ASPECTS OF THE SPAWNING OF WESTERN ATLANTIC BUTTERFLYFISHES (PISCES: CHAETODONTIDAE)

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Synopsis

The status of knowledge of spawning among the five shallow water *Chaetodon* species in the western Atlantic is reviewed. Spawning has been observed for three species in Puerto Rico, St. Croix and the Bahamas, with possible courtship in a fourth. *Chaetodon aculeatus* spawned near the time of sunset over objects on the reef as single female/male pairs or as two females and one male, with pair spawning in rapid succession. Spawning occurred during much of the lunar month from February to April and it is uncertain whether any lunar periodicity to spawning exists. Male-male aggression was noted. Spawning sites (coral heads) were alternated daily and it is likely that females spawn only once every two days. A single female produced as many as 2090 eggs in a single spawning. *Chaetodon capistratus* spawned during much of the lunar month from February to April. It spawned about 5 min after *C. aculeatus*, occasionally using the same sites, and alternated sites daily. A female produced as many as 3710 eggs in one spawning. *Chaetodon striatus* spawned from February to April but it is unknown if it has any lunar spawning cycle. No predation attempts by piscivores on spawning adults were seen. Predation by *Melichthys niger* on eggs of *C. striatus* occurred. No egg predation was observed for *C. aculeatus* and *C. capistratus*. With an assumed four month reproductive season, alternate day spawning and observed egg production values, *C. aculeatus* and *C. capistratus* produce respectively about 100 000 and 200 000 eggs per large female per year. The reproductive strategy of smaller species may be to produce moderate numbers of eggs per day over a spawning season of at least a few months while larger species may produce more eggs per day for a shorter period.

Introduction

Despite their diversity and conspicuous presence on most coral reefs, the reproductive biology of the butterflyfishes (Chaetodontidae) is poorly known. Thresher (1984) has summarized recent information on the family. There are five shallow water species of *Chaetodon* in the western Atlantic and aspects of their reproduction discussed in this paper are summarized in Table 1. Aiken (1983) provided data on gonadal condition of various *Chaetodon* spp. near Jamaica, based on trap collections, but did not observe actual spawning. Neudecker & Lobel (1982) described spawning of *Chaetodon aculeatus* and *C. capistratus* while Colin & Clavijo (1988) described spawning in the two preceeding species as well as *C. striatus*. This paper reports additional information concerning spawning of western Atlantic species and attempts to discuss spawning strategies of chaetodontids in comparison with other reef fishes.

Materials and methods

Observations and collections were made in Puerto Rico, St. Croix, U.S. Virgin Islands and the Bahamas. Puerto Rican observations were made on a shelf edge reef at 18 m depth off southwestern Puerto Rico in an area described in detail by Colin & Clavijo (1988). Observations in St. Croix were made from the Hydro-Lab habitat on the east wall of the Salt River submarine canyon at 18 m depth. In the Bahamas work was carried out from the Caribbean Marine Research Center on Lee Stocking Island, Exumas, on a reef ledge at 12–18 m depth facing Exuma Sound.

Table 1. Spawning and courtship occurrences of shallow water western Atlantic species of *Chaetodon*. FM = full moon, AFM = after full moon, BFM = before full moon, NM = new moon.

Species	Location	Months	Lunar phase	Temp. (°C)	Source
C. aculeatus	Puerto Rico	April 78', 79'	FM-8AFM	25.5	Colin & Clavijo (1988)
	St. Croix	Sept. 1978	4 AFM (probable spawn)	28–29	pers. obs.
	St. Croix	Feb. 1980	1–3 BFM		Neudecker & Lobel (1982)
	St. Croix	Oct. 1980	11 BFM (courtship only)		I.E. Clavijo, pers. comm.
	Bahamas	Feb. 1988	3–4 AFM	24.3	pers. obs.
	Bahamas	April 1988	1 AFM–14 AFM (NM)	23.5–24.2	pers. obs.
	Bahamas	May 1988	11 AFM, 15 BFM	25.0	pers. obs.
C. capistratus	Puerto Rico	April 1979	5 BFM	25	Colin & Clavijo (1988)
	St. Croix	Feb. 1980	9, 8, 4, 1 BFM		Neudecker & Lobel (1982)
	Jamaica	much of year	(gonads)		Aiken (1983)
	Bahamas	April 1988	2 AFM–14 AFM (NM)	23.5–24.2	pers. obs.
	Bahamas	May 1988	11 AFM, 15 BFM	25.0	pers. obs.
C. ocellatus	Jamaica	Jan, May (ND March, Apr., June), some other months.			Aiken (1983)
	Bahamas	May 1988 (ripe)	12 AFM	25.5	pers. obs.
	N. Carolina	May 1978 (ripe)	1 week BFM, FM	18–20	S.W. Ross (pers. comm.)
C. striatus	Puerto Rico	Feb–March 1979	9–11 BFM; 3 AFM	24–25	Colin & Clavijo (1988)
		Feb. 1988 (courtship only)	10–11 AFM	26.7	pers. obs.
	Jamaica	Jan. Feb. peak, some active all months			Aiken (1983)
	Bahamas	May 1988 (ripe)	13 AFM	25.5	pers. obs.
C. sedentarius	Puerto Rico	Mar. Apr, June	1–5 BFM (courtship)		
	Jamaica	Jan., May, Sept. (a few ripe)			Aiken (1983)
	N. Carolina	May 1978 (ripe)	1 week BFM, FM	18–20	S.W. Ross (pres. comm.)

Observations were made while SCUBA diving. Spawning behavior was recorded using an 8 mm video camera. Temperatures were measured using calibrated recording thermographs in Puerto Rico and the Bahamas. Time of events was determined to 2 min accuracy using calibrated watches.

Eggs were collected using a short handled dip net 15 cm in diameter with 210 micron mesh. This was used to strain the water in the area of egg release within 5–10 seconds of release. The net with captured eggs was then everted inside a plastic bag to retain the eggs. Eggs were returned to the laboratory in the plastic bags, filtered from the water using 250 micron mesh and preserved in alcohol. Once in alcohol, the eggs became opaque and were easily counted in a petri dish.

Results

Accounts of individual species

Chaetodon aculeatus. The longsnout butterflyfish is the chaetodontid most often seen to spawn. Colin & Clavijo (1988) observed spawning in Puerto Rico in April 1978 and 1979 while Neudecker & Lobel (1982) saw it from 13 February to 1 March 1980 in St. Croix. More recently, I observed this species spawning in the Bahamas during February, April and May 1988 (n = 34 spawns). Spawnings were observed 1 and 3 days before the new moon (Neudecker & Lobel 1982) and daily from the day of the full moon to at least the day after the new moon (Colin & Clavijo 1988, personal observation). Neudecker & Lobel (1982) reported spawning by *C. aculeatus* not to occur between 9 and 11 days before the full moon in February and 2 days after the full moon in early March. No attempt has yet been made to determine if individuals are spawning during the entire period from after the new moon until near the time of the full moon, but this should be done before any firm statements can be made regarding lunar periodicity of its spawning.

Spawning was not observed on three evenings in July 1988 at Lee Stocking Island on phases of the moon and at sites where it had been observed in April and May. There may be some limited spawning occurring during the summer or fall periods. I observed one probable spawning by *C. aculeatus* in St. Croix in September 1978 and I.E. Clavijo (personal communication) also saw two instances of courtship without apparent spawning there in October 1980.

Spawning behavior also appears to be variable. Neudecker & Lobel (1982) reported an ascent of less than one meter with the male underneath the female and both fish quivering for about one sec while releasing gametes. My observations indicate that pairs of *C. aculeatus* often circle several times with the fish oriented laterally, the snout of the male touching the caudal fin of the female before he moves slightly underneath her for gamete release. The pair did not always move upward with the male pushing the female at gamete release, but rather the male orients behind the female with his snout touching her caudal fin. They circle laterally with the males' snout continuing to touch the female until gamete release. During one spawning the pair 'made a short slow "dash" into the water column to release gametes' (A. Gronell in Thresher 1984, personal observation). In the spawnings I observed there was considerable variation in vertical ascent, from less than 10 cm to as much as 50–60 cm, with much of the actual rise coming during the circling phase prior to gamete release. At gamete release the female is stationary, angled upwards with the male below her with his snout near her vent area. He moves forward while the eggs are released, leaving the female in the water column. There were no false starts to spawning as occurs in some other reef fishes (Colin & Clavijo 1988). In all cases where spawning was positively observed, the female was visibly swollen with eggs before spawning.

Chaetodon aculeatus typically spawned near or above objects on the bottom. One pair in Puerto Rico spawned above a large sponge *Xestospongia muta.* In the Bahamas it spawned along a steep rocky reef face which extended from 12 m depth to a sandy plain at 18 m. This sand extended offshore to the shelf break another 300–400 m offshore, so the actual spawning site was well inside the edge of the insular shelf. Small coral heads, ranging from only about 50 cm to 1.5 m in height, projected up

from both the edge and upper surface of the ledge. Fish spawned both along the edge of the face and over heads located 10–15 m inside the reef edge at depths of 10–12 m.

Spawning occurred just before or at the time of sunset, generally about 5 minutes before *Chaetodon capistratus* spawned. Fish spawned once per day, as both male-female pairs and in several instance as two females spawning consecutively with one male.

Without exception, the spawning sites at the Lee Stocking Island study area were utilized only on alternate days. Whether individual fish were utilizing different sites on alterate days or if spawning by individuals took place only every other day could not be positively determined, but based on anecdotal evidence, I feel it is likely alternate day spawning by an individual females is probably the case. There were four coral heads, all within 15 m of each other, that were utilized for spawning and each was monitored continuously during the period when spawning would occur from the day of the full moon to the new moon in April 1988. In addition, spawning sites nearby were monitored intermitently. Fish appeared at the spawning site about 10–15 minutes prior to spawning and remained within a few meters of that site until after spawning had occurred. The spawning sites from the previous night were not utilized by any fish or visited during the half hour prior to spawning.

One coral mound was utilized only by a trio of fish, a single male and two females, with one female considerably smaller than the other (estimated standard length 45 mm vs. 55 mm). This trio was observed spawning on seven occasions, on a two day cycle, and unless disturbed by egg collection, spawnings of the two females occurred within one minute. On 4 days the large female spawned first and on 3 days the small one was first. There was no aggressive interaction between the two females. The small female, the only individual which confidently could be identified, was never seen to spawn elsewhere on nights she did not spawn amongst the trio.

In a nearby area, about 40 m from the primary observation sites, three *C. aculeatus* (presumed to be 2 males and 1 female) were found in which one male fought for a prolonged period with the second, who was with an associated female. Within the hour before sunset the presumed intruding male attempted to court the female while the second male kept trying to drive him from the vicinity. On the first day observed, the female was visibly swollen with eggs and fighting between the two males was fierce. The male with the female repeatedly attempted to drive the intruding male away from the vicinity of the female, and occasionally the female also directed an attack at the intruding male. More aggressive actions were used by the male when the intruder did not retreat. This involved raising the dorsal spines, angling the body forward to orient the spines toward the facing male and charging forward. The two males often ended up spinning, their dorsal fins meeting while both in this posture, until one fish was spined and broke the exchange off. This aggressive behavior was observed for over 30 min with intervals where the males faced one another about 1 m apart without attacking. Both males were battered with wounds to the body and dorsal fin membranes, with the intruder appearing worse. The next day, a presumed non-spawning day for the female, both males were present in the same area, but beyond weak attempts to drive one another away, there was little aggression between them. The following day, 2 days after the initial fierce encounter, the female was again swollen with eggs (supporting alternate day spawning by individuals) and the males fighting as aggressively as two days before. On this evening the defending male was seen to successfully mate with the female.

The eggs were 0.74–0.76 mm in diameter, clear, with a single oil globule, 0.16 mm diameter. The embryos hatched between 26 and 36 h after spawning at 25° C.

Chaetodon capistratus. Spawning by the foureye butterflyfish has been reported previously by Neudecker & Lobel (1982) in St. Croix in February 1980 from 9–4 days before the full moon and by Colin & Clavijo (1988) in Puerto Rico in April 1979, 5 days before the full moon. Additional spawnings have been seen in the Bahamas in April and May 1988 from the day after the full moon until

the day after the new moon (n = 14 spawns). Spawning was not observed at the Lee Stocking Island site in July 1988 at locations and on lunar phases where spawning had been seen in April and May.

There are differences reported in spawning behavior of *C. capistratus*. Neudecker & Lobel(1982) reported it to forage in monogamous pairs and spawn in those pairs only. Colin & Clavijo (1988) found that in Puerto Rico it occurs in social groups of as many as 15 individuals with no consistent pairing, indicating some flexibility in social activity and spawning. A social system similar to that observed by Colin & Clavijo (1988) was reported by Gore (1982) from Jamaica and Grand Cayman island. These differences in social system in different areas could be due to density of adults on the reef which cause the pairing of fish to break down. At Lee Stocking Island the social system of *C. capistratus* was similar to that described by Neudecker & Lobel (1982) in St. Croix with pairs foraging together before spawning, and spawning occurring only as isolated pairs.

There was little courtship prior to spawning. Like *C. aculeatus*, at gamete release the female remained nearly stationary, while the male moved forward and downward, possibly serving to mix the eggs and sperm. Close observation of the eggs on release indicate they emerge as a dense stream several centimeters in length, rather than as a single burst or cloud. They quickly begin to diffuse away from the center of the stream so that within about 10 sec the dense stream of eggs is no longer identifiable. Within a few seconds more the clear eggs are nearly invisible to a human observer.

Spawning by *C. capistratus* occasionally occurred at the same sites as *C. aculeatus*, but unless disturbed by an observer, took place about 5 minutus after the latter. At the same sites, *C. capistratus* spawned slightly higher (50–100 cm above objects) than *C. aculeatus*. Like *C. aculeatus*, this species alternated spawning sites each evening and it believed this is due to females spawning only on alternate evenings. Just before the time of spawning some pairs of *C. capistratus* were found in the study area in which neither fish was visibly swollen with eggs. These occurred almost alongside pairs in which one fish was noticeably swollen with eggs and adds some support to the argument that during the spawning season females spawn only every other night. In all cases in which pairs spawned, the female was easily identified by her egg-swollen condition. Despite possible alternate-night spawning by individual females, there were different pairs of *C. capistratus* spawning each night. The eggs were 0.76–0.77 mm in diameter, clear, with a single oil globule 0.18 mm diameter.

Chaetodon ocellatus. The spawning of the spotfin butterflyfish has not been observed. Robins et al. (1986) reported coloration differences between sexes with males having a dark spot at the posterior edge of the dorsal fin, but other works (Allen 1979, Burgess 1978) do not report any sexual dichromatism. In most mature pairs I have seen, assumed to be male and female, plus actual male/female pairs speared and sexed, both individuals possess the black spot on the dorsal fin edge.

During April 1988, when I was regularly observing spawning by *C. aculeatus* and *C. capistratus*, there were several *C. ocellatus* present in the Lee Stocking Island study area and no courtship behavior or visibly swollen females were seen. I am fairly certain *C. ocellatus* was not spawning during this period from the full moon to new moon. At south Cat Island, Bahamas a slightly swollen female *C. ocellatus* was observed on 13 May 1988, two days before the new moon. This fish, 113 mm SL, was collected (along with a 116 mm SL male) at sunset and approximately 19 000 partially hydrated eggs were hand stripped with light pressure from the fish. Certainly this pair was near the time of spawning, but the partially hydrated state of the eggs indicates that spawning was still some hours away. It is possible that spawning may occur at dawn due to the incomplete hydration of these eggs at sunset.

S.W. Ross (personal communication) found gonad development indicating imminent spawning among *C. ocellatus* collected at 38–62 m depth in Onslow Bay, North Carolina during the week before the full moon in May 1978. He found females 111–137 mm SL had ovaries comprising 1.1–8.1% of body weight. Moe (1976) reported the eggs of *C. ocellatus* to be 0.6–0.7 mm in diameter based on eggs taken in the laboratory.

Chaetodon sedentarius. A few instances of possible courtship by a large pair of the reef butterflyfish were seen in Puerto Rico. One fish of probable male/female pairs chased the other, placing its snout on the posterior margin of the anal fin. These instances occurred 1–5 days before the new moon in March, April and June (Colin & Clavijo 1988). S.W. Ross (personal communication) collected female *C. sedentarius* at 38–62 m depth off Onslow Bay, North Carolina with ovaries comprising 3.1–8.3% of body weight during the week before the full moon in May 1978.

Chaetodon striatus. The courtship and spawning of the banded butterflyfish was observed on three occasions on a shelf edge coral reef off southwestern Puerto Rico (Colin & Clavijo 1988). There was no elaborate courtship with pairs of nearly equal-sized fish progressively swimming closer to one another over several minutes. Prior to this, they ranged widely over the reef, covering as much as 50 m in one direction within a few minutes, swimming 50–100 cm above the bottom. The male would occasionally approach the visibly swollen female and touch his snout to her caudal fin. A pair would undergo a few false starts in which the spawning ascent was initiated but broken off prior to gamete release. During the spawning ascent the male was behind the female, his snout touching her caudal fin, while the fish rose at a slight angle. After gradually rising off the bottom, they spawned as much as 7–8 m above the bottom. They were not oriented with nor did they start their ascent from any projection above the surface of the reef. At the release of gametes, the male gave a flip of his caudal fin which may have helped to mix the gametes. After release the fish swam down to the substratum.

Spawnings in Puerto Rico were seen 3 days after the full moon in February 1979 and 9 and 11 days before the full moon in March 1979. In addition, courtship similar to that seen previously was observed 10 and 11 days after the full moon in February 1988. Females were also heavy with eggs, but observers had to leave the site before spawning was observed.

During April 1988 a single pair of *C. striatus* were checked daily for any signs of courtship or spawning activity at the Lee Stocking Island study site from the time of the full moon to the new moon. Neither fish was ever found to be swollen with eggs and near the time of dusk no courtship activity was seen. Almost certainly this pair was not spawning during the period of observation. On 14 May 1988, one day before the new moon, a moderately swollen female *C. striatus* was seen at south Cat Island, Bahamas and collected along with a male. The female produced approximately 5 500 partially hydrated eggs by hand stripping.

In Puerto Rico the eggs were collected, but not measured, and the embryos hatched in about 30 h at 26° C. At 72 h after hatching the eyes were pigmented and the yolk absorbed.

Hybridization

Among western Atlantic species, only a single probable hybrid individual has been reported (Clavijo 1985). It probably represents a cross between *C. ocellatus* and *C. striatus* with the color pattern containing elements of both probable parent species. Since spawnings of chaetodontid species that have been observed have been well separated in time and space, it is unlikely that hybrid *Chaetodon* are the result of chance mixing of eggs and sperm from separate spawnings. More likely they are the result of a suitable mate of the same species not being available to an isolated individual.

Egg numbers per spawning

Eggs were collected using a hand net from individual females immediately after release and the numbers captured from each spawning varied considerably. When the gamete cloud was released by the pair, collection would commence, if possible, within 5 sec so the net could be brought through the area of concentrated eggs while they were still visible. In such cases, most (if not all) released eggs were collected.

Among *C. aculeatus* spawns, the eggs collected per spawn ranged up to 2090 (n = 13) with 9 collec-

tions over 500 eggs (531, 545, 654, 692, 1109, 1540, 1630, 1933 and 2090). Four collections numbered less than 200 eggs and since definite egg clouds were seen on release, it is assumed that most of the eggs were not collected from these spawns. The smallest female (approximately 45 mm standard length, SL) observed spawning produced at least 692 and 225 eggs on two nights when her eggs were collected. A full-size female (approximately 55 mm SL) produced 1933 eggs and two nights later 2090 eggs (presumed to be the same fish based on size, general appearance and spawning location). The question of whether a single female spawns nightly (as opposed to alternate nights) cannot be answered based on my data, but I am confident the same females were spawning at least on alternate evenings.

Counts of *C. capistratus* eggs collected from large females (approximately 80 mm SL) were 110, 450, 610 and 3710 (n = 4) with the lower numbers, again, almost certainly due to a large part of the eggs released not being collected.

Aiken (1983) reported estimated total egg numbers from ovaries of four species of *Chaetodon* from Jamaica. For *C. capistratus* total egg numbers ranged between 2900 and 12900. The differences with actual numbers of eggs collected above imply that a significant number of eggs are retained in the ovaries and are probably not yet ready for release. Larger species, such as *C. ocellatus* had roughly one order of magnitude more eggs (up to 64000) in its ovaries than *C. capistratus*.

Predation on eggs and spawning adults

No attempts by piscivores to prey on spawning adults have been seen. Predation on the eggs of *C. striatus* by the black durgeon, *Melichthys niger*, was seen on two occasions immediately after release of the eggs (Colin & Clavijo 1988). The *M. niger* stationed themselves close behind the pair of *C. striatus* who were gradually rising into the water column to spawn and made no effort to escape or deter the egg predators. At the instant of gamete release, the *M. niger* immediately swam to the cloud of gametes and picked at what were assumed to be the eggs for a few minutes. The *C. striatus* made no effort to protect their eggs and the observers remained far away from the spawning so they had negligible effect on the fishes.

No instances of egg predation were noted for 'undisturbed' spawns (where no attempt was made to collect eggs, otherwise egg collection would have interrupted egg predators) by either *C. aculeatus* (n = 17) or *C. capistratus* (n = 8) at the Lee Stocking Island site.

Discussion

Seasonality and lunar periodicity

The seasonality and lunar periodicity of spawning by western Atlantic butterflyfish are not well defined. From available information it does seem likely there are seasonal spawning peaks. Aiken (1983) implied seasonal peaks from his data while Colin & Clavijo (1988) over nearly three years found spawning by chaetodontids only during the winter and spring in Puerto Rico (February to April). At other times, though, a probable spawning by *C. aculeatus* in September (personal observation) and courtship in October (I.E. Clavijo personal communication) in St. Croix were seen, implying a small amount of spawning may occur during the 'off' season.

The alternation of spawning sites and/or bidaily spawning by *C. aculeatus* and *C. capistratus* signal caution in determining accurately when spawning is occurring. For example, Neudecker & Lobel (1982) reported *C. aculeatus* in St. Croix to spawn on two evenings (two days apart) at the same site. Subsequently they reported the fish not to spawn on three evenings, 5–7 days later. If each female spawns every other night, as suspected, then this would explain the lack of spawning by the pair on two of the three nights when spawning was reportedly not seen (5 and 7 days after). Whether or not spawning occurred on the remaining evening would then become the sole basis for making the statement that spawning does not occur during the first quarter of the moon. Similarly another instance of non-spawning by *C. aculeatus* was report-

ed after the full moon in March (Neudecker & Lobel 1982) and could have been due again to either lack of spawning or alternate night spawning. Consequently the data here (and most reef fish spawning data based on observations) can only be considered positive data and negative spawning data must be viewed with caution. Ideally, comparative data, such as gonad indices, should support any conclusions concerning negative spawning. Similarly, spawning observations on a particular phase of the moon do not imply lunar periodicity unless, using consistent and sensitive techniques, significant variation in spawning activity was detected over the course of the lunar month.

A few comparisons can be made regarding spawning patterns between western Atlantic and Indo-Pacific species. Hawaiian and western Atlantic *Chaetodon* do seem to share a similar reproducive season with spawning during the winter and spring. Lobel (1978) reported three species of Hawaiian *Chaetodon* (*C. fremblii, C. multicinctus* and *C. unimaculatus*) to spawn during the week before the full moon in February and March. Ralston (1981) found *Chaetodon miliaris,* an Hawaiian endemic, to spawn, based on gonad samples, between January and May with a peak during February and March and no apparent lunar periodicity. Based on gonadal evidence, Tricas (1986) found *C. multicinctus* to spawn between October and May with a semilunar periodicity.

There is little information for chaetodontids in the southern hemisphere. Thresher (1984) briefly described spawning by *Chaetodon rainfordii* and *Heniochus acuminatus* on the Great Barrier Reef, but did not give details of timing. Near Port Moresby, Papua New Guinea, I found *Chaetodon unimaculatus* and *Chaetodon kleinii* swollen with eggs and undergoing typical chaetodontid courtship at the new moon in June when water temperatures were at their yearly minimum (24–25° C). Spawning was never observed, but based on the swollen condition of the females, almost certainly occurred.

Most observations of butterflyfish spawning have been during periods of winter low water temperatures (Ralson 1981, Tricas 1986, Neudecker & Lobel 1982, Colin & Clavijo 1988, this paper) of around 23–26° C which tends to correlate with the period of most active spawning by many reef fishes (Walsh 1987, Colin & Clavijo 1988, Munro et al. 1973). *C. aculeatus* and *C. capistratus* at the Lee Stocking island site were spawning in May when water temperatures were 24–25.5° C but were no longer spawning during July at which time water temperatures were 27.5–29.5° C. It would be interesting to see how well the spring rise in water temperatures correllates with the cessation (or great reduction) in spawning by these two species.

S.W. Ross (personal communication) found ripe females of *C. ocellatus* and *C. sedentarius,* which were almost certainly near the time of spawning, at 38–62 m depth off North Carolina in May 1978 when water temperatures measured at the collection sites were 18–20° C. Winter minimums in this area are near 8–12° C so the observed temperatures represent a significant rise over the yearly minimums. During summer, water temperatures at these depths may not rise significantly or may actually become lower than those observed during May due to upwelling of colder water.

Fricke (1986) reports spawning by *Chaetodon chrysurus* in the Red Sea to first be noticed in June and July during the period of warmest water temperatures. These are only 24–26° C (Fishelson et al. 1987), similar to temperatures recorded in areas where chaetodontids are spawning during winter and spring.

It seems that chaetodontids do not actively spawn at water temperatures above about 26° C and the seasonality of their spawning may be different in response to particular temperature regimes. In areas where water temperatures do not reliably reach the minimums found in true tropical areas, such as along the North Carolina coast, spawning may still proceed, possibly during the warmest period of the year.

Various reasons have been suggested to account for prevalence of winter spawning seasonality in many reef fishes in tropical areas, including increased primary production during winter, occurrence of particular current regimes to either disperse or retain the eggs and larvae near their point of origin and the influence of glacial conditions adapting spawning to present day low water tem-

peratures (see Thresher 1984 for review plus Colin & Clavijo 1988). An additional hypothesis is that spawning by many reef fishes with pelagic eggs at the yearly minimum water temperatures of most reef areas insures embryos have developed to the point at which they are able to initiate feeding (eyes pigmented, mouth and gut functional) at a time where they have a full day ahead (morning) rather than when first feeding would have to be deferred or halted prematurely (night or late afternoon). Aquiring sufficient food and continuing to feed for an entire day may be crucial in allowing larvae to survive the first night after yolk is absorption.

Spawning styles

There may be a change in the reproductive patterns of butterflyfishes with increasing size. Small species may spawn often, perhaps as often as every other day, producing modest numbers of eggs throughout a lengthy period of the year. Large species produce much greater numbers of eggs per spawning but spawn less often, perhaps only a few times a year. Between large and small there is a variation with frequency of spawning smaller numbers of eggs being traded for more eggs produced at greater intervals.

The presence of visibly swollen females is the surest sign of imminent spawning aside from actual observation of the spawning (Fricke 1986). If data on swollen females are acceptable to indicate probable spawning occurrence (in addition to actual observations of spawning) there is even stronger evidence for differences in spawning styles with size among chaetodontids. In the western Atlantic, the two smallest species, *C. aculeatus* and *C. capistratus*, spawned regularly during the period of coolest water temperatures. The three larger species, though, were not observed as often to spawn or have visibly swollen females.

At the Lee Stocking Island only *C. aculeatus* and *C. capistratus* were seen to spawn and to have visibly swollen females. A few pairs of *C. ocellatus* and *C. striatus* were present at this study site, but none were ever seen be swollen. Almost certainly they were not spawning on the same days as *C. aculeatus* and *C. capistratus*. *C. striatus* has been seen to spawn and to have swollen females only in Puerto Rico in February and early March. Colin & Clavijo (1988) saw it spawning on only three occasions in a portion of their study area that was under regular observation for surgeonfish spawning and it is unlikely the species was spawning there regularly (daily or alternate days). Qualitatively the Puerto Rico study indicates that the frequency of spawning by *C. striatus* there is less than what was observed in the Bahamas for the two small species.

The numbers of eggs produced per year by *C. aculeatus* and *C. capistratus* can be estimated based on the limited data available. These species have a four to six month active spawning season with observed spawning occurring from February and to at least May. Each female probably spawns every other day and a full-size adult female of *C. aculeatus* and *C. capistratus* produces approximately 1500 and 3000 eggs per spawning respectively. This results, for each species respectively, in about 100 000 and 200 000 eggs per year per individual. The spawning style of these two small species appears to be to produce gametes on a regular basis (spawning occurred every day for both species whether individuals spawned each day or not) for a period of one third to one half of the year.

The remaining shallow-water western Atlantic *Chaetodon* may have a different style. In the Bahamas in April 1988 *C. striatus* and *C. ocellatus* (no *C. sedentarius* pairs present) were not actively spawning in the same area as *C. aculeatus* and *C. capistratus*. The data available indicate the three larger species produce more gametes per spawning than the two smaller species. The eggs released by a large *C. ocellatus* in a single spawning number in the tens of thousands and it seem likely these larger species produce a larger number of eggs per day on fewer days per year.

Tricas (1986) examined egg numbers produced by Hawaiian *C. multicinctus*. After actively spawning in October and November there was a possible reduction in spawning activity for about a month in December or January. This is followed by a yearly peak in March. He found apparent semilunar periodicity to spawning based on occurrence of postovulatory follicles in female specimens with spawn-

ing occurring about nine days prior to one day after the new moon and again nine days before to the day of the full moon. The data indicate that females do not spawn on successive nights and in fact may spawn only a single to a few times during each of the semi-lunar periods. Tricas (1986) found evidence of increased egg production per female during the peak of the spawning period. During the spawning season seven females injected with gonadotropins, held for 24 h in aquaria and then hand stripped of ova, produced between about 2 000 and 20 000 eggs with about 10 000 eggs coming from average size adult females (85–90 mm SL). Assuming that (1) the spawning season of *C. multicinctus* runs from mid-October to mid-May with a brief hiatus or reduction in activity in December or January, (2) spawning occurs on a semilunar cycle with two spawnings per female during each semilunar period, (3) there are reductions in spawning activity and egg numbers produced per spawn early and late in the spawning season and (4) the average females produces about 10 000 eggs per spawning during the peak of the reproductive season, the annual egg production is very roughly estimated at 200 000 to 300 000 eggs per female.

Bauer & Bauer (1981) found female angelfishes (Pomacanthidae) of the genus *Centropyge* in the aquarium to daily produce 50 to over 100 eggs. For six species this resulted in an estimated production of 20 000–50 000 eggs per female per year. Members of *Centropyge* are smaller than most chaetodontids and produce perhaps only about 20% the number of eggs per year as the smaller Atlantic chaetodontids. They may, however, spawn more regularly than small chaetodontids and have a more extended spawning season resulting in a style where even fewer eggs are produced over a more extended period.

Almost a continuum can be seen among fishes producing pelagic eggs from small species which produce their modest number of eggs over a much longer period to large species, such as groupers, which spawn once or a few times per year yet produce eggs numbering two orders of magnitude greater than species such as those of *Centropyge* at that time. Variation of spawning style with size appears to be the case even among the limited size range of chaetodontids, although data are still very limited.

Suggestions for future research

There is an obvious need for a detailed long term study of spawning activity by chaetodontids to both determine patterns within and among species. With five readily accessible species in the western Atlantic, it would be very feasible to include all of them in such a study and a wide range of spawning styles would probably be present within those.

Many aspects to chaetodontid spawning biology are suitable for investigation if the proper techniques are used. It is relatively easy to obtain eggs of some species, opening possibilities to study early development and conduct experimental work on the embryos and larvae which would be impossible using ichthyoplankton collections due to the relative rarity of chaetodontids in such collections.

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Chaetodon capistratus from the Carribean. Photo by P.S. Lobel.