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LUNAR SPAWNING OF THE THREADFIN, *POLYDACTYLUS SEXFILIS*, IN HAWAII[1]

Recent evidence indicates that lunar spawning rhythms are more common in fishes than was once thought. Johannes (1978) listed 50 species of teleost fishes with lunar spawning rhythms, most of them tropical and all of them marine or catadromous. In the course of developing methods for culturing the threadfin, *Polydactylus sexfilis* (Cuvier and Valenciennes), we found that this species displayed a lunar spawning rhythm (May 1976). The lunar pattern of spawning had been indicated by a previous field study (Lowell 1971) and is consistent with fishermen's lore (Hosaka 1944), but proof was lacking and details of the rhythm were unknown. In this paper we present detailed information on the lunar spawning of *P. sexfilis* along with observations of spawning behavior, using results from captive fish.

Polydactylus sexfilis is a much sought-after food fish in Hawaii and supports an important sport fishery as well as a small commercial fishery (Rao[2]). Information on the life history of this species (Lowell 1971; Morris and Kanayama[3]) indictates that spawning takes place close to shore. The larvae and juveniles lead a pelagic existence for about 3 mo, juveniles moving to shallow inshore areas at fork lengths (FL) between about 50 and 100 mm. The fish become sexually mature males at 20-25 cm FL and subsequently undergo a sex reversal, passing through a hermaphroditic stage and becoming functional females between 30 and 40 cm FL. Adults inhabit inshore rocky and sandy areas, frequently in zones of turbulence.

Methods

Juvenile *P. sexfilis* were captured by seine on reef flats along windward Oahu in September and October 1970 and reared to sexual maturity in tidal ponds at Coconut Island, in Kaneohe Bay, Oahu. The fish were daily fed chopped squid or smelt, commercial trout chow (40% protein), or trout chow supplemented with chopped squid. In May 1973, 30 mature fish (18 females and 12 males) were transferred to a 18-m^3 nylon net enclosure suspended from Styrofoam[4] floats and anchored off the leeward (southwest) side of Coconut Island. In June and July 1973, a small number of these fish were removed to laboratory tanks and used in experiments on hormone-induced spawning. During this work, ovarian biopsy samples were examined which contained residual eggs and indicated that the fish had been spawning spontaneously. In order to monitor any such spawning, an airlift egg collector was installed (May et al.[5]) in the center of the net in July 1973 and operated continuously (except for a few days when equipment malfunctioned) between 14 July 1973 and 31 December 1975. *Polydactylus sexfilis* produces pelagic eggs, so that the collector obtained a sample of eggs at each spawning. Every morning the entire contents of the collector were harvested and examined under a dissecting microscope, and the number of *P. sexfilis* eggs was estimated by sub-

[1]Contribution No. 552, Hawaii Institute of Marine Biology.

[2]Rao, T. R. 1977. Enhancement of natural populations of moi (*Polydactylus sexfilis*) in Hawaii through the release of hatchery-reared juveniles - a feasibility study of sea ranching. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 33, 46 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

[3]Morris, D. E., and R. Kanayama. 1964-69. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Projects No. F-5-R-11 to F-5-R-17, Div. Fish Game, State of Hawaii. Division of Fish and Game, Honolulu, Hawaii.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]May, R. C., G. S. Akiyama, and M. T. Santerre. 1976. A simple method for monitoring the spawning activity of fish in net enclosures. International Milkfish Workshop-Conference, May 19-22, 1976, Tigbauan, Iloilo, Philipp. Working Pap. 10, p. 133-138. Southeast Asian Fisheries Development Center, Kalayaan Building, Dela Rosa corner Salcedo Sts., Makati, Metro Manila, Philipp.

sampling. In 1976 and 1977, the collector was operated only during the spawning periods, which were predictable on the basis of data collected during the previous years. Eggs of *P. sexfilis* were distinguished from occasional eggs of other species by their diameter (800-825 μm) and by comparing hatched larvae with larvae obtained from hormone-induced spawnings; the identification was further corroborated by rearing larvae to the juvenile stage on several occasions. Since *P. sexfilis* undergoes a male-female sex reversal, additional males were added to the population each year to maintain a female to male sex ratio between 1:1 and 1.5:1 during the spawning season. In 1976, additional males were not added until the third spawning month, so data on spawning were not available for the first two spawning months of that year. At the end of this study in December 1977, the population of spawners numbered 57.

In order to determine the exact time of day when spawning occurred, water was sampled from the holding net continuously with a centrifugal pump at 10 l/min and passed through a small collecting basket (500-μm nylon mesh) on a barge anchored next to the net. The collecting basket was monitored visually, and the time when eggs first appeared was noted. The superstructure of the barge provided a barrier between the observer and the holding net, so that activities associated with monitoring the basket did not disturb the spawners in the net.

Results

Lunar Spawning Rhythm

Eggs of *P. sexfilis* were first observed in the collector from 23 to 25 July 1973. Subsequently the fish were found to spawn at night over a period of 3-7 (in one instance, 10) days once each month, always in proximity to the last quarter phase of the moon (Figure 1), and in a spawning season that extended from May or June to October (Table 1). Because the lunar month is 29.5 days long and does not coincide exactly with the calendar month, the calendar dates of spawning (Table 1) were generally 1-3 days earlier in each succeeding month. The first spawning of each monthly series was usually preceded by 1 or 2 days on which the fish fed less actively than normal. Counts of *P. sexfilis* eggs from the collector were made in August 1973, and thereafter. Judging from the samples obtained by the collector, relatively few eggs were produced on the first and last days of spawning, with a peak usually on the second or third day (Figure 1). However, because the eggs collected represented only a sample of the total number of eggs produced, it is possible that the peaks reflected some sampling variability.

The time of spawning relative to the lunar cycle appeared to change as the spawning season progressed. The first spawning series of the year always began (Figure 2) on the day of the last quarter (in one case the egg collector malfunctioned prior to the last quarter, and it is possible that the first day of spawning occurred earlier). In subsequent months the series began 1-4 days prior to

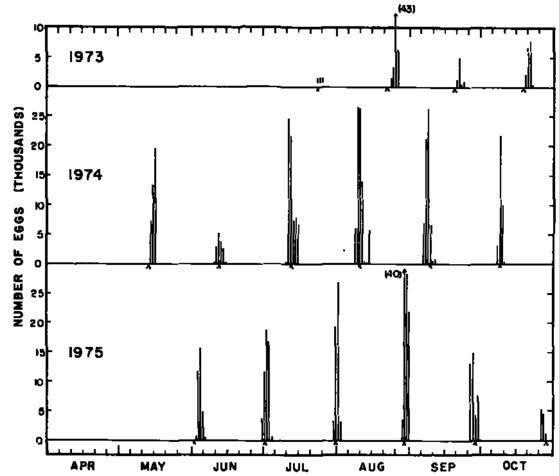

FIGURE 1.—Numbers of *Polydactylus sexfilis* eggs obtained by the airlift egg collector between August 1973 and October 1975. In July 1973, eggs were noted on 3 days but were not counted. Carets indicate the time of the last quarter phase of the moon.

TABLE 1.—Dates on which eggs were produced by captive *Polydactylus sexfilis* during study period. For each spawning month, the upper date is the first observed day of spawning, the lower date the last day.

Year	Spawning month I	II	III	IV	V	VI
1973	(1)	(1)	(1)	22 Aug. 25 Aug.	19 Sept.[2] 22 Sept.	18 Oct.[2] 21 Oct.
1974	13 May 15 May	9 June 14 June	9 July[2] 14 July	7 Aug. 13 Aug.	5 Sept. 10 Sept.	6 Oct. 9 Oct.
1975	1 June[2] 5 June	29 June 3 July	29 July 1 Aug.	27 Aug. 30 Aug.	25 Sept.[2] 29 Sept.	25 Oct. 27 Oct.
1976	(1)	(1)	17 July 20 July	15 Aug. 18 Aug.	13 Sept.[2] 16 Sept.	13 Oct. 16 Oct.
1977	9 May 14 May	7 June[2] 11 June	6 July 11 July	4 Aug. 13 Aug.	3 Sept. 7 Sept.	1 Oct. 5 Oct.

[1]Data not available.
[2]Collector malfunctioned on previous day; initial spawning day possibly earlier.

the last quarter (Figure 2). In April 1974 the collector obtained several thousand eggs over a 3-day period about 12 days before the last quarter; although the eggs were of the same diameter as *P. sexfilis* eggs, the larvae were not reared for positive identification. In view of the consistency of subsequent spawning data, and the low ovarian weights which two previous studies found in *P. sexfilis* in April (Lowell 1971; Morris[6]), we believe these were eggs of another species.

Some of the eggs found in the collector were transparent, buoyant, and developing normally, while others sank and were opaque and obviously not viable. Among the spawnings in which 1,000 or more eggs were collected, an average of 52% of the eggs were viable (range, 0-98%). The airlift collector apparently damaged the eggs to some extent. For example, on 13 June 1974, when 75% of the eggs from the collector were viable, eggs obtained by dip net at the time of spawning showed over 90% viability. It is not known how many of the fish in the net participated in each spawning or whether the same fish spawned each month, although Kanayama[7] believed that individual *P. sexfilis* spawned more than once in a season.

[6]Morris, D. E. 1964. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-11, Div. Fish Game, State of Hawaii, 15 p. Division of Fish and Game, Honolulu, Hawaii.

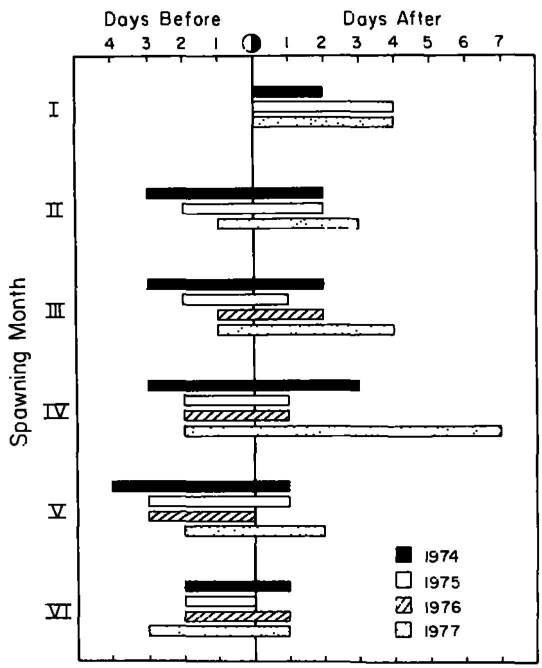

FIGURE 2.—Duration of spawning of *Polydactylus sexfilis* relative to the time of the last quarter (◑) for the six spawning months in 1974, 1975, and 1977. Data are given only for the last four spawning months of 1976.

Time of Spawning

The developmental stage of eggs found in the collector in the morning indicated that spawning had occurred shortly after sunset. Visual monitoring of water sampled continuously from the net on 34 spawning nights showed that with few exceptions the fish spawned between 2030 and 2130 h (Figure 3, Table 2). The times recorded were those when eggs were first observed in the collector; it is possible that additional spawnings took place slightly later on the same night, and behavioral observations (see below) indicated that this may have been true on at least some nights. The time of spawning did not vary with the time of sunset (Figure 3) and appeared unrelated to the time of moonrise (which occurred generally between 2300 and 0400 h during the spawning season).

[7]Kanayama, R. 1967. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-15, Div. Fish Game, State of Hawaii, 9 p. Division of Fish and Game, Honolulu, Hawaii.

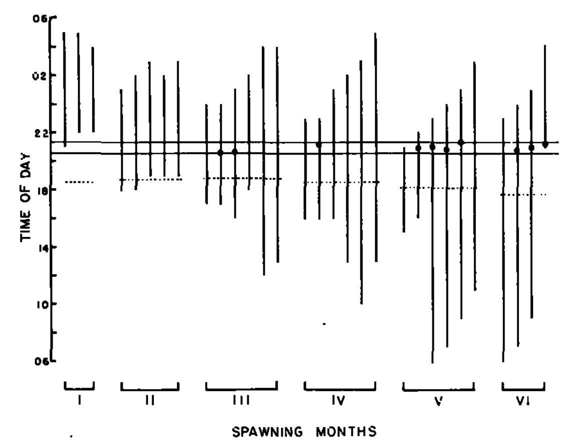

FIGURE 3.—Times of spawning of *Polydactylus sexfilis* during the six spawning months (roman numerals) of 1974 in relation to the tidal cycle. Dots indicate observed times of spawning in 1974, and the horizontal lines delineate the time of spawning as indicated by data from 1974, 1975, and 1977 (see Table 2). Dotted horizontal lines show the times of sunset in 1974. Vertical lines for each spawning night indicate time between the evening high and low tides, i.e., the duration of the outgoing tide, as measured by a tide gage at Coconut Island in 1974.

TABLE 2.—Times of first spawning in a captive population of *Polydactylus sexfilis* on nights in 1975 and 1977. Where a single time is given, the egg collector was examined continuously; in other cases, the collector was examined at intervals of 5-15 min. Numbers in parentheses indicate times of peak fish activity, presumed to be the exact time of spawning.

Date	Time of first spawning	Date	Time of first spawning
1975.		26 Sept.	2045-2100 (2052)
2 June	2115-2118	27 Sept.	2054-2100
3 June	2110-2115	28 Sept.	2050-2054 (2053)
4 June	2110-2115	29 Sept.	2135-2140 (2138)
5 June	2115-2120	26 Oct.	2050-2100 (2056)
30 June	2115-2120	27 Oct	2105-2110 (2107)
2 July	2125-2130 (2127)	1977:	
3 July	2140-2145	7 June	2105
30 July	2045-2100 (2058)	9 July	2147
31 July	2120-2125	10 July	2140
28 Aug.	2115-2118 (2117)	6 Aug.	2050
29 Aug.	2129	4 Sept.	2103
30 Aug.	2115-2118 (2117)	3 Oct.	2038

Data from a tide gage located at Coconut Island were available for 1974 and showed that spawning nearly always took place on the outgoing tide (Figure 3). Although tide gage data were not available for subsequent years, tides predicted from tide tables showed patterns similar to the 1974 tide gage data. For 1975, 1976, and 1977, the time of spawning (i. e., 2030-2130 h) was compared with predicted tides and again found to occur mostly during the outgoing tide. Spawning occurred on the outgoing tide in 73% of the spawning nights during 1974-77.

Spawning Behavior

Observations of spawning behavior were made initially by watching bioluminescence caused by the fish's movement; later, direct observations were made by shining lights on the water at the time of spawning. The level of activity of the fish gradually increased beginning around 2015 h and culminated in the spawning act as determined by the appearance of eggs in the centrifugal pump samples. Occasionally the fish broke the surface of the water during the period of increased activity. During courtship the fish swam rapidly around the net in a circular manner in groups of two or three. They appeared to be chasing one another, and often one fish would contact another from behind, either dorsally or ventrally, with snout. Spawning appeared to take place between pairs rather than among larger groups of fish. Increased activity usually continued for 20 or 30 min after eggs were first noted.

Discussion

The captive population of *P. sexfilis* was clearly spawning with a well-defined lunar rhythm. Other evidence implies that this is a natural behavior for this species. Lowell (1971) set gill nets weekly in certain shoal areas of Oahu from April to August 1970 and reported that exceptionally large catches of *P. sexfilis* per effort occurred "after the full moon and continuing until the last quarter (1 week duration)," and because of the stage of gonadal development among fish in such catches, he termed them "spawning runs." In July 1970, female fish caught 3 days before the last quarter all had well-developed ovaries, but fish caught 4 days after the last quarter had spent ovaries. Fishermen seem to have been aware of the habits of *P. sexfilis* for a long time: Hosaka (1944:117) stated, "Moon light nights are best for moi (= *P. sexfilis*) fishing, and this is especially true when the moon is in the last quarter phase."

Spawning at the time of the last quarter phase of the moon appears to be rare among fishes. Of the 50 lunar spawners which Johannes (1978) listed, only two besides *P. sexfilis* spawned on the last quarter; both of these are species of *Amphiprion*, and one spawned on the first as well as the last quarter. Since the various species covered in Johannes' list occurred in different geographic locations, the variations in spawning days, taken together with variations in spawning times, could reflect local adaptations such as would occur if egg or larval survival were related to tides or currents.

The coincidence of spawning in *P. sexfilis* with the outgoing tide indicates that the remarkably precise timing of spawning may act as a mechanism for offshore dispersal of eggs and larvae. Lowell (1971) noted that there was a strong, oceanward current at his sampling site during falling tide, when he estimated spawning occurred, and results of ichthyoplankton surveys indicated that *P. sexfilis* eggs and larvae are not found in inshore waters in Hawaii (Leis and Miller 1976; Miller et al.[8]; Watson and Leis[9]). Johannes (1978)

[8]Miller, J. M., W. Watson, and J. M. Leis. 1973. Larval fishes. *In* S. V. Smith (editor), Atlas of Kaneohe Bay, a reef ecosystem under stress, p. 101-105. Univ. Hawaii Sea Grant Tech. Rep. 72-1. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

[9]Watson, W., and J. M. Leis. 1974. Ichthyoplankton of Kaneohe Bay, Hawaii: a one-year study of the fish eggs and larvae. Univ. Hawaii Sea Grant Tech. Rep. 75-1, 178 p. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

pointed out that spawning on outgoing tides is a common phenomenon among coastal marine fishes in the tropics, and he believed it evolved as a strategy for ensuring that eggs and larvae are transported away from the heavy concentration of predators in shallow water. Johannes noted that nocturnal spawning is also common in tropical reef fishes and serves to reduce predation both on the eggs and on the spawners.

The first *P. sexfilis* spawning of the year appears to be anomalous in that it occurs relatively late with respect to the last quarter. If offshore transport confers an important selective advantage on *P. sexfilis*, the lateness of the first spawning is maladaptive because it results in release of eggs early relative to the outgoing tide (see Figure 3). The initial phase of the spawning season may thus result in few viable offspring and could represent a gradual initiation of the main spawning season, delayed perhaps by the lower water temperatures which usually prevail during the first spawning month (Bathen[10]).

No observations on the spawning behavior of a polynemid fish have been published previously. In *P. sexfilis* the sexes apparently pair and spawn after a brief courtship involving rapid following and nosing of one fish by another. The spawning behavior of this species is similar in many respects to that of the Pacific bonito, *Sarda chiliensis*, including behaviors described by Magnuson and Prescott (1966) as "circle swimming," "tail nosing," and "following." The circling behavior noted among *P. sexfilis* may have been imposed by the confinement of the net enclosure, but *S. chiliensis* also showed tight circling behavior at the time of gamete release in a very large tank at Marineland of the Pacific, and circling prior to spawning occurs naturally in mullets (Helfrich and Allen 1975) and some (perhaps many) other tropical fishes (R. E. Johannes, Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96844. Pers. commun., December 1977). The circling behavior during spawning observed in captive *P. sexfilis* thus may not be abnormal for this species but may, as Magnuson and Prescott (1966) theorized for *S. chiliensis*, serve to enhance the probability of fertilization.

[10]Bathen, K. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. Univ. Hawaii. Hawaii Inst. Mar. Biol., Tech. Rep. 14, 353 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

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