UNIVERSIDADE ESTADUAL DE SANTA CRUZ

PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO

PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

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IDENTIFICAÇÃO E MAPEAMENTO DE AGREGAÇÕES REPRODUTIVAS DE DUAS FAMÍLIAS DE PEIXES DE ALTO VALOR COMERCIAL: EPINEPHELIDAE E LUTJANIDAE

ILHÉUS - BAHIA

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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutora em Ecologia e Conservação da Biodiversidade.

Orientador: Prof. Dr. Alexandre Schiavetti.

Co-orientadores: Profª. Drª Fabiana Cézar Félix-Hackradt e Prof. Dr. Mauricio Hostim-Silva.

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O48 Oliveira, Inajara Marques Bezerra.
Identificação e mapeamento de agregações reprodutivas de duas famílias de peixes de alto valor comercial: Epinephelidae e Lutjanidae / Inajara Marques Bezerra Oliveira. – Ilhéus, BA: UESC, 2021.
120f. : il.

Orientador: Alexandre Schiavetti.
Tese (Doutorado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade.
Inclui referências e apêndice.

1. Biodiversidade marinha – Conservação. 2. Garoupa (Peixe). 3. Peixes – Reprodução. 4. Pesca. 5. Áreas protegidas. I. Título.

CDD 333.956

ILHÉUS – BAHIA

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Ilhéus, 28 de maio de 2021.

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Aos meus pais, Mônica Marques e Francisco Inajá Bezerra (*in memoriam*), que sempre me apoiaram e acreditaram em mim.

“Mar, metade de minha alma
É feita de maresia”
(Sophia de Mello)

AGRADECIMENTOS

A Deus, pela força e graça infinita que me trouxeram até aqui.

Ao meu orientador, Alexandre Schiavetti, por acreditar no nosso projeto e me ensinar tanto sobre etnoecologia, ser um orientador que acolhe e por contribuir imensamente com o meu crescimento profissional.

À minha co-orientadora, Fabiana C. Félix Hackradt, por todo o conhecimento compartilhado, por estar sempre presente e disponível mesmo com duas nenéns em casa. Obrigada por acreditar no meu potencial. Foi um aprendizado gigante ser sua orientanda nos últimos seis anos.

Ao meu co-orientador Mauricio Hostim, pela acolhida e auxílio sempre que preciso no Espírito Santo.

Ao meu orientador na Universidad de Murcia, José Antonio Garcia Chartón, por todo o suporte e por me receber na Espanha de forma tão acolhedora e amiga. Obrigada por todas as conversas e direcionamentos nas minhas análises.

A Carlos Hackradt, por toda a contribuição durante a escrita dos capítulos.

À Universidade Estadual de Santa Cruz (UESC) e ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade pela oportunidade de cursar esse doutorado.

Às secretárias do Programa Iky e Amábille pela ajuda, profissionalismo e prontidão sempre que preciso.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado e bolsa de doutorado sanduíche (PDSE).

A todos os financiadores desse projeto de pesquisa: FAPES (Edital FAPES/SEAMA nº 02/2016 - PPE Gerenciamento Costeiro), IdeaWild e Rufford Foundation.

Ao Instituto Chico Mendes de Biodiversidade (ICMBio) e projeto GEFMar, pela colaboração com a logística para a realização das entrevistas no Espírito Santo, além da permissão de uso dos dados de desembarque. Em especial a todos os coletores dos portos, Dudu, Bruno, Vinicius e Nilamon.

Aos proprietários, mestres e tripulações da frota capixaba que gentilmente cooperaram neste projeto compartilhando seu precioso conhecimento.

À minha mãe e meus irmãos, por todo incentivo, amor e apoio incondicional. Vocês são minha grande motivação para buscar sempre mais. Ao meu pai, Inajá (*in memoriam*), porque sei que estaria orgulhoso de mim e o quanto investiu em nossa educação.

Ao meu grande amor e companheiro, Du. Tem sido uma jornada incrível partilhar a vida com você. Obrigada por ser meu maior incentivador, acreditar em mim mais do que eu mesma e ser colo pronto para me acolher nos momentos de dificuldade. Em extensão, agradeço imensamente a sua família, por toda torcida, apoio e carinho.

À Amanda, minha grande parceira dessa jornada. Obrigada por dividir, motivar e me inspirar ao longo desses quatro anos. Esse período teria sido mais difícil e muito menos leve sem a sua companhia diária! Obrigada, Maca.

À um dos meus grandes presentes da graduação, Marina. Obrigada por sua amizade e por toda a troca que sua presença traz. Por todos os áudios que me motivaram, alegraram ou só distraíram e me resgataram de dias cansativos.

Aos amigos que ganhei em Murcia e que fizeram minha estadia, mesmo em um momento difícil de pandemia, muito mais divertida e prazerosa. Obrigada por me acolherem com tanto carinho, Virginia, Irene, Victor, Auri, Valeria, Hayfa e Guti.

Ao grupo do Laboratório de Ecologia e Conservação Marinha (LECoMar) e do Laboratório de Etnoconservação e Áreas Protegidas (LECAP), por todas as reuniões, campos e pela contribuição com o trabalho através de sugestões nas apresentações.

A André e Manu pela ajuda no campo dos BRUVS e a Fabrício pelo apoio no campo e sugestões no capítulo de revisão.

A todos os colegas da turma 2017.1.

Em especial a Jessyca, Ramon, Karis, Indira, Zé, Rafa Sena, Juliane, Elisa, Jana, Maísa e Thaiane. Amigos queridos que me apoiaram durante toda a minha trajetória.

A Robson e Juliana, pela paciência infinita e ajuda com minhas dúvidas no ArcGis.

Por fim, à Lolinha, meu amor e companhia diária. Sua presença me acalmou e alegrou em diversos momentos.

A Todos Aqueles Que De Alguma Maneira Contribuíram Com a Minha Caminhada, Minha Eterna Gratidão!

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RESUMO GERAL

Agregações reprodutivas são eventos temporários e imensamente vulneráveis na história de vida da maioria dos peixes recifais com alto valor comercial. Esses encontros breves podem abrigar até milhares de indivíduos em períodos e locais específicos onde toda ou grande parte de sua atividade reprodutiva anual ocorre. Ao longo do tempo, os pescadores também passaram a se reunir para aproveitar a relativa facilidade de captura de um grande número de peixes, muitas vezes explorando-os até o seu esgotamento. Nesse contexto, os objetivos dessa tese foram: (i) revisar a literatura sobre eventos de agregação reprodutiva de espécies das famílias Epinephelidae e Lutjanidae ao redor do mundo, padrões globais e o papel das áreas marinhas protegidas; (ii) identificar possíveis áreas de agregação reprodutiva de espécies das famílias Epinephelidae e Lutjanidae no estado do Espírito Santo através do conhecimento ecológico local e (iii) utilizar dados de desembarque e variáveis ambientais como indicadores de agregações reprodutivas no sul da Bahia e no estado do Espírito Santo. A partir de uma revisão da literatura de estudos que identificaram agregações reprodutivas, através de indicativos diretos e indiretos, foi possível observar que mais da metade das agregações ocorrem principalmente no Caribe e no Indo-Pacífico e fora de áreas marinhas protegidas. Assim, os oceanos Atlântico Sul e Índico carecem de maior investimento em pesquisas que busquem entender a distribuição espacial e temporal de eventos de agregação reprodutiva e, a partir dessas descobertas, estabelecer medidas de proteção para todas as espécies que apresentam esse comportamento, em particular para aquelas que já se encontram sob algum nível de ameaça. Além disso, foi possível observar padrões sazonais e ambientais para diversas espécies dessas famílias. Utilizando indicativos indiretos para a identificação de possíveis áreas de agregação reprodutiva, pudemos acessar, através do conhecimento ecológico local de 51 pescadores capixabas, 31 possíveis áreas de agregação reprodutiva de garoupas e vermelhos, concentradas principalmente na região do Banco dos Abrolhos. O badejo-quadrado (*Mycteroperca bonaci*) e a guaiúba (*Ocyurus chrysurus*) foram identificados como os principais recursos para os pescadores entrevistados. Ainda nessa região, utilizamos a captura por unidade de esforço (CPUE) e variáveis ambientais para identificar possíveis locais de agregação reprodutiva, além das principais características ambientais associadas a esses eventos. Os resultados demonstraram que valores elevados de CPUE estão relacionados principalmente ao tipo de fundo de áreas de recifes, rodolitos, montes submarinos e fundos inconsolidados. Além disso, foi possível corroborar uma das áreas de agregação reprodutiva identificadas pelos pescadores através dos dados de CPUE para *M. bonaci*. A identificação dessas áreas é urgente, uma vez que possibilita a criação e implementação de medidas de conservação e manejo eficazes. Além disso, garantir a preservação desse fenômeno é de suma importância para as comunidades locais dependentes dos recursos pesqueiros recifais.

Palavras-chave: garoupas, vermelhos, CEL, pesca, sobre-explotação, AMP.

ABSTRACT

Spawning aggregations are temporary and immensely vulnerable events in the life history of most reef fish with high commercial value. These brief encounters can house up to thousands of individuals in highly specific periods and locations where all or a huge part of their annual reproductive activity takes place. Over time, fishermen also came together to take advantage of the relatively easy catch of a large number of fish, often exploiting them until they are locally extinct. In this context, the objectives of this thesis were: (i) to review the literature on spawning aggregation events of Epinephelidae and Lutjanidae families around the world, looking for global patterns and analyzing the role of marine protected areas on the maintenance of these spawning aggregations; (ii) to identify possible spawning aggregation areas of Epinephelidae and Lutjanidae species in the Espírito Santo state (southeastern Brazil) through local ecological knowledge and (iii) to use landing data and environmental variables as indicators of spawning aggregations in southern Bahia (in northeastern Brazil) and in Espírito Santo. A literature review indicated that more than half of the spawning aggregations occur mainly in the Caribbean and Indo-Pacific and outside marine protected areas. Thus, the South Atlantic and Indian oceans need greater investment in research to understand the spatial and temporal distribution of spawning aggregations to propose better protection actions mainly for threatened species. In addition, it was possible to observe seasonal and environmental patterns for several species of these families. Using indirect signs 51 fishers from Espírito Santo were able to identify, 31 possible areas of spawning aggregation of groupers and snappers, concentrated mainly in the Abrolhos Bank. Black grouper (*Mycteroperca bonac*i) and yellowtail snapper (*Ocyurus chrysurus*) were identified as the main resources. We used capture per unit of effort (CPUE) and environmental variables to identify possible spawning aggregation sites and the main environmental characteristics associated with these events. High CPUE values were mainly related to reefs, rhodoliths, seamounts, and unconsolidated substrate where spawning aggregations occurred. CPUE data corroborated the localization of one of the spawning aggregations of *M. bonaci* identified by local fishers. The identification of spawning areas is of paramount importance to implement management and conservation plans considering local communities that depend on these resources.

Keywords: groupers, snappers, LEK, fishery, overexploitation, MPA.

INTRODUÇÃO GERAL

O fenômeno da agregação reprodutiva é caracterizado como uma concentração de indivíduos coespecíficos, reunidos com o propósito de reprodução (Colin et al., 2003). É previsível no tempo e no espaço e a densidade de indivíduos que participam desse evento é pelo menos quatro vezes maior do que a encontrada fora do período de agregação (Domeier, 2012). Diversos animais utilizam a agregação como uma estratégia reprodutiva, incluindo crustáceos (por exemplo, caranguejos vermelhos da Ilha Christmas, Adamczewska & Morris, 2001), moluscos (por exemplo, sépia-gigante-australiana, Hall & Hanlon, 2002), e peixes (por exemplo, o budião gigante, *Cheilinus undulatus*, Colin, 2010).

Dentre as espécies de peixes conhecidas por apresentarem esse comportamento, pelo menos 100 espécies de peixes recifais, pertencentes a 20 famílias diferentes, formam agregações reprodutivas (Colin & Bell, 1991; Gladstone, 1996; Sadovy de Mitcheson & Colin, 2012). Embora dentro do próprio grupo existam diferenças com relação ao tamanho dessas agregações e distâncias de migração, tal fenômeno é crucial para o ciclo de vida de todas as espécies envolvidas (Domeier & Colin, 1997). Adicionalmente, a alta concentração de indivíduos contidos nesses grupos servem como oportunidades fáceis para os pescadores retirarem grandes quantidades de peixes rapidamente e com pouco esforço (Sadovy de Mitcheson et al., 2008), muitas vezes explorando-as até a sua extirpação (Erisman et al., 2020).

Em função de poucas espécies já terem sido adequadamente estudadas, as hipóteses relacionadas aos benefícios da desova em agregações giram em torno da redução das ameaças predatórias e/ou aumento do sucesso reprodutivo (Shapiro et al., 1993). No entanto, a reprodução em agregação pode render mais de um benefício ou acarretar mais de um custo (Molloy et al., 2011). Como consequência da ausência de estudos comparativos, a maioria das hipóteses permanecem amplamente não testadas, sendo apoiadas de forma anedótica ou meramente por especulação (Claydon, 2004).

Domeier & Colin (1997) classificaram as agregações reprodutivas em residentes e transientes, com base na constância em que o evento ocorre, no período em que persiste, e na distância que os peixes migram até o local de agregação. Sugere-se que as agregações residentes deslocam os indivíduos para um local próximo a sua área de vida adulta, enquanto as transientes geralmente envolvem migrações de longa distância, chegando até a 250 km (Colin, 1992; Carter et al., 1994). As agregações transientes são caracterizadas por ocorrerem sazonalmente, diferente das residentes, que podem ocorrer diariamente por semanas, meses ou até durante todo o ano (Sadovy de Mitcheson & Colin, 2012).

Evidências científicas de eventos de agregação reprodutiva podem ser obtidas através de dois tipos de sinais: diretos e indiretos (Colin et al., 2003). Indicativos diretos podem ser observações no momento da desova e presença de oócitos hidratados nas gônadas de fêmeas coletadas no local (Heyman et al., 2004). Em função da dificuldade de presenciar esses eventos, que na maioria das vezes ocorrem em um ambiente com pouca luminosidade (ao entardecer), indicativos indiretos também são considerados para a identificação das agregações reprodutivas: comportamentos de corte conspícuos, como mudanças de coloração (Archer et al. 2012, Heppell et al., 2012); comportamentos agonísticos (Rowell et al., 2018); produção de sons (Schärer et al. 2012); abdômen inchado nas fêmeas (Erisman et al., 2007); aumento no índice gonadossomático (Claro & Lindeman, 2003, Heyman et al., 2004); assim como abundância elevada (Domeier & Colin, 1997).

Apesar da extrema relevância destas descobertas e caracterizações para implementações de medidas eficazes de manejo, encontrar agregações reprodutivas na área marinha é uma atividade muito difícil, lenta e de custo elevado (Sala et al., 2001). Nesse sentido, a utilização do conhecimento ecológico local e de dados provenientes da pesca para a identificação dessas agregações se apresentam como ferramentas capazes de fornecer informações essenciais sobre a história de vida, ecologia e biologia dessas espécies (Claro & Lindeman, 2003; Boomhower et al., 2007; Robinson et al., 2011). Além disso, essas ferramentas se destacam como principais fontes de informação para iniciar estudos em áreas onde esse fenômeno ainda é desconhecido ou mesmo pouco estudado.

É possível observar o progresso nos estudos de agregações reprodutivas de peixes recifais ao longo do tempo principalmente nas regiões do Caribe e Indo-Pacífico (Erisman et al., 2015) e particularmente sobre duas espécies: a garoupa de nassau, *Epinephelus striatus* e garoupa leopardo, *Plectropomus leopardus*, respectivamente. No entanto, ainda há poucas informações sobre a dinâmica dos padrões de desova e os efeitos da pesca em agregações em áreas como o Pacífico Sudeste, o Atlântico Sudeste e o Índico (Sadovy de Mitcheson et al., 2008; Granados-

Dieseldorff et al., 2013). Como resultado dessa concentração espacial de estudos, as abordagens de gestão pesqueira para agregações reprodutivas têm sido baseadas em particularidades de poucos locais e espécies estudadas (Molloy et al., 2011).

Se o *status* de uma população local for desconhecida ou se uma espécie já se encontra ameaçada pela sobrepesca, é imprescindível uma abordagem preventiva. Nesse contexto, o estabelecimento de áreas marinhas protegidas, proibições de venda, proteção de habitats associados a áreas de agregações (ou seja, montes submarinos, quebra da plataforma, promontórios) e/ou o estabelecimento de limites de captura podem ser indispensáveis para auxiliar as populações a reconstruírem seus estoques. Infelizmente, existe uma ausência de dados para a maioria das espécies registradas com comportamento de agregação reprodutiva e, nesse sentido, abordagens conservadoras precisam ser consideradas (Sadovy de Mitcheson et al., 2008).

As famílias Epinephelidae e Lutjanidae são compostas por espécies com alto valor comercial, que apresentam o comportamento de agregação como estratégia reprodutiva e que estão sob intensa pressão pesqueira (Sadovy & Vincent, 2002; Erisman et al., 2010). Adicionalmente, constituem grande parte da captura de peixes recifais na zona costeira de ambientes tropicais e subtropicais e são caracterizadas por realizarem agregações transientes (Coleman, 2000), geralmente representando o esforço reprodutivo total dos indivíduos participantes (Domeier & Colin, 1997; Domeier, 2012). Compreender a localização e o período das agregações reprodutivas é primordial para garantir que sejam protegidas de forma adequada. O contexto de escassez de dados e *status* geralmente desatualizado das espécies que apresentam comportamento de agregação não devem constituir barreira para a implementação de medidas de manejo (Turnbull & Samoilys, 1997).

Esta tese é composta por três capítulos e tem como objetivo geral identificar possíveis áreas de agregação reprodutiva de espécies das famílias Epinephelidae e Lutjanidae e entender os principais padrões que influenciam a ocorrência desse fenômeno ao redor do mundo. No **capítulo 1** foi realizada uma revisão buscando analisar a distribuição geográfica de trabalhos publicados sobre agregações reprodutivas, avaliar a relação entre as características ambientais e localização e período das agregações reprodutivas. Além de, identificar lacunas de conhecimento acerca do estudo desses eventos e analisar o nível de proteção das agregações reprodutivas conhecidas.

Nos **capítulos dois e três**, buscamos identificar possíveis áreas de agregação reprodutiva de epinefelídeos (garoupas) e lutjanídeos (vermelhos) no Brasil através de sinais indiretos de identificação. Assim, no capítulo dois analisamos, através do uso de entrevistas semiestruturadas, se o conhecimento ecológico local pode determinar áreas potenciais de agregações no estado do Espírito Santo (localizado na região sudeste; Figura 1). No capítulo três, buscamos avaliar dados de desembarque. Especificamente buscou-se abordar as seguintes questões: (i) os dados de pesca são indicadores adequados e viáveis de agregação reprodutiva de garoupas e vermelhos no Brasil ?; e (ii) quais variáveis ambientais podem ser usadas para caracterizar possíveis agregações reprodutivas? Essas questões foram avaliadas para as espécies de garoupas (badejo quadrado (*M. bonaci*) e garoupa (*E. morio*) e vermelhos (cioba (*L. analis*), dentão (*L. jocu*), guaiúba (*O. chrysurus*)) na costa leste brasileira. Além disso, incluímos uma avaliação e descrição dos dados de pesca para caracterizar os padrões temporais e espaciais de capturabilidade das espécies.

Figura 1. Realização de entrevistas com pescadores nos munícipios de Anchieta e Piúma/ES.

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Capítulo 1

Distribution of spawning aggregations of Epinephelidae and Lutjanidae families: Global patterns and marine protected areas

Artigo a ser submetido para Global Ecology and Conservation (A2, IF 2.5).

Distribution of spawning aggregations of groupers and snappers: Global patterns and marine protected areas

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ABSTRACT

Several reef fish migrate in order to form spawning aggregations. These events generally occur in predictable locations in time and space. Moreover, environmental characteristics such as geomorphological features, lunar and tide cycles and sea temperature are associated with this predictability. Species with high commercial value and aggregating behavior, such as those included in the Epinephelidae and Lutjanidae families, have suffered from overfishing for decades. In an attempt to minimize these impacts, several management actions have been implemented, e.g., seasonal closures, fishing bans and establishment of marine protected areas. In this sense, the present work aimed at: i. analyzing the geographic distribution of published works on spawning aggregations in the world; ii: identifying seasonal patterns in the occurrence of spawning aggregations in the northern and southern hemispheres; iii. evaluating the correlation between environmental characteristics and the periods/places of reproductive aggregation; iv. analyzing the protection level of known aggregations. This literature review summarizes the latest advances in the study of reef fish spawning aggregations in the world, with a greater focus on aggregations identified through direct signs of groupers and snappers. Eighty-nine studies of Epinephelidae and Lutjanidae families were identified, which focused on 34 species. Of these, 86 studies identified aggregations by direct signs and 57 by indirect signs. Most studies were documented in the Caribbean (n = 48) and Indo-Pacific (n = 22). For both families, full moon and spring had a strong relationship with fish spawning aggregation (FSA) events. The average temperature and depth where FSA occur are 26°C and 26 m for Epinephelidae and 28°C and 31 m for Lutjanidae, respectively, mostly in coral reefs and promontories. Only 44.4% of all known aggregations occur within marine protected areas, while 55.6% occur outside protected areas or were not mentioned in the study. Therefore, this review represents a contribution to groupers and snappers spawning aggregations worldwide. It was possible to show that, Southwest Atlantic and the Indian Ocean, more research is needed to understand how FSA area are spatially and temporarily distributed to support the management of threatened species.

Keywords: Epinephelidae, Lutjanidae, Conservation, Overfishing

INTRODUCTION

Several reef fish aggregate to reproduce in specific times and places (Carter et al., 1994; Sadovy, 1994; Domeier & Colin, 1997; Tuz-Sulub & Brule, 2015; Nanami et al., 2017). In the last decades, the phenomenon of reef fish spawning aggregations (FSA) has received increasing attention, not only for its ecological and fishing importance, but also because many aggregations have decreased or even disappeared over time (Colin, 1996; Sala et al., 2001; Aguilar-Perera, 2006; Russell et al., 2012). Even though other factors contribute to the loss of FSA, such as habitat degradation and other forms of disturbances, the greatest threat to reef fish spawning aggregations appears to be commercial overfishing (Sadovy, 1994; Luckhurst, 2002).

One of the main reasons responsible for the fast decline of populations, since the aggregations have become fishing targets, is the fact that fish are usually captured before spawning. This curbs the population a chance to maximize reproductive success and to stocking the environment with new individuals (Koenig et al., 1996; Sadovy, 1996; Rhodes et al., 2005). Moreover, many spawning aggregation-forming species have complex life cycles that increase their susceptibility to extinction (Sadovy, 1997; Armsworth, 2001; Huntsman et al., 1999; Coleman et al., 2000; Sadovy de Mitcheson et al., 2020). Due to the size selection of fishers to larger individuals on aggregations, catches of protogynous or protandrous species generally consists of individuals of the same sex, thus impacting the sex ratio at the time of spawning and thereby reducing the reproductive success (Coleman et al., 1996; Koenig et al., 1996; Vincent & Sadovy, 1998).

There are particularities that are strongly related to the occurrence of spawning aggregation events and its predictability (Domeier & Colin, 1997), such as significant geomorphological features (shelf edges or reef projections) (Colin et al., 1987), sea temperature (Hereu et al., 2006; Feeley, 2018), lunar (Beets & Friedlander, 1999, Archer et al., 2012, Biggs & Nemeth, 2016) and tidal (Heyman et al., 2005) cycles, site fidelity, and seasonality. This characteristics represents an easy opportunity for fishermen withdraw a lot of fish, quickly and with relatively little effort (Sadovy de Mitcheson et al., 2008). Moreover, added to the development of fishing gear technology, the fishing activity directed to these aggregations increased considerably, becoming even more efficient. This overfishing caused the population decline of several FSA species (Johannes et al., 1999; Sala et al., 2001; Claro & Lindeman, 2003).

Within this context, several actions have been thought of as a way to curb this threat. In the Tropical Western Atlantic and Indo-Pacific, a wide variety of management measures have been implemented over the years aiming to protect FSA (Domeier et al., 2002). These measures range from seasonal (Beets & Friedlander, 1999) or permanent (Koenig et al., 2000; Pet et al., 2005) closures of places where aggregations occur, gear restrictions (Erisman et al., 2014), seasonal/annual prohibitions sales of species that aggregate (Johannes et al., 1999), to a combination of these actions (Rhodes & Sadovy, 2002).

However, the best approach to these resources conservation tends to vary according the region where they are located. Especially, considering the information gaps in the reproductive behavior of different species and concerns about the decline in stocks caused by overfishing, it is imperative that there are preventive approaches that can guarantee sustainable management (Rhodes et al., 2012). Unfortunately, for species that already suffer from intensive fishing and/or are threatened, multiple conservation measures must be applied both during and outside the aggregation period to minimize the risk of overfishing of the species (Russel et al., 2012) .

Among these measures, the local community support, involved in the fisheries decision and enforcement process, stands out as a key tool for the successful monitoring and recovery of populations (Hamilton et al., 2011; Granados-Dieseldorff et al., 2013). Aburto-Oropeza et al. (2011) for example, demonstrated that working together with local fishermen achieved success in a marine protected area over 10 years, increasing marine biomass by more than 450%. Therefore, the appropriate management for a given location or species inevitably depends on local, social, and economic factors, as well as on the biology and conservation status of the target species and each case should be analyzed individually.

Colin et al. (2003) proposed a set of divisions related to the type of sign found to identify spawning aggregation events. Direct signs provide accurate evidence of FSA occurrence (i.e.: visualization of spawning during the dive in aggregation sites and/or presence of post-ovulatory follicles in females). Indirect signs require additional evidence that can confirm the purpose of the aggregation. Examples of indirect signs include swollen abdomen in females, change in color pattern, courtship behavior, significant increase in relative abundance or increase in catches at certain times of the year and in constant fishing areas (Colin et al., 2003; Sadovy de Mitcheson et al., 2008).

In particular, Epinephelidae and Lutjanidae families, represent an important group, with high commercial and consumption value, and which has been under strong fishing pressure for decades (Sadovy & Vincent, 2002). Moreover, they support an important part of coastal reef fishing in tropical and subtropical environments and are characterized by transient aggregations as a reproductive strategy (Coleman, 2000). This behavior encompasses long migrations to the spawning location, lasting from days to weeks and generally represents the total reproductive effort for the participants individuals (Domeier & Colin, 1997; Domeier, 2012).

Although several relationships have already been established in literature that indicate the locations and times of aggregations occurrence, it is important to point out that many questions still remain unanswered. For each generality or hypothesis raised about this phenomenon, there is a case that says exactly the opposite (Colin, 2011). In addition, what happens in one location does not necessarily occur in another with the same features, besides it is needed to consider the unknown plasticity of reproductive ecology locally. For example, Boomhower et al. (2010) sought to detect FSA through geomorphological features, however it was not possible to identify a direct sign of spawning aggregation for any species.

Moreover, characteristics such as lunar phase or temperature can vary from place to place. Therefore, the present work has as objectives for the species of Epinephelidae and Lutjanidae families: i. analyze the geographical distribution of published works on spawning aggregations in the world; ii: identify seasonal patterns in the occurrence of spawning aggregations in the northern and southern hemispheres; iii. evaluate the correlation between environmental characteristics (e.g. lunar patterns) and the periods/places of spawning aggregation; iv. analyze the protection level of known aggregations.

Review of spatial and temporal patterns of spawning aggregations of epinephelids and lutjanids

It was used as a basis, searches carried out on the Web of Science, Google Scholar and Scopus platforms, published throughout the period available in these databases until January 2021. For the bibliographic survey, the following keywords were used: “spawn* aggregation*” or “gathering” and “reef fish*” Or “Epinephelidae” or “Serranidae” or “Lutjanidae”. Moreover, the

Science and Conservation of Fish Aggregations (SCRFA) database and secondary citations were used in the analyzed articles to obtain complementary information.

We identified 89 studies related to spawning aggregations of Epinephelidae and Lutjanidae focusing on 34 species (21 and 13, respectively) (Table 1). Among these, 85 spawning aggregation have been identified through direct signs and 57 through indirect signs. It is important to note that the same work can investigate more than one species and use direct, indirect or both signals.. Most studies were documented in the Caribbean (n = 48) and Indo-Pacific (n = 22).

Only studies reporting direct signal to identify spawning aggregations were analyzed. Indirect signals without confirmation of the spawning event and/or gonadal analysis may still represent other types of behavior, such as food migration for example (Colin et al., 2003). For the seasonality analysis, the following division was considered: December, January and February (winter/summer); March; April and May (spring/autumn); June, July and August (summer/winter); and September, October and November (spring/autumn) for the northern and southern hemispheres, respectively.

Table 1: Studies of spawning aggregations of the families Epinephelidae and Lutjanidae identified in the literature review.

Species	**Family**	**Reference**	**Direct or Indirect**
Epinephelus fuscoguttatus (Brown-marbled grouper)	Epinephelidae	Pet et al., 2005	Indirect
		Robinson et al., 2008	Direct
		Mangubhai et al., 2011	Indirect
		Hamilton et al., 2012	Indirect
		Rhodes et al., 2014	Indirect
		Hughes et al., 2020	Direct
Dermatolepis dermatolepis (Leather bass)	Epinephelidae	Aburto - Oropeza & Hull, 2008	Indirect
		Erisman et al., 2009	Direct
Epinephelus guttatus (Red hind)	Epinephelidae	Colin, 1987	Direct
		Sadovy et al., 1994	Direct
		Shapiro et al., 1993	Direct
		Luckhurst, 1998	Direct
		Beets & Friedlander,1999	Direct
		Nemeth, 2005	Indirect
		Eristhee et al., 2006	Direct
		Nemeth et al., 2007	Indirect
		Cushion et al., 2008	Direct
		Kadison et al., 2009	Direct

		Luckhurst & Trott, 2009	Indirect
		Boomhower et al., 2010	Indirect
		Tuz-Sulub & Brulé, 2015	Direct
Epinephelus itajara (Goliath grouper)	Epinephelidae	Bullock et al., 1992	Direct
		Félix Hackradt & Hackradt, 2008	Indirect
		Bueno et al., 2016	Direct
		Malinowski et al., 2019	Direct
Epinephelus marginatus (Dusky grouper)	Epinephelidae	Zabala et al., 1997	Direct
		Pelaprat, 1999	Direct
		Hereu et al., 2006	Direct
Epinephelus ongus (White-streaked grouper)	Epinephelidae	Nanami et al., 2013	Direct
		Nanami et al., 2014	Direct
		Ohta & Ebisawa, 2015	Direct
		Nanami et al., 2017	Indirect
Epinephelus polyphekadion (Camouflage grouper)	Epinephelidae	Rhodes & Sadovy, 2002	Direct
		Robinson et al., 2008	Direct
		Hamilton et al., 2012	Indirect
		Rhodes et al., 2012	Indirect
		Rhodes et al., 2014	Indirect
		Hughes et al., 2020	Direct
Epinephelus striatus (Nassau grouper)	Epinephelidae	Smith, 1972	Direct
		Olsen & La Place, 1979	Indirect
		Colin, 1987	Indirect
		Colin, 1992	Direct
		Tucker et al., 1993	Direct
		Carter et al., 1994	Direct
		Sadovy & Colin, 1995	Direct
		Aguilar-Perera & Aguilar-Davila, 1996	Indirect
		Sala et al., 2001	Direct
		Claro & Lindeman, 2003	Indirect
		Whaylen et al., 2004	Direct
		Medina-Quej et al., 2004	Indirect
		Starr et al., 2007	Direct
		Whaylen et al., 2007	Direct
		Cushion et al., 2008	Direct
		Heyman & Kjerfve, 2008	Direct
		Boomhower et al., 2010	Indirect
		Heyman et al., 2010	Direct
		Archer et al., 2012	Direct
		Egerton et al., 2017	Indirect
Mycteroperca bonaci (Black grouper)	Epinephelidae	Smith, 1972	Direct
		Eklund et al., 2000	Indirect
		Sala et al., 2001	Direct
		Claro & Lindeman, 2003	Indirect
		Brule et al., 2003	Direct

		Whaylen et al., 2004	Indirect
		Paz & Sedberry, 2008	Direct
		Heyman & Kjerfve, 2008	Direct
		Luckhurst, 2010	Indirect
		França & Olavo, 2015	Indirect
Mycteroperca jordani (Gulf grouper)	Epinephelidae	Sala et al., 2003	Indirect
Mycteroperca microlepis (Gag grouper)	Epinephelidae	Gilmore & Jones, 1992	Indirect
		Koenig et al., 1996	Direct
Mycteroperca olfax (Sailfin grouper)	Epinephelidae	Salinas-de-León, 2015	Direct
Mycteroperca phenax (Scamp)	Epinephelidae	Gilmore & Jones, 1992	Indirect
Mycteroperca prionura (Sawtail grouper)	Epinephelidae	Sala et al., 2003	Direct
Mycteroperca rosacea (Leopard grouper)	Epinephelidae	Sala et al., 2003	Direct
		Erisman et al., 2007	Direct
		TinHan et al., 2014	Indirect
Mycteroperca tigris (Tiger grouper)	Epinephelidae	Sadovy et al., 1994	Direct
		Sala et al., 2001	Indirect
		White et al., 2002	Direct
		Matos-Caraballo et al., 2006	Indirect
		Whaylen et al., 2007	Direct
		Heyman & Kjerfve, 2008	Indirect
		Tuz-Sulub & Brulé, 2015	Direct
		Starr et al., 2018	Direct
Mycteroperca venenosa (Yellowfin grouper)	Epinephelidae	Sala et al., 2001	Indirect
		Claro & Lindeman, 2003	Indirect
		Whaylen et al., 2004	Indirect
		Starr et al., 2007	Direct
		Cushion et al., 2008	Direct
		Heyman & Kjerfve, 2008	Direct
		Scharer et al., 2012	Direct
		Tuz-Sulub & Brulé, 2015	Direct
Plectropomus areolatus (Squaretail coralgrouper)	Epinephelidae	Pet et al., 2005	Direct
		Rhodes & Tupper, 2008	Direct
		Mangubhai et al., 2011	Indirect
		Hamilton et al., 2012	Indirect
		Rhodes et al., 2014	Indirect
		Hughes et al., 2020	Direct
Plectropomus leopardus (Leopard coral-trout)	Epinephelidae	Samoilys & Squire, 1994	Direct
		Samoilys, 1997	Direct
		Zeller, 1998	Direct
		Frisch & van Herwerden, 2006	Direct
Plectropomus maculatus (Spotted coral grouper)	Epinephelidae	Frisch & van Herwerden, 2006	Direct
Plectropomus punctatus	Epinephelidae	Robinson et al., 2008	Direct

(Marbled coral grouper)			
Lutjanus synagris (Lane snapper)	Lutjanidae	Claro & Lindeman, 2003	Indirect
Lutjanus analis (Mutton snapper)	Lutjanidae	Claro & Lindeman, 2003 Burton et al., 2005 Graham, 2008 Heyman & Kjerfve, 2008 Boomhower et al., 2010 Graham, 2012 Granados-Dieseldorff et al., 2013 França & Olavo, 2015 Feeley et al., 2018 França et al., 2021	Indirect Indirect Direct Direct Indirect Direct Indirect Indirect Direct Direct
Lutjanus apodus (Schoolmaster snapper)	Lutjanidae	Boomhower et al., 2010	Indirect
Lutjanus argentiventris (Yellow snapper)	Lutjanidae	Sala et al., 2003	Direct
Lutjanus bohar (Two-spot red snapper)	Lutjanidae	Sakaue et al., 2016	Direct
Lutjanus cyanopterus (Cubera snapper)	Lutjanidae	Claro & Lindeman, 2003 Heyman et al., 2005 Kadison et al., 2006 Heyman & Kjerfve, 2008 Boomhower et al., 2010 Heyman et al., 2010 Biggs & Nemeth, 2016	Indirect Direct Indirect Direct Indirect Direct Direct
Lutjanus fulvus (Blacktail snapper)	Lutjanidae	Cimino et al., 2018	Indirect
Lutjanus gibbus (Humpback red snapper)	Lutjanidae	Nanninga & Spaet, 2016	Direct
Lutjanus griseus (Grey snapper)	Lutjanidae	Claro & Lindeman, 2003	Indirect
Lutjanus jocu (Dog snapper)	Lutjanidae	Carter & Perrine, 1994 Claro & Lindeman, 2003 Whaylen et al., 2004 Kadison et al., 2006 Whaylen et al., 2007 Heyman & Kjerfve, 2008 Heyman et al., 2010 França & Olavo, 2015 Biggs & Nemeth, 2016 França et al., 2021	Direct Indirect Indirect Indirect Direct Direct Direct Indirect Direct Direct
Lutjanus novemfasciatus (Pacific dog snapper)	Lutjanidae	Sala et al., 2003	Direct
Ocyurus chrysurus (Yellowtail snapper)	Lutjanidae	Heyman & Kjerfve, 2008	Direct

Symphorichthys spilurus (Sailfin snapper)	Lutjanidae	Sakaue et al., 2016	Direct

Seasonality

One of the main factors associated with the decline of populations forming spawning aggregations is their predictability. A unique event in the year for many species that allows fishers to obtain their largest catches. Over the decades, this behavior has led to several places being exhausted (Coleman et al., 1996; Sala et al., 2001; Sadovy de Mitcheson & Colin, 2012; Erisman et al., 2015; Robinson et al., 2015; Sadovy de Mitcheson et al., 2020).

For epinephelids (18 of 21 analyzed species) and lutjanids (9 of 13 analyzed species), the spawning season occurs mainly between spring and summer (in each hemisphere), with some species (from both families) extending their reproductive period until autumn and winter (Figure 1). For epinephelids, in the northern hemisphere, the studies analyzed showed that there are species of the family spawning throughout the year. In the southern hemisphere, although there is a concentration of spawning in the spring/summer, four species aggregating in the winter (*P. areolatus*, *E. polyphekadion*, *E. fuscoguttatus*, *P. leopardus*) and three in the autumn (*P. areolatus*, *E. polyphekadion*, *E. fuscoguttatus*) (Figure 1). For lutjanids, only one study was identified through direct indication of aggregation in the southern hemisphere (Nanninga & Spaet, 2016), with spawning in the spring of each year. In the northern hemisphere, aggregations for reproductive purposes are concentrated in the spring/autumn period, but with small variation when we observe summer and winter (Figure 1).

According to Grimes (1986), it is possible to observe two evident patterns of reproductive seasonality in lutjanids. Populations and species showing prolonged spawning in the summer, and on the other hand, species that reproduce all year round with pulses in spring and autumn. In addition, reef fish may show plasticity regarding reproductive strategies. Since the strength and direction of natural selection differs by geographic location, it is suggested that there may be a subsequent change in the reproductive mechanisms employed. What may be a strong selection pressure in the Caribbean may be absent or diminished in importance in the Pacific (Carter & Perrine, 1994).

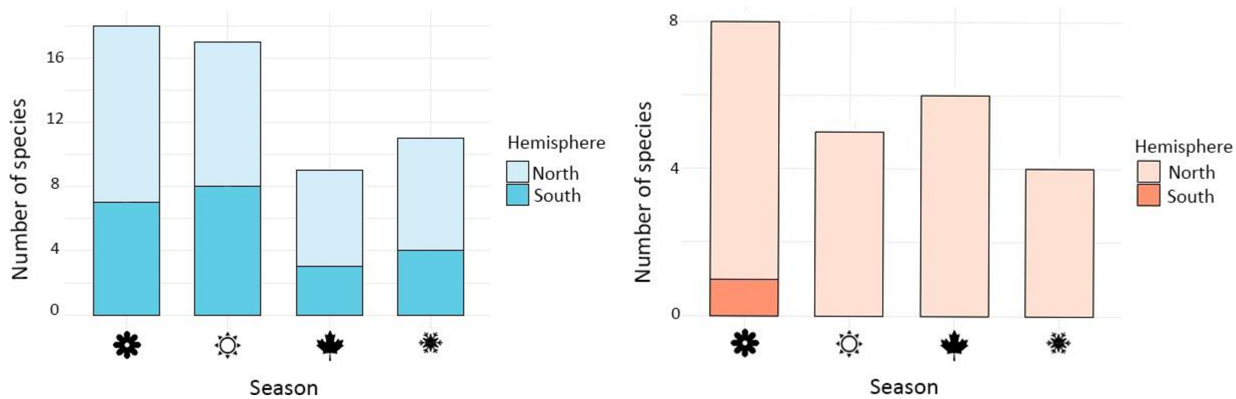

Figure 1. Number of species in each season (spring, summer, fall and winter, in this order) forming spawning aggregations in the northern and southern hemispheres. Blue: Epinephelidae; Orange: Lutjanidae.

It is important to note that this is an overview of the places and times where the spawning episodes occurred, according to the division considered for the months corresponding to the seasons in each hemisphere, without considering the particularities of each location. Spawning aggregations will probably be influenced by a combination of oceanographic and atmospheric factors (currents, topography, seasonal temperature, salinity, and climate) with biological factors (specific needs regarding food, social structure, predation, physiology, and genetics). Additionally, species included in this review have a tropical and sub-tropical distribution with stable environmental conditions in comparison with temperate and cold regions, not favoring clear seasonal patterns.

Lunar period

For both families, the full moon phase shows a strong relationship with FSA events (Figure 2). The new moon also showed a strong relationship for the epinephelid and no relationship with lutjanids. For this last family, four species (out of a total of five analyzed) were observed aggregating during the full moon, followed by *Lutjanus cyanopterus* and *Symphorichthys spilurus* spawning on the last quarter (Figure 2).

Although strong relationship between lunar phases and aggregation periods for spawning has already been well-known, some studies have shown little or no relationship between lunar periodicity and the formation of spawning aggregations. For example, no relationship was found with formation or reproductive activity and the lunar cycle for the dusky grouper (*Epinephelus marginatus*) (Herue et al., 2006), *Paralabrax clathratus* (Erisman & Allen, 2006), *Mycteroperca rosacea* (Erisman et al., 2007) and *Lutjanus jocu* (Carter & Perrine, 1994). Sala (2003) showed that in Mexico, factors such as day length of or temperature may be more relevant to encourage spawning. However, in some species like *E. striatus*, the spawning seasonality is strongly correlated with the full moon, as well as with the temperature, not the month itself (Sadovy & Eklund, 1999).

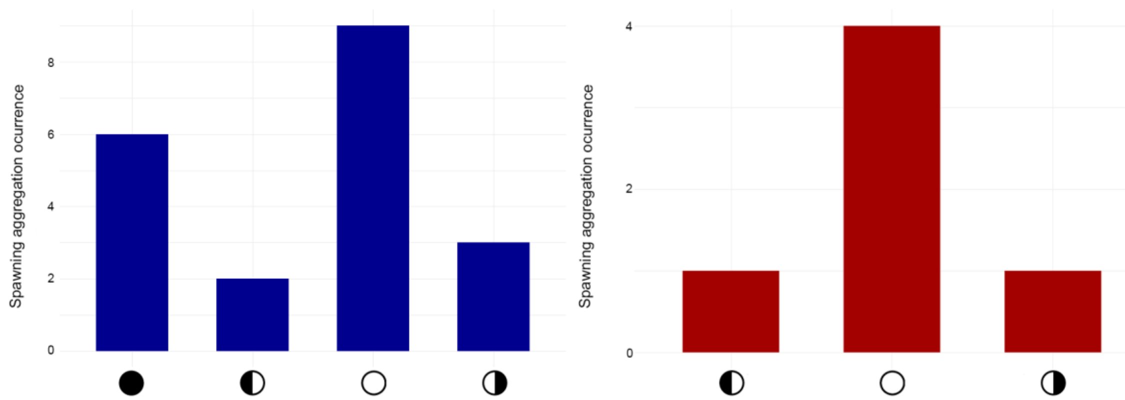

Figure 2 . Number of spawning aggregations reported by lunar phase. Blue: Epinephelidae; Red: Lutjanidae. In sequence: New moon, First quarter moon, Full moon, and Last quarter moon.

Temperature

Among several environmental factors that trigger events of spawning aggregations, such as the lunar phase, tidal amplitude, the seasonal temperature variation, undoubtedly plays an important role (Louisy & Culioli, 1999; Pelaprat, 1999; Hereu et al., 2006). The water temperature determines the rates of many fish metabolic functions, such as, the rate of embryonic growth, hatching and food dynamics (Leggett & Dublois, 1994; Yoseda et al., 2006).

According to Hereu et al. (2006), episodes with extreme limits, such as powerful currents or low temperatures, have the ability to inhibit spawning activity and aggregation formation. Due to the low annual temperature variation in the Indo-Pacific, species such as *P. areolatus* can have long periods of aggregation, which can extend throughout the year, but always with lunar periodicity (Johannes et al., 1999; Hughes et al., 2020). Conversely, *E. striatus* spawning has a greater relationship with the moon phase and temperature (Sadovy & Eklund, 1999).

From the analyzed studies, the temperature averages were 26ºC and 28ºC for Epinephelidae and Lutjanidae, respectively (Figure 3). For one of the most studied species, the Nassau grouper (*E. striatus*), spawning occurs consistently at about 25ºC. Other species, such as *E. guttatus*, are reported to spawning over a wider temperature range (between 21°C and 26 °C). Additionally, other species did not show such a close relation with temperature, but for many, conclusive data were not found. In Roviana Lagoon (Solomon Islands), none of the three species of grouper studied (*P. areolatus, E. fuscoguttatus and E. polyphekadion*) showed any relation between daily water temperatures and the aggregation formation pattern (Hamilton, 2012).

For lutjanidae, there was a lower temperature range for the analyzed species. Unfortunately, not all studies reported water temperature during spawning, with many species having only one record for both families. Additionally, it should be considered that shelf edge areas, where most fish aggregate, usually have colder water at depths close to the aggregation areas. Thus, fish can adjust their temperature by simply varying the depth in which they are. In this context, Starr et al. (2007) documented an interesting example in Lighthouse Reef, Belize, where the Nassau grouper changed from shallow water depth (less than 30 m) to deeper waters (60-70 m) after spawning in January. Several possible reasons for this change can be suggested, and the selection of a preferred temperature may be one of them.

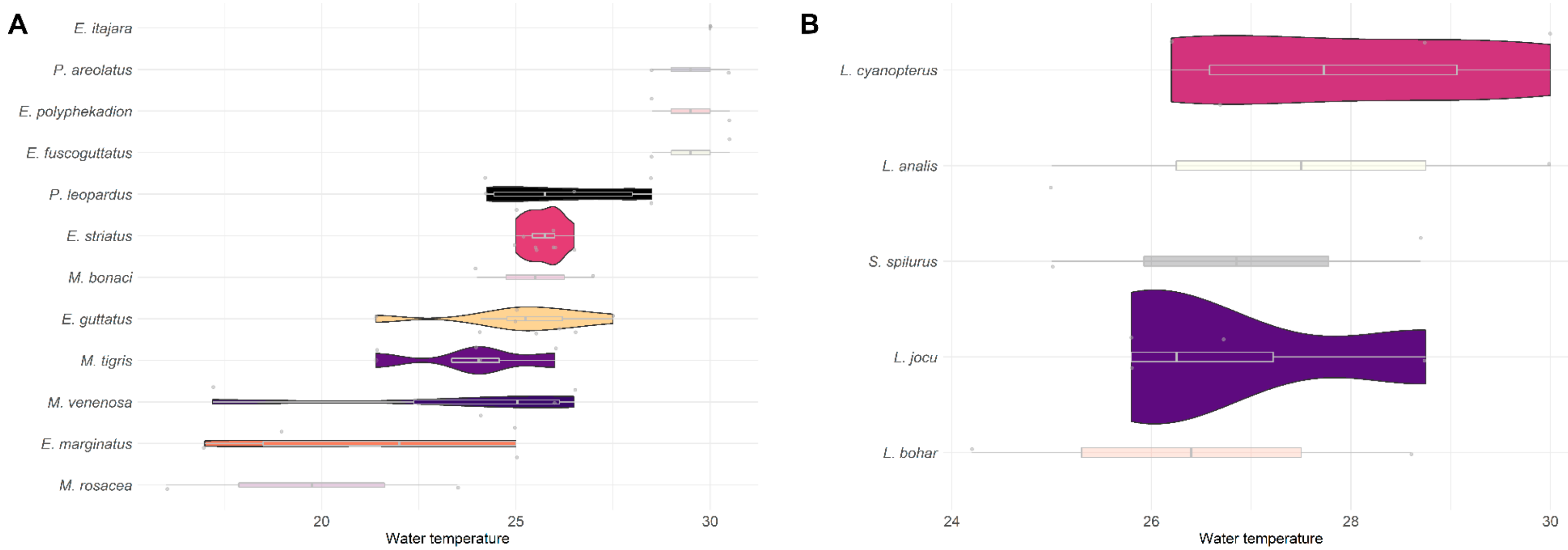

Figure 3. Temperature variation at sites of spawning aggregations. A: Epinephelidae; B: Lutjanidae.

Depth

Spawning aggregations were found on an average of 26 m to the Epinephelidae (18 species analyzed) and 31 m to the Lutjanidae (8 species analyzed) (Figure 4). The maximum depth observed was 60 m for *M. bonaci* (gonadal analysis of individuals obtained through fishing - Brule et al., 2003) and 45 m for *L. analis* (Graham, 2008; 2012) and *L. jocu* (Carter & Perrine, 1994). For Lutjanidae, only one study was observed for five species (*O. chrysurus* – Heyman & Kjerfve, 2008; *S. spilurus* - Sakaue et al., 2016; *L. bohar* - Sakaue et al., 2016; *L. argentiventris* - Sala et al,. 2003 and *L. novemfasciatus* - Sala et al., 2003) that presented the depth where the aggregation was found, and it was not possible to generate the range or mean for these species (Figure 5).

Diving is the main methodology used to visualize spawning in spawning aggregations (Carter & Perrine, 1994; Erisman et al., 2007; Graham, 2012; Salinas-de-León, 2015; Starr et al., 2018). This tool has several limitations, one of which is the relationship between the time the diver can be submerged and the depth at which he is. Therefore, it is important to take this factor into consideration since the depths presented may represent the context of this limitation. For example, Erisman et al. (2009), through the use of a small submersible they were able to observe the spawning of *D. dermatolepis* at a depth between 45-47 meters, a range that does not represent the usual and safe depth in which the spawning visualization methodology is applied.

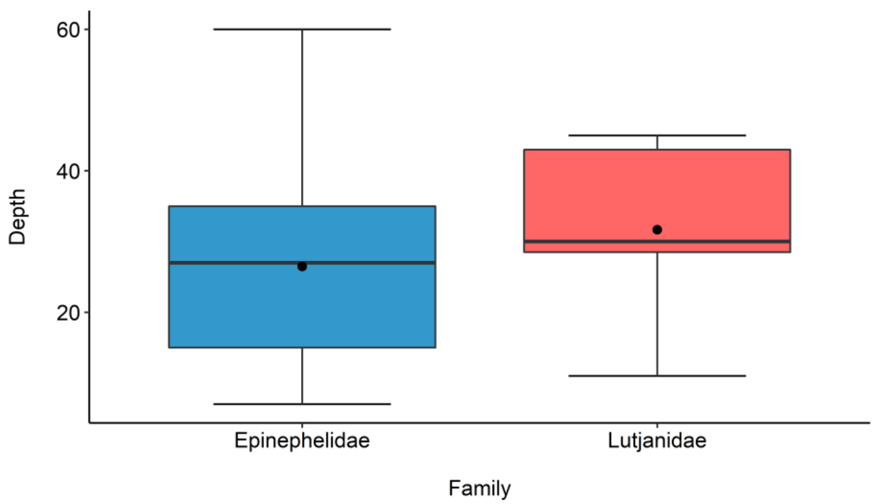

Figure 4. Depths where spawning aggregations were identified for Epinephelidae and Lutjanidae (n = 11). Black dots represent mean depth.

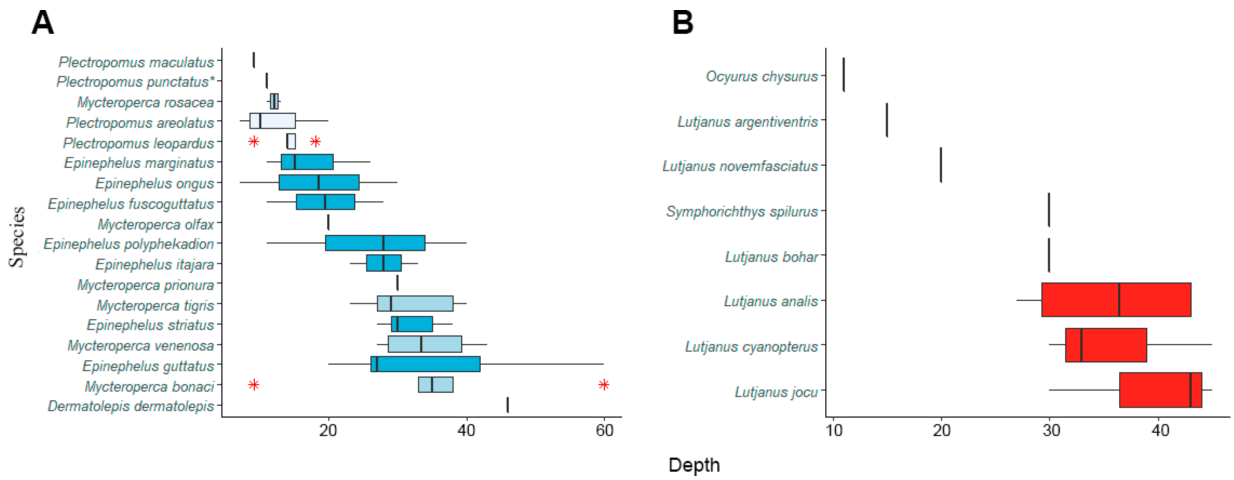

Figure 5. Depths at which spawning aggregations were identified for species of Epinephelidae (A) and Lutjanidae (B). Red asterisks represent outliers.

Habitat

Spawning areas are likely to be selected due to certain characteristics (Randall & Randall, 1963), but the continued use of sites can be traditional and learned (Warner, 1988; 1995). Although almost all studies are able to fit into four broad descriptions of reef structures (channels and passages, walls, promontories and reef slopes), this is quite subjective and dependent on scale (Claydon, 2004). The absence of studies with detailed descriptions of the places where spawning aggregations occur do not yet allow this assessment to be done accurately (Colin, 2011). Furthermore, limited evidence indicates that, among the seemingly equivalent reef structures, only a few of them can actually harbor aggregation (Colin, 1992). However, most studies tend to focus on few locations and often presents generalities (Colin, 2011).

It is also interesting to reflect on the fact that the shallower areas of the marine environment are relatively new, since it was only a few thousand years ago that these sites appeared, after the sea level rose (Pauly, 1990). Therefore, it is observed that these innermost areas of the reef were not available during the lowest sea levels. According to Sadovy & Colin (1995), the use of a site can boost the success sometimes, while other sites can be advantageous on other occasions. Since it is very difficult to monitor the reproductive success of spawning in a given place, a combination of historical aspects of ecology, species biology and geomorphology of reef environments is considered. In this study, spawning aggregations were mostly reported in coral reefs and reef promontories for both families (Figure 6).

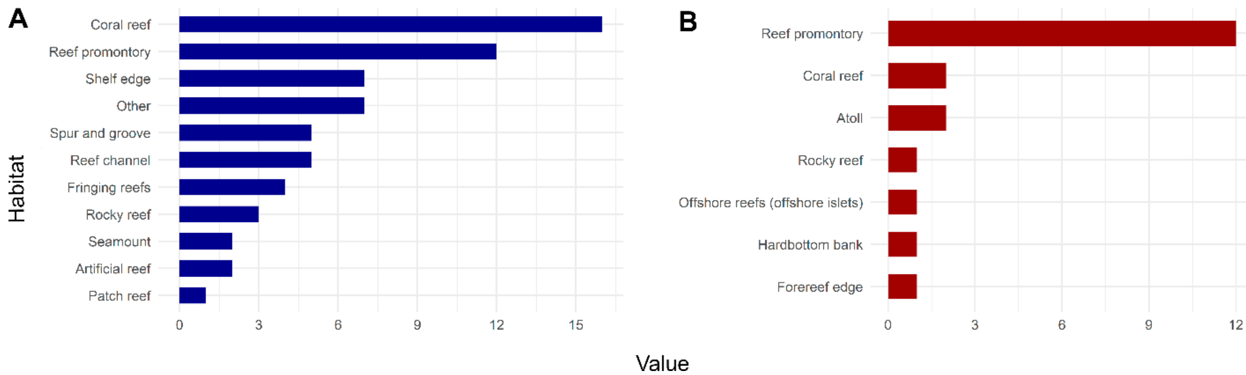

Figure 6. Number of spawning aggregations registered in each habitat type. Epinephelidae (A) and Lutjanidae (B).

Threats

Among the several factors threatening spawning aggregations, overfishing represents the main driving force. Families with great commercial value, such as epinephelids, have in addition to the risk common to all, particularities of their biology, such as longevity and protogyny, that put them in further danger (Huntsman & Schaaf, 1994; Sadovy, 1997; Huntsman et al., 1999; Coleman et al., 2000; Armsworth, 2001). Habitat degradation and climate change are examples of additional threats to FSA.

Recent interest by commercial companies resulted in technologically advanced methods for identifying locations of aggregation areas, which seems to have accelerated overfishing (Johannes et al., 1999). Considering the size selection through the use of fishing gear built for this purpose, the capture of protogynous species tends to be composed mainly of large individuals of the same sex, which affects the sexual proportion at the time of spawning and hence reducing the reproductive success (Coleman et al., 1996; Vincent & Sadovy, 1998; Armsworth, 2001). Actually, even low levels of selective fishing in protogynous males have negative consequences on the population dynamics of fishing stocks (Alonzo & Mangel, 2004). In addition, BOFFFFs (big old fat fecund female fish) in general produce larger eggs than smaller mature females. Their eggs can also develop into larvae with higher growth rate and less susceptibility to hunger (Hixon et al., 2014).

Disproportionate removal of males and females can have deleterious consequences for population persistence and, consequently, for fishing productivity (Bobko & Berkeley, 2004; Hixon et al., 2014). The loss of the largest individuals within the population makes reproduction unfeasible until another individual's sex transition ends. Thus, as a direct consequence, during the entire sex change period, all reproductive potential is lost.

Sustainable management of spawning aggregations takes to arrive, but it is urgent, since the implementation of marine protected areas (MPA) alone and in the absence of seasonal closures, effort and surveillance are insufficient (Gruss et al., 2014). For the Nassau grouper, the locations of many spawning aggregations have been known for at least a century. However, about 33% of these aggregations no longer exist due to fishing pressure and their decline is well documented in the literature (Aguilar-Perera, 1996; Carter et al., 1994; Paz & Grimshaw, 2001; Sadovy & Eklund, 1999; Sala et al., 2001). The Cayman Islands is one of the few places where the Nassau grouper still aggregates to the thousands (Whaylen et al., 2004). In contrast, *P. leopardus* spawning aggregation is possibly less vulnerable to fishing compared to other groupers (for example, *P. areolatus*, Johannes et al., 1999; *Mycteroperca tigris*, Sadovy et al., 1994; *Epinephelus striatus*, Sadovy, 1994), because aggregations are relatively smaller, and seem to disperse in the morning (Samoilys, 1997) and also a fraction of the population seems to present a different reproductive strategy, not aggregating for spawn and staying during the year within a defined home range (Zeller, 1998).

MPA and Conservation

Marine protected areas have been considered a very useful tool for fisheries management and conservation, especially in reef environments (Jennings, 2009; Hackradt et al., 2014). MPAs should be determined by several environmental aspects, geomorphology, and behavioral characteristics of focal species (Zeller, 1997; Russ, 2002; Nanami et al., 2014). However, as overfishing and threats to biodiversity are a major concern, no-take MPAs are often implemented before all relevant scientific information on fauna and habitat is available (Eklund et al., 2000). In the context of spawning aggregations, MPAs located in spawning sites are a tool used by managers to reduce fishing effort and rebuild stocks (Sluka et al., 1997; Beets & Friedlander, 1999; Heyman & Requena, 2002; Cho, 2005; Gell & Roberts, 2003; Burton et al., 2005; Nemeth, 2005).

Restrictions on fishing imposed in protected marine areas make it possible to reduce and/or mitigate the effects of overfishing, especially when considering protogynous fish groups that are particularly susceptible (Coleman et al., 1996; Koenig et al., 1996), and continue to be strongly taken by fishing (Morris et al., 2000; Alonzo & Mangel, 2004). Additionally, the suitable design of the protected area is essential, preferably covering the entire extent of fish movement (catchment area) during the reproductive period, and not just the spawning site (Gruss et al., 2014; Di Franco et al., 2018).

Although some FSA areas have shown signs of recovery after being heavily fished (Beets & Friedlander, 1999; Sadovy de Mitcheson et al., 2020), this is still an exception in view of other examples where this objective has not been achieved (Nemeth et al., 2006; Graham et al., 2008). Despite the adoption of closures and other management measures (eg Luckhurst, 1996; Paz & Grimshaw, 2001; Claro & Lindeman, 2003), there is still no evidence to suggest that the recovery of FSA is guaranteed. Additionally, the few FSA that have shown to recover from near extinction took decades to do so (Colin et al., 2003; Burton et al., 2005). Moreover, the dynamics of aggregation formation is still largely unknown, that is, the reasons which allows that a locality harbors FSA and others do not, despite having similar environmental characteristics (abiotic and geomorphologic). These inconsistencies create substantial problems for the implementation of certain types of management (e.g., quotas and access permissions).

Nemeth (2005) demonstrated that the effective seasonal protection of *E. guttatus* spawning aggregation site in St. Thomas (US Virgin Islands) showed an increase of more than 60% in the average density and biomass over 10 years. On the other hand, poorly supervised sites may not fulfill the proposed goal of the protection area and continue to allow population decline (Nemeth et al., 2006). In this context, Grüss et al (2014) demonstrated through a review of MPAs designed to protect FSA that, mostly MPAs were inadequate to conserve aggregations mainly by deficient supervision (Golbuu & Friedlander, 2011; Mangubhai et al., 2011), problems in the design of the area (Eklund et al., 2000; Nemeth et al., 2006; Hutchinson & Rhodes, 2010), lack of measures to control fishing mortality outside the aggregation period (Rhodes & Sadovy, 2002; Heyman & Wade, 2007; Hamilton et al., 2011) and the exploration of the portion of the population that resides in FSA sites outside the spawning period (Heyman & Wade, 2007; Marshak & Appeldoorn, 2007; Claro et al., 2009; Rhodes et al., 2011).

In our study, of the 54 studies identified with direct indicative of spawning aggregation for the families studied, only 44.4% occur within MPA, while 55.6% occur outside the protected areas or were not mentioned in the study. Despite having almost half of all aggregation areas protected, this number in practice may be even lower since the effectiveness of protection is low due to the lack of enforcement and monitoring. Also, it is possible that not known aggregations sites tend to occur in a higher proportion outside and from MPAs.

Although this topic is of great relevance worldwide, the studies regarding the spawning aggregation of these two families are basically concentrated in the Caribbean and the Indo-Pacific, with Lutjanidae having less representatives than Epinephelidae (Figure 7). Considering that in many studies, the first steps taken towards the discovery of new areas of aggregation come through interviews with fishermen, it is possible that because lutjanids have longer breeding periods and naturally gregarious behavior, fishermen do not recognize a moment specific for their capture, being abundant throughout the year, and for this reason they do not guide studies focused on areas of lutjanids aggregation.

On the Caribbean Sea 61.3% of the FSA reported occur outside MPAs. However, there are active measures that aim at reducing fishing intensity on target species. *Epinephelus striatus* and *E. guttatus* represent the species with the largest number of protective measures in the region (as a result of the intense fishing pressure they suffer), such as seasonal closures (*E. striatus* and *M. venenosa* in Puerto Rico; *E. guttatus* in US Virgin Islands) and seasonal fishing ban (from December to March for *E. striatus* in Belize; *E. guttatus* in Mexico). Some species like *M. bonaci* are protected as a result of the closure of fishing with a focus on the Nassau grouper (Paz & Sedberry, 2008).

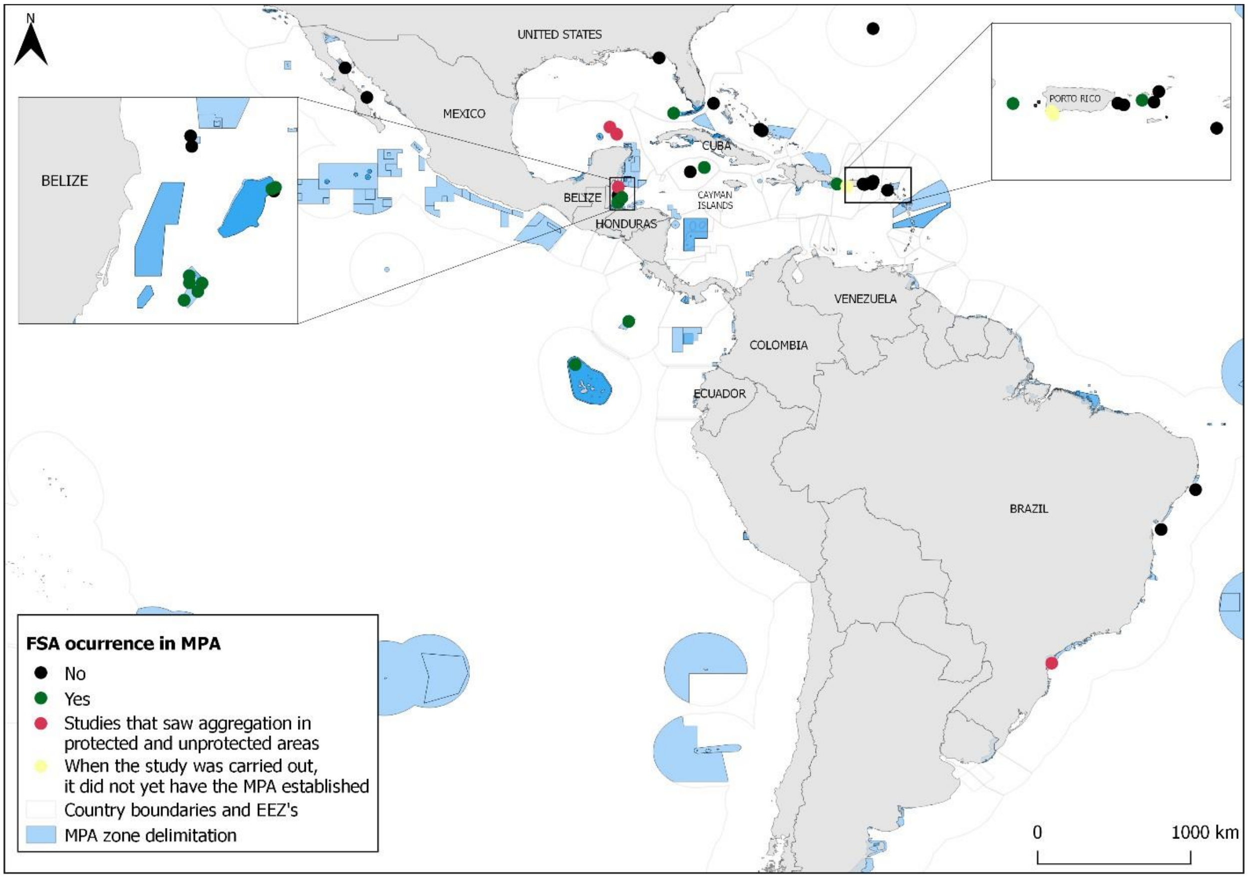

Figure 7. Map focusing on the area of the Tropical Atlantic and Eastern Pacific, presenting studies that take place inside or outside protected marine areas.

In the Indo-Pacific, on the other hand, although there is a lower concentration of studies, about 53.8% of the aggregations are within protected areas (Figure 8). In addition to MPAs, laws that seek to mitigate overfishing in the region are also in place, such as seasonal bans on capture and sale (between October and January for *P. areolatus*, *E. polyphekadion* and *E. fuscoguttatus* - Hughes et al., 2020). Moreover, in this region, community protection is widely used as a reliable tool for the management of marine resources (Cohen & Foale, 2011). Thus, it is also necessary to consider that the prohibition of fishing in several regions has, in addition to ecological issues, social consequences, since local fishermen who fish in spawning aggregations often depend on that extra annual income. Therefore, any order aimed at protecting aggregations must take these factors into account (Colin, 1992).

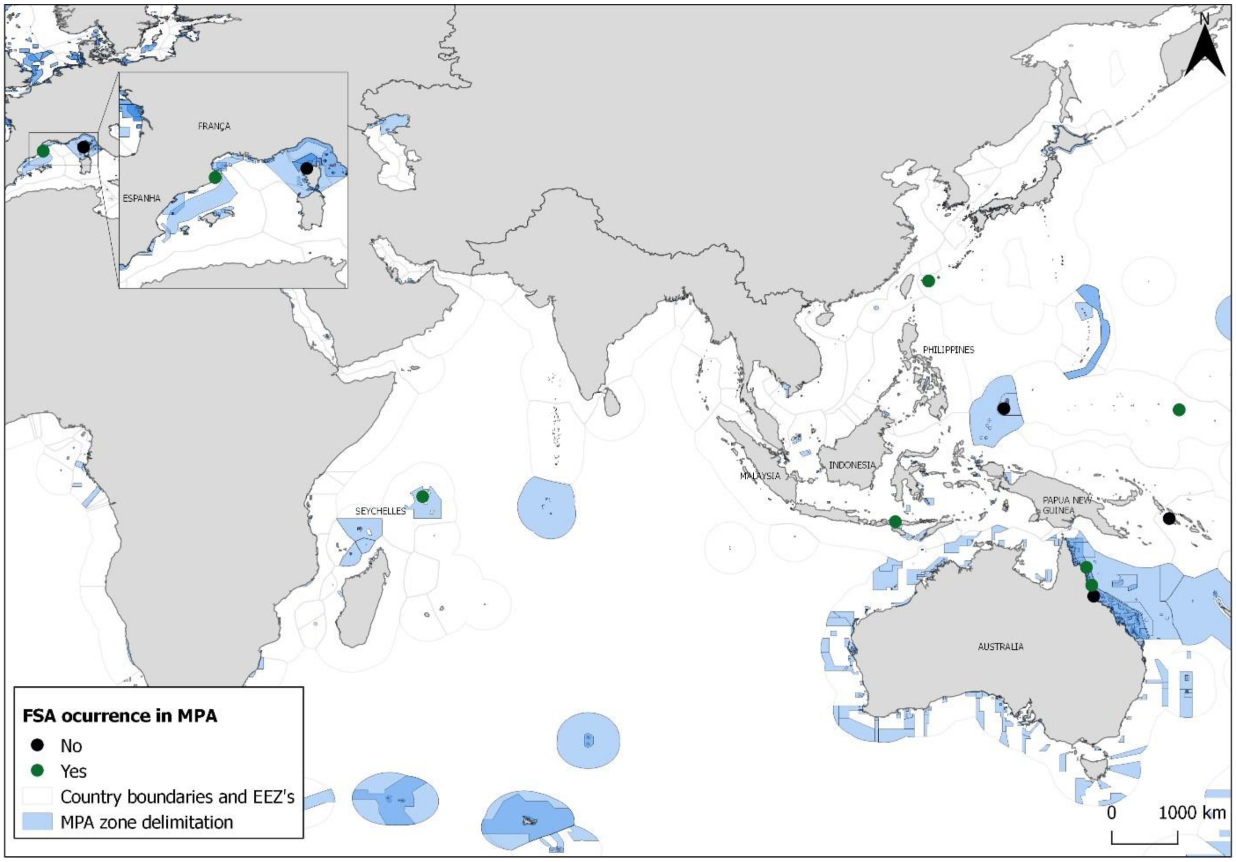

Figure 8. Map focusing on the Mediterranean and Indo-Pacific areas, presenting studies that occur inside or outside protected marine areas.

MPAs represent powerful tools for protection of critical habitats, species, and ecological functions, and do not necessarily entail total restrictions on fishing. Several other options can be applied in spawning aggregation areas in order to protect them and still allow controlled exploitation of the resource. For example, temporal and/or spatial prohibitions, size and weight limits, quotas and bag limits, possession and fishing prohibitions are also options to be considered as possibilities to curb overfishing during aggregation events (Beets & Friedlander, 1999; Grüss et al., 2014).

Conclusions

Spawning aggregations tend to occur at predictable and specific locations and times (Sadovy de Mitcheson et al., 2008). Among the various environmental characteristics that are directly linked to this phenomenon, the time (seasonal and lunar) of fish spawning is considered a fundamental component of reproductive success (Donahue et al., 2015). The two families studied showed a strong relationship with the full moon during their reproductive periods. During this lunar phase, the tidal amplitudes and currents are greater, in addition, the full moon provides more intense night light, allowing the fish to communicate more effectively visually, through coloring patterns and courtship behaviors (Colin, 2011). The sum of these characteristics can also help to carry eggs and larvae slightly floating in the water column and make it possible to increase the species dispersion range (Domeier & Colin, 1997; Félix-Hackradt et al., 2013; Caló et al., 2013).

Among the main types of habitat that harbor spawning aggregations annually, coral reefs and reef promontories were the most common for both families (Kadison et al., 2009; Rowell et al., 2015; Tuz-Sulub & Brulé, 2015). Most of the studies already conducted on spawning aggregations of the Epinephelidae and Lutjanidae families are mainly concentrated in the Caribbean and Indo-Pacific. The South Atlantic and Indian Ocean despite representing a *hotspot* of marine biodiversity (Moura, 2002) still does not have sufficient research to understand the particularities of its marine fauna, especially on species that exhibit spawning aggregation behavior. Also, intense traditional coastal fisheries insufficiently monitored (regarding catches, areas, species etc.) may play a key role on the profound data deficiencies on the southwestern and southeastern Atlantic (Previero & Gasalla, 2018).

Finding spawning aggregations in large marine areas is difficult due to the high costs of equipment, transport, diving and climatic unpredictability. Therefore, this review represents a contribution to the spawning aggregations of the Epinephelidae and Lutjanidae families around the world. It was possible to show that particularly in the Southwest Atlantic and the Indian Ocean, there is still room for further research to understand how FSAs are spatially and temporally distributed. In addition to contributing to the proposition of management measures, data related to the time of reproduction and location of aggregations contribute to support the management of endangered species

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Capítulo 2

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

Artigo publicado na Fisheries Research, em março de 2021 (doi.org/10.1016/j.fishres.2021.105937)

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

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ABSTRACT

Local knowledge is a fundamental source of information for starting spawning aggregation studies in areas where this phenomenon is still unknown or little studied. Among the species that present this reproductive strategy, groupers and snapper represent two of the most relevant components of artisanal and commercial capture worldwide and are highly susceptible to overfishing. We conducted interview-based surveys to examine if local ecological knowledge can determine potential areas of spawning aggregations in southeast Brazil. Fifty-one local fishermen targeting groupers and snappers were asked about spawning aggregation areas and seasonality using charts and geographic information system (GIS) analysis. Information was obtained for 31 potential spawning aggregation sites, where black grouper (*Mycteroperca bonaci*) represented the most important resource for the fishermen interviewed, followed by yellowtail snapper (*Ocyurus chrysurus*). In addition, red grouper (*Epinephelus morio*), mutton snapper (*Lutjanus analis*) and dog snapper (*Lutjanus jocu*) were also mentioned as important resources that have spawning in aggregation as a reproductive strategy. The main possible spawning aggregation areas indicated occur within the Abrolhos Bank, the largest and richest reef complex in the South Atlantic. The lack of published records of spawning aggregations in Brazil, hinders the suitable implementation of measures that can protect this phenomenon and consequently the perpetuation of these and potentially other species. Therefore, additional studies and particularly in situ validation, are needed to determine the occurrence and status of the aforementioned aggregations.

Keywords: Ethnoecology, Snappers, Groupers, Brazil, Artisanal

1. Introduction

Spawning aggregations represent an important stage in the life cycle of several reef fish species. This event is defined by a significant increase in the density of individuals of the same species, at least four times greater when compared to that found in the same area outside the breeding period (Domeier and Colin, 1997; Domeier, 2012). They occur all over the world although they are more documented in tropical waters including the Gulf and Caribbean (Erisman et al., 2015). In addition, reef fish spawning aggregations supports some of the most significant and productive commercial, recreational, and subsistence fisheries around the world (Sadovy De Mitcheson and Colin, 2012). It's also crucial to the livelihoods and food security of small-scale fishers (Rhodes and Tupper, 2007).

It is characterized by occurring faithfully in the same place and at the same time year after year. This predictability favors its intense exploitation, making it possible to obtain a high fishing yield with minimal effort (Sadovy et al., 1994; Sadovy and Eklund, 1999; Colin et al., 2003; De Mitcheson et al., 2008). Other factors that contribute to this extensive exploitation emerged from the evolution of fishing gear with the advent of new technologies, such as autonomous diving equipment and increasingly sensitive tools for fish detection. Thus, the fishing activity directed to these aggregations improved considerably, becoming increasingly effective. This pressure inevitably led to the deterioration of the reproductive stock of several species (Johannes et al., 1999; Sadovy and Eklund, 1999; Sala et al., 2001; Claro and Lindeman, 2003), such as the classic and widely studied case of the Nassau grouper, *Epinephelus striatus*, where intense fishing over aggregation areas has led its near extinction in many Caribbean locations (Sadovy et al., 1994; Sala et al., 2001; Luckhurst, 2002).

One way to mitigate these impacts is through the identification and characterization of aggregation sites, since these studies represent a valuable step towards the conservation of several fish species with high commercial value during a critical moment in their life cycle (Domeier and Colin, 1997). Despite the relevance of this characterization, finding spawning aggregations in the marine area is a very difficult and costly activity (Colin et al., 2003). In this sense, the use of local ecological knowledge in studies to identify this events are established as a tool capable of providing essential information about the life history, ecology and biology of these species (Claro and Lindeman, 2003; Boomhower et al., 2007). Furthermore, local knowledge is a fundamental source of information for starting aggregation studies in areas where this phenomenon is still unknown or even little studied.

In this context, Epinephelidae and Lutjanidae families (groupers and snappers) harbor numerous species with spawning aggregation behavior, of high commercial value and which have suffered over time with intense fishing pressure (De Mitcheson et al., 2013; IUCN, 2020). All these factors, combined with the absence of studies seeking to identify breeding areas, contribute to these species being increasingly at risk of disappearing and/or suffering irreversible consequences in their reproductive dynamics due to overfishing. In addition, in particular for epinephelids, selective fishing tends to remove larger and older individuals, causing serious consequences for the population structure (Armsworth, 2001) such as low fertilization rates for eggs produced by the population (Shapiro et al., 1988), insufficient sperm count and social disturbance (Sadovy, 2005; De Mitcheson and Erisman, 2012).

In Brazil, because of the extensive coastal zone, there are still few studies targeting the phenomenon of spawning aggregation. Most of them in the South/Southeast of the country and mainly aimed at the goliath grouper, *Epinephelus itajara* (Felix-Hackradt and Hackradt, 2008; Bueno et al., 2016; Giglio et al., 2016). However, reports from fishermen and diving operators refer to the presence of several other species aggregations along the country's coast (Reuss-Strenzel and Assunção, 2008; Gerhardinger et al., 2009; De Salles et al., 2010; França and Olavo, 2015). Thus, fishermen represent an invaluable source of information and assistance for this discovery, and, together with the scientific community, they must be the main actors in protecting their own resources (Heyman et al., 2004).

Located along the central coast of Brazil, the state of Espírito Santo is considered one of the largest fishing centers and emerges as a major center of marine biodiversity. This high diversity is strongly related to the fact that it is a transition area between tropical communities (southern limit of Abrolhos Bank) and subtropical (Floeter and Gomes, 1999; Floeter et al., 2007). Despite the existence of conservation units in the region, varying between restricted use (Abrolhos Marine National Park, Recife de Fora Marine Park and Santa Cruz National Wildlife Refuge) and of sustainable use (Environmental Protection Area of Caraíva and Trancoso, Environmental Protection Area Ponta da Baleia, Corumbau Marine Extractive Reserve and Environmental Protection Area Costa das Algas), there is a national deficit on fishing data, along with a lack of a systematic fisheries monitoring and enforcement, which further threatens these stocks (Sadovy De Mitcheson and Colin, 2012).

Considering that this reproductive phenomenon is critical for the resilience of diverse marine fish populations, its identification and conservation is urgent. For many species, aggregations represent the main annual source of reproduction and can allow, when well-managed, the sustainability of many traditional fisheries (De Mitcheson and Erisman, 2012; Erisman et al., 2017). In this context, we seek to elucidate if local ecological knowledge can determine potential areas for spawning aggregations of species from Epinephelidae and Lutjanidae families in southeast Brazil.

2. Material and methods

2.1. Study area

The study area comprises the entire Espírito Santo state (located between the coordinates - 17◦52′ and - 21◦17′ latitude and - 41◦54′ and - 39◦38′ longitude) covering a coastline of 521 km with 14 coastal municipalities and about 50 fishing communities. It also has 36 fishing ports along its coast (De Freitas Netto and Di Beneditto, 2007). In the state, the fishing fleet is the largest oceanic fleet in the country, with around twelve thousand active fishermen. It is estimated that, at various points along this long coastline, a significant part of the population lives directly or indirectly from fishing (Knox and Trigueiro, 2014).

The marine environment of Espírito Santo harbors a large fish diversity (Floeter et al., 2007; Pinheiro et al., 2018). In addition, it is known that the continental shelf of the state has a wide variation in width, with the region to the south of Sao Mateus being narrower (50 - 60 km), while the region to the north has a more extensive platform, with more than 240 km and associated with the Abrolhos region (Sobreira and França, 2006). The main marine habitats are characterized by paleo valleys, hard bottoms/reefs and rocky promontories (Moura et al., 2013; Bastos et al., 2015). Among the rivers present on Espírito Santo’s coast, the Doce river emerges as the most significant, with an average flow ranging from 190 m^3/s (September) to 650 m^3/s (January) (Pinto et al., 2015).

2.2. Interviews with the fishermen

For the interviews, the ports with the highest landings of species from the two families studied were visited. The selection was made by analyzing the data developed by the Protected Marine and Coastal Areas project (GEFMar - World Bank). At the port, the goal was to interview fishermen targeting groupers and snappers. These ports are located in eight municipalities in Espírito Santo: São Mateus, Santa Cruz, Vila Velha, Guarapari, Anchieta, Piúma, Marataízes and Itaipava and were visited between August 2018 and March 2019.

Interviews were conducted using a semi-structured questionnaire (16 questions) due to the flexibility provided by this format (Young et al., 2016). There was no stipulated time for the interview, the duration depended on the development of each response plus the availability of the interviewed fisherman. In addition, fishermen were asked to mark in nautical charts, referring to the fishing zone in which they operate (obtained through the Brazilian Navy website - https://www.mar.mil.br), the points where they used to carry out largest catches, as well as the main seasons of the year where the largest fisheries of each species are concentrated. A clipboard containing a series of photos of fish with high commercial value in the state was used so that they could identify the species, thus avoiding errors to the different common names attributed to the same species in different regions. Furthermore, when possible, the geographical coordinates of the main fishing spots were obtained directly.

Fishermen are already used to working with the Meros do Brasil project (www.meros.com.br) and with the monitoring of fishing landings developed by the Protected Marine and Coastal Areas project (GEFMar - World Bank). This relationship previously established with the local researchers and fishermen allowed them to provide reliable information regarding these families. The interviews were conducted individually in order to avoid the influence of other fishers. Finally, the fishermen were categorized by the time of experience: beginners (≤ 15 years of practice); intermediate (16–30 years) and experienced (≥ 31 years; (Bender et al., 2013); artisanal (≤ 8 days of sea autonomy) and industrial (≥ 9 days of sea autonomy), and whether or not they depend on fishing as a source of income. This study was approved by the Human Research Ethics Committee of the Federal University of Espírito Santo under protocol nº. 89595217.2.0000.5063.

2.3. Fishermen's Knowledge Mapping and Analysis

The mind maps resulting from the interviews were transferred to a Geographic Information System (GIS). As a result, information on capture points and areas of occurrence of the species could be distributed in space. In addition, in order to highlight the main possible areas of aggregation, a kernel density map was built, separated by family. The maps were overlaid and analyzed using the QGIS 2.18.26 program.

The association between the number of responses and the level of experience (beginners, intermediate and experienced) of each fisherman, the level of experience and if they noticed the change in fish size over time, the fishery category (artisanal or industrial), financial dependence on fishing (yes or no) and the importance of species (black grouper – *Mycteroperca bonaci*, yellowtail snapper – *Ocyurus chrysurus* and others) was tested using the Chi-square test (χ^2 <3.840, p = 0.05). The analysis was performed using t

he R Studio software (R Core Team, 2019).

3. Results

3.1. Profile of Fishermen Interviewed

A total of 51 fishermen were interviewed. The age between them ranged from 28 to 68 years (mean = 47 years) and the fishing experience ranged from 12 to 46 years (mean = 27 years). Among them, 14 % were beginners, 50 % intermediate and 36 % experienced. For 92.3 % of the fishermen, the source of income comes exclusively from fishing, while the rest (7.7 %) have other sources to complement family income (Table 1).

Among the most referenced species associated with the behavior of spawning in aggregations, black grouper represented the greatest importance for the interviewees, since it was mentioned in first place in 47 % of the interviews and 78 % of the fishermen mentioned the species in some another important position (Fig. 1). Then, yellowtail snapper appears in second place, being mentioned in first place in 37 % of the interviews and 53 % of the interviewees mention the species in some other important position. Other species such as red grouper, dog snapper and mutton snapper were also identified as major species that have aggregation behavior.

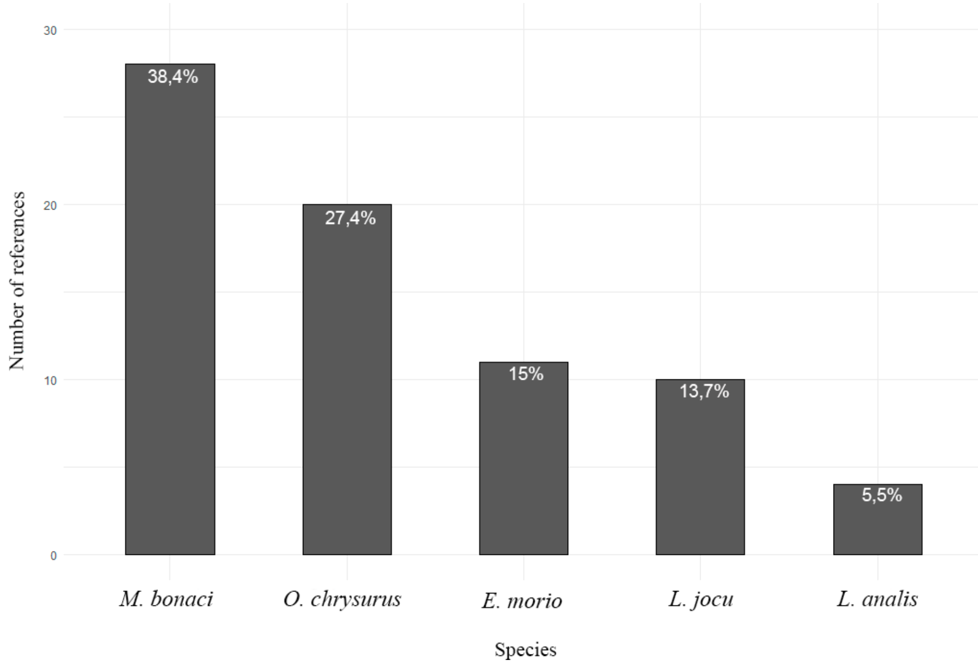

Fig. 1: Number of species references from Epinephelidae and Lutjanidae families in interviews with fishermen in the study area.

3.2. Spawning aggregations "potential" locations

Most fishermen were aware that certain species of reef fish aggregate to spawn in specific times and places. Nevertheless, there were also reports of what they believe to be feeding aggregation, where they reported that several species migrate from the Northeast to the Southeast in search of food. A total of 31 possible spawning aggregation sites were cited by fishers with 27 possible locations for groupers and four possible locations for snappers. These locations were, in most cases, related to areas near or at the shelf edge. The main area is located in the south of the state of Bahia (Abrolhos region) for the Epinephelidae family. Concerning the Lutjanidae family, the areas are concentrated in the north of Espírito Santo and south of Bahia (Fig. 2).

Table 1: Parameters and their distribution across interviews.

Fisher experience	Number (%)	Age Mean, range	% of fishing ports represented	Artisanal/Industrial
<15	7 (14%)	40, 28-58	37,5	Industrial
16-30	26 (50%)	44, 30-60	100	Artisanal/Industrial
>31	18 (36%)	55, 43-68	62,5	Artisanal/Industrial

The most cited place among respondents was a fishing grounds located at the Royal Charlotte Bank, near Santa Cruz Cabrália, being mentioned in 27.45 % of the interviews. The chi-square p values obtained regarding the number of responses by the fishermen were 0.141; 0.326; 0.731 and 0.041 for the type of fleet, change in fish size over time, dependence on fishing and species, respectively. Therefore, it was only possible to observe that the main species mentioned differed according to the interviewees experience.

Among the locations indicated by fishermen as possible aggregation areas, the Kernel density map indicates two main zones located on the Abrolhos region. One to the north and coastal, between the municipalities of Porto Seguro and Santa Cruz Cabralia and another to the south and farthest from the coast (Fig. 3). Regarding the seasonality of the catch record, the months of June and July were identified as the spawning season for black grouper. As for yellowtail snapper, the months of December, January, February, September were identified (Fig. 3).

When fishermen were asked which fishing modality/fishing gear contributes to the decrease or disappearance of some species, the most common reasons given for these changes were due to the use of predatory fishing gear such as trawling, balloon fishing, lobster net, compressor fishing and mainly trawlers from the south of Brazil.

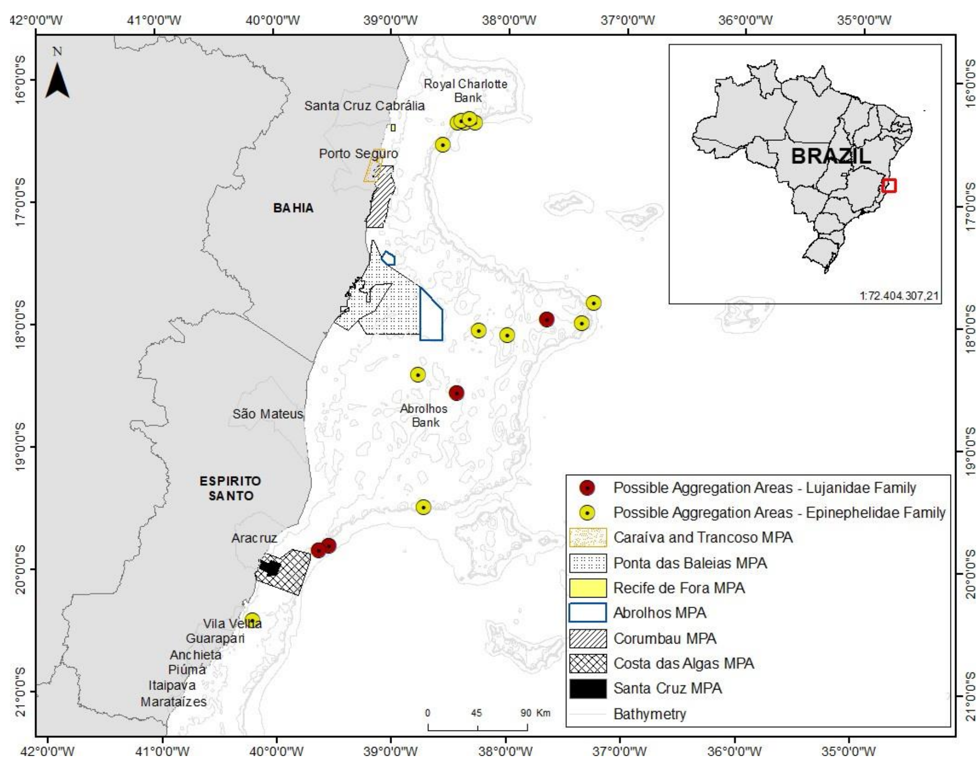

Fig. 2: Areas cited as possible fish aggregation areas of the families Epinephelidae (yellow dots) and Lutjanidae (red dots). Cities listed in the state of Espírito Santo represent the locations where interviews were conducted with fishermen.

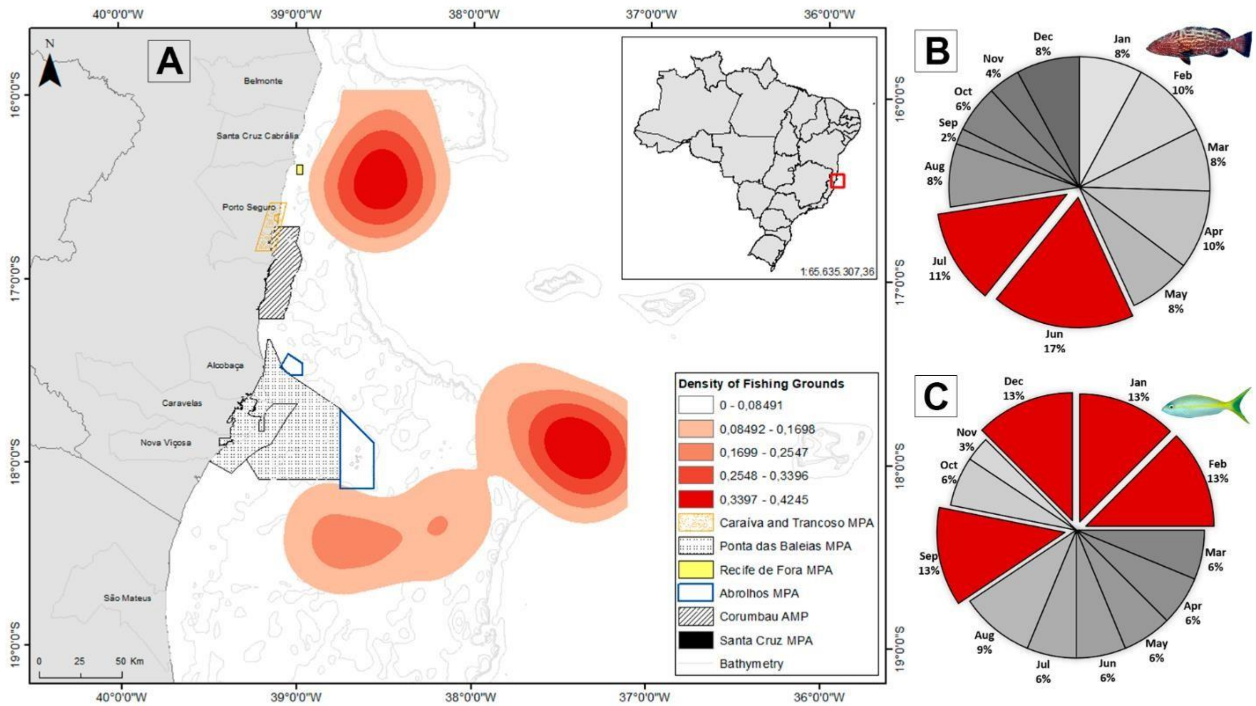

Fig. 3: A: Kernel density map of possible spawning aggregation locations for the Epinephelidae and Lutjanidae families; seasonality indicated for B: *Mycteroperca bonaci* and C: *Ocyurus chrysurus.*

4. Discussion

Our results demonstrated through the Local Ecological Knowledge the existence of several areas with great potential to host spawning aggregation, mainly directed to two species, black grouper (currently listed as vulnerable in Brazil) and yellowtail snapper. In addition, the main areas mentioned occur in the Abrolhos region, an area that encompasses the largest and richest coral complex in the South Atlantic and the oldest of the few marine protected areas in Brazil (Moura et al., 2013; Pinheiro et al., 2018). However, despite this relevance, currently, there is no management actions that encompass the whole Abrolhos region ecosystem neither a national policy for collection of fisheries data.

The use of local ecological knowledge has been applied for decades as the main starting point in the search to identify places of aggregation where there is little or no data about this phenomenon (Johannes et al., 1999; Sala et al., 2001; Rhodes and Sadovy, 2002; Heyman et al., 2004). The great practical difficulties in finding these places, makes scientists and managers interested in studying them, resort on the local knowledge of fishermen in the early stages of their work. This is especially significant when considering the short time and the high accuracy of geographic events (Johannes et al., 1999; Robinson et al., 2004; Hamilton et al., 2005, 2011; Sadovy de Mitcheson et al., 2008).

In Brazil, there are few studies with *in situ* validation of spawning aggregation sites, most of them carried out through traditional knowledge and/or fishing landing data (Reuss-Strenzel and Assunçao, 2008; Osório & Borgonha, 2010; Ferreira et al., 2014). Giglio et al. (2016) mapped, through 98 reports, locations of aggregation of the goliath grouper, *Epinephelus itajara,* in seven states on the Brazilian coast, most of them through information from professional divers and fishermen. Only two of these locations were confirmed *in situ* (Félix-Hackradt and Hackradt, 2008; Bueno et al., 2016).

With the information obtained by fishermen, it is possible to observe a greater number of possible aggregation areas for the Epinephelidae family. This shows that it is the most sought-after resource by most fishermen. Additionally, the fact that the reproductive period of this family is more easily distinguishable in time due to the species, in general, have annual spawning (Sadovy et al., 1994), exhibit naturally non-gregarious behavior (Rhodes and Tupper, 2008) and, in many cases, territorial (Archer et al., 2012), in addition to its high economic value (Sala et al., 2001), makes the aggregations of the studied epinephelids more recognizable in time and space. The opposite is true for species of the Lutjanidae family, such as yellowtail snapper, where their regular abundance and gregarious behavior can camouflage the reproductive objective of their aggregations in specific locations.

With the exception of red grouper, all four main species cited by fishermen (black grouper, yellowtail snapper, dog snapper and mutton snapper) are identified as having aggregation formation as a breeding strategy (Claydon, 2004). Precisely, the interviewees assertion that, in certain places in the state, year after year, abundant catches of groupers and snappers are recurrent at the same times, suggests that spawning aggregations of several species may be formed in these places. According to 28 % of interviewees, black grouper had the highest catch volumes between June and July, a period in which individuals with developed gonads were also reported by fishers during interviews. The results obtained through the interviews are supported by several reproductive biology works of the mentioned species. Freitas et al. (2011, 2018) identified the period from winter to spring as the reproductive phase of black grouper and red grouper, with the highest gonadosomatic rates occurring in August and September. Teixeira et al. (2004), proved that the reproductive season of black grouper occurs between the months of April and September.

Regarding Lutjanids and specifically yellowtail snapper, several studies have shown that the species of this family have longer breeding periods, often occurring year round (*O. chrysurus*, García Cagide et al., 2001; *Lutjanus fulvus*, Cimino et al., 2018; *Lutjanus jocu*, Claro and Lindeman, 2003; Biggs and Nemeth, 2016) or with some more expressive pulses in certain months (*Lutjanus bohar*, Sakaue et al., 2016; *Lutjanus cyanopterus*, Heyman and Kjerfve, 2008; Biggs and Nemeth, 2016). Possibly for this reason, we observe that fishermen do not recognize a specific time for snappers capture, being abundant throughout the entire year. However, it was possible to observe that the months of September and February were more relevant among the interviewees as the reproductive period for snappers. This information is corroborated by a study carried out in the Abrolhos bank that identified two reproductive peaks for snappers, the most intense between September and October and the other between February and March (Freitas et al., 2011).

Regarding the potential spawning sites, the fishers highlighted a total of 31 locations for the different species mentioned. Among these places, it is worth mentioning a fishing ground located in front of Santa Cruz Cabrália (Bahia), acknowledged by 27.4 % of the fishers. Due to intense reference of this particularly fishing ground, it was possible to confirm its location by comparing geographical coordinates with more than one fisherman. It is located near to platform breaks (about 60 km from the coast), which further reinforces its prominence since areas close to the open ocean and at the shelf edge are in general a common place for many species spawning aggregations (De Mitcheson et al., 2008; Kobara & Heyman, 2010).

It is important to note that 90 % of the main aggregation points informed are in the Abrolhos Region (including Royal Charlotte and Abrolhos Bank), the richest and most extensive reef complex in the South Atlantic (Pinheiro et al., 2018). Several studies have already demonstrated the importance of Marine Protected Areas (MPA) for the biomass export and the fishing activity maintenance of numerous species (García-Charton et al., 2004; Nemeth, 2005; Claudet et al., 2008) and fish spillover (Hackradt et al., 2014). Claro and Lindeman (2003) did an extensive work using LEK and were able to identify 21 aggregation sites on the Cuban platform for eight groupers and snappers species, subsequently using this information for the design of marine reserves, since the LEK contributes data on seasonality, number and size of individuals, as well as reproductive behavior and changes over time in the status of aggregations (De Mitcheson et al., 2008).

In addition, in this study, LEK data are reliable in the sense that they dialogue and are cross-referenced with fisheries and seabed data (unpublished data), where the largest observed catches are in accordance with information's provided by fishermen. Regarding Abrolhos region, the presence of marine protected areas does not promote total fishing restrictions. In many of them is allowed to fish (the case of Extractive Reserves, in which some controlled and sustainable uses are allowed inside MPA limits). Alternative methods for protection of spawning aggregation areas can also be represented by temporal and/or spatial bans, since this areas are predictable in time and space (Beets and Friedlander, 1999; Graham et al., 2008; Grüss et al., 2014), which reinforces the need of studies like this.

4.1 Conclusions

The lack of published records of spawning aggregations in Brazil, hinders the adequate implementation of measures that can protect this phenomenon and consequently the perpetuation of the species that present this reproduction strategy. In addition, possible management measures capable of mitigating damage from overfishing include bans on fishing in known spawning sites, prohibitions on species sale during periods identified as their reproduction peak and inclusion of spawning aggregation sites in permanent marine reserves (Heyman, 2014).

Our work demonstrates that local ecological knowledge is fundamental in the search for potential areas of spawning aggregation, especially considering places without previous studies that can guide the *in-situ* exploration and validation of these aggregations. Therefore, further work is needed to corroborate the information obtained, and it is suggested to start from the indicated places presented by the interviewed fishermen (please look Colin et al., 2003; Kobara et al., 2013). Conservation and management strategies must originate from these works, which will necessarily include the fishing communities, the main users of the resources and their greatest knowledge

(Colin et al., 2003; Kobara et al., 2013). These, in turn, will benefit the most since the protection of spawning aggregations will guarantee the continuity of fishing as an economically viable activity.

Acknowledgements

We thank the Areas Marinhas e Costeiras Protegidas project (GefMar) for the collaboration. We are grateful to the owners, captains and crews of the Capixaba's fleet who kindly cooperated on this project by sharing his precious knowledge. Special thanks to Carlos Eduardo Stein and Bruno da Hora for the essential help during the trips for the interviews.

Funding: The authors thank Rufford Foundation nº 24449-1 for funding the study. This study was also financed in part by the Coordenaçao de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Finance Code 001. We thank the support by FAPES - Coastal Management Program (grant no. 607/2016), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) for the grants provided for MHS (grant no. 312278/2017-9) and AS (grant no. 310464/2020-0).

CRediT authorship contribution statement

Inajara Marques Bezerra: Conceptualization, Investigation, Funding acquisition, Writing - review & editing. **Mauricio Hostim-Silva:** Conceptualization, Writing - review & editing. **Jessyca Luana Silva Teixeira:** Writing - review & editing. **Carlos Werner Hackradt:** Conceptualization, Writing - review & editing. **Fabiana C. Félix- Hackradt:** Conceptualization, Writing - review & editing. **Alexandre Schiavetti:** Methodology, Investigation, Writing - review & editing.

Declaration of Competing Interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary material

➔ Questionnaire to be applied in interviews with groupers and snappers fishermen in Espírito Santo, Brazil.

Name:_________

Age: ________

1. How long have you been fishing? ___________

( ) Beginner (<15 years)

( ) Intermediate (16-30 years)

( ) Experience (> 30 years)

2. How big is your vessel? ______________

3. How many days do you usually spend at sea? ________________

4. How many people participate in the fishery? _____________

5. Is fishing your only source of income? ( ) Yes ( ) No

6. How would you describe the current state of fish stocks regarding abundance?

( ) Unchanged ( ) Decline ( ) Growing

7. Among these species, which ones do you know that make spawning aggregations?

  

8. Where do these aggregations occur (show on map)?

9. When do these aggregations occur (month/season for each species)?

Sp1____________Sp2____________Sp3____________Sp4____________

10. Do you know a place that was once considered a spawning aggregation site, but nowadays it is no longer? ( ) Yes ( ) No

Where?________

11. Do you know anyone who fishes in aggregations? Who? _______________________

12. Do you think there was a decrease in individuals' size, taking into account when you started fishing until today?

13. Do you know any species that were fished a lot in the past and today are fished less or have disappeared in this region?

( ) Yes ( ) No

If so, which species?____

14. Do you know any species that was previously discarded or was only used as bait or was not fished (because it had no commercial value) and today is a fishing target?

( ) Yes ( ) No

If so, which species? ___________________________________

15. Could you tell which fishing modality/fishing gear contributes to the decrease or disappearance of some species?

16. What do you attribute the change of fishery target to other species of less economic interest in the past?

( ) decrease of fish by fishing ( ) pollution ( ) others ____________________

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Capítulo 3

The use of CPUE and environmental variables as indicators of snapper and grouper spawning aggregations in the Tropical Southwestern Atlantic

Artigo a ser submetido para Marine Environmental Research (A1, IF 2.7).

The use of CPUE and environmental variables as indicators of snapper and grouper spawning aggregations in the Tropical Southwestern Atlantic

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ABSTRACT

Many species of the snapper-grouper complex migrate to form transient spawning aggregations, which are characterized as a concentration of individuals that gather up to thousands at specific times and locations for reproduction. The predictability of this events is often targeted by local fisher, making them extremely vulnerable to overfishing. In poorly studied sites, as the Brazilian coast, indirect signs that identify aggregation locations, such as fishery data and geomorphological characteristics, can be used to find these areas. Therefore, this study aimed to identify periods and locations of possible spawning aggregations areas of *Lutjanus analis*, *Lutjanus jocu*, *Ocyurus chrysurus*, *Mycteroperca bonaci* and *Epinephelus morio* from the analysis of catch per unit of effort (CPUE) and environmental variables data available from the eastern Brazilian coast. Among the sites observed, Abrolhos bank represented the main fishing area for the species studied. For *M.bonaci*, it was possible to corroborate a fishing ground previously identified by fishermen as a possible aggregation area. For snappers, variations were found throughout the year, but with no peaks year-round. Additionally, the results showed that high CPUE values are mainly related to structures of reef, rhodolith beds, seamounts and unconsolidated bottoms. This study indicated that the use of fishing data, when available, can represent an important tool for investigation of possible spawning aggregations. Unfortunately, Brazil has a long history lack of fishing data, which makes it even more difficult to implement efficient management measures. Additional studies that prioritize the exploration of these places identified here are important to confirm the spawning character of these aggregations.

Keywords: Reef; Rodolith Beds; Brazil;Lutjanidae; Epinephelidae

1. Introduction

Fishes from the snapper-grouper complex (Lutjanidae - Epinephelidae) play significant roles in commercial, recreational, and subsistence fisheries around the world (Coleman, 1999). These species have biological, ecological, and behavioral characteristics that make them particularly vulnerable to overfishing, such as low rates of growth and high longevity, in addition to spawning aggregation behavior (Coleman et al., 1996; Lindeman et al., 2000; Sadovy & Cheung, 2003; Sadovy de Mitcheson et al., 2008).

Several snapper and grouper species migrate long distances to form massive, transient spawning aggregations (Colin, 2003). Reproduction in aggregations is characterized by gatherings of up to thousands conspecific individuals occurring predictably at the same time and location year after year, and representing a critical phase in the life history of several tropical reef fishes (Claydon, 2004). These events often represent the total reproductive effort for the participating individuals (Domeier & Colin, 1997; Domeier & Speare, 2012). The predictability of this phenomenon makes them especially vulnerable to fishing (Burton et al., 2005; Sadovy de Mitcheson & Colin, 2012), and, once identified, the intense fishing pressure on these populations can lead to their extinction if not managed in time (Chollet et al., 2020).

The identification of fish spawning aggregations may be assessed by indirect signals such as an increase of at least four times in relation to the mean relative abundance and catches observed during the non-reproductive period as indicative of a possible reef fish spawning aggregation (FSA) (Domeier, 2012). Moreover, in areas where it has not yet been possible to spatially identify sites of spawning aggregation and there is no exploitation of this event, an alternative to start searching for these sites may occur through the use of fishery dependent and/or independent data and geomorphological characteristics of the environment (Heyman et al., 2004; Boomhower et al., 2010; Kobara & Heyman, 2010; Robinson et al., 2011; Tobin et al., 2013).

Studies carried out in the Caribbean have shown that the majority of spawning aggregations occur on shelf-edge reef promontories (Carter et al., 1994; Heyman & Kjerfve, 2008). Additionally, a compilation carried out by Nemeth (2009) concluded that most species with high commercial value, such as members of the snapper-grouper complex, spawn in three main habitats: reef channels, promontories along with fringing reefs and external reef slopes.

The increase in fish density occurring in spawning aggregation events results, in most cases, in increase of catch per unit effort (CPUE) and catchability of target species during this period (Arreguín-Sánchez, 1996). The synergy between CPUE peaks and the intense pressure on these stocks, allows fishermen to extract large amounts of fish quickly and with minimal effort (Erisman et al., 2012). Additionally, the consequences of overfishing resulting from constant and intense withdrawal of these individuals includes reduction in the mean length (Sadovy, 1994; Graham et al., 2008), changes in sex ratio (Koenig et al., 1996), and declines in abundance (Claro et al., 2009). The global database of the Society for the Conservation of Fish Aggregations (SCRFA, 2014) shows that within the exploited aggregations 39% and 32% show evidence of declines in density for snapper and groupers, respectively. In addition, it is known that 2% and 5% of them are gone (Russell et al., 2014).

Brazil is a potent fishing nation, although, basic data about fish species caught or the fleet size operating on its coast are difficult to obtain. This occurs mainly because the last time the Brazilian government collected national-scale data on its fishing activities was thirteen years ago. Missing and flawed data threatens commercially valuable fish, endangered species, and undermines the development and adoption of adequate policies. The time and location of spawning aggregations is a strategic information to guide conservation measures needed to maintain sustainable fisheries (Erisman et al., 2017; Farmer et al., 2017; Grüss et al., 2018).

In spite of their importance and vulnerability, there are no direct measures to protect marine FSAs in Brazil, and very little is known about their conservation status. In this way, the present study aimed at adressing the following questions: (1) are fisheries data good and viable indicators of FSA in Brazil?; and (2) which environmental variables can be used to characterize these possible FSAs? Those questions were evaluated for snappers (Mutton snapper (*L. analis*), Dog snapper (*L. jocu*), Yellowtail snapper (*O. chrysurus*)) and groupers (Black grouper (*M. bonaci*) and Red grouper (*E. morio*)) species at the eastern Brazilian coast. In addition we also included an assessment and description of fisheries data to characterize temporal and spatial patterns of species catchability.

2. Materials and methods

2.1 Study area

The study was carried out on the eastern coast of Brazil, between the extreme southern coast of Bahia (Prado city) and the entire coastal zone of Espírito Santo state. This region includes a continental shelf platform of ~ 200 km wide, named Abrolhos Bank which represents an exception to the narrow continental shelf (~ 40 km wide) present in other Brazilian regions (Vital et al., 2010). Additionally, it harbors the largest coral reef complex in the South Atlantic and has a complex benthic habitat mosaic with reefs in diverse shapes and dimensions (e.g., *chapeirões* and fringing reefs) (Leão et al., 2003; Pinheiro et al., 2018).

The area has 20 904 km^2 of rhodolith beds, in addition to unconsolidated sediments, *buracas*, mangroves and seaweed banks (Bastos et al., 2013; Moura et al., 2013). This ecosystem is home to nearly 20 coral species and 300 fish species (Leão & Kikuchi, 2001; Moura & Francini-Filho, 2005; Dutra et al., 2006, Cavalcanti et al., 2013; Previero et al., 2013). It is also possible to observe the presence of seamounts of volcanic origin that have submerged banks on their tops (such as Minerva and Rodger Banks). Similarly, in Espírito Santo state, the Vitória-Trindade Chain is found, composed of a sequence of 30 seamounts and considered an oceanic hotspot (Pinheiro et al., 2015). Moreover, this area harbors the second highest density of coastal marine protected areas along the Brazilian coast (Zapelini & Schiavetti, 2014).

2.2 Fishery data

We used two data sets: fishing landing databases from the monitoring program carried out with fishermen in the municipalities of Prado, Alcobaça, Barra de Caravelas, and Ponta de Areia, the latter two falling within the Caravelas municipality, between the years 2005-2007, made by the Conservation International Brazil Marine Program and the monitoring program carried out by the Marine and Coastal Protected Areas Project (GEFMar – World Bank) between the years 2017 and 2018 on the coast of Espírito Santo. Fishers marked their fishing grounds by stock on a nautical chart, which were later transformed into fishing spots. For each record, CPUE (total production in kg per number of fishermen × fishing trip duration in days) were calculated (Table 1). For this map, a grid was created, and each fishing point was plotted, per stock. The quadrants received fictitious names in order for subsequent analyses to be conducted. The program used to compute the data was ArcGIS 9.3.

Table 1. Number of landings, CPUE average and CPUE average x 4 per species as an indicator of spawning aggregation events (Domeier, 2012).

Species	N (Landings)	Average CPUE	Average x 4
Mycteroperca bonaci	306	5,17	20,68
Epinephelus morio	309	4,68	18,72
Ocyurus chrysurus	506	12,07	48,28
Lutjanus jocu	236	2,42	9,68
Lutjanus analis	173	2,48	9,92
Total	**1530**	**-**	**-**

2.3 Environmental data

Since there is a lack of environmental data for these fishing locations, satellite data were used. Monthly average sea surface temperature (SST) (2003– 2007) data derived from the Terra-Modis level 3 (version 4) (Terra- Moderate-resolution Imaging Spectroradiometer) satellite and chlorophyll-a data derived from the Aqua-Modis level 3 satellite were downloaded from the NASA Goddard Space Flight Centre (GSFC) through the following website http://oceancolor.gsfc.nasa.gov/cgi/. These data are 4 km pixel resolution products in .cdf format. Regarding depth, the values were generated from a GEBCO global bathymetry model (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). The spatial resolution is approximately 0.4 km. Moreover, regarding the bottom type data, the shelf morphology was used based on Bastos et al. (2015).

2.4 Statistical analysis

Each fishery was considered a sampling unit in the data analysis. In addition, only landings from fishing trips with positive catches of the target families (groupers and snappers) were analyzed. Boxplots were used to investigate the monthly and annual variation of CPUE values. Thus, for the analysis, outliers and extreme outliers was considered extraordinary fisheries in possible areas of spawning aggregation. They are represented by values that exceed 1.5 and 3.0 times the amplitude of the data distribution of the analyzed sample (França & Olavo, 2015). From the calculation of the CPUE global average for each species, considering the entire sampled period

(2005-2007; 2017-2018), a reference value was generated, later established as a criterion for identifying possible spawning aggregation areas. For that, we used the proposed by Domeier (2012), which is at least four times the global average value of CPUE.

The study area was divided into quadrants of 10 x 10 km^2, where information was extracted by species and by quadrant: sum of CPUE; average temperature of the five years worked; chlorophyll average (2003- 2020); average depth and bottom type. Bottom type factor was classified into four categories: reef, rodolith, seamount slope and unconsolidated. Then transformed into a compositional variable (totalizing 100%), later transformed into arcsine to dilute the zeros effect and standardized so that the variables are inserted in the same order of magnitude.

In order to evaluate the influence of the environmental variables on CPUE, data were averaged by quadrant and tested using generalized linear models (GLM). Since the CPUE data had an asymmetric distribution, we used a Box-Cox transformation (Box & Cox, 1964). As data were averaged by specie, we used a Gaussian distribution error which is more appropriate when dealing with continuous measures than others.

Multiple regression was used to identify the environmental variables with a significant influence in the CPUE for each species. The CPUE was exhaustively regressed to all possible combinations of environmental variables and best model was selected using the akaike information criteria (AIC) and ranked by AIC weights. Previously to model selection we tested for multicollinearity among Depth, Chlorophyll, SST, Reef, Rodolith, Seamount Slope and Unconsolidated in the full model using Variation Inflation Factors (VIF) for CPUE. All the statistical analyses were carried out in R software (R Core Team, 2019).

3. Results

3.1 Fishery characterization

The analysis of outliers and extreme outliers of the CPUE distribution for all species, where large CPUE peaks represented exceptional catches were used as an indicator of possible spawning aggregations events. The real names of the fishing grounds are not disclosed with the intention of protecting the aggregation areas themselves, since to date there are no protection measures in place for these areas.

Catch of *M. bonaci* ($F = 2.81$; $p < 0.05$) and *E. morio* ($F = 2.67$; $p < 0.05$) varies with season. *Post-hoc* analysis identified increased catches in summer and fall and between winter and summer ($p < 0.05$), respectively. *O. chrysurus*, *L. jocu* e *L. analis* showed no significant difference between the catch and the seasons of the year ($p > 0.05$).

For all species, except *M. bonaci* (63.1 kg/year in 2005), 2007 was the year with the lowest average yield (13.65, 131.18, 26.51 and 32.85 kg/year for *E. morio*, *O. chrysurus*, *L. jocu* and *L. analis*, respectively). The years 2017 and 2018 stood out as the years with the highest annual production averages for all species (478.4, 513.14, 512.15 and 197.78 kg/year for *M. bonaci*, *E. morio*, *O. chrysurus* and *L. jocu* respectively) with the exception of *L. analis*, which had 2005 as the year with the highest annual average (155.53 kg/year) (Figure 1a-o). Effort kept the same pattern for all species (except for *O. chrysurus*) where the first three years of the series showed less effort when compared to the two most recent years. For *O. chrysurus*, effort remained balanced during all years sampled (Figure 1h).

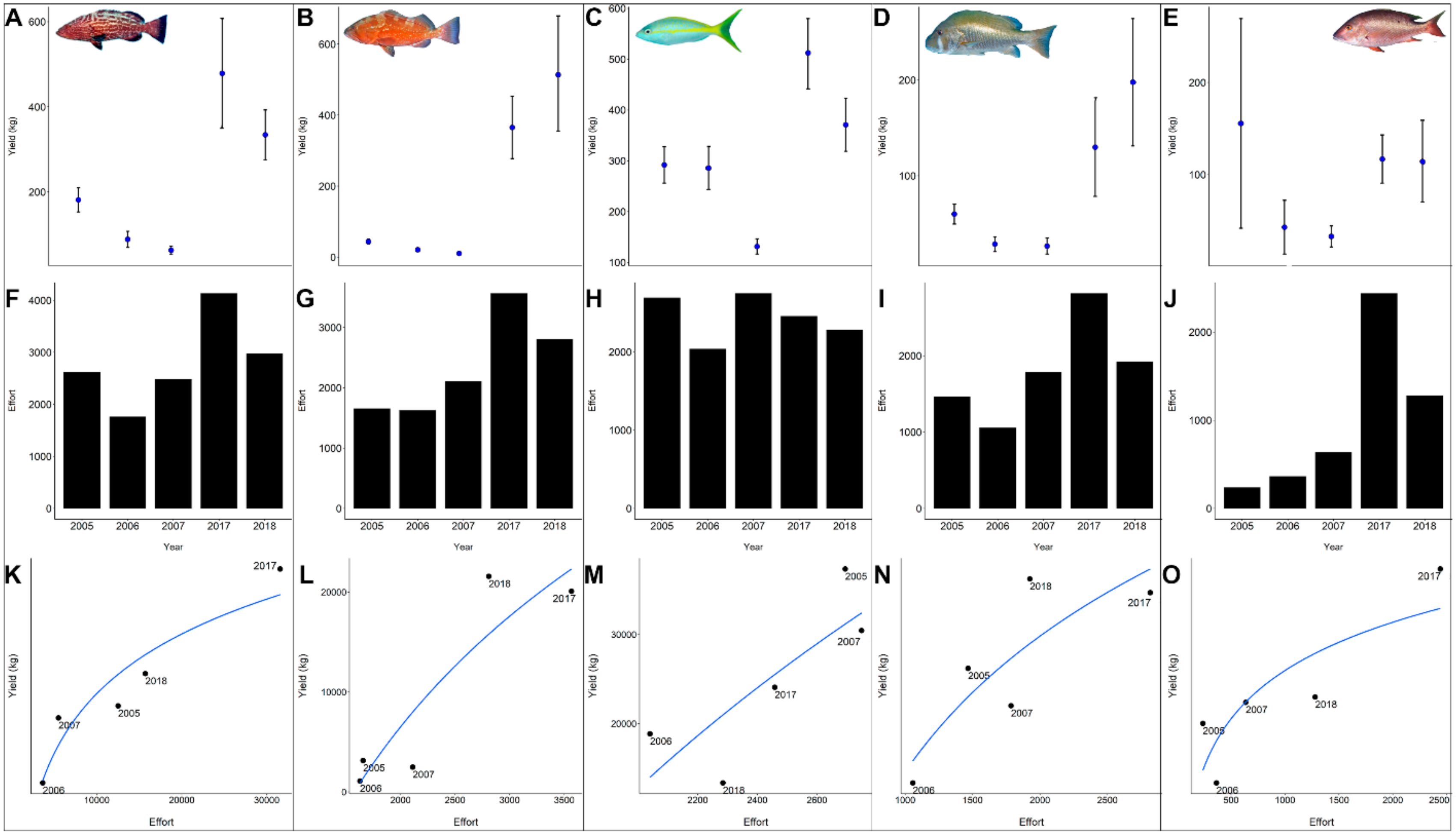

Figure 1: A-E: time series trends in annual yield (kg/year; ± SE); F-J: total annual fishing effort (nº of fishermen × nº of fishing days); K-O: relationship between annual yield (kg/year) and effort (nº of fishermen × nº of fishing days) for the period 2005-2007; 2017-2018.

Mycteroperca bonaci

A total of 306 landings was reported for black grouper, recorded between 2005-2007; 2017-2018. Winter (June to August) was the season that presented the highest monthly CPUE average. It was observed only for July maximum values (vertical line) that exceeded the reference value of four times the global average (20.6 kg / fisherman per day) (Figure 2b). In addition, the occurrence of extreme outliers indicating huge catches (in possible spawning aggregation areas) was observed in February, March, and June to August. Particularly, July/2005 and August/2017 presented extraordinary catches for the species, indicating possible fishing in an area of spawning aggregation, deserving a deeper investigation. The exploration of outliers and extreme outliers on the map demonstrated that the areas with the highest CPUE values are concentrated in the Abrolhos bank, with the highest CPUE value in the shelf break of Royal Charlotte bank, in front of the city of Porto Seguro (Figure 3).

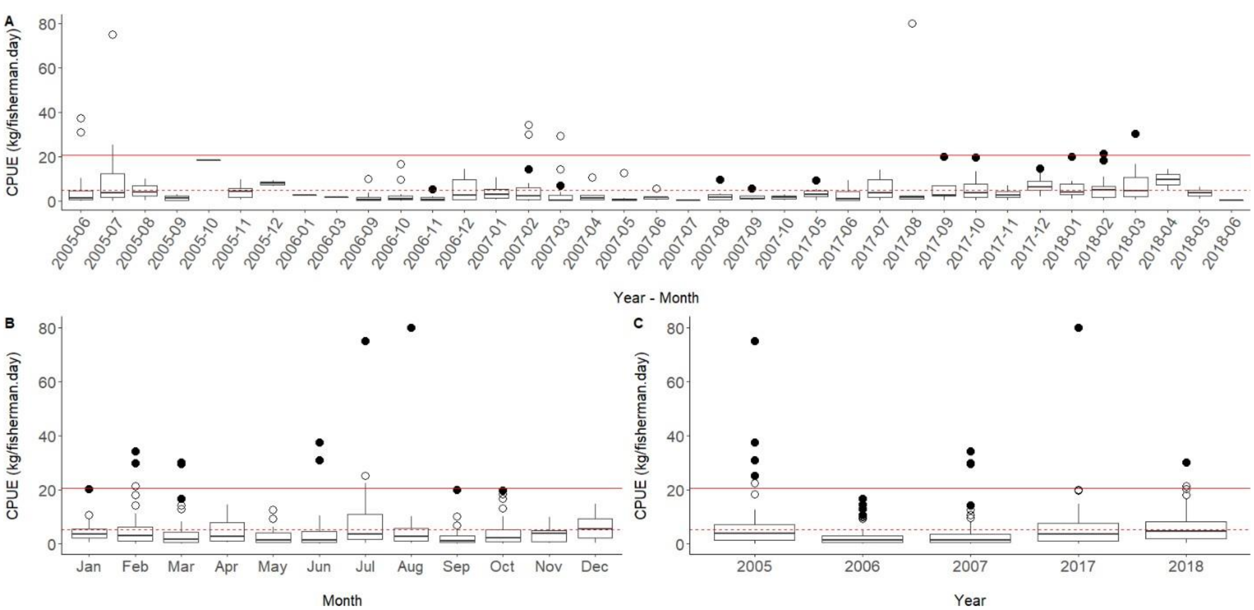

Figure 2. Distribution of Black grouper (*Mycteroperca bonaci*) CPUE per landing, grouped by Year and month (A), by month (B), and by year (C) between 2005-2007; 2017-2018 (n = 306). In red, the dashed line indicates the global mean CPUE for the species (5.1 kg/fisher per day) and the solid line indicates the value four times higher than the global mean CPUE (20.6 kg/ fisher per day). (o) Represents outliers. (•) Represents extreme outliers.

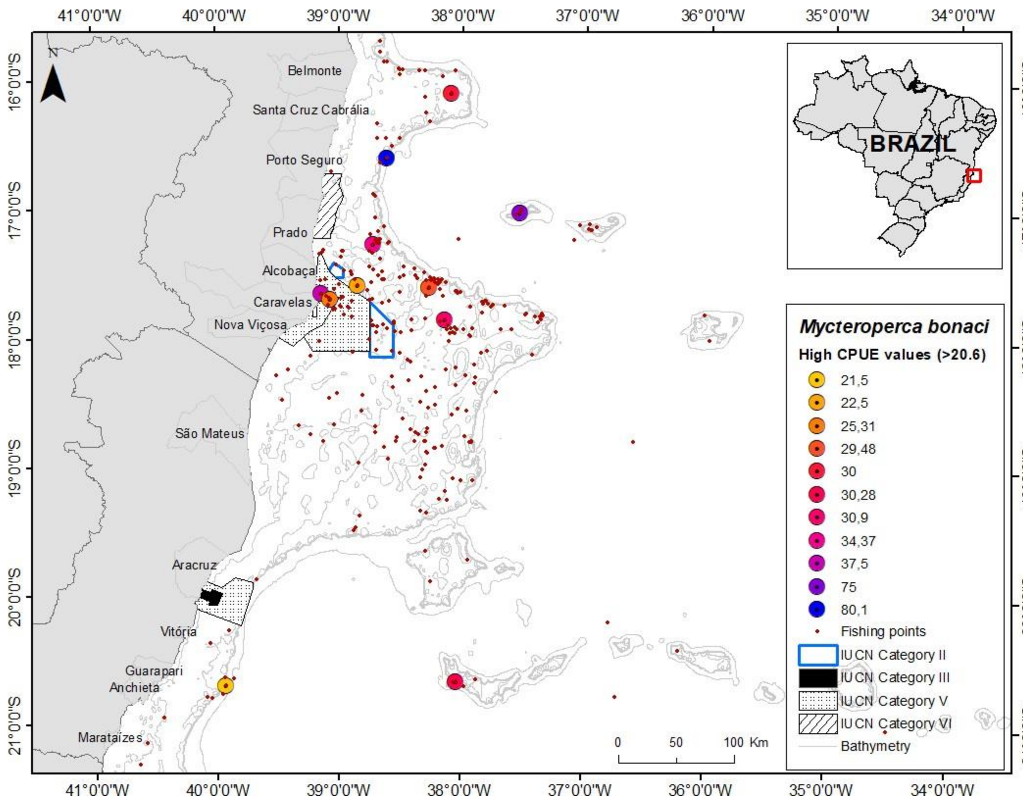

Figure 3. Map of fishing points and highest CPUE values for *Mycteroperca bonaci* in the study area. Category II: National Park; Category III: Natural Monument or Feature; Category V: Protected Landscape/Seascape and Category VI: Protected area with sustainable use of natural resources.

Epinephelus morio

A total of 309 landings for red grouper were analyzed during the five years studied (2005-2007; 2017-2018). The maximum values that exceeded the established reference of four times the global average of CPUE as indicative of spawning aggregation (18.7 kg/fisher per day) were observed in October. Additionally, it is possible to see an extraordinary catch in February/2007 (Figure 4b). Extreme outliers were observed especially in late summer (January and February) and during winter (June and August). Observing the map, it is possible to identify that all fishing grounds are dispersed throughout the Abrolhos bank, with its most extreme value in the region next to the continental shelf break in front of the city of Prado (Figure 5).

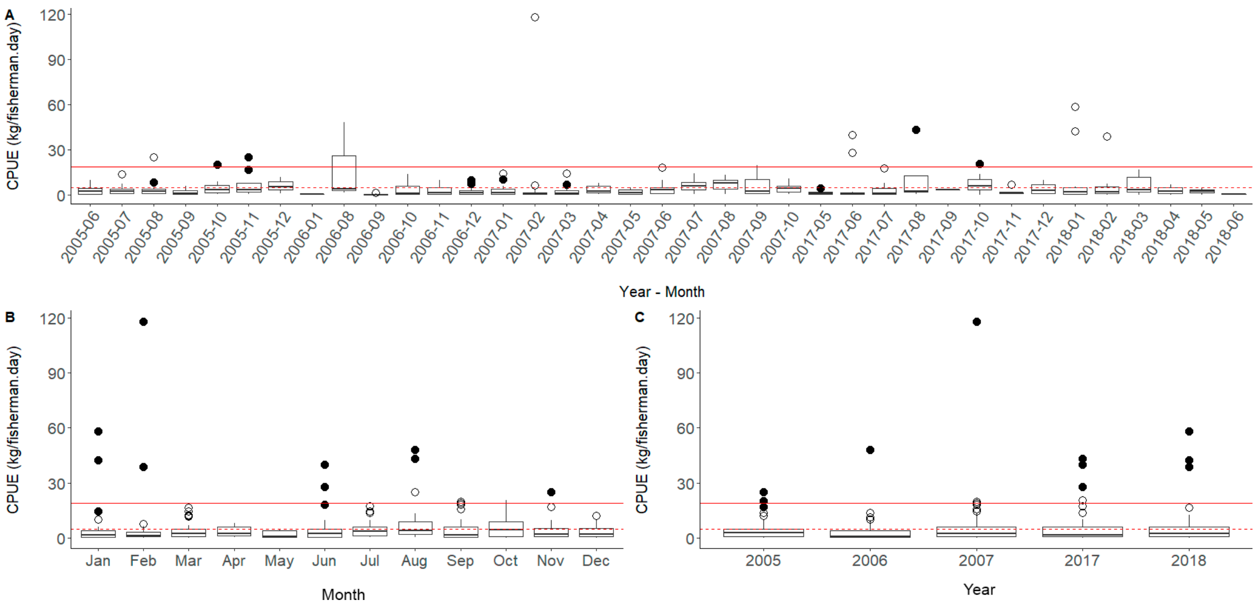

Figure 4. Distribution of Red grouper (*Epinephelus morio*) CPUE per landing, grouped by Year and month (A), by month (B), and by year (C) between 2005-2007; 2017-2018 (n = 309). In red, the dashed line indicates the global mean CPUE for the species (4.6 kg/fisher per day) and the solid line indicates the value four times higher than the global mean CPUE (18.7 kg/fisher per day). (o) Represents outliers. (•) Represents extreme outliers.

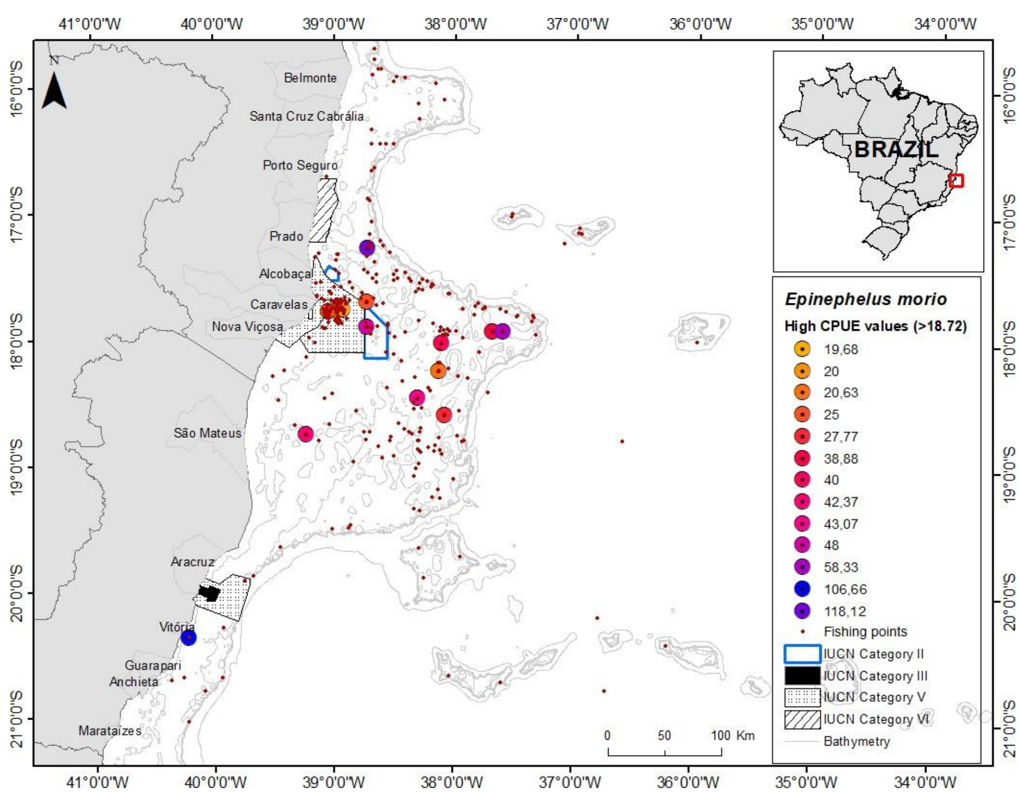

Figure 5. Map of fishing points and highest CPUE values for *Epinephelus morio* in the study area. Category II: National Park; Category III: Natural Monument or Feature; Category V: Protected Landscape/Seascape and Category VI: Protected area with sustainable use of natural resources.

Ocyurus chrysurus

Data for 506 landings were obtained for yellowtail snapper during the sampled years (2005-2007; 2017-2018). It is possible to observe few values of extreme outliers for this species, but present in several months throughout the year. Higher recordings, above the value of four times the global CPUE mean (48.28 kg/fisher per day), was found in February, March, June to August and October. On the map it is possible to identify that the areas with the highest CPUE values are concentrated in the north of the Abrolhos Bank and in the Royal Charlotte Bank, with the highest CPUE value in front of the city of Belmonte (Figure 7).

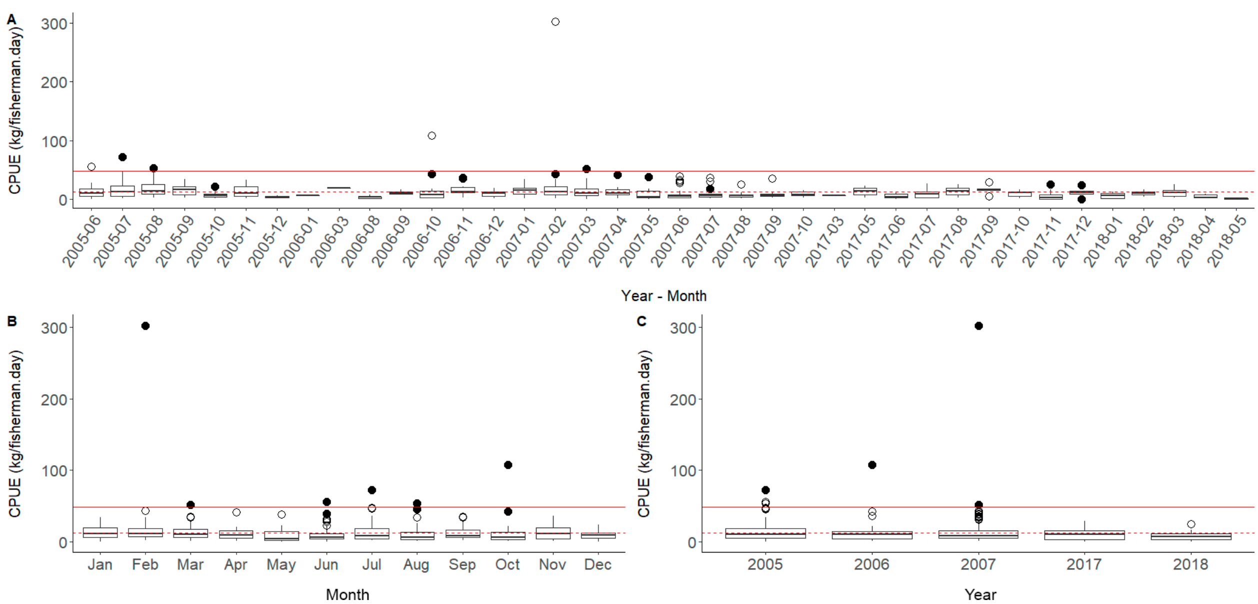

Figure 6. Distribution of yellowtail snapper (*Ocyurus chrysurus*) CPUE per landing, grouped by Year and month (A), by month (B), and by year (C) between 2005-2007; 2017-2018 (n = 506). In red, the dashed line indicates the global mean CPUE for the species (12 kg/fisher per day) and the solid line indicates the value four times higher than the global mean CPUE (48.2 kg/fisher per day). (o) Represents outliers. (•) Represents extreme outliers.

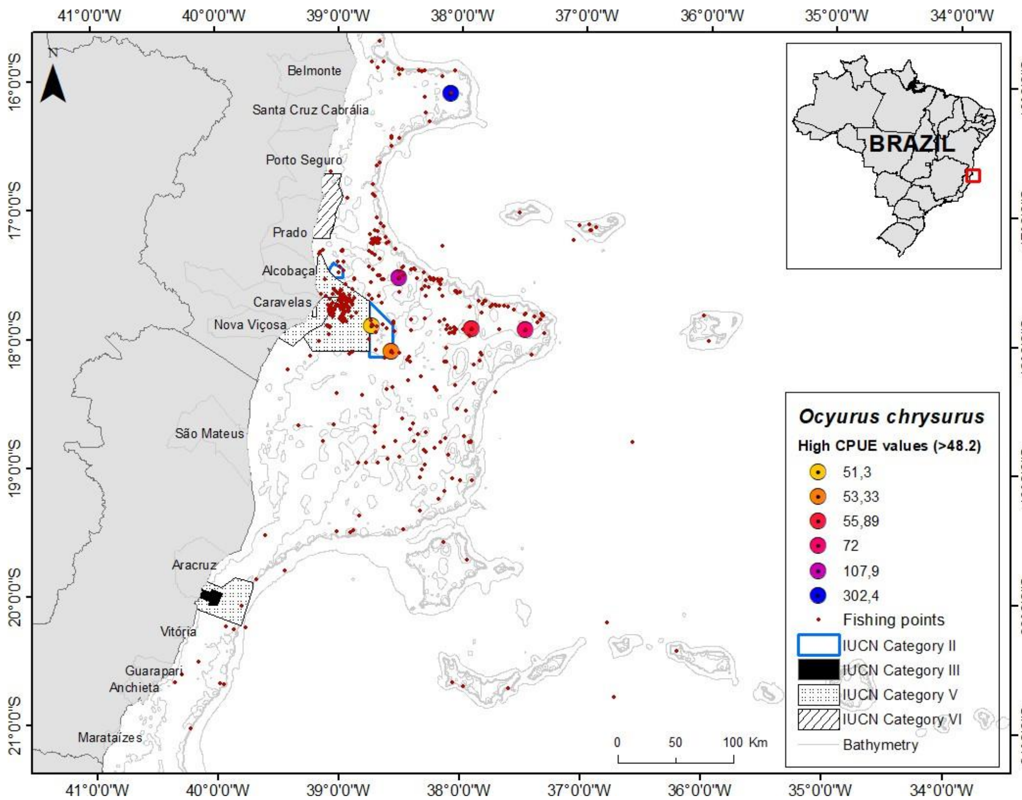

Figure 7. Map of fishing points and highest CPUE values for *Ocyurus chrysurus* in the study area. Category II: National Park; Category III: Natural Monument or Feature; Category V: Protected Landscape/Seascape and Category VI: Protected area with sustainable use of natural resources.

Lutjanus jocu

For dog snapper, a total of 236 landings were analyzed between 2005-2007; 2017-2018. It was observed only for May and July maximum values (vertical line) that exceeded the reference of four times the global average (9.6 kg / fisher per day) (Figure 8). Extreme outliers were observed almost throughout the year, with the exception of February, April, and September alone. However, the highest values are concentrated in winter (June to August). Watching the map, it is possible to identify that the area near the Abrolhos Marine Park delimitation represents an important fishing ground for the species (Figure 9).

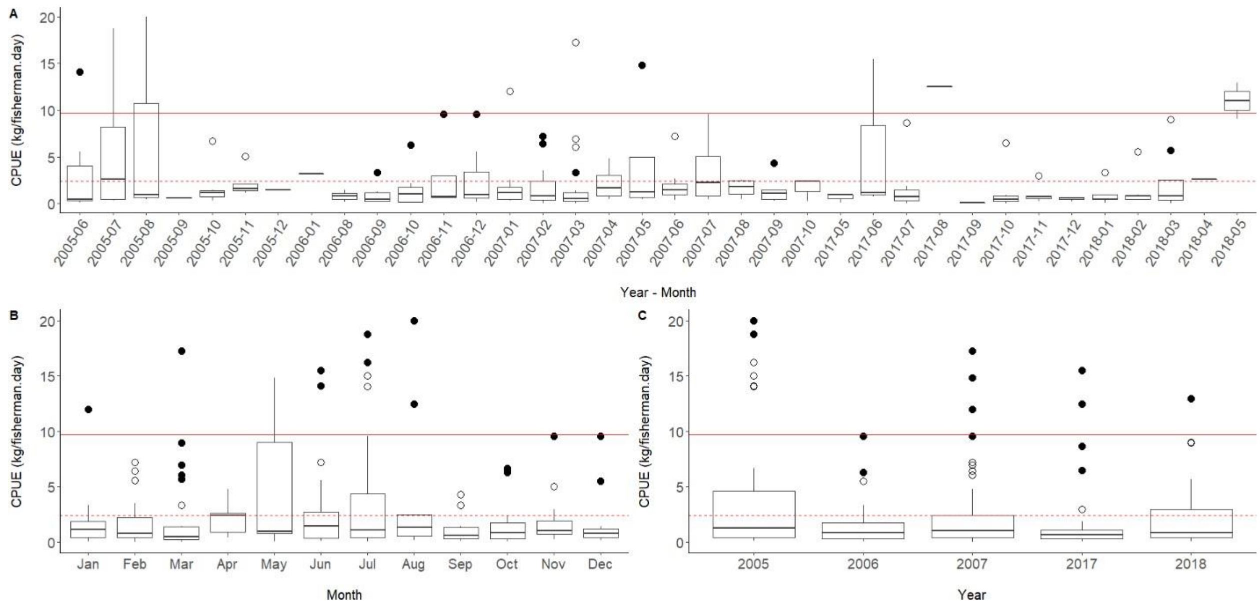

Figure 8. Distribution of dog snapper (*Lutjanus jocu*) CPUE per landing, grouped by Year and month (A), by month (B), and by year (C) between 2005-2007; 2017-2018 (n = 236). In red, the dashed line indicates the global mean CPUE for the species (2.4 kg/fisher per day) and the solid line indicates the value four times higher than the global mean CPUE (9.6 kg/fisher per day). (o) Represents outliers. (•) Represents extreme outliers.

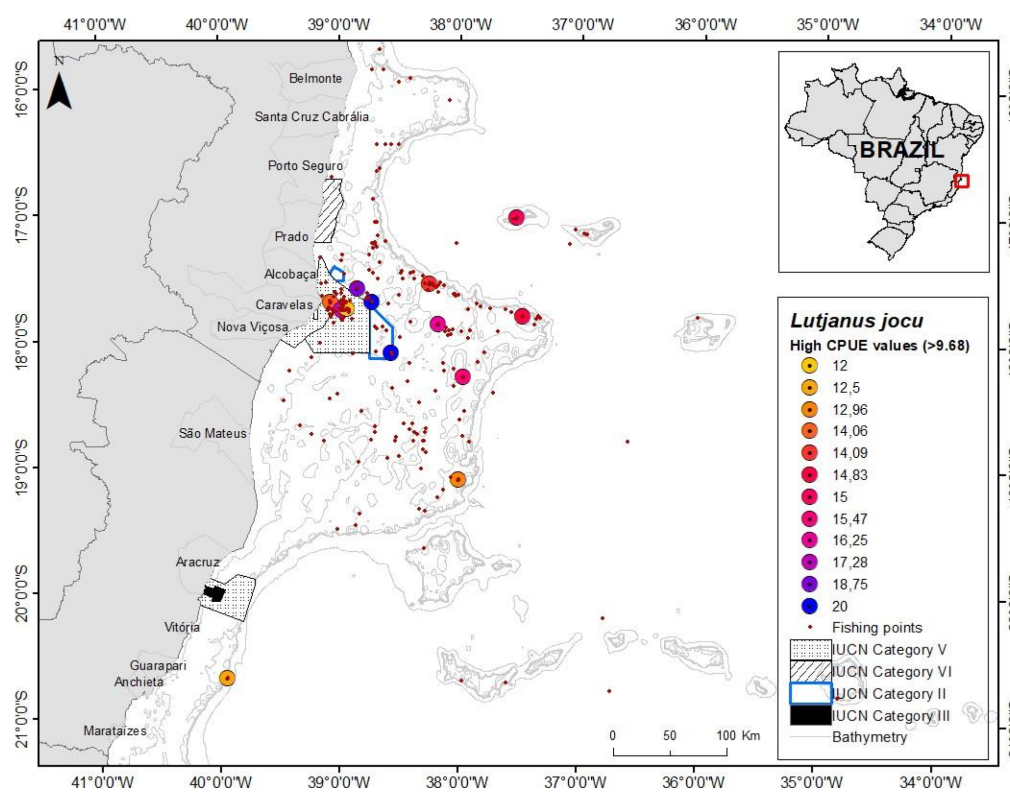

Figure 9. Map of fishing points and highest CPUE values for *Lutjanus jocu* in the study area. Category II: National Park; Category III: Natural Monument or Feature; Category V: Protected Landscape/Seascape and Category VI: Protected area with sustainable use of natural resources.

Lutjanus analis

A total of 173 landings with catch of mutton snapper, recorded between 2005-2007; 2017-2018, were analyzed. In particular, it was possible to observe in the months of June to August and October the presence of values well above the established criterion as indicative of reproductive aggregation for the species (CPUE of 9.94 kg / fisher per day). The largest catches are concentrated in the second half of the year, with less pronounced CPUE peaks from December to May (Figure 10). The investigation of these outliers and extreme outliers allowed the identification of the main areas where this fishery occurs. It is possible to observe on the map that the areas with the highests CPUE values are concentrated in the coast and next to the marine park borders, with the highest CPUE value in the region located between the cities of Alcobaça and Caravelas (Figure 11).

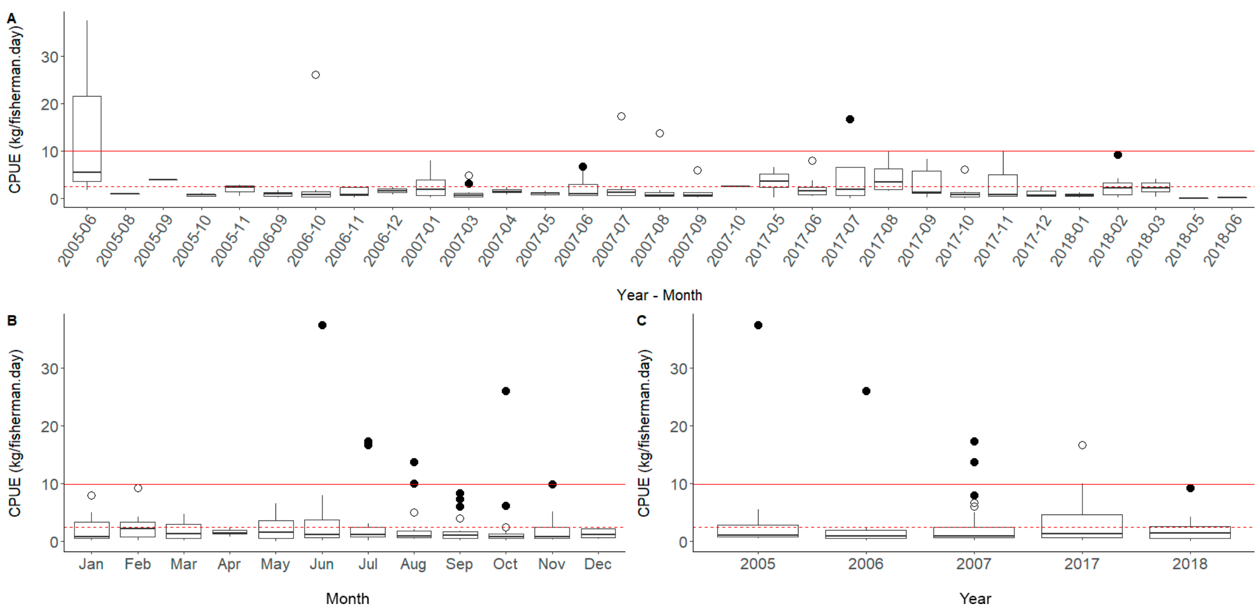

Figure 10. Distribution of mutton snapper (*Lutjanus analis*) CPUE per landing, grouped by Year and month (A), by month (B), and by year (C) between 2005-2007; 2017-2018 (n = 173). In red, the dashed line indicates the global mean CPUE for the species (2.4 kg/fisher per day) and the solid line indicates the value four times higher than the global mean CPUE (9.9 kg/fisher per day). (o) Represents outliers. (•) Represents extreme outliers.

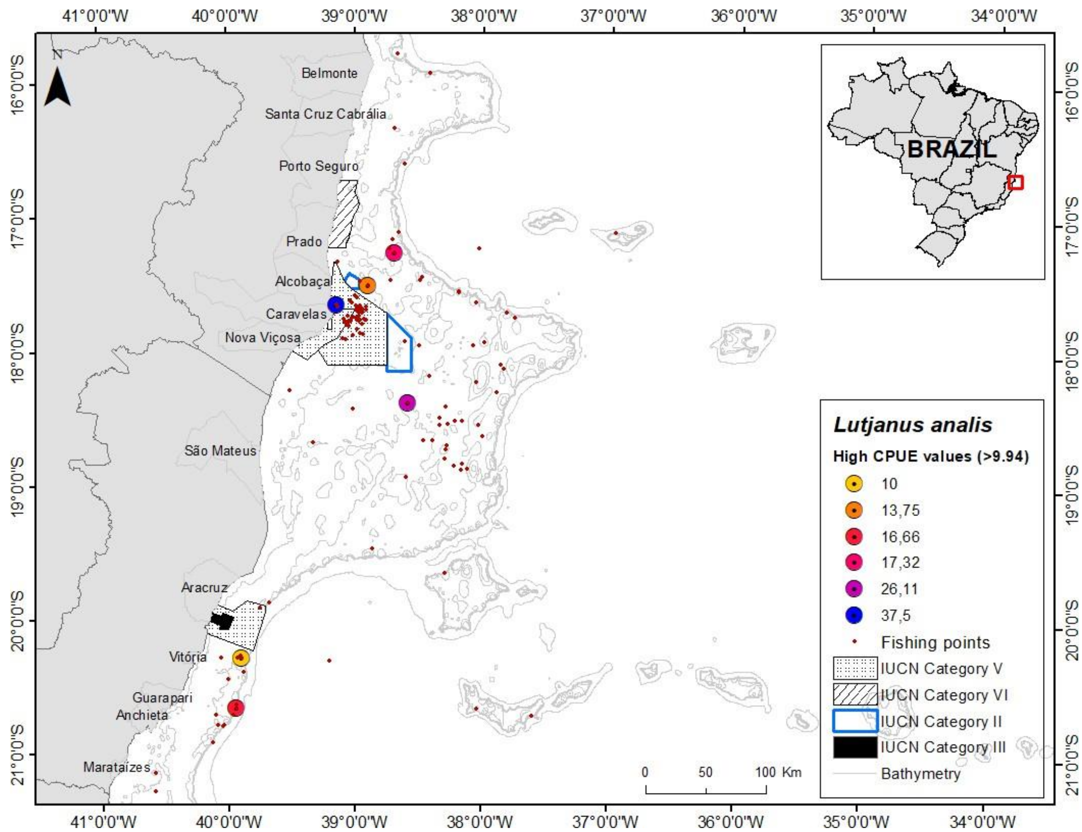

Figure 11. Map of fishing points and highest CPUE values for *Lutjanus analis* in the study area. Category II: National Park; Category III: Natural Monument or Feature; Category V: Protected Landscape/Seascape and Category VI: Protected area with sustainable use of natural resources.

3.2 Relationships between environmental variables and CPUE

The relationships with environmental variables and CPUE for each species are shown in Table 1. In most cases, models retained more than one predictor variable, with variables related to bottom type (reef, rodolith and unconsolidated) as the most important influential ones. *M. bonaci* was related to all four bottom types, as well as *L. analis*; *E. morio* was positively related to reef, rodolith and unconsolidated; *O. chrysurus* was positively related to SST, Depth, Rodolith, Unconsolidated and Reef and *L. jocu* was positively related to Chlorophyll, Rodolith, Unconsolidated, Reef and SS.

Table 2. Results of GLM fitted models between total CPUE and each specie with environmental variables: Depth, Cholo - Chlorophyll, SST – Sea Surface Temperature, Reef, Rod - Rodolith, SS – Seamount Slope, Unc – Unconsolidated Substrate. AICc: Akaike's information criterion; Df: number of model parameters; Wi: AICc weight.

Species	**Term**	**AICc**	**Df**	**W_i**
Mycteroperca bonaci	Reef + SS + Unc + Rod	702.9	6	0.323
Epinephelus morio	Reef + Rod + Unc	625.3	5	0.289
Ocyurus chrysurus	SST + Depth + Rod + Unc + Reef	689.2	7	0.426
Lutjanus analis	Rod + Reef + Unc + SS	276.1	6	0.125
Lutjanus jocu	Chlo + Rod + Unc + Reef + SS	487.1	7	0.355

4. Discussion

The use of CPUE as an indirect sign of spawning aggregation events has been widely used (Eristhee et al., 2006; Graham, 2008; Kadison et al., 2009; Erisman et al., 2017), especially when considering areas that have been poorly studied. In situ research is a difficult and very costly activity, which makes studies focused on this event even more difficult. The identification of extreme values of CPUE allowed the analyses of possible spawning aggregation locations and times for the five species evaluated, which can be directly associated with the spawning processes or the movement to the spawning aggregation sites (França & Olavo, 2015; França et al., 2021).

The lack of a continuous landings database (by species) for commercial fisheries in the entire Brazilian coast hinders detailed assessments and management of long-term trends in landings of aggregating species. However, the data we have compiled provides a means to analyses possible periods of aggregation of two families of reef fish with high commercial value. Several groups of species that have aggregation as a breeding strategy, such as snappers and groupers have supported commercial fishing for more than fifty years (Arvizu-Martinez, 1987; Cisneros-Mata, 2010), contributing significantly to commercial reef fish fisheries all over the world (Díaz-Uribe et al., 2007; Erisman et al., 2010).

Among the sites observed throughout the monitoring periods (2005-2007; 2017-2018), inarguably the Abrolhos region represents the main fishing area for the species studied. This area harbors the most productive fishing grounds, presenting extremely high and periodic catch rates. These same possible aggregation sites were identified by Previero & Gasalla (2018) as harboring the largest fisheries for *Lutjanus jocu*, *L. synagris*, *Ocyurus chrysurus*, *Cephalopholis fulva*, *Epinephelus morio* and *Mycteroperca bonaci*. Moreover, the Abrolhos region encompass the largest coral reef in the South Atlantic and supports large fisheries for diverse reef organisms (Moura et al., 2013). Considering the topographic and structural complexity of this region (Bastos et al., 2015), this can be considered an ideal habitat for the occurrence of spawning aggregation events (Kobara & Heyman et al., 2010).

For the relationship between the largest catches and the environmental characteristics, it is essential to consider that the points obtained through fishermen do not represent the exact fishing point, but rather the identification of the main fishing ground exploited. Despite this, the result obtained through GLM is consistent with that found in the literature, where the structural bottom complexity, where the spawning aggregations are located and usually occur, are very relevant to their occurrence (Claydon, 2004; Kobara & Heyman et al., 2010). For the others selected characteristics, such as temperature, depth, and chlorophyll, which are also described as related to spawning aggregation events, only *O. chrysurus* and *L. jocu* showed a significant relationship for the increase of CPUE and the presence of these characteristics.

Hamilton et al. (2012) for example did not find correlation between daily water temperatures and the pattern of aggregation formation for *E. fuscoguttatus*, *E. polyphekadion* or *P. areolatus*. Regarding the depth, it is suggested that the movement between the extracts may be related to the escape of predators or parasite infestations, release of fertilized eggs in specific oceanic strata or with currents that increase larval survival and/or retention (Semmens et al., 2006; Starr et al., 2007; Nemeth, 2009). Additionally, chlorophyll is related to the feeding of the larvae after the release and eggs fertilization.

Epinephelidae family

Black grouper and red grouper have been intensively fished in the Abrolhos region since the 1980s (Costa et al., 2003; Martins et al., 2005). However, despite the catch inconsistency of data in Brazil, it has already been possible to notice an intense drop in catch since the 70s through both CPUE and local ecological knowledge (Costa et al., 2003; Bender et al., 2013; Zapelini et al., 2019). At Abrolhos Bank, *M. bonaci* and *E. morio* represented 1.5% and 0.4% of the total fish biomass, respectively (Francini-Filho & Moura, 2008).

The highest CPUE recorded for *M. bonaci* (80.1 kg/fisher per day) corresponds to a withdrawal of 8010 kg (16 times the average for that year) in a single fishery. This fishing ground was identified by fishermen (Bezerra et al., 2021) as an area of spawning aggregation for the species. In addition, the month corresponding to this fishery (August/2017), also corresponds to the reproductive period of the species (Freitas et al., 2011). In the Caribbean, there are records of reproductive aggregation between December and February, with a peak between January and February (Smith, 1972; Sala et al., 2001; Heyman & Kjerfve, 2008, Paz & Sedberry, 2008). Therefore, in both hemispheres the reproduction of the species occurs during the winter.

It has been suggested that, unlike many grouper species, *E. morio* does not exhibit spawning aggregation behavior (Brule et al., 1999). Red grouper has been described as nonmigratory polygynous spawning (Sadovy et al., 1994; Coleman et al., 1996). However, particularities of red grouper spawning behavior are still unknown in its entirety. The highest CPUE recorded (118.1 kg/fisher per day) corresponds to a catch of 945 kg in February (late summer). In the Gulf of Mexico, the months identified as the grouper's spawning period were from March until May (spring) (Jhonson et al., 1998). In Brazil, Freitas et al. (2011), identified in the Abrolhos Banck through GSI, the period between July and October (with peak between August and September), i.e. winter and early spring, as the reproductive season of the species.

Lutjanidae family

Snappers are central targets for fisheries worldwide (Claro & Lindeman, 2003) and intensively captured by marine fisheries on the Brazilian coast (Fredou et al., 2009). This family represents up to 38% of fishing landings in the Abrolhos region (Costa et al., 2003). In addition, several studies have been able to demonstrate family overfishing in Brazil (Rezende & Ferreira, 2003; Klippel et al., 2005).

Despite the spawning aggregation of *O. chrysurus* not being deeply studied as is the case of some species of the same family (*L. cyanopterus* Biggs & Nemeth, 2016; Heyman & Kjerfve, 2008; Heyman et al., 2005; Heyman et al., 2010 and L. *analis* Feeley et al., 2018; Graham, 2008, Graham 2012; Granados-Dieseldorff et al., 2013; Heyman & Kjerfv, 2008), the highest CPUE value (302.4 kg/fisher per day) found for the yellowtail snapper corroborates the reproductive period identified by Freitas et al. (2011) in Brazil, and with the months of higher yields founded by Costa et al. (2003). In the Caribbean, Heyman & Kjerfve (2008) identified the months of February and March (late winter) as the reproductive period of yellowtail snapper.

It is possible to observe that there is not a large variation between the CPUE values above average x 4 (spawning aggregation indicative) for this family, which shows a possible balance between the catches, without huge peaks year-round. This result is supported through works developed in the Caribbean, where there are records of spawning aggregation throughout the year for dog snapper (Carter & Perrine, 1994; Heyman & Kjerfve, 2008; Heyman et al., 2010; Biggs & Nemeth, 2016;), cubera snapper, *Lutjanus cyanopterus* (Heyman et al., 2010) and two-spot red snapper, *Lutjanus bohar* (Sakaue et al., 2016).

For the mutton snapper, in the Caribbean and Gulf of Mexico, there are records of spawning aggregation from March to August, with peaks between April and June (Graham, 2008, 2012; Heyman & Kjerfve, 2008; Feeley et al., 2018). In Brazil, Freitas et al. (2011) suggested the period between spring and autumn as the reproductive season of the species. Teixeira et al. (2010) identified through GSI, that the spawning season occurs between November and April, with a spawning peak in March.

For all species (with the exception of *O. chrysurus*), the years 2017 and 2018 had the highest yield and effort ratio compared to the other years analyzed demonstrating the use of a greater effort for fishing in the region. However, it is necessary to consider the difference between the fleets that made the catches in the first three years (2005-2007), which represents a small-scale fleet with effort almost three times less than the employee in the last two years (Freitas, 2009; Previero & Gasalla, 2018). The fleet responsible for the capture in the years 2017 and 2018, from the state of Espírito Santo, is characterized by being the largest oceanic fleet in the country, it has greater sea autonomy, which guarantees a larger catch among the species analyzed.

5. Conclusions

Encouraged by the absence of long-term fishing data, the intense and excessive exploitation of the stocks of these two families may present a false perception of stability. This misconception can be seen through the high yield of recent years analyzed, falling on the already solid concept of illusion of plenty, where fishing may be exploring spawning aggregation sites (Erisman, 2011). Currently, the two studied species of the Epinephelidae family are within a national moratorium that prohibits fishing, transportation, landing and commercialization of any species individuals of under 60 cm and 45 cm for *M. bonaci* and *E. morio*, respectively (decree 445/2014).

This study has demonstrated that when available, fishing data can be a powerful weapon in exploring possible areas of spawning aggregation. Additionally, the results showed that high values of CPUE are mainly related to structures of reef, rhodolith beds, seamounts and unconsolidated bottoms. Brazil has a history of overfishing, aggravated by the difficulty of inspecting fishing and coastal management. Additional studies that focus on these places and periods are needed to confirm the spawning character of these aggregations.

6. Acknowledgements

This study was financed in part by the Coordenaçao de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Finance Code 001. We thank the support by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the grant provided for AS (grant nº. 310464/2020-0). We thank the Areas Marinhas e Costeiras Protegidas project (GefMar) for the collaboration.

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CONSIDERAÇÕES FINAIS

Os resultados apresentados nessa tese poderão contribuir para o manejo de espécies e processo de tomada de decisão de áreas prioritárias como o Banco dos Abrolhos, por possivelmente abrigarem eventos de agregação reprodutiva de garoupas e vermelhos. Em regiões pouco estudadas e tão extensas como a costa brasileira, o conhecimento ecológico local e o acesso a dados de pesca demonstraram ser ferramentas poderosas para a identificação de possíveis áreas de agregação reprodutiva, direcionando futuras investigações *in situ* para a identificação direta e caracterização desses eventos.

Através da revisão de literatura realizada no **primeiro capítulo** foi possível observar os últimos avanços no estudo das agregações reprodutivas no mundo e principalmente como a maioria dos locais onde elas ocorrem não estão situados em áreas marinhas protegidas ou mesmo quando apresentam algum nível de proteção (fechamentos sazonais e/ou proibição da pesca), sofrem com a ausência de fiscalização. Além disso, foi possível demostrar que o Atlântico Sudoeste e o Oceano Índico carecem de investigações que busquem entender como esses eventos estão distribuídos espacial e temporalmente em sua costa.

No **segundo capítulo**, pudemos identificar através do conhecimento ecológico dos pescadores capixabas, 31 possíveis áreas de agregação reprodutiva de epinefelídeos e lutjanídeos. Além disso, foi demonstrado que o Banco dos Abrolhos representa a principal área de pesca e o badejo-quadrado (*M. bonaci*), juntamente com a guaiuba (*O. chrysurus*), os dois principais recursos pesqueiros entre os entrevistados.

Por fim, o **terceiro capítulo** teve como objetivo investigar a captura por unidade de esforço de cinco espécies de alto valor econômico e explorar a influência das variáveis ambientais como um indicativo de possíveis áreas de agregação. Para ambas as famílias, as principais variáveis ambientais selecionadas pelas espécies foram aquelas relacionadas aos tipos de fundo (recife, rodolitos e fundos inconsolidados) e condizem com o já proposto na literatura. Adicionalmente, para o badejo-quadrado, o pesqueiro com o maior valor de CPUE corrobora com uma área de agregação identificada pelos pescadores no segundo capítulo dessa tese.

Os estudos dos eventos de agregação reprodutiva tendem a ser complexos em função da difícil logística das atividades marinhas, além de financeiramente onerosos. Em função disso, o uso de metodologias alternativas na busca da identificação desses locais, são fundamentais para nortear posteriores confirmações visuais desses eventos. Portanto, é urgente a compreensão de que o resultado advindo da continuidade da sobrepesca sobre espécies que realizam agregação reprodutiva é o declínio populacional e futuro desaparecimento dessas espécies. Nesse sentido, o manejo dessas populações deve ser visando um plano de gestão pesqueira abrangente, adequado as circunstâncias locais e temporais, que exclui permanentemente a pesca de peixes reprodutivamente ativos em áreas de agregação reprodutiva.