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INVITED REVIEW

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Biophysical connectivity of snapper spawning aggregations and marine protected area management alternatives in Cuba

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Abstract

The ability of larvae to move beyond the spatial range of adult migrations can be critical to the resilience of populations that aggregate to spawn. We reviewed the literature and unpublished information on larval transport modeling, reef fish spawning aggregations, and marine protected area (MPA) management to identify alternatives for Cuban spawning site conservation. Larval transport information is available at annual and decadal scales for eight Cuban sites for five species of snappers. Connectivity patterns were examined: (a) within Cuban regions, (b) among Cuban regions, and (c) among other countries. We compared this information with the distribution of protected areas relative to spawning sites, site management attributes, and potential alternatives. Of eight focal spawning sites, seven are in protected areas and one is proposed. Southeast and north-central Cuba had highest estimated within-region retention levels. Southwest and northwest sites exported relatively more larvae out-of-region. Southern regions produced larvae that reached Jamaica, the Cayman Islands and Haiti. All northern regions can export larvae to the southern Bahamas. The regions and sites within are geomorphologically diverse with variable fishing and socio-economic attributes. Information on stock status and protected area efficacy is limited and field assessments of aggregation status are needed for multispecies spawning sites. Few management plans address spawning conservation or network connectivity opportunities for MPAs. An alternative is development of one or more regional workgroups of protected area specialists, fishery scientists, expert fishers, and other stakeholders. Temporal closures of fisheries before and during spawning season could also amplify effectiveness of current gear- and zoning-based management tools.

KEYWORDS
connectivity, Cuba, larval transport, Lutjanidae, MPA, snapper, spawning aggregation

1 | INTRODUCTION

For many highly valuable snapper and grouper reef fisheries, annual aggregations for spawning are increasingly impacted by fishing with multiple demographic implications (Sadovy de Mitcheson et al., 2008; Sala, Ballesteros, & Starr, 2001). Spawning aggregations of snappers (Lutjanidae) support some of the most valuable reef fisheries in Cuba, with at least 20 spawning aggregation sites known for five species (Claro & Lindeman, 2003). The negative consequences of fishing spawning aggregations are documented in over 40 years of data by Cuban region: during the 1970s, snapper catches surpassed 7,500 metric tons (mt) annual and are currently >3,000 mt despite decades of management efforts (Claro, Sadovy de Mitcheson, Lindeman, & Garca-Cagíde, 2009; Claro & Valle, 2014).

Biophysical modeling of larval transport from known spawning sites has clarified fundamental dispersal patterns from primary Cuban snapper aggregations (Paris, Cowen, Claro, & Lindeman, 2005) including a decade of annual oceanographic variability (Kough, Claro, Lindeman, & Paris, 2016). However, most aggregations modeled in these studies remain fished before and during spawning (Claro et al., 2009). There is an opportunity to integrate these connectivity findings with Cuban spawning aggregation and marine protected area (MPA) management information to identify potential alternatives for managers.

Marine and coastal protected areas encompass approximately 25% (ca. 1,744,390 ha) of the Cuban shelf including estuaries, coastal lands, and marine open-water areas (CNAP, 2013), exceeding the 10% by 2020 challenge for MPAs globally under Aichi Target 11 of the Convention on Biological Diversity. The degree to which individual MPAs address IUCN and NOAA guidelines for management across biological, socio-economic and governance categories is often associated with local-scale identification of specific objectives (Pomeroy, Parks, & Watson, 2004). Cuban MPAs often have well developed planning structures with PA management objectives including biodiversity and socio-economic factors (Perera-Valderrama et al., 2018).

There is evidence of effective fishery protection in areas of the large Parque Nacional Jardines de la Reina (PNJDR; Pina-Amargós, González-Sansón, Martín-Blanco, & Valdivia, 2014). Puritz (2017) examined management effectiveness between PNJDR and PN Punta Frances (PNPF) concluding that potentially higher performance at JDR was primarily due to contributions of ecotourism to park management. Management effectiveness for other marine issues has also been assessed in PNPF (Angulo-Valdés & Hatcher, 2013). However, few MPA plans in Cuba address fishery spawning conservation and management effectiveness.

The Cuban MPA system is under the coordination of the National Center of Protected Areas (CNAP), with many MPAs co-managed by the National Enterprise for the Protection of Flora and Fauna (ENPFF; Hidalgo Ceruto, 2014; Perera-Valderrama et al., 2018) and other agencies. Fishery rule-making involves the Office of Fishery Regulation, Ministry of Food (formerly Industrial Fisheries). These agencies have also developed fishery management tools (e.g., net bans, size limits, effort limits) to improve protection of spawning areas and pre-spawning migrations (Claro, 2001; Claro & Lindeman, 2008; Claro et al., 2009) among efforts to resolve continuing declines in many Cuban fisheries (Baisre, 2018).

We reviewed existing oceanographic, fishery, and management information to: (a) detail connectivity patterns at three spatial scales: within Cuban regions, among Cuban regions and among other countries, (b) identify the distribution of managed areas relative to spawning sites, status of spawning aggregations, and site management attributes, and (c) integrate connectivity and MPA information to identify potential alternatives for fishery and protected area managers to better sustain these economic and ecological resources.

2 | CONNECTIVITY AND MANAGEMENT BY REGION AND SITE

Biophysical larval transport models have estimated regional snapper settlement and connectivity at annual and decadal scales for 8 of 20 known snapper spawning sites on the Cuban shelf (Kough et al., 2016; Paris et al., 2005). Models use spawning phenology and larval attributes, and estimate habitat effects using overlaid maps (Lindeman et al., 2006; Paris et al., 2005). Dispersal has been examined for *Lutjanus synagris* (lane), *L. analis* (mutton), *L. griseus*, *L. cyanopterus* and *L. jocu* (a grey-cubera-dog snapper complex was used in some cases for species that can share spawning sites and times, Kough et al., 2016). This information was compared to the distribution of each spawning area and the MPAs they are within (Figure 1) and to the aggregation status and fishery management attributes for the northern and southern coasts.

2.1 | Northwest Cuba

One spawning site was modeled following Paris et al. (2005) and Kough et al. (2016) in this region: Corona de San Carlos within the Archipiélago de Los Colorados. This site is used by four snapper and three grouper species (Claro & Lindeman, 2003). Mean retention, the proportion of settling larvae that originated within the same region, was 18% (3%–60% over years and species) over 10 years (Table 1), lowest of the four regions studied. In terms of export to other Cuban regions, the north-central received 10%–80% from the northwest over 10 years, the southwest also received occasional larvae. Larvae exported off-island from the northwest primarily travelled to the Bahamas (20%–80% annually, Table 1). There was limited export (0%–5%) across the Florida Current to Florida, occuring in 3 of 10 years (Kough et al., 2016).

2.1.1 | Corona de San Carlos

This area, 150 km west of Havana, is the most well known in the region and is a multispecies spawning site for lane, mutton, grey and cubera snapper and yellowfin (*Mycteroperca venenosa*), black (*M. bonaci*) and Nassau (*Epinephelus striatus*) grouper (Serranidae). There is some tourism in the area and commercial and subsistence fishing.

There may be management opportunities via the proposed Refugio de Fauna Cayo Levisa—Corona San Carlos (Figure 1). More information is needed on the aggregation status of the primary species since there is evidence the site can be fished during spawning (R. Claro, unpublished data) and small size limits for many Cuban reef fishes allow harvests of pre-spawning individuals (Alvarez-Lajonchère, 2014). Alternatives for long-term socioeconomic benefits, in addition to potential PA creation, include protection of pre-spawning migrations (Table 1).

2.1.2 | Other northwest aggregations

Cabo San Antonio, projecting into the Yucatan Straits in westernmost Cuba was not modeled. This site is within the Área Protegida de Recursos Manejados Península de Guanahacabibes. Larval export destinations potentially include northwest and southwest Cuba, The Bahamas, Florida, and Mexico. Traditionally, mutton and other species were fished at Cabo San Antonio, we do not know the current status of those aggregations.

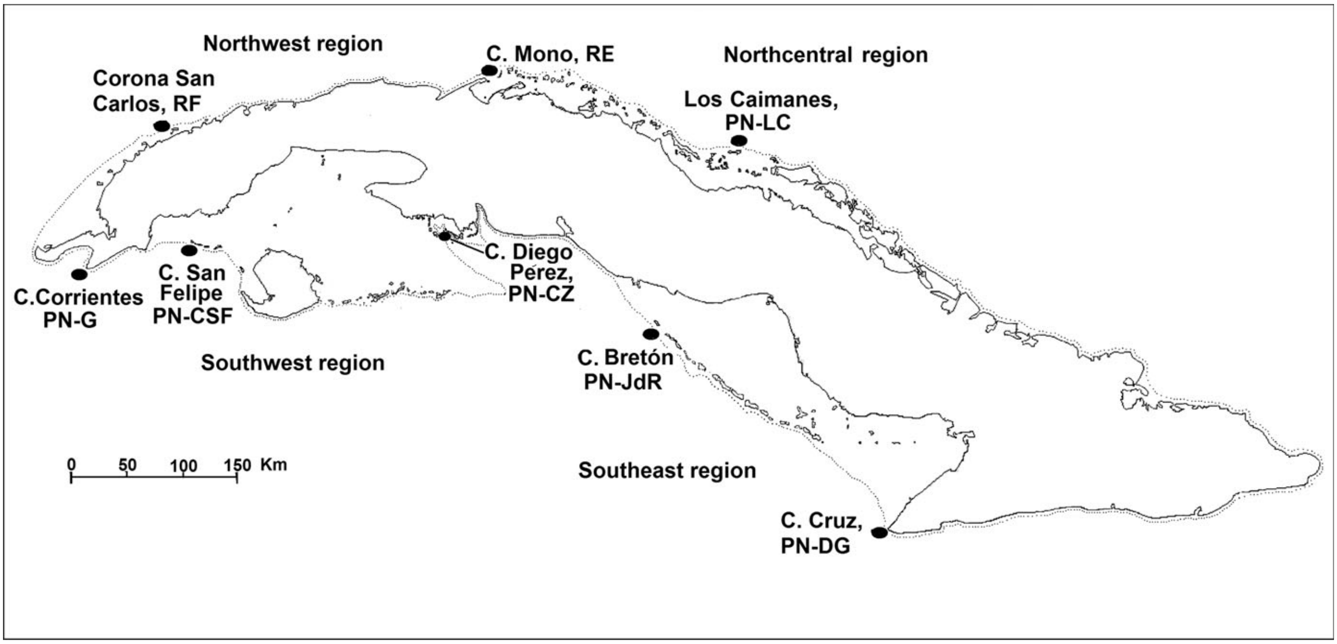

FIGURE 1 North and south coasts of Cuba with eight modeled spawning sites and associated protected areas. RF, Refugio de Fauna; RE, Reserva Ecológica; PN, Parque Nacional; PN-G, Parque Nacional Guanahacabibes; PN-CSF, Cayos de San Felipe; PN-CZ, Ciénaga de Zapata; PN-LC, Los Caimanes; PN-JdR, Jardines de la Reina; PN-DG, Desembarco del Granma

2.2 | North-central Cuba

The north coast of Cuba has a prominent north-central reach with large tropical lagoon systems (the Archipiélago de Sabana-Camagüey and estuaries within). Two aggregation sites have been modeled: Cayo Mono-Punta Hicacos and a multispecies site in PN Los Caimánes, 225 km to the east. Spawning sites in the north-central region are often closer to the mainland and easier to reach than many southern coast sites.

Mean within-region retention was relatively high: 48% (18%–97% range), in 10 years of model runs (Table 1; Kough et al., 2016). There may be limited larval export from north-central to northwest Cuba (0%–20% over 10 years of runs). Off-island export of larvae ranged from 10%–60% annual to the Bahamas (Kough et al., 2016, Figure 2).

2.2.1 | Cayo Mono

Off the north tip of Peninsula de Hicacos (Varadero Beach), 135 km east of Havana, Cayo Mono is a spawning site for mutton and lane snapper, and Nassau and yellowfin grouper (Claro & Lindeman, 2003). Well known for tourism, the area has also been used by commercial and subsistence fishers for decades. The spawning site is now in the Reserva Ecologica Cayo Mono-Galindo (Figure 1) but is not within the no-take areas and there can be little protection along the pre-spawning migration routes (Table 1). Information is limited on aggregation status, although a large mutton snapper fishery existed here previously (Claro et al., 2009).

2.2.2 | Cayo Caiman

Spawning sites for several species are within a "Zona de Conservacíon Estricta" within PN Los Caimanes (Figure 1; Quirós Espinosa & Rodríguez Moya, 2007), but there can be challenges from fishing due to a lack of resources. The principal pre-spawning staging area is outside park boundaries where important species (lane, mutton and grey snapper) can be fished. These species are also fished along other migration pathways outside reserve boundaries. Information on current fishery status is limited, although there have been long-term regional declines for several lutjanids (Claro et al., 2009). Management alternatives include temporal and/or additional spatial closures on fishing before and during spawning peaks.

2.2.3 | Other north-central aggregations

Six additional spawning sites are known from the region but have not been modeled. All sites have lane snapper, with mutton, grey and cubera occurring at a few (Claro & Lindeman, 2003). To the east, Cayo Mégano de Nicolao and Boca de Sagua are 45 and 130 km east of Cayo Mono. To the centre of the northern island, Cayo Lanzanillo and Cayo Fragoso are within the national Refugio de Fauna Lanzanillo-Pajonal-Fragoso. Over 200 km to the east of C. Caimán are Cayo Paredón and C. Sabinal with limited information on spawning aggregations. Some sites can provide substantial larval outflow to the Great Bahamas Bank and Turks and Caicos, depending on oceanographic dynamics in the Old Bahamas Channel (Kough et al., 2016; Paris et al., 2005).

TABLE 1 Larval snapper connectivity estimates, MPA placement and management attributes for northern Cuban shelf regions

Northern Cuban Site and species		Connectivity (% annual settlement/10 year) Within region	Among regions	Among countries	Aggregation and management attributes Aggreg. status	Within PA?	Threats and management	Alternatives include
Northwest region								
Corona San Carlos	*L. analis*, *L. synagris*, *L. griseus*, *L. cyanop.*	Stays in Northwest region: mean retention 18% (3%–60%); lowest of regions studied	Exports to: *N-central:* 10%–80% *Southwest:* 0%–40%	Exports to: *Bahamas:* 20%–80% *Florida:* 0%–5%	Declines Declines Declines Unknown	Proposed within local Refugio de Fauna	Very limited protection for spawning aggregations of multiple species. Size limits too small with little effect	Ensure the RF includes multi-species spawning protection year-round. Protect pre-spawn migrations. Incentives for fishers and tourism support
North-central region								
Cayo Mono	*L. analis*, *L. synagris*	Stays in N-central region: 48% mean retention (18%–97%)	Exports to: *Northwest* 0%–20%	Exports to: *Bahamas:* 10%–60% *Hispanola:* 0%–10%	Declines Unknown	Yes, RE Cayo Mono-Gallindo (2010)	Limited protection at site or on migration pathways. A large *L. ana.* aggregation fishery existed previously	Work with RE to ensure no take protection. Increase fisher-incentives and RE resources
Cayo Caiman	*L. analis*, *L. synagris*, *L. griseus*, *L. cyanop.*				Declines Declines Unknown Unknown	Yes, PN Los Caimanes (2008)	Fishing prohibited at sites. Limited protection at sites and on migration pathways. Small size limits	Increase PN resources and fisher-incentives. Temporal closure during spawning peak

Notes. Sources include: Claro et al. (2001), Claro & Lindeman (2003), Claro et al. (2009), CNAP (2013), Alvarez-Lajonchère (2014), Kough et al. (2016).
(20xx): year protected area approved.
PA, Protected Area; PN, Parque Nacional; RF, Refugio de Fauna; RE, Reserva Ecològica.

2.3 | Southwest Cuba

This region encompasses the narrow westernmost shelf and the wide Golfo de Batabanó. Three sites were modeled from west to east: Cabo Corrientes near Cuba's westernmost margin; Cayo La Cucaña within Cayos de San Felipe on the west-southwest margin of the Golfo de Batabanó; and Cayo Diego Pérez, 220 km to the east, on the deep ocean intrusion south of the Ciénaga de Zapata (Figure 1). These three spawning areas are all within national parks. The Golfo de Batabanó has been the primary snapper fishery in Cuba for decades based largely on lane snapper (Claro et al., 2009).

Mean within-region retention was estimated to be 28% (4%–83%) for four species pooled in 10 years of model runs (Table 2), suggesting more temporally and spatially variable levels of self-recruitment in comparison to the southeast. Models show export of 0%–65% to northwest Cuba by advection through the Yucatan Straits (see Kough et al., 2016 for model videos in supplemental materials). The southeast region received 0%–35% from the southwest annually. Larvae advected to the north largely arrived in the Bahamas (0%–25%). Export in some years also reached Jamaica, Hispaniola, the Cayman Islands and Mesoamerica (Kough et al., 2016; Paris et al., 2005).

2.3.1 | Cabo Corrientes

The site is within the PN Península de Guanahacabibes (Figure 1) and fishing is prohibited. Mutton snapper are fished outside, but close to the reserve along pathways to the spawning site. The existence of an important dive resort (Maria la Gorda) in the area helps reinforce regulations as does the PN. Some fishing is still present and densities of snapper and grouper above 30 cm on reefs near the spawning area have been found to be low (Rojas & Monteagudo, 2009).

2.3.2 | Cayos de San Felipe

Drop-offs close to Cayo La Cucaña are used by several snapper species for spawning and are within the PN Cayos de San Felipe (Figure 1, Table 2). In five species of snappers, de la Guardia et al. (2018) found high catches of pre-spawning fishes, especially in mutton and cubera snapper, and suggested more precautionary management. de la Guardia et al. (2018) also recorded a new spawning site west of the PN for at least mutton, lane and cubera snapper.

2.3.3 | Cayo Diego Pérez

A major spawning site for lane snapper is within the PN Ciénaga de Zapata, close to Cayo Diego Pérez along the edge of the Golfo de Cazones. The geomorphology includes the deep undersea Cazones canyon penetrating into the shelf, a highly exposed shelf release site for propagules. Extremely large pre-spawning migrations of lane snapper have long been fished outside and inside the park boundaries. Fishing limits have helped avoid extinction of the aggregation, however long-term overfishing has resulted in lowered production (Claro & Valle, 2014). Alternatives include closure of the lane snapper fishery in the east Golfo de Batabanó during the 5th lunar cycle (Table 2).

2.3.4 | Other southwest aggregations

At least five unmodeled snapper and grouper spawning aggregation sites exist. From east to west, these are Puntalón de Cayo Guano, an offshore area near a second site at Banco de Jagua, both used by mutton snapper and some groupers; Cayo Ávalos, east of Isla de la Juventud, is used by mutton, grey and cubera snapper; and Los Indios to the west is used by lane and mutton snapper. Near Los Indios is PN Punta Francés where a Nassau grouper aggregation (Claro & Lindeman, 2003), has declined or may be extinct. Punta Francés has been examined in terms of management effectiveness (Angulo-Valdés & Hatcher, 2013; Puritz, 2017), but not spawning aggregations. Information on these aggregation sites is limited, but regional data show decades of declines due to fishing of spawners and pre-spawners (Claro et al., 2009).

2.4 | Southeast Cuba

Two distant sites were modeled: Cayo Bretón on the western margin of the Archipiélago Jardines de la Reina and Cabo Cruz on the east edge of the southeast shelf (Figure 1). This is the second most important region for the national lane snapper fishery: 600–900 mt annual in the 1970s, about 200–300 mt more recently (Claro, Baisre, Lindeman, & García-Arteaga, 2001; Claro & Valle, 2014).

Mean within-region retention was estimated to be 50% (2%–99%) in 10 years of model runs (Table 2). This was the largest regional level of retention (Figure 3 in Paris et al., 2005; Kough et al., 2016). Current models suggest export is primarily to the southwest region (Paris et al., 2005; Figure 3 in Kough et al., 2016). Larvae exported off-island are predicted to periodically settle in Jamaica, Hispaniola and the Cayman Islands (Kough et al., 2016; Paris et al., 2005).

2.4.1 | Cayo Bretón

This site is used by mutton, lane, grey, dog and cubera snapper within the western margin of the Jardines de la Reina (Figure 1), and has been in the PNJDR boundaries since 2012. There is evidence of enforcement success for some reef fishes in the eastern park (Pina-Amargós et al., 2014). Relative isolation and high within-region retention (Kough et al., 2016; Paris et al., 2005) may underlie the relative stability of regional catches (Claro & Valle, 2014). PN management has been evaluated with a focus on public-private partnerships and eco-tourism (Puritz, 2017), fishery spawning was not a focus.

2.4.2 | Cabo Cruz

This site is in the PN Desembarco del Granma near the edge of the narrow southeast shelf and the broad Golfo de Guacayanabo to the

TABLE 2 Southern Cuban shelf regions: larval snapper connectivity estimates, MPA placement and management attributes

Southern Cuban Site and species		Connectivity (% annual settlement/10 year) Within region	Among regions	Among countries	Aggregation and management attributes Aggreg. status	Within PA?	Threats and management	Alternatives include
Southeast region								
Cabo Cruz	*L. analis*, *L. synagris*	Stays in Southeast region: 50% mean retention (2%–99%)	Exports to: *Southwest:* 0%–25%	Exports to: *Jamaica:* 0%–75% *Hispanola:* 0%–20% *Cayman I.:* 0%–8%	Limited information	Yes, PN Desembarco del Granma (2001)	Primary impacts on *L syn* are during the pre-spawning migrations. Fishing quotas possibly too high and size limits too small	Closure during spawning peak: 5th lunar cycle for *L. ana*., usually May; 6th cycle for *L syn.*, usually June
Cayo Bretón	*L. analis*, *L. griseus*, *L. cyanop.* *L. jocu*				Declines Declines Declines Unknown	Yes, added to PN Jardines de la Reina (2012)	Limited protections at the spawning site in recently included area. Size limits too small	Increase PN resources and fisher incentives. Manage fishing on migration routes
Southwest region								
Cayo Diego Pérez	*L. synagris*	Stays in Southwest region: 28% mean retention (4%–83%)	Exports to: *Northwest:* 0%–65% *Southeast:* 0%–35% *Northcentral:* 0%–15%	Exports to: *Cayman I.:* 0%–20% *Bahamas:* 0%–25%	Major declines over decades	Yes, PN Ciénaga de Zapata (2008)	Heavy fishing on pre-spawners. Effort limits helped avoid extinction of aggs. but fishing is common	Closure for *L. syn.* in the E Golfo de Batabano during 5th lunar cycle. Increase PN resources
Cayos de San Felipe	*L. analis*, *L. synagris*, *L. cyanop.*				Declines	Yes, PN Cayos de San Felipe (2010)	Effort limits helped avoid extinction of aggs. but not long-term overfishing	Increase PN resources and consider temporal closures
Cabo Corrientes	*L. analis*, *L. griseus*, *L. cyanop.*				Limited information	Yes, PN Guana-hacabibes (2010)	Fishing prohibited in PN. Effective protection often in reserve, but pre-spawn migrations can be heavily fished	Increase PN resources. Expand zoning and manage fishing on migration routes. Incentivize further efforts with dive tourism industry

Notes.. Sources include: Alvarez-Lajonchère (2014), Angulo-Valdés & Hatcher (2013), Claro & Lindeman (2003), Claro et al. (2001, 2009), CNAP (2013), de la Guardia et al. (2018), Kough et al. (2016), Pina-Amargós et al. (2014), Puritz (2017).

west (Figure 1). The site is used by lane, mutton, cubera and other snappers and groupers (Claro & Lindeman, 2003). There are not specific regulations to protect migrating fishes or the spawning site, but aggregation fishing may not be as pronounced as other regions due to (a) limited land access because of the PN, and (b) the distance by sea for many boats. Temporal fishery closures may be of value (Table 2).

2.4.3 | Other southeast aggregations

We did not model larval transport from the other known spawning site in this region: Bajo Mandinga, used by at least two snapper species (Claro & Lindeman, 2003). The site is on the shelf edge towards easternmost Cuba. There is little information on this site.

3 | LARVAL OUTFLOWS FROM CUBA TO THE GREATER CARIBBEAN

Larval export from snapper populations on the Cuban shelf likely contributes to the replenishment of smaller shelf fisheries in Jamaica, the Caymans, and Haiti from southeast Cuba, and the Bahamas and Turks and Caicos from northern Cuba (Kough et al., 2016). Cuba's shelf areas are much larger than most of these islands. Connections to Mexico, Belize, and the Colombian Archipelago were not common, although each species had at least one site and year when possible (Kough et al., 2016).

The multispecies snapper and grouper spawning sites of Cuba are marine conservation focal points for coordinated international management in the northwest Caribbean. Complicated metapopulation biology reflects (a) annually variable species-specific connectivity with other countries, (b) the large region-scale shelf areas and diversity of Cuban habitats, and (c) the effects of over 60 years of fishing removal, not only upon numbers of fishes but also habitats and demographic structure (e.g., Koenig et al., 2000).

The southeast US is a destination for Cuban snapper larvae but with low relative volume and frequency at annual and decadal scales (Table 1; Paris et al., 2005; Kough et al., 2016). This system involves the energetic front of the Florida Current, complex interactions among cyclonic and anticyclonic eddies (Kourafalou, Androulidakis, Kang, & Le Hénaff, 2018) and the timing of spawning events (Donahue, Karnauskas, Toews, & Paris, 2015). Offshore meandering of the Florida Current in the southern Florida Straits may occasionally entrain pulses of reef-fish larvae from the Florida Keys to Cuba, but transport in the opposite direction appears more sporadic (Limouzy-Paris, Graber, Jones, Röpke, & Richards, 1997; Sponaugle, Paris, Walter, Kourafalou, & d'Alessandro, 2012). The southward meandering of the Florida Current front needs to coincide with lunar spawning cycles (Vaz et al., 2016).

Oceanographic data sets are sparse and hydrodynamic modeling scales are relatively coarse except for the ~900 m grid of the South Florida Keys Hybrid Coordinate Ocean Circulation Model (FKey-HyCOM, Kourafalou & Kang, 2012) which covers northwest Cuba. Models operating in the Caribbean are not resolving important observed sub-mesoscale eddy variability (e.g., Graber & Limouzy-Paris, 1997). High resolution models incorporating tidal forcing are needed to further address regional connectivity in Cuba (e.g., Lindo-Atichati, Curcic, Paris, & Buston, 2016).

4 | LARVAL CONNECTIVITY, PROTECTED AREAS, AND INFORMATION NEEDS

Integrating connectivity predictions with aggregation information and MPA attributes may help inform managers on prioritizing candidate sites for increased protection. Of the eight focal spawning sites, seven are in PAs, and one is proposed (Tables 1 and 2). Aggregation sites inside areas with prohibited fishing are at PN Los Caimanes and PN Guanahacabibes and enforcement can be variable (Tables 1 and 2). More on-site fishery data and socio-economic fieldwork is needed at primary spawning sites.

Connectivity information can inform coordinated MPA management. Consider two functioning but depleted aggregation sites with similar habitats and fishing pressures but differing larval connectivity pathways. One shows high local retention, but limited export out of region and the other has low local retention yet receives and sends larvae to other aggregations. Managers interested in sustained harvests might try to protect the stock with higher local retention since it will be more self-supporting with more pronounced local benefits. Alternatively, managers interested in sustaining exogenous stocks may protect the more connected aggregation site.

An area may quickly be replenished by diverse larval sources and also export to other locations, while depletion of a region with only a high export spawning site may impact the spawning aggregation network and disrupt its connectivity (Holstein, Paris, & Mumby, 2014). Krueck et al. (2017) reviews various studies and develops approaches to select priority locations that include alternative dispersal patterns, population threats, and site versus network based optimization strategies; such analyses can be applied to Cuban spawning aggregations.

Cuba's northwest region had the lowest mean retention level (Table 1). This region receives settlers from Cabo San Antonio, Cabo Corrientes, and possibly from Cayos de San Felipe (Kough et al., 2016), is weakly connected to the Florida Keys (Paris et al., 2005; Kough et al., 2016), and exports much larvae to the Bahamas (Donahue et al., 2015). High export and intermediate inflows from other regions facilitate external and internal replenishment (Holstein et al., 2014), making such areas logical candidates for aggregation protection.

Uncertainty from the limited information on the status of these aggregations coupled with variable oceanography suggests that precautionary management principles apply. Much connectivity information remains coarse since the percentage recruitment in most regions is a mix of two or more modeled sites and several species combined. Finer scales of hydrodynamic information are needed from more resolved nearshore oceanographic models and time series. Examination of hurricane effects upon regional connectivity suggests that August and September storms have complex affects upon larval dispersal and survival in most of the regions studied (C. B. Paris, R. Claro, A. S. Kough, K. C. Lindeman, unpublished data). More population genetics information can also aid Cuban connectivity studies (García-Machado, Ulmo-Díaz, Castellanos-Gell, & Casane, 2018).

Groups of lane, grey and mutton snapper can use relatively wide staging areas over days during spawning (Claro & Lindeman, 2003) and migration routes often cross MPA boundaries with many opportunities for aggregation overfishing. With the fishing of large pre-spawning migrations, understanding the potential for demersal supply from catchment areas is important (Nemeth, 2012). Coordinated field surveys of aggregation status at primary sites and migration paths are needed to identify which species and sites are most threatened. Tagging studies are needed to map migrations to the spawning areas. Structured interviews with experienced fishers can apply local ecological knowledge to spawning aggregation management (Hamilton, Sadovy de Mitcheson, & Aguilar-Perera, 2012). Examination of fishery productivity-susceptibility indicators can assist identification of focal species and regions (Puga et al., 2018) and could be applied to aggregation fisheries.

We are unaware of an example of a snapper aggregation in Cuba that has been fished to extinction. Even more reduced than the snappers, Nassau grouper have been fished very heavily since the 1960s and annual catches decreased from 1,400 mt in the 1960s to <10 mt by the 2000s (Claro et al., 2009). Information on the status of most Nassau aggregations in Cuba is very limited. Adults may still be caught in very low numbers at some sites. A priority research need for both snappers and groupers is assessment of those aggregations most at risk for extinction and the deployment of management tools that can increase aggregation resilience.

5 | POTENTIAL MANAGEMENT ALTERNATIVES

Protected area work in Cuba has been advanced by long-standing coordination among CNAP, ENPFF, the Office of Fisheries Regulations, and other agencies. A principal feature of PA's in Cuba is a criterion for the protection of critical population sites for species of high economic and conservation priority (CNAP, 2013). Multispecies reef fish spawning sites for prominent fisheries with major ecological and economic significance meet this criterion (e.g., Heyman & Kjerfve, 2008; Sadovy de Mitcheson et al., 2008).

Marine protected area management planning and effectiveness evaluation can involve dozens of biological, socio-economic, and governance indicators (Pomeroy et al., 2004). Management indicators for Cuban MPAs (Angulo-Valdés & Hatcher, 2013; Puritz, 2017) do not typically include status of spawning aggregations. Future planning for spawning site management should have value including: (a) biological status assessments requiring new fishery-independent resources, and (b) workgroups with local stakeholders.

One or more working groups of protected area specialists, fishery scientists, expert fishers and other local stakeholders are logical alternatives. Such groups could evaluate biophysical information and further interagency coordination specific to spawning monitoring and outreach. Network planning, climate change issues and estimation of the opportunity-costs of taking no adaptive conservation actions could also be coordinated.

A variety of fishery management alternatives have arisen in the eight site summaries and Tables 1 and 2. In some instances, the creation of specially zoned spawning reserves within existing protected areas may be called for (Claro, 2001). Downstream, spawning reserves were recently implemented for grouper and snapper species in the southeast U.S. using a new amendment to the federal Snapper-Grouper Fishery Management Plan (SAFMC, 2016). These five reserves were developed by a workgroup of scientists and expert fishers convened by a fishery agency. These “spawning special management zones” complement temporal spawning closures already in place for some species.

Cuban shelf regions are not homogeneous and can show large within-region geomorphic variation (e.g., the Golfo de Batabanó), as well as among-region variation. There is also much biological variability. Spawning peaks for lane and mutton snappers vary among regions and management should adaptively reflect this variation (Claro & Lindeman, 2003).

Species-scale fishing differences are also important for management. For example, lane and grey snapper aggregations are usually fished at pre-spawning staging areas, while mutton and cubera snappers are fished primarily at spawning sites (but also in channels between keys, close to spawning sites; Claro et al., 2009). Therefore, fishery rules limit set nets and long trawls on pre-spawning migration routes, but pre-spawners are fished with other gears (Claro & Lindeman, 2008; Claro & Valle, 2014).

Therefore, in regions where migrating routes and/or staging areas are vulnerable, spawning season closures may be more effective than only MPAs at the spawning site. Such temporal closures could be most practical for the protection of aggregations with more diffuse staging areas (C. Bretón, Corona San Carlos, Cayo Mono, others).

Additional management challenges will emerge if coastal tourism accelerates around the island. The construction of new cruise ship terminals and land infrastructure at some offshore sites should ensure that economically valuable spawning aggregations and migration paths are not structurally modified as at the site of a Nassau grouper aggregation in Mahahual, Mexico (Aguilar-Perera, 2006).

Revenue streams for PA management can be generated from park admission and hotel green fees (Honey & Hogenson, 2017; Lindeman, Tripp, Whittle, Moulaert-Quiros, & Stewart, 2003), as done in national marine parks of Mexico for decades. Alternative livelihood efforts via ecotourism (e.g., catch-release fishing guides) can also be supported by commercial ventures (e.g., the Avalon Hotel, PN Jardines de la Reina). In PN Los Caimanes, one management objective encourages alternative income sources including potential aquaculture and ecotourism to reduce fishing pressure (A. Quirós Espinosa, personal communication).

The available information suggests that inclusion of spawning aggregation conservation as an early planning objective is appropriate not only in various MPA management plans but also as an indicator of management effectiveness for such sites. In addition, some of the more prominent spawning sites in Cuba (Cayo Diego Pérez, C. Corrientes, Corona de San Carlos, Caimanes, C. Bretón, others) appear to meet core criteria for IUCN Key Biodiversity Areas (IUCN, 2016). These and other recognitions of the economic and biodiversity value of these sites could further mobilize needed resources to sustain spawning aggregations for economic and environmental benefits.

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