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Title: Five decades of reef observations illuminate deep-water grouper hotspots

Running Head: Grouper hotspots

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Abstract:

Fish often aggregate to spawn, feed, rest, or avoid predation. Direct observations of very high counts of large-bodied grouper on deep shipwrecks, however, do not fit into typical descriptions of spawning-, resource-, or predation-driven aggregations. To investigate whether these observations are rare or part of an underlying pattern, we synthesized five decades (1969 - 2019) of direct observations of groupers on deep-water (50 - 300 m) habitats along the southeastern United States (Cape Hatteras, NC to Cape Canaveral, FL). The direct observations, which included 439 remotely-operated vehicle transects, 235 human-occupied vehicle transects, and 881 hook-and-line drops, revealed six hotspots of deep-water groupers on three shipwrecks, two artificial reefs, and one boulder field. Grouper counts at these hotspots (0.10 - 5.40 grouper per linear m surveyed) exceeded counts of grouper outside of hotspots (<0.01 - 0.02 grouper per linear m surveyed) by multiple orders of magnitude. Commonalities among the sites with grouper hotspots included that all are relatively isolated structures surrounded by unconsolidated sediments and located in shelf-edge to upper-slope depths. Thus, it appears that these isolated habitats, despite their small spatial footprint, represent a disproportionate abundance of deep-water groupers. Future research efforts should determine how groupers derive sufficient resources from, and thus co-occur on, these small habitats and how these aggregations relate to the large-scale dynamics of these populations.

Keywords: Aggregation; deep reefs; deep-water fish; isolated habitat; rocky reef; shipwreck

1. Introduction

Understanding why species form groups in certain habitats or at certain times is a fundamental goal of ecology (Allee, 1927; Wilson, 1975). In marine environments, fish aggregations are often associated with spawning activity, prey exploitation, or resting, as well as school formation for feeding or predation avoidance. Fish spawning aggregations are defined as concentrations (i.e., at least four times the density or abundance of fish outside the gathering) of conspecifics that occur repeatedly and predictably in time and space and result in a mass reproductive event (Michael L. Domeier, 2012). Prominent spawning aggregations with abundances often numbering in the thousands include normally solitary Nassau grouper (*Epinephelus striatus,* Serranidae) (Smith, 1972; Waterhouse et al., 2020; Whaylen et al., 2007), as well as mutton snapper (*Lutjanus analis,* Lutjanidae) (Burton, Brennan, Muñoz, & Parker, 2005; Graham, Carcamo, Rhodes, Roberts, & Requena, 2007) and other species across diverse taxa (Claydon, 2004; Michael L. Domeier, 2012), which repeatedly spawn *en masse* at predictable times and places.

Fishes also aggregate to take advantage of high prey densities or to seek refuge around habitats that provide access to food resources and shelter from predation. For example, fishes such as albacore and skipjack tuna (*Thunnus alalunga,* Scombridae*; Katsuwonus pelamis,* Scombridae; (Fielder & Bernard, 1987)) and whale sharks (*Rhincodon typus,* Rhincodontidae*;* (Heyman, Graham, Kjerfve, & Johannes, 2001; Hoffmayer, Franks, Driggers, Oswald, & Quattro, 2007)) aggregate to exploit food resources. While some aggregations occur in open water, aggregations for shelter and food often occur in habitats with an abundance of these resources, such as seamounts where complex topography interacts with water flow creating biologically productive, prey-rich waters (Clark et al., 2010) or coral reefs that not only provide shelter but also concentrated food resources (Demartini & Anderson, 2007; Hamner, Jones, Carleton, Hauri, & Williams, 1988; Sandin & Pacala, 2005). Some fish species commonly move in schools, which are thought to increase swimming efficiency (Hemelrijk, Reid, Hildenbrandt, & Padding, 2015), decrease predation risk (Parrish, 1989; Parrish & Edelstein-Keshet, 1999) and increase per capita food consumption (Major, 1978). Others, such as grunts (Haemulidae), often shelter during resting periods in crevices or undercuts of reefs in large groups, or shoals, which likely provide refuge from predation and increased energetic efficiency (Helfman, Collette, Facey, & Bowen, 2009; Helfman & Schultz, 1984; Ogden & Ehrlich, 1977).

Aggregations of typically non-schooling fish species outside of spawning events and around habitats that do not appear to offer extensive prey or shelter are rarely reported. Direct observations of very high counts of large-bodied groupers, such as snowy grouper (*Hyporthodus niveatus,* Serranidae) and Warsaw grouper (*H. nigritus,* Serranidae) (Figure 1) (Johnson et al., 2020) residing on deep, small, and isolated shipwrecks, seem to contradict the notion that aggregations outside of spawning events and away from habitats with prey and shelter are rare. Snowy and Warsaw grouper are generally not believed to be schooling fishes nor are they known to form spawning aggregations (Coleman, Koenig, Eklund, & Grimes, 1999; Farmer et al., 2017; Farmer & Karnauskas, 2013; Kolmos, Wyanski, White, & Mikell, 2019; Sadovy, 1990; Sedberry, Pashuk, Wyanski, Stephen, & Weinbach, 2006). We investigated whether observations of high grouper counts on deep reefs were rare, predictable, or common (but previously overlooked) by reviewing count data of typically non-schooling deep-water groupers that showed no evidence of spawning.

Our objective was to synthesize direct observations of large-bodied groupers on deep artificial and natural southeastern US Atlantic (hereafter SEUS) reefs. Specifically, we asked: 1) Where have aggregations of large-bodied deep-water groupers been observed on reef habitats in the SEUS?, 2) How do grouper counts at "aggregation reefs" compare to counts observed elsewhere in the SEUS?, 3) What characteristics are unique about the reefs where high counts of deep-water groupers occur?, and 4) Is there scientific literature suggesting the existence of aggregations beyond those identified in our direct observations?

2. Synthesizing five decades of observational data

We convened a group of subject matter experts who had directly collected or had access to relevant SEUS data that were collected over five decades (1969-2019). We established criteria for which data should be included in the synthesis based on survey method, species, reef depth, and reef type. We included data from visual surveys using human-occupied vehicle (HOV) transects and remotely-operated vehicle (ROV) transects that allowed grouper identification to genus or species. Transect widths were likely similar across ROV and HOV transects because both types of vehicles carried similar video cameras so collected data in comparable fields of view. Transect length often differed by survey or site, so we standardized resulting fish counts per linear m of transect length. We also included hook-and-line data, even though these data are not directly comparable to transect-type data, because hook-and-line data provided additional information on sites with and without high grouper catches. We excluded data, such as those collected by fishery echosounders, for which we were not able to identify fish to fine taxonomic levels. We also excluded fish trap and stationary or bottom-lander video data since these observations cannot be directly compared to density metrics from transect-type data. Given that the initial observations (Johnson et al., 2020) were of high counts of large-bodied groupers in deep habitats, we focused on grouper species within the genera *Epinephelus, Hyporthodus,* and *Mycteroperca,* all within the family Serranidae (Fricke, Eschmeyer, & Van der Laan, 2020). We included observations from structured habitats, including natural rocky reefs, artificial reefs, and shipwrecks, on the shelf edge and upper slope between 50 and 300 m deep off the SEUS states (Cape Hatteras, North Carolina (NC) to Cape Canaveral, Florida (FL)).

3. Reefs with grouper hotspots

Our synthesis group reviewed 439 ROV transects, 235 HOV transects, and 881 hook-and-line drops (Figure 2; Table 1; Data S1) to determine where aggregations of large-bodied, deep-water groupers had been observed. From these data, we identified six reef sites that we categorized as hosting grouper aggregations (Figure 2). Our use of the term "aggregation" to describe a group of conspecifics gathered in counts higher than those of a mating pair or family (e.g., social unit) (Wilson, 1975) or higher counts than observed elsewhere implies that these reefs host high grouper counts and does not imply the reason for these gatherings (e.g., spawning, resources). Further, our use of the term 'aggregation' is distinct from the use of the term related to whether artificial reefs aggregate or produce fish biomass (Bohnsack, 1989; Layman, Allgeier, & Montaña, 2016). Because grouper counts on the six identified aggregation reefs were very high, especially in comparison to other nearby structured habitats, we also use the term "hotspot" to describe the reefs with aggregations. Our use of the term "hotspot" refers to reefs with high counts typical of aggregations, rather than high biodiversity (Stuart-Smith et al., 2013). Here, we provide narrative details and quantitative summaries of grouper aggregations observed on the six hotspots.

3.1. Snowy Wreck

The "Snowy Wreck" is an unidentified metal hulled shipwreck (likely a coastal cargo carrier) about 100 m long (based on 2011 multibeam survey, S.W. Ross, unpublished data) lying off Cape Fear, NC on coarse sand bottom (Figure 2). The base of the wreck, some of which is buried, is about 255 m deep. The upper structure of the wreck rises to at least 241 m, and a cargo derrick rises vertically from the wreck to at least 235 m. Strong currents continually sweep the wreck making ROV surveys difficult; in general only the down current side of the wreck could be viewed during ROV dives. The wreck was heavily fished, mostly for snowy groupers (hence the name), until 2009 after which fishing was prohibited as part of the "Snowy Grouper Wreck Marine Protected Area" (SAFMC, 2020).

The first visual survey of the Snowy Wreck using an ROV occurred on 24 August 2004 (Quattrini & Ross, 2006). Due to weather and currents, only part of the wreck could be covered by one 30 min ROV video transect, estimated to be 60 m long, which ranged along the south side of its upper deck and hull and along the sand-wreck interface. During this transect, 0.72 snowy grouper, mostly large juveniles or small adults (ca. <90 cm TL), per linear m surveyed, hereafter "grouper per m," (43 individual snowy grouper / 60 m transect) were counted (Figure 3). These fish were scattered over the whole of the wreck area surveyed. No other grouper species were observed.

The Snowy Wreck was observed again with ROV transects on 13 July 2012, 15 June 2016, and 31 October 2017 after fishing was prohibited. During these surveys, the ROV traversed lengthwise along the north side of the shipwreck, including the upper decks, middle hull, sand-wreck interface, and vertical derrick. The surveys revealed huge aggregations of large adult (many > 1 m TL) snowy grouper packed into the wreck structure, hovering along the derrick and swimming over the wreck and a short distance out into the adjacent sand (Figure 1B). These fish were so dense that individuals had to be counted at separate parts of the wreck to reduce double counting. In 2012, 2.40 snowy grouper per m (240 individual snowy grouper / 100 m transect) were observed (Figure 3). During the 2016 survey, 5.40 snowy grouper per m (540 individual snowy grouper / 100 m transect) were observed (Figure 3). Two yellowedge grouper (*H. flavolimbatus,* Serranidae) were also encountered during the 2016 survey. During the most recent survey on 31 October 2017 (S.W. Ross and R. Mather, unpublished data), the grouper were both so dense and moving so quickly it was necessary to subdivide the collected data into nine horizontal transects, ranging from 6 m to 30 m long, and two vertical transects of 4 m and 8.9 m. Across these eleven transects, a mean of 3.7 snowy grouper per m were enumerated (Figure 3). More specifically, the horizontal transects resulted in 1.0 to 8.2 (mean 3.4 fish per m) snowy grouper per m, and the two vertical transects yielded 3.1 to 7.7 snowy grouper per m. In three places where the volume of water could be estimated and where grouper were hovering in place, grouper densities were 1.5, 1.6, and 1.8 fish per m^3 (e.g., Figure 1B). In addition to snowy grouper, one each large yellowedge grouper and Warsaw grouper were observed on the wreck in 2017.

On three dates (13 June 2017, 5 August, 2018, and 1 August 2019), hook-and-line sampling was conducted at the Snowy Wreck. Fishing was performed using high-low bottom rigs with size-8/0 J-hooks baited with cut Atlantic Menhaden (*Brevoortia tyrannus,* Clupeidae) and shortfin squid *Illex* sp. Out of seven total drops of a two-hook rig, nine snowy grouper were caught (catch per unit effort = 1.3 fish/drop; range 650-1020 mm TL).

3.2. Underwater Battlefield (U-*576*, SS *Bluefields*)

On 24-26 and 28 August 2016, HOVs collected video of fish communities on two deep shipwrecks (Johnson et al., 2020). The two World War II era shipwrecks, the U-*576* and the SS *Bluefields*, sank in 1942 and rest 241 m from each other off NC (Figure 2). The German submarine U-*576* rests in slightly shallower water (210 m) than the Nicaraguan freighter SS *Bluefields* (245 m). The HOVs traversed lengthwise along each shipwreck collecting video along transects illuminated by continuous lighting that allowed for species identification.

Across four transects along the 67-m long U-*576*, we observed between 0.46 grouper per m (31 individuals / 67 m transect) and 0.75 grouper per m (50 individuals / 67 m transect; Figure 4). The grouper species observed on the U-*576* shipwreck consisted of snowy grouper and Warsaw grouper (Figure 1A), as well as several grouper that we could not positively identify. On the nearby and larger (76 m long) shipwreck SS *Bluefields,* between 0.17 grouper per m (13 individuals / 76 m transect) and 0.68 grouper per m (52 individuals / 76 m transect) were observed per transect (Figure 4). Similarly to the U-*576,* the species present on the SS *Bluefields* were snowy grouper and Warsaw grouper with the addition of yellowedge grouper.

3.3. Intentionally-Sunk Barges (Shallow Barge, Deep Barge)

In April 2014, two barges were sunk approximately 7.2 km away from each other inside an area designated as the Charleston Deep Artificial Reef MPA off South Carolina (Figure 2). Prior to deployment of the barges, this area was devoid of hard bottom. For simplicity, we have named these barges the “shallow barge” and the “deep barge” since they were sunk in 85 and 100 m of water, respectively. Both barges were surveyed with a ROV on 13 June 2016, 26 June 2017, and 16 May 2018. The ROV traversed lengthwise along each barge in a single transect each year to collect video data of fish communities. Both barges are approximately 80 m in length, but the total distance traversed was 116 m on the shallow barge and 138 m on the deep barge. Additional structures, such as convex containers, were attached to the barges when they were deployed to create a more complex fish habitat. Some of these structures became detached from the barges upon landing on the seafloor which accounts for the additional distance traversed by the ROV.

On the shallow barge, we observed a maximum of 0.18 grouper per m (21 individuals / 116 m transect) and a minimum of 0.10 grouper per m (12 individuals / 116 m transect; Figure 5) across all three surveyed years. The grouper species observed on the shallow barge consisted of scamp (*Mycteroperca phenax*), yellowedge grouper, gag (*M. microlepis,* Serranidae), and snowy grouper. There were also a few grouper that could not be positively identified to species. On the deep barge, a maximum of 0.36 grouper per m (49 individuals / 138 m transect) and minimum of 0.14 grouper per m (20 individuals / 138 m transect) were encountered across the three years (Figure 5). The grouper species present on the deep barge were yellowedge grouper, misty grouper (*H. mystacinus,* Serranidae), Warsaw grouper, snowy grouper, scamp, and gag.

3.4. Snowy Hole

During August and September 1979, HOV surveys were conducted at 13 natural reef sites off NC (Parker & Ross, 1986). These authors reported fish abundance as numbers per hectare, which may overestimate counts; therefore, the raw data from the 10 deeper stations (≥ 50 m) that met our inclusion depth criteria were reexamined. The one grouper aggregation observed was at station 9, known colloquially as "Snowy Hole" (Figure 2), where one 69-min transect was accomplished over a depth range of 125-137 m on 31 August 1979. The aggregation at Snowy Hole consisted of 150 large individual snowy grouper, which occurred at the only reef of this dive where the habitat was low-profile scattered boulders, estimated to be ≤ 900 m^2 in area. Because the transect length is unknown, however, we cannot provide grouper in units of fish per m but instead report 150 snowy grouper across the approximate habitat area. Since this small rock patch was known to fishermen and contained commercially valuable fishes, we assume that it had been fished regularly before the 1979 surveys.

4. Placing grouper hotspots in context

To place grouper counts inside hotspots within a larger regional context (e.g., the context of counts outside of hotspots, Figure 6), we compared grouper counts from hotspots to non-hotspot counts from several datasets. These datasets include: 1) South-East Fisheries-Independent Survey (SEFIS) ROV surveys of shelf-edge natural reefs (October 2010); 2)

Sedberry HOV surveys of shelf-edge and upper-slope natural reefs (July 1985, September 2001, July – August 2002, August 2003, August 2004); 3) NOAA Panama City ROV surveys of shelf-edge and upper-slope natural reefs (April – May 2004, June 2006, August 2007, July 2008, November 2009, May 2010, July 2012, July 2013, June 2014, June 2015, July 2016, June 2017, May 2018); and 4) hook-and line surveys of natural reefs (May – October 2017-2019) (Table 1, Figure 6; Data S1). These surveys adhere to our synthesis search criteria of depths 50-300 m within the SEUS region. The first three datasets reported mean counts per linear m surveyed, which we could directly compare to grouper counts per linear m surveyed from hotspot sites (e.g., number of individuals / transect length). The fourth dataset reported CPUE, which we could directly compare to hook-and-line data from hotspot sites.

Mean grouper counts per m surveyed outside of hotspots were markedly lower than counts per m surveyed on hotspot reefs. Outside of hotspots, mean grouper counts on shelf-edge reefs ranged from 0.01 - 0.02 per m, whereas mean grouper counts on deeper reefs located on the upper slope outside of hotspots ranged from <0.01 - 0.01 grouper per m (Figure 7). We used a variety of data sources so could not include them into an overall analysis of grouper counts on hotspots versus outside of hotspots. Instead, we focused our analysis on one data source where we could make comparison using means and associated standard error. The dataset that we selected was the Panama City ROV dataset, containing eight observations from grouper hotspots and 229 observations from outside of hotspots. A basic analytical comparison revealed that mean grouper counts per m on hotspots were 1.12 ± 0.67, whereas mean counts outside of hotspots were 0.01 ± 0 0.001 (Figure S1). Hook-and-line surveys of shelf edge reefs outside of hotspots similarly yielded a lower CPUE for snowy grouper than found on the Snowy Wreck hotspot (0.07 vs. 1.3 CPUE). Overall, count metrics were several orders of magnitude higher on hotspots than outside of hotspots.

Although several additional surveys met our depth criteria, these surveys did not report grouper in comparable units, but rather grouper per hectare or counts per transects of unrecorded length (e.g., time reported). These surveys, including: 1) S.W. Ross *Johnson Sea Link* HOV surveys of shelf edge natural reefs (August 1983); 2) Quattrini and Ross ROV (April 2004) & HOV surveys of shelf edge natural reefs (September 2001, August 2002, August 2003, June 2004); as well as the aforementioned Parker and Ross (1986) HOV surveys of shelf edge natural reefs exclusive of "Snowy Hole" (August – September 1979) (Table 1), revealed low counts of grouper, such as 1-8 grouper per hectare (Parker & Ross, 1986), which provide further support for patterns of low grouper counts on non-hotspot sites (Data S1).

5. Unique traits of reefs with hotspots

Given that large-bodied grouper hotspots did not occur on the majority of sites, we examined the traits of the hotspots habitats. The aggregations mostly occurred on isolated, deeper habitats (Table 2), and in fact, all of the deeper, isolated habitats that we examined supported aggregations. For example, the shipwrecks (Snowy Wreck, U-*576,* SS *Bluefields*) and artificial reefs (deep barge, shallow barge) are small patches of artificial habitat surrounded by large expanses of sandy, unconsolidated and unstructured habitat. Likewise the natural reef habitat at Snowy Hole is a field of small rubble boulders surrounded by a large expanse of sand. While all six instances of hotspots occurred on isolated habitats, this does not mean that hotspots of deep-dwelling, large-bodied groupers cannot occur on continuous, non-isolated habitats. Additionally, five of the six hotspots are artificial habitats, yet because artificial habitats are inherently small and isolated, it remains unknown whether habitat isolation or reef type is the better predictor of hotspots. While fishing pressure likely co-varies with the survey data (decreased in the MPA and potentially increased elsewhere during the decades of this synthesis), there was no known striking commonality in fishing pressure (e.g., open vs. closed) among the hotspots, yet as all hotspots are isolated and in deep waters, fishing pressure could hypothetically be limited in comparison to less isolated and shallower habitats.

6. Additional hotspot evidence from literature

Other examples of grouper hotspots in the SEUS have been reported. Commercial fishing catch data from a site off NC called "Adrian's Mark" suggests that this site once hosted a grouper aggregation (Epperly & Dodrill, 1995). Whether this site is a natural reef or a shipwreck is unknown, but it is reportedly a small, isolated feature (~48 m x 56 m) with a maximum relief of 2-3 m, at a depth of 194 m (based on 2019 multibeam survey, Harter and David, unpublished data). In a series of 32 commercial fish trips, during the period 7 June 1985 – 2 April 1986, 25,333 kg of snowy grouper were caught from the site using hook and line; the maximum daily catch was 382 individuals, totaling 3,225 kg (Epperly & Dodrill, 1995). Catch declined on Adrian's Mark over time, with estimates that over 80% of the snowy grouper biomass had been removed from the site by April 1986 (Epperly & Dodrill, 1995). Whereas it is unreported in the peer-reviewed publication (Epperly & Dodrill, 1995), a fishermen who participated in the Adrian's Mark commercial fishing trips confirmed that nearly all of the snowy grouper caught from this hotspot were in spawning condition with fully developed gonads, suggesting that this aggregation may have been related to spawning (K. Brennan, personal observation).

Capture-recapture data reported by a recreational fishing charter captain on a fishing trawler shipwreck off FL, called the "Sebastian Shipwreck," provides evidence of another SEUS grouper hotspot (Shertzer, Bacheler, Kellison, Fieberg, & Wiggers, 2018). Over a 10 year period (1994 - 2004), the captain tagged 196 Warsaw grouper and harvested many more grouper from the shipwreck, which rests in ~49 m (slightly shallower than our inclusion criteria) off the Atlantic coast of FL. Of these tagged grouper, 71 (36%) were recaptured with 30 recaptured once, 24 recaptured twice, 10 recaptured three times, 5 recaptured four times, 1 recaptured five times, and 1 recaptured six times, all on the same shipwreck. The large number of fish caught and the high percentage of recaptures is evidence of a likely Warsaw grouper aggregation that is persistent on or exhibits a high degree of site fidelity to this small, isolated shipwreck.

7. Implications and next steps

Our evaluation of 439 ROV transects, 235 HOV transects, and 881 hook-and-line drops collected over five decades revealed six hotspots of deep-water grouper off the SEUS. Grouper counts on these hotspots, which include three shipwrecks, two artificial reefs, and one boulder field, exceeded counts of grouper outside of hotspots by many orders of magnitude. Sites hosting aggregations of grouper were all deep (i.e., shelf-edge, upper-slope) reefs with small spatial footprints surrounded by large expanses of unconsolidated substrates. Evidence of additional hotspots in the SEUS on small shipwrecks and isolated deep-water sites supports this general pattern. It is unknown how these rare grouper aggregations contribute to overall population dynamics or how such immense numbers of groupers can co-occur and sustain themselves on small habitats.

We propose five potential explanations for why deep-water groupers may aggregate at hotspot locations in the SEUS. These explanations are not mutually exclusive and may all contribute to the realized benefits of such aggregations. First, groupers may aggregate at hotspots for feeding purposes. Most large-bodied groupers consume a combination of fish and invertebrate prey (Spanik, 2018), and some of these prey species tend to be found in higher densities on and in immediate proximity to shipwrecks, artificial reefs, and natural hardbottom areas compared to surrounding unconsolidated habitats (Lindquist et al., 1994; Lindquist et al., 1994; Posey & Ambrose, 1994). Still, it is difficult to imagine that there can be enough prey resources available at these grouper aggregation sites to support such immensely high densities of large-bodied groupers. Some grouper species, such as snowy grouper, are known to feed on species of crabs that are exclusively found over unconsolidated habitats, as well as squid that are presumably eaten higher in the water column (Bielsa & Labisky, 1987; Dodrill, Manooch, & Manooch, 1983Bielsa & Labisky, 1987). Coupled with observations of snowy grouper dispersing off of isolated habitats at night (K. Brennan, personal observation), this evidence suggests that perhaps grouper supplement food resources at hotspots by feeding on prey horizontally or vertically separated from these hotspots. This possibility is supported by observations that snowy grouper near the Snowy Wreck hotspot generally have narrow home ranges, with tagging data revealing that horizontal movements of individuals are usually restricted to several km^2 even over multi-year timescales (B. Runde, personal observation, unpublished data).

Second, groupers could use the hotspot sites as refuge from predators. Large-bodied groupers have very few predators in the open ocean, but sharks are likely the biggest threat and are relatively common in deep areas of the SEUS. For instance, eight acoustically tagged white sharks (*Carcharodon carcharias,* Lamnidae) and one acoustically tagged tiger shark (*Galeocerdo cuvier,* Carcharhinidae) were detected near the Snowy Wreck over an 18-mo period (Runde, Michelot, Bacheler, Shertzer, & Buckel, 2020). Moreover, most of the predation upon recently released reef fishes from hook-and-line fishing on artificial and natural reefs in the Gulf of Mexico and Atlantic was due to sharks (Bahaboy, Guttridge, Hammerschlag, Van Zinnicq Bergmann, & Patterson III, 2020; Runde et al., 2020). Such distributional behavior is supported by experimental evidence that gag exhibit density-dependent habitat selection, primarily for shelter, on shallow (13 m) artificial reefs in the northeast Gulf of Mexico (Lindberg et al., 2006). Shipwrecks, artificial reefs, and natural hardbottom areas, such as the hotspots identified here, likely afford groupers cover and protection from potential predators.

A third explanation for grouper aggregations at hotspots could be a bioenergetic strategy related to reef structure. Groupers living in habitats lacking vertical relief cannot avoid ocean currents, and therefore must expend energy to remain at the same location. Groupers around a structured habitat, like a shipwreck, on the other hand, can seek shelter on the downstream side of a wreck out of the current, and would therefore spend less energy. This is analogous to trout sheltering in lower-current areas of rivers behind boulders, rocks, or woody debris (Lehane, Giller, O'Halloran, Smith, & Murphy, 2002). This notion is supported by echosounder surveys on shallower shipwrecks (< 100 m) on the NC continental shelf, where large fish (> 29 cm) were detected closer to shipwrecks with stronger magnitude currents and further from structure with weaker currents (Paxton, Taylor, Peterson, Fegley, & Rosman, 2019).

Fourth, groupers could be aggregating at these hotspots for reproduction or spawning purposes. Snowy grouper spawning likely occurs between March and October, with peak spawning between May and August (Farmer et al., 2017) but may begin as early as late January and likely ends in early October (Kolmos et al., 2019). Multiple studies have identified female snowy grouper in spawning condition, but none have confirmed the presence of spawning aggregations, courtship, or spawning activity (Farmer et al., 2017; Kolmos et al., 2019). Observations, however, of mostly spawning adult snowy grouper with fully-developed gonads caught on Adrian's Mark in April – September 1985 (K. Brennan, personal observation) suggest that snowy grouper may form spawning aggregations, yet it is unknown whether these grouper may have been present prior to April as part of a resident population or whether they were an aggregation staging to spawn. Aggregations detected from HOV and ROV surveys on the Snowy Wreck (August 2004, July 2012, July 2016), underwater battlefield shipwrecks (August 2016), intentionally-sunk barges (July 2016, June 2017, May 2018), and Snowy Hole (August – September 1979) temporally coincide with the likely spawning period (Table S1), but none of these visual surveys provided information on whether the grouper were in spawning condition. Observations from the Snowy Wreck of an aggregation on 31 October 2017, however, fall just outside of the likely spawning season (Table S1). Gonads from snowy grouper caught with hook-and-line on the Snowy Wreck in June 2017 visually appeared to be ripening, and later examination indicated the presence of stage III oocytes (vitellogensis; J. Locascio, personal observation). Fish caught at the same site in August 2018 were released with unknown gonad condition, and several others from August 2019 were retained without gonad examination but anecdotally were not females in spawning condition. Sampling snowy grouper hotspots during the winter months, when sampling is limited due to poor offshore weather conditions, may help answer these questions. Of the other grouper species detected on hotspots (Warsaw, yellowedge, misty, gag, scamp), only scamp and gag are known to form spawning aggregations (Coleman et al., 1999; Farmer et al., 2017). Low counts of scamp (0.05-0.14 individuals per m) and gag (0.02 individuals per m) observed on the hotspots suggest that they were not part of a spawning aggregation at the time of observation. Possibly, however, some of these species, like Warsaw, snowy, yellowedge, and misty grouper, may spawn *en masse,* but supporting evidence is limited. A shallower-dwelling grouper species, the goliath grouper (*Epinephelus itajara,* Serranidae), has been documented to aggregate around artificial structures in off Florida (Collins, Barbieri, McBride, McCoy, & Motta, 2015; Koenig, Coleman, & Kingon, 2011) and Brazil (Giglio et al., 2014), as well, and it has been, likewise, debated whether these observations are associated with spawning in small groups, *en masse,* or potentially another behavior (M. L. Domeier, Maria, & Nasby-Lucas, 2006).

Lastly, fishing pressure or lack thereof may also help explain the presence of grouper aggregations on select reefs. Hotspots identified herein are small areas surrounded by expanses of unconsolidated substrate. These small, isolated grouper aggregation sites may be much more difficult for fishers to find compared to aggregation sites near or connected to large, naturally occurring ledges or other hardbottom areas, such as the shelf break. Since the hotspots are in deep water, they are also located far from shore and are harder for fishers to access. Hypothetically, this could allow aggregations to persist on small, deep features, whereas aggregations formerly on larger features have now been reduced or eliminated by fishing pressure. Clearly, fishing can dramatically reduce or eliminate grouper aggregations, as documented at Adrian's Mark in the 1980s (Epperly & Dodrill, 1995), and by the reduced numbers of snowy grouper at the Snowy Wreck during the pre-MPA 2004 survey (Quattrini & Ross, 2006) compared to later surveys. Thus, it is impossible to know whether groupers are selecting isolated locations for their aggregations or that only the isolated aggregations now remain due to many decades of heavy fishing. On the contrary, the U-*576* and SS *Bluefields* shipwrecks, which were commonly and collectively referred to by fishermen as the "Jack Frost Wreck," began to be fished in the 1970s and were heavily fished by the 1980s (K. Brennan, personal observation), and yet they remain as hotspots as recently as 2016, though it is important to note that stricter trip limits for snowy grouper have been in place since 2006 (SAFMC, 2006). The Snowy Wreck was fished until 2009 when it was designated as part of an MPA, and aggregations were encountered both before (2004) and after (2012, 2014, 2017) MPA designation. Future research should investigate how fishing pressure relates to hotspots and the scale of aggregations and could involve the use of hydrophones to record boat traffic as a metric for fishing pressure.

It is unclear how (or if) the species-specific abundances of groupers occupying hotspots, or the number of species-specific grouper hotspots, relate to the abundance or distribution of the broader populations of those species. If those relationships were known and consistent over time, aggregation sites could be monitored as an index of abundance for the population. Unfortunately, such determinations would likely be exceedingly difficult, requiring some combination of knowledge of the number, distribution, and location of hotspots (how many sites are there, and does the number of sites vary over time?), temporal variability in abundance (how does site-specific abundance vary within and across years, with relevance for determining monitoring approaches?), and, preferably, ground-truthing of species-specific indices of abundance or biomass generated from hotspot-site monitoring with population-level indices of abundance or biomass derived from one or more other sources (do aggregations behave in concordance with population trends, or might aggregations exhibit hyperstability even in low population status?). In the near-term, case studies involving specific hotspots would be informative to provide insight into temporal variability in abundance and the degree to which specific sites are affected by, or can recover from, targeted fishing efforts. For example, a cross-comparison of abundance over time at the Snowy Wreck, a grouper hotspot that experienced targeted fishing but was subsequently protected as an MPA, and Adrian's Mark, an unprotected aggregation site that continues to experience fishing effort (G.T. Kellison, personal observation), could provide insight into the resilience of site-specific aggregations. For the Snowy Wreck, at least, while data are limited, the pre- and post-MPA surveys suggest a huge increase in grouper numbers after the habitat was protected (Quattrini & Ross, 2006). If new artificial reefs are deployed at comparable depths to the hotspots identified here, monitoring the new artificial reefs could provide additional insight into temporal variability, including colonization, of potential new hotspots. This approach towards documenting colonization of potential hotspots could also help determine inter- and intra- specific species interactions.

Evaluating observational data collected over five decades was challenging, largely because it required synthesis of diverse datasets that not only used different methods (ROV, HOV, hook-and-line) but that were also collected over a timeframe when technology rapidly changed. To ensure that all data were comparable, we examined ROV and HOV data in units of counts per linear m surveyed and hook-and-line data separately as CPUE. Using count per m for the ROV and HOV data allowed us to evaluate the presence of grouper aggregations from differing survey designs (time, distance, etc.), survey dates, fields of view, and gear (camera, video, in-person counts) since not all datasets reported densities. It is possible that additional datasets could have provided further evidence of hotspots on the SEUS.

Our synthesis revealed that hotspot sites with small spatial footprints and isolated spatial arrangements may represent disproportionate abundances of deep-water groupers. Despite our documentation of grouper hotspots on select SEUS reefs and several examples of additional grouper hotspots reported in the literature, descriptions of similar observations from other regions or other survey methods are rare. We encourage communication and publication of similar observations or data from other regions to better elucidate the extent to which this phenomenon occurs globally and whether it also occurs in other large-bodied grouper or other marine fauna. Future research can help solve the puzzle of why deep-water grouper aggregate on small, isolated habitats and how the aggregated grouper both derive resources from these sites and relate to large-scale population dynamics.

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Tables:

Table 1: Direct observational datasets over five decades that were analyzed for hotspots of groupers. The survey date(s), methods, and effort are indicated for each site, as is the source of data. Reef type (i.e., artificial or natural), reef sites, and geographic location are provided. Data sources, as well as the location within this paper where the dataset is referenced, are also given.

Dataset	Survey date(s)	Survey method	Survey effort	Reef type	Reef site(s)	Depth (m)	State(s)	Data source	Reference section
Parker & Ross	1979	HOV	13 transects	natural	Snowy Hole, shelf-edge reefs	52-152	NC	Parker & Ross, 1986. NEGS.	3.4
Ross JSL	1983	HOV	10 transects	natural	shelf-edge reefs	52-95	NC	SW Ross unpublished data	4
Sedberry	1985, 2001-2004	HOV	189 transects	natural	shelf-edge reefs, upper-slope reefs	50-79, 197-207	SC, GA, FL	Schobernd & Sedberry, 2009. Ocean Exploration Cruise Report	4
Quattrini & Ross	2001-2004	HOV & ROV	17 transects (HOV); 10 transects (ROV)	artificial, natural	Snowy Wreck, shelf-edge reefs, upper-slope reefs	57-253	NC	Quattrini & Ross, 2006.	3.1, 4
NOAA Panama City	2004, 2006-2010, 2012-2018	ROV	265 transects	artificial, natural	Snowy Wreck, Charleston Barges, shelf-edge reefs, upper-slope reefs	50-252	NC, SC, GA, FL	Reports to the SAFMC; some in Bacheler et al., 2016.	3.1, 3.3, 4
SEFIS	2010	ROV	163 transects	natural	shelf-edge reefs	50-66	SC, GA, FL	Bacheler et al. 2016.	4
Underwater Battlefield	2016	HOV	6 transects	artificial	U-*576*, SS *Bluefields*	210, 245	NC	Johnson et al. 2020.	3.2
Ross Snowy	2017	ROV	11 transects	artificial	Snowy Wreck	252	NC	SW Ross unpublished data	3.1
Hook & Line	2017-2019	Hook-and-line	881 drops	artificial, natural	Snowy Wreck, Snowy MPA, shelf-edge reefs	250, 60-140	NC	Runde, Rudershausen, Buckel unpublished data	3.1, 4

Table 2: Characteristics of hotspots. For each reef, the reef type (artificial, natural, unknown), depth, fishing pressure (open, closed), and isolation (isolated or not) are provided.

Hotspot	**Reef type**	**Depth (m)**	**Current fishing pressure**	**Isolation**	**Reference section**
Snowy Wreck	Artificial	250	Protected; unfished (closed to fishing since 2009)	Isolated	3.1
Underwater Battlefield (U-*576*, SS *Bluefields*)	Artificial	210, 245	Fished	Isolated	3.2
Intentionally-Sunk Barges (Shallow Barge, Deep Barge)	Artificial	85, 100	Protected; unfished (closed to fishing since 2017)	Isolated	3.3
Snowy Hole	Natural	125-137	Fished	Isolated	3.4

Figures:

Figure 1: Observations of hotspots characterized by high snowy grouper counts on: A) the shipwreck U-*576* in 210 m depth off North Carolina in August 2016 and B) the Snowy Wreck in 250 m depth off North Carolina in October 2017. See Section 3 ("Reefs with grouper hotspots") for site details.

Figure 2: Locations of artificial (triangles) and natural (circles) reefs surveyed over five decades that were evaluated for presence of grouper hotspots. Sites where hotspots were observed are in red with labels in black text, whereas sites where hotspots were not observed appear in gray. Contour lines represent 100 m depth intervals. The area considered in this study was bounded by Cape Hatteras, NC to the north and Cape Canaveral, FL to the south.

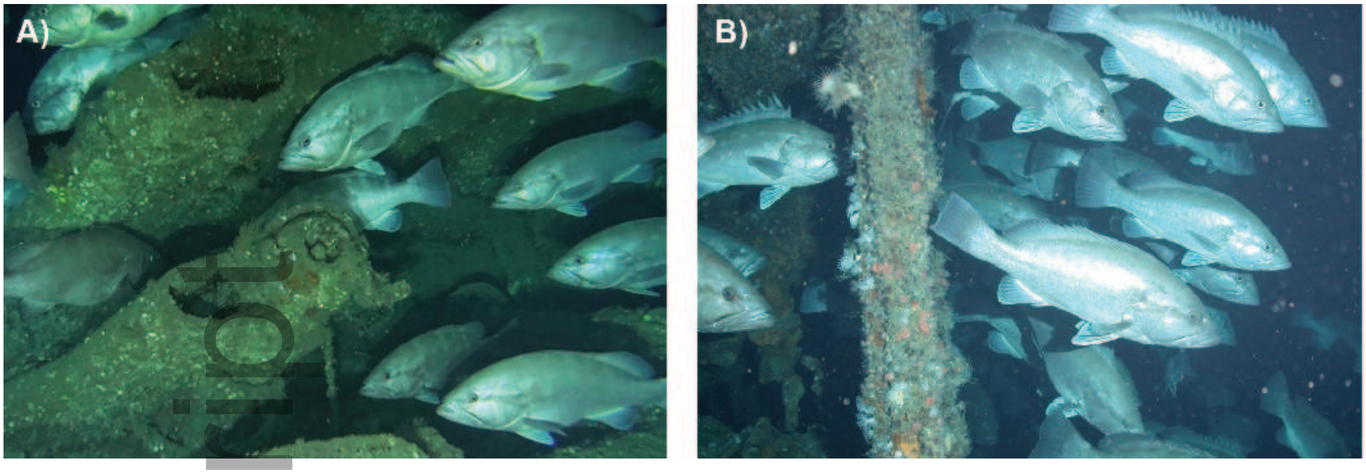
Figure 3: Counts of snowy grouper per linear m surveyed on the Snowy Wreck hotspot located off North Carolina by year. Each bar corresponds to one survey transect, with the exception of 2017 which corresponds to the mean snowy grouper count per m observed across eleven transects designated post-data collection. The Snowy Wreck was protected from fishing in 2009.

Figure 4: Counts of large-bodied groupers per linear m surveyed on two hotspots: A) U-*576* shipwreck and B) SS *Bluefields* shipwreck located off North Carolina by replicate transects (e.g., U-*576* transect 1 = U1, SS *Bluefields* transect 1 = B1). Each bar corresponds to one HOV transect. UnID refers to grouper that we were not able to identify to species level.

Figure 5: Counts of large-bodied groupers per linear m surveyed on two hotspots: A) shallow barge and B) deep barge, both located off the coast of Charleston, South Carolina. Each bar corresponds to one ROV transect. UnID refers to grouper that we were not able to identify to species level.

Figure 6: Grouper on natural reefs without observed hotspots: A) on the shelf edge off Florida and B) on the upper slope off South Carolina from NOAA Panama City ROV dives.

Figure 7: Mean grouper count per linear m surveyed outside of hotspots from three datasets: 1) SEFIS ROV, 2) Sedberry HOV, and 3) NOAA Panama City ROV. Text above each bar indicates the total number of transects used to calculate the mean count per m for reefs on the shelf edge and upper slope. Error bars represent ± 1 SE. See Data S1 for species-specific counts.



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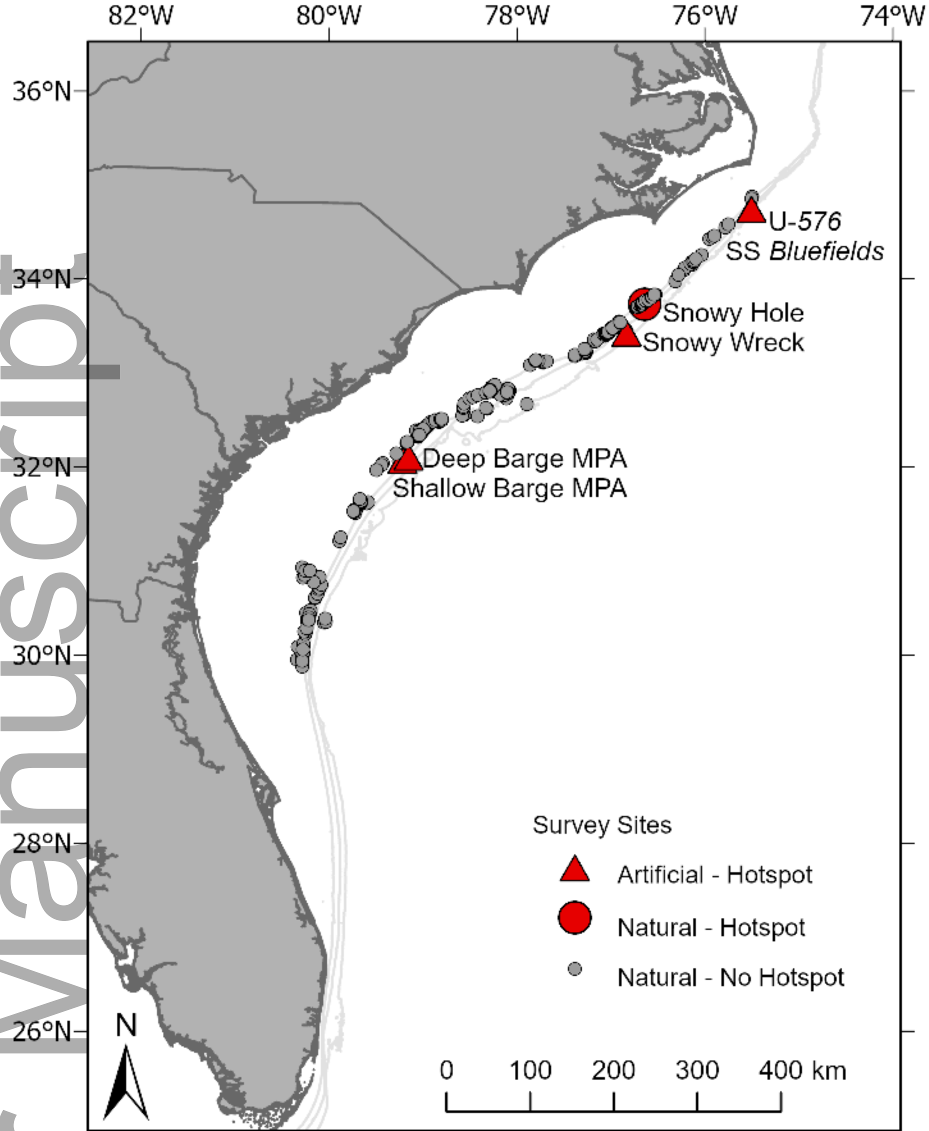

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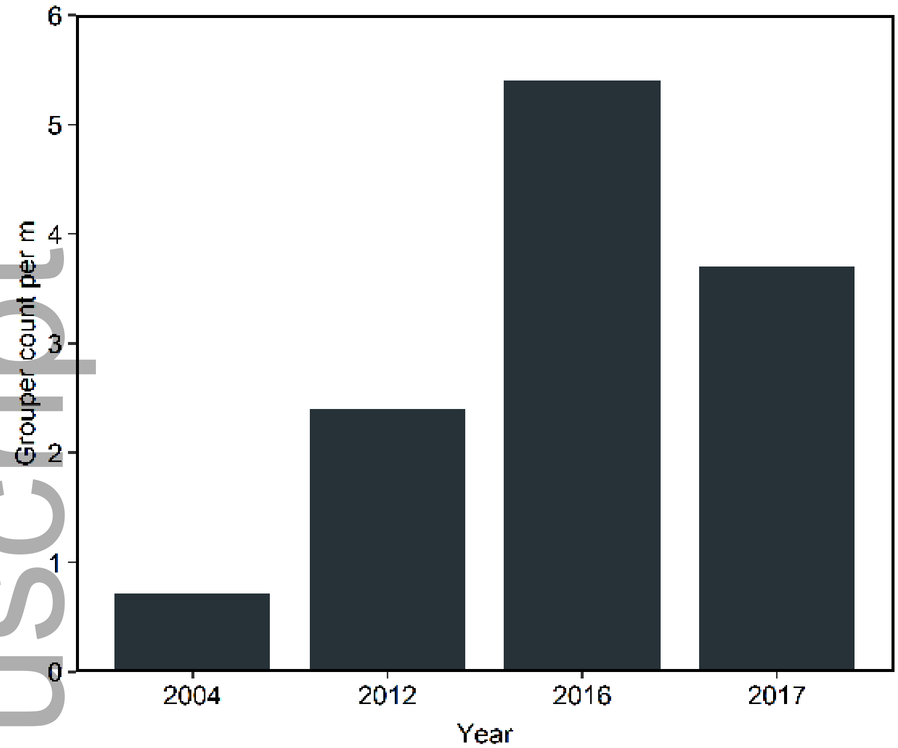

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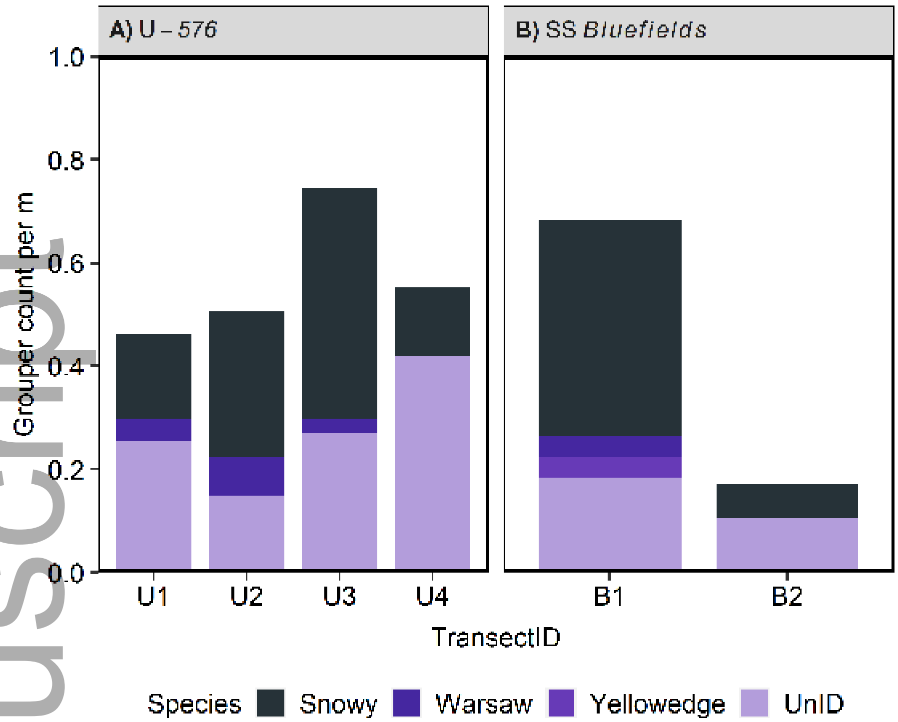

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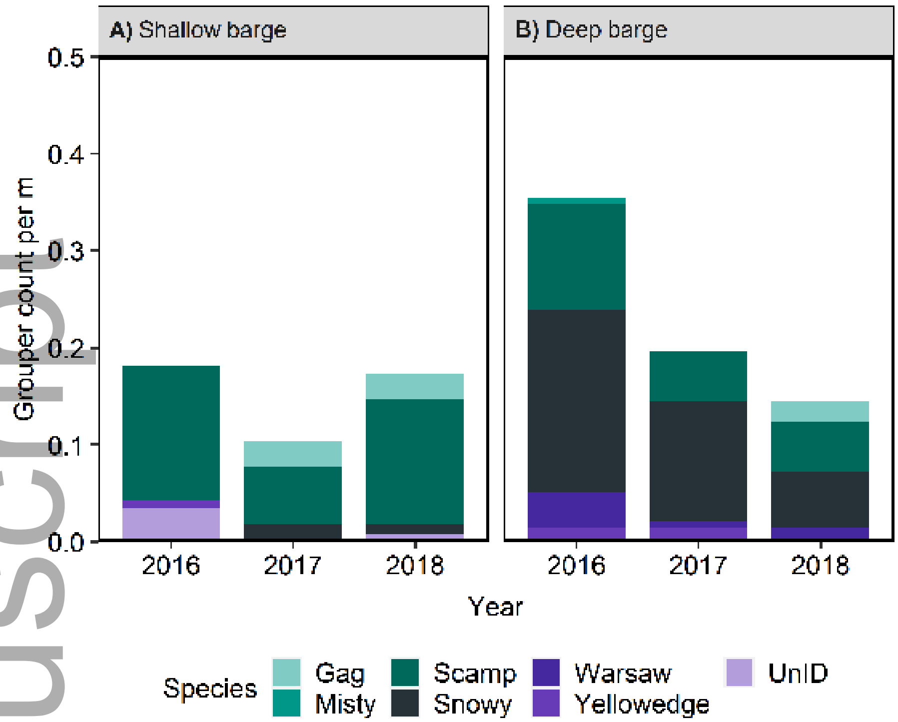

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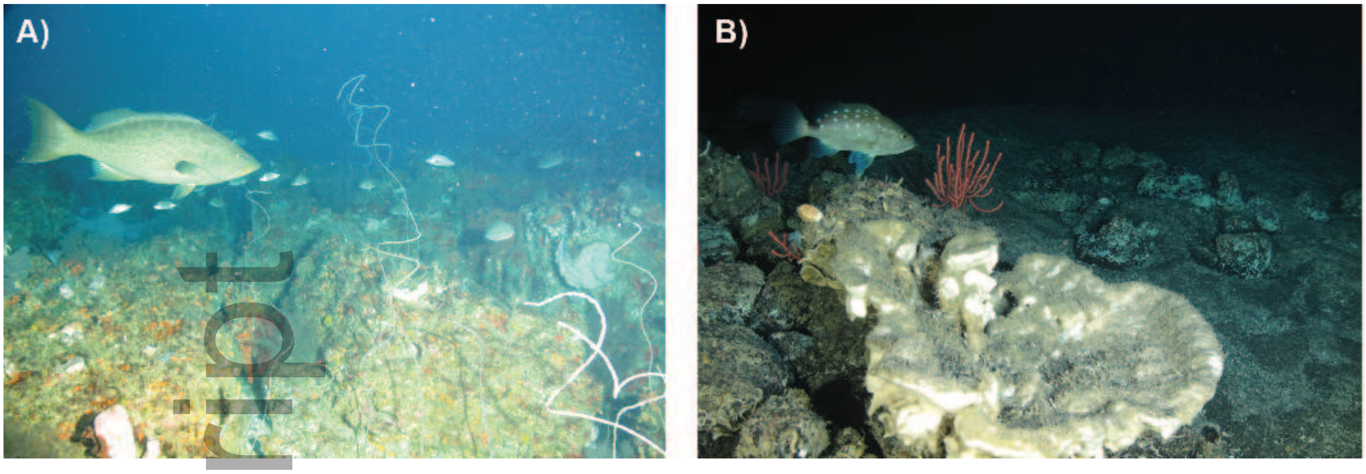

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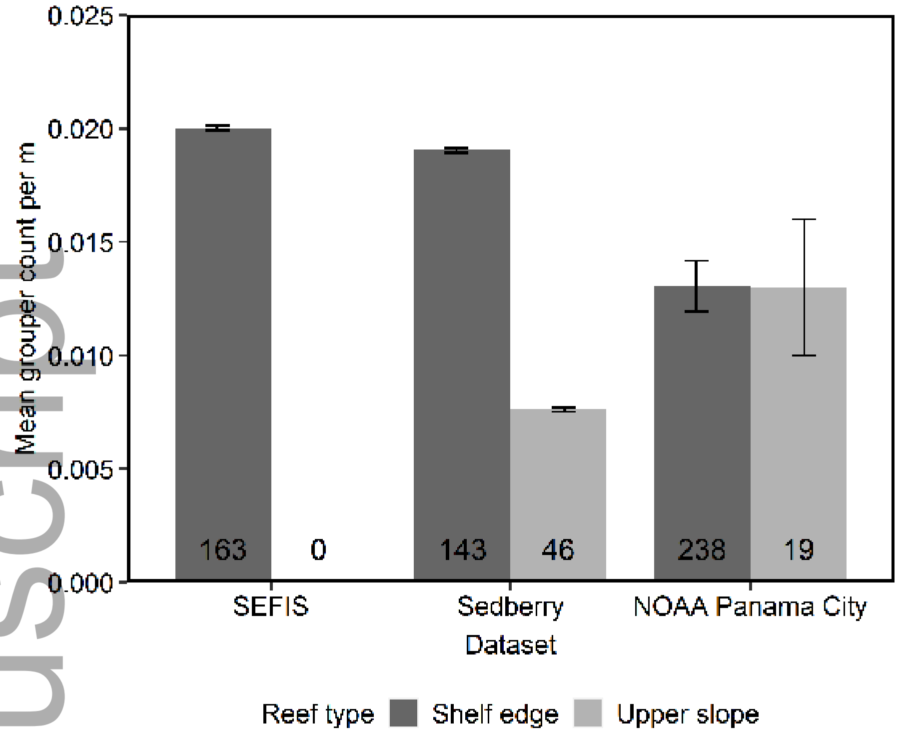

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