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RESEARCH

Impending extirpation of an isolated Nassau grouper (*Epinephelus striatus*) population at Glover's Atoll, Belize, based on two decades of monitoring

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Abstract Nassau grouper (*Epinephelus striatus*) was once among the most abundant and commercially important reef fish species in the Caribbean region. Overextraction at their fish spawning aggregations (FSAs) has contributed significantly to dramatic regionwide declines in their populations, resulting in widespread local extirpations, nominal presence in catch composition and categorization as an IUCN critically endangered species. This study reviews over 20 years of fishery-dependent and fishery-independent observations to examine the status of a spatially isolated population of Nassau Grouper inhabiting Glover's Atoll, Belize (which is wholly encompassed by Glover's Reef Marine Reserve) and utilizing a single well-documented reproductive site. Nassau grouper at Glover's Reef Marine Reserve has decreased in abundance by 85% at the spawning site and decreased in density to virtually undetectable levels across all habitats and management zones despite seasonal and spatial closures, upper and lower size limits and collaborative monitoring and enforcement since 2003. Nassau grouper is also extremely rare in fisher catches both at Glover's Reef Marine Reserve ($n = 118$ over 20 years) and nationally (18 of 18,383 fish observed at landing sites between 2017 and 2020), with juvenile fish comprising over 75% of the sampled individuals. The population at Glover's Reef Marine Reserve continues to decline on a trajectory towards local extirpation. Closure of management gaps, including chronic enforcement resource deficits, may not guarantee recovery but has been a necessary precursor to recovery of other FSAs in the Caribbean.

Keywords *Epinephelus striatus* · Belize · Critically endangered species · Population decline · Fisheries conservation · Fish spawning aggregations · Marine protected areas

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Introduction

The Nassau grouper (*Epinephelus striatus*) was once one of the most commercially important reef fish species in the Wider Caribbean region, including Belize (Craig 1969; Carter et al. 1994). It travels long distances from home reefs during its spawning season (December–March) to form transient fish spawning aggregations (FSAs)—dense, seasonal gatherings of mostly sexually mature conspecifics that are critical to reproductive success. Many large-bodied, mid-to-high trophic-level species within the commercially important grouper/snapper complex form FSAs (Sadovy et al. 2008, 2018; Chollett et al. 2020; Nemeth et al. 2023; Sadovy De Mitcheson et al. 2024), and Nassau grouper were once known to form particularly large aggregations, numbering tens of thousands of spawning fish (Fulton 2023; Sadovy De Mitcheson et al. 2024). These spawning events occur in response to environmental and physiological cues and are usually highly predictable in both timing and location. This predictability, combined with the high densities of large fish, makes them highly sought after by fishers, but also highly vulnerable to recruitment overfishing, where fishing effort causes a reduction in the number of the large, fecund individuals in a population to the degree that the production of recruits is notably impaired (Pauly 1994; Hixon et al. 2014; Sherman et al. 2016; Tewfik et al. 2019; Stock et al. 2021). Heavy exploitation of FSAs and spawning migration routes has led to tremendous declines in Nassau grouper populations and local extirpations of FSAs across their range (Colin et al. 2003; Sadovy and Domeier 2005; Aguilar-Perera 2006; Kobara and Heyman 2010; Cheung et al. 2013; Nemeth et al. 2023). These declines are associated with the loss of ecosystem services to the fishing and tourism sectors and the destabilization of trophic balance on coral reefs (Tupper 2002; Rudd and Tupper 2002; Sadovy and Domeier 2005; Gill et al. 2015; Babcock et al. 2018).

Several national and international efforts to regulate fishing pressure on Nassau grouper and their FSAs have been implemented in response to the species' declining populations (Green Reef Environmental Institute 2001; Gibson et al. 2007; Burns Perez and Tewfik 2016; Fulton 2023). Nassau grouper was added to the USA Endangered Species List in 2016 and to Appendix III of the Specially Protected Areas and Wildlife (SPAW) Protocol of the Cartagena Convention in 2017 (Somma et al. 2021; Sadovy De Mitcheson et al. 2024). It was also upgraded from 'Endangered' to 'Critically Endangered' by the International Union for Conservation of Nature (IUCN) in the 2018 Red List of Threatened Species (IUCN 2012; Sadovy et al. 2018; Harms-Tuohy et al. 2022). This was based on existing time series of data on FSA populations across the region and an estimated generation length of 17 years. IUCN modelling exercises projected regional population declines of 95% over the course of three generations (1980–2031) (Sadovy et al. 2018).

In light of these recent assessments, regional fisheries management organizations have called upon member states to regulate levels of exploitation through improved fisheries management measures including size limits, spatial closures and seasonal closures. The Western Central Atlantic Fisheries Commission of the United Nations Food and Agriculture Organization (WECAFC) finalized and endorsed a Regional Fish Spawning Aggregation Management Plan with focus on Nassau grouper and mutton snapper (*Lutjanus analis*) in 2022. WECAFC also endorsed recommendations to upgrade these two species to Group 1 in their Data Collection Reference Framework, conferring upon them the highest institutional priority for regional conservation and management action (WECAFC 2023; Sadovy De Mitcheson et al. 2024). The Caribbean Regional Fisheries Mechanism (CRFM) and the Caribbean Regional Activity Center for the SPAW Protocol (CAR-SPAW-RAC) have since taken steps to formally align with WECAFC's management plan and recommendations for FSAs, obliging their member states to do the same (Somma et al. 2022; Headley 2024).

The decline of this species is clearly exemplified in the waters of Belize in Central America, where Nassau grouper has had a long-documented history of commercial exploitation since at least the 1920s (Craig 1966; Carter et al. 1994; Burns Perez and Tewfik 2016). Fisheries records indicate that Nassau grouper was once the most caught fish in the country, with estimated catches of over 30,000 fish/year from a single aggregation site, Caye Glory, in the 1960s (Craig 1966, 1969; Sadovy et al. 2018). Caye Glory was estimated to have over 100,000 spawning fish each spawning season—the apparent upper range of Nassau grouper FSA size across their geographic range, with aggregations typically ranging from 10,000 to 30,000 fish.

However, the massive Caye Glory FSA had been considered "overfished" as early as the 1950s, following decades of intense harvest involving hundreds of vessels over 6–8 weeks of the spawning season (Craig 1969; Sadovy et al. 2018). By 1986, the aggregation had declined to fewer than 20,000 fish—just one-fifth of its estimated size two decades earlier (Carter et al. 1994; Heyman and Wade 2007). Annual reported catch at the site also fell from over 45,000 kg to less than 14,000 kg between the 1950s and 1986 (Carter and Marrow 1991).

Other populations of Nassau grouper in Belize exhibited notable declines by the 1970s, attributed to heavy fishing pressure and the introduction of the spear gun in the 1960s (Burns Perez and Tewfik 2016). Population assessments at the end of the twentieth century indicated that Nassau grouper had only been found in numbers exceeding 1,000 fish at two of nine traditionally recognized FSA sites in Belize–Northeast Point at Glover's Atoll (also known as Glover's Reef), and Sandbore at Lighthouse Reef Atoll. Low numbers or complete absence of Nassau groupers were reported from seven other known sites, including at Caye Glory, the one-time focus of the fishery (Sala et al. 2001; Heyman and Wade 2007; Burns Perez and Tewfik 2016; Sadovy et al. 2018). Presently, aggregations numbering over 1,000 fish are considered large, with reports of 100 to 1000 considered the norm (Fulton 2023).

Between 2003 and 2009, three pieces of specific legislation have been passed in Belize which encapsulate most of the generally recommended protective measures for the conservation of Nassau grouper and its FSAs (Nemeth et al. 2023; Sadovy De Mitcheson et al. 2024). These legislative measures were proposed and supported by the Belize National Spawning Aggregation Working Group, a coalition comprising several NGOs and fisher co-operatives in partnership with the Belize Fisheries Department (Gibson et al. 2007, p. 200). The working group and its associates have consistently monitored eight of the thirteen protected FSAs over the past two decades, and regularly report findings to decision-makers to inform management (Gibson et al. 2007; Burns Perez and Tewfik 2016; Phillips 2023). Area closures and/or special licenses for traditional fishers protect thirteen traditional FSA fishing sites and a nation-wide closed season has been implemented for Nassau grouper from December 1st until March 31st of the following year. This closed season reflects the period during which Nassau grouper migrates to and from FSAs in Belize (Fisheries (Nassau Grouper Protection) Regulations, 2003; Heyman and Wade 2007).

Protection also includes a minimum size limit (50.8 cm / 20 inches) to protect juvenile/subadult fish and a maximum size limit (76.2 cm / 30 inches) to protect large, highly fecund individuals, i.e. mega-spawners or BOFFFFs (big old fat fecund female fish) (Froese 2004; Hixon et al. 2014). The disproportionately high fecundity of mega-spawners makes them a conservation priority to sustain recruitment levels and allow potentially rapid recovery of impacted populations (Froese 2004; Hixon et al. 2014; Sadovy De Mitcheson et al. 2024). In addition, Nassau grouper must be landed whole to facilitate enforcement of size regulations, and all other fish species landed as fillets must retain a skin patch to allow confirmation that they are not Nassau grouper (Burns Perez and Tewfik 2016; Fisheries (Nassau Grouper & Species Protection) Regulations, 2009; Fisheries (Spawning Aggregation Site Reserves) Order, 2003).

Belize is considered a regional leader in Mesoamerica with respect to the conservation of Nassau grouper and their fish spawning aggregations (Fulton et al. 2020; González-Bernat et al. 2020; Fulton 2023). Management measures put in place for Nassau grouper over the past two decades (i.e. size limits to protect juveniles and mega-spawners, seasonal fishery closure, year-round closure of traditionally fished aggregation sites, landing of whole fish) reflect regional best practice recommendations (Sadovy De Mitcheson et al. 2024) and were meant to rebuild populations of this ecologically, culturally and formerly economically significant species (Gibson et al. 2007; Burns Perez and Tewfik 2016).

If these measures had worked as intended, over the past two decades, the population should exhibit a trend of stabilization or increase, with concurrent increase in the number of protected mega-spawners (total length > 76 cm) at the spawning site over time. In addition, studies suggest that larval retention is greatest near the fish spawning aggregations where the larvae are produced. As such, Northeast Point may serve as a critical source of larval recruits to Glover's Atoll (Karnauskas et al. 2011; Jackson et al. 2014; Chollett et al. 2020). Increases in aggregation size should also be reflected in patch reef and fore reef habitats throughout GRMR, including spillover from the no-take zone into fished areas driven by density-dependent dynamics. Concurrently, Nassau grouper should become more frequent and of larger mean size in fisher catch (Waterhouse et al. 2020).

The aim of this study is to examine the effectiveness of the past two decades of management in achieving recovery of the Nassau grouper population at Glover's Atoll, for which the Northeast Point FSA has been identified as the sole accessible reproductive site (Starr et al. 2007). Our findings are intended to provide context for future adaptive management and conservation strategies for this critically endangered species and its associated livelihood and ecosystem service provisioning.

Methods

Marine resource management in Belize

Management of marine fisheries resources in Belize occurs largely within the context of its National Protected Areas System (NPAS) and Managed Access (MA) program. The NPAS comprises a network of terrestrial and marine protected areas with varying restrictions on user activities (Wildtracks Belize 2019), including over twenty marine protected areas (MPAs) variously designated as marine reserves, marine natural monuments, marine national parks and protected spawning aggregation sites (Ylitalo-Ward 2020). The MA program was introduced after the NPAS and has been layered over the pre-existing MPA network. Since 2016, it has divided Belize's Exclusive Economic Zone (EEZ) into nine Territorial Use Rights for Fishing areas (TURFs, known locally as Managed Access Areas). Licensed commercial fishers must choose to operate within two of the eight shallow water managed access areas. A deepwater area outside of the main barrier reef and atolls (MA Area 9) remains open access. The program was intended to (1) reduce fishing effort; (2) increase revenue for fishers via increased landings and larger fish sizes, *inter alia*; (3) promote stewardship of marine resources by fishers through tenure rights to the MA Areas; and (4) increase fisher participation in decision-making through MA working groups and committees (Castañeda et al. 2011; Karr et al. 2017; Wade et al. 2019; Bowman et al. 2021; Alves et al. 2022a). However, no formal limits have been instituted on the number of active fishing licenses in any managed access area to date.

Site description

Glover's Reef Marine Reserve (GRMR; designated Managed Access Area 8) encompasses the full extent of Glover's Atoll, which is the southernmost of Belize's three atolls (Fig. 1) and one of the most isolated reef systems in Belize. GRMR has international significance as a SPAW Protocol-listed protected area (CAR-SPAW-RAC 2021) and is also one of seven MPAs which constitute the "Belize Barrier

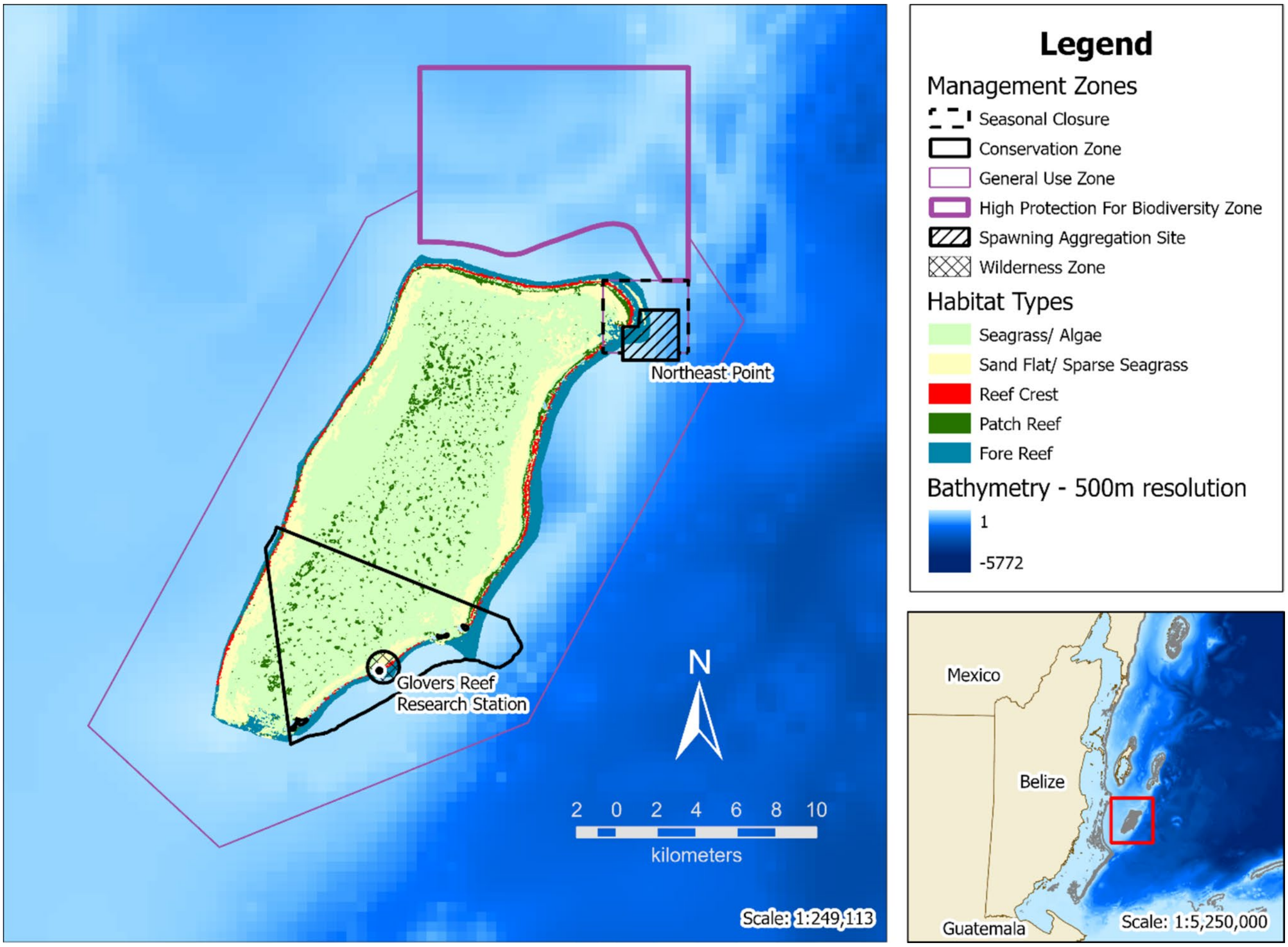


Fig. 1 Map of Glover's Reef Marine Reserve, including bathymetry, management zones and simplified habitats. The spawning aggregation protection zone is demarcated at the Northeast of the atoll. Enforcement personnel are stationed 20 km southwest at the Glover's Reef Research Station on Middle Caye

Reef Reserve System", a UNESCO World Heritage Site (Byron and Osipova 2013). Despite its title, the World Heritage Site does not include the entirety of Belize's Barrier Reef and associated atolls, to which we will refer throughout this article.

GRMR is located 45 km east of the nearest fishing community (the town of Dangriga in central Belize), 20 km east of the main Belize Barrier Reef, and 25 km southwest of Lighthouse Reef Atoll. The surrounding water is 300–400 m in depth to the north and west, while the eastern shelf of the atoll descends rapidly to depths exceeding 1000 m (Fig. 1) (Tewfik et al. 2019). The atoll has an area of approximately 350km^2 (as defined by the 200 m depth contour) and features five sandy cayes which occur on the south-eastern reef crest. The lagoon has a maximum depth of ~ 20 m and is dotted with over 850 patch reefs interconnected by seagrass and algae beds on the lagoon floor. Shallow sandflats (< 10 m depth) with sparse seagrass run along the back reef, while the reef crest is broken in three places by major tidal channels. Outside the reef crest, the fore reef extends out to a prominent shelf at ~ 15–30 m and descends rapidly thereafter (Tewfik et al. 2019; McClanahan and Muthiga 2020).

GRMR is managed by the Belize Fisheries Department, which maintains a patrol unit at the Glover's Reef Research Station on Middle Caye (Fig. 1). In 2011, 141 persons were licensed for commercial fishing in GRMR (Castañeda et al. 2011; Tewfik et al. 2020a). The number of licensed fishers increased to 168 in 2019 (Tewfik et al. 2020a), and to 532 in 2024 (Alicia Eck-Nunez, Belize Fisheries Department, pers. comm.).

The marine reserve has been divided into six management zones with differing levels of restriction on fishing activity. The General Use Zone (GUZ) is the largest zone, expanding across most of the atoll. Commercial fishing is permitted within the GUZ, but the usage of long lines, traps, nets, and spear guns (as of 2009) is prohibited. In 2021, the GUZ was expanded to include a 4-km buffer zone around the entire atoll for the management of the shark fishery (Fisheries

(Amendment) Regulations, 2021). The Conservation Zone (CZ) is designed to protect several ecologically and recreationally important features of the atoll. It is located in the southern portion of the reserve and excludes commercial fishing while permitting catch-and-release sportfishing (e.g. bonefish, tarpon, permit) (Wildtracks Belize 2019; McClanahan and Muthiga 2020). The Wilderness Zone is located within the CZ and is centred around Middle Caye. This zone includes the only significant mangrove habitat on the atoll and excludes all activities except scientific research. Most recently, a "High Protection for Biodiversity" Zone was added in the deep water north of the atoll (Fisheries Resources (High Protection for Biodiversity Marine Reserves) Order, 2022), which excludes all activities except scientific research and sport fishing (Fisheries Resources (High Protection for Biodiversity Marine Reserves) Regulations, 2022).

Northeast Point is a multi-species Fish Spawning Aggregation (FSA) site located approximately 1 km east of the northeast elbow of Glover's Atoll at a depth of 24–43 m (Shcherbina et al. 2008; Kobara and Heyman 2010). It is surrounded by a Spawning Aggregation Site Zone which is no-take year round (Fisheries (Spawning Aggregation Site Reserves) Order, 2003) and a Seasonal Closure Zone which is closed to fishing from December 1st-March-31st.

While best known for the prominent Nassau grouper aggregation, other grouper species have been regularly recorded at Northeast Point including black (*Mycteroperca bonaci*), yellowfin (*Mycteroperca venenosa*) and tiger grouper (*Mycteroperca tigris*) (Sala et al. 2001; Burns Perez and Tewfik 2016). These other species have also been identified as being overfished nationally (Tewfik et al. 2022).

Assumptions

The appropriateness of the methodology for assessment of the peak number of spawning fish at GRMR relies upon the following assumptions. While presented in brief below, these assumptions are expanded upon in the supplementary materials (Online Resource 1).

Assumption 1 Spatially isolated population with single spawning site

Surveys of the entire perimeter of the atoll confirmed that Northeast Point is the only accessible FSA for this species. Tagging studies did not observe reproductive migrations to any other point on the atoll or post-spawning emigration from the atoll (Sala et al. 2001; Starr et al. 2007).

Assumption 2 No effect of temperature on spawning behaviour across the time series

Temperature is believed to influence spawning behaviour, with an optimal temperature range for Nassau grouper reproduction between 25 and 26 °C (Carter et al. 1994; Colin et al. 2003; Nemeth et al. 2007; Dahlgren et al. 2016).

We assumed no change in water temperature of sufficient magnitude to shift spawning phenology or location. To test this assumption, we analysed primary in situ temperature data collected from Northeast Point during December–January from 2011 to 2022 using temperature loggers (HOBO Pendant 64 K Temp-Light Data Logger UA-002-64) anchored to a buoy at 27.5 m depth. We statistically examined temperature trends across spawning seasons in R version 4.2.2 using a box-and-whisker plot and Spearman's rank correlation, applying a significance threshold of 0.05.

Assumption 3 Unchanged spawning phenology across the time series

We assumed the spawning season (i.e. December–March), peak spawning months (i.e. January and February) and spawning period (3–10 days after the full moon/DAFM) remained stable across the time series (Carter et al. 1994; Sala et al. 2001; Heyman et al. 2004; Heyman and Adrien 2006; Whaylen et al. 2007; Nemeth et al. 2007; Starr et al. 2007). Tagging, acoustic telemetry and passive acoustic studies conducted at GRMR provide specific evidence in support of this assumption (Starr et al. 2007; Eric Appeldoorn-Sanders, University of Puerto Rico, unpubl. report).

Assumption 4 A truncated survey period is sufficient to detect population trends

Surveys at Northeast Point FSA are carried out from the third until the eighth day after the full moon (DAFM) in January and February, following protocols described by Heyman et al. (2004). The surveys strategically prioritize the first six days of the eight-day spawning period during the two peak months to optimize resource expenditure. This survey period has been adopted at the national level by the Belize Fisheries Department and the National Belize Spawning Aggregation Working Group (FAO/WECAFC 2024). Challenging weather conditions prevented sampling on some days during each planned survey period. We assume that peak abundance was captured in most years, resulting in data which reasonably reflect long-term trends in aggregation size (see Online Resources 1, 2). We further assume that the entire aggregation at Northeast Point was detectable by the survey team conducting underwater visual census on SCUBA.

Assumption 5 Limited impact of observer bias on results

Survey teams for fishery-independent surveys at the FSA and in habitats across the atoll consisted of core members who participated over multiple years, supported by trained contractors as needed. Although team composition varied across each time series (~20 years), all divers underwent formal training in survey protocols prior to fieldwork, and calibration exercises were conducted to maximize consistency in observer performance. However, observer identity information was not available for most of the visually estimated data, limiting our ability to assess observer bias. While inter-observer variability is a known limitation of UVC methods (Prato et al. 2017; Jessop et al. 2022), our results have been interpreted with this source of uncertainty in mind.

Abundance at the FSA

Visual census of spawning aggregations was conducted by a team of 4–6 divers who located and then visually estimated the abundance of Nassau grouper at the site. Divers conducted a roving transect of the known aggregation area starting from a fixed location approximately 1–2 h before dusk. Surveys were occasionally conducted earlier in the day depending on resource availability and weather conditions, which can be extremely challenging at this exposed location.

Divers were trained in fish counting techniques during annual courses conducted by the Belize Spawning Aggregation Working Group, and adjusted their methods based on fish behaviour—whether individuals were densely schooling in the water column or dispersed across the benthos. In estimating total numbers, divers aimed to count all individuals, often using a reference group of 10–20 fish and extrapolating that count across the three-dimensional structure of the aggregation (Heyman et al. 2004; Belize Spawning Aggregation Working Group 2011).

If the fish were dispersed across a large area, divers were split into two teams. One team surveyed an area of spur and groove formations (20–26 m depth), known to be utilized by the fish as a staging point at the start of the aggregation period and favoured by smaller individuals. Maintaining a maximum dive depth of ~28 m, the other team explored the deeper reef slope (down to ~45 m) adjacent to this staging area. This area is utilized by larger fish and is the site of courtship behaviours including colour change, sparring and ascent into the water column for spawning. Immediately after the dive, independent estimates of abundance were collected from each diver, and the mean of these estimates was considered the "mean count" for that day. The highest mean count in any year, based on approximately 7.6 ± 0.7 (SE) survey dives each year, was assumed to be a reasonable proxy for the maximum number of fish engaging in breeding behaviours at the aggregation in that year (Colin et al. 2003; Heyman et al. 2004, Online Resource 2). The highest mean count was plotted against year, and a linear regression was performed in R version 4.2.2 against a significance value 0.05.

Mean counts from all surveys in January and February were plotted versus year in a box plot using R version 4.2.2.

FSA individual size surveys

Monitoring teams also visually estimated the size distribution of all individuals seen within the FSA from 2005 to 2011 using 10-cm bins of total length. Divers carried slates and tallied individuals by size class during each survey. To ensure accuracy, divers were trained to estimate the size of fish using models of known length during exercises both above and below water and were required to pass a size estimation test with a score of 75%. Answers were considered correct within 3 cm of the true size (Heyman et al. 2004). This methodology was abandoned after 2011 in order to prioritize accuracy of abundance estimates during the short (<15 min) survey dives (Belize Spawning Aggregation Working Group 2011).

A cost-effective laser calliper sizing system was tested and adopted in 2017 to measure a subset of individuals within the aggregation (Heppell et al. 2012). The apparatus featured two parallel submersible lasers mounted under a pair of handheld underwater video cameras (for redundancy) operated by a single diver (Fig. 2e). Fish were sampled opportunistically, including at the densest parts of the aggregation. The operator placed the two laser points perpendicular to the lateral surface of a fish while recording video at less than 5 m from the subject. During review of the video footage, data collectors used a paused video frame and the known distance between the two parallel laser points on the fish's body to extrapolate the actual total length of the individual animal (Fig. 2).

Individuals were considered immature ("subadult") when their total length was less than the legal minimum size limit (50.8 cm), "legal sized adult" between 50.8 and 76.2 cm, and a "mega spawner" when total length exceeded the maximum size limit (76.2 cm). The legal minimum size limit is based on known life history research on the mean length at which 50% of individuals achieve sexual maturity (L_m) (Carter et al. 1994; Sadovy and Eklund 1999; Sadovy De Mitcheson et al. 2024). 'Mega-spawners' are defined as highly fecund individuals 110% of optimal size, where optimal size describes the length which will allow maximum yield and revenue from mature individuals in the catch (Froese 2004, p. 200).

Visual size estimate data (2004–2011) were transformed in R version 4.2.2 from 10 cm bins to serial instances of the mean value of their bins (i.e. one fish in bin "1 cm-10 cm" = one fish of estimated length 5.5 cm). This transformed dataset and the laser calliper size dataset were combined and plotted versus year in a boxplot using R version 4.2.2 to examine size distribution, while

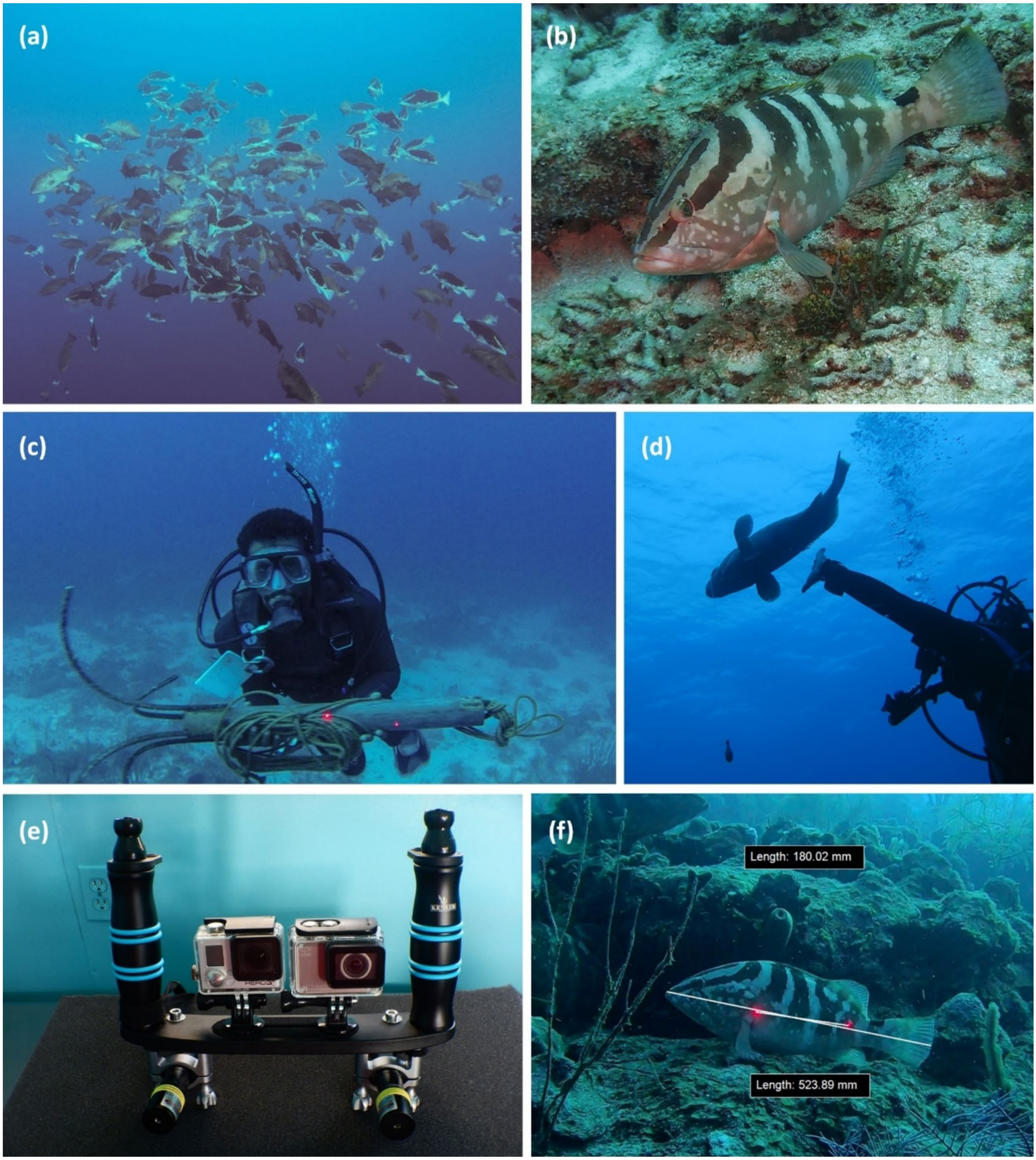


Fig. 2 **a** Aggregating Nassau grouper at Northeast Point, showing colour changes for spawning. **b** Nassau grouper **c** Diver with discarded anchor from a vessel which had been fishing at Northeast Point during the spawning season in 2017. **d** Nassau grouper at Northeast Point with fishing hook in its mouth during the spawning season. **e** Laser calliper apparatus used to take individual measurements of Nassau grouper at Northeast Point **f** Nassau grouper with parallel lasers on lateral surface. Fixed distance (180 mm) between points is used as a reference for estimation of total length. Photo Credit: A. Tewfik/WCS Belize (a,c,d,e); M. Phillips/WCS Belize (b,f)

proportional distribution of age classes was plotted in Microsoft Excel for Microsoft 365 MSO (Version 2309 Build 16.0.16827.20150). Finally, linear regression was carried out in R version 4.2.2 on the mean annual fish size from 2005 to 2022 versus year. This was done to test for overall trends in size over time against a significance threshold of 0.05.

Reef habitat surveys

Broader reef fish surveys, as part of reef health monitoring, provided trends in abundance and length of Nassau groupers in reef habitats across GRMR from 2004 to 2020. Belt transect data were collected by snorkelers on 28 shallow (2–4 m) patch reefs from 2004 to 2014 using the AGRRA protocol (Tewfik et al. 2017). Ten patch reefs occurred in the CZ and the remaining 18 were in the GUZ. Dive teams surveyed eight to ten 30 m x 2 m transects at fixed sites, laid haphazardly across the patch reef at a uniform depth (approx. 3 m). Each transect was separated from others by at least 5 m. Divers were trained in size estimation using plastic cut outs both above and below water, and estimated fish size in bins with the aid of a marked T-bar (Almada-Villela et al. 2003; Acosta 2004; Tewfik et al. 2017).

Data collection was expanded in 2015 to include fore reef (< 15 m) sites accessed by SCUBA using experienced surveyors. The selection of sites was also modified. Eighteen fore reef sites (six on the leeward side of the atoll and twelve on the windward side) were placed roughly 2 km apart from each other, with equal distribution of sites between the fished general use zone and the unfished conservation zone. Seven patch reef sites were selected in the conservation zone, and seven were selected in the general use zone.

Density of Nassau groupers in each management zone category was plotted against year for each habitat, and linear regressions were performed in R version 4.2.2 against a significance threshold 0.05, assuming a linear relationship exists between density and year in each habitat. We assessed the potential for observer bias by fitting a series of generalized linear mixed models comparing total fish abundance at each site in each year, with and without observer identity included as a random effect. In the subset of years where observer identity was consistently recorded at the sample unit level, some models showed improved fit when observer was included. However, across most of the time series, observer information was either missing or grouped (i.e., multiple observers assigned to a single observation), with overlapping observers across groups and years. Given this inconsistency, we elected to exclude observer identity as a random effect from models of species-specific density, which used the full dataset.

Ontogenetic distribution patterns were examined by plotting length across all years versus frequency of observations from patch reefs, fore reefs and the FSA from 2017 to 2023 in Microsoft® Excel® for Microsoft 365 MSO (Version 2309 Build 16.0.16827.20150). Shapiro–Wilk tests of normality were performed on length/frequency data from each habitat using R version 4.2.2 against a significance value 0.05.

Fishery-dependent data

GRMR catch data

Catch surveys were conducted on the fishing grounds (i.e. general use zone) within Glover's Atoll from 2004 to 2019. The number, length and weight of Nassau groupers encountered in fisher catches were recorded, as well as the gear type with which they had been caught. Catch was analysed for mean length (L_x) and referenced against known size at first maturity (L_m) as a general length-based indicator of overfishing (L_x/L_m). Values < 1.0 indicate that the average individual in the catch is smaller than the length at maturity (i.e. overfishing) (Babcock et al. 2018; Tewfik et al. 2020b, 2022). Size observations were plotted versus year in a boxplot using R version 4.2.2 to examine size distribution over time.

Fish market landings data

Fish total length data were collected from fishers and vendors at community markets in six of the major traditional fishing communities (Caye Caulker, Corozal, Belize City, Dangriga, Placencia, and Punta Gorda) across Belize from 2017 to 2020. Random sampling was conducted by trained data collectors 2–3 times weekly throughout the year in each community, capturing information on catch from fishing grounds across Belize. The dataset comprised over 18,000 fish from 90 species (Tewfik et al. 2020b, 2022). Data collectors aimed to measure as much of the catch as fishers and vendors would allow and provided mobile phone credit as an incentive for participation. Observations of Nassau groupers were extracted from this dataset for further analysis.

Results

Spawning phenology-temperature

Temperature data were available during the spawning season (December–March) for the years 2011–2014, 2019 and 2022 (Fig. 3). Spearman's rank correlation returned a statistically significant positive relationship between year and temperature/°C (Spearman's rho = 0.653; p value < 2.2e-16). Mean temperature at the site (27.5 m depth) increased from 26.5 in 2011 to 27.4 in 2022, an annual mean temperature increment of less than 0.1 °C/year.

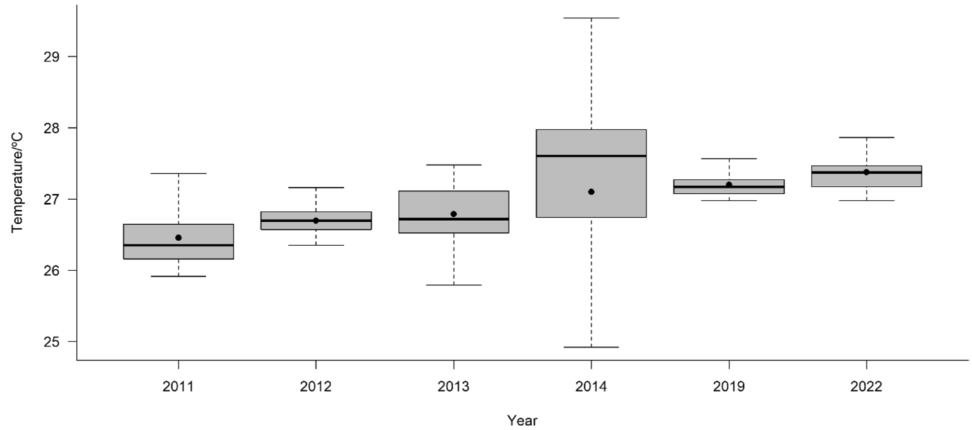


Fig. 3 Box & whisker plot of available temperature logger data from Northeast Point, Glover's Reef Marine Reserve during the 2011–2022 spawning seasons. No data were collected in 2015–2018, 2020 nor 2021. Grey boxes indicate upper (75%) and lower quartile (25%) of size data. Median and mean values are represented by black bars and black circles, respectively. Whiskers represent maximum and minimum value within 1.5 times interquartile range

Abundance at the FSA

Regular fluctuations were observed in the time series of highest annual mean counts of Nassau grouper (Fig. 4). Peak counts of ~ 3000 fish occurred in 2000, 2006 and 2010. After 2010, the peak counts decreased to 1842 fish in 2014, before declining again to much lower peaks of ~ 900 fish in 2018 and 2020 and 463 in 2023. The highest mean counts exhibit a statistically significant (p value < 0.001) pattern of decline from 2000 to 2023 (Fig. 4). The annual variability in the January and February counts are described in Fig. 5. Declines in maximum counts are accompanied by reductions in variance, median, and mean values across the time series, with maximum counts as outlier values in 2006, 2011 and 2022 only.

Data on mean counts throughout the survey period for the entire time series are presented in the supplementary materials (Online Resource 2).

Size data from FSA

The mean proportion of adults within the legal harvest size slot across all years was 65%. Subadults and mega-spawners accounted for mean proportions of 21% and 14% of measured individuals across all years, respectively (Fig. 6). The use of laser callipers has confirmed the presence of relatively few mega-spawner Nassau groupers from 2017 to 2023 (Fig. 7). Linear regression of mean fish size versus year yielded no significant correlation ($r^2 = 0.009$, $p = 0.314$).

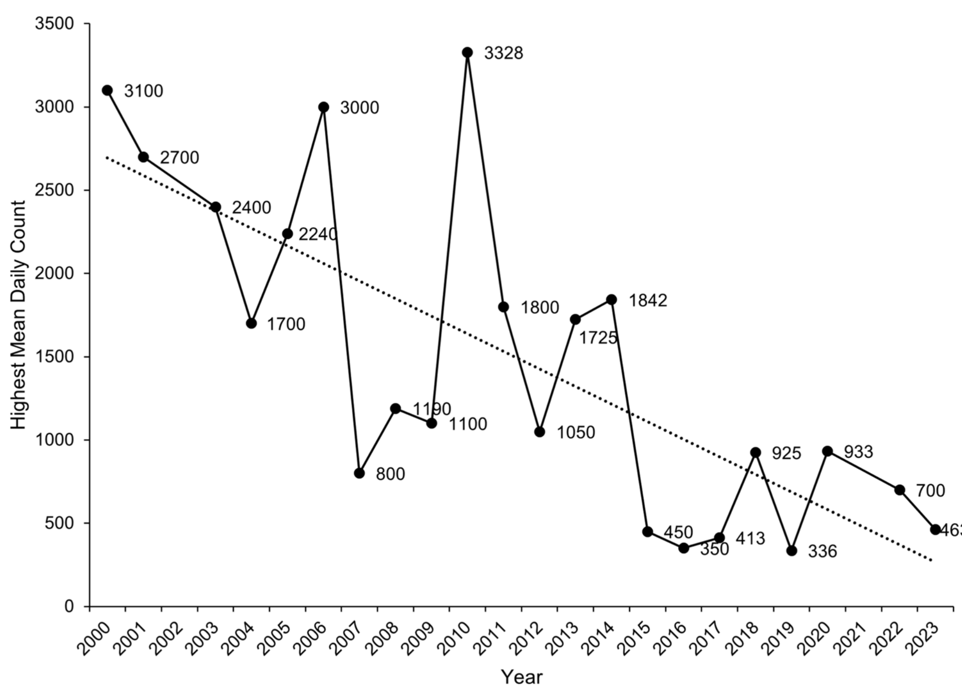


Fig. 4 Highest mean daily counts of Nassau grouper recorded at Northeast Point, Glover's Reef Marine Reserve during the 2000–2023 spawning events. No data were collected in 2021. Linear regression trendline: $y = 105.56 \times x + 213813.4$. Multiple $r^2 = 0.531$. p value < 0.001. Mean number of survey events per year was 7.6 ± 0.7 (SE)

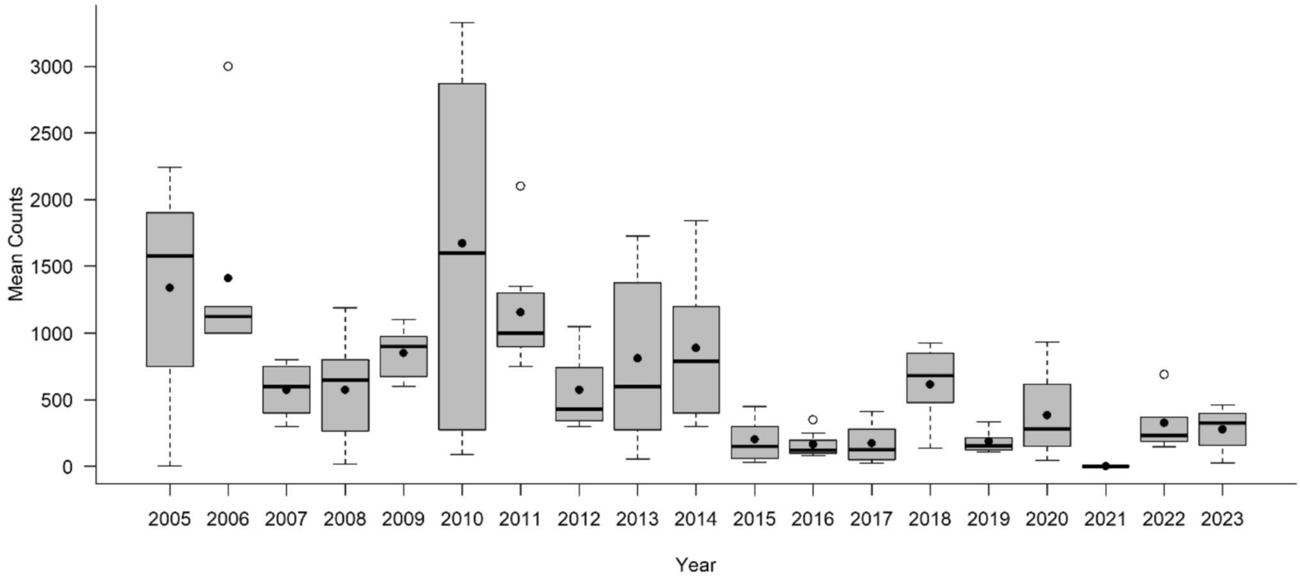


Fig. 5 Box & whisker plot of all January and February mean counts of Nassau grouper at Northeast Point, Glover's Reef Marine Reserve during the 2000–2023 spawning events. No data were collected in 2021. Grey boxes indicate upper (75%) and lower quartile (25%) of size data. Median and mean values are represented by black bars and black circles, respectively. Whiskers represent maximum and minimum value within 1.5 times interquartile range; white circles show outliers

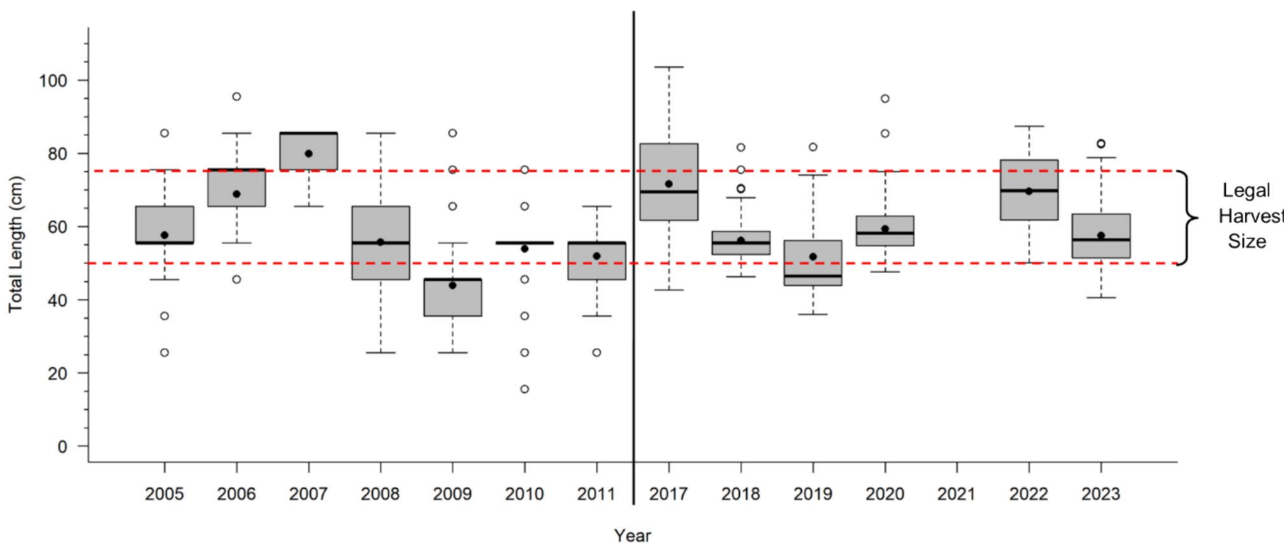


Fig. 6 Box plot showing size distribution of Nassau grouper at Northeast Point, Glover's Reef Marine Reserve. Dotted red lines represent legal size limits. Grey boxes indicate upper (75%) and lower quartile (25%) of size data. Median and mean values are represented by a black bar and black circle, respectively. Whiskers represent maximum and minimum value within 1.5 times interquartile range; white circles show outliers. Size data were collected from 2005 to 2011 using visual size estimation, while 2017–2022 data were derived using laser callipers. The gap in the x-axis (2012–2016) indicates years where no size data were collected using either method. No data were collected in 2021

Reef habitat surveys

Habitat type Mean size (total length/cm) of individuals becomes larger in ascending order from patch reefs (24.3 ± 0.6) to fore reefs (42.4 ± 2.5) to the spawning site (60.9 ± 0.5). The assumption of normal distribution was false ($p \leq 0.05$) for all three length frequencies (Fig. 8). Only 3.35% of all individuals observed on patch reefs and fore reefs (maximum depth 15 m) were above the legal harvest size, which coincides with the mean length at which Nassau

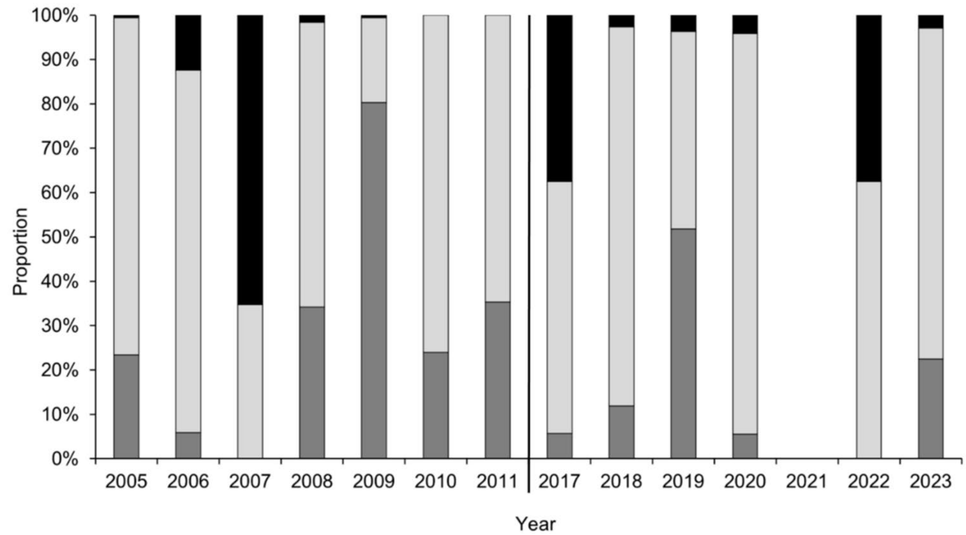


Fig. 7 Proportional distribution by size classes of the Nassau grouper at the Northeast Point FSA from 2005 to 2023. Black = Mega-spawners. Light grey = Legal sized adults. Dark Grey = subadults (see main text). Size data collected from 2005 to 2011 using visual size estimation, while 2017–2022 employed laser callipers. The gap in the x-axis (2012–2016) comprises years where no size data were collected using either method. No data were collected in 2021

groupers achieve sexual maturity (L_m). Patch reef sites also exhibited lower mean density of Nassau groupers (2.92 individuals/ha) than fore reef sites (7.08 individuals/ha) (Fig. 9).

Management zone Annual trends (individuals/ha) indicated that for both patch reefs and fore reefs, average density of Nassau groupers populations is lower in the general use zone (GUZ), where fishing of Nassau groupers is permitted from April to November, than in the conservation zone (CZ), where they experience legal protection from fishing year-round.

The results of linear regression of density versus time in each management zone and habitat are summarized in Table 1. A statistically significant negative trend exists between density and year in the GUZ in both patch eef and fore reef habitats, with population densities eventually becoming too low to be detected by the survey methodology (Fig. 9). The presence of Nassau grouper has not been detected in surveys of patch reefs in the GUZ since 2013, nor in GUZ fore reef surveys since 2017. In the conservation zone, no clear linear relationship was supported between density and year. Previous studies indicate no statistically significant differences in habitat quality between the GUZ and the CZ at Glover's Reef Marine Reserve (McClanahan and Muthiga 1998, 2020; McClanahan and Karnauskas 2011), eliminating this from consideration as a potential confounding factor.

Fishery-dependent data

GRMR catch data

Over the course of fifteen years (2004–2019) and 309 days of total survey effort, 119 Nassau groupers were observed in fisher catches across the GUZ fishing grounds in Glover's Reef Marine Reserve. These individuals had been caught using Hawaiian slings ($n = 10$), spear guns ($n = 100$) and fishing line ($n = 9$). The dataset indicates that 66% of individuals in the catch were below the minimum size limit/size at maturity (L_m) of 50.8 cm (Fig. 10). Average size (L_x) across all years (2004–2019) was 47.3 cm ($L_x/L_m = 0.946$) indicating overfishing (Babcock et al. 2018). Only five Nassau groupers were recorded in the catch data from 2010 to 2019 (Fig. 11).

Fish market landings data

Surveys of fish at six community markets resulted in measurements of 18,383 individuals during 628 days of survey effort between 2017 and 2020 (Tewfik et al. 2022). Only 18 Nassau grouper were identified in this dataset, and they were captured using fishing lines ($n = 11$), spear guns/Hawaiian slings ($n = 4$) and fish traps ($n = 1$), with the gear of capture for the remaining three specimens unknown. Only 4 of 18 (22%) were above the minimum size limit (50.8 cm), and two of these were larger than the maximum size limit (76.2 cm).

Discussion

Belize has implemented a range of regulatory, conservation and management measures aimed at rebuilding Nassau grouper populations. The anticipated population rebuilding outcome rested upon the assumption that recruitment and survival rates for Nassau grouper were high enough for seasonal and spatial closures and size limits and other measures to support population recovery. Contrary to expectations, the size of the spawning aggregation at GRMR continues to decline. Observations of the species have also declined in fishery-independent monitoring surveys, in fisher catches

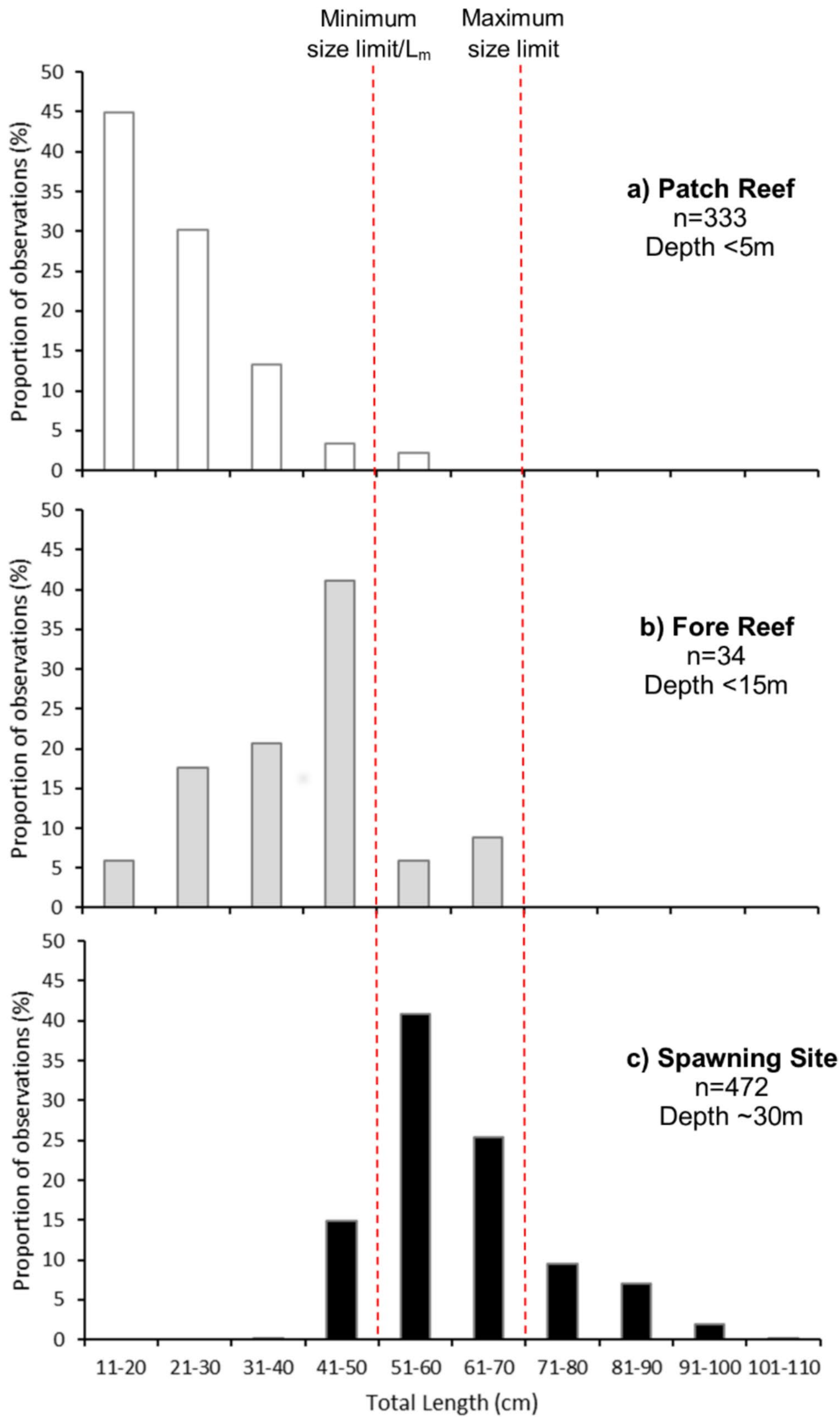


Fig. 8 Proportional distribution of length frequencies of Nassau groupers in patch reef survey data collected 2004–2022 ($n = 333$), fore reef survey data collected 2015–2023 ($n = 34$ and laser calliper data from Northeast Point FSA collected 2017–2023 ($n = 472$). Mean size of individuals is higher in ascending order from patch reefs (24.3 ± 0.6) to fore reefs (42.4 ± 2.5) to the spawning site (60.9 ± 0.5). Shapiro–Wilk tests of normality returned $p < 0.001$ for patch reef length frequencies, $p = 0.038$ for fore reef, and $p < 0.001$ for FSA

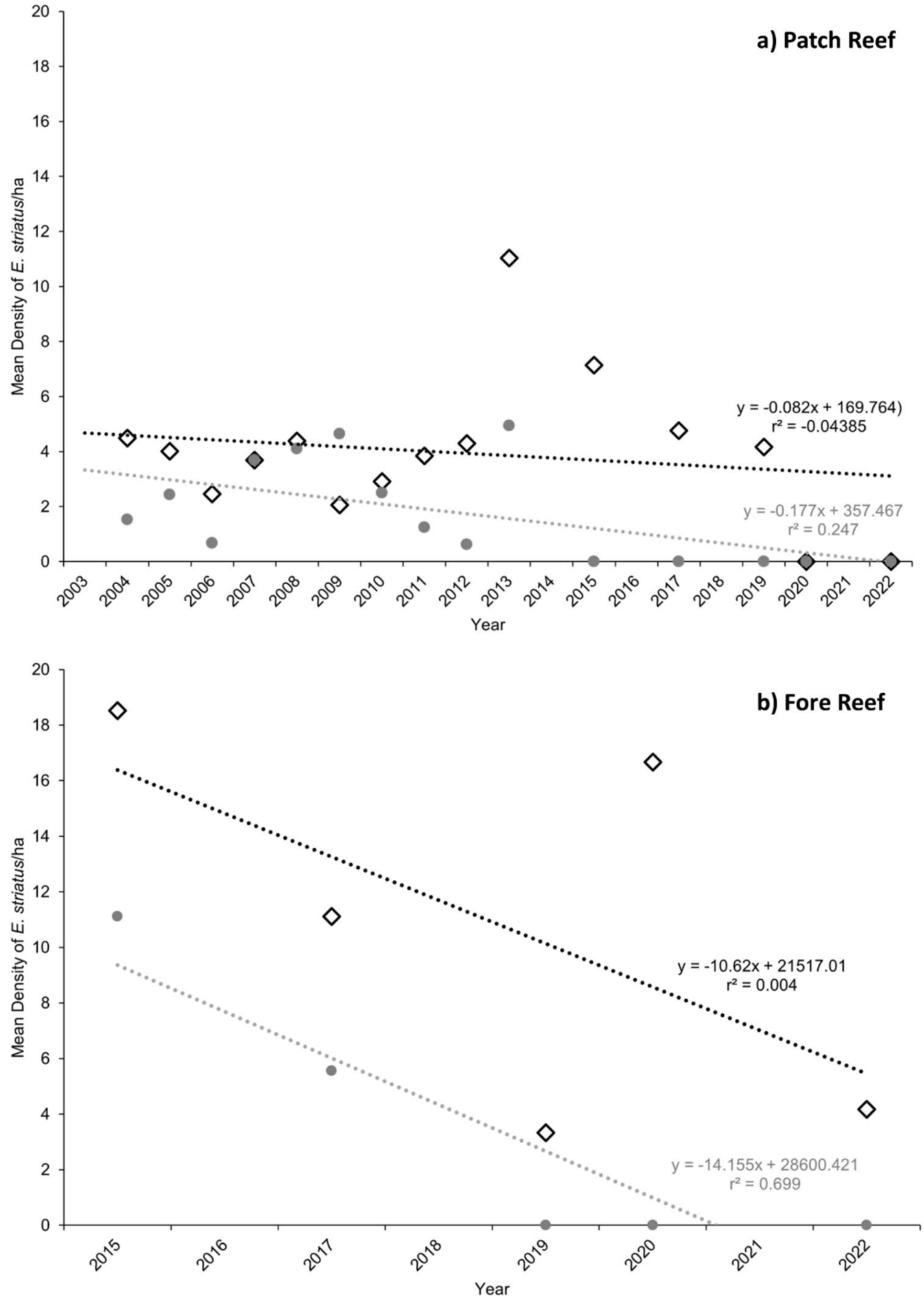


Fig. 9 Density of Nassau groupers in reef survey data from Glover's Reef Marine Reserve collected 2004–2022. Grey circles = General Use (fished) zone; hollow diamonds = Conservation (fishing restricted) zone. Black trendlines = linear regression of Nassau grouper density in Conservation Zone. Grey trendlines = linear regression of Nassau groupers density in General Use Zone. Test statistics are summarized in Table 1

Table 1 Summary of linear regression of density of Nassau groupers versus year in reef survey data from Glover's Reef Marine Reserve collected 2004–2022. CZ = Conservation Zone. GUZ = General Use Zone

Density ~ year (habitat type—management zone)	Residual std. error	Degrees of freedom	Multiple r^2	Adjusted r^2	F-statistic	p value
Patch reef—CZ	2.729	13	0.031	-0.044	0.412	0.532
Patch reef—GUZ	1.589	13	0.301	0.247	5.592	0.034
Fore reef—CZ	56.89	3	0.253	< 0.004	1.017	0.388
Fore reef—GUZ	23.84	3	0.774	0.699	10.3	0.049

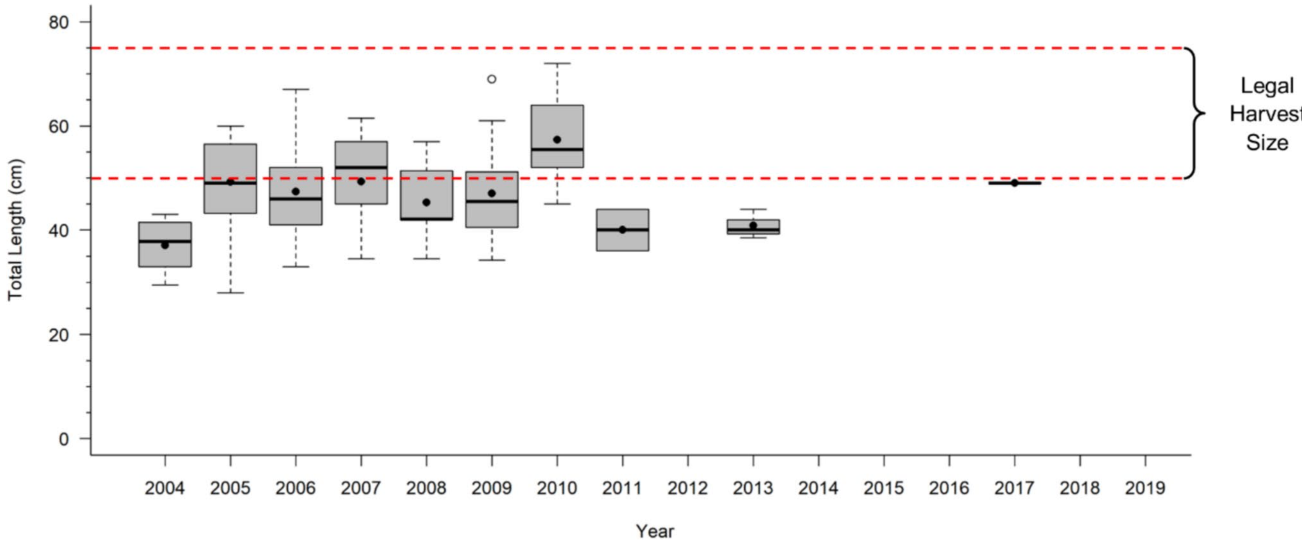
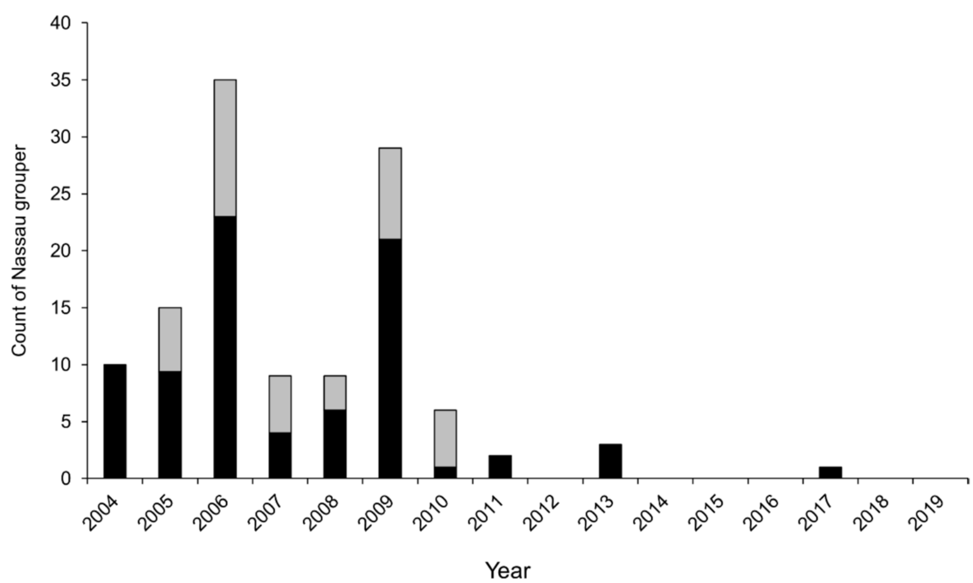


Fig. 10 Box plot showing size distribution of Nassau groupers (n = 119) in fishery-dependent dataset from Glover's Reef Marine Reserve 2004–2019. Red dotted lines indicate legal size limits (50–76 cm). Grey boxes indicate upper (75%) and lower quartile (25%) of size data. Median and mean values are represented by a black bar and black circle, respectively. Whiskers represent maximum and minimum value within 1.5 times interquartile range; white circles show outliers

Fig. 11 Bar graph showing total number/year and proportional distribution of legal catch and undersized catch of Nassau grouper (n = 119) in fishery-dependent dataset from Glover's Reef Marine Reserve 2004–2019. Black portion = undersized catch (< 50 cm). Grey portion = legal catch (50–74 cm). No mega spawner oversized (> 76 cm) individuals were recorded



at the atoll, and at markets across Belize during the open season (Babcock et al. 2013, 2018; Tewfik et al. 2017, 2022; Fulton et al. 2020; Fulton 2023).

Post-larval Nassau groupers are not likely to migrate to or from the atoll across significant expanses of deep water, which suggest that population trends are negligibly influenced by transient juveniles and adults from other areas (Starr et al. 2007; Waterhouse et al. 2020). Literature review and analysis of available primary and secondary data provide no evidence to suggest significant change in spawning behaviour or phenology (i.e. spawning season, peak months or spawning period during the lunar month). Mean temperature during the spawning season was confirmed to gradually increase during January and February at Northeast Point from 2011 to 2022. However, the magnitude of this increase was low-less than 0.1 °C per year. Further, spawning of Nassau groupers was observed at Northeast Point on 23–24 February 2022 (7–8 days after full moon) despite temperatures at depth being approximately 27 °C. A recent study in the US Virgin Islands cited interannual variability in monthly temperatures and a limited temperature range (25.4–28.0 °C) as confounding factors in attempts to carry out modelling exercises on the movement patterns of Nassau grouper during the spawning season (Nemeth et al. 2023). As such, the gradual and negligible change in temperature observed across our time series is therefore unlikely to statistically explain trends in aggregation size or spawning phenology at Northeast Point.

The results presented reflect the best information available at present on this well-documented spawning aggregation site. Passive and active acoustic monitoring methods in combination with visual surveys represent the most ideal combination of methods for additional investigation of spawning behaviour at Northeast Point throughout the entire spawning season (Schärer et al. 2012). Future studies should also consider the potential formation of additional spawning groups which might remain undetected by SCUBA-based visual surveys.

Abundance and size trends

Early population models predicted that the Northeast Point Nassau grouper aggregation would comprise fewer than 50 individuals by 2009 if pre-regulation fishing pressure was maintained, with complete extirpation anticipated by 2013 (Sala et al. 2001). The aggregation has survived a full decade beyond that prediction. However, despite the establishment of various legal protections beginning in 2003, abundance of Nassau grouper at Northeast Point exhibits an ongoing and statistically significant decline of 85%.

Further, in 2001, the aggregation had already declined by 79% since 1975. A local expert fisher and guide (Danny Westby, subsequently involved in numerous in-water surveys), estimated a count of 15,000 aggregating fish in 1975, shortly after the aggregation came under regular exploitation by fishers from the communities of Hopkins and Dangriga (Sala et al. 2001). Therefore, the overall change in abundance from 15,000 to 463 fish between 1975 and 2023 (48 years) represents a decrease of ~ 97% at the only Nassau grouper spawning site at Glover's Atoll (Starr et al. 2007). This is comparable to the result of a 95% regional decline over 50 years described in the 2018 IUCN Red List assessment for this species (Sadovy et al. 2018).

Despite their significant decrease in abundance, the Nassau grouper at Northeast Point FSA have been observed to engage in spawning and spawning-associated behaviours, including grouping, colour change and courtship as recently as 2023. However, should their numbers continue to decrease, a recognizable spawning aggregation may cease to form (Sala et al. 2001; Chollett et al. 2020). The diminished breeding group at the FSA may already be functionally compromised as a source of self-recruitment to GRMR due to the low numbers of spawning fish (Karnauskas et al. 2011; Jackson et al. 2014). While distant FSAs might contribute to larval recruitment on the atoll through pelagic dispersal, this contribution is likely to be limited due to their own decreasing population densities, the geographic isolation of GRMR and the documented importance of self-recruitment for this species (Sala et al. 2001; Froese 2004; Waterhouse et al. 2020; Sadovy De Mitcheson et al. 2024; Karnauskas et al. 2011; Jackson et al. 2014).

With respect to size data, across all years, most of the individuals measured at the FSA were sexually mature (TL > 50 cm), and mega-spawners were consistently present (TL > 76 cm). Unfortunately, the available dataset does not present a clear trend in the mean size of breeding individuals over time, nor do they permit an empirical assessment of change in the prevalence of mega-spawners (Fig. 7). However, other datasets allow us to examine size and abundance trends in the wider population.

Nassau grouper require a range of habitats and a changing suite of prey items across their ontogeny, and managers must be mindful to take the entire life history and population biology into consideration to achieve effective ecosystem-based protection (Legare et al. 2011; Nemeth 2012; Sadovy 2016; Sherman et al. 2016; Sadovy De Mitcheson et al. 2024). Reef surveys revealed a pattern of smaller fish in shallow, lagoon patch reef environments and larger individuals on deeper fore reefs (Fig. 8). Patch reefs and the surrounding lagoon thus constitute largely juvenile/subadult habitat, while the fore reef represents habitat for larger and older adult Nassau grouper, including mature fish that would migrate to the FSA seasonally. Individuals measured during surveys of the shallow fore reef (< 15 m) are generally smaller than the fish encountered at the spawning aggregation (Fig. 8). Sexually mature Nassau grouper tagged at Northeast Point were found to inhabit the fore reef at depths as great as 140 m during non-spawning months (Starr et al. 2007). As such, it can be inferred that much of the breeding population of Nassau grouper lives beyond the depth range of general SCUBA-based reef surveys at GRMR. This habitat versus depth distribution is consistent with documented patterns of ontogenetic distribution and movement from shallow seagrass and patch reef environments to deeper fore reefs as individuals mature (Tupper 2002; Legare et al. 2011; Sadovy et al. 2018; Blincow et al. 2020; Harms-Tuohy et al. 2022).

In both patch reef and fore reef environments, Nassau grouper density was higher in surveys of the CZ, where it experiences legal protection from fishing, while the species has disappeared from surveys in the GUZ, where fishing is permitted outside the closed season (Fig. 9). Other studies at GRMR support these findings, showing statistically significant and positive effects of the CZ on the relative biomass and size of Nassau grouper (Tewfik et al. 2017; McClanahan and Muthiga 2020).

Additionally, researchers conducting baited remote underwater video at depths ranging from 3 to 40 m have indicated similar observations. Nassau groupers are attracted to the baited cameras at all depths, and the frequency of observations of this species has decreased from 2009 to 2020 (Demian Chapman, Mote Marine Laboratory, unpubl. data). As such, it can be inferred that relative abundance of Nassau grouper at all post-larval life stages is decreasing throughout its habitat range at GRMR.

Decreasing habitat quality and overfished prey populations across management zones and habitats may also play a role in the observed decline by inhibiting recruitment and survival of post-larval fish and thus future population recovery (Carter and Marrow 1991; McClanahan and Muthiga 1998, 2020; Sherman et al. 2016; Bruno et al. 2019). Coral reefs—including those at GRMR—face well-documented global stressors, including nutrient enrichment, climate-related impacts and an ubiquitous phase shift from hard coral dominated reefs to reefs where macroalgae and turf algae are increasingly preeminent (Lapointe 2004; Lapointe et al. 2004, 2021; Vermeij et al. 2010; Alves et al. 2022b; Ban et al. 2023).

The Nassau grouper fishery

Existing size limits were intended to prevent growth overfishing (i.e. excessive harvest of juveniles) and recruitment overfishing (i.e. excessive harvest of sexually mature/breeding fish, especially mega-spawners) of this species (Pauly 1994; Babcock et al. 2013, 2018; Burns Perez and Tewfik 2016; Tewfik et al. 2017; Wildtracks Belize 2019). However, catch data from GRMR indicate that fishers have been primarily harvesting individuals below the legal size since at least 2004. This is likely to be linked to the location of the traditional fishing grounds in shallow lagoon/patch reef areas (Tewfik et al. 2017; Babcock et al. 2018), which serve primarily as juvenile/subadult habitat for this species but are also the primary fishing grounds for the key export fisheries of queen conch (*Aliger gigas*) and spiny lobster (*Panulirus argus*). Lobster and conch fishers are known to opportunistically capture preferred finfish species, including groupers and snappers, with hawaiian slings and spear guns (Babcock et al. 2013; Tewfik et al. 2017; Geers et al. 2020).

At the national level, similar patterns emerge. Decreasing abundance of Nassau grouper is supported by its limited presence in country-wide market surveys, and fish below the minimum size limit are predominant among the few fish in the national catch, just as they are in the GRMR catch. However, the presence of fish above the maximum size limit (76.2 cm) in the country-wide dataset also suggests that fishers do not always release mega-spawners when they are caught. These results have been validated in discussion with traditional fishers, who generally do not carry fish measurement tools, as Nassau grouper is the only finfish with a size limit regulation in Belize. Fishers also indicated that they consider them to be very rare in their catch (FAO/WECAFC 2024). Line fishers have the option to release Nassau groupers to avoid potential penalties, while others (e.g. spear fishers) may choose to retain and sell their catch, having relied on an ad hoc judgement of length (FAO/WECAFC 2024). It must be noted that the impact of trophy hunting and consumption by recreational fishers (i.e. tour boats, charter fisheries, guides) on Belize's reef fisheries has not been properly assessed. Recreational fisheries are also largely unregulated, apart from strict catch and release regulations for bonefish, permit and tarpon (Babcock et al. 2013; Perez-Cobb et al. 2014; Geers et al. 2020; Tewfik et al. 2022).

Enforcement, compliance and policy

Illegal, unreported, and unregulated (IUU) fishing remains a concern with respect to the management of Nassau grouper at GRMR (Fig. 2), with ongoing reports of the presence of local and foreign fishing boats at Northeast Point during the spawning season (Phillips 2023; Fulton 2023; FAO/WECAFC 2024, Eric Appeldoorn-Sanders, University of Puerto Rico, unpubl. report). Local infractions related to Nassau grouper are considered infrequent both at the national and site level (FAO/WECAFC 2024; Hampton Gamboa, Belize Fisheries Department, pers. comm.). Night fishing by boats from Honduras and Guatemala is considered frequent, and has been notoriously difficult to control because of Northeast Point's challenging sea conditions during December to March, the distance of the site from enforcement assets based ~ 20 km south at Middle Caye, and chronic management resource deficiencies (Tewfik et al. 2017; Azueta et al. 2020; Fulton et al. 2020; FAO/WECAFC 2024; Hampton Gamboa, Belize Fisheries Department, pers. comm.). Enforcement units in Belize are often restricted in their ability to patrol Northeast Point and other remote sites by limited fuel allocations and lack of equipment for night patrols, though attempts are made by NGO partners to supplement resource gaps (Paz and Truly 2007; Tewfik et al. 2017; Azueta et al. 2020; Phillips 2023; BFSF 2024; FAO/WECAFC 2024). Ongoing IUU fishing mortality incurred upon the Northeast Point FSA is impossible to assess but is likely to contribute directly to the decline of the spawning aggregation and the decrease in recruitment. The GRMR management plan indicates that stakeholders consider illegal and unsustainable fishing of Nassau grouper at the FSA to be "High" in both scope and severity, and that these trends may be difficult to reverse (Wildtracks Belize 2019).

Despite upgrades in international conservation priority for Nassau grouper and ongoing population declines in national and regional waters over the past two decades, there have been no significant changes to the regulations which govern the Nassau grouper fishery in Belize since 2009 (FAO/WECAFC 2024). The only relevant policy change has been a general increase in penalties for fisheries infractions enacted under the Fisheries Resources Act (No. 7 of 2020). Management of Nassau grouper was given high priority in the guidelines for development of a multi-species finfish management plan (UNCTAD 2022). However, this plan is yet to be developed and operationalized into legal force, and the lack of a management plan which mandates specific indicators, benchmarks and trigger points for action is cited as a weakness of finfish and FSA management in Belize (Geers et al. 2020; UNCTAD 2022; FAO/WECAFC 2024). Further, given the strength of Belize's existing protective regulations, the only significant legal advancement which could be made under the new Fisheries Resources Act (2020) would be a total closure of the Nassau grouper fishery—a resource-intensive measure requiring extensive collaborative effort, deft consultations and effective stakeholder engagement.

While fishery closures are often unpopular measures, the minimal contribution of Nassau grouper to national catch composition suggests that a ban would have a negligible impact on fisher livelihoods. Fishery-dependent data suggest that Nassau grouper has not provided substantial economic benefits as an export or local finfish product for decades (Heyman and Wade 2007; Tewfik et al. 2020b, 2022). Decreasing abundance and average size of Nassau grouper in reef environments also has notable impacts on the tourism industry. Their presence on dive sites is highly valued by snorkellers and SCUBA divers, who demonstrate willingness to pay higher prices for encounters with this and other large charismatic species (Rudd and Tupper 2002; Schuhmann et al. 2013; Gill et al. 2015; Shideler and Pierce 2016). A fishery closure is not a novel proposition (Sala et al. 2001; Paz and Truly 2007). However, as with the existing regulations, the effectiveness of a closure are likely to be contingent on Belize's ability to address persistent barriers to effective enforcement (BFSF 2024; FAO/WECAFC 2024).

Further, even with a national fishery closure, illegal transboundary fishing poses a persistent threat to Belizean fishery resources—a threat which has not been tangibly addressed in many years (Perez 2009; Heyman and Granados-Dieseldorff 2012; Wade et al. 2019; Geers et al. 2020). Recovery of declining Nassau grouper populations in Belize may only be possible through transboundary enforcement collaborations with neighbouring countries, regional harmonization of regulations, and significant outreach and livelihood interventions in communities which engage in illegal activities (Fulton et al. 2020; González-Bernat et al. 2020; Fulton 2023; FAO/WECAFC 2024; Sadovy De Mitcheson et al. 2024). The Mesoamerican reef spans four countries, which suggests that this species, which is dispersed by planktonic larvae and capable of migrating over 300 km along contiguous reef tracts to spawn, is a transboundary resource whose fate in Belize has direct implications for its overall status in neighbouring countries, and vice versa (Bolden 2001; Fulton et al. 2020). This is supported by genetic studies which indicate a relatively distinct Mesoamerican sub-population, providing rationale for regional management approaches (Jackson et al. 2014; Sadovy De Mitcheson et al. 2024).

Conclusions

Our examination of fishery-dependent and fishery-independent data, including a continuous 20-year monitoring of the only Nassau grouper FSA at GRMR, suggests that the existing management measures, begun in 2003, have not been effective in the restoration of this isolated population. Fish surveys have shown declines in the presence of Nassau grouper across habitats and management zones, including at the spawning site, and their virtual disappearance from fished areas. Spatial isolation from the main barrier reef complex and declining habitat quality further detract from the resilience of this population to extant threats (McClanahan and Muthiga 1998, 2020; Tewfik et al. 2017; Chollett et al. 2020; Alves et al. 2022b). Ongoing and frequent IUU fishing at the Northeast Point FSA highlights the need for more effective enforcement and compliance strategies, including the pursuit of harmonized regional management. The trend of decline points to imminent extirpation of Nassau grouper from Glover's Atoll unless novel management interventions succeed in fostering recovery (Tewfik et al. 2017; Fulton et al. 2020; FAO/WECAFC 2024; Sadovy De Mitcheson et al. 2024).

Effective FSA recovery in response to increased management has been documented in other places, including the Cayman Islands (Waterhouse et al. 2020). However, it must be noted that despite FSA recovery only being documented in well-managed areas, management does not guarantee that recovery will occur, especially once a recognizable spawning aggregation has ceased to form (Chollett et al. 2020; Nemeth et al. 2023). The extirpation of Nassau grouper FSAs has already been observed at other sites in Belize, including Rocky Point and Gladden Spit (Burns Perez and Tewfik 2016; FAO/WECAFC 2024), and at the global scale, almost 60% of known extirpated FSAs have not recovered even where they benefit from spatial and seasonal protections (Cheung et al. 2013; Chollett et al. 2020). Successes in the declaration of protected areas and establishment of spatial, temporal and gear regulations do not guarantee mitigation of threats to biodiversity, including the ecological impacts of human activity (Zupan et al. 2018; Relano and Pauly 2023; Hughes et al. 2023; Ban et al. 2023).

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Author contribution M.P. wrote the main manuscript text and prepared all figures, with editing by A.T. All authors participated in data collection. All authors reviewed and approved the manuscript before submission.

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Data availability The data that support the findings of this study are available from the Wildlife Conservation Society upon reasonable request.

Declarations

Conflict of interest The authors declare no competing financial or non-financial interests.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study. All methods were purely observational, and involved no lethal collections nor veterinary procedures.

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