

Detection of Fishing Effects on a Nassau Grouper Spawning Aggregation from Southern Quintana Roo, Mexico

ALFONSO AGUILAR-PERERA
*Department of Marine Sciences
University of Puerto Rico
Mayagüez, Puerto Rico 00681-9013*

ABSTRACT

In the tropics, spawning aggregations represent ideal opportunities to target commercially important fishes, to the level that intense and effective fishing can eliminate much of the population. The commercially important Nassau grouper forms large seasonal spawning aggregations at specific locations along the coral reefs of the western Atlantic and Caribbean. In the Mexican Caribbean, the effects of the gillnet fishery on the Nassau grouper, taken during its annual aggregations, were analyzed from 1991 to 1997. Fishing effects on grouper mean size and sex ratios were not clear. Mean size for both sexes decreased and later increased apparently in response to both fishing and variable recruitment. The size-selectivity of gillnets against both small and large individuals may have masked the impact of fishing on population size structure. The sex ratio was female-biased for the overall period and remained close to unity for each individual reproductive season, but sex ratio may not be a good indicator of exploitation in this primarily gonochoristic species. However, landings substantially declined and the aggregation disappeared from its traditional site; both of these are suggestive of serious problems. Although several factors could be involved, fishing is strongly implicated as probable cause for these changes. Fishery managers seriously need to consider the establishment of marine reserves as an alternative to protect all the known Nassau grouper aggregations along the southern coast of Quintana Roo, Mexico.

KEY WORDS: Fishing, Nassau grouper, spawning aggregations, Mexico

Determinacion del los Efectos de la Pesca en Agregaciones de Desove del Mero de Nassau a lo Largo de la Costa Sur de Quintana Roo, México

En los trópicos, las agregaciones de desove representan oportunidades ideales para capturar peces de importancia comercial, a grado tal que la pesca intensa y efectiva puede eliminar gran parte de su población. El mero de Nassau, de importancia comercial, forma agregaciones de desove estacionales en sitios específicos a lo largo del arrecife coralino en el Atlántico oeste y Caribe. En el Caribe mexicano, se analizaron los efectos de la pesca con redes sobre el mero de Nassau, capturado durante sus agregaciones anuales, de 1991 a 1997. No fueron claros los efectos de la pesca sobre la talla media y proporción en sexos del mero.

La talla media para ambos sexos disminuyó y luego incrementó, en respuesta tanto a la pesca como a un reclutamiento variable. La selectividad por talla de las redes contra individuos pequeños y grandes quizá haya enmascarado el impacto de la pesca sobre la estructura poblacional por tallas. La proporción en sexos estuvo sesgada hacia hembras durante todo el período y se mantuvo cercana a la unidad para cada estación reproductiva, pero la proporción en sexos quizá no sea un buen indicador de explotación en esta especie primordialmente gonocórica. Los desembarques disminuyeron substancialmente y la agregación desapareció del sitio tradicional, lo que sugiere que existen problemas serios. Si bien, varios factores podrían estar involucrados en tal desaparición, la pesca queda implicada como una causa probable de tales cambios. El manejo pesquero necesita tomar seriamente en consideración el establecimiento de reservas marinas como una alternativa para proteger todas las agregaciones conocidas del mero de Nassau a lo largo de la costa sur de Quintana Roo, México.

PALABRAS CLAVES: Pesquería, el mero de Nassau, agregaciones de desove, Quintana Roo, México

INTRODUCTION

Traditional subsistence fishing is a widespread human exploitative activity in the tropics. Intense fishing pressure affects the targeted marine organisms (Russ 1991, Jennings and Lock 1996) by reducing their density and abundance (Russ and Alcalá 1989, McClanahan 1994), biomass (Jennings et al. 1995), altering sex ratios (Thompson and Munro 1983), and decreasing body mean size and catch rates (Koslow et al. 1988). Intense fishing has severe consequences for commercially important groupers because of their longevity, slow growth, large age at maturity, and their aggregating behavior during reproduction (Ralston 1987, Sadovy 1994; Coleman et al. 1996).

In the western Atlantic, several groupers exhibit an aggregating behavior: Nassau grouper, *Epinephelus striatus* (Smith 1972), Red hind, *Epinephelus guttatus* (Shapiro et al. 1993), Goliath grouper, *E. itajara* (Sadovy and Eklund 1999, Nelson et al., 2001), Tiger grouper, *Mycteroperca tigris* (Sadovy et al., 1994; Sala et al., 2001), Yellowfin grouper, *M. venenosus* (Sala et al. 2001), and Black grouper, *M. bonaci* (Eklund et al. 2000, Sala et al. 2001). They form briefly, seasonal aggregations to spawn at predictable times and places in the coral reefs (Shapiro 1987, Domeier and Colin 1997). Such aggregating behavior and high site fidelity during reproductive seasons may increase chances for their overexploitation (Coleman et al. 1996).

The Nassau grouper, one of the most commercially important, shallow-water grouper in the western Atlantic (Munro 1973, Thompson and Munro 1978, Sadovy and Eklund 1999), concentrates in hundreds or even thousands of individuals at what seem to be traditional spawning aggregation sites in the coral reef (Smith 1972; Olsen and La Place 1979, Sadovy and Eklund 1999). The aggregation forms for a

period of days prior to spawning during full moon days of December and January, and abruptly dissipates after the reproductive season (Colin 1992, Carter et al. 1994; Aguilar-Perera and Aguilar-Dávila 1996, Sadovy and Eklund 1999, Sala et al. 2001). Many reported Nassau grouper aggregation sites in the western Atlantic show severe landing declines (Sadovy 1999), and many have completely disappeared due to overexploitation (Sadovy and Eklund 1999). As a consequence, the Nassau grouper is a candidate for the U.S. Endangered Species List (Sadovy and Eklund 1999) and considered as threatened by the American Fisheries Society (Musick et al. 2000).

In the Mexican Caribbean (eastern Yucatan Peninsula), of the seven Nassau grouper aggregation sites located along the southern coast of Quintana Roo (Aguilar-Perera 1994), one of the most exploited and the only studied is located off Mahahual, close to northern Belize. Fishermen heavily exploited Nassau groupers from this aggregation site for more than 80 years (Aguilar-Perera 1994, Aguilar-Perera and Aguilar-Dávila 1996, Aguilar-Perera 2000, Sosa-Cordero and Cárdenas-Vidal 1996). Current studies on its stock are relatively scarce as to establish fishery management regulations to protect it.

While direct effects of fishing pressure on fishes are known (Russ 1991, Jennings and Lock 1996), and being more critical during spawning seasons of aggregating groupers (Coleman et al., 1996), relatively few is known of the Nassau grouper in the Mexican Caribbean (Aguilar-Perera 2000). Thus, the primary aim of this study was to examine its population structure based on the commercial gillnetting catch and to determine if changes in mean size and sex ratio relate to the effects of persistent and heavy fishery exploitation.

MATERIAL AND METHODS

Nassau groupers were sampled from the commercial catch in Mahahual (18°43' N; 87°42' W), southern Quintana Roo, Mexico, exclusively during reproductive seasons (e.g., spawning aggregations) each December and January from 1991 - 1997 (except January 1994, 1995 and December 1996, due to logistic constrains). For capturing Nassau groupers, the fishermen used gillnets (15 cm in mesh size) that regularly set in the afternoon (1500 hrs) and hauled early in the morning (0500 hrs) the following day. In some cases during mornings, fishermen would remove groupers as the gillnet was hauled, set it back in the water, and haul it again in the afternoon. Gillnets were deployed in the fore reef, perpendicularly to the reef crest, southern to the traditional grouper spawning aggregation site of Mahahual (Aguilar-Perera 1994, Aguilar-Perera and Aguilar-Dávila 1996).

Since sampling was entirely fishery-dependent, there were some constraints in fishing effort that substantially precluded the sampling. Number of boats, fishermen, and gillnets were variable every fishing season. For instance, in December 1991 and January 1992, at least six boats with two gillnets (150 m long, 5 m wide each) were used by fishermen, while in December 1995 and January 1996, only three boats with one gillnet (200 m long, 5 m wide) were used. Such a decrease in fishing effort was explained by the difficulty for the fishermen in easily finding the grouper

aggregation.

At the landing site, grouper total length (TL) and standard length (SL) were measured to the nearest centimeter, and body and gonad weights were recorded to the nearest gram. Fish were sexed either macroscopically by gently squeezing and externally examining their abdomens or microscopically in laboratory, following embedding in paraffin, sectioning at 4–5 μm , and staining in hematoxylin and eosin. The Kolmogorov-Smirnov two sample test (D), t-test (t), χ^2 , and ANOVA were used to compare the fish size-frequency distributions, mean size, sex ratio, and length variations between reproductive periods, respectively (Sokal and Rohlf 1995).

RESULTS

The total sample was comprised by 778 Nassau groupers ranging from 39 to 88 cm TL (sexes combined). Of these, 338 (43.4 %) were males (39 to 86 cm TL) and 440 (56.5%) were females (46 to 88 cm TL). A subsample of 412 groupers (52.9 %; sexes combined) ranged from 1.3 to 10.2 kg. Of these, 178 were males (1.3 to 10.2 kg) and 233 were females (1.8 to 9.6 kg). Size-frequency distributions between females and males were not significantly different (Kolmogorov-Smirnov two sample test). Mean total length did not differ significantly between sexes within each reproductive season (t-test; Table 1). However, mean total length for both sexes combined was significantly different between reproductive seasons (ANOVA, $p < 0.0001$). There was a significant decrease in mean total length for males in December 1993, while significant differences for females were found in December 1993 and 1994 (Tukey test, $p < 0.05$). Mean total length for both sexes slightly increased during subsequent reproductive seasons.

Size-frequency distributions, sexes combined, showed a slightly shift to smaller sizes between December and January within a single reproductive season (Figure 1). In December 1991, mean size was 58.1 cm, while in January 1992 there was a mean size of 59.21 cm. However, size-frequency distributions were not significantly different. In contrast, in December 1992 and January 1993, size-frequency distributions were significantly different (Kolmogorov-Smirnov: $D = 0.226$, $p < 0.01$). Mean size in December 1992 (57.7 cm) was significantly smaller than that of January 1993 (60.8 cm; t-test, $p < 0.01$).

The overall sex ratio of females ($n = 440$) to males ($n = 338$) was 1.3:1, which was significantly biased towards females (χ^2 , $p < 0.001$). Nonetheless, during most reproductive seasons, the sex ratio was close to unity (1:1), except for December 91-January 1992 ($n = 224$, χ^2 , $p < 0.001$) and December 1995-January 1996 ($n = 61$, χ^2 , $p < 0.01$), where a female-biased ratio for the former and a male-biased ratio for the latter were significant. Sex ratios for each reproductive season are shown in Table 2.

Table 1. Mean observed total length (TL, cm), standard deviation (SD) and percentage, for Nassau grouper female and male by reproductive season (December 1991 - January 1997).

Reproductive season	Female				Male			
	Mean	SD	N	%	Mean	SD	N	%
December 91-January 92	58.2	5.371	147	33.4	58.2	5.992	77	22.7
December 92-January 93	58.3	5.614	167	37.9	58.6	5.043	126	37.2
December 93	55.4	4.108	60	13.6	54.7	4.277	57	16.8
December 94	57.5	3.733	39	8.8	56.1	3.279	31	9.1
December 95-January 96	60.8	6.825	20	4.5	58.5	5.329	41	12.1
January 97	60.0	6.218	7	1.6	58.3	2.732	6	1.7
Grand Mean/Total	58.7	5.433	440	57.8	57.8	5.176	338	

N = number of fish

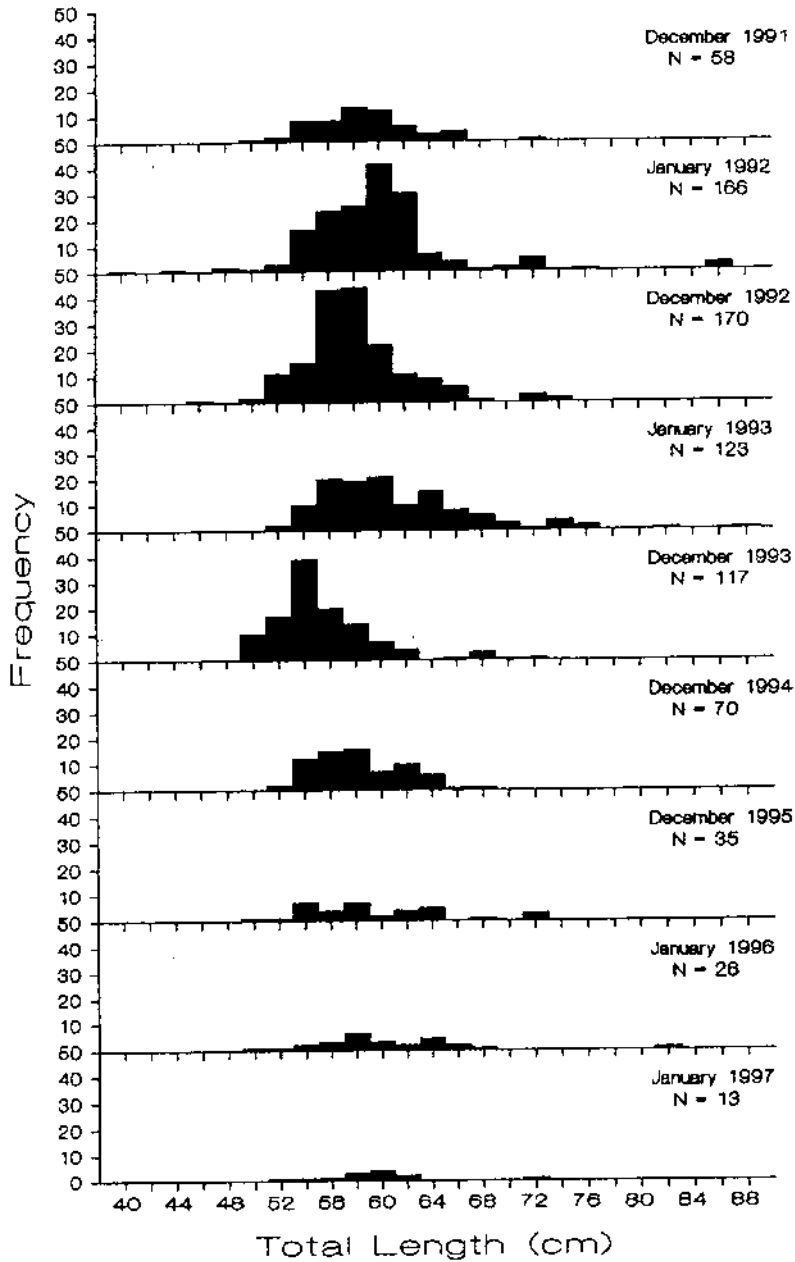


Figure 1. Length-frequency distributions of male and female Nassau grouper, *Epinephelus striatus*, taken from the spawning aggregation by the gillnetting fishery of Mahahual, Quintana Roo, Mexico (from Aguilar-Perera, 2000).

Table 2. Nassau grouper, *Epinephelus striatus*, sex ratios for each reproductive season and fish aggregation arrival dates to the traditional aggregation site at Mahahual, Quintana Roo. Sampling was conducted around full moon days only.

Reproductive season	N		Sex ratio F : M	Sampling	Full moon day	Grouper arrival date
	F	M				
Dec 91-Jan 92	147	77	1.9:1*	23-26 Dec; 19-25 Jan	21 Dec/19 Jan	23 Dec/19 Jan
Dec 92-Jan 93	187	126	1.3:1	10-15 Dec; 6-12 Jan	10 Dec/ 8 Jan	19 Dec/6 Jan
Dec 93	60	57	1:1	28-31 Dec	27 Dec	28 Dec
Dec 94	39	31	1.2:1	18-21 Dec	17 Dec	18 Dec
Dec 95-Jan 96	20	41	0.48:1**	6-8 Dec; 5-8 Jan	16 Dec/7 Jan	6 Dec/5 Jan
Jan 97	7	6	1.1:1	21 Jan	23 Jan	21 Jan

F = female, M = male. N = number of fish. Dec = December, Jan = January. Significant, female-biased (*). Significant, male-biased (**).

DISCUSSION

Nassau grouper mean size trend was not a good indicator of fishing effects because of the influence of annual recruitment variability. Females and males were similar in size, not only for the overall study, but also during each reproductive season. However, there was a decline in mean size for females during December 1993 and 1994, and for males during December 1993. An apparent increase in mean size for both sexes was observed during December 1995 and January 1997. It is possible that a combination of persistent fishing pressure and grouper annual recruitment variations could account for such differences in mean size. Moreover, during last months of the study sample size was so small (around 13 individuals), due to grouper landing decline, that it could confound mean size comparisons with the previous reproductive seasons. There were no more elements as to conclude that the mean size fluctuations could be solely due to fishing pressure.

According to Carter et al. (1994), in Belize the Nassau grouper mean sizes for both sexes were similar within a given area, or at a specific aggregation site; thus it is possible to detect size decline in areas of higher exploitation. When the exploitation is very high, juveniles (< 30 cm TL) largely comprised the catch (Sadovy and Eklund 1999). In Belize, Nassau grouper mean sizes of exploited aggregations were smaller (> 42 cm standard length [SL]) than those of non-exploited aggregations (52 cm SL) (Carter et al. 1994). In the Mexican Caribbean, although mean sizes apparently declined, juveniles were not present in the commercial catch, and mean size for both sexes was greater than that of groupers from Belize. In a previous study in Mahahual, Mexico, Sosa-Cordero and Cárdenas Vidal (1996) found that mean size between females and males was significantly different during 1991 - 1990, with females slightly larger than males. However, they concluded that their results were preliminary, with shortcomings derived from a small sample size (180 individuals only).

In the present study of Mahahual, juvenile absence from catches could be due to either gillnet selectivity for larger sizes (> 30 cm) or the presence of only mature groupers. However, a couple of individuals (< 30 cm) were observed in the coral reefs close the aggregation site. One interesting aspect found in this study, in relation to mean size, is that the size-specific Nassau grouper catchability (i.e., the extent to which a stock is susceptible to fishing) with gillnets would potentially be equivalent for both sexes, meaning that the fishery was not size-selective for a particular sex.

Sex ratio was not a good indicator of fishing effects. The overall sex ratio of Nassau grouper in the Mexican Caribbean was significantly female-biased (1.3:1), but when viewed for each reproductive season it was close to unity, with two exceptions (December 1991 - January 1992; December 1995 - January 1996). The gillnet fishery reflected a significantly overall female-biased sex ratio. However, most reproductive seasons reflected a uniform sex ratio. Compared to other Nassau grouper populations around the western Atlantic, the sex ratio in this study was among the closest to unity, while the most female-biased (4:1) was reported in heavily exploited areas of Cuba (Claro et al. 1990).

In general, the sex ratio is female-biased in exploited populations, while in lightly or relatively non-exploited populations is close to unity, suggesting that the normal sex

ratio in non-fished adult populations is approximately 1:1 (Sadovy and Colin 1995, Sadovy and Eklund 1999). However, care is needed when assessing sex ratios at aggregations because of possible gear selectivity, differences between the sexes in time spent at aggregation sites or migration patterns (Sadovy and Eklund 1999). In the Mexican Caribbean, differences between sexes in time spent at aggregation sites could have affected the estimation of sex ratio. According to Bardach (1958), males may precede females to spawning sites. This may explain the sudden appearance of a male-biased sex ratio observed in the Mexican Caribbean during the December 1995 - January 1996. Sosa-Cordero and Cárdenas-Vidal (1996) also documented a male-biased sex ratio (1: 1.5) in Mahahual during 1990-91.

While the mean size trend and sex ratio were not good indicators of fishing effects on the Nassau grouper from Mahahual, the aggregation disturbance (i.e., disappearance) and landing declines (Aguilar-Perera and Aguilar-Dávila 1996) were indicative of serious problems. Such situation is similar to that of the rest of the Nassau grouper aggregations in the western Atlantic (Sadovy and Eklund 1999). In this sense, concerns about the possibility of overexploitation of the Nassau grouper from Mahahual are high (Aguilar-Perera 2000). Fishing at this aggregation site started in the 1920s, but it attained commercial importance in the 1950s, when Nassau grouper landings obtained by hook and line for one season reached about 24 t (Aguilar-Perera 1994). The average weight of the groupers caught from 1991-1997 was 4 kg (Aguilar-Perera, 2000); thus, 24,000 kg represents around 6,000 individuals. In 1988, 4 t (1000 individuals) were caught in 1988 using spearfishing only (Aguilar-Perera 1994), and 2 t (500 individuals) in 1992 using gillnets (Aguilar-Perera and Aguilar-Dávila 1996). However, in 1997 less than 100 kg (25 individuals) were caught with gillnets only. It is important to mention that not only the fishing gear used, but also the number of fishermen varied along this period of 50 years.

During the 1990 - 1991 season, a grouper aggregation comprised by 1,000 groupers was found at the traditional site (Aguilar-Perera 1994), but eventually no longer appeared at this site, and only sparse fish groups (2 or 3 of less than 100 individuals) were found at the deep fore reef (15 m), moving from south to north following the deep fore reef contour (Aguilar-Perera and Aguilar-Dávila 1996). Such a progressive decline in fish abundance at this aggregation has greatly diminished the fishermen's ability to exploit it. Moreover, in late 1996 the Mexican Fishery Department applied a severe fishing ban, which not allowed the fishermen to exploit the Nassau grouper during the aggregation.

In the western Atlantic, of the more than 60 Nassau grouper aggregation sites known, many (25 %) no longer form (Sadovy and Eklund 1999). Since these aggregations are found at predictable places and times in short periods, removed with a variety of fishing gears, and heavily exploited for more than 50 years, they are especially susceptible to heavy fishing pressure, and consequently to overexploitation. In the Mexican Caribbean, as in many areas of the western Atlantic, the fishermen mainly exploit Nassau groupers during the reproductive (i.e., aggregating) season (December and January). For more than 80 years, the grouper

aggregation from Mahahual was exploited with different types of fishing gears (Aguilar-Perera 1994), including hand lines, spearguns, and gillnets (Aguilar-Perera and Aguilar-Dávila 1996). Spearfishing (Sluka and Sullivan 1998) and fish traps (Thompson and Munro 1978) are more devastating for larger and smaller groupers, respectively, because both gears are highly size-selective. In the Mexican Caribbean, gillnets selected a vast array of Nassau grouper sizes (39 cm to 88 cm TL) according to the mesh size used (e.g., 15 cm).

Fishing effects are more striking on fishes that aggregate to spawn (Coleman et al. 1996), since they show high site fidelity and concentrate their annual reproductive activity during aggregations. Heavy selective pressure concentrates on mature Nassau groupers susceptible to capture from easily located spawning aggregations. Since heavy fishing on these aggregations is one of the main causes of fish depletion and stock collapse, a complete protection for them is strongly recommended as a management strategy in the western Atlantic (Sadovy 1999). Such protection needs also to be enforced during non-aggregating seasons, with additional management regulations, such as: minimum sizes, gear restrictions and quota limits (Sadovy, 1994). Furthermore, comprehensive studies on biological, fishery, and socio-economic aspects are important for an effective management (Sadovy 1994, Aguilar-Perera 1994). In the Mexican Caribbean, new research for the aggregation site off Mahahual (including the other known sites along the southern coast of Quintana Roo), must rely on using the side-scan sonar technology and geographic information systems (GIS) for habitat mapping, and telemetry (ultrasonic tagging) to determine the Nassau grouper home range and potential aggregation site sharing along the Mexican coast (including Belize).

Recently, a management alternative increasingly accepted to protect spawning areas involves establishing "no-take" (or fully protected) marine reserves (Jennings 2001, Roberts et al. 2001). Any identified and documented spawning area represents a known "source" of larvae for the replenishment of local populations, while the adjacent areas could be "sinks". Thus, both should be protected as a marine reserve (Roberts 1998). Density and biomass of larger groupers in the Florida Keys and the Bahamas were significantly greater in marine reserves than in heavily exploited areas (Chiappone et al. 2000). Nassau grouper size, reproductive output (number of eggs per hectare), and average biomass inside a marine reserve in the Bahamas were significantly greater than those of outside (Sluka et al. 1997). Since the Nassau grouper migrates considerable distances to reproduce (Bolden, 2000), a network of marine reserves (including spawning sites) is recommended for conservation and management purposes. In addition to establishing reserves for the Nassau grouper in the Mexican Caribbean, it could be important to evaluate the nonextractive value of this grouper as a tourist attraction through diving, offering the fishermen an alternative to obtain economic revenue. In this sense, very interesting perspectives have proposed in Belize (Sala et al. 2001) and Turks and Caicos (Rudd and Tupper 2002).

Avoiding fishing pressure on the Nassau grouper spawning aggregations, establishing a network of "no-take" marine reserves, and applying additional

management regulations during non-aggregating periods, need to be strongly enforced to assure that potential recruits could incorporate via either pelagic (eggs and larvae) or benthic (adults) stages to replenish grouper populations not only in the Mexican Caribbean, but also in adjacent countries (e.g., Belize and Honduras) within the Mesoamerican Barrier Reef System.

ACKNOWLEDGMENTS

Many people provided assistance for this work, I am especially grateful to J. Schmitter-Soto, W. Aguilar-Dávila, D. Ceballos-Carrillo, H. Herrera, L. Canul, A. Sosa, C. Ramón, and M. Collí (Chandés). R. S. Appeldoorn provided very helpful advice, supported on final stages of this work, and generously helped drawing Figure 1. In Mexico, this work was partially funded by the former Centro de Investigaciones de Quintana Roo (now El Colegio de la Frontera Sur) and the Consejo Nacional de Ciencia y Tecnología.

LITERATURE CITED

- Aguilar-Perera, A. 1994. Preliminary observations on the spawning aggregation of Nassau grouper *Epinephelus striatus* at Mahahual, Quintana Roo, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:112-122.
- Aguilar-Perera, A. and W. Aguilar-Dávila. 1996. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fish* 45:351-361.
- Aguilar-Perera, J. A. 2000. Stock analysis for an aggregating reef fish, the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) from the Mexican Caribbean. MS Thesis, University of Puerto Rico, Mayagüez, Puerto Rico. 85 pp.
- Bardach, J.E. 1958. On the movements of certain Bermuda reef fishes. *Ecology* 39:139-146.
- Bohnsack, J. 1996. Maintenance and recovery of reef fishery productivity. Pages 283-313 in: Polunin, N.V.C. and C.M. Roberts (eds.). *Reef Fisheries*. Chapman and Hall, London, England.
- Bolden, S.K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fisheries Bulletin* 98:642-645.
- 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. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:65-111.
- Chiappone, M., R. Sluka, and K. Sullivan Sealy. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series* 198:261-272.
- Claro, R., A. García, L. Sierra, and J. García. 1990. Características biológico-pesqueras de la cherna criolla, *Epinephelus striatus* (Bloch) (Pisces:

- Serranidae) en la plataforma cubana. *Ciencia Biología* 23:23-43.
- Coleman, F.C., C.C. Koenig, and L.A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fish* 47:129-141.
- Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fish* 34:357-377.
- Domeier, M.L. and P.L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60:698-726.
- Eklund, A.E., 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.
- Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. *Reviews in Fisheries Biology and Fisheries* 10:209-231.
- Jennings, S. and J.M. Lock. 1996. Population and ecosystem effects of reef fishing. Pages 192-218 in: Polunin, N.V.C. and C.M. Roberts (eds.). *Reef Fisheries*. Chapman and Hall, London, England.
- Jennings, S., E.M. Grandcourt and N.V.C. Polunin. 1995. The effects of fishing on diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14: 225-235.
- Koslow, J.A., F. Hanley, and R. Wicklund. 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. *Marine Ecology Progress Series* 43:201-212.
- McClanahan, T.R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13:231-241.
- Munro, J.L. 1973. The spawning season of Caribbean reef fishes. *Journal of Fish Biology* 5:69-84.
- Musick, J.A. et al. (seventeen authors). 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America. *Fisheries* 25:6-30.
- Nelson, J.S., E.J. Crossman, H. Espinoza-Pérez, L.T. Findley, C.R. Gilbert, R.N. Lea, and J.D. Williams. 2001. Recommended change in the common name for a marine fish: Goliath grouper to replace jewfish (*Epinephelus itajara*). *Fisheries* 26:31.
- Olsen, D.A. and J.A. LaPlace. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. *Proceedings of the Gulf and Caribbean Fisheries Institute* 31:130-144
- Ralston, S. 1987. Mortality rates of snappers and groupers. Pages 375-404 in: Polovina, J.J. and S. Ralston (eds.). *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado USA.
- Roberts, C.M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries* 23:16-19.
- Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294:1920-1923.

- Rudd, M.A. and M.H. Tupper. 2002. The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coastal Management* 30:133-151.
- Russ, G.R., 1991. Coral reef fisheries: effects and yields. Pages 601-635 in: Sale, P.F. (ed.). *The ecology of fishes on coral reefs*. Academic Press, San Diego, California USA.
- Russ, G.R. and A. Alcalá. 1989. Effects on intense fishing pressure on an assemblage of coral reef fishes. *Marine Ecology Progress Series* 56:13-27.
- Sadovy, Y. 1994. Grouper stocks of the western Central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:43-64.
- Sadovy, Y. 1999. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper, in the Caribbean and western Atlantic. *Proceedings of the Gulf and Caribbean Fisheries Institute* 45:5-22.
- Sadovy, Y. and P.L. Colin. 1995. Sexual development and sexuality in the Nassau grouper. *Journal of Fish Biology* 46: 961-976.
- Sadovy, Y. and A. Eklund. 1999. Synopsis of the biological data on the Nassau grouper *Epinephelus striatus* (Bloch, 1792) and the Jewfish, *E. itajara* (Lichtenstein, 1822) NOAA Tech. Rep. NMFS 146. 65 pp.
- Sadovy, Y., P.L. Colin, and M.L. Domeier. 1994. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). *Copeia* 1994:511-516.
- 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. 1987. Reproduction in groupers. Pages 295-328 in: Polovina, J.J. and S. Ralston (eds.). *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, Colorado USA.
- 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.
- Sluka, R.D., M. Chiappone, K.M. Sullivan, and R. Wright. 1997. The benefits of a marine fishery reserve for Nassau grouper *Epinephelus striatus* in the central Bahamas. *Proc. 8th Int. Coral Reef Symposium* 2:1961-1964.
- Sluka, R. and K.M. Sullivan. 1998. The influence of spear fishing on species composition and size of groupers on patch reefs in the upper Florida keys. *Fisheries Bulletin* 96:388-392.
- Smith, C.L. 1972. A spawning aggregation of the Nassau grouper *Epinephelus striatus* (Bloch). *Transactions of the American Fisheries Society* 101:257-261.
- Sokal, R.R. and F.J. Rohlf. 1995. *Biometry*. The principles and practice of statistics in biological research, 3rd Edition. Freeman & Co., New York, New York USA. 850 pp.
- Sosa-Cordero, E. and J. Cárdenas-Vidal. 1996. Estudio preliminar de la pesquería de mero *Epinephelus striatus* del sur de Quintana Roo. *Proceedings of the Gulf and Caribbean Fisheries Institute* 44:56-72.

- Thompson, R. and J.L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology* 12:115-146.
- Thompson, R and J.L. Munro. 1983. The biology, ecology and bionimics of the hinds and groupers, Serranidae. Pages 59-81 in: J.L. Munro (ed.). *Caribbean Coral Reef Fisheries Resources* (ICLARM Stud. Rev. 7) ICLARM, Manila, Philippines.