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On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific

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Synopsis

Surgeonfish spawning was observed at Palau, Lizard Island, Escape Reef (all Pacific Ocean) and Aldabra (Indian Ocean). Seven species, all fairly exclusively benthic feeding, defended feeding territories to some extent, and some of them formed territorial groups composed of 1 male + $\geqslant 1$ female. One other species ate both benthic algae and zooplankton, and both sexes appeared to be nonterritorial, except that males defended temporary spawning territories. The primary spawning rhythm appeared to be a restriction of spawning to part of the day. Ebb-tide spawning rhythms were evident where distinct tidal currents flowed on and off a reef; at one such site (Palau), a secondary tidal rhythm of spawning overlaid and combined with the primary rhythm to produce an apparent semi-lunar rhythm of spawning. Peaks of spawning of three Palauan species were on days when tidal heights/amplitudes were either less than or no different from the mean. Fishes that lived in intertidal areas (including some from heterosexual territorial groups) migrated to and massed and spawned at the intertidal/subtidal interface. Some fishes spawned in pairs, either in their (intertidal and subtidal) feeding territories or in temporary spawning territories at the reef edge. Many that migrated to the reef edge were (temporarily) nonterritorial there, and spawned in groups [1 female (sometimes more?) + many males]. Predatory fishes and zooplanktivorous fishes attacked spawning fishes and fed on fresh ova. At Palau, egg predators attacked group, rather than pair spawnings. Pulses of massed group spawning may reduce the rate of egg predation per group spawning. Two different types of color change by both sexes were associated with the two basically different patterns of spawning – in pairs and in groups.

Introduction

The surgeonfishes (Acanthuridae) are characteristic and abundant members of tropical reef communities throughout the world. There are about 75 species of these diurnally active fishes (Nelson 1976). The scientific literature contains only a few, fairly rudimentary reports on the spawning behavior of these fishes, principally on *Acanthurus triostegus*, *Zebrasoma scopas* and *Ctenochaetus striatus* (Randall 1961a, b, Johannes 1978, Lobel 1978, Robertson et al. 1979).

This report deals with the spawning activity of eight Indo-Pacific species. It describes and discusses where on reefs they spawn, the relationship of spawning activity to time of day and to tidal and lunar cycles, predator-prey interactions that occur during spawning activity, and the form of courtship and the spawning behavior. The eight species are: *A. nigrofuscus* (Forsskål), *A. lineatus* (Linnaeus), *A.*

triostegus (Linnaeus), *C. striatus* (Quoy & Gaimard), *C. strigosus* (Bennett), *Z. scopas* (Cuvier), *Z. veliferum* (Bloch), and *Paracanthurus hepatus* (Linnaeus).

Materials and methods

Most data were obtained at two locations, Aldabra Atoll in the western Indian Ocean and Palau in the western Pacific. The study sites at these two areas I will refer to as Aldabra and Palau, and, unless otherwise indicated, my remarks are confined to fishes at those sites. The Aldabra site has been described elsewhere (Robertson et al. 1979). Palau (lat. 7°30'N, long. 134°30'E) is one of the western Caroline Islands. The Palau site consisted of a 1.5 km stretch of outer reef edge that extended southwest from the lighthouse that marks the eastern entrance to the Malakal harbor channel, near Koror Island. Extending inwards from the outer reef edge, which faces the open ocean, there is an intertidal reef flat that is up to 0.75 km wide. The outer edge has a variable form; in some places it consists of slope-sided spurs of reef that project seawards for 20–50 m, while in other areas it is a fairly straight-edged cliff, 5–7 m high.

The tidal range at Aldabra is up to 3 m (Farrow & Brander 1971), while that at Palau was up to about 2 m during the study period (Tide Tables, Office of the District Administrator, Koror). At both sites tidal currents were very distinct and the tidal flood and ebb currents were on and off the reef (on/off-reef flow) rather than parallel to the axis of the reef edge (an along-reef flow).

In addition, less intense observations were made at two other areas on the northern part of Australia's Great Barrier Reef, Lizard Island (lat. 14°38'S, long. 145°28'E) and Escape Reef (lat. 15° 50'S, long. 145°49'E). Surgeonfish spawning was observed at two sites on the outer edge of Lizard Reef (a narrow fringe of reef around a cluster of four islands) a few hundred meters southeast of North Point, and the eastern tip of South Island. Spawning was also observed at the western side of Macgillivray reef, which is about 2 km east of Lizard Island.

At Lizard Island the tidal range was about 2 m during the study period. On each of 48 days during this 8-week period, I was present for 4–6 h between 0900–1730 h on the leeward (northwest) side of Macgillivray reef. The current between 0–10 m depth at that site invariably was an along-reef current, regardless of the stage of the tide. The wind came mostly from a southerly direction during the 8-week period, and on 40 of the 48 observation days the current also came from the south, regardless of the stage of the tide. Only on days when the wind blew from the northwest did the current in that study area change; then it flowed from the northwest during both ebb and flood tides. A lack of change in current direction associated with an ebb/flood change in the tidal cycle was also noted on three days at the outer edge of South Island.

All observations were made while snorkelling. Data were collected at Aldabra from July 1975 through January 1976, at Palau from January through April 1980, at Lizard Island during mid December 1979 and January-March 1982, and at Escape Reef during December 1981.

The distributions of surgeonfishes in intertidal and shallow subtidal areas at Aldabra and Palau were determined by counting fishes in segments of belt transects. Each transect was run across the intertidal reef flat and down the subtidal reef slope, in a line perpendicular to the outer edge of the reef. The single Aldabra transect was run out to the lower limit of coral growth on the reef slope, at a depth of 25 m, while the three Palau transects ended in about 10 m of water. The Aldabra transect was 10 m wide, while each Palauan transect was 5 m wide. On the Aldabra transect a count was made of the number of individuals of each species in each of a series of transect segments. Those segments varied from 25 m in length in inner reef flat areas (where there were very few fishes) to 10 m in length in the outer reef flat and reef slope. All Palauan transect segments were 5 m in length. Each species was recorded as being present or absent in each of those segments. Counts of fishes were made during flood tides, when fishes were sexually inactive and were in their normal feeding areas.

The Aldabra transect spanned six zones of four different types of substrate. The intertidal reef flat comprised two zones of seagrass and two banks of dead coral rubble. At its seaward edge, the reef flat gave way to the reef crest, a flat area of smooth rock. This reef crest and the innermost 100 m of the subtidal reef slope were relatively free of live coral. There were large amounts of live coral on the lowermost parts of the reef slope (see also Robertson et al. 1979).

The Palau transects spanned four main habitats. Two intertidal zones comprised the reef flat, with a substrate of dead and live coral intermixed with small sand patches, and the reef crest, an area of bare, smooth rock with little coral that had a small rubble bank at its inner edge. The two subtidal zones consisted of a shallow upper reef slope that, at the outer reef edge, gave way to the lower reef slope. The lower slope ran down into deep water. The upper slope, which was covered by a 1–2 m of water at low tide, consisted of a mixture of coral beds and barer areas of coralline rock that contained scattered small coral growths. The lower reef slope consisted of beds of live coral and large patches of sand.

No systematic observations were made of the presence/absence of surgeonfish spawning at different stages of the tidal cycle and different times of day at Aldabra. At Palau, an effort was made to sample systematically for evidence of such correlations and notes were made of amounts of spawning activity of all species at different stages of the tide and times of day. In addition, intensive observations were made of spawning activity by *A. nigrofuscus* and *Z. veliferum* at the outer reef edge. A study area of roughly 500 m^2 was set up there on the tip of a shallow (3 m depth of high tide) spur of reef that projected out into deep water. One series of five high tide observations and another of four low tide observations were made on the spawning activity of those two species in that area. Each observation period of 6.0–6.5 h spanned a high or a low tide. During each 0.5 h segment of each period, the following data were recorded: (1) the number of individuals of the two species present in the study area at the beginning of the segment; (2) the direction of current flow at the beginning of the segment (which was determined using a tethered current meter suspended 0.5 m below the surface); and (3) the presence or absence of spawning and courtship by each species throughout the time segment.

Table 1. Maximum size of surgeon fishes collected at Aldabra and Palau.

Species	Aldabra		Palau	
	Weight (g)	Standard length (mm)	Weight (g)	Standard length (mm)
Acanthurus nigrofuscus	63	113	33	65
Acanthurus lineatus	289	186	294	183
Acanthurus triostegus	122	134	no data	
Ctenochaetus striatus	205	161	178	162
Ctenochaetus strigosus	120	133	no data	
Zebrasoma scopas	78	119	57	111
Zebrasoma veliferum	342	198	216	171

Results

Acanthurus nigrofuscus

Acanthurus nigrofuscus is a small surgeonfish (Table 1). The largest specimen that I collected at Palau weighed only about half as much as the largest speared at Aldabra. Normally, the body and fins of this fish are uniformly colored in dark grey. The fish's cheeks bear a scattering of small, indistinct orange spots and its iris is dark. Its diet consists of fleshy microalgae, principally red algae (Robertson & Gaines, unpublished data).

At Aldabra, this species was found in shallower subtidal areas and in the outer section of the intertidal part of the transect (Fig. 1). Adults were largely restricted to intertidal areas (Robertson et al. 1979). At Palau, *A. nigrofuscus* was widely distributed throughout intertidal and subtidal areas (Fig. 2).

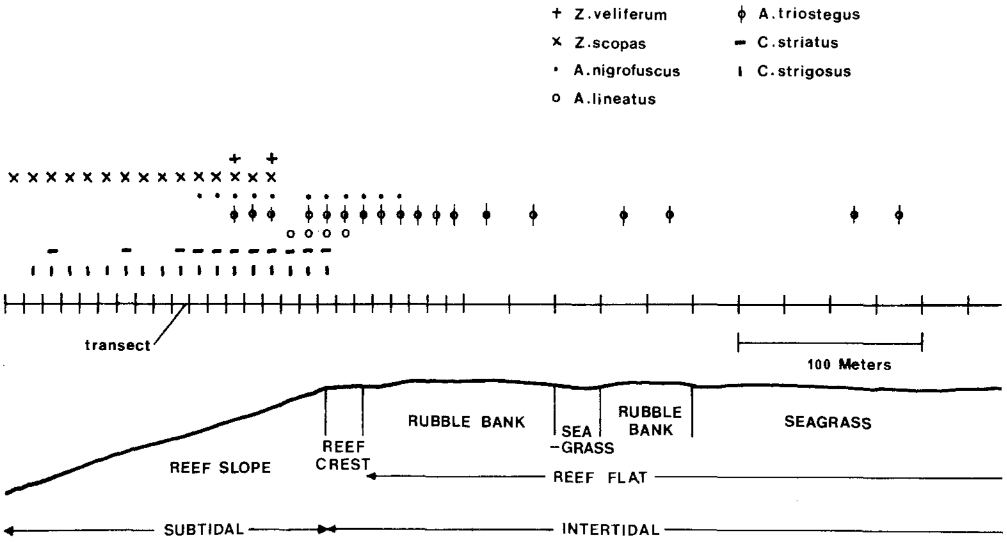

Fig. 1. Zonation of surgeonfishes at Aldabra. The presence of a species in a 10-m or 25-m segment of the transect is indicated by that species' symbol.

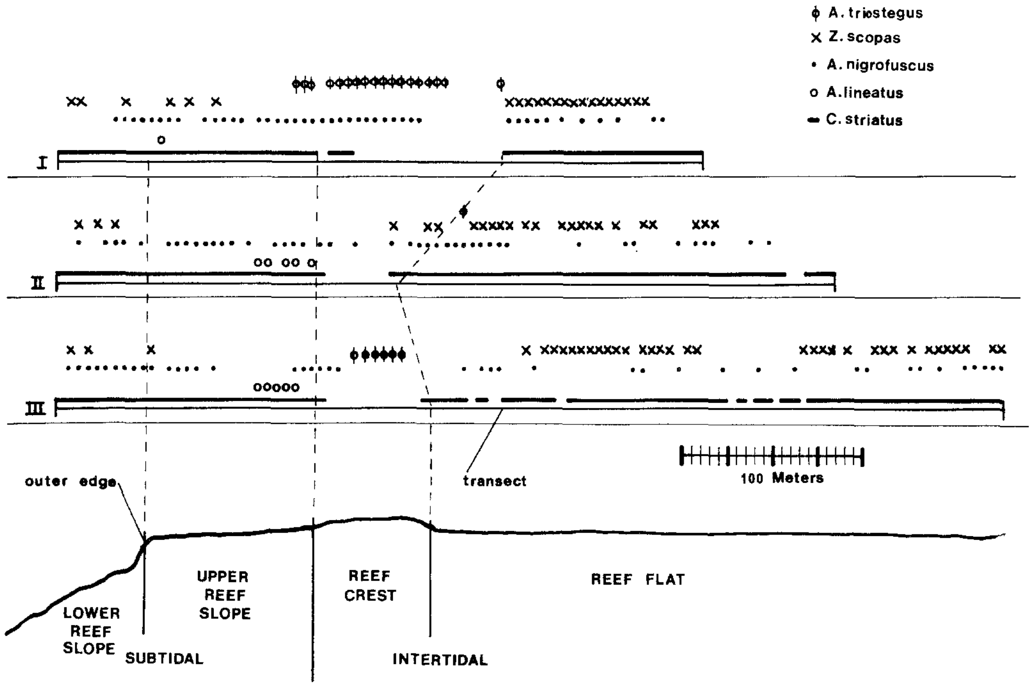

Fig. 2. Zonation of surgeonfishes at Palau. The presence of a species in a 10-m segment of the three transects is indicated by that species' symbol.

At Aldabra and Palau, adults of both sexes commonly defended feeding territories, either as single fish or in groups of up to five individuals. The members of a group shared the same feeding area, and aggressively resisted attempts of other conspecifics to feed in that area. No data were obtained on how long individuals of this species remained as members of a particular group, although limited data on this question were obtained for other species (see below). At Palau, multi-individual groups comprised a male plus one or more smaller females (Robertson, in preparation). At Aldabra, the composition of territorial groups was more variable, in terms of both the number of fish of each sex and their relative sizes (Robertson et al. 1979). Most adults at Palau were territorial, although nonterritorial and weakly territorial fish were numerous in a few areas of shelter-poor habitat. In addition, schools of up to about 30 adults were occasionally seen feeding on the upper reef slope during low tides, when they may have been driven from intertidal areas by lowered water levels. Both territorial and nonterritorial fish were common at Aldabra. Strongly territorial fish excluded conspecifics (other than members of the same group) from their feeding areas, and excluded or attempted to exclude other surgeonfishes that fed on the same types of algae as they (e.g., *A. triostegus*, *Z. scopas*).

At Aldabra, pair spawning was observed on five days during November and December. It occurred during afternoon ebb tides, in the first two or three hours after the tide had turned. During those spawning periods, fish moved from intertidal areas down onto the reef slope at depths of 5–7 m. Group spawning was observed on one occasion in a large aggregation of fish that formed at the mouth of Passe Dubois, which is one of the channels that drain the Aldabra lagoon. That channel mouth was about 2 km from the main study area.

The *A. nigrofuscus* migrated from distances of up to at least 300 m to that spawning site. There they formed a loose aggregation of several thousand individuals that milled about in an area of approximately 0.25 ha, 2–3.5 h after high tide. The substrate in this area, which was in about 5 m of water, consisted of a scattering of boulders on a sand and rubble bottom. Clusters of fish in this aggregation performed group spawnings over a period of at least 45 min, beginning at 1230 h. Those spawnings tended to be pulsed, with periods of activity by the whole aggregation of fish that lasted for up to 20 seconds interspersed with periods of inactivity of several minutes.

Spawning by *A. nigrofuscus* was observed on over

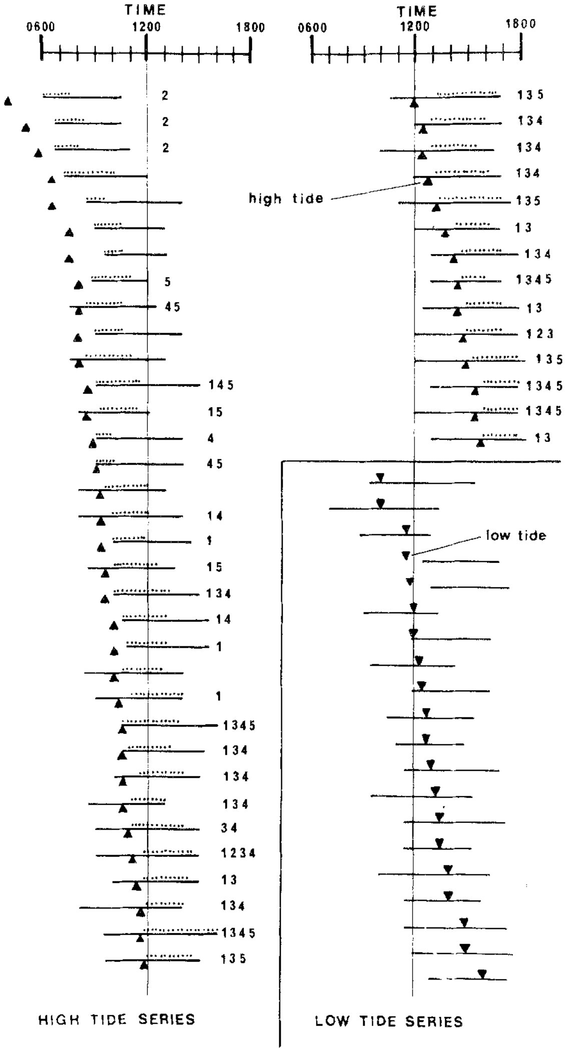

Fig. 3. Spawning activity of surgeonfishes at Palau during ebb tides at different times of the day. Observation of spawning on a particular day by a particular species is indicated by its number: 1 = *A. nigrofuscus*, 2 = *A. lineatus*, 3 = *C. striatus*, 4 = *Z. scopas*, 5 = *Z. veliferum*. Each triangle marks the time of the high or low tide (defined as the middle of slack water). Each horizontal line indicates the period over which observations were made. Each dotted line indicates the period during which spawning by surgeonfishes and labroid fishes was observed.

a dozen days at Lizard Island. On one day at North Point, the fish moved from inshore areas onto the outermost tip of a shallow (less than 2 m depth) spur of reef that jutted out from the general line of the reef edge. The reef face dropped abruptly into 15 m of water at the edge of this spur. A milling aggregation of several hundred fish formed at this spur tip between 1500–1600 h, when an along-reef current was running. Six pulses of group spawnings by the aggregation were observed. Each pulse lasted about 15 seconds and consisted of 1–2 dozen separate group spawnings. The fish moved several meters off the edge of the reef during each pulse, then rushed back to the substrate in the shallows as soon as it ended. A small (ca. 1.3 m total length) carcharinid shark attacked the *A. nigrofuscus* during one of these spawning pulses, rushing up into the mass of fish, then coming to a halt and biting rapidly and repeatedly at them. The shark's activity did not appear to noticeably disrupt the spawning pulse and after the attack commenced the fish continued spawning for several seconds before they returned to the reef. On two days pair and group spawnings were observed between 1600–1730 h at the outer edge of the fringing reef near South Island. These spawnings began 2–3 h before high tide. The current flowed along-reef on both occasions. At the Macgillivray Reef site, group spawning was only observed between 1500–1700 h; it occurred during both flood tides (n = 3) and ebb tides (n = 6) on the subtidal reef slope.

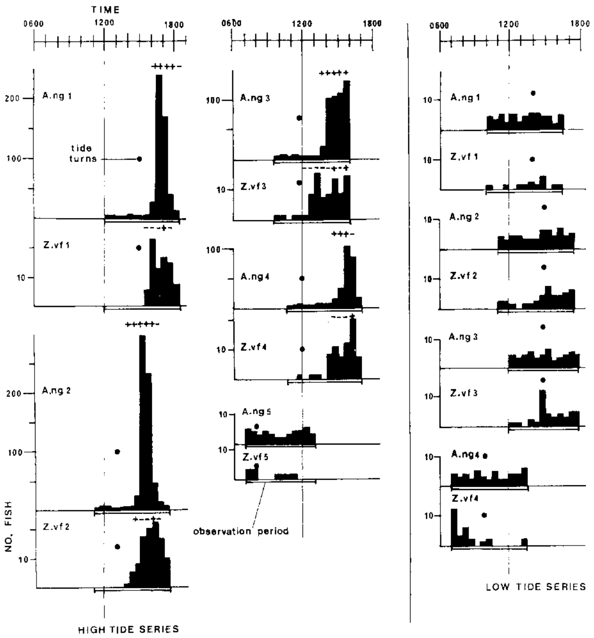

Fig. 4. Formation of spawning aggregations of two surgeonfishes at the reef edge at Palau. The numbers of individuals counted at 30-minute intervals in a 500-m^2 study area are shown. A.ng. = *A. nigrofuscus*, Z.vf. = *Z. veliferum*. Each horizontal bar indicates a complete observation period; ● tide turns = middle of slack water; + = spawning observed during 30-minute interval, ▬ = courtship observed, but not spawning.

Table 2. Amounts of ebb-tide spawning activity by three surgeonfishes when high tide occurred at different times of the day at Palau.

Hour during which high tide occurred	Number of days on which different amounts[1] of spawning activity were observed								
	Acanthurus nigrofuscus			*Acanthurus lineatus*			*Ctenochaetus striatus*		
	–	+	++	–	+	++	–	+	++
<0600	4	0	0	0	0	3	4	0	0
0600–0700	2	0	0	2	0	0	2	0	0
0700–0800	2	0	0	2	0	0	2	0	0
0800–0900	7	2	0	9	0	0	9	0	0
0900–1000	1	4	0	5	0	0	4	1	0
1000–1100	3	6	0	9	0	0	4	5	0
1100–1200	0	2	4	5	1	0	0	6	0
1200–1300	0	1	5	6	0	0	0	3	3
1300–1400	0	0	3	3	0	0	0	0	3
1400–1500	0	1	5	5	1	0	0	0	6
1500–1600	0	0	3	3	0	0	0	0	3
1600–1700	0	0	2	2	0	0	0	0	2

[1] Amounts of spawning: – = nothing, + = a few pair or group spawnings, + + = massed group-spawning activity.

At Palau, *A. nigrofuscus* spawned only during ebb tides, 1–4 h after the tide had turned. No spawning occurred on early morning ebb tides and the amount of activity per tide gradually increased as the time of the high tide advanced through the day. The greatest amounts of spawning occurred during mid to late afternoon ebb tides (Figs. 3, 4, Table 2). This afternoon spawning activity was observed during a 5–7 day period that ended 2–4 days before the full and new moons (Fig. 5). On those days of peak spawning, the height of the high tide usually was less than the mean height of high

Table 3. Tidal amplitudes[1] and heights of high tides on days of peak spawning activity[2] by *Acanthurus nigrofuscus* and *Ctenochaetus striatus.*

	Number of days tide was $<\bar{x}$ value of tides for each tide series[3]		Number of days tide was $>\bar{x}$ value of tides for each tide series[3]
High tide height	28	*	4
Tidal amplitude	19	NS	13

[1] Tidal amplitude = height of high tide – height of subsequent low tide.

[2] Peak spawning days = last 4 days of each of eight series of days on which high tide occurred during the day (see Fig. 5). Although not all 32 days were sampled, mass spawning was observed on all 21 days that were sampled.

[3] Tide series = each of eight series of daytime high tides (see Fig. 5).

X^2, $* = P<0.01$, NS = not significant.

tides on other days, although tidal amplitudes (the difference between the height of each high tide and subsequent low tide) typically were neither greater nor less than the mean amplitude of tides on other days (Table 3). During those afternoon spawning periods, large numbers of fish migrated to the outer reef edge from more inshore areas and aggregated there 1.5–4 h after the high tide (Fig. 4). Those migrating fish moved in distinct streams a few meters wide between the reef edge and areas as much as 400 m in from the reef edge. As at Aldabra and Lizard Island, group spawning activity in the large aggregations of Palauan fish occurred in pulses of up to several scores of spawnings.

At Palau, pair spawnings were observed in both subtidal areas down to depths of 8 m and intertidal areas as much as 150 m in from the outer reef edge. Group spawnings essentially were restricted to the upper reef slope within about 20 m of the outer edge (Fig. 5). All of the pair spawnings at Palau involved a territorial male that either held a feeding territory by itself or with one or more females. Prior to each of eight pair spawnings, the pair was observed for up to 20 minutes and for 10 minutes after it. Each of those eight pairs spawned above its jointly defended feeding territory. In addition, some males evidently were setting up temporary pair-spawning territories at the outer reef, although no spawnings by such individuals were observed. Those territories were occupied only for the duration of a spawning period.

Zooplanktivorous fishes that commonly fed on the freshly spawned eggs of wrasses and parrotfishes at Palau (Robertson & Foster, in prepara-

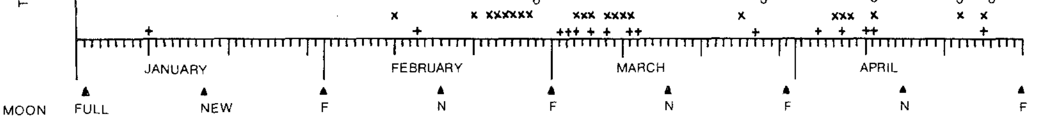

Fig. 5. Spawning of surgeonfishes at Palau in relation to the lunar cycle and different tidal heights/amplitudes. The observation of spawning by a species on a particular day is indicated by its symbol (lack of a symbol on any day does not necessarily mean that observations were made and that no spawning was seen). Bar labelled 'afternoon high tides' refers to days on which massed spawning by *A. nigrofuscus* and *C. striatus* was observed (or would be expected to occur) during the afternoon. In each of the eight complete series of tides, the height of high tides that occurred between 0530 and 1700 are shown, as well as the tidal amplitude (= difference between a high tide and the subsequent low tide). Times of full and new moons are indicated by triangles. Data on tides are from tide tables, Office of the District Administrator, Koror.

Table 4. Levels of attack by egg predators on pair and group spawnings of surgeonfishes immediately after the spawning act, at Palau.

Species spawning	Percentage of gamete clouds attacked by zooplanktivorous fishes[1]	
	Pair mating (n)	Group mating[2] (n)
Acanthurus nigrofuscus	4.0 (25)*	42.2 (718)
Ctenochaetus striatus	4.9 (123)*	27.1 (240)
Zebrasoma scopas	5.7 (53)	no data
Zebrasoma veliferum	0 (19)	no data

[1] These included the following: Pomacentridae – *Abudefduf saxatilis, Chromis caerulea, C. atripectoralis, Ambliglyphidodon curacao*; Labridae – *Thalassoma hardwicki, T. amblycephalus*; Lutjanidae – *Caesio coerulaureus, C. erythrogaster, C. lunaris, Pterocaesio chrysozonus*; Scombridae – *Rastrelliger kanagurta*; Balistidae – *Melichthys vidua*; Exocoetidae – one unidentified hemiramphine; Dussumieridae – at least one unidentified species.
[2] A group mating has ≥ 4 participants.
X^2, * = $P<0.01$.

tion) often attacked freshly spawned ova of *A. nigrofuscus*, and group released products of this species were attacked more often than were pair released gametes (Table 4). Spawning fishes were themselves attacked by piscivorous fishes. Attacks were observed on group spawning *A. nigrofuscus* by the following piscivores: *Carcharinus melanopterus, Cephalopholis argus, Caranx melampygus, Lutjanus bohar* and an unidentified belonid. No attacks by the spawning *A. nigrofuscus* on either egg predators or piscivores were observed.

The sexual identities of participants in pair spawnings were established from their relative sizes, the relative size of males and females in territorial groups having been determined by collection of specimens (Robertson, unpublished data). The identities of the sexes in group spawnings were determined by the collection of eight males and three females at Palau. I observed 25 pair spawnings and several hundred separate group spawnings at Aldabra, 21 pair spawnings and several thousand separate group spawnings at Palau, and 6 pair spawnings and 100–200 separate group spawnings at Lizard Island. Unlike the situation in *C. striatus*, and the two *Zebrasoma* spp. (see below), I saw no cases of a second male participating in the pair spawning of a territorial male *A. nigrofuscus*.

A pair-spawning male begins courtship by making a series of rapid approaches to the female. Each approach ends with him swimming rapidly about very near her while spreading his median fins and twitching his body from side to side. Frequently he rushes rapidly up and down in the water column in the same manner as during the spawning rush. A female begins responding by ceasing to feed and slowly rising a few cm above the substrate and staying there for a few seconds. The male responds to this rising by making further approaches and displays. Bouts of this combined activity increase in frequency and duration until eventually the female starts to rise vertically with her head up. The male responds by rushing to her side and the two make a rapid vertical dart up for about 1 m, then dart back to the substrate, separating as they go. Mating occurs at the peak of this rush, which may be 2–3 m above the substrate. Immediately following the mating, the male often rushes about the female and displays further to her in the manner described above.

No color changes were noted among the females during the courtship and pair spawnings observed at Palau and Lizard Island. Males typically underwent a distinct color change when courting and pair spawning, although the extent to which they developed this color change varied considerably and spawnings were seen in which almost no change from the normal pattern was observed. The color pattern developed by pair-spawning males took the following form during courtship (Fig. 6). The body was slightly paler than normal, and the cheeks and throat and pelvic and anal fins were very pale grey. The fish's dorsal and caudal fins were the same color as its body (Fig. 6). In more extreme cases, the iris became very pale and facial paling spread backwards behind the pectoral fin, and the tail, dorsal fin, and top of the back paled also (Fig. 6). The most characteristic part of this color change was the paling of the face, throat, and pelvic fins.

Group spawning involved a different set of movements and color changes to those in pair spawning, especially by the male. In a large aggregation of fish

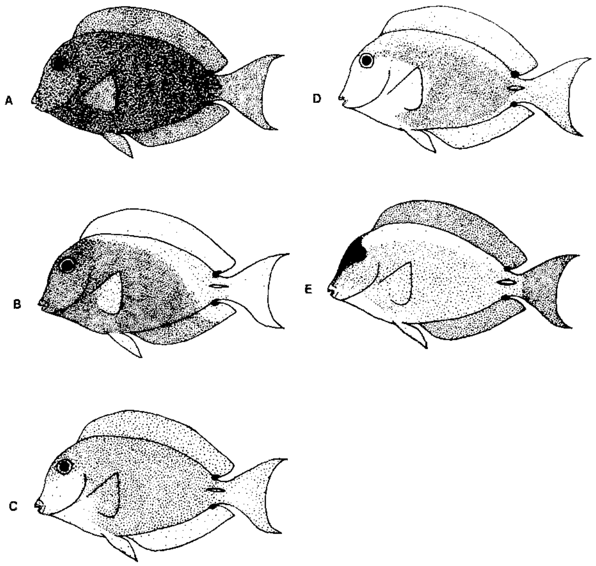

Fig. 6. Color patterns of *Acanthurus nigrofuscus.* A = normal dark-phase pattern; B = pattern of aggressive fish; C = moderate development of pattern of pair-spawning territorial male; D = extreme development of pattern of pair-spawning male; E = pattern of group-spawning, nonterritorial male.

that were milling about up to several meters off the bottom, a group of males with their median fins somewhat spread would be seen closely and persistently following a female, clustering against her and behind her and rubbing themselves against her. The female's response varied. Sometimes she attempted to elude the males, at other times she came to a halt and rose slowly up until she was 1–2 m above the substrate. This rising led to a tightening of the cluster of fish, with the female at the center-front. This rising cluster sometimes broke up and returned to the substrate and, at other times, made a series of short, hesitant upward movements followed by a nearly vertical rush for 1–2 m. These upward rushes often terminated within 1 m of the surface, as much as 4–5 m above the substrate. At the peak of the rush, milt was released as the fish abruptly turned and rushed back down, separating as they went. The cloud of milt released during group spawning was larger, more noticeable and more persistant than that released during pair spawning. Group spawnings typically had about 6–15 participants. During pulses of group spawning, the first spawnings took the form described above. Later spawnings often consisted of fish that were milling about erratically in midwater beginning to rise more or less independently, then rushing together from as much as several meters apart and making a mating rush.

Prior to and during group spawnings, males often developed a distinctive color pattern that was different to that exhibited by pair-spawning males. At its most extreme, the pattern took the following form (Fig. 6). Most of the body and face was colored more or less as normal. The eyes, a small area around them, and a stripe along the center of the nose of the fish to the anterior base of the dorsal fin were almost black. The belly and pelvic fins were pale grey. Sometimes the inner two-thirds of the anal fin also paled. The top of the body, from above the eyes backwards, was very pale grey. The most distinctive elements of this color pattern were the pale back and dark facial mask. The intensity to which group-spawning males developed this pattern varied considerably. Females did not change color in any readily recognizable manner while males were clustering about them preparatory to group spawning. However, as they rose and began to start the spawning rush, females sometimes weakly developed the pale area on the top of the back that group-spawning males developed so characteristically.

Territorial fish that were attacking conspecifics often did not change color in any readily noticeable manner. However, paling of the face and chest was evident in aggressive pair-spawning males. At Lizard Island I frequently observed sexually inactive fish involved in aggressive interactions. When attacking unresisting intruders, such territorial individuals usually developed pale tails and/or dorsal fins. When attacking fishes (of other species as well as conspecifics) which aggressively resisted such attacks, the territorial fish's dorsal fin and tail, and pelvic fins paled markedly, as did the posterior part of the anal fin, the caudal peduncle and back (Fig. 6). In extreme cases of such paling, the iris also became pale.

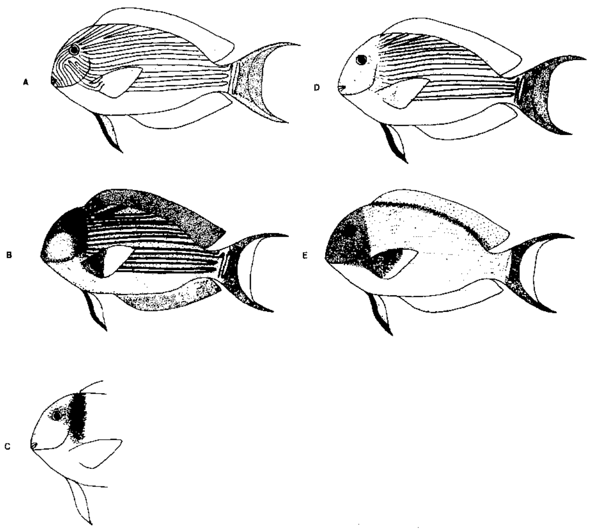

Fig. 7. Color patterns of *Acanthurus lineatus.* A = normal pattern; B = pattern of aggregating, weakly aggressive fish; C = head pattern of fish fighting with an aggressively resisting conspecific; D = pattern of fish chasing unresisting intruder from its territory; E = pattern of group-spawning fish.

Acanthurus lineatus

Acanthurus lineatus is a moderately large member of its genus. It achieved about the same maximum size at Aldabra and Palau (Table 1). This species' normal color pattern is complex. While it appears bright and conspicuous when the fish is close to the observer, it gradually blends into the substrate as the distance between fish and observer increases. The body is yellowish. There are about 10 blue-centered black stripes that run from the face along the upper two-thirds of the body and continue onto the base of the dorsal fin. The iris is gold. The belly is pale bluish-grey with a yellow-orange tint ventrally. The dorsal and anal fins are bluish grey, while the pelvic fins are orange with a black leading edge. The pectoral fin has an orange inner half with several blue stripes, while the outer half is hyaline. The tail has a dark grey center and pale grey upper and lower edges (Fig. 7). Overall, the head is paler than the body. The fish has considerable powers of rapid color change. At both Aldabra and Palau the diet of *A. lineatus* consisted largely of small, fleshy, red algae that grew in a turf on dead coral substrates (Robertson 1981a).

At both Aldabra and Palau this species was restricted to the interface between intertidal and subtidal sections of the reef (Figs. 1, 2). It lived in the same types of areas at other sites where I have seen it – Lizard Island, Escape Reef, Heron Island (on the southern part of the Australian Great Barrier Reef), and at Guam (Mariana Islands, western Pacific.

Adults of both sexes at Aldabra and at Palau defended feeding territories, invariably as single individuals (Robertson et al. 1979, Robertson, in preparation). At both sites virtually all adults appeared to be territorial, although a few nonterritorial fish were detected at Aldabra (Robertson et al. 1979). Fish also defended territories singly at Heron Island, Lizard Island, and Guam. At both Aldabra and Palau the territories of this species were aggregated in colonies (Robertson et al. 1979). At both those sites, territories were defended against a large range of herbivorous fishes that fed on benthic algae—acanthurids, siganids, scarids, and balistids (Robertson et al. 1979, Robertson 1981a).

Spawning by *A. lineatus* was observed at Palau on five days during February-April and on one day at Escape Reef. At Palau, all spawnings occurred during the first 1–3 h of ebb tides. We observed over 150 early morning group spawnings, which all occurred between 0550–0655 h on days when the high tide was earlier than 0600 h. All of those days were shortly before full moon. Johannes (1981) observed *A. lineatus* spawning at another site around 0700 h at new moon. In addition, I observed two group spawnings during a midday ebb tide and a single pair spawning during a midafternoon ebb tide (Fig. 3, Table 1). Courtship, on the other hand, occurred during ebb tides at various times of the day—it was noted on 18 ebb tides that began ebbing anywhere from midmorning to late afternoon. High tides that would allow spawning before 0700 h during the first half of an ebb tide occurred over a 3–5 day period that ended 1–2 days before new and full moons (tide information from Koror Tide Tables).

On each of the three days in which early morning spawning was observed, the height of the high tide was less then the mean height of high tides of the daytime series of high tides that followed that day. In addition, the tidal amplitude on each of those three days was less than the amplitude of all daytime tides of the series that followed it (see Fig. 5 for tide series).

All of the spawnings that I observed took place above or within 15 m of colonies of *A. lineatus* at the outer edge of the reef (see Fig. 2). Spawning activity occurred in water 3–7 m deep, on the upper reef slope and shallow part of the lower slope. At the site where the spawnings were observed, colonies of *A. lineatus* were scattered along both the inner and outer parts of the upper reef slope. Because of the large numbers of fish milling about above the colony area during the spawning periods, I suspect that fish were migrating from the inshore colonies to the outer colonies to spawn at the outer edge.

In each of the three early morning spawning periods, spawning activity was pulsed, i.e., there were short bouts of high levels of activity separated by relatively long periods of inactivity. I defined a pulse as two or more matings that were separated by no more than 5 seconds. Of 120 early morning spawnings, 16.7% were not in pulses, 15.8% were in pulses of 2–5 matings, 11.7% were in pulses of 6–10, and 55.8% occurred in pulses of 11–20 acts. All of the matings in the large pulses occurred within a total of 10–15 seconds.

Group spawnings of *A. lineatus* were attacked by some of the egg predators listed in Table 2. I did not see any attacks on those egg predators by the spawning fish or attacks by piscivores on the spawning fish.

The single *A. lineatus* pair spawning that I saw at Palau took the following form. For about 10 minutes before the mating, the (presumed) female intermittently moved up 0.5–1 m from the substrate and hung there in the water column for half a minute or so. The male moved around in the water about half a meter above her while frequently making short upward movements accompanied by short bursts of lateral jerking of his tail and abrupt lowerings of his pelvic fins. This behavior was similar to that of male *C. striatus*. Eventually the female adopted a head-up attitude, started to move up further, then rapidly increased speed as the male rushed to her side from 1–2 m away. The pair rushed vertically up for 1–2 m, then abruptly turned and darted back to the bottom, separating as they went. Milt was produced at the top of the rush, about 3 m above the bottom. Prior to this mating both male and female changed color in the same manner, although the change was slightly more pronounced in the male.

Group spawning was preceded by the fish moving up off the substrate and swimming rapidly about in a milling mass in the upper levels of the water column. They individually began moving up to the water's surface and down again in sweeping curves. Bouts of this curving gradually increased in frequency and velocity and led into spawning. In a mating, a group of 4–10 fish that were scattered about as much as 3–5 m apart in midwater rushed together in a rising movement that led into a vertical rush of 0.5–1 m. The rush terminated at or just below the water's surface, in water depths of 3–7 m. Then the fish abruptly turned and swam rapidly back down to midwater, separating as they went. A cloud of milt was released at the apex of the rush.

The male and female involved in each pair spawning had contiguous territories that were located at the seaward edges of colonies. Each pair spawning took place above the territories of the two fish. Two group spawnings and one pair spawning were seen at Escape Reef, between 1600–1700 h at the seaward edge of the reef when water was flowing off the reef out to sea. These spawnings took the same form as spawning seen at Palau. As the species was abundant at the Escape Reef site, the spawnings represented very low-level activity by that population.

Acanthurus lineatus undergoes a variety of color changes during social interactions (Fig. 7). A territory holder that is chasing unresisting intruders develops a pale head and dark tail. The iris is bright. The black of the body stripes deepens, the blue of these stripes brightens, and the dorsal and anal fins and base of the pectoral fin darken. Milling aggregations of up to a dozen weakly aggressive fish sometimes form in *A. lineatus* colonies, particularly when a territory vacancy is being contested. A fish in one of these aggregations develops a very dark head with a pale cheek. The ground color of the body darkens, the black of the body stripes thicken and darken and the blue centers of the stripes brighten. The dorsal and anal fins darken considerably. The tail darkens basally and on the upper and lower lobes, and its center pales. The inner half of the pectoral fin turns very dark and the iris also darkens (Fig. 7). A strongly aggressive fish that is fighting with an aggressively resisting conspecific develops the same body and fin colors as a milling fish but a different head color. The shoulder bears a broad, very dark bar. This darkening extends forward around the eye, but is not as intense as in the shoulder bar. The nose and forehead are slightly darker than normal and the iris is bright (Fig. 7). Detailed observations were made on color change by only one set of pair-spawning fish (although the other pair did not develop colors like those of group spawners; see below). Both fish developed darkening of the eyes and a small surrounding area, mainly in front of the eye. Slight darkening of the dorsal and anal fins, and of the base and lobes of the tail also occurred. At Lizard Island, fish were often observed behaving in the same manner as the males did before pair spawning, and those fish displayed the same color pattern as the pair spawners. As far as I could tell, all participants in group spawning activity developed the same very distinctive color pattern. This pattern was displayed by both the rising and curving fish and the spawners. The fish's body and anal fin became extremely pale, the stripes on the body having almost disappeared. The head and inner two-thirds of the pectoral fin turned almost black, as did the inner third of the dorsal fin and the base and filaments of the tail (Fig. 7).

Acanthurus triostegus

Acanthurus triostegus is a medium-sized *Acanthurus* species (Table 1). Normally, a member of this species has a pale grey-green body with a white belly and pale grey-green fins. There are five strongly delineated black bars on the head and body and two black dots on the caudal peduncle (Fig. 8). At Aldabra this species' diet consisted of small fleshy microalgae (Robertson & Gaines, unpublished data).

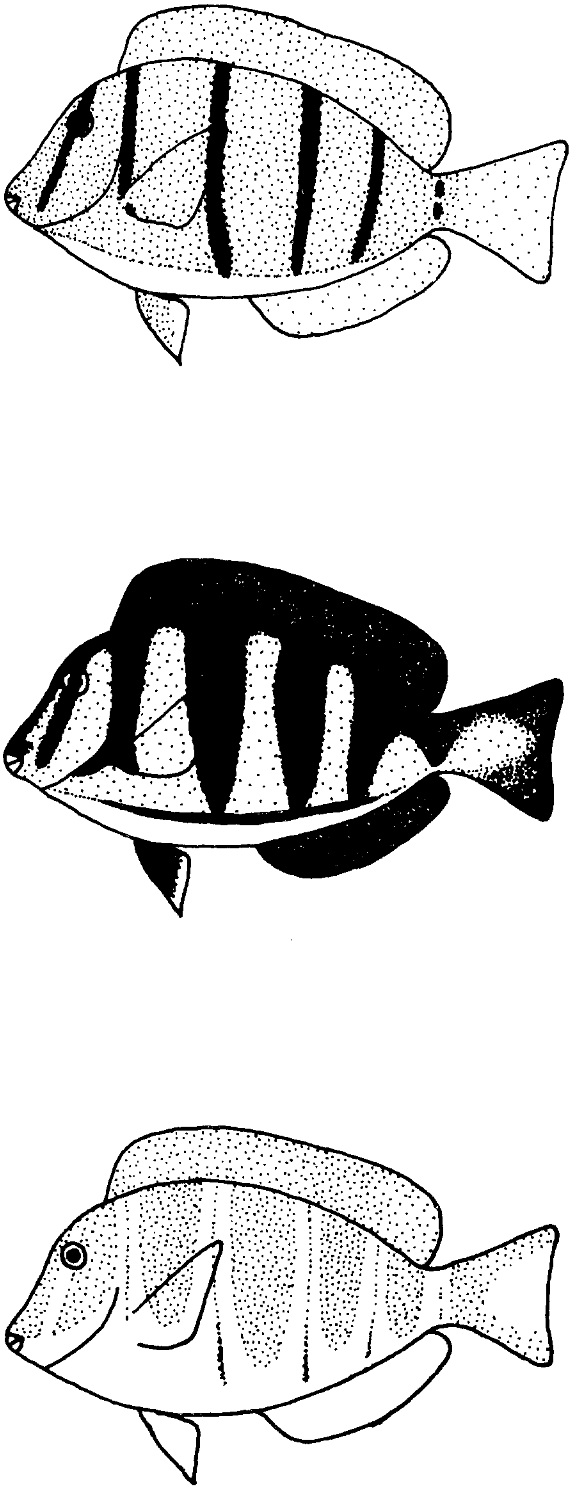

Fig. 8. Color patterns of *Acanthurus triostegus*. Upper = normal pattern; middle = pattern developed by group-spawning males; lower = pattern developed by aggressive territorial fish.

At Aldabra, *A. triostegus* was abundant and widely distributed through intertidal and shallow subtidal areas (Fig. 1). *Acanthurus triostegus* was not abundant at Palau, where it was restricted to the intertidal reef crest (Fig. 2).

At Aldabra three different social classes of fish were observed. First, many fish in both intertidal and subtidal areas were territorial and defended feeding areas against conspecifics. Territories were defended either by single males or by groups of up to six fish. There was no regular pattern apparent of group composition in terms of sexual makeup and relative size of the sexes (Robertson et al. 1979). Second, single nonterritorial fish fed in intertidal areas. Third, large schools of up to 1,000 or more adults of both sexes roamed through subtidal areas feeding in the territories of other species of surgeonfishes (Robertson et al. 1979). Membership in one of these social classes was not an all or none phenomenon, because tagged territorial fish were regularly observed to intermittently abandon their feeding territories and join feeding schools.

Spawning of this species was observed only at Aldabra, on four days during November and December. It was recorded during ebb tides that occurred between midday and dusk. On one occasion, a group of eight fish in the subtidal portion of the main study area group-mated four times and two of them pair mated once. On the other three occasions, mass spawning activity was observed at the mouth of Passe Dubois, at the same site as mass spawning by *A. nigrofuscus* was seen (see above). On the day that spawning by *A. nigrofuscus* was observed, spawning by *A. triostegus* occurred concurrently. The *A. triostegus* migrated to the Passe Dubois site from distances of up to at least 2 km. Fish that migrated from the vicinity of the main study area moved in a dense, 5–10-m-wide stream, along the intertidal rubble bank adjacent to the reef crest (see Fig. 1). On the day that I saw the greatest numbers of fish at the spawning ground that must have been several tens of thousands of fish in an area of about 0.25 ha. Group spawning activity in those large aggregations occurred in pulses, and the entire aggregation often engaged in repeated group matings for 5–10 seconds. Individual group spawnings in this aggregation typically involved 10–20 fish. I observed attacks on members of the spawning aggregation by *Caranx melampygus* and several unidentified species of groupers.

The single pair spawning observed took the following form. The pair rose up about 2 m in the water column with the (presumed) male repeatedly approaching the female. These approaches ended with the male making a short upward movement while twitching his tail laterally and dropping his pelvic fins. After a series of such approaches, the male came up against the shoulder of the female and the two rushed up at a 60° angle, for about 1.5 m, then abruptly turned and separately darted back down. Milt was released at the turning point of the rush, about 6 m above the substrate. The female of this pair had normal coloration while the bars on the body of the male were a little more intensely colored than usual.

Group spawnings by *A. triostegus*, of which perhaps a thousand were seen, took essentially the same form as those of *A. nigrofuscus*. Milt was released at the peak of the spawning rush within 1 m of (and often right at) the water's surface. Water depth at the spawning ground was 5–7 m. Males of *A. triostegus* undergo a distinct color change prior to and during group spawning. The vertical bars on the body and face darken and thicken while the dorsal, anal, pelvic and caudal fins become blackened (Fig. 8). Randall (1961a) described such a color pattern by group-spawning males in the Taumotu Archipelago. This color pattern is radically different to that developed by territorial fish (of both sexes) at Aldabra and at Randall's (1961a) site. Territorial fish undergo a partial reversal of the normal color pattern, especially when aggressively active. The dark vertical bars become very pale while the spaces between those bars darken a little (Fig. 8).

Ctenochaetus striatus

Ctenochaetus striatus is a surgeonfish of moderate size (Table 1). When socially inactive the fish is uniformly and drably colored in medium to dark grey-brown, and has some faint light-colored spots on the face (Fig. 9). Its diet consisted of sediment and detritus (Robertson & Gaines, unpublished data).

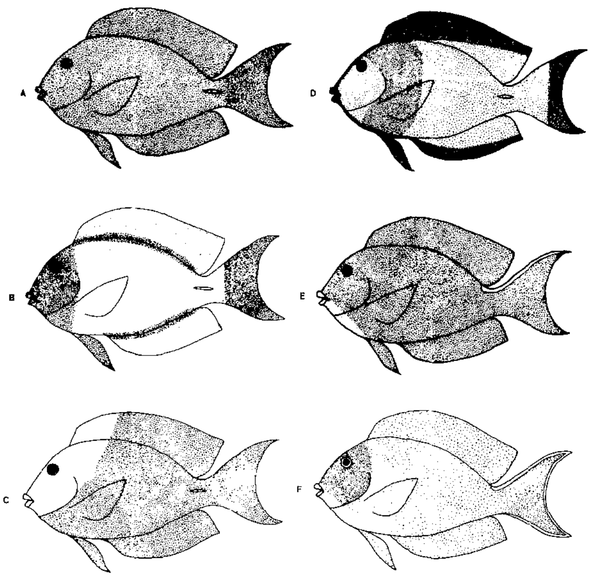

Fig. 9. Color patterns of *Ctenochaetus striatus.* A = normal pattern; B = pattern of fish chasing unresisting intruder from its territory; C = pattern of fish fighting with a resisting conspecific; D = pattern of group-spawning males; E = moderate development of pattern of pair-spawning male; F = extreme development of pattern of pair-spawning male.

At Aldabra this species was restricted to shallow subtidal areas (Fig. 1), while at Palau it was distributed throughout both intertidal and subtidal zones (Fig. 2). At the latter site, it probably was the most abundant surgeonfish present.

At both Aldabra and Palau, adults of *C. striatus* often defended feeding territories, either singly or in groups of up to six fish. These multi-individual groups contained a single male and one or more smaller females (Robertson et al. 1979). Territories were defended against conspecifics, other congeners, other detritivorous surgeonfishes (*Acanthurus tennenti, A. nigrocaudus*) and parrotfishes. In addition, nonterritorial and weakly territorial fish were seen at Aldabra and Palau.

I saw spawning at Aldabra on 11 days during August-December. These occurred between 0900–1900 h during ebb tides, 2–3.5 h after the tide had turned. Pair spawning was noted on all those days, while group spawning was seen only during five late-afternoon ebb tides. Spawning occurred on the reef slope where this species had its feeding grounds.

At Lizard Island, pair spawning of *C. striatus* occurred concurrently with *A. nigrofuscus* spawning at the North Point site. At Macgillivray Reef, *C. striatus* feeding areas were restricted to intertidal areas and subtidal areas within 15 m of the intertidal (Robertson, unpublished data). Beginning at about 1400 h, males moved from these feeding areas down to the base of the reef slope, in about 7 m depth of water about 50 m out from the intertidal area, where they set up temporary spawning territories. Pair and group spawning occurred in and near those territories from about 1500 h onwards and sexual activity was not seen before 1400 h. Spawning occurred during both ebb tides (n = 9) and flood tides (n = 3) on all days that I visited that spawning ground.

Spawning was observed frequently at Palau, during all months of the study period. It only occurred on ebb tides and was restricted to afternoon ebb tides. The greatest amounts of spawning occurred during mid- to late afternoon ebb tides (Fig. 3, Table 2). This afternoon spawning activity occurred during the same 4–7 day period prior to the full and new moon as the peak of spawning by *A. nigrofuscus* occurred in (Fig. 5), although it peaked a day or two later than that of *A. nigrofuscus* (Table 2). During these afternoon spawning periods, thousands of fish migrated from inner reef areas and aggregated along the outermost 25 m of the upper reef slope (Fig. 2), where they group spawned en masse. Group-spawning activity in these large aggregations was pulsed in the same way as in aggregations of *A. nigrofuscus*, *A. lineatus*, and *A. triostegus*.

Except at Macgillivray Reef, all of the pair spawnings that I saw appeared to involve territorial males and the females of each male's group. At Palau, 15 different pairs of fish were each observed for up to 10 minutes prior to their pair mating and for 5 minutes afterwards. Each of those pairs fed together in a shared feeding territory before and after the spawning and mated in the water column immediately above that territory. Similar observations were made on 12 pairs (including one tagged pair) at Aldabra, with the same results. As well as fish that had migrated from inshore areas, group spawning aggregations at the reef edge in

Palau also contained males and females from territorial groups that were resident in the areas where the aggregations formed.

Zooplanktivorous fishes commonly attacked fresh gametes of *C. striatus* at Palau and group spawnings suffered higher rates of such predation than did pair spawnings (Table 4). Also, fish that were spawning there were attacked by at least one piscivorous fish, *Caranx melampygus.* I did not observe any attacks by the spawning *C. striatus* on the egg predators or piscivores.

I observed 40 pair matings and over 35 group matings by *C. striatus* at Aldabra, over 120 pair matings and thousands of separate group matings at Palau, and over 30 pair matings and several dozen group matings at Lizard Island. The identity of the sexes in pair matings was established by the collection of fish in territorial groups at Aldabra and Palau. Group-spawning males developed a specific color pattern (see below) that Randall (1961b) described. I confirmed this by spearing seven and eight males bearing this color pattern at Aldabra and Palau, respectively. At Palau, two fish that were thought to be females had their identities confirmed when I speared them.

Sexual interactions that culminated in pair spawning by *C. striatus* took the following form. The first indications were the male, initially alone but later followed by the female, rising up slowly a meter or two in the water and hanging there for a minute or two. After the female had risen, she would remain hanging in midwater for a few seconds and then go down to the substrate and resume feeding. These bouts of rising gradually increased in frequency and duration and the male began making approaches to the female, approaches that ended with him coming to a halt a little above her and making an abrupt rising movement for 10–15 cm, during which he raised his head, (laterally) twitched the rear portion of his body and momentarily spread his pelvic and unpaired fins. Occasionally he also circled, by rapid pectoral-fin sculling, round above the female, moving up and down in the water a little as he did so. The female usually responded to these male behaviors by rising further in the water. Eventually she lifted her head and began rising further, and started to accelerate as the male began to move rapidly towards her from up to several meters away. The two fish sped up as the male came up against the side of the female. Then they rushed vertically up for 1–2 m, abruptly turned and darted back to the substrate, separating as they went. Gametes were released at the peak of the rush, which was up to 5–6 m above the bottom.

While the pair was rising, neighboring territorial males often approached them. The male of the rising pair responded by driving away such intruders. Sometimes, an intruder darted to the pair as they began their mating rush and joined them, either as they released gametes or immediately afterwards. Wandering males that exhibited the male group-spawning color pattern (see below) also interfered in pair spawnings in this same manner. Secondary clouds of sperm were seen to be released by these interfering males. Such interference was observed at Aldabra and Lizard Island, and occurred in 24.8% of the pair matings seen at Palau.

Group spawnings in *C. striatus* had essentially the same form as those of *A. nigrofuscus* and *A. triostegus.*

Ctenochaetus striatus changed color in two quite different ways when being aggressive. Although fish that chased unresisting individuals sometimes did not change color, usually the body and outer two-thirds of the dorsal and anal fins turned pale caramel, and a pale blue-grey bar developed immediately behind the pectoral fin. The head, tail, and base of the dorsal and anal fins remained dark (Fig. 9). Fish that were fighting with equally aggressive conspecifics typically developed paling that covered the face and extended back onto the anterior part of the dorsal fin (Fig. 9). During interactions between the pair that led up to pair spawning, the male often, but not invariably, changed colors. In the pair spawnings seen at sites other than Macgillivray Reef the change was relatively slight: the male's lips and throat became very pale and a pale cream line developed along the top of his caudal peduncle and upper edge of his tail (Fig. 9). At Macgillivray Reef, pair-spawning males also developed the very pale mouth and throat; as well, the body and dorsal and anal fins turned paler than normal and the pale edging of the tail extended round the entire fin (Fig. 9). Females underwent no

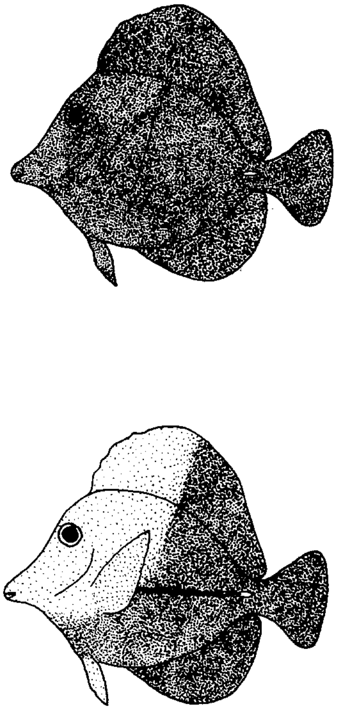

Fig. 10. Zebrasoma scopas. Upper = normal pattern; lower = pattern of a fish fighting with a resisting conspecific.

situation-specific color change during courtship and pair spawning and usually were of light to medium color. During group spawnings and the interactions that preceded them, males developed the following color pattern. The body and face became pale, except for a broad dark bar that ran down the body just behind the operculum. That bar varied in intensity and size and sometimes was absent. The outer edge of the body and face had a dark band around it and the pelvic fins and outer edges of the dorsal, anal and caudal fins were dark (Fig. 9, see also Randall 1961a). Females, on the other hand, did not appear to change color while engaging in group spawning.

Ctenochaetus strigosus

Ctenochaetus strigosus was observed only at Aldabra. It reached a considerably smaller size than *C. striatus* (Table 1). It was drably colored in the same manner as *C. striatus*. Those two species could readily be distinguished in the field because the tail is truncate in *C. strigosus* and lunate in *C. striatus*. The diets of these two species were essentially the same (Robertson and Gaines, unpublished data).

Ctenochaetus strigosus was restricted to the subtidal portion of the study area, and extended into deeper areas than did *C. striatus* (Fig. 1). *C. strigosus* defended feeding territories. Groups composed of a male and 1–3 smaller females defended jointly used feeding areas (Robertson et al. 1979). Those feeding areas were defended against conspecifics and *C. striatus*, although some sharing of feeding areas between the two *Ctenochaetus* species was also noted.

Spawning was observed during ebb tides on three days in August. It occurred between 0900–1600 h, at depths of 6–8 m on the reef slope where the species had its feeding areas. A total of 12 pair matings were observed and I never saw any activity that suggested that group matings might also occur. At least seven of these pair spawnings involved a male and one of the females that he shared a feeding territory with—in each of those seven cases, the pair was observed for 10 minutes after the spawning and they resumed feeding together in a territory immediately below the spawning site.

Interactions between the male and female *C. strigosus* that culminated in pair mating took essentially the same form as those in *C. striatus*. Gametes were released 4–6 m above the substrate. No color changes by either the male or female *C. strigosus* were observed during those pair-spawning interactions.

Zebrasoma scopas

Zebrasoma scopas is one of the smaller surgeonfishes. Fish at Palau achieved a smaller size than those at Aldabra (Table 1). Usually it has a dull black-brown body, although the head is sometimes paler than the rest of the body. All fins are the same color as the body, except the pectoral which is dull reddish-brown. The iris is a dull red-brown. The caudal spine is white (Fig. 10). At Aldabra and Palau, *Z. scopas*' diet consisted of fleshy benthic microalgae, principally reds (Robertson & Gaines, unpublished data).

At Aldabra this species was restricted to the subtidal reef slope (Fig. 1), while it was widespread throughout intertidal and subtidal areas at Palau (Fig. 2).

At both Aldabra and Palau, adults defended feeding territories against conspecifics, *Z. veliferum* and several *Acanthurus* spp., including *A. nigrofuscus* and *A. triostegus*. At Aldabra all territories were occupied by groups of 2–3 fish while those at Palau were defended by 1–4 fish. Multi-individual groups at both sites consisted of a male and one or more smaller females (Robertson et al. 1979, Robertson, in preparation). Single territorial fish at Palau were of both sexes (Robertson, unpublished data). All fish at Aldabra were territorial. At Palau, nonterritorial fish were seen in compact schools of 50–75 individuals that fed in intertidal areas. Adult males and females can easily be distinguished in this species because males alone possess an elongate patch of short, dense bristles immediately in front of the caudal spine. Using this characteristic, I estimated that three schools of *Z. scopas* each contained at least 80% males.

Spawning was observed at Aldabra on nine days during August-December. All of the 18 matings seen were pair matings. They were seen on ebb tides, between 1100–1800 h. Two of the matings were between members of two tagged pairs that each defended a joint territory. Subsequent to each of another six matings, I followed the pair of fish for about 10 min. In each case they resumed feeding together in a territory immediately below the spawning site. All the spawnings were observed in subtidal habitat normally occupied by the species.

At Palau over 50 pair matings were recorded, as well as a single group spawning. Zooplanktivorous fishes attacked a small percentage of those pair spawnings at Palau (Table 4). No aggressive or predatory interactions were seen between sexually active *Z. scopas* and either zooplanktivores or piscivores. At least 15 of those pair spawnings were between members of (15 different) territorial groups, because the pairs were observed for about 10 min after spawning, and each resumed feeding together in a territory on the substrate directly below the spawning site. The pair matings occurred in subtidal areas down to depths of at least 10 m and in intertidal areas as much as 300 m in from the outer reef edge. The single group spawning took place about 20 m in from the outer reef edge. No large-scale spawning migrations by *Z. scopas* living inshore from the reef edge were evident. However, on one occasion I did note the movement during a spawning period of small numbers of fish from inshore areas across the upper reef slope towards the outer edge.

Spawning at Palau was observed on 22 days during February-April, and did not seem to be restricted to any particular part of the lunar cycle (Fig. 5). It took place during the first 1–3.5 h after the tide had peaked and begun to ebb, and was observed between midmorning and late afternoon (Fig. 3).

At Lizard Island, a total of six pair-spawnings were seen at the same South Island site and the same time of day as those of *A. nigrofuscus*. Courtship occurred frequently at Macgillivray Reef, but only after 1500 h, and one pair-spawning was observed there, at 1545 h, on an ebb tide.

Interactions between a pair of *Z. scopas* that led up to pair spawning took the following form. The two fish began leaving the substrate and slowly rising up to 2 m above it. The male usually initiated such rising. They hung in the water column for a few seconds, then returned to the substrate. During these bouts of rising, the male frequently approached the female and made short, slow rushes at her, expanding his median fins and fluttering his tail from side to side as he came near her. After a number of bouts of this rising with the male displaying to the female, the mating occurred. Two forms were observed. In one, after the pair had risen the female darted to the side of the male from up to a meter away, the two rapidly rushed up together at 60–90° for about 20–50 cm, then the female broke rapidly away and rushed to the bottom. In the second form, the male approached the female and came up against her so that the two were side by side. The two fish, with their backs tilted apart and their bellies close together, rose slowly for a few centimeters, then the female broke away with a flick of her tail and darted to the substrate. Milt was released at the apex of both of these types of pair movements, each of which ended 1–4 m above the bottom.

At Lizard Island, socially active *Z. scopas* often underwent distinct color changes. When chasing single, unresisting intruders of their own or other species, territorial *Z. scopas* often did not change or, if they did, developed slight paling of the head. When they were attacking nonaggressive feeding schools of *A. nigrofuscus*, a territorial *Z. scopas* usually developed a pale head, anterior back and anterior half of the dorsal fin, and a thin dark line appeared along its midside (Fig. 10). Its iris usually did not change color. When a fish was fighting with an aggressive conspecific (or member of another species), a territorial fish not only developed a pale front, but also changed its iris color to iridescent orange. Territorial fish at Palau also developed an orange iris when attacking territory-holding conspecific neighbors, but showed no obvious change in body color. No changes in the color of the body and fins of the courting and spawning fish was noted at Aldabra and Palau. At Lizard Island, both members of a courting or spawning pair usually developed slight paling of the head region and also developed orange irises. Male *Z. scopas* at Palau sometimes developed an orange iris while courting with their females, especially when also chasing neighboring males that were approaching the courting pair. Such approaching males were attempting to interfere in pair matings and I saw one successful interference at Palau.

The single group spawning that was seen at Palau was not accompanied by any color change of the participants. The four participants were part of a group of about a dozen that were moving about together near the outer reef edge. The fish briefly clustered together a few centimeters above the substrate, then made a short, vertical rush up for about 50 cm and darted back down, separating as they went.

Zebrasoma veliferum

Zebrasoma veliferum is a moderately large surgeonfish (Table 1). It probably reached much the same weight at Aldabra and Palau, although large Palauan specimens were shy and were not speared. This species tends to be rather dully colored. Its fins are dark brown and its body is dark brown with a series of pale bars that are palest and broadest anteriorly (Fig. 11). The fish can rapidly change color and lighten the pale bars or darken them until they almost merge into the rest of the body. *Zebrasoma veliferum*'s diet consisted of fleshy green and red algae (Robertson & Gaines, unpublished data).

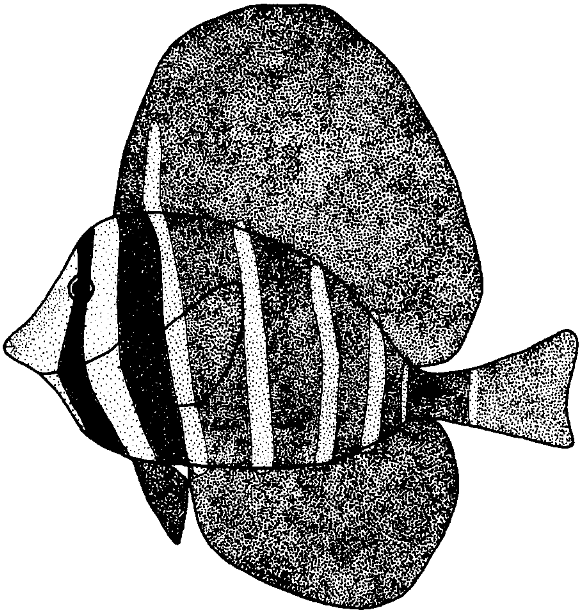

Fig. 11. Zebrasoma veliferum, normal pattern.

This species was observed only in subtidal areas at Aldabra (Fig. 1). Its avoidance reaction to humans was so strong at Palau that it was not recorded on the transects there. However, it was common in both intertidal and subtidal areas there.

At Aldabra, pairs of adult fish, consisting of a male and a large female, defended joint feeding territories against conspecifics (Robertson et al. 1979). At Palau, many adults defended feeding territories against conspecifics, either as single fish or in pairs. Those territories were on the upper and lower reef slopes. There, also, it appeared that the male was smaller than his pair partner (Robertson, in preparation). A large proportion of the adult population also formed feeding schools of 50–100 fish that roamed throughout intertidal areas and subtidal areas down to depths of at least 15 m.

At Aldabra, pair spawning was observed during two days in September. It occurred on ebb tides, between 1500–1800 h, on the reef slope in up to 10 m depth where the fish normally fed. At Palau, spawning was restricted to the first 1.5–5 h of ebb tides (Fig. 3, 4). It was observed between 1030–1800 h on 15 days during January-April, and occurred during most stages of the lunar cycle (Fig. 5). During spawning periods, fish migrated from inner reef areas to the outer edge (Fig. 4). Migrating males established small (5–15 m diameter) territories on the outermost 20 m of the upper reef slope. Those territories were spawning territories; the males did little feeding in them and they were occupied and defended only for the duration of each spawning period. Pair spawnings were seen both by males that established temporary territories and males that were more permanently paired with females and lived immediately below the outer reef edge. Three spawnings by different pairs of Aldabran fish and four spawnings by two pairs of fish at Palau evidently were in the water column over each pair's territory because I observed the pair feeding together in a known pair-territory immediately below the spawning site for 10 minutes after the spawning. At Palau, females also moved from intertidal areas out to the reef edge to males' temporary spawning territories, mated in them and then left again.

We did not see any attacks by zooplanktivorous fishes on the fresh gametes of *Z. veliferum* at Palau (Table 4), or attacks by piscivores on the spawning fishes or *Z. veliferum* attacking zooplanktivores or piscivores.

Three matings were seen at Aldabra and another 19 at Palau. The sexes of the participants in the Aldabran spawnings were established from known size relations between the males and females of pairs. At Palau, I speared four males that were holding spawning territories along the outer reef edge to establish their sex. The males that held reef-edge spawning territories were all large and moderately large fish (n = 40). Even so, they tended to court and mate with females that were larger than they – the male was noticeably smaller than the female in 23 such pairs, there was no noticeable difference between the sizes of the two fish in another six pairs, while the male was larger than the female in seven pairs. In four of the latter seven pairs, the female was a small fish. Neighboring territorial males frequently attempted to approach a courting pair that was preparing to spawn. The male of the pair responded to these approaches by vigorously attacking the intruding male. In one of the matings at Palau, an intruding male interfered in the same manner as males of *C. striatus* and *Z. scopas* were seen to do in conspecifics' spawnings.

Courtship and pair mating proceeded as follows in *Z. veliferum*. The male began rising up and hanging in the water column up to several meters above the substrate. Eventually he was followed up by the female. The two often remained in midwater for several minutes, then returned to the bottom. As the female rose further up, the male responded by approaching her and erratically circling round above and within several meters of her, using his pectoral fins for locomotion. He also occasionally approached her and briefly quivered the posterior half of his body from side to side, moving slightly upwards as he did so. Finally, the female rose well above the bottom. The male rushed to her side and the two moved rapidly up for 1–2 m, then abruptly separated and swam back to the bottom. Milt was released at the apex of this rush. The rush terminated within about 1 m of the water surface, in water depths of up to 7 m. Sometimes the final part of the spawning rush was horizontal because the fish had risen right to the surface of the water during it. During the later stages of courtship, and at the mating, both members of the pair developed the same color pattern—the light bars on the face and body became pale, while the fins and the rest of the body remained dark. Territorial fish, on the other hand, usually were dark overall when attacking conspecifics.

Paracanthurus hepatus

Three *Paracanthurus hepatus* were collected at Escape Reef, the largest being a male of 176 g (SL = 175 mm). The body of this brilliantly colored fish (Fig. 12) is bright, electric blue, with a broad pitch-black stripe that runs from the eye along the back to the base of the tail. There is a large blue oval patch in the center of this body stripe. The tail and caudal peduncle are bright yellow with black upper and lower edges. The dorsal and anal fins are blue basally and sooty distally; while the pelvic fins are blue anteriorly and grey-brown posteriorly. The pectoral fin has a black leading edge, a blue center and a yellow posterior edge.

At Escape Reef, which is an outer-barrier reef, this species was seen only along the seaward edge of the reef. There it was observed feeding both in the water column up to about 10 m above the bottom and on the substrate. The stomachs of the three specimens collected there contained a mixture of zooplankton and small, fleshy types of benthic algae.

The behavior of an aggregation of 25–30 *P. hepatus* was observed on two days at Escape Reef. When not sexually active, these fish were spread out singly or in small transient groups along about 100 m of reef edge. They mingled freely and showed no signs of territoriality. In this same area, this loose aggregation broke up into 5–8 subgroups during the two periods of sexual activity that I observed. Each group, which remained in an area of approximately 100–200 m^2 separated by 10–20 m from other groups, contained a sexually active male and 2–7 smaller fish, all of which seemed to be females. The male of each group chased away males from neighboring groups and other large solitary intruders, which may also have been males. Movement of females in and out of a group during the course of a day's spawning period was noted.

Spawning was observed on two days at Escape Reef, between 1645–1815 h. It began about 30 min after high tide when water was moving off the reef to the open sea. Matings occurred in 7–8 m of water within 15 m of the outer edge of the reef, which is a 20-m-high vertical face. Spawning also was observed on one day in February at Macgillivray Reef, between 1600–1700 h, beginning about 3.5 h after high tide. It occurred on the lee side of the reef on the reef slope in 5 m of water 25 m out from the edge of the intertidal part of the reef. In addition, courtship was observed at exactly the same site and during the same time period on another three days during February and March, both shortly before and shortly after low tide. The fish spawning at that site had migrated at least 100–200 m from the seaward side of Macgillivray Reef, as the seaward side was the only place they were seen outside the spawning period.

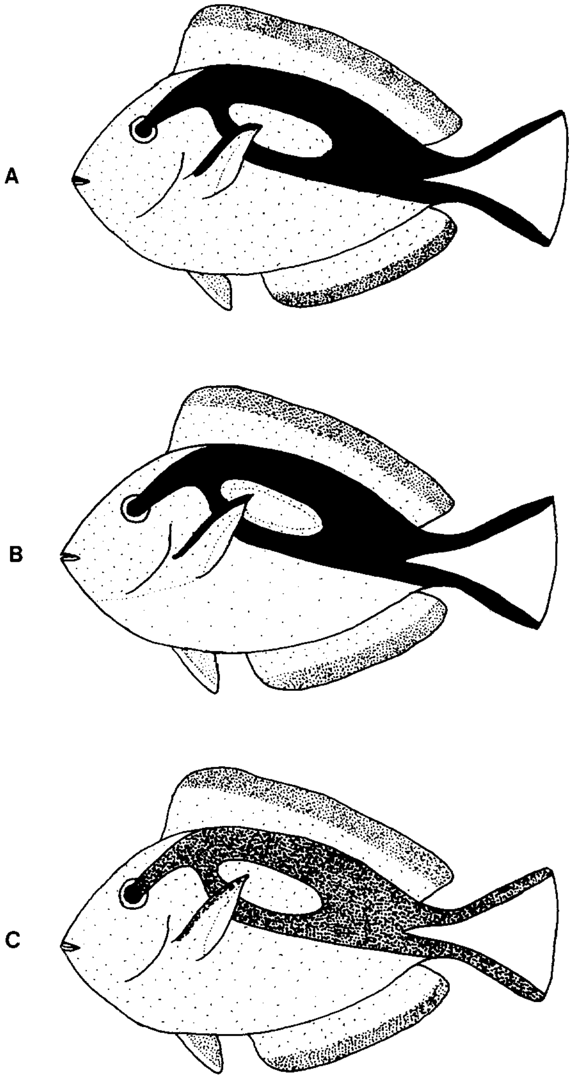

Fig. 12. Color patterns of *Paracanthurus hepatus*. A = normal pattern; B = pattern of pair-spawning male; C = pattern of pair-spawning female.

The sexual identities of participants in pair spawnings were established by spearing one male and two ripe females at Escape Reef; a comparison of those freshly speared fish did not reveal any sexually dimorphic external features. I saw 22 pair spawnings at Escape Reef, and four pair spawnings at Macgillivray Reef. No behavior was seen that indicated that group spawnings might occur.

The sequence of interactions that leads up to pair spawning takes the following form. The male is moving around in the middle levels of the water column above the group of fairly inactive females. He begins making approaches to any female that moves up in the water and circles around her. During these approaches the male's dorsal, anal and pelvic fins are depressed, the pectoral fins are expanded and held rigidly pointing down and out away from the body. He moves slowly forward by shallow, rapid, fluttering beats of the expanded tail. When near a female the male often leans his back sufficiently towards her that she can see the top of his stiffly extended pectoral fin. The approaches and circlings also are interspersed with the male coming to a halt, briefly twitching his body from side to side, then expanding all his fins and shooting forward in a stiff motion provided by jerky beats of his tail. After about 30 min of the male behaving in this manner, females begin to respond positively by rising up to him when he approaches. Some of these risings lead into spawnings. The female begins rising at about 45°, using her pectoral fins for locomotion while the rest of her fins are depressed. As she rises the female begins to speed up, the male rushes to her side and the two take off in a rapid spawning rush about 0.5 m long. During this rush the fish are side by side and use their tails for locomotion. At the end of the rush, the two abruptly turn, releasing gonadal products as they do, then separately speed back downward for about 1 m. Immediately after a mating the male sometimes makes further rushes similar to the spawning rush. Spawning activity in the larger groups sometimes occurs in bursts; one female rising is rapidly followed up by several more and up to three females each mate with the male in less than one minute. The apex of the spawning rush typically is close to the water's surface: 15 were within 0.3 m of the surface, another 9 were 0.3–1 m from the surface, and the remaining 2 were about 1.5 m below it. Fish that spawn right at the surface often rise up to it before beginning a spawning rush, in which case, the rush is almost horizontal. Rushes that begin further below the surface typically angle up at 45°–60° above the horizontal.

Both the male and female change color during courtship and spawning. In the male, the blue on the body fades everywhere except on the head and around the outer edge of the oval patch in the black body stripe (Fig. 12). In the female, the blue color remains as normal, but the black of the body stripe fades to a dark silvery-grey (Fig. 12). Insufficient numbers of aggressive interactions involving males were seen to be able to determine whether specific color changes occur under different social contects.

Discussion

The localization of spawning in space

Spawning by the study species did not occur at random throughout the water column over an entire reef. Rather, it was often localized at specific sites on the reef and in a specific part of the water column.

Spawning migrations
At all three sites the surgeonfishes that lived in inshore areas commonly migrated to the outer edge of the reef to spawn at the interface between shallow and deep areas of the reef. At Palau many wrasses and parrotfishes made similar large-scale migrations to the same sites (Robertson & Foster, unpublished data). In many cases, the migration was more or less directly between the inshore area and the nearest part of the reef edge. In some instances, however, the surgeonfishes also travelled along the reef edge to a specific part of it where they concentrated to spawn. At Palau, fishes living below the interface at which the inshore fishes aggregated to spawn were not observed to move up to that interface or into deeper areas to spawn. At Macgillivray Reef, fishes migrated from intertidal and shallow subtidal areas down to the base of the reef slope, at the lower limit of coral growth.

There were exceptions to this tendency for inshore-living fishes to make spawning migrations. Individuals of three species that lived in territorial harem groups in intertidal areas at Palau often spawned in their territories. This tendency was strong in *Z. scopas*, which rarely appeared to migrate. Some *A. nigrofuscus* and *C. striatus* living in harem groups in intertidal areas spawned in their feeding territories. However, many such fish migrated during spawning periods. Whether or not particular harem females showed both patterns of spawning behavior or only one was not established. In all species for which data are available, fishes that lived in harem groups in subtidal areas apparently spawned in their feeding territories.

Spawning migrations are widespread among reef fishes that produce pelagic eggs (Colin & Clavijo 1978, Johannes 1978 and references therein, Nakazono 1979, Nakazono & Tsukahara 1974, Robertson & Hoffman 1977, Robertson, 1981b, Warner & Robertson 1978, Warner et al. 1975). Although Johannes (1978) indicated that species smaller than about 25 cm in length do not make spawning migrations, the information presented here and by several of the authors referred to above shows that such is not the case. Johannes' information on migrations concerns mainly species that fisherman seek, which tend to be large. However, there may be qualitative and quantitative differences in the tendency for species of different sizes to make such migrations.

Predation on the pelagic eggs of reef fishes immediately after the eggs have been produced is a common occurrence (Hobson 1965, Matsuoka 1972, Moyer 1975, Colin 1976, Meyer 1977, Robertson & Hoffman 1977, Colin 1978, Nakazono 1979).

Both the acanthurids dealt with here and other reef fishes that migrate generally release eggs at sites where they are thought to have the best chance of being rapidly carried away from a reef and reef-based egg predators, vertebrate and invertebrate, mobile and sessile (Randall & Randall 1963, Jones 1968, Warner et al. 1975, and see Johannes 1978 for review). These sites include reef edges, especially down-current edges, prominences of reef and the mouths of lagoon channels.

The formation of a long-term heterosexual group requires some degree of mating fidelity of the female to the male of her group. Such fidelity may occur in surgeonfishes because males can control a female's access to a limiting resource (food) or because males defend females against other males (Emlen & Oring 1977, Robertson & Hoffman 1977). The 'permanent' territoriality of most surgeonfishes considered here serves a resource (food) defense function, since territories are defended by single fish, and by both sexes in a heterosexual group, and feeding areas are defended against a variety of species that have similar diets. Mate monopolization may arise through resource defense in these fishes.

For a female of a surgeonfish harem that lives at a preferred spawning ground there may be little or no benefit to leaving her feeding area and spawning elsewhere. At both Aldabra and Palau, various harem-living surgeonfishes spawned in their feeding territories when those territories were at or near the spawning grounds used by migratory fish. However, if a female's feeding area is located where only low-quality spawning sites are available then the benefits of a spawning migration may greatly exceed its costs. Perhaps for this reason many *A. nigrofuscus* and *C. striatus* that lived in intertidal areas made spawning migrations. Some of the individuals living in those intertidal areas spawned in their harem territories, although how the spawning rates of the males that maintained harems there compared to those of males living in preferred spawning grounds remains unknown. *Z. scopas* that lived in intertidal areas showed a slighter tendency to migrate than did *C. striatus* and *A. nigrofuscus* living in the same areas. If the resource defence hypothesis of harem formation in the herbivorous surgeonfishes is correct, then a male's ability to control resources should be greater in *Z. scopas* than in the other two species. This remains to be tested.

Spawning near the water's surface

There is a widespread tendency for reef fishes to move up off the bottom when spawning planktonic eggs, which has been attributed to the advantage of releasing eggs away from egg predators that live on reefs (Jones 1968, Ehrlich 1975, Robertson & Hoffman 1977, Johannes 1978). That tendency to mate up off the bottom was universal among the acanthurids dealt with here. Most of those spawning fishes did not merely move a fixed distance above the substrate, but attempted to release their gametes near the water's surface. First, during a spawning rush performed in deeper water the fish typically moved further up off the bottom than they did when in shallow water. Although fishes in deeper water often did not mate close to the surface, increasing risks of predation on them as they moved away from the shelter of the substrate may have inhibited them from moving very far up. Second, the fishes that had spawning migrations at Palau congregated at the outer limit of the shallow portion of the reef. If they were attempting to release eggs at the extreme outer limits of the reef, then they should have migrated down the reef slope; instead, they stopped where the water's surface was still in close proximity to the substrate. Third, although fishes did migrate down to the base of the subtidal reef slope at Macgillivray Reef, the water where they spawned was quite shallow and eggs were released within a few meters of the water's surface. Spawning migration of labroid fishes from shallow to deeper areas of reef are known, however (Randall & Randall 1963, Colin 1978), and at least one such migration appears to be associated with depth variation in the distribution of zooplanktivorous fishes that eat eggs (Jones 1981). Migration to different depths also may be related to depth variation in current patterns.

There are several possible reasons why the upper level of the water column usually may be the most suitable place for spawning. First, for freshly released, concentrated eggs the risk of predation from zooplanktivorous reef fishes may be least there. Many zooplanktivorous reef fishes rely on the reef for shelter and tend to restrict their feeding to the middle and lower levels of the water column (Stevenson 1972, Emery 1973, Hobson 1974, Hobson & Chess 1978, personal observations). Observations on the rates of predation by zooplanktivores on egg clusters released in different parts of the water column could show whether this effect is operating. Second, surgeonfishes spawning at the reef edge at Palau released their eggs into a mass of water that was moving off the reef into deep water. If surface water tends to move off the reef in a more uniform and rapid manner than subsurface water, it would be advantageous for surgeonfishes to spawn close to the surface to minimize the time that their eggs are exposed to those zooplanktivorous fishes that do not move out into deep water. Pelagic fish eggs generally are positively buoyant (Lagler et al. 1977) and both fertilized and unfertilized eggs of *Acanthurus triostegus* have been shown to be so (Randall 1961a). If surgeonfish eggs make their way to the surface fairly rapidly after being released then predation risks from zooplanktivorous fishes immediately after spawning may be the major factor determining where in the water mass spawning occurs. If eggs are neutrally buoyant or rise only slowly, then the avoidance of subsurface water that could retain eggs near a reef also could be of importance.

Spawning rhythms

Diel rhythms

Among the species studied, spawning typically was restricted to a certain time of day, and two, possibly three, types of diel rhythms were detected. First, *A. lineatus* typically spawned just after sunrise. Second, spawning by *A. nigrofuscus* and *C. striatus* peaked during the afternoon. Third, the two *Zebrasoma* species spawned between midmorning and dusk; the data are insufficient to show whether those two species had a peak of spawning activity during the afternoon i.e., whether this pattern was essentially an imprecise version of the *A. nigrofuscus/C. striatus* pattern. The more limited data from Aldabra and Lizard Island indicate that *C. striatus*, *A. nigrofuscus* and *Z. scopas* are afternoon spawners at those locations. Thus, except for *A. lineatus*, early- to mid-morning spawning was generally avoided by surgeonfishes and afternoon was the time of greatest activity. Afternoon spawning also appears to be the case for most other day-spawning reef fishes that have planktonic eggs (see Randall & Randall 1963, Reinboth 1973, Nakazono & Tsukahara 1974, Moyer & Shepard 1975, Colin 1976, Robertson & Hoffman 1977, Lobel 1978, Moyer & Nakazono 1978, Robertson & Warner 1978, Warner & Robertson 1978, Robertson 1981b). However, a significant number of exceptions to this pattern also exist (see Meyer 1977, Nakazono 1979, Thresher 1979, Dubin 1981, Jones 1981). At both Palau and Lizard Island morning spawning was common among wrasses and parrotfishes, although the relative amounts of morning and afternoon activity by these species were not determined.

Exposure to strong solar radiation is known to have deleterious effects on some fish eggs and embryos and nocturnal spawning may represent a response to this problem (see Ferraro, 1980, for review). The amounts of intra- and interspecific variation in the timing of spawning by various surgeonfishes throughout the day make it unlikely that the timing of their spawning at Palau represents such an adaptive response.

It has been argued that spawning during late afternoon or dusk reduces egg predation because the feeding efficiency and general activity of zooplanktivorous fishes is reduced at that time (Robertson & Hoffman 1977, Lobel 1978). Very few data are available that deal with diel activity patterns of zooplanktivores. Stevenson (1972), in a study of the activity of one common zooplanktivorous damselfish from the Caribbean, found that the level of feeding was lower in the afternoon than in the morning, although increased current velocity exerted a strong influence on that level and could intensify afternoon feeding. If a pattern of afternoon feeding being less than morning feeding is common to many zooplanktivorous reef fishes, then afternoon spawning by fishes that produce prey eggs may be an adaptation that reduces the risk of egg predation.

In some situations, afternoon spawners may gain a reduction in egg predation in another way. Zooplanktivores actively feed when currents bring oceanic material onto a reef. At sites such as Palau, eggs spawned on afternoon ebb tides will be exposed to predation from fishes that have already fed during a morning flood tide that brought in oceanic water and that are more likely to be sated than during the morning.

If there is a general advantage to afternoon spawning, why is *A. lineatus* the radical exception, particularly since zooplanktivorous fishes do consume its eggs? I suggest that *A. lineatus* behaves differently because it is responding to a problem that it experiences much more acutely than the remainder of the study species do—strong, continuing pressures of competition for food from other fishes. The response of *A. lineatus* to that competition is to spawn at the time of day when that pressure is least. The following observations lead to this hypothesis.

First, the territory of an *A. lineatus* contains a concentrated food supply that must be continuously defended against a broad range of herbivorous fishes, to avoid being depleted (Robertson et al. 1979). In comparison to *A. lineatus* the other species dealt with here maintain less concentrated food supplies, defend food against fewer species, and do not attempt to completely exclude as many species from their territories (Robertson et al. 1979, Robertson, unpublished data). Second, at Aldabra and Palau, other herbivorous surgeonfishes did not begin feeding until about an hour after dawn (personal observation). This may be the general case for herbivorous fishes (see Montgomery 1980, Taborsky & Limberger 1980, Nursall 1981). Third, competitors of *A. lineatus*, such as *A. nigrofuscus* and *Z. veliferum*, did not make spawning migrations to the reef edge at dawn. Other competitors such as parrotfishes did make such dawn migrations, but my impression is that many fewer of them did so then than at other times of the day.

If this hypothesis is correct, then the following predictions should be upheld: (1) The feeding activity of competitors of *A. lineatus* (various parrotfishes, rabbitfishes and surgeonfishes) should be lower during the morning period when *A. lineatus* spawns than during (a) the equivalent period prior to sunset and (b) the main part of the day. (2) The density of food competitors in the vicinity of *A. lineatus* territories should be lower during its dawn spawning periods than at other times of day at the same stage of the tidal cycle. (3) When *A. lineatus* territories are experimentally vacated, the rate of depletion of food shortly after the vacation should be less in territories that are vacated at the start of the dawn spawning period than in territories that are vacated at other times of the day. (4) Other territorial surgeonfishes that attempt to maintain exclusive-use territories and that face pressures from interspecific food competitors of similar intensity to those that *A. lineatus* must cope with should also restrict their spawning to around dawn. Nonherbivorous surgeonfishes and herbivorous surgeonfishes that are not ecologically and behaviorally similar to *A. lineatus* should not restrict their spawning to the same time of the day that *A.*

lineatus does.

There are four surgeonfishes which are ecologically similar to *A. lineatus* and which might therefore be expected to spawn at dawn. In the Red Sea, *A. sohal*, which is closely related to *A. lineatus* (Randall 1956), seems to be an ecological analog of *A. lineatus* (see Vine 1974). *Acanthurus glaucoparieus* from the Pacific Ocean and *A. leucosternon* from the Indian Ocean are two highly aggressive species that defend feeding territories against a wide range of herbivorous fishes. However, the pressure from competitors that these two face probably is not as strong as that with which *A. lineatus* must cope; they tolerate feeding by some species that *A. lineatus* excludes and the resources of their territories are not as concentrated as those in *A. lineatus* territories (Robertson et al. 1979, Robertson, in preparation). In addition, both *A. glaucoparieus* and *A. leucosternon* form heterosexual pairs which jointly defend territories that often are near the outer edge of the shallow sections of reef. Thus they may be able to accomplish spawning without leaving their territories and engaging in the types of activity that *A. lineatus* does prior to group spawning. The fourth species is *Acanthurus achilles*, from the western Pacific, which appears to resemble *A. glaucoparieus* and *A. leucosternon* in its ecology and social organization (see Jones 1968, Barlow 1974). *Acanthurus glaucoparieus* was common at Palau but was not seen to spawn there.

An alternative possibility is that early-morning spawning represents a mechanism by which some herbivorous reef fishes minimise their loss of feeding activity – they spawn during that part of the day that is least suitable for feeding.

Tidal rhythms

A common tidal rhythm of spawning was evident among all surgeonfishes studied at Palau and Aldabra: spawning occurred only during the first half of ebb tides. Numerous wrasses and parrotfishes also exhibited this same rhythm at Palau (Fig. 5, and Robertson & Foster, in preparation). At the Lizard Island sites no tidal spawning rhythm was evident. Although all three locations had substantial tidal ranges and predictable tides, only at Lizard Island were tidal flows along-reef rather than on off-reef. The presence/absence of a tidal spawning rhythm reflects the advantages that arise when fishes spawn so that their eggs move off a reef very soon afterward. At sites that have on off-reef tidal flow that is distinct and predictable, fishes spawn only during off-reef flows (this study, Randall 1961, Robertson 1974, Robertson & Choat 1974, Choat & Robertson 1975, Lobel 1978, Thresher 1979). When currents are along-reef, fishes do not have such a change in flow patterns to respond to (this study). Also, tidal rhythms of spawning (by labroid fishes) are absent when tidal current patterns are weak, unpredictable or overridden by currents generated by other factors (Robertson & Hoffman 1977, Robertson 1981b, Jones 1981).

Semi-lunar rhythms

At Palau, most *Acanthurus lineatus* spawning occurred on days 9–13 of the lunar cycle, and possibly days 24–27 as well. Peaks of spawning by *A. nigrofuscus* and *C. striatus* occurred shortly before the moon changes, on days 6–12 and 20–26 of the lunar cycle. Those two species and the two *Zebrasoma* species spawned throughout the lunar cycle except for the few days immediately after new and full moons.

These semi-lunar spawning rhythms are different to those that Johannes (1978) reported for some other Palauan fishes that produce planktonic eggs. He indicated that 19 species, including *Acanthurus xanthopterus*, spawned at and just after the new and/or full moon, although one of those 19 also spawned just before full moon. He also reported that at two Pacific locations (one of which is in the general vicinity of Palau), *C. striatus* spawns at and just after full moon, i.e., at a different stage of the lunar cycle to that at which it spawns at Palau.

Johannes (1978) developed the argument that two factors contribute to semi-lunar rhythms of spawning by reef fishes: tidal height and tidal current velocity. Noting that certain species spawn around the moon changes, he proposed that spawning is restricted to the times of the lunar cycle when spring tides (a) maximize the rate of movement of eggs off a reef and (b) keep eggs furthest up in the water column above reef-based predators. The data presented here on the spawning of the Palauan surgeonfishes do not show such a correlation between semi-lunar rhythms of spawning and either high tide height or tidal amplitude (which is probably an indicator of tidal current velocity). First, the early morning tides on which *A. lineatus* spawned en masse were smaller (i.e., had lower highs and lower amplitudes) than tides during the rest of the day. Second, on days when *A. nigrofuscus* and *C. striatus* concentrated their spawning the high tides usually were smaller than those at other times of day and the tidal amplitudes were not consistently different from those at other times of day. These data lead me to make two alternative suggestions. First, the tidal range invariably is sufficiently large at Palau that even 'small' tides produce tidal flows that are strong enough to rapidly flush surgeonfish eggs off a reef. Many fishes migrate to the outer edges of reefs to spawn and the reduction in duration of exposure of eggs to reef-based egg predators that derives from such migrations probably far outweighs any reduction that would come from restricting spawning to large tides. Thus, those fishes would gain little or no advantage by restricting their spawning to large tides. Second, semi-lunar rhythms of spawning exhibited by the Palauan surgeonfishes are tertiary rhythms that derive from a combination of (a) primary, diel rhythms and (b) a secondary, tidal rhythm, i.e., there are only two periods during the lunar month when the 'right' time of day and the 'right' tidal current flow coincide and favorable conditions for spawning exist.

Variation in the daily timing of spawning by a particular species, the preciseness of diel spawning rhythms and the degree of coincidence of the rhythms of different species at different sites may reflect variation in the magnitude and temporal patterning of egg-predation risks. The size of those risks may be related not only to (a) the population densities and spatial distributions of egg predators, but also (b) the relative importance of mobile versus sessile egg predators, (c) the degree of spatial localization of spawning, and (d) the predictability of temporal variation in the feeding activity of egg predators. While mobile egg predators may be able to take advantage of highly localised spawning it may not be economical for them to respond to dispersed spawning by altering their activity. Highly localised spawning by migratory fishes may most typically occur on reefs that (a) support large populations of fishes, and (b) have predictably changing current flows. The availability of non-egg foods for egg predators will be determined in part by certain characteristics of current patterns – the strength, duration, and origin of the water flow. Consequently the predictability of changes in these characteristics may determine whether spawning fishes can take advantage of periods when egg predators are least likely to attack their eggs.

Here I have emphasized how predictable variation in the risk of predation on freshly spawned planktonic eggs may be an important factor selecting for spawning at specific times, stages of the tide and locations. Other factors probably also have strong influences on spawning activity and may sometimes override the effects of egg predation that are considered here. These factors include mechanisms that reduce egg predation, e.g., toxicity of eggs (Moyer & Zaiser 1981), defense of eggs, losses of feeding activity by spawners, and variation in risks of predation on spawners that depend on the spatial distributions and activity patterns of piscivores.

Relative amounts of predator-prey interactions during pair- and group spawnings

During spawning of fishes that produce planktonic eggs, attacks are often seen on both eggs (see above) and on the spawning fishes (Randall & Randall 1963, Moyer 1974, Meyer 1977, Robertson & Hoffman 1977, Colin 1978). At Palau, zooplanktivorous fishes commonly attacked the freshly released eggs of surgeonfishes, wrasses and parrotfishes, and predatory fishes attacked the spawners. Robertson & Foster (in preparation) found that the numbers of some predatory and zooplanktivorous fishes on the spawning grounds at Palau increased during spawning periods.

Many zooplanktivorous reef fishes normally feed by picking individual items out of the water column (Davis & Birdsong 1973, Hobson 1974, personal observations). An examination of data presented by

Hobson & Chess (1978) shows that, although pelagic fish eggs are a major component of the diet of diurnally feeding zooplanktivorous reef fishes, those fishes tend to eat fewer planktonic fish eggs than would be expected on the basis of their relative abundance in the water column. Hobson & Chess's (1976) data show a similar situation with respect to temperate, near-shore zooplanktivorous fishes, although the discrepancy between abundance of eggs in fish stomachs versus that in the water column is even more pronounced than among the tropical reef fishes. Hobson & Chess (1976) have suggested that small size and transparency reduce rates of predation on many types of diurnal zooplankters, including fish eggs. I suggest that because many pelagic fish eggs are small, transparent, and nonmotile, a planktivorous fish cannot economically concentrate feeding on them when they are dispersed. However, those eggs are highly concentrated in the water column immediately after they are released and then can be more easily located and economically fed upon by such fishes. Thus the time at which eggs are most susceptible to predation from the broadest range and greatest numbers of mobile predators may be immediately after they are released.

Among the Palauan surgeonfishes pair spawnings were much less susceptible to attacks by egg predators than were group spawnings. The chance that during an attack an egg will be eaten is likely to be higher in a group spawning than in a pair spawning because (a) it seems that group spawnings typically have only one female participant and (b) spawnings typically are attacked by groups of up to a score or more of zooplanktivores rather than by single fish. This possibility could be tested by determining egg numbers in attacked and nonattacked group spawnings and pair spawnings, and comparing the numbers of egg predators attacking them and the duration of those attacks. There are at least two possible reasons for the difference in frequency of attacks on pair and group spawnings. (1) Group spawnings may be easier for egg predators to locate. The large number of participants may make group spawnings more conspicuous and/or the larger and more persistent cloud of sperm from a group spawning may be easier to locate. (2) The reward to a zooplanktivore may be greater from a group spawning than from a pair spawning. (a) If more than one female sometimes participate in a group spawning, the average number of eggs in a group spawning should be greater than in a pair spawning. (b) Sperm clouds are larger and more dense in group spawnings, which have many more male participants than pair spawnings, and it is conceivable that zooplanktivores might actively seek and drink sperm when it is present in large concentrations. Further, large numbers of pair and group spawnings of many different species occur simultaneously during a day's spawning period that lasts several hours. If zooplanktivorous fishes are likely to gain a greater reward from a group spawning than from a pair spawning, then they may direct their attention preferentially towards group spawnings and attack pair spawnings less often than would be expected on the basis of their relative abundance.

Pair spawnings of many Palauan wrasses and parrotfishes were performed mainly by territorial males. Those males drove away from their territories both egg predators and predatory fishes that were capable of preying on females (Robertson & Foster, unpublished data). I did not observe attacks by spawning surgeonfishes on egg predators or fish predators. Several factors may contribute to this behavioral difference between 'nondefender' males of surgeonfishes and 'defender' males of wrasses and parrotfishes.

First, the pair spawnings and spawning individuals of surgeonfishes may be less susceptible to predation than are those of the defender labroids. Such differences in susceptibility could be due to differences in (a) the likelihood and/or size of the reward to a predator from a single spawning act, (b) the ease with which a spawning and the spawning fish can be located and approached by a predator, (c) the small-scale location of spawning, because different types of sites may facilitate or hinder predators' activities. Further, predators might be expected to direct their attention preferentially towards species whose males spawned at the highest rates, because that type would potentially offer the greatest rewards. However, we might also expect that, because to a male with low spawning rate each spawning is of higher value than to one with a high spawning rate, the former type of male should be more likely than the latter to attack predators. Such an effect might promote attacks by egg predators on species whose males had high spawning rates. Territorial males of some species of labroids can have very high frequencies of pair spawning during a day's spawning period (Warner et al. 1975). Most pair spawnings by the surgeonfishes considered here were intraharem spawnings. Because harem sizes of those fishes are small, pair-spawning rates of individual males are probably low, and predators may not be attracted to them as strongly as they are to some labroids that have high frequencies of pair spawning. *Zebrasoma veliferum* was an exception to the extent that, at Palau, males migrated to the reef edge and established spawning territories there. However, they did not appear to have high spawning frequencies.

Second, when females can freely choose among a variety of males at a spawning ground, the chosen males may be those that tend to perform risk-bearing activities that directly benefit females, activities such as protecting the female from fishes that may eat her, and protecting her spawn. When females have less choice, males may not be so likely to perform such activities. The ability of females to choose mates freely during pair spawnings was more evident among many of the labroid fishes than among the surgeonfishes.

The surgeonfishes at all three study sites and many wrasses and parrotfishes at Palau appeared to employ one tactic that may lower rates of egg predation on group spawnings: massed performance of group-spawning in pulses. Robertson & Foster (in preparation) found that, at Palau, in spawning pulses of *Scarus sordidus* the percentage of group spawnings that were attacked by egg predators was inversely proportional to the number of spawnings per pulse. The effect of this pulsing on risks of predation on the group-spawning fishes themselves was not determined, although we might expect that pulsing would also reduce those risks by predator swamping (Darling 1938).

Even though pulsing of group spawning does reduce egg predation, group spawnings generally suffer much higher rates of egg-predator attack than do pair spawnings. One might therefore expect females to avoid group-spawning activity in favor of pair spawning. Yet, group spawning was the predominant mode of spawning in four of the species studied, there was very little pair spawning in two of those species, and there was no indication of universal and pronounced attempts by females of those species to avoid group spawning.

There are at least two factors that may contribute to this preponderance of group spawning. First, the presence of numerous male participants in a group spawning may reduce the risk of a predator attacking a female, and when risks of fish predation are high, females may actively choose to spawn in a group. Second, it simply may be too costly for females to try to avoid group spawning. The density of males often is so high on spawning grounds that many of them can and do easily join a pair spawning and effectively turn it into a group spawning. A territorial male may not be able to prevent either neighboring territorial males or the large numbers of nonterritorial males from joining his group spawning (see Warner & Robertson 1978). High densities of territorial males in one Caribbean parrotfish appear to facilitate their interference in each other's pair spawnings (Robertson & Warner 1978). Robertson et al. (1979) suggested that high densities in colonies of *A. lineatus* would greatly facilitate similar interference (and effectively eliminate any advantage a male might gain by 'permanently' pairing with one or more females) and predicted that group spawning should predominate in that species.

Color change in relation to sexual and social behavior

The few papers that consider the color changes of surgeonfishes in relation to their social and sexual behavior give only incomplete and fragmentary accounts, do not indicate the existence of more than one male color pattern associated with spawning, and do not consider the functional significance of those color changes (Randall 1961a, b, Nursall 1974, Barlow 1974, Robertson et al. 1979). The data presented here are sufficient to make some preliminary interpretations of the functions of surgeonfish color change.

The existence of differently colored male fishes spawning in two different ways could indicate that two species were spawning in the same area. In the species dealt with here, this seems highly unlikely: Pair- and group-spawning activities intergrade rather than being completely separate entities; within a presumed species, males with one color pattern regularly join in the spawnings of males bearing the other pattern; pair-spawning males sometimes change color to the pattern of group-spawning males, and pair-spawning males are territorial toward 'conspecific' males bearing either pair-spawner or group-spawner color patterns.

Two quite different patterns of color exhibited by males of the one species are associated with two basically different patterns of spawning behavior. Pair spawning typically involves a male who spawns in a territory (which may be either permanent or temporary) with females of a harem and/or visiting females. Group spawning, on the other hand, involves nonterritorial fishes, although they may only be temporarily nonterritorial. In pair spawning the male often, though not invariably, undergoes a specific color change. If he exhibits a color change it often is either a slight change or not a full development of the potential change. Pair-spawning females usually do not change color in any specific manner. *P. hepatus* may be an exception, although more work is needed to show that the color pattern a female of this species shows prior to spawning is specific to that social context. Group-spawning males develop a specific, distinctive color pattern that is different to, and often more conspicuous than that developed by pair-spawning males. Females that are group spawning sometimes do not appear to change color (*A. triostegus* and *C. striatus*?), sometimes show a tendency to develop the same color pattern as group-spawning males (*A. nigrofuscus*?) and sometimes evidently show consistent development of much the same coloration as group-spawning males (*A. lineatus*). The color pattern developed by group-spawning fishes is different to that developed by aggressive, territorial conspecifics. Further, the color pattern exhibited by territorial courting males often contains elements that are different to those of the color pattern displayed by sexually inactive conspecifics that are involved in uncontested defense of their feeding territories. Although pair-spawning males do sometimes develop elements of such 'aggressive' coloration, this development appears to be associated with active territory defense that occurs concurrently with courtship.

These patterns of color change may function in the following manner. Specific color patterns that are developed by sexually active individuals distinguish them from sexually inactive conspecifics. Males are competing for females and typically have low thresholds of responsiveness to females. This particularly applies to promiscuous species (Selander 1972, Trivers 1972). Consequently there probably has been weaker selection for female surgeonfishes to develop sexual color patterns than for males to do so. Group-spawning males often are territorial when sexually inactive and their distinctive spawning coloration may serve to advertise their change to a nonterritorial condition. Pair-spawning males, on the other hand, do not undergo such a behavioral-state change. Consequently, two different patterns of color changes serve to distinguish these different states of sexually active males. It may be particularly important for group-spawning males to advertise their change because it facilitates the aggregation of fish, and mass activity appears to be advantageous (see above). Thus the male 'group-spawner' pattern often is more conspicuously developed than the 'pair-spawner' pattern. Within a species, advertisement presumably benefits males that attract passing females to temporary spawning territories more than males that spawn in permanent territories with their harems of resident females, which may be why the former class of male sometimes develops more extreme coloration (e.g., *C. striatus*). The tendency of females to develop specific colors when group spawning but not when pair spawning may also be a reflection of advantages that might come from promoting the aggregation of fish during group-spawning activity. Perhaps it may also be advantageous for females, which seem to be in the minority in a group spawning, to resemble males to reduce the risk of predation on them that might arise from predators tending to select odd prey (Salt 1967). All species dealt with here do not fit these general patterns neatly, *Z. scopas* being the most anomalous case.

Since the available information is quite limited in a number of cases, more detailed analyses are required of color change in relation to intra- and interspecific interactions in a wide range of contexts.

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