Quantitative Observations of Predation during Spawning Rushes of the Labrid Fish *Thalassoma cupido* at Miyake-jima, Japan

Jack T. Moyer

(Received June 30, 1986)

Abstract A rapid upward spawning rush is a nearly universal phenomenon among reef fishes that spawn pelagic eggs. Although spawning rushes have long been considered to have evolved as a defense against egg predators and/or attacks on the spawning fishes by piscivores, these hypotheses have never been tested in the field. We analysed piscivore attacks during three motor patterns associated with group spawning of the labrid fish *Thalassoma cupido* at Miyake-jima, Izu Islands, Japan. Egg predation on group spawnings was also quantified. Of 206 piscivore attacks on spawning fishes by seven predator species, 171 (83.1%) occurred during 461 spawning rushes (1/2.7 spawning rushes). No attacks were successful during spawning rushes, and only four kills were made in 206 attacks summed from all three motor patterns associated with spawning, amounting to a piscivore success rate of only 1.9%. In contrast, gametes from 90 of 213 spawnings (42.3%) were consumed by nine species of planktivorous fishes. Spawning fish seemed not to recognize egg predators and made no attempt to avoid them, often spawning in the midst of waiting aggregations of damselfishes. Our data indicate that the rapidly of the spawning rush of *T. cupido* serves as an excellent defense against piscivores, but is ineffective against egg predators. Evidence is presented from observations of seven other species suggesting that spawning ascents provide little protection against water column egg predators in predator-rich environments.

A temporary spawning ascent into the water column is a nearly universal phenomenon among reef fishes spawning pelagic eggs. This behavioral pattern is usually referred to as the "spawning rush" (Robertson and Hoffman, 1977; Johannes, 1978; Colin, 1982; etc.), although in some species, e.g. ostraciids (Moyer, 1984a) and pomacanthids (Moyer and Nakazono, 1978), such ascents are extremely slow. Several hypotheses have been offered to explain the common occurrence of the "spawning rush", especially for those species for which the ascent is truly a rush (reviewed by Thresher, pp. 359–360). The two most widely accepted hypotheses to account for the evolution of the spawning rush are as follows: (1) an upward ascent permits pelagic eggs to be released far enough above the substratum to minimize consumption by egg predators, and (2) the height and speed of the ascent should minimize the risk of attack by piscivores during the time the spawning fish are exposed in the water column away from shelter (Jones, 1968; Ehrlich, 1975; Robertson and Hoffman, 1977; Johannes, 1978).

As pointed out by Thresher (1984), the risk-of-predation hypothesis is currently widely accepted and self-perpetuating in the ichthyological litera-ture (e.g. Keenleyside, 1979), but has yet to be tested in the field.

It was our purpose in this study to collect quantitative data on both egg predation and piscivore attacks on a group-spawning labrid species (*Thalassoma cupido*) in an attempt to determine whether or not upward spawning rushes in this species provided protection against piscivores and/or egg predators.

Methods

The site chosen for our study has been well documented as a spawning site for labrid fishes (Meyer, 1977; Moyer and Yogo, 1982; Tribble, 1982; Moyer, 1984b), and both egg predation and piscivore attacks have been noted in all of the above studies. The site, located in Igaya Bay, Miyake-jima, one of the Izu Islands of southern Japan (34°05′N, 139°30′E), has been described in detail by Tribble (1982). Large boulders, smaller rocks, cliffs, crevices, caves, coral outcroppings, and lush algal meadows provide adequate shelter not only for spawning labrids, but also for piscivores and potential egg predators. Population densities of most reef piscivores and egg predators

would seem to be related to the availability of adequate shelter, and one would expect a greater attack rate on fishes spawning where such conditions exist than in areas where predator shelters are minimal. Our qualitative observations support this prediction. The study site was chosen due to the high probability of attacks on spawning fishes and their eggs by piscivores and planktivorous fishes in a location with adequate shelter for both the attacker and the attacked; the more attacks observed, the greater the reliability of our statistical analyses.

Within the study area was a large boulder (2 m high, 3 m long, and 2 m wide) which was used daily as the spawning site by an estimated 1000–3000 group spawning *T. cupido*. Our data were collected exclusively from spawnings occurring at this boulder. Motor patterns associated with the spawning behavior of *T. cupido* and analysed for susceptibility to predation are as follows:

1. Bobbing (Meyer, 1977). Aggregations of fish approaching the spawning site swim in a peculiar up-and-down bobbing motion, moving back-and-forth over the spawning boulder, often for several minutes, prior to spawning. Bobbing groups frequently join other similar aggregations, or small numbers of individuals may break away to form a separate group (Meyer, 1977).

2. Milling (Meyer, 1977). Just prior to the spawning rush, from <5->40 fish break away from the bobbing groups, invariably led by a gravid female. These fish move forward and slightly upward with accelerated fin movements, coming together into a tight milling mass and swimming in a conspicuous agitated manner. The spawning rush follows within a few seconds after these milling groups form.

3. Spawning rush. Some or all of the milling fish suddenly dash very rapidly upward 13 cm to 1.5 m into the water column (Meyer, 1977), release gametes at the apex of the rush, and return extremely rapidly to the algal-covered substratum. Each spawning aggregation consists of one female and from 2->20 males. The entire spawning rush, from initial ascent to return to the shelter of the algal substratum takes about 1 sec (Meyer, 1977; Moyer, pers. obs.).

The large number of spawnings at the boulder seemed to attract both egg predators and piscivores. Using SCUBA and lying motionless within 2 m of the boulder, we recorded the number of spawning rushes, the number of attacks made on spawning fish by piscivores during each of the three identified motor patterns, and the number of spawnings in which gamete clouds were preyed upon within 5 sec of gamete release. Such a time interval is conservative, since gamete clouds were frequently visible for more than 10 sec.

Five one hour observations were made on consecutive days from Aug. 26–30, 1981, amounting to 300 min of data collection. Statistical methods follow Sokal and Rolf (1981).

Results

Piscivore attacks. Of the total 461 group spawnings observed, 206 were attacked by any one of seven piscivore species during any one of the three motor patterns (Table 1). Piscivore attacks were made on 171 (37.1%) of the spawning rushes; all were unsuccessful, i.e. no kills were made. Attacks on bobbing aggregations were observed 23 (5.0%) times, four (17.4%) of which resulted in kills. Only 12 (2.6%) attacks were made on milling aggregations and none were successful. The total of four kills from 206 attacks amounts to a mere 1.9% piscivore success rate (Table 1).

If the probabilities of piscivore attack were equal for all stages of the spawning sequence, then we would expect the total of 206 attacks to be divided equally among the three motor patterns. Our observed frequencies of attack differed significantly from these expected frequencies (Goodness of Fit test, using the G-statistic; P<0.01, df=2). In particular, the number of attacks made during the spawning rush was far greater than that expected (Table 2).

If one considers the actual amount of time available for piscivores to attack during each of the three motor patterns, the expected frequencies of attack are dramatically altered (Table 2). We estimated that each spawning event at the boulder lasted, on the average, 5 min (300 sec), comprising spawning rush (1 sec), milling (5 sec just prior to the rush), and bobbing (bobbing aggregations were continuously present on the spawning boulder, but for the purpose of this analysis we allocate only the remaining 294 sec to bobbing, thus providing a conservative estimate). During the total 18,000 sec of observation time, piscivores, therefore, had access to bobbing fish for 15,244 sec

(98.0% of total time), to milling fish for 2,305 sec (1.67%), and to rushing fish for 461 sec (0.33%). Using expected frequencies of attack calculated from these proportions, we found that the observed frequency of attacks differed significantly from those expected (P<0.01). While the greatest number of attacks (98% of total) would be expected during bobbing, the greatest number of attacks (83.01% of total) were actually observed during the spawning rush, amounting to one attack every 2.7 spawning rushes; all of these were unsuccessful (Table 2).

Our data show that the greatest risk of attack came during the 1 sec spawning rush. We suggest that the agitated milling behavior just prior to the spawning rush excited the potential predator and the rapid upward dash that followed elicited an attack response. Close observations of the piscivores *Synodus ulae* and *Sebasticus marmoratus* disclosed that during the bobbing stage, these predators remained motionless, but while the labrids were milling, "nervous" twitches of the caudal fins of the predators were common. Also during milling, *S. marmoratus* often moved

slightly forward, and *S. ulae* frequently "danced" in its pelvic fins. At the first moment of the upward rush, these predators dashed forward toward the spawning aggregations from distances varying from 60 cm to 3 m. Invariably they arrived at the point of apex of the spawning rush at about the same moment that the spawning aggregation had returned to the shelter of the algal substratum. No observed attack on fish in the spawning rush was even remotely close to being successful. The four kills (two by *Synodus ulae* and two by *Scorpaenopsis cirrhosa*) were from short ambush attacks (2–10 cm) on bobbing labrids that approached too close within the algae to the well camouflaged predators. Concentrated study over two spawning seasons disclosed that *S. cirrhosa* is strictly an ambush predator; none of >10 attacks covered a distance of more than 6–7 cm, thus making attacks during bobbing the only possible attack method by this species. However, because we cannot totally discount the possibility of an occasional attack during other motor patterns, and because inclusion of *S. cirrhosa* did not alter significance of

Table 1. Piscivore attacks on group spawning *Thalassoma cupido* at Miyake-jima, Japan. Successful attacks (i.e., kills) shown in parentheses.

| Species | Family | Motor patterns | | | Total |
		Bobbing	Milling	Upward rush	
Synodus ulae	Synodontidae	9 (2)	5 (0)	156 (0)	170 (2)
Epinephelus fasciatus	Serranidae	2 (0)	1 (0)	7 (0)	10 (0)
Sebastiscus marmoratus	Scorpaenidae	2 (0)	3 (0)	0 (0)	5 (0)
Scorpaenopsis cirrhosa	Scorpaenidae	3 (2)	0 (0)	0 (0)	3 (2)
Gymnothorax eurostus	Muraenidae	3 (0)	3 (0)	2 (0)	8 (0)
Aulostomus chinensis	Aulostomidae	0 (0)	0 (0)	3 (0)	3 (0)
Cheilio inermis	Labridae	4 (0)	0 (0)	3 (0)	7 (0)
Column totals		23 (4)	12 (0)	171 (0)	206 (4)

Table 2. Goodness of fit tests (G-statistic) analyses of piscivore attack rate on group spawning *Thalassoma cupido* at Miyake-jima, Japan.

| Motor pattern | Based on total attacks | | Based on proportion time/motor pattern[1] | |
	Observed frequency	Expected frequency	Observed frequency	Expected frequency
Bobbing	23	68.7	23	201.9
Milling	12	68.7	12	3.4
Upward rush	171	68.7	171	0.7
Totals	206	206	206	206

1 Proportion of time available for piscivore attack per motor pattern=98% for bobbing, 1.7% for milling, and 0.3% for upward rush. See text for details.

tests, the data from this species were included in our statistics.

It appears that group spawning *T. cupido* attract piscivores. In more than 2000 h of underwater observations during various studies at Miyake-jima, only two piscivore attacks on non-spawning, foraging *T. cupido* have been observed (.001 attacks/h) (Moyer, pers. obs.), yet 206 attacks were witnessed in 5 h of observations of spawning fish (41.2 attacks/h). This almost certainly results from the fact that spawning sites and times are predictable and that thousands of labrids migrating daily along well-defined pathways to and from the spawning site attract predators.

Egg predation. Attempts to collect data on egg predation were made from 213 spawnings over a period of 180 min. Spawning aggregations of *T. cupido* apparently did not recognize egg predators, and often rushed directly into aggregations of waiting damselfishes. In fact, on one occasion, an upward dashing labrid aggregation collided into the abdomen of a waiting *Pomacentrus nagasakiensis*. Egg predators gathered daily over the spawning site, rushing to white clouds of gametes where they hovered, rapidly opening and closing their mouths. The aggregating egg predators remained with a particular cloud of gametes often for more than one minute, presumably consuming most, if not all of the eggs in the cloud. Species observed preying on gamete clouds included the pomacentrids *Pomacentrus nagasakiensis, P. coelestis, Chromis flavomaculata, C. chrysura, Amphiprion clarkii,* and *Dascyllus trimaculatus*; the anthiine *Anthias squamipinnis*; and the pomacanthids *Centropyge interruptus* and *C. tibicen*. A total of 90 gamete clouds was preyed upon from 213 spawnings (42.3%). This figure would probably have been higher except for the fact that spawning rushes usually occurred in clusters, and egg predators were attracted to the first 1–2 spawnings in a cluster, ignoring the rest as they consumed the gametes already available to them.

No noticeable attempts were made by spawning fish to avoid egg predators, and large numbers of propagules were lost to the nine species of egg predators observed at the site.

Discussion

It could be argued that, because of the extremely high likelihood of attack during the spawning rush of group spawning *T. cupido*, the spawning rush is a poor anti-predator tactic. This, however, is a weak argument due to the fact that it is the success or failure of piscivores (i.e., kills), not the number of attacks, that determines whether or not the defense is adequate. Because spawning fish must rise in the water column to spawn, for reasons perhaps related to dispersal of eggs and larvae (Barlow, 1981), the evolutionary "problem" facing spawning individuals is one of how to release gametes in the water column without falling prey to piscivores. The rapid spawning rush provides the solution to the problem. The complete absence of kills during 167 attacks on spawning *T. cupido* in this study is clear evidence that the spawning rush is a very successful anti-predator defense.

Although the rapid speed of the upward spawning rush of *Thalassoma cupido* at Miyake-jima clearly provided protection against piscivores, egg predation was common. Other studies at the same study site provide similar results. Bell (1983) observed only unsuccessful attacks by *S. ulae* on pair spawning labrids (*Cirrhilabrus temminckii*), but Moyer (pers. obs.) frequently observed predation on *C. temminckii* eggs. Tribble (1982) recorded nine unsuccessful attacks by *S. ulae* on spawning rushes of the labrid *Coris dorsomaculata*, and further noted that egg predation by five planktivorous fishes posed a problem for that species. Moyer (1984b) recorded egg predation on 37 of 136 spawnings (27.2%) of the labrid *Pteragogus flagillifera* and showed that excessive egg predation in territories of dominant males periodically alternated the relative spawning success of the three most successful males. Yet, no successful attacks by piscivores were observed during the study, although unsuccessful attacks by *S. ulae* delayed spawnings by several minutes in some instances (Moyer, 1984b).

Moyer (unpublished), in more than 500 h of observations of the reproduction of pomacanthid fishes in a variety of tropical and warm temperate locations, observed only one piscivore attack (unsuccessful), by a large carangid on *Centropyge shepardi* at Guam. However, at certain locations, egg predation on pomacanthid spawnings is not uncommon. Predation on gametes from six out of 16 spawnings (37.5%) of *Centropyge bispinosus* by the lutjanid *Macolor niger* was recorded by Moyer at a specific site at Mactan Island, Philip-

pines. Moyer (1984c) also found egg predation by the pomacentrid *Amblyglyphidodon aureus* to pose a problem for spawning individuals of the pomacanthid *Genicanthus lamarck*, also at Mactan Island. At Miyake-jima, the pomacentrid *Pomacentrus nagasakiensis* was seen to prey on 11 of 31 spawnings (35.8%) of the pomacanthid *Centropyge ferrugatus* at a specific pinnacle and on 11 of 28 spawnings (39.3%) of *Centropyge tibicen* at the same pinnacle (Moyer, unpublished). Bell and Colin (1985) commonly observed predation on eggs of spawning *Caesio teres* at Enewetak Atoll. It appears that spawning ascents are not effective defenses against egg predators. However, swamping of egg predators with clusters of spawnings may be a partially effective defense (Warner and Moyer, in prep).

Sites where egg predators and/or piscivores are abundant are apparently not common. Moyer has observed more than 800 spawnings of 15 species of pomacanthid fishes, with only the few above-mentioned examples of predation, and R. Warner (pers. comm.) recorded data on more than 500 spawnings of the labrid fishes *Thalassoma cupido* and *Stethojulis interrupta* over a flat sandy habitat at Miyake-jima without a single observation of piscivore or egg predation. Bell and Colin (1985) found no piscivore attacks on spawning fishes at a well used spawning site at Enewetak Atoll, Marshall Islands. The lack of predator pressures over wide geographical areas does not negate the selective advantages of anti-predator defenses if predation on eggs and spawning fishes is prevalent in sufficient frequencies at locations elsewhere to make such defenses adaptive, particularly in view of supposed wide dispersal of larval fishes. For example, propagules spawned at low predation sites could conceivably settle and later spawn in areas of high risk.

Bell and Colin (1985) suggest that a strategy for optimal egg predator avoidance would result in spawnings at periods of maximum current velocity. This was not the case in their study at Enewetak Atoll, nor is it so at Miyake-jima. Barlow (1981) and others have suggested that a spawning ascent facilitates maximum dispersal of gametes and larvae. Our observations do not discount this hypothesis; however, a rapid upward dash is not necessary to achieve a dispersal function. Our data from Miyake-jima provide evidence that, due to speed, the rapid spawning rush,

though seemingly ineffective against egg predators, functions as an excellent defense against piscivores in a predator-rich environment.

Literature cited

Barlow, G. W. 1981. Patterns of parental investment, dispersal, and size among coral-reef fishes. Env. Biol. Fish., 6: 65–86.

Bell, L. J. 1983. Aspects of the reproductive biology of the wrasse *Cirrhilabrus temminckii* at Miyake-jima, Japan. Japan. J. Ichthyol., 30: 158–167.

Bell, L. J. and P. L. Colin. 1985. Mass spawning of *Caesio teres* (Pisces: Caesionidae) at Enewetok Atoll, Marshall Islands. Env. Biol. Fish., 15(1): 69–74.

Colin, P. L. 1982. Aspects of the spawning of western Atlantic reef fishes. NOAA Tech. Mem. NMFS-SEFC-80, March, 1982: 69–78.

Ehrlich, P. R. 1975. The population biology of coral reef fish. Ann. Rev. Ecol. System., 6: 211–248.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish., 3: 65–84.

Jones, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica, 4: 309–361.

Keenleyside, M. H. A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, Berlin., 208 pp.

Meyer, K. A. 1977. Reproductive behavior and patterns of sexuality in the Japanese labrid fish *Thalassoma cupido*. Japan. J. Ichthyol., 24: 101–112.

Moyer, J. T. 1984a. Social organization and reproductive behavior of ostraciid fishes from Japan and the western Atlantic Ocean. J. Ethol., 2: 85–98.

Moyer, J. T. 1984b. Comparative reproductive strategies of labrid fishes from benthic plant and coral reef communities. Doctoral Dissertation, Univ. of Tokyo., 208 pp.

Moyer, J. T. 1984c. Reproductive behavior and social organization of the pomacanthid fish *Genicanthus lamarck* at Mactan Island, Philippines.

Copeia, 1984: 194–200.

Moyer, J. T. and A. Nakazono. 1978. Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. Japan. J. Ichthyol., 25: 25–39.

Moyer, J. T. and Y. Yogo. 1982. The lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyake-jima, Japan. Z. Tierpsychol., 60: 209–226.

Robertson, D. R. and S. Hoffman. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z. Tierpsychol., 45: 298–320.

Sokal, R. R. and F. J. Rolf. 1981. Biometry. 2nd ed. Freeman and Co., San Francisco., 859 pp.

Thresher, R. E. 1984. Reproduction in reef fishes. T. F. H. Publ., Neptune City, 399 pp.

Tribble, G. W. 1982. Social organization, patterns of sexuality, and behavior of the wrasse *Coris dorsomaculata* at Miyake-jima, Japan. Env. Biol. Fish., 7: 29–38.

(Tatsuo Tanaka Memorial Biological Station, Ako, Miyake-jima, Tokyo 100–12, Japan)

三宅島におけるニシキベラ産卵中の捕食の定量的観察

Jack T. Moyer

浮性卵を産む礁魚の多くは, 産卵の際に雌雄が上方へ突進する (spawning rush). この行動は親魚と卵が捕食されないための防衛行動であると考えられているが, 未だ検証されていない. 本研究では 1981 年に三宅島においてニシキベラのグループ産卵を 461 回観察し, 他魚種による親魚の捕食を定量的に調べた. その結果, 7 種の魚が合計 206 回親魚を襲うのが観察された. この内 171 回は spawning rush 中の魚に対して行われたが, 一度も成功しなかった. spawning rush 前の bobbing や milling 中の親魚に対しては 35 回の攻撃があったが, これにより 4 尾の親魚が捕食された. すなわち, 全体としての捕食者の成功率は 1.9% にすぎなかった. これに対し, 卵は 9 種のプランクトン食性魚類の捕食を受け, その頻度は 213 回中 90 回 (42.3%) に達した. 以上の結果から, spawning rush は親魚の捕食者に対する防衛としては有効であるが, 卵の捕食者に対してはほとんど効果のないことが判明した. この他 7 種の礁魚の spawning rush と卵捕食との関係についても述べた.

(100-12 東京都三宅島阿古 田中達男記念生物実験所)