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SPAWNING AGGREGATIONS AND REPRODUCTIVE BEHAVIOR OF REEF FISHES IN THE GULF OF CALIFORNIA

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ABSTRACT

Spawning aggregations numbering up to tens of thousands of reef fishes have disappeared throughout the tropics due to fishing, causing the collapse of their populations and of commercial fisheries in many regions. Although there is a wealth of information on spawning aggregations in the Caribbean and the Indopacific, there are almost no data on spawning aggregations of commercial reef fishes in the Tropical Eastern Pacific. Here we describe aggregations and the reproductive behavior of eight species of reef fishes in the Gulf of California, Mexico. The serranids *Mycteroperca prionura* and *M. rosacea*, the snapper *Lutjanus novemfasciatus*, and the jacks *Caranx sexfasciatus* and *Seriola lalandi* form spawning aggregations of 12 to >1000 individuals on islands, exposed coastal rocky reefs, and seamounts. The serranids *Paranthias colonus* and the snapper *L. argentiventris* spawn in schools with densities similar to these during non-reproductive periods. We observed aggregations of the serranid *M. jordani* but did not observe spawning. Some spawning aggregations of these and other species (such as *Epinephelus itajara* and *Stereolepis gigas*) have now disappeared from the Gulf of California due to fishing. Our findings suggest the existence of undocumented spawning aggregations throughout the Tropical Eastern Pacific that sustain varied levels of fishing pressure. These spawning aggregations must be identified and protected in order to ensure the replenishment of fish populations.

Many species of reef fishes, including groupers, snappers, and jacks, aggregate to spawn at specific locations and times throughout the tropics (e.g., Johannes, 1978a; Carter et al., 1994; Carter and Perrine, 1994; Sadovy, 1994; Domeier and Colin, 1997). Fishers in the Indopacific and the tropical Western Atlantic have targeted these aggregations, and have accumulated a wealth of knowledge on the reproductive biology of reef fishes, often for decades to centuries (Johannes, 1978b, 1981; Sadovy, 1994). This traditional knowledge of fish reproduction served the purposes of making fisheries more effective as well as ensuring their sustainability, although in recent times this knowledge made fish populations more vulnerable to over-exploitation. Presently, understanding the reproductive biology of fishes is of paramount importance to establish minimum catch sizes, when to implement closed seasons, and where to locate marine reserves. Marine reserves, if they are to ensure the viability of fish populations, need to include the places where fishes spawn (Carr and Reed, 1993; Bohnsack, 1998; Dayton et al., 2000). The link between theory and application, however, has been hindered by the fact that these larval sources are not known for most species. Dismissing the use of these kinds of basic natural history data in fisheries management can result in accelerated depletion of exploited fish populations. The Nassau grouper provides an excellent Caribbean example of how regulations addressing minimum catch size failed by ignoring the fact that most of the fishery was carried out on spawning aggregations (DeLoach, 1999). Likewise, trawling in the Gulf of Mexico destroys habitat that is essential for the reproduction of the gag (Koenig et al., 1996). It is therefore imperative to understand where, when and how fish species repro-

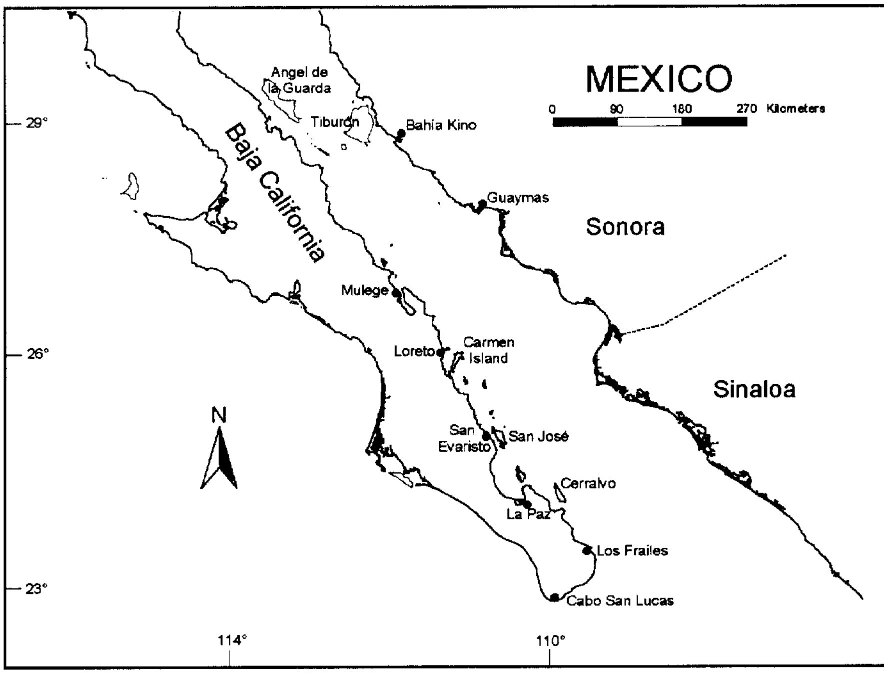

Figure 1. Map of the Gulf of California, México.

duce in order to manage fisheries adequately and develop conservation measures that ensure the replenishment of vulnerable populations. Here we present the first description of the reproductive behavior of commercial reef fishes and report on spawning aggregations of reef fishes in the Gulf of California.

The Gulf of California, or Sea of Cortés, located in northwestern Mexico (Fig. 1), is a subtropical sea which harbors an extraordinary fish fauna of approximately 900 species (Thomson et al., 2000). Although the Gulf of California has a relatively low human population density, its waters are subjected to intense commercial and sport fishing. Fisheries include commercial offshore and nearshore fisheries targeting mainly tuna, jacks, sharks, rays, groupers and snappers; and a sportfishing industry targeting pelagic species such as billfish, tuna and dorado, and reef fishes such as groupers and snappers. Despite the importance of its fishery resources not much is known about the reproductive biology of reef fishes in the Gulf of California (Thresher, 1984; Thomson et al., 2000). The objective of this study was to determine (1) whether spawning aggregations of commercial species of reef fishes occur in the Gulf of California, and (2) where, when and how these species reproduce. By obtaining information on basic natural history from local fishers and conducting diving surveys, our aim was to obtain basic information on sources of larvae to be used in the design of marine reserves.

Material and Methods

The commercial species of reef fishes we chose to focus our study on were the groupers *Epinephelus itajara*, *Mycteroperca jordani*, *M. prionura*, and *M. rosacea*; the seabass *Stereolepis* *gigas*; the snappers *Lutjanus argentiventris* and *L. novemfasciatus*; and the jacks *Caranx sexfasciatus* and *Seriola lalandi*. Although *C. sexfasciatus* and *S. lalandi* are considered pelagic species, they commonly frequent reefs; and since they are commercially important species in the Gulf of California we included them in our study. We also collected information on the creolefish *Paranthias colonus* which is commonly fished for bait in the fisheries that target the above species. We present descriptions of the behavior associated with spawning, the habitats where spawning occurs, the timing of spawning, and the existence of spawning aggregations. Additionally, when possible we also analyze the status of the fishery and of the spawning aggregations. We considered spawning aggregations to be concentrations of fish that involve abundances higher than are found during non-reproductive periods (Domeier and Colin, 1997, suggest that "any increase in density of spawning fish greater than 3-fold constitutes a spawning aggregation"). However, in this study we also included species that form aggregations throughout the year, and that spawn in densities similar to those during non-reproductive periods, because nothing was published with regard to their reproductive habitats, and because they are also commercially important species.

The study had two components: interviews with local fishers and divers, and diving surveys. Since there was no published information on the reproductive behavior of commercial reef fishes in the Gulf of California, we began by obtaining information from local fishers. Fishers represent a very useful source of knowledge with regard to spawning aggregations of fishes (Johannes, 1981). We carried out five trips to interview fishers as well as sport divers in towns and small fishing camps throughout the gulf: Cabo San Lucas, Los Frailes, Cabo Pulmo, El Sargento, La Paz, El Pardito, San Evaristo, Loreto, Guaymas, and Bahía Kino (Fig. 1). Although on a few occasions we interviewed large groups of fishers at the same time, we preferred to conduct individual interviews. After interviewing several fishers at a fishing camp we analyzed the information obtained and searched for general and consistent patterns. The interviews did not follow a rigid structure, and we never asked directly about the existence of spawning aggregations to prevent biased answers. However, we followed a method (R. Johannes, pers. comm.) consisting of introducing ourselves as scientists less knowledgeable than fishers with regard to the life of fishes, and then asking general questions about their fishery to break the tension (fishers were often reluctant to give information because they had the feeling that this information could be used for implementing regulations). After this introduction we asked about the best seasons and places for fishing, and the occurrence of reproduction of commercial species during those times.

Once we obtained consistent information about specific places, habitats, and seasons where and when commercial reef fishes spawn, we conducted diving surveys to verify this information. Although we conducted only five trips dedicated exclusively to searching for spawning aggregations, the observations presented here were obtained during 20 diving trips carried out in the Gulf of California, Mexico, from April 1994 to May 2001. Diving surveys covered all types of rocky habitats to a depth of 50 m throughout the gulf, from Isla Angel de la Guarda to Cabo San Lucas in the southernmost tip of Baja California. We covered a region of 800 km and conducted 1,321 man-dives.

Observations on fish distribution, behavior, courtship and spawning were made using SCUBA. Video camcorders (8 mm and digital) without additional illumination were used to record behavior. Fishes used for measurements and gonad collection were obtained at the aggregation sites by commercial or sport fishers.

To determine whether density of fish in these aggregations was higher than that during non-reproductive periods, we used data collected in September 1999, 2000 and 2001 as part of a long term monitoring program (unpubl. data) at the sites where we observed the aggregations. We also used data collected at other sites and times during 1999–2001 to determine the average density of these species in rocky habitats in the Gulf of California. The abundance of fish species was quantified using line-transects (Harmelin-Vivien et al. 1985). At each site, fish abundance was recorded on replicate 50×5 m transects ($n = 4$–6) using SCUBA. Each diver swam over the bottom and haphazardly chose a starting point, where it put down a weight attached to a 50 m fiberglass measuring tape. The diver unreeled the tape while swimming on a linear direction, and recorded the abundance and estimated the size of all fish species within a 5 m path on a waterproof paper sheet attached to a plastic binder. Sizes were estimated with the help of a plastic ruler attached to the binder, and pooled in 5 cm size classes.

Since fishing spawning aggregations of commercial fishes in the Gulf of California is not regulated, we believe it is not appropriate to describe here the location of the spawning aggregations we studied. As we will discuss below, several spawning aggregations of large commercial fishes have disappeared without being noticed by scientists and managers, and most of them are steadily declining in the Gulf of California. Some of these aggregations are already fished intensively, using even gillnets to surround entire seamounts and catching tons of fish in a few days. However, some of the aggregations we observed were not fished, and a few are unknown to local fishers.

Results

SERRANIDAE: *MYCTEROPERCA JORDANI*.—The gulf grouper (local names: *baya* and *garropa*), *M. jordani,* is a large grouper that can attain 150 cm, and is distributed from La Jolla, California, to Mazatlán, Sinaloa (Heemstra and Randall, 1993). Its normal color pattern is entirely gray, frequently having large ovoid, darker blotches, and occasionally dark lines radiating from the eye. The gulf grouper inhabits rocky bottoms, usually below 30 m in summer, but frequenting depths as shallow as 5 m by late fall (Thomson et al., 2000). They are more common on fields of large boulders with high availability of shelter, usually on the limit between rocky reefs and deeper sandy or muddy bottoms, and on offshore seamounts. They are voracious predators, eating slipper lobster (*Scyllarides astori*) and large fishes; on one occasion a gulf grouper was caught with juvenile (60 cm) hammerhead sharks in its stomach (Thomson et al., 2000). Fishermen report that the gulf grouper used to be commonly found in shallow waters, but that intense fishing has restricted them to deeper waters. Our surveys along the gulf show that gulf groupers are rare in the southern gulf, and more common (although not abundant) in the area of the Midriff islands. The gulf grouper is a species prized by anglers and spearfishers. Indeed, it is the target of illegal spearfishers fishing at night using lights and hooka. Fishing is presently being conducted more intensively on the Midriff Islands and in the area around Guaymas, Sonora. The species has been included in the list of species at risk of the American Fisheries Society (Musick et al., 2000).

We observed one aggregation of gulf groupers on a rocky reef in the region of the Midriff Islands below 25 m in depth, on 14 May 1994, 4 d before the full moon (Table 1). The aggregation had more than 20 gulf groupers of sizes between 100 and 150 cm. Density of gulf groupers at this aggregation was 5.5 groupers 250 m^{-2}. In other seasons, we observed a mean density of only 0.25 ± 0.25 (mean ± SE) gulf groupers 250 m^{-2} at the same site. Density of gulf groupers in rocky habitats in the Gulf of California in 1999–2001 was 0.02 ± 0.01 groupers 250 m^{-2}. The habitat where the aggregation occurred is a rocky reef of abrupt relief, with overhangs and large rocks, colonized by gorgonians (*Muricea* spp.) and black coral (*Antipathes galapagensis*). The groupers exhibited instantaneous color changes associated with presumed courtship, from the normal dark gray coloration with darker blotches and lines radiating from the eye, to a distinct lighter gray coloration with a white patch below the dorsal fin, light fins, and dorsal, anal and caudal fins with black margins (Fig. 2). The color changes were realized in less than a second. No spawning was observed, probably because no observations were made at dusk, the usual time of spawning in groupers (Johannes, 1978). Although no spawning

Table 1. Characteristics of aggregations of commercial reef fish species in the Gulf of California. Asteriscs indicates spawning aggregations with fish densities larger than during non-reproductive periods. See text for more detailed descriptions.

Species	Depth (m)	Habitat	Duration (d)	Months of formation	Sign of spawning	Time of spawning	Lunar phase	Fish numbers	Area (m^2) of aggregation
*Caranx sexfasciatus**	10–20	Offshore islands	?	Jul–Sep	Spawning observed	All day	Full	500–1,500	10,000
Lutjanus argentiventris	15	Rocky reefs, boulders	?	May–Jun	Spawning observed	Dusk	Last quarter	>30	500
*Lutjanus novemfasciatus**	20	Offshore reefs	?	Sep	Spawning observed	Afternoon	Last quarter	12	500
*Mycteroperca prionura**	20–40	Rocky reefs, boulders	7	Apr–May	Hydrated eggs	?	First to last quarter	14–100	600
Mycteroperca jordani	20–35	Rocky reefs, boulders	?	May	Not observed	-	Around full	7–20	1,000
*Mycteroperca rosacea**	5–20	Rocky reefs, seamounts	?	Mar–May	Hydrated eggs	?	New–full	100–400	1,000–10,000
Paranthias colonus	5–25	Seamounts, rocky reefs	?	May	Spawning observed	Afternoon	Full	> 1,000	1,000–10,000
*Seriola lalandi**	10–20	Rocky reefs, seamounts	?	Apr	Hydrated eggs	?	Full	80	>10,000

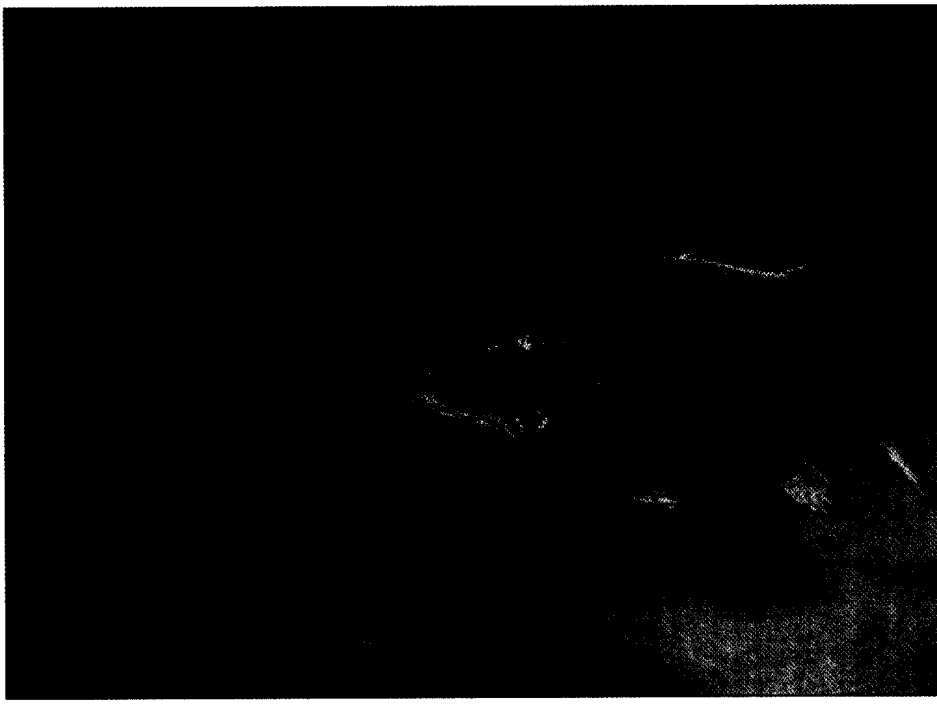

Figure 2. Gulf grouper, *Mycteroperca jordani*, (1.5 m total length) exhibiting conspicuous dark lines radiating from the eye.

was observed, we assume this was a spawning aggregation because of the presumed courtship behavior and the unusually high abundance of gulf groupers at the site (more than 20 times the density observed during other periods).

Additional instances of rapid changes in coloration in gulf groupers were observed in a non-aggregation setting within days around the full moon in May 2001, on two seamounts between 20 and 30 m depth. We observed up to three gulf groupers on each seamount, but no obvious intraspecific interactions. However, one of the biggest groupers (140 cm) exhibited a coloration consisting of gray body, white dorsal and anal fins, a snow white semicircular patch below the dorsal fin, and conspicuous dark lines radiating from the eye (Fig. 2). These patterns of color change were similar to those exhibited by other species in the genus *Mycteroperca* (Gilmore and Jones, 1992).

We observed two other aggregations of gulf groupers in the southern Gulf of California in May 2000, 4 d after the full moon (Table 1). One of these aggregations was on a steep sandy slope with large scattered rocks at 20–25 m, and was composed of seven individuals. A spearfisher caught four gulf groupers at this site that same year, the sizes ranging from 69 to 118 cm. No gonads were made available for examination. The other aggregation was located on a rocky reef at 10 m depth, subjected to strong surge, and only 100 m away from shore. This aggregation was composed of seven individuals, with six individuals measuring about 80 cm, and one of 1 m in length. Groupers in these two aggregations were swimming frantically, although we did not observe any color changes or interaction between individuals.

SERRANIDAE: *MYCTEROPERCA PRIONURA*.—The sawtail grouper (local name: *pinta*), *M. prionura*, is a large grouper growing up to 1 m in length which ranges from the Midriff Islands to Southern Jalisco (Heemstra and Randall, 1993). Its normal coloration is whitish, with a combination of small brown-red spots and large oval brown blotches. The sawtail grouper inhabits rocky bottoms to a depth of 50 m, being more common on fields of large boulders colonized by gorgonians (*Muricea* spp. and *Pacifigorgia* spp.) and black coral (*Antipathes galapagensis*). They are more abundant in the central and northern gulf than in the southern gulf. There are no previously published studies on the biology or the ecology of this species. The sawtail grouper has been included in the list of vulnerable species of the American Fisheries Society (Musick et al., 2000). It is an appreciated food species, although presently its abundance is so low that it does not support a specific fishery. The main fishing threats include illegal spearfishing using lights and hooka at night, which takes place from La Paz to the Midriff Islands.

We located two aggregations of sawtail grouper, one in the southern Gulf of California and another in the central gulf. The smallest aggregation (14 individuals) occurred on an island at 20–25 m depth, on 25–27 May 2000 (waning crescent) (Table 1). The sawtail groupers were concentrated in a small area of approximately 600 m^2. We dived on the same spot on 13 June 2000, but the groupers had already left the site. We observed only one sawtail grouper at the same site during other months of the year. Density of sawtail groupers in rocky habitats in the Gulf of California in 1999–2001 was 0.02 ± 0.01 (mean ± SE) individuals 250 m^{-2}. The groupers aggregated on a rocky reef with spectacular relief, formed by large rocks up to 10 m in height and 12 m in diameter over a sandy bottom at 25 m with a 15° slope, which became very steep (>40°) at about 35 m. The reef was colonized by high numbers of gorgonians, mainly *Muricea apressa* and *M. hebes*. The size range of the individuals aggregating at this site was estimated from 40 to 80 cm in length, with a mean size of 66 cm. Most individuals spent the day swimming around the top of a large rock. One individual of about 70 cm had a distinct coloration with dark head (Fig. 3). We observed putative courtship behavior where two individuals (75 and 80 cm in length) approached swimming in opposite directions; when both fishes were side by side, one of them tilted sideways, shaking the anterior part of the body for a few seconds. After this interaction the fishes swam away and remained at several meters from each other. About ten individuals were swimming around the flat top of that large rock, and remained stationary for several minutes at a time. We did not observe spawning at this site.

The second aggregation we observed twice, on 3 April 1994 and 16–17 April 2000 (Fig. 3, Table 1). The first date corresponded to the waning crescent phase of the moon, whereas the second dates were the 2 d before the full moon. In April 2000 the aggregation disappeared four days after the full moon. This aggregation occurred on a field of large boulders between 20 and 40 m depth, the limit between the rocky shore and a deeper sandy bottom, on an area of approximately 1 ha. The rocks were dominated overwhelmingly by black corals, although there were numerous smaller suspension feeders such as sponges, tunicates, gorgonians and hydroids. In April 1994, the aggregation had about 100 sawtail groupers (mean ± SE, 5.00 ± 0.63 groupers 250 m^{-2}), whereas in April 2000 we censused about 70 groupers (4.50 ± 0.56 groupers 250 m^{-2}). Density of sawtail groupers at the same site during other times was 0.17 ± 0.17 individuals 250 m^{-2}. Individuals were between 56 and 90 cm, with a mean size of 74 cm. Examination of eight females in April 2000 showed full gonads with hydrated eggs, which indicates this is a spawning

Figure 3. Field of black coral (*Antipathes galapagensis*) harboring a spawning aggregation of the sawtail grouper, *Mycteroperca prionura*. Note several groupers swimming among black corals and two yellowtail jacks (*Seriola lalandi*) on the background.

aggregation. Most individuals in the aggregation had enlarged abdomens and a few individuals exhibited a dark headed color phase (Fig. 4). The main observed interaction between individuals consisted of the head tilts side by side. We also observed a big grouper (90 cm) chasing away smaller individuals, both with normal coloration, with head tilts for a few meters, and then swimming back to where the chase started. At the very moment when the chase ceased both groupers flashed a dark head for a couple of seconds. During the day, sawtail groupers were swimming between boulders and several meters above the bottom, covering a distance of less than 100 m. No individuals were observed in similar types of bottom anywhere else nearby, which suggests that the spawning site is very restricted in space.

Because of the high productivity of the region during April–May, the upper 10 m had a phytoplankton bloom. Although the water was clear below that upper plankton layer, when we dived at dusk it was too dark to see effectively, and spawning was not observed.

SERRANIDAE: *MYCTEROPERCA ROSACEA*.—The leopard grouper (local name: *cabrilla sardinera*), *M. rosacea*, grows up to 1 m. It is by far the most abundant and intensely fished grouper in the Gulf of California. Its normal coloration is gray-brown with numerous small brown spots; on the upper half of the body there are irregular dark saddles with narrow whitish streaks between them (Allen and Robertson, 1994). A small percentage of leopard groupers are entirely golden yellow (golden phase). We have observed golden individuals from 18 to 80 cm in length. The leopard grouper is distributed from Bahía Magdalena on the Pacific coast of Baja California throughout the gulf from the northernmost rocky reefs (Rocas Consag) to southern Jalisco (Thomson et al., 2000). The leopard grouper inhabits preferentially rocky bottoms down to a depth of 50 m. Adult groupers feed upon other fishes, and seasonally (between February and May–June) they attack

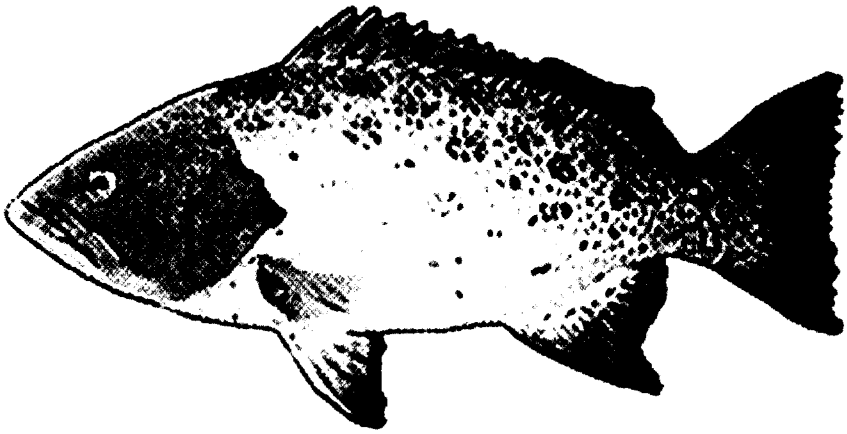

Figure 4. Dark head phase of the sawtail grouper, *Mycteroperca prionura*.

schools of sardines (*Harengula thrissina*) and anchovies (*Cetengraulis mysticetus*) (Hobson, 1968; Parrish, 1992). Fishers knew the locations of many of these feeding aggregations. Several spawning aggregations in the southern and central Gulf of California are presently fished using gillnets, and using a diver to circle the fish.

Our examinations of fished individuals suggests that males (mean length ± SD, 41.5 ± 10.4 cm, n = 34) have smaller sizes than females (46.7 ± 8.3 cm, n = 24; t-test, $P < 0.001$). Thomson et al. (2000) report that recent examinations of gonads show that the leopard grouper is gonochoristic, in contrast with the typical pattern of epinepheline groupers. The proportion of sexes in any population is not known. There seems to be a higher proportion of males in fisheries catches, but this dominance in the catch could be an artifact of the more aggressive feeding behavior exhibited by males.

Leopard groupers aggregate to spawn on exposed islets, rocky promontories and capes between 5 and 20 m close to sharp drop-offs, shallow rocky reefs (<20m) surrounded by sand close to islands, and shallow seamounts (with the top shallower than 20 m) (Table 1). The bottoms where spawning aggregations occur encompass fields of medium to large boulders and rocky reefs colonized by fleshy algae (dominated by a few species of the seasonal brown alga *Sargassum*) and/or gorgonians (mainly *Muricea* spp.). We have located 13 spawning aggregations of leopard grouper in the Gulf of California, from the bay of La Paz to the Midriff Islands, however the amazingly high abundance of juveniles along the entire gulf (authors' unpubl. data) suggests that they must aggregate to spawn in many other places. The observed aggregations encompassed from 100 to > 400 individuals, with densities varying from 15.75 ± 2.07 (mean ± SE) to 22.25 ± 2.68 groupers 250 m^{-2}. Average density of leopard groupers in rocky habitats in the Gulf of California during 1999–2001 was 5.08 ± 0.43 groupers 250 m^{-2}. Leopard groupers with enlarged abdomens were obtained at all the aggregation sites. They contained hydrated eggs, which indicates that all the studied aggregations are spawning aggregations. Fishers who indicated to us the location of most of the studied aggregations already knew that leopard groupers were spawning at these sites during that time. Spawning activity occurred around

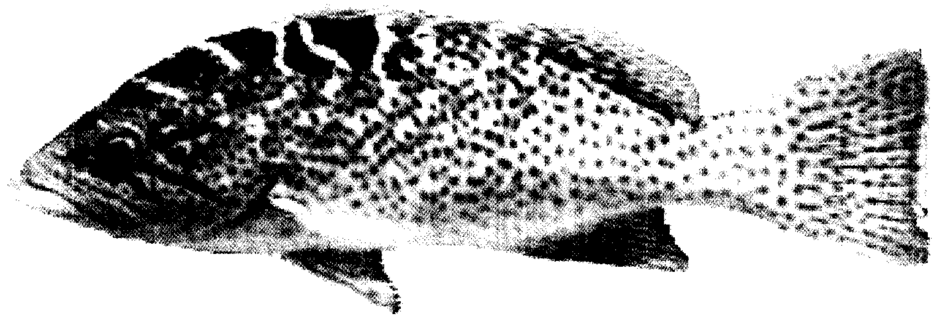

Figure 5. Color phase of leopard groupers, *Mycteroperca rosacea*, exhibited during territorial pre-spawning behavior.

both new and full moons. The timing of spawning shifted latitudinaly, with leopard groupers in the southern gulf spawning from March to May, and groupers in the Midriff Islands spawning only in May.

Leopard groupers form feeding schools of up to several tens of individuals at dusk throughout the year, and do not appear to be territorial. However, during the spawning season a few presumed males of about 50 cm in length exhibited a striking coloration and were more active than other conspecifics. Their coloration was distinct with a pale ventral and posterior half of the body and fins, and brown blotches in the anterior upper half of the body, which was darker than usual, contrasting strikingly with the light rings around the blotches. They also exhibited darker blotches around the eye, in some cases forming a radiating pattern (Fig. 5). Leopard groupers exhibiting the golden phase (Thomson et al., 2000) were observed in the aggregations, although there were at most one or two golden individuals per aggregation. The presumed males had abdomens from slightly to clearly enlarged, whereas larger individuals had clearly enlarged abdomens. Larger individuals spent most of their time swimming from near the surface to the bottom, or remaining stationary in the water column. Leopard groupers were observed feeding on small pelagic fishes during that time. During spring 1999, when the Gulf of California was subjected to La Niña conditions with colder water rich in nutrients, leopard groupers fed upon clouds of mysid shrimps. Groupers swam slowly between gorgonians, and suddenly swam up with mouth agape to swallow hundreds of mysids. Therefore enlarged abdomens in smaller groupers could be caused by feeding.

During the day, presumed males displayed aggression towards other individuals with similar size and similar or normal coloration, chasing them away if they entered their territories. Territories were 10 to 20 m wide. The bodies of these presumed territorial males were slightly bent laterally in an angle of about 20°. Sometimes these individuals carried out fast rises of about 6 m in height without interacting with any other grouper, coming back to the bottom as suddenly as they rose. These territorial males did not exhibit any aggressive behavior towards bigger females. When males and females interacted during the day, males either ignored females or exhibited a courtship where the male first approached the female with a lateral display, swimming in the opposite direction. When both fishes were side by side, the male tilted sideways in an inclined position, shaking the head. After a few seconds, females usually swam away slowly.

At dusk, the aggressive behavior of presumed males ceased, and most individuals started swimming towards the surface in a swimming frenzy where groupers swam up and down at high speed. Leopard groupers became extremely wary at that time and did not allow us to approach. Since most of our observations were carried out in years and seasons with high concentration of nutrients, the upper 10–15 m had rich phytoplanktonic communities and hence there was very poor visibility at dusk. Thereby we were not able to observe the spawning proper.

SERRANIDAE: *PARANTHIAS COLONUS.*—The Pacific creolefish (local name: *verdillo*), *P. colonus*, growing to at least 36 cm, is the most abundant fish at many rocky reefs in the Gulf of California (Thomson et al., 2000). It has a salmon-red color, darker on the upper half, and a row of five light spots. The creolefish is distributed from Southern California to Peru and the Galápagos Islands (Heemstra and Randall, 1993). This species is commonly fished on seamounts and exposed rocky reefs subjected to strong currents. It was first fished as bait for large fishes such as other groupers, but recently it is fished for food because larger fishes are increasingly rarer in some locations.

P. colonus forms schools of >1000 individuals throughout the year, mainly on seamounts and steep rocky reefs. Although these aggregations cannot be considered spawning aggregations following the definition of Domeier and Colin (1997), we included them in this study because reproduction of the Pacific creolefish was not described, and it is a species targeted by fishers. In May 2000 and 2001 we observed the reproduction of *P. colonus* within two days before and after the full moon on a seamount and an offshore islet in the southern Gulf of California (Table 1). Courtship started during daylight (3 pm) either on a school in the water column or on the bottom (20–25 m depth), where groups of 3–6 individuals gathered and swam in one direction. Courtship involved changes in coloration among the following three phases: (1) normal red coloration, (2) dark body where the five light spots stand out, and (3) light body with dark irregular spots. After initial formation of groups, schools of 8–20 fish gathered in the water column, swimming and approaching each other. These small schools united and separated several times. After several such interactions, a group of 8–20 fish swam towards the surface and spawned at about 15 m above the bottom (Fig. 6). Some solitary individuals swimming close to the spawning groups joined the group and spawned. About 10 groups of fish participated in the spawning. These spawning rushes were repeated frequently (up to 3 groups spawning in 20 s). We observed cannibalistic behavior when the emission of gametes was followed by predation of eggs by a couple of adult *P. colonus*. We also observed three *M. jordani* (>80 cm in length) attacking reproductive adults of *P. colonus* on one of the spawning schools on a seamount.

SERRANIDAE: *EPINEPHELUS ITAJARA* AND POLYPRIONIDAE: *STEREOLEPIS GIGAS.*—Fishers in fishing camps south of La Paz reported the historical existence of spawning aggregations of the goliath grouper *E. itajara* and the black sea bass *S. gigas* in the southern Pacific coast of Baja California. These aggregations have now been extinguished as no groupers have been seen returning to these spawning sites. *S. gigas* are fished only in the northern gulf presently, in the region of the Midriff Islands. *S. gigas* also forms spawning aggregations in the coast of California (Domeier, in press). Our interviews also revealed that *E. itajara* has not been fished or observed in most of the gulf since 1995. However, both species are still fished on the Pacific coast of Baja California.

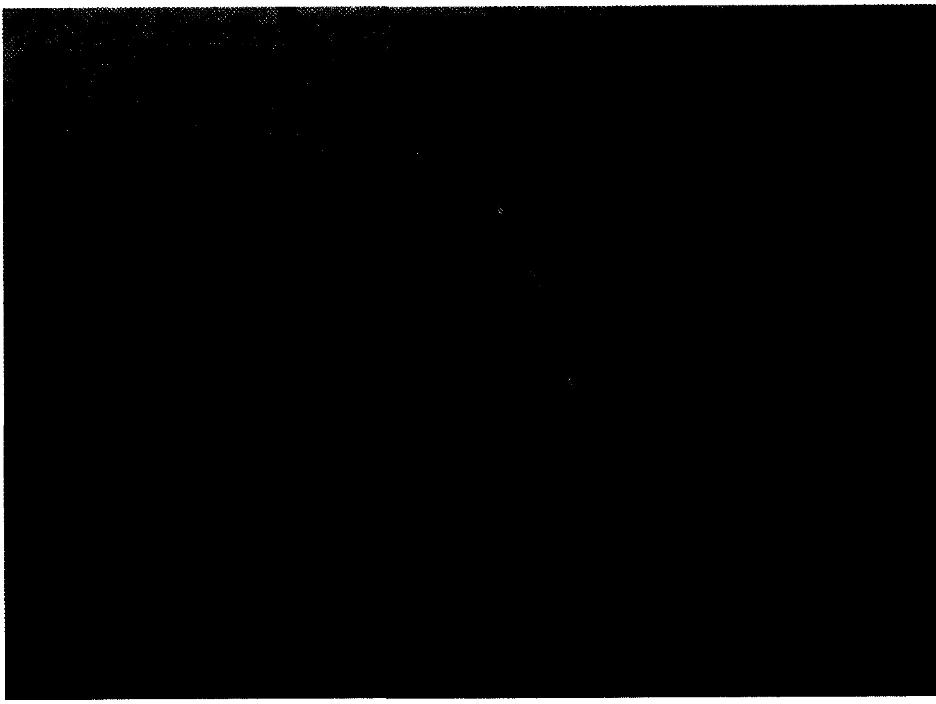

Figure 6. Group spawning of the creolefish *Paranthias colonus* over a seamount at a depth of 10 m. The larger aggregation of creolefish appears on the background.

CARANGIDAE: *CARANX SEXFASCIATUS*.—The bigeye crevalle jack (local name: *jurel*), *C. sexfasciatus*, is a pelagic predator that can reach 80 cm. It is iridiscent blue-green on back, shading to silvery white below (Allen and Robertson, 1994). This jack is distributed widely in the tropical Indo-Pacific. The diet of this species consists of shrimp, mantis shrimp, and small fish and fish larvae. It is a species of commercial importance, fished using spearfishing, hook and line, gillnets, and longlines throughout the year. Fishermen told us that in some locations they gillnet spawning aggregations that occur on seamounts, since seamounts are relatively easy to encircle with the nets. The total catch of jacks in the gulf sums up to 900 t annually (Mexico's Fisheries Statistics), although we cannot be sure how many correspond to the bigeye crevalle jack, since all jacks are pooled into a single category in the fisheries statistics.

The bigeye crevalle jack forms stationary schools of up to thousands of individuals during daylight. These schools travel throughout the gulf, and it is unlikely to see them in the same reef for more than a few weeks. In the Gulf of California, these schools aggregate at specific reefs in summer to spawn. From July to September 1998–2000 we observed one spawning aggregation of varying size between 500–1500 individuals between 60 and 80 cm in length on an offshore islet (Table 1). During the rest of the year individuals of this species are seldom seen, thus confirming this is a spawning aggregation (sensu Domeier and Colin, 1997). In all of our observations, visibility was about 30 m, there were 4-kt currents with varying direction, and water temperature was between 28 and 31°C. Observations of reproductive behavior were conducted daily from the full moon to

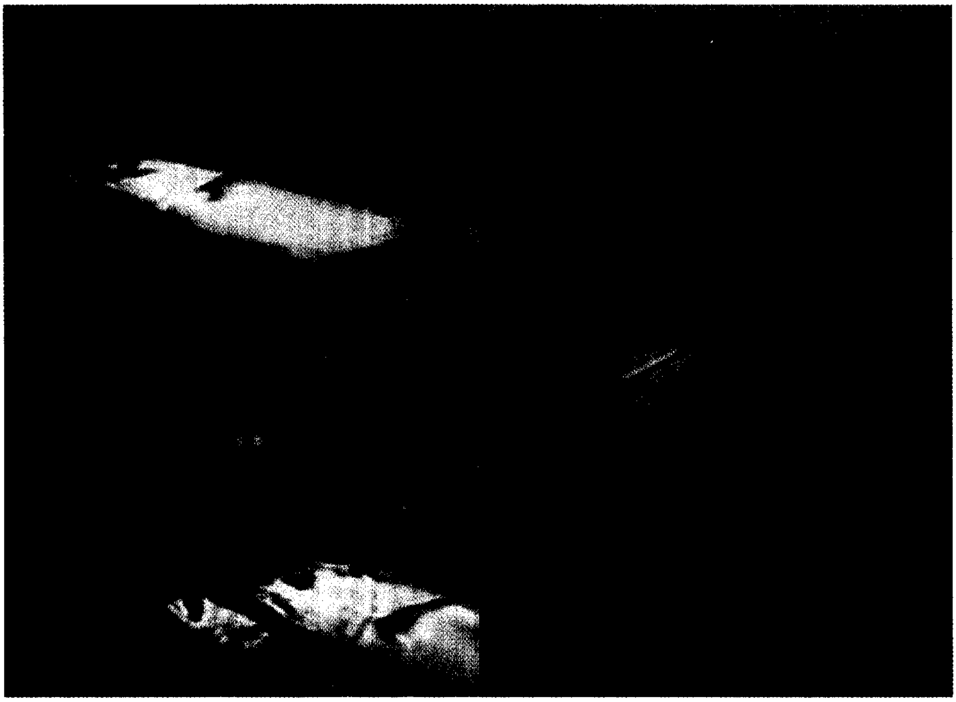

Figure 7. Reproductive behavior of the bigeye crevalle jack *Caranx sexfasciatus*: (a) Pairs of jacks leaving a spawning aggregation, showing both normal and dark phase; (b) a pair of *C. sexfasciatus* swimming prior to spawning.

the waning crescent. The aggregation was composed of one or two main schools swimming in compact formation. The coloration of the jacks was the normal silvery-gray. Almost continuously and during daylight, several pairs left the school in different directions. At one moment in time, there were 30 pairs leaving the school. One of the individuals in the pair swam on the side and below the other. The jack below became entirely black in less than a second (Fig. 7). This color change has been observed in other jacks during reproduction in South Africa (Talbot and Williams, 1956) and Palau (Johannes, 1981). Pairs swam at different speeds, both slowly and fast. Occasionally, 2–3 silver individuals left the school swimming towards a pair that just left the big school. The black individual immediately left the pair and chased the jacks that were approaching, going back to its partner right afterwards. We observed fish spawning in pairs, where the jacks pressed their ventral surfaces together and spawned, then returning to the big school. We did not observe mass spawning involving the entire school. During the day the school stayed between 10 and 20 m in depth over a bottom of 30 m, and in the late afternoon the school moved to offshore, deeper waters, hence our observations were made only when the school was in shallow waters.

CARANGIDAE: *SERIOLA LALANDI*.—The yellowtail amberjack (local name: *jurel de castilla*), *S. lalandi*, is a fast-swimming, pelagic jack that grows to at least 150 cm. The yellowtail is an elongated fish with blue upper back, sides and belly silvery to white, a narrow bronze stripe along the middle of the body, and yellowish fins (Allen and Robertson, 1994). The yellowtail is circumglobal in temperate and tropical waters, and is very prized among anglers. In the gulf, they are caught near rocky points, and on drifting offshore rafts of the brown alga *Sargassum*. In the southern and central gulf, several spawning aggregations are circled and fished using gillnets and a diver.

Female yellowtail mature at 698 mm fork length in Australia (Gillanders et al., 1999), between 580 and 670 mm in New Zealand (McGregor, 1995), and at 506 mm in California (Baxter, 1960). All *Seriola* species studied to date appear to be spring-summer spawners (Gillanders et al., 1999). In southern Africa, they appear to exhibit migrations to spawning grounds (Garratt, 1988).

Yellowtail school offshore, near islands and on seamounts at different times of the year throughout the Gulf of California. We observed one aggregation of yellowtail around an island in the central gulf on 15–17 April 2000 (starting three days before the full moon) (Table 1). The aggregation was composed of approximately 80 individuals (mean density ± SE, 2.00 ± 0.64 yellowtail 250 m^{-2}), of sizes ranging from 75 to 105 cm. We did not observe any change in coloration or interaction between individuals, mainly because of the poor underwater visibility conditions. However, macroscopic examination of five ripe individuals confirmed that gonads were full, and eggs hydrated. We examined two males (98 and 102 cm), which released sperm profusely on the deck when their bellies were pressed. The other three individuals caught were females (77, 98, and 101 cm) with hydrated eggs 1 mm in diameter. Density of yellowtail at the same site during other times was 0.00 ± 0.00 (mean ± SE) fish 250 m^{-2}. Average density of yellowtail in rocky habitats in the Gulf of California during 1999–2001 was 0.003 ± 0.003 ind 250 m^{-2}. Therefore we can confirm that the studied aggregation was a spawning aggregation.

LUTJANIDAE: *LUTJANUS ARGENTIVENTRIS*.—The yellow snapper (local name: *pargo amarillo*), *L. argentiventris*, is the most common snapper in the Gulf of California. It has a rose anterior half body, and pale yellow to golden posterior half, and can grow to 66 cm. The yellow snapper is distributed from the Gulf of California to Peru, inhabiting rocky bottoms down to at least 60 m in depth (Thomson et al., 2000), and feeds upon fishes, crustaceans and mollusks. Juvenile yellow snappers are found exclusively in mangroves, coastal lagoons, and very sheltered bays. This species is fished from May to September using hook and line, spearguns, longlines, and gillnets. Fishermen report aggregations of several hundred ripe individuals in May and June in the southern gulf.

Thomson et al. (2000) report activities presumably related to courtship during winter months when large adults dart in and out of small caves. We have observed this kind of behavior repeatedly and can confirm that it is related to spawning. Yellow snappers may be solitary, hiding in crevices or caves, or may form small schools, always near shelters. However, in May 25, 2000 (last quarter of the moon) we saw, during daylight, a school of 30 ind (mean ± SE, 16.00 ± 1.29 snappers 250 m^{-2}) swimming frenetically in and out of a crevice on a large rocky reef at a depth of 15 m, in the southern Gulf of California (Table 1). At dusk, within 1 h before sunset, yellow snappers rushed towards the surface to group spawn, then returned to the crevice. We observed gamete release near the surface. Snappers formed a sort of a living conveyor belt between the crevice and shallow waters: as some snappers swam towards the surface, some others swam back into the crevice. Density of yellow snappers at the same site during other times was 9.50 ± 3.87 snappers 250 m^{-2}. Average density of yellow snappers in rocky habitats in the Gulf of California during 1999–2001 was 2.23 ± 0.36 snappers 250 m^{-2}. Although density of yellow snappers at the aggregation site was twice the average density observed during non-reproductive periods, it cannot be considered a spawning aggregation proper following the definition of Domeier and Colin (1997), who suggest that a spawning aggregation must show a 3-fold difference in density. In any case, the yellow snapper aggregates to spawn at densities larger than those during non-reproductive periods.

LUTJANIDAE: *LUTJANUS NOVEMFASCIATUS*.—The Pacific dog snapper (local name: *pargo dentón*), *L. novemfasciatus*, is the largest snapper in the Gulf of California, growing to 100 cm. The dog snapper has large canine teeth, olive-brown to copper red body, and 8–9 dusky bars on the upper half (Allen and Robertson, 1994). It is distributed throughout the Gulf of California to Peru, inhabiting rocky reefs to a depth of at least 60 m. Juveniles inhabit mangroves, coastal lagoons, and very sheltered bays. The dog snapper feeds on large invertebrates (mantis shrimps, crabs) and fishes. Juvenile dog snappers feed upon larvae of other fishes in the habitat provided by roots of mangroves. It is a species very appreciated commercially and is fished with nets and spears.

Large dog snappers commonly inhabit bottoms of large boulders, rocky walls with profusion of shelter, and seamounts. We observed spawning on a vertical wall located at 20 m on an offshore islet in the southern Gulf of California. The spawning occurred during daylight (2 pm) on 21 September 2000 (last quarter of the moon), and involved a school of 12 snappers in an area of approximately 500 m^2 (Table 1). Snappers were between 70 to 90 cm in length, and displayed two distinct colorations: a very dark grayish body, and a dark body with pale ventral sides. Usually dog snappers swim quickly into shelter when surprised by divers, but in this occasion they remained outside the rocky wall, oblivious to the presence of divers. The snappers were schooling outside the wall, and one of them left the school and swam to the bottom. This individual remained stationary 1 m above the rocky bottom at the base of the vertical wall at 20 m, and was then approached by two smaller individuals. Before the smaller snappers reached the large snapper, the latter started to swim quickly along the bottom. Once the small snappers reached the large snapper, they got side by side, and the two smaller snappers pressed their ventral sides against both sides of the large snapper in a horizontal position. After only a few seconds of ventral contact they spawned, then slowed down and separated calmly swimming in different directions, and eventually returned to the school. The entire process lasted less than 30 s. Immediately after the first spawning event, another group of three snappers left the school and spawned. We observed four group spawning events, involving all individuals in the school. After these four spawnings, the school dispersed and we did not observe it again. Density of dog snappers at the same site during other times was 0.33 ± 0.21 snappers 250 m^{-2}. Average density of dog snappers in rocky habitats in the Gulf of California during 1999–2001 was 0.13 ± 0.05 snappers 250 m^{-2}. Since density of snappers at the spawning site was 18 times higher than density during non-reproductive periods, we can confirm this aggregation was a spawning aggregation.

DISCUSSION

Here we report the existence of spawning aggregations of large commercial reef fishes in the Tropical Eastern Pacific. The only spawning aggregations of commercial fishes previously described for the Gulf of California were these of large Sciaenidae such as the totoaba, which spawn on soft shallow bottoms near the delta of the Colorado River (Barrera-Guevara, 1990; Cisneros-Mata et al., 1995).

In the Gulf of California, the serranids *M. prionura* and *P. colonus*, the jacks *C. sexfasciatus* and *S. lalandi* spawned around the full moon, although aggregations of *M. prionura* and *C. sexfasciatus* were observed at least until the last quarter. In contrast, the spawning of *M. rosacea* did not show any clear relationship with moon phases, and *L. argentiventris* and *L. novemfasciatus* were observed spawning during the last quarter. The weak relationship between spawning and the phases of the moon in the Gulf of California might be attributable to the fact that tidal amplitudes commonly associated with full and new moons in the tropical Pacific (Johannes, 1978) are not as important in the southern and central gulf. Carter and Perrine (1994) found a similar pattern on the timing of aggregations of *Lutjanus jocu* in Belize. In the Gulf of California, other factors such as duration of the day or temperature may be important in triggering spawning of the species investigated in this study.

The leopard grouper *M. rosacea* was found to spawn at different times in different regions of the gulf. *M. rosacea* spawns first in the south of the gulf, and spawning is delayed in sites situated farther north. These observations suggest that spawning is related to temperature, since warming of sea surface is also delayed along the latitudinal gradient. Similar latitudinal patterns have been found for the Nassau grouper, *E. striatus*, in the Caribbean. *E. striatus* spawns in December and January in the Bahamas, in January and February in the Cayman Islands, and in May and July in Bermuda (Bardach et al., 1958; Colin, 1992; Carter et al., 1994). We speculate that temporal patterns of spawning in *M. rosacea* might change as a function of the oceanographic climate, since the Gulf of California is subjected to significant interannual fluctuations in oceanographic conditions (mainly El Niño and La Niña). This implies that fisheries regulations for *M. rosacea* that take into account reproductive seasons have to incorporate variations in the timing of spawning from year to year.

The reproductive behavior of reef fishes is well known by, and has become an important part of traditional fishing cultures (Johannes, 1978b, 1981). Fishers have targeted spawning aggregations of reef fishes and wiped them out in many places in the Caribbean and the Indo-Pacific. However, in some Pacific islands local fishers understood the importance of protecting the aggregations for the viability of the fish populations and for the sustainability of their fisheries, and thus held fishing the spawning aggregations as a taboo (Johannes, 1978b, 1981; Johannes et al., 1999). In the Gulf of California, only the Seri people, centered in the coast around Tiburón Island in the area of the Midriff Islands, have a secular fishing tradition. In the rest of the gulf, and especially in Baja California, reef fish fisheries are a relatively modern activity. Although a pearl fishery started in the early XVI century and subsistence fishing may have occurred for centuries among indigenous peoples, commercial fisheries of reef fishes date only from the XX Century (Cariño Olvera, 1996). Although multigenerational knowledge is lacking in the coast of Baja California, local fishers have been effective at locating and targeting spawning aggregations of groupers, jacks, and snappers.

A number of spawning aggregations of large reef fishes may have disappeared without being noticed by biologists and fisheries managers. As we gathered from interviews with fishers in the southern Gulf of California and the southern Pacific coast of Baja California, there used to be spawning aggregations of the groupers *Epinephelus itajara* and *Mycteroperca jordani*, which have now disappeared. *E. itajara* has not been fished in most of the gulf for 5 to 10 yrs, and *M. jordani* and *M. prionura* are fished mostly in the central gulf where fishing pressure has not been as high as along the coast around La Paz and Cabo San Lucas. However, a few spearfishers still target one aggregation of *M. jordani* in the southern gulf. In contrast, it appears that spawning aggregations of *M. prionura* are mostly unknown by commercial fishers, although targeted by sportfishers. In many places, young fishers had no knowledge of fisheries of large groupers that are now rare or non-existant.

Since there are no historical data on spawning aggregations of the species we investigated, we cannot determine what the pre-fishing sizes of these aggregations were. However, the large differences in abundance between present aggregations suggest that some aggregations are in a critical state. Of the two aggregations of *Mycteroperca prionura* we observed, the aggregation located near a large fishing community had only 14 individuals whereas the aggregation located in a more remote island had 100 individuals in 1994, and 70 individuals in 2000. The average size of the *M. jordani* observed during our dives in the southern gulf is >80 cm, suggesting that successful reproduction and recruitment may not have occurred for many years. All species of groupers investigated in this study except the abundant *M. rosacea* were included in the list of species at risk of the American Fisheries Society (Musick et al., 2000).

The previous absence of reports on spawning aggregations of large reef fishes in the Tropical Eastern Pacific might be simply a consequence of the lack of studies designed specifically to describe spawning aggregations. It would not be surprising if we found other species of large groupers and snappers form spawning aggregations throughout the Eastern Pacific. And evidently, the species investigated in this study must aggregate to spawn in other regions as well. To prevent the disappearance of spawning aggregations of large reef fishes, as has been the case in the Caribbean (Sadovy, 1994; Colin, 1996), spawning aggregations in the Tropical Eastern Pacific must be identified and monitored. Furthermore, they should be included in marine reserves that should serve as sources of larvae to ensure the replenishment of the populations of these large vulnerable species.

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Literature Cited

Allen, G. R. and D. R. Robertson. 1994. Fishes of the Tropical Eastern Pacific. Univ. Hawaii Press, Honolulu. 332 p.

Bardach, J. E., C. L. Smith and D. W. Menzel. 1958. Bermuda fisheries research program final report. Bermuda Trade Development Board, Hamilton. 59 p.

Barrera-Guevara, J. C. 1990. The conservation of *Totoaba macdonaldi* (Gilbert, 1891) (Teleostei:Sciaenidae), in the Gulf of California, Mexico. J. Fish Biol. 37: 201–202.

Baxter, J. L. 1960. A study of the yellowtail *Seriola dorsalis* (Gill). Fish Bull. U.S. 110: 96.

Bohnsack, J. A. 1998. Application of marine reserves to reef fisheries management. Austr. J. Ecol. 23: 298–304.

Cariño Olvera, M. M. 1996. Historia de las relaciones hombre-naturaleza en Baja California Sur, 1500–1940. Univ. Autonoma de Baja California Sur-Promarco, La Paz. 229 p.

Carr, M. H. and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges - Examples from temperate reef fishes. Can. J. Fish. Aquat. Sci. 50: 2019–2028.

Carter, J., G. J. Marrow and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. Proc. Gulf Carib. Fish. Inst. 43: 65–111.

________ and D. Perrine. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. Bull. Mar. Sci. 55: 228–234.

Cisneros Mata, M. A., G. Montemayor Lopez and M. J. Roman Rodriguez. 1995. Life History and Conservation of *Totoaba macdonaldi*. Cons. Biol. 9 806–814.

Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces, Serranidae) and its relationship to environmental conditions. Environ. Biol. Fishes 34: 357–377.

_________. 1996. Longevity of some coral reef fish spawning aggregations. Copeia 1996: 189–192.

Dayton, P. K., E. Sala, M. J. Tegner and S. Thrush. 2000. Marine reserves: Parks, baselines, and fishery enhancement. Bull. Mar. Sci. 66: 617–634.

DeLoach, N. 1999. Reef fish behavior. New World Publications, Jacksonville, Florida. 359 p.

Domeier, M. L. and P. L. Colin. 1997. Tropical reef fish spawning aggregations: Defined and reviewed. Bull. Mar. Sci. 60: 698–726.

Garratt, P. A. 1988. Notes on seasonal abundance and spawning of some important offshore linefish in Natal and Transkei waters, southern Africa. New Zealand J. Mar. Sci. 7: 1–8.

Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the Epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 51: 83–103.

Gillanders, B. M., D. J. Ferrell and N. L. Andrew. 1999. Size at maturity and seasonal changes in gonad activity of yellowtail kingfish (Seriola lalandi; Carangidae) in New South Wales, Australia. New Zealand J. Mar. Freshw. Res. 33: 457–468.

Harmelin-Vivien, M. L., J. G. Harmelin, C. Chauvet, C. Duval, R. Galzin, P. Lejeune, G. Barnabe, F. Blanc, R. Chevalier, J. Duclerc and G. Lasserre. 1985. Evaluation visuelle des peuplements et populations de poissons: methodes et problemes. Rev. Ecol. (Terre Vie) 40: 467–539.

Heemstra, P. C. and J. E. Randall. 1993. FAO Species Catalogue, vol. 16. Groupers of the world (Family Serranidae, Subfamily Epinephelinae). FAO Fish. Synopsis, no. 125. 382 p.

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

____________. 1978b. Traditional marine conservation methods in Oceania and their demise. Ann. Rev. Ecol. Syst. 9: 349–364.

____________. 1981. Words of the Lagoon. Fishing and marine lore in the Palau district of Micronesia. Univ. California Press, Los Angeles, California. 245 p.

____________., L. Squire, T. Graham, Y. Sadovy and H. Renguul. 1999. Spawning aggregations of groupers (Serranidae) in Palau. Mar. Cons. Res. Ser. Publ. #1, The Nature Conservancy. 144 p.

Koenig, C. C., F. C. Coleman, L. A. Collins, Y. Sadovy and P. L. Colin. 1996. Reproduction of the gag (*Mycteroperca microlepis*) (Pisces:Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. ICLARM Conf. Proc., Manila. 48: 307–323.

McGregor, G. 1995. Is the northern region the kingfish capital of the Pacific? Part 1: the fish. Seafood New Zealand June 1995:28-30.

Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala, T. W. Scmidt, G. R. Sedberry, H. Weeks and S. G. Wright. 2000. Marine, estuarine and diadromus fish stocks at risk of extinction in North America (Exclusive of Pacific Salmonids). Fisheries 25: 6–30.

Sadovy, Y. 1994a. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces:Serranidae). Copeia 1994: 511–16.

_________.1994b. Grouper stocks of the Western Central Atlantic: The need for management and management needs. Proc. Gulf Carib. Fish. Inst. 43: 43–64.

Talbot, F. H. and F. Williams. 1956. Sexual color differences in *Caranx ignobilis* (Forsk). Nature 178: 934.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 2000. Reef fishes of the Sea of Cortez. The Univ. Texas Press, Austin. 353 p.

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

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