

Nassau Grouper (*Epinephelus striatus*) in St. Thomas, US Virgin Islands, with Evidence for a Spawning Aggregation Site Recovery

ELIZABETH KADISON, RICHARD S. NEMETH, JEREMIAH BLONDEAU, TYLER SMITH, and JACQUI CALNAN
Center for Marine and Environmental Studies, University of the Virgin Islands
2 John Brewers Bay, St. Thomas, United States Virgin Islands

ABSTRACT

The exploitation by fishing of fish spawning aggregations has caused many to disappear over the last fifty years, and has been a primary cause of dramatic stock declines of several large snapper and grouper species Caribbean-wide. In the USVI and Puerto Rico, the major Nassau grouper (*Epinephelus striatus*) spawning aggregation sites were fished to extinction in the 1970s, and although the species is now federally protected, most sites show no signs of recovery. In 2003, Nassau grouper were found aggregating in small numbers to spawn on an offshore reef south of St. Thomas called the Grammanik Bank. The bank was seasonally, from February to May, closed to all bottom fishing beginning in 2005 due to the aggregating of the yellowfin grouper (*Mycteroperca venenosa*) on the site. Since 2005, increased numbers, a significantly greater mean size, and a larger size range of Nassau grouper have been documented on the bank. The fish are spatially and temporally mixed with yellowfin grouper during courtship, and it is believed this behavior may be an artifact of decreased numbers of Nassau, now using the yellowfin as surrogate aggregation members. It is doubtful that any other large Nassau grouper spawning aggregation sites remain in the USVI, so the effectiveness of the Grammanik Bank fishing closure may play a significant role in the recovery of local stocks.

KEYWORDS: Serranidae, spawning stocks, protected species, marine protected areas

Evidencia de recuperación de una agregación reproductiva del Mero Cherna (*Epinephelus striatus*) en el Banco Grammanik de las Islas Vírgenes de EU

La explotación pesquera del Mero Cherna ha causado la desaparición de varias agregaciones reproductivas lo cual ha reducido dramáticamente los abastos de esta especie a través del Caribe. En las Islas Vírgenes de EU la agregación de desove mas grande del Mero Cherna se pescó hasta su extinción en los años 1970 y aunque actualmente la especie esta protegida a nivel federal, aun no se observa la recuperación de su población. Apenas cinco kilómetros hacia el este de el lugar de agregación tradicional se han observado Meros Cherna agregados para desovar en el Banco Grammanik donde tradicionalmente se pesca el Guajil Aletiamarillo (*Mycteroperca venenosa*). En el año 2005 el Consejo de Pesca del Caribe prohibió toda pesca de fondo desde el 1º de febrero al 30 de abril y se prohibió la pesca de nasas durante el año completo en el Banco Grammanik. Desde entonces hemos documentado un aumento en la abundancia al igual que el tamaño promedio, tamaño máximo y menor tamaño mínimo del Mero Cherna. Los Meros Cherna se mezclan con el Guajil Aletiamarillo temporal y espacialmente al igual que en los comportamientos de cortejo. Creemos que esto se debe a los números reducidos del Mero Cherna que se asocian a los Guajiles como miembros sustitutos de su agregación de desove. Es poco probable que existan otras áreas de agregación reproductiva significativas del Mero Cherna en las Islas Vírgenes de EU, por lo tanto la efectividad del cierre a la pesca en el Banco Grammanik juega un rol sumamente importante en la recuperación de los abastos locales de esta especie.

PALABRAS CLAVES: Serranidae, los abastos reproductivo, especie protegidas, manejo de áreas protegidas marinas

Évidence de Récupération D'agrégation de Frai Pour un Merou de Nassau (*Epinephelus striatus*) Sur la Banque Grammanik, Îles Vierges Américaines

L'exploitation des agrégations de reproduction de mérours Nassau par les pêcheurs au cours des cinquante dernières années a provoqué la disparition de nombreuses agrégations, et a été la principale cause de la baisse dramatique des stocks de Nassau dans toute la Caraïbe. Dans les îles Vierges américaines, le site principal d'agrégations de mérours Nassau a été pêché jusqu'à l'extinction en 1970, et bien qu'actuellement sous protection fédérale, il ne montre aucun signe de reprise. Cinq kilomètres à l'est, par ailleurs, des mérours de Nassau ont été trouvés agrégeant à se reproduire sur la Grammanik Bank, un récif où le mérour albacore (*Mycteroperca venenosa*) est traditionnellement pêché durant leur période de reproduction. Bien qu'illégal à récolter, des mérours Nassau ont été capturés comme prises accessoires et poché à partir du site par les pêcheurs pêchant l'albacore. En 2005, le Conseil de gestion des pêcheries dans les Caraïbes a fermé la banque à tous de pêche de fond à partir du 1er février au 30 avril annuellement et les pièges à poissons toute l'année. Depuis, nous avons documenté un nombre accru de mérours Nassau sur la Grammanik Bank, ainsi qu'une taille moyenne plus grande, une plus grande taille maximale, et une plus petite taille minimum. Des données d'étiquette hydro-acoustique et externe indiquent que les poissons sont venus de l'ouest et du nord. Les mérours Nassau sont spatialement et temporellement mélangés avec les mérours albacore lors de la séduction, et nous pensons que ce comportement pourrait être un objet de diminution du nombre de Nassau, en utilisant l'albacore comme membres d'agrégation de substitution. Il est incertain que les autres grands sites d'agrégation de frai de mérours Nassau restent dans les îles Vierges américaines, car l'efficacité de la fermeture de la pêche à Grammanik Bank pourrait jouer un rôle important dans la reconstitution des stocks locaux.

MOTS CLÉS: Serranidae, zone de protection marine, bio-diversité

INTRODUCTION

The once prolific Nassau grouper (*Epinephelus striatus*), historically dominant both culturally and economically in Caribbean fisheries, is today commercially extinct over much of its historic range (Sadovy and Eklund 1999). Although protected in federal waters of the United States (US) since the 1990s, the Nassau is still considered to be one of the most threatened groupers worldwide (Morris et al. 2000), is listed as endangered on the IUCN Red List, and is a candidate for the US Endangered Species Act.

Overexploitation by fishing of spawning aggregations is believed to have played a major role in the collapse of local grouper and snapper fisheries in some areas (Sadovy 1997, Sadovy and Domeier 2005). Strong spawning aggregation site fidelity in both space and time as well as unusually high densities of normally solitary fish, greatly increase vulnerability to fishing during this life history phase. Aggregations, lasting only a few weeks of the year, represent most if not all of the annual reproductive effort of many large groupers, including the Nassau (Sadovy and Eklund 1999). In the United States Virgin Islands (USVI), a large Nassau grouper spawning aggregation site located south of St. Thomas was extirpated in the 1970s, and although additional aggregation sites have been reported anecdotally, the demise of this site was believed to have been instrumental in the collapse of the Nassau grouper fishery in St. Thomas waters (Olsen and LaPlace 1978).

In 2003, on a coral reef called the Grammanik Bank located on the southern edge of the Puerto Rican shelf edge

approximately 14 km south of St. Thomas (Figure 1), a small aggregation of Nassau grouper was documented (Nemeth *et al.* 2006). This bank is located approximately 4 km east of the historic Nassau grouper spawning site, Yellowfin grouper (*Mycteroperca venenosa*), tiger grouper (*M. tigris*), yellowmouth grouper (*M. interstitialis*), dog snapper (*Lutjanus jocu*) and cubera snapper (*L. cyanopterus*) were also found aggregating to spawn on the Grammanik Bank (Nemeth *et al.* 2006, Kadison *et al.* 2007). Groupers had been largely unexploited on this reef prior to 2000, however in March and April of 2000 and 2001, fishermen reported catches of up to 20,000 lbs of yellowfin grouper and over 1,000 lbs of Nassau grouper (Kenneth Turbe, USVI fisherman Pers. comm.). The Grammanik Bank was closed to all bottom fishing from February 1 through April 30 in 2005 by the Caribbean Fisheries Management Council as an emergency measure (Federal Registry Vol. 70, No. 2), that became permanent in 2006. In 2006, the USVI also implemented territorial fishing regulations that further protected the Nassau grouper, including prohibiting all harvest of the fish in local waters, prohibiting filleting of fish at sea, and prohibiting the harvest and sale of red grouper (*E. morio*), black grouper (*M. bonaci*), tiger grouper (*M. tigris*), yellowfin grouper (*M. venenosa*) and yellowedge grouper (*E. flavolimbatus*) from February through April each year (USVI Department of Planning and Natural Resources, Rules and Regulations, Title 12). These regulations made it more difficult to catch and sell Nassau grouper in the legal, open market, thereby potentially increasing the local spawning stock. This report

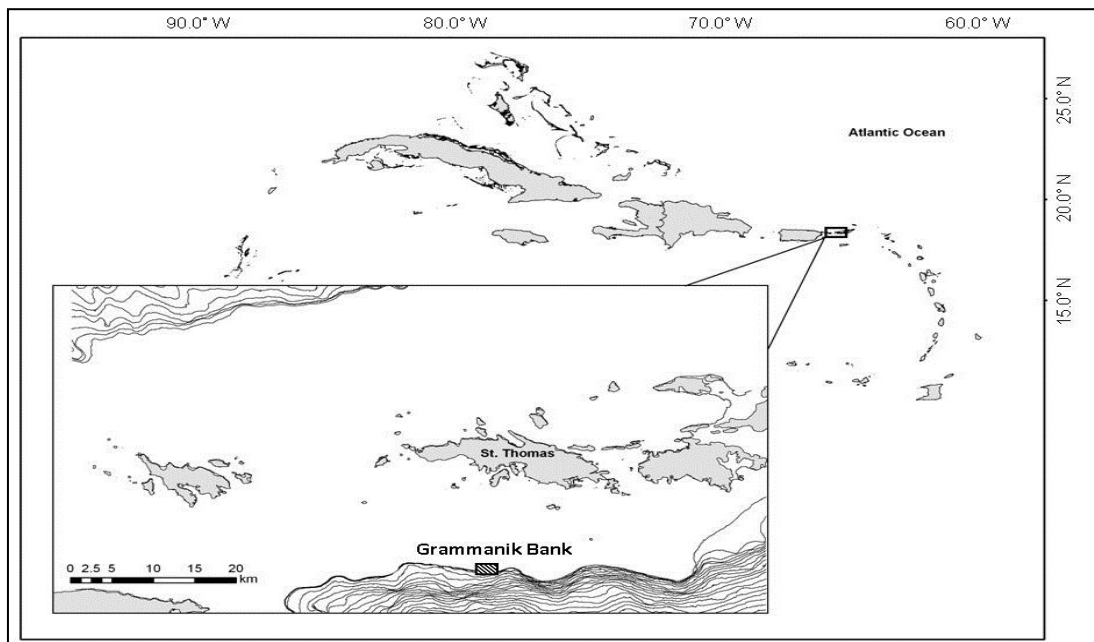


Figure 1. Map of the location of the study area, the Grammanik Bank, south of St. Thomas, USVI.

Table 1. Nassau grouper collected from the Grammanik Bank from 2004-2009 in February, March and April, with sex and recaptures shown.

	Total number collected	Males	Females	Unsexed	Sex ratio F : M	Tag Recaptures	% of catch recaptured-tagged same season	% of catch recaptured-tagged previous seasons
2004	63	19	44	0	2.3 : 1.0	5	8%	0%
2005	132	85	47	0	1.8 : 1.0	23	17%	0%
2006	189	85	100	4	1.2 : 1.0	38	17%	3%
2007	86	33	53	0	1.6 : 1.0	17	9%	10%
2008	80	30	46	4	1.5 : 1.0	27	8%	26%
2009	118	44	63	11	1.4 : 1.0	46	13%	25%
Total all years combined	668	258	391	19	1.5 : 1.0	160		

represents preliminary findings on changes in the Nassau grouper population aggregating on the Grammanik Bank since these protective measures were implemented, based on monitoring from 2004 through 2009.

METHODS

Dive surveys on technical NITROX or closed circuit re-breathers were conducted around the full moon each year from January through April, 2004 through 2009. Surveys generally were conducted over 2 to 11 days, beginning the day of the full moon until new moon, timed to document the arrival and departure of fish. Occasional dives were made outside of this period to confirm that grouper were not present in numbers and no reproductive activity was taking place. In 2004 and 2005, roving dive surveys were used along the 1.7 km bank to locate and characterize the main aggregation area. During the 2006 and 2007, spawning seasons, belt transects (1.2km x 50m) were conducted by divers using diver propulsion vehicles once or twice daily, to determine the grouper distribution across the reef and to estimate the spawning population size. In 2007, 2008 and 2009, in addition to transects, dives were made from mid-afternoon to sunset on and around the spawning site. Number of fish, coloration, and courtship behavior were recorded and videoed. Groupers were collected daily during the same time period each year using standard Antillian fish traps baited with bonito (*Sarda sarda*) and squid. Captured Nassau grouper were measured, sexed using a portable field ultrasound (Whiteman et al. 2005), and tagged through the dorsal fin pterygiophores with numerically coded external Floy dart tags. The fish were released close to the collection site using a release cage that could be opened remotely when it reached the sea floor, thereby minimizing predation (Nemeth 2006). Spawning population changes from 2004 through 2009

were compared using the number of fish observed in underwater surveys and population characteristics including sex ratio and mean size of fish collected over five years of monitoring.

RESULTS

Between 2004 and 2009, over 200 dive surveys were conducted and 670 traps deployed. Six hundred and sixty-eight Nassau grouper were collected and tagged (Table 1). Surveys and trap catches revealed that Nassau aggregated on the Grammanik Bank in February, March and April. They arrived on and around the full moon, peaked in number from 2 - 8 days after the full moon (dafm), and departed from 10 to 12 dafm. In some years small numbers of fish were observed in January and May. The number of Nassau grouper observed in visual surveys increased slowly from 2005 through 2007 but was dramatically higher in 2008 and especially 2009 (Figure 2). They were approximately 2-5% as abundant as yellowfin in 2004, 15% as abundant in 2008 and 25% - 30% as abundant in February 2009. Spatially, Nassau grouper were patchily mixed across the reef with yellowfin during the day. In late afternoon, approaching sunset, from 4 to 11 dafm. Nassau grouper moved west, along with yellowfin, to the southern, seaward edge of the shelf. Fish exhibited courting and spawning colorations described by Sadovy and Eklund (1999) including barred (typical non-courtship), white bellied, dark and bi-colored. They were observed occasionally swimming singly or in pairs elevated 5 - 10 m above the bottom, and joined spawning aggregations of yellowfin toward dusk, rising from the bottom to 20 m in depth. Although yellowfin were observed in spawning rushes within the larger aggregation on several occasions, Nassau grouper were not observed actually spawning. Spawning

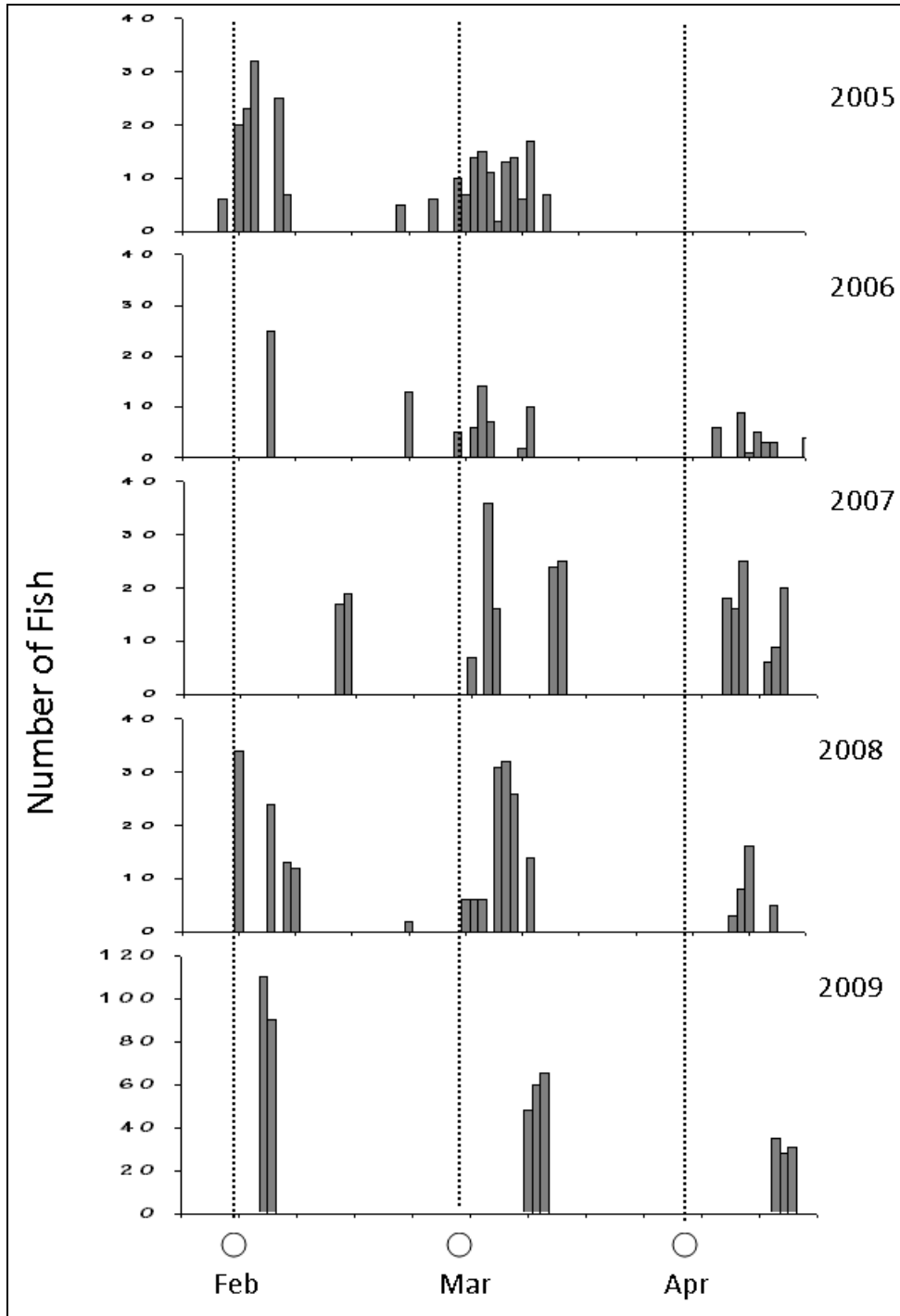


Figure 2. Underwater visual surveys conducted during February, March and April on the Grammanik Bank from 2004 through 2009 with bars indicating total number of Nassau grouper observed per day. Counts from dives repeated at the same location on the same day were not included more than once.

began late in the day, generally within 10 min of sunset, and occurred under poor light conditions. Dives were terminated while spawning was underway every evening it was observed, and it probably continued much longer, into the night.

Traps were baited and set differentially to target different species of co-occurring groupers, so over all catch per unit effort (CPUE) was not a clear indicator of changes in the Nassau grouper spawning population size. Nearly all male Nassau collected on the bank had ripe gonads and

females had enlarged, developed ovaries when viewed with the ultrasound. Of 22 Nassau grouper that died in the field, eight were ripe males, ten were developing females, three were spent females and one was a resting female. The ratio of females to males collected decreased every year from 2.3:1.0 in 2004 to 1.4:1.0 in 2009, with the exception of 2006 when the female to male ratio was as low as 1.2:1.0 (Table 1). The mean size of Nassau collected on the bank in 2004 was 60.0 ± 0.8 cm TL, which was not significantly different than the mean size collected in 2005 (59.4 ± 5.7 cm TL), however both years had significantly smaller mean fish size than each of the following years, 2006 through 2009 (Kruskal Wallance, $H = 43.3$, $p < 0.001$; Dunn's Method, $p < 0.05$). Mean fish size did not significantly change from 2006 through 2009 (Kruskal Wallance, $H = 3.7$, $p = 0.30$). The size range of collected fish also increased after 2005, with more, smaller fish present in the aggregating population of 2009 (Figure 3). Nassau grouper recaptured with Floy tags varied as a percentage of the whole catch each year but in general the number recaptured within the season decreased and the number of fish recaptured with tags from previous years increased from 2005 to 2009 (Table 1).

DISCUSSION

The documentation of the Grammanik Bank spawning aggregation site represents not only the sole Nassau aggregation site in US waters, but probably one of the only remaining in the eastern Caribbean.

Fewer than 80 historic or current spawning aggregations of Nassau grouper are known, most of which occur (or occurred) in the Bahamas, Cuba, or Meso-America (Sadovy and Eklund 1999). Traditional aggregations off Puerto Rico, St. Thomas and St. Croix, fished to extinction in the 1970's and 80's, have not been re-established on their historic sites. Spawning aggregations in the northeast Caribbean outside of US waters are reported to occur only in the British Virgin Islands and Antigua (Monro and Blok 2003), however these sites are without scientific confirmation and virtually nothing is known of them.

The Nassau grouper spawning aggregation site on the Grammanik Bank is of disputed age and origin. Local fishermen claim that the bank is not a historical location for spawning, but rather the Nassau used the area approximately 4 km to the west exclusively, that was fished out by 1980. It is hypothesized that the Nassau now utilizing the Grammanik Bank are a small sub-population of that original spawning group that was separated, or followed the activity of the other reproductively active groupers (i.e. yellowfin) east to the Grammanik Bank when their own numbers diminished. This theory is plausible given reports that grouper have been found to move away from highly exploited banks to spawn (Aguilar-Perera 1994), as well as observations of fish migrating to spawning aggregations in schools of 25 to 500 in other areas, suggesting learned

migration route behavior (Colon 1992, Carter *et al.* 1994, Starr *et al.* 2007). However, there are also a few fishermen that concede the Nassau grouper always spawned on the Grammanik Bank to some extent in December and January, and in fact were fished there "secretly" for years. There are no reports of Nassau being harvested historically past the month of January, after which spawning populations of yellowfin, believed ciguatoxic, moved onto the aggregation sites each year.

Nassau grouper spawning in the Caribbean region is highly synchronized and generally occurs around the full moon or between the full and new moon, during two consecutive months between November and February (Smith 1972, Olsen and LaPlace 1978, Colin 1992, Carter *et al.* 1994, Tucker *et al.* 1993, Aguilar-Perera 1994, Domeier and Colin 1997, Sala *et al.* 2001, Sadovy and Eklund 1999, Whaylen *et al.* 2004, Starr *et al.* 2007). Ripe and spent ovaries have been collected in April and May off Jamaica however (Thompson and Monro 1978) and in September off Cuba (Claro *et al.* 1990). Although historically in the Virgin Islands Nassau spawning occurred in December and January, followed by yellowfin grouper in February as has been reported on other aggregation sites around the Caribbean (Colin 1992, Carter and Perrine 1994, Fine 1992, Sala *et al.* 2001, Whaylen *et al.* 2004, Haymen and Kjerfve 2008) a shifting of seasonality has obviously taken place on the Grammanik Bank. Temperature is an important stimulus for Nassau grouper spawning, more so than day length (Tucker 1994), and optimal temperature for Nassau grouper reproduction is between 24 and 27°C (Colin 1992, Tucker *et al.* 1993, Tucker 1994, Sadovy and Eklund 1999). The temperature on the Puerto Rican shelf drop south of St. Thomas was relatively stable from January through April between 2004 and 2009 on the Grammanik Bank and ranged from 25 to 27°C during those months (Nemeth, unpublished data). If Nassau grouper originally followed yellowfin to the Grammanik Bank aggregation site during February, March and April, environmental cues might not prevent a shifting away from the traditional yellowfin spawning period to earlier in the year, especially if numbers of Nassau grouper were low.

Multispecies spawning aggregation areas, as described by Haymen and Kjerfve (2008), are sites that are uniquely desirable for aggregation, broadcast spawning, via presumably, enhanced success of egg and larval dispersal to nursery areas, larval survivability and, or adult survivability. Typically several fish species are separated temporally and spatially (with some overlap) within a very discrete area to spawn (Whaylen *et al.* 2004, Haymen and Kjerfve 2008). Little is known of the environmental, physiological or biological processes that initiate and maintain these seasonal and spatial partitions. Although we have noticed the beginning of some limited grouping over the last two seasons, with increasing numbers of

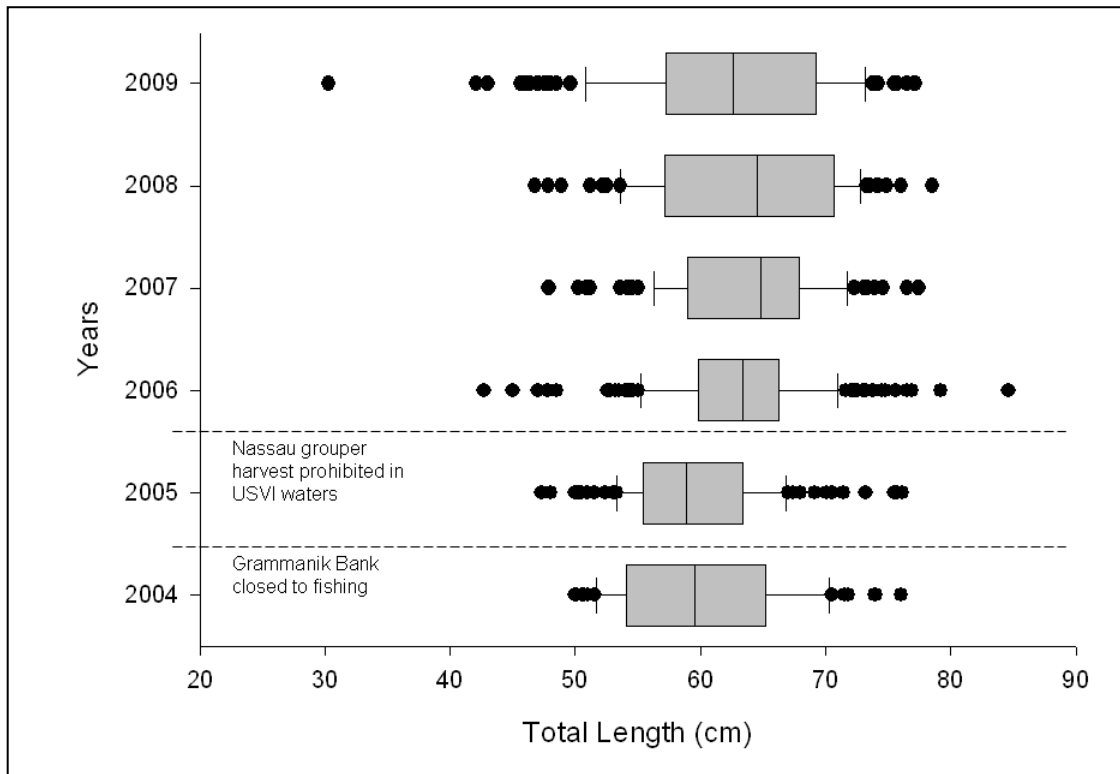


Figure 3. Box plot of mean Nassau grouper total length with boxes representing 25th and 75th percentile. Outliers as black dots are represented with black dots.

Nassau, the two species (Nassau and yellowfin grouper) are on the Grammanik Bank are generally mixed during the day and into the afternoon courtship period. It is again speculated that this behavior is an artifact of relatively low numbers of Nassau, using yellowfin grouper as surrogate aggregation members to act as cues to trigger reproduction.

We believe that Nassau grouper are actually spawning on the Grammanik Bank based on at least some site fidelity (as indicated by tag returns), reproductive condition, spawning coloration, and courtship behavior. Although small in terms of number of fish, which reportedly can reach thousands to tens of thousands on healthy aggregation sites (Smith 1972, Sadovy and Eklund 1999, Whaylen *et al.* 2004), the Grammanik Bank aggregation appears to be slowly rebuilding from the over-exploitation of previous years. Divers in 2009 reported numbers of Nassau that tripled those of previous years. Sex ratios have improved (moved toward unity) and mean size has significantly increased since 2004 and 2005, indicating a decreased level of exploitation (Sadovy and Eklund 1999). In addition, the presence of younger cohorts on the aggregation site in 2009 suggest the possibility of continuity and perhaps the rebounding of a healthy Nassau grouper spawning aggregation.

Because there is no legal harvest of Nassau grouper in US waters, fisheries data is lacking regarding the effectiveness of the protective measures put in place by the

Caribbean Fisheries Management Council in 2005 and the territorial government in 2006. Since 2008, fishermen in St. Thomas report that they catch and release Nassau of all sizes regularly (Dave Olsen, St. Thomas Fisherman's Association Pers. comm.), and data from fisheries independent surveys around the territory indicate that there are limited numbers of adult and juvenile Nassau on offshore and nearshore reefs in St. Thomas and St. John. On St. Croix, where no Nassau grouper aggregation is believed to exist, fishermen and dive operators agree that grouper are almost completely absent from their isolated shelf (Gerson Martinez, fisherman Pers. comm., Michele Pugh, dive business owner and operator Pers. comm.). Only one has been observed in six years of fish surveys conducted annually on 14 sites around St. Croix (Nemeth Unpub. data). If it is in fact the only remaining spawning site in the USVI, the aggregation on the Grammanik Bank may not only be a very important source of larval recruitment for eastern Caribbean stocks, it may also be a proxy for the health of the Nassau grouper population in the northern Virgin Islands.

ACKNOWLEDGMENTS

We thank NOAA, NMFS, Puerto Rico SeaGrant, National Health Foundation, and VI EPSCoR for funding research over the past 6 years. Also we would also like to acknowledge UVI researchers: Liz Whiteman and Steve Herzlieb, and Fishermen: Kenny Turbe, Bobby Vante, Mante Turbe and Dean Greaux.

LITERATURE CITED

- Aguilar-Perera, A. 1994. Preliminary observations of the spawning aggregation of Nassau grouper, *Epinephelus striatus*, at Majahual, Quintana Roo, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:112-122.
- 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.
- Carter, J., G. J. Marrow and V. Pryor. 1994. Aspects of the ecology and reproduction of the Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:64-111.
- Claro, R. and K.C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper (Lutjanidae and Serranidae) species on the insular shelf of Cuba. *Gulf and Caribbean Research* **14**(2):91-106.
- 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. Colon. 1997. Tropical fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**:698-726.
- Heyman, W.D. and B. Kjerfve. 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science* **83**:531-551.
- Kadison, E., R. Nemeth, S. Herzlieb and J. Blondeau. 2007. A preliminary description of the temporal and spatial dynamics of *Lutjanus cyanopterus* (Pisces: Lutjanidae) and *L. jocu* spawning aggregations on a site in the USVI. *Revista de Biología Tropical* **54**:69-78.
- Munro, J.L. and L. Blok. 2003. The status of stocks of groupers and hinds in the northeast Caribbean. *Proceedings of the Gulf and Caribbean Fisheries Institute* **56**:283-294.
- Morris, A.V., C.M. Roberts and J.P. Hawkins. 2000. the threatened status of groupers (Epinephelinae). *Biodiversity and Conservation* **9**:919-942.
- Nemeth, R.S. 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series* **286**:81-97.
- Nemeth, R.S., E. Kadison, S. Herzlieb, J. Blondeau and E. Whiteman. 2004. Status of yellowfin (*Mycteroperca venenosa*) and Nassau (*Epinephelus striatus*) grouper spawning aggregations in the US Virgin Islands with notes on other species. *Proceedings of the Gulf and Caribbean Fisheries Institute* **57**:543-558.
- Olsen, D.A. and J.A. LaPlace. 1978. A study of a Virgin Islands fishery based on a breeding aggregation. *Proceedings of the Gulf and Caribbean Fisheries Institute* **31**:130-144.
- Sadovy, Y. 1997. 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* **43**:43-65.
- Sadovy, Y. and A. Eklund. 1999. Synopsis of biological data on the Nassau grouper *Epinephelus striatus* (Bloch 1792) and the jewfish *Epinephelus itajara* (Lichenstein 1822). NOAA-NMFS Technical Paper 146. Silver Spring, Maryland USA, 65 pp.
- Sala, E., R. Starr and E. Ballesteros. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26**:23-30.
- Starr R. M., E. Sala, E. Ballesteros, and M. Zabala. 2007. Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. *Marine Ecology Progress Series* **343**:239-249.
- 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.
- Tucker, J.W. 2004. Spawning by captive serranid fishes; a review. *Journal of the World Aquaculture Society* **25**:345-359.
- Tucker, J.W., P.G. Bush, and S.T. Slaybaugh. 1993. Reproductive patterns of Cayman Islands Nassau grouper (*Epinephelus striatus*) populations. *Bulletin of Marine Science* **52**:961-969.
- Whiteman, E., C.A. Jennings, and R.S. Nemeth. 2005. Sex structure and potential female fecundity in an *Epinephalus guttatus* spawning aggregation: applying ultrasound imaging. *Journal of Fish Biology* **66**:983-995.
- Whaylen, L., C.V. Pattengill-Semmens, B.G. Bush and M.R. Boardman. 2004. Observations of a Nassau grouper (*Epinephelus striatus*) spawning aggregation site in Little Cayman, including multi-species spawning information. *Environmental Biology of Fish* **70**:305-313.