

## Social Organization and Spawning Behavior of the Pteroine Fish *Dendrochirus zebra* at Miyake-jima, Japan

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**Abstract** Social organization and reproductive behavior of the lionfish *Dendrochirus zebra* were studied at Miyake-jima, one of the Izu Islands of Japan. Individuals of this species are solitary predators that hunt over wide home ranges that overlap greatly with other members of the species, both male and female. Large males are often found within specific areas in the midst of their much wider home ranges. Such "activity centers" are not defended, and cannot be considered as territories. During daylight, females in spawning condition come to specific locations, termed "rendezvous sites", within the activity center of a particular male, where they are met by that male or by one of many smaller subdominant males. Spawning occurs after sunset in areas of moderate off-shore currents. Males compete for females, often fighting. Wounds inflicted by venomous spines of rival males can result in injury that may affect the spawning success of the injured male.

Females spawn two mucous sacks, each containing a few thousand eggs. These are released after a short upward dash. Tests showed that many well-known egg predators were repulsed by the mucus. It is hypothesized that the upward spawning rush is an anti-predator defense, and that certain fish, perhaps sharks, might occasionally prey on lionfishes.

Although lionfishes (Scorpaenidae: Pteroinae) are common and frequently observed residents of tropical reefs throughout the Indo-West Pacific region, surprisingly little is known about them. Some research has dealt with their toxins, e. g. Halstead (1970), but information on their behavior appears to be limited to the studies of Fishelson (1975) and Brandt (1976), both of which relied heavily or entirely upon aquarium observations. Fishelson (1978) also examined the reproductive physiology of the pteroine *Dendrochirus brachypterus* (Cuvier). Little is available on the social organization of any of the lionfishes other than passing references to their solitary or gregarious nature, depending upon the species (e. g. Fishelson, 1975).

The paucity of information on the sociobiology of pteroine fishes, as well as the general lack of information on social organizations of upper-level consumers in the reef community, led us to undertake a detailed study of *Dendrochirus zebra* (Quoy et Gaimard) at Miyake-jima (34°05' N, 139°30' E), one of the Izu Islands of southern Japan.

### Methods and materials

All behavioral observations were made using

SCUBA. From one to five (usually three) dives of from 40~80 min were made daily, ocean conditions permitting, from June to mid-October, 1980, amounting to a total of 191 hours of underwater observations. Two dives were made daily at fixed times. A population census was taken in the study area every day at mid-day (11:00~13:00 h), and spawning observations were attempted beginning shortly before sunset and terminating from twenty to fifty-five minutes after sunset every evening. Lights were not used. In addition, dives were made at all hours of daylight in order to obtain information on diurnal activities of our study animals.

After a period of several days of habituating our animals to our presence, each individual observed on the mid-day census was measured and examined for specific identifiable characteristics. Measurements were made from a distance of 3~10 cm with a hand-carried ruler (Fig. 1A). Each individual was measured 5~10 times over a period of three weeks in order to assure accuracy of measurements. With the exception of male No. 11, our measuring technique was tolerated by all of the estimated 32 adult fish in our study population. Small juveniles (50~65 mm in total length) were not included in the

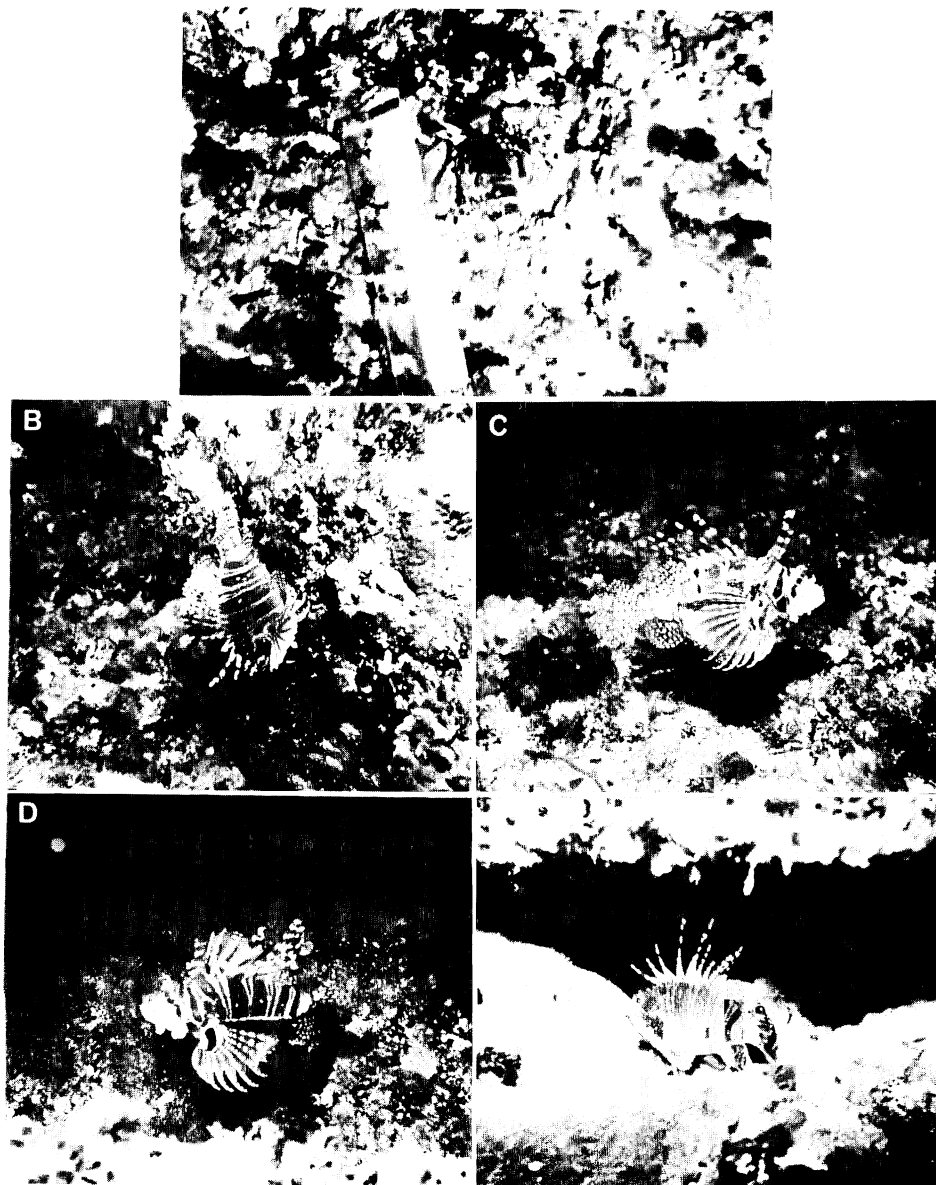


Fig. 1. A: Method of measuring *Dendrochirus zebra* individuals during mid-day census. B: Male #2. Note broken third dorsal spine. C: Male #5. Note absence of third dorsal spine. D: Male #11. Note broken first dorsal spine. E: Male #12. Note broken second dorsal spine and eighth dorsal spine. From color transparencies by J. T. Moyer (A~D) and M. J. Zaiser (E).

study.

Most individuals could be recognized by specific characteristics (Fig. 1B~F, Table 1), so that we were able to accurately identify all males (N=15) and eight of the estimated 17 females in the population. We estimated the total number of identically appearing females on

the basis of the maximum number of a particular size and color pattern observed on specific census dives. This technique gives us an *absolute* minimum figure, but the possibility exists that we may have overlooked some individuals.

Mucous egg sacks were collected at selected spawnings in plastic bags, and eggs were counted

under a binocular dissecting microscope. Water temperatures and depths were measured with commercial gauges. All photographs were taken by the authors (as indicated) using a Nikonos III camera.

#### The study site

The study site (Fig. 2) consisted of an area of approximately 11,875 square meters, about 35% of which was made up of a substrate of small (60 cm<sup>2</sup>) to medium-sized (1 m<sup>2</sup>) boulders. The remainder consisted of small volcanic and coral rubble on sand and areas of bare sand. A few large volcanic boulders (up to 2.5 m in height) were widely scattered throughout the study site. Depths ranged from 5~15 m. A moderate current usually flowed seaward, passing over the sandy areas of the site on the seaward side of Male #15's Rock, Anemone Rock, and Male #1's Boulder, and moving in the direction of Yogo's Corner (see Fig. 2). The site, on the northwest side of Miyake-jima, was relatively

well-sheltered from heavy wave action resulting from prevailing winds from the southwest and northeast. Water temperatures at the time of the study ranged from 18°~29°C.

#### Results

##### Social organization

*Dendrochirus zebra* is a solitary predator that feeds primarily upon crabs, shrimp, and small fishes (personal observations). Individual home ranges are large (e. g. Male #15 was observed in numerous locations over an area 115 m × 75 m in size), and greatly overlap those of other individuals, both male and female. Individuals do not defend territories, although certain large males (e. g. Nos. 1, 5, 11, and 12) had definite areas of peak activity within their much wider home ranges. Chance meetings between fish of the same sex are inevitable during feeding and reproductive activities. Females tolerate other females when such accidental meetings occur, but they cannot be considered as gregarious,

Table 1. Characteristics of specific males and females.

Sex	No.	Total length	Spots behind pectorals		Broken dorsal spines	Other characteristics
			Left	Right		
M	1	220 mm	1	1	None	Very dark. Pectoral spots faint.
M	2	200 mm	2	1	3rd $\frac{1}{2}$ broken	
M	3	160 mm	1	1	None	Many spots on pectoral fin
M	4	180 mm	1	1	None	Similar to #3, but larger
M	5	210 mm	1	1	No 3rd spine	Pectoral spots dull
M	6	160 mm	1	1	None	Right pectoral spot dull
M	7	160 mm	3	2	None	Left pectoral spots dull. One dull spot on right pectoral
M	8	200 mm	1	1	None	Very dark
M	9	200 mm	1	1	3rd $\frac{1}{2}$ broken	Differs from #2 by pectoral spots
M	10	180 mm	1	1	None	Permanent scar
M	11	200 mm	1	0	1st near base	Dark, aggressive to observer
M	12	200 mm	0	1	2nd and 8th	
M	13	130 mm	2	2	None	
M	14	100 mm	1	1	None	Smallest male
M	15	140 mm	2	2	None	Slightly larger than #13
F	3	100 mm	1	1	None	
F	4	160 mm	1	1	None	Right pectoral spot dull
F	5	180 mm	1	1	None	Very large female
F	6	140 mm	2	1	None	
F	7	120 mm	1	1	None	
F	8	130 mm	1	1	None	
F	9	150 mm	2	2	None	
F	10	140 mm	2	3	None	

and never form feeding groups.

Male-male interactions during feeding and courtship hours are always extremely agonistic in nature. Fights are quite common (Fig. 5), resulting in numerous broken spines, ripped fins, and other wounds. The locations and appearance of broken spines made identification of individual males relatively easy (Fig. 1). Females rarely, if ever, fight, and no females with broken spines or other wounds were observed. Male competition for females is intense, and a considerable amount of male activity is concerned with locating, defending, courting, and spawning with females. By contrast, females spend most of their active time feeding.

#### Diel activity and reproduction

*Dendrochirus zebra* is primarily a nocturnal predator, however a considerable amount of important activity occurs during daylight hours. Diurnal activity is mostly for the purpose of temporary pairing prior to the evening spawning period. However, females were occasionally observed feeding at mid-day, particularly during periods after storms or cold water and during peaks in spawning activity. Although both males and females may be active in the daytime, males are considerably more mobile, changing their locations several times during the day, as they attempt to locate females in pre-spawning condition.

Both males and females often begin actively hunting about 3 h before sunset. Males that have located females for spawning may temporarily leave them at this time, but only for short periods of 5~10 min.

**Sexual dimorphism.** Males of *D. zebra* are generally larger than females, but so much overlapping in size occurs that size alone is not an indication of sex (Fig. 3). Males seem to have more robust heads and jaws, but sex-determination on the basis of this character is uncertain at best. Females in spawning condition display a temporary pre-spawning coloration. The entire head and operculum become creamy-white, except for a dark stripe through the eye. Facial appendages under the eye become a brilliant white (Figs. 6, 7), turning silvery at the spawning period. Tips of the first four dorsal spines also turn brilliantly white, and the abdomen pales near the vent. The abdomen becomes swollen with eggs (Fig. 7). Females quickly

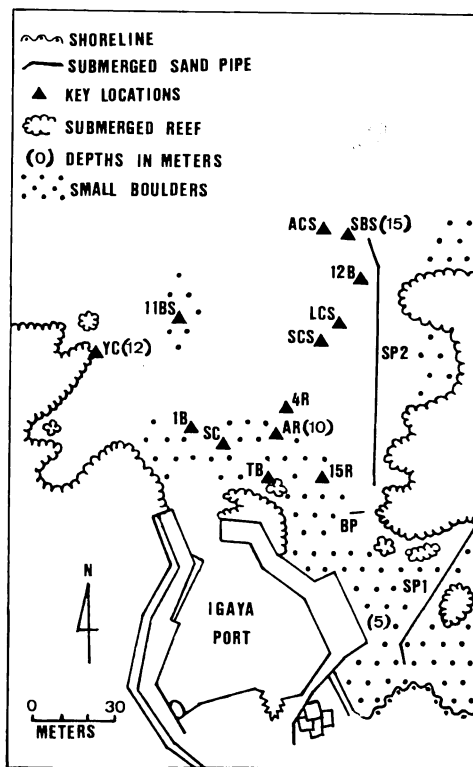


Fig. 2. Map of study site. SP, Sand Pipe; BP, Broken Pipe; 15R, Male #15's Rock; TB, Triggerfish Boulder; SC, Soft Coral; AR, Anemone Rock; 1B, Male #1's Boulder; 4R, Male #4's Rock; YC, Yogo's Corner; 11BS, Male #11's Boulders; SCS, Small Coral on Sand; LCS, Large Coral on Sand; 12B, Male #12's Boulder; SBS, Small Boulders on Sand; ACS, Arch Coral on Sand.

revert to normal coloration immediately after spawning.

**Rendezvous sites.** Solitary females of relatively small size that move in spawning condition at night over a very large home range could conceivably fail to make contact with a male and thus be unable to spawn. Individuals of *Dendrochirus zebra* avoid this problem by making use of specific rocks and boulders on the reef as rendezvous sites, where males find females in pre-spawning coloration during daylight hours. Eight such sites were found in the study area. These sites were named as follows: Male #1's Boulder, Soft Coral, Anemone Rock, Male #11's Boulders, Male #12's Boulder, Small Coral on

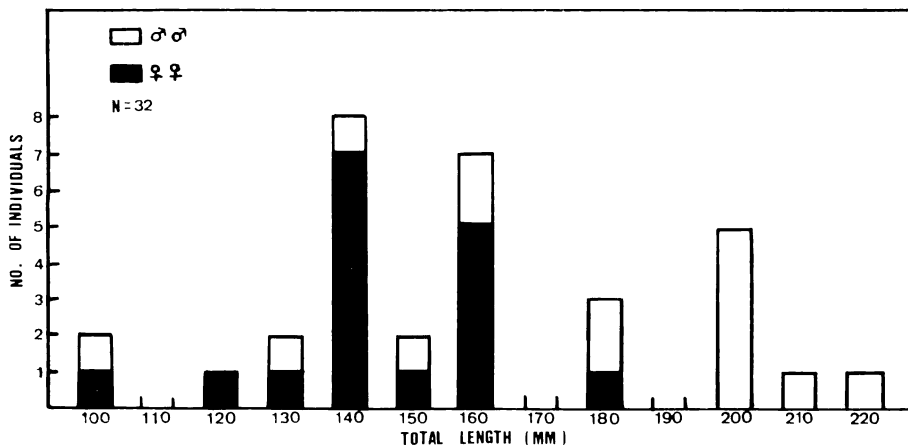


Fig. 3. Length frequency of the sexes of *Dendrochirus zebra*. Dark bars indicate females, open bars indicate males.

Sand, Large Coral on Sand, and Arch Coral (see Fig. 2). Often 2~3 females and a male were found at the same site during the mid-day census, giving the initial erroneous impression that *D. zebra* is a gregarious species. Females that were not ready to spawn did not visit these sites, seeking shelter during daylight at random locations on the reef.

**Strategies of dominant males.** Four large males (Nos. 1, 5, 11, and 12) appeared to be dominant over the other 11 males in the population. This dominance was usually expressed in nocturnal confrontations. The dominant fish, usually larger, darkened his body color and approached his rival. Usually the body color of the subdominant fish immediately faded in appeasement coloration, and he rapidly fled. Occasionally, lengthy chases followed (e.g. male #1 chased male #6 over a distance of 30 m on Sept. 18), but more often, the aggressor quickly returned to feeding or courtship. On some occasions, the subdominant fish temporarily challenged the stronger male. This invariably occurred in the presence of a female during courtship, but only if the rivals were of similar size. Both fish took on the dark aggressive coloration, widely flaring their opercula, causing their foreheads to drop and their entire face to broaden in appearance. At the same time, the pectoral fins were extended and rotated forward (Fig.: 5A), presenting a broad, spectacular posture. Invariably, the subdominant male

moved a few meters away, turned and fled. Fig. 5A shows a confrontation over a female between males #9 and #12, both 200 mm in total length (T. L.). #9 fled a few moments after the photograph was taken, but returned twice to challenge #12 before giving up the female.

Each of the four dominant males ranged widely over the study area at night, but centered most diurnal and pre-spawning activities into a fairly small location apart from his three dominant rivals. Such locations cannot be called territories because they were not defended against other males or females, and hunting ranges of the four dominant males overlapped. All four areas contained rendezvous sites, but even these important sites were not defended by the dominant male of a particular area. We identify these areas of activity by the term "activity center". The activity centers of the four dominant males can be seen in Fig. 2 as follows: Male #1 dominated the area from the Soft Coral to the submerged reef to the west. Male #5 dominated the area from Soft Coral to Anemone Rock and Male #4's Rock south to Triggerfish Boulder. Male #11's activity center was from Male #11's Boulders to Yogo's Corner, and male #12's area of domination was found between Small Coral on Sand to Arch Coral and Small Boulders on Sand (Fig. 2).

During daylight hours, the dominant male moved from rendezvous site to rendezvous site within his activity center in search of females



Fig. 4. Rendezvous site at Anemone Rock. Male #5 and a 140 mm female. From color transparency by J. T. Moyer.

in prespawning condition, spending short periods of time with each such female encountered (Fig. 4). Subdominant males were sometimes present in the vicinity of white-faced females at this time, but these were tolerated during morning and early afternoon. By three hours before sunset, when females often began actively hunting, subdominant males had usually departed. We never observed a confrontation during daylight hours, and cannot say what caused the departure of the subdominant male.

About one hour before sunset, the dominant male was usually with a female in spawning condition. Courtship began about 30 min before sunset (see Courtship and spawning behavior, p. 60). Immediately after spawning, the male moved out over the sand between the various activity centers to look for another female.

It is important to emphasize that activity centers should not be confused with territories or home ranges. They were not defended, and all four dominant males regularly fed and courted females in areas far from their activity centers in broadly overlapping home ranges.

**Strategies of subdominant males.** Large subdominant males (e. g. #2, #4, #9, and #10) were often observed in the activity centers of dominant males, both on the mid-day census and at the spawning time. During morning and early afternoon, no noticeable attempt was made to avoid detection by the dominant male, but at sunset and after, the appearance of the dominant male brought immediate appeasement and flight by his smaller rival. These large subdomi-

nant males concentrated their activities in specific areas. Male #2 was seen frequently in the activity centers of both males #1 and #5. Male #4 appeared regularly at #4's Rock and other locations in #5's activity center until Sept. 24, when he was found in extremely weakened condition from wounds inflicted by the spines of another male, possibly #5. He remained for three days on the same rock and then disappeared. He was not seen again for 15 days (Oct. 11), when he was observed courting a white-faced, egg-swollen female at Small Boulders on Sand (Fig. 2), deep within male #12's activity center.

Male #9 competed for females in the activity center of male #12, but was not often seen. Interestingly, male #11 was seriously wounded in a fight (apparently by male #5) on the night of Oct. 11, and male #9 appeared conspicuously in the midst of #11's Boulders shortly after. Male #11 was not seen after Oct. 12. He had been an extremely pugnacious animal and was very dangerous to measure. On Oct. 12, he was in such weakened condition that he could be accurately measured from a distance of 2 cm with no response whatsoever. On the same day, male #5 was repeatedly rubbed on the dorsal spines with our ruler without response. It is clear that venomous effect of spinal wounds greatly affects reproductive fitness for at least a few days.

Unlike other large subdominant males, #10 appeared infrequently at random locations over the study site in the activity centers of all four dominant males.

Small subdominant males changed locations

Table 2. Dates and locations of specific individuals of *Dendrochirus zebra*

Sex.	No.	1B	SC	AR	4R	15R	BP
M	1	8/25.26.28. 30.9/1.2.13. 20.22.10/2.9	9/5				
M	2	10/13	9/2.5.25	8/24			
M	3		8/26	8/25.30			
M	4			8/24.25	8/28.9/1.2.5. 7.8.9.13.15. 16.18.22		9/24.25.26
M	5		8/26	8/28.29.31.9/1 9/5.20.22.25	9/6.13.17. 10/10.11.12.13 10/14		
M	6		9/14				9/17
M	7						
M	8						
M	9	9/14					
M	10		9/24				
M	11						
M	12						
M	13						
M	14						
M	15					9/13.14.16.17	
F	3						
F	4	8/25		8/26.28.29.31 9/1.5.6.25			
F	5	8/25.28.9/16 9/17.22.24 10/11	8/26.29.10/10 10/13.14	8/31			
F	6		8/28.29	9/23.24		8/31	
F	7		9/24	8/28.29.30.9/1 9/8.9.13			
F	8			9/14.10/13			
F	9						
F	10						

regularly, appearing during census dives in widely separated locations on consecutive days. Exceptions were #6 and #15, who occupied favored rocks during daylight for a few days at a time.

The spawning strategy of both large and small subdominant males was to attempt to remain with females in spawning condition until the spawning time. If driven away by a dominant male, they would remain nearby until after sunset, and the attempt to locate another female and spawn. That they were frequently successful is

shown in Table 3.

**Strategies of females.** Females are solitary predators. When not in spawning condition they are secretive and not commonly observed. They hunt over wide areas, usually among boulders, and except for periods of spawning, show no apparent preference for specific locations, unlike the behavior of males.

When in spawning condition, females move to rendezvous sites where they are usually joined by males. Females generally arrive at specific

Moyer and Zaiser: Lionfish Behavior

at mid-day census of study site, Aug. 25~Oct. 14, 1980. See Fig. 2 for location abbreviations.

SCS	LCS	12B	SBS	ACS	11BS	Other
						10/6.10.13
						9/16.17.20 8/28.9/17 10/8.9 9/21
					10/6.11	8/25.9/7.15 9/26.10/1
	9/18					8/25.26.9/6 9/23.10/12 8/21
9/24	9/17			10/1	10/8	
		9/7	9/5	9/22	10/13	
9/7.15.16. 10/7.8.9				10/2		9/6
	9/7				9/22.24.26. 10/6.7.11.12	
	9/9.14.15.17. 9/20	9/2.6.8.13.14 9/23.24.25 10/11.12.14	9/16.22.10/1 10/2.6.10.13	9/21.10/8		
				9/16		9/9
					10/9.11.14 9/23.10/1.8 10/13	9/24.25.26 10/6.10 8/29.9/25
	9/17.20.21.23 10/10					9/16.18.26 10/2.5.8.9
					10/9	
						9/1.5.7.26
						10/7.9.12
	9/16			9/6.14	10/2.10.12	9/7.21.10/6
	9/8.9.13.15			9/20	10/1.9.10.11 10/14	9/26.10/2
	9/22				10/11.14	9/23.24.10/6 9/22
9/14						

rendezvous sites by mid-morning, often moving away to feed about three hours before sunset. Two or three females may use the same rendezvous site at the same time with no noticeable agonism, and they remain non-agonistic even during chance meetings over the sand during the spawning time. For example, on Oct. 10, as we watched male #5 courting a 160 mm female, a 140 mm female, also white-faced and swollen with eggs, swam directly up to the larger female. They rested on the sand side-by-side. As the

smaller female swam slowly away, male #5 abandoned the larger female and began to court the smaller one. They were followed by the larger fish as they swam out into the current. #5 spawned with the smaller female, immediately returning to court the larger one.

An individual female will spawn with different males at different times (Table 3). However, many females show definite preferences. Female #5 most frequently appeared at Male #1's Boulder (Table 2). On one occasion, she was observed



with male #2 near Anemone Rock at the mid-day census, and again 30 min before sunset. Five minutes before sunset she moved to male #1's Boulder, and later apparently spawned with male #1.

If a female has not been discovered by a male by sunset, she feeds for a few minutes and then moves out over the sand, where she is usually found by a searching male. It seems that gravid females sometimes go unnoticed throughout the spawning period. We have often found females with enormously-swollen abdomens and silvery-tipped facial appendages at rendezvous sites on mid-day census dives. All such females waited until sunset to spawn. We have no examples of diurnal spawning.

#### Courtship and spawning behavior

Although courtship has been observed at noon, *D. zebra* reproductive activity normally takes place from about 30 min before sunset to more than 55 min after sunset. As sunset nears, the male has usually found a gravid female, and the two rest side-by-side on a rock or boulder. The female usually initiates courtship behavior by suddenly swimming away from the male. The

male follows close behind (Fig. 6A), frequently speeding up to circle around her (Fig. 6B). After swimming several meters, the female may stop swimming and rest on the substrate. The male then circles close to her, often brushing her body or spines with his pectoral or pelvic fins (Fig. 6C). Such tactile stimulation usually results in renewed movement by the female. Often a female may remain quiescent until several minutes after sunset. In such cases, the male initiates courtship by circling the female (Fig. 7A). On two occasions we observed the male using his head in attempts to push the female up from the substrate.

With the exception of very small individuals, e. g. #7 and #8, females lead males away from feeding areas among boulders to areas of moderate current over sand or sand and rubble. As the female arrives at a suitable spawning location, she rises about 10 cm above the substrate, continuing her forward movement. The male moves up next to her, their heads side-by-side. A short, usually rapid upward rush of from 20~50 cm follows (Fig. 7B). Of seven observed spawning rushes, two were slow enough

Table 3. Actual and probable spawnings of specific *Dendrochirus zebra*.<sup>1)</sup>

Date	Male	Female	Interactions between courting male and other male	Sunset time	Spawning time or end of observation	Min. before or after sunset	Nearest location	Height of rise
6/24	?	?	None	19 : 01	18 : 35*	-26 min	BP	±30 cm
7/26	?	?	None	18 : 51	19 : 18	+27 min	BP	—
8/12	1	?	Displays to #2	18 : 34	19 : 02	+28 min	over sand	—
8/13	2	?	None	18 : 33	19 : 02	+29 min	over sand	—
8/22	1	3	Fights with #5	18 : 22	18 : 42*	+20 min	BP	±40 cm
8/28	5	?	None	18 : 14	18 : 47	+33 min	over sand	—
8/30	4	3	None	18 : 12	18 : 38*	+26 min	BP	±30 cm
9/ 1	4	3	None	18 : 09	18 : 18*	+ 9 min	BP	±20 cm
9/ 8	5	4	None	17 : 59	18 : 30	+31 min	over sand	—
9/15	5	?	None	17 : 49	18 : 20	+31 min	over sand	—
9/15	14	3	None	17 : 49	18 : 34	+45 min	SP 1	—
9/16	1	4	Drives away #2	17 : 47	17 : 48	+ 1 min	4R	—
9/16	12	9	Drives away #9	17 : 47	18 : 28	+38 min	ACS	—
9/17	5	7	None	17 : 46	17 : 55*	+ 9 min	SC	±40 cm
9/24	12	?	None	17 : 36	18 : 11	+35 min	LCS	—
9/25	2	3	None	17 : 34	18 : 06*	+32 min	SC	±40 cm
10/ 6	5	?	Drives away #2	17 : 18	17 : 45	+27 min	4R	—
10/ 7	1	?	None	17 : 17	17 : 45	+28 min	near 1B	—
10/10	5	?	None	17 : 13	17 : 28*	+15 min	4R	±50 cm

<sup>1)</sup> Probable spawnings include all observations of long courtship that were discontinued due to darkness.

\* Spawning actually observed.

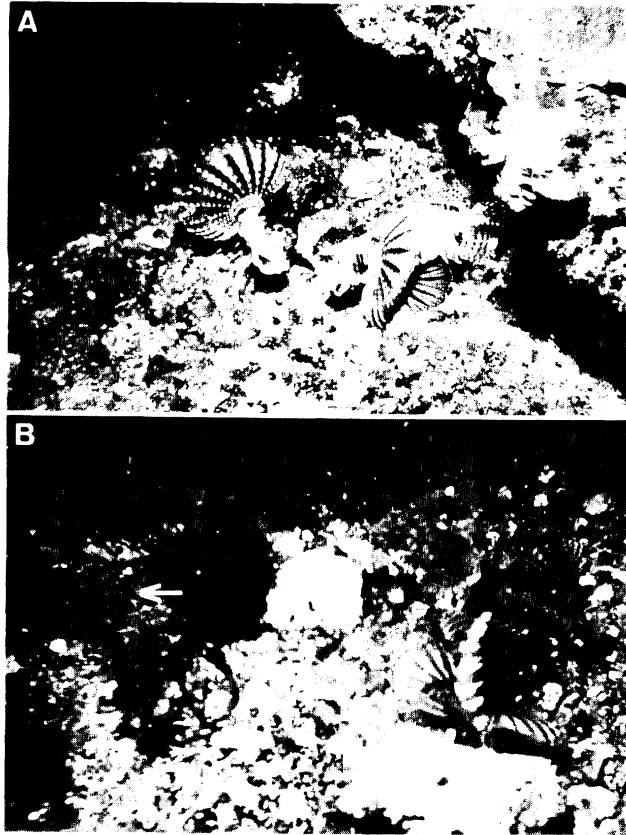


Fig. 5. Agonistic posture and fighting behavior of males of *Dendrochirus zebra*. A: Male #9 (left) confronts Male #12 (right). Note gill rakers of #12, visible under flared operculum. B: Male #5 attacks Male #1. Female #3 moves slowly away (arrow). From color transparency by J. T. Moyer.

to permit detailed observations. These plus photographs make it possible to describe the spawning in detail. After a short rise, the male drops his head slightly below the female's, turns his ventral surface toward the still-rising female, who turns her abdomen toward his, passing closely over the now-descending male. (Fig. 7C, Fig. 8) Two hollow mucous egg sacks are released by the female as their vents pass. Whether their vents actually come into contact could not be determined. On one occasion, the male pushed the female upward with his head to begin the spawning rush.

Fights between males are quite common during the spawning period. For example, on Aug 22, the #1 male was courting the #3 female near Broken Pipe (Fig. 2) when the pair was discovered by male #5. Both dominant males were relatively far from their activity centers. They confronted

each other in aggressive postures and, after a moment, #5 lowered his head, turning his spines forward, and rushed forward (Fig. 5B) driving his anterior dorsal spines deep into the flesh of his opponent. Both fish had to shake their bodies in order to dislodge the spines. Seconds later, the attacked male (#1) spawned while the attacker looked on.

Spawnings are promiscuous in nature (Table 3). For example, our data show that male #5 spawned with at least four different females, and female #3 spawned with a minimum of five males. Spawnings occurred between 26 min before and 32 min after sunset, and courtship displays that almost certainly ended in spawnings, were observed until 55 min after sunset, when observations were abandoned for safety reasons. Only a single spawning was observed before sunset.

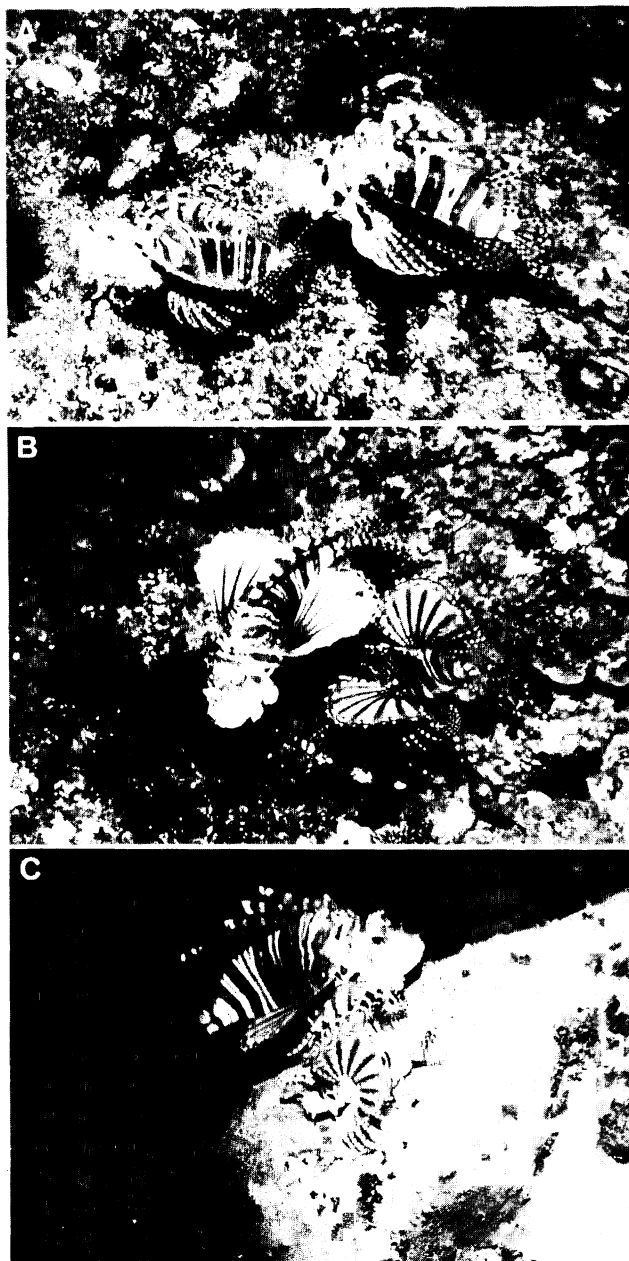


Fig. 6. A: Male follows female toward spawning site. Note white face of female. B: Male circles female. Note egg-swollen abdomen of female. C: Male brushes female with pelvic fins. Note silvery-white facial appendages on female. From color transparencies by J. T. Moyer.

Egg sacks from a female of 100 mm contained about 2200 eggs each, or a total of about 4,400 eggs. A 140 mm individual spawned about 6000 eggs. When examined under the dissecting microscope, the mucous sacks appeared as hol-

low tubes, with two layers of eggs around the hollow center. One layer appeared to be in contact with the outer surface of the sack, and the other with the inner surface, within the tube. It is assumed that the entire tube is flooded with

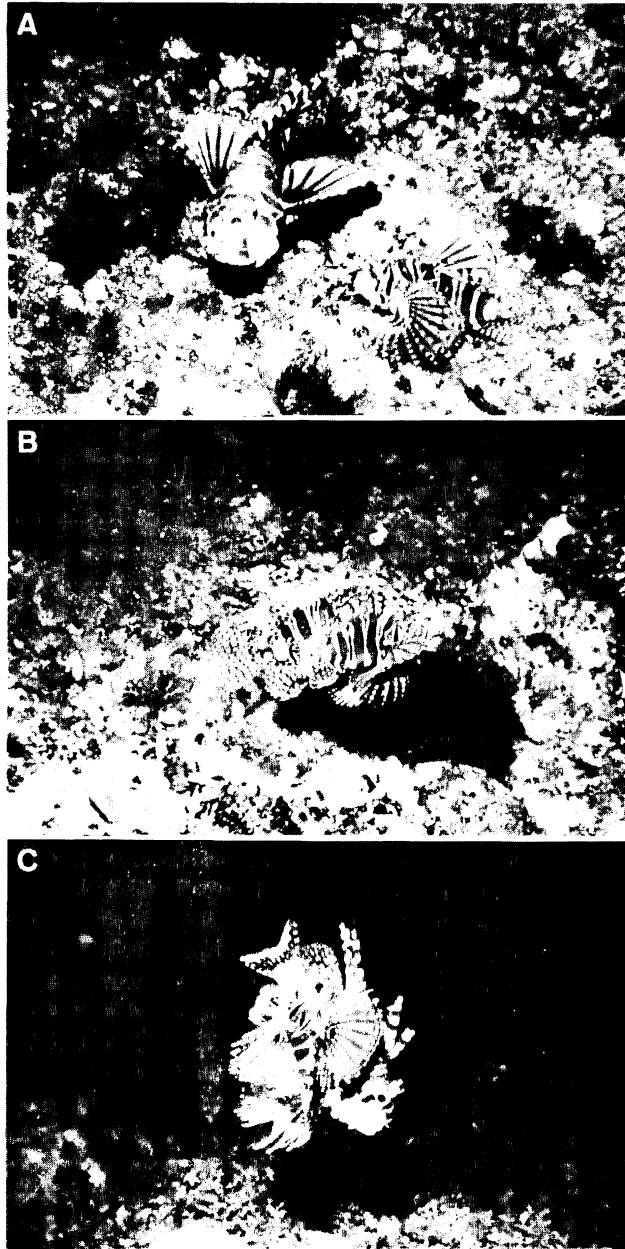


Fig. 7. A: Male circles female. Note female's white face. B: Beginning of spawning rush. Female (right) with egg-swollen abdomen. C: Spawning of *Dendrochirus zebra*. Male descends as female expels eggs in mucous sack. Color transparencies by J. T. Moyer.

sperm, and that the eggs either reach the surface of the tube or the sperm can penetrate a possible thin layer of mucus over the eggs.

Spawnings were observed in water temperatures ranging from 21°C to 29°C in depths of

from 5~13 m. Although females were found at rendezvous sites throughout the study, peaks were noticeable within five days before or after the full and new moons, near periods of maximum tidal flow, suggesting a weak semi-lunar

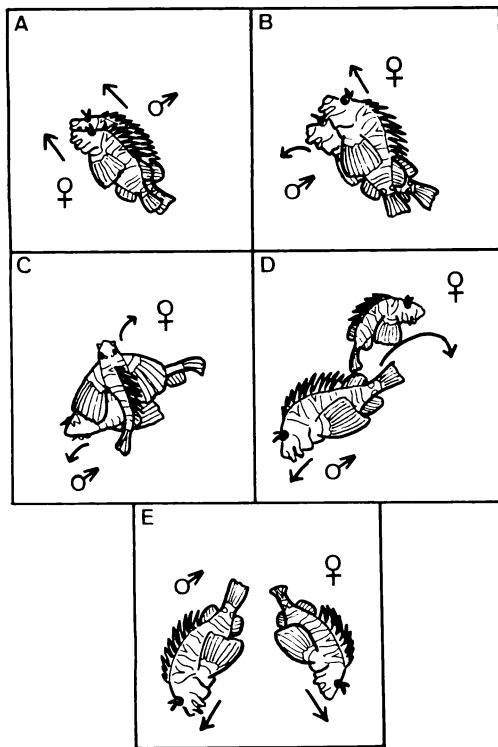


Fig. 8. Sequential stages of upward rush and spawning of *Dendrochirus zebra*. A: Beginning of spawning rush. B: Male lowers head and begins to turn abdomen towards female. C: Female passes male, abdomens close together or touching. Gametes are released at this time. D: Male begins descent as female passes over him. E: Female follows male in descent. Drawings by M. J. Zaiser.

cycle (Fig. 9). A single female may spawn more than once in each spawning cycle, but we were unable to determine exactly how often or at what intervals females spawned. Female #3 was observed spawning three times in ten days, of which two spawnings were seen in three days (Table 3).

**The mucous egg sack and predation**

One cannot help but wonder why a gamete-launching species would concentrate several thousand eggs into two fairly conspicuous mucous sacks. Although egg predators are at a minimum after dark, several potential egg predators were active in the study site, e. g. *Canthigaster rivulatus* (Temminck et Schlegel), *C. coronatus* Vaillant et Sauvage, and *Navodon*

*modestus* (Günther). A single such predator could quickly destroy 50% of the spawn. To test the possibility of predation on the mucous egg sacks, we offered the spawn of a 140 mm female to a variety of hungry, tank-trained aquarium fish (Table 4). The fish were offered the mucous egg sacks at their normal feeding time. They rushed to the surface to get food, as was their habit, nibbling at the fingers of the observers. In one test, all fish in the tank swam rapidly away from the egg sack to the far end of the aquarium as soon as the mucous tube touched the water. This tank contained such well-known egg predators as *Thalassoma cupido* (Temminck et Schlegel), *T. amblycephalus* (Bleeker), and *Abudefduf vaigiensis* (Quoy et Gaimard). A stripey, *Microcanthus strigatus* (Cuvier), approached the egg sack after 2 min and touched it with his mouth, instantly fleeing. In another test, two carangids and an oplegnathid immediately touched the egg sack with their lips and quickly fled. The egg sacks were removed from the aquaria within 5 min to protect the test fish from possible toxins in the mucus. Shortly after these tests, the fish in both aquaria readily ate other foods. The biochemical composition of the mucus is presently under study. Our results strongly suggest that the mucous egg sacks of pteroine fishes and possibly other scorpaenids are repulsive to egg predators.

Table 4. List of fish species and families used in egg-predation tests.

- Muraena pardalis* (Muraenidae)
- Gymnothorax kidako* (Muraenidae)
- Oplegnathus punctatus* (Oplegnathidae)
- Kuhlia mugil* (Kuhliidae)
- Anthias nobilis* (Serranidae)
- Girella mezina* (Girellidae)
- Girella melanichthys* (Girellidae)
- Kyphosus cinerascens* (Kyphosidae)
- Longirostrum delicatissimus* (Carangidae)
- Amphiprion clarkii* (Pomacentridae)
- Abudefduf vaigiensis* (Pomacentridae)
- Abudefduf sordidus* (Pomacentridae)
- Thalassoma cupido* (Labridae)
- Thalassoma amblycephalus* (Labridae)
- Microcanthus strigatus* (Scorpididae)
- Heniochus acuminatus* (Chaetodontidae)
- Sufflamen frenatus* (Balistidae)
- Pterois volitans* (Scorpaenidae)

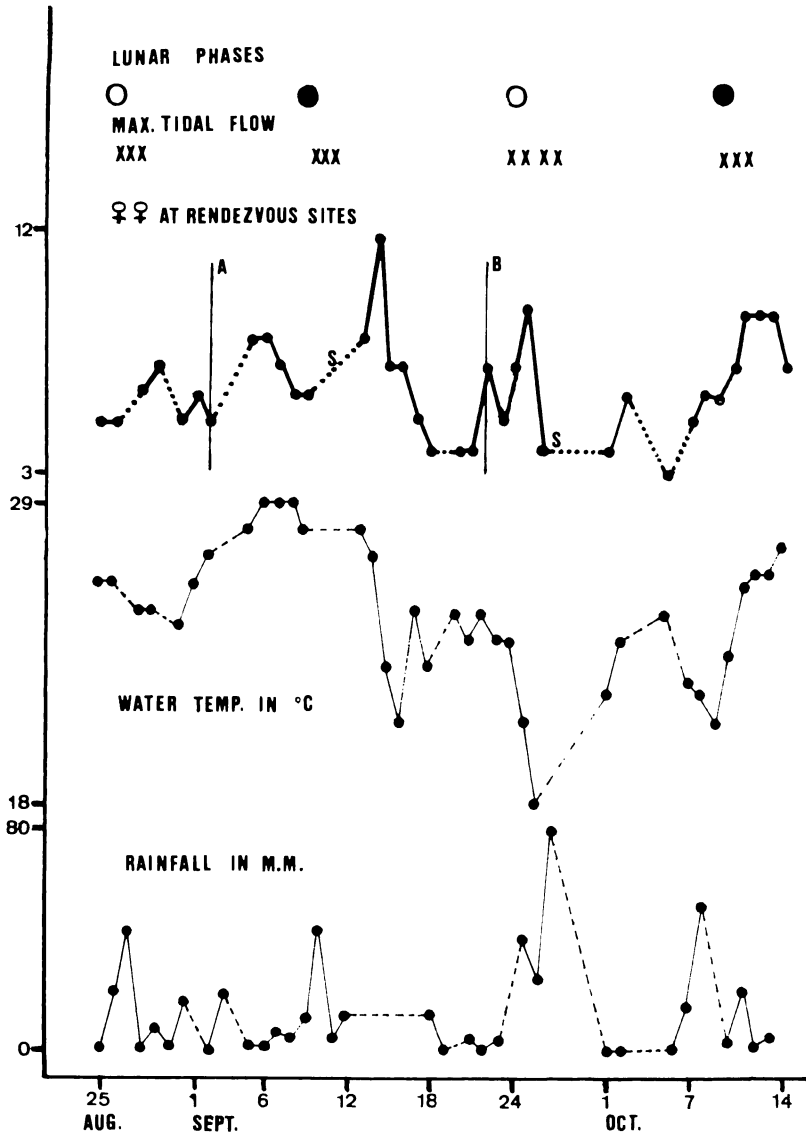


Fig. 9. Graph showing spawning peaks of females and possible ecological influences on spawning, based on counts of females at rendezvous sites at mid-day census. A, date of discovery of Male #12's activity center; B, date of discovery of Male #11's activity center; S, major storms (including heavy surge and fresh water flow from five rivers that empty into Igaya Bay).

### Discussion

#### Comparison of *Dendrochirus zebra* and *D. brachypterus*

It is of interest to compare the spawning behavior of *Dendrochirus zebra* with that of *D. brachypterus* studied by Fishelson (1975) and Brandt (1976). Studies of the latter relied heavily or entirely upon aquarium observations,

while our work with *D. zebra* was limited entirely to observations in nature. Comparisons may, therefore, be somewhat misleading.

**Social organization.** Fishelson (1975) notes that *D. brachypterus* is gregarious, occurring in small groups of 3~6 fish. Such groups are composed of "a dominant male, some females, and some small males" (Fishelson, 1975). He

later points out that during the spawning period just after sunset, a male will often court a female for a short time and then “. . . move to another” suggesting that they remain in close association in the evening as well.

By contrast, *D. zebra* is solitary, appearing in small groups only at rendezvous sites during the daytime. Such temporary aggregation is simply for the purpose of locating a mate for the evening spawning, and does not represent gregarious tendencies in this species. At night, if not in courtship with a member of the opposite sex, individuals hunt by themselves, and remain solitary during daylight when not in spawning condition.

**Sexual dimorphism.** Descriptions of sexual dimorphism by Fishelson (1975) and photographs appearing both in the works of Fishelson (1975) and Brandt (1976) indicate close similarities between *D. brachypterus* and *D. zebra*. Males tend to be dark, while females become pale around the vent and white-faced with silvery facial appendages. These colors are conspicuous even after dark and males can easily distinguish females in spawning condition.

**Courtship and spawning.** Although similar in some ways, e. g. circling of females by males, courtship and spawning of *D. zebra* and *D. brachypterus* differ in many important respects. *D. brachypterus* males lead females slowly to the surface and females follow, pectoral fins “trembling” (Fishelson, 1975). Having reached the surface, the spawning pair swim in circles, the male pushing his body against the female, and occasionally nipping at her silvery facial appendages. They spawn upside-down at the surface. Although lacking specific details, Brandt (1976) also reports courtship and spawning at the water surface in the aquarium. Thus, the courtship and spawning of *D. brachypterus* differ considerably from the short spawning rush of *Dendrochirus zebra*.

#### Spawning and predation

The fact that, when feeding in areas near shore, all but the smallest females of *D. zebra* move during courtship to areas of moderate currents, sometimes a great distance away, suggests that even with the seemingly repulsive nature of the mucous egg sacks, egg-predation is a factor in the spawning strategy of this species. The advantages of spawning off-shore in areas of rapid

egg-transport by currents have been treated in detail by Randall and Randall (1963), Robertson and Hoffman (1977), Johannes (1978), and others and need not be repeated here. As for *D. zebra*, it is significant that the mucous egg sack begins to break up within 12 h after spawning, a time period that allows for safe dispersal of eggs far from potential reef predators, e. g. pomacentrids and labrids.

It has been hypothesized that the rapid upward rush of labrids and scarids serves the dual purpose of protecting the eggs from egg-predators and the spawning fish from piscivores (e. g. Ehrlich, 1975). Such an hypothesis raises certain questions when applied to *D. zebra*. If the mucous egg sack is, indeed, repulsive to egg predators, why is it necessary to release spawn with a rapid rush away from the substrate? Furthermore, the spines of *D. zebra* inflict severe, toxic wounds, so why is it necessary for the fish to protect itself from predation with a short (20~50 cm spawning rush)?

Egg predators are probably not common on the reef at night, and the seemingly repulsive mucus probably serves as an effective deterrent to egg-predation while the eggs are carried away from the reef by currents. We suggest that the upward rush is a defense against piscivorous predators.

Allen and Eschmeyer (1973) reported different responses by different fish species to lionfish venom. After injection, holocentrids, serranids, and mullids all died within 10~30 min. However, a pomacentrid (*Epibulus*) survived injections in repeated experiments of increasing dosage. The toxins of pteroine fishes obviously are a powerful weapon against predation. However, if a single relatively common predator on the reef was able to prey on lionfishes without discomfort, a cryptic spawning strategy would have important survival value. Hammerhead sharks (Sphyrnidae) are known to feed repeatedly upon sting rays (Trygonidae) and individuals have been caught with numerous sting ray spines imbedded in their mouths and face (Norman and Fraser, 1949; Grant, 1978; Anderson, personal communication). Black-tip and white-tip reef sharks (Carcharhinidae) are common nocturnal predators over most of the tropical Indo-West Pacific, and hammerheads and, rarely, tiger sharks (Carcharhinidae) occasionally occur close

to shore at night at Miyake-jima (see Randall and Helfman, 1973; Randall, 1977; and personal observations). Tests of lionfish toxins on sharks would be of great interest.

#### The intraspecific role of toxin

Quite obviously, the toxic spines of the Pteroinae serve as an impressive defense against predation. However, our observations support the hypothesis that the venom also plays an active role in male-male competition for females. Allen and Eschmeyer (1973) report that regardless of the dosage, injections of venom into pteroinae fishes resulted merely in increasing the respiration rate by 3~4 times and reducing swimming activity of the fish. Fishelson (1975) reported that males impaled by the spines of a rival showed no changes in behavior.

Our results indicate that among *Dendrochirus zebra*, wounds from venomous spines of male rivals result in relatively long-lasting ill effects on the attacked fish, although the immediate effect might not appear severe. For example, male #1 spawned seconds after being stabbed by male #5 on Aug. 22 (Fig. 5B). However, the wounded male #4 remained stationary for three days after being attacked on the night of Sept. 23, and was not observed in the study site for 15 days after leaving his recuperatory rock.

It seems especially significant that the number of females observed in Male #11's Boulders decreased suddenly after he was wounded on the night of Oct. 11, while at the same time an increase of females was noticed in the activity center of male #1. Furthermore, the large 200 mm male #9, that usually was found in the vicinity of male #12's activity center, suddenly appeared in Male #11's Boulders. Smaller males (Nos. 2, 3, 6, 8, 10, 14, and 15) were also found wounded and then not seen for several days. Fighting is common among *D. zebra* males, and certainly results in sudden changes in reproductive fitness among the male population, some of which may become permanent.

#### Mating strategies and food resources

*Dendrochirus zebra* is an upper-level predator that hunts both by ambush and by slow, time-consuming stalking (personal observations). Prey consist mainly of crabs and shrimp, but we have also observed successful attacks on apogonids and the pomacentrid *Pomacentrus coelestis*. Food is obviously neither abundant nor

clumped in specific locations. The best hunting grounds appeared to be among small boulders (see Fig. 2). In an hour of hunting, an individual might make 4~5 attacks on potential prey, but only 2~3 kills (personal observations). Specific individuals showed a tendency to hunt in different areas within their wide home ranges on different nights, suggesting that intensive use of a particular area by even a single individual might exhaust or alert the food supply. Territoriality and defense of food resources are therefore not practical, eliminating the potential for monopolization of mates ("resource defense polygyny", Emlen and Oring, 1977).

*Dendrochirus zebra*, therefore, is a solitary, opportunistic, wide-ranging predator, competing for food with other conspecifics that share widely overlapping home ranges. The solitary nature of the species' feeding habits results in a promiscuous mating system, where male and female often come together in chance meetings after dark, and where a large male may discover and interrupt the spawning attempts of a smaller rival. The chance of females in spawning condition remaining undiscovered throughout the night is lessened by the existence of rendezvous sites at numerous locations. These sites are dominated by specific males at different locations over the overlapping ranges of the population. Rendezvous sites increase a particular female's chance of spawning at an early hour with the dominant male. However, this will not happen if the dominant male chooses to court another female. Smaller, subordinate males may quickly locate and court such a female, or she may go unnoticed throughout the night.

Rendezvous sites are best located at areas that meet both feeding and spawning requirements, i. e. among small boulders that shelter crabs, shrimp, and small fish, and in or close to moderate currents. Male #11's Boulders are ideally located because both requirements are met at the same location. Male #12's activity center is favorably located for similar reasons, but feeding grounds are more limited. The activity centers of both male #1 and male #5 border feeding grounds among boulders to the south and spawning grounds in moderate currents to the north.

The agonistic behavior associated with male-male encounters is clearly related to competition



over females. The peaceful, totally non-aggressive nature of rare chance meetings between females during the spawning time increases the average spawning success of both females. Whether a particular male courts one or the other female is irrelevant, because he will eventually spawn with both.

#### Lunar periodicity

Our data suggest a weak semi-lunar spawning periodicity. Although females appear at rendezvous sites in spawning condition throughout the month peaks are found near the spring tides associated with the full and new moons. A more clear periodicity might be expected in the tropics, where water temperatures and day-length are less variable. The strong spring tides would result in more rapid transport of eggs away from shallow water predators before breaking away from the mucous sacks. A weakening of the tendency for lunar periodicity in Miyake-jima populations as compared to tropical populations appears to be the case with *Amphiprion clarkii* (Moyer, 1980) and *Apogon cyanosoma* (personal observations). Long periods of cold winter waters result in a shortened, intensified breeding season in these species, with the result that selective pressures for a clean lunar cycle are weakened (Moyer, 1980).

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### 三宅島におけるキリンミノの社会構造と産卵習性

Jack T. Moyer • Martha J. Zaiser

キリンミノは単独で生活する肉食性魚類である。広範な生活域を所有するが、個々の生活域は同種の他の個体と大部分重複する。大型の雄はとくに広い生活域を所有し、その中央の特定の場所に所在することが多

い。しかしその場所は防衛されてはいず、従ってなわばりとは見做しにくい。産卵間近な雌は上記の特定の場所内の“rendezvous sites”と名付けられえる地点で、優位の大型の雄または低順位のやや小型の雄に日中に出会う。産卵は日没後、沖へ向かう緩潮の流れる場所で行われる。雄は雌をめぐる争い、毒棘で傷つけられた雄は産卵行動に支障を来すように思われる。産卵時の雌は短距離を急上昇して、数千個の卵を含む粘液質の卵嚢を2個産出する。この粘液によって卵が捕食を免れ得ることを簡単な実験によって確かめた。また産卵時の急上昇が魚食魚の捕食を防ぐのに役立つことを論じた。

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