



Fig. 6. Anti-Parallel Rest behavior in a pair of *Paracirrhites forsteri* during courtship atop a coral boulder at Pago Bay, Guam.

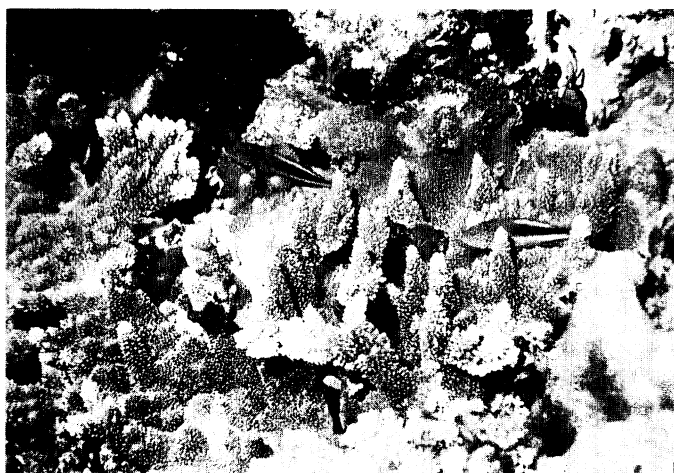


Fig. 7. Lead and Follow behavior by a pair of *Paracirrhites forsteri* during courtship at Pago Bay, Guam. The female, on the right, is leading the male, on the left.

although females in some groups were larger than males in others. Protogynous hermaphroditism is suspected and under investigation.

Non-sexual polychromatism existed. Two distinct color morphs and an intermediate form were observed at various localities. One color morph was identified by a body coloration of light pink to reddish-brown, with a white stripe along the flank; the other lacked the white stripe along its flank and its body color was reddish-olive. Intermediates were reddish-olive with a white stripe along the flank. Social groups tended to segregate by color morph in relation to depth (Donaldson,

in prep.). Social groups of mixed morph composition, including intermediates, were occasionally observed along "borders" shared by both.

Courtship and spawning commenced just prior to or after sunset, with 2-8 bouts lasting 5-360 seconds and spawning occurring 2 minutes before to 6 minutes past sunset (N=4 spawns observed). Courtship patterns used were few in number (Table 2) and courtship was relatively simple compared to *P. forsteri*. Generally, the male approached the female (Fig. 8) and the two assumed Parallel Rest. The male, and occasionally the female, engaged in Looping, which ended in



Fig. 8. Pair formation during Approach behavior by a male *Paracirrhites arcatus* at Tanguisson Reef, Guam. The male is on the left.

Parallel Rest. The pair then waited a few seconds, and then they began Lifting. After Lifting a few times they ascended 1–1.4 m into the water column. At the top of the ascent the pair quickly turned downward, released a small cloud of gametes, and swiftly returned to the same coral head. After spawning the male either waited a few minutes and then left to court another female at a different coral head or settled with the female in between the branches for the night. Some males courted more than one female at the same coral head. For example, one male at Tanguisson Reef, Guam, courted four females in succession at the same large *P. elegans* coral which he shared with one of the females; the other three females migrated to that coral head at sunset from their home areas centered at an adjacent *P. eydouxi* coral (one female) or in less favored *Porites rus* corals a few meters away.

In social groups with more than one female, males usually courted but did not spawn with each female every night. Observed spawnings were few since this species became relatively shy during courtship periods. Reproductive behavior may have been affected by the presence of an observer. This presence may have contributed to the reluctance of the female to complete spawning despite persistent courtship attempts by the male. Alternately, lack of spawning success may simply be a function of a corresponding lack of female readiness.

***Paracirrhites hemistictus*.** This species exists in

two non-sexually derived color morphs (Randall, 1963), the lightly colored “*hemistictus*” phase and the darker “*polystictus*” phase (see Myers, 1989, for color photographs of each). Both tended to segregate by depth, and aggressive interactions between morphs were observed at borders between depth zones. The “*polystictus*” morph occurred in shallower water near the reef margin while the “*hemistictus*” morph occurred in slightly deeper waters (Donaldson, unpubl. ms.). Intermediate color morphs have been reported (Marshall, 1950).

This species occurs from French Polynesia west to Christmas Island, Indian Ocean (Randall, 1955, 1963; Allen and Steene, 1979). Two color morphs, but not the intermediate, were observed at Ponape, Guam, Saipan and Moorea; courtship behavior has been observed at Tanguisson Reef, Guam and Wing Beach, Saipan. Spawning has not been observed, but it is assumed to be pelagic, as with *P. arvatus* and *P. forsteri*.

Male body sizes were larger than those of females (Table 3) within groups, although the largest females’ body size often approached that of the males in the *P. hemistictus-polystictus* morph; body sizes of the *P. hemistictus-hemistictus* morph could not be obtained but males appeared to be larger than females within the few social groups observed.

Males held relatively large territories (up to 150 m<sup>2</sup>) in which females had smaller home areas. Territories and home areas were usually centered around a large *Pocillopora* spp. coral or

*Millepora* spp. hydrozoan, a large boulder, or a prominent ledge in the spur and groove zone.

At Tanguisson Reef, Guam, a social group of the "polystictus" phase, consisting of one male and four females, shared a very large *Pocillopora eydouxi* coral in the spur and groove zone just below the reef margin at a depth of 2 m. The male and the two largest females often patrolled the area around this coral while the other females remained in distinct home areas between the coral's branches. In addition, two melanistic *P. forsteri* females, a male and a female *Cirrhitus polystictus*, three *Exalljas brevis* (Blenniidae) and four *Plectroglyphidodon johnstonianus* (Pomacentridae) shared this coral. At sunset, the male and largest female joined the remaining females in the coral and courtship commenced. Females interacted aggressively with one another at this time, with the largest female dominating the others; interactions with the two melanistic *P. forsteri* females also occurred.

Courtship patterns observed included Parallel Rest, Perpendicular Rest, Head-up and Lead and Follow. Courtship included long periods of waiting during bouts; courtship was relatively simple, rather like that of *P. arcatus* and not that of *P. forsteri*. This species was very wary and many courtship attempts were aborted, either because of interruption by a coral's other residents (at Tanguisson Reef) or a female's possible reaction to the presence of either cruising predators or the observer (Tanguisson Reef and Wing Beach).

*Cirrhitus pinnulatus*. This species is widely distributed, from Hawaii to the Red Sea and occurs in three distinct subspecies (Randall, 1963). Others in the genus have relatively small distributions, and endemism is common. *Cirrhitus pinnulatus* is a reef margin-inhabiting species that occurs in the spur and groove zone at or below the edge of the reef. This species has been described as nocturnal (Kluzinger 1870, cited in Randall, 1963; Harry, 1953; Randall, 1963) but numerous observations of populations at Wing Beach, Saipan, Tanguisson Reef, Guam, and Aiwo Reef, Nauru, indicated that this species is active socially during daylight hours through dusk and is often seen darting between corals, boulders, and cuts in the edge of the reef (pers. obs.).

Members of the genus *Cirrhitus* are among the largest of the cirrhitids, and this species is no

exception. Individuals that exceeded 280 mm TL have been collected. Sexual dimorphism in body size existed (Table 3), with males larger than females within groups, although large female body sizes approached those of males.

Social organization, courtship and some spawning behavior were observed at Wing Beach; additional observations of social behavior were made at Tanguisson Reef, and Aiwo Reef. Territorial interactions occurred between males in adjacent territories. Females had smaller home areas within male territories and defended courtship sites (Fig. 9) just prior to and after sunset. Generally, larger females dominated these sites if they were shared.

Observations of courtship behavior in this species were difficult to make because of its wary behavior; only three spawnings were actually observed from over 30 hours of courtship observations. Males tended to prefer courtship with larger females and often chased smaller females from courtship sites until after courtship with the larger females was completed. Courtship began just before sunset and concluded after dusk.

Observed courtship patterns were few in number (Table 2). Males approached waiting females at shared courtship sites or single females at unshared sites, and then waited, occasionally shifting position about the site. The courtship pattern was paired and sequential; the pair assumed the Parallel Rest, Anti-parallel Rest or Perpendicular Rest motor patterns. After a few seconds, both male and female began Lifting, always from the Parallel Rest position, and, in one instance, were observed to make a rapid ascent 1.5 m into the water column. At the apex of this ascent, just below the surface of the water, the pair turned downward and released a small cloud of gametes, before quickly dashing back to the substratum at the courtship site. Numerous courtship attempts did not lead to spawning. Also, males often did not attempt to court every female in the harem.

*Oxycirrhites typus*. This species is distributed from the Gulf of California west to the Red Sea (Randall, 1963), and occurs in deep-slope habitats (20–150 m). *Oxycirrhites typus* was observed at Papua New Guinea and Ponape. This species is an obligate coral-dwelling hawkfish (Donaldson, unpubl. ms.) and is strongly site-attached to gorgonians and antipatharian corals. Sexual di-

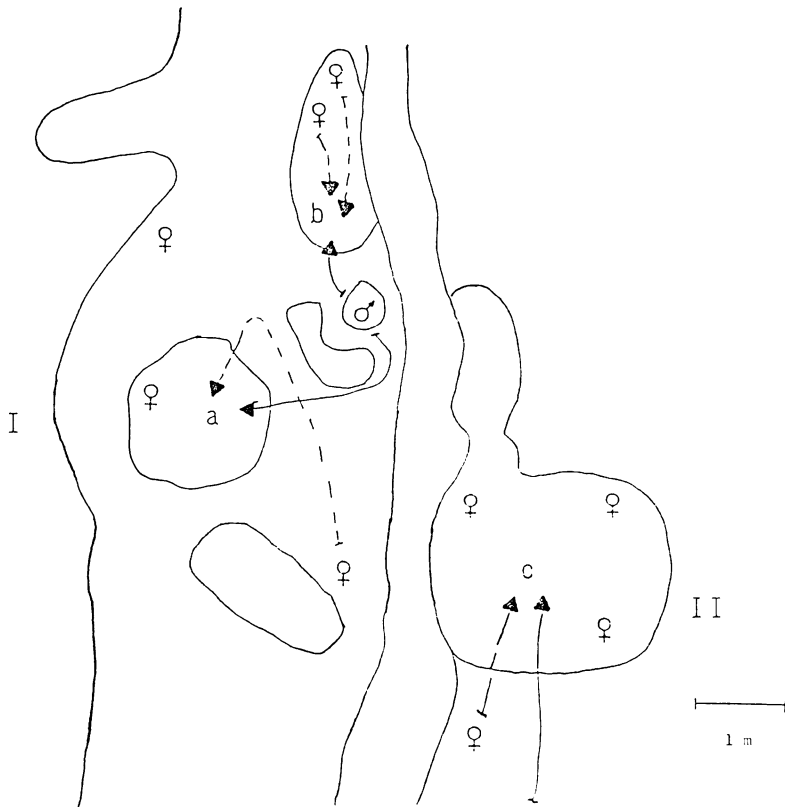


Fig. 9. Spatial patterns and movement of males and females of two adjacent social groups of *Cirrhitus pinnulatus* in the spur and groove zone at Wing Beach, Saipan, Mariana Islands. I, social group no. 1 with two courtship sites, a and b; II, social group no. 2 with a single courtship site, c. Solid lines indicate paths taken by males from resting sites to courtship sites; dashed lines indicate paths taken by females from resting sites to courtship sites (summarized from ca. 16 hours of observation).

morphism in body size occurred within social groups, but differences between male and female body sizes were less pronounced compared with other species (Donaldson, unpubl. ms.; Table 3).

Although this species is usually observed in pairs, it is also harem and has a mating system of facultative monogamy. This system is influenced by the availability and size of corals as suitable habitat in a given area (Donaldson, 1989).

Lobel (1974) reported that this species spawned demersally in an aquarium, although spawning was inferred rather than observed. Donaldson and Colin (1989) determined that this species spawns pelagically in pairs and that courtship is sequential within harems.

*Neocirrhites armatus*. This brightly colored

species was commonly observed at Guam, Saipan, and Moorea, where it occurred in close association with *Pocillopora eydouxi* and *P. elegans* corals (Donaldson, unpubl. ms.). This species favored *P. verrucosa* and *P. eydouxi* in Fiji (Carlson, 1975). *Neocirrhites armatus* is considered an obligate coral dwelling species (Donaldson, unpubl. ms.).

Social groups consisted of a single dominant male and up to four females. More commonly, this species was found in pairs or in small harems consisting of a single male and two females, often with a pair in a single coral head and the second female in an adjacent one. Group size within coral heads depended upon coral size; groups with more than three individuals within the same coral occurred rarely, and then only if the coral was

quite large or if coral densities were low because of loss to predatory *Acanthaster planci* starfish or habitat destruction by man. Group size also depended upon the proximity of neighboring corals (Donaldson, unpubl. ms.). The species demonstrated facultative monogamy (Donaldson, 1989).

Sexual dimorphism in body size was evident, with males being larger than females within groups (Donaldson, 1989). Protogynous hermaphroditism was indicated and is currently being investigated.

Territoriality within corals was pronounced, particularly at the approach of sunset. Both males and females defended portions of the coral from intra- and interspecific intruders, of which many of the latter were refuging in the branches of the coral for the night. Intraspecific interactions, particularly between females in corals supporting more than a pair, also increased at this time prior to the onset of courtship.

Some courtship behavior was observed. This behavior was paired and sequential. A male approached a female, either by moving into her home area within the coral, or by swimming along the substratum to a female in an adjacent coral. Once pair formation occurred, the male and female engaged in Parallel Rest, Anti-parallel Rest, and Perpendicular Rest. Males also chased females between the branches of the coral. Alternately, females engaged in Lead and Follow through the coral branches. Courtship behavior was interspersed with long periods of waiting for several seconds to a few minutes. Rapid dashes just above the edge of the coral were observed, but pelagic spawning was not confirmed. This species has been suggested as a possible demersal spawner (G. W. Barlow, pers. comm.) because of its strong association with corals and the high visibility of its color pattern in daylight, which may render it vulnerable to predators. Demersal spawning, by laying eggs in a nest within the branches of a resident coral, may reduce the risk of predation of adults. However, no evidence of demersal spawning was observed. Further, both males and females have been observed moving between corals during daylight and at sunset. If such movement is possible then pelagic spawning, by making a rapid dash above the coral, may also be so. Making such an ascent at dusk would also reduce the chance of preda-

tion by visually-oriented predators, since the red coloration of this species renders it difficult to see during periods of darkness (pers. obs.).

*Amblycirrhitus bimacula*. This species, occurring from Hawaii to east Africa, is one of the most widely distributed cirrhitids; it is also one of the most rarely observed species, although it does appear with regularity in collections made with rotenone. One reason for the rarity of observations, at least at the localities visited, is that this species is a reef-margin inhabitant that tended to be found in the spur and groove areas just below the surf zone. This habitat usually experienced wave activity often in excess of that which could be tolerated by divers. *Amblycirrhitus bimacula* is considered a non-coral dwelling species, but one social group, consisting of a single male and a smaller female, was observed in a large *P. eydouxi* coral at 10 m on Tanguisson Reef. The social organization of this species is unknown, but it may be harem in the spur and groove zone and facultatively monogamous in corals.

The pair of *A. bimacula* observed in the *P. eydouxi* coral at Tanguisson Reef was territorial, particularly at sunset, toward other resident fishes and non-resident fishes refuging for the night. Resident fishes included *Caracanthus unipinna* (Caracanthidae), *Sebastapistes albobrunnea* (Scorpaenidae) and *Pomacentrus vaiuli* (Pomacentridae). Non-resident intruders included *Cephalopholis urodeta* (Serranidae), and *Acanthurus nigrofuscus* (Acanthuridae).

Pre-courtship behavior was observed in the Tanguisson Reef pair, although this species was shy and difficult to approach. As sunset approached, the male and female moved to the lower portion of the coral near the base of its branches. Then, the male left the coral, patrolled a 2 m<sup>2</sup> area around the coral, and then returned to the base of the coral and into the branches where the female waited. Three such patrols were observed. The reason for this behavior is unknown. The male may have been searching for an adjacent female, as has been observed in coral-dwelling *Cirrhitichthys oxycephalus*, but no other females were detected in the area. While the male patrolled, the female occasionally left the coral and followed the male for a short period of time.

Spawning was not observed but the behavior is presumed to be paired and pelagic.

### Discussion

**Social organization.** The patterns of social organization and behavior of the Cirrhitidae (summarized in Table 4) are consistent with those of a number of small, benthic reef-dwelling fishes. Those hawkfishes described herein are harem, with social groups consisting of a single dominant male and one or more females. The number of females within a harem is influenced by habitat availability and use. Local population densities are probably regulated by both, as is recruitment of individuals, as either post-larval juveniles or displaced adults, to harems. In obligate coral-dwelling species, habitat availability and use contributed to the formation and use of a mating system based upon facultative monogamy. In non-obligate and non-coral dwelling species these factors seemed to have less influence, and other considerations, such as the cost of maintaining a harem relatively to the size of that harem, may have been more important.

Variation in the size of harems and corresponding mating systems between populations of some species at different localities could have resulted from geographic variation. This variation in harem size may be in response to the availability of suitable habitat (i.e. corals), and the absence of potential competitors for that habitat at some localities. For example, *Cirrhitichthys oxycephalus* was an obligate coral-dwelling species at some localities, such as Lizard Island, the Papuan Barrier Reef, and Nauru, and occurred in pairs or in small harems consisting of a single male and two females. In the latter case one female shared a coral with the male while the second female resided in an adjacent coral. A potential competitor for the corals, the obligate coral-dwelling species *Neocirrhites armatus*, was not observed at these localities. At Guam, where both species occur, *N. armatus* inhabited *Pocillopora* corals and *C. oxycephalus*, when seen, inhabited the substratum beneath these corals, and was harem.

Sexual dimorphism in body size within social groups was pronounced in all species and seems indicative of protogynous hermaphroditism (Thresher, 1984), although body size dimorphism does not provide conclusive evidence of this (Sadovy and Shapiro, 1987). Kobayashi et al. (1985) reported, in an abstract, hermaphroditism in four species of cirrhitids from Japan, but

details have not been published.

**Reproductive behavior.** Cirrhitids share a number of features of reproductive behavior (Table 3), including: (1) onset of courtship and spawning just prior to or after sunset; (2) paired, sequential courtship in harems; (3) pelagic spawning, resulting in pelagic eggs and larvae in probably all species; (4) daily courtship that may be regulated by seasonal effects in relation to latitudinal variations in water temperature rather than any adherence to a lunar cycle; and (5) no apparent variation in the general pattern of courtship and spawning.

Courtship and spawning just prior to or after sunset is a consistent feature in all cirrhitids studied (Thresher, 1984; Donaldson, 1986a, 1987; Donaldson and Colin, 1989). This behavior is also a consistent feature of courtship of many other pelagically-spawning reef fishes (Moyer et al., 1983; Thresher, 1984). Possible reasons for spawning during this narrow time window are related to the use of the spawning ascent motor pattern. Pelagic spawning releases eggs for dispersal (Barlow, 1981), for maximum potential survival in waters having patchy resources (Doherty et al., 1985) or for predation avoidance (Johannes, 1978; see Shapiro et al., 1988, for a critical review of all three hypotheses), but it also exposes them to potential predation by diurnal planktivores (Thresher, 1984). Such predators appeared to be relatively less common at sunset than during daylight at the localities visited. At sunset, diurnal planktivores found shelter for the night and did not appear to feed upon cirrhitid eggs in the water column. Similar patterns of diurnal planktivore behavior at sunset have been reported elsewhere (see review in Thresher, 1984).

Pelagically-spawning fishes are also exposed to potential predation from piscivores while making the spawning ascent (see reviews in Keenleyside, 1979; Thresher, 1984), but the effectiveness of such predators in taking spawning adults may be poor (Moyer, 1987). Rapid ascents to minimal heights during periods of low light levels allowed spawning hawkfishes to release eggs above the substratum quickly with minimal exposure to predators; more often, predation potential may have been more keen while hawkfishes were courting on or near the substratum. *Cirrhitichthys falco* and *C. aprinus* males were occasionally attacked by larger fishes, though

Table 4. Summary of social organization and reproductive behavior characteristics of ten species of Pacific Cirrhitidae. \* Male (M); females (F); juveniles (J). \*\* Data from Donaldson (1989).

Species	Localities studied	Mating system	Group size M: F: J*	Male Territory?	Female site?
<i>Cirrhitichthys aprinus</i>	Miyake-jima; Motupore Is.; Guadalcanal	harem	1: 2: 1-9	yes	yes
<i>Cirrhitichthys falco</i>	Guam; Miyake-jima; Lizard Is.; Motupore Is.; Guadalcanal	harem	1: 1-7: 1-6	yes	yes
<i>Cirrhitichthys oxycephalus</i>	Nauru; Lizard Is.; Motupore Is.	harem/facultative monogamy	1: 1-6	yes	yes
<i>Paracirrhites forsteri</i>	Guam; Nauru; Lizard Is.; Guadalcanal; Fiji	harem/facultative monogamy (?)	1: 1-5	yes	yes
<i>Paracirrhites arcatus</i>	Guam; Tinian; Saipan; Nauru; Lizard Is.; Moorea; Motupore Is.	harem/facultative monogamy (?)	1: 1-3	yes	yes
<i>Paracirrhites hemistictus</i>	Guam; Saipan; Moorea; Ponape	harem	1: 1-3	yes	yes
<i>Cirrhites pinnulatus</i>	Saipan; Nauru; Guam	harem	1: 2-8	yes	yes
<i>Neocirrhites armatus</i>	Guam; Tinian; Moorea	facultative monogamy/harem	1: 1-4	yes	yes
<i>Oxycirrhites typus</i> **	Motupore Is.; Ponape	facultative monogamy/harem	1: 1-2	?	yes
<i>Amblycirrhites bimaculata</i>	Guam	facultative monogamy /harem (?)	1: 1	?	yes

Species	Courtship before (-) or after (+) sunset	Spawning time before (-) or after (+) sunset	Adult body size (range, mm TL)		Site attachment	Microhabitat type
			male	female		
<i>Cirrhitichthys aprinus</i>	- +	- +	60-100	40-85	strong	non-coral dweller
<i>Cirrhitichthys falco</i>	- +	- +	55-80	35-60	strong	non-coral dweller
<i>Cirrhitichthys oxycephalus</i>	+	+	45-55	35-50	strong /very strong	non-coral dweller /obligate coral dweller
<i>Paracirrhites forsteri</i>	- +	+	80-180	60-145	strong /very strong	non-obligate coral dweller
<i>Paracirrhites arcatus</i>	+	+	50-95	40-70	strong /very strong	non-obligate coral dweller
<i>Paracirrhites hemistictus</i>	+	?	200-240	120-220	strong	non-obligate coral dweller/non-coral dweller
<i>Cirrhites pinnulatus</i>	- +	- +	150-210	60-170	strong	non-coral dweller
<i>Neocirrhites armatus</i>	- +	?	44.5-70	37-62	very strong	obligate coral dweller
<i>Oxycirrhites typus</i> **	- +	+	65-99.5	52-92	very strong	obligate coral dweller
<i>Amblycirrhites bimaculata</i>	-	?	55 (n=1)	48 (n=1)	strong /very strong	non-coral dweller /obligate coral dweller

unsuccessfully, as they moved between females in a harem. Attacked fishes escaped by erecting their dorsal spines; erect dorsal spines also were apparent in fishes of both sexes during and at the end of the spawning ascent (Donaldson, 1987).

Courtship occurred daily in localities at lower latitudes. Daily courtship and spawning occurs in other small harem reef fishes, such as the pomacanthids of the genus *Centropyge* (Moyer et al., 1983). Seasonality in the courtship of cirrhitids is expected only at higher latitudes where local water temperatures influence spawning readiness. Seasonality in water temperatures may also influence the maintenance of social structure during non-breeding periods, by acting as a stimulus for sex-reversal. Such effects have been described from a population of protogynous *Parapercis snyderi* (Pinguipidae) from Japan (Nakazono et al., 1985).

Spawning frequency may not be a daily event in some species of cirrhitids, however, even if daily courtship does occur. Donaldson (1986a, 1987) found, with some exceptions, that male *C. falco* spawned daily with each female in its group. Both *C. oxycephalus* in season (Thresher, 1984, pers. obs.) and *C. aprinus* (this paper) appear to spawn daily, as does *O. typus* (Donaldson and Colin, 1989). The same cannot be said of other cirrhitids or any of the same cirrhitids at different localities. Observations of *C. oxycephalus* at Lizard Island, *P. forsteri* at Guam, Nauru and Lizard Island, *P. arcatus* at Guam and Nauru, and *C. pinulatus* at Saipan indicated that, although males courted females on a daily basis, they do not successfully spawn with each female. The reason for this is unclear, though the presence of an observer may be a factor. Another possibility is the lack of female readiness. In some species females may not be physiological capable of spawning on a daily basis, although this limitation seems unlikely in view of the spawning patterns of other cirrhitids. More likely, females may choose not to spawn because of a potential risk of predation during courtship. Recognition of potential predators in or near the courtship site may compel a female to delay or forego spawning, despite vigorous courtship by the male.

Although cirrhitids have three forms of microhabitat preference there is consistency in both social and reproductive systems. Hawkfishes are

harem, even if the "harem" consists of a single female, and all appear to practice sequential courtship resulting in paired pelagic spawning during sunset hours. This consistency contrasts sharply with the social organization and mating systems of the Pomacanthidae, where considerable variation exists, and results from local selection pressures (Moyer et al., 1983).

The use of many of the same motor patterns by members of the family in different genera requires further analysis. While one pattern, male approach, was common to all species, six other patterns occurred in up to 90% of all species and 14 in up to 60%; seven patterns were seen in only one species and may prove to be species-specific (Table 2). Caution must be used in stating species-specificity of motor patterns since those observed in only a single population or species may be influenced by geographic variation, or be found in other species once the entire family is surveyed, and may also be influenced by geographic variation.

Examination of the relative use and sequence of use of shared patterns by each species may be more useful (Fitzsimons, 1976) than simply looking for species-specific behaviors. Difference in pattern use between species may explain how reproductive isolation among members of the family as possible.

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#### 太平洋産ゴンベ科魚類数種の繁殖行動と社会組織

Terry J. Donaldson

太平洋産ゴンベ科魚類10種は、1尾の雄と1-数尾の雌からなるグループで生活する。サンゴ内に生息する2種では、一夫一妻になることもしばしば観察されたが、残りの種はたいてい一夫多妻（ハレム）であった。雄はグループ内のどの雌よりも大きい。他のグループの雌と比べると必ずしもそうではなかった。雄は雌たちの行動圏を囲む範囲を、なわばりとして防衛し、その中で雌は各々の求愛場所を互いに防衛していた。求愛は日没後に始まり、暗くなると終了した。求愛行動は必ず1尾の雄と1尾の雌のペアで行われたが、雄は一タのうちにグループ内の雌たちと連続的に求愛を交わした。産卵行動が観察された8種では、いずれも上昇して浮性卵を産むことが確認された。

編 集 後 記 ・ Editorial notes

本号からこれまでの活版に代わって電算写植・オフセット印刷になりましたが、できればいかがでしょうか。少なくともこの切り替えにより、編集作業の方は能率が良くなり、ありがたいことと思っております。この

折に「投稿規定」と「原稿作成上の注意」も一部改訂いたしました。投稿される方は必ず目をお通し下さるようお願いいたします。

訂 正 ・ Errata

魚類学雑誌 36 巻 4 号に次の誤りがありました。お詫びして訂正いたします。

Japanese Journal of Ichthyology, 36(4), Donaldson:

page 449, Fig. 7, 2nd line, read “left” and “right” for “right” and “left,” respectively.