaetodontoplus mesoleucus* protogynous?

Observations of natural sex change in pomacanthids are scarce, even in field studies of long duration (e.g., Aldenhoven, 1984; Moyer and Nakazono, 1978; Moyer and Zaiser, 1984). No direct proof of hermaphroditism was obtained in this study; however, some indirect lines of evidence point to typical pomacanthid protogyny. Males are invariably larger than and dominant over females within social groups, and social groups larger than male-female pairs are always size-dominance hierarchies. Motor patterns, habitat utilization, temporal reproductive cycles, social behavior, etc., are very nearly identical to most other substratum-oriented pomacanthids (see below). Further studies will almost certainly disclose protogyny in *Chaetodontoplus*.

In situations such as that described from *Chaetodontoplus mesoleucus* at Bantayan Island, however, sex change would occur infrequently. Aldenhoven (1986), writing about *Centropyge bicolor*, has suggested that ultimately a female will change sex if and when it is to her advantage to do so; i.e., if her reproductive fitness is potentially improved. As pointed out by Moyer (1987) such a "choice" is dependent upon proximal mechanisms, as follows: a) a female must be able to avoid aggressive interactions with a dominant male (Shapiro, 1979; Moyer and Zaiser, 1984) while b) aggressively dominating a smaller female (Moyer and Zaiser, 1984). In addition, there is

probably an as yet unidentified time interval within which the sex-changing female must escape domination by another conspecific, either male or female (Moyer, 1987). In male-female pairs and in social groups with only two females and a male, i.e. in Bantayan Island situations, such proximal factors apparently do not normally occur. An exception would be, for example, a situation in which the male in a two-female group was in frequent conflict with a neighboring male ("aggressive neglect," Warner and Hoffman, 1980; Moyer, 1984a) and if the two females were clumped (Moyer and Zaiser, 1984). Such a scenario was not found to occur at Bantayan Island, and sex change, if it occurs, most likely results almost exclusively from the death or disappearance of a male.

Rendezvous sites. Rendezvous sites are known to be used by at least six pomacanthid species (Thresher, 1982; Moyer, 1987). They are also reported in studies of ostraciids (Moyer, 1984b) and scorpaenids (Moyer and Zaiser, 1981). In all cases, such sites were used to facilitate location of mates in situations where population densities were low and/or home ranges were quite large over a monotonous topography and when diel spawning periods were of relatively short duration (Moyer, 1984b) or after dark, when location of mates would otherwise be difficult (Moyer and Zaiser, 1981). Future studies will certainly disclose the use of rendezvous sites to be a common reef fish tactic under similar conditions.

Pomacanthid relationships. The close similarities of *Chaetodontoplus mesoleucus* in various aspects of spawning behavior and resource utilization to other pomacanthid fishes further emphasize the confounding phylogenetic complexities within the family (see Moyer, 1987). As shown long ago by Konrad Lorenz, an analysis of the motor patterns used in courtship can be useful in tracing phylogenetic relationships (Lorenz, 1941). In nearly all pomacanthid species reported to date, including *C. mesoleucus*, motor patterns associated with spawning are almost identical. The mid-water habitat of the planktivorous *Genicanthus* spp. is reflected in a vestigial post-spawning downward dash that consists merely of a slight dip of a few cm, followed usually by continued mid-water foraging by females and further courtship by males (Moyer, 1984c). Another interesting modification seems to occur in the subgenus

Centropyge Fraser-Brunner (genus *Centropyge*). In those species for which data are available, i.e. *C. tibicen*, *C. nox*, *C. flavissimus*, and *C. vrolicki*, the male rotates his body 180° on the long axis at the moment of spawning, resulting in a simultaneous male-female downward dash, with both fish reaching the substratum at the same time (Moyer, unpublished data). This differs from all other species of pomacanthids for which data are available, representing six of seven pomacanthid genera, and including *Chaetodontoplus*, in which males turn 90° on the long axis when spawning, leading females to the substratum in the downward dash (or in the case of *Genicanthus*, in the vestigial dip). This suggests the possibility that, phylogenetically, the subgenus *Centropyge* has diverged from an ancestor of another subgenus *Xiphipops* Fraser-Brunner type, all of which rotate the body 90°.

The social organization of a particular species is not a good indicator of phylogenetic relationships as such, due to the important role of the habitat in placing constraints on population size, sex ratio, and thus, in the composition of social groups. Most pomacanthids for which data are available, however, display almost identical social systems, further indicating the close relationships within the family. Behaviorally, *Chaetodontoplus mesoleucus* is a member of this large group of pomacanthid species that includes, among others, all species of *Centropyge* for which information is available, *Holacanthus tricolor*, *Pomacanthus imperator*, *P. sexstriatus*, and *Pygoplites diacanthus* (Table 2). These species all have the polygamous potential for single male, multi-female social groups arranged in size-dominant hierarchies, with all species in the group sharing nearly identical reproductive behavior. Most display either permanent or temporary sexual dichromatism, or both. For the sake of comparison, I propose that this group be considered to represent the pomacanthid general, unspecialized behavioral type. Divergence from the "general" type is found in the planktivorous genus *Genicanthus*, as demonstrated by multi-male social groups in *G. lamareck*, *G. semifasciatus*, and *G. caudovittatus* (Specialized 1 in Table 2; Moyer, 1984c). This important modification appears to result from a mid-water habitat (Moyer, 1984c). *Genicanthus melanospilos*, however, is found in single-male social groups with bachelor males, possibly as a

Table 2. Social organization, sexual dimorphism, behavioral type, and sex change in thirty-one species of marine angelfishes (Pomacanthidae). Modified and updated from Moyer (1987); * Early sex change demonstrated. For the details of behavioral type, see text. Source: 1, This paper; 2, Aldenhoven (1984); 3, Bruce (1980); 4, Carlson (1982); 5, Debelius (1978); 6, Gronell and Colin (1985); 7, Hioki et al. (1982); 8, Hourigan and Kelley (1985); 9, Lobel (1978); 10, Lutnesky (pers. comm.); 11, Moyer (1981); 12, Moyer (1984); 13, Moyer (1987); 14, Moyer and Nakazono (1978); 15, Moyer et al. (1983); 16, Moyer and Zaiser (1984); 17, Neudecker and Lobel (1982); 18, Randall (1975); 19, Shen and Liu (1976); 20, Suzuki et al. (1979); 21, Thresher (1982); 22, Moyer et al. (in prep).

Species	Social organization (Max. population density)			Sexual dichromatism		Sexual size dimor- phism	Behav- ioral type	Proto- gynous hermaph- rodite	Location	Source
	Obligate monogamy	Single male/ multi-female	Multi-male, multi-female	Per- manent	Tem- porary					
<i>Chaetodontoplus mesoleucus</i>		×		no	no	yes	general	?	Philippines	1
<i>Centropyge argi</i>		×		no	yes	yes	general	?	Curacao	15
<i>C. bicolor</i>		×		no	yes	yes	general	yes*	Ponape, Lizard I., Papua New Guinea	2, 13
<i>C. bispinosus</i>		×		yes	yes	yes	general	yes	Lizard I., Philippines, Enewetak	2, 13, 21
<i>C. ferrugatus</i>		×		yes		yes	general	yes*	Miyake-jima, Okinawa	13
<i>C. flavicauda</i>		×		yes	?	yes	general	?	Miyake-jima	13
<i>C. flavissimus</i>		×		no	yes	yes	general	?	Enewetak, Guam	13, 21
<i>C. heraldi</i>		×		yes	?	yes	general	?	Enewetak	21
<i>C. interruptus</i>		×		yes	no	yes	general	yes*	Miyake-jima	14
<i>C. loriculus</i>		×		yes	?	yes	general	?	Enewetak	21
<i>C. multifasciatus</i>		×		no	no	yes	general	?	Enewetak, Philippines, Papua New Guinea	13, 21
<i>C. multispinis</i>		×		yes	?	yes	general	yes	Aldabra, Eilat	3, 13
<i>C. nox</i>		×		no	yes	yes	general	?	Philippines, Papua New Guinea	13
<i>C. potteri</i>		×		no	yes	yes	general	?	Hawaii	9, 10, 13
<i>C. shepardi</i>		×		yes	yes	yes	general	yes	Gaum	11, 13
<i>C. tibicen</i>		×		yes	yes	yes	general	yes*	Miyake-jima, Philippines	13, 16
<i>C. vrolicki</i>		×		no	yes	yes	general	yes	Miyake-jima, Okinawa, Philippines	13, 21

<i>Genicanthus caudovittatus</i>		×	yes	no	yes	Spe- cialized 1	yes	Eilat	3, 5, 18
<i>G. lamarck</i>		×	yes	no	yes	Spe- cialized 1	yes	Philippines	12, 18, 20
<i>G. melanospilos</i>		×	yes	no	yes	general	yes	Papua New Guinea	7, 13, 18
<i>G. personatus</i>	?	?	yes	no	yes	?	yes	Aquarium	4, 18
<i>G. semifasciatus</i>		×	yes	no	yes	Spe- cialized 1	yes	Miyake-jima	12, 18, 19, 20
<i>Holacanthus ciliaris</i>		×	no	?	yes	general	?	Curacao Panama	15
<i>H. passer</i>		×	yes	no	yes	Spe- cialized 2	?	Sea of Cortez	15
<i>H. tricolor</i>		×	yes	yes	yes	general	yes*	Virgin I., Puerto Rico, Panama	8, 15, 17
<i>Pomacanthus arcuatus</i>		×	no	yes	yes	Spe- cialized 3	?	Panama, Puerto Rico	15
<i>P. imperator</i>		×	yes	yes	yes	general	?	Enewetak	21
<i>P. narvachus</i>		×	no	?	yes	general	?	Philippines, Papua New Guinea	13
<i>P. paru</i>		×	×	no	no	yes	Spe- cialized 3?	Cayman I.,	22
<i>P. sexstriatus</i>		×	no	?	yes	general	?	Lizard I., Philippines, Papua New Guinea	13
<i>Pygoplites diacanthus</i>		×	no	no	yes	general	?	Enewetak, Philippines, Papua New Guinea	6, 13

result of smaller body size and a corresponding greater dependence upon the substratum for shelter (Moyer, 1987).

At least some eastern Pacific *Holacanthus* (Specialized 2 in Table 2) and both species of western Atlantic *Pomacanthus* (Specialized 3 in Table 2) also diverge from the general pattern; e.g., *Holacanthus passer* forms lek-like groups over part of its range in the Sea of Cortez (Moyer et al., 1983), *Pomacanthus arcuatus* is promiscuous along the east coast of Central America (Moyer et al., 1983), and *P. paru*, reported as monogamous by Moyer et al. (1983) and others, is polygamous at Grand Cayman Island, and probably promiscuous in dense populations (Moyer et al., in prep.).

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- (Tatsuo Tanaka Memorial Biological Station, Ako, Miyake-jima, Izu Islands 100–12, Japan)
- フィリピンのパンタヤン島におけるチリメンヤッコの社会行動と繁殖行動およびキンチャクダイ科の類縁関係
Jack T. Moyer
- フィリピンのパンタヤン島におけるチリメンヤッコ *Chaetodontoplus mesoleucus* の生息場所は、変異に乏しい単純な構造のインサング類とウミトサカ類からなる小さなパッチ・リーフである。ここでは雄と雌のペアが普通で、性比はわずかしか雌に偏らない。しかし、雄1尾、雌2尾よりなるグループも見られ、本種が本来は複婚であることが分かる。社会グループが少数の個体によって構成されるのは、本種の生息場所の構造が単純であることによると考えられる。本種は地形の複雑なサング礁では見られなかった。本種の社会行動と繁殖行動は性転換を行うその他のキンチャクダイ科魚類とよく類似しており、また体長による順位関係も認められることから、雌性先熟であることが示唆される。31種のキンチャクダイ類の行動を比較すると、本報告のチリメンヤッコを含め多くの種が類似した行動を示し、それらは一般型に類別されるが、タテジマヤッコ属、東太平洋のスマレヤッコ属、西大西洋のサザナミヤッコ属は行動が特殊で一般型と異なっている。また、アブラヤッコ属のアブラヤッコ亜属は先祖型の *Xiphipops* 亜属から派生したと考えられることの根拠を示すとともに、チリメンヤッコとキンチャクダイ類の性的二型やランデブー・サイトについても論議した。
- (100-12 東京都三宅村阿古 田中達男記念生物実験所)