



Fish Spawning Aggregations in the Southeast Florida Coral Reef Ecosystem Conservation Area: A Case Study Synthesis of User Reports, Literature, and Field Validation Efforts

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The formation of fish spawning aggregations (FSAs) is an essential part of the life history of many economically important fish species; however, their status are often poorly described in the literature either due to their occurrence in remote locations, during seasons with unsafe ocean conditions, or because they move on space and time scales that are difficult to predict and validate. Even in areas that are relatively accessible and heavily fished, such as southeast Florida, regionally relevant information describing FSA dynamics is generally absent from the literature and unaccounted for in existing management plans. We propose that this can be attributed to the fact that information is often held by stakeholders or found in unpublished manuscripts and reports. These sources are not widely disseminated and are therefore difficult to locate and integrate into fisheries management decisions. In this paper, we present a case study demonstrating the value of regional data syntheses as a tool to improve management activities in southeast Florida. Specifically, we engaged with local stakeholders to collect reports of FSA occurrence, and used Web of Science queries to collate information describing the reproductive dynamics of locally occurring snapper and grouper species. Reports were combined with regional FSA literature and provided to managers as a support tool to anticipate FSA occurrence, and to guide policy development and future FSA research. Resource users identified 13 potential aggregations from five species, but Web of Science queries revealed a paucity of information. Echosounder, camera, and fisheries dependent surveys were then used to corroborate reportedly active cubera snapper (*Lutjanus cyanopterus*), hogfish (*Lachnolaimus maximus*), and gag grouper (*Mycteroperca microlepis*) aggregations. Variability in the spatiotemporal aspects of FSA occurrence make them difficult to study, but this may also explain how certain species have avoided detrimental impacts from aggregation fishing. These data represent a first

step toward describing FSAs that have historically occurred in the Southeast Florida Coral Reef Ecosystem Conservation Area and can be used by managers to prioritize future research efforts focused on species or hotspots of multispecies activity along the northern extent of the Florida Reef Tract.

Keywords: fish spawning aggregations, South Florida, fisheries management, local knowledge, snapper grouper complex, fishing

INTRODUCTION

The formation of Fish Spawning Aggregations (FSAs) is a vital part of the life cycle of many fish species, with each spawning event representing 33–100% of the annual reproductive investment for transient aggregating species (Domeier and Colin, 1997; Sadovy de Mitcheson et al., 2013). This reproductive strategy is shared by over 150 species world-wide (Claydon, 2004), and sites are often used by multiple species, either simultaneously or across multiple seasons (Johannes, 1978; Kobara et al., 2013; Farmer et al., 2017). Despite the documented occurrence of nearly 1,000 aggregations across the globe, the status of approximately 50% of them are unknown due to the difficulty associated with locating FSAs and conducting field research that characterizes their biological and ecological dynamics (Russell et al., 2014).

Location is thought to be primarily dictated by the optimization of larval dispersal into environments where predation risk is minimized and food encounter rate in a heterogeneous landscape is maximized (Johannes, 1978; Karnauskas et al., 2011; Sadovy De Mitcheson and Colin, 2013). However, fluctuations in oceanographic features (e.g., changes in flow direction and speed, temperature, etc.) are known to drive spatiotemporal patterns of occurrence (Heyman and Kjerfve, 2008; Karnauskas et al., 2011). For instance, changes in tidal period or short-term upwelling events may disperse aggregated spawners over a period of a few hours, or shift their focal spawning area, making detection increasingly difficult. Beyond the environmental factors complicating FSA detection, aggregating species exhibit varying degrees of site fidelity and seasonality (Farmer et al., 2017). Certain species within the snapper-grouper complex, such as mutton snapper (*Lutjanus analis*) and goliath grouper (*Epinephelus itajara*), are known to maintain localized “home ranges” during discrete spawning periods (Koenig et al., 2017; Feeley et al., 2018), though other species such as gray snapper (*L. griseus*), yellowtail snapper (*Ocyurus chrysurus*), and hogfish (*Lachnolaimus maximus*) aggregate on a range of habitats, have relatively large spawning home-ranges and protracted spawning seasons (Muñoz et al., 2010; Farmer et al., 2017).

While hundreds to thousands of individuals have been documented traveling for weeks, over great distances (10–100 km) during specific times of the year for the sole purpose of spawning (Sadovy De Mitcheson and Colin, 2013), pinpointing their precise location in space and time is difficult without substantial effort and resources. Even in cases where high-resolution spatial and temporal information on aggregation occurrence have been provided in historical reports from

resource users, documentation of FSA formation and spawning can take years, especially where heavy fishing pressure has depressed abundance (Burton et al., 2005; Heyman and Kjerfve, 2008; Feeley et al., 2018). For example, a collaborative multi-agency effort to document the recovery of a mutton snapper aggregation near Dry Tortugas National Park, Florida required approximately 10 years of consistent study before spawning was observed in 2009 (Feeley et al., 2018). Prior to the formation of the Tortugas South Ecological Reserve (TSER) in 2001, commercial fishing on Riley’s Hump (the focal point of the TSER) had consistently occurred for over a decade (Burton et al., 2005). Following sharp declines in mutton snapper landings during the spawning season, concerned fishers approached the Florida Keys National Marine Sanctuary with reports of the decline and began assisting with the implementation of legislation that closed off the region surrounding Riley’s Hump. With endorsement from the commercial fishing community, a comprehensive monitoring program was developed. Over the following 10 years period, mutton snapper and numerous other aggregating species, including ocean triggerfish (*Canthidermis sufflamen*), cubera snapper (*L. cyanopterus*), permit (*Trachinotus falcatus*), and horse-eye jacks (*Caranx latus*) were observed at the aggregation site (Feeley et al., 2018).

Similar to the successes seen in the Dry Tortugas, stakeholder involvement has led to the recovery of FSAs throughout the world (Russell et al., 2014). However, the dynamics of FSA occurrence are still poorly understood in many regions, even those that are easily accessible and widely discussed within the fishing community. The paucity of information can be attributed to biotic and abiotic factors that drive spatial and temporal variability as described, but a significant obstacle to successful FSA management and identification is the lack of peer-reviewed syntheses that combine stakeholder reports, relevant peer-reviewed sources, and gray literature sources to describe regionally specific FSA dynamics. Syntheses such as these may be generated as part of an agency report or technical review, but they are not widely disseminated in peer-reviewed journals due to their scope and are therefore difficult to locate and integrate into current and future FSA management activities. Large spatial-scale reviews are useful and represent a valuable tool to broadly describe the reproductive dynamics of selected species, but regionally specific reviews may provide the level of detail needed to make appropriate management decisions that address local resource needs.

In this paper, we present a case study in support of regional FSA syntheses. Using the FSA research guidelines presented by the Society for the Conservation of Reef fish Aggregations (Collins et al., 2003), we gathered information from

peer-reviewed literature, gray literature sources, and stakeholders to inform regional management decisions and develop an FSA validation field survey in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA). Specifically, we used multiple queries from Web of Science and engaged with local fishers and SCUBA divers to collect historical and current reports of FSA formation in the ECA. Reports from stakeholders were combined with information from regional FSA literature and provided to managers as a geospatial report of the occurrence of FSAs that could be used to guide conservation goals and future FSA research¹. Field echosounder surveys, camera surveys, on-water fishing surveys, and trip-interviews were used to validate and assess reportedly active spawning aggregations, for which we had reports with meaningful spatial information. These data represent a first step toward describing FSAs that have historically occurred in the ECA and can be used by managers to prioritize future research and management efforts focused on individual species or hotspots of multispecies activity along the northern extent of the Florida Reef Tract.

The Southeast Florida Coral Reef Ecosystem Conservation Area—A Case Study

The Southeast Florida Coral Reef Initiative (SEFCRI) includes a collaborative advisory team and Technical Advisory Committee tasked with identifying and implementing priority actions needed to reduce key threats to coral reef resources off southeast Florida. The region extends along 150 km of coastline from the northern boundary of Biscayne National Park off Miami-Dade County, to the St. Lucie inlet in Martin County (**Figure 1**) (SEFCRI 2012). This portion of the Florida reef tract was designated as the Southeast Florida Coral Reef ECA by the Florida Legislature in 2018. The SEFCRI team consists of governmental agencies, non-profit organizations, recreational and commercial fishing and diving stakeholders, and marine industry leaders, focused on providing recommendations to the Florida Department of Environmental Protection (FDEP) Coral Reef Conservation Program (CRCP) resource managers, related to priority projects consistent with their Charter. The SEFCRI Technical Advisory Committee is made up of subject matter experts who advise the SEFCRI Team on technical topics related to coral reef threats. Founded in 2004, the SEFCRI and FDEP CRCP have completed over 140 projects pertaining to awareness and appreciation (i.e., outreach and education), land-based sources of pollution, maritime industry and coastal construction, and fishing, diving and other uses. However, a state-adopted regional management plan has not been developed prior to the designation of the ECA, leaving the northern extent of the Florida Reef Tract largely under managed and under protected.

The Florida Reef Tract is comprised of nursery, spawning, and foraging habitats for a diverse assemblage of tropical and sub-tropical species (Arena et al., 2007). Characterized by three distinct limestone reefs and nearshore ridge complex habitats that occur at increasing distances from shore, increasing in

complexity seaward, the Florida Reef Tract is dominated by micro/macro-algae cover, interspersed with soft-coral colonies, sponges, and stony coral species, and bordered by expanses of sandy unconsolidated soft bottom (Walker and Gilliam, 2013). State waters within the ECA also contain an extensive network of artificial reef complexes, both intentionally and unintentionally sunk (Walker et al., 2009) (**Figure 2**). These structures vary in spatial extent (i.e., footprint), vertical relief, overall complexity (rugosity) and age, but both natural and artificial reef habitats in the region are “hotspots” of fish aggregation, production and biodiversity in a heterogeneous (patchy) landscape of small and isolated islands (Arena et al., 2007; Walker et al., 2009).

Recognizing the importance of protecting sensitive living marine resources, SEFCRI launched the “Our Florida Reefs” campaign in 2013 to engage stakeholders, ocean users and the general public in a collaborative community planning effort that identified knowledge gaps and management priorities for the region (Reisewitz and Harper, 2013). Among the gaps outlined by the team, delineating habitats used by fish (specifically recreationally and commercially important species) during spawning were specifically highlighted as a research priority for integration into the final management plan recommendation. Spawning habitats are already identified as a federal management priority with the provision of the Essential Fish Habitat amendment to the Magnuson Stevens Act in 2002 (Federal Register vol. 67, no. 12, 2002) and subsequent reauthorization in 2006, though information related to the spatial and temporal aspects of FSAs in the ECA are essentially absent from the scientific literature despite their ecological importance.

MATERIALS AND METHODS

Study Region and Target Species

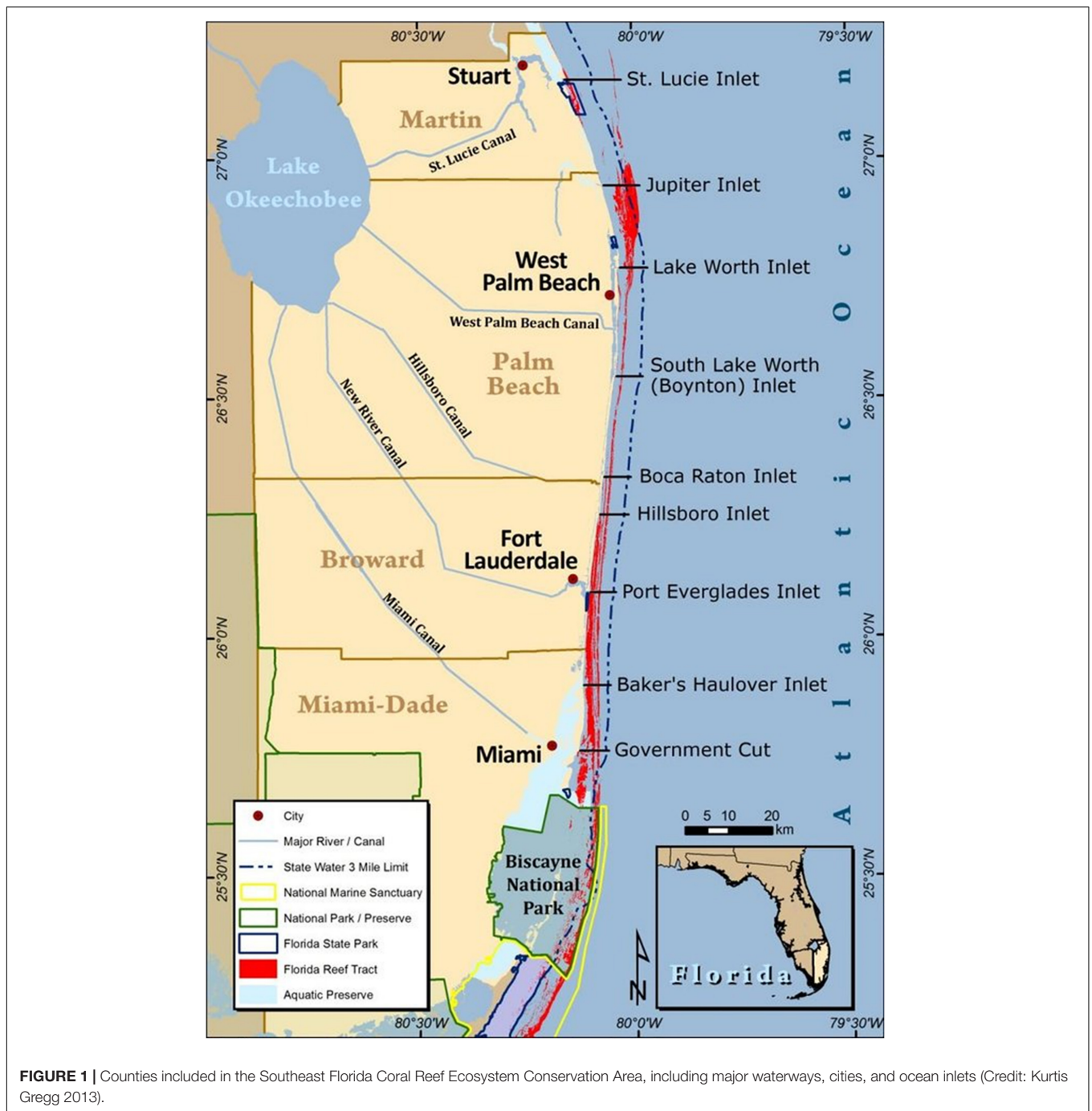
Data collection and reports used for this synthesis were constrained to coastal state waters and adjacent federal waters (≤ 75 m depth) between the northern and southern boundaries of the ECA (**Figure 1**). Focal species were selected based on initial review of reports from users, government reports, theses and peer-reviewed publications from reports of spawning aggregation occurrence in the study region. Select taxa were within the Snapper-Grouper Complex managed by the US South Atlantic Fishery Management Council (Gould and Brawner, 1983): gray snapper, mutton snapper, cubera snapper, gag grouper (*M. microlepis*), and hogfish. Though hogfish are classified as a wrasse (Family: *Labridae*), they are a managed species of significant economic value within the snapper-grouper complex. Goliath grouper aggregations were not included in this synthesis, as their aggregations are well described in the literature, and they are currently protected from harvest.

Data Collection

Literature Review and User Reports

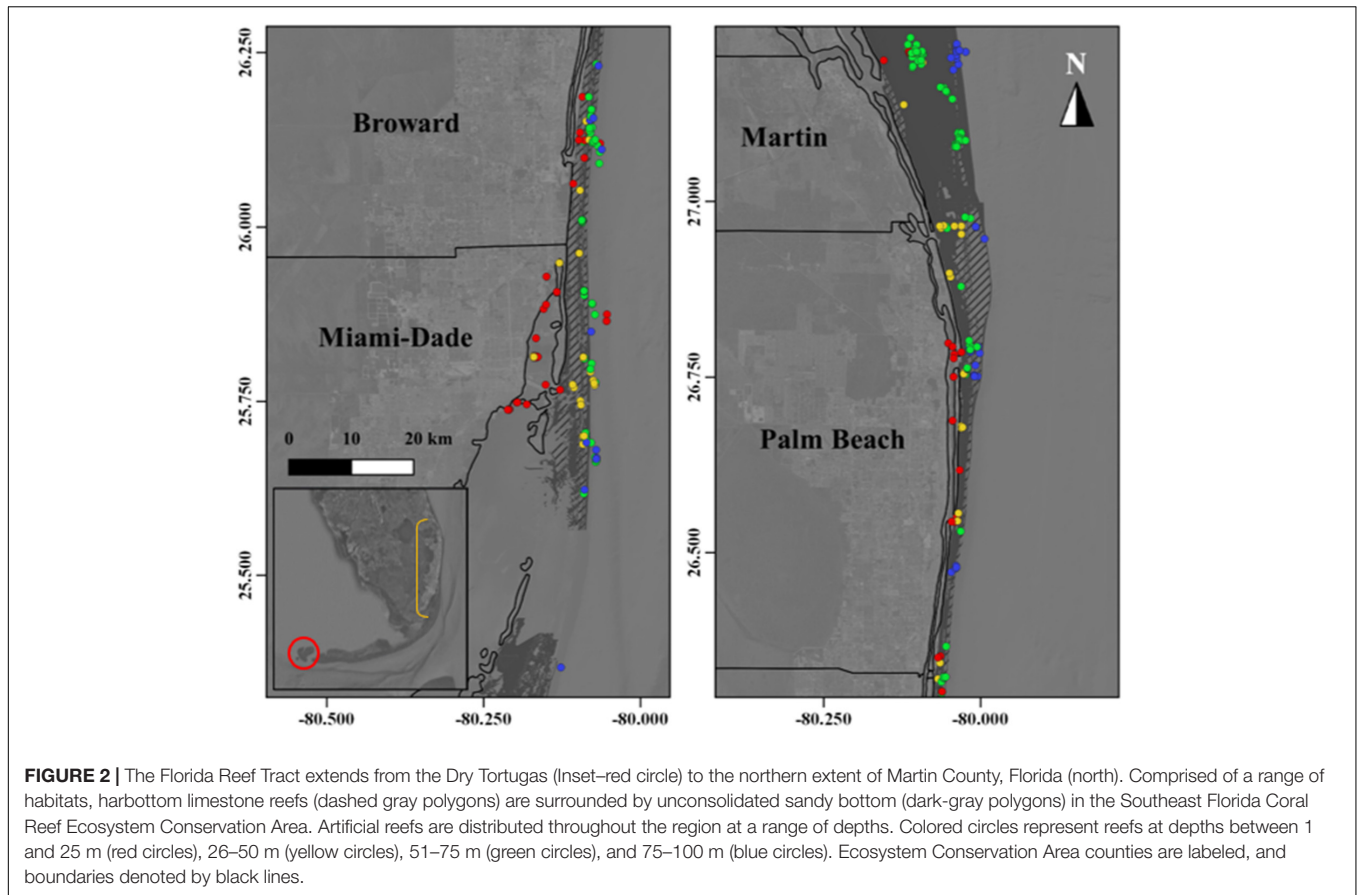
A keyword search was performed on Web of Science to compile available FSA literature pertaining to the ECA (**Table 1**). The

¹<https://ourfloridareefs.org/tool/>



search results were considered relevant and retained if they included species of interest occurring in the ECA. Those that pertained to the south Florida region and the species of interest were preserved, and location, time of aggregation occurrence, FSA size (geographic extent and relative abundance), and study dates were all recorded. Scientists in the region known to study snapper and grouper reproduction were also contacted to identify internal government reports and unpublished data sources that may contain relevant information pertaining to FSA spatiotemporal dynamics.

Anecdotal user reports were collected by means of direct interview and through the collection of second-hand reports from resource users in the region. Contacts were initially identified by established scientists working in the region, and additional contacts were generated through resource user interviews. Contacts included retired and active commercial fishers, charter guides, recreational anglers, and SCUBA diving shops. The information collected from users included species, location, time of aggregation occurrence, FSA magnitude, and age of the report.



Spawning Aggregation Validation

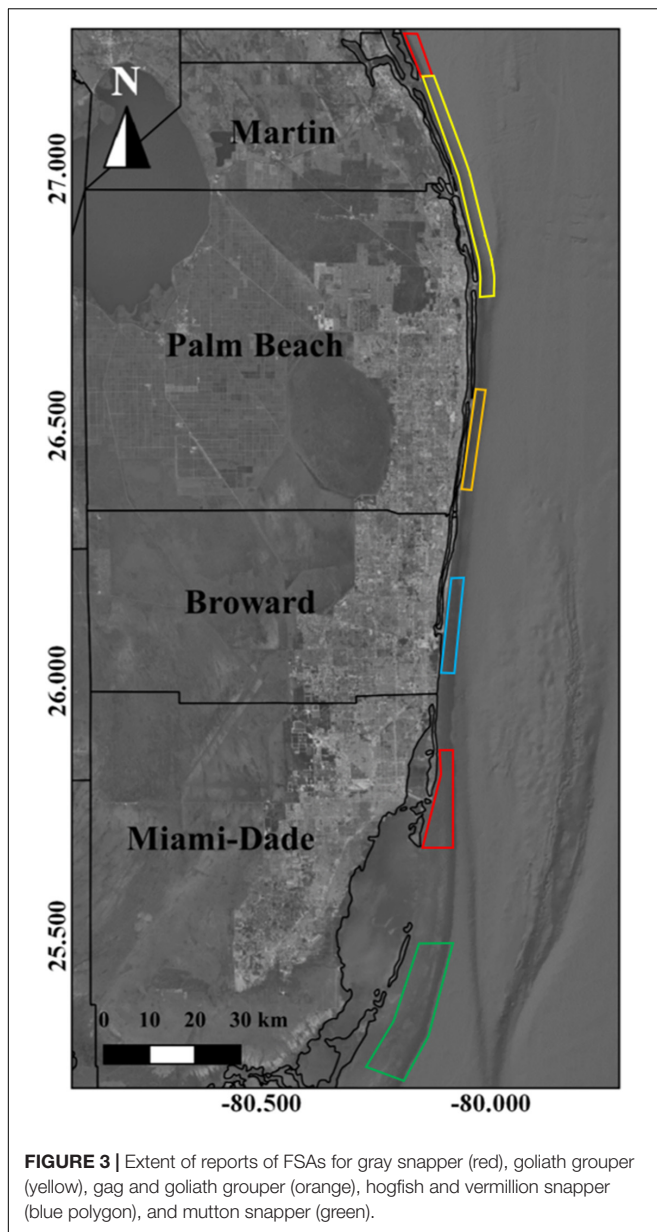
Validation efforts were performed using a combination of echosounder transects paired with 360° unbaited remote underwater video (URUV) surveys, drop cameras, fisheries observer surveys, and dockside interviews. All four methods were used to explore and confirm the occurrence of a gag grouper spawning aggregation that was reportedly active near Boynton Beach, Florida between January, and March of 2016. Paired echosounder and URUV/drop camera surveys were conducted near Jupiter, Florida on a reported gray snapper aggregation site, between July and September 2016. Observer surveys paired with dockside interviews were used to confirm the occurrence of cubera and mutton snapper aggregations offshore of Homestead, Florida between May and October of 2014 and 2015 (Figure 3).

TABLE 1 | A keyword search was performed in Web of Science (Clarivate Analytics, 2018) to identify primary literature relevant to spawning aggregation activity in the Southeast Florida Coral Reef Initiative Ecosystem Conservation Area.

Keywords	Citations
Fish spawning Aggregations + Florida	69
Spawning + Florida + Snapper	18
Spawning + Florida + Grouper	29

Duplicate entries returned in the second and third queries were removed from their respective tallies and included in the first query.

Echosounder surveys consisted of parallel linear transects, spaced approximately 25–30 m apart, that bisected the reefs and surrounding habitat centered on the geographic position where aggregations were reported to occur (Figure 4). Survey extent and transect line lengths varied by site and were determined by precision of report. Echosounder data were collected with calibrated 38 and 120 kHz split-beam echosounders (SIMRAD EK60/EK80), operating at 0.256 μs pulse duration with a 10° and 7° beam-angle, respectively. The transducers were deployed from a pole mount, approximately 1 m below the surface. Echosounder surveys were primarily used as a tool to identify areas of increased fish biomass for camera (URUV and drop camera) surveys. Specifically, an adaptive sampling approach was implemented, where echosounder data were monitored for the presence of backscatter indicating fish aggregations, and cameras were immediately deployed when elevated backscatter was observed. The URUV system consisted of a weighted (10 kg of lead weights) aluminum tripod, with three GoPro Hero 3 action cameras (170° horizontal field of view). The cameras were mounted on a platform attached to the top of the tripod, that allowed for 360° viewing of the surrounding habitat. The overall height of the URUV was approximately 1 m, to allow for unobstructed viewing over low lying visual obstructions (Supplementary Material). GoPro Hero 3 action cameras were also used for drop camera surveys. The three cameras were arranged on a weighted



pipe to create a 360° video and deployed over the side with polypropylene rope. The pipe was deployed to the bottom, then recovered to suspend approximately 1–2 m over the substrate while the survey vessel held position over the site. Data collected during camera deployments were processed by a trained analyst proficient in reef fish identification, and the presence of aggregating target species was recorded along with additional reef fish species relative abundance (based on the maximum number of conspecifics seen in a single frame) (Ellis and DeMartini, 1995).

Fisheries observer surveys consisted of on-water surveys aboard a charter fishing vessel. The observer recorded fishing pressure and landings at the reported aggregation, and reproductive state of fish that were harvested using standard

gonad assessment protocols consistent with Lowerre-Barbieri et al. (2011). In addition to on-water surveys, participating charter fishers were interviewed upon returning from fishing activities and the reproductive state of harvested fish was assessed. Biweekly interviews were made during the aggregation period to confirm the occurrence of aggregation activity and consisted of general questions related to: (1) the targeted species, (2) locations and timing of any aggregations observed, (3) depth where aggregation fishing took place, (4) observations of milt or eggs flowing from captured fish, (5) size of aggregation(s), (6) age of report (i.e., when did they see an aggregation relative to when they were interviewed), (7) a general description of habitat where aggregations were observed (e.g., artificial reef or natural reef), (8) and observations of notable behaviors exhibited by aggregating fish (**Supplementary Material**).

RESULTS

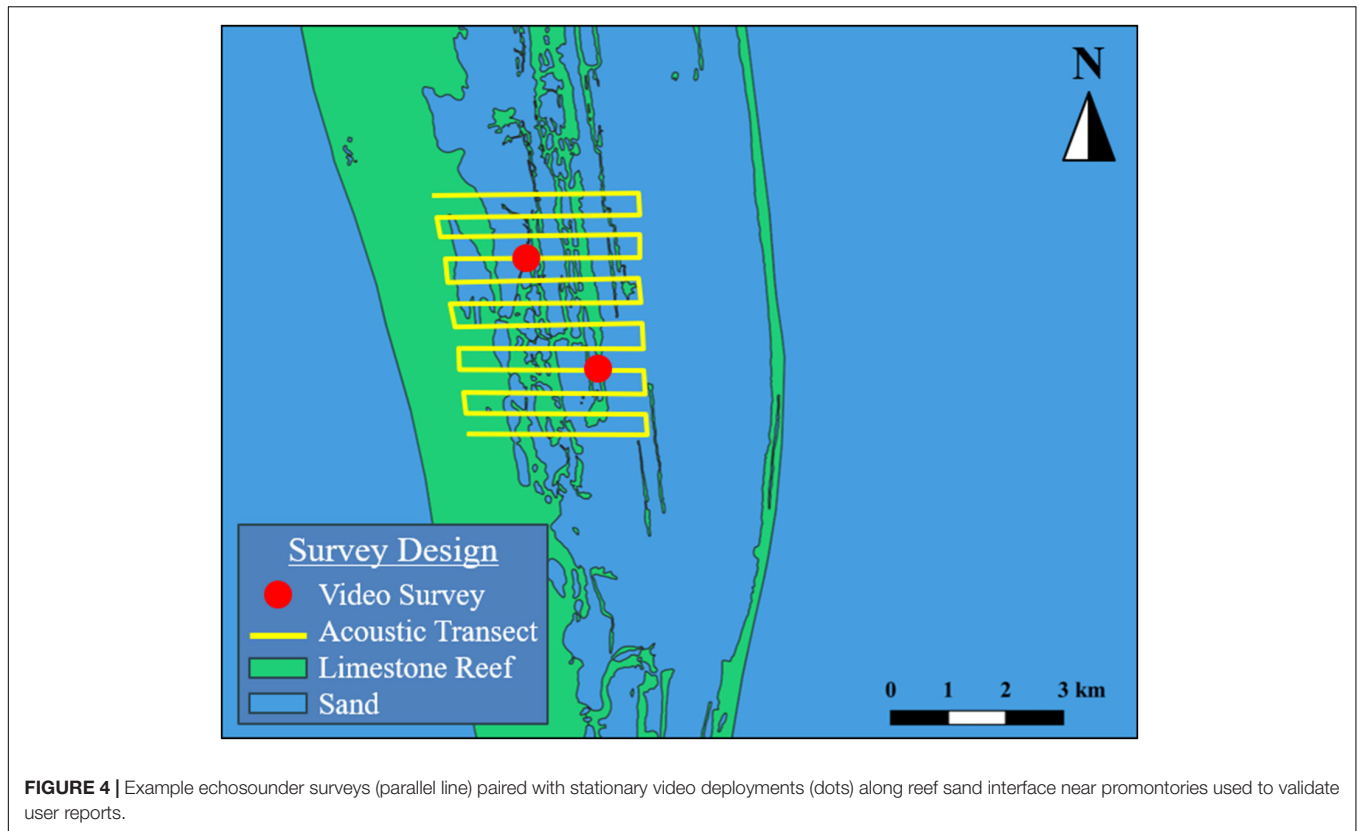
Literature Review

Between the three Web of Science queries conducted, 178 articles were identified. Several of these articles were represented in multiple queries, reducing the total unique sources to 116 peer-reviewed journal articles (**Table 2**). Only 27 of these studies related to the target species, 24 of which were conducted outside of our current study region. The three remaining articles focused on mutton snapper age, growth, and mortality (Burton, 2002); and the life history, movement and management of gray snapper (Faunce and Serafy, 2007; Luo et al., 2009). No articles pertaining to the target species spawning in the ECA were identified, but eight articles related to spawning were identified from other regions in the coastal United States (i.e., Gulf of Mexico and South Atlantic). Nine additional Florida-centric references offer insight into the life history, management, movement, spawning, and general ecology of the study species and those grouper and snapper found in the ECA that are taxonomically similar (**Table 3**). Goliath grouper are not among the target species in this review, but they are known to spawn in the ECA. Seven studies characterizing aspects of goliath grouper life history, management, movement, spawning, and ecology were identified by our queries, four of which were conducted in the ECA. Black and red grouper were also excluded from our synthesis due to an absence of aggregation reports in the study region, but 11 studies characterizing their life history, management, movement, spawning, and ecology were identified. Those studies were conducted near the West Florida Shelf, Dry Tortugas, Florida Keys, Puerto Rico, and US Virgin Islands.

Five articles describing hogfish life history, movement and habitat use in the eastern Gulf of Mexico, Eastern United States, and Florida Keys were identified outside of the Web of Science query, but information pertaining to spawning in the ECA is absent from the literature.

Unpublished Theses

Potential spawning locations for various snapper species along the east coast of Florida were identified by



Tishler-Meadows (2012) who presented a survey that capitalized on fishers' ecological knowledge and identified 51 potential spawning locations for red snapper (*L. campechanus*) (27), gray snapper (19), mutton snapper (8), cubera snapper (6), and vermilion snapper (3). Nine of the reported aggregations were considered multi-species aggregations, four of which occurred just beyond the northern extent of the ECA. Species included in these aggregations were gray and mutton snapper (3), and gray, mutton and cubera snapper (1). Eight gray snapper aggregations, nineteen mutton snapper, and three cubera snapper aggregations were reported to occur within the northern extent of the ECA. Due to confidentiality agreements with fishers, the precise location of reported aggregations were not presented, thus it is uncertain whether all the reported aggregations lie within the ECA. Direct evidence of spawning (gametes released in water column) was only observed at two of the reported spawning sites (gray snapper), but advanced stage gonadal development was observed at 49 of the reported sites (all species). Reproductive seasonality varied for all species when compared to conspecific spawning periods in other regions throughout the United States and Greater Caribbean, but reports peaked between June and July, and ranged from April to September (Table 4).

Towne (2018) examined age and growth of hogfish in southeast Florida. The field effort was limited in scope, and focused on the expected peak of the spawning season between March and May (McBride and Richardson, 2007). Evidence of spawning in the ECA was presented, based on observations of

courtship behavior by divers. Personal communication with the author (i.e., Towne) confirms that both male and female hogfish had fully developed gonads during the spring season, based on a macroscopic assessment of reproductive stage from harvested specimens. This interpretation is consistent with the observed spawning period identified in the Florida Keys, Puerto Rico, and eastern Gulf of Mexico (Colin, 1982; McBride and Richardson, 2007; Muñoz et al., 2010; Collins and McBride, 2015). Four additional reports related to hogfish were identified, including the most current Southeast Data, Assessment, and Review (SEDAR) hogfish stock assessment (SEDAR 37) (Cooper et al., 2012). An addendum to SEDAR 37 was released in 2018, though this pertained to the West Florida Shelf hogfish stock (Addis et al., 2018). Information related to spawning in the study area was absent from the identified reports.

User Reports

From 2014 through 2016, 13 potential aggregations were identified for the five different study species, between the southern extent of Miami-Dade County and the northern extent of Martin County (Table 5 and Figure 3). Reports were collected from long-time professional fishers (>10 years of experience) and members of the South Atlantic Fisheries Management Council with connections to the fishing community. Reports were also provided by state and federal fisheries biologist that work primarily with the focal species. Goliath grouper spawning aggregations in Palm Beach County were identified by resource users as economically and ecologically important, and have

TABLE 2 | All web of science query results.

Query	Cross-reference	Citation	Relevancy	Subject	
FSA + Florida		Adams et al., 2009. <i>Mar Eco Prog Series</i> . 389: 213–222	I		
		Aguilar-Perera, 2004. <i>Proc of the 55th GCFI</i> . 543–556	I		
		Allee et al., 2012. Seafloor Geomorphology as Benthic Habit. 435–448	II and V	MG and S	
		Baumberger et al., 2010. <i>Copeia</i> . (1): 41–46	I		
		Bryan et al., 2015. <i>Env Bio of Fishes</i> . 98(11): 2,263–2,276	I		
		Bueno et al., 2016. <i>J of Fish Bio</i> . 89(1): 876–889	II and III	S	
		Buitrago et al., 2006. <i>Estuarine Coastal and Shelf Sci</i> . 66(3–4): 634–642	I		
		Burton, 2002. <i>Fish Res</i> . 59(1–2): 31–41	V	LH and MG	
		Carson et al., 2011. <i>Fishery Bul</i> . 109(4): 416–428	II and V	MV and E	
		Manuel Castro-Perez et al., 2018. <i>Latin Amer J of Aquatic Res</i> . 46(4): 717–726	II and IV and V	F	
		Chiappone et al., 2000. <i>Mar Eco Prog Series</i> . 198: 261–272	II	MG	
		Coleman et al., 2011. Pro Geo. 63(4): 456–474	II and IV	S and MG	
		D'Alessandro et al., 2010. <i>Mar Eco Prog Series</i> . 410: 159–175	II and V	LH	
		Danylchuk et al., 2011. <i>Mar Bio</i> . 158(9): 1,981–1,999	I		
		Domeier, 2004. <i>Fish Oceanography</i> . 13(5): 287–294	I		
		Donahue et al., 2015. <i>Plos One</i> . 10(6)	II and IV	LH and S	
	6		Eklund et al., 2000. <i>Bul of Mar Sci</i> . 66(3): 721–728	III	S
	5		Farmer and Ault, 2011. <i>Mar Eco Prog Series</i> . 433: 169–184	II and IV	MV
	4		Farmer and Ault, 2018. <i>Canadian J of Fish and Aquatic Sci</i> . 75(3): 375–388	II and IV	MV
			Farmer et al., 2017. <i>Plos One</i> . 12(3)	II and V	S and MG
			Feeley et al., 2009. <i>J of Fish Bio</i> . 74(10): 2,415–2,421	I	
			Feeley et al., 2018. Fish Res. 204: 209–223	II and V	S and MG and MV
			Fitzhugh et al., 2005. <i>Bul of Mar Sci</i> . 77(3): 377–396	II and V	LH and MV
			Flaherty et al., 2014. <i>Estuaries and Coasts</i> . 37(1): 206–228	II and V	MV and E
			Frias-Torres, 2013. <i>Oryx</i> . 47(1): 88–95	III	
	7		Gleason et al., 2011. Pro Geo. 63(4): 443–455	II and IV	S
			Gledhill and David, 2004. <i>Proc of the 55th GCFI</i> . 614–625	II	MG
			Grüss et al., 2018. <i>Scientific Reports</i> . 8	II and IV	S and MG
			Hare and Walsh, 2007. <i>Canadian J of Fish and Aquatic Sci</i> . 64(9): 1,234–1,247	I	
			Hernandez et al., 2013. <i>Ices J of Mar Sci</i> . 70(3): 628–635	I	
			Holt, 2008. <i>Trans of the Amer Fish Soc</i> . 137(2): 551–561	I	
			Koenig et al., 2011. <i>Bul of Mar Sci</i> . 87(4): 891–911	III	MG and E
			Koenig et al., 2000. Bul of Mar Sci. 66(3): 593–616	II	MG and S
	8		Koenig et al., 2017. <i>Bul of Mar Sci</i> . 93(2): 391–406	III	S and E
			Leichter et al., 2008. <i>Mar Eco Prog Series</i> . 356: 123–138	I	
	2		Lindeman et al., 2000. <i>Bul of Mar Sci</i> . 66(3): 929–956	IV	LH and MG and S
			Locascio and Mann, 2011. <i>Fishery Bul</i> . 109(3): 327–338	I	
			Lowerre-Barbieri et al., 2016. <i>Eco App</i> . 26(4): 979–995	I	
			Lowerre-Barbieri et al., 2003. <i>Trans of the Amer Fish Soc</i> . 132(5): 940–952	I	
			Mann et al., 2016. <i>Listening in the Ocean</i> . 309–324	II	E
			McGovern et al., 2005. <i>Bul of Mar Sci</i> . 76(1): 47–59	III	MV
			Molloy et al., 2009. <i>Mar Eco Prog Series</i> . 392(): 253–262	II	
		Muñoz et al., 2010. Bul of Mar Sci. 86(1): 93–116	II and V	MV and MG and S and E	
		Murchie et al., 2012. <i>Telemetry Techniques</i> . 389–412	I		
		Nelson et al., 2011. <i>Aquatic Bio</i> . 12(2): 97–108	II and III	E	
		Paris et al., 2005. <i>Mar Eco Prog Series</i> . 296: 93–106	I		
		Peebles et al., 1996. <i>Mar Eco Prog Series</i> . 131(1–3): 61–73	I		
		Potts and Burton, 2017. <i>Peerj</i> . 5	III	LH	
		Provancha and Hall, 1991. <i>Env Bio of Fishes</i> . 31(1): 41–54	I		
		Reed et al., 2007. <i>Bul of Mar Sci</i> . 81(3): 481–496	I		
		Reed et al., 2005. <i>Cold-Water Corals and Ecosystems</i> . 443–465	II		
		Rowell et al., 2012. <i>Mar Eco Prog Series</i> . 462: 241–250	I		
		Sadovy de Mitcheson et al., 2013. <i>Fish and Fish</i> . 14(2): 119–136	II and IV	MG	

(Continued)

TABLE 2 | Continued

Query	Cross-reference	Citation	Relevancy	Subject
Spawning + Florida + Grouper		Sanchez et al., 2017. <i>Fishery Bul.</i> 115(2): 186–195	III	S and E
		Saucier and Baltz, 1993. <i>Env Bio of Fishes.</i> 36(3): 257–272	I	
		Saul et al., 2013. <i>Fish Res.</i> 143: 12–20	II	
		Sedberry et al., 2001. <i>American Fisheries Symposium.</i> 25: 3–23	II	
		Shulzitski et al., 2009. <i>Fishery Bul.</i> 107(4): 501–509	II and V	MV
		Switzer et al., 2015. <i>N Amer J of Fish Mgmt.</i> 35(6): 1,132–1,143	II and V	LH and E
		Taylor et al., 2001. <i>N Amer J of Fish Mgmt.</i> 21(1): 70–75	I	
		Todd et al., 2014. <i>J of Mar Res.</i> 72(6): 445–475	I	
		Tupper, 2002. <i>Proc of the 53rd GCFI.</i> 606–622	II	MG
		Tzadik et al., 2017. <i>Estuaries and Coasts.</i> 40(6): 1,785–1,794	III	LH
		Wall et al., 2014. <i>J of Fish Bio.</i> 85(5): 1,470–1,488	III	MV and E
		Walters et al., 2009. <i>Trans of the Amer Fish Soc.</i> 138(1): 88–98	I	
		Walters et al., 2013. <i>Mar Eco Prog Series.</i> 479: 191–202	I	
		Woodson, 2018. <i>Annual Review of Mar Sci.</i> 10: 421–441	I	
		Young et al., 2014. <i>Mar Eco Prog Series.</i> 505: 227–240	I	
		Young et al., 2016. <i>Trans of the Amer Fish Soc.</i> 145(2): 400–415	I	
		Barbour and Adams, 2012. <i>Mar Eco Prog Series.</i> 457: 241–250	I	
		Bullock and Murphy, 1994. <i>Bul of Mar Sci.</i> 55(1): 30–45	II and III	LH
		Crabtree and Bullock, 1998. <i>Fish Bul.</i> 96(4): 735–753	III	LH and S
		Degidio et al., 2017. <i>N Amer J of Aquaculture.</i> 79(3): 205–215	I	
		Gilmore and Jones, 1992. <i>Bul of Mar Sci.</i> 51(1): 83–103	II and V	E
		Gruss et al., 2017. <i>Fish Res.</i> 193: 129–142	II and III and IV	LH and MV
		Kadison et al., 2017. <i>Plos One.</i> 12(7)	II and III	MG
		Mann, 2016. <i>Effects of Noise on Aquatic Life.</i> 875: 673–678	I	
		Marancik et al., 2012. <i>Fish Bul.</i> 110(1): 1–20	II and III	LH and MV
		Nelson et al., 2012. <i>Mar Bio.</i> 159(2): 365–372	I	
		Pichorim and Suzuki, 2015. <i>Oceans 2015 – Genova.</i>	III	MG
		Porch et al., 2006. <i>Fish Bul.</i> 104(1): 89–101	III	MG
		Renan et al., 2016. <i>Trans of the Amer Fish Soc.</i> 145(6): 1,252–1,265	II and V	MG
		3 Shideler and Pierce, 2016. <i>Ocean and Coastal Mgmt.</i> 129: 36–43	III	MG and F
		Strelcheck et al., 2003. <i>Fish Res.</i> 60: 255–265	II and V	LH
		Wall et al., 2011. <i>Mar Eco Prog Series.</i> 431: 243–254	II and III	MV and S and E
		Weisberg et al., 2014. <i>Continental Shelf Res.</i> 88: 11–23	II and V	LH
	Ziskin et al., 2011. <i>Trans of the Amer Fish Soc.</i> 140(2): 384–398	II and III	MG	
Spawning + Florida + Snapper		Allman and Grimes, 2002. <i>Fish Bul.</i> 100(3): 391–403	II and V	LH and MV
		Amezcuea et al., 2006. <i>Fish Res.</i> 77(3): 293–300	I	
		Ault et al., 1998. <i>Fishery Bul.</i> 96(3): 395–414	I	
		1 Bohnsack et al., 1994. <i>Bul of Mar Sci.</i> 54(3): 982–1,018	II	F
		Burton et al., 2005. Fishery Bul. 103(2): 404–410	II and V	S
		Collins et al., 2003. <i>Proc of the 54th GCFI.</i> 580–591	I	
		Denit and Sponaugle, 2004. Trans of the Amer Fish Soc. 133(6): 1,339–1,355	II and V	LH and S
		Faunce and Serafy, 2008. <i>Estuarine Coastal and Shelf Sci.</i> 79(1): 93–100	V	LH and E
		Garlock et al., 2017. <i>Fish Res.</i> 186: 460–467	I	
		Hostetter and Munroe, 1993. <i>Fishery Bul.</i> 91(1): 45–64	I	
		Johnson et al., 2013. <i>Trans of the Amer Fish Soc.</i> 142(1): 50–58	I	
		Jue et al., 2014. <i>Mar Bio.</i> 161(8): 1,905–1,918	II and V	E
		Karnauskas et al., 2017. <i>Mar and Coastal Fish.</i> 9(1): 50–67	I	
		Le Port et al., 2014. <i>Mar Eco Prog Series.</i> 515: 203–215	I	
		Lee et al., 1994. <i>Bul of Mar Sci.</i> 54(3): 621–646	II	LH
		9 Locascio and Burton, 2016. <i>Fishery Bul.</i> 114(1): 103–116	II and III	S and E
		Luo et al., 2009. <i>Mar Eco Prog Series.</i> 380: 255–269	V	MV
	Manooch et al., 1998. <i>Fish Res.</i> 38(1): 19–32	I		

(Continued)

TABLE 2 | Continued

Query	Cross-reference	Citation	Relevancy	Subject
		McGovern et al., 2002. N Amer J of Fish Mgmt. 22(4): 1,151–1,163	I	
		McGovern et al., 1998. Fishery Bul. 96(4): 797–807	II and V	LH
		Nadon et al., 2015. Plos One. 10(8)	I	
		Pinkard and Shenker, 2001. Amer Zoologist. 41(6): 1,556–1,557	I	
		Powell, 2003. Fish Bul. 101(3): 704–711	I	
		Powell et al., 2004. Fishery Bul. 102(1): 142–155	I	
		Rotman et al., 2003. World Aquaculture Society	I	
		Saillant et al., 2010. Ices J of Mar Sci. 67(6): 1,240–1,250	I	
		Turano et al., 2000. J of the World Aquaculture Soc. 31(1): 59–68	I	
		Vaughan et al., 1998. Fishery Stock Assessment Models. 15: 121–136	I	
		White and Palmer, 2004. Bul of Mar Sci. 75(3): 335–360	I	

Cross-reference numbers correspond to citations seen in Table 3. Bold citations relate to spawning in the United States but not the Southeast Florida Coral Reef Initiative Ecosystem Conservation Area. Roman numerals within relevancy have been divided into five categories.

I, irrelevant to study; II, out of study region; III, not related to target species; IV, multi-species spawning information; V, related to target species. Subject codes correspond to E, ecology; F, fishing; LH, life history; MG, management; MV, movement; S, spawning.

TABLE 3 | Literature related to target and non-target (taxonomically similar) species found in Florida.

Subject	Region	Species	Citation
Fisheries	Florida keys	Mixed assemblage	Bohnsack et al., 1994
Life history–Management–Spawning	Key West–Dry Tortugas	<i>Mycteroperca</i> Spp.	Lindeman et al., 2000
Management–Fisheries	Jupiter	<i>Epinephelus itajara</i>	Shideler and Pierce, 2016
Movement	Dry Tortugas	<i>Mycteroperca bonaci</i> <i>Lutjanus analis</i>	Farmer and Ault, 2018 Farmer and Ault, 2011
Spawning	Florida keys	<i>Mycteroperca bonaci</i> <i>Mycteroperca bonaci–Lutjanus analis</i>	Eklund et al., 2000 Gleason et al., 2011
Spawning–Ecology	Jupiter Dry Tortugas	<i>Epinephelus itajara</i> <i>Mycteroperca bonaci–Epinephelus morio</i>	Koenig et al., 2017 Locascio and Burton, 2016

Mixed assemblages include species from the families Lutjanidae, Serranidae, Haemulidae, and Balistidae. Citations correspond to specific citations found in Table 2.

been reported here, but were not a priority study species identified by the SEFCRI due to the harvest moratorium currently in place. One vermillion snapper (*Rhomboplites aurorubens*) aggregation was also reported to occur during the summer months, but precise information pertaining to timing and location could not be verified, and it was not prioritized as a study species.

Spawning Aggregation Validation

Only three aggregations out of the 13 identified were reported to be active with precise spatial information and selected for field validation. A gag grouper aggregation reported to occur near Boynton Beach, Florida was not observed despite multiple attempts to confirm their presence during the expected reproductive season in 2016. Echosounder surveys ($n = 8$) were conducted over an approximately 60 km² region between January and March during full moon periods. URUV surveys ($n = 19$) were conducted at high relief reef locations where small schools were detected, though gag grouper were not observed in URUV data. Video data consistently revealed a mixed reef fish assemblage and high-density schools of tomtates (*Haemulon aurolineatum*) (Figure 5). Bi-weekly interviews with a collaborating SCUBA diving shop during

the 2016 and 2017 season ($n = 10$) also indicated that gag grouper were never seen aggregated at the suspected aggregation site.

Paired echosounder and URUV surveys near Jupiter, Florida were also used to validate a reported gray snapper aggregation occurring over a discrete natural reef area (approx. 1.5 km²), between July and September 2016 ($n = 6$). No areas of concentrated backscatter were identified by echosounders, but URUV ($n = 5$) and drop camera surveys ($n = 5$) were performed near high-relief reef-sand interfaces (i.e., promontories), where gray snapper were expected to aggregate. Gray snapper were not observed in videos, and subsequent resource user interviews indicated that gray snapper in the study area are not often isolated to discrete regions as described by the original source.

A cubera and mutton snapper aggregation was reported to occur offshore of Homestead, Florida. The report indicated that the aggregations occurred annually from April to July (mutton snapper), and August–September (cubera snapper) during full moons. However, the mutton snapper aggregation had not been reported as active for several years, and both FSAs were heavily fished since the early 2000's (no specific date could be provided). Researchers joined a recreational fishing charter on

TABLE 4 | Spawning seasonality for study species found in the Southeast Florida Coral Reef Ecosystem Conservation Area.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Sources
Grouper													
Gag	█	█	█	█									Koenig et al., 2000
*Black	█	█	█										Koenig et al., 2000
*Goliath							█	█	█	█			Koenig et al., 2017
Snapper													
Cubera					█	█	█	█	█				Lindeman et al., 2000
Gray					█	█	█	█	█				Lindeman et al., 2000
Mutton					█	█	█	█	█				Lindeman et al., 2000
hogfish	█	█	█	█	█	█	█						Towne, 2018

Regions in gray denote the reported spawning season, while black boxes indicate peak periods in spawning activity.

*Black and goliath grouper were not focal species, but due to their occurrence in the study region, spawning seasons have been included. An example source has been provided, though others can be found in the literature.

TABLE 5 | Anecdotal reports of spawning aggregations in the Southeast Florida Coral Reef Ecosystem Conservation Area collected between 2014 and 2016.

Species	Location	Depth	Seasonality	Type	FSA Size	Age of report
<i>Lutjanus analis</i>	Homestead	60 m	April–July	Spawning	10’s–100’s	1990’s–present
	Discrete aggregation occurs over known artificial reef and has been heavily targeted for years. The report indicates that the duration and catchability of snapper has declined in recent years. This is also a multi-species aggregation site <i>Lutjanus cyanopterus</i>					
<i>L. cyanopterus</i>	Homestead	60 m	Aug–Oct	Spawning	10’s–100’s	1990’s–present
	This is a multi-species aggregation site (<i>L. analis</i> ; above). The aggregation has been heavily targeted for years, and a decline in catchability and the duration of aggregation occurrence has decreased					
	Jupiter	5 m	June–Oct	Pre-spawning/unknown	<100	2010–present
	A range of sizes are seen aggregating in Jupiter Inlet coincidentally with common snook aggregations. Individuals are reported to average 75 cm total length					
<i>L. griseus</i>	Miami	20 m	June–Sept	Spawning	100’s–1,000’s	2010–present
	Aggregations are reported to form near natural limestone reefs southeast of Government Cut. Aggregations do not exhibit high site fidelity					
	Fort Lauderdale	20 m	Aug–Sept	Spawning	100’s–1,000’s	2010–present
	Aggregations occur near natural limestone reefs. Targeted by recreational charters at night. Information on site fidelity is unknown					
	Jupiter	20 m	June–Sept	Spawning	100’s–1,000’s	2010–present
	Aggregations are reported to form near natural limestone reefs. Aggregations do not exhibit high site fidelity					
<i>Lachnolaimus maximus</i>	Fort Lauderdale	5–20 m	March–May	Spawning	<20	2016–present
	Small aggregations were observed on reef features across a wide range of depths. Reports indicate that individual length and aggregation size (abundance) increased with depth					
<i>Epinephelus itajara</i>	West Palm Beach–Jupiter	15–45 m	July–October	Spawning	<100	1980’s–present
	Well documented aggregations occur on natural and artificial reefs throughout Palm Beach and Martin County					
<i>Mycteroperca microlepis</i>	Boynton Beach	10–20 m	Jan–April	Pre-spawning/Spawning	≤100	1970’s–present
	Believed to be pre-spawning aggregations comprised of a range of sizes. Multiple aggregations have been reported on natural and artificial reefs at various depths. Their occurrence has declined in recent years, despite the annual harvest restrictions					
<i>Rhomboplites aurorubens</i>	Fort Lauderdale	20–30 m	May–September	Unknown	100’s–1,000	2015
	Aggregation’s reportedly form on artificial reefs south of Port Everglades. Only one source available and has not been validated					

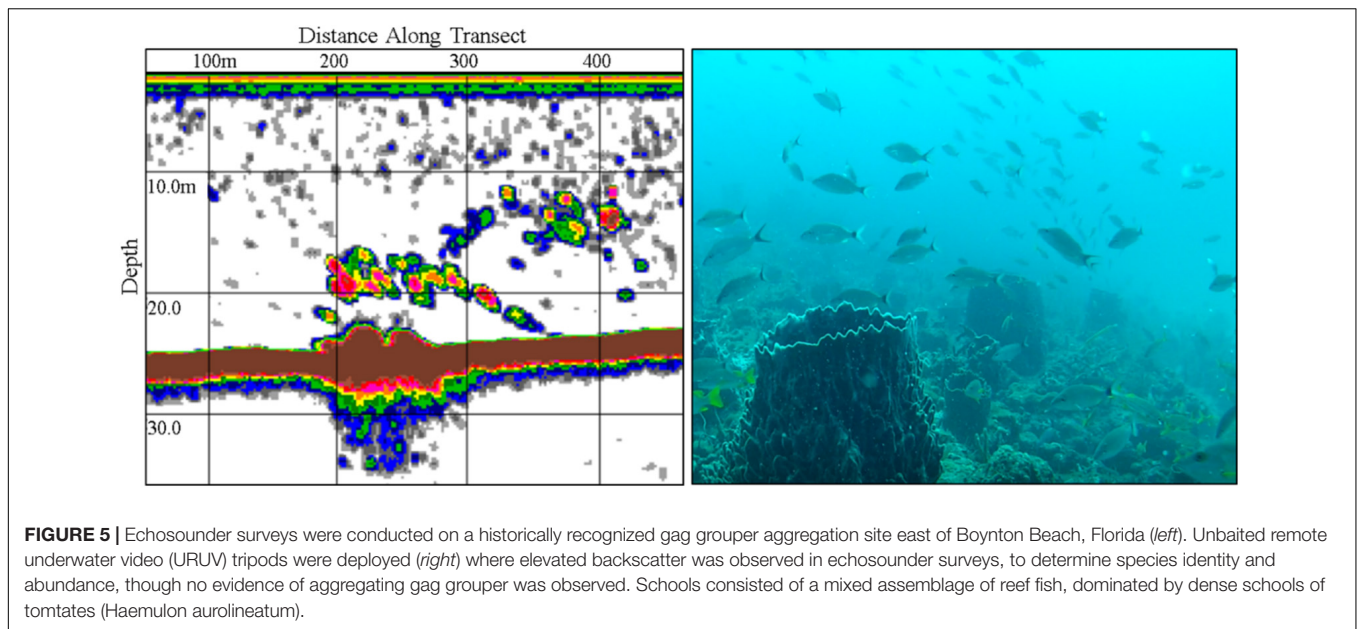
Aggregation descriptions are included.

two occasions, in August 2014 and 2015, during full moon overnight fishing charters to confirm the occurrence of the cubera snapper FSA. Biweekly interviews were also conducted to assess the status of the cubera snapper aggregation. During field surveys, eight mature cubera snapper were captured (four each year), and four were harvested (two from each year). All eight fish were >80.0 cm total length, and the four harvested cubera snapper were spawning capable males with fully ripe gonads, qualified using the classification system developed by Domeier and Colin (1997). Surveys were not conducted in

September of 2014 and 2015, or in the 2016 season, based on reports from the charter captain that the aggregations had not formed.

DISCUSSION

Information related to commercially and recreationally important snapper and grouper reproduction (specifically spawning aggregations) in the ECA is essentially absent from



the peer-reviewed literature based on our Web of Science queries and a thorough review of additional primary and gray literature sources. No research specifically characterizing the spatial aspects of spawning aggregation formation (for the focal species), and their seasonality in the ECA was identified. However, numerous literature sources describing spawning seasonality in other regions were available and used to develop a calendar to forecast FSA seasonality, which showed a high degree of overlap with the reports of FSA occurrence provided by fishers. The information available in the literature was primarily limited to research describing life-history, movement, and seasonality of reproductive development. Thus, the paucity of data identified is likely an accurate reflection of the state of FSA science in the ECA.

When compared to the number of current and historical aggregations reported throughout the region by users, it is clear that a focused effort is required to confirm the presence of and characterize the state of regional FSAs that may still occur. Considering the high degree of spatiotemporal variability associated with FSA formation, it is not unreasonable to presume that aggregations were missed by our field and interview approach, which were dependent on up-to-date user reports distributed over a large geographical area for many species. While user reports do offer the highest spatial and temporal resolution, a lack of reports is not necessarily sufficient evidence to conclude that aggregations are not occurring in the reported region. This is exceptionally true in cases where users are not actively targeting the species of interest. For example, the gag grouper fishery is closed from January through April to protect their populations from exploitation during the reproductive season². This precluded any targeted fishing by commercial and recreational anglers during the study period, which may

²<https://safmc.net/regulations/regulations-by-species/gag-grouper/>

have produced spawning reports useful to our field efforts had the fishery been open. Thus, in the case of the reported gag grouper aggregation near Boynton Beach, Florida, we were solely dependent on SCUBA diving charter reports and our own exploratory field surveys across a wide expanse of continuous reef. Had the commercial and recreational fishing community been targeting the inshore gag grouper fishery at the time, it is possible that field survey efforts may have been more successful.

Fish Spawning Aggregations have also been historically reported to occur near natural and artificial promontories, which function as recurrent spawning sites for various species. Indeed, spawning aggregations have been found near promontories in the Florida Keys (Feeley et al., 2018), northeast Florida (Koenig et al., 2000), and west Florida (Coleman et al., 1996), while in contrast, there are fewer promontories along the northern extent of the Florida Reef Tract, and fewer confirmed reports of spawning aggregation occurrence. This may explain why aggregations reported to occur in the study region are difficult to locate and exhibit lower site fidelity (i.e., they are not concentrated on discrete features). Furthermore, while high relief features do occur along the northern extent of the Florida Reef Tract, some features that may be ordinarily attractive to aggregating species occur beyond their typical spawning depths. For example, Tishler-Meadows (2012) reported gray snapper aggregations at depths between 15 and 60 m, but this is deeper than reported spawning depths in Florida Keys, Dry Tortugas, and Cuba (9–37 m) (Domeier and Colin, 1997; Lindeman et al., 2000; Claro and Lindeman, 2003).

In addition to abiotic considerations, species-specific reproductive behaviors and regional differences may further hinder our ability to detect aggregations. For instance, gray snapper aggregations are known to be less predictable in time and space, as they spawn repeatedly over protracted time periods and exhibit lower fidelity to discrete locations

(Domeier and Colin, 1997; Sadovy De Mitcheson et al., 2008; Farmer et al., 2017). They may form aggregations on large swaths of reef for short periods of time and inadvertently avoid exploitation because their occurrence is unpredictable, brief, and their movements are frequent. Even with respect to species that typically form predictable aggregations in discrete areas (i.e., mutton and cubera snapper), detection along continuous reefs has been historically difficult. For example, a black grouper aggregation was observed on one occasion by researchers near Key Largo, Florida (Eklund et al., 2000), but a subsequent study between 2008 and 2012 was only able to re-locate the aggregation on one occasion, despite repeated diver surveys paired with echosounder surveys over the 4 years period (Taylor et al. Unpubl. data).

Anthropogenic factors may also explain why FSAs have remained undetected and thus understudied in the ECA. Specifically, FSA identification (initial detection by managers and scientists), and subsequent investigation, has typically been tied to reports from resource users participating in targeted aggregation fishing activities that have occurred over extended periods. Drawing from examples found in the literature, aggregation fishing had occurred for extended periods, and only after decreases in catches became noticeable to resource users, did reports reach fisheries managers and scientists. At that point, most of the aggregations reported in the literature were overfished, extirpated, or were suffering substantial losses due to on-going fishing activities (Luckhurst, 1998, 2010; Burton et al., 2005; Nemeth, 2005). In the context of reports gathered during this study, only the cubera and mutton snapper aggregations identified near Homestead, Florida were reported by fishers as heavily fished, and had been for over a decade (*Binder personal comm.*). The user indicated that both cubera and mutton snapper abundance at the aggregation site had decreased steadily over a 10-years period and indicated that management intervention was needed to protect the two resources.

No users indicated that aggregating species in the ECA were consistently fished beyond the two reported cases. Indeed, despite the generally high pressure exerted on fishery resources in south Florida, specifically the snapper and grouper fisheries, very little evidence of on-going aggregation fishing was documented. A paucity of information in the media (i.e., newspapers and social media) also suggests that aggregating species are not exposed to aggregation fishing activity within the ECA. Conversely, media sources (newspaper, radio broadcast, and social media) and charter fishing services widely publicize and offer permit and mutton snapper aggregation fishing opportunities in the Florida Keys, which have resulted in heavy fishing pressure during spring and summer full moon periods at discrete FSA sites. Thus, it is plausible that the variability of aggregation occurrence, which is driven by ephemeral hydrodynamic events (i.e., current changes, upwelling, etc.) and the heterogeneous landscape (i.e., limited promontories and expanses of continuous reef interspersed with sandy substrate), mitigates aggregation fishing activity in the ECA.

Potentially the largest obstacle hindering effective FSA assessments and effective conservation has been the lack of real-time data streams in regions of concern (Kobara et al., 2013). Reports from resource users, that make their

livelihoods using coastal resources, offer a wealth of real-time information collected over expansive geographical areas (Gerhardinger et al., 2006). Additionally, individuals from the local fishing community are capable of tracking fine-scale changes in environmental factors, using decades of experience (in some cases), to interpret environmental conditions that dictate where target fish schools may be on a given day. Indeed, numerous studies have successfully utilized local and traditional knowledge from fishers to achieve a baseline understanding of the spatial and temporal dynamics of aggregations (Johannes, 1978; Lindeman et al., 2000; Sadovy De Mitcheson et al., 2008; Freitas et al., 2011), and invested resource users have contributed directly to the recovery of FSAs throughout the United States and Greater Caribbean (Lindeman et al., 2000; Burton et al., 2005; Nemeth et al., 2006; Feeley et al., 2018).

Fish Spawning Aggregations represent “hotspots” of fish production during ephemeral periods in time and space that often support multiple aggregating spawning species, and play a role in promoting overall ecosystem health through the stimulation of fish biomass and biodiversity (Schärer et al., 2010; Archer et al., 2015; Grüss et al., 2018). Unfortunately, FSAs also represent attractive targets to fishers, and there are many cases of decline and extirpation after extended periods of excessive fishing (Sadovy De Mitcheson et al., 2008). An erosion of trust between resource users and managers has resulted in challenges assimilating their knowledge into assessments and management process (Boonstra and Nhung, 2012; Jagers et al., 2012). The SEFCRI was specifically created to bridge that gap between resource users and managers and develop effective long-term solutions to coastal and fisheries management issues. Cooperation between users and managers that result in actionable reports from users for field investigations are essential to the future of integrated fisheries management, especially with respect to protecting FSAs. The approach presented here is an important first step toward understanding the spatiotemporal dynamics of regional FSA occurrence, and represents a thorough synthesis of information describing the state of knowledge for recreational and commercially important aggregating species found in the ECA. These data can be used to inform future management plan development, and we hope that these data will be used as a framework for future studies focused on improving our understanding of FSA dynamics in south Florida.

DATA AVAILABILITY STATEMENT

The identity of resource users and precise locations of reported aggregations are not provided due to the sensitivity of this material. The data layers described herein can be found at: <https://www.arcgis.com/apps/webappviewer/index.html?id=0825dda753674dabbd184ea5cae8a8c8&extent=-9381939.8924%2C2833900.6103%2C-8442681.6888%2C3250941.0367%2C102100>.

AUTHOR CONTRIBUTIONS

BB gathered reports, carried out fieldwork and prepared the manuscript. JT NOAA partner assisted with the manuscript

preparation. KG SEFCRI partner assisted with the manuscript preparation. KB project principal investigator advised BB (Ph.D. student) and assisted with manuscript preparation. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.671477/full#supplementary-material>

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Conflict of Interest: KG was employed by ERT Inc. during the time of field data collection and manuscript preparation.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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