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Social organization, patterns of sexuality, and behavior of the wrasse *Coris dorsomaculata* at Miyake-jima, Japan

Gordon W. Tribble[1]

Tatsuo Tamaka Memorial Biological Station, Ako, Miyake-jima, Izu Islands, Japan 100–12

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Synopsis

The wrasse *Coris dorsomaculata* was investigated at Miyake-jima, Japan. This species is sexually dichromatic and males arise from sex-changed females. Individuals were found living in harems which may be maintained through the defense of food by dominant males. The behavior of this species was similar to other studied wrasses, with the exception of a post-spawning display by males and the regular formation of multi-male aggregations in the late afternoon. Reproductive activity appeared to be affected by the warm-temperate climate at the study area. When day length was long, the spawning time coincided with outgoing tidal currents. When day length was short, the daily spawning time became fixed.

Introduction

The reproductive biology of tropical labroid fishes (wrasses and parrotfishes) has been intensively investigated in recent years due to the wide range of social systems exhibited by these fishes, their complex life history patterns, diurnal habits, and overall abundance (Randall & Randall 1963, Robertson 1972, Reinboth 1973, Robertson & Choat 1974, Moyer & Shepard 1975, Warner et al. 1975, Meyer 1977, Reinboth 1977, Robertson & Hoffman 1977, Robertson & Warner 1978, Warner & Robertson 1978, Thresher 1979). Much of the work on the relationships between life history patterns, social organization, and resource utilization is based on studies of terrestrial vertebrates (Emlen & Oring 1977, reviewed in Warner 1980); work of this sort on reef fishes is not common [but see Barlow 1975a (Serranidae), Barlow 1975b (Scaridae), Robertson & Hoffman 1977 (Labridae), Moyer & Nakazono 1978 (Pomacanthidae), Thresher 1979 (Labridae)].

Much of the research on the reproductive ecology of wrasses has focused on members of the genus *Thalassoma* (Robertson & Choat 1974, Warner et al. 1975, Meyer 1977, Robertson & Hoffman 1977, Warner & Robertson 1978). Most other labrid genera, particularly in the Indo-Pacific, are less well known (but see Robertson 1972, Nakazono & Tsukahara 1974, Robertson & Choat 1974, Moyer & Shepard 1975).

From August to December 1979, I investigated the social and reproductive biology of the wrasse *Coris dorsomaculata*. Reinboth (1970, 1975) has histologically investigated sex change in the Medi-

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[1] Present address: 4074 Puu Eleele Pl, Honolulu, Hawaii 96816, U.S.A.

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terranean species *C. julis*, and Randall (1976) has reviewed Hawaiian members of the genus. This paper considers the relationships between environmental factors, social organization, and patterns of sexuality for *Coris dorsomaculata*. Several behavioral aspects of this species are also investigated. Further, the effects of the warm-temperate climate at the study site on reproductive activity are examined.

Some confusion exists regarding the nomenclature of this species. *Coris dorsomaculata* Fowler 1908 has also been referred to as *C. multicolor* Rüppell (1835). However, the latter name does not correctly apply to this species (Randall, personal communication).

Methods and materials

All work was done on the west coast of Miyake-jima (35°05′N, 139°30′E), Izu Islands, Japan. Observations were made using scuba, totaling more than 150 hours, from August 7 to December 17, 1979. Observations were not made when the water visibility fell below two meters. Depth, temperature, and field notes were recorded underwater on plastic slates. Sunrise and sunset times, plus tidal cycle information, were obtained from local government publications.

Observations were made at two sites at Igaya Bay. Site 1, described by Moyer (1975), was 12 m deep. The bottom was sandy with a few large boulders and many smaller rocks. Coral growth was restricted to flat encrustations of faviid corals and occasional colonies of branching *Acropora*. Overall, leafy algae were predominant.

Site 2 was located at the base of a large vertical lava wall, 15-20 m deep, which had a broad, poorly defined base of lava and coral debris. This terminated in a zone of irregular rocks, small cobble, and sand. Coral growth was slightly more luxuriant than at Site 1, but leafy algae still predominated. A contour drawing of this site was presented in Moyer & Nakazono (1978).

Four social groups of *Coris dorsomaculata* were observed during the study. Two groups at Site 1 (1A and 1B) were watched from August 15 to December 17; two groups at Site 2 were observed between September 5 and December 17.

In situ sex determination of fish was made on the basis of body coloration (see below). Fish usually bore some distinctive markings and could be individually recognized, although some fish were tagged with plastic beads for rapid identification. These were caught with a fence net, tagged, and their standard lengths (SL) measured. Thirty fish were marked with different combinations of up to three small colored beads attached to tissue just posterior to the nape with a needle and thin monofilament line. They were returned to the site of collection immediately after tagging. Tagged fish were easy to recognize and their behavior was not noticibly affected. Also, three of the tags remained in place for over a year after the initial tagging.

Between October and December, 95 fish were collected with a small multiprong spear and Hawaiian sling for gonad examination. Testes were characterized by their smooth texture, whitish color, and relatively small size. Ovaries were recognized by their yellow color, large size, and the presence of small but distinct eggs. Individuals lacking developed gonads were considered to be immature. An analysis of gut contents was performed on 30 of the speared fish. Fish within 40 m of either study area were not speared.

The area occupied by a particular social group was determined by direct observation and mapping. The size of the enclosed area was determined to within 25 m^2 by visual reference to pipes of known length lying on the bottom.

The occurrence of spring and neap tides was based on the phase of the moon. Spring tides were considered to be the ones that occurred two days prior to, the day of, and two days after, the new and full moon. Similarly, neap tides were defined as the ones that fell within a five-day period bracketing the first and third quarters of the lunar cycle.

Results

Social organization

Individuals of *Coris dorsomaculata* were found in male-dominated social groups resembling harems. Groups consisted of 10-13 females living in an area occupied by a single male (Table 1). Male territories did not overlap spatially, and agonistic encounters

Table 1. Harem size and female density of the four observed harems as of September 15, 1979.

Harem	Size of male (mm SL)	Number of females in harem	Territory size (m^2)	Females m^{-2}
1A	160	13	300	0.053
1B	148	10	225	0.044
2A	133	10	140	0.071
2B	145	11	150	0.073

between neighboring males occurred 15 times during 35 hours of observation. Only one of 386 observed spawnings occurred between individuals from different social groups.

The composition of harems changed over time. After 10 weeks of observation, 15 of 27 individually recognized females could not be found despite intensive searching. This did not appear to be a result of tagging mortality; survivorship was 55% (n = 20) in tagged fish and 57% (n = 7) in untagged fish. Seven of the missing fish disappeared during a large typhoon[2]. In addition, 12 predatory attacks on *C. dorsomaculata* were seen, all by the lizardfish *Synodus ulae*. Nine of these attacks occurred while individuals were either engaged in courtship or spawning. Also, between August and November, nine females changed harems. Eight of these changes occurred after large storms. Only four of these females stayed in the new harem for longer than a week. New females that stayed in a harem for less than a week were not seen spawning with the resident male.

The size of male territories changed over time (Fig. 1). Major territorial expansions by a male were coincident with the absence, and presumed death, of a neighboring male. After three months of observation, four of seven original males were absent. In the two cases where a known male disappeared and the following events observed, a neighboring male was seen in the missing male's territory within a day of his absence. Females in the newly occupied territory were incorporated into the new male's harem.

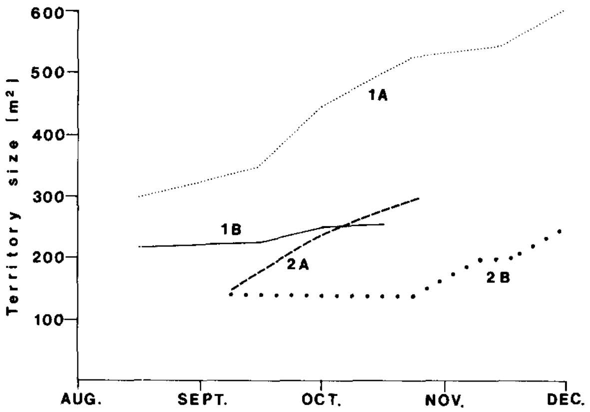

Figure 1. Changes in the size of the four male territories observed between August and December 1979. Males 1B and 2A disappeared during the study and were presumed dead.

Patterns of sexuality

Coris dorsomaculata is sexually dichromatic. Males are found entirely and exclusively in the terminal color phase (Fig. 2). The dichromatism is partial (sensu Robertson & Hoffman 1977); both sexes have the same pattern of body coloration. The terminal phase is distinguished by a bright yellow band on the anterior margin of the dorsal fin and several blue patches ventrally. In addition, the lateral body colors are more prominent in males. Male coloration is permanent and does not change during courtship or other social activities.

This species appears to be monandric (sensu Reinboth 1970), in that all males appear to result from sex-changed females (Fig. 3). Regardless of color phase, males were not present in size classes smaller than 120 mm SL.

The minimum size of sexually active females decreased during the study. Only females larger than 80-85 mm SL were observed spawning during August and September (n = 129). Small females were seen in the territories at this time, but they were not observed spawning. By the end of the study, females as small as 55 mm SL were seen spawning. Females 55-75 mm SL were involved in 43% (n = 130) of the spawnings seen during November and December. This smaller size class contained 57% (n = 30) of the known females larger than 55 mm SL.

Three females were recaptured about 11 months after the initial tagging; their average growth was 51

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[2] Tribble, G.W., L.J. Bell & J.T. Moyer. The submarine effects of a major typhoon at Miyake-jima, Japan. Manuscript.

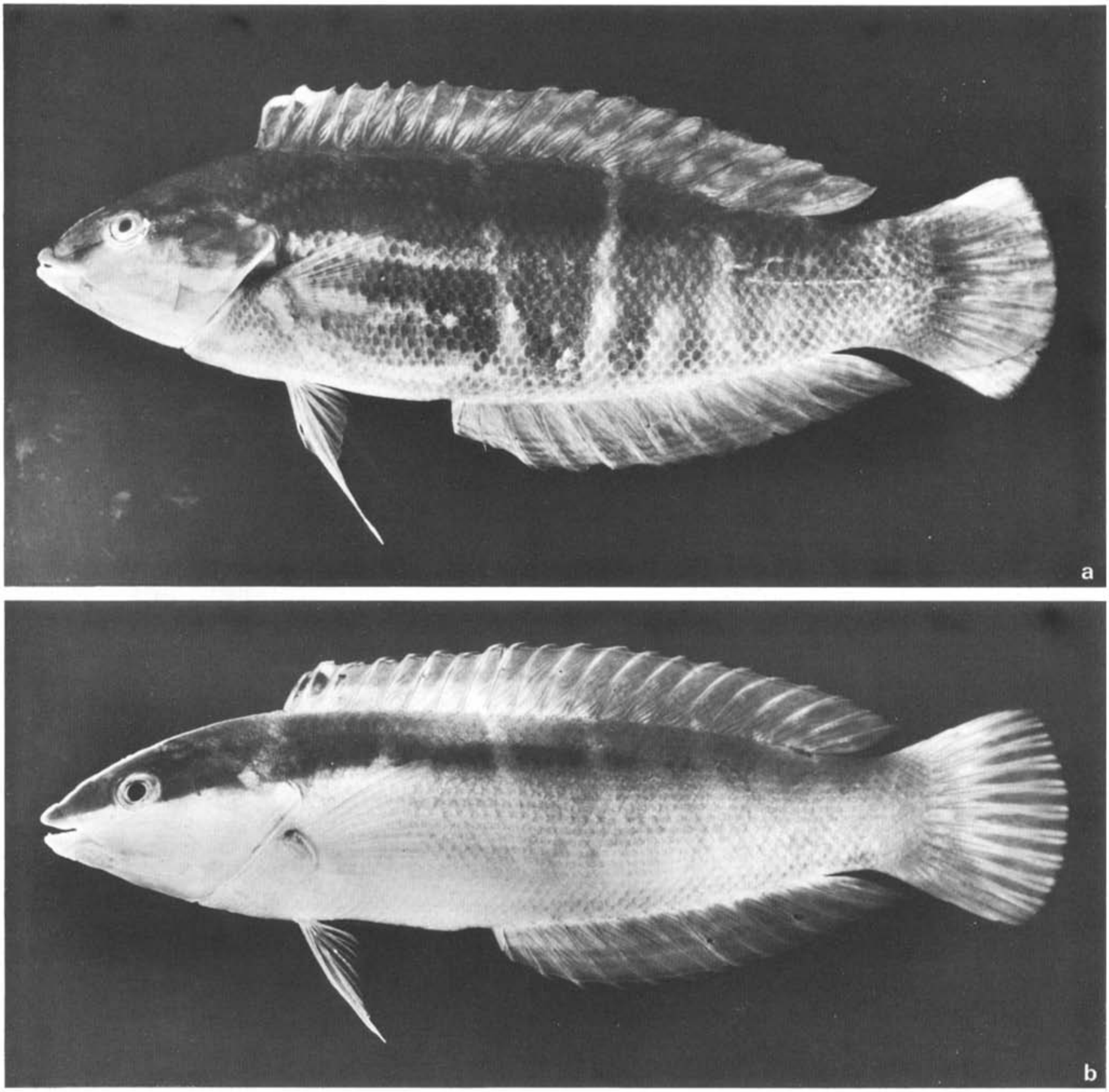

Fig. 2. Differences in color patterns between male and female *C. dorsomaculata*: 2a - male, 142 mm SL, collected at Miyake-jima, Japan, 22.5.1975 and 2b - female, 87 mm SL, collected at Sesoko Is. Okinawa, on 26.5.1975. Photos by John Randall.

mm SL (Table 2). Extrapolated linearly, this computes to an annual growth rate of 56 mm SL. All three had become males, and the territories held by these males overlapped somewhat with the home ranges that they occupied as females (Table 2).

Reproductive activity

Over 385 spawnings were observed, all between a male and female. The spawning sequence appeared typical of pair-spawning labrids (summarized in Robertson & Hoffman 1977). It was initiated when

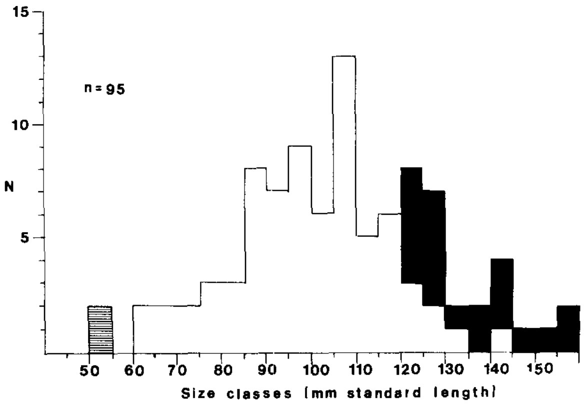

Fig. 3. Patterns of sexuality of *C. dorsomaculata.* Horizontal stripes denote immature fish, the clear areas represent females, and the shaded areas denote males. Sex was determined by visual inspection of gonads.

a female rose 20-50 cm above the substrate with her fins extended and body oriented 45° relative to a horizontal axis. The resident male approached and assumed an orientation similar to, but above, the female. Immediately prior to spawning, the male lightly touched the nape of the female with either his pelvic fins or the isthmus of his throat. A rapid upward rush at a 45° angle was initiated by the female (Fig. 4). Gamete release occurred at the apex of the rush, about a meter from the starting point.

On five occasions, planktivorous fishes were attacked by a male when they attempted to eat the zygotes. Attacks were directed at the damselfishes *Pomacentrus nagasakiensis* and *Chromis flavomaculata,* the butterflyfish *Chaetodon nippon,* and the sharpnose puffer *Canthigaster rivulatus.*

During the spawning period, males often swam in an accelerated arc, similar to the 'looping' of *Thalassoma bifasciatum* described by Reinboth (1973). These acts were significantly more frequent when the water visibility exceeded 5 m ($\bar{x}=8.0$ acts per 15 min, $n=90$) than when water visibility was 2-5 m ($\bar{x}=2.4$ acts per 15 min, $n=16$; $P<0.001$, approximate t-test, Sokal & Rolf 1969). Spawning was followed by a similar up and down swimming motion 93% ($n=190$) of the time. In this display, the male quickly swam farther up in the water column immediately after gamete release with his dorsal fin extended, while the female returned to the bottom. This post-spawning display was either absent or barely noticeable when the water visibility was less than 4 m. Both of these acts resembled the rapid upward rush of the male during spawning.

Spawning occurred near rocky areas throughout male territories, and was not restricted to a single fixed site. On days when the visibility exceeded 10 m, the females in one harem moved before spawning to a point farthest away from where an aggregation of planktivorous damselfishes and groupers usually occurred. They did not move to this site when the water was turbid.

The number of non-foraging related aggressive acts by males, directed at females, was significantly higher during spawning periods: 7.5 acts per 15 min ($n=72$) vs 1.8 acts per 15 min ($n=71$; $P<0.001$, approximate t-test). In such acts, the male swam directly at a female and either circled or pursued her for a few seconds. The behavior appeared ritualized, and the male did not strike the female. There appeared to be a decrease in male aggression towards females during non-spawning months (Moyer, personal communication).

On six occasions, a male was seen quickly chasing and hitting a female. Five of these attacks were directed at harem members near territorial borders. One attack was directed at a female that had just spawned with a male from an adjacent territory.

The spawning season lasted from early June to early February. Bottom temperatures in the bay during this time ranged from 20-29° C (Moyer, personal communication). Between August and

Table 2. Sex change, growth, and spatial shifts of three individuals recaptured approximately 11 months after tagging. All three were found at Site 1.

Initial tagging date	Initial sex	Initial size (mm SL)	Recapture date	Sex at recapture	Length at recapture (mm SL)	Net growth (mm)	Percent spatial overlap between 1979 and 1980 home ranges
8-23-79	F	102	7-30-80	M	146	44	60
9-09-79	F	96	7-30-80	M	147	51	50
9-09-79	F	97	7-30-80	M	154	57	10

December, spawning occurred between 1100 and 1630 h daily. The duration of the daily spawning period ranged from 12-145 min, the average length being 60 min ($\sigma = 36$, $n = 31$).The number of spawnings observed in these periods ranged from 2-18 ($\bar{x} = 5.8$ spawnings per period, $\sigma = 3.8$, $n = 31$). There was no significant correlation between the length of a spawning period and the number of spawnings in that period.

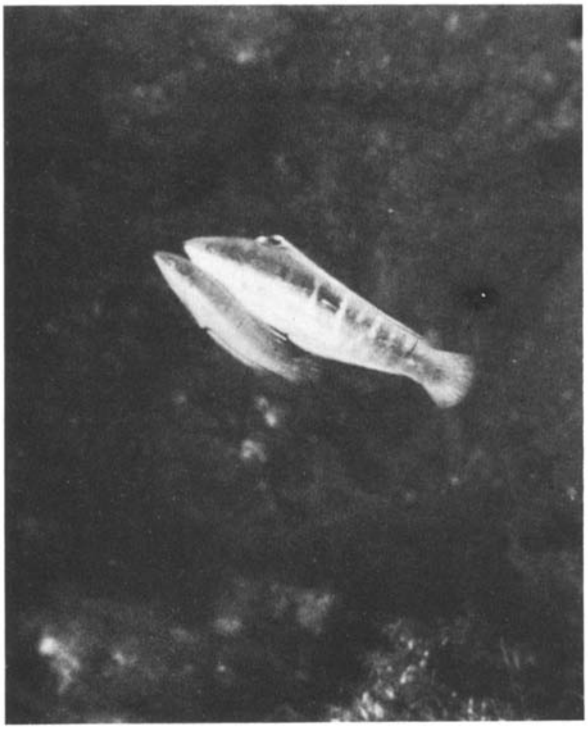

Fig. 4. The rapid upward rush preceding gamete release. Note the lead position and extended genital papillae of the female. See text for details. Prints made from Ektachrome slide taken by Jack Moyer.

During August and September, the daily spawning time changed in accordance with the tidal cycle (Fig. 5). *Coris dorsomaculata* spawned with the incoming tide; at the two study sites, such a tide produced an outgoing current. Males were seen performing courtship displays throughout the day on days when the spawning time changed from late afternoon to morning. The mean number of spawnings by a male did not differ between days with spring and neap tides ($P > 0.1$, t-test). However, during August and September, the duration of the spawning period on days with spring tides ($\bar{x} = 36.2$ min, $n = 6$) was significantly shorter than the length of the spawning period on neap tide days ($\bar{x} = 79.8$ min, $n = 5$; $P < 0.001$, t-test). In addition, the average number of spawnings per minute was higher on days with spring tides (Fig. 6). Thus, on days with spring tides, reproductive activity occurred relatively rapidly over a shorter period of time, whereas spawning was more protracted on days with neap tides.

From late September until the end of the breeding season, the daily spawning time became fixed between 1100 and 1300 h daily (Fig. 5). Also, the tidal cycle had no discernable effect on either the length of the spawning period ($P > 0.1$, t-test) or the

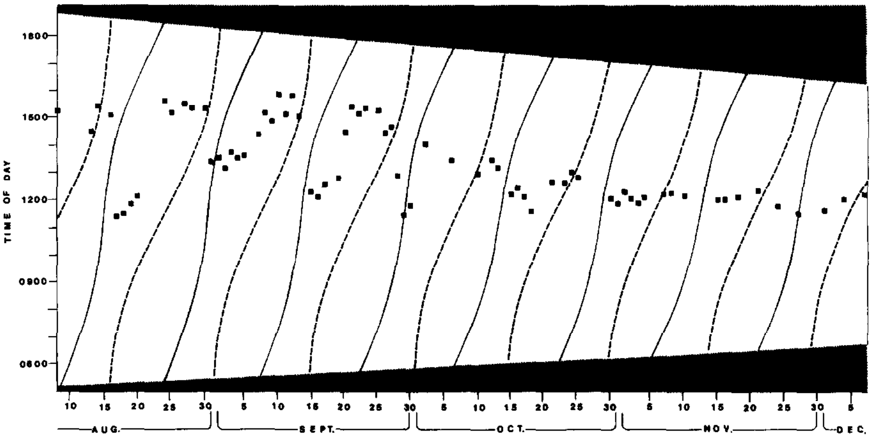

Fig. 5. Relationship between the tidal cycle, day length, and spawning time. Squares show the mean time of observed spawnings on a day. Shaded areas represent the time preceeding sunrise and following sunset. Dashed and unbroken lines represent the time of low and high tide, respectively. For example, on August 25, the mean time of spawning was at 1509. This was during the incoming tide, three hours after low tide. See text for details.

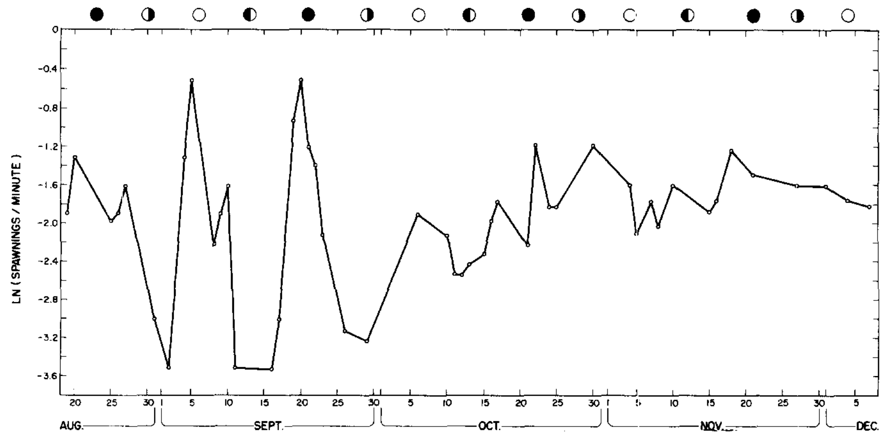

Fig. 6. Relationship between the number of spawnings per minute and the tidal cycle. Only days with three or more observed spawnings are shown. Circles at top represent the lunar phase; darkened circles show the new moon, open circles show the full moon. Half-darkened circles represent the first and third quarter moon phases. New and full moons correspond with spring tides, while quarter moons correspond with neap tides. See text for details.

average number of spawnings per minute (Fig. 6).

Non-reproductive activity

When not engaged in reproductive activity, individuals of *C. dorsomaculata* spent most of their time feeding. They fed almost exclusively on hard-bodied benthic invertebrates (Table 3), often turning over small rocks to find food. They were also seen picking prey items exposed by the barbels of foraging goatfishes, which they often followed. On several occasions, fish were observed breaking open relatively large prey items by grasping them with their anterior canine teeth and hitting the prey against a rock with a rapid sideways motion of the head. Larger fish often displaced smaller individuals from feeding sites; males displaced females with a frequency of 0.5 times per 15 min (n = 86). Levels of feeding aggression were slightly higher during spawning periods ($0.1 > P > 0.05$, approximate t-test).

Table 3. Average percent composition of gut contents of 30 adults (93-144 mm SL) collected between 1200-1700 h, October 9-15. 1979.

Average percent composition	Food type
35	Crustaceans: small decapods and amphipods
31	Gastropods: cone and top shells <5 mm
19	Others: ophiuroids, polychaetes, echinoids and invertebrate egg masses
14	Unidentified
Trace	bivalves, bryozoans, pycnogonids

Three of the four regularly watched males left their harems daily, one to two hours before sunset, and joined multi-male aggregations of up to six individuals. Larger females were also occasionally present. Males in such groups often converged on each other and swam side-by-side for up to 5 m. Individuals swam rapidly and close together, bodies occasionally touching. Recognizably agonistic interactions between males in these aggregations were not observed.

About one half-hour before sunset, individuals of *Coris dorsomaculata* buried themselves in the sand. Similar behavior in the congeners *C. julis* and *C. formosa* has been photographically analyzed by Reinboth (1972a, 1972b). The fish apparently do not have specific nocturnal resting sites; seven fish, each watched on four different occasions, did not reuse the same spot. However, successive resting sites were located within 5 m of each other.

Discussion

Behavior

In general, the behavior of *C. dorsomaculata* is typical of other studied labrids. Several workers have observed 'looping' by males during spawning periods (Reinboth 1973, Robertson & Hoffman 1977, Thresher 1979). This courtship display possibly serves to attract females or entice them to spawn (Reinboth 1973) and appears similar in form and function to 'signal jumping' observed in damselfishes (Abel 1961, Moyer 1975). In addition, ritualized aggression by males towards females has been noted in two other wrasses, both of which live in harems (Robertson & Hoffman 1977, Thresher 1979), and occasional violent attacks by a male on females were noted in harems of the wrasse *Labroides dimidiatus* (Robertson & Hoffman 1977). Such male aggression may function as a means of social control to keep females subordinate, and perhaps inhibits sex change (Robertson 1972, Shapiro 1977, 1980). Lastly, the spawning sequence of *C. dorsomaculata* is similar to most other pair-spawning wrasses (Randall & Randall 1963, Breder & Rosen 1966, Reinboth 1973, Nakazono & Tsukahara 1974, Robertson & Choat 1974, Moyer & Shepard 1975, Reinboth 1977, Robertson & Hoffman 1977, Warner & Robertson 1978, Thresher 1979).

Coris dorsomaculata appears to differ from other studied labrids in that males perform a prominent post-spawning display. Similar to 'looping' and strongly resembling the overall spawning act, this display may serve to attract females or demonstrate male reproductive success.

The formation of multi-male aggregations is interesting in that participating males leave their territories. Some damselfish have been observed exhibiting similar behavior (Clarke 1971, Keenleyside 1972, Sale 1978, Thresher 1980). Males of the wrasse *Halichoeres maculipinna* that were contesting a vacated territory engaged in side-by-side swimming (Thresher 1979) that is apparently similar to that of *C. dorsomaculata* in aggregates. The formation of multi-male aggregates and the close side-by-side swimming of *C. dorsomaculata* may be a means of establishing or reinforcing dominance without having to engage in agonistic, territorial encounters. The death of a male, perhaps noted through his absence from an aggregation, provides other males with a potential opportunity to expand their harems. Thus, it would benefit a male to join an aggregate if he could both determine his status in relation to other males and keep track of such males on a day to day basis while avoiding agonistic encounters.

Social organization

Emlen & Oring (1977) ascribe the development of a polygynous mating system to the defense, by males, of either females or resources required by females. In the case of *C. dorsomaculata*, food appears to be the defended resource. Individuals were commonly seen fighting over food items, and larger fish often displaced smaller ones from feeding sites. Spawning and nocturnal resting sites do not appear to be defended; individuals were not seen fighting over such sites. Also, spawning was not restricted to specific sites and individuals did not use the same nocturnal resting sites every day. It is possible that females themselves are the defended resource ('female defense polygyny', sensu Emlen & Oring 1977). If only females are defended, one would expect males not to defend areas without females. During the study, however, a male was seen defending a large area even after the females previously occupying it disappeared.

The development of harems in *C. dorsomaculata* as a result of defended food resources appears similar to the situation reported for the cleaner wrasse *Labroides dimidiatus* (Robertson 1972, Robertson & Hoffman 1977). In this case, as well as in the present report, ascribing the development of a polygonous social and mating system to a specific parameter has been done using only observational or correlative data. One experimental approach would be to remove all the females from a territory; female defense would be negated if the male did not abandon the territory.

Monandry and sexual dichromatism

The apparent monandry of this species may be a consequence of its haremic social and mating system. Small males would be unlikely to maintain harems and probably have few, if any, chances to spawn. Thus, an individual would have greater reproductive success if it was a sexually active female when small and changed to a male only when there was a chance to secure a harem. There are no reports of a diandric fish with a haremic mating system; primary (non-hermaphroditic) males seem to occur only where opportunities exist for small males to achieve some reproductive success

(Randall & Randall 1963, Reinboth 1973, Warner et al. 1975. Thresher 1979). One possible exception to this is the diandric wrasse *Halichoeres maculipinna*, reported by Thresher (1979) to live in harems. However, he also noted that several initial phase fish spawned synchronously with the spawning pair in 'all but a few cases'. This, in conjunction with observations of group spawning by Warner & Robertson (1978), suggests that *H. maculupinna* may not be haremic.

Patterns of sexuality for the genus *Coris* as a whole are unresolved. Randall (1976) noted the absence of small males in Hawaiian members of the genus. However, Reinboth (1970, 1975) has clearly shown that the Mediterranean species *C. julis* is diandric. Obviously, histological investigations of the gonads of Pacific members of *Coris* are desirable.

The presence of a prominent and distinct male color phase in this species may be a result of the changing composition of social groups. In this study, males occasionally enlarged their territories and increased the size of their harems. Also, some females changed harems. Thus, a male which is distinctly colored may have a better chance, for example, of attracting a female displaced by a storm. Distinctly colored males may therefore have a higher reproductive success than non-distinct ones. This is in contrast with the haremic wrasse *Labroides dimidiatus*, in which females do not change harems and a distinct male color phase is absent (Robertson & Hoffman 1977).

Seasonal effects on reproductive behavior

During the middle of summer, when day length is longest, *C. dorsomaculata* adjusts its daily spawning time to coincide with outgoing tidal currents. Thus, when the temporal limitations of day length allow, spawning occurs at a time that increases the probability of offshore dispersal of progeny. This has been noted in other reef fishes (Randall 1961, Randall & Randall 1963, Johannes 1978), and seems to serve both as a means of larval dispersal and to reduce predation on young by reef-dwelling planktivores. The defense of spawned eggs by males supports this idea, as does the movement of females in one harem to a site distant from groups of planktivorous fishes. That fish modify their reproductive behavior in order to maximize offshore dispersal of gametes is also supported by the observation that during spring tides the duration of the spawning period is shorter and the average number of spawnings per minute is higher. Outgoing tidal currents resulting from spring tides are generally stronger than those resulting from neap tides, and thus provide for maximum offshore dispersal of eggs. Neap tides produce relatively weak currents, so the benefits of concentrating reproductive activity into a short period are not as strong as with spring tides.

As day length decreases during fall the spawning time becomes fixed at midday, implying that individuals restrict reproductive activity to parts of the day when the light is brightest. During early morning and late afternoon, the sun is low on the horizon and ambient light levels are decreased. It is during this time that most piscivorous fishes seem to feed (Hobson 1974, 1975). The high proportion of predatory attacks that occurred while individuals were either spawning or in courtship suggests that they are particularly vulnerable during periods of reproductive activity. Thus, the temperate climate where the study was conducted may have resulted in two patterns of sexual activity: a variable spawning time to facilitate offshore movement of zygotes when day length is long, and a fixed spawning time at midday to minimize the risk of predation on spawning adults when day length is short.

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