Courtship and spawning behaviors of carangid species in Belize

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Many species of reef fish aggregate seasonally in large numbers to spawn at predictable times and sites (Johannes, 1978; Sadovy, 1996; Domeier and Colin, 1997). Although spawning behavior has been observed for many reef fish in the wild (Wicklund, 1969; Smith, 1972; Johannes, 1978; Sadovy et al., 1994; Aguilar Perera and Aguilar Davila, 1996), few records exist of observations on the courtship or natural spawning for the commercially important family Carangidae (jacks) (von Westernhagen, 1974; Johannes, 1981; Sala et al., 2003). In this study, we present the first observations on the natural spawning behavior of the economically-valuable permit (*Trachinotus falcatus*) (Linnaeus, 1758) from the full to new moon period at reef promontories in Belize, with notes on the spawning of the yellow jack (*Carangoides bartholomaei*) (Cuvier, 1833), and the courtship of five other carangid species.

Permit belong to the family Carangidae and are broadly distributed in the western Atlantic Ocean from Massachusetts to southeastern Brazil, including the Caribbean Sea and Gulf of Mexico (Smith, 1997). Considered an inshore pelagic species (Valdez Muñoz and Mochek, 2001) that spawns offshore, permit utilize a range of habitats that include coastal mangroves and seagrass beds, reef flats, and fore-reef areas during their life-cycle (Crabtree et al., 2002). Permit are reported to feed during the day and may show similar feeding characteristics to the closely related *T. carolinus* that displays a clear circadian rhythm entrained to the light phase during its feeding period (Heilman and Spieler, 1999). According to otolith analysis of fish caught in Florida, permit live to at least 23 years and reach a maximum published fork length of 110 cm and a weight of 23 kg (Crabtree et al., 2002).[1,2] Permit are gonochoristic and Crabtree et al. (2002) recorded 50% sexual maturity for females at 547 mm FL or 3.1 years and males at 486 mm FL and 2.3 years. Permit exhibit a protracted spawning season from March to September in Cuba (García-Cagide et al., 2001) and from March to July in Florida (Crabtree et al., 2002). High gonadosomatic indices recorded for March and maturation of oocytes noted in late June–July (Crabtree et al., 2002) support the observations by García-Cagide et al. (2001) that permit are batch spawners and have an asynchronous cycle of vitellogenesis. Spawning cued by the full moon has been recorded in many species of reef and inshore fish (Johannes, 1978, 1981; Moyer et al., 1983; Crabtree, 1995; Hoque et al., 1999). Macroscopic gonadal analysis and observations on the timing of courtship and spawning in several carangid species in the wild (Johannes, 1981; Sala et al., 2003), coupled with gonadal sampling observations on the captive spawning behavior of the related bluefin trevally (*Caranx melampygus*) (Moriwake et al., 2001), further indicate that permit and other carangids display circa lunar periodicity when spawning naturally.

Permit represent a valuable resource for recreational fishermen throughout their range. In Florida, recreational fisheries land more than 100,000 fish per year, but declines in landings from 1991 to date prompted regulation (Crabtree et al., 2002) and a move towards catch-and-release of fish. As such, Belize is rapidly becoming known as a world-class flyfishing location due to its abundance of permit. The fishery is highly lucrative: flyfishers pay up to US$500 per day in Belize to catch and release a permit. This niche tourism industry has also become an economic alternative for local fishermen (Heyman and Graham[3]). Consequently, information on the timing and behavior of reproduction of permit can underpin conservation efforts that focus on a vulnerable stage in their life cycle.

[1] The IGFA (International Game Fishing Association) notes a record length for permit of 122 cm FL. 2001. Database of IGFA angling records until 2001. IGFA, Dania Beach, Florida, 33004.

[2] The United Nations notes a maximum weight of 36 kg for a permit. (Cervigón, F., R. Cipriani, W. Fischer, L. Garibaldi, M. Hendrickx, A.J. Lemus, R. Márquez, J. M. Poutiers, G. Robaina and B. Rodriguez. 1992. Fichas FAO de identificación de especies para los fines de la pesca. Guía de campo de las especies comerciales marinas y de aquas salobres de la costa septentrional de Sur América, 513 p. FAO, Rome.

[3] Heyman W. D., and R. T. Graham. 2000. The voice of the fishermen of Southern Belize, 44 p. TIDE (Toledo Institute for Environment and Development), P.O. Box 150, Punta Gorda, Belize.

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Materials and methods

Turneffe Elbow (17°09′N, 87°54′W) and Gladden Spit (16°35′N, 88°00′W) are two sites located on the Belize Barrier Reef that were monitored for abundance and behavior of many species of spawning reef fish between 1999 and 2002. Both sites are promontories with a sloping reef shelf that drops off steeply at a depth of 35–45 m to over 1000 m into the southern tip of the Cayman Trench. According to the spawning aggregation criteria developed by Domeier and Colin (1997), Turneffe Elbow and Gladden Spit attract, respectively, an estimated 13 and 27 species of reef fish that aggregate seasonally to spawn (Graham, 2003).

We logged over 270 hours of underwater monitoring of reef fish spawning aggregations at Turneffe Elbow and Gladden Spit, primarily from the full-moon to the new-moon from March to July from 2000 through 2002. Additional dives took place variously over the course of 3–5 days during the same lunar period from 1999 to 2002. Most dives for monitoring spawning aggregations took place between 0830 and 1100 hours, at midday, and between 1600 to 1730 hours of each diving day. Dives began 150–250 m north of both spawning aggregation sites and proceeded to the south along the reef platform edge. Dive depth usually began at about 30 m and decreased to 15 m as the dive progressed because of SCUBA decompression constraints. Dives normally lasted between 35 and 50 minutes. Horizontal and vertical visibility rarely dropped below 20–25 m.

Results and discussion

During 10 dive surveys (15 diving hours) at Turneffe Elbow, we observed a large school of 250 to 500 permit aggregating on the reef promontory (Table 1). The aggregated fish slowly swam into the south current along the south-facing sloping fore-reef shelf at 5–15 m depth and the steep drop-off located at ~30–35 m. The school streamed down to the spur and groove formations at about 20 m depth on the reef shelf and rose up into the upper water column again. Permit were loosely grouped and displayed little fear of divers, a behavior commonly observed among a range of other fish species that aggregate to spawn (Graham, 2003). Several individuals displayed a dark patch located above and behind the pectoral fin on both flanks. Permit displayed this same behavior coloration change during each encounter.

On 22 August 2000, 7 days after the full moon, at ~1730 (41 minutes before sunset at 1811 hours local time) we conducted our standard north to south fish census dive at a depth of ~20–30 m along the fore-reef drop off. During all dives horizontal and vertical visibility was at least 20 m and often over 40 m. We observed a school of ~300 permit descend from 5–15 m depth above the fore-reef drop-off to 25 m directly on the shelf edge. At ~1745 hours (26 min before sunset) within-group activity increased as permit schooled densely on the edge of the reef drop-off. At ~1750 hours, a subgroup of eight permit left the dense school and ascended in the water column to ~18 m depth. The lead individual initiating the ascent was ~100 cm FL and was pursued by seven fish ranging from ~55 to 75 cm FL. The pursuing fish nuzzled the larger fish's vent as it rose in the water column. All fish displayed a dark flank patch behind their pectoral fins. The lead permit then ceased its ascent at ~15 m, tilted its head down slightly and convulsed rapidly, releasing a puff of gametes. Pursuing permit tried to position their vents as closely as possible to the lead individual's while releasing their gametes. The resulting gamete cloud was less than 50 cm in diameter and dispersed within seconds (Fig. 1). Following gamete release, all fish descended quickly to the main school still located ~25 m below. Within moments this behavior was repeated and observed in two smaller groups of permit before all observations ceased because of a lack of light.

At Gladden Spit, we observed slightly different permit spawning behavior. On 7 April 2002 (10 days after the full moon), the aggregation remained in a restricted area ~100 m north of where we previously witnessed the spawning of several species of fish and ~30 m east of where we have also observed groupers *Epinephelus striatus*, *Mycteroperca tigris*, *M. venenosa,* and *M. bonaci* aggregate to spawn (Graham, 2003). Ambient water temperature was 27.7°C as measured by a temperature logger (Onset Corp. Tidbit data logger) moored at the spawning site at 30 m depth.

At least 300 permit—many of them large individuals (~70–90 cm FL)—schooled densely into a ball at ~1700 hours (66 minutes before sunset local time) near the reef shelf drop-off at a depth of ~40–48 m. Subgroups comprised five to nine fish, and the lead fish was much larger than the pursuers. Subgroups rapidly rose up on the periphery of the school, spawned at the apex of the aggregation, and descended towards the bottom of the school again. Spawning was more frenetic than that observed at Turneffe Elbow. Permit subgroups behaved in the same manner as that observed at Turneffe during spawning, and all spawning individuals displayed a large dark flank patch behind the pectoral fins.

Based on our observations of courtship and spawning behavior, our estimate of spawning season for permit in Belize may stretch from February to the end of October, beyond the period of March to September as suggested by García-Cagide et al. (2001) and Crabtree et al. (2002). Permit may also reach larger sizes than published by Crabtree et al. (2002); we estimated the largest individual permit observed at Turneffe Elbow in Belize to be ~120 cm FL, which may indicate that permit exceed a lifespan of 23 years.

We could not determine if the lead permit was female and the pursuing permit were males because no individuals were caught for gonadal analysis. However, carangids are gonochoristic and it is highly likely that the lead fish in the spawning rush was female. García-Cagide et al. (2001) noted that spawning females are often larger than mature males in several species of

Figure 1

Subgroup of eight permit (*Trachinotus falcatus*) immediately following spawning at Truneffe Elbow, Belize. The subgroup detached itself from the main aggregation to spawn in midwater at ~15 m. The larger fish led the ascent to 15 m; all fish in the subgroup hovered at that depth, released gametes, and returned to the main school at a depth of ~25 m. The arrow indicates the dark patch behind the pectoral fin that each fish sports during spawning.

reef fish. This is also supported by our observations of gonochoristic spawners such as the cubera snapper (*Lutjanus cyanopterus*) and the dog snapper (*L. jocu*) that display a pattern of group, broadcast spawning where larger females are swollen with roe and lead the subgroup spawning ascents (Graham, 2003).

Group spawning behavior in the yellow jack (*C. bartholomaei*) closely resembled that of permit. We recorded yellow jacks schooling at Gladden Spit on only two occasions (Table 1). On 7 April 2002, we observed that the yellow jacks spawned at ~1705 hours (61 minutes before sunset local time) at Gladden Spit, less than 50 m south of the school of spawning permit. The jacks schooled densely at ~40–45 m and subgroups of 5 to 8 fish detached themselves from within the school, ascending rapidly to ~35 m, releasing gametes at the apex, and descending into the school again. Observations ceased shortly thereafter because of depth constraints and decreasing light.

Not all species of carangids are group spawners. Pair spawning has been observed in species such as *C. ignobilis* and *Alectis indicus* in the Pacific (von Westernhagen, 1974) and *C. sexfasciatus* in the Gulf of California (Sala et al., 2003). We have also observed on numerous occasions pair courtship in crevalle jack (*C. hippos*), horse-eye jack (*C. latus*), and bar jack (*Carangoides ruber*) in schools exceeding 1000 fish, in rainbow runner (*Elagatis bipinnulata*) in schools of up to ~300 fish, and occasionally greater amberjack (*Seriola dumerili*) in schools numbering ~120 individuals, primarily following during the full-moon and waning moon periods between February and October (Table 1). These five species displayed extended pair courtship within and outside a large aggregation of conspecific fish as they swam along the edge of the reef drop-off. All courting pairs observed showed similar behavior. The chasing fish nuzzled the gonopore of the lead fish (whose head and upper body half had turned black but whose fins were lighter, Fig. 2, A and B) during prolonged chases, often swimming close to and at a perpendicular angle to the lead fish. *Seriola dumerili* also displayed dichromatism; the pursuing fish turned a vivid electric blue and exhibited a scrawled pattern on its upper flanks, similar to that displayed by the scrawled filefish (*Aluterus scriptus*). Occasionally, 1–10 individuals that did not display coloration changes followed the courting pairs. These five species may also pair spawn because their courtship behavior parallels that of *C. sexfasciatus*, observed by Sala et al. (2003) to spawn in pairs from the full moon to waning crescent periods from July to September. However, we did not observe any release of gametes during all pair courtship behavior.

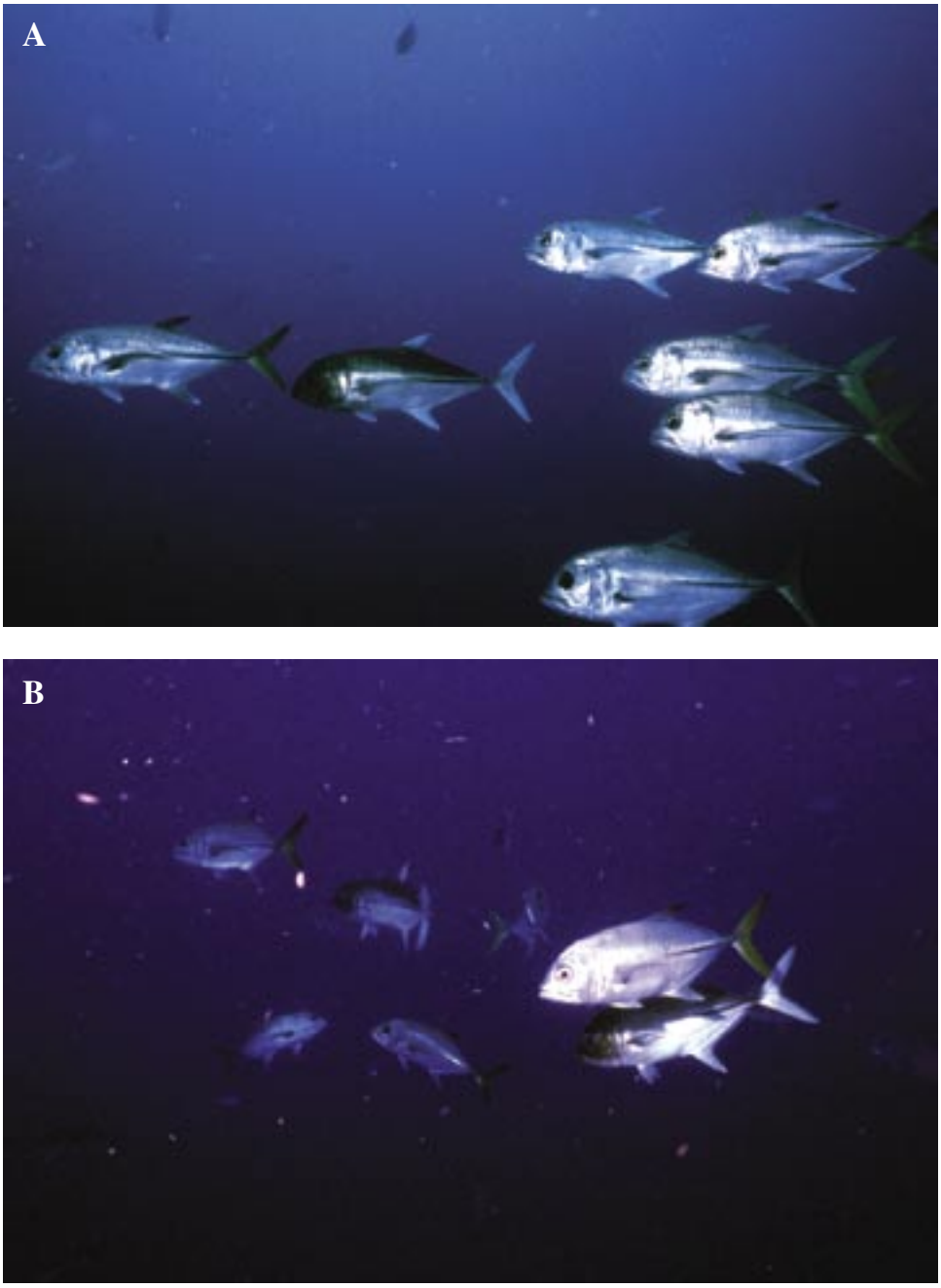

Figure 2

Pair courtship behavior in the horse-eye jack (*Caranx latus*) at Gladden Spit, Belize. The pursuing fish often swims slightly behind the lead and their flanks touch. The lead fish (**A**) remains silver colored, and the pursuing fish (**B**) takes on a very dark coloration around the head and upper flank during courtship.

Conclusions

Our observations confirm that permit spawn offshore at reef promontories that support other reef fish spawning aggregations. Permit demonstrate group broadcast spawning behavior and spawning events take place close to sunset. Further observations indicate that other species of carangids, such as yellow jack are also group broadcast spawners, occupying the same spatiotemporal spawning niche as permit. If observed courtship behav-

Table 1

Timing and lunar phase of observations on the schooling, courtship, and spawning of seven carangids at two reef promontories in Belize from April 1999 to July 2002. fm = full moon; dafm = days after full moon; dbfm = days before full moon. Sch = schooling; C = courting and color change; Spawn = spawning observed.

Date		Dive start time	Moon phase	Location	Species	Behavior
2 Apr	1999	12:04	2 dafm	Gladden	Yellow jack	Sch
3 Apr	1999	10:25	3 dafm	Gladden	Crevalle	Sch
5 Apr	1999	16:40	5 dafm	Gladden	Crevalle, horse-eye, rainbow runner	Sch
2 May	1999	16:50	2 dafm	Gladden	Bar jack, crevalle	Sch
5 May	1999	5:40	5 dafm	Gladden	Horse-eye, crevalle	Sch, C
30 May	1999	12:45	fm	Gladden	Amberjack, bar jack	Sch, C
3 Jun	1999	9:10	4 dafm	Gladden	Horse-eye, bar jack	Sch
4 Jun	1999	15:30	5 dafm	Gladden	Crevalle	Sch
30 Jun	1999	12:00	2 dafm	Gladden	Bar jack, horse-eye	Sch
27 Sep	1999	16:30	2 dafm	Gladden	Crevalle, amberjack	Sch, C
28 Sep	1999	10:50	3 dafm	Gladden	Crevalle, bar jack, horse-eye	Sch
		16:30	3 dafm	Gladden	Horse-eye, amberjack	Sch, C
24 Mar	2000	17:15	4 dafm	Gladden	Horse-eye	Sch, C
17 Apr	2000	16:25	1 dbfm	Gladden	Horse-eye, crevalle	Sch, C
18 Apr	2000	16:25	fm	Gladden	Bar jack, rainbow runner	Sch
19 Apr	2000	17:10	1 dafm	Gladden	Horse-eye	Sch, C
20 May	2000	17:00	2 dafm	Gladden	Crevalle	Sch, C
23 May	2000	16:45	5 dafm	Gladden	Amberjack	Sch, C
24 May	2000	16:21	6 dafm	Gladden	Bar jack	Sch
25 May	2000	~16:30	7 dafm	Gladden	Crevalle	Sch
26 May	2000	16:00	8 dafm	Gladden	Horse-eye, crevalle	Sch, C
23 Jun	2000	17:30	7 dafm	Gladden	Bar jack	Sch, C
18 Aug	2000	15:36	3 dafm	Gladden	Bar jack	Sch
		15:36	3 dafm	Gladden	Horse-eye, rainbow runner	Sch, C
19 Aug	2000	~12:00	4 dafm	Gladden	Bar jack, crevalle	Sch
20 Aug	2000	15:00	5 dafm	Turneffe	Horse-eye	C
		15:00	5 dafm	Turneffe	Permit	Sch
20 Aug	2000	17:00	5 dafm	Turneffe	Permit	Sch, C
		17:00	5 dafm	Turneffe	Amberjack, bar jack	Sch, C
21 Aug	2000	15:00	6 dafm	Turneffe	Crevalle, horse-eye	Sch, C
		15:00	6 dafm	Turneffe	Permit	Sch
22 Aug	2000	17:30	7 dafm	Turneffe	Horse-eye	C
		17:30	7 dafm	Turneffe	Permit	Spawn
14 Oct	2000	17:30	1 dafm	Gladden	Horse-eye, crevalle	C
15 Oct	2000	17:30	2 dafm	Gladden	Rainbow runner	C
17 Oct	2000	16:30	4 dafm	Turneffe	Horse-eye, crevalle	C
		16:30	4 dafm	Turneffe	Permit, amberjack	Sch
18 Oct	2000	16:30	5 dafm	Turneffe	Horse-eye, crevalle, amberjack, permit	C
13 Dec	2000	16:30	2 dafm	Gladden	Horse-eye	Sch
9 Apr	2001	16:00	1 dafm	Gladden	Horse-eye	C
8 May	2001	11:15	1 dafm	Gladden	Crevalle	C
9 May	2001	~10:30	2 dafm	Gladden	Crevalle	Sch
7 Jun	2001	17:00	1 dafm	Gladden	Crevalle, bar jack, horse-eye	Sch

continued

Table 1 (continued)

Date	Dive start time	Moon phase	Location	Species	Behavior
8 Jun 2001	17:00	2 dafm	Gladden	Amberjack, crevalle, horse-eye	Sch, C
9 Jun 2001	11:00	3 dafm	Gladden	Crevalle, horse-eye	Sch
10 Jun 2001	17:50	4 dafm	Gladden	Crevalle, horse-eye	Sch, C
3 Oct 2001	~17:00	1 dafm	Turneffe	Horse-eye	C
6 Feb 2002	16:00	9 dafm	Turneffe	Horse-eye, permit	Sch
7 Feb 2002	8:30	10 dafm	Turneffe	Horse-eye, permit	C
	16:30	10 dafm	Gladden	Horse-eye, crevalle, bar jack	Sch
28 Mar 2002	16:48	fm	Gladden	Crevalle, permit	Sch
	16:48	fm	Gladden	Horse-eye	C
29 Mar 2002	16:30	1 dafm	Gladden	Crevalle, bar jack, horse-eye	Sch
30 Mar 2002	16:45	2 dafm	Gladden	Crevalle, horse-eye	Sch
31 Mar 2002	16:40	3 dafm	Gladden	Horse-eye	Sch
1 Apr 2002	16:35	4 dafm	Gladden	Bar jack, horse-eye	Sch
3 Apr 2002	9:40	5 dafm	Gladden	Bar jack, horse-eye	Sch
7 Apr 2002	10:30	9 dafm	Gladden	Bar jack	Sch
	16:30	9 dafm	Gladden	Permit, yellow jack	Spawn
	16:30	9 dafm	Gladden	Bar jack	Sch
6 May 2002	9:40	9 dafm	Gladden	Horse	Sch
27 May 2002	12:18	1 dafm	Gladden	Horse-eye	C
30 May 2002	11:07	4 dafm	Gladden	Horse-eye	Sch
31 May 2002	16:20	5 dafm	Gladden	Crevalle	Sch
1 Jun 2002	16:15	6 dafm	Gladden	Bar jack, rainbow runner	Sch
2 Jun 2002	16:15	7 dafm	Gladden	Bar jack, horse-eye	Sch
29 Jun 2002	12:00	5 dafm	Turneffe	Permit, horse-eye	Sch
1 Jul 2002	15:00	7 dafm	Gladden	Bar jack, crevalle, horse-eye	Sch

ior is included, the spawning season for permit and horse-eye jacks is protracted from February through October, and the five other carangid species described in the present study spawned within this period. Protection of permit stocks throughout their life cycle, and particularly during their spawning season, underpins the associated rapidly growing and economically lucrative flyfishing tourism. Future directions of study should include a study of permit movement patterns between feeding and spawning grounds and mortality rates of catch-and-release fishing.

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