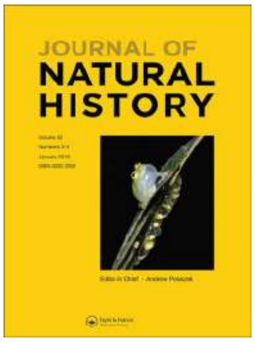

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Fish aggregations and reproductive behaviour on mesophotic coral ecosystems of a southwestern Atlantic Oceanic archipelago

Hudson T. Pinheiro[a,b,c], Bart Shepherd[d], João Batista Teixeira[c,e], Caio R. Pimentel[b,e], Pedro Henrique C. Pereira[f], Carlos E. Stein[c], José Amorim Reis-Filho[g], Ricardo C. Garla[h], Raphael M. Macieira[e], Stephanie D.T. Delfino[e], Tommaso Giarrizzo[i], Jean-Christophe Joyeux[e], João Luiz Gasparini[j] and Luiz A. Rocha[b]

[a]Center for Marine Biology, University of São Paulo, São Sebastião, SP, Brazil; [b]Department of Ichthyology, California Academy of Sciences, San Francisco, CA, USA; [c]Associação Ambiental Voz da Natureza, Vitória, ES, Brazil; [d]Steinhart Aquarium, California Academy of Sciences, San Francisco, CA, USA; [e]Departamento De Oceanografia E Ecologia, Universidade Federal Do Espírito Santo, Vitória, ES, Brazil; [f]Projeto Conservação Recifal (Reef Conservation Project), Recife, PE, Brazil; [g]ICHTUS Soluções Em Meio Ambiente, Salvador, BA, Brazil; [h]Departamento De Botânica E Zoologia, Univ. Federal Do Rio Grande Do Norte, Natal, RN, Brazil; [i]Núcleo De Ecologia Aquática E Pesca Da Amazônia, Univ. Federal Do Pará, Belém, PA, Brazil; [j]Instituto De Biodiversidade E Sustentabilidade, Univ. Federal Do Rio De Janeiro, Macaé, RJ, Brazil

ABSTRACT

Dozens of marine fish species are known to form spawning aggregations, a behaviour that often increases the species vulnerability to fisheries. Therefore, it is widely recommended for aggregation sites to be considered a conservation priority, and implementation of management measures on those sites is essential. Here, we report for the first time the reproductive behaviour of the marbled grouper *Dermatolepis inermis*, observed at a lower mesophotic coral ecosystem of Fernando de Noronha, an oceanic tropical archipelago in the southwestern Atlantic. The event was characterised by an aggregation of six adult fish, displaying courtship behaviour and reproductive colouration. We also recorded an aggregation of about 20 dog snappers *Lutjanus jocu* at the same site, but no reproductive behaviour was observed. Finally, another aggregation was observed in the island's upper mesophotic reefs, with 25 terminal phase individuals of the Brazilian endemic parrotfish *Sparisoma amplum*. Our report reinforces the biological importance of mesophotic coral ecosystems, and highlights the urgent need of governmental policies for studying, monitoring, and protecting those reefs.

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Management; deep reefs; marine-protected area; remotely operated vehicle; spawning aggregation; oceanic island

Introduction

Spawning aggregations (following Domeier 2012) occur when individuals of a species move or migrate in large numbers to reproductive grounds or areas at certain times of the year and/or lunar phases (Sadovy De Mitcheson et al. 2008; Colin 2012a), and seem to

CONTACT Hudson T. Pinheiro ✉ htpinheiro@gmail.com

have evolved independently in many animal classes, including fishes (Choat 2012). Aggregations are, therefore, optimum spreading points for parasites and feeding grounds for predators (e.g. Womble et al. 2005; Nemeth 2012), including humans (Iwata et al. 2010). Overfishing on spawning aggregations is just one of the potential human impacts to these species, due to closely related threats pre and post reproduction. Other vulnerable behaviours associated with these aggregations include reproductive migration (e.g. salmon runs), pre-spawning aggregations (e.g. bonefish; Lombardo et al. 2020) and larval or juvenile recruitment into (e.g. European glass eel; Briand et al. 2007) or out (e.g. shrimp, prawn and many fishes; Gillanders et al. 2003) of juvenile habitats.

Currently, 13 families of reef fishes are known to form spawning aggregations (Sadovy de Mitcheson and Colin 2012), which can involve anywhere from a few dozen to many thousands of adult fish (Domeier and Colin 1997). During these events, fish engage in intricate swimming patterns, quick and drastic colour changes, sound-signalling, and physical contact (Deloach and Humann 2002; Molloy et al. 2012). Reproductive grounds are usually in prominent coastal geomorphological features (Domeier 2012), such as reef passes, channels, promontories, and outer reef-slope drop-offs adjacent to the continental slope (Sadovy De Mitcheson et al. 2008; Reis-Filho et al. 2021).

The protection of spawning aggregations is considered to be a high conservation priority because stocks can be quickly depleted by fisheries targeting reproductive grounds (Sala et al. 2001; Drazen et al. 2003; Whaylen et al. 2004). However, aggregations are increasingly targeted by recreational and commercial fishers using a wide range of gear to supply both local and international markets (Sadovy de Mitcheson and Erisman 2012). As reef fishes can migrate distances over 200 km to reach spawning grounds, overfishing spawning aggregations can have region-wide implications (Stump et al. 2017). Despite the biological importance of those spawning aggregations, their location and timing are still poorly understood, reducing our ability to establish conservation priorities and implement management measures. Among the common management strategies to safeguard this critical event in a species' life history, marine protected areas and seasonal closures have been successfully implemented, recovering threatened spawning aggregation sites and endangered populations worldwide (Beets and Friedlander 1998; Luckhurst and Trott 2008; Waterhouse et al. 2020).

Although hundreds of spawning aggregation sites have been reported in the northwestern Atlantic, there is very limited information available for the southwestern Atlantic (Bezerra et al. 2021; Reis-Filho et al. 2021) and, consequently, few fishing regulations exist in this entire region (Freitas et al. 2011). In Fernando de Noronha Archipelago, off northeastern Brazil, conservation of marine natural resources is enforced by a large National Marine Park, which covers about 70% of its shallow waters (<50 m depth). However, most mesophotic coral ecosystems around the islands are completely open to fishing, which is practiced mainly with hand lines and trolling (Dominguez et al. 2016).

In 18 October 2019, during a scientific expedition to assess the fish biodiversity of Fernando de Noronha's mesophotic ecosystems (see Pimentel et al. 2020), we observed for the first time the reproductive behaviour of the marbled grouper *Dermatolepis inermis* (Valenciennes, 1833) (Figure 1A). The behaviour was recorded using a remotely operated underwater vehicle (ROV) between 95 and 100 m depth, at the northern edge of the insular shelf, in a complex habitat of large horizontal crevices, with extensive black coral cover, and colder temperatures compared to surface waters (~18°C at the bottom, vs 28°C at the

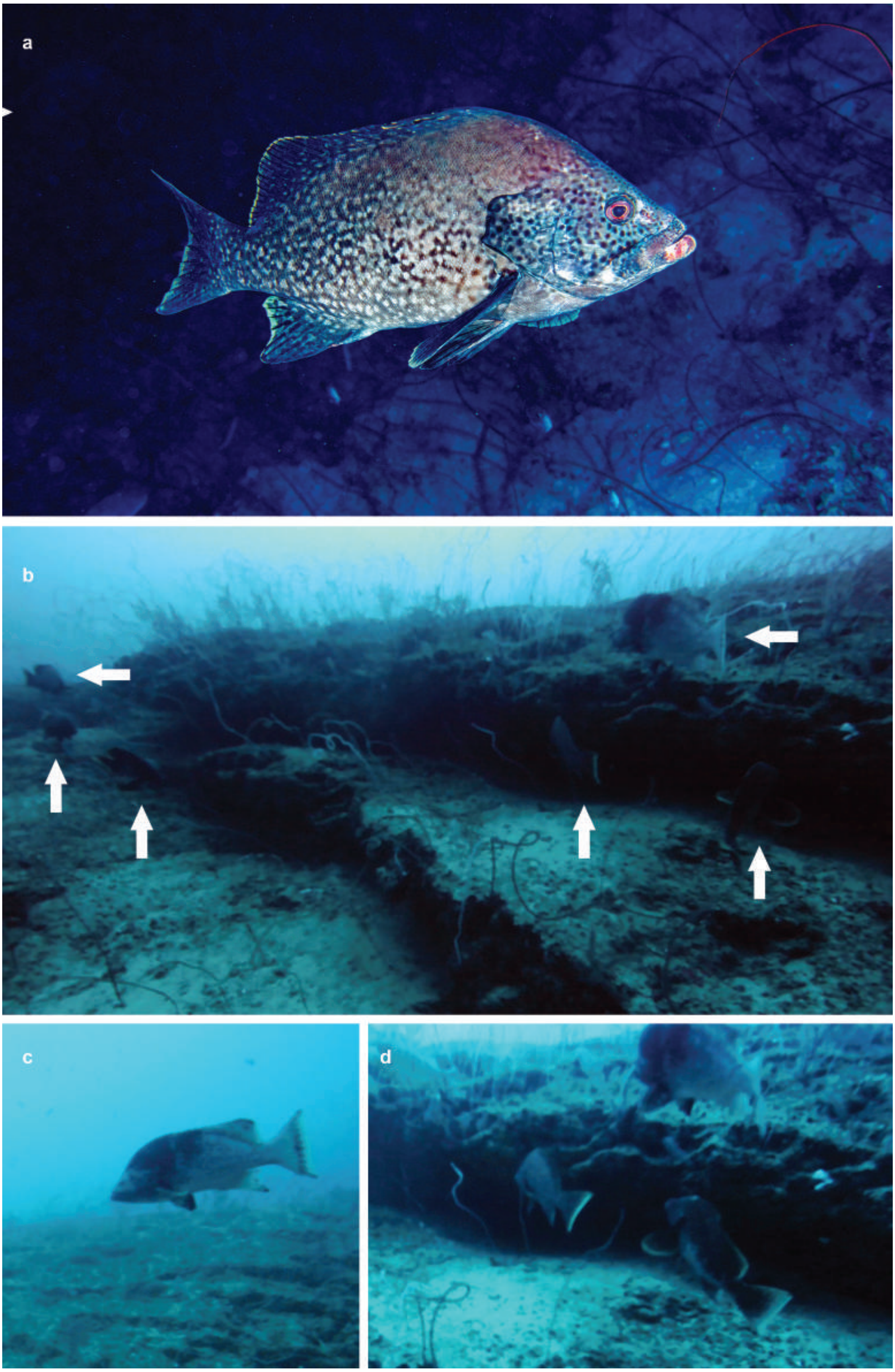

Figure 1. The marbled grouper *Dermatolepis inermis* in lower mesophotic reefs of the Fernando de Noronha Archipelago (A), and the aggregation site with six fish in the field of view (B), including individuals with the tuxedo colour pattern (C), and yellow fin margins and white belly (D). Photo by L. A. Rocha (A) and frames from videos recorded by J. B. Teixeira (B – D).

surface) (Figure 1B). The event, recorded five days after the full moon, was characterised by a large individual fish displaying the 'tuxedo' colour pattern (described in Kline et al. 2011) (Figure 1C) and courtship behaviour (body shaking and rubbing). Another five smaller adult fish presenting strong yellowish margins in their fins were in the field of view, with two of them showing white belly colour patterns (Figure 1D). The fish exhibiting the tuxedo colour pattern interacted with two individuals before swimming towards three others nearby, which seemed characteristic of haremic behaviours (https://youtu.be/awa-sbw8fo8).

In addition, we documented two other aggregations in the mesophotic zone of the archipelago. Also, in 18 October 2019, an aggregation of about 20 individuals of the dog snapper *Lutjanus jocu* (Bloch & Schneider, 1801) was observed descending in the water column from about 70 m depth to the ledge environment, located at approximately 90 m depth. Although dog snappers usually aggregate and spawn during the full moon, and their spawning behaviour involves a quick ascent in the water column, no obvious reproductive behaviour was recorded (https://youtu.be/awa-sbw8fo8). In May 2018, on a previous field trip, an aggregation of the Brazilian endemic parrotfish *Sparisoma amplum* (Ranzani, 1841) consisting of at least 25 adult individuals (Figure 2) was observed hovering and feeding on the substratum at 35 m depth, at Laje do Bode dive spot (Figure 2; https://youtu.be/awa-sbw8fo8). Surprisingly, only terminal phase individuals (males) were recorded during this aggregation, and no intraspecific aggression or territorial behaviours were seen. These events, in which we observed over 20 fish of each species in few square metres, presented a much higher density than is usually found in reefs of the archipelago. There, the average density (fish/100 m^2 ± SD; methods as in Pinheiro et al. 2016) for *L. jocu* and *S. amplum*, respectively, is 1.6 ± 2.4 and 0.2 ± 0.7 on mesophotic reefs (31–100 m depth; N = 35 transects), and 0.8 ± 1.5 and 1.2 ± 2.0 on shallow reefs (0–30 m depth; N = 94 transects). Therefore, these observations represent the first aggregations ever recorded for these species at Fernando de Noronha Archipelago.

Colour patterns, courtship behaviour, group size, and presumed sex ratio in our marbled grouper observation match the characteristics reported for the rock hind *Epinephelus adscensionis* (Osbeck, 1765) in the Gulf of Mexico (Kline et al. 2011). Similar colouration during reproduction was also reported for the mutton hamlet *Alphestes afer* (Bloch, 1793) (Medeiros et al. 2009) and Nassau grouper *Epinephelus striatus* (Bloch, 1792) (Whaylen et al. 2004) in the western Atlantic. Reproductive and foraging aggregations have also been reported for the closely related *Dermatolepis dermatolepis* (Boulenger, 1895) in tropical oceanic islands and seamounts of the Eastern Pacific (Aburto-Oropeza and Hull 2008; Erisman et al. 2009; Quimbayo et al. 2014), where aggregations of 10 to 70 individuals were observed at the summits of seamounts (Aburto-Oropeza and Hull 2008; Erisman et al. 2009). Moreover, there are indications that the dog snapper and parrotfish aggregations we observed could also be related to reproductive events: 1) several lutjanids often share the same aggregation sites with grouper species (Sadovy De Mitcheson et al. 2008); 2) pre-aggregation events involving sex-segregation have been reported for some species (Casadevall et al. 2017), and parrotfish spawning aggregations usually occur in areas where feeding aggregations occur (Domeier and Colin 1997).

Unlike the spawning aggregations of *Epinephelus, Mycteroperca*, and *Plectropomus* groupers that are commonly reported in shallow waters (summarised in Domeier 2012), the use of mesophotic habitats could be one of the strongest limiting factors to spawning observations in the species we report here. Studies describing spawning aggregations in

Figure 2. Aggregation with dozens terminal phase individuals of the parrotfish *Sparisoma amplum* in Fernando de Noronha Archipelago, southwestern Atlantic. Photos by P.H.C. Pereira.

these habitats are limited because they require the use of ROV, submersibles or technical diving (Colin 2012b). A pair of dog snappers was previously observed spawning in shallow waters of Fernando de Noronha Archipelago, and in this case, the absence of an aggregation was attributed to the lack of nearby optimal spawning habitat (Krajewski and

Bonaldo 2005). The ledge of insular shelves might promote opportunities for a rapid advection of fertilised eggs by currents, and could explain the preference for these habitats by *Dermatolepis* and *Lutjanus* in the Fernando de Noronha Archipelago.

The group size of spawning aggregations reported here are much smaller than most reported elsewhere for the same families. For instance, the density we reported for *D. inermis* in Fernando de Noronha's lower mesophotic reefs was 1.1 (1.5) fish (SD) 100 m^{-2} ($N = 18$ transects), lower than found for *D. dermatolepis* (Aburto-Oropeza and Hull 2008) and other groupers in the Pacific (Sadovy de Mitcheson et al. 2020). Although previous spawning aggregations of *D. dermatolepis* in the Eastern Pacific were recorded in a variety of lunar phases (Erisman et al. 2009), about 50% of the world's spawning aggregation events take place around the full moon (Sadovy De Mitcheson et al. 2008). Thus, we may have simply observed the few remaining individuals from a larger aggregation that happened in the preceding days. The smaller group sizes and lower density of individuals reported here could also be related to the widespread nature of the ledge habitat around the Archipelago – larger aggregations are commonly related to limited suitable habitat for spawning (Nemeth 2012). Although *D. inermis* might be considered historically rare in Fernando de Noronha (RG, per. obs.), declines in group size and fish density could be a sign of overfishing (Reis-Filho et al. 2021), as fishing debris was reported in 18% of the transects in Fernando de Noronha's mesophotic zone (Pimentel et al. 2020). Exploited populations are more susceptible to overfishing in oceanic sites due isolation and high dependency on self-recruitment processes (Schultz and Cowen 1994) and, therefore, the lack of protection of Fernando de Noronha's deep reefs increases their vulnerability.

Mesophotic reefs of Fernando de Noronha, as with most of the world's deep reefs, shelter a distinct assemblage of species compared to that found on shallow reefs, including many endemics (Rocha et al. 2018; Pimentel et al. 2020), and important aggregation and reproductive grounds, as reported here. Proactive and integrative management of aggregations and fishing resources through long-term monitoring, appropriate fishery policy, and extensive fisher and community consultation and outreach, are among the best solutions for achieving conservation and sustainable development (Russell et al. 2012). For Fernando de Noronha, working in partnership with local stakeholder groups to extend the Marine National Park to include mesophotic habitats, such as ledges and walls, is one way to protect the island's unique fauna and ensure fishing sustainability through a potential spillover process.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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ORCID

Hudson T. Pinheiro http://orcid.org/0000-0002-3143-1474
Bart Shepherd http://orcid.org/0000-0002-8918-1551
Tommaso Giarrizzo http://orcid.org/0000-0002-5116-5206
Luiz A. Rocha http://orcid.org/0000-0003-4011-569X

References

Aburto-Oropeza O, Hull PM. 2008. A probable spawning aggregation of the leather bass *Dermatolepis dermatolepis* (Boulenger) in the Revillagigedo Archipelago, México. J Fish Biol. 73:288–295. doi:10.1111/j.1095-8649.2008.01909.x.

Beets J, Friedlander A. 1998. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ Biol Fishes. 55(1–2):91–98. doi:10.1023/A:1007404421518.

Bezerra IM, Hostim-Silva M, Teixeira JLS, Hackradt CW, Félix-Hackradt FC, Schiavetti A. 2021. Spatial and temporal patterns of spawning aggregations of fish from the Epinephelidae and Lutjanidae families: an analysis by the local ecological knowledge of fishermen in the Tropical Southwestern Atlantic. Fish Res. 239:105937. doi:10.1016/j.fishres.2021.105937.

Briand C, Bonhommeau S, Castelnaud G, Beaulaton L 2007. An appraisal of historical glass eel fisheries and markets: landings, trade routes and future prospect for management. Proceedings of the Institute of Fisheries Annual Conference, Westport, Ireland, pp 21.

Casadevall M, Sarrà-Alarcón L, Delgado E, Matallanas J. 2017. The sexual segregation of the European eel, *Conger conger* (Linnaeus, 1758) (Anguilliformes, Congridae) and female semelparity in the north-west Mediterranean. J Fish Res. 1(1):5–14.

Choat JH. 2012. Spawning aggregations in reef fishes; ecological and evolutionary processes. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 85–116.

Colin PL. 2012a. Timing and location of aggregation and spawning in reef fishes. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 117–158.

Colin PL. 2012b. Studying and monitoring aggregating species. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 285–330.

Deloach N, Humann P. 2002. Reef fish behavior: identification, Florida, Caribbean, Bahamas. 1st ed. Jacksonville: New World Publications.

Domeier ML. 2012. Revisiting spawning aggregations: definitions and challenges. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 1–20.

Domeier ML, Colin PL. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci. 60:698–726.

Dominguez PS, Zeineddine GC, Rotundo MM, Barrella W, Ramires M. 2016. A pesca artesanal no arquipélago de Fernando de Noronha (Pe). Bol Inst Pesca. 42:241–251. doi:10.20950/1678-2305.2016v42n1p241.

Drazen JC, Goffredi SK, Schlining B, Stakes DS. 2003. Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda Escarpment: a reproductive hot spot. The Biological Bulletin. 205 (1):1–7. doi:10.2307/1543439.

Erisman BE, Konotchick TH, Blum S. 2009. Observations of spawning in the leather bass, *Dermatolepis dermatolepis* (Teleostei: epinephelidae), at Cocos Island, Costa Rica. Environ Biol Fishes. 85:15–20. doi:10.1007/s10641-009-9463-x.

Freitas MO, de Moura RL, Francini-Filho RB, Minte-Vera CV. 2011. Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantic. Sci Mar. 75:135–146. doi:10.3989/scimar.2011.75n1135.

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser. 247:281–295. doi:10.3354/meps247281.

Iwata Y, Ito K, Sakurai Y. 2010. Is commercial harvesting of spawning aggregations sustainable? The reproductive status of the squid *Loligo bleekeri*. Fish Res. 102(3):286–290. doi:10.1016/j.fishres.2009.12.010.

Kline Rj, Khan IA, Holt GJ, Osorio D. 2011. Behavior, color change and time for sexual inversion in the protogynous grouper (*Epinephelus adscensionis*). PLoS ONE. 6(5):e19576. doi:10.1371/journal.pone.0019576.

Krajewski JP, Bonaldo RM. 2005. Spawning out of aggregations: record of a single spawning Dog Snapper pair at Fernando de Noronha Archipelago, Equatorial Western Atlantic. Bull Mar Sci. 77:165–167.

Lombardo SM, Adams AJ, Danylchuk AJ, Luck Ca, Ajemian MJ. 2020. Novel deep-water spawning patterns of bonefish (*Albula vulpes)*, a shallow water fish. Mar Biol. 167:187. doi:10.1007/s00227-020-03799-3.

Luckhurst BE, Trott TM 2008. Seasonally-closed spawning aggregation sites for red hind (*Epinephelus guttatus*): bermuda's experience over 30 years (1974 – 2003). Proceedings of the 61st Gulf and Caribbean Fisheries Institute, Gosiers, Guadeloupe 331–336.

Medeiros DV, Nunes JACC, Sampaio CLS. 2009. A mutton hamlet *Alphestes afer* (Bloch, 1793) reproductive event in northeast Brazil. Pan-Am J Aquat Sci. 4:212–215.

Molloy PP, Côté IM, Reynolds JD. 2012. Why spawn in aggregations? In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 57–84.

Nemeth RS. 2012. Ecosystem aspects of species that aggregate to spawn. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef Fish Spawning Aggregations: biology, Research and Management. New York: Springer; p. 21–56.

Pimentel CR, Rocha LA, Shepherd B, Phelps TAY, Joyeux J-C, Martins AS, Stein CE, Teixeira JB, Gasparini JL, Reis-filho JA, et al. 2020. Mesophotic ecosystems at Fernando de Noronha Archipelago, Brazil (South-western Atlantic), reveal unique ichthyofauna and need for conservation. Neotrop Ichthyol. 18:e200050. doi:10.1590/1982-0224-2020-0050.

Pinheiro HT, Goodbody-Gringley G, Jessup ME, Shepherd B, Chequer AD, Rocha LA. 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. Coral Reefs. 35:139–151. doi:10.1007/s00338-015-1381-0.

Quimbayo JP, Zapata FA, Floeter SR, Bessudo S, Sazima I. 2014. Reef fish foraging associations at Malpelo. Bol Invest Mar Cost. 43:183–193.

Reis-Filho JA, Miranda RJ, Sampaio CLS, Nunes JACC, Leduc AOHC. 2021. Web-based and logbook catch data of permits and pompanos by small-scale and recreational fishers: predictable spawning aggregation and exploitation pressure. Fish Res. 243:106064. doi:10.1016/j.fishres.2021.106064.

Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P. 2018. Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science. 361:281–284. doi:10.1126/science.aaq1614.

Russell MW, Luckhurst BE, Lindeman KC. 2012. Management of spawning aggregations. In: Sadovy Y, Mitcheson D, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 371–404.

Sadovy de Mitcheson Y, Erisman B. 2012. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In: Sadovy De Mitcheson Y, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. New York: Springer; p. 225–284.

Sadovy de Mitcheson Y, Colin PL. 2012. Reef fish spawning aggregations: biology, research and management. New York: Springer. Fish & Fisheries Series 35.

Sadovy de Mitcheson Y, Colin PL, Lindfield SJ, Bukurrou A. 2020. A decade of monitoring an Indo-Pacific grouper spawning aggregation: benefits of protection and importance of survey design. Front Mar Sci. 7:1–23. doi:10.3389/fmars.2020.571878.

Sadovy De Mitcheson Y, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC. 2008. A global baseline for spawning aggregations of reef fishes. Conserv Biol. 22:1233–1244. doi:10.1111/j.1523-1739.2008.01020.x.

Sala E, Ballesteros E, Starr RM. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries. 26:23–30. doi:10.1577/1548-8446-(2001)026<0023:RDONGS>2.0.CO;2.

Schultz ET, Cowen RK. 1994. Recruitment of coral reef fishes to Bermuda: local retention or long distance transport. Mar Ecol Prog Ser. 109:15–28. doi:10.3354/meps109015.

Stump KS, Dahlgren CP, Sherman KD, Knapp CR. 2017. Nassau grouper migration patterns during full moon suggest collapsed historic fish spawning aggregation and evidence of an undocumented aggregation. Bull Mar Sci. 93(2):375–389. doi:10.5343/bms.2016.1042.

Waterhouse L, Happell SA, Pattengill-Semmens CV, McCoy C, Bush P, Johnson BC, Semmens BX. 2020. Recovery of critically endangered Nassau grouper (*Epinephelus striatus*) in the Cayman Islands following targeted conservation actions. Proc Nat Acad Sci. 117(3):1587–1595. doi:10.1073/pnas.1917132117.

Whaylen L, Pattengill-Semmens CV, Semmens BX, Bush PG, Boardman MR. 2004. Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. Environ Biol Fishes. 70(3):305–313. doi:10.1023/B:EBFI.0000033341.57920.a8.

Womble JN, Willson MF, Sigler MF, Kelly BP, VanBlaricom GR. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. Mar Ecol Prog Ser. 294:271–282. doi:10.3354/meps294271.