Spawning Aggregation Sites of Snapper and Grouper Species (Lutjanidae and Serranidae) on the Insular Shelf of Cuba

Rodolfo Claro
Instituto de Oceanologia, Cuba

Kenyon C. Lindeman
Environmental Defense, Miami, Florida

SPAWNING AGGREGATION SITES OF SNAPPER AND GROUPER SPECIES (LUTJANIDAE AND SERRANIDAE) ON THE INSULAR SHELF OF CUBA

Rodolfo Claro[1] and Kenyon C. Lindeman[2]
[1]*Instituto de Oceanología, CITMA, 1ra #18406, Playa, La Habana, Cuba*
[2]*Environmental Defense, 14630 SW 144 Terr., Miami, Florida 33186 USA*

ABSTRACT Twenty-one spawning aggregation sites on the Cuban shelf were identified for eight species of snappers (*Lutjanus*) and groupers (*Epinephelus* and *Mycteroperca*) using information from experienced fishers and field studies. Three sites are on the southeastern shelf, eight on the southwest shelf bordering the Golfo de Batabanó, two in the northwest, and eight in the north-central region along the margins of the Archipiélago de Sabana-Camagüey. These numbers may reflect sampling effort as much as absolute aggregation numbers, with most effort concentrated in the southwest and north-central regions. Additional studies, particularly field assessments, are needed to determine the current status and consistency of occurrence of many of these aggregations. Most sites occur near the shelf drop-off at depths of 20–50 m, over reef substrates. Some sites involve sequential use by multiple species over several seasons of the year. Fishing activities have impacted many of these aggregations, both during spawning events and during pre-spawning migrations. This information is being applied in the design of marine reserve networks for several Cuban archipelagos. Intraspecific variations in aggregation formation occur temporally among differing regions of Cuba. Such variations reinforce the need for expanded research efforts on spawning aggregations.

INTRODUCTION

Many species of reef fishes are known to aggregate in large numbers at specific times and places to reproduce. In snappers (Lutjanidae) and groupers (Serranidae), spawning aggregation sites are often located near the outer reef edge or reef passes (Johannes1978). Some sites may be used by many species, either simultaneously or at differing times of the day, month or year (Domeier and Colin 1997). The relatively predictable nature of these concentrations makes them extremely vulnerable to overexploitation. A substantial number of snapper and grouper aggregations have been degraded or eliminated in the Caribbean, particularly, aggregations of Nassau grouper (Sadovy 1994a, Sadovy and Eklund 1999).

In the northern Caribbean, substantial impacts to spawning aggregations of snapper or grouper species have been documented in Puerto Rico (Shapiro et al. 1993, Sadovy 1994b), the US Virgin Islands (Beets and Friedlander 1999), Mexico (Aguilar-Perera and Aguilar-Davila 1996), Belize (Sala et al. 2001, Heyman et al. 2001) and the lower Florida Keys (Lindeman et al. 2000). In addition, fishing gear damage to habitats associated with spawning can be significant as demonstrated in east-central Florida (Koenig et al. 2000). The degradation or elimination of aggregations and their habitats can have highly negative impacts on populations over varying spatial scales since these sources of fishery production are highly concentrated in both space and time. Aggregations can also be heavily impacted by fishery removal of migrating pre-spawners in route to aggregation sites, as in lane snapper in southwest Cuba (Claro 1981a, Claro et al. 2001a).

Snappers and groupers are the most important commercial and recreational fishing resources of the Cuban shelf. There is more information on the biology, fisheries and management of these species than any other commercial fishes in Cuba (Claro et al. 2001b). Some aspects of their reproductive strategy are similar to other species (grunts, jacks) that can spawn near the shelf edge (García-Cagide et al. 2001). Knowledge of migration routes, characteristics of spawning aggregations, spawning behavior and dispersal patterns of larvae are key elements for assessing the design of marine reserve networks around the large shelf systems of Cuba. Information on sites and timing of snapper and grouper spawning aggregations has been accumulated for centuries by Cuban fishers. For example, Vilaró Díaz (1884) mentioned aggregation sites for some commercial species. However, the available information for Cuba has not been gathered, evaluated in a standard manner, or applied towards coordinated management goals.

Obtaining and standardizing information on the distribution and timing of spawning aggregations in Cuba is essential to developing strategies for confirming the current status of aggregations and developing precautionary management measures. On the basis of empirical data and information from fishers, the present paper identifies spawning aggregation sites for species of *Lutjanus, Epinephelus,* and *Mycteroperca.* Details of

spawning seasonality and potential dispersal processes are also discussed in the context of potential management measures and the population biology of key species in Cuba, particularly lane snapper (*Lutjanus synagris*), mutton snapper (*Lutjanus analis*), and Nassau grouper (*Epinephelus striatus*).

Methods

Geographic regions

The Cuban shelf has an approximate area of 67,831 km^2 (Núñez Jiménez 1982). The shelf has four particularly wide areas bordered by extensive reef lines, with each wide area separated by long, narrow shelf stretches (Claro et al. 2001b). Two of the wide-shelf areas occur on the south coast, the Golfo de Batabanó to the west and the area including the Golfo de Ana Maria and Golfo de Guacanayabo to the east, and two occur on the north coast, the Archipiélago Los Colorados in the northwest and the Archipiélago Sabana-Camagüey in the north-central region (Figure 1).

In southeastern Cuba, a narrow shelf with a very steep dropoff occurs from the easternmost point (Punta Maisi) west to Cabo Cruz. Immediately to the west, the Golfo de Guacanayabo, unlike most other wide-shelf areas in Cuba, is not rimmed by keys, sand banks and reefs, but has a steep slope to the shelf edge. The adjacent Golfo de Ana Maria is fringed by the Archipiélago Jardines de la Reina reef system (Figure 1), an array of keys, sand banks, and reef crests separating much of the gulf from the open sea. The bottom is mostly muddy in central areas with seagrasses near the mainland and the keys. Together, these two southeastern gulfs have a total area of about 18,000 km^2. To the west, the Golfo de Batabanó is the largest submerged area of the Cuban shelf, with an area of about 20,870 km^2. This massive lagoon is fringed by and includes more than 670 islands and keys that comprise the Archipiélago Los Canarreos to the east of Isla de la Juventud and the Cayos Los Indios and San Felipe to the west (Figure 1). Depths reach 15 m in some channels but typically average 3–6 m. Sand-mud bottoms with extensive seagrasses dominate the lagoon habitats. A wide array of reef habitats extend from the channels between the keys to the shelf edge.

The northwest shelf, much of it bordered by the Archipiélago Los Colorados, is not as wide as the other three wide-shelf areas, but in the westernmost area, substantial shallow shelf areas are present at the Golfo de Guanahacabibes (Figure 1). To the east, the most substantial shelf area is within the Archipiélago Sabana-Camagüey, a long reef system with more than 2500 islands, keys, and islets (a total area of about 10,115 km^2). The keys fringe the shelf for more than 460 km, forming over ten significant bays and lagoons. These lagoons have a maximum depth of 2–3 m with many shoals emergent at low tide. North of the keys, a narrow belt of rocky bottom with sandy areas, sparse seagrass beds, and numerous reef crests and fore reefs extends to the shelf edge.

Identification of Spawning Aggregation Sites

Criteria for identifying spawning aggregations include both direct and indirect evidence (Domeier and Colin 1997). Direct evidence includes several different types of observations within large species groups at discrete sites: observations of simultaneous gamete extrusion among multiple individuals, identification of hydrated eggs, or identification of post-ovulatory follicles. Direct evidence is preferred but is also much less common than indirect evidence for many commercial species. Indirect evidence often includes information provided by veteran fishers on spawning and pre-spawning aggregations. This information can be valuable (Johannes 1998), but should be obtained and evaluated with care (e.g., heavy chumming can create artificially-induced "aggregations") and substantiated whenever possible via independent sources. Additional types of indirect evidence can be of use, including dense migrations of pre-ovulatory individuals en route to spawning sites (Starck 1970, Claro et al. 1981a,b).

Published information on spawning sites was limited or unavailable for almost all species on the Cuban shelf. Due to this paucity of information and logistical constraints on direct observations of snapper and grouper spawning, much of the evidence for spawning aggregation site locations and timing, fishing characteristics, and aggregation status was obtained through interviews with experienced fishers from different regions of Cuba, often in conjunction with biological studies carried out from 1970 to 2000 (e.g., Olaechea and Quintana 1975, Claro 1981a,b, Claro 1982, Claro 1983a,b, García-Cagide and Claro 1983, Claro et al. 1990, García-Cagide and García 1996, García-Cagide et al. 1999a,b). These fishers averaged over 20 years of commercial net, trap, or hand-line experience. In most cases, the information was checked with at least three fishers independently.

Only sites with unusually high catches of fishes with running-ripe or enlarged gonads during known spawning peaks were identified as potential spawning aggregation sites. Periodically, fishers identified the site where they saw or caught aggregated pre-spawners during their spawning migration, but the spawning site itself was not
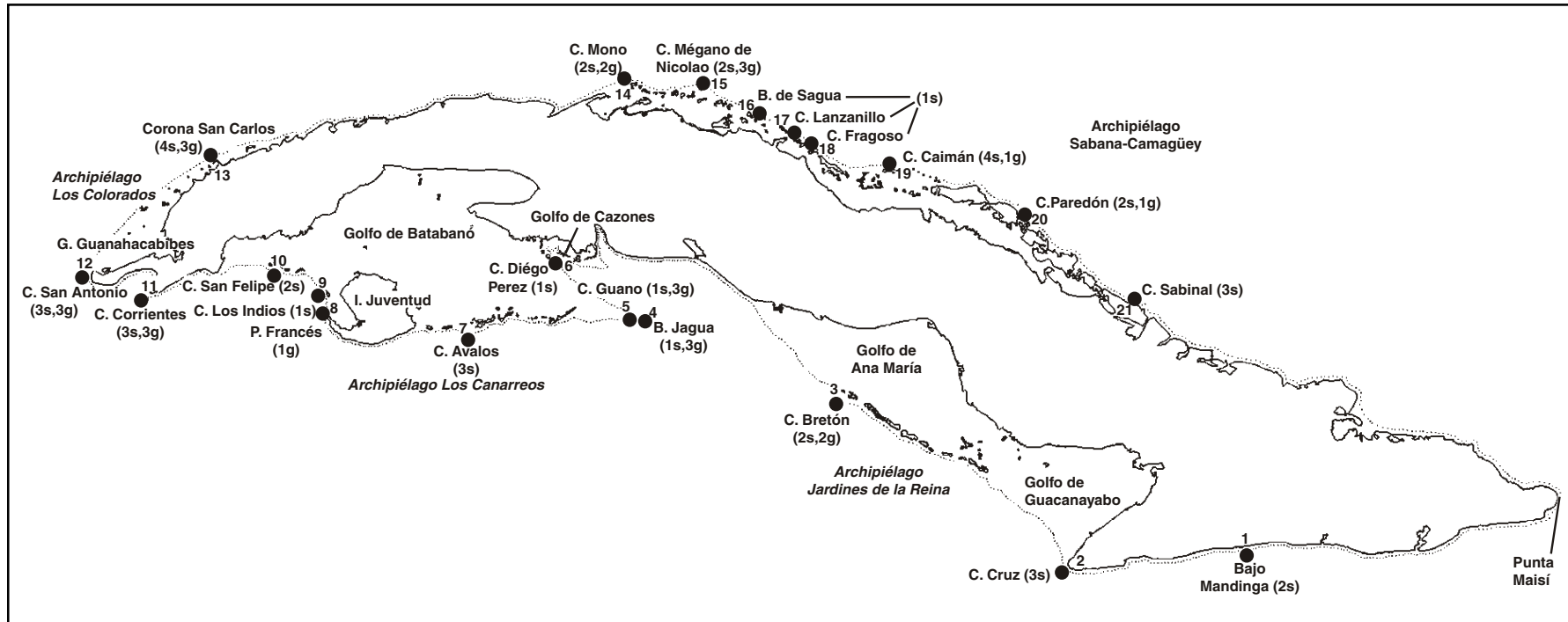
Figure 1. Spawning aggregation sites on the shelf of Cuba. Numbers in parenthesis indicate the number of species known to aggregate at each site. s: snappers; g: groupers. Dotted line indicates the shelf edge.

exactly known. Many sites are very remote, but in some cases we obtained direct documentation by site visits during aggregation occurrence, particularly in southwest and north-central areas. All aggregation information from fishers was checked against detailed monthly catch statistics that were available at the provincial level (unpubl. data, Ministerio de Industria Pesquera, Claro et al. 2001a) . This information was particularly useful for identifying peaks in monthly catches that reflected the occurrence of spawning aggregations. Data at the monthly level are currently only available through 1985. In addition, other references with related spawning information from Cuba were consulted as relevant (e.g., Vilaró Díaz, 1884, García-Cagide et al. 2001).

RESULTS

Southeastern Cuba

Three spawning aggregation sites have been identified in this region. Two are along the narrow shelf of southeastern Cuba and one is within the western side of the Archipiélago Jardines de la Reina reef system (Figure 1).

Bajo Mandinga. South of the Sierra Maestra mountain range, this is an oceanic promontory located about 3 km south of the Chivirico and Cayo Damas villages. The shallow and very narrow shelf is covered by well-developed coral reefs to 30 m depth. Mutton snapper in May–June and cubera snapper (*Lutjanus cyanopterus*) in July–August move along the coast from east and west to aggregate at the top of the promontory at 15–25 m depths where they are fished with hook and line (Table 1).

Cabo Cruz. This site is located on the westernmost shelf of the Granma Province, at the eastern entrance of the Golfo de Guacanayabo. This area has a rocky-sandy bottom until the drop-off at about 20–25 m depth. Important aggregations of lane snapper with ripe gonads are caught in June and July close to shore on the shallow shelf using set nets and trawls. Fishers say movements occur from the Golfo de Guacanayabo to Cabo Cruz. Smaller aggregations of mutton and cubera snapper are also caught at this site (Table 1). Some groupers are known to spawn in this area, although no large schools have been documented.

Cayo Bretón. This site is near the western margin of the Archipiélago Jardines de la Reina and has traditionally been an important fishing area during spawning aggregations for at least four species of groupers and snappers during the winter and summer, respectively (Table 1). We were able to dive in a large mixed aggregation of cubera (about 60%) and dog snapper, *L. jocu*, (about 40%) during July 1986 at 25–30 m over the reefs

bordering the shelf drop-off. More than 1000 fish, all larger than 60 cm FL, moved in a circle in an area of about one hectare during daylight hours. No spawning signals were observed during the dive. All fishes caught with spear gun from both species had ripe gonads, as did all fishes caught with hook and line by commercial fishers. Fishers from the area believe that spawning takes place in the early evening because fishes stop taking baited hooks at this time.

Southwestern Cuba

Eight aggregation sites have been identified in this area, many on the margin of the reef systems to the east and west of Isla de la Juventud (Figure 1). This region has traditionally been a leading producer of lane snapper, Nassau grouper, and mixed cubera and gray snapper catches from spawning aggregations (Figure 2).

Banco de Jagua. A steep rise, Banco de Jagua, is located at the easternmost drop-off of the southwest shelf with an upper platform at a depth of 14–20 m. Although not as well-known as the Puntalón de Cayo Guano (details in next site), fishers state that the same grouper and snapper species also spawn here at the same times (Table 1) and can attain larger sizes. Aggregations at both sites are fished mainly with large baited traps. Fishers claim that when substantial Nassau grouper aggregations still existed, the fishes moved upward to the traps and filled them before the gear reached the bottom. Hook-and-line also was used to catch groupers at both sites.

Puntalón de Cayo Guano. This site, about five km west of Banco de Jagua, is a well-known aggregation site for several commercial species. Traditionally, fishers caught Nassau grouper during the full moon of December and January. Large aggregations were common every year at this site until the 1970s, but fish aggregations decreased, probably as an artifact of the overfishing of this species across the whole shelf (Claro 1991). Smaller aggregations of the yellowfin grouper and black grouper also occur at this site. These three species occur in the area with ripe gonads from December to March, but the peak spawning of each species occurs in different months (Table 1). The spawning of all grouper species here occurs around the full moon, based on fisher observations of peak densities.

Cayo Diego Pérez. The spawning aggregations of lane snapper near Cayo Diego Pérez, southeastern border of the Golfo de Batabanó, are the most-studied in Cuba (Claro 1981a, 1982, García-Cagide and Claro 1983). Spawning migrations of the lane snapper from the middle of the gulf to the eastern shelf drop-off at the Golfo de Cazones (Figure 1), have been followed by fishers for

TABLE 1

Regions and sites on the Cuban shelf with spawning aggregations of snapper and grouper species. Numbers in parenthesis refers to site locations in Figure 1. * = peak spawning month.

Spawning site	Habitat	Species	Spawning season	Spawning peak	Moon	Time	Primary gear used on aggregations	Aggregation status
Southeast region								
Bajo Mandinga (1)	Slope reef, high coral	Cubera snapper	Jun–Sep	Jul–Aug	Full	Night	Hook and line	Declined
19º56´–76º24´	cover, 20–30 m depth	Mutton snapper	May–Aug	May*–Jun	Full to ¾	Sunset	Hook and line	Slightly declined
Cabo Cruz (2)	Sandy, rocky, coral	Lane snapper	Apr–Sep	Jun*–Jul	¼ to full	Sunset	Trawls and traps	Declined
19º50´–77º47´	heads, 30–40 m depth	Mutton snapper	May–Aug	May*–Jun	Full to ¾	Sunset	Hook and line	Slightly declined
		Cubera snapper	Jun–Sep	Jul*–Aug	Full	Night	Hook and line	Declined
Cayo Bretón (3)	Slope reef, high coral	Cubera snapper	Jun–Sep	Jul*–Aug	Full	Night	Hook and line	Declined
21º05´–79º29´	cover, 20–30 m depth	Dog snapper	Year round	Jul–Aug	Full	Night	Hook and line	Declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Slightly declined
		Black grouper	Jan–Mar	Feb–Mar	Full	?	Hook and line, traps	Sharply declined
Southwest region								
Banco de Jagua (4)	Oceanic bank, rocky	Mutton snapper	Apr–Sep	May*–Jun	Full to ¾	Sunset	Hook and line	?
21º35´–80º41´	bottom, moderate coral	Nassau grouper	Dec–Feb	Dec–Jan*	Full	?	Hook and line, traps	Sharply declined
	cover, 14–25 m depth	Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
		Black grouper	Jan–Mar	Feb–Mar	Full	Sunset	Hook and line, traps	Declined
Puntalón de Cayo Guano (5)	Slope reef, high coral	Mutton snapper	Apr–Sep	May*–Jun	Full to ¾	Sunset	Hook and line	Sharply declined
21º35´–80º50´	cover, 30–40 m depth	Nassau grouper	Dec–Feb	Dec–Jan*	Full	Sunset	Hook and line, traps	Declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
		Black grouper	Jan–Mar	Feb–Mar	Full	?	Hook and line, traps	?
C. Diego Pérez (6)	Slope reef, high coral	Lane snapper	Apr–Sep	Apr–May*	¼ to full	Sunset	Trawls and set nets on migration route	Sharply declined, recovering
22º02´–81º30´	cover, 20–30 m depth							
C. Avalos (7)	Slope reef, high coral	Mutton snapper	Apr–Sep	May–Jun	Full to ¾	Sunset	Hook and line, set nets	Slightly declined
21º27´–82º09´	cover, 20–30 m depth	Cubera snapper	Jun–Sep	Jul–Aug	Full	Night	Hook and line, set nets	Declined
		Gray snapper	Jun–Sep	Jul*–Aug	Full	Night	Set nets	Declined
P. Francés (8)	Slope reef, high coral	Nassau grouper	Dec–Feb	Dec–Jan*	Full	Sunset	Hook and line, traps	Sharply declined
21º38–83º14´	cover, 20–30 m depth							
Los Indios (9)	Slope reef, high coral	Lane snapper	May–Sep	May–Jun*	¼ to full	Sunset	Trawls and set nets on migration route	Sharply declined, recovering
21º48´–83º14´	cover, 20–30 m depth							
C. San Felipe (10)	Slope reef, high coral	Mutton snapper	Apr–Aug	May*–Jun	Full to ¾	Sunset	Hook and line	
21º54´–83º23´	cover, 20–30 m depth	Lane snapper	May–Sep	May–Jun*	¼ to full	Sunset	Trawl and set nets	Slightly declined

TABLE 1. (Continued)

Spawning site	Habitat	Species	Spawning season	Spawning peak	Moon	Time	Primary gear used on aggregations	Aggregation status
Southwest region (continued)								
Cabo Corrientes (11)	Sandy, rocky, coral	Mutton snapper	Apr–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns	Sharply declined
21°44´–84°34´	heads, 25–40 m depth	Cubera snapper	Jul–Sep	Jul*–Aug	Full	Night	Hook and line	Slightly declined
		Dog snapper	Year round	Jul–Aug	Full	Night	Hook and line	Declined
		Nassau grouper	Dec–Feb	Dec–Jan*	Full	Sunset	Hook and line, traps	Declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	Night	Hook and line, traps	Declined
		Black grouper	Dec–Mar	Feb–Mar	Full	Night	Hook and line, traps	Declined
Northwest region								
Cabo San Antonio (12)	Slope reef, high coral	Mutton snapper	May–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns	Declined
21°54´–84°57´	cover, 25–40 m depth	Cubera snapper	Jul–Sep	Jul*–Aug	Full	Night	Hook and line, sp. guns	Declined
		Dog snapper	Year round	Jul–Aug	Full	Night	Hook and line, traps	Declined
		Nassau grouper	Dec–Feb	Dec–Jan	Full	Sunset	Hook and line, traps	Sharply declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
		Black grouper	Jan–Mar	Feb–Mar	Full	?		Declined
Corona de San Carlos (13)	Slope reef, sandy, rocky, coral heads,	Mutton snapper	May–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns, trawls	Declined
22°54´–83°36´	20–30 m depth	Lane snapper	Apr–Oct	May*	¼ to full	Sunset	Trawls, hook and line	Sharply declined
		Gray snapper	Jun–Sep	Jul*–Aug	Full	Night	Trawls, hook and line	Declined
		Cubera snapper	Jun–Sep	Jul*–Aug	Full	Night	Hook and line	Declined
		Nassau grouper	Dec–Feb	Dec–Jan	Full	Sunset	Hook and line, traps	Sharply declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
		Black grouper	Jan–Mar	Feb–Mar	Full	?	Hook and line, traps	Declined
North-central region								
Punta Hicacos- Cayo Mono (14)	Slope reef, sandy, rocky, coral heads,	Mutton snapper	May–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns	Declined
23°18´–81°03´	25–40 m depth	Lane snapper	Apr–Sep	May–Jun*	¼ to full	Sunset	Trawls, set nets, traps	Declined
		Nassau grouper	Dec–Feb	Dec*–Jan	Full	?	Hook and line, traps	Sharply declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
C. Mégano de Nicolao (15)	Slope reef, high coral cover, 20–	Mutton snapper	May–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, trawls	Slightly declined
23°16´–80°25´	30 m depth	Lane snapper	May–Sep	May–Jun*	¼ to full	Sunset	Trawls, set nets	Declined
		Nassau grouper	Dec–Feb	Dec*–Jan	Full	Sunset	Hook and line, traps	Sharply declined
		Yellowfin grouper	Jan–Mar	Jan–Feb	Full	?	Hook and line, traps	Declined
		Black grouper	Jan–Mar	Feb–Mar	Full	?	Hook and line, traps	Declined

TABLE 1. (Continued)

| Spawning site	Habitat	Species	Spawning season	Spawning peak	Moon	Time	Primary gear used on aggregations	Aggregation status
North-central region (continued)								
Boca de Sagua (16) 23º05´–80º06´	Slope reef, moderate coral cover, 25–35 m depth	Lane snapper	May–Sep	May–Jun*	Full	Sunset	Trawls, set nets, traps	Declined
C. Lanzanillo (17) 22º58´–79º47´	Slope reef, moderate coral cover, 20–30 m depth	Lane snapper	May–Sep	May–Jun*	Full	Sunset	Trawls, set nets, traps	Declined
C. Fragoso (18) 22º50´–79º-35´	Slope reef, moderate coral cover, 20–30 m depth	Lane snapper	May–Sep	May–Jun*	Full	Sunset	Trawls, set nets, traps	Declined
C. Caimán Grande (19) 22º45´–78º-52´	Slope reef, high coral cover, 20–30 m depth	Mutton snapper	May–Aug	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns	Slightly declined
		Cubera snapper	Jun–Sep	Jul*–Aug	Full	Night	Hook and line, sp. guns	Declined
		Gray snapper	Jun–Sep	Jul*–Aug	Full	Night	Trawls, set nets	Declined
		Lane snapper	May–Sep	May–Jun*	Full	Sunset	Trawls, set nets	Sharply Declined
		Nassau grouper	Dec–Feb	Dec*–Jan	Full	Sunset	Hook and line, traps	Sharply declined
C. Paredón (20) 22º30´–78º09´	Slope reef, high coral cover, 20–30 m depth	Lane snapper	May–Sep	May–Jun*	¼ to full	Sunset	Trawls, traps	Declined
		Cubera snapper	Jun–Sep	July*–Aug	Full	Night	Hook and line, traps	Declined
		Nassau grouper	Dec–Jan	Dec*–Jan	Full	Sunset	Hook and line, traps	Sharply declined
C. Sabinal (21) 21º46´–77º19´	Slope reef, high coral cover, 20–30 m depth	Lane snapper	May–Sep	May–Jun*	¼ to full	Sunset	Trawls, set nets	Declined
		Mutton snapper	May–Sep	May–Jun*	Full to ¾	Sunset	Hook and line, sp. guns	Slightly declined
		Cubera snapper	Jul–Sep	Jul–Aug	Full	Night	Hook and line, sp. guns	Declined
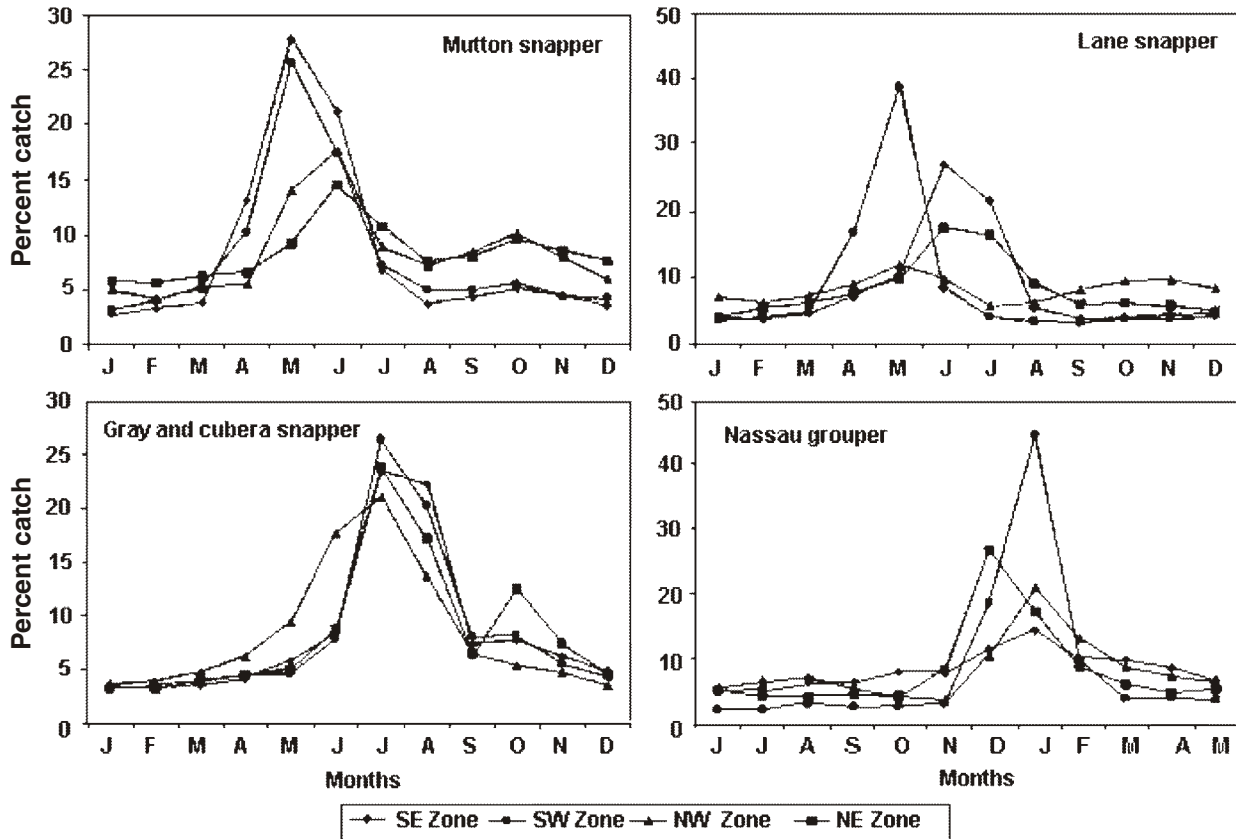
Figure 2. Monthly variation of catches of mutton snapper, lane snapper, mixed cubera and gray snappers, and Nassau grouper (mean values from 1962 to 1985) from the four fishery statistical zones of the Cuban shelf.

many decades. Several days before the fifth full moon of the year, usually in May, aggregations of lane snapper begin to move from the central part of the Golfo de Batabanó to the east, usually close to the keys. Once near the spawning area, at the margin of the Golfo de Cazones, large schools of lane snapper move around during the day, close to Cayo Diego Pérez, for about eight-ten days.

Direct observations on fish aggregations, gonad analysis (Claro 1981a, 1982), daily tagging and recovery of fishes (A. Olaechea, unpublished data), showed that every day at noon, the schools moved from the shallow (3–6 m depth) seagrass beds close to the keys, to the drop off. Spawning occurs after sunset and fish return to the shallow waters (perhaps to avoid predators such as sharks and barracudas) where they remain until the next afternoon. Histological analysis of gonads showed the release of about 4–5 batches of eggs in a similar number of days (Claro 1982, García-Cagide and Claro 1983, García-Cagide et al. 2001). After release of all batches, lane snapper dispersed to feeding areas in the Golfo de Batabanó. Siam Lahera (1986) found that the highest percentage of lane snapper with ripe gonads at the border

of Golfo de Cazones occurred when water temperatures at depths of 20–30 m were between 26.7–27.3°C. The existence of a local upwelling and frontal system at the eastern Gulf of Cazones (Siam Lahera and Ramírez 1987) may favor the development and recruitment of fish larvae.

Since the mid-1970s, when lane snapper stocks in the Golfo de Bataban were overfished, aggregations have seriously declined (Claro 1991, Claro et al. 2001a). In the last seven years, the abundance of lane snappers migrating to the site may have increased based on limited information, although aggregation sizes don't reach the levels of the 1960s and early-1970s. Some other snappers, including mutton, gray (*Lutjanus griseus*) and yellowtail (*Ocyurus chrysurus*) may spawn at the same shelf drop-off near Diego Pérez. A notable number of ripe adults of these species are caught in the adjacent shallow areas during their spawning season (Claro 1981b, l983a,b), but there is no clear documentation of spawning aggregations. These fishes may spawn in small groups in this area.

Cayo Avalos (Cabezo Sambo). A shallow offshore reef south of Cayo Avalos, Cabezo Sambo, is a well-known spawning site for several species. At the south drop-off of the reef, spawning aggregations of some intensively fished species occur (Table 1). These aggregations are fished heavily by hook and line. Prior to reaching the aggregation site, pre-spawning fishes migrating to the outer spawning site are also caught with set nets at the channels between the keys separating the inner Golfo de Batabanó from the outer shelf. This activity is now regulated by banning the use of set nets across channels during spawning migrations.

Punta Francés. At the southwest tip of the Isla de la Juventud (Figure 1), this is one of the oldest marine reserves in Cuba (although small with an area of about 6,000 ha) and the reefs are in good condition. However, tourist diving activities are increasing as well as cruise ship visits. Close to the western tip of the peninsula (about 3 km west of the reserve boundary), aggregations of Nassau grouper are reported to occur in December and January. At least in the last ten years, the aggregations have declined as result of overfishing outside the reserve according to both fishers and dive operators. Vilaró Díaz (1884) mentioned the occurrence of Nassau grouper aggregations south of Isla de Pinos (currently Isla de la Juventud) in possible reference to the same site, but did not give precise locations.

Cayos Los Indios and Cayo San Felipe. Spawning aggregations of lane snapper have been fished for many decades close to Los Indios and San Felipe, usually one month later than at Cayo Diego Pérez. Mutton snapper aggregations are also known from San Felipe with peak spawning in May. Vilaró Díaz (1884) reported spawning aggregations of Nassau grouper south of La Coloma, which appears to refer to Cayo San Felipe. This area is known as one of the most important sites for spawning of spiny lobster (*Panulirus argus*) in Cuba. Ripe spiny lobster are found all year but the spawning peak occurs in spring-summer (Cruz-Izquierdo et al. 1987, Cruz-Izquierdo 1999). Although spawning may occur along the whole edge of the shelf in this area, it is assumed that a deep-water population is the main source of reproduction (González Sansón et al. 1991).

Cabo Corrientes. A well-known spawning site for mutton snapper is located at Cabo Corrientes, south of the Reserva de la Biosfera Península de Guanahacabibes at depths of 25–40 m. The spawning site is located at the tip of the narrow shelf bordering the peninsula (Figure 1), over sandy bottom. We visited the site during mutton snapper spawning events in June 1973 and 2001. The aggregations were present at least 8–10 days, beginning

two to three days before the full moon. Several other important snapper and grouper species also aggregate at this site and are fished by hook-and-line and traps (Table 1).

Fishers state that the fishes migrate to this site from the east along the narrow shelf, and from the Ensenada de Corrientes to the west. During the migrations, some species are heavily fished by sport and commercial fishers. The site is near the southwest corner of the mouth of the Yucatan Channel and the currents are strong and complex. Anticyclonic circulation systems can form in the Ensenada de Corrientes. In addition, eggs and larvae may also be transported to the east by the Cuban countercurrent, or to the west into the Yucatan Straits.

Northwestern Cuba

Two spawning aggregation sites were identified in this region (Figure 1), although the enormous length of the Archipiélago Los Colorados suggests additional lutjanid and serranid spawning sites are present.

Cabo San Antonio. The same species that aggregate at Cabo Corrientes are reported to aggregate at Cabo Antonio, at the westernmost margin of Cuba. These aggregations form at depths of 30–40 m over well-developed coral habitats. Peak spawning months are also the same as at Cabo Corrientes (Table 1). Fishers assume that the fishes aggregating here come mainly from the north coast. This site is located in an area of complex current systems that can transport eggs to the east along the south coast, or to the northeast or northwest.

Corona de San Carlos. This site is traditionally known as important for spawning aggregations of mutton snapper and other species. It is located offshore, about 19 km northeast of Puerto Esperanza on the shelf near oceanic waters. Close to the shelf drop-off, the bottom has spur and grove reef structures, with poorly-developed coral cover. These topographic features are common to some other spawning sites on the north shelf of Cuba (Punta Hicacos, Mégano de Nicolao, Cayo Caimán, C. Paredón, and C. Sabinal).

Large schools of adult mutton snapper, 50–70 cm FL or more, are visible over the reef at 25–35 m depths close to the shelf drop-off in May and June (Claro 1981b). According to fishers, snappers are intensively caught with hook-and-line when strong currents occur. Aggregations start arriving at the site 3–4 days before the full moon and decrease in quantity until the third quarter of the moon, as at Cabo Corrientes and Cabo San Antonio. Presumably, spawning occurs at sunset or early night. Unlike lane snapper, that move daily to shallow waters after the release of one batch (Claro 1982, Garcia-Cagide

et al. 2001), mutton snappers stay at the slope reef until spawning is completed. The same behavior has been observed in other large species (e.g., cubera and dog snappers). Corona de San Carlos is also a well-known spawning site for several other snapper and grouper species (Table 1) and the margate (*Haemulon album*). Most of the aggregations have declined since the 1980s, particularly that of Nassau grouper.

North-central Cuba

Eight spawning aggregation sites were identified in this region. All were on the outside border of the extensive Archipiélago Sabana-Camagüey reef system (Figure 1).

Punta Hicacos-Cayo Mono. These offshore reefs are known as spawning aggregation sites for mutton snapper, but other important species also aggregate on these reefs (Table 1) (see also Vilaró Díaz 1884). Fishes aggregate at 25–50 m depth over a submerged peninsula of sandy-rock bottom with patch reefs. This reefs are heavily fished, mainly by sport fishers from nearby resorts on the Peninsula de Varadero.

Cayo Mégano de Nicolao. Northeast of Bahía de Cádiz, Mégano de Nicolao is an offshore sand-rock area bordered by well-developed coral reefs very close to the shelf drop-off at 25–30 m depth. Several species (Table 1) may aggregate throughout the area, but the main groups are known from north of Cayo Mégano. Schools of lane snapper with ripe gonads are usually fished in the shallow waters, close to Cayo Blanquizal (south of Mégano de Nicolao), during their migrations to the spawning site.

Boca de Sagua, Cayo Lanzanillo and Cayo Fragoso. There is evidence of lane snapper group spawning from all of these sites based on fisher observations and catches. Since this species moves to shallow waters during the day, the precise location of the spawning sites is unclear. North of the keys bordering the lagoons, there is a largely sandy bottom extending to the shelf border, with some well-developed slope reefs from 15 to 30 m depths where some of the spawning appears to occur. Schools are fished in the shallow waters close to the keys north of Bahía de Sagua, Cayos Jutías, el Pajonal, Cayo Lanzanillo and Bahía Nazabal. The aggregations usually fished at Cayo Lanzanillo and Cayo Fragoso may move to spawn in the same offshore sites.

Cayo Caimán Grande. Located north of Bahía de Buenavista and Cayos de Santa María, this site is possibly one of the most important in north-central Cuba. There is a wide shelf of sand and rock bottom with dispersed coral heads, several rocky keys called Los Caimanes, and some reef crests. North of the shallow crest reefs, the bottom is usually covered with corals almost continuously until the shelf drop-off. The shelf drop-off is bordered by well-developed coral reefs at 15–25 m depths. The adjacent southwest inner shelf area supports the largest catches of mutton snapper in north-central Cuba (Claro et al. 2000). Significant concentrations of juveniles of mutton, lane and yellowtail snappers are common in the northern part of Bahía Buenavista, Pasa Las Piraguas and in channels between the keys. These areas are important nursery areas for many species which migrate as adults to the adjacent Bahía San Juan de los Remedios. The degradation of environmental conditions in the Bahía de Buenavista from various anthropogenic sources (Claro et al. 2000) may have affected the lane snapper fisheries in the area. Fishers also reported large schools of mojarras (*Gerres cinereus, Eugerres* spp.) spawning in the shallow shelf at depths of 2–5 m, close to Cayo Santa María, on sandy bottom.

Cayo Paredón. Offshore of the reef crests, largely sand bottom extends to the shelf drop-off at 40–50 m, an area with rocky bottom and sparse coral heads. The spawning site is located north of Cayo Paredón where the shelf protrudes to the north. Aggregations of lane snapper are often fished in shallow water seagrasses bounded to the north by several crest reefs and to the south by several keys (Cayo Paredón del Medio to Cayo Paredón Grande) separated by narrow channels. Currents may favor recruitment to the south and southwest of this site, but nursery areas in the inner lagoons have been seriously degraded by increased salinity and pollution.

Cayo Sabinal. Annual spawning migrations of mutton snapper and cubera snapper (Table 1) are fished in channels (Pasa Las Calaveras and Pasa Sabinal) that connect the lagoons (Bahía La Gloria and Ensenada de Sabinal) with the outer shelf. These schools move parallel to the shelf until the Laguna Tortuguilla, and later move north to the shelf drop-off, at 25–35 m depths. The slope reef, once well-developed, has been seriously degraded by coral diseases and algal overgrowth (Claro et al. 2000). Aggregations have declined in size, but are still fished during the spawning peak.

DISCUSSION

Twenty-one spawning aggregation sites were identified around the Cuban shelf. By region, three sites are on the southeast shelf, eight on the southwest, two on the northeast, and eight on the north-central shelf. The spatial distribution of known aggregation sites reflects both fishing and validation efforts, with most effort concen-

trated in southwest and north-central areas that have long-term fishing operations or were less remote. Many of the aggregation sites were first identified in the 1980s and many remain quite remote. Assessment of current aggregation status has been limited by a lack of boats and communication opportunities with local fishers. Additional studies, particularly field assessments, are needed to determine the current status and consistency of occurrence of many of these aggregations.

Behaviors and Habitats

Various behaviors can characterize the migrations to sites, the pre-spawning assembly of individuals on-site, the spawning act itself, spawning frequency over both daily and weekly time-scales, and subsequent adult dispersal. Generally, very little comparative information is available on any of these attributes. This lack of information can lead to situations where limited data are overextrapolated and critical biological variation is not recognized within and among species.

Available information suggests most snapper and grouper species in Cuba form transient aggregations and spawn in groups (following Domeier and Colin 1997). However, gray snapper may exhibit simple migratory spawning as discussed in Domeier et al. (1996) and Domeier and Colin (1997). There are clearly differences in the behavior of schools of mutton and lane snapper during the course of spawning aggregations, with mutton staying at the shelf edge and lane migrating into shallow water on a daily basis (Claro 1981b, Claro 1982, García-Cagide et al. 2001). Direct observations of spawning events have been rare in Cuba and more information on the population size of past and current spawning aggregations is needed. Descriptions of spawning in snappers exist from work in Belize with dog and cubera snapper (Carter and Perrine 1994, Heyman et al. 2001).

Detailed information on habitat attributes that favor spawning aggregations is lacking. Almost all sites in Cuba are near the shelf edge and many are in remote areas far from urban centers. All the known spawning sites are located near the shelf break, between 20 and 50 m depth, mostly between 25 and 35 m over hard or sand bottoms (Table 1). Colin and Clavijo (1988), Shapiro et al. (1988), and Colin (1996) have pointed out that key spawning areas do not necessarily contain unique structural habitat features. In Cuba, areas with aggregations also do not appear to have habitat structure that exceeds other areas in quality. Positioning of spawning areas across the outer shelf may be as important as fine-scale habitat features. Many of the described spawning sites in Cuba are located near current systems that contain eddies or other recircu-

lation features (García-Díaz et al. 1991, Victoria and Penié 1998) which can retain eggs and larvae close to the shelf and favor recruitment to nearby shallow areas. Such scenarios have been predicted for the spawning of lane snapper at the border of the Golfo de Cazones (Claro 1982) and mutton snapper at Corona de San Carlos (Claro 1981b). The correlation of spawning aggregation site locations with habitat features and geomorphological attributes at higher spatial scales requires more investigation.

Timing of Spawning and Intraspecific Variations

Although many species have a protracted spawning season (Table 1), all species have a well defined peak, usually over one or two months. This peak is often clearly reflected in fisher descriptions and commercial catches (unpubl. data, Ministerio de Industria Pesqueria; Figure 2), and is also coincident with biological studies of reproduction in Cuba (García-Cagide et al. 2001). In some instances, peak spawning months are the same in differing regions. Examples include the gray and cubera snappers (reported together in Cuban fishery statistics) that have maximum catches associated with spawning in July throughout the island. Also, the dog snapper is found with ripe gonads year round (García-Cagide et al. 1999) but has only been observed and fished in aggregations during July-August.

The timing of peak spawning in some snapper species, however, varies among differing regions of the Cuban shelf. Monthly catches from 1962 to 1985 indicate that mutton snapper has a spawning peak in May on the south-central and southeastern shelf, but peaks in June in other regions of Cuba (Figure 3; unpubl. data, Ministerio de Industria Pesquera). Catch data and fisher observations also demonstrate geographic variation in the timing of peak spawning in lane snapper. Maximum yields from spawning aggregations of lane snapper in the northwest and south-central regions occur in May, but on the southeast, north-central and southwest shelf areas, peak spawning takes place in June (Figure 3) and occasionally in July (unpubl. data, Ministerio de Industria Pesquera). For example, in the eastern Golfo de Batabanó, the largest lane snapper aggregations occur in May at the margin of the Golfo de Cazones, but they occur in western areas of the Golfo de Batabanó in June. García-Díaz (1981) reported that temperature in the Cazones-Casilda basin is higher than in other oceanic waters around Cuba; this difference may trigger earlier gonad maturation in fishes at this site (lane, mutton, and yellowtail snappers begin initial spawning in this area in April).
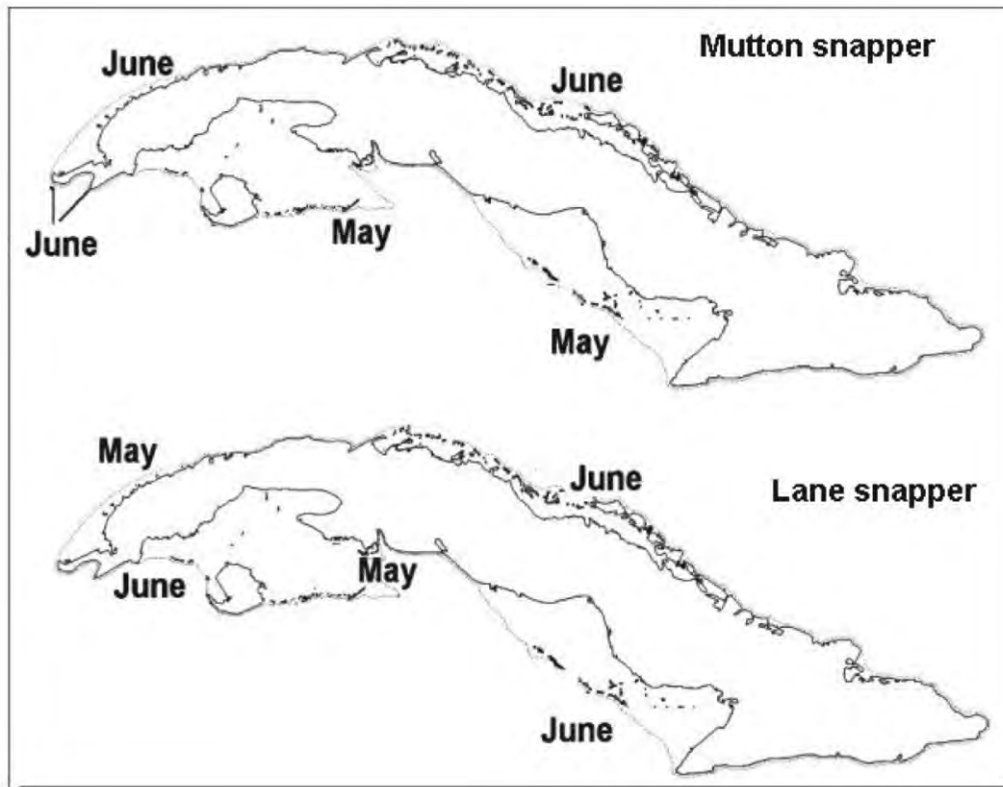
Figure 3. Intraspecific variations in peak spawning months of mutton and lane snapper among differing shelf regions of Cuba.

Variations in spawning peaks in groupers of the Cuban shelf are not as well defined as in snappers. In Nassau grouper, the spawning peak traditionally occurred in January in all regions except the northeast (with a spawning peak in December, Table 1). It is now difficult to assess such attributes of Nassau grouper spawning since catches are much lower than in the 1960s and early 1970s (Figure 4, Figure 8.14 in Claro et al. 2001). In addition, data from earlier years are potentially confounded by catch reports that included Nassau grouper captured in the Bahamas.

Mechanisms triggering variations in spawning timing are not well known and are potentially a function of age, local population size, intra- and interannual climate and current variations, and differing shelf geomorphologies (Grimes 1987, Koenig et al. 2000, Eklund et al. 2000, García-Cagide et al. 2001). Unfortunately there is a lack of information on how environmental conditions may influence spawning aggregations for most species. Sadovy and Eklund (1999) and García-Cagide et al., (2001) have suggested that water temperature is an important factor, but further information is needed before mechanisms influencing aggregation details can be confidently identified.

Interspecific Variations in Egg Release

Complex differences in gametogenesis can induce subtle variations in spawning patterns among species. In particular, differences in oogenesis can alter the amounts and timing of egg releases among seemingly similar congeneric species. Prior work in Cuba has identified several patterns of oogenesis that characterize the majority of economically valuable marine fishes of Cuba (García-Cagide et al. 2001). Two of these patterns, Type A and Type D, apply to snapper and grouper species in Cuba and appear similar (several egg batches are released by individual females over a 5 to 10 day period during only one month). However, the underlying physiological patterns of oogenesis differ between these types. In Type A species, oocytes mature at different rates, while in Type D species, all oocytes mature at once but ovulate at different rates.

The significance of these differences in evaluating spawning can be summarized, in part, as follows. Type A species (black grouper, yellowfin grouper, tiger grouper, yellowtail snapper, and dog snapper) may be able to release 7 or 8 egg batches over the course of one spawning aggregation. In contrast, Type D species (Nassau grouper, gray, mutton, and lane snapper) may only release 4
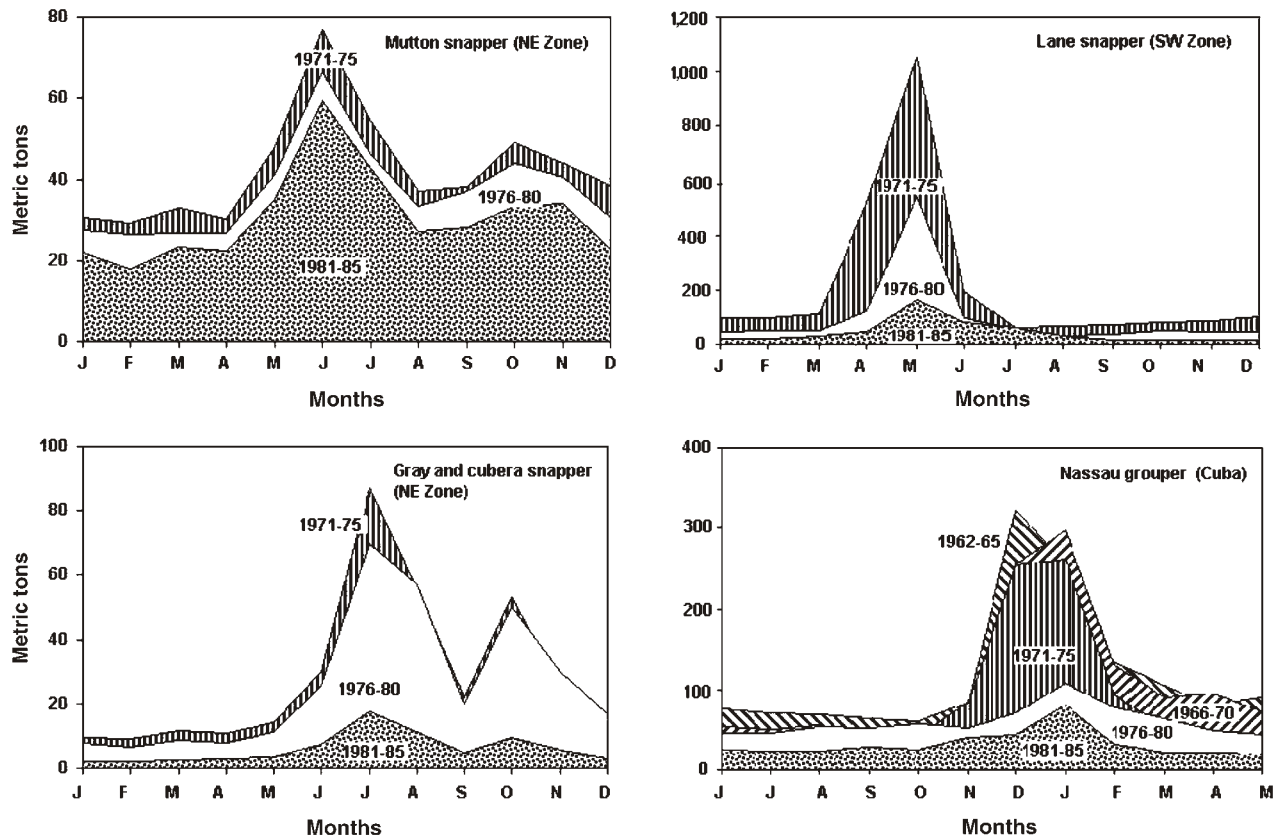
Figure 4. Monthly variations of catches of mutton, lane, mixed cubera and gray snappers (mean values for five year periods from 1971 to 1985) and Nassau grouper (1962–1985) for the Cuban shelf.

or 5 egg batches per spawning aggregation (García-Cagide et al. 2001). Much more research on both fine-scale temporal variation in egg releases and total egg production within and among species is needed to better understand spawning aggregation patterns, and their application to ecological theory and fishery management.

Overfishing of Cuban Spawning Aggregations

Degradation or elimination of spawning aggregations is one of the most damaging of population-level impacts. Not only can regional-scale population sustainability be threatened, management efforts to re-build populations can be degraded if local or long distance sources are significantly compromised. Long-term economic damage to local communities can result, as well as complex degradation of the reef ecosystem. Fishers also target areas where migrating pre-spawners are concentrated while moving to the spawning site. Such migration bottlenecks can be heavily fished, with impacts that rival fishing of actual spawning groups (Claro 1981a, Claro 1991).

Nassau grouper fisheries in the wider Caribbean represent a classic example of the consequences of over-fishing spawning aggregations (Sadovy 1994a, Sadovy and Eklund 1999, Sala et al. 2001). A similar situation exists in Cuba. Figure 4D shows the seasonal variation of Nassau grouper catches in Cuba from 1962 to 1985. The top annual catches were traditionally obtained during the spawning period and at various spawning sites (Table 1). As a result of concentrated fishing of spawning aggre-gations, catches decreased from more than 2,000 metric tons annually in the 1960s to less than 100 metric tons in the late 1990s (Claro et al. 1990, Claro et al. 2001a). Although monthly data is not readily available for recent years, available evidence suggests that Nassau grouper spawning aggregations are not recovering in substantial manners (e.g., Figure 8.14 in Claro et al. 2001a).

Until 1970, fishing trawlers caught more than 90% of the lane snapper aggregations on the shallow shelf close to Cayo Diego Pérez before and during the fifth full moon of the year. Later, long set nets, several km in length, were placed across the migration routes of lane snapper so that most of the aggregations were caught

before arriving at the spawning site (Claro 1982). During the late 1960s and until 1976, from the second quarter to 3–4 days after the full moon of May, more than 60% of the total annual catch of lane snapper in the Golfo de Batabanó, was obtained from these aggregations. Catches reached more than 1500 ton per spawning event from 1970 to 1976 (Claro 1982, 1991). These effort levels lead to catastrophic local overfishing of this species. Efforts to rebuild this lane snapper population have existed for over 25 years using several measures (a closed season during the reproductive period, size and fishing effort limits); yet, annual catches still fall far short of prior production levels (Claro et al. 2001a).

Gray and cubera snapper have also been overexploited on the Cuban shelf as result of intense fishing effort on aggregations (Figure 4C, Claro et al. 2001a). Traditionally, more than 40% of the annual catch was obtained in July-August during spawning aggregations. Both species are fished heavily during their migration to the spawning sites in channels between the keys, and cubera snapper is also fished with hook and line at the spawning site. A fishing closure in July has now been in place for several years, but this measure does not yet appear to be enough for the recovery of these stocks.

Management Applications

Fishers have passed down information on spawning aggregations for centuries. Only recently have scientists taken advantage of this information (Johannes 1978, 1998, Claro 1981a,b, Lindeman et al. 2000, Heyman et al. 2001). In addition to focusing the spatial locations of research, consistent interactions with experienced fishers can increase stakeholder involvement if related or unrelated regulatory measures arise at later intervals. Increased communication before regulations are developed can dilute the mistrust some fishers feel towards agency staff or scientists, and ultimately result in better design and implementation of marine reserves, particularly when fishers are brought into the process early and participate in the development of co-management plans.

Spawning aggregations are particularly important focal points for the siting of marine reserves because they are concentrated production sites and are relatively predictable in space and time. Examinations of source-sink dynamics and marine protected area design have focused on both larval production (Roberts 1997) and habitat-specific demographic variables (Crowder et al. 2000). These approaches encompass complex physical and biotic relationships that vary temporally (Lipcius et al. 1997). There is agreement on the need to identify and protect sites of concentrated production, particularly

given the many current threats from overfishing and habitat degradation. Active spawning aggregations, due to their discrete nature and high productivity, are clearly important source areas. This emphasizes the need to validate aggregation information when available. Use of these areas may vary temporally under natural conditions or be fully eliminated due to fishing pressure, therefore, efforts to confirm the existence of nominal aggregation sites and monitor their production through time will be essential to optimal reserve design and management.

The use of aggregation information also incorporates connectivity goals more directly into the design of interlinked networks of reserves. The long, complex configuration of the Cuban shelf, with its various archipelagos and associated circulation regimes may favor the retention of larvae within some Cuban regions (Lindeman et al. 2001), although some larvae from western spawning sites are certainly transported externally (e.g., north to at least the Florida Keys). We are using spawning aggregation sites from several Cuban archipelagos as release sites in larval transport modeling at the laboratory of R. Cowen (in prep.). Many of the spawning aggregation sites identified here are also under evaluation in a national initiative to establish a network of marine reserves around the Cuban shelf. For example, spawning sites of lane snapper near Cayo Diego Pérez at the Golfo de Cazones shelf-edge and the adjacent shallow seagrass meadows, are critical habitats for the reproduction, recruitment and juvenile growth of many commercial fishes of the Golfo de Batabanó (García-Arteaga et al. 1990, García-Cagide et al. 2001). The remaining spawning habitats in these areas deserve the protection afforded by no-take fishery reserves and are potential components of a marine reserve network in southern Cuba. Multi-use zoning alternatives that provide protection for key spawning aggregations are being incorporated into management planning for proposed reserves within all of the primary archipelagos of the Cuban shelf.

LITERATURE CITED

Aquilar-Perera, A. and W. Aguilar-Davila. 1996. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Pisces, Serranidae), in the Mexican Caribbean. Environmental Biology of Fishes 45:351–361.

Beets, J. and A. Friedlander. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environmental Biology of Fishes 55:91–98.

Carter, J. and D. Perrine. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. Bulletin of Marine Science 55:228–234.

Claro, R. 1981a. Ecología y ciclo de vida de la biajaiba, *Lutjanus synagris* (Linnaeus) en la plataforma cubana. II. Biología pesquera. Informe Científico-Técnico, Academia de Ciencias de Cuba 177:1–53.

Claro, R. 1981b. Ecología y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. c 186:1–83.

Claro, R. 1982. Ecología y ciclo de vida de la biajaiba, *Lutjanus synagris* (Linnaeus), en la plataforma cubana. IV. Reporte de Investigaciones, Instituto de Oceanología, Academia de Ciencias de Cuba 5:1–37.

Claro, R. 1983a. Ecología y ciclo de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma cubana. I. Identidad, distribución y hábitat, nutrición y reproducción. Reporte de Investigaciones, Instituto de Oceanología, Academia de Ciencias de Cuba 7:1–30.

Claro, R. 1983b. Ecología y ciclo de vida de la rabirrubia, *Ocyurus chrysurus* (Bloch), en la plataforma cubana. I. Identidad, distribución, hábitat, reproducción y alimentación. Reporte de Investigaciones, Instituto de Oceanología, Academia de Ciencias de Cuba 15:1–34.

Claro, R. 1991. Changes in fish community structure by the effect of fishing activity. Tropical Ecology 32: 36–46.

Claro, R., A. García-Cagide, L.M. Sierra, and J.P. García-Arteaga. 1990. Características biológico-pesqueras de la cherna criolla *Epinephelus striatus* (Bloch) (Pisces: Serranidae) en la plataforma cubana. Ciencias Biológicas 23:23–43.

Claro, R., K. Cantelar-Ramos, F. Pina-Amargós, and J.P. García-Arteaga. 2000. Biodiversidad y manejo de la ictiofauna del Archipiélago Sabana-Camagüey. Instituto de Oceanología, CITMA, Cuba, 89 p.

Claro, R., J.A. Baisre, K.C. Lindeman, and J.P. García-Arteaga. 2001a. Cuban fisheries: historical trends and current status. pp. 194-219 In: R. Claro, K.C. Lindeman, and L.R. Parenti, eds. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, DC, USA, 253 p.

Claro, R., K.C. Lindeman, and L.R. Parenti, eds. 2001b. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, DC, USA, 253 p.

Colin, P.L. 1996. Longevity of some coral reef fish spawning aggregations. Copeia 1996:189–192.

Colin, P.L. and I.E. Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico. Bulletin of Marine Science 43:249–279.

Crowder, L.B., S.J. Lyman, W.F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66:799–820.

Cruz-Izquierdo, R. 1999. Reclutamiento, procesos oceánicos y su relación con el pronóstico de la pesquería de la langosta, *Panulirus argus* (Latreille, 1804) en Cuba. Doctoral Thesis, University of Habana, La Habana, Cuba.

Cruz-Izquierdo, R., J.A. Baisre Alvarez, E. Díaz Iglesias, R. Brito Pérez, C. García Díaz, W. Blanco Aviles, and C. Carrodegas Rodríguez. 1987. Atlas biológico-pesquero de la langosta en el Archipiélago Cubano. Ministerio Industria Pesquera, La Habana, Cuba, 125 p.

Domeier, M.L. and P.L. Colin. 1997. Tropical reef fish spawning aggregations: Defined and reviewed. Bulletin of Marine Science 60:698–726.

Domeier, M.L., C.C. Koenig, and F.C. Coleman. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other western Atlantic snappers (Lutjanidae). p. 189–201 In: F. Arreguín-Sánchez, J. Munro, M.C. Balgos, and D. Pauly, eds. Biology, Fisheries and Culture of Tropical Groupers and Snappers. ICLARM Conference Proceedings 48:449 p.

Eklund, A.M., D.B. McClellan, and D.E. Harper. 2000. Black grouper aggregations in relation to protected areas within the Florida Keys National Marine Sanctuary. Bulletin of Marine Science 66:721–728.

Elizarov, E. and J.A. Gómez. 1971. Acerca de la dinámica de las aguas que rodean a Cuba [in Russian]. In Soviet-Cuban Fish. Res., VNIRO-CIP, Pishevaia Promichlennost, Moscow, vol. 3, p. 130–141.

García-Arteaga, J.P., R. Claro, L.M. Sierra, and E. Valdés-Muñoz. 1990. Características del reclutamiento a la plataforma de los juveniles de peces neríticos en la región oriental del Golfo de Batabanó. En Asociaciones de peces en el Golfo de Batabanó (R. Claro, ed.), Editorial Academia, La Habana, Cuba, p. 96–122.

García-Cagide, A. and R. Claro.1983. Datos sobre la reproducción de algunos peces comerciales del Golfo de Batabanó. Reporte de Investigaciones, Instituto de Oceanología, Academia de Ciencias de Cuba 12:1–20.

García-Cagide, A, and T. García. 1996. Reproducción de *Mycteroperca bonaci* y *M. venenosa* en la plataforma cubana. Revista de Biología Tropical 44:771–780.

García-Cagide, A., R. Claro, and J. P. García-Arteaga.1999a. Características biológicas del bonací gato, *Mycteroperca tigris* (Pisces: Serranidae) en la plataforma SW de Cuba. I. Características generales, reproducción. Revista de Investigaciones Marina 20:8–14.

García-Cagide, A., R. Claro, and J.P. García-Arteaga. 1999b. Biología del jocú, *Lutjanus jocu* (Pisces: Lutjanidae) en las zonas NE y SW de la plataforma cubana I. Distribución, hábitat, reproducción y dinámica de los indicadores morfofisiológicos. Revista de Investigaciones Marina 20:22–29.

García Cagide, A., R. Claro, and B.V. Koshelev. 2001. Reproductive patterns of fishes of the Cuban shelf. p. 71–114 In: R. Claro, K.C. Lindeman, and L.R. Parenti, eds. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, DC, USA, 253 p.

García-Díaz, C. 1981. Temperatura de las aguas oceánicas de Cuba. II. Aguas sub-superficiales. Revista Cubana de Investigaciones Pesqueras 6:16–35.

García-Díaz, C., A.L. Chirino, and J.P. Rodríguez. 1991. Corrientes geostróficas en la ZEE al sur de Cuba. Revista de Investigaciones Marinas 12:29–38.

González Sansón, G., A. Herrera Moreno, E. Díaz-Iglesia, R. Brito Pérez, G. Gotera González, C. Arrinda Montes y D. Ibarzabal Bombalier. 1991. Bioecología y conducta de la langosta (*Panulirus argus*, Lat.), en las zonas profundas del borde de la plataforma en la región suroccidental de Cuba. Revista de Investigaciones Marinas 12:140–153.

Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review. p. 239–294. In: J.J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, CO, USA.

Heyman, W.D., R.T. Graham, B. Kjerfve, and R. E. Johannes. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Marine Ecology Progress Series 215:275–282.

Johannes, R.E. 1978. Traditonal marine conservation methods in Oceana and their demise. Annual Review of Ecology and Systematics 9:349–364.

Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore fin fisheries. Trends in Ecology and Evolution 13:243–246.

Koenig, C.C., F.C. Coleman, C.B. Grimes, G.R. Fitzhugh, K.M. Scanlon, C.T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelfedge reefs of Florida. Bulletin of Marine Science 66:593–616.

Lindeman, K.C., R. Pugliese, G.T. Waugh, and J.S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bulletin of Marine Science 66:929–956.

Lindeman, K.C., T.N. Lee, W.D. Wilson, R. Claro, and J.S. Ault. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: evidence for partial retention in grunts and snappers. Proceedings of the Gulf and Caribbean Fisheries Institute 52:732–747.

Lipcius, R.N., W.T. Stockhausen, D.B. Eggleston, L.S. Marshall, and B. Hickey. 1997. Hydrodynamic decoupling of recruitment, habitat quality, and adult abundance in the Caribbean spiny lobster: source-sink dynamics? Marine and Freshwater Research 48:807–815.

Núñez Jiménez, A. 1982. Cuba: la Naturaleza y el Hombre: el Archipiélago. Editorial Letras Cubanas, La Habana, 691 p.

Olaechea, A. and M.A. Quintana. 1975. Desarrollo gonadal de la biajaiba en la plataforma suroccidental de Cuba. Centro de Investigaciones Pesqueras, MIP, Cuba.

Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. Science 278:1454–1457.

Sadovy, Y. 1994a. Grouper stocks of the western central Atlantic: the need for management and management needs. Proc. Gulf and Caribbean Fisheries Institute 43:43–65.

Sadovy, Y. 1994b. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). Copeia 1994:511–516.

Sadovy, Y. and A. Eklund. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Techical Reports NMFS 146, 65 p.

Sala, E., E. Ballesteros, and R.M. Starr. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries 26:23-30.

Shapiro, D.Y., D.A. Hensley, and R.A. Appeldoorn. 1988. Pelagic spawning and egg transport in coral-reef fishes: a skeptical overview. Environmental Biology of Fishes 22:3–14.

Shapiro, D.Y., Y. Sadovy, and M.A. McGehee. 1993. Size, composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). Copeia 1993:399–406.

Siam Lahera, C. 1986. Comportamiento de la temperatura del agua en las cercanías del Cayo Diego Pérez. Centro de Investigaciones Pesqueras, Ministerio de Industria Pesquera, La Habana, Cuba.

Siam Lahera, C. and N. Ramirez. 1987. Distribución de las masas de agua alrededor de Cuba. Centro de Investigaciones Pesqueras, Ministerio de Industria Pesquera, La Habana, Cuba.

Starck, W.A. 1970. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. Studies in Tropical Oceanography University of Miami 10:1–150.

Victoria del Río, I. and I. Penié. 1998. Hidrología. In: M. Vales, A. Alvarez, L. Montes, and A. Ávila, eds. Estudio Nacional sobre la Diversidad Biológica en la República de Cuba. PNUMA/CENBIO/IES/AMA/CITMA, La Habana, Cuba, p. 117–125.

Vilaró Díaz, D.J. 1884. Corrida y arribazón de algunos peces cubanos. Manuel Gómez de la Maza, La Habana, Cuba, 15 p.