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Cubera snapper (*Lutjanus cyanopterus*) aggregation at Riley's Hump, Tortugas South Conservation Area: indirect evidence for multispecies spawning aggregation recovery

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ABSTRACT.—Studying previously fished multispecies aggregation sites provides insight on how to manage them to ensure their continued reproductive success. Riley's Hump is a historically overexploited multispecies aggregation site situated in the no-take Tortugas South Conservation Area, Florida Keys National Marine Sanctuary. This paper summarizes opportunistic observations of a cubera snapper (*Lutjanus cyanopterus*) aggregation collected from 2011 to 2020. By utilizing a variety of methods, collaborative multi-agency partnerships, and repeated visits to the aggregation site, we gathered indirect (echosounder) and direct (divers, ROV) evidence of significant biomass that persists across multiple months and years, from spring through fall, at the cubera snapper aggregation site. The persistent biomass present at Riley's Hump during known cubera spawning months, color morphs associated with reproduction, and female morphs with visibly distended abdomens, suggests that this location is currently a significant, and likely spawning aggregation site for this species, although direct confirmation of spawning remains to be obtained. In addition to cubera snapper, we confirmed the regular presence of multiple species of apex predators (e.g., Carangidae, Carcharhinidae, Epinephelidae). These observations provide further indirect evidence that the current no-take management designation of Riley's Hump has been successful at maintaining a healthy ecosystem, characterized by snapper, grouper, and other species undertaking critical spawning activities, and higher trophic level species associated with this location and the activities and habitats that occur there. The multispecies spawning aggregations and deep reef habitats of Riley's Hump can serve as a conservation "bright spot" for fish populations in the greater Florida region.

Reef fishes are known to form aggregations for the purposes of feeding or reproduction (Fisher et al. 2018). Many commercially and recreationally important species of the snapper-grouper complex form seasonal spawning aggregations where peaks in reproductive effort occur (Sadovy 1996, Nemeth 2009). Some of the same aggregation sites are used by multiple species throughout the year, and as such, represent productivity hotspots characterized by large numbers of fish attracted for reproduction, apex predators attracted to the spawning fish, and planktivores attracted to the pulses of eggs released during spawning (Nemeth 2012, Erisman et al. 2015, Grüss et al. 2018). The predictable nature of these multispecies spawning aggregations makes the fish that use them vulnerable to overexploitation (Sadovy de Mitcheson and Erisman 2012, Grüss et al. 2014, Pittman and Heyman 2020). Once aggregations have been fished to sufficiently low numbers, they may be unable to recover (Aguilar-Perera 2006, Waterhouse et al. 2020), although examples of recovery following successful protection are growing (Feeley et al. 2018, Sadovy de Mitcheson et al. 2020). Studying previously fished multispecies aggregation sites provides insight on how to manage these species to ensure their continued reproductive success (Nemeth 2005, Kadison et al. 2006, Stock et al. 2021).

Riley's Hump is a multispecies fish aggregation site situated in the Tortugas South Conservation Area (formerly Tortugas South Ecological Reserve) of the Florida Keys National Marine Sanctuary (FKNMS, Fig. 1). Riley's Hump's status as a historic overexploited multispecies aggregation site is based on fisherman interviews and catch data (Lindeman et al. 2000, Domeier 2004, Burton et al. 2005). In 2001, the

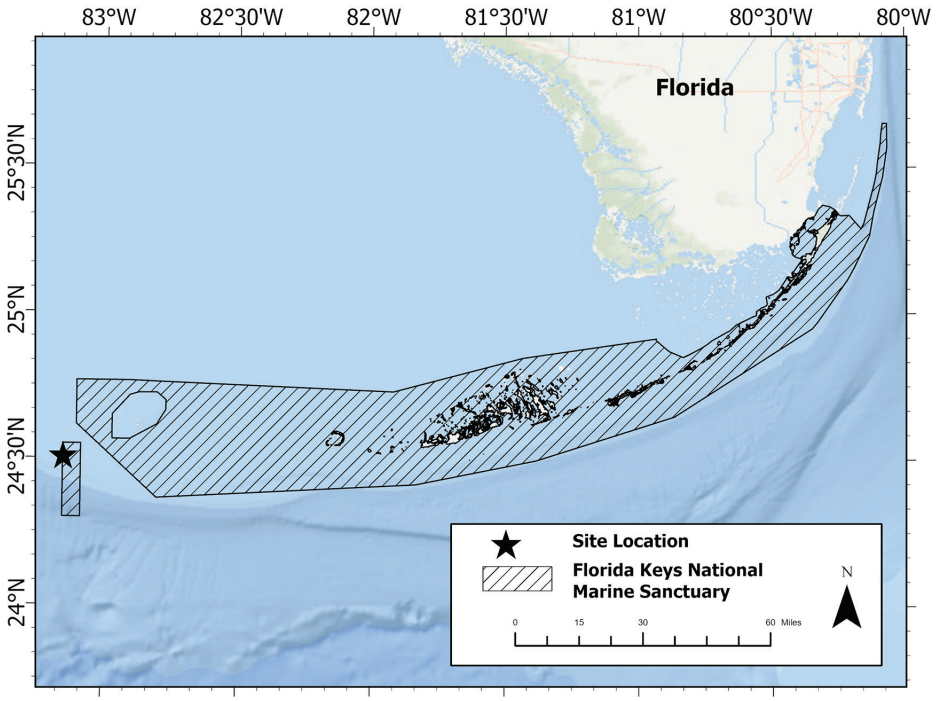

Figure 1. Overview of Southeast Florida with the management boundary for Florida Keys National Marine Sanctuary. A black star represents the study site and general location of Riley's Hump in the northern region of the Tortugas South Conservation Area.

Tortugas South Ecological Reserve was implemented, creating a no-take marine reserve that encompassed Riley's Hump (Florida Keys National Marine Sanctuary 2001). Vessels may only enter if they remain in continuous transit with fishing gear stowed, and diving and snorkeling are prohibited. Scientists have been monitoring Riley's Hump since its protection to determine if recovery of a multispecies spawning aggregation is possible.

Since its closure in 2001, various observation methods have recorded evidence of recovery of the multispecies aggregation site at Riley's Hump. Early on, diver observations were used to record species richness and abundance at Riley's Hump (Burton et al. 2005). Due to the difficulty of maintaining direct observation year-round at this remote aggregation site, these efforts have been complemented with additional technology since 2008 when the National Oceanic and Atmospheric Administration (NOAA) implemented hydrographic survey and seafloor mapping in the Tortugas Bank region, and included water column echosounding to characterize fish and fish aggregations associated with seafloor features. To monitor spatial and temporal movements of mutton snapper (*Lutjanus analis*), the Florida Fish and Wildlife Conservation Commission (FWC) began deployments of acoustic receivers in 2008 (Feeley et al. 2018), and Mote Marine Laboratory deployed passive acoustic hydrophones in 2010 to document grouper sound production (Locascio and Burton 2016).

Eight years after protection was in place, acoustic telemetry documented mutton snapper (*L. analis*) migrations to Riley's Hump during their spawning season while scientists additionally confirmed and recorded spawning rushes using underwater video (Feeley et al. 2018). Further evidence of the recovery of this multispecies spawning aggregation site came from the use of passive acoustic hydrophones which recorded peaks in courtship calls for black grouper (*Mycteroperca bonaci*), red hind (*Epinephelus guttatus*), and red grouper (*Epinephelus morio*) during their spawning season (Locascio and Burton 2016, Sanchez et al. 2017). Additional diver observations recorded elevated numbers and spawning coloration of jacks (blue runner, *Caranx crysos*; horse eye jack, *Caranx latus*; crevalle jack, *Caranx hippos*); nesting behavior of ocean triggerfish (*Canthidermis sufflamen*); and elevated numbers of permit (*Trachinotus falcatus*), dog snapper (*Lutjanus jocu*), and cubera snapper (*Lutjanus cyanopterus*) at Riley's Hump (Feeley et al. 2018).

To augment direct diver observations on portions of Riley's Hump that are deeper than typical recreational dive limits (approximately 40 m), additional tools such as direct observations by rebreather divers, as well as indirect methods including remotely operated vehicles, drop cameras, and acoustic sonar surveys were opportunistically deployed. Through these diverse tools, it became apparent that cubera snapper were aggregating at a deeper, upper mesophotic reef area adjacent to Riley's Hump during their reported spawning season (generally March–September [May–August in the Florida Keys], Lindeman et al. 2000, Heyman et al. 2005, Kadison et al. 2006). Initial hydrographic multibeam mapping of the area revealed a terrace and ledge feature adjacent to the main rise of Riley's Hump. Water column echosounding during the mapping surveys also indicated high abundance of fishes over the feature. This paper summarizes opportunistic observations of a cubera snapper aggregation made using multiple methods and platforms from 2011 to 2020. Additional reports of other species aggregations in high densities are also reported. Together with previous studies documenting spawning aggregations or reproductive

behavior of species including mutton snapper, black grouper, red grouper, permit, and jacks (Burton et al. 2005, Locascio and Burton 2016, Feeley et al. 2018), this study supports the idea that carefully placed conservation areas can help protect vital phases in the life history of managed stocks, adding to the accumulating direct and indirect evidence of the importance of the Tortugas South Conservation Area for multiple species and the greater South Florida tropical marine ecosystem.

Methods

Site Description.—Riley's Hump is an irregularly shaped upper mesophotic reef located adjacent to the Dry Tortugas, Florida (24.6285°N, 82.8732°W, 137 km west of Key West, Florida), at the far western edge of the island chain and reef tract of the Florida Keys. Bottom depths range from 30 to 65 m. Riley's Hump is inside the Tortugas South Conservation Area of the Florida Keys National Marine Sanctuary and has been under protection from fishing and anchoring since 2001. Additional details of the study site can be found in Mallinson et al. (2003), Domeier (2004), and Burton et al. (2005). We utilized the following vessels for operations: the NOAA Ship Nancy Foster, a 56.8 m former US Navy torpedo test vessel; the MV Spree, a 30.2 m aluminum-hulled vessel converted from use for oil field services to a live-aboard dive platform; the RV Peter Gladding, a 17.4 m catamaran operated by the FKNMS and typically used for law enforcement activities in the lower Florida Keys.

Seafloor and Spatial Planning.—Hydrographic multibeam surveys were conducted over Riley's Hump and the surrounding area during several missions on the NOAA Ship Nancy Foster from 2010 to 2017. Processed bathymetric soundings were gridded to 2 m resolution and visualized in a GIS (ArcGIS Pro v3, Esri).

All data were visualized over the bathymetric maps. For this paper, due to the sensitivity of the data, the geographic coordinates are not included with the maps. Additionally, the orientation of the maps has been rotated while still conveying the size and geomorphology of the study feature. Both of these measures were taken to protect the exact location of this feature.

Fishery Echosounder Surveys.—Fishery echosounder surveys and transects were conducted opportunistically during complementary missions to assess the fish communities within the Tortugas South Conservation Area. The Simrad EK60 splitbeam echosounder operating at 120 kHz was mounted on the hull of a research vessel (NOAA Ship Nancy Foster), or using an overboard pole mount on a charter vessel (MV Spree). A minimum pulse length of 128 microseconds and maximum pulse rate was used to optimize vertical resolution and detection of targets near the seabed. Survey transects either followed the orientation of the feature, or were set perpendicular to the orientation of the ledge. Survey effort in line kilometers varied by year, and surveys were conducted during various times of day.

Splitbeam echosounder data were processed in Echoview (v12 and v13, Echoview, Pty Ltd, Hobart, Tasmania). Bottom and surface lines were created to delineate the seabed and eliminate surface bubbles from vessel wakes in the water column. The lines were manually reviewed and edited to exclude additional noise in the water column and near the seafloor. The data were thresholded at −60 dB to isolate the individual fish and fish schools in the water column. Fish schools and individual

fish targets were detected using a user-defined detection algorithm and manually scrutinized for valid detection (Taylor and Ebert 2012). Data from sequential pings were aggregated into 50 m intervals along survey transects and exported as text files with spatial position and magnitude of backscatter in units of Nautical Area Scattering Coefficient (NASC). NASC is roughly proportional to relative abundance of fish in the water column, but does not attempt to apportion backscatter to individual fish species or densities (MacLennan et al. 2002, Fernandes et al. 2016). The splitbeam echosounder surveys represent a "slice" through the water column (about 12% swath over water depth), which reflects a narrow cross-section of fish and fish schools along a transect.

Diver Observations.—We used both open-circuit scuba and closed-circuit rebreather systems for diver observations. Dives were conducted opportunistically around the full moon from March through July of 2011 through 2015, often in conjunction with surveys targeting mutton snapper who are known to aggregate for spawning at Riley's Hump around the full moon from late spring to early summer (Domeier 2004, Burton et al. 2005, Feeley et al. 2018). Cubera snapper in Belize and St. Thomas, United States Virgin Islands have also been found to aggregate for spawning in the late afternoon around the full moon (Heyman et al. 2005, Kadison et al. 2006). Dives were conducted between other methodologies (ROV surveys, echosounder surveys, equipment service dives, etc) on research trips, resulting in non-standardized dates and times across years. Initially, elevated numbers of cubera snapper were observed by rebreather divers in March 2011, and divers also observed an apparent cubera snapper aggregation in 2012 when retrieving equipment associated with another project monitoring grouper courtship sounds (Locascio and Burton 2016). Subsequently, we used the echosounder (described above) to document elevated biomass along a feature that encompassed the sites from 2011 and 2012 and deployed divers where elevated biomass was seen with the echosounder to provide species identification. Videos were collected by divers with either GoPros or various underwater point and shoot digital cameras (e.g., manufactured by Olympus, Sony, Canon). Diver videos were analyzed for MaxN, the maximum number of fish seen in a single frame (Ellis and Demartini 1995). MaxN was used to determine counts of cubera snapper to avoid overinflating counts of the same fish swimming back into the frame multiple times in one video (Ellis and Demartini 1995, MacNeil et al. 2020). Since different cameras may have different fields of view and a correction factor for these differences could not be calculated after the fact, MaxN numbers between observation days present relative differences.

Baited Remote Underwater Video.—Stationary baited remote underwater video (BRUV) camera arrays consisted of two independent stereo-video systems powered by 12V DC batteries. The stereo-video systems were mounted 180° to one another inside an aluminum frame. Each stereo-video system consisted of paired color, digital video cameras (Arecont® 2105 day/night). The digital video camera recorded continuous video using Luxriot® digital video software (.lxa format) during the deployment. In addition to the two stereo-video camera systems, two GoPro cameras recording continuous video were also mounted within the aluminum frame at 180° to each other, and 90° to the stereo cameras, resulting in the ability to record video in all directions from the aluminum frame. Camera arrays were baited with

approximately 1.8 kg of round sardinella (*Sardinella aurita*) and bait was refreshed between camera deployments. These underwater camera arrays were baited in the afternoon and deployed overnight for approximately 14 hours on 18 and 20 August 2016. Videos were reviewed for cubera snapper sightings using the same MaxN methods of the diver videos.

ROV Video Surveys.—Two types of remotely operated vehicles (ROVs) were used to record cubera snapper activity at Riley's Hump. A smaller SeaBotix LBV 150SE ROV was used in 2012 but the variable and oftentimes strong currents at the site made it difficult to operate. Subsequent ROV deployments utilized a larger ROV. In August 2017 and again in September 2020, transects were run along the feature of interest from the NOAA Ship Nancy Foster using a survey-class Sub-Atlantic Mohawk 18 ROV. The ROV speed was approximately 0.1 m/s along the transect, with interruptions to allow for closer examination of fish species. Forward video on a tilt bar was recorded in HD (720p) on the ship. Navigational information was provided by offsets from an ultra-short baseline (USBL) using differentially corrected GPS positions from the ship, allowing fish counts to be positioned relatively along the transect using matched time stamps between the video and ROV navigation data. Videos were reviewed for the presence of cubera snapper in aggregation and analyzed similarly to the diver observations with MaxN.

Results

Due to variable conditions at Riley's Hump and the opportunistic nature of our sampling, we utilized fishery echosounder, closed circuit and open circuit scuba, drop cameras, BRUVs, and multiple types of ROV. Across all years and months sampled, we observed consistently high relative biomass (as determined with the echosounder) mostly associated with a distinct benthic feature. Paired diver observations confirmed cubera snapper, sometimes aggregated in the 100s, and other species associated with this elevated biomass. Additional details are provided below.

Synthesis of recent seafloor mapping surveys revealed a prominent ledge feature adjacent to Riley's Hump (Fig. 2). The plateau is about 54 m at the shallowest with a steep sloped ledge that drops to maximum depth at the base substrate at about 65 m (Fig. 3). The shape of the feature is like an "elbow" with one segment 0.7 km in length, a change in orientation of roughly 150 degrees, followed by a 1.3 km long segment. The elbow represents the highest relief ledge at about 9-m rise from the base substrate. The ledge height decreases from the elbow out to the ends of the feature where there is no apparent relief.

Fishery Echosounder Surveys.—Sixteen fishery echosounder surveys were conducted using various survey designs intended to identify locations of high relative abundance of fish in the water column (Table 1). The surveys along and perpendicular to the feature revealed aggregations of fish in the water column and close to the seabed. In most surveys, direct observations of species in these aggregations were not performed. On a few occasions, the echosounder surveys were preceded or followed by visual observations. These results are described in the next section on diver and camera surveys. Here we summarize the general observations of the distribution

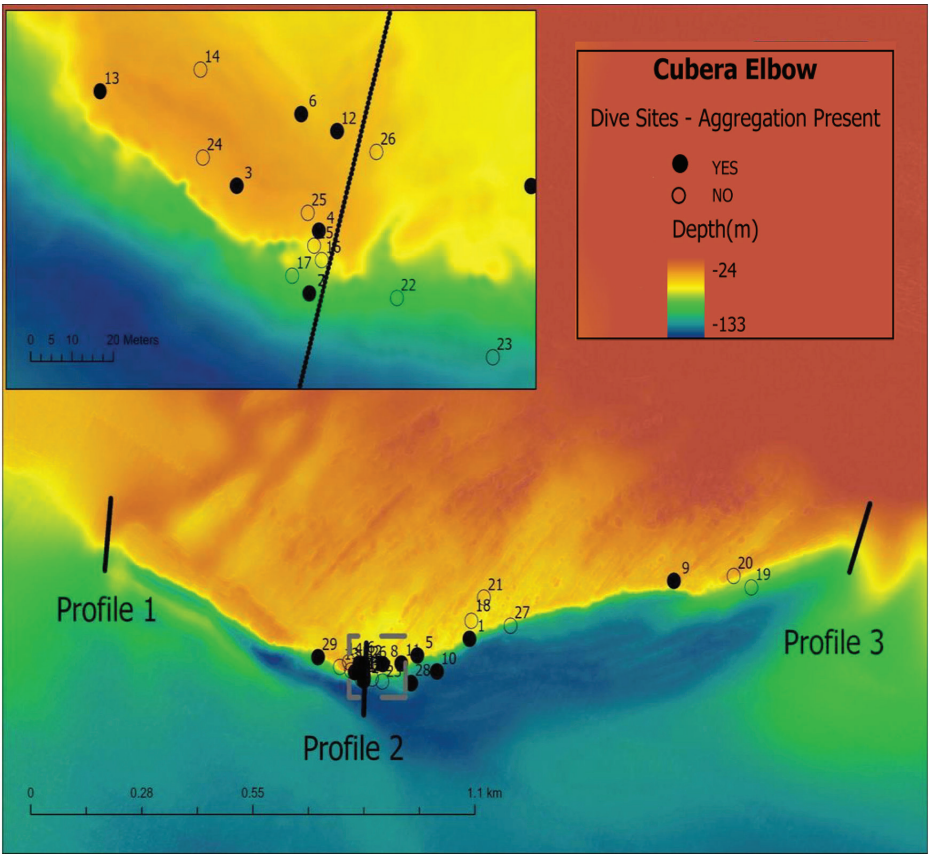

Figure 2. Overview of dive stations on the ledge feature at Riley's Hump. Black circles show dives where cubera snapper (*Lutjanus cyanopterus*) were observed in aggregation, while clear circles indicate dives where cubera snapper were not seen. The locations of the three bathymetric profiles detailed in Figure 3 are indicated.

of relative abundance as indicated by the NASC metric from the analysis of the echosounder surveys.

In 2011, high relative abundance, as indexed by NASC, was observed close to the elbow but also distributed along the escarpment feature (Fig. 4A). In 2012, a single transect along the feature was used to identify aggregations and then transects were run perpendicular to the escarpment at the peak observations to further assess the relative abundance and distribution. Smaller aggregations of fish were observed in the vicinity of the elbow, but also at either end of the feature. A single observation of dispersed large fish targets high in the water column was also observed (Fig. 4B). In 2013, more extensive surveys were possible, spanning 4 days and morning and evening periods. High relative abundance was observed primarily within 0.5km of the elbow (Fig. 4C). A single survey was conducted in 2015 and focused several transects on a portion of the escarpment. Highest relative abundance was located within 0.25 km of the elbow (Fig. 4D). A single transect along the entire length of the escarpment was surveyed twice in 2017 (Fig. 4E). High relative abundance was observed along extended tracks of the escarpment with peaks at the elbow but with additional high relative abundance observed at each end of the escarpment. A

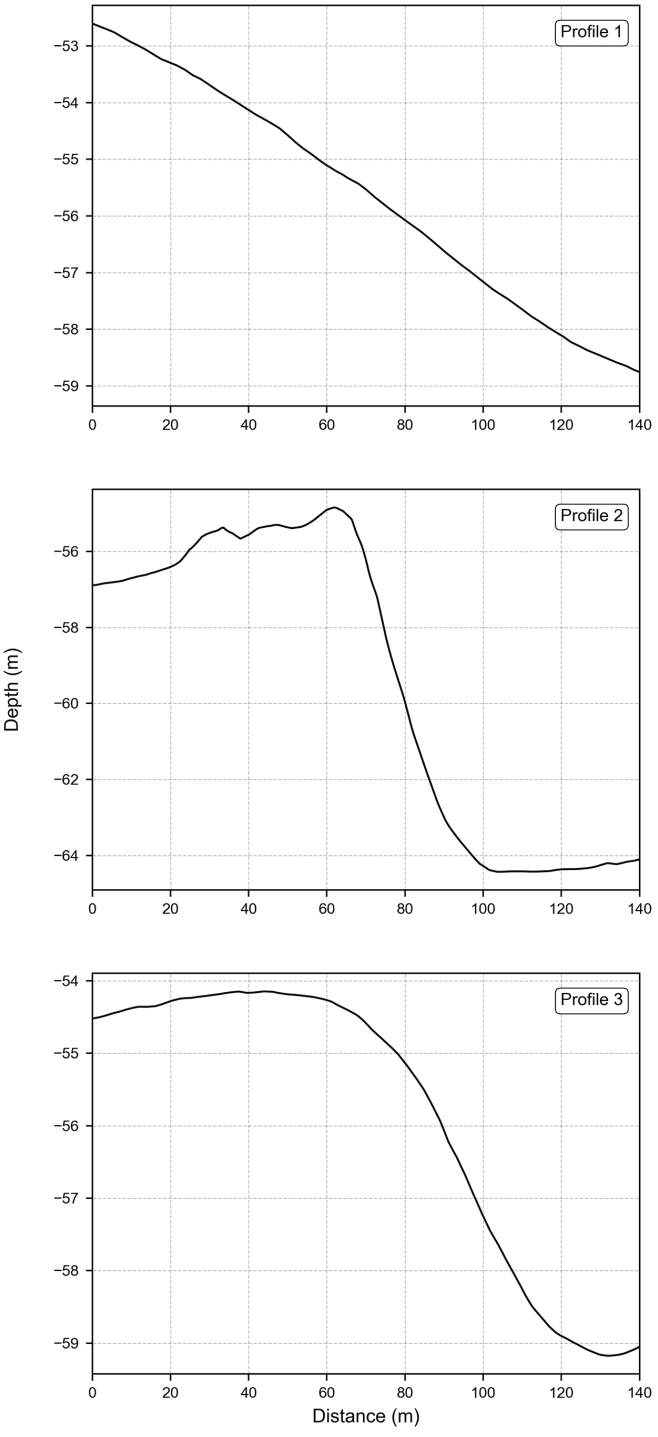

Figure 3. Bathymetry and profile of the ledge feature at Riley's Hump. The locations on the ledge of the three bathymetric profiles are indicated in Figure 2.

Table 1. Summary of survey effort using echosounders. Time is in Coordinated Universal Time (UTC). Nautical Area Scattering Coefficient (NASC) values are median and maximum values. Additional site observations by divers or remotely operated vehicle (ROV) are provided for context. *Maximum number of fish seen in a single frame (MaxN) = 24 cubera snapper but about 500 estimated from divers. + ROV dive completed the morning after (08/03/2017 14:14 UTC) the acoustic sample.

Date	Time (start)	Survey duration (min)	Linear km	NASC median (max)	Cubera snapper observations (MaxN, method, time, site)
03/21/2011	13:26	150	19.2	165 (4,449)	24*, divers, 19:38, 8
07/17/2011	22:11	133	14.1	147 (5,143)	- - -
08/02/2012	10:00	80	14.7	69 (3,294)	200, ROV, 13:17, 11
07/23/2013	20:22	16	1.8	704 (17,951)	94, divers, 20:54, 2
07/23/2013	22:21	129	15.5	140 (15,337)	- - -
07/24/2013	20:12	93	11.4	39 (1,055)	- - -
07/24/2013	22:43	78	8.1	103 (3,756)	- - -
07/25/2013	21:12	37	4.2	115 (3,648)	41, divers, 19:47, 1
07/26/2013	21:18	161	16.2	152 (9,587)	102, divers, 18:08, 7
06/17/2015	23:32	50	10.4	400 (15,649)	- - -
08/02/2017	11:10	22	4.9	1,163 (42,014)	- - -
08/02/2017	21:54	23	5.1	1,077 (20,506)	19, ROV, 14:14+, 28
11/09/2018	11:22	62	8.0	85 (17,263)	- - -
11/09/2018	16:51	34	7.2	103 (8,015)	- - -
11/09/2018	22:31	49	9.4	115 (17,764)	- - -
09/11/2020	20:00	45	8.9	381 (6,409)	16, ROV, 19:13, 29

single survey was conducted in 2018 that included several repeated transects along a portion of the elbow and escarpment. High relative abundance was observed along the surveyed portion of the feature (Fig. 4F). Finally, a single survey was conducted in 2020 along a transect that was covered twice. High relative abundance was limited to the elbow feature (Fig. 4G).

Diver/BRUV/ROV.—The cubera snapper aggregation site at Riley's Hump was often characterized by low visibility and strong currents that precluded scuba diving surveys, and currents were also often found to be too strong for the smaller SeaBotix ROV. Fortunately, currents and visibility at the site were highly variable, sometimes changing between days, so repeated visits over multiple days often proved successful at observing and documenting the cubera snapper aggregation. The largest portion of the cubera snapper aggregation formed in approximately 60 m depth but individuals could be observed rising 15–18 m off the bottom in groups of approximately 20 individuals. We observed light color morph fish (females) with visibly distended abdomens (Fig. 5C–E) swimming in the water column pursued by numerous dark color morph fish (presumed males, Heyman et al. 2005).

Our opportunistic surveys at Riley's Hump spanned ten years and included observations across seven years that revealed large (100s of individuals) aggregations of cubera snapper present in five of seven years and smaller groups (<20 individuals) of cubera snapper present in two years (Table 2). MaxN varied from a low of 16 recorded with ROV in 2020 to a high of 376 fish recorded by rebreather divers in 2012 (Fig. 5A, B), and rebreather divers estimated 500 cubera snapper (not MaxN) from their dive on the aggregation observed in 2011. While the geospatial location of these cubera snapper aggregations varied among years and included a potential staging area that spanned a distance of approximately 1.5 km (Fig. 2), our repeated visits across years allowed us also to infer a primary aggregation site, based on elevated

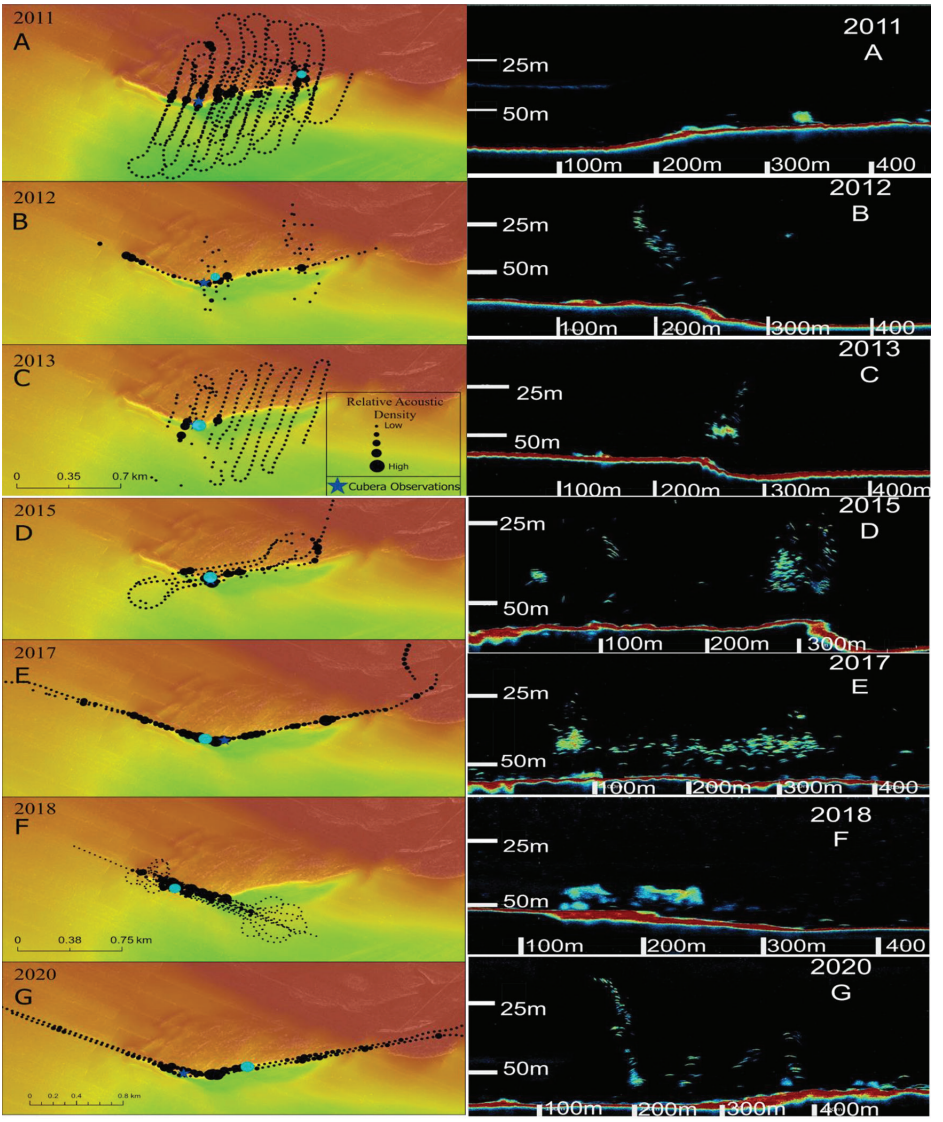

Figure 4. Relative acoustic density of fish during (A) 2011, (B) 2012, (C) 2013, (D) 2015, (E) 2017, (F) 2018, (G) 2020. Bathymetry is presented as in the color ramp in Figure 2. Relative density is presented as proportionally sized points that are normalized across all surveys. Each panel represents multiple surveys conducted on a single or several days as noted in Table 1. Blue stars show locations of cubera snapper (*Lutjanus cyanopterus*) aggregations confirmed via divers or ROV. Right panels are excerpts from the corresponding echogram showing fish schools and seabed in the vicinity of the turquoise circle on the corresponding map. Red line is the seabed and relative acoustic density is shown from blue-green (low) to orange (high).

numbers and biomass of fish (relative to other sites) and observations of females with visibly distended abdomens (Fig. 4).

We observed cubera snapper aggregations in the months of March, July, August, and September. Our observations generally coincided with the full moon (Table 2) and were targeted for the late afternoon. Most of our observations of cubera

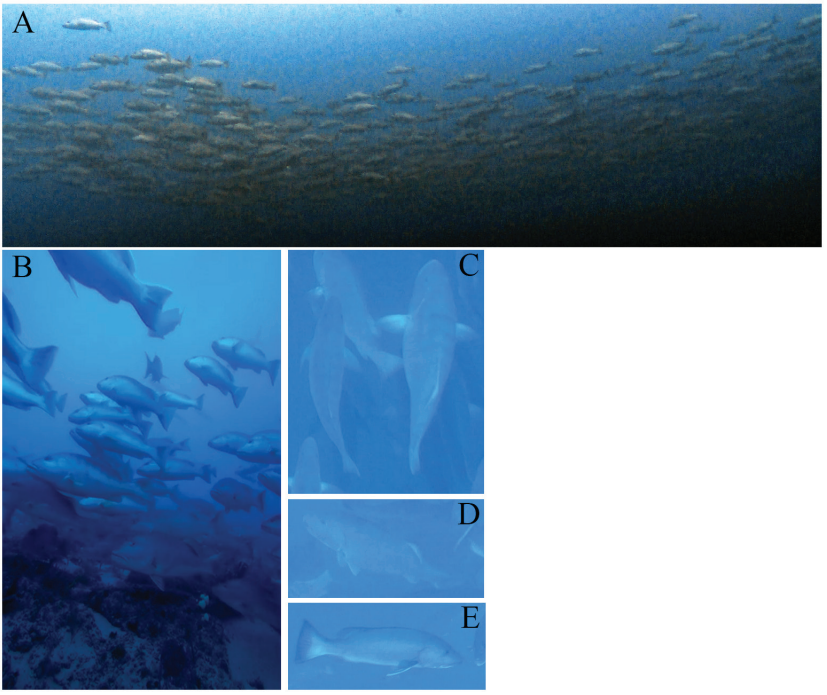

Figure 5. Cubera snapper (*Lutjanus cyanopterus*) aggregation at Riley's Hump seen in overview consisting of (A) 376 individuals and (B) detail of aggregation. (C) Female cubera snapper illustrating distended abdomen (on right) associated with hydrated oocytes, (D) side view of another female cubera snapper with distended abdomen for comparison with (E) a cubera snapper where the distended abdomen is not observed. Photo credits: (A) Jean Anne Booth/Spree Expeditions, (B) FWC, (C–E) Paul Barbera/FWC.

snapper in aggregation were made near the day of the full moon and up to five days following or prior to the full moon. However, in 2012 and 2020 we observed cubera snapper aggregations two to three days following the third quarter moon (9-10 days following the full moon, Fig. 6). Additionally, although most of our observations of cubera snapper aggregations were targeted for the late afternoon, we also specifically visited the site during morning hours on five occasions to determine if aggregations were limited to afternoon periods. These morning observations confirmed that aggregations could be observed at this time as well (Table 2).

A variety of predatory fish species were regularly associated with the cubera snapper aggregation site. These included species that were seen high in the water column over the site as well as at depth intermingling with the cubera snapper aggregation and included at least 24 species of apex predators (e.g., Carangidae, Carcharhinidae, Epinephelidae, Table 3). A number of these predators were found associated with the highly rugose benthos (Fig. 7) in the vicinity of the aggregation.

Discussion

The protection of fish spawning aggregations can provide disproportionate benefits to fisheries conservation and management via discrete protection of a large number of individuals of a population that typically lead more solitary lives, during a life-history

Table 2. Details of diver/baited remote underwater video (BRUV)/remotely operated vehicle (ROV) deployments from Riley's Hump, 2011–2020. * in MaxN column indicates additional explanatory information available in the Notes column.

Date	Dive site	Time (EST)	MaxN of cubera snapper observed	Observation type	Full moon	Days before (–) or past (+) full moon	Notes
21 Mar, 2011	8	15:38	24*	Rebreather divers	19 Mar, 2011	+2	Divers estimated 500 cubera snapper and also observed 8 Caribbean reef sharks, 15 scamp grouper, 8 black grouper
12 Jul, 2012	9	14:45	376	Rebreather divers	03 Jul, 2012	+9	- - -
13 Jul, 2012	9	13:00	110	Rebreather divers	03 Jul, 2012	+10	- - -
02 Aug, 2012	11	9:17	200	ROV - Seabotix	01 Aug, 2012	+1	- - -
03 Aug, 2012	12	9:26	35	Drop Camera	01 Aug, 2012	+2	- - -
03 Aug, 2012	12	14:23	40	Drift diver surveys	01 Aug, 2012	+2	- - -
23 Jul, 2013	2	16:54	94	Drift diver surveys	22 Jul, 2013	+1	- - -
25 Jul, 2013	1	15:37	41	Drift diver surveys	22 Jul, 2013	+3	- - -
25 Jul, 2013	5	16:05	63	Drift diver surveys	22 Jul, 2013	+3	- - -
25 Jul, 2013	1	16:38	73	Drift diver surveys	22 Jul, 2013	+3	- - -
26 Jul, 2013	7	14:08	102	Drift diver surveys	22 Jul, 2013	+4	- - -
26 Jul, 2013	2	15:42	53	Drift diver surveys	22 Jul, 2013	+4	- - -
27 Jul, 2013	2	8:13	89	Drift diver surveys	22 Jul, 2013	+5	- - -
27 Jul, 2013	6	9:21	68	Drift diver surveys	22 Jul, 2013	+5	- - -
02 Jul, 2015	13	17:30	*	Drift diver surveys	02 Jul, 2015	0	Cubera snapper seen in aggregation, along with bull and sandbar sharks, but strong current precluded dive operations
03 Jul, 2015	10	16:50	*	Drift diver surveys	02 Jul, 2015	+1	Cubera snapper seen in aggregation, along with multiple sharks including sandbar shark, but no video or photos were successfully captured for analysis
04 Jul, 2015	7	14:30	53	Drift diver surveys	02 Jul, 2015	+2	- - -
04 Jul, 2015	7	19:03	23	Drift diver surveys	02 Jul, 2015	+2	- - -
05 Jul, 2015	2	17:44	25	Drift diver surveys	02 Jul, 2015	+3	- - -
05 Jul, 2015	2	18:48	97	Drift diver surveys	02 Jul, 2015	+3	- - -
06 Jul, 2015	2	14:27	74*	Drift diver surveys	02 Jul, 2015	+4	Divers observed ~300 cubera snapper in tight school
06 Jul, 2015	2	18:51	135	Drift diver surveys	02 Jul, 2015	+4	- - -
06 Jul, 2015	2	19:21	144	Drift diver surveys	02 Jul, 2015	+4	- - -
18 Aug, 2016	3	18:20	19	BRUV	18 Aug, 2016	0	- - -
20 Aug, 2016	4	19:37	150	BRUV	18 Aug, 2016	+2	- - -
03 Aug, 2017	28	9:03	19	UNCW ROV Mohawk 18	07 Aug, 2017	-4	ROV video track along length of ledge feature suggests most complex benthic topography occurs near primary aggregation site
11 Sep, 2020	29	15:13	16	UNCW ROV Mohawk 18	02 Sep, 2020	+9	- - -

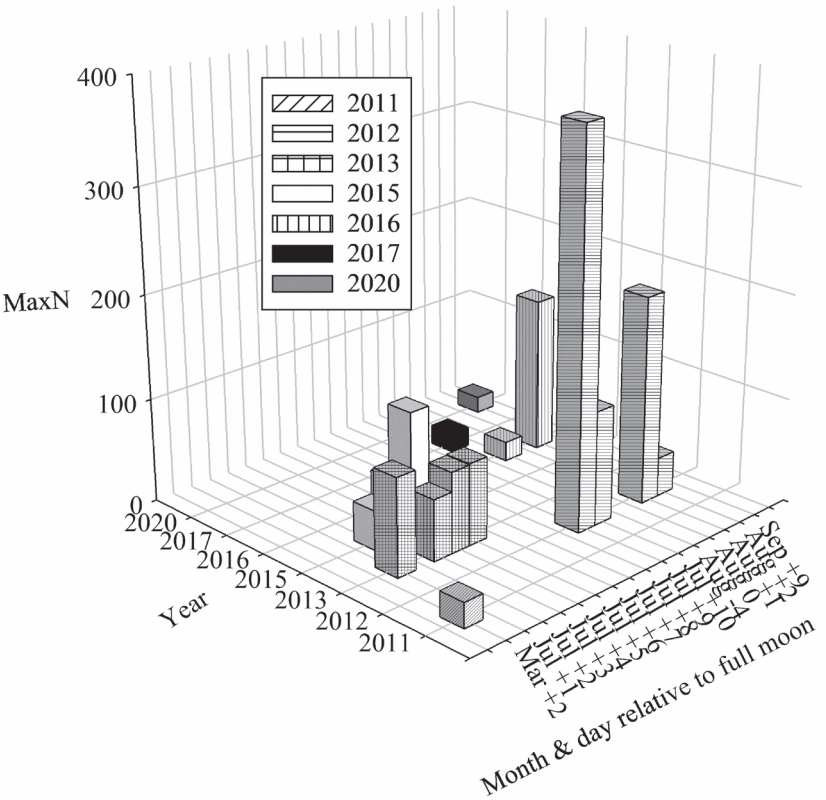

Figure 6. Relative abundance (MaxN, *z*-axis) of cubera snapper at Riley's Hump from 2011 to 2020. *X*-axis shows different months as well as days before (–) or following (+) the full moon. Once in 2012 and on three occasions in 2013 and 2015, repeat visits were made on the same days and MaxN for these instances are averages.

stage that is highly vulnerable to overexploitation, yet critical to the maintenance of population health (Erisman et al. 2015, Sadovy de Mitcheson et al. 2020). Given the finite resources available for conservation and management, locations that are the sites of spawning aggregations for multiple species are particularly important as local hotspots of productivity and biodiversity (Myers et al. 2000, Erisman et al. 2015, Wagner et al. 2020). Spawning aggregations can convey local and downstream ecological benefits through the regular, repeated release of massive quantities of energy-rich gametes, and with the attraction of planktivores, megaplanktivores, and apex predators, distributing nutrients to pelagic and benthic ecosystems across numerous trophic levels (Nemeth 2012, Erisman et al. 2015, Fuiman et al. 2015, Grüss et al. 2018). Yet spawning aggregations can be dynamic and ephemeral and often occur in locations with frequently changing abiotic and biotic conditions, making study of aggregations difficult and requiring years of research with a variety of methods to effectively characterize such factors as spawning site locations, timing of spawning, peak spawning activity, and approximate sizes of spawning aggregations (Sadovy de Mitcheson et al. 2020).

At Riley's Hump in the remote Tortugas South Conservation Area, we encountered these logistical challenges over the years and often between consecutive days. In

Table 3. Species associated with the cubera snapper aggregation as determined from diver/baited remote underwater video (BRUV)/remotely operated vehicle (ROV) deployments at Riley's Hump from 2011 to 2020.

Genus species	Common name	Location observed	Notes
Carangidae			
Alectis ciliaris	African pompano	Water column	Solitary or groups <3 fish
Caranx bartholomaei	Yellow jack	Water column	Large schools (multiple hundreds of fish)
Caranx crysos	Blue runner	Water column	Large schools
Caranx latus	Horse eye jack	Water column + benthos	Large schools
Caranx hippos	Crevalle jack	Water column	Small schools (10–30 fish)
Elagatis bipinnulata	Rainbow runner	Water column	Large schools
Seriola dumerili	Greater amberjack	Water column + benthos	Medium schools (<100 fish)
Seriola rivoliana	Almaco jack	Water column + benthos	Medium schools (<100 fish)
Carcharhinidae			
Carcharhinus falciformis	Silky shark	Water column	Solitary or groups <3 fish
Carcharhinus leucas	Bull shark	Water column + benthos	Solitary or groups <3 fish
Carcharhinus perezi	Reef shark	Water column + benthos	Solitary or groups <10 fish
Carcharhinus plumbeus	Sandbar shark	Water column + benthos	Solitary or groups <3 fish
Negaprion brevirostris	Lemon shark	Water column + benthos	Solitary or groups <3 fish
Sphyrnidae			
Sphyrna mokarran	Great hammerhead shark	Water column	Solitary
Scombridae			
Euthynnus alletteratus	Little tunny	Water column	Large schools
Sphyraenidae			
Sphyraena barracuda	Great barracuda	Water column + benthos	Solitary or small schools
Epinephelidae			
Epinephelus itajara	Goliath grouper	Benthos	Solitary or groups <3 fish
Epinephelus morio	Red grouper	Benthos	Solitary or groups <3 fish
Mycteroperca bonaci	Black grouper	Benthos	Solitary or groups <5 fish
Mycteroperca interstitialis	Yellowmouth grouper	Benthos	Adults solitary, groups of <5; or as juveniles in groups of <3
Mycteroperca phenax	Scamp	Water column + benthos	Adults solitary, or in groups (20–30 individuals); juveniles solitary or groups of <10
Lutjanidae			
Lutjanus analis	Mutton snapper	Benthos	Solitary or groups <5 fish
Lutjanus buccanella	Blackfin snapper	Benthos	Juveniles; Small schools of 20–30 fish
Lutjanus jocu	Dog snapper	Benthos	Solitary or groups <5 fish

some cases underwater visibility or strong currents at the study site prevented us from safely conducting operations. In other cases underwater conditions allowed for field operations but we were unable to locate cubera snapper at a particular day's initial chosen dive site. Cubera snapper and other transient spawning species are known to utilize a larger staging area in preparation for spawning together with a discrete spawning site location, as well as multiple spatially distinct spawning sites among years within a larger but consistent spawning staging area (Heyman et al. 2005, Kadison et al. 2006, Nemeth 2012, Biggs and Nemeth 2016). This geospatial variability can make it challenging to locate spawning aggregation sites but in this study we often overcame this logistical challenge with our paired echosounder-diver deployments. Echosounder surveys were used first to locate elevated biomass and subsequent diver surveys reported species composition. By utilizing a variety of different methods, collaborative multi-agency partnerships, and repeated visits to

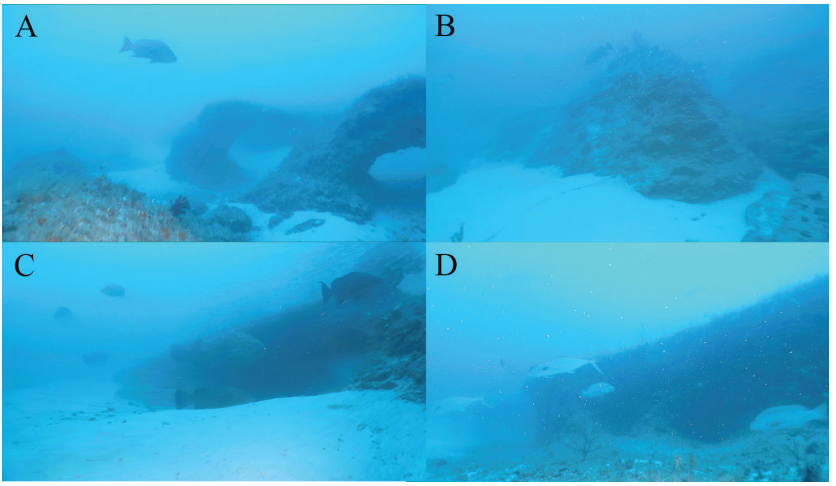

Figure 7. Representative habitats of the cubera snapper (*Lutjanus cyanopterus*) aggregation grounds at Riley's Hump. (A, C) Note the high relief, rugose reef features interspersed with sand, including extensive undercuts. (B) An adult yellowmouth grouper (*Mycteroperca interstitialis*) provides scale for the coral mound, while (C) two goliath grouper (*Epinephelus itajara*) provide scale for the undercut feature. Also in C clockwise from center left are an almaco jack (*Seriola rivoliana*), scamp grouper (*Mycteroperca phenax*), goliath grouper, scamp, black grouper (*Mycteroperca bonaci*), goliath, and black grouper. (D) Two greater amberjack (*Seriola dumerili*), two cubera snapper, a scamp grouper, and an unidentified shark (Carcharhinidae) are visible. ROV video taken along the entire feature suggests that the most complex topography is located near the primary aggregation site. Photo credits: NOAA.

the aggregation site, we were able to gather indirect (echosounder) and direct (divers, ROV) evidence of significant biomass that persists across multiple months and years, from spring through fall, at the cubera snapper aggregation site. The persistent biomass present at Riley's Hump during known cubera spawning months suggests that this location is currently a significant, and likely spawning aggregation site for this species. We completed fishery echosounder surveys over seven years (encompassed within a span of ten years) and obtained paired diver or ROV confirmation of species composition for five of these events. Those species (e.g., *L. cyanopterus*, *E. itajara*, *M. bonaci*, *M. phenax*, *S. dumerili*, *S. rivoliana*, *C. perezi*) observed at the site during our initial visit in 2011 with rebreather divers generally persisted across our study period, were present during repeated visits across the study period, and were also observed with ROV in 2020. These observations provide further indirect evidence (see below) that the current management designation of Riley's Hump, a historically depleted multispecies spawning aggregation site protected as a no-take zone, has been successful at maintaining a healthy ecosystem, characterized by snapper, grouper, and other species undertaking critical spawning activities, and higher trophic level species associated with this location and the activities and habitats that occur there.

While we did not directly observe spawning by *L. cyanopterus* in our study, we did observe two conditions that are accepted for concluding that an aggregation is assembled for spawning (Domeier and Colin 1997, Colin et al. 2003): 1) a >3-fold increase in density over densities typically observed for the species; 2) direct or indirect evidence of spawning. Whereas previous literature characterizes cubera snapper as generally solitary reef dwellers (Allen 1985, Boomhower et al. 2010), we observed repeated aggregations of cubera snapper that were estimated with MaxN

to contain a range from 16 to 376 fish from a single frame of video (Fig. 5A), and up to 500 individuals estimated by divers in situ, demonstrating marked increases in density (>>3-fold) over those typically observed. The second criterion deemed acceptable for confirmation of spawning was indirect and included two observations: behaviors and color patterns associated with reproduction, and females with swollen abdomens indicative of hydrated oocytes (Domeier and Colin 1997, Colin et al. 2003). For cubera snapper at Riley's Hump, this indirect evidence includes our observations of behaviors and color phases previously identified with courtship (Heyman et al. 2005): dark color morphs (males) pursuing light color morph (female) fish with visibly distended abdomens (Fig. 5C–E). Direct confirmation of spawning for the cubera snapper aggregation remains to be obtained. This can consist of direct observations of spawning including gamete release, or collections of females with either hydrated oocytes, or with the presence of post-ovulatory follicles in the ovaries (Domeier and Colin 1997, Colin et al. 2003).

Additional aspects of our study suggest the aggregation of cubera snapper is assembled for spawning. We observed cubera snapper aggregating during March through September, months of the year that cubera snapper have been confirmed to spawn in Belize and the Caribbean (Heyman et al. 2005, Kadison et al. 2006, Boomhower et al. 2010) and are believed to spawn (based on abundant catches of fish with running ripe or enlarged gonads) at Riley's Hump (Lindeman et al. 2000) and Cuba (Claro and Lindeman 2000). We observed the cubera snapper aggregations from four days prior to the full moon and up to ten days following the full moon, and this aggregation timing associated with the full moon is consistent with confirmed or suspected (as above) spawning aggregations in the Northern Hemisphere (Domeier and Colin 1997, Claro and Lindeman 2000, Lindeman et al. 2000, Heyman et al. 2005, Kadison et al. 2006, Boomhower et al. 2010, Biggs and Nemeth 2016). We observed cubera snapper in smaller numbers utilizing a larger area together with discrete locations of larger aggregations, consistent with previous studies that reported larger staging areas with discrete spawning site locations (Heyman et al. 2005, Kadison et al. 2006, Nemeth 2012, Biggs and Nemeth 2016). The location and morphology of the feature we believe to be the primary spawning site shares physical similarities with other fish spawning aggregation sites in the wider Caribbean. The main cubera snapper aggregation site at Riley's Hump is found in approximately 54 m depth and represents the highest relief portion of a ledge that rises 9-m from the base substrate, superficially resembles an "elbow" with an approximately 150-degree angle, and imagery of the benthos reveals highly rugose features visibly scoured by currents, with deeper habitats adjacent to the primary spawning site. In the wider Caribbean fish spawning aggregations are known to occur at distinctive bathymetric features, with fishes in the snapper grouper complex tending to form multi-species aggregations in 20–60 m depth close to the inflection point (i.e., promontories) along the edges of convex, steep shelf-edge dropoffs adjacent to relatively deep water (Kobara and Heyman 2010, Kobara et al. 2013, Chollett et al. 2020). Our cubera snapper observations also included additional species such as dog snapper that are known to aggregate for spawning together with cubera snapper, the two species using similar locations and peak spawning times (Heyman et al. 2001, Paris et al. 2005). Although certain species of snapper such as the yellowtail snapper (*Ocyurus chrysurus*) are known to form large aggregations for feeding, cubera snapper do not exhibit this feeding behavior. Finally, the regular presence of a variety of species

of sharks, including species (bull, lemon, white) known to congregate around prey aggregation sites (Graham and Castellanos 2012, Pickard et al. 2016, Feeley et al. 2018, Schilds et al. 2019) is consistent with other long-established spawning aggregations that are visited by large predators attracted by and attempting to feed on aggregating fishes (Heyman and Kjerfve 2008, Nemeth et al. 2010, Graham and Castellanos 2012, Erisman et al. 2015, Mourier et al. 2016, Pickard et al. 2016, Schilds et al. 2019).

Echosounders are a useful remote sensing tool to quickly survey and capture the distribution and relative abundance of fish in the water column. For densely aggregated, but sparsely distributed groups of fish, the echosounder can enhance the detection and location of a targeted group over very large areas. When coupled with direct visual observations, echosounder surveys can provide estimates of species-specific density and abundance (Fernandes et al. 2016, Scoulding et al. 2023). Detailed patterns of aggregation size, shape and proximity to seabed features can be captured and visualized in maps and 3D models (Taylor et al. 2006, Taylor and Ebert 2012, Egerton et al. 2017). Our repeated surveys over a range of time scales documented apparent shifts in the position of the highest relative densities over a day and night, across season and years; however, the highest densities were still within 0.3 km from the point of the elbow. The relative densities could be composed of a number of large-bodied aggregating and schooling species that were observed by divers such as schooling jacks and the cubera snapper. The echosounder likely also encountered large schools of smaller bodied fishes associated with the benthic habitats, but the acoustic response for these smaller fishes would contribute proportionally lower relative backscatter compared to the large-bodied fishes.

As the largest western Atlantic snapper, cubera snapper are classified by the International Union for the Conservation of Nature (IUCN) Red List as Vulnerable with a decreasing population trend primarily due to the intensive fishing of spawning aggregations, with United States Atlantic catches declining by 60% in the last 20 years, and the spawning potential ratio in the Florida Keys estimated at 5% of total (Lindeman et al. 2016). Further declines are believed possible based on continued targeting of spawning aggregations unless protective measures are established and enforced (Lindeman et al. 2016). In the Gulf of Mexico, the cubera snapper population was classified as Data Deficient with decreasing population trend, indicating that monitoring of the abundance of this species and the status of spawning aggregations is needed to better estimate population trends and regional extinction risk (Lindeman et al. 2016). In the United States, fishery management is robust with comprehensive research and stock assessment programs; the United States has one of the highest management budgets per landed tonnage of wild-capture fisheries, estimates annual catch limits for the vast majority of fishes in United States federal fisheries management plans, and has established accountability measures that are triggered when recorded annual harvest exceeds annual catch limits (Methot et al. 2014, Melnychuk et al. 2023). Although Data Deficient, United States fishery management should be poised to respond to future concerns of cubera snapper population status. Future studies of the cubera snapper aggregation at Riley's Hump should directly confirm spawning activity with either observations of spawning, or collections of females from the aggregation with hydrated oocytes; verify the temporal persistence of the main aggregation site, better characterize the spatial extent of the staging area, and determine if additional locations (outside the main aggregation site) within the staging area continue to be active-acoustic tagging of cubera snapper could

help address these questions. Although we observed cubera snapper aggregations across a ten-year time span, the opportunistic nature of the study meant that we usually targeted summer months (typically July) around the full moon. The full moon corresponds with peak cubera snapper spawning aggregations in the Northern Hemisphere (*see above*) but studies of cubera snapper in the Southern Hemisphere have reported spawning aggregations associated with the new as well as full moon (Malafaia et al. 2021, Motta et al. 2022). Future work with cubera snapper at Riley's Hump might determine if aggregation behavior is restricted to the full moon or if cubera snapper also aggregate with the new moon, which could have future implications for managers interested in refining spawning season closures. Sufficient enforcement of management regulations and effective monitoring programs are key components in the conservation of fish spawning aggregations (Colin et al. 2003, Heyman et al. 2004, Erisman et al. 2015). The remote location of many spawning aggregation sites (including Riley's Hump) makes both monitoring and enforcement challenging, but the development of advanced technologies such as remote time lapse video and automated image analysis/machine learning may make the coordination of these activities more feasible and cost effective by alleviating the need for site visits to exclusively involve extensive diving operations. Simple camera deployments and retrievals can be supplemented with more extensive operations targeted around peak spawning periods (Sadovy de Mitcheson et al. 2020, Prior et al. 2023, Saulnier et al. 2025).

Today's coral reef ecosystems are in global decline and face a multitude of local threats including overfishing, pollution, and destructive fishing practices, compounded by the overarching impacts of global environmental change (Eddy et al. 2021, Culhane et al. 2024, Mello et al. 2025). Major impacts of global environmental change such as warming ocean temperatures (including marine heatwaves), ocean acidification, and coral bleaching, which can lead to coral disease and death, arguably represent the most significant threats to coral reefs and their inhabitants in the modern era (Hughes et al. 2017, Knowlton et al. 2021, Mills et al. 2023). In the past 50 years, the human population has doubled (IPBES 2019) and monitored wildlife populations have declined by 73% (WWF 2024). In marine ecosystems, overexploitation is the leading cause of biodiversity loss (IPBES 2019) and a recent evaluation of the Gulf of Mexico at the large marine ecosystem scale determined it to be experiencing ecosystem overfishing (Link 2021). The recovering multispecies spawning aggregation sites associated with Riley's Hump are located upstream from the main Florida Keys reef tract, and oceanographic conditions in the area have been shown to facilitate the retention and transport of larvae released from the Tortugas region to the Florida Keys, as well as to both the southeast and (to a lesser extent) west coasts of Florida (Lee et al. 1994, Domeier 2004, Bryan et al. 2015). As such, the spawning aggregations at Riley's Hump may contribute to the resilience of the regional coral reef ecosystem and recently (Jan 2025), the entire western boundary of the Tortugas South Conservation Area was proposed to be expanded by one mile, in part to capture the spawning aggregation sites and important deep reef habitats described here (Florida Keys National Marine Sanctuary 2025). The multispecies spawning aggregations and deep reef habitats of Riley's Hump, regularly visited by numerous species of apex predators, and including observations of bull, great hammerhead, and white sharks (this study, Feeley et al. 2018), can also be used as an indicator of ecosystem health and may serve as a baseline to assess the status of

marine ecosystem health in other areas of Florida and the Gulf of Mexico (Sadovy and Domeier 2005, Erisman et al. 2015). If sufficient and continued enforcement is available to protect the multispecies spawning aggregations of Riley's Hump, this important site might serve as a conservation "bright spot" (Cinner et al. 2016, Pittman and Heyman 2020) and regional monitoring network for fish populations in the greater Florida region.

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