Social Organization, Reproductive Behavior, and Zoogeography of Some Indo-Pacific Hawkfishes (Cirrhitidae).

Terry John Donaldson
Louisiana State University and Agricultural & Mechanical College

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Social organization, reproductive behavior, and zoogeography of some Indo-Pacific hawkfishes (Cirrhitidae)

Donaldson, Terry John, Ph.D.
The Louisiana State University and Agricultural and Mechanical Col., 1988
Social organization, reproductive behavior, and zoogeography of some Indo-Pacific hawkfishes

(Cirrhitidae)

A dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by

Terry John Donaldson
B.S., Michigan State University, 1977
M.S., The University of Guam, 1981
December, 1988
The text of this dissertation consists of five manuscripts, three of which have been published. "Distribution and species richness patterns of Indo-West Pacific Cirrhitidae: support for Woodland's hypothesis" first appeared in 1986 in the book *Indo-Pacific Fish Biology*, edited by Uyeno et al. "Courtship and spawning behavior of the hawkfish Cirrhichthys falco at Miyake-jima, Japan" was published in the Japanese Journal of Ichthyology in 1986. "Social organization and reproductive behavior of the hawkfish Cirrhichthys falco (Cirrhitidae)" was published in the Bulletin of Marine Science and appeared in 1987. The remaining chapters have been submitted for publication and appear here in the style of the journals to which they were submitted: "Reproductive behavior and social organization of some Pacific hawkfishes (Cirrhitidae)" (Japanese Journal of Ichthyology); "Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae)" (Environmental Biology of Fishes).

These studies benefitted greatly from the assistance of many people. I am especially grateful to J. M. Fitzsimons, J. T. Moyer and J. E. Randall for guidance and help in ways too numerous to mention. P. L. Colin,
R. F. Myers, J. P. O'Neil, R. E. Thresher, the members of my advisory committee, J. M. Fitzsimons, C. F. Bryan, J. V. Remsen, M. S. Hafner, R. W. Hastings and C. Wilson, and the staff and students of the Section of Ichthyology and the Museum of Natural Science, are also thanked for their time and consideration.

The following institutions are thanked for the use of their facilities or collections: Antenne du Museum et des Hautes Etudes (Moorea), Australian Museum, B. P. Bishop Museum, California Academy of Sciences, CSIRO Marine Laboratories (Hobart), Lizard Island Research Station, Motupore Island Research Station, Tatsuo Tanaka Memorial Biological Station, Tokyo University Museum, University of Guam Marine Laboratory, University of the South Pacific, University of Washington School of Fisheries, and the Western Australian Museum. The Division of Aquatic and Wildlife Resources of the Government of Guam, the Division of Fish and Wildlife of the Commonwealth of the Northern Marianas, and the Great Barrier Reef Marine Park Authority, Australia, granted necessary collecting permits.

This study was funded by generous awards from the Coypu Foundation, the Japan Airlines 50th 747 Asian Studies Scholarship, the Museum of Natural Science and the Department of Zoology and Physiology of Louisiana.
State University, and M. C. and S. Wilkins, to whom I am extremely grateful.

Finally, I thank my wife, Grace Constantino Donaldson, for help, encouragement and understanding.
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Abstract

The social organization and reproductive behavior of ten species of hawkfishes was studied at several Pacific localities. In addition, the zoogeography of all Indo-West Pacific cirrhitids was considered in relation to both the Indo-Malayan triangle as a center of species diversity and the isolation of the Pacific and Indian ocean basins during Quaternary events.

Patterns of hawkfish distribution and species richness, reflected in high levels of endemism in both the Pacific and Indian ocean basins, support the hypothesis that the Indo-Malayan triangle is not so
much a center of speciation as one of the confluence of
two distinct centers of distribution.

Patterns of hawkfish social organization and
reproductive behavior indicated that members of the
family were haremic or facultatively monogamous,
depending upon habitat association and habitat size.
Habitat associations included obligate coral-dwelling,
non-obligate coral-dwelling or non coral-dwelling.
Sexual dimorphism in body size was evident, with males
being larger than females within social groups, but not
always between social groups. Males maintained
territories in coral heads or on the substratum.
Females within a male-dominated social groups
maintained home areas within these territories and
defended courtship sites from conspecific females in
most species. Hawkfishes had sequential courtship,
commencing prior to or after sunset, and spawning was
pelagic. Courtship motor patterns observed included
those shared by most members of the family and some
which may have been species specific.
Introduction

The studies reported here have demonstrated that the social organization and reproductive behavior of hawkfishes (Cirrhitidae), a small but widely distributed group of perciforms, show minor variation within and between species across the geographic range of the family. In contrast, the social organization and reproductive behavior of relatively large, widely-distributed families of reef fishes (e.g., the Labridae) are usually variable both within and between species and genera. Among typical reef fishes, variation in social organization may include the use of solitary, paired (monogamous and non-monogamous), harem, or multi-male heterosexual social groups (Fricke, 1975; see summary in Thresher, 1984) that determine the form of mating system practiced within taxa. Variation in reproductive behavior is determined largely by the spawning class (Thresher, 1984) to which the species belongs, i.e., live-bearing, laying or scattering demersal eggs, or spawning pelagic eggs by benthic broadcasting or pelagic ascent.

Variation in both social organization and reproductive behavior may result from non-unidirectional selection pressures (Moyer et al., 1983) across the range of a species, genus, or family. Variation within a species is expected if that species
is broadly distributed and if populations of that species are geographically isolated. Variation within genera is expected if congeners have both allopatric and sympatric distributions; variation in allopatric species may result from geographic isolation whereas variation in sympatric species, at least in reef fishes with pelagic larvae, may result from differential use of habitat types or selection for reproductive isolating mechanisms. Variation within the family, particularly at the generic level, may result from responses to selective pressures in different habitat types, from geographical isolation of incipient genera derived from a common ancestor, or from polyphyletic origins within the family.

Variation in social organization and reproductive behavior has been observed in large reef fish families such as the wrasses (Labridae), damselfishes (Pomacentridae) and gobies (Gobiidae) (Thresher, 1984). Members of each of these widely distributed and speciose families occur in a variety of habitat types and have considerable potential for variation in social and reproductive traits. But what of smaller, monophyletic families of reef fishes with broad distributions? Moyer et al. (1983) provided an example of widespread variation in social organization and mating systems within the relatively small family Pomacanthidae. Members of this family had social
organizations that included apparent monogamy, male-dominated harems, lek-like mating systems, and explosive promiscuous breeding assemblages. Such variation was attributed to responses to a lack of unidirectional selection pressures over the range of a species. Variation in social organization and reproductive behavior may occur in other small families of reef fishes subject to similar conditions.

Although variation may occur in social organization and reproductive behavior among members of a family, variation in the mechanism used in spawning seldom varies. Reproductive strategies that determine spawning class, generally characteristic of the family level, have been described as being evolutionarily conservative with few tropical shallow-water groups showing within-family differences (Thresher, 1984).

Thresher (1984) listed the Clinidae, Antennaridae, and Muraenidae as having such differences. The Clinidae have members that are either demersal spawners or live bearers; the Antennaridae have members that are either demersal or pelagic spawners. The Muraenidae differ by spawning pelagic eggs in the water column or by benthic broadcasting pelagic eggs. Two additional families may have spawning-class differences as well. The Tetraodontidae may spawn demersal eggs or scatter them; the Balistidae may lay demersal eggs or spawn pelagically. Tropical families that show latitudinal
shifts from pelagic to demersal spawning include the Labridae, Sparidae, and, possibly, the Diodontidae (Thresher, 1984). However, tropical reef fishes generally do not vary in the type of spawning class used at the family level.

The Cirrhitidae, a tropical family of reef fishes, may show some variation in both social organization and type of spawning class. Members of this family are widely distributed on coral and rocky reefs in the tropics and subtropics. The family is small, numbering 34-35 species, but the number of genera, 9-10, is relatively large. The Cirrhitidae is monophyletic, yet has four or five monotypic genera and demonstrates a remarkable degree of endemism (Randall, 1963; Springer, 1982). Little has been published regarding the social organization and reproductive behavior of this family, yet conflicting reports indicate or suggest that its members may be harematic or monogamous, and may spawn pelagically or demersally (Lobel, 1973; Amesbury and Myers, 1983; Thresher, 1984; Randall, 1985; Barlow, 1986). If all reports are valid, then the Cirrhitidae may be unique among small tropical perciform families in showing such variation. Threshzer (1984) questioned the validity of a report indicating demersal spawning in at least one hawkfish species, Oxycirrhites typus, and contended that this possibility was unlikely in a small monophyletic family in which pelagic spawning had
been observed for one other species, the haremic Cirrhitichthys oxycephalus. Others (various, pers. comm.) have suggested that O. typus and another monotypic species, Neocirrhites armatus, may lay demersal eggs and be monogamous. Both species appear to be unique among cirrhitids in that they are found in close association with certain coral species. This association seems to favor an alternate strategy in which the social organization is based upon monogamy, and is conducive to laying demersal eggs rather than spawning pelagically.

The purpose of these studies was to determine if the family Cirrhitidae shows variation in both social organization and reproductive behavior, including variation in spawning class type. If variation in these characters was found to exist, the next step was to describe possible mechanisms that may contribute towards this variation across the range of those species examined. These descriptions required a detailed analysis of the zoogeographical relationships among members of this family, and a determination of the social organization and reproductive behavior of hawkfishes in different genera distributed in the central and western Pacific.
Permission to microfilm the following article of my dissertation has been requested from the publisher, The Ichthyological Society of Japan:

Distribution and species richness patterns of Indo-Pacific Cirrhitidae: support for Woodland's hypothesis.
Distribution and Species Richness Patterns of Indo-West Pacific Cirrhitidae: Support for Woodland's Hypothesis*

Terry J. DONALDSON

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Louisiana State University, Louisiana, U.S.A.

Abstract  Traditional views of Indo-West Pacific region reef fish zoogeography depict the existence of a center of diversity marked by high species richness. This center occurs in an area bounded by New Guinea, the Philippines, and the Malayan Peninsula (the Indo-Malayan triangle). Presumably, new and successful species are created here at rates faster than those of other areas, resulting in higher species richness within the Indo-Malayan triangle.

Woodland (1983) offered an alternative hypothesis to explain this phenomenon in fishes. His view was that the level of species richness in this area is inflated and actually represents the pooling of species numbers from two distinct centers of distribution in confluence. These centers, one each in the Pacific and Indian oceans, are marked by higher levels of endemism when compared with the Indo-Malayan triangle. These levels may be the result of allopatric speciation, made possible by the isolation of the two oceanic basins because of Quaternary events.

An examination of the distributions of Indo-West Pacific cirrhitids revealed high species richness in the Indo-Malayan triangle but low levels of endemism when compared with distributions centered in the Pacific and Indian oceans. The existence of two distinct centers of distribution, based upon high levels of endemism, is offered in support of Woodland's hypothesis.

Fishes of the family Cirrhitidae occurring in the Indo-West Pacific have ranges which in a general sense, seem indicative of two distinct centers of distribution. This pattern is inconsistent with traditional views of Indo-West Pacific reef fish zoogeography which depict the existence of a single center of diversity marked by high species richness. This center, located in the southwestern corner of the Indo-Pacific province (Briggs, 1974), occurs in an area bounded by New Guinea, the Philippines and the Malayan Peninsula. It has been referred to as the "fertile triangle" (Briggs, 1974) or Indo-Malayan area (Woodland, 1983). Species richness in this Indo-Malayan area, when compared with other Indo-West Pacific Region provinces, as defined by Briggs (1974), or even the "Polynesian area" of the Indo-Pacific province, is exceptional. Presumably high species richness exists because new and successful species were created at rates faster than those of other areas (Woodland, 1983) resulting in higher species richness. Woodland (1983) offered an alternative hypothesis to explain the phenomenon of high species richness in the Indo-Malayan area. His view was that the level of species richness for this area was inflated and actually represented the pooling of species numbers from two distinct centers of distribution in confluence. These centers of distribution, one each in the Pacific and Indian oceans, are marked by higher percentages of
endemism when compared with percentages of endemism from the Indo-Malayan area. High levels of endemism may have been the result of allopatric speciation, made possible by the nearly total isolation of both oceanic basins because of Quaternary events (Woodland, 1983).

Woodland (1983) predicted that close examination of distribution and species richness patterns of some other taxa would also indicate that: 1) richness values would be inflated in the Indo-Malayan area because of confluence, and 2) distribution patterns would indicate two centers of distribution, one in the Indian Ocean and the Pacific oceans, rather than a single center of diversity in the Indo-Malayan area.

I examined the patterns of distribution, species richness, and endemism of Indo-West Pacific hawkfishes (Cirrhitidae) to determine if additional support for Woodland’s hypothesis existed.

Natural history. The Cirrhitidae is a family of small to moderately-sized fishes (50-550 mm SL) which inhabit coral and rocky reefs in tropical and subtropical waters. Most are benthic and are often found living in close association with coral heads, although at least one species, *Cyprinocirrhis polyacis* (Bleeker) is a planktivorous water column forager (Randall, 1963). The Cirrhitidae is comprised of some 34-35 species in 9-10 genera (Randall, 1963; Springer, 1982). Four genera, *Cyprinocirrhis*, *Isocirrhitus*, *Neocirrhitus*, and *Oxykirrahitus*, are monotypic. In addition, the Indo-West Pacific *Amblycirrhitus* has 4-5 species, *Cirrhitus* has 4 species, *Cirrhitoaps* has 2 species, *Cirrhitechthys* has 7-8 species, and *Paracirrhitus* has 7-8 species. *Amblycirrhitus (?)* (= *Cirrhitus*) *wilhelmi*, originally described from Easter Island (Lavenberg and Yanez, 1972) but also found to occur at Rapo, Ilots du Bass, and Pitcairn Island, may actually represent a new genus (Cressey and Randall, 1978; Springer, 1982; Randall, pers. comm., April, 1985). Presently, the family Cirrhitidae is undergoing a revision (Randall, ms.).

Briggs’ provinces and the distribution of the Cirrhitidae. Briggs (1974) recognized eight provinces within the Indo-West Pacific Region (Table 1). A province was defined as an area having 10% or more endemic species. The Indo-Polynesian province was envisioned as having boundaries which included a huge area that spanned from Polynesia (excluding Hawai’i, the Marquesas, and Easter Island) westward into the Indian Ocean as far as the Persian Gulf, with species richness highest in the Indo-Malayan area. Peripheral areas (i.e., Polynesia and the central Indian Ocean) were marked by lower levels of species richness. Despite these remarkable differences within the province, the Indo-Malayan area was not considered distinct from the peripheral areas because the latter generally did not possess species that were not also found in the former. A closer examination of the patterns of cirrhitid distribution seems to contradict this.

The distribution of Indo-West Pacific cirrhitid species among the eight provinces defined by Briggs (1974) is given in Table 1. Only 14 of 24 Indo-Polynesian cirrhitid species occur in the Indo-Malayan area. Eight of these species are widely distributed in the Indo-West Pacific Region. Nine additional species occur in the “Polynesian” area of the province exclusive of the Indo-Malayan and “Indian Ocean” areas. One remaining species is limited to the Indian Ocean area exclusive of the Indo-Malayan and Polynesian areas. These non-Indo-Malayan area species are endemic to their respective areas. Those in the Polynesian area, when viewed as Pacific-plate endemics (Springer, 1982), contribute to the highest level of endemism of any Indo-West Pacific shorefish family.

Woodland’s hypothesis and the distribution of the Cirrhitidae. If we follow Woodland’s (1983) separation of the Indo-Polynesian province into two distinct provincial areas, we see that one is centered in the Pacific Ocean and the other in the Indian Ocean (I have
Table 1. Hawkfish (Cirrhitidae) distribution among Indo-West Pacific Region provinces as defined by Briggs (1974).

<table>
<thead>
<tr>
<th>Province</th>
<th>No. species</th>
<th>No. endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Sea</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>W. Indian Ocean</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>Indo-Polynesian</td>
<td>24</td>
<td>14</td>
</tr>
<tr>
<td>NW Australian</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Lord Howe-Norfolk Is.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Marquesas</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Hawaiian</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Easter Island</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>


Table 2. Hawkfishes (Cirrhitidae) endemic to areas of the Indo-West Pacific Region and levels of endemism within those areas.

<table>
<thead>
<tr>
<th>Area</th>
<th>Endemic species</th>
<th>No. spp.</th>
<th>No. endemics</th>
<th>% endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polynesian</td>
<td><em>Amblycirrhitus unimaculatus</em>  <em>Cirrhites albofasciatus</em>  <em>Cirrhitops fasciatus</em>  <em>Cirrhitichthys aureus</em>  <em>Isocirrhitus sexfasciatus</em>  <em>Paracirrhites bicolor</em>  <em>P. nilssoni</em>  <em>P. xanthus</em></td>
<td>20</td>
<td>8</td>
<td>40</td>
</tr>
<tr>
<td>Indo-Malayan</td>
<td><em>Amblycirrhitus oxyrhynchus</em>  <em>Paracirrhites ambycephalus</em></td>
<td>14</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>Indian Ocean</td>
<td><em>Amblycirrhitus indicus</em>  <em>Cirrhitus punctatus</em>  <em>Cirrhitichthys bleekeri</em>  <em>C. callitrus</em>  <em>C. guichenoti</em></td>
<td>13</td>
<td>5</td>
<td>38</td>
</tr>
</tbody>
</table>

modified the latter to consist of the Indian Ocean area, plus the Western Indian Ocean province since inclusion of the two seems desirable; see Klausewitz, 1978:35). By listing endemic species for each area, and for the Indo-Malayan area, and comparing levels of endemism with those of the Indo-Malayan area (Table 2), we see the following:

1) the Indian Ocean center of distribution possesses 13 species, eight of which are wide-ranging regional species, and five or 38% of which are endemic.

2) the Pacific Ocean center of distribution possesses 20 species; eight are wide-ranging regional species, four species are shared with the Indo-Malayan area, and eight or 40% are endemic.

3) the Indo-Malayan area possesses 13–14 species; eight are wide-ranging regional species; 3–4 are shared with the Pacific center of distribution; one species, *Cirrhitichthys serratus* Randall, may be synonymous with *C. falco* Randall, but is treated here as a fourth species. Two species, or 14%, are endemic.
Endemism and centers of distribution. High levels of endemism in both the Pacific (Polynesian) and Indian ocean centers of distribution and the low level of endemism in the Indo-Malayan area are indicative of two distinct faunal distributions which are in confluence within the Indo-Malayan area. It should be noted that this pattern does not establish strict boundaries which separate each center of distribution nor does it specify the exact location of each distributional center. However, the nature of these centers can be determined by a consideration of cirrhitid faunal elements that seem indicative of each of the centers. Two large genera, *Cirrhitichthys* and *Paracirrhites*, are considered here.

Four of the eight Indo-West Pacific species of *Cirrhitichthys* occur in the Indian Ocean area. Three of these are endemic species (Table 2). Four species also occur in the Polynesian area, but only one species is endemic (Table 2). Three species occur in the Indo-Malayan area, yet none of these are considered endemic. A single species, *C. oxycephalus* (Bleeker), is present in all three areas.

Six of the seven Indo-West Pacific species of *Paracirrhites* occur in the Polynesian area and three are endemic (Table 2). Only two species occur in the Indian Ocean area and none are endemic. Four species occur in the Indo-Malayan area, one of which is endemic (Table 2). Only two species, *P. forsteri* (Schneider) and *P. arcautus* (Cuvier), occur in all of these areas, although one species, *P. hemistictus* (Günther), occurs in two distinct color morphs in the Pacific and Indo-Malayan areas and also at Cocos-Keeling and Christmas Islands in the eastern Indian Ocean (Randall, 1963; Allen and Steene, 1979). The two latter localities possess both Pacific Ocean and Indo-Malayan affinities (Randall, 1963; Allen and Steene, 1979; Springer, 1982).

Centers of distribution and congeneric relationships. It is possible that, in view of the relative endemism and distribution patterns of *Cirrhitichthys* and *Paracirrhites*, the former genus has a distribution which is centered in the Indian Ocean area, and the latter genus has a distribution which is centered in the Polynesian area. Presumably, separately-centered distributions could have resulted from speciation events brought on by the isolation of both areas because of Quaternary lowerings of sea levels in the Indo-Malayan area, and other associated factors as discussed in Woodland’s (1983) treatment of the Siganidae. These speciation events could be relatively recent. An examination of congeneric relationships to determine which species are more closely related to one another within a genus could support the concept of rapid post-Quaternary speciation.

Within the genus *Cirrhitichthys* we find that *C. callius* Regan and *C. bleekeri* Day are more closely related to each other and also to *C. aureus* (Temminck et Schlegel), a western Pacific species. Randall (1963:442) suggested that all three species could conceivably be subspecies of a single species in continuous distribution from the Red Sea to Japan. The remaining Indian Ocean area endemic, *C. guichenoti* (Sauvage), seems more closely related to the wide-ranging *C. oxycephalus*.

The endemic Polynesian area *Paracirrhites* are more closely related to each other when compared with wide-ranging members of the genus. Randall (1963) recognized a *P. arcautus* species complex consisting of the wide-ranging and polymorphic *P. arcautus*, and *P. xanthus* Randall, *P. bicolor* Randall, and *P. nisus* Randall. The latter three species appear to be endemic to an area bounded by the Society, Tuamotu, Line and Phoenix islands. Springer (1982) assigned these endemics to sibling species groups on the basis of comments in Randall (1963). Springer considered *P. xanthus* and *P. amblycephalus* (Bleeker), the latter a rare allopatric Indo-Malayan area endemic, to be more closely related. *Paracirrhites nisus* and *P. bicolor* were also considered to be more closely related and sympatric in at least part of their respective ranges.
Table 3. Wide-ranging species of the family Cirrhitidae of the Indo-West Pacific Region.

<table>
<thead>
<tr>
<th>Species</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oxycirrhites typus</td>
<td>Red Sea to Mexico</td>
</tr>
<tr>
<td>Cirrhitichthys oxycephalus</td>
<td>Red Sea to Mexico and Colombia</td>
</tr>
<tr>
<td>Amblycirsirrhus bimacula</td>
<td>Red Sea to Hawaii</td>
</tr>
<tr>
<td>Paracirrhites forsteri</td>
<td>Red Sea to Hawaii</td>
</tr>
<tr>
<td>P. arcatus</td>
<td>Red Sea to Hawaii</td>
</tr>
<tr>
<td>Cirrhitus pinnulatus</td>
<td>Red Sea to Hawaii</td>
</tr>
<tr>
<td>Cirrhitops fasciatus</td>
<td>Madagascar, Mauritius, Japan, Hawaii</td>
</tr>
<tr>
<td>Cyprinocirrhites polyactis</td>
<td>E. Africa, Japan to NE Australia</td>
</tr>
</tbody>
</table>

By comparison, the pattern of distribution of sibling species pairs of cirrhitid species contrasts with that of siganids within the same centers of distribution. Woodland (1983) found one member of each of five sibling species pairs occurring in the Pacific and Indian oceans respectively. In the Cirrhitidae, the daughter species of both *Cirrhitichthys* and *Paracirrhites* may have evolved separately from isolated peripheral populations within their respective centers of distribution. Such a possibility appears to exist for siganids of the subgenus *Lo* (Woodland, 1983).

Although many species of cirrhitids have distributions which seem limited to either the Polynesian, Indian Ocean, or Indo-Malayan areas, at least eight species in five genera (Table 3) are widely distributed in the Indo-West Pacific Region. Two of these species, *Cirrhitichthys oxycephalus* and *Oxycirrhites typus* Bleeker, have ranges which extend from the Red Sea well into the Eastern Pacific Region (Randall, 1963). Just why some members of a genus are wide-ranging and others are narrowly-endemic is open to speculation. For the Siganidae, Woodland (1983:715) proposed that, in the case of allopatric speciation, one could predict that new species could evolve rapidly in physically isolated areas. Further, he viewed isolation as a function of the species' potential for colonization. If this view were accepted, then it should be possible to correlate a species' "lifestyle" (Woodland, 1983:715) with its distribution and subsequent potential to speciate. Those species which appear to be successful colonists should possess adaptations which would promote dispersal and allow sufficient gene flow between separate populations to inhibit speciation. This pattern seems true of wide-ranging cirrhitid species. Conversely, those species whose populations seem prone towards speciation would possess limited distributions because of the lack of adaptations which promote dispersal, colonization, and gene flow. This pattern seems true of those species endemic to distinct centers of distribution.

Such possibilities were found to exist for the Siganidae (Woodland, 1983). One wide-ranging species, *Siganus argenteus* (Quoy et Gaimard), possesses a distinct pre-juvenile stage which seems adapted for an extended pelagic existence. This species, and *S. spinus* (Linnaeus), another widely-distributed species, both spend considerable time in the pelagic realm and may be dispersed widely before settling out on coral reef flats. In contrast, those siganids of the subgenus *Lo* lack this adaptation and seem more prone to speciation because of the effects of isolation.

The existence of a similar adaptation which could promote dispersal and reduce speciation potential in the Cirrhitidae may exist in some species. Leis and Rennis (1983) reported two specializations in larvae of wide-ranging *Cirrhitops fasciatus* (Bennett), *Amblycirsirrhus bimacula* (Jenkins), *Cyprinocirrhites polyactis*, and possibly, a species of *Paracirrhites*. One specialization was the presence of a gas bladder, an organ of obvious dispersal value, which was absent from adults. The second was the presence of a chin barbel in
the larvae of some species; the function of this organ was not readily apparent.

Ideally, the larvae of all Indo-West Pacific cirrhitid species should be identified and examined to determine if similar kinds of specialization are limited to wide-ranging species. A determination of lineages within both *Cirrhitichthys* and *Paracirrhites* should be made to establish the probable identity of ancestral species from which daughter species evolved in either the Polynesian or Indian Ocean areas. Further, a comparative analysis of the behavior and ecology of endemic *Cirrhitichthys* and *Paracirrhites* within these areas is desirable. Patterns of behavior which would determine habitat utilization among isolated populations of species in either genus in the absence of those of the other could be examined to determine what selection pressures exist that would effectively prevent potential colonists from successfully colonizing either center of distribution. Finally, the determination of the exact centers and boundaries of both distributional areas, perhaps by continued sampling of isolated areas in each, should be made and compared with those determinations made for other taxa.

Acknowledgments

I wish to thank J. E. Randall, W. H. LeGrande, the Department of Ichthyology of the California Academy of Sciences, the Tatsuo Tanaka Memorial Biological Station and the University of Guam Marine Laboratory for their assistance. This paper benefitted from discussions with J. E. Randall, J. T. Moyer, D. J. Woodland, T. Roberts, E. Fischer, and R. F. Myers. J. M. Fitzsimons kindly reviewed the manuscript. I gratefully acknowledge the generous support provided by the Japan Airlines 50th 747 Asian Studies Scholarship, the Organization Relief Fund of the Louisiana State University Graduate School, and the LSU Museum of Natural Science. This is contribution no. 61 of the Tatsuo Tanaka Memorial Biological Station and contribution no. 221 of the University of Guam Marine Laboratory.

Literature Cited


Permission to microfilm the following article of my dissertation has been requested from the publisher, The Ichthyological Society of Japan:

Courtship and spawning of the hawkfish Cirrhichthys falco at Miyake-jima, Japan.
Courtship and Spawning of the Hawkfish

*Cirrhitichthys falco* at Miyake-jima, Japan

Terry J. Donaldson
(Received December 28, 1985)

The hawkfish *Cirrhitichthys falco* Randall (Cirrhitidae) occurs from Japan (Masuda *et al.*, 1975) south to the Philippines (Randall, 1963), the Marianas (Myers and Shepard, 1980), Pohnpei (Gawel, unpubl. ms.), Fiji (Springer, 1982) to northeastern Australia (Russell, 1983) as far as Sydney (R. E. Thresher, pers. comm.). Although this species occurs at Miyake-jima, Izu Islands, Japan (34°05'N, 139°30'E) it is rare and may often be mistaken for *C. aprinus* (Bleeker).

Courtship and spawning behavior of cirrhitid fishes has been largely limited to aquarium observations. Lobel (1974), Takeshita (1975) and Tanaka *et al.* (1985a) reported on courtship and spawning of *Oxycirrhites typus* (Bleeker); Suzuki *et al.* (1980) reported spawning behavior of *Cirrhitichthys aureus* (Temminck et Schlegel); Tanaka *et al.* (1985b) reported spawning behavior of *Cirrhitoptes hubbardi* (Schultz).

Field studies of cirrhitid courtship and spawning behavior have begun to appear. Thresher (1984) briefly mentioned courtship of *Paracirrhites arcatus* (Cuvier) from One Tree Island, Great Barrier Reef and has also provided a detailed description of courtship and spawning of *Cirrhitichthys oxycephalus* (Bleeker) occurring in the Gulf of California. Here I report courtship and spawning behavior of a congener, *Cirrhitichthys falco*, at Miyake-jima.

Study area and methods

Courtship and spawning behavior of *C. falco* were studied on seven consecutive days between 6-12 August 1985 in Igaya Bay. All observations were made at a single site located ca. 100 m NE of the pier at Igaya Port at a depth of 10 m. The courtship and spawning site, henceforth referred to as the rendezvous site (Moyer, 1980, 1984), consisted of a rocky outcropping located atop a large boulder (ca. 2.5 m high) immediately adjacent to an abandoned pipeline. A number of sea anemones (*Parasicyonis* spp.) were clustered on the seaward margin of the boulder, directly beneath the outcropping. The adjacent substratum consisted of five smaller boulders (ca. 0.5-2.0 m high), mixed volcanic rubble, sand, and various algae. A slight to moderate current, made stronger occasionally by the effects of passing swells generated by storms well offshore, flowed seaward past the site. Water temperatures ranged from 23 to 26°C.

Observations were made using SCUBA, and data were recorded on plastic slates and by underwater photography. Two dives were made daily, usually between 10:30-14:00 h and 17:45-19:00 h. The first dive consisted of a population census and observations of habitat utilization, territorial boundaries, and aggressive behavior, while the second dive was devoted to observations of courtship and spawning.

Results

Social organization and aggressive behavior. Two fish, a male (designated as M1, ca. 80 mm SL) and a female (F1, ca. 70 mm SL) were observed near and at the rendezvous site. No other conspecifics were present in the area. The female occupied a small territory (ca. 3 m²) immediately beneath the outcropping on the shoreward side of the boulder. She was quite secretive and rarely left the shelter of a small hole located in this area. The male foraged over a territory, ca. 25 m², adjacent to and including the rendezvous site. No active territorial defense against conspecifics was observed. The male did defend parts his territory against some interspecific intruders. Many territorial interactions were with a neighboring congener, a large male (ca. 90 mm SL) *C. aprinus*, which occurred at the rendezvous site and at a common territorial boundary shared with this species. Defense was particularly pronounced just prior to and after sunset when courtship between M1 and F1 was about to commence. Males of both species interacted aggressively with one another but not with the female *C. falco*.

Courtship and spawning. Five distinct motor patterns were recognized during male-female interactions: 1) Parallel Rest, 2) Nudging, 3) Circling, 4) Hopping and 5) Spawning. Circling and Parallel Rest were also seen in interactions be-
tween male *C. falco* and *C. aprinus*. Motor patterns are described as follows:

1) **Parallel Rest.** The male and female aligned themselves on the substratum in a position parallel to one another (Fig. 1A). Occasionally, the male was positioned slightly behind the female. This motor pattern often preceded the performance of other motor patterns and always preceded spawning.

2) **Nudging.** During Nudging the male placed his snout against the flank of the female at a point directly beneath the soft dorsal fin (Fig. 1B) while both the male and female remained motionless. The behavior was seen soon after pair formation and was often repeated during a courtship encounter. This motor pattern is similar to that reported for *C. oxycephalus* by Thresher (1984).

3) **Circling.** The male positioned his snout near the caudal fin of the female and vice versa; together they swam in a circular fashion (Fig. 1C) around the rendezvous site and made frequent stops to Parallel Rest. This motor pattern frequently occurred while the male and female were engaged in Hopping.

4) **Hopping.** The male and female engaged in short swimming bouts, resembling hopping, around the rendezvous site. The male was positioned slightly behind the female as they swam (Fig. 1D). Hopping was often preceded and followed by Parallel Rest displays. This motor pattern was also reported for *C. oxycephalus* by Thresher (1984).

5) **Spawning.** After the last Parallel Rest display the male and female ascended into the water column to a height of 20-50 cm, pointed their snouts downward (Fig. 1E) from the parallel rest position, and released a cloud of gametes before quickly returning to the substratum.

Courtship and spawning events involved only M1 and F1 although the male *C. aprinus* attempted courtship with F1 on a number of occasions but was always driven off by M1. Time of courtship commencement ranged from one minute before sunset to 20 minutes past sunset over a period of seven days and lasted between 2-16 minutes before spawning occurred (Table 1). Typically, either M1 or F1 arrived at the rendezvous site first and was joined immediately by the other. On one occasion M1 was observed to herd F1 towards the rendezvous site from a position directly below the site.

Once at the rendezvous site the pair first exhibited the Parallel Rest motor pattern for 5-20 s and then the male nudged the female. Hopping and Circling followed with intervals of Parallel Rest and Nudging and ended in the Parallel Rest for a period of 10-40 s. The spawning ascent immediately followed the last Parallel Rest display. Spawning times varied between 4-22 minutes past sunset (Table 1). After the release of gametes, the small white cloud was visible for 3-9 s. Egg predation was not observed.

After returning to the substratum the male attempted to court the female again on five of seven evenings when spawning was observed. The male assumed the Parallel Rest position and nudged the female. However, this second attempt at courtship was never successful; either the female returned to her shelter beneath the rendezvous site or the courtship behavior was interrupted by the approach of the male *C. aprinus* or other

### Table 1. Temporal patterns of courtship and spawning of the hawkfish *Cirrhitichthys falco* at Miyake-jima, Japan.

<table>
<thead>
<tr>
<th>Date</th>
<th>Water temperature</th>
<th>Sunset</th>
<th>Courtship onset (Min past sunset)</th>
<th>Duration (Min)</th>
<th>Spawning (Min past sunset)</th>
<th>No. interruptions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre-spawn</td>
</tr>
<tr>
<td>6-VIII-85</td>
<td>26°C</td>
<td>18:41h</td>
<td>-1</td>
<td>5</td>
<td>+4</td>
<td>0</td>
</tr>
<tr>
<td>7-VIII-85</td>
<td>26°C</td>
<td>18:40h</td>
<td>0</td>
<td>15</td>
<td>+15</td>
<td>0</td>
</tr>
<tr>
<td>8-VIII-85</td>
<td>26°C</td>
<td>18:39h</td>
<td>+20</td>
<td>2</td>
<td>+22</td>
<td>3*</td>
</tr>
<tr>
<td>9-VIII-85</td>
<td>23°C</td>
<td>18:38h</td>
<td>+15</td>
<td>7</td>
<td>+22</td>
<td>0</td>
</tr>
<tr>
<td>10-VIII-85</td>
<td>23°C</td>
<td>18:37h</td>
<td>+13</td>
<td>3</td>
<td>+16</td>
<td>0</td>
</tr>
<tr>
<td>11-VIII-85</td>
<td>23°C</td>
<td>18:36h</td>
<td>+9</td>
<td>3</td>
<td>+12</td>
<td>1*</td>
</tr>
<tr>
<td>12-VIII-85</td>
<td>23°C</td>
<td>18:35h</td>
<td>+2</td>
<td>16</td>
<td>+18</td>
<td>2</td>
</tr>
</tbody>
</table>

* C. *cirrhitocephalus* (male); b, *Epinephelus fasciatus*; c, *Anthias (Franzia) squamipinnis* (male); d, *A. (F.) squamipinnis* (female); e, *Stegastes alternatus*; f, *Pempheris oualensis.*
Donaldson: Courtship and Spawning of Hawkfish

Fig. 1. Motor patterns observed during courtship and spawning of the hawkfish *Cirrhitichthys falco* at Miyake-jima, Japan. A) Parallel Rest, B) Nudging, C) Circling, D) Hopping and E) Spawning. (Male denoted by M; female denoted by F).

Interspecific interactions. Courtship behavior was often interrupted by the presence of the male *C. aprinus* or other species of fishes, resulting in variable durations in time before spawning occurred (Table 1). The male *C. aprinus* interrupted courtship both before and after the spawning; interruption took the form of swift charges at M1 and attempted courtship with F1 before M1 was able to drive the male *C. aprinus* away. Courtship motor patterns displayed by the male *C. aprinus* included the Parallel Rest and Hopping. Other species of fishes in the area interrupted courtship both before and after M1 and F1 spawned (Table 1). Courting male and female *Anthias* (Franzia) *squamipinnis* (Peters), foraging *Epinephelus fasciatus* (Forsskål) and territorial *Stegastes alius* (Okada et Ikeda) all interrupted *C. falco* during the first bout of courtship prior to spawning; an aggregation of *Pempheris oualensis* Cuvier interrupted post-courtship displays after spawning on one occasion.

Discussion

Social organization and mating system in Cirrhitidae. The occurrence of a male-female pair of *C. falco* at the spawning site was consistent with observations of this species made at Guam, Mariana Islands although social groups of up to six individuals have also been seen (pers. obs.). Thresher (1984) reported social groups of one male and up to seven females for *C. oxycephalus* in the Gulf of California. I have seen male-female pairs only of the following other species of cirrhitids: *O. typus* at Pohnpei, Caroline Islands; *Paracirrhites hemisticus* (Günther) at Pohnpei and Guam; *P. forsteri* (Schneider) at Pohnpei and Guam; *Neocirrhites armatus* Castelnau at Guam. However, *N. armatus*, *P. arcatus*, *P. forsteri* and *P. hemisticus* have been observed also in groups of one male and up to four females at Guam. J. T. Moyer (pers. comm.) reported sightings of two *C. aprinus* social groups at Igaya Bay, Miyake-jima during 1984–85. Each social group consisted of one male and two females. Both social units disappeared during a typhoon in June, 1985. This same typhoon may account for the attempts made by the male *C. aprinus* at courting the female *C. falco*; the former may have lost his mate(s) by the typhoon. Moyer (1981) observed interspecific spawning between a male *Centropyge*
shepardi Randall et Yasuda and a female C. bispinosus (Günther) at Guam, where the latter species is rare and the former is common. Moyer hypothesized that such interspecific spawnings usually involve females of rare species and males of common species. Such spawnings may occur as a result of constraints imposed by energy expenditure in the production of eggs versus sperm; females should engage in interspecific spawnings only when male conspecifics are absent whereas males can afford to be less discriminating in choosing mates.

Thresher (1984) considered C. oxycephalus to possess a mating system of male-dominated socially controlled hermaphroditism. Kobayashi et al. (1985) recently reported the existence of protogynous hermaphroditism in C. falco and in C. aureus, C. aprinus and Cirrhitops hubbardi as well. Donaldson (unpubl. ms.) has recently described the mating and social systems of P. arcatus, P. forsteri, P. hemistictus, and N. armatus.

Male defense of both the rendezvous site and the female was indicated in C. falco, but the relative importance of defending one over the other is uncertain. J. T. Moyer (pers. comm.) reported that males of C. aprinus at Miyake-jima travelled over "well-known" paths in given areas but did not engage in intraspecific territorial defense of these areas although they did defend females from male conspecifics.

Interspecific comparisons of courtship and spawning. Four of the C. falco courtship and spawning motor patterns observed at Miyake-jima are relatively consistent with those observed for C. oxycephalus in the Gulf of California (Thresher, 1984). These patterns are Parallel Resting, Nudging, Hopping and the spawning ascent. Male C. oxycephalus approached females at a single spawning site and, in succession, nudged, hopped, and rested before executing the spawning ascent. Two of the motor patterns, Nudging and the spawning ascent, seem common of pelagic-spawning reef fishes in general. Males of C. aprinus apparently nudge females by lying over their bodies (J. T. Moyer, pers. comm.); I have observed males of N. armatus performing a similar pattern during courtship. The significance of the Nudging motor pattern is uncertain, although Thresher (1984) speculated that it served to stimulate egg movement in the female prior to spawning. The spawning ascent allows free-floating eggs to escape predation from bottom-dwelling organisms by their release into the water column above the substratum. The height of the release may be constrained by the risk of predation on the spawning adults (Thresher, 1984). Emery (1973), Robertson and Hoffman (1977), Moyer and Yogo (1982) and Thresher (1984) reported that predators often attacked spawning individuals; the probability of such attacks may be minimized by rapid ascents to minimal heights that would allow spawning adults to avoid the risk of predation while conveying an anti-predation advantage to the free-floating eggs released during the ascent (Thresher, 1984). A test of this hypothesis on small site-attached species seems warranted.

Acknowledgments

I wish to thank J. T. Moyer, J. E. Randall, P. L. Colin, L. J. Bell-Colin, D. Y. Shapiro, J. M. Fitzsimons, M. C. Wilkins and S. de C. Wilkins for their advice, comments and assistance. G. B. Constantino kindly prepared Fig. 1. I also thank the Tatsuo Tanaka Memorial Biological Station for its hospitality. This work was made possible through the generous support of the Japan Airlines 50th 747 Asian Studies Scholarship and the LSU Museum of Natural Science. This is contribution no. 64 of the Tatsuo Tanaka Memorial Biological Station.

Literature cited


Moyer, J. T. 1981. Interspecific spawning of the pygmy angelfishes Centropyge shepardi and C.
Donaldson: Courtship and Spawning of Hawkfish


(Section of Ichthyology, Museum of Natural Science and Department of Zoology and Physiology, Louisiana State University, Baton Rouge, Louisiana 70893, USA.)

三宅島におけるサラサゴンベの求愛・産卵行動

Terry J. Donaldson

1985年8月、伊豆諸島の三宅島においてサラサゴンベ（ゴンベ科）の産卵行動がはじめて観察された。1週間の調査期間中、雄（体長8cm）と雌（7cm）のペアが産卵場所となる洞を中心として定住していた。毎日、日没前後になると、ペアは定まった洞の上で一連の求愛行動を始め、3-16分後に20-50cm高さを保持して放射状に散らばった。産卵前後には、雌が産卵状態の雄がこの間求愛することや、その後の魚種による干渉もしばしば観察された。本種の社会構造、繁殖行動および求愛・産卵行動を他のゴンベ科の魚種と比較して考察した。
12 September, 1988

Dr. William J. Richards,
Editor
Bulletin of Marine Science
Rosenstiel School of Marine and Atmospheric Science
University of Miami
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Terry J. Donaldson
Section of Ichthyology

Title:

SOCIAL ORGANIZATION AND REPRODUCTIVE BEHAVIOR OF
THE HAWKFISH CIRRHITICHTHYS FALCO (CIRRHITIDAE)

Terry J. Donaldson

ABSTRACT

The social organization and reproductive behavior of the hawkfish Cirrhitichthys falco Randall (Cirrhitidae) was studied at Tanguisson Reef, Guam and at additional Pacific localities. Single males dominated social groups of 1–7 females; "sneaker" males and juveniles were also present in some social groups. Male-male social interactions were rare and limited to encounters between dominant males and sneaker males, rather than adjacent dominant males. Male-female, female-female and male-juvenile interactions were usually limited to the onset of dusk. Interspecific interactions were also common at this time.

Courtship and spawning behavior was sequential and occurred daily at the Tanguisson site, commencing just after sunset and continuing until darkness. Thirteen motor patterns were utilized during courtship resulting in pelagic spawning.

Social organization and reproductive behavior of cirrhitid fishes are largely unknown. Reproductive behavior has been described from aquarium studies of only three species: Oxycirrhites typus (courtship and spawning—Lobel, 1974; Takeshita, 1975; Tanaka et al., 1985a); Cirrhitichthys aureus (spawning—Suzuki et al., 1980); and Cirrhitops hubbardii (spawning—Tanaka et al., 1985b). Recently, field studies of cirrhitid reproductive behavior and social organization have been reported. Thresher (1984) described courtship and spawning behavior of Cirrhitichthys oxycephaIus occurring in the Gulf of California and briefly described courtship behavior of Paracirrhites arcatus at One Tree Island, Great Barrier Reef. Y. Yogo (pers. comm.) has described the courtship and spawning of Cirrhitichthys aureus in Japan. Donaldson (unpubl. ms.) has described the social organization and reproductive behavior of Paracirrhites arcatus, P. forsteri and P. hemistictus at Guam, Mariana Islands, and Cirrhitichthys aprinus at Miyake-jima, Izu Islands, Japan. Donaldson (1986) also reported courtship and spawning behavior of a single pair of Cirrhitichthys falco occurring at Miyake-jima. The purpose of this paper is to describe the social organization and reproductive behavior of C. falco occurring at a number of western Pacific localities.

Cirrhitichthys falco occurs from Japan (Masuda et al., 1985) south to the Philippines and Marianas (Randall, 1963; Myers and Shepard, 1980), Ponape (pers. obs.), Fiji (Springer, 1982), Papua New Guinea (pers. obs.) and northeastern Australia (Russell, 1983) as far south as Sydney Harbour (R. E. Thresher, pers. comm.).

METHODS

Cirrhitichthys falco was studied between 1 December 1985 and 1 August 1986 at Guam, Mariana Islands. The principal study site was located at Tanguisson Reef in an area some 25–50 m beyond the reef margin on a gentle reef slope at a depth of 8–10 m. A field of underwater communications cables lay within and adjacent to the southern boundary of the site. The substratum consisted of coral pavement, loose coral boulders, live coral (primarily Pocillopora elegans, P. eydouxi and Porites rus), hydrozoans (Milipora platyphylla and M. laifolia), dead coral (mostly Acropora and Pocillopora spp. killed by Acanthaster planci), and various algae (primarily cyanophytes). Numerous holes and small pockets or caves were present in the pavement. Current activity ranged from slight to moderate but increased dramatically from the effects of passing storms which generated large ground swells and heavy surf, often rendering the site inaccessible. Water temperatures ranged from 25–27°C.
Table 1. Locality data of *Cirrhitichthys falco* social groups in this study

<table>
<thead>
<tr>
<th>Locality</th>
<th>Habitat</th>
<th>Substratum</th>
<th>Depth (m)</th>
<th>No. groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanguisson Reef, Guam</td>
<td>Reef slope</td>
<td>pavement/rock/coral</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Igaya Bay, Miyake-jima, Izu Islands,</td>
<td>Patch reef</td>
<td>pavement/rock/coral</td>
<td>5-8</td>
<td>1</td>
</tr>
<tr>
<td>Japan</td>
<td>Sunken ship</td>
<td>encrusted deck</td>
<td>3-15</td>
<td>2</td>
</tr>
<tr>
<td>Guadalcanal, Solomon Islands</td>
<td>Reef slope/flat</td>
<td>pavement/rock/coral</td>
<td>2-10</td>
<td>6</td>
</tr>
<tr>
<td>Papuan Barrier Reef, Papua New Guinea</td>
<td>Reef slope/flat</td>
<td>pavement/rock/coral</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Lizard Island, Great Barrier Reef</td>
<td>Reef slope</td>
<td>sand/rock/coral</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>Yonge Reef, Great Barrier Reef</td>
<td>Reef slope</td>
<td>sand/rock/coral</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Supplemental observations of *C. falco* social organization were made at Miyake-jima, Japan (August 1985 and September 1986), Guadalcanal, Solomon Islands (October 1986), the Papuan Barrier Reef, Papua New Guinea (November 1986), and Lizard Island and Yonge Reef, Great Barrier Reef, Australia (December 1986). Locality data are summarized in Table 1.

Observations were made using SCUBA, and data were recorded on plastic slates and by underwater photography. One or two dives were made daily, surf conditions permitting, at 1000-1630 h and 1715-1915 h, except at Guadalcanal where dives were made between 0800-1200 h. Individual fish were recognized by a combination of factors: relative body size, color pattern, and location within the study area, or by use of color-coded glass bead tags. A population census and observations of social behavior and habitat use were usually made during the first dive. Social behavior, courtship and spawning were observed and photographed under low light conditions during the second dive. Current fish names follow Randall (1963), and Myers (in press).

**RESULTS**

**Social Organization and Interaction.**—Fifteen social groups were studied at various localities (Table 1). Group sizes ranged from 2-10 individuals, including mature males, "sneaker" males, mature females and juveniles. Single dominant males controlled 1-7 females within a group. Mean group size, consisting of dominant males and mature females, was 3.9 (±1.7) individuals. Sneaker males were observed in only one social group, at Tanguisson Reef, having appeared late in the study at this locality. Juveniles, present as individuals at all localities, were socially active in only two social groups, one each at Tanguisson Reef and Lizard Island.

Male body sizes (*X* = 65.0 ± 8.8 mm TL; *N* = 17) were greater compared to

Table 2. Mean (range; *N*) onset of courtship in minutes past sunset for social groups of *Cirrhitichthys falco* at Tanguisson Reef, Guam (Data are pooled from social groups of two different sizes and compositions)

<table>
<thead>
<tr>
<th>Courtship attempt</th>
<th>Group composition</th>
<th>1 male/3 females</th>
<th>1 male/5 females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>13.2 (9-23; <em>N</em> = 21)</td>
<td>11.6 (4-18; <em>N</em> = 9)</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>15.7 (12-20; <em>N</em> = 16)</td>
<td>15.1 (8-24; <em>N</em> = 6)</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>19.4 (14-25; <em>N</em> = 14)</td>
<td>15.7 (11-19; <em>N</em> = 7)</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td>18.4 (15-22; <em>N</em> = 7)</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td>21.9 (18-26; <em>N</em> = 7)</td>
</tr>
</tbody>
</table>
females ($X = 51.8 \pm 12.1$ mm TL; $N = 43$; three additional females were not measured) but males in some groups were smaller than females in other groups. Intra- and interspecific social behavior was recorded at Tanguisson Reef only. Interactions between males was rare and restricted to encounters between a dominant male in a large social group (one male, five females and two juveniles) and two sneaker males. These encounters occurred when either of the sneaker males attempted courtship with one or more of the females present in the group and was challenged by the dominant male. Encounters between dominant males were nonexistent, owing to the relative distance (2–13 m) between territories held by dominant males. Male-female interactions within groups were more common, especially during the time just prior to the onset of male-female courtship. Females often gave threat displays towards the approaching male; threats consisted of a female exposing her body flank laterally toward the male while erecting her dorsal fin. Males responded by aggressively herding females towards a particular spawning site. Males attacked juveniles within the group at this time. Female-female interactions within social groups were most often observed. These interactions occurred prior to or during courtship between the male and one of the females in the presence of another female. For example, two females from a social group consisting of a male and three females often shared the same courtship site; occasionally, either female would attack the other when the male approached during the courtship period or when courtship was underway. In addition, a large female in one social group appeared to display courtship patterns towards another, smaller female within that same group.

Interspecific interactions also occurred with regularity. Encounters at locations associated with courtship and spawning occurred just prior to or after sunset. Male and female *C. falco* often interacted with species that utilized a portion of the spawning site for crepuscular refuging. These species included the chaetodontids *Chaetodon reticulatus*, *C. ephippium*, *C. bennetti* and a labrid, *Pseudochelinus hexataenia* which also engaged in mating at the same site. In addition, interactions with foraging predators, including the holocentrid *Sargocentron spiniferum* and the very abundant serranid *Cephalopholis urodelus*, occurred. On a number of occasions the latter species attacked *C. falco* during unsuccessful twilight feeding attempts which were repulsed when the *C. falco* firmly erected its dorsal spines; the serranid then switched to displays of agonistic behavior to which the *C. falco* responded defensively.

### Courtship and Spawning Motor Patterns

Thirteen motor patterns were recognized during the courtship and spawning interactions observed at Tanguisson Reef: (1) Parallel Rest, (2) Anti-Parallel Rest, (3) Perpendicular Rest, (4) Lead and Follow, (5) Circling, (6) Hopping, (7) Passing, (8) Nudging, (9) Mounting, (10) Tail Beating, (11) Lifting, (12) Quivering, and (13) Spawning. Parallel Rest (Fig. 1A), Nudging, Circling, Hopping and Spawning have already been described for *C. falco* (Donaldson, 1986). Circling and Hopping were seldom observed in the Tanguisson Reef population. The remaining motor patterns are described as follows: ANTI-PARALLEL REST. The male and female positioned their bodies parallel to one another but faced in opposite directions (Fig. 1B). PERPENDICULAR REST. The male positioned its body perpendicular to that of the female and pointed its snout towards her flank. This motor pattern often occurred in conjunction with Lead and Follow and preceded Nudging and Mounting. LEAD AND FOLLOW. The female positioned herself slightly ahead and to the side of the male and swam in short bursts just above the substratum around the courtship site with the male following close behind (Fig. 1C). The female also used this behavior to attract the
male to a spawning site and during interrupted courtship or when the male broke off courtship and attempted to move on to another female. **Passing.** The male, starting from the Parallel Rest position, swam in front of the stationary female, exposed his flank to her, looped behind the female and returned to the Parallel Rest position but on the opposite side from where it started. Occasionally, the male swam over the female's dorsal fin and looped around her opposite flank before coming to rest alongside that flank. This motor pattern commonly occurred during courtship periods of 60 sec or more. **Mounting.** The male placed his lower flank in a position atop the female on either side of her dorsal fin by moving from the Nudging position and pressed his body against her's. **Tail Beating.** The male rapidly beat his caudal fin against the female during Mounting, or against the substratum or water to maintain the mounted position. **Lifting.** Both male and female extended their pectoral fins against the substratum, lifted their bodies briefly and then lowered them again by relaxing their pectoral fins. This motor pattern occurred either singly or in a few rapid bursts, the latter often just prior to the spawning ascent. **Quivering.** The male's flank quivered rapidly for 1–2 sec during mounting. This motor pattern appeared to communicate male readiness prior to the spawning ascent and females usually responded by Lifting before executing the ascent.

**Courtship and Spawning Behavior.**—Courtship of *C. falco* at Tanguisson Reef usually commenced when the male appeared at one or more of the spawning sites after sunset and was met by the female who resided near that site. If two females shared a common spawning site the male courted only one at a time; occasionally, both females would attempt to participate in courtship at the same time and the male either switched back and forth between the two or chased one off in favor of the other.

Courtship proceeded sequentially on a daily basis with the male moving from one female to the next after each courtship attempt. There was no apparent order of visitation from one day to the next. Courtship attempts in one social group were occasionally interrupted by the intrusion of one or two sneaker males which lived on the periphery of the social group. These males often attempted to court females and experienced occasional success.

Typical courtship began after pair formation when a male and female assumed the Parallel Rest position. The male nudged the female, who responded with the Lead and Follow pattern. The pair reassumed the Parallel Rest position and then the male continued with a sequence consisting of the following patterns: Nudging, Mounting, Perpendicular Rest and Passing. Hopping and Circling were rarely observed. Prior to the spawning ascent the male executed the following patterns: Mounting, Tail Beating and Quivering. Then, from either the mounted or Parallel Rest positions both male and female began Lifting, followed by a quick burst of swimming upwards into the water column to a point 5–30 cm above the substratum. At this point both male and female turned their snouts downward and released gametes which formed a small white cloud that was visible for 3–5 sec. Following gamete release the pair quickly swam, with erected dorsal spines, back down to the spawning site (Fig. 1D) and rested for 5–70 sec, and often in the Parallel Rest position. Afterwards, the male made his way to any remaining

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Figure 1. Courtship and spawning motor patterns of *Cirrhitichthys falco*: A, upper) Parallel Rest; B, lower) Perpendicular Rest; C, upper) Lead and Follow; D, lower) descent from spawning ascent; note erect dorsal spines used to deter predators.
Table 3. Mean duration (±SD; N) of courtship leading to spawning in seconds for social groups of *Cirrhitichthys falco* at Tanguisson Reef, Guam (Data are pooled from social groups of two different sizes and compositions)

<table>
<thead>
<tr>
<th>Courtship no.</th>
<th>1 male/3 females</th>
<th>1 male/5 females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>108.2 (77.2; N = 20)</td>
<td>112.8 (104.7; N = 9)</td>
</tr>
<tr>
<td>2</td>
<td>75.9 (68.2; N = 15)</td>
<td>58.3 (65.8; N = 9)</td>
</tr>
<tr>
<td>3</td>
<td>49.3 (54.2; N = 14)</td>
<td>39.5 (20.9; N = 6)</td>
</tr>
<tr>
<td>4</td>
<td>—</td>
<td>59.2 (46.4; N = 6)</td>
</tr>
<tr>
<td>5</td>
<td>—</td>
<td>88.8 (56.2; N = 7)</td>
</tr>
</tbody>
</table>

females within the social group and repeated the courtship sequences while the spent female found shelter against a rock or in a *Porites rus* coral head. The male sought similar shelter after completing spawning attempts with all of the females in his group.

The onset of first courtship (Table 2) ranged between 4–23 minutes past sunset. Mean courtship duration in successful attempts (Table 3) ranged between 39.5–112.8 sec. Spawning times (Table 4) occurred as early as 6 and as late as 28 minutes past sunset, depending upon the size of the social group and the number of females visited. Not all courtship and spawning attempts were successful. Males averaged 3.6–6.1 attempts per day and achieved spawning success 63.9–76.1% of the time depending upon group size (Table 5).

**DISCUSSION**

**Social Organization and Interaction.**—*Cirrhitichthys falco* occurred in male-dominated social groups of 1–7 females. Groups consisting of a male-female pair were probably atypical and the result of biotic (i.e., predation upon other group females or the successful sequestering of a group female by a sneaker male) or abiotic

Table 4. Mean time (range; N) of spawning in minutes past sunset for social groups of *Cirrhitichthys falco* at Tanguisson Reef, Guam (Data are pooled from social groups of two different sizes and compositions)

<table>
<thead>
<tr>
<th>Spawning no.</th>
<th>1 male/3 females</th>
<th>1 male/5 females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15.2 (11–24; N = 20)</td>
<td>13.3 (11–19; N = 9)</td>
</tr>
<tr>
<td>2</td>
<td>17.6 (13–22; N = 16)</td>
<td>16.3 (9–24; N = 9)</td>
</tr>
<tr>
<td>3</td>
<td>20.1 (14–25; N = 15)</td>
<td>16.6 (12–20; N = 7)</td>
</tr>
<tr>
<td>4</td>
<td>—</td>
<td>19.8 (16–23; N = 6)</td>
</tr>
<tr>
<td>5</td>
<td>—</td>
<td>22.8 (19–28; N = 5)</td>
</tr>
</tbody>
</table>
Table 5. Courtship success in social groups of *Cirrhitichthys falco* at Tanguisson Reef, Guam (Data are pooled from social groups of two different sizes and compositions)

<table>
<thead>
<tr>
<th>Group composition</th>
<th>Variable</th>
<th>1 male/3 females</th>
<th>2 male/5 females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Courtship attempts/day (X; ±SD, N)</td>
<td>3.6 (1.4; N = 71)</td>
<td>6.1 (1.5; N = 61)</td>
</tr>
<tr>
<td></td>
<td>Courtship attempts/day resulting in spawning (X; ±SD, N)</td>
<td>2.6 (0.7; N = 49)</td>
<td>3.9 (1.8; N = 37)</td>
</tr>
<tr>
<td></td>
<td>Percent success</td>
<td>76.1</td>
<td>63.9</td>
</tr>
</tbody>
</table>

factors (i.e., disturbed weather, such as typhoons, which catastrophically affects the composition of a group). Male-dominated social groups are undoubtedly quite common within the family itself. *Cirrhitichthys oxycephalus* existed in social groups consisting of one male and two females at Lizard Island, Great Barrier Reef (pers. obs.) and one male and seven females in the Gulf of California (Thresher, 1984). *Cirrhitichthys aprinus* at Miyake-jima, Japan occurred in groups of one male and two females (J. T. Moyer, pers. comm.) and I have observed this species in groups of one male and four females in Papua New Guinea. Other cirrhitids, including *Cirrhitus pinnulatus*, *Neocirrhites armatus*, *Oxycirrhites typus*, *Paracirrhites arcatus*, *P. forsteri* and *P. hemistictus* have been observed in male-dominated social groups of two or more females, although male-female pairs have also been observed (Donaldson, unpubl. ms.).

Male-male social interactions, although infrequent, appeared to be related to mate defense insofar as such interactions occurred only in the presence of females. Male *C. falco* at Miyake-jima appeared to defend both the female and the spawning site (Donaldson; 1986). Male *C. aprinus* at Miyake-jima defended females from male conspecifics but otherwise did not engage in territorial defense (J. T. Moyer, pers. comm.). The same appears true of *C. aprinus* in Papua New Guinea (pers. obs.).

Male-female social interactions appeared related to courtship activities. Males were aggressive only if females resisted courtship attempts. At Tanguisson Reef, a single large female in a social group consisting of one male and five females became aggressive towards the male late in the study. This behavior almost always occurred around sunset and in the presence of another female. The behaviors performed by the aggressive female resembled those observed during male-sneaker male interactions. These behaviors included lateral displays, raised dorsal fins, chasing and nipping. The use of these behaviors in this particular situation coupled with observations of apparent courtship directed by the aggressive female towards the other female present, suggest that the aggressive female may have been undergoing early sex change (Moyer and Zaiser, 1984). Kobayashi et al. (1985) reported protogynous hermaphroditism in *C. falco*. Thresher (1984) suggested that this mechanism operated in populations of *C. oxycephalus* as well.

Female-female interactions appeared related to both spawning site defense and access to a courting male. These interactions were particularly pronounced just prior to and during courtship in social groups with females who shared spawning sites or where separate spawnings sites were in close proximity to one another. Similar patterns of behavior have been observed in social groups of *N. armatus*, *P. arcatus*, *P. forsteri* and *P. hemistictus* at Tanguisson Reef (pers. obs.).

*Sex Ratio.*—Sex ratios of *C. falco* indicated an inferred mating system of protogynous hermaphroditism that favored single dominant males with access to one
or more females in a social group. The appearance of successful sneaker males in these social groups affected dominant male fitness by reducing the number of females available to him. In addition, females in larger social groups fractioned by successful sneaker males may have had improved fitness owing to increased access to available males during spawning periods without waiting for males shared with other females.

Sneaker males may have been dominant males from social groups dissolved by the loss of females to predation or other selective pressures, or they may have been the product of early sex change. Moyer and Zaiser (1984) reported early sex change in the pomacanthids *Centropyge interruptus* and *C. tibicen* and its effects upon the social organization of those species. Fishes undergoing early sex change may have left their social group and joined another, in which the dominant male was absent, and assumed control of that group before the resident dominant female could begin sex change and assert control herself.

Early sex change may operate upon the social organization of *C. falco* but it might do so in a different manner. Large females within social groups may undergo sex change despite the presence of the dominant male. Such females, as newly developed males, may then attempt to gain control of one or more females within its own social group or it may leave that social group and sneak females from others. Sneaking may be successful if it is done in large social groups with many females. Preliminary studies have indicated that dominant males in such groups have greater difficulty in controlling females if group size is too great and that losses to sneaker males occur more commonly in large groups compared to smaller groups (pers. obs.).

Juveniles in social groups exist as a pool of potential mates but are not regarded by males as such until they reach a certain size or age and become sexually active. Rather, they are frequently attacked by dominant males, particularly in the presence of females during courtship periods, or are otherwise ignored. Because of this, juveniles offer considerable potential to sneaker males seeking to form social groups.

**Courtship and Spawning Behavior.**—The motor patterns present in the repertoire of *C. falco* at Tanguisson Reef may be classed into three functional groups: readiness assessment, stimulation and spawning. Readiness might be determined by Parallel Rest, Anti-Parallel Rest, Perpendicular Rest, Hopping, Circling, Lead and Follow, Passing and possibly, Quivering. Similar forms of resting and hopping are present in the courtship repertoire of *C. oxycephalus* and appear to provide a similar function (Thresher, 1984). Parallel Rest, Hopping and Circling were previously observed in the courtship of *C. falco* at Miyake-jima (Donaldson, 1986). Stimulation may be achieved by Nudging, Mounting, Quivering and Tail Beating. Thresher (1984) hypothesized that the form of nudging present in the repertoire of *C. oxycephalus* stimulated egg movement in females prior to spawning. Male *C. aprinus* also nudge females in courtship (J. T. Moyer, pers. comm.; pers. obs.) perhaps to a similar end. Similar behavior has been observed in the courtship of *P. forsteri* (Donaldson, unpubl. ms.). Lifting and the spawning ascent are of the third class of behaviors. Lifting also occurs in *P. forsteri* (Donaldson, unpubl. ms.) where it appears to allow the pair to coordinate the timing of the spawning ascent. The ascent itself, a generalized pattern commonly used by many reef fishes, allows free-floating eggs to enter the water column and escape immediate predation from bottom-dwelling predators (Thresher, 1984).

Courtship and spawning at dusk, commencing just after sunset and continuing into darkness, has been observed in Miyake-jima conspecifics (Donaldson, 1986)
and in *C. o. oxycephalus* of the Gulf of California (Thresher, 1984) and the Great Barrier Reef (pers. obs.). This pattern is probably common of all cirrhitids (Donaldson, unpubl. ms.) and in many other families of reef fishes as well. The reasons for spawning at this time, when light levels are low, are unclear. Possible advantages include reduced planktivore activity and thus reduced levels of planktivory upon pelagic eggs (Johannes, 1978; Lobel, 1978), and lower predation pressure upon adults (Johannes, 1978; Lobel, 1978), although the degree of threat offered by potential predators at this time is subject to debate (Thresher, 1984; Moyer, unpubl. ms.). Planktivores were relatively uncommon during *C. f. falco* courtship and spawning at Tanguisson Reef, but potential predators, particularly the serranid *Cephalopholis urodelus* and various carangids of the genus *Caranx*, were almost always in evidence. Obviously, both hypotheses require critical testing.

The relationship between social group size and male reproductive success, expressed particularly in the relative differences in the onset of courtship, the duration of courtship and the successful completion of sequential spawning acts in a limited daily time period, between groups of different sizes, cannot be adequately addressed here. However, there is some indication that male reproductive success is greater in groups of moderate size where the benefits of controlling more than one female are not outweighed by the costs of controlling too many.

**Acknowledgments**

I thank P. L. Colin, A. D. Constantino, G. B. Constantino, E. Eckhoff, G. R. Grimm, P. Moreton, J. T. Moyer, R. F. Myers, R. H. Richmond and C. A. Wilkins for their help in the field. C. Birkeland, J. H. Choat, P. L. Colin, A. D. Constantino, P. Doherty, E. Eckhoff, L. G. Eldredge, B. Kojis, N. Quinn and R. H. Richmond provided logistical support. A. Gronell, J. T. Moyer, R. F. Myers, J. E. Randall, D. Y. Shapiro, R. E. Thresher, Y. Yogo and two anonymous reviewers offered advice and comments. J. M. Fitzsimons kindly proofed the manuscript and offered constructive criticism. S. Bullock, R. N. Clayshulte, L. Collin, K. Dummitt, G. R. Grimm, J. Leis, "Kiwi House" of LIRS, J. T. Moyer, R. F. Myers, R. H. Richmond and especially C. A. Wilkins, M. C. Wilkins, and S. Wilkins are thanked for their excellent hospitality. The Division of Aquatic and Wildlife Resources, Government of Guam and the Great Barrier Reef Marine Park Authority are thanked for permitting the collection of specimens. Research was conducted through the facilities of the Tatsuo Tanaka Memorial Biological Station, the University of Guam Marine Laboratory, the Motupore Island Research Station, the Lizard Island Research Station and the Australian Museum, and was generously supported by the Japan Air Lines 50th 747 Asian Studies Scholarship and the Louisiana State University Museum of Natural Science. This is Contribution No. 68 of the Tatsuo Tanaka Memorial Biological Station and No. 239 of the University of Guam Marine Laboratory.

**Literature Cited**


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Reproductive Behavior and Social Organization of Some Pacific Hawkfishes (Cirrhitidae)

Terry J. Donaldson

Abstract. Ten species of Pacific hawkfishes occur in small social groups consisting of a single male and one or more females. Facultative monogamy occurred regularly in two obligate coral-dwelling species whereas the remaining species were largely haremic. Males had larger body sizes than females within groups but not always between groups. Males defended territories in which females had home areas. Females defended courtship sites within a male's territory against neighboring females of the same social group. Courtship was paired and sequential within groups, commencing just prior to or after sunset and concluding at dusk. Spawning, when observed, was pelagic.

Studies of hawkfish reproductive behavior have been largely limited to brief accounts based upon aquarium observations of a few species (see review in Donaldson, 1987). Field studies of reproductive behavior and social organization have appeared recently. These new studies have dealt primarily with members of the genus Cirrhitichthys, including C. oxycephalus (Thresher, 1984), C. falco (Donaldson, 1986a, 1987) and C. aureus
(Y. Yogo, pers. comm.), and a monotypic species, *Oxyccrrhites typus* (Donaldson and Colin, in press).

All species examined so far are similar behaviorally and socially in a number of features. They are organized into social groups or harems consisting of a single dominant male and one or more females of various body sizes; in some instances, the harem mating system is replaced by one of facultative monogamy (Donaldson, unpubl. ms). Courtship is paired and sequential; it commences just prior to or after sunset and concludes before dusk with pelagic spawning. This information has been derived from studies of a single obligate coral-dwelling species, *Oxyccrrhites typus*, and two species, *Cirrhithichthys falco*, and *C. oxycephalus*. Of these two, the former does not live in close association with corals and may be classified as a non coral-dwelling hawkfish, whereas the latter may be either a non coral-dwelling hawkfish or a non-obligate coral-dwelling species depending, upon geographic locality (Donaldson, unpubl. ms).

This study was undertaken to describe the social organization, mating system and spawning mode of this family of reef fishes, and to determine the possible influence of microhabitat preferences upon hawkfish reproductive and social behavior. The data reported represent intensive studies of certain species and relatively limited observations of infrequently
encountered species or those found in reef habitats that are often hostile to divers. However, these descriptions provide a general insight into the organization of reproductive and social systems for all hawkfish species.

Methods

Between August 1985 and January 1988, observations of reproductive behavior and social organization of 10 species of hawkfishes were made at several Pacific Ocean localities, including: the Mariana Islands (Guam, Saipan, and Tinian), Japan (Miyake-jima, Izu Islands), Caroline Islands (Ponape, Ant, and Pakein), Nauru Island, Solomon Islands (Guadalcanal), Papua New Guinea (Motupore Island and the Papuan Barrier Reef), Great Barrier Reef (Lizard Island and Yonge Reef), Fiji (Suva, Viti Levu), and the Society Islands (Moorea). Observations were made by SCUBA diving or snorkelling in shallow (1-30 m) depths. Data were recorded on plastic slates and by underwater still photography. Sunset times were determined from meteorological tables. Hawkfish were sexed by behavioral observations during courtship periods or by extrusion of gametes of fishes collected temporarily prior to sunset (those fishes sexed by the latter method were not observed for reproductive behavior on the same day of capture and
release). Fishes were also collected with handnets, monofilament barrier nets, and quinaldine-alcohol solution for body size measurement (mm TL = total length), and, at some localities, tagging. Measurements were made with calipers; tagging was accomplished by suturing small, color-coded glass beads through the dorsal musculature of anesthetized fishes. Fishes were then released at their original collection sites.

Pacific hawkfishes

The Cirrhitidae includes at least 35-36 species in 9-10 genera. Hawkfishes are distributed worldwide on coral and rocky reefs in tropical and subtropical waters (Randall, 1963; Springer, 1982; Donaldson, 1986b). As many as 26 species in all genera occur in the central and western Pacific. Those species considered here include: Cirrhichthys apinus, C. falco, C. oxycephalus, Cirrhitus pinnulatus, Neocirrhites armatus, Oxy cirrhites typus, Paracirrhites arcatus, P. forsteri and P. hemistictus. Brief notes on Amblycirrhitus bimacula are also included. Studies of the reproductive behavior and social organization of C. oxycephalus, C. falco, and O. typus have been published (Thresher, 1984; Donaldson, 1986a, 1987; Donaldson and Colin, in press), and additional information is included here. Many of these species, with the
exception of C. aprinus, C. falco, N. armatus and, to a lesser extent, P. hemistictus, are widely distributed in both the western Pacific and Indian oceans (Donaldson, 1986b).

Courtship and spawning motor patterns

Twenty-eight cirrhitid motor patterns of courtship and spawning were recognized from descriptions by Thresher (1984), Donaldson (1986a, 1987), Donaldson and Colin (in press) and those included here. Motor patterns types were identified as: Assessment and Synchronization, Stimulation, and Spawning (Table 1; see also, Figs. 1-3, 5, 8-11). Species repertoires for these patterns appear in Table 2. Analyses of pattern use during courtship and spawning bouts will appear elsewhere (Donaldson, in prep.).

Species accounts

Genus Cirrhitichthys

Cirrhitichthys aprinus

This species was observed on coral reefs and encrusted shipwrecks in Papua New Guinea and Guadalcanal, and at Miyake-jima, where it occurred in male-dominated harems consisting of 2-6 individuals. Males defended territories of up to 25 sq m against
neighboring males. Females and juveniles held individual home areas within male territories, and each female had its own courtship site or shared one with a neighboring female.

Social interactions were usually confined to female-female aggressive encounters within harems at shared or bordering courtship sites. Male-female aggressive encounters were rare and limited to a time just prior to the onset of courtship. Males usually did not interact with juveniles except when the latter interfered with the courtship of adults. Male-male interactions were uncommon and depended upon the relative proximity of neighboring territories. For example, on encrusted shipwrecks (Fig. 4) territorial boundaries tended to be rather close, sometimes less than 1.5 m apart, because of the limited amount of habitable space compared with a natural substratum; male-male interactions tended to be more frequent. Males and females usually remained separate during daylight hours, but as sunset approached, males made multiple brief visits to females by moving from one to the next in succession.

Sexual dimorphism in body sizes (Table 3) was evident, with males having larger body sizes than adult females within harems, but not necessarily between harems. This size difference may be indicative of protogynous hermaphroditism, but not necessarily so
(see Sadovy and Shapiro, 1987); this possibility is currently under investigation.

Occasionally, *C. aprinus* harems included congeners or vice versa. Harems occurring on small shipwrecks at Bootless Inlet, Papua New Guinea, included single *C. falco* or *C. oxycephalus* females in addition to female *C. aprinus*. Female *C. aprinus* were present in harems of *C. falco* at Miyake-jima, and a male *C. aprinus* regularly attempted courtship with a female *C. falco* when conspecific females were absent (Donaldson, 1986a). Interspecific courtship however, was infrequent at Papua New Guinea, and encounters between species of different sexes were marked by female-directed aggression by *C. aprinus* males.

Daily courtship has been observed at both Papua New Guinea and Miyake-jima localities. Courtship commenced just prior to or after sunset and concluded at dusk. Courtship was paired and sequential, with males making multiple (2-31) brief visits to each female at individual courtship sites. During these visits or bouts, the male approached the female, circled her and came to Parallel Rest, Anti-parallel Rest, or Perpendicular Rest. The male then either left the female for another or continued courtship with the same by Circling and Nudging. The female responded with Lead-and-Follow, and then joined the male in Parallel Swim, Parallel Rest, or Perpendicular Rest, followed by
Nudging. Gradually, courtship intensified as the number of bouts with each female increased. Males engaged in Passing, Nudging, Mounting, and Tail Beating prior to assuming Parallel Rest and then the Head-up pattern (Fig. 5). From this position, the pair rapidly rose 0.25-1.0 m above the substratum (or perpendicularly away from the substratum if it the deck of a sunken ship), turned, and spawned by releasing a small cloud of visible gametes, which rapidly dispersed. After spawning was completed, the pair quickly dashed back to the substratum. Once there, the female quickly moved into shelter; the male, after pausing a few seconds, either moved to the next female or, if all courtship within the harem was completed, moved into shelter as well.

When spawning did not occur, females pursued departing or passing males, occasionally drove them back toward their individual courtship sites, and resumed courtship. Alternately, females refused courtship from males, despite intense aggressive courtship behavior, if potential predators were near. Similar behavior has been observed in social groups of the congener C. falco and C. oxycephalus (pers. obs.). Courtship behavior patterns were similar (Table 2) to those of C. falco (Donaldson, 1986a, 1987), although fewer patterns were used in any given courtship bout. Courtship bouts were shorter in duration but more
numerous compared with _C. falco_ and _C. oxycephalus_ (Donaldson, unpubl. data). Occasionally, a male continued to court the same female after spawning before moving on to another female.

Spawning began 24 minutes before to 34 minutes after sunset for first spawns and ended 11 before to 34 minutes after sunset for the last. Pelagic spawning ascents tended to be both higher and faster than those observed of _C. falco_ (pers. obs.).

Predation attempts on courting males by scorpaenids and serranids occasionally occurred as males moved past ambush sites located between female courtship sites or during courtship at those sites. Observed predation attempts were unsuccessful, although courtship was usually interrupted. Males avoided predation attempts by rapidly erecting their dorsal spines and then quickly withdrawing from the immediate area. Males also moved along different "paths" between courtship sites if predators were near. At Bootless Inlet, Papua New Guinea, female congeners, resident in a male's territory, usually elicited courtship from the male when he passed. Males did not respond to this behavior, although male _C. aprinus_ have been observed in courtship with female _C. falco_ at Miyake-jima (Donaldson, 1986a). Interspecific spawnings may yield viable offspring; eggs of _C. aprinus_ and _C. falco_
cross-fertilized in the laboratory resulted in 30% fertility (P. Colin, pers. comm.).

Cirrhitichthys falco and C. oxycephaulus

Social organization and reproductive behavior of both C. falco and C. oxycephaulus have been described (Donaldson, 1986a, 1987; Thresher, 1984). The former species was observed at Miyake-jima, Guam, Guadalcanal, Papua New Guinea, and the Great Barrier Reef. The latter species was observed at Nauru, Guadalcanal, Papua New Guinea, and the Great Barrier Reef.

Both species were sexually dimorphic in body size (Table 3), with males being larger within groups rather than between groups.

Cirrhitichthys falco occurred in social groups of 2-8 individuals (Donaldson, 1987). Observations of C. oxycephaulus at Nauru and Lizard Island revealed a social organization that differed from that described for this species in the Gulf of California (Thresher, 1984). At the latter locality, social groups consisted of a male and up to seven females; courtship occurred at one or more corals within the male’s territory. At Nauru and Lizard Island, social groups consisted of a male and two females; a male and one female shared a single coral while a second female lived in a coral up to 3 m away. During courtship periods, particularly at Lizard Island (Fig. 6), the male first made his way to
the second female and courted her before returning to court the first female. Courtship with the second female occurred either at her coral or at a point halfway between the two corals; courtship with the first female always occurred at her coral. Usually the male completed courtship and spawning with the second female before doing so with the first. Occasionally, courtship attempts with the second female were rejected, and the male switched back and forth between both females until courtship with either one was completed or he moved into refuge with the first female as darkness fell. In addition, the first female occasionally followed the male out of her coral in "apparent attempts to lure" the male back to her courtship site.

Genus Paracirrhites

*Paracirrhites forsteri*

This wide-ranging species occurs from the Red Sea to Hawaii (Randall, 1963, 1985). Social groups of this species were observed at Guam, Saipan, Nauru, Guadalcanal, Papua New Guinea, Fiji, and Moorea; a single adult was observed at Miyake-jima and was probably a stray recruit carried north from southern Japan or Okinawa as a larva by the Kuroshio Current. Courtship and spawning were observed at Tanguisson Reef and Pago Bay, Guam; Aiwo Reef; Nauru; and North Point
Reef, Lizard Island. These hawkfishes were sexually dimorphic in body size (Table 3), with males larger than females within harems. Social groups were male-dominated and consisted of a single male and 1-3 females within the male's territory. Males held relatively large territories that included one or more large, prominent coral heads (Pocillopora eydouxi or Acropora palifera). Males moved between these coral heads and used them for feeding sites, refuge, and courtship sites with resident females. Large males (> 150 mm TL) usually had two or more females; pairs were defined with caution because some males had second females in coral heads up to 15 m away. Juveniles, recognized by their distinctive coloration, were present within male territories but rarely interacted with adults. Juvenile coloration was maintained by unattached individuals to 80 mm TL; adult coloration was assumed when juveniles joined social groups.

Male-male interactions occurred along territorial borders more often than in most other cirrhitids. This may be a result of increased mobility in members of this genus compared to others. Male-female interactions were limited to brief, non-aggressive encounters when individuals entered a coral inhabited by another. Female-female interactions were infrequent and limited to encounters at commonly shared courtship sites at sunset whether the male was present or not. Such
interactions were often intense, however. For example, at North Point, Lizard Island, a melanistic female (130 mm TL) frequently interacted aggressively with a larger (145 mm TL) female when the latter approached the coral used as a courtship site by both and as a residence for the former, as well as the male (Fig. 7). The larger female often chased the melanistic female off the coral prior to courting with the male. The melanistic female responded by interrupting courtship between the larger female and the male, and then attempted courtship with the male. When this occurred, both the larger female and the male chased the melanistic female from the coral head and then continued courtship while the melanistic female waited on a coral boulder 2.5 m away. After spawning, the larger female immediately returned to her home area, about 15 m away. The male remained in the coral and was joined by the melanistic female. However, by this time it was usually dark, and no further courtship attempts were observed. The male always showed a preference for the larger female over the melanistic female. Occasionally, he was observed swimming towards her home area if she had not yet arrived to commence courtship, and even if the melanistic female was present and attempting courtship with the male.

Generally, courtship of P. forsteri commenced 16 minutes before to 58 minutes after sunset and was not
always successful. Courtship consisted of one or more bouts, each 4-1800 seconds, with each female. Bouts leading to successful spawning ranged from 152-758 seconds. Spawning occurred 11-47 minutes past sunset.

Most courtship patterns in _P. forsteri_ were also used by other species (Table 2). Patterns that appeared unique to _P. forsteri_ included an exaggerated form of Looping, and Figure-8 passing. The former (Fig. 8) consisted of swimming in a single loop outside of a coral in which both male and female rested, exiting the coral from the front, relative to the direction in which both fish were facing, and returning from the back. Males executed this pattern from the Parallel Rest position in the presence of the female; females usually executed this pattern immediately after arrival of the male in her coral head. Figure-8 passing, performed by males only, consisted of two loops, one each on either side of the coral, made so that the male passed directly in front of the resting female before executing the second loop.

Courtship commenced when the male approached the waiting female and settled into her coral head, or when the female arrived in a male's coral. Occasionally, the male's color would pale. Both male and female would then line up parallel to one another and then rest for a few to several seconds. The male and female often shifted position in the coral head, usually by
jumping or hopping between the coral branches or on the surface of the coral, before coming to rest parallel, anti-parallel (Fig. 9), or perpendicular to one another. Courtship continued with Looping, Figure-8 passing, or Lead-and-Follow (Fig. 10), interspersed with periods of rest or waiting. Just prior to spawning, the male and female assumed Parallel Rest, raised themselves into the Head-up pattern, and began Lifting by raising and lowering their bodies, in synchrony, by flexing of the pectoral fins. After a few lifts, the pair executed a spawning ascent and quickly rose 1.5-2.5 m into the water column. At the top of the ascent, both turned, heads down, released a cloud of gametes, and quickly swam for the coral. Once in the coral, the pair rested for a few minutes. The male then either left to court additional females or remained with the female and settled in between the branches of the coral for the night; in some instances, such as after a bout at Lizard Island, the female left the male and returned to her own home area (Fig. 7).

**Paracirrhites arcatus**

This species was common at Guam, Saipan, Nauru, the Papuan Barrier Reef off Motupore Island, the outer Great Barrier Reef (Yonge Reef), and Moorea; it was less commonly observed at Guadalcanal. Courtship and spawning was observed only at Guam and Nauru.
Social organization at all localities consisted of male-dominated harems of one or more females, with each female living in a coral and having a home area within the male's territory. The male moved freely between female-occupied corals in this territory and usually shared a coral with one of the females. Favored corals included Pocillopora eydouxi, P. elegans, or Stylophora mordax. Juveniles within the boundaries of a territory were usually found in smaller P. verracosa or Acropora spp. corals, which were not utilized by adults.

Aggressive interactions were few and usually limited to border encounters between neighboring males. Males and females were never observed in aggressive interactions with one another. Females rarely interacted aggressively with one another, even just prior to or during courtship periods. Generally, each female's courtship coral was far enough away from the next to avoid interaction. Aggressive interactions did occur when more than one female shared a coral as a shelter or as a site for courtship with the male.

Sexual dimorphism in body size was pronounced (Table 3), with males larger than females, 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 their respective depth of distribution (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 sec and spawning occurring 2 minutes before to 6 minutes past sunset. 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. 11) and the two assumed Parallel Rest. The male, and occasionally the female, engaged in Looping, which ended in Parallel Rest. The pair then waited a few seconds and then began Lifting. After Lifting a few times they ascended 1-1.5 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 shared with two of the females; the other two females migrated to that coral head at sunset from their home areas centered in less favored _Porites rus_ corals a few meters away (Fig. 12).

In social groups with more than one female, males usually courted but did not spawn with each female every night. Observed spawnings were few, because 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. Both tended to segregate by depth, and aggressive interactions between different morphs were observed at
borders between depth zones. The latter "polystictus" morph occurred in shallower water near the reef margin whereas 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. arcatus_ 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 sq m) in which females had smaller home areas. Territories and home areas were usually centered around a large _Pocillopora_ spp. coral or _Millipora_ 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 (Fig. 13). 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 _Exallias 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, Anti-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 wary and many courtship attempts were aborted, either because of interruption by the coral's other residents or a female's possible reaction to the presence of either cruising predators or the observer.
Cirrhitus pinnulatus

This species is widely distributed, from Hawaii to the Red Sea and occurs as three distinct subspecies (Randall, 1963). Other species in the genus have relatively small distributions. Cirrhitus pinnulatus is a reef margin 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, as 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 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. 14) just prior to and after sunset. Generally, larger females dominated these sites if were shared by both females.

Observations of courtship behavior in this species were difficult to make because of its wary behavior. 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 around 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, 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; 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 dimorphism in body size occurred within social groups, but differences between male and female sizes were less pronounced than in 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, unpubl. ms).

Lobel (1974) reported that this species spawned demersally in aquaria, although spawning was inferred rather than observed. Donaldson and Colin (in press) described courtship and spawning behavior, and determined that this species spawns pelagically in pairs, using sequential courtship within harems.
Neocirrhites armatus

This brightly colored species was commonly observed at Guam, Saipan, and Moorea, where it occurred in close association with corals (Pocillopora eydouxi and P. elegans; Donaldson, unpubl. ms). This species favored P. verracosa 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 starfish (Acanthaster planci) or habitat destruction by man. Group size also depended upon proximity to neighboring corals (Donaldson, unpubl. ms). This species demonstrated facultative monogamy (Donaldson, unpubl. ms).

Sexual dimorphism in body size was evident, with males being larger than females within groups (Donaldson, unpubl. ms; Table 3). 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, Perpendicular Rest, and Circling. Males also chased females among 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. Head-up and Quivering were observed, followed by rapid dashes just above the edge of the coral, but pelagic spawning was not confirmed. This species has been suggested to be 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 occurs, then pelagic spawning by making a rapid dash above the coral may be possible. Making such an ascent at dusk would also reduce the chance of predation by visually-oriented predators, because the red coloration renders them difficult to see during periods of darkness (pers. obs.).

*Amblycirrhitus bimacula*

This species, found 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 I visited, is that this species is a reef-margin inhabitant that tended to be found in 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 (Fig. 15) 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 urodela* (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 sq m 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 haremic, 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 to harems, as either post-larval juveniles or displaced adults. In obligate coral-dwelling species, habitat availability and use may have 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 relative to the size of that harem, may have been more important (Donaldson, in prep.).
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, whereas 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 haremic.

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) briefly reported 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 4), 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, in press). 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 plantivore 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. 

Cirrhichthys falco and C. aprinus males were occasionally attacked by larger fishes, although 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 haremic 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 cooler water temperatures inhibit spawning. 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 synderi* from Japan (Nakazono et al., 1985).

Spawning frequency, however, may not be a daily event in some species of cirrhitids 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, in press). 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. pinnulatus* at Saipan indicated that although males court females on a daily basis, they do not successfully spawn with each female. The reason for this is unclear, although the presence of an observer may be a factor. Another possibility is the lack of
female readiness. In some species females may not be physiologically 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 patterns of microhabitat preference, there is consistency in both social and reproductive systems. Hawkfishes are haremic, 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, in which 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 (Donaldson, in prep.). Here, it is evident that a certain number of patterns may be required for courtship and spawning to take place. Although one pattern, male approach, was common to all species, six other patterns occurred in 70-90% of all species. Four
of these shared patterns were used for assessment and synchronization (Circling, Lead-and-Follow, Parallel Rest and Anti-Parallel Rest), and two for spawning (Head-up and Ascent). Observed patterns used for stimulation were shared by 40-60% of all species (Nudging, Mounting, Tail Beating, and Quivering). Two assessment and synchronization patterns (Perpendicular Rest and Parallel Swim) and one spawning pattern (Lifting) also were observed in 40-60% of the species. Assessment and synchronization patterns were the most variable in all species where they were observed. Eight occurred in 20-30% of all species and seven were seen in only one species. Those patterns seen in only a single species may prove to be species-specific. Caution must be used in stating species-specificity of motor patterns because those observed in only a single population or species may be influenced by geographic variation, or may be found in other species once the entire family is surveyed. The lack of patterns in the repertoires of some species, particularly Paracirrhites hemistictus "polystictus" and Amblycirrhitus bimacula, is most probably an artifact resulting from too few observations of reproductive behavior in these species.

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. Differences in pattern
use between species may explain how reproductive isolation among members of the family was possible.

Acknowledgments

I am grateful to P. L. Colin, J. T. Moyer, R. F. Myers, J. E. Randall and R. E. Thresher for stimulating discussions and help in many ways. L. Bell, J. H. Choat, R. N. Clayshulte, P. L. Colin, G. B. Constantino, F. Cushing, P. Doherty, E. Eckhoff, L. G. Eldredge, R. Galzin, G. R. Grimm, A. Gronell, B. Irish, C. E. Lennert, J. T. Moyer, R. F. Myers, R. H. Richmond, P. Ryan, H. Sanger, R. Sakamoto, V. Tyndzik and C. Wilkins provided assistance in the field. J. M. Fitzsimons, C. F. Bryan, R. W. Hastings, J. V. Remsen, M. S. Hafner and C. Wilson all commented on the manuscript. G. B. Constantino offered valued encouragement. The following institutions are thanked for their assistance and support: the Tatsuo Tanaka Memorial Biological Station, the University of Guam Marine Laboratory, the Lizard Island Research Station, the Australian Museum, the Motupore Island Research Station, the Department of Biological Sciences of the University of the South Pacific, the B.P. Bishop Museum, and the Centre de l'environment d'Opunohu, Antenne de Musee, Moorea. The Great Barrier Reef Marine Park Authority, the Division of Fisheries and
Wildlife of the Commonwealth of the Northern Marianas, and the Division of Aquatic and Wildlife Resources of the Government of Guam, issued necessary permits. Research was supported by the Coypu Foundation, the Japan Air Lines 50th 747 Asian Studies Scholarship, the LSU Museum of Natural Science, and M.C. and S. Wilkins, to whom I am grateful. This is contribution no. 000 of the Tatsuo Tanaka Memorial Biological Station and contribution no. 000 of the University of Guam Marine Laboratory.

Literature cited


(Section of Ichthyology, Museum of Natural Science, and Department of Zoology and Physiology, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803 USA; and the Tatsuo Tanaka Memorial Biological Station, Ako, Miyake-jima, Izu Islands, Tokyo 100-12, Japan)
Table 1. Courtship and spawning motor patterns of Pacific Cirrhitidae. References: 1) Thresher (1984); 2) Donaldson (1986a); 3) Donaldson (1987); 4) Donaldson and Colin (in press); 5) this paper.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Description</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ASSESSMENT AND SYNCHRONIZATION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Approach</td>
<td>male approaches female at onset of courtship, stops just in front of her, and faces her</td>
<td>1,2</td>
</tr>
<tr>
<td>Parallel Rest</td>
<td>male and female align parallel to one another</td>
<td>2,4,5</td>
</tr>
<tr>
<td>Anti-parallel Rest</td>
<td>male and female align parallel to one another but facing opposite directions</td>
<td>3,4,5</td>
</tr>
<tr>
<td>Perpendicular Rest</td>
<td>male aligns perpendicular to female</td>
<td>3,5</td>
</tr>
<tr>
<td>Parallel-swim</td>
<td>male and female swim parallel to one another around courtship site</td>
<td>4,5</td>
</tr>
</tbody>
</table>
Table 1, cont'

<table>
<thead>
<tr>
<th></th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parallel-hover</td>
<td>male and female hover parallel to one another above substratum</td>
</tr>
<tr>
<td>Tail Stand</td>
<td>male and female align parallel to one another, vertically, balancing upon substratum with their caudal fins</td>
</tr>
<tr>
<td>Tilt</td>
<td>male tilts body toward female</td>
</tr>
<tr>
<td>Head-to-Head</td>
<td>male and female aligned 180° apart, facing each other</td>
</tr>
<tr>
<td>Tail-to-Tail</td>
<td>male and female align 180° apart, facing away with caudal fins touching</td>
</tr>
<tr>
<td>Curl</td>
<td>male curls his body so that the flank is exposed to an approaching female</td>
</tr>
<tr>
<td>Color Change</td>
<td>head of male or female pales upon approach of partner</td>
</tr>
<tr>
<td>Jump</td>
<td>male or female jump quickly in place upon approach of partner</td>
</tr>
</tbody>
</table>
Table 1, con't

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circling</td>
<td>Male and female circle one another, often touching one another's caudal fins with their snouts</td>
<td>2, 4, 5</td>
</tr>
<tr>
<td>Lead-and-Follow</td>
<td>Female leads male around courtship site on substratum</td>
<td>3, 4, 5</td>
</tr>
<tr>
<td>Hopping</td>
<td>Male and female swim parallel to one another by hopping along substratum at courtship site</td>
<td>1, 2, 5</td>
</tr>
<tr>
<td>Passing</td>
<td>Male swims from one side of female at parallel rest, passes in front of the female, and comes to rest at her opposite side</td>
<td>3, 5</td>
</tr>
<tr>
<td>Looping</td>
<td>Male swims out from parallel rest in a wide loop, up to 3 m away from female, and comes to rest on her opposite side</td>
<td>4, 5</td>
</tr>
<tr>
<td>Figure 8</td>
<td>Male performs double looping pattern, either clockwise or counter-clockwise relative to the female</td>
<td>5</td>
</tr>
</tbody>
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Table 1, con't

<table>
<thead>
<tr>
<th>Chase Male</th>
<th>female chases after passing or retreating male just prior to onset of courtship or during a lapse in courtship, respectively</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chase Female</td>
<td>male aggressively chases female around courtship site at onset of courtship</td>
</tr>
</tbody>
</table>

**STIMULATION**

<table>
<thead>
<tr>
<th>Nudging</th>
<th>male nudges female's flank or operculum with his snout (see Fig. 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mounting</td>
<td>male positions his body across dorsal fin and upper flank of female (see Fig. 2)</td>
</tr>
<tr>
<td>Tail Beating</td>
<td>male beats caudal fin vigorously against water while mounting female</td>
</tr>
<tr>
<td>Quivering</td>
<td>male quivers his body, usually while nudging or mounting</td>
</tr>
</tbody>
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Table 1, con't

**SPAWNING**

<table>
<thead>
<tr>
<th>Task</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>Head Up</td>
<td>Male and female, in parallel rest, raise their heads upwards towards the vertical and wait, just prior to the spawning ascent</td>
</tr>
<tr>
<td>Lifting</td>
<td>Male and female, in parallel rest and head up, lift their bodies by flexing their pectoral fins.</td>
</tr>
<tr>
<td>Ascent</td>
<td>Male and female rise in parallel, the male often pushing his body or snout against the female, into the water column; at the apex of ascent the pair turn downward and release gametes; after gamete release the pair return to the substratum together (see Fig. 3)</td>
</tr>
</tbody>
</table>
Table 2. Courtship and spawning motor patterns observed in ten species of Pacific hawkfishes. Species abbreviations: CA- *Cirrhitichthys aprinus*; CP- *C. falco*; CO- *C. oxycephalus*; PF- *Paracirrhites forsteri*; PA- *P. arcatus*; PHP- *P. hemistictus "polystictus"*; CP- *Cirrhitus pinnulatus*; OT- *Oxycephalus typus*; NA- *Neocirrhites armatus*; AB- *Amblycirrhitus bimacula* (n.o. = not observed; % = percent of total species where pattern was observed).

<table>
<thead>
<tr>
<th>Pattern</th>
<th>CA</th>
<th>CF</th>
<th>CO</th>
<th>PF</th>
<th>PA</th>
<th>PHP</th>
<th>CP</th>
<th>OT</th>
<th>NA</th>
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<tbody>
<tr>
<td>Approach</td>
<td>x</td>
<td>x</td>
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<td>Parallel Rest</td>
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<td>Anti-Parallel</td>
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<td>x</td>
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<td>Parallel Swim</td>
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<td>Parallel Hover</td>
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<td>Tail Stand</td>
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<td>Head-to-Head</td>
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<td>Table 2, con't</td>
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<td>PHP</td>
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<td>Looping</td>
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<td>Figure 8</td>
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<td>Chase Male</td>
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<td>Tail Beating</td>
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<td>x</td>
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<td>Head Up</td>
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<td>x</td>
<td>x</td>
<td>x</td>
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<td>Ascent</td>
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<td>x</td>
<td>x</td>
<td>x</td>
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<td>n.o.</td>
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<td>Total</td>
<td>16</td>
<td>17</td>
<td>12</td>
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<td>15</td>
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Table 1. Mean ( 
± S.D.) body sizes (mm TL) of male and female hawkfishes (Cirrhitidae).

<table>
<thead>
<tr>
<th>Species</th>
<th>Body size</th>
<th>t-value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
</tr>
<tr>
<td>Cirrhitichthys aprinus</td>
<td>72.4 ± 13.5</td>
<td>50.9 ± 12.2</td>
<td>3.93</td>
</tr>
<tr>
<td></td>
<td>n = 7</td>
<td>n = 21</td>
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<tr>
<td>Cirrhitichthys albo</td>
<td>65.7 ± 9.4</td>
<td>52.8 ± 10.1</td>
<td>14.20</td>
</tr>
<tr>
<td></td>
<td>n = 18</td>
<td>n = 36</td>
<td></td>
</tr>
<tr>
<td>Cirrhitichthys oxycephalus</td>
<td>61.8 ± 2.6</td>
<td>42.5 ± 5.3</td>
<td>2.77</td>
</tr>
<tr>
<td></td>
<td>n = 9</td>
<td>n = 15</td>
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</tr>
<tr>
<td>Cirrhitus pinipunctus</td>
<td>190.7 ± 25.9</td>
<td>104.3 ± 32.7</td>
<td>31.37</td>
</tr>
<tr>
<td></td>
<td>n = 14</td>
<td>n = 64</td>
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<tr>
<td>Paracirrhitus areatus</td>
<td>84.7 ± 12.5</td>
<td>49.6 ± 11.7</td>
<td>6.01</td>
</tr>
<tr>
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<td>n = 38</td>
<td>n = 57</td>
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</tr>
<tr>
<td>Paracirrhitus forsteri</td>
<td>140.6 ± 25.6</td>
<td>98.4 ± 31.2</td>
<td>5.30</td>
</tr>
<tr>
<td></td>
<td>n = 20</td>
<td>n = 44</td>
<td></td>
</tr>
<tr>
<td>Paracirrhitus hemistictus</td>
<td>207.5 ± 18.9</td>
<td>152.5 ± 32.4</td>
<td>3.09</td>
</tr>
<tr>
<td>(polyistictus- morph)</td>
<td>n = 4</td>
<td>n = 8</td>
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<tr>
<td>Paracirrhitus typus*</td>
<td>78.3 ± 18.2</td>
<td>61.5 ± 7.9</td>
<td>(no test)</td>
</tr>
<tr>
<td></td>
<td>n = 3</td>
<td>n = 4</td>
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</tr>
</tbody>
</table>

(* data from Donaldson and Colinn, in press)
Table 4. Summary of social organization and reproductive behavior characteristics of ten species of Pacific Cirrhitidae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Localities studied</th>
<th>Mating system</th>
<th>Group size</th>
<th>Male</th>
<th>Female</th>
<th>courtship site</th>
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</thead>
<tbody>
<tr>
<td>Cirrhitichthys aprinus</td>
<td>Miyake-jima; Motupore Is; Guadalcanal</td>
<td>haremic</td>
<td>1:2-5:1-9</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Cirrhitichthys falco</td>
<td>Guam; Miyake-jima; Lizard Is; Motupore Is; Guadalcanal</td>
<td>haremic</td>
<td>1:1-7:1-6</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Cirrhitichthys oxycephalus</td>
<td>Nauru; Lizard Is; Motupore Is.</td>
<td>haremic/facultative monogamy</td>
<td>1:1-6</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>P. forsteri</td>
<td>Guam; Nauru; Lizard Is; Guadalcanal; Fiji</td>
<td>haremic/facultative monogamy (?)</td>
<td>1:1-5</td>
<td>yes</td>
<td>yes</td>
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<tr>
<td>Paracirrhitus arcatus</td>
<td>Guam; Tinian; Saipan; Nauru; Lizard Is; Hoeren Notupore Is.</td>
<td>haremic/facultative monogamy (?)</td>
<td>1:1-3</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Paracirrhitus hemistictus</td>
<td>Guam; Saipan; Moorea; Ponape</td>
<td>haremic</td>
<td>1:1-3</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Cirrhitus pinnulatus</td>
<td>Saipan; Nauru; Guam</td>
<td>haremic</td>
<td>1:2-8</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Neocirrhitus armatus</td>
<td>Guam; Tinian; Moorea</td>
<td>facultative monogamy/haremic</td>
<td>1:1-4</td>
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<td>yes</td>
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<tr>
<td>Oxyocirrhitus typus</td>
<td>Motupore Is; Ponape</td>
<td>facultative monogamy/haremic</td>
<td>1:1-2</td>
<td>?</td>
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<td></td>
</tr>
<tr>
<td>Amblyocirrhitus bimacula</td>
<td>Guam</td>
<td>facultative monogamy/haremic (?)</td>
<td>1:1</td>
<td>?</td>
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* Male: Females: Juveniles
<table>
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<tr>
<th>Courtship before (-) or after (+) sunset</th>
<th>Spawning time before (-) or after (+) sunset</th>
<th>Adult body size (range, mm TL)</th>
<th>Site attachment</th>
<th>Microhabitat type</th>
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<td>60-100</td>
<td>strong</td>
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<tr>
<td>- +</td>
<td>- +</td>
<td>55-80</td>
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<td>non-coral dweller</td>
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<tr>
<td>+</td>
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<td>45-55</td>
<td>strong/very strong</td>
<td>non-coral dweller/obligate coral dweller</td>
</tr>
<tr>
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<td>+</td>
<td>80-180</td>
<td>strong/very strong</td>
<td>non-obligate coral dweller</td>
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<tr>
<td>+</td>
<td>+</td>
<td>50-95</td>
<td>strong/very strong</td>
<td>non-obligate coral dweller</td>
</tr>
<tr>
<td>+</td>
<td>?</td>
<td>200-240</td>
<td>strong</td>
<td>non-obligate coral dweller/non-coral dweller</td>
</tr>
<tr>
<td>- +</td>
<td>- +</td>
<td>150-210</td>
<td>strong</td>
<td>non-coral dweller</td>
</tr>
<tr>
<td>- +</td>
<td>?</td>
<td>44.5-70</td>
<td>very strong</td>
<td>obligate coral dweller</td>
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<tr>
<td>- +</td>
<td>+</td>
<td>65-99.5</td>
<td>very strong</td>
<td>obligate coral dweller</td>
</tr>
<tr>
<td>-</td>
<td>?</td>
<td>n.a. n.a.</td>
<td>strong/</td>
<td>non-coral dweller/</td>
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</tbody>
</table>

n.a. = not available
Fig. 1. Nudging behavior by a male during courtship of Cirrhichthys falco at Tanguisson Reef, Guam, Mariana Islands.
Fig. 2. Mounting behavior by a male during courtship of *Cirrhichthys falco* at Tanguisson Reef, Guam, Mariana Islands.
Fig. 3. Spawning ascent in a pair of *Cirrhichthys falco* at Tanguisson Reef, Guam, Mariana Islands. A, beginning of ascent from the head-up pattern; B, half-circle above the substratum; C, vertical rise, with the male pushing against the female; D, turn and release of gametes; E, descent towards the substratum.
Fig. 4. Spatial pattern of five male-dominated social groups of *Cirrhitichthys aprinus* on the hull of a shipwrecked landing craft off Lion Island, Bootless Inlet, Papua New Guinea. Hull surfaces, indicated in part, appear in schematic form. Parts b-d are at right angles to parts a-a'. Female home areas and approximate courtship sites of social group I are indicated; ovals represent soft corals inhabited by one or more juveniles within the male's territory.
Fig. 5. Head-up behavior prior to a spawning ascent by a pair of *Cirrhilichthys aprinus* at Igaya Bay, Miyake-jima, Izu Islands Japan. The female's body is hidden by the male's (forefront).
Fig. 6. Spatial pattern and movements of male and female *Cirrhithichthys oxycephalus* prior to and during courtship at North Point reef, Lizard Island, Great Barrier Reef, Australia.  

a, Pocillopora coral inhabited by the male and female-1;  
b, Acropora coral inhabited by female-2 and visited by the male prior to courtship;  
c, coral rock which served as a courtship site for the male and female-2;  
d-f, coral rocks where female-1 waited for the return of the male prior to courtship (after courtship and spawning had been completed with female-2).  
Solid lines indicate the paths taken by the male; dashed lines indicate paths taken by both females.
Fig. 7. Spatial pattern and movements by *Paracirrhites forsteri* prior to and during courtship and spawning at North Point reef, Lizard Island, Great Barrier Reef, Australia. 

a, *Pocillopora eydouxi* coral inhabited by the male and melanistic female (female-m), which was used as a courtship site for the male and female-1 and was also the site of agonistic encounters between the two females; b, coral inhabited by female-1 during daylight hours and after courtship and spawning with the male had been completed; c, "meeting place" where the male greeted female-1 prior to moving to the courtship site; d-e, waiting sites on coral boulders used by female-m while the male and female-1 courted. Solid lines indicate paths taken by the male; dashed lines indicate paths taken by the females.
Fig. 8. Looping behavior by a pair of *Paracirrhites forsteri* during courtship at Pago Bay, Guam, Mariana Islands. The male is on the left of the coral, the female is on the right.
Fig. 9. Anti-parallel Rest behavior in a pair of *Paracirrhites forsteri* during courtship atop a coral boulder at Pago Bay, Guam, Mariana Islands.
Fig. 10. Lead-and-Follow behavior by a pair of *Paracirrhites forsteri* during courtship at Pago Bay, Guam, Mariana Islands. The female, on the right, is leading the male, on the left.
Fig. 11. Pair formation during Approach behavior by a male *Paracirrhites arcatus* at Tanguisson Reef, Guam, Mariana Islands. The male is on the right.
Fig. 12. Spatial pattern and movement of male and female _Paracirrhites arcatus_ prior to courtship at Tanguisson Reef, Guam, Mariana Islands. 

a, _Pocillopora elegans_ coral inhabited by the male and female-1, which also served as the courtship site; 

b-d, _Porites rus_ coral inhabited by females 2-4 during daylight hours prior to the onset of courtship; 

e, _Pocillopora eydouxi_ coral visited by both the male and female-1 prior to the onset of courtship; 

f, coral rock formation, ca. 1 m in height. Solid lines indicate paths taken by males and females prior to the onset of courtship. All females remained at the courtship site until dawn of the following day.
Fig. 13. Spatial pattern and movement of male and female *Paracirrhitidae hemistictus* (polystictus-phase) to a large *Pocillopora eydouxi* coral in the spur and groove zone at Tanguisson Reef, Guam, Mariana Islands. The coral, resting upon a spur, served as the courtship site for this harem. Grooves between the spurs measured approximately 1-1.5 m deep. The solid line indicates the path of the male enroute to the coral from his perching site on an adjacent spur; dashed lines indicated paths taken by the two largest females from their perching sites adjacent to the courtship site.
Fig. 14. 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.
Fig. 15. Spatial pattern and movement of a pair of *Amblycirrhitus bimacula* prior to courtship at Tanguisson Reef, Guam, Mariana Islands.

- a, *Pocillopora eydouxi* coral where the pair resided; 
- b, rock where the male waited prior to courtship; 
- c–d, sites where the female waited for the male to return (rock and pavement, respectively); 
- e–f, surrounding coral rocks.

Solid lines indicate paths of the male; dashed lines indicate paths of the female.
Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae)

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Key words: Behavior, Harem, Mating system, Social organization, Reproduction
Synopsis

Obligate coral-dwelling hawkfishes have been hypothesized to be monogamous. This hypothesized mating system is at odds with what is known of those of other cirrhitids. *Neocirrhitus armatus*, which inhabits *Pocillopora* spp. corals, and *Oxycirrhitus typus*, which inhabits gorgonians and antipatharian corals, were examined for evidence of a monogamous mating system. Life history criteria that favor monogamy in reef fishes (Barlow 1986) were examined for these two species. Facultative monogamy was found in both. In this mating system, males are limited in their ability to acquire and maintain females, and thus have only a single mate, but may acquire additional females if conditions for doing so are favorable.
**Introduction**

Some workers (e.g. Thresher 1984, Barlow 1986) have predicted that certain hawkfish species, specifically those found exclusively in corals, usually as paired adults, are monogamous. Two obligate coral-dwelling species, *Neocirrhitus armatus* and *Oxycirrhitus typus*, are likely candidates. Both are frequently observed in pairs when encountered. However, the possibility that either or both species are monogamous is at odds with what is known of the social organization and mating system of other members of the Cirrhitidae. The purpose of this paper is to examine the social organization and mating system of these two cirrhitids to determine if these species are unique from the rest of the family.

Hawkfishes (Cirrhitidae) are a monophyletic fish group consisting of 34-35 species in 9-10 genera (Springer 1982). They are distributed largely in the tropical and subtropical Indo-West Pacific, although three species occur in the tropical Atlantic and a single species is endemic to the eastern Pacific (Randall 1963, Lubbock 1978, Springer 1982, Donaldson 1986a). Hawkfishes occur on coral and rocky reefs, and various species have been classified as having one or more of three major types of microhabitat preference (Donaldson unpublished ms): obligate coral-dwelling species, non-obligate coral-dwelling species, and non coral-dwelling species. Recent studies have indicated that hawkfishes are
protogynous hermaphrodites (Thresher 1984, Kobayashi et al. 1985, Y. Yogo pers. comm., Sadovy & Donaldson unpublished data). Those non coral-dwelling and non-obligate coral-dwelling species studied so far are haremic, with social groups consisting of a single male and one or more females (Thresher 1984, Donaldson 1986b, 1987).

Monogamy and reef fishes

Monogamy in reef fishes has been reviewed recently by a number of authors (Gronell 1984, Thresher 1984, Driscoll & Driscoll 1988), but evidence of "exclusive matings between one male and one female" (Thresher 1984) exists for only a few taxa. Monogamy has been described for a few pomacentrids, including Amphiprion (Fricke 1974, Moyer & Bell 1976, Fricke & Fricke 1977) and Acanthochromis (Thresher 1984), and in syngnathids of the genus Corythoichthys (Gronell 1984). Much of the literature on monogamy in reef fishes emphasizes short (at time of courtship; see Gronell 1984) and long-term pairing. This is true of the Acanthuridae (Robertson et al. 1979), Apogonidae (Thresher 1984, Kuwamura 1985), Chaetodontidae (Fricke 1973, Reese 1975, Burgess 1978, Tricas 1985, Driscoll & Driscoll 1988), Gobiidae (Lassing 1976, Schmale in Thresher 1984), Pomacanthidae (Strand 1978 in Thresher 1984), and Serranidae (Donaldson in press) to name a few.
Thresher (1984) and Gronell (1984) reviewed or described five hypotheses that might explain the formation of monogamous systems in reef fishes. These hypotheses center around the following: biparental care of offspring, resource defense, low density and low mobility of individuals, hybridization avoidance and increased reproductive efficiency.

Barlow (1984, 1986) discussed monogamy in both freshwater fishes and marine reef fishes. His points, with respect obligate coral-dwelling hawkfishes, are considered here.

In Barlow’s definition, monogamy in fishes occurs when a pair of fishes remains together through a reproductive cycle that includes biparental care of offspring, or when a pair of fishes spawned together with the same partners, during short intervals of time, over a long period without practicing parental care of offspring. Barlow found that freshwater fishes conformed to the former condition, whereas marine reef fishes to the latter. With reef fishes, monogamy may result from two causes: the pattern of dispersion of females in a given area, and the subsequent inability of the male to secure access to more than one female because of that pattern (Barlow 1986).

Barlow (1986) listed certain life history criteria that can be applied to describe potentially monogamous species. Fishes should be relatively small in body size, and be strongly site-attached or territorial. They should spawn
without seasonality or with weak seasonality over a long period of time and produce planktivorous eggs or larvae that disperse without parental care. These criteria were considered in relation to known life history patterns of _N. armatus_ and _O. typus_.

Methods

Populations of obligate coral-dwelling hawkfishes were surveyed at six localities in the central and western Pacific to determine the proportion of adults occurring in pairs within the same coral. In addition, fishes were observed repeatedly over time at a number of study sites to determine their social organization, site fidelity, social behavior, and reproductive behavior. Observations were made using scuba, and data were recorded on plastic slates and by underwater photography.

Species accounts

Neocirrhites armatus

This brightly colored species is distributed from French Polynesia (Society Islands and Tuamotu Archipelago) west to the Phoenix Islands, northeast Australia, Fiji, the Mariana Islands, Wake Island, and southern Japan (Randall 1963, Carlson 1975, Myers & Shepard 1981, Masuda et al. 1985). _Neocirrhites armatus_ is an obligate coral-dweller, preferring corals of the genus _Pocillopora_, especially _P._
Neocirrhites armatus was surveyed and observed at the following localities and sites: Guam, Mariana Islands (Tanguisson Reef, Gun Beach, Agana Bay, Cabras Island, Luminao Reef, Anae Island and Pago Bay); Saipan, Mariana Islands (the Grotto); Tinian, Mariana Islands (Herman's Beach, Tachogna Beach); Moorea, Society Islands (outer reef on E. and W. sides of Tareu Pass, Opunohu Bay). This species was relatively common at Guam, particularly at Tanguisson Reef and Pago Bay, and at Moorea, but was less common elsewhere. Relative abundance in general seemed limited by the availability of live Pocillopora corals; these corals were often dead, damaged, or absent from many sites because of the activities of man or the crown-of-thorns starfish, Acanthaster planci.

Corals were surveyed to determine the number of individuals occurring in each coral. Of 166 sampled corals containing N. armatus, 45.2% had fish that occurred in pairs, 42.2% singly, 10.8% as a single male and two females (triplets), 1.2% as a single male and three females, and 0.6% as a single male and four females. The differences are significant (Chi-square goodness-of-fit; $X^2 = 160.9$, $p < 0.001$, df = 4). The number of individuals occurring in the same coral head seemed limited by both the size of the coral and the availability of suitable corals (Donaldson unpublished ms).
Social groups at Guam, Tinian, and Moorea were male-dominated and ranged in size from 2-5 individuals ($X = 2.4 \pm 0.57$ SD, $n = 44$). Social groups occupied 1-4 corals, depending upon coral size and relative proximity to one another (Donaldson unpublished ms). Social groups consisting of a single male and two or more females were more common if corals were large (> 50 cm in diameter) or scarce.

Individuals living alone in coral heads may have been associated with other individuals in the following ways: 1) paired with others living singly in adjacent corals, 2) grouped with pairs living in adjacent corals, or 3) grouped with social groups consisting of two or more females, either living together in the same coral or in two or more adjacent corals. In the first example, paired fishes were believed to be monogamous; in the second, a male living with a female often made visits to a second adjacent female during courtship periods but returned to the coral where the first female resided. Similar behavior of the cirrhitid Cirrhitichthys oxycephalus has been observed at Lizard Island, Great Barrier Reef (pers. obs.). In the third example, the male visited each of the females in adjacent coral heads during courtship periods but returned to its own coral head when courtship had been completed. This behavior has also been observed in three non-obligate coral-dwelling species, Paracirrhites arcatus, P. forsteri and P. hemistictus (Donaldson unpublished ms).
Body sizes of this species were small and sexual dimorphism was present within pairs or social groups. Males were larger ($\bar{X} = 53.8 \pm 15.9$ (SD) mm TL, $n = 51$) than females ($\bar{X} = 49.6 \pm 6.4$ (SD) mm TL, $n = 77$), and the differences were significant (T-test, $t = 2.08$, $p < 0.05$).

*Neocirrhites armatus* had strong site fidelity to specific coral heads (Donaldson unpublished ms). Carlson (1975) has also indicated strong site fidelity among members of a Fiji population. Duration of residence for some pairs, triplets, and individuals in the same coral heads at Tanguisson Reef, Guam, exceeded 2.5 years (Donaldson unpublished ms). This species was both intra- and interspecifically territorial, defending all or part of the coral head from intruders. Interactions between individuals in pairs or social groups within the same coral were less intense than those from outside the coral (Donaldson unpublished data). Preliminary experimental introductions at Tanguisson Reef indicated that males and females defended vigorously against introduced males and larger females; males tended to ignore smaller females and juveniles, although resident females defended against both. Resident females that lived alone in corals excluded larger or equally sized females. These females tended to ignore smaller females and juveniles and often allowed them to stay (Donaldson unpublished data).

Courtship was paired, and began just prior to or after sunset. Courtship concluded after dusk throughout the year.
at Tanguisson Reef, Guam. There was no apparent
seasonality. Males in social groups of two or more females
courted females in sequence and often made multiple visits
to each if they shared the same coral or occupied a second
coral less than 1.5 m away (Donaldson unpublished ms).
Pelagic spawning has not yet been confirmed. This species
most likely spawns pelagically, as do other cirrhitids
(Thresher 1984, Donaldson, 1986b, 1987, Donaldson & Colin in
press), only after dark, when the deep red coloration of
this species may afford cryptic coloration against
visually-oriented predators. It could be a demersal
spawner, laying eggs within the coral where it resides, but
I have seen no evidence of such spawns. Life history
characteristics are summarized in Table 2.

**Oxycirrhites typus**

This uncommonly seen species has one of the widest
distributions of any cirrhitid and occurs from the tropical
eastern Pacific westward to the Red Sea (Randall 1963).
Oxycirrhites typus is an obligate coral-dwelling hawkfish
that lives on gorgonians and antipatharian corals in deep
slope (20-150 m) habitats (Randall 1963, Thomson et al.

Oxycirrhites typus was surveyed at the Papuan Barrier
Reef, east of Port Moresby, Papua New Guinea (see Donaldson
& Colin in press, for details of the study sites), and at
Mwahn Channel, Ponape, Caroline Islands. This species was
observed at depths of 20-28 m at three sites in Papua New Guinea and 48 m at a single site at Ponape. The distribution of these hawkfishes at each locality seemed limited by the availability of suitably-sized corals. This hawkfish was absent from gorgonians with diameters were less than 1.8 m and antipatharians less than 1.6 m in height (pers. obs.). Fewer *O. typus* individuals could be surveyed and observed compared to *N. armatus* because of: a) there were no suitable corals in large numbers at the localities examined and, b) individuals occurred at depths which limited observation time because of diver-safety considerations.

In corals that supported one or more *O. typus* (*n* = 10), 40% had fish that were paired (one male and one female), and 60% had single fish. Of the paired fishes, three pairs consisted of two adults and one consisted of a female and a juvenile. Of the single fishes in corals, two were paired together socially and lived in adjacent corals, three were part of a male-dominated harem, and one was alone. The paired individuals not occurring on the same coral each used separate corals, but migrated to a common coral for courtship and spawning. Afterwards, they remained in that coral for an undetermined length of time but returned to their separate corals by morning (Donaldson & Colin in press). Those individuals from the harem lived in corals adjacent to one another; during the courtship period, the male visited each female in sequence before returning to his
own coral for the night (Donaldson & Colin in press).
Social group coral use is illustrated in Figure 1; social
group sizes ($\bar{X} = 2.2 +/- 0.45$ (SD), $n = 5$) are given in
Table 1.

This species appeared to be sexually dimorphic for body
size within pairs or groups of adults. Males were slightly
larger ($\bar{X} = 78.3 +/- 18.2$ (SD) mm TL, $n = 3$) than females ($\bar{X}
= 61.5 +/- 7.9$ (SD) mm TL, $n = 4$). Sample sizes were too
small to attempt statistical analyses.

*Oxycirrhites typus* appeared to have strong site
fidelity where suitable corals were few in number. However,
at one site the male and female of a single pair lived
separately in more than one coral and moved between those
corals on different days. These two hawkfishes were the
only *O. typus* present, although corals at this site were
common. Both male and female favored a single coral over
others and met at a common coral only during courtship.
Territoriality was not observed in pairs or in the harem.
It was not possible to make experimental introductions of
individuals into corals where pairs resided because of the
relative scarcity of individuals in the area.

Courtship began just prior to or after sunset at Papua
New Guinea and concluded at dusk (Donaldson & Colin in
press). Courtship and spawning may occur year round in the
tropics and seasonally higher latitudes, where water
temperatures during cooler parts of the year may be an
influence. Spawning was paired and pelagic (Donaldson &
Colin in press) and not demersal, as has been previously indicated (Lobel 1974, Randall 1985). Eggs and larvae were pelagic (Donaldson & Colin in press). Life history characteristics are summarized in Table 2.

Discussion

Obligate coral-dwelling cirrhitids such as Neocirrhites armatus and Oxycirrhites typus have characteristics that satisfy those life history criteria proposed by Barlow (1986), yet are monogamous only under certain circumstances, which are discussed here. Both species are strongly site-specific, often used the same coral for shelter, feeding and reproduction, but they tend to occur in monogamous pairs if suitable corals are too few or too small. If corals are more plentiful, are of a larger size, or are in close proximity to one another, then multi-female harems may occur. Territoriality has not been observed in Oxycirrhites typus, thus far. Neocirrhites armatus is territorial, and defends space against intruders if alone, or, if not, against one or more mates or harem members in addition to intruders. Males may strongly defend against intruding males or large females, but not necessarily against smaller females, which are potential mates if they can be accommodated within the coral or in a nearby coral. Females will defend against both males and females, regardless of size. This behavior is indicative of male
choice as a function of monogamy in reef fishes (Barlow 1986) or size-selective territoriality (R. E. Thresher personal communication). Males ultimately will spawn with as many females as possible but may be limited in their ability to do so. Such a condition allows for the appearance and maintenance of a monogamous mating system (Barlow 1986). Two potential limitations, with respect to the cirrhitids described here, are: (1) the availability of females, in relation to the availability of suitable corals, and, (2) the possibility that large females may undergo early sex change and succeed in sneaking or stealing females from the dominant male (Moyer & Zaiser 1984, Donaldson 1987). Females are expected to exclude other females since they are potential competitors for access to both the same male, and the limited space that can be shared with that male, and failure to exclude rival females will result in a lowering of fitness. The success that a female has in excluding rival females may reinforce a monogamous mating system. The failure to do so may result in the formation and maintenance of a harem system, although the probability of this occurring may also be limited by size, availability and proximity of suitable corals to support that system.

Both _N. armatus_ and _O. typus_ have relatively small body sizes compared to many other cirrhitids (see Randall 1963). _Neocirrhites armatus_ is sexually dimorphic for size, and _O. typus_ appears to be so, with males larger than females.
within pairs or groups, though not always between pairs or
groups. This dimorphism could be indicative of protogynous
hermaphroditism and is currently under investigation.

Similar patterns of size dimorphism between sexes occur in
*Cirrhitichthys falco* (Donaldson 1987), *C. aprinus*, *C.
oxycephalus*, *Paracirrhites arcatus*, *P. forsteri*, *P.
hemistictus*, *Amblycirrhitus bimacula* and *Cirrhitus*
pinnulatus (pers. obs.).

*Oxycirrhites typus* spawns pelagically, and releases
eggs that hatch into pelagic larvae; *N. armatus* is assumed
to have the same pattern of reproduction. Pelagic eggs and
larvae may be produced (see Shapiro et al. 1988 for critical
review) providing dispersal of adults (Barlow 1981),
predation avoidance of eggs and larvae (Johannes 1978) and
reducing the probability of failure in larval survival
(Doherty et al. 1985). Regardless, the need for parental
care of larvae is eliminated, as is the need for progeny to
be immediately adapted to the reef environment (Barlow
1986). The pattern of producing pelagic eggs and larvae
may, in the absence of parental care, contribute towards
monogamy but not exclusively so. This same pattern also
occurs in haremic cirrhitids (Thresher 1984, Donaldson

Courtship by both species is frequent and, at least for
*N. armatus*, lacks seasonality at low latitudes. Similar
patterns have been observed (Donaldson 1986b, 1987) for
haremic *C. falco* at Guam (lower latitude: 13° 23' N) and
Miyake-jima, Japan (higher latitude: $34^\circ 05'$). Hawkfishes that release small packets of propagules on a daily basis may realize greater fitness by compensating for relatively small body sizes even though the daily fecundity of females is lowered. At higher latitudes, females with relatively larger body sizes, and thus relatively greater fecundities, may be able to compensate for the inability to spawn throughout the year because of a shorter breeding season. Larger body sizes may contribute to greater daily fecundity if there is not also latitudinal variation in egg sizes (see Thresher 1988). Although frequent spawning may contribute towards monogamy, it too is not exclusive to this mating system.

Possession of life history characteristics that satisfy those criteria proposed for a monogamous mating system does not mean necessarily that monogamy will occur. Monogamy in reef fishes may occur if a) defense of a resource is enhanced by pairing (e.g., Robertson et al. 1979), b) pairing reduces the opportunity for hybridization between closely related species (Fricke 1973), c) reproductive efficiency is enhanced, as has been demonstrated for syngnathids of the genus Corythoichthys (Gronell 1984), and d) pairing allows for more successful parental care (see Gronell 1984, for review). Two of these conditions are irrelevant with respect to obligate coral-dwelling hawkfishes: hybridization is unlikely in both species because they are monotypic genera; and parental care is
probably absent in both because _O. typus_ spawns pelagically and _N. armatus_ presumably does as well. The likelihood of increased success at defending a resource and increased reproductive efficiency are both under investigation.

Monogamy may also occur if it is a function of male choice in relation to the density and distribution of females (Barlow 1986). In obligate coral-dwelling hawkfishes male choice will also depend upon the density and dispersion of suitably sized corals that can support potential mates. This dependence is in agreement with the Low Density with Low Mobility hypothesis, which states that monogamy may be selected for when individuals are widely dispersed, have restricted mobility, and have social units whose size may be influenced by available habitat (Ghiselin 1969, Wilson 1975; see summaries in Gronell 1984, and Thresher 1984). Such monogamy can be facultative (see Thresher 1984 for examples in other taxa, i.e., labrids); males will be monogamous only if they cannot acquire and support additional females. Males can acquire additional females if the corals in which they reside are large enough to accommodate additional females, or if suitable corals supporting single females are within close proximity to resident corals. If paired females are unsuccessful in defending resident corals from new females, a harem mating system will also result. Female success in "sequestering males" by territorial defense against intruding females then, may serve to maintain monogamy once it is established.
Acknowledgments

I am grateful to G.W. Barlow, J. T. Moyer, D. Y. Shapiro, and R.E. Thresher for comments and discussions on group size and social organization in fishes. C. Birkeland, P. L. Colin, G. B. Constantino, E. Eckhoff, R. Galzin, G. R. Grimm, and C. E. Lennert are thanked for diving assistance. M. C. Wilkins, S. Wilkins, and the staff of the University of Guam Marine Laboratory, the Motupore Island Research Station, and the Centre de L'Environnement, Antenne du Museum et des Hautes Etudes, are thanked for their kind hospitality. J. M. Fitzsimons, R. W. Hastings, C. F. Bryan, J. V. Remsen, M. S. Hafner and C. Wilson all commented upon the manuscript. The additional comments of two anonymous reviewers are greatly appreciated. Research was supported by the generous assistance of the Coypu Foundation and the Japan Air Lines 50th 747 Asian Studies Scholarship. This is contribution no. 000 of the Tatsuo Tanaka Memorial Biological Station and contribution no. 000 of the University of Guam Marine Laboratory.

References Cited


systems. Env. Biol. Fish. 4: 125-170.


Table 1. Social group sizes of the obligate coral-dwelling hawkfishes *Neocirrhites armatus* and *Oxycirrhites typus*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Group Size</th>
<th>No. of Groups</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Neocirrhites armatus</em></td>
<td>2</td>
<td>30</td>
<td>66.6</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>12</td>
<td>26.6</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>2</td>
<td>4.4</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>1</td>
<td>2.4</td>
</tr>
<tr>
<td><em>Oxycirrhites typus</em></td>
<td>2</td>
<td>4</td>
<td>80.0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1</td>
<td>20.0</td>
</tr>
</tbody>
</table>

(* $X^2 = 48.3$, $p < 0.001$, df = 3*)
Table 2. Summary of life history characteristics of two obligate coral-dwelling hawkfishes. M = male; F = female.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Neocirrhites armatus</th>
<th>Oxycirrhites typus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site attachment</td>
<td>very strong</td>
<td>very strong</td>
</tr>
<tr>
<td>Territoriality</td>
<td>strong</td>
<td>not seen</td>
</tr>
<tr>
<td>Adult body size (range; mm TL)</td>
<td>M- 44.5 - 70.0</td>
<td>M- 65.0 - 99.5</td>
</tr>
<tr>
<td>(range; mm TL)</td>
<td>F- 37.0 - 62.0</td>
<td>F- 52.0 - 92.0</td>
</tr>
<tr>
<td>Sexual dimorphism (body size)</td>
<td>M greater than F</td>
<td>M greater than F</td>
</tr>
<tr>
<td>(within groups)</td>
<td></td>
<td>within groups</td>
</tr>
<tr>
<td>Courtship periodicity</td>
<td>daily</td>
<td>daily</td>
</tr>
<tr>
<td>Seasonality in courtship</td>
<td>lacking</td>
<td>at higher latitudes</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(?)</td>
</tr>
<tr>
<td>Courtship type</td>
<td>paired, sequential</td>
<td>paired, sequential</td>
</tr>
<tr>
<td>Spawning type</td>
<td>pelagic (?)</td>
<td>pelagic</td>
</tr>
<tr>
<td>Eggs and larvae</td>
<td>planktonic (?)</td>
<td>planktonic</td>
</tr>
<tr>
<td>Social organization (range in group size)</td>
<td>2-5</td>
<td>2-3</td>
</tr>
<tr>
<td>Mating system</td>
<td>facultative monogamy/</td>
<td>facultative monogamy/</td>
</tr>
<tr>
<td></td>
<td>male-dominated harem</td>
<td>male-dominated harem</td>
</tr>
</tbody>
</table>

Fig. 1. Social organization and coral use in *Oxycirrhites typus*: A- monogamous pair in the same gorgonian; B- monogamous pair in separate coral heads at Horseshoe Reef, Papua New Guinea (male in a gorgonian; female in an antipatharian; arrows indicate the paths taken by both male and female to the antipatharian coral used as a courtship and post-spawning refuge site); C- male and a two-female harem in separate corals at Loloata Island, Papua New Guinea (male and female no. 1 in antipatharians; female no. 2 in a gorgonian; arrows indicate the path taken by the male enroute to courtship with both females, and the path taken to his coral after courtship was completed). Data are from Donaldson & Colin (in press).
Summary and Conclusions

The social organization, reproductive behavior, and zoogeography of the Cirrhitidae were studied to determine if variation occurred in the social organization and reproductive behavior of Pacific hawkfishes. Observed patterns of social organization and reproductive behavior, including spawning class (Thresher, 1984), did not show major variation within species and between species, in the taxa examined. However, minor variation was observed in the social organization and reproductive behavior of this group. This variation could have been the result of geographic isolation, particularly in the use of specific courtship patterns. Patterns of species distribution and richness, which indicated a high level of endemism in both the Indian and Pacific ocean basins as a result of Quaternary events, support this view. Two genera, Cirrhitichthys and Paracirrhites, show remarkable speciation in each basin, respectively. Geographically isolated species, subjected to non-unidirectional selection, evolve social and mating systems and behaviors that can be quite variable. An example would be the Pomacanthidae, another small wide-ranging family, which had social systems as variable as apparent monogamy, harems, lek-like mating assemblages.
and explosive promiscuous mating assemblages (Moyer et al., 1983).

Those hawkfish species studied here, representing 10 species in six genera from the central and western Pacific, appear to have the same patterns of social organization and reproductive behavior, including spawning class. In this study, spawning class refers to the mechanism by which spawning is achieved; for cirrhitids, there were two possibilities: pelagic and demersal spawning. Despite species-specific associations with three different habitat types, there was a lack of major variation. These associations, i.e., obligate coral-dwelling, non-obligate coral-dwelling, and non coral-dwelling, may provide sources of non-unidirectional selection, particularly for geographically isolated species or populations of species. Those hawkfishes studied appear to have social systems in which male-dominated harems prevail. Some variation in social organization existed among obligate coral-dwelling species. Monogamy was found to exist, but it was facultative in nature and probably depended upon habitat size (Donaldson, in prep.), as well as a male's ability to obtain and maintain mates. In the species studied, reproductive behavior was similar between species and genera, in that it consisted of sequential courtship, in which the male courted each female in his social group in sequence.
This courtship commenced just prior to or after sunset and resulted in pelagic spawning. Although pelagic spawning has not been confirmed for *Neocirrhites armatus*, courtship behavior of this species suggests that it is likely. Thus, variation in the type of spawning class in cirrhitids probably does not exist, and spawning class should be regarded as an evolutionarily conservative character (Thresher, 1984).

Although spawning class is a fixed characteristic, variation may frequently occur in courtship behavior patterns, both within and between species. Such variation may be a function of geographic isolation and non-unidirectional selection at the local level. An analysis of variability in courtship pattern use in relation to habitat associations among different species and geographic localities (Donaldson, in prep.) shows potential in describing the evolution of courtship behavior within the family.
BIBLIOGRAPHY


Anemonefisches Amphiprion bicinctus. Z. 
Tierpsychol. 36: 429-513.

Fricke, H.-W. 1975. Sozialstructur und okologische 
Spezialisierung von verwandten Fischen 

Fricke, H.-W. and S. F. Fricke. 1977. Monogamy and 
sex change by aggressive dominance in coral reef 

Ghiselin, M. T. 1969. The evolution of 
hermaphroditism among animals. Q. Rev. Biol. 44: 
189-208.

fishes of southern Indonesia and northwestern 
Australia. Australian Development Assistance Bureau, 
Indonesian Directorate General of Fisheries, and the 

Gronell, A. M. 1984. Courtship, spawning and social 
organization of the pipefish, Corythoichthys 
intestinalis (Pisces: Syngnathidae) with notes on 

Harry, R. R. 1953. Ichthyological field data of 
18. 190 pp.


leucosternon and Zebrasoma scopas): their feeding strategies and social and mating systems.
Env. Biol. Fish. 4: 125-170.


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Aiwo, Nauru (1986)

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E. Ricketts Award, Illinois State University (1982)
Phi Sigma Society (1982)
Society of Sigma Xi (1982)
California Academy of Sciences-NSF Visiting Researcher Award (1982-1983)
Phi Sigma Society Award (1983)
Friends of the Hopkins Research Station, Stanford University Scholarship (1983)
Japan Airlines 50th 747 Asian Studies Scholarship (1985)
Louisiana State University Graduate School Organization Relief Fund (1985)
Coypu Foundation grant (1985)
Papers Given


Distribution and species richness patterns of Indo-West Pacific _Cirrhitidae_: support for Woodland's hypothesis. Second Indo-Pacific Fish Biology Conference, Tokyo (1985)

Social organization and reproductive behavior of the hawkfish _Cirrhitichthys falco_ (Cirrhitidae). Second Indo-Pacific Marine Biology Conference, Guam (1986)


Seminars Given

Hawkfish zoogeography. University of Guam Marine Laboratory (September, 1985)

Reproductive behavior of _Cirrhitichthys falco_ at Miyake-jima, Japan. University of Guam Marine Laboratory (April, 1986)

Hawkfish behavior. Marianas Audobon Society (September, 1986)

Social organization and reproductive behavior of hawkfishes. Louisiana State University Museum of Natural Science (November, 1987)

Hawkfish reproductive behavior. Southeastern Louisiana University (March, 1988)

Do lizardfishes lek like birds? Louisiana State University Museum of Natural Science (September, 1988)

Miscellaneous

Member, Sponsoring Committee, Fourth Biennial Conference on the Behavioral Ecology and Ethology of Fishes, Normal (1983)

Thesis

Agonistic behavior of the freshwater prawn *Macrobrachiumlar* in relation to size and sex.

Publications


International Conference on Indo-Pacific Fishes.
Ichthyological Society of Japan, Tokyo.


DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Terry John Donaldson

Major Field: Zoology

Title of Dissertation: Social Organization, Reproductive Behavior and Zoogeography of Some Indo-Pacific Hawkfishes (Cirrhitidae)

Approved:

[Signatures]

Major Professor and Chairman
Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

November 16, 1988