

Diurnal Periodicity of Spawning Activity in Free-spawning Labrid Fishes

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The reproductive strategies of coastal marine fishes were reviewed and discussed by Johannes (1978). He proposed six types of reproductive behavior in relation to predator avoidance. Labrid fishes (family Labridae) exhibit either of two types; demersal spawning with egg-guarding or spawning near shelter. In the former type, adhesive eggs are attached to a substrate (nest) and cared for by male-parents. This type has been observed for several Mediterranean and northern European species (Fiedler, 1964; Breder and Rosen, 1966; Sjolander et al., 1972; Potts, 1974). Many other labrids including approximately all of the tropical species exhibit the latter type, in which gametes are released free into the water at the top of an upward spawning dash (Randall and Randall, 1963; Breder and Rosen, 1966; Youngbluth, 1968; Reinboth, 1973; Moyer, 1974; Nakazono and Tsukahara, 1974; Robertson and Choat, 1974; Moyer and Shepard, 1975; Meyer, 1977; Warner and Roberston, 1978; Thresher, 1979; Nakazono, 1979).

The timing of daily spawning in these free-spawners either depends on the tidal cycle or is fixed at a certain period of day. Robertson and Hoffman (1977), in comparing three species of labrids, have suggested that the timing depends on local conditions, e. g. presence or absence of a strong predictably timed tidal current. They have discussed the biological meanings of these timings in relation to the predation risk upon both eggs and spawning adults.

However, factors affecting the timing of spawning in many other labrids, especially those spawning independently of the tidal cycle, have not yet examined comparatively, though they seem to vary considerably.

The purpose of this paper is to review the diurnal periodicities of spawning in free-spawning labrids, and to examine their causal factors.

First, I describe the spawning times of several labrids that were observed in two localities of Japan. Second, available information concerning these times is arranged, and causal factors are discussed.

Observations

Underwater observations using SCUBA were carried out at Shirahama (33°42'N; 135°20'E) from 1972 to 1980, and at Kuroshima Island (24°25'N; 124°10'E) in November 1978. Spawning of seven species of labrids and two species of scarids were observed.

At Shirahama, observations were made at the shallow rocky reefs in the vicinity of the Seto Marine Biological Laboratory (see Kuwamura, 1981). *Labroides dimidiatus* was most intensively studied, and 40 spawnings and pseudo-spawnings (no release of eggs) of the species were observed. Spawning occurred from May to September, pseudospawnings occurring from April to November. Both spawning and pseudospawning occurred restrictedly between 10:58 and 13:17, except one pseudospawning at 14:54, independent of the tidal cycle (Kuwamura, 1981). Seasonal change of the spawning time was not apparent, though the very late pseudospawning mentioned above was observed in November at the end of the sexually active period. Eggs were once observed being fed upon by a school of the jack mackerel *Trachurus japonicus*, just after spawning. Adult fish were not attacked by predators either while mating or at other periods during the day. However, when tagged individuals were released at their collection site, attacks by the lizardfish *Synodus variegatus* were observed twice, one successful and the other unsuccessful.

In *Thalassoma cupido* only "group spawning" (see Nakazono, 1979) were observed about ten times. They occurred between 09:00 and 12:30, from May to July. "Pair spawnings" (see Nakazono, 1979) of *Halichoeres tenuispinis* were observed five times. They occurred between 10:30 and 12:30, from May to August. Both species spawned at various stages of the tidal cycle. No predator was observed attacking eggs and/or spawning adults of the two species. Because observations are limited, it may be premature to conclude the diurnal periodicity

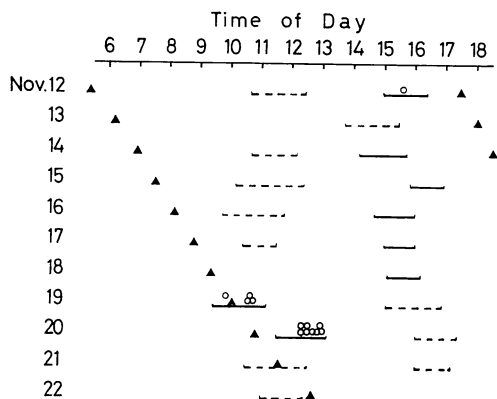


Fig. 1. Spawning times of labrids and scarids at Kuroshima Island, observed during the period from November 12 to 22, 1978. The segment of a line shows the duration of surveys at the lagoon moat (broken line) and at the reef flat and slope (solid line). Each circle represents one spawning observed. The triangle indicates the time of high tide.

of spawning time in the two species, but it seems that they spawn at a fixed time of day, independent of the tidal cycle.

At Kuroshima Island, 19 surveys, each continuing one to two hours, were conducted from November 12 to 22, 1978. Observations were made at various periods of day at various habitats of the barrier reef (see Fig. 1). Spawning was observed in: *Labroides bicolor* once at 09:55 (just before high tide); *L. dimidiatus* once at 12:34 (1.5 h after HT); *Thalassoma amblycephalus* three times at 12:28~12:55 (1.5~2 h after HT); *T. lutescens* three times at 12:31~12:55 (1.5~2 h after HT); *T. quinquevittata* once at 15:40 (2 h before HT); and two scarid species, *Scarus chlorodon* once at 10:39 (0.5 h after HT); *S. lunula* three times at 10:41~12:28 (0.5~1.5 h after HT). Most of these were pair spawning. The exceptions were two "triple spawnings" (see Nakazono, 1979) in *S. lunula*. No predation upon eggs and spawning adults was observed.

Spawning of these labrids and scarids occurred only at the offshore edge of the reef flat, and was restricted to a time period within two hours before or after high tide (Fig. 1). Though the present observations are by no means sufficient, it seems that the timing of daily spawning

in the labrids and scarids of Kuroshima depends on the tidal cycle, at least on the reef flat and slope.

Discussion

Synchronous spawning of coexisting species.

The most conspicuous example of synchronous spawning has been reported from the coral cay of Heron Island, the Great Barrier Reef (Robertson and Choat, 1974; Choat and Robertson, 1975). In that area, many species of labrids and scarids spawn shortly after high tide when the outgoing current is at its peak. For example, the spawning time of *L. dimidiatus* changes day by day from early morning to late afternoon, according to the advance of the tidal cycle, and it has two spawning periods on some days when there is one high tide a little before dusk and another just before dawn (Robertson, 1974). *L. dimidiatus* at the Aldabra Atoll also spawns shortly after high tide (Robertson and Hoffman, 1977).

Although observations are limited at present, labrids and scarids at Kuroshima Island probably spawn at the similar stage of the tidal cycle. In addition to the species of the present study, one more species of scarid at Kuroshima has been also known to spawn shortly after high tide (Yogo et al., 1980).

At Florida (USA) three species of labrids spawn around midday, but only on calm days when the tide is going out (Thresher, 1979). This finding suggests the possibility that some species, which are known to spawn at a fixed time of day, may be also depending on an outgoing current.

The above examples demonstrate that many species in an area spawn depending on the same environmental factor, i. e. the outgoing current. The advantage of spawning at the time when the tide is going out has been discussed from the viewpoint of the avoidance of predation upon eggs by reef-attached planktivores (Robertson and Hoffman, 1977; Johannes, 1978; Lobel, 1978; Yogo et al., 1980) or the long-distance dispersal of eggs (Barlow, 1981).

Intraspecific variation in spawning time. In *L. dimidiatus* spawning occurs shortly after high tide at Heron and Aldabra (Robertson and Hoffman, 1977) and probably at Kuroshima (present study), but it occurs around noon, indepen-

dent of the tidal cycle, at Shirahama (Kuwamura, 1981). No predictable outgoing current was recorded at the time shortly after high tide or around noon in the vicinity of the study area at Shirahama (Nakamura, 1958, 1959, 1960). Moreover, spawnings in aquaria, in which there are no currents depending upon the tidal cycle, also occur around noon (Hioki, 1979).

Similar variation is found in *T. lutescens*: it spawns probably depending on the tidal cycle at Kuroshima (present study), while it spawns at the fixed time (10:30~11:30) of day at Miyake-jima (Moyer, personal communication). *Halichoeres bivittatus* and *H. maculippina* spawn around midday, only on calm days when the tide is going out, at Florida (Thresher, 1979), while they spawn in the mid-afternoon at the San Blas Islands off Panama (Warner and Robertson, 1978), where the strong predictably timed tidal currents are lacking (Robertson and Hoffman, 1977).

The above cases show that even within a species the timing of daily spawning can vary geographically depending upon local conditions, as has been suggested by Robertson and Hoffman (1977) between different species in different areas.

Spawning times of *T. cupido* and *H. tenuispinis* also vary among several localities of Japan (see Table 1). This geographical variation in spawning time of the two species can not be explained by the presence or absence of a predictable offshore current, and spawnings occur independent of such currents. There is no clear relationship between the spawning time and the latitude or longitude at each locality (see Table 1). At present, it is unknown what differences in local conditions are related to variations in spawning times.

In some temperate labrids the timing of daily spawning changes seasonally. At Miyake-jima *Coris dorsomaculata* spawns with the incoming tide, which produces an outgoing current, between 11:00 and 16:30 during August and September, while it spawns at the fixed time between 11:00 and 13:00 from late September to December (Tribble, in press). No detailed information is available as to the seasonal change of the strength and predictability of the outgoing current in that area. Therefore, it can not be concluded at present whether the seasonal variation of *C. dorsomaculata*'s spawning time has

resulted from the change of day-length or change of currents, or both.

At Miyake-jima, *Halichoeres melanochir* also changes its spawning time seasonally: it spawns about 14:00~15:00 in mid-June, and about 15:00~17:00 during late July and August (Moyer and Yogo, in press). The change of day-length may possibly affect both physiological and behavioral conditions of the fish. Such seasonal change of spawning time may also be found in other labrids in the temperate waters if detailed studies are made. For example, it may not be rejected that *L. dimidiatus* at Shirahama also changes its spawning time seasonally, as a very late pseudospawning occurred at the end of spawning season.

Different spawning times among coexisting species. In contrast to synchronous spawnings in areas previously mentioned, spawning times of several labrid species differ from each other in some other areas; e. g. the San Blas Islands off Panama and several localities of Japan (see Table 1).

Although the strength and predictability of outgoing currents in these areas are not always known precisely, from the viewpoint of topographical conditions outgoing currents seem to be weaker and unpredictable there, as compared with coral cays such as Heron Island. In these areas, even if there is a predictable outgoing current, the different spawning times of various species show that there are some species whose spawning times do not depend on the current. The light intensity or the length of time after sunrise seems to be a proximate cause of the fixed spawning time of day in these species.

It seems to be rather difficult to explain the biological meaning or ultimate cause of these fixed spawning times, as compared with that in the synchronous spawning.

Hioki (1979) has suggested the possibility that the different spawning times between *H. tenuispinis* and *T. cupido* in Suruga Bay are related to the avoidance of interspecific spawnings. However, this does not seem to be a primary cause, as both spawned at the same time of day at Shirahama, and no spawning between them was observed.

Referring to the hypothesis that piscivorous fishes feed most successfully at dawn or dusk, while the feeding ability of planktivorous fishes is reduced at that time due to risk of predation they

Table 1. Examples of different spawning times of coexisting labrid species within an area. Sources of information are given in parentheses: 1. Hioki (1979); 2. Kuwamura (1981); 3. Meyer (1977); 4. Moyer (1974); 5. Moyer (personal communication); 6. Moyer and Shepard (1975); 7. Moyer and Yogo (in press); 8. Nakazono (1979); 9. Nakazono and Tsukahara (1974); 10. Robertson and Hoffman (1977); 11. Tribble (in press); 12. Warner and Robertson (1978); 13. Yogo (observations, in Meyer 1977); 14. Present study.

Locality	Species	Maximum standard length (cm)	Spawning time	Source
San Blas Islands (9°30'N; 78°30'W)	<i>Thalassoma bifasciatum</i>	12	midday	(10, 12)
	<i>Halichoeres maculippina</i>	12	mid-afternoon	(12)
	<i>H. bivittatus</i>	15	mid-afternoon	(12)
	<i>H. poeyi</i>	15	mid-afternoon	(12)
	<i>Clepticus parrae</i>	19	mid to late afternoon	(10, 12)
	<i>Bodianus rufus</i>	24	very late afternoon	(12)
Amakusa (32°22'N; 130°03'E)	<i>T. cupido</i>	15	mid-afternoon	(13)
	<i>Stethojulis interrupta terina</i>	10	14: 00~15: 00	(8)
Shirahama (33°42'N; 135°20'E)	<i>T. cupido</i>	15	09: 00~12: 30	(14)
	<i>H. tenuispinis</i>	15	10: 30~12: 30	(14)
	<i>Labroides dimidiatus</i>	9	11: 00~13: 00	(2)
Tsuyazaki (33°51'N; 130°29'E)	<i>Pseudolabrus japonicus</i>	16	08: 00~10: 00	(8)
	<i>H. tenuispinis</i>	12	09: 00~10: 00 & 15: 00~16: 00	(8)
	<i>Pteragogus flagellifer</i>	16	15: 00~16: 30	(8, 9)
Miyake-jima (34°05'N; 139°30'E)	<i>T. cupido</i>	15	08: 30~12: 00	(3, 4)
	<i>Macropharyngodon negrosensis</i>	9	mid-morning	(5)
	<i>T. lutescens</i>	15	10: 30~11: 30	(5)
	<i>Coris dorsomaculata</i>	15	11: 00~16: 30*	(11)
	<i>M. moyeri</i>	9	early afternoon	(5)
	<i>H. melanochir</i>	15	14: 00~17: 00*	(7)
	<i>Pseudojuloides elongatus</i>	11	mid-afternoon	(5)
	<i>P. cerasinus</i>	11	mid-afternoon	(5)
	<i>Cirrhilabrus temminckii</i>	15	late afternoon	(6)
<i>Pseudocheilinus hexataenia</i>	10	just before sunset	(5)	
Suruga Bay (35°03'N; 138°48'E)	<i>T. cupido</i>	12	08: 00~09: 40	(1)
	<i>H. tenuispinis</i>	15	16: 00~17: 00	(1)
	<i>C. temminckii</i>	8	16: 00~18: 00	(1)

* Seasonal change occurs. See text for details.

face (see Hobson, 1974, etc.), Robertson and Hoffman (1977) suggested that the different timing of *T. bifasciatum* and *C. parrae*'s spawning periods at the San Blas Islands (see Table 1) was determined by differences in the strength of predation risks to spawning individuals of each species. They hypothesized that a substrate-associated species (*T. bifasciatum*) would be more prone to predation when spawning in mid-water than those fishes that normally live up in the water column (*C. parrae*). Differences in the strength of reliance upon the substrate

seem to be partly related to differences of body-size between the two species.

In all six species studied in the San Blas Islands there can be found a tendency that larger species spawn later in the afternoon (Table 1). Spawning at dusk may reduce the risk of predation on eggs (Robertson and Hoffman, 1977; Lobel, 1978; Moyer, 1979), but only larger species seem to be able to spawn at that time when crepuscular piscivores are active instead of planktivores. It is probably because smaller species are more vulnerable to predation than larger ones (Hob-

son, 1974; Johannes, 1978; Moyer, 1979). Body-size has been suggested to determine the reproductive strategies of fishes in two aspects: 1) migrating spawning or non-migrating spawning (Johannes, 1978), and 2) broadcasting pelagic eggs or guarding demersal eggs (Barlow, 1981). As mentioned above, I suggest that body-size also determines the timing of daily spawning.

The above "size hypothesis" in spawning time seems to be applicable to labrid species in some other areas (e. g. Shirahama), but there are several exceptions (see Table 1). For example, a small species, *Pseudocheilinus hexataenia*, spawns just before sunset at Miyake-jima. The upward spawning dash of this species is very short and rapid (Moyer, personal communication), and probably reduces the predation risk upon spawning adults by crepuscular piscivores. The pattern of spawning behaviour also seems to be related to the timing of spawning period. No sufficient explanation for other exceptional species can be given at present.

Closing comments. This brief review has shown that two main environmental factors, i. e. the outgoing current and day-length or light intensity, are affecting the timing of labrid spawning periods, but that factors are complex and remain unknown in many cases, especially in areas where the spawning time differs among species. The ultimate cause of the timing seems to be possibly explained from the viewpoint of the avoidance of predation upon eggs and/or spawning adults. However, this anti-predation hypothesis has not yet been satisfactorily substantiated. Many authors have observed actual predation on eggs and/or spawning adults of labrids (Moyer, 1974; Meyer, 1977; Robertson and Hoffman, 1977; Nakazono, 1979; Moyer and Yogo, in press; Tribble, in press; Suzuki, personal communication; present study). However, presence or absence of predation at spawning does not deny nor support the hypothesis, as such facts give no information about whether eggs and adults would be fed upon more or less if spawning would occur at other periods of the day. Detailed information is needed on the feeding strategies and activity patterns of both piscivorous and planktivorous fishes in relation to the spawning time of labrids in each locality.

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ベラ科魚類の産卵時刻

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和歌山県白浜および八重山諸島黒島において観察した計7種のベラ類と2種のブダイ類の産卵時刻を報告し、従来の知見と合わせて浮遊卵を産むベラ類の産卵時刻をきめる要因について考察した。

沖へ向かう強い潮流が定期的にある地方ではその時刻に合わせて産卵するのに対し、そのような潮流が明瞭でない地方では、種ごとに異なった一定時刻に産卵する傾向がみられた。前者の産卵時刻の意味は卵の分散および捕食回避の面から説明しうるが、後者については不明な点が多く、ここでは卵および親魚に対する捕食圧との関係から、体の大きさや産卵時の上昇行動の速度と距離が影響していることを示唆した。種内における産卵時刻の地理的変異や季節変化についても若干の考察を行った。

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