

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 m² 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

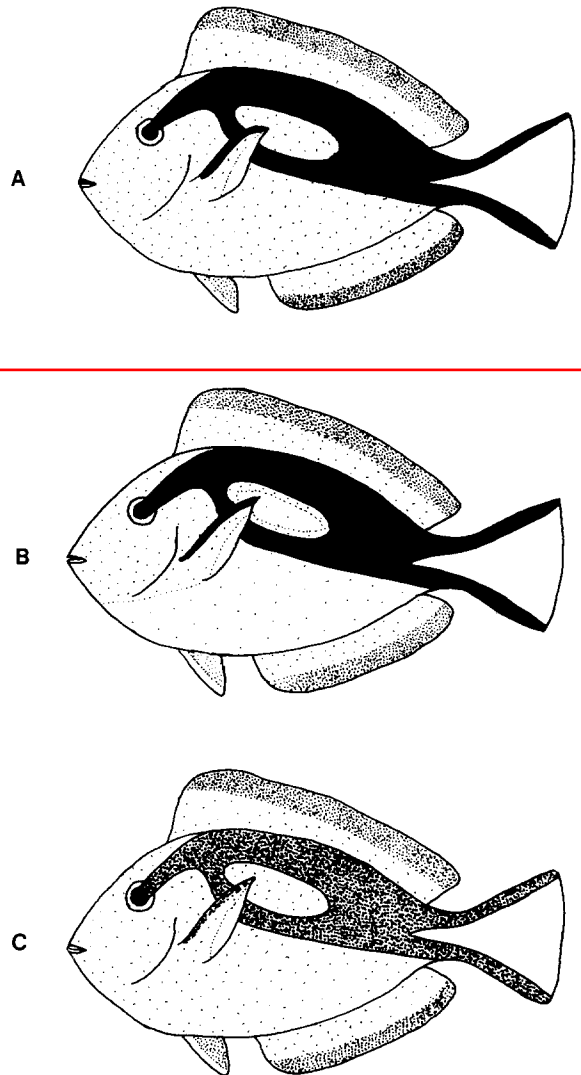


Fig. 12. Color patterns of *Paracanthurus hepatus*. A = normal pattern; B = pattern of pair-spawning male; C = pattern of pair-spawning female.

spawning period.

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 contexts.

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 mi-