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PADRÕES ESPAÇO-TEMPORAIS DE MOVIMENTAÇÃO DE PEIXES RECIFAIS: telemetria acústica como subsídio para efetividade de áreas marinhas protegidas

Recife
2021

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, Centro de Tecnologia e Geociências, como requisito parcial para obtenção do título de Doutor em Oceanografia.

Área de concentração: Oceanografia Biológica

Orientadora: Profa. Dra. Beatrice Padovani Ferreira
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RESUMO

O movimento dos peixes e as mudanças resultantes no uso do habitat são influenciados por uma variedade de processos biológicos e ecológicos, incluindo disponibilidade de recursos reprodução, competição, predação e ontogenia. Assim, o movimento é um fator chave que molda a distribuição e estrutura das populações de peixes e influencia nos benefícios proporcionados pelas medidas de conservação e manejo, como a implementação de áreas marinhas protegidas (AMPs). Portanto, métodos de estudo que permitam a identificação dos padrões de deslocamento das espécies, como a telemetria acústica, auxiliam o planejamento e a avaliação de AMPs. Para o presente estudo, foi inicialmente realizada uma revisão bibliográfica sistemática abordando o uso da telemetria acústica no monitoramento de peixes em AMPs. Observou-se que a telemetria acústica tem sido utilizada principalmente para avaliar a efetividade da proteção fornecida pelas AMPs para as populações de peixes e para investigar padrões espaço-temporais no comportamento das espécies. No entanto, esta tecnologia ainda é relativamente cara e os estudos realizados por países em desenvolvimento, como o Brasil, ainda são escassos. Assim, a telemetria acústica foi utilizada de forma pioneira em recifes de corais no Brasil com o objetivo de contribuir com o aporte de informações sobre a ecologia do movimento de peixes para subsidiar medidas de manejo de AMPs no país. Entre dezembro 2016 e outubro de 2017, 20 *Sparisoma axillare* e 9 *Lutjanus alexandrei* foram marcados internamente com transmissores acústicos e monitorados por receptores instalados nos recifes costeiros de Tamandaré-PE, inseridos na APA Costa dos Corais. O primeiro objetivo foi verificar as variações espaço-temporais na movimentação e uso do habitat e, assim, avaliar a efetividade de uma área *no-take*, a Zona de Preservação da Vida Marinha de Tamandaré (NTZ), para essas espécies. Ambas as espécies apresentaram um elevado índice de residência no curto prazo, indicando uma alta fidelidade espacial até o momento em que elas permanentemente deixam de ser detectadas. A ausência de sinais pode indicar um deslocamento para recifes mais profundos (migração ontogenéticas e reprodutivas), mortalidade por predação ou mortalidade por pesca quando os peixes ultrapassam os limites da NTZ. A área de vida utilizada pelas espécies foi pequena e ambas apresentaram subgrupos espacialmente separados dentro das populações. Em média, o percentual da área de vida inserida na NTZ foi de 88% para *S. axillare* e 95% para *L. alexandrei*, sugerindo uma boa proteção no período em que os indivíduos permaneceram em seu interior. O estudo também analisou as variações em curta escala temporal (ciclos de 24h) na movimentação, ocupação espacial e comportamento das duas espécies. Um comportamento claramente diurno foi observado para *S. axillare*, apresentando valores significativamente maiores para movimentação, área de vida e equabilidade espacial durante o dia. Por outro lado, para *L. alexandrei* foi possível identificar dois grupos de indivíduos com comportamentos opostos: peixes primariamente diurnos e peixes primariamente noturnos. É esperado que os resultados desta tese forneçam subsídios para a conservação das espécies, para o planejamento de futuras AMPs e para o manejo adequado da APA Costa dos Corais e da NTZ.

Palavras-chave: monitoramento acústico; *Sparisoma axillare*; *Lutjanus alexandrei*; ecologia do movimento; área de vida; variação nictemeral.

ABSTRACT

Fish movement and the resulting changes in habitat use often occur at different spatial and temporal scales. These dispersive behaviors may be influenced by a variety of biological and ecological factors, including resource availability, reproduction, competition, predation, and ontogeny. Thus, movement is a key factor that shapes the distribution and structure of fish populations and influences the extent of the benefits provided by conservation and management measures, such as the implementation of marine protected areas (MPAs). Therefore, the use of methodologies that allow the identification of species movement patterns, such as acoustic telemetry, provides information on the planning and evaluation of MPAs. For the present study, a systematic review on literature was initially carried out addressing the use of acoustic telemetry on the monitoring of fish species within MPAs. It was observed that acoustic telemetry has been used mainly to evaluate the effectiveness of the protection provided by MPAs to fish populations and to investigate spatial and temporal patterns in the species behavior. Recent technological advances have made possible an increase in the number of species and individuals tagged by study, as well as longer monitoring periods. However, this technology is still relatively expensive, and studies conducted by developing countries, such as Brazil, are still scarce. Thus, from December 2016 to October 2017, 20 *Sparisoma axillare* and 9 *Lutjanus alexandrei* were internally tagged with acoustic transmitters and passively monitored by an array of receivers deployed in the coastal reefs of Tamandaré-PE, within the Costa dos Corais MPA. This study aimed to verify the spatial-temporal variations in movement and habitat use and thus evaluate the effectiveness of a no-take area (NTZ), for these species. Both species presented a high residence index on the short-term, indicating they were full-time residents to the monitored area until detections were permanently lost. The absence of detections may indicate an emigration to deeper reefs (ontogenetic and reproductive migrations), predation mortality or fishing mortality when fish left the NTZ. Home range used by both species were small and both presented spatially segregated subgroups within the populations. On average, the percentage of home range within the NTZ was 88% for *S. axillare* and 95% for *L. alexandrei*. Diel variations were also observed in the movements, spatial occupation, and behavior of the two species. A clearly diurnal behavior was observed for *S. axillare*, with significantly higher values for movement, home range and spatial equitability during the day. On the other hand, a period of higher activity was not observed at species level for *L. alexandrei*. However, multivariate analyses revealed an individual-level heterogeneity in the activity patterns of most fish. Thus, two groups of individuals with opposite behaviors were identified: primarily diurnal fish and primarily nocturnal fish. It is expected that the results of the present thesis provide subsidies for species conservation, planning of future marine protected areas in the region and for the management of Costa dos Corais MPA and NTZ.

Keywords: acoustic monitoring; *Sparisoma axillare*; *Lutjanus alexandrei*; movement ecology; home range; diel variability.

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LISTA DE ABREVIATURAS E SIGLAS

AMP	Área marinha protegida
APR	Aggregated patch reefs
CD	Centroid distances
COA	Center of activity
CR	Core range
BR	Barrier reef
FFT	Fast Fourier Transformation
HR	Home range
I_R	Residency index
I_{WR}	Weighted residency index
KUD	Kernel utilization distribution
MPA	Marine protected area
NTZ	Área no-take/no-take zone
OI	Overlap index
SPR	Scattered patch reefs
SUR	Single unit reef

SUMÁRIO

1 INTRODUÇÃO

O movimento é um fator chave que molda a dinâmica, estrutura e padrões de distribuição das populações de peixes e influencia a extensão dos benefícios proporcionados pelas medidas de conservação e manejo (HALPERN, 2003; GRÜSS *et al.*, 2011; DI LORENZO *et al.*, 2016). As espécies podem apresentar padrões de deslocamento de curta e larga escalas espaço-temporais que incluem desde os ciclos diários de deslocamentos entre áreas de alimentação e repouso (HITT *et al.*, 2011a; WELSH; BELLWOOD, 2014; ROOKER *et al.*, 2018), migrações reprodutivas (FEELEY *et al.*, 2018; BRYAN *et al.*, 2019) e deslocamentos *cross-shelf* para recifes de maior profundidade ao longo da plataforma continental (FRÉDOU; FERREIRA, 2005; ASCHENBRENNER *et al.*, 2016a, 2016b).

1.1 MOVIMENTO E ÁREA DE VIDA

A área utilizada por um indivíduo durante suas atividades diárias regulares (p. ex. alimentação, reprodução, repouso, interações sociais e cuidado parental) compreende a área de vida ou *home range* deste animal (Burt, 1943; KRAMER; CHAPMAN, 1999; Powell, 2000). Dentro do seu *home range*, um indivíduo pode ainda apresentar áreas de uso preferencial (áreas núcleo ou *core range*) nas quais permanece durante a maior parte do tempo (SAMUEL *et al.*, 1985). Uma das possíveis vantagens de se estabelecer um *home range* está no rápido acesso aos recursos disponíveis, como fontes de alimento e abrigo, dentro de uma área de elevada familiaridade, aumentando assim as chances de sobrevivência do indivíduo (KRAMER; CHAPMAN, 1999).

Os padrões de movimentação e tamanho do *home range* das espécies podem variar de acordo com diversos processos biológicos e ecológicos, tais como: tamanho corporal (LIU; SADOVY, 2005; FROEHLICH *et al.*, 2019), ontogenia (DAHLGREN; EGGLESTON, 2000; ORTIZ; TISSOT, 2008), comportamento social (AFONSO *et al.*, 2008a; WELSH; BELLWOOD, 2012a, 2012b); reprodução (AFONSO *et al.*, 2008b; RHODES *et al.*, 2012), competição (ABESAMIS; RUSS, 2005; Jones, 2005), variações circadianas (HITT *et al.*, 2011a, 2011b; DAVIS *et al.*, 2017), disponibilidade de recursos (p. ex., alimento e abrigo, DAHLGREN; EGGLESTON, 2000; MEYER *et al.*, 2010), risco de predação (HAMMERSCHLAG *et al.*, 2010; BOSIGER; MCCORMICK, 2014; ROOKER *et al.*, 2018) e distribuição dos habitats e estrutura da paisagem marinha (PITTMAN *et al.*, 2014; POPPLE; HUNTE, 2005).

1.2 ESTUDOS COM TELEMETRIA ACÚSTICA

A telemetria acústica, é uma tecnologia que permite coletar informações sobre o comportamento e ecologia dos animais, incluindo o rastreamento do movimento, uma das mais importantes condições prévias para as decisões de manejo (KRAMER; CHAPMAN, 1999; DI FRANCO *et al*., 2018). Além de permitir, também, entender os sinais e efeitos das mudanças nos ecossistemas, ou seja, analisar como os animais respondem aos fatores ambientais e antropogênicos. Esta técnica envolve a colocação de dispositivos eletrônicos ("transmissores" ou "tags") nos animais que transmitem dados de forma autônoma para as estações de registro (HUSSEY *et al*., 2015).

A telemetria acústica passiva utiliza um arranjo de receptores (hidrofones) omnidirecionais, fixados ao substrato, capazes de registrar ininterrupta e simultaneamente a presença de diversos indivíduos marcados dentro de um raio máximo de alcance do receptor (HEUPEL *et al*., 2006; HEUPEL; WEBBER, 2012). Cada transmissor emite um sinal codificado único possibilitando a identificação individual dos peixes marcados, e pode ainda transmitir dados como pressão, temperatura e aceleração através de sensores específicos que podem ser integrados aos transmissores. Os receptores armazenam a data e o horário no qual os sinais são captados, sendo assim possível determinar os padrões de movimentação e o período que cada indivíduo permanece na área estudada ao se analisar os registros fornecidos por todo o conjunto de receptores.

Diversos estudos têm utilizado a telemetria acústica como ferramenta para estimar e avaliar diferentes aspectos relacionados à ecologia do movimento em peixes marinhos como: fidelidade espacial e residência (Alós *et al*., 2011; MARCH *et al*., 2011; ABECASIS *et al*., 2013; HARASTI *et al*., 2015), tamanho do *home range* (ABECASIS *et al*., 2009; TOPPING and SZEDLMAYER, 2011; VILLEGAS-RÍOS *et al*., 2013), padrões diários de atividade (ALÓS *et al*., 2012; Gandra *et al*., 2018; HITT *et al*., 2011a; ROOKER *et al*., 2018), uso do habitat (ALÓS *et al*., 2011; MARCH *et al*., 2010; Marshell *et al*., 2011), eventos de mortalidade (KHAN *et al*., 2016), ontogenia (HUIJBERS *et al*., 2015), migrações sazonais e reprodutivas (ARENDT *et al*., 2001; MOULTON *et al*., 2017; FEELEY *et al*., 2018).

Um fator importante por trás do crescimento dos estudos de rastreamento de animais marinhos tem sido a necessidade de dados de distribuição e movimentação para informar a política de gerenciamento e conservação de espécies (ABECASIS *et al*., 2014, 2015; Di Lorenzo *et al*., 2016; Hays *et al*., 2019). As Áreas Marinhas Protegidas (AMPs) são áreas espacialmente delimitadas do ambiente marinho estabelecidas por razões gerais de conservação. Em 2010, a Convenção sobre Diversidade Biológica (CBD), adotou o Plano Estratégico de Biodiversidade 2011-2020, que inclui as Metas de Biodiversidade de Aichi. A Meta 11 de Aichi solicitou que 10% das áreas costeiras e marinhas fossem conservadas até 2020 através de sistemas de áreas protegidas efetivamente gerenciados, ecologicamente representativos e bem conectados, e integrados às paisagens e paisagens marinhas mais amplas (SCBD, 2010). Assim, um importante campo de estudo para avaliar esses atributos é o monitoramento remoto de organismos marinhos, incluindo o monitoramento acústico de peixes.

1.3 MOVIMENTO E EFETIVIDADE DE ÁREAS MARINHAS PROTEGIDAS

A criação de zonas marinhas de não captura ou *no-take zones* (NTZs) tem sido considerada uma das ferramentas mais eficazes na restauração e preservação da biodiversidade em ambientes de recifes de coral (HALPERN; WARNER, 2003; LESTER *et al*., 2009; EDGAR *et al*., 2014). Desde o estabelecimento das primeiras NTZs, um grande conjunto de evidências tem mostrado que essas áreas são eficazes no aumento do tamanho, abundância e biomassa dos peixes (POLUNIN; ROBERTS, 1993; GELL; ROBERTS, 2003; HALPERN, 2003), recuperando populações de espécies ameaçadas (AFONSO *et al*., 2011; ANDERSON *et al*., 2014), ajudando a restaurar a complexidade dos ecossistemas através do restabelecimento de cascatas tróficas (HARBORNE *et al*., 2008; LELEU *et al*., 2012) e promovendo um aumento geral da resiliência e complexidade dentro de seus limites (HUGHES *et al*., 2007; MICHELI *et al*., 2012; BARNETT; BASKETT, 2015).

A eficácia das NTZs para a reconstrução e conservação das populações de peixes está inerentemente ligada ao movimento de peixes que elas pretendem proteger (GREEN *et al*., 2015). Os peixes recifais são diversos e possuem sistemas sociais complexos que se modificam ao longo de seus ciclos de vida, conectando habitats e ecossistemas através de movimentos migratórios (JONES *et al*., 2010; KIMIREI *et al*., 2013). Os movimentos dos peixes, e as mudanças resultantes no uso do habitat, frequentemente ocorrem em diferentes escalas espaciais e temporais e são influenciados por uma variedade de processos ambientais, biológicos e ecológicos (DAHLGREN; EGGLESTON, 2000; ABESAMIS; RUSS, 2005; BOSIGER; MCCORMICK, 2014)

Como o uso e o movimento do habitat podem variar consideravelmente entre as espécies, os benefícios das AMPs são específicos das espécies, sendo então necessário entender o tempo e a escala de movimentos exibidos pelas espécies de interesse para prever o valor dessas medidas de conservação (GREEN *et al*. 2015). Se as NTZs forem relativamente pequenas em área ou não representarem os habitats essenciais, os movimentos regulares das espécies podem não ser totalmente englobados e os indivíduos estarão constantemente expostos a um potencial risco de mortalidade por pesca, comprometendo assim a capacidade da área protegida de promover o crescimento e a sobrevivência dos peixes dentro de seus limites (KRAMER; CHAPMAN, 1999; HALPERN; WARNER, 2003). Por outro lado, uma das principais contrapartidas esperadas das NTZs é sua capacidade de beneficiar a pesca local e a biodiversidade fora de seus limites através da exportação de adultos (*spillover*) (GOÑI *et al*., 2008; EDGAR *et al*., 2014), e assim ajudar a restaurar as capturas em uma escala local (GELL; ROBERTS, 2003; DI LORENZO *et al*., 2016). Neste contexto, o conhecimento sobre os movimentos de peixes a curto e longo prazo e os padrões de utilização do espaço é um elemento-chave para o planejamento, gerenciamento e avaliação das NTZs em ambientes recifais.

1.4 VARIAÇÕES NICTEMERAIS

As comunidades de peixes apresentam variações nictemerais, ou seja, dentro de um período de 24 horas, na composição e abundância das espécies (HOBSON, 1972; TRAVERS *et al*., 2006; AZZURRO *et al*., 2013) associadas às flutuações de intensidade luminosa entre períodos diurnos e noturnos (MCFARLAND *et al*., 1979; HOBSON *et al*., 1981; RICKEL; GENIN, 2005; SCHMITZ; WAINWRIGHT, 2011).

Para a maioria das espécies de peixes, os padrões de atividade tendem a ser diurnos, noturnos ou crepusculares, de acordo com o período em que apresentam maior atividade alimentar (HOBSON, 1965; MACFARLAND, 1991). Entretanto, variabilidades intraespecíficas nestes padrões podem ser impulsionadas por diversos fatores (REEBS, 2002), como a ontogenia (MAGNAN; FITZGERALD, 1984; ROUSSEL; BARDONNET, 1999), mudanças nas condições ambientais (por exemplo, sazonalidade, temperatura) (FRASER *et al*., 2011, 1993), e fatores biológicos como o risco de predação, disponibilidade de presas e competições intraespecíficas (FOX; BELLWOOD, 2011; KOECK *et al*., 2013; WILLIAMS-GROVE; SZEDLMAYER, 2016).

O ciclo nictemeral é um dos principais fatores ambientais que regem os padrões de atividade e de ocupação e uso dos habitats pelos peixes (MEYER *et al*., 2007; HARVEY *et al*., 2012; HONDA *et al*., 2016). O tamanho da área de *home range* e as distâncias percorridas variam entre os tipos de comportamento e períodos do dia, tais como alimentação ativa durante o dia ou repouso à noite (DAVIS *et al.*, 2017). Os padrões de atividades diários também estão relacionados aos usos diferenciais da paisagem marítima entre o dia e a noite, promovendo assim a conectividade biológica entre os habitats (HITT *et al.*, 2011a, 2011b).

Desta forma, o conhecimento sobre os padrões nictemerais de movimentação de espécies pode ter implicações importantes para o manejo e conservação das espécies e ecossistemas, assim como no desenho de redes efetivas de AMPs e no planejamento espacial marinho.

1.5 O PRESENTE ESTUDO

No presente estudo, foram utilizados levantamentos visuais e telemetria acústica passiva para investigar a densidade e os padrões de movimento de duas espécies de peixes de recifais, o bobó ou peixe-papagaio *Sparisoma axillare* (Steindachner, 1878) (Labridae) e a baúna *Lutjanus alexandrei* Moura & Lindeman, 2007 (Lutjanidae). Ambas as espécies são endêmicas da costa brasileira (MOURA et al., 2001; MOURA; LINDEMAN, 2007) e altamente visadas pelas atividades pesqueiras locais (SILVEIRA, 2018).

A área monitorada está localizada no complexo de recifes de corais de Tamandaré - Pernambuco, situado ao largo da costa nordeste do Brasil (8° 44' S, 35° 6' W), e inclui as formações recifais dentro e no entorno da Zona de Preservação da Vida Marinha de Tamandaré, uma NTZ de 2,7 km² estabelecida em 1999, na qual todas as atividades extrativistas e recreacionais são proibidas. A NTZ está situada dentro de duas grandes AMPs: a APA federal Costa dos Corais e APA estadual de Guadalupe (ambas estabelecidas em 1997), e é também o núcleo da área marinha do Parque Natural Municipal do Forte Tamandaré (estabelecido em 2003). Cerca de 30% da área da NTZ é composta por formações de recifes de coral, as quais estão concentradas no lado norte e são contíguas aos recifes não protegidos fora da NTZ. Os recifes costeiros de Tamandaré estão dispostos em um padrão de três linhas paralelas à costa, com morfologias, profundidades e coberturas de substrato característicos de cada linha (ver MAIDA; FERREIRA, 1997).

1.5.1 **Objetivo geral**

Avaliar os padrões espaço-temporais na movimentação de *S. axillare* e *L. alexandrei* utilizando telemetria acústica, e assim aferir a efetividade de proteção da área *no-take* localizada nos recifes costeiros de Tamandaré-PE.

1.5.2 Objetivos específicos

a) Realizar um levantamento bibliográfico dos artigos científicos que utilizaram telemetria acústica em peixes em áreas marinhas protegidas no mundo e no Brasil.
b) Identificar os países com maior número de publicações e os principais objetivos dos estudos selecionados pelo levantamento bibliográfico.
c) Identificar o número de espécies e indivíduos marcados, além do tempo de monitoramento nos estudos selecionados.
d) Estimar e comparar, através de censos visuais, as densidades de indivíduos de *S. axillare* e *L. alexandrei* nos recifes do interior e exterior da área *no-take* localizada em Tamandaré-PE.
e) Identificar, através da telemetria acústica, a existência de subgrupos de indivíduos espacialmente distintos dentro das populações destas espécies.
f) Estimar e comparar o índice de residência, tamanho da área de vida e tamanho da área núcleo entre as espécies e subgrupos de indivíduos.
g) Correlacionar os comprimentos totais dos peixes com os tamanhos das áreas de vida e áreas núcleo.
h) Estimar e comparar a sobreposição espacial das áreas de vida e áreas núcleo entre os subgrupos.
i) Estimar e comparar o percentual das áreas de vida e áreas núcleo inseridos no interior da área *no-take* entre as espécies e subgrupos.
j) Identificar padrões de curta escala temporal (nictemeral - 24h) na periodicidade das detecções paras as espécies.
k) Estimar e comparar o índice de residência, frequência de detecção, taxa de movimentação, tamanho da área de vida e equabilidade espacial entre os períodos diurno e noturno para ambas as espécies.
l) Identificar a existência de subgrupos de indivíduos com padrões de atividade nictemeral distintos dentro das populações
m) Estimar e comparar a sobreposição espacial das áreas de vida dos indivíduos durante os períodos diurno e noturno.

1.6 ESTRUTURA ORGANIZACIONAL DA TESE

Os resultados da tese estão apresentados em formato de três artigos científicos. No primeiro artigo, intitulado “The use of acoustic telemetry to monitor fish species in marine protected areas: a systematic review with notes on Brazilian perspectives”, é apresentada uma revisão sistemática da literatura científica relativa ao uso da telemetria acústica no monitoramento de peixes marinhos, com destaque para sua aplicação em AMPs, discutindo a expansão global, principais aplicações e os recentes avanços do método. O Brasil acaba de atingir a marca de 20% de sua Zona Econômica Exclusiva (ZEE) inserida em AMPs, portanto o uso da telemetria acústica nas AMPs brasileiras também é discutido, bem como o papel das redes de monitoramento colaborativo globais e regionais. No segundo artigo, intitulado “Use of acoustic telemetry to evaluate fish movement, habitat use, and protection effectiveness of a coral reef no-take zone in Brazil”, levantamentos visuais e telemetria acústica foram empregados para investigar a densidade e os padrões de movimentação de duas espécies de peixes recifais, o peixe-papagaio *S. axillare* e a baúna *L. alexandrei*, em uma NTZ recifal. Os principais objetivos deste estudo foram estimar a residência, o movimento e o *home range* de ambas as espécies, para estimar a eficácia da proteção fornecida pela NTZ para estas espécies. No terceiro artigo, intitulado “Diel activity and habitat utilization by two reef fish species within a marine protected area in Brazil”, a telemetria acústica é utilizada para investigar a variabilidade nictemeral nos padrões de atividade das espécies alvo do estudo. Os peixes-papagaio são espécies tipicamente diurnas que forrageiam ativamente durante o dia e procuram abrigo à noite. Por outro lado, peixes do gênero *Lutjanus* são geralmente classificados como predadores noturnos, que permanecem abrigados em habitats de alta complexidade estrutural, como recifes, durante o dia e que se dispersam entre o recife e o fundo de areia adjacente para se alimentar à noite.

2 ARTIGO 1 – THE USE OF ACOUSTIC TELEMETRY TO MONITOR FISH SPECIES IN MARINE PROTECTED AREAS: A SYSTEMATIC REVIEW WITH NOTES ON BRAZILIAN PERSPECTIVES

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ABSTRACT

Inferring pathways used by organisms within ecosystems is essential to the design, management, and evaluation of Marine Protected Areas (MPAs). This study aimed to present a systematic review on the literature regarding the use of acoustic telemetry to monitor marine fish movement and its application on MPAs. Searches were conducted on electronic databases. The first studies using telemetry on marine fish date back to the 60's, while application on MPAs only appeared 30 years later. However, over the last decade, studies in MPAs accounted for 20% of the overall acoustic telemetry publications on marine fish species. Recent technological development has had an important impact on those results. The number of studies inside MPAs followed the number of general studies and coverage areas of MPAs declared around the world, although frequency of studies did not match MPA coverage in some countries. Developed countries scored more studies, probably due to the relative high cost of acoustic telemetry. Studies in Brazilian MPAs are scarce, with only one study available on elasmobranchs. Brazil has recently increased its MPA coverage to 26%, so it is expected to increase the need for MPA effectiveness studies. Brazilian participation on global tracking networks may help filling this gap.

Keywords: fish movement, remote monitoring, MPA effectiveness, tracking networks.

RESUMO

O estudo da movimentação animal nos ecossistemas é uma importante ferramenta para a criação, manejo e avaliação de Áreas Marinhas Protegidas (AMPs). Este trabalho objetivou apresentar uma revisão bibliográfica sistemática na literatura científica abordando o uso de telemetria acústica para monitorar a movimentação de peixes e sua aplicação em AMPs. Para isso, foram realizadas pesquisas em bases de dados eletrônicas. Os primeiros estudos usando telemetria acústica em peixes datam da década de 60, porém esta técnica só foi aplicada em AMPs 30 anos depois. Na última década, estudos em AMPs representaram 20% do total de publicações com telemetria acústica com peixes em ambientes marinhos. O desenvolvimento tecnológico recente teve um importante impacto nestes resultados. O aumento no número de estudos realizado em AMPs foi congruente com o crescente número de estudos gerais de telemetria e com o aumento em áreas declaradas como AMPs globalmente. No entanto, não foi observada relação entre a frequência de estudos e a cobertura de AMP em alguns países. Países desenvolvidos produziram mais estudos, provavelmente devido ao alto custo da telemetria acústica. Estudos no Brasil foram escassos, com apenas um estudo em elasmobrânquios. Recentemente, o Brasil elevou sua cobertura marinha protegida para 26%, portanto, espera-se que isso impulsione estudos avaliando a efetividade de AMPs e que a participação brasileira em redes globais de telemetria ajude a preencher esta lacuna.

Palavras-chave: movimento de peixes, sensoriamento remoto, efetividade de AMPs, redes de telemetria

INTRODUCTION

Movement is a key factor that shapes several aspects of fish behavior such as habitat use, home range size, reproduction, and diel and seasonal activity patterns, (MARSHELL *et al*., 2011; LEE *et al*., 2015; DI LORENZO *et al*., 2016; GANDRA *et al*., 2018) and therefore, influences the dynamics, structure, and distribution patterns of fish populations. Telemetry, i.e., the remote measurement of biological variables, a technology that allows gathering information on the biology and behavior of the animals, including movement tracking, one of the most important preconditions for management decisions (SPEDICATO *et al*., 2005). It involves placing electronic devices (“transmitters” or “tags”) on animals that autonomously transmit data to data logging or relay-receiving stations (HUSSEY *et al*., 2015).

One important driver behind growth in marine animal tracking studies has been the need for distribution and movement data to inform conservation policy and management (HAYS *et al.*, 2019). Marine Protected Areas (MPAs) are spatially delimited areas of the marine environment that are established for general conservation reasons, but expectations often include increased fishery catches in adjacent areas (EDGAR *et al.*, 2007). In 2010, the Convention on Biological Diversity (CBD), adopted the Strategic Plan for Biodiversity 2011-2020, which includes Aichi Biodiversity Targets. Aichi Target 11 called for 10% of coastal and marine areas to be conserved by 2020 through effectively managed, ecologically representative, and well-connected systems of protected areas, and integrated into the wider landscapes and seascapes (SCBD, 2010). Thus, one important field of study to assess those attributes is the remote monitoring of marine organisms, including fish.

The present study aimed to present a systematic review on the scientific literature concerning the use of acoustic telemetry to monitor fish movement and its application on the design and assessment of MPAs, discussing the global expansion and recent advancements of the method. Brazil has just reached the mark of 20% of its Exclusive Economic Zone (EEZ) under a designated MPA (SOARES; LUCAS, 2018), therefore the use of acoustic telemetry as a tool in Brazilian MPAs is also discussed as well as the role of global and regional collaborative tracking networks.

MATERIALS AND METHODS

In October 2020, two searches were conducted on electronic databases (Web of Science and SCOPUS) to identify the up-to-date relevant scientific literature on the use of acoustic telemetry to monitor fish species in marine or estuarine environments (Search 1) and specifically in marine protected areas (Search 2). Searches were conducted on the fields Title, Abstract and Author’s keywords, and only articles published in English language were selected. The terms used on both searches are presented in Table I.

Search 1 returned a total of 1,203 publications after removals of duplicates. The article’s titles, abstracts and keywords were then screened, and 897 studies remained for analysis. For the Search 2, the systematic review followed the steps defined in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (MOHER *et al.*, 2009) (Figure 1). Articles were filtered for the quantitative analysis based on the following exclusion criteria: the study (I) addressed species other than fish (e.g., cuttlefish), (II) were not conducted in already implemented or designated (with well-established borders) marine protected areas and (III) evaluated MPA effectiveness based on simulation models. For each eligible article (N = 157) the following data were compiled: year of publication, study location (country or territory), main objective, habitat type, species, number of tagged fish, overall duration of the study, application of other field methods (e.g., satellite tracking, mark-recapture) and partnership with tracking networks. Additionally, information on the size of implemented or designated MPAs for the countries listed in the articles were obtained from the Marine Protection Atlas website (MPAtlas.org, 2020).

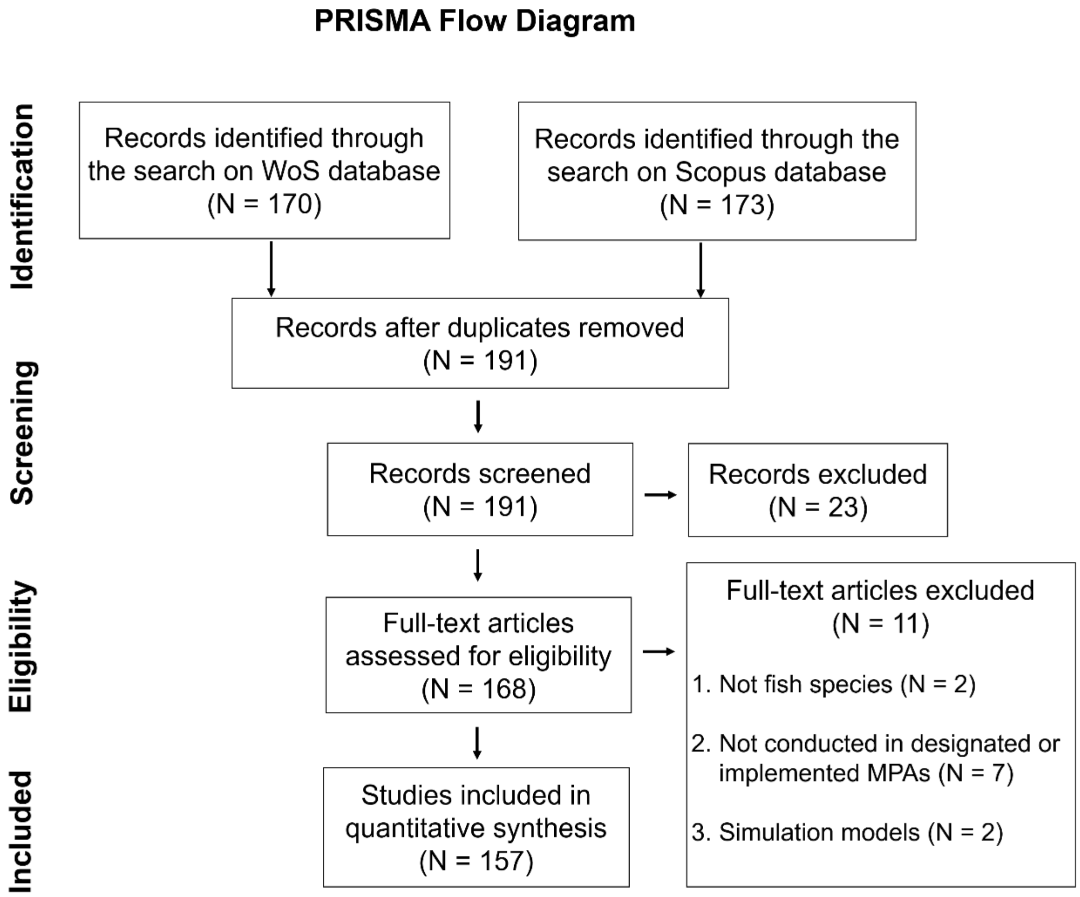
Table 1 – Combination of terms used on the two searches performed on the Web of Science and Scopus databases. Searches were conducted on Title, Abstract and Author's keywords fields.

Search 1: acoustic telemetry on fish species in marine and estuarine environments
(acoustic OR ultrasonic OR sonic)
AND
(telemetry OR tracking OR tagging)
AND
(fish OR fishes OR shark* OR ray* OR elasmobranch* OR salmon* OR trout* OR eel* OR grouper* OR cod* OR catfish* OR bass)
NOT
(freshwater OR river* OR lake* OR dam* OR stream* OR hydroelectric* OR reservoir*

Search 2: acoustic telemetry on fish species in marine protected areas
(acoustic OR ultrasonic OR sonic)
AND
(telemetry OR tracking OR tagging)
AND
(fish OR fishes OR shark* OR ray* OR elasmobranch* OR salmon* OR trout* OR eel* OR grouper* OR cod* OR catfish* OR bass)
AND
mpa OR marine protected area* OR marine reserve* OR marine park* OR marine sanctuary

Fonte: O Autor

Figure 1 - PRISMA flow diagram for systematic review, including sample sizes and exclusion criteria.



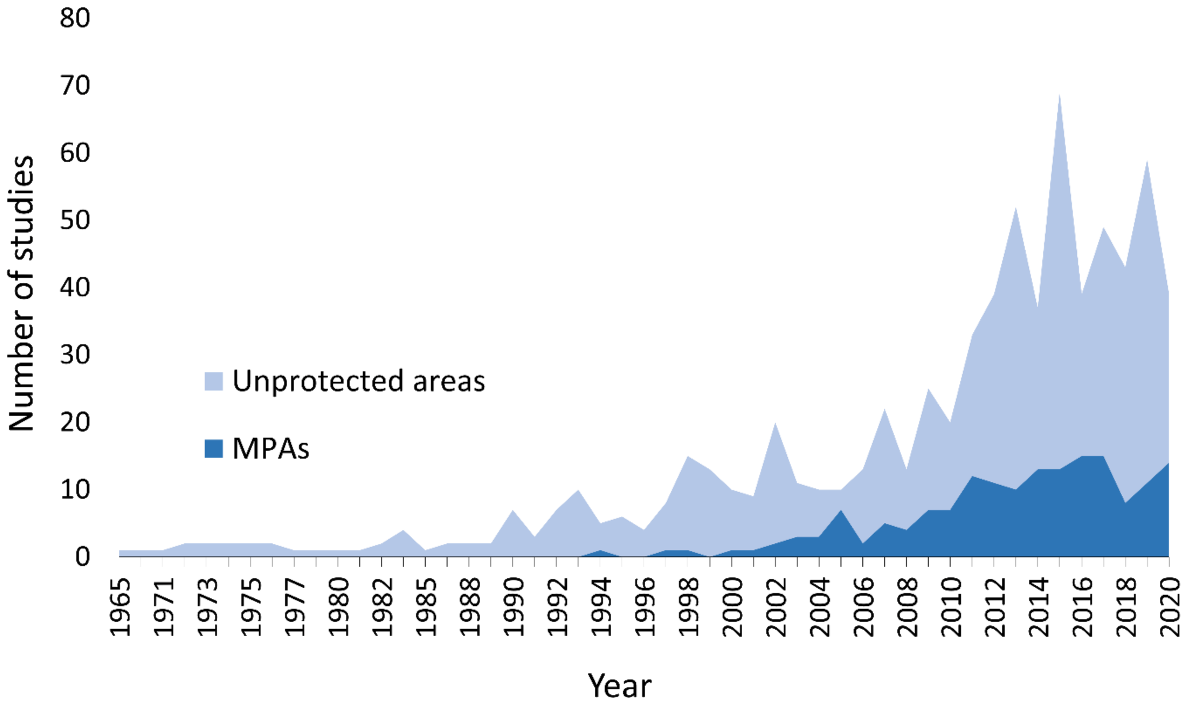
Fonte: O Autor

RESULTS

Studies using acoustic telemetry on fish species in marine or estuarine environments (Search 1, n = 897) were first published in the 1960's. The number of studies remained relatively low for the following decades (1965 – 1989) (Figure 2) with an average of less than 2 publications per year. During the 1990's, the number of publications increased fourfold (8 publications/year) and has been growing exponentially over the last decades: 2000-2009 (18 publications/year) and 2010-2020 (55 publications/year).

Studies reporting the use of acoustic telemetry to monitor fish species inside MPAs (Search 2, n = 157) were first published in the 1990's (Figure 2). Since then, the number of publications has increased from 3.4 per year (2000-2009) to 11 publications per year (2010-2020). All the results presented hereafter refer exclusively to the publications yielded by the second search, that is, the ones related to MPAs.

Figure 2 – Increase in the number of acoustic telemetry studies conducted on fish species in marine and estuarine environments (Search 1, light blue) and specifically in marine protected areas (MPAs) (Search 2, dark blue) since 1965.

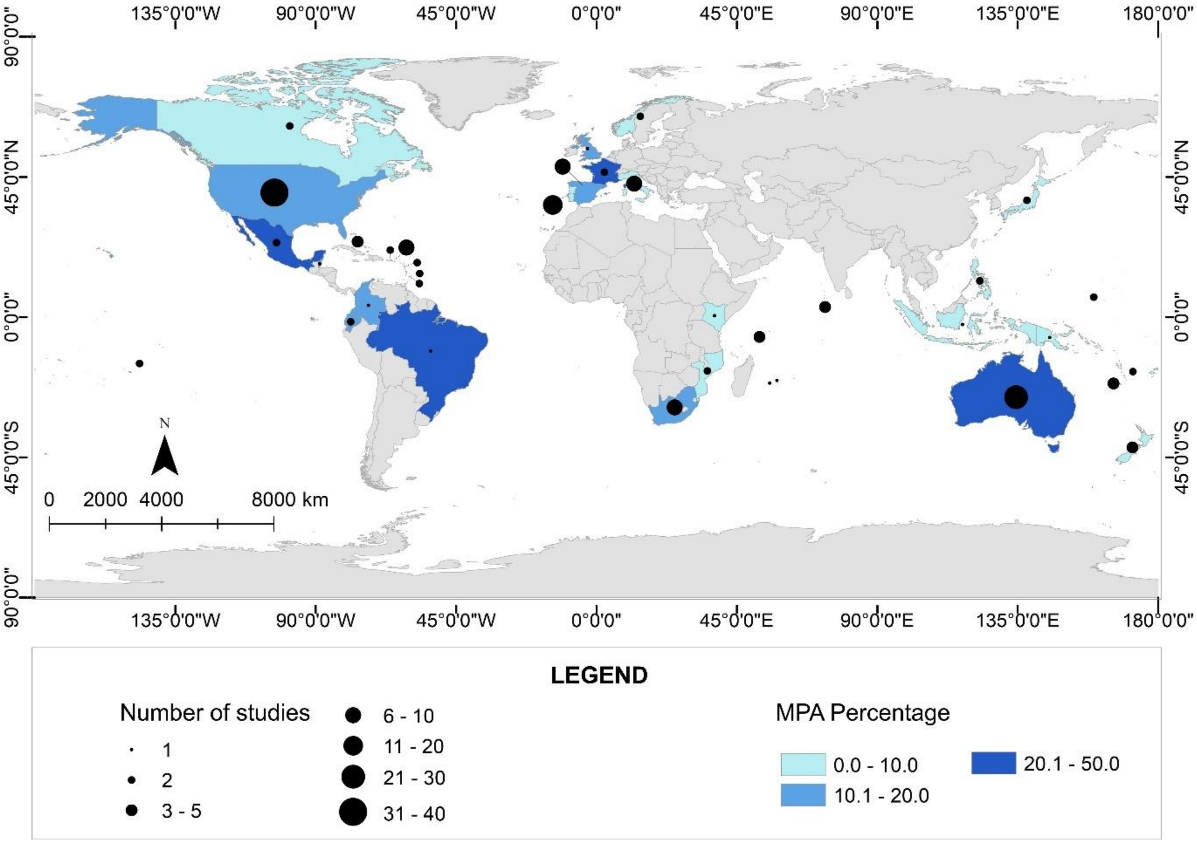


Fonte: O Autor

The found MPAs were located in 36 countries and territories. Three countries were responsible for 55% of the studies: United States of America (national waters and overseas territories; 28.5%, N = 45), Australia (19%, N = 29) and Portugal (7.5%, N = 12), whereas two-thirds of the countries published only one or two studies (Figure 3). There was no correspondence between the percentage of MPAs (relative to the area of the EEZ of each country) and number of studies. While countries with low percentage of MPAs (e.g., Portugal, Italy, and Spain) have a relatively high number of publications, other countries such as Brazil, Mexico and France have low numbers of studies despite the high percentage of their EEZ designated as MPAs.

Regarding the type of habitat covered by the MPAs, the majority of studies were conducted on coral or rocky reef habitats (73.2%, N = 115), followed by fewer studies (10.2%) on unconsolidated substrate areas (*e.g.*, seagrass or macroalgae beds, sand/mud bays and estuaries), mixed habitats (10.2%) (*i.e.*, mostly coral/rocky reefs associated to seagrass, sand or mangroves), open ocean, submerged banks or seamounts (3.8%) and fjords or sounds (2.6%). A total of 140 fish species (31 chondrichthyan and 109 teleost species) were acoustically monitored inside MPAs. The most studied families in terms of both number of studies and species were: Epinephelidae (28 studies and 17 spp.), Carcharhinidae (25 studies and 12 spp.), Sparidae (21 studies and 10 spp.), Lutjanidae (19 studies and 13 spp.) and Labridae (17 studies and 15 spp.). Many species (20%) are under some level of threat, according to the criteria adopted by the international Union for conservation of Nature's Red List of Threatened Species – IUCN red list (Critically Endangered = 3 spp., Endangered = 3 spp. or Vulnerable = 22 spp.), whereas some others are classified as Near Threatened (11.5%, 16 spp.), Least concern (57.8%, 81 spp.), Data Deficient (5.7%, 8 spp.) and Not Evaluated (5%, 7 spp.).

Figure 3 – Global map showing the locations (countries or territories) where the studies using acoustic telemetry on fish species were conducted in marine protected areas (MPAs). Shades of blue (light blue to dark blue) indicate the percentage of each country's Exclusive Economic Zone covered by MPAs. The number of studies is proportional to the black circle's size. Three territories (not distinguishable on the map) had more than 50% of theirs EEZ covered by MPAs: Martinique (99.7%), Chagos Archipelago (98.02%), and New Caledonia (94.25%). Data source information: Coordinate System GCS WGS 1984; units: Degrees; datum: WGS 1984.

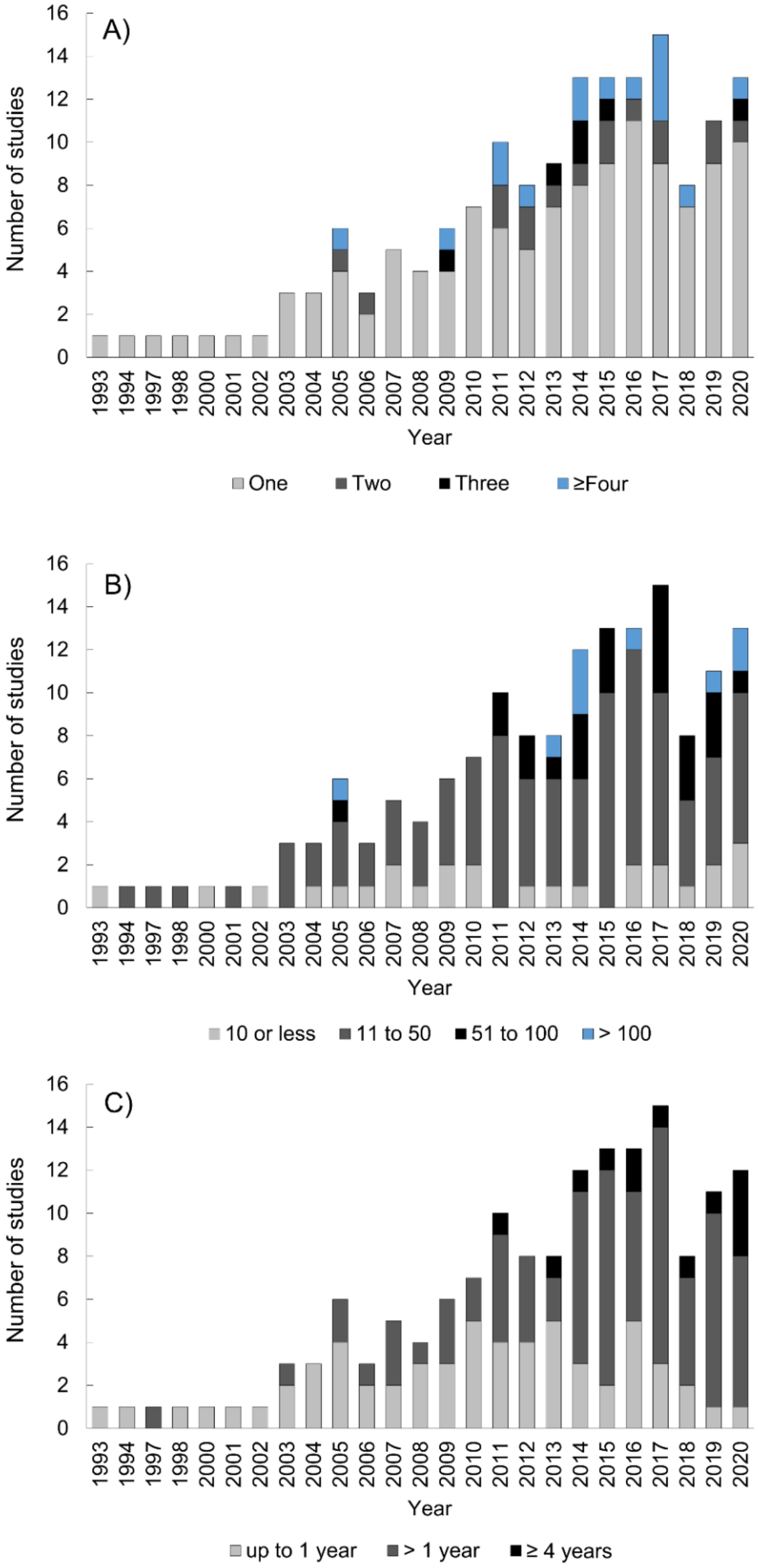


Fonte: O Autor

Acoustic telemetry has been mainly used as a tool to evaluate the protection effectiveness afforded by the MPAs to fish populations (55.4%, N = 87) as well as to investigate spatial and temporal aspects of fish behavior (38.2%, N = 60). The majority of studies were performed in (or included) no-take zones (112 out of 157). Fewer studies (3.8%) focused on the assessment of specific human impacts (e.g., feeding activity and fishing mortality), on the development of analytical methods (2%), and tag retention time (0.6%). In most cases, studies were conducted on a single species at a time (76.4%, N = 120), with less studies tagging simultaneously two (10.2%), three (3.8%) or four or more species (9.6%). Although less numerous, the number of studies with a multi-specific approach has increased over the past decade (Figure 4-A). A recent increase in the number of tagged individuals per study (Figure 4-B) and in the overall duration of the studies (Figure 4-C) was also observed.

Among the studies analyzed, 18 (11.5%) were part of a regional or global tracking network: the Integrated Marine Observatory System (IMOS) in Australia (n = 13), the Acoustic Tracking Array Platform (ATAP) in South Africa (n = 2), the Ocean Tracking Network FACT node (Florida Atlantic Coast Telemetry Network) (n = 2) and the US Caribbean Acoustic Network USCAN (n =1).

Figure 4 – Number of published acoustic telemetry studies per year in relation to the: (A) Number of tagged species, (B) Number of tagged individuals and (C) Duration of the studies.



Fonte: O Autor (2021)

DISCUSSION

The onset of studies in acoustic telemetry on fish species in marine or estuarine environments was in the 1960's (BASS; RASCOVICH, 1965). In subsequent decades, the number of studies remained low, experiencing an accelerated growth in the two last decades. Indeed, in recent decades, technological developments in miniaturization (MARCH *et al*., 2011), battery engineering and hard and software development have enabled this development and the monitoring of aquatic organisms in a multitude of environments (HUSSEY *et al*., 2015).

However, studies using acoustic telemetry inside marine protected areas (MPAs) only started three decades later, in the 1990's (HOLLAND *et al*., 1993), following the increase in the coverage area by MPAs declared worldwide (WORM, 2017; O'LEARY *et al*., 2018). During the last decade, studies in MPAs accounted for 20% of the total number of published studies using fish acoustic telemetry in marine or estuarine environments.

The geographic distribution of those studies, however, was uneven. Although studies in MPAs were distributed across several countries and territories, three developed countries (United States of America, Australia, and Portugal) concentrated 55% of the studies. The high number of studies in MPAs did not match the relative total area of MPAs of those countries either, as the three added covered only 28.4% of MPA area in the world: US (13.9%), Australia (14.2%) and Portugal (0.3%) (MPAtlas.org, 2020). Indeed, countries with lower MPA areas (e.g., Portugal, Italy, and Spain) had a higher number of studies in their MPAs in comparison with developing countries such as Brazil and Mexico, that showed a low number of studies despite the high percentage of their EEZ designated as MPAs. This difference is possibly related to the relative high cost of those studies, that even with technological improvements, remain expensive and limited to few manufactures located in developed countries (GARCIA *et al*., 2014; HELLSTRÖM *et al*., 2016).

It was observed that the main objective of the studies conducted on MPAs was to evaluate the protection effectiveness afforded to fish populations and most of them were performed in (or included) no-take zones. A high percentage of studies were concentrated on coral or rocky reef habitats, probably as those habitats typically harbor more territorial species (SALE, 2002; BURGER; GOCHFELD, 2001), thus allowing for most cost-effective designs, and have shown positive effects deriving from MPA establishment (STENECK *et al*, 2018). Accordingly, the majority of studied families of bony fish in terms of both number of studies and species, were reef associated (e.g. groupers, snappers, and parrotfishes) (LA MESA *et* *al*., 2012; GARCIA *et al*., 2014; KENDALL *et al*., 2017). In addition, 20% of the species were under some level of threat according to IUCN Red List criteria, indicating that those status make studies even more necessary (AFONSO *et al*., 2011; DALY *et al*., 2020).

Another interesting finding was the increase, in the last decade, of the number of studies with a multi-specific approach. This application is especially important for studies dealing with the design and spatial effectiveness of MPAs. Data from acoustic telemetry show the overlap in the spatial occupation of prey and predator species, aggregations and movement of threatened species, essential information for marine spatial planning (HUSSEY *et al*., 2015). Another finding was the increase in the duration of the tracking period, also derived from technology improvement, and allowing for studies to encompass a significant period of life of individuals (PITTMAN *et al*., 2014).

In the last decade there was also an increase in the establishment of acoustic tracking networks, with the first study on MPAs, as part of a network, published in 2011 (FIELD *et al*. 2011). Since then, 18 studies were published as a result of regional or international partnerships. Two countries that concentrated the higher number of studies, US and Australia, also concentrated the networks cited. In Brazil, in spite of the still low number of published studies to date, a tracking network was created as part of the Ocean Tracking Network (OTN), a Canadian based initiative that aims to form a global partnership that documents the movement and survival of aquatic animals to both understand how these populations are being influenced by changing environmental conditions and to support their sustainable management (IVERSON *et al*., 2019).

Indeed, Brazil in spite of the higher percentage of MPAs (26% of EEZ, although only 3.3% are considered fully or highly protected) (SOARES; LUCAS, 2018) had only one study applying fish acoustic telemetry inside a MPA identified in the Search 2, out of the five studies detected for Brazil in Search 1. The study assessed the activity patterns of sharks inside the Marine Park of Fernando de Noronha (GARLA *et al*., 2017). In addition, another study on rays on the Saint Peter and Saint Paul Archipelago was identified (MENDONÇA *et al*., 2018). However, at the time of the study, the area had not yet been declared a protected area, and no mention was made to MPA in the study, so it was not added to the survey. It is worth mentioning that since 2018 the region has become a MPA (SOARES; LUCAS, 2018). Also, two other acoustic telemetry studies conducted on elasmobranchs species inside Brazilian MPAs (GARLA *et al*., 2006; WETHERBEE *et al*., 2007) were not identified on both searches as the surveyed terms (i.e., acoustic* OR sonic* OR ultrasonic*) were not mentioned on the articles' researched fields (title, abstract and author's keywords).

In Brazil, effectiveness of MPAs in terms of increase in the abundance and biomass of fish inside its boundaries has been relatively well documented (FLOETER *et al*., 2006; PRATES *et al*., 2007; ANDERSON *et al*., 2014), but reports on benefits through spillover to adjacent areas and effectiveness in terms of biodiversity protection and fisheries benefits are scarce. Also, connectivity of Brazilian MPAs through larval dispersion has been discussed (ENDO *et al*., 2019), as well as its implication on the design of a representative MPA system (MAGRIS *et al*., 2020).

The present study has shown that acoustic telemetry, as an effective technique to study fish movement, has been applied in the assessment of MPAs worldwide. In spite of comparatively high costs in relation to other techniques (e.g., UVC, mark-recapture and larval dispersal modelling) the results are unique and can also show direct benefits for adjacent areas (REYIER *et al*., 2020). Moreover, considering the impacts in marine habitats caused by human actions, including climate change, acoustic telemetry arises as an important tool in inferring and predicting how organisms and communities rearrange themselves when faced with environmental changes (HUSSEY *et al*., 2015).

Brazil still has a low number of studies in marine acoustic telemetry in general, with most of them addressing elasmobranchs species (FERREIRA *et al*., 2013; AFONSO; HAZIN, 2014; MENDONÇA *et al*., 2018) and only one study regarding bony fishes (PINHEIRO *et al*., 2018). So, in order to boost such kind of studies, a partnership with an international acoustic tracking network was established in 2015 (IVERSON *et al*., 2019; PINHEIRO *et al*., 2018) aiming mutual benefits among partners, through national and international data interchange and collaboration. In that sense, it is expected that incentives for MPA effectiveness studies and Brazilian participation on networks may help to fill this gap.

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3 ARTIGO 2 – USE OF ACOUSTIC TELEMETRY TO EVALUATE FISH MOVEMENT, HABITAT USE, AND PROTECTION EFFECTIVENESS OF A CORAL REEF NO-TAKE ZONE IN BRAZIL

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ABSTRACT: Movement is a key factor that shapes the distribution and structure of fish populations and influences the extent of the benefits provided by conservation and management measures, such as the implementation of marine no-take zones (NTZs). In the present study we used visual surveys and acoustic telemetry to investigate density and movement of two Brazilian endemic and highly targeted reef fish species inside and outside a coral reef NTZ, and subsequently infer the effectiveness of the NTZ for protecting these species. To do so, we conducted visual surveys on protected and unprotected reefs between 2016 and 2017. Moreover, we tagged 20 gray parrotfish *Sparisoma axillare* and 9 Brazilian snapper *Lutjanus alexandrei* with acoustic transmitters and passively monitored them from December 2016 to October 2017. For both species, fish densities were significantly higher within the NTZ. Also, both species presented high residence index (RI) on the short-term, indicating they were full-time residents to the monitored area until detections were permanently lost. The absence of detections may indicate relocation to deeper reefs, predation, or fishing mortality when fish left the NTZ. Home ranges (HR) were small (0.10 to 0.45 km²) and both species presented spatially segregated subgroups within the populations. On average, the percentage of HR within the NTZ was 88% for *S. axillare* and 95% for *L. alexandrei*. Our results showed that small NTZs that harbor part of target species life cycle are an effective measure to conserve reef fish populations, and also highlighted the importance of fisheries management outside NTZs.

Keywords: Acoustic monitoring. Marine protected area. Parrotfish. Snapper. Home range. Spatial ecology. Reserve effect.

INTRODUCTION

The creation of marine no-take zones (NTZs) has been considered one of the most effective tools in restoring and preserving biodiversity on coral reefs environments (HALPERN; WARNER, 2003; LESTER *et al*., 2009; EDGAR *et al*., 2014). Since the establishment of the first NTZs, a large body of evidence has shown that those areas are effective in increasing fish size, abundance, and biomass (POLUNIN; ROBERTS, 1993; GELL and ROBERTS, 2003; HALPERN, 2003), recovering endangered species populations (AFONSO *et al*., 2011; ANDERSON *et al*., 2014), helping to restore the complexity of ecosystems through reestablishment of trophic cascades (HARBORNE *et al*., 2008; LELEU *et al*., 2012) and promoting an overall increase in resilience and complexity within their boundaries (HUGHES *et al*., 2007; MICHELI *et al*., 2012; BARNETT and BASKETT, 2015).

Effectiveness of NTZs for rebuilding and conserving fish populations is inherently linked to the movement of fishes that they are intended to safeguard (GREEN *et al*. 2015). Reef fish are diverse and have complex social systems that evolve during their life cycles, connecting habitats and ecosystems through migratory movements (JONES *et al*., 2010; KIMIREI *et al*., 2013). Fish movements and resulting changes in habitat use often occur at different spatial and temporal scales, and these dispersive behaviors are influenced by a variety of biological and ecological processes including ontogeny (DAHLGREN; EGGLESTON, 2000), reproduction (AFONSO *et al*., 2008; RHODES *et al*., 2012), competition (ABESAMIS; RUSS, 2005), predation (BOSIGER; MCCORMICK, 2014; ROOKER *et al*., 2018), and resource availability (MEYER *et al*., 2000).

Because habitat use and movement may vary considerably among species, benefits of Marine Protected Areas (MPAs) are species specific and understanding the timing and degree of movements displayed by species of interest is needed to predict the value of these conservation measures (GREEN *et al*. 2015). If NTZs are relatively small in area or unrepresentative of essential habitats, regular movements of species may not be totally encompassed, and individuals will be constantly exposed to a potential risk of fishing mortality, thus compromising the ability of the protected area to promote fish growth and survival within its limits (KRAMER; CHAPMAN, 1999; HALPERN; WARNER, 2003). On the other hand, one of the main trade-offs expected from NTZs is their ability to enhance local fisheries and biodiversity outside their boundaries through spillover, and thus help to restore lost catches and fishing areas from previous degradation and from exclusion of fishing territories (GELL; ROBERTS, 2003; DI LORENZO *et al.*, 2016). In this context, knowledge on fish short- and long-term movement and site-utilization patterns is a key element to the design, management, and evaluation of coral reef NTZs.

Passive acoustic telemetry allows the continuous and simultaneous tracking of individuals within a monitored area over different time scales (TOPPING *et al.* 2005; HEUPEL *et al.* 2006), and the approach has been commonly used to assess NTZs effectiveness (e.g., DI FRANCO *et al.*, 2018; LEA *et al.*, 2016) by evaluating different aspects of fish movement ecology as site fidelity (ABECASIS; ERZINI 2008; MEYER *et al.* 2010; HARASTI *et al.* 2015), residency (MARCH *et al.* 2011; ABECASIS *et al.* 2013), home range size (TOPPING; SZEDLMAYER 2011; VILLEGAS-RÍOS *et al.* 2013; GARCIA *et al.* 2014), habitat preference (MARCH *et al.* 2010; ALÓS *et al.* 2011; MARSHELL *et al.* 2011; ROOKER *et al.* 2018), mortality events (KHAN *et al.*, 2016; TICKLER *et al.*, 2019), and reproductive and ontogenetic migrations (RHODES *et al.*, 2012; HUIJBERS *et al.*, 2015; NANAMI *et al.*, 2018).

In the present study, visual surveys and passive acoustic telemetry were used to investigate density and movement patterns of two Brazilian endemic and highly targeted by local fisheries coral reef fish species, gray parrotfish *Sparisoma axillare* (Steindachner, 1878) (Labridae) and Brazilian snapper *Lutjanus alexandrei* Moura & Lindeman, 2007 (Lutjanidae), within a coral reef NTZ, in Brazil. The primary goals of this study were to estimate residency, movement patterns, and home range to assess the effectiveness of the current NTZ for protecting these species.

MATERIALS AND METHODS

Study area

The monitored area was located on the Tamandaré coral reef complex off Pernambuco state coast, in the northeast of Brazil (8° 44’ S, 35° 6’ W), and included the main reef formations inside and around a 2.7km² well-enforced no-take zone (NTZ) established in 1999 (Figure 1). The NTZ is situated within two larger multiple-use marine protected areas (MPAs): the Coral Coast MPA and the Guadalupe MPA (both established in 1997) and is also the core of the marine area of the Municipal Natural Park of Tamandaré Fort (established in 2003). About 30% of the NTZ area is covered by coral reef formations, which are mostly located on its north side and are contiguous to the reefs outside the NTZ. The establishment of other NTZs is part of the management strategy of the large Coral Coast MPA, and after the establishment of this first zone, other three zones have been created in other municipalities.

Four distinct reef areas comprised the seascape within the NTZ:

(1) scattered patch reefs (SPR) – low relief shallow zone (depth range: 1 - 3 m), reefs are surrounded by broad sand areas;

(2) aggregated patch reefs (APR) – reefs are clustered, separated by narrow sand corridors distributed over a deeper area (8 m deep and reefs grow up to 7 m high) that becomes shallower towards north and outside the no-take zone (3 m deep and reef tops may reach the surface);

(3) single unit reef (SUR) – represented by a high complexity and relatively isolated single unit reef structure, composed by an eroded reef top exposed during low tide. On the leeward side, overhanging ledges shade the systems of interconnected caves that open on the windward side to a spur-and-groove system. A wide and shallow (1 – 2 m) enclosed lagoon is also present on the southern side. Depth ranges from 4 m on the leeward side (back reef) to 12 m on the windward side;

(4) barrier reef (BR) – consisting of elongated reef formation which is subjected to stronger wave action. Southward inside the NTZ, the reef top is deeper (6 m) with an irregular surface composed of boulders and crevices. Depth drops towards the northern border and outside the no-take zone the reef top is flattened and shallower (up to 3 m deep). Eastward, beyond the last line of receivers, depth increases continuously up to 8 m.

Reef fish surveys

Visual fish surveys using belt transects of 100 m^2 (5 m wide by 20 m long) were used to compare fish density and size composition for the two target species. During surveys, S. *axillare* and *L. alexandrei* individuals were identified, counted, and total length was estimated and recorded by trained divers. A minimum of four replicates transects were performed at each diving site, with no sampling taking place when underwater visibility was lower than 4 m. A total of 314 transects were conducted during two consecutive dry seasons (January to April 2016 and September 2016 to March 2017). A total of 130 transects were conducted within the NTZ, corresponding to the SUR area (NTZ1 = 98 transects) and patch reefs area (SPR and APR areas, NTZ2 = 32 transects). Visual surveys outside the NTZ totaled 184 transects and were performed on the reefs located beyond the southern (SZ = 48 transects) and northern (NZ1 = 74 and NZ2 = 62 transects) borders of the NTZ (Figure 1).

Acoustic monitoring system

From December 2016 to August 2018, an array of 17 omnidirectional acoustic monitoring receivers (VR2W-69kHz, VEMCO) were used to monitor the movements and habitat use of *S. axillare* and *L. alexandrei* tagged individuals (Figure 1). Preliminary range tests conducted inside the NTZ demonstrated that, in addition to distance between receivers and transmitters, tide level also had a negative effect on detection probability. A minimum detection rate of 50% was obtained for transmitters at 150 m of distance and therefore this range was used as a guideline to design the array. At 300 m, average detection probability dropped to below 5% during high tide hours (GIACALONE *et al*., 2016).

In most cases, receivers positioning allowed for overlapping detection ranges and the total area covered by the array was approximately 1 km², including more than 80% of the reef area within the NTZ and the reef formations adjacent to its northern border. To identify fish movement from within the NTZ to unprotected areas, 3 receivers were placed outside the NTZ, on the reef continuum beyond its northern boundary. Depth inside the monitored area ranged from 1 to 12 meters.

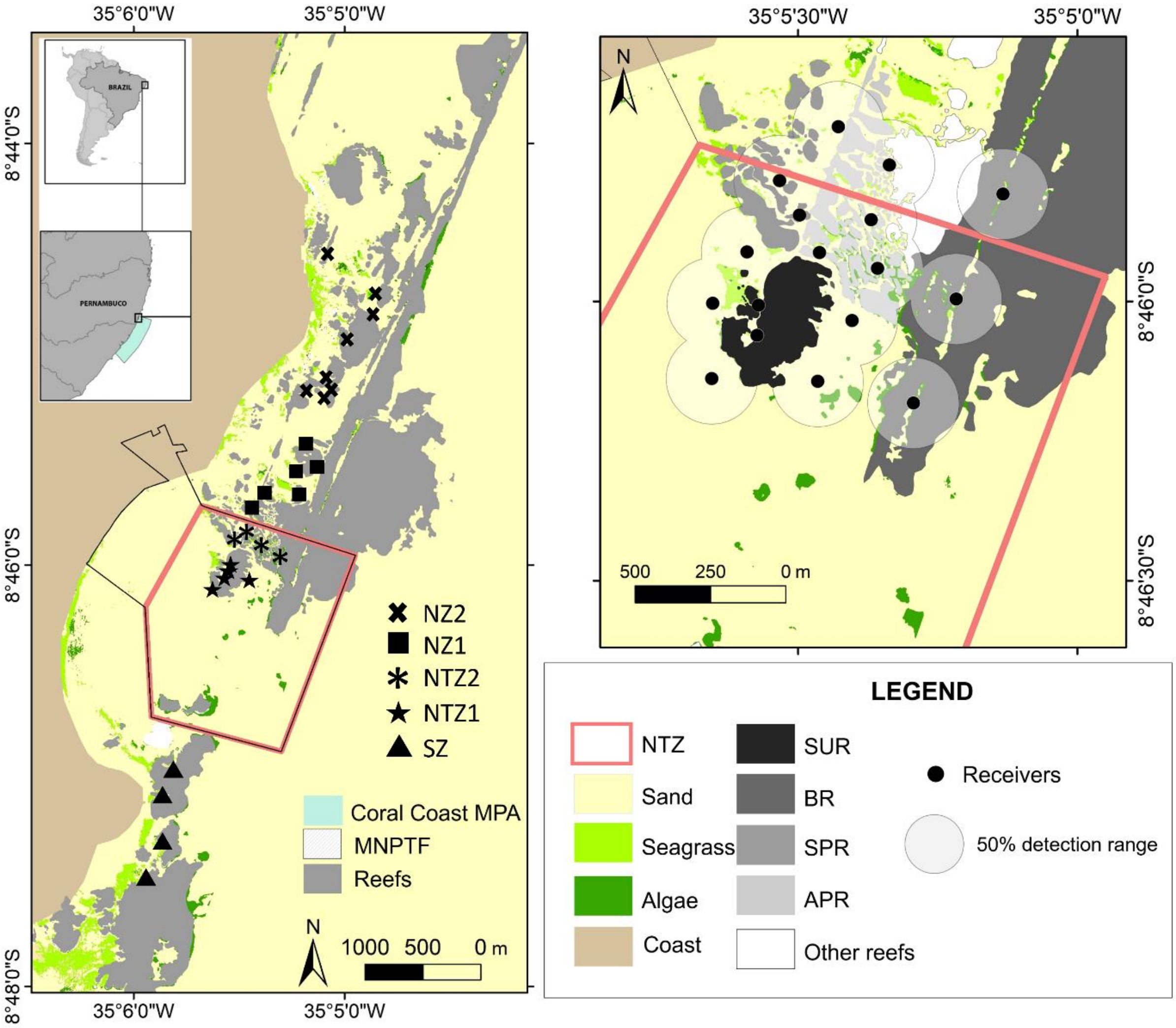
As reef tops may be exposed (or just below the surface) during low tide, receivers were placed over the sandy bottom around the reefs, moored in a PVC pipe attached to a concrete base to ensure vertical positioning and avoid dragging. Data downloads, battery checks and clearing of fouling organisms took place every 1-2 months. One receiver located at the southernmost part of the BR reefs (Figure 1) was lost during the 2017 winter due to severe sea conditions.

Fish collection and tagging

From December 2016 to May 2017, 20 gray parrotfish, *S. axillare* and 9 Brazilian snappers, *L. alexandrei* were caught and tagged. All fish were caught exclusively inside the NTZ (Figure 1). To reduce possible school influence on parrotfish behavior (WELSH; BELLWOOD, 2012a) and better represent the local population, collections of *S. axillare* were equally distributed among reef areas (5 individuals per area). For *L. alexandrei,* fish were captured in the SUR (n = 5), SPR (n = 3) and APR (n = 1) areas.

Individuals were caught with hand nets by SCUBA divers, during the night period, when fish were either “sleeping” (*S. axillare*) and/or with reduced flight capability (*L. alexandrei*). This way, impact was minimized, as only fish from the target species and with a desirable body size were caught. This collection method reduced the disturbance to the local fish community and the risk of injury caused by fishing gears. Individuals were transported to a research facility on land and kept in 1,000 L holding tanks with direct seawater and monitored for 24 hours prior to tag implantation.

Figure 1 – Map of the study area in the Tamandaré coral reef complex off the northeast coast of Brazil. Left panel: locations of the Coral Coast MPA, Municipal Natural Park of Tamandaré Fort (MNPTF) and the NTZ. It is also shown where the fish surveys were conducted at the different reef zones: South zone (SZ, triangles), No-take zone 1 (NTZ1, stars), No-take zone 2 (NTZ2, asterisks), North zone 1 (NZ1, squares) and North zone 2 (NZ2, crosses). Right panel: locations of the acoustic receivers (black dots) and 50% detection range (light grey shaded area). Reef areas: Single unit reef (SUR), barrier reef (BR), scattered patch reefs (SPR) and aggregated patch reefs (APR).



Fonte: O Autor (2021)

Sparisoma axillare were implanted with individually coded V9-4L acoustic transmitters (30-90 s. delay, 476 days expected lifetime, VEMCO Ltd., Canada) while L. *alexandrei* were implanted with V8-4L acoustic transmitters (30-90 s. delay, 150 days expected lifetime, VEMCO Ltd., Canada). Prior to surgery, fish were transferred to a smaller tank and anesthetized in a seawater and eugenol solution (0.04 ml L^{-1}), weighted (total weight, nearest g) and measured (total length, nearest mm). Individuals were then placed in a "V" shaped bed and 6 - 9 scales were plucked from the ventral midline to expose tag insertion area. Transmitters were cleaned in povidone-iodine and then surgically inserted into the peritoneal cavity through a 1.5 - 2.0 cm incision, which was closed with 2 or 3 stitches of absorbable 4/0 monofilament suture. Direct seawater flow was maintained through the gills by a water pump allowing fish to breath normally throughout surgery procedure. After surgery, individuals were returned to the holding tanks and observed for a 24 h period prior to release. Releases occurred the following morning, at each individual's capture site. All tagged *S. axillare* were initial phase females, with a mean size of 26.5 ± 2.3 cm TL (24.2 to 33 cm) and mean weight of 296.3 ± 73.5 g (Table 1). *Lutjanus alexandrei* sex was not determined and mean size and weight was 22.5 ± 2.3 cm TL (19.5 to 25.2 cm) and 186.3 ± 60.3 g, respectively (Table 2). For all individuals, the tag-to-body relationship never exceeded 2% ($\bar{x}$ = 1.49% ± 0.38, range = 0.83 - 1.95%) of fish total weight in air, as recommended by the transmitter's manufacturer.

Data analysis

Fish density among reef sites was compared using the non-parametric Kruskal-Wallis and post-hoc Dunn's pairwise ranked tests. For the purpose of analyses, *S. axillare* were divided in two size categories: ≤20 cm and >20 cm, as followed by the Reef Check protocol (FERREIRA *et al*., 2018) and *L. alexandrei* as a single category.

For the acoustic telemetry data, prior to analysis, spurious detections (i.e., any detection from a single fish occurring alone within a 24h period) were removed to prevent any false-positive detections (MARCH *et al*., 2011; HARASTI *et al*., 2015). Detections obtained within the first 24h post-release were also excluded from all individuals to avoid potentially negative effects of tagging procedure on fish behavior (HONDA *et al*., 2016).

To identify groups of individuals with distinct spatial occupation patterns within each species, the relative number of detections on each receiver was calculated for each fish. Proportions were then arcsine-square root transformed and a similarity matrix among fish was built for each species based on Bray-Curtis similarity index. Statistically distinct spatial groups were then identified through hierarchical cluster analysis followed by a SIMPROF procedure (CLARKE; GORLEY, 2006). Differences in fish total length (cm) was tested among spatial groups for each species using analysis of variance (ANOVA) and Student's t test.

Permanence within the monitored area was quantified for each fish by two indices as performed by ABECASIS *et al*. (2013): (1) a residency index (I_R) expressed as the number of days an individual was actually detected (D_D) divided by the individual's detection period (number of days between release and the last detection - D_P) and (2) a weighted residency index (I_{WR}) calculated as: $I_{WR} = (D_D/D_{max}) \times (D_P/D_{max})$, where D_{max} is the maximum number of possible monitoring days for each species based on estimate battery life (*S. axillare* V9's lifetime = 476 days and *L. alexandrei* V8's lifetime = 150 days). The end of study date was considered as D_{max} when the removal of the receivers' array occurred before the transmitter's expected lifetime was over. For both indices, values range from 0 (no residency) to 1 (permanent residency).

To estimate the extent of space used by each individual, centers of activity (COAs) were firstly calculated for each fish at 60 min intervals (SIMPFENDORFER *et al*. 2002). This method uses the weighted means of the number of detections registered by each receiver to provide estimated hourly fish positions (mean latitude and longitude). Then, the nonparametric kernel utilization distribution (KUD) was used to calculate home range (HR, defined as 95% KUD) and core range (CR, defined as 50% KUD) areas, based on the COAs estimates over the entire individuals' detection periods. KUDs were estimated based on bivariate fixed kernels (WORTON, 1989) over a 25 x 25 m cell grids and a fixed bandwidth smoothing factor (h) of 150 m (corresponding to the 50% detection probability range). As observed during diurnal and nocturnal dives in the monitored reefs, both species are highly reef attached and the use of bare sand/mud areas are limited to the immediate reef vicinity. Therefore, the entire 95% and 50% KUD areas were considered an overestimation of the actual home range used by both species. To produce more reliable HR and CR estimates, areas of interest were selected by excluding from the 95% and 50% KUDs the surrounding sand covered areas located more than 50 m away from any reef formation. The selection of an area of interest reduced the HR and CR areas of *S. axillare* by 25.1 ± 10.6 % CI and 21.2 ± 10.4 % CI, respectively. For *L. alexandrei*, HR and CR areas were reduced by 34.0 ± 13.6 % CI and 24.9 ± 16.3 % CI, respectively. The majority of seagrass and macroalgae patches present in the monitored area were included within the 50 m limit range. Finally, individual HR and CR areas were overlapped with the NTZ boundary to assess the percentage of HR and CR areas located inside the no-take zone.

To investigate space-use sharing between the different spatial groups within species, mean HR and mean CR areas were calculated for each spatial group based on the total number of COAs estimated for all fish from the group. Estimates of mean HR and CR followed the same procedures used to calculate individual KUDs. An overlap index (OI) was then calculated for each spatial group as: $OI = OV_{(KUDi,\ KUDi+1)} \div (KUD_i + KUD_{i+1})$, where $OV_{(KUDi,\ KUDi+1)}$ is the overlap area between the mean HR or CR areas of two spatial groups and $(KUD_i + KUD_{i+1})$ is the combination of the two spatial groups mean HR or CR areas. Values range from 0 (no overlap, groups are spatially segregated) to 1 (mean HR or CR are completely overlapped and groups show no spatial segregation).

KUD analyses were performed using the Home Range Tools extension for ArcGIS (RODGERS *et al*., 2015). Selection of KUD areas of interest, overlap between HR and CR areas and NTZ boundary, as well as the overlapped and combined mean HR and CR areas were obtained using geoprocessing tools on ArcGIS 10.4.

Differences on I_R, I_{WR}, HR and CR areas between species and among spatial groups were assessed using analysis of variance (ANOVA) and Student's t test (or the non-parametric Kruskal-Wallis and Mann-Whitney U test whether parametric assumptions were not met). Also, Spearman's rank correlations were used to investigate if fish total length was significantly correlated with I_{WR}, I_R, HR and CR. Analyses were conducted in Statistica v. 8.0 (Statsoft Inc. 2007) and PRIMER v. 6.1 (CLARKE; GORLEY, 2006). Significance was tested at $\alpha = 0.05$.

Ethics Statement

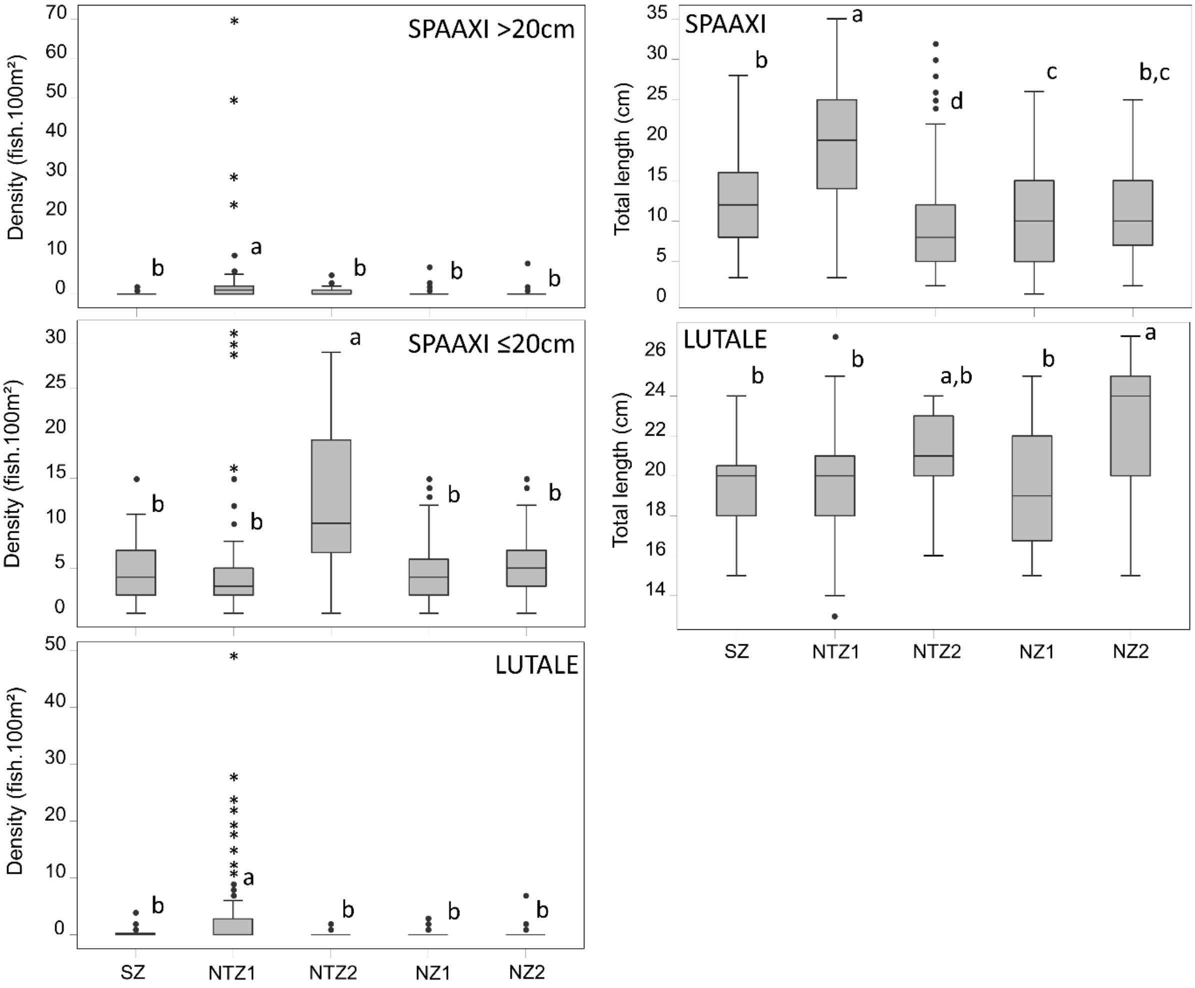
This research was approved by Ethics Committee and Animal Use of the Federal University of Pernambuco (CEUA-UFPE Number: 23076.007810/2015-01) and Chico Mendes Institute for Biodiversity Conservation (ICMBIO – Sisbio License: 45992).

RESULTS

Reef fish surveys

Fish densities for both species were significantly higher inside the Tamandaré NTZ, with *Sparisoma axillare* >20 cm forming large roving schools along reef crests and *Lutjanus alexandrei* aggregating in large numbers to rest inside caves. Outliers and extreme outliers indicate the occurrence of those schools, which for *S. axillare* could aggregate up to 70 individuals (Figure 2, left panel). Densities were significantly higher on NTZ1 (corresponding to the SUR area) for *S. axillare* >20 cm ($H = 36.2$, $p < 0.001$) and for *L. alexandrei* ($H = 39.8$, $p < 0.001$), and on NTZ2 (corresponding to SPR and APR areas) for smaller *S. axillare* ≤20 cm ($H = 37.5$, $p < 0.001$) (Figure 2, left panel). For *S. axillare*, fish TL was also significantly higher on NTZ1 (H = 36.2, p < 0.001) whereas larger *L. alexandrei* were observed on NZ2 (H = 16.5, p < 0.01) (Figure 2, right panel).

Figure 2 – Fish density (left panel) and total length (right panel) of *Sparisoma axillare* (SPAAXI) and *Lutjanus alexandrei* (LUTALE) obtained by the visual surveys performed in the Tamandaré coral reef complex. For density estimates, *S. axillare* was divided in two size categories (>20 and ≤20 cm). Sites inside the NTZ: NTZ1 and NTZ2. Sites outside the NTZ: North Zones (NZ1 and NZ2) and South Zone (SZ). Letters indicate the results of Dunn's pairwise ranked tests. Box plots legend: solid line within the box indicates the median, box represents the interquartile range (low = 25th percentile, upper = 75th percentile), whiskers extend to the largest value within 1.5x the interquartile range, outliers outside this range are represented by black dots, and extreme outliers (values beyond 3x the interquartile range) are drawn as asterisk.



Fonte: O Autor (2021)

Acoustic telemetry

The tagging and monitoring data of the 20 gray parrotfish (*S. axillare*) and 9 Brazilian snappers (*L. alexandrei*) individuals are summarized on Tables 1 and 2, respectively. Three *S.*

axillare were detected for a short period of 6 days or less (SPAAXI #02, #12 and #14). Other *S. axillare* (SPAAXI #05) was assumed to be dead a few days after tagging in a detectable location in the array, as this fish was continuously being detected by only one receiver and detection ceased only after the transmitter's estimated lifespan was over. Therefore, these four *S. axillare* individuals were excluded from all subsequent analysis. Only one fish (SPAAXI #11) seemed to have its monitoring discontinued by the receiver loss, as this fish was being recorded exclusively by this receiver and ceased to be detected only 3 days before the last date of download. Two other *S. axillare* individuals were constantly being detected by the lost receiver, however for both fish detection ceased more than 40 days prior to receiver loss. The remaining 16 *S. axillare* and all 9 *L. alexandrei* were monitored for 16 to 187 days, from December 2016 to October 2017 (Figure 3-A, B).

Table 1 – Summary of the monitoring data for *Sparisoma axillare* tagged individuals (n = 20) in the coastal reefs of the Tamandaré coral reef complex. Total length (TL, cm), detection period (DP), days detected (DD), weighted residency index (IWR), residency index (IR), number of centers of activity (COAs), percentage of home range located inside the NTZ (%HRin) and percentage of core range located inside the NTZ (%CRin). Fish that prematurely left the array, lost the tag, or died (†). Not available (NA).

Fish ID	TL (cm)	Date released (d/m/y)	No. of Detections	D_P	D_D	I_{WR}	I_R		COAs	Home range (km²)		Core range (km²)	
							All	Outside NTZ		All	% HR_{in}	All	% HR_{in}
SPAAXI #01	26.2	13/12/2016	13,002	51	51	0.01	1.00	-	837	0.10	100%	0.02	100%
SPAAXI #02†	26.1	13/12/2016	87	01	01	NA	NA	NA	NA	NA	NA	NA	NA
SPAAXI #03	25.5	12/01/2017	4,091	18	18	0.001	1.00	-	314	0.14	100%	0.04	100%
SPAAXI #04	25.0	12/01/2017	1,252	25	25	0.003	1.00	-	212	0.44	98.9%	0.11	100%
SPAAXI #05†	31.5	14/01/2017	34,234	480	325	NA	NA	NA	NA	NA	NA	NA	NA
SPAAXI #06	25.0	14/01/2017	733	23	23	0.002	1.00	0.13	111	0.34	86.8%	0.07	99.7%
SPAAXI #07	27.7	14/01/2017	942	17	17	0.001	1.00	0.18	117	0.42	85.1%	0.07	97.2%
SPAAXI #08	33.0	20/01/2017	437	107	62	0.03	0.58	0.07	158	0.40	80.8%	0.07	100%
SPAAXI #09	27.0	20/01/2017	63	26	20	0.002	0.77	-	37	0.25	100%	0.07	100%
SPAAXI #10	25.4	20/01/2017	490	55	50	0.01	0.91	-	217	0.18	100%	0.05	100%
SPAAXI #11	27.5	20/01/2017	125	91	39	0.02	0.43	-	65	0.16	100%	0.04	100%
SPAAXI #12†	25.0	20/01/2017	19	06	04	NA	NA	NA	NA	NA	NA	NA	NA
SPAAXI #13	25.2	26/01/2017	180	56	39	0.01	0.70	-	86	0.28	82.9%	0.07	100%
SPAAXI #14†	29.0	26/01/2017	484	03	02	NA	NA	NA	NA	NA	NA	NA	NA
SPAAXI #15	25.0	30/03/2017	7,190	58	58	0.02	1.00	0.26	840	0.22	72.1%	0.05	97.9%
SPAAXI #16	24.5	30/03/2017	12,353	180	34	0.03	0.18	0.01	377	0.21	78.7%	0.05	99.9%
SPAAXI #17	26.8	30/03/2017	13,821	38	38	0.01	1.00	-	555	0.19	100%	0.06	100%
SPAAXI #18	24.3	28/04/2017	3,017	159	151	0.14	0.95	0.03	711	0.31	84.1%	0.06	100%
SPAAXI #19	25.6	28/04/2017	717	28	25	0.004	0.89	0.61	136	0.45	58.8%	0.10	49.0%
SPAAXI #20	24.2	28/04/2017	866	187	134	0.15	0.71	0.01	355	0.34	86.6%	0.07	100%

Fonte: O Autor (2021)

Table2 – Summary of the monitoring data for *Lutjanus alexandrei* tagged individuals (n = 09) in the coastal reefs of the Tamandaré coral reef complex. Total length (TL, cm), detection period (DP), days actually detected (DD), weighted residency index (IWR), residency index (IR), number of centers of activity (COAs), percentage of home range located inside the NTZ (%HRin) and percentage of core range located inside the NTZ (%CRin).

Fish ID	TL (cm)	Date released (d/m/y)	No. of Detections	D_P	D_D	I_{WR}	I_R		COAs	Home range (km²)		Core range (km²)	
							All	Outside NTZ		All	% HR_{in}	All	% HR_{in}
LUTALE #01	24.0	13/12/2016	3,122	24	24	0.03	1.00	-	276	0.15	100%	0.05	100%
LUTALE #02	21.5	13/12/2016	29,810	152	146	0.99	0.96	-	1,400	0.19	100%	0.06	100%
LUTALE #03	24.5	12/01/2017	14,154	135	135	0.81	1.00	-	1,801	0.15	100%	0.03	100%
LUTALE #04	25.2	12/01/2017	3,261	127	119	0.67	0.93	-	1,066	0.40	86.2%	0.08	100%
LUTALE #05	23.1	12/01/2017	1,893	19	17	0.01	0.89	-	113	0.26	100%	0.07	100%
LUTALE #06	24.5	14/01/2017	39,736	143	143	0.91	1.00	0.74	2,139	0.27	74.2%	0.05	99.2%
LUTALE #07	19.5	30/03/2017	45,837	150	150	1.00	1.00	-	2,345	0.15	100%	0.05	100%
LUTALE #08	20.4	28/04/2017	2,032	107	94	0.45	0.88	-	582	0.19	96.9%	0.04	100%
LUTALE #09	19.5	05/05/2017	885	16	16	0.01	1.00	-	126	0.12	100%	0.03	100%

Fonte: O Autor (2021)

Even with a shorter transmitter's battery lifespan, *L. alexandrei* had a higher number of detections per fish ($\bar{x}$ = 15,637 ± 18,018 SD) and longer detection period ($\bar{x}$ = 97 ± 59.5 SD days) than *S. axillare* ($\bar{x}$ = 3,705 ± 5,002 SD detections and $\bar{x}$ = 70 ± 58.3 SD days), though individual variation within each species was high (Tables 1, 2). Based on the relative number of detections for each fish at each receiver, hierarchical cluster analysis followed by a SIMPROF procedure revealed four significantly distinct clusters for *S. axillare*: Barrier reef (BR), scattered patch reefs (SPR), aggregate patch reefs (APR) and single unit reef (SUR) (Figure 3-C), and two significantly distinct clusters for *L. alexandrei*: SPR and SUR (Figure 3-D), which corresponded to groups of individuals with distinct spatial occupation patterns. For both species, spatial groups were mostly composed by the individuals captured in the same reef area. Only one *S. axillare* (SPAAXI #19, Fig. 3-C) and two *L. alexandrei* (LUTALE #05 and #08, Figure 3-D) had more detections on reef areas other than their original capture locations. Fish SPAAXI #04 was not included in any spatial group. Neither species showed significant difference in fish total length among spatial groups: *S. axillare* (ANOVA, F = 2.39, p = 0.12) and *L. alexandrei* (Students' t test, t = 0.82, p = 0.44).

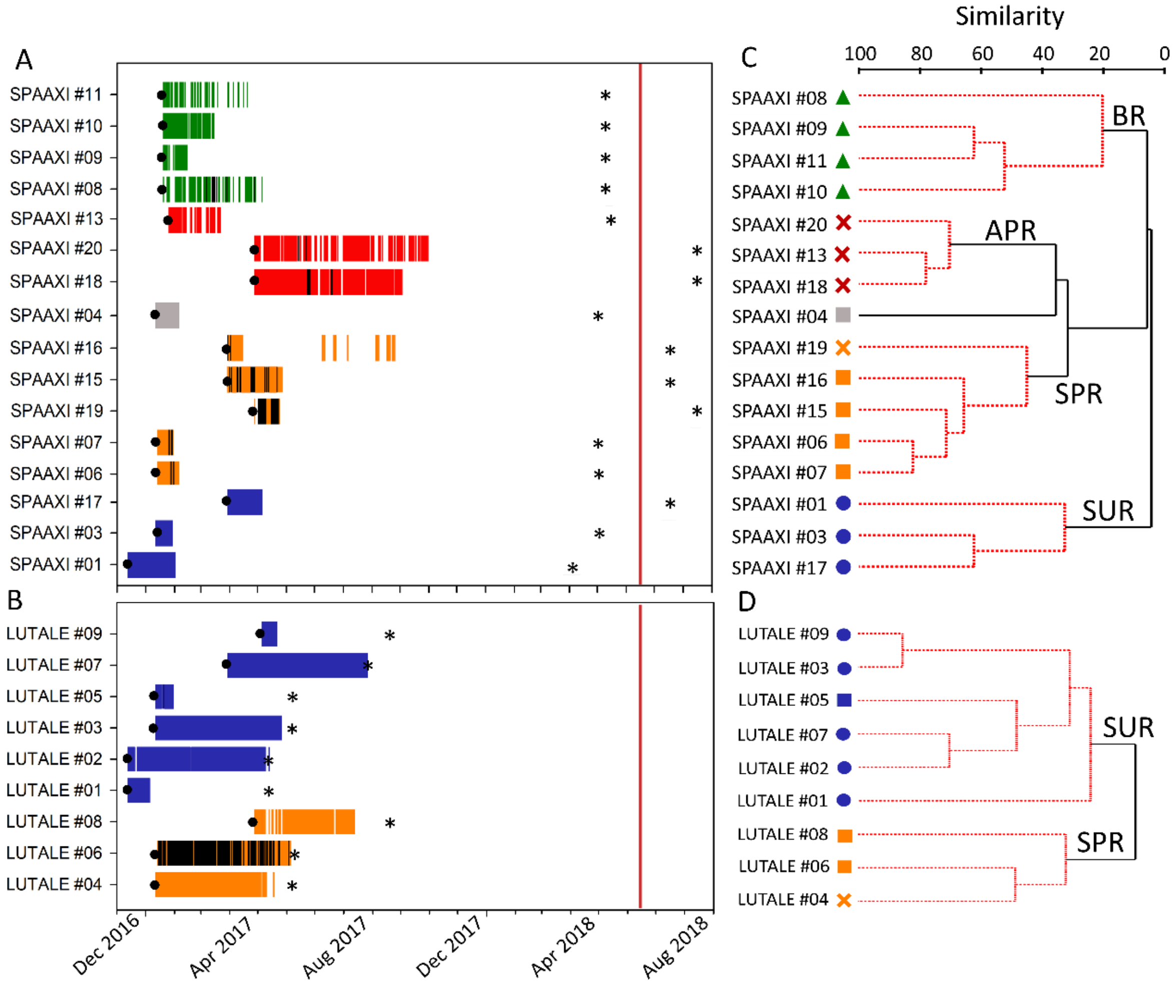
On average, *S. axillare* individuals were detected on 11% ± 9.7 SD of the maximum number of monitoring days (V9's lifetime = 476 days, or end of the study), resulting in low I_{WR} values for the species (0.03 ± 0.05 SD) (Table 1, Figure 3-A). For *L. alexandrei*, I_{WR} values were considerably higher ($\bar{x}$ = 0.54 ± 0.42 SD) as fish remained in the monitoring area for 62.5% ± 39 SD of the maximum number of monitoring days (V8 transmitter's expected lifetime = 150 days) (Table 2, Figure 3-B). For both species, no significant differences on I_{WR} were observed among fish groups: *S. axillare* (Kruskal-Wallis, H = 4.04, p = 0.25) and *L. alexandrei* (Mann-Whitney, U = 8, p = 0.90).

Both species had high residency index (I_R) values (*S. axillare*, $\bar{x}$ = 0.82 ± 0.24 SD and *L. alexandrei*, $\bar{x}$ = 0.96 ± 0.05 SD) (Tables 1, 2), with no significant difference between them (Mann-Whitney, U = 52, p = 0.24). For *S. axillare*, higher I_R values were observed for SUR group (I_R = 1 for all fish), followed by SPR ($\bar{x}$ = 0.82 ± 0.35 SD) and APR ($\bar{x}$ = 0.79 ± 0.14 SD) groups, whereas lower values were obtained for BR group ($\bar{x}$ = 0.67 ± 0.21 SD). Significant differences on I_R were observed between SUR and BR (Mann-Whitney, U = 0, p = 0.02) and SUR and APR (Mann-Whitney, U = 0, p = 0.03) groups. For *L. alexandrei*, no statistical difference was found between the two groups (Mann-Whitney, U = 5, p = 0.30). No correlations were found between fish total length and I_{WR} (Spearman rank correlation; *S. axillare*, r_s = -0.02, p = 0.93 and *L. alexandrei*, r_s = -0.01, p = 0.97) or I_R (Spearman rank correlation; *S. axillare*, r_s = -0.42, p = 0.10 and *L. alexandrei*, r_s = 0.07, p = 0.85).

Nine individuals were recorded outside the NTZ, but only three of them (all from SPR groups) left the protected area on a regular basis: SPAAXI #15 (26% of monitoring period), SPAAXI #19 (61%) and LUTALE #06 (74%) (Table 1, 2, Figure 3-A, B). Fish SPAAXI #19 also had highest number of detections outside the NTZ (65% of all detections). All *S. axillare* and *L. alexandrei* from SUR groups were never detected outside the NTZ.

The estimated home range (HR, 95% KUD) areas ranged from 0.10 to 0.45 km² ($\bar{x}$ = 0.28 ± 0.11 km² SD) for *S. axillare* (Table 1) and from 0.12 to 0.40 km² ($\bar{x}$ = 0.21 ± 0.09 km² SD) for *L. alexandrei* (Table 2). Regarding the core range (CR, 50% KUD) estimates, areas ranged from 0.02 to 0.11 km² ($\bar{x}$ = 0.06 ± 0.02 km² SD) for *S. axillare* (Table 1) and from 0.03 to 0.08 km² ($\bar{x}$ = 0.05 ± 0.02 km² SD) for *L. alexandrei* (Table 2). Both HR and CR sizes did not differ significantly between species (Student's t test, t = 1.48, p = 0.15 and t = 1.31, p = 0.20, respectively) or among spatial groups within each species (Table 03). For *S. axillare*, no correlations were found between fish total length and HR (Spearman rank correlation; r_s = 0.16, p = 0.54) or CR size (Spearman rank correlation; r_s = -0.11, p = 0.67) (Figure 4-A). For *L. alexandrei*, influence of fish total length on HR and CR sizes were relatively stronger, yet not significant (Spearman rank correlation; r_s = 0.62, p = 0.09 and r_s = 0.37, p = 0.33, respectively) (Figure 4-B).

Figure 3 – Detection plots of fish daily presence-absence at the monitored area (A,B) and hierarchical cluster analysis followed by a SIMPROF procedure (C,D) indicating the formation of significantly distinct groups of fish with distinct spatial occupation patterns (red dotted lines) for tagged *Sparisoma axillare* (A,C) and *Lutjanus alexandrei* (B,D) in the coastal reefs of Tamandaré-PE. Fish groups and correspondent colors: barrier reef (BR, green), aggregate patch reefs (APR, red), sparse patch reefs (SPR, orange) and single unit reef (SUR, blue). Fish SPAAXI #04 (gray) was not included in any group. Symbols on C and D indicate the capture/release areas: BR (triangles), APR (cross), SPR (squares) and SUR (circles). Fish release dates (black circles), days with detections outside the NTZ (black bars), transmitter's estimated lifetime (465 days for *S. axillare* V9 and 150 days for *L. alexandrei* V8) (asterisks) and removal of receiver array (end of study, vertical red line) are also shown.



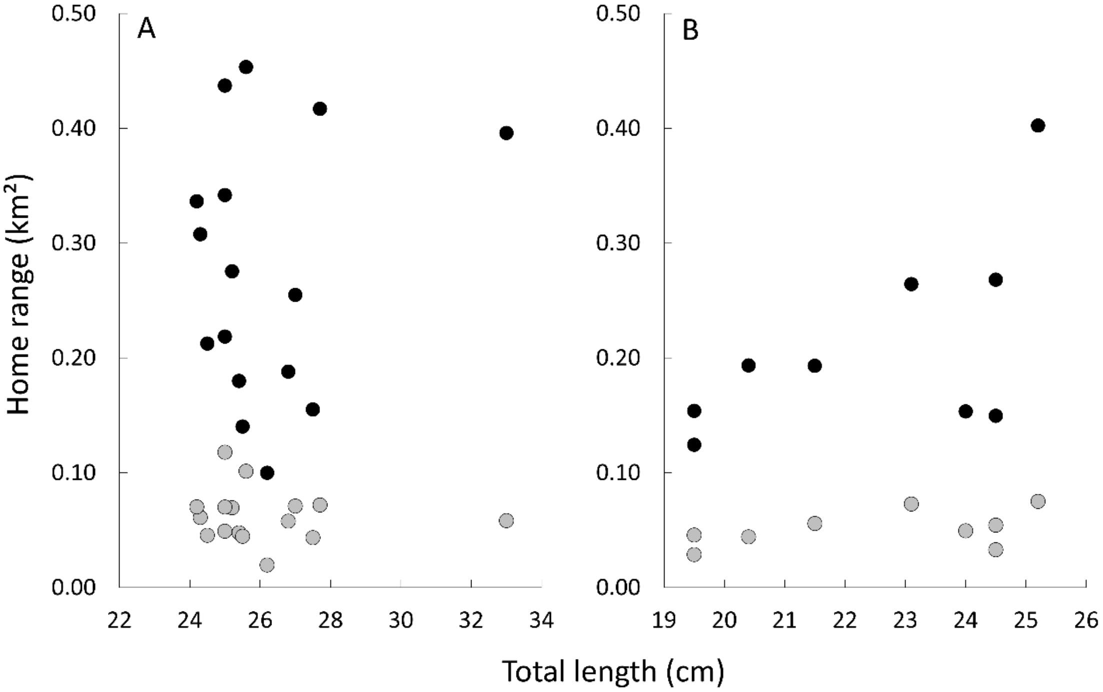
Fonte: O Autor (2021)

Table 3 – Mean (± SD) home range and core range areas for *Sparisoma axillare* and *Lutjanus alexandrei* spatial groups. Single unit reef (SUR), sparse patch reefs (SPR), aggregate patch reefs (APR) and barrier reef (BR). Results of ANOVA and Student's t test are shown.

Source	SUR	SPR	APR	BR	ANOVA		
					df	F	P
Sparisoma axillare							
Home range	0.14 ± 0.04	0.33 ± 0.11	0.31 ± 0.03	0.25 ± 0.11	3	2.92	0.08
Core range	0.04 ± 0.02	0.07 ± 0.02	0.07 ± 0.01	0.05 ± 0.01	3	1.84	0.19
					Student's t test		
Lutjanus alexandrei					df	t	P
Home range	0.17 ± 0.05	0.29 ± 0.10			7	2.30	0.06
Core range	0.05 ± 0.02	0.06 ± 0.02			7	0.91	0.39

Fonte: O Autor (2021)

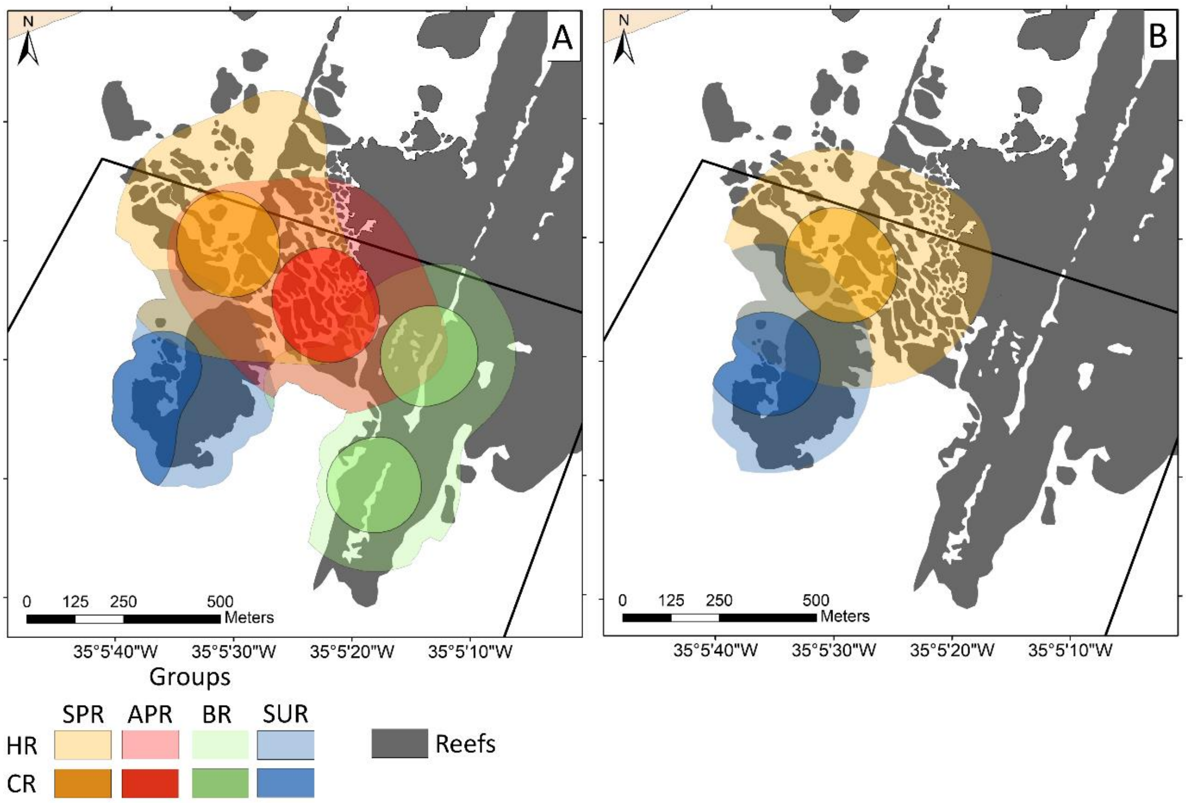
Figure 4 – Relationship between total length and home range (black circles) and core range (grey circles) size for *Sparisoma axillare* (A) and *Lutjanus alexandrei* (B) in the coastal reefs of Tamandaré-PE.



Fonte: O Autor (2021)

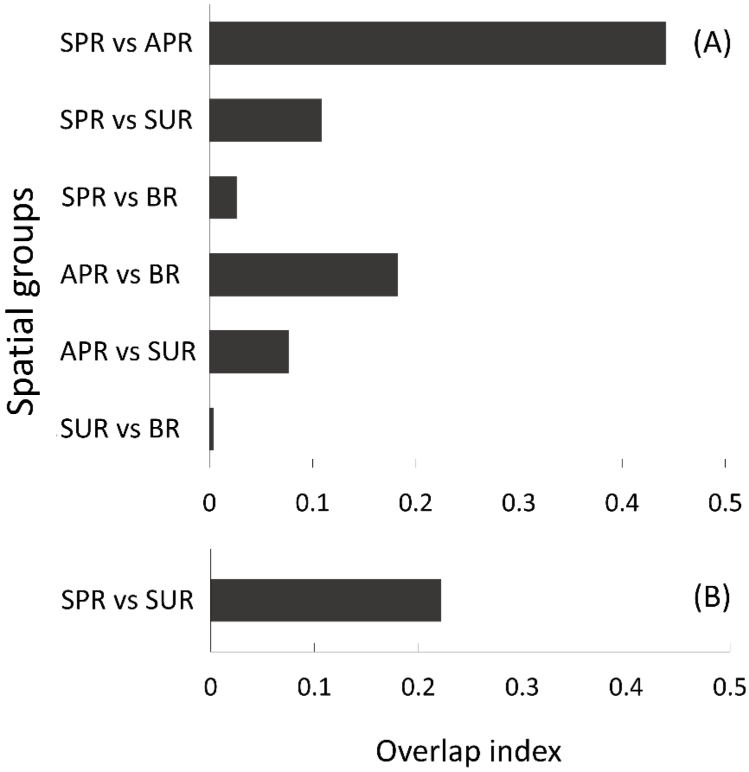
In general, fish from the different spatial groups used more intensively their respective capture/release reef areas (Figure 5-A, B). Therefore, low overlap index (OI) values were observed among the mean home range areas of the spatial groups for both *S. axillare* ($\bar{x}$ = 0.14 ± 0.16 SD) and *L. alexandrei* (OI = 0.22) (Figure 6). A moderate overlap (OI = 0.44) was only observed between *S. axillare* SPR and APR home range areas. For both species, fish from the different spatial groups used completely distinct mean core range areas resulting in no overlap (Figure 5-A, B).

Figure 5 – Home range (HR, 95% KUD) and core range (CR, 50% KUD) areas estimated for the *Sparisoma axillare* (A) and *Lutjanus alexandrei* (B) spatial groups in the coastal reefs of Tamandaré-PE. Sparse patch reefs (SPR, orange), aggregate patch reefs (APR, red), barrier reef (BR, green) and single unit reef (SUR, blue). Black line represents the NTZ boundary.



Fonte: O Autor (2021)

Figure 6 – Overlap index between mean home range areas for *Sparisoma axillare* (A) and *Lutjanus alexandrei* (B) spatial groups in the coastal reefs of the Tamandaré coral reef complex. Sparse patch reefs (SPR), aggregate patch reefs (APR), barrier reef (BR) and single unit reef (SUR).

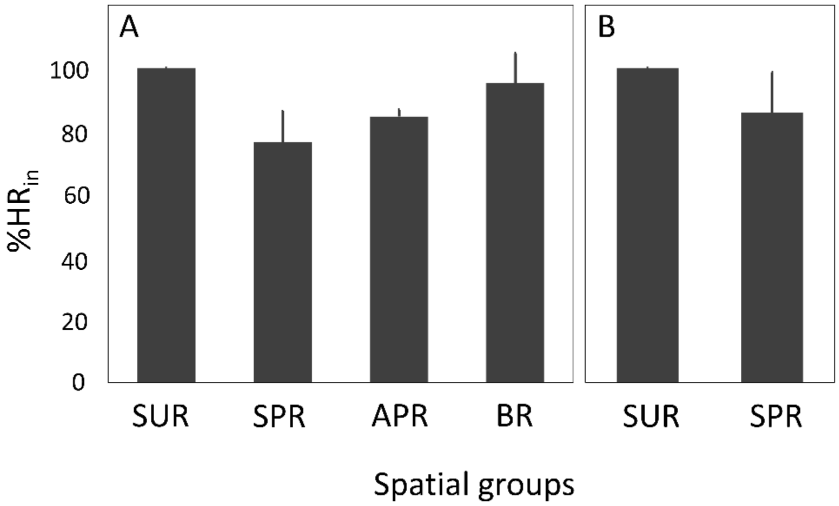


Fonte: O Autor (2021)

Regarding the percentage of fish HR and CR located inside the NTZ (%HR_{in} and %CR_{in}, respectively), all *L. alexandrei* and most *S. axillare* individuals (except for SPAAXI #19) had a %HR_{in} higher than 70% (*S. axillare*, $\bar{x}$ = 88.4 ± 6 % CI and *L. alexandrei*, $\bar{x}$ = 95.2 ± 4.5 % CI) and a %CR_{in} over 95% (*S. axillare*, $\bar{x}$ = 96.5 ± 6.2 % CI and *L. alexandrei*, $\bar{x}$ = 99.9 ± 0.1 % CI) (Tables 1 and 2). No significant differences between species were observed for both %HR_{in} (Mann-Whitney, U = 45, p = 0.16) and %CR_{in} (Mann-Whitney, U = 52, p = 0.24). For *S. axillare*, all fish from the SUR spatial group had their HRs located entirely inside the NTZ, whereas one fish from BR and all fish from SPR and APR spatial groups had part of their HRs outside the NTZ (Figure 7-A). Similarly, all *L. alexandrei* from SUR group used only areas inside the NTZ, while all fish from SPR had part of their HRs beyond the NTZ boundary (Figure 7-B). Significant differences on %HR_{in} were observed among *S. axillare* spatial groups (Kruskal-Wallis, H = 7.8, p = 0.04), specifically between SUR and SPR (Mann-Whitney pairwise, U = 0, $p > 0.03$). For *L. alexandrei*, significant difference on %HR_{in} was also found between SUR and SPR groups (Mann-Whitney pairwise, U = 0, $p > 0.03$).

Regarding the $\%CR_{in}$, only five *S. axillare* (all from SPR group) and one *L. alexandrei* (also from SPR) had part of their CRs outside the NTZ.

Figure 7 – Mean percentage of home range areas located inside the Tamandaré NTZ (%HRin) for *Sparisoma axillare* (A) *and Lutjanus alexandrei* (B). Single unit reef (SUR), sparse patch reefs (SPR), aggregate patch reefs (APR) and barrier reef (BR). Error bars indicate 95% confidence interval.



Fonte: O Autor (2021)

DISCUSSION

Positive effects of NTZs for fish communities, characterized by increased fish density and larger body-size within the protected area, have been well documented worldwide (HALPERN, 2003; LESTER *et al*., 2009; MALCOM *et al*., 2018; GILCHRIST *et al*., 2020) and in Brazil (FLOETER *et al*., 2006; ANDERSON *et al*., 2014, 2020). Present results also revealed a positive effect on fish density and size for both *S. axillary* and *L. alexandrei* within the NTZ, corroborating previous studies in the area (FERREIRA and MAIDA, 2007). The UVCs also highlighted a distinct preference of juveniles *S. axillare* for the patch reef zones (SPR and APR), whereas larger *S. axillare* and *L. alexandrei* showed markedly higher densities in the SUR area where large schools of both species are observed during the day. Fish distribution is contagious, non-normal, and this pattern is determined by large variances associated with the belt transect fish counts related to the formation of large schools in fixed places at determined times of the day (authors pers. obs.). Indeed, this pattern has been previously described to be a characteristic of many reef fish that seek shelter and school for protection or feeding (MCCLANAHAN *et al*., 2007; BECK *et al*., 2014). Juvenile and subadult *S. axillare* were more abundant in the patch reef areas (SPR and APR) of the NTZ, indicating a preference for this habitat that forms a continuous inside-outside the NTZ. This area is less complex than the SUR area, where interconnected caves form an intricate network of shelters and passages and harbor greater densities of large-bodied *S. axillare* individuals as well as *L. alexandrei*. However, this area is also occupied by larger predatory fish (FERREIRA *et al*., 2007; authors pers. obs.), therefore the patch reef areas appear to be the safest zone for small-bodied fish.

The acoustic monitoring results revealed an overall low site fidelity for *S. axillare* as fish remained in the NTZ for less than 40% of the 476 days estimated V9's lifetime and 50% of individuals went undetected in less than 40 days. *L. alexandrei* were relatively more site attached as two fish were monitored throughout the entire V8 transmitter's expected lifetime (150 days) and four individuals for longer than 70% of that period. After 100 days of monitoring, two-thirds of *L. alexandrei* individuals were still present in the NTZ. Despite the low I_{WR} values for *S. axillare* and some *L. alexandrei* individuals (LUTALE #01, #05 and #09), nearly all tagged individuals showed high I_R on the short-term, indicating that both species were full-time residents in the monitored area until detections were permanently lost. Comparable detection periods were observed for the congeneric species *Sparisoma cretense* in a similar sized marine reserve (0.83 km^2) on the Mediterranean (LA MESA *et al*., 2012) and for *Sparisoma viride* and *Lutjanus apodus* in a relatively larger (9.56 km^2) Caribbean marine reserve (GARCIA *et al*., 2015). However, long-term studies have shown high residency of up to 937 days for *Sparisoma cretense* (AFONSO *et al*., 2008) and up to 363 to 1,096 days for others *Lutjanus* species at natural and artificial habitats (TINHAN *et al*., 2014; HUIJBERS *et al*., 2015; WILLIAMS-GROVE and SZEDLMAYER, 2016).

A decline in the number of detected fish throughout the monitoring period is usually observed in acoustic telemetry studies (TINHAN *et al*., 2014; GARCIA *et al*., 2015; WOLFE; LOWE, 2015), which can be mostly explained by natural mortality (e.g., predation), fishing mortality and emigration beyond receivers' detection range (e.g., ontogenetic, or reproductive migrations) (KHAN *et al*., 2016; BROWNSCOMBE *et al*., 2019). Another possibility is that fish disappearance could be due to transmitter malfunctioning or premature failure of battery, however equipment failure is not addressed as a relevant reason of detection loss in studies using similar equipment (AFONSO *et al*., 2016; KHAN *et al*., 2016). Moreover, in this study the transmitters used in two *L. alexandrei* and the one used on SPAAXI #05 were detected throughout their entire estimated battery lifetime. For the three *S. axillare* with noticeably short detection periods (SPAAXI #02, #12, #14) and for SPAAXI #05, that was assumed to be dead a few days after release, anticipated mortality as a consequence of tagging procedure might also be considered (KHAN *et al*., 2016; BROWNSCOMBE *et al*., 2019).

Mortality by predation is an expected effect of NTZs as the initial increase in the abundance of prey attracts and even sustains large populations of predators (RUSS; ALCALA, 1996; STENECK, 1998). On the Tamandaré reef complex, large top predators as Goliath groupers (*Epinephelus itajara*), Green moray eels (*Gymnothorax funebris*), Cubera snappers (*Lutjanus cyanopterus*) and Great barracudas (*Sphyraena barracuda*) are commonly seen inside the NTZ, as well as signs of predation attempts in the resident prey fishes (authors pers. obs.). Seven parrotfish (SPAAXI #02, #03, #07, #13, #14, #16, #17) had their last detections while sheltering at nighttime. Since parrotfishes are strictly diurnal (HOBSON, 1975), it seems unlikely that these individuals would leave the monitoring area during the night, then mortality by predation seems to be a reasonable explanation for fish disappearance in the present study.

Illegal fishing can also be a reason for detection loss on acoustic telemetry studies conducted inside no-take zones, especially for those areas with limited enforcement as large and remotely located NTZs (TINHAN *et al*., 2014; TICKLER *et al*., 2019). Although illegal fishing can also be a reason for detection loss on acoustic telemetry studies, fishing mortality inside the NTZ is unlikely as the area is relatively small, with well-defined boundaries (visually delimited by floating buoys) and located close to the shore in front of the research facility. Such characteristics make the NTZ a fully enforced area that is easily monitored from both boat and land. However, fishing is allowed at the immediate vicinity of the NTZ, so mortality by fisheries would be expected to occur as a consequence of spillover or even due to short displacements to the open area. Those species are important fish targets, and *S. axillare* is one of the main caught species by both spear and hook-and-line fishing in the region (SILVEIRA, 2018). *Sparisoma axillare* and *L. alexandrei* individuals (mostly from SPR and APR groups) were detected outside the NTZ and had part of their HR and CR beyond its northern border, indicating a potential for fish spillover through those areas (AFONSO *et al*., 2008; LA MESA *et al*., 2012). So, the results suggest that fishing mortality at the unprotected reefs contiguous to the SPR and APR areas are likely to occur.

Emigration to areas outside the receiver's detection range are also likely related to movements toward the deeper reefs beyond the last line of receivers in the BR area. Snappers commonly perform ontogenetic migrations from shallow coastal to deeper reef areas (FRÉDOU; FERREIRA, 2005; ASCHENBRENNER and FERREIRA, 2015; ASCHENBRENNER *et al*., 2016a, 2016b). *Lutjanus alexandrei* has been shown to spend its first years in estuarine/mangrove areas, moving to reefs during their third or fourth year of life (ASCHENBRENNER *et al*., 2016a, 2016b) a movement that continues gradually to deeper areas as the species is observed up to depths of 50 meters at sizes larger than 33 cm TL (MOURA; LINDEMAN, 2007; FERNANDES *et al*., 2012). So, it seems that the NTZ may act as a stepping stone during the ontogenetic migration, where individuals can exhibit high site fidelity for a certain time before possibly moving to deeper areas. This would result in a higher period of residency in the shallow reefs of the NTZ and lower spillover in the short-term. Snappers are known to perform reproductive migrations from home sites to aggregation sites during well-defined spawning seasons (BIGGS; NEMETH, 2016). The length at first sexual maturity for *L. alexandrei* is estimated around 20 cm TL and the species has a clear spawning season (from November to March, with a peak in February) during which fish may aggregate, as indicated by an increase on fisheries landings for the species in the same period (FERNANDES *et al*., 2012). In the present study, the monitoring period of six adults *L. alexandrei* (size range from 21.5 to 25.2 cm TL) overlapped the spawning season. The disappearance of two of those individuals (LUTALE #01 and #05, both with markedly short I_{WR}) during the spawning season could then be related to reproductive migrations to aggregation sites outside the NTZ, as suggested for *L. apodus* in Martinique (GARCIA *et al*., 2014).

For *S. axillare*, the time of residency in the NTZ seems to be sufficient for a significant mortality reduction, resulting in an increase in both size and abundance. As shallow reefs areas are occupied mainly by juveniles and initial phase females, this benefit is verified only for this part of the population, although terminal phase males are most likely present in the deeper areas of BR, where UVC were not conducted during this study due to limiting conditions. Moreover, ontogenetic and reproductive movements to deeper areas are likely to occur, and as suggested through this study, would represent spillover from the NTZ.

Several parrotfish species have complex social systems (van ROOIJ *et al*., 1996; MUMBY; WABNITZ, 2002) and movement patterns related to social interactions and reproductive behavior may play an important role in space used by individuals (AFONSO *et al*., 2008). First maturation size for female *S. axillare* is estimated at 25 cm TL and reproduction occurs all over the year (VERAS unpub. data). Therefore, most tagged individuals were mature females and reproductive migrations might be an important factor determining movements and residency time for this species at shallow reef areas. Nine *S. axillare* were last detected during daylight hours on the receivers at BR or on the receiver located at the easternmost part of APR area, which could indicate a permanent relocation to the unmonitored deeper reefs inside and outside the NTZ. Also, the lower I_R registered for APR and BR fish groups might be related to frequent short-term displacements to the deeper portions of the BR area beyond the receivers' monitoring ranges. Such movements could possibly lead to low survival rates due to spillover movements at deeper areas. Indeed, the unmonitored deeper portion of the BR area contiguous to the NTZ is recognized by the local fishermen as a major fishing ground for larger parrotfish (> 20 cm TL).

Acoustic telemetry is recognized as an effective tool for examining fish movements and habitat use at a variety of marine environments, as well as to assess the protection effectiveness of NTZs to different fish species (DI FRANCO *et al.*, 2018). However, acoustic telemetry is still relatively expensive, and the number of available acoustic receivers might be a limiting factor on the spatial extent of the study. Moreover, on morphologically complex high-relief habitats as coral reefs, the detection range of the receivers might be affected by the existence of physical barriers to the signal propagation thus creating acoustic dead zones (WELSH *et al.*, 2012; SELBY *et al.*, 2016). In the present study, the capability to detect cross-boundary movements and the extent of fish displacements at unprotected areas might have been limited by the low number of receivers deployed outside the NTZ that resulted in gaps on acoustic coverage, particularly at deeper areas. Similarly, possible relocations towards deeper reefs may have been undetected due to the non-overlapping listening ranges of the last line of receivers at BR area. Therefore, an expansion of the acoustic array to areas outside the NTZ as well as to deeper reef areas within the NTZ are necessary to a better understanding on the extent of spill-over and cross-shelf movements performed by *S. axillare* and *L. alexandrei* individuals, as well as the identification of the pathways utilized during those movements.

Both *S. axillare* and *L. alexandrei* used small HRs (up to 0.45 km² and 0.40 km², respectively) with most activity limited to core range areas of up to 0.12 and 0.07 km², respectively, usually corresponding to the fish capture locations. Although relatively small, the reefs within the NTZ were shown to harbor spatially segregated subgroups of individuals for both species. The use of distinct reef areas by groups of fish has been shown for other reef fish species (EGLI; BABCOCK, 2004; HAMMERSCHLAG-PEYER; LAYMAN, 2010; PILLANS *et al.*, 2017). Site-attached species may benefit from the continued use of small HR and CR areas by the prompt access to resources (e.g., food and shelter) within a familiar reef area (KRAMER; CHAPMAN, 1999). Additionally, low overlapping on space use among fish subgroups may reduce intraspecific competition and therefore improve the overall fitness of the population (WELSH; BELLWOOD, 2012b).

Sparisoma axillare mean HR size (0.25 ± 0.10 km²) were comparable to the HR estimated for *S. cretense* (LA MESA *et al*., 2012), however about 6 to 30 times greater than the previously reported by other acoustic telemetry studies on parrotfish species (AFONSO *et al*., 2008; WELSH; BELLWOOD, 2012b; GARCIA *et al*., 2014; DAVIS *et al*., 2017). Mean HR for *L. alexandrei* (0.19 ± 0.08 km²) were equivalent to the estimated for *Lutjanus apodus* (GARCIA *et al*., 2014) and *Lutjanus campechanus* (FROEHLICH *et al*., 2019), although about 6 to 50 times greater than the observed by other studies on *Lutjanus* species (HAMMERSCHLAG-PEYER; LAYMAN, 2010; HITT *et al*., 2011a; TOPPING; SZEDLMAYER, 2011). Such differences on HR sizes might be related to specific environmental and ecological features of the different studied sites and to species-specific requirements and behavior (ZELLER, 1997). However, it could also be a consequence of the different methods used to detect the acoustic signals. A common characteristic of the above-mentioned studies with markedly smaller HRs estimates was the utilization of active acoustic tracking instead of a multi-receiver passive monitoring array as used in the present study. During the active tracking, acoustic signals are detected by a hydrophone connected to a receiver on the surface and fish position fixes are recorded using a GPS as fish are individually tracked. However, the monitoring period for each fish is usually limited to a few tracking sections (from one to a few days) of short duration (generally no more than 24h) (BROWNSCOMBE *et al*., 2019). Therefore, this method identifies fine-scale movement patterns over limited time intervals which may not encompass the entire individuals' activity space and then provide underestimated HRs. On the other hand, estimates of fish positions within passive monitoring acoustic arrays are related to the detection ranges of the receivers and are then subject to a higher level of uncertainty (up to hundreds of meters). In the present study, such uncertainties were incorporated on the estimative of the utilization distributions (KUD_{95} and KUD_{50}) as a kernel bandwidth of 150m (corresponding to the 50% detection probability range) and, therefore, could have resulted in overestimated home ranges.

Low variability on HR and CR sizes were observed among individuals within each species. For *S. axillare* both HR and CR were uncorrelated to fish total length, as previously observed for *S. cretense* (AFONSO *et al*., 2008) and *Chlorurus microrhinos* (WELSH; BELLWOOD, 2012b). Indeed, for adult populations of *S. cretense* HR size seemed to be related to individual type of social behavior (*i.e.*, group fish or territorial fish) instead of body length (AFONSO *et al*., 2008). For *L. alexandrei*, a moderate positive relationship between HR and fish total length was observed, though it was only marginally significant ($r_s = 0.62$, $p = 0.09$). Such positive relationship is often attributed to an increase on resources requirements of larger individuals (WAKEMAN *et al*., 1979; KRAMER; CHAPMAN, 1999) and were also observed for *L. campechanus* (TOPPING; SZEDLMAYER, 2011; PIRAINO; SZEDLMAYER, 2014; FROEHLICH *et al*., 2019) and *Lutjanus decussatus* (NANAMI; YAMADA, 2008). However, other studies on snappers have found no influence of body length on HR size (HAMMERSCHLAG-PEYER; LAYMAN, 2010; Hitt *et al*., 2011a), so other factors like competition (JONES, 2005), individual learning and behavior (BROWN; LALAND, 2003; PARSONS *et al*., 2003) as well as resources availability and seascape structure (HITT *et al*., 2011b; PITTMAN *et al*., 2014) could also explain HR variability within fish populations. It is possible that the results reported here were influenced by the small number of tagged fish, which is a recurrent issue in acoustic telemetry studies (LUO *et al*., 2009; HAMMERSCHLAG-PEYER; LAYMAN, 2010). Moreover, for both species the minimum fish sizes suitable for tagging were limited by the transmitters' sizes in order to not exceed the 2% tag/body mass threshold and were then biased to larger individuals. Thus, further investigation on a higher number of individuals comprising a broader size scale (including juvenile and/or sub-adult individuals present in the NTZ) would provide a better understanding on how HR size varies within S. *axillare* and *L. alexandrei* populations inhabiting the shallow coastal reefs of Tamandaré.

This study was the first to investigate movements and habitat use of teleost coral reef fishes by means of acoustic telemetry in Brazil and provides invaluable insights on the efficiency and functioning of the NTZ established in the coastal reefs of Tamandaré. The effect of the Tamandaré NTZ in terms of increasing fish density and size was shown; however, our findings also highlight the importance of fisheries management outside the NTZ where fishing pressure is high (SILVEIRA, 2018) and capable of promoting a rapid decline in *S. axillare* and *L. alexandrei* populations. In addition, due to ontogenetic migrations, protection for areas that shelter older life stages of both species are necessary to maintain healthy stocks capable of continuing to sustain a high fishing pressure. Protection of larger areas in order to encompass the reef continuum seems to be necessary although the implementation of large NTZs or the increase of the size of existing NTZs is not an easy task. Recent works have highlighted the need to protect spawning areas (FRANÇA *et al*., 2021) and deeper habitats (EDUARDO *et al*., 2018) on Brazilian coral reef complexes. The establishment of more NTZs along the Northeastern coast of Brazil is part of the management plan of the large Coral Coast MPA and therefore this study indicates the importance of considering both isolation and connectivity in the design of new protected areas, as well as the relevance of including a heterogeneity of reef habitats.

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4 ARTIGO 3 – DIEL ACTIVITY AND HABITAT UTILIZATION BY TWO REEF FISH SPECIES IN A MARINE PROTECTED AREA IN BRAZIL

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ABSTRACT: The diel cycle is one of the major environmental factors that drives reef fish activity patterns and spatial occupation. In the present study, we used acoustic telemetry to investigate the diel variability in the activity patterns of two poorly known endemic Brazilian reef fish species, the gray parrotfish *Sparisoma axillare* and the Brazilian snapper *Lutjanus alexandrei*. From December 2016 to October 2017, 20 *S. axillare* and 9 *L. alexandrei* were tagged with acoustic transmitters and passively monitored in a marine protected area in Brazil. Detections were divided into diurnal and nocturnal periods, and then four diel activity pattern indicators were calculated for each fish: detections per hour, movement rate, home range and spatial equitability. A clearly diurnal behavior was observed for *S. axillare*, with significantly higher values for movement, home range and spatial equitability during the day. On the other hand, a period of higher activity was not observed at species level for *L. alexandrei*. However, multivariate analyses suggested an individual-level heterogeneity in the activity patterns of most fish. Thus, an intra-population mixed day/night activity pattern was observed for *L. alexandrei* indicating that biological factors may interact to determine individual fish behavior.

Keywords: Acoustic telemetry. Diel periodicity. Movement. No-take zone. Home range. Labridae. Lutjanidae.

INTRODUCTION

Reef fish assemblages are known to undergo conspicuous day-night shifts on species composition and abundance (HOBSON, 1972; TRAVERS *et al*., 2006; AZZURRO *et al*., 2007; MYERS *et al*., 2016) associated to the fluctuations of light intensity between diurnal and nocturnal periods (MCFARLAND *et al*., 1979; HOBSON *et al*., 1981; RICKEL; GENIN, 2005).

For most fish species, activity patterns tend to be either diurnal, nocturnal, or crepuscular (HOBSON, 1965; MACFARLAND, 1991). However intra-specific variability in diel patterns may be driven by many factors (REEBS, 2002), such as ontogeny (MAGNAN; FITZGERALD, 1984; ROUSSEL; BARDONNET, 1999), changes in environmental conditions (*e.g.*, seasonality, temperature,) (FRASER *et al*., 1993, 2011), and biological factors such as predation risk, prey availability and intra-specific competition (FOX; BELLWOOD, 2011; KOECK *et al*., 2013; WILLIAMS-GROVE; SZEDLMAYER, 2016).

The diel cycle is one of the key environmental factors that drives reef fish activity patterns and spatial occupation (MEYER *et al*., 2007a; HARVEY *et al*., 2012; HONDA *et al*., 2016). The size of home range and covered distances varies between behavioral types and time of activities, such as feeding during the day or sheltering at night (JONES, 2005; DAVIS *et al*., 2017). Diel activity patterns are also related to differential uses of the seascape between day and night promoting biological connectivity among habitats (VERWEIJ *et al*., 2006; HITT *et al*., 2011b).

Parrotfish are typically diurnal species that forage actively during the day and seek shelter at night (DUBIN; BAKER, 1982; LINDHOLM *et al*. 2006; HOWARD *et al*. 2013, DAVIS *et al* 2017). On the other hand, snappers are widely assigned as primarily nocturnal feeders (HOBSON, 1965; ROOKER, 1995; HITT *et al*., 2011a; ROOKER *et al*. 2018). Juvenile and adult snappers usually shelter on habitats of high structural complexity such as reefs and mangroves roots by day and often move to nearby seagrass beds or sand plains (ROOKER; DENNIS, 1991; ROOKER *et al*., 2018), or disperse among the reef and adjacent sand bottom (HITT *et al*., 2011a, 2011b). However, plasticity is expected for the snappers as some species are diurnally active or with mixed diel behaviors (STARCK; DAVIS, 1966, MUELLER 1994, WILLIAMS-GROOVE, 2016).

In the present study, we used acoustic telemetry to investigate the diel variability in the activity patterns of two poorly known endemic Brazilian reef fish species, the gray parrotfish *Sparisoma axillare* (Steindachner, 1878) (Labridae) and the Brazilian snapper *Lutjanus alexandrei* Moura & Linderman, 2007 (Lutjanidae). Both *S. axillare* and *L. alexandrei* are important resources for the artisanal fisheries in Northeast Brazil (SILVEIRA, 2018). The study was conducted within a no-take zone, where positive effects of protection such as the increase in fish size and density have been reported for both species (Chapter 3). The knowledge on species diel patterns may have important implications for management and conservation of species and ecosystems, including the design of marine protected areas and marine spatial planning.

MATERIALS AND METHODS

Study area

The monitored area is located on the Tamandaré coral reef complex off Pernambuco state coast, in the Northeast Brazil (8° 44’ S, 35° 6’ W), and include the main reef formations inside and around a 2.7km² well-enforced no-take zone (NTZ) established in 1999 (Figure 1). Two multiple-use marine protected areas (MPA) also encompass the studied reefs: Municipal Natural Park of Tamandaré Fort MPA (established in 2003) and Coral Coast MPA (created in 1997, subjected federal regulation). About 30% of the NTZ area is covered by coral reef formations, which are located on its north side and are contiguous to the reefs outside NTZ.

Tamandaré coral reefs are distributed along three lines with an overall formation that resembles fringing reefs as they run parallel to the coast and present a shallow lagoon between first and third reef lines with a poorly developed spur-and-groove system in some areas of the fore reef. These reefs raise as isolated columns forming patch reefs or pinnacles from depths of 1 to 12 m and extend up to 7 m high. Their tops might be exposed at low tides or be permanently submerged a few meters below the surface. Reef tops expand laterally as overhanging edges creating shaded areas and caves of variable sizes that are used as shelter by many reef fish species. Where these reefs are densely aggregated, their tops coalesce creating larger barriers with extensive systems of interconnected caves below their surfaces (MAIDA; FERREIRA, 1997).

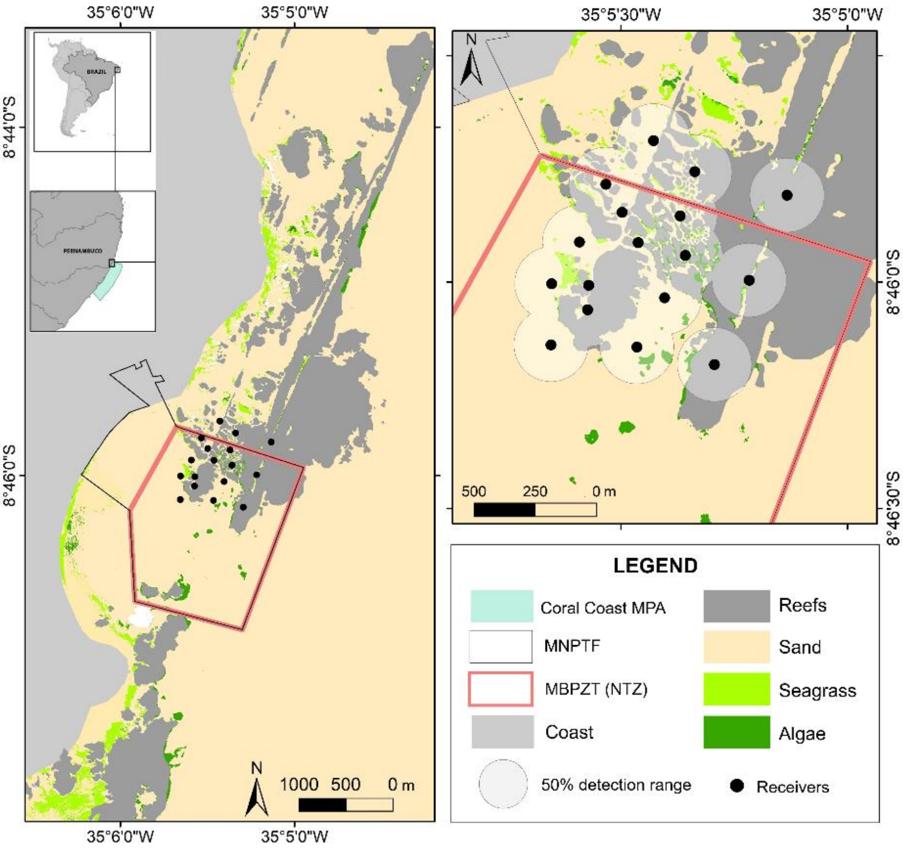
The region has a semidiurnal tide cycle and is classified as mesomareal with a tidal range of approximately 1.7 - 2.5 m at spring tide and 0.6 - 1.4 m at neap tide. During low tide, the third line of reefs act as a barrier protecting areas within the lagoon from wave and current actions, thus maintaining a calm and clear water condition. As the tide rises and incoming waves overcome the reef crest, turbulence inside the inner lagoon increases. The climate is tropical with mean annual precipitation of 200 cm and two distinct seasons: a rainy winter (May – September with 70-75% of annual precipitation) and a dry summer (August - April). Mean temperature ranges from approximately 30 °C in summer to 26 °C in winter.

Acoustic monitoring system

An array of 17 omnidirectional acoustic monitoring receivers (VR2W-69kHz, VEMCO) were deployed (from December 2016 to August 2018) to monitor the movements of *S. axillare* and *L. alexandrei* (Figure 1). Preliminary range tests conducted inside the NTZ demonstrated that, in addition to distance between receivers and transmitters, tide level also had a negative effect on detection probability. A minimum detection rate of 50% was obtained for transmitters at a distance of 150 m and therefore this range was used as guideline to design the array. At 300 m, average detection probability dropped to below 5% during high tide hours (GIACALONE *et al*., 2016). Also, no diel differences were observed on detection efficiency (Wilcoxon signed-rank test, $W = 236$, $p = 0.45$).

In most cases, receivers positioning allowed for overlapping detection ranges and total area covered by the array was approximately 1 km^2, including more than 80% of the reef area inside the NTZ and the reef formations adjacent to its northern border. Depth inside monitored area ranged from 1 – 12 meters. As reef tops may be exposed (or just below the surface) during low tide, receivers were placed over the sandy bottom around the reefs, moored in a PVC pipe attached to a concrete base to ensure vertical positioning and avoid dragging. Data download, battery check and clearing of fouling organisms took place every 1-2 months.

Figure 1 – Map of the study area in the Tamandaré coral reef complex off the northeast coast of Brazil. Left panel: locations of the Coral Coast MPA, Municipal Natural Park of Tamandaré Fort (MNPTF) and the NTZ. Right panel: locations of the acoustic receivers (black dots) and 50% detection range (light grey shaded area).



Fonte: Autor (2021)

Fish collection and tagging

Between December 2016 and May 2017, 20 *S. axillare* and 9 *L. alexandrei* were caught exclusively inside the NTZ (Figure 1). Individuals were caught with hand nets by divers on SCUBA during nighttime. At this period, fish are either "sleeping" (*S. axillare*) and/or with reduced flight capability (*L. alexandrei*). This way, impact was minimized, as only fish from target species and with a desirable body size were selected and easily caught. This capture method reduced the disturbance to local fish community and the risk of injury caused by fishing gears. Individuals were transported to a research facility on land and kept in 1,000 L holding tanks with direct seawater flow to be monitored for 24 hours prior tag implantation. *Sparisoma axillare* were implanted with individually coded V9-4L 69 kHz acoustic transmitters (30-90 s. delay, 476 days expected lifetime, VEMCO Ltd., Canada) while *L. alexandrei* were implanted with V8-4L 69 kHz acoustic transmitters (30-90 s. delay, 150 days expected lifetime, VEMCO Ltd., Canada). Prior surgery, fish were transferred to a smaller tank and anesthetized in a seawater and eugenol solution (0.04 ml L^{-1}), weighted (total weight, nearest g) and measured (total length, nearest mm). Individuals were then placed in a "V" shaped bed and 6 - 9 scales were plucked from the ventral midline to expose tag insertion area. Transmitter was cleaned in povidone-iodine and then surgically inserted into the peritoneal cavity through a 1.5 - 2.0 cm incision, which was closed with 2 or 3 stitches of absorbable 4/0 monofilament suture. Direct seawater flow was maintained through the gills by a water pump allowing fish to breath normally throughout surgery procedure. After surgery, individuals were returned to holding tanks and observed for a 24h period prior to release. Releases took place during early morning at the same sites of capture. All tagged *S. axillare* were initial phase females with a mean size of 26.5 ± 2.3 cm TL and mean weight of 296.3 ± 73.5 g. *Lutjanus alexandrei* sex was not determined and mean size and weight was 22.5 ± 2.3 cm TL and 186.3 ± 60.3 g, respectively (Table 1). For all individuals, the tag-to-body relationship never exceeded 2% ($\bar{x}$ = 1.49% ± 0.38, range = 0.83 - 1.95%) of fish total weight in air, as recommended by the transmitter's manufacturer.

Data analysis

Prior to analysis, spurious detections (i.e., any detection from a single fish occurring alone within a 24 h period) were removed to prevent any false-positive detections (MARCH *et al*., 2011; HARASTI *et al*., 2015). Detections obtained within the first 24 h post-releasing were also excluded from all individuals to avoid potentially negative effects of tagging procedure on fish behavior (HONDA *et al*., 2016).

In order to identify short-term periodicity patterns in the time series, detections from the entire acoustic array were pooled into hourly bins and analyzed for each fish by applying the Fast Fourier Transformation (FFT) (AFONSO *et al*., 2009; GARCIA *et al*., 2015). In this analysis, predominant periods of cyclical patterns - for example, diel (24 h) or tidal (12 h) patterns - are indicated as peaks in the power spectra. Hamming window were selected as smoothing filter to reduce the amplitude of spectral leakages (artificially introduced high-frequency components) and produce clearer spectral responses.

Detections were then separated into the different phases of the day – diurnal, nocturnal and crepuscular (dawn and dusk). The duration of each phase was estimated daily using the civil twilight timetable (available at the Geoscience Australia website) for the study site coordinates (http://www.ga.gov.au/geodesy/astro/sunrise.jsp; accessed 15 June 2018). During the monitoring period, the average length of diurnal period was slightly longer than the nocturnal period (12h05min for daytime and 11h10min for nighttime) while dawn and dusk had an average duration of 00h21min each. Because of the short duration of crepuscular phases and the impossibility of estimating centers of activity (based on 60 min bins) that fall entirely within dawn and dusk, detections from these periods were excluded from the following analysis.

Permanence within the monitored area was quantified for each fish by a residency index (I_R) expressed as the total number of days an individual was detected divided by the individual's detection span (number of days between release and the last detection) (AFONSO *et al.*, 2008; ALÓS *et al*., 2012). I_R values range from 0 (no residency) to 1 (permanent residency) and were calculated to assess day and night overall residency (detections obtained for each period over the entire acoustic array). Differences on I_R between day and night was assessed for each species using a Wilcoxon signed-rank test.

To investigate diel variability in fish behavior (i.e., at which phases of the day fish were likely to be more active or resting), the following activity pattern indicators were estimated for each individual for diurnal and nocturnal phases: detection frequency (h^{-1}), spatial evenness, movement rate ($m.h^{-1}$) and home range (km^2). Mean hourly detection frequencies were obtained daily and standardized dividing the number of detections by the duration of each period. Overall spatial evenness was calculated based on a diversity index of space use adapted from Pielou's evenness index (TINHAN *et al*., 2014), and indicates how fairly the detections are distributed among the receivers for day and night phases over the entire detection span. Values range from 0 to 1, with results closer to 0 suggesting a strong site attachment while values closer to 1 indicate that the monitored area is being evenly used. Prior to movement rate and home range analysis, Centers of Activity (COAs) were calculated for each fish at 60 min intervals (SIMPFENDORFER *et al*., 2002). This method uses the weighted means of the number of detections registered by each receiver to estimate fish position (mean latitude and longitude) within the selected time interval. For each day, the hour bins that comprised the sunrise and sunset periods were excluded to avoid the possibility that a single COA could include detections from both diurnal and nocturnal periods. Mean hourly movement rate was then estimated as the sum of the linear distances between pairs of consecutive COAs divide by the duration of each phase (GANDRA *et al*., 2018). To reduce the underestimation of individuals' movement rates, only the phases of the day with a minimum of four calculated COAs were selected to this analysis. Overall home range (defined as 95% KUD) areas were calculated for daytime and nighttime based on COAs estimates over the entire individual's detection period, using the nonparametric kernel utilization distribution (KUD). Utilization distributions were estimated based on bivariate fixed kernels (WORTON, 1989) over a 25 x 25 m cell grids and a fixed bandwidth smoothing factor (h) of 150 m (corresponding to the 50% detection probability range). As observed during diurnal and nocturnal dives in the monitored reefs, both species are highly reef attached and the use of bare sand/mud areas are limited to the immediate reef vicinities. Therefore, the entire 95% KUD areas were considered an over-estimation of the actual home range used by both species. To produce more reliable home ranges estimates, the surrounding sand covered areas located more than 50 m away from any reef formation were excluded from the 95% KUD area. This method reduced the diurnal and nocturnal HRs of *S. axillare* by 26.4 ± 8.9 % and 25.9 ± 8.9 %, respectively. For *L. alexandrei*, diurnal and nocturnal HRs were reduced by 36.7 ± 8.1 % and 31 ± 5.8 %, respectively. The majority of seagrass and macroalgae patches present in the monitored area were included within the 50 m limit range. Hourly movement rate and home range analysis were performed using the Home Range Tools extension for ArcGIS 10.4 (RODGERS *et al*., 2015). All the activity pattern indicators were only estimated for fish with a number of COAs >20 for each phase of the day.

To account for the lack of independency between diurnal and nocturnal data, the differences in the activity pattern indicators (detection frequency, spatial evenness, movement rate and home range) were tested between species and daily phases using a repeated measures permutational multivariate analysis of variance (RM-PERMANOVA) as suggested by ANDERSON *et al*. (2008). Three factors were included in the design: "Species" (between-subjects, fixed, with two levels: *S. axillare* vs *L. alexandrei*), "FISH ID" (between-subjects, random, nested in "Species" with 18 levels: 09 *S. axillare* and 09 *L. alexandrei* individuals) and "Daily Phase" (within-subjects, fixed, two levels: Day vs Night). Data were normalized to eliminate the scale differences among activity pattern indicators, and analysis was then performed based on a Euclidean distance dissimilarity matrix. P (Monte Carlo) values were obtained with 9999 permutations of residuals under a reduced model. For all significant factors, permutational pair-wise t-tests were performed. The effects of "Species" and "Daily Phase" on each activity pattern indicator were also analyzed by a Two-way Mixed-Design ANOVA. Data were $\log_{10}$ (X+1) transformed to meet normality (Shapiro-Wilk test). As the within-subjects factor "Daily Phase" had only two levels (Day vs Night), the assumption of sphericity was not a requirement. Tukey's HSD test was used to identify significant differences among means.

Principal Components Analysis (PCA) and hierarchical cluster analysis were then used to investigate whether there were groups of individuals with distinct diel activity patterns within a species (i.e., fish with a primarily diurnal or primarily nocturnal behavior). Analyses were carried out for each species based on the same dataset (and data treatments) previously used for the RM-PERMANOVA. The significance of diel variability in fish activity patterns was tested between- and within-groups using RM-PERMANOVA and Two-way Mixed-Design ANOVA, following the same procedures describe above.

Overlap index (OI) and centroid distances (CD) were used to investigate space-use sharing between diurnal and nocturnal home ranges (HITT *et al.*, 2011b; ALÓS *et al.*, 2012). Overlap index was calculated for each fish as: $OI = OV_{(HRd,\ HRn)} \div (HR_d + HR_n)$, where $OV_{(HRd,\ HRn)}$ is the overlap area between day and night home ranges and $(HR_d + HR_n)$ is the combination of day and night home ranges. Values range from 0 (no overlap and diel migrations between discrete day and night HRs are likely to occur) to 1 (diel HRs are completely overlapped, and fish show high site fidelity). Centroids distances were measured as the linear distances between diurnal and nocturnal HRs. The overlapped and combined HR areas, centroids coordinates, and distance measurements were obtained using geoprocessing tools on ArcGIS 10.4. Comparisons of OI and CD between species and between *L. alexandrei* behavioral groups (i.e., Primarily Diurnal and Primarily Nocturnal) were made using Student's t-tests. Relationship between OI and fish total length was assessed using Pearson's correlation coefficient.

Analysis was conducted in Statistica v. 8.0 (Statsoft Inc. 2007) and PRIMER v. 6.1 with the PERMANOVA+ package software. Data was reported as mean ± standard error (S.E.) and significance was tested at $\alpha = 0.05$.

Ethics Statement

This research was approved by Ethics Committee and Animal Use of the Federal University of Pernambuco (CEUA-UFPE Number: 23076.007810/2015-01) and Chico Mendes Institute for Biodiversity Conservation (ICMBIO – Sisbio License: 45992).

RESULTS

The tagging and monitoring data of the 20 gray parrotfish (*S. axillare*) and 9 Brazilian snappers (*L. alexandrei*) are summarized on Table 1. Three *S. axillare* were detected for a short period of 6 days or less (SPAAXI #02, #12 and #14) which suggests that these fish may have lost their tags, prematurely left the monitoring area, or died either by predation, fishing or as a consequence of tagging procedure. Other *S. axillare* (SPAAXI #05) was assumed to be dead few days after tagging as this fish was continuously being detected by only one receiver and detection ceased only after the transmitter's estimated lifespan was over. Therefore, these four *S. axillare* individuals were excluded from all subsequent analysis. The remaining 16 *S. axillare* and all *L. alexandrei* individuals were monitored between 16 and 187 days, from December 2016 to October 2017 (Table 1).

Sparisoma axillare was more consistently detected during the day ($I_{R\ day}$, $\bar{x} = 0.80 \pm 0.06$) than at night ($I_{R\ night}$, $\bar{x} = 0.51 \pm 0.09$) (Wilcoxon signed-rank test, W=108, p<0.01), while no diel variability on I_R was observed for *L. alexandrei* ($I_{R\ day}$, $\bar{x} = 0.86 \pm 0.05$ and $I_{R\ night}$, $\bar{x} = 0.94 \pm 0.03$ S.E.). After pooling detections to hourly bins, a total of 4,608 centers of activity (COAs) were obtained for *S. axillare* and 8,758 for *L. alexandrei*. Both species showed higher numbers of COAs during daytime.

The Fast Fourier Transformation analysis revealed a primary 24h rhythmicity on hourly detections for 80% (13 out of 16) of *S. axillare* and 90% (8 out of 9) of *L. alexandrei* individuals (Table 1). The remaining individuals (except SPAAXI #19) presented a secondary 24h peak on spectral density. A 12h periodicity, could also be observed in several fish of both species.

All *L. alexandrei* and nine *S. axillare* (SPAAXI #01, #03, #06, #07, #15, #16, #17, #18 and #20) (Table 2) were selected for the activity pattern indicators estimates (i.e., hourly detections, movement rate, home range and spatial evenness) and all subsequent analysis. Seven *S. axillare* were excluded from analysis due to the low number of COAs (<20) obtained during nighttime.

Table 1 – Summary of the monitoring data for the *Sparisoma axillare* (n = 20) and *Lutjanus alexandrei* (n = 09) individuals monitored in the costal reefs of Tamandaré-PE. TL: total length (cm); TW: total weight (g); I_R: residency index; COAs: centers of activity; D: day; N: night. Fast Fourier Transformation (FFT) analysis shows the dominant peaks in decreasing order of amplitude. Fish IDs in bold text indicate the eligible individuals for the activity patterns indicators estimates. † Individuals that prematurely left the array, lost the tag, or died. NA: not available.

Fish species and ID	**TL (cm)**	**Date released (d/m/y)**	**Detection span (days)**	**No. of detections**		**No. of receivers**		**I_R**		**No. of COAs**		**FFT**
				D	**N**	**D**	**N**	**D**	**N**	**D**	**N**	
Sparisoma axillare												
SPAAXI #01	26.2	13/12/2016	51	5554	7017	07	02	1.00	0.98	437	283	24h
SPAAXI #02†	26.1	13/12/2016	01	84	02	03	01	NA	NA	NA	NA	NA
SPAAXI #03	25.5	12/01/2017	18	2714	1302	05	02	0.94	1.00	141	127	24, 12h
SPAAXI #04	25.0	12/01/2017	25	1197	24	10	03	1.00	0.80	164	11	24, 12h
SPAAXI #05†	31.5	14/01/2017	480	19197	14559	01	01	NA	NA	NA	NA	NA
SPAAXI #06	25.0	14/01/2017	23	606	120	07	02	1.00	0.78	35	33	12, 24h
SPAAXI #07	27.7	14/01/2017	17	370	566	08	04	0.94	1.00	72	84	24h
SPAAXI #08	33.0	20/01/2017	107	419	18	05	02	0.57	0.01	142	07	24h
SPAAXI #09	27.0	20/01/2017	26	63	-	03	-	0.77	-	34	-	24h
SPAAXI #10	25.4	20/01/2017	55	456	32	03	02	0.89	0.09	189	12	24h
SPAAXI #11	27.5	20/01/2017	91	122	03	01	01	0.42	0.01	56	02	24h
SPAAXI #12†	25.0	20/01/2017	06	19	-	02	-	NA	NA	NA	NA	NA
SPAAXI #13	25.2	26/01/2017	56	137	40	03	04	0.63	0.23	62	17	24h
SPAAXI #14†	29.0	26/01/2017	03	66	412	02	06	NA	NA	NA	NA	NA
SPAAXI #15	25.0	30/03/2017	59	5056	1945	07	06	1.00	0.98	526	216	24h
SPAAXI #16	24.5	30/03/2017	180	6959	5026	05	06	0.12	0.18	168	163	24, 12h
SPAAXI #17	26.8	30/03/2017	38	6816	6769	07	04	1.00	1.00	310	204	12, 24h
SPAAXI #18	24.3	28/04/2017	159	1792	1175	06	02	0.90	0.58	449	212	24, 12h
SPAAXI #19	25.6	28/04/2017	28	628	75	08	01	0.89	0.36	112	13	12h
SPAAXI #20	24.2	28/04/2017	187	866	61	08	02	0.68	0.23	285	42	24h
Lutjanus alexandrei												
LUTALE #01	24.0	13/12/2016	24	113	3009	04	04	0.83	1.00	36	205	24h
LUTALE #02	21.5	13/12/2016	152	23144	6666	05	05	0.95	0.80	976	199	24, 12h
LUTALE #03	24.5	12/01/2017	135	12144	2010	06	06	0.99	0.96	1179	526	24h
LUTALE #04	25.2	12/01/2017	101	832	2309	09	06	0.89	1.00	144	677	24, 12h
LUTALE #05	23.1	12/01/2017	19	397	1496	09	06	0.84	0.89	53	49	12, 24h
LUTALE #06	24.5	14/01/2017	143	3151	36585	08	08	0.89	1.00	342	1484	24h
LUTALE #07	19.5	30/03/2017	150	16840	28997	04	04	1.00	0.96	1248	998	24, 12h
LUTALE #08	20.4	28/04/2017	107	288	1744	01	04	0.50	0.83	80	448	24, 12h
LUTALE #09	19.5	05/05/2017	16	775	110	04	04	0.81	1.00	89	25	24h

Fonte: Autor (2021)

Table 2 – Mean (± S.E.) values of the activity patterns indicators (hourly detections, movement rate, home range and spatial evenness) estimated for the selected *Sparisoma axillare* and *Lutjanus alexandrei* individuals in the coastal reefs of Tamandaré-PE.

Fish species and ID	**Detections (h^{-1})**		**Movement rate ($m.h^{-1}$)**		**Home range (km^2)**		**Spatial Evenness**	
	Day	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**
Sparisoma axillare								
SPAAXI #01	8.71±0.63	12.7±1.35	64.92	0.97	0.09	0.05	0.16	0.01
SPAAXI #03	12.1±1.45	6.65±0.66	56.09	3.16	0.13	0.07	0.35	0.15
SPAAXI #06	2.11±0.47	0.48±0.12	31.35	2.19	0.36	0.17	0.36	0.03
SPAAXI #07	1.74±0.40	2.93±0.52	89.05	3.72	0.41	0.18	0.54	0.04
SPAAXI #15	7.29±0.54	2.89±0.58	34.23	2.76	0.21	0.18	0.26	0.09
SPAAXI #16	34.1±3.49	25.4±2.85	28.26	1.11	0.21	0.18	0.15	0.02
SPAAXI #17	15.0±1.52	15.3±1.32	43.79	2.95	0.15	0.13	0.27	0.26
SPAAXI #18	1.02±0.13	0.66±0.09	27.79	1.62	0.33	0.20	0.44	0.10
SPAAXI #20	0.51±0.07	0.05±0.01	22.93	1.90	0.33	0.19	0.48	0.08
Mean ± S.E.	9.17±3.56	7.44±2.89	44.3±7.29	2.26±0.32	0.25±0.04	0.15±0.02	0.33±0.05	0.09±0.03
Lutjanus alexandrei								
LUTALE #01	0.38±0.09	10.9±1.19	58.65	3.46	0.12	0.12	0.32	0.01
LUTALE #02	13.0±0.94	3.92±0.37	13.87	21.19	0.15	0.19	0.10	0.39
LUTALE #03	7.32±0.60	1.27±0.12	12.27	49.28	0.07	0.17	0.04	0.40
LUTALE #04	0.67±0.08	1.92±0.12	64.48	9.73	0.46	0.21	0.61	0.17
LUTALE #05	1.87±0.44	7.65±1.18	46.13	7.70	0.23	0.19	0.60	0.19
LUTALE #06	1.89±0.25	21.4±0.56	27.45	8.47	0.37	0.17	0.37	0.05
LUTALE #07	9.56±0.48	15.7±1.29	10.83	8.74	0.13	0.14	0.06	0.01
LUTALE #08	0.26±0.06	1.51±0.16	3.37	1.79	0.17	0.18	0.00	0.04
LUTALE #09	4.31±0.99	0.54±0.12	14.47	39.93	0.07	0.14	0.03	0.43
Mean ± S.E.	4.37±1.53	7.19±2.46	27.9±7.57	16.7±5.62	0.19±0.05	0.17±0.01	0.24±0.08	0.19±0.06

Fonte: Autor (2021)

The repeated measures PERMANOVA showed a significant interaction between factors “Species” and “Daily Phase” (Table 3). Pair-wise tests revealed that significant difference between species was restricted to the nocturnal phase and a diel variability was observed only for *S. axillare*. Mixed-design ANOVAs of each activity pattern indicator found significant differences between diurnal and nocturnal phases for movement rate, home range and spatial evenness (Table 3). Tukey HSD tests showed that such differences were due to significantly higher values obtained during daytime for *S. axillare*, whereas no differences were observed for *L. alexandrei* (Figure 2). Also, no diel variability on number of hourly detections was observed for both species.

For *S. axillare*, the Principal Component Analysis (PCA) followed by a hierarchical clustering arranged the individuals’ diurnal and nocturnal activity patterns in two distinct and temporally homogeneous groups: a high activity-diurnal group and a low activity-nocturnal group (Figure 3). The first two axes of the PCA explained nearly 89% of the total variation. PC1 (that explained 56.5% of the variation) was characterized by an increase on movement rate, home range and spatial evenness values (positive loadings and similar magnitudes) from the low activity-nocturnal group (lower scores) towards the high activity-diurnal group (higher scores). Detection frequency, however, showed a negative relationship with the other variables (negative loading). PC2 was mostly driven by detection frequency and explained 32.4% of the variation. Therefore, it was observed that all *S. axillare* individuals displayed a clear diurnal behavior characterized by higher values for the activity pattern indicators, except for the number of hourly detections.

On the other hand, a phase of the day of more intense activity could not be observed for *L. alexandrei* at species level (Figure 2). However, PCA indicated an individual-level heterogeneity on the diel behavior for most fish (Figure 4). PC1 contributed with 67.9% of the 84% total variability explained by the two axes and, as observed for *S. axillare*, was positively related to movement rate, home range and spatial evenness (positive loadings), but negatively related to the detection frequency (negative loading). Thus, a primarily diurnal or nocturnal behavior could be observed for 7 individuals (LUTALE #1, #2, #3, #4, #5, #6, #9) by having their respective day and night activity patterns plotted far apart from each other and on opposite sides along the PC1. Also, hierarchical clustering revealed two distinct, but temporally mixed groups (i.e., diurnal and nocturnal activity patterns within the same cluster). The High Activity group comprised the daily phases when individuals had higher home range, movement rate and spatial evenness values, but lower detection frequency. In this group were included the diurnal activity pattern of LUTALE #1, #4, #5 and #6 and the nocturnal activity pattern of LUTALE #2, #3, #9. In contrast, the Low Activity group was composed by the respective periods of reduced activity for the abovementioned individuals. Both diurnal and nocturnal activity patterns of LUTALE #7 and #8 were also included within the Low Activity group, therefore suggesting an absence of diel variability for these individuals. *Lutjanus alexandrei* individuals were then classified into three distinct behavioural groups: Primarily Diurnal fish (composed by LUTALE #1, #4, #5 and #6), Primarily Nocturnal fish (LUTALE #2, #3, #9) and Cathemeral/Undefined fish (LUTALE #7 and #8). Repeated measures PERMANOVA conducted between Primarily Diurnal and Primarily Nocturnal groups showed a significant effect for the interaction “Behavioral Group x Daily phase” (Table 4). Following pairwise tests yielded significant diel variability within both groups as well as differences between groups during diurnal and nocturnal phases. Moreover, mixed-design

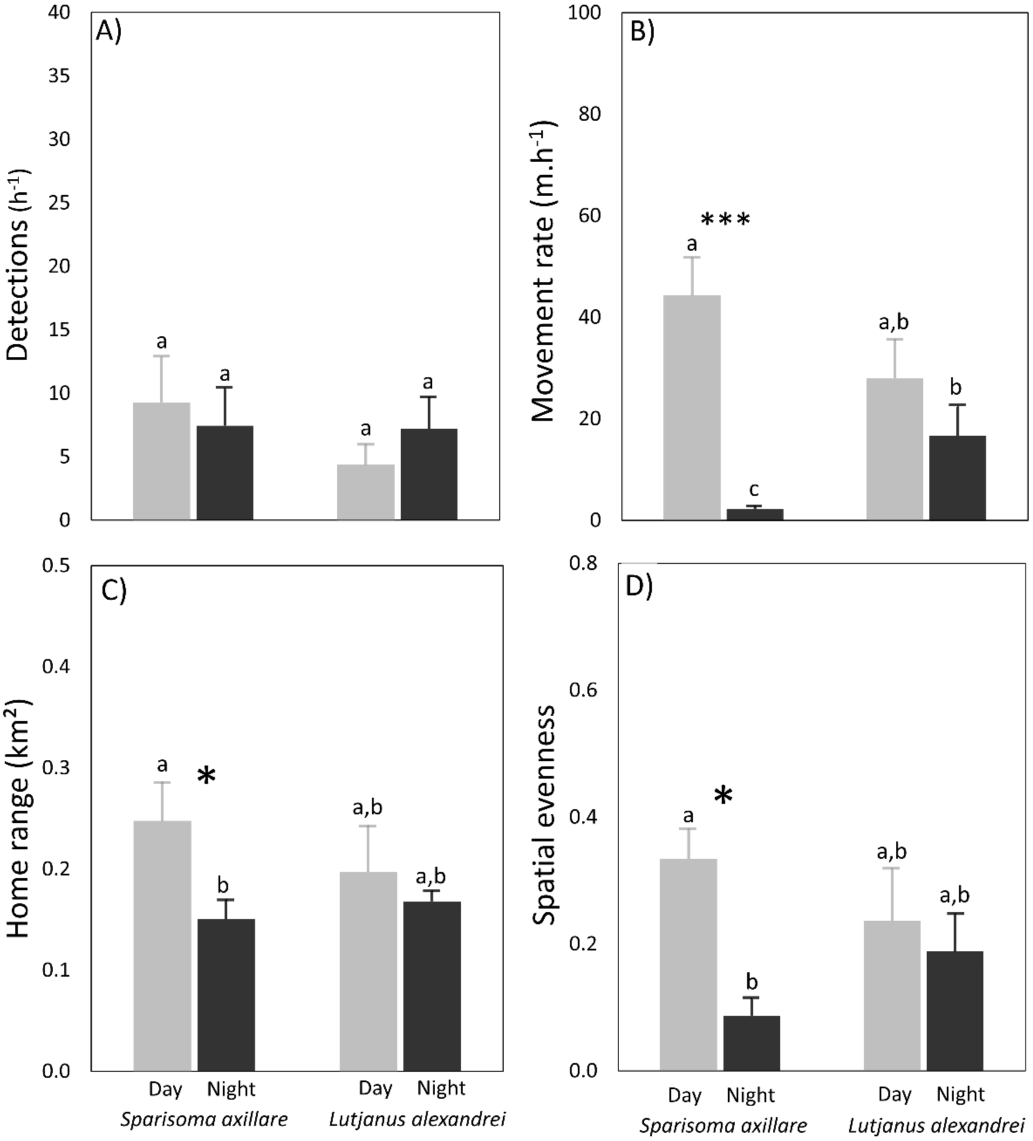
ANOVAs showed that all the activity pattern indicators had significant interactions between factors “Behavioral Groups” and “Daily Phases” (Table 4), emphasizing the opposite diel behavior between the two groups. Both groups showed significant diel variabilities for detection frequency and spatial evenness (Figure 5). Movement rate was significantly higher during the day for the Primarily Diurnal individuals and no differences were observed for home range size. No differences in fish total length were found between the behavioral groups (Student’s t test, t = 179, p = 0.13). Cathemeral/Undefined group was not considered in analysis due to the low sample size.

Table 3 – Mixed-design ANOVA results for the effects of “Species” (between-subject factor, two levels: *Sparisoma axillare* and *Lutjanus alexandrei*) and “Daily phases” (within-subjects factor, two levels: day and night) on the activity patterns indicators: detections (h^{-1}), movement rate ($m.h^{-1}$), home range (Km²) and spatial evenness. Significant values are shown in bold text.

RM-PERMANOVA	Source	df	MS	Pseudo-F	P(MC)	Unique perms
Main test	Species	1	1.47	0.37	0.76	8166
	Daily phase	1	25.2	10.7	**0.001**	9946
	Fish ID (Species)	16	3.99	1.69	0.05	9910
	Species x Daily phase	1	11.8	5.01	**0.02**	9958
	Res	16	2.35			
	Total	35				
Pair-wise test	**Species (*S. axillare* x *L. alexandrei*)**			**t**	**P(MC)**	**Unique perms**
	Within day			1.21	0.22	8154
	Within night			1.78	**0.04**	8142
	Daily pahse (day x night)					
	Within *S. axillare*			6.59	**<0.001**	9919
	Within *L. alexandrei*			0.75	0.52	9950
Mixed-design ANOVA	**Source**	**df**	**MS**	**F**	**P**	**Tukey HDS**
Detections (h^{-1})	Species	1	0.09	0.30	0.59	
	Daily phase	1	0.002	0.03	0.86	
	Species x Daily phase	1	0.19	2.09	0.17	Fig. 02 (A)
	Error	16	0.09			
Movement rate ($m.h^{-1}$)	Species	1	0.19	1.97	0.18	
	Daily phase	1	4.20	45.4	**<0.001**	Day > Night
	Species x Daily phase	1	1.71	18.5	**<0.001**	Fig. 02 (B)
	Error	16	0.09			
Home range (km²)	Species	1	0.001	0.20	0.66	
	Daily phase	1	0.004	6.58	**0.02**	Day > Night
	Species x Daily phase	1	0.001	2.37	0.14	Fig. 02 (C)
	Error	16	0.001			
Spatial evenness	Species	1	0.001	0.01	0.94	
	Daily phase	1	0.02	5.78	**0.03**	Day > Night
	Species x Daily phase	1	0.01	3.03	0.10	Fig. 02 (D)
	Error	16	0.004			

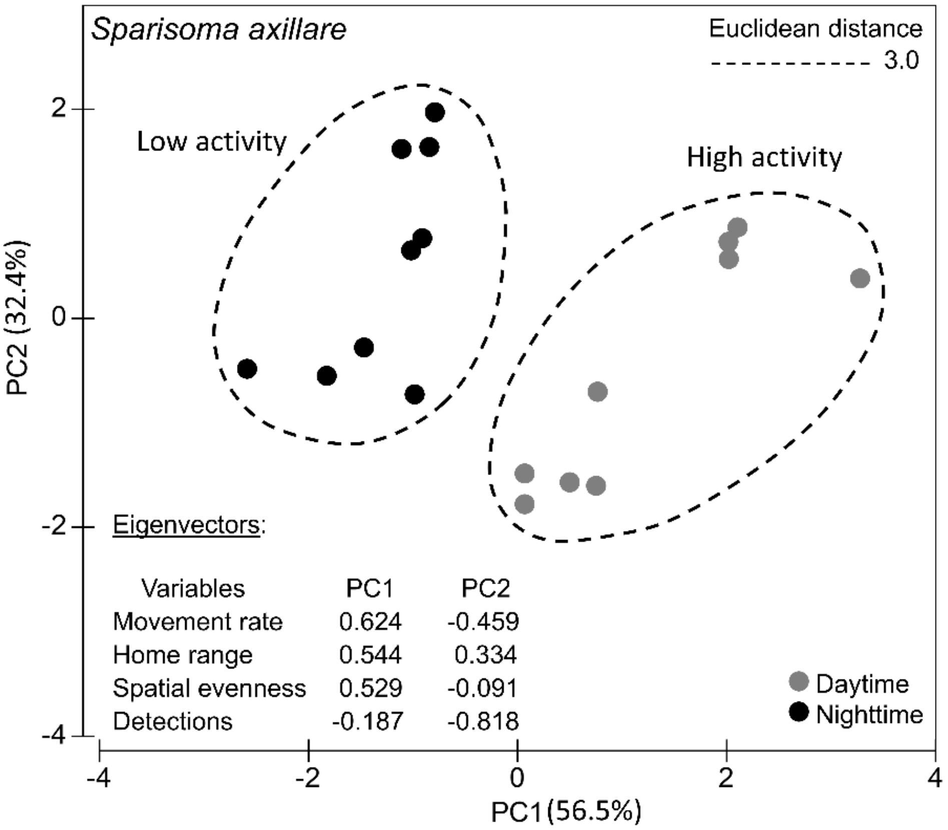
Fonte: Autor (2021)

Figure 2 – Bar plots of the mean (±S.E.) values for the activity pattern indicators estimated for *Sparisoma axillare* (n = 9) and *Lutjanus alexandrei* (n = 9) during day (light grey bars) and night (dark grey bars) phases: Detections (h^{-1}; A), movement rate ($m.h^{-1}$; B), home range (Km^2; C) and spatial evenness (D). Letters (a, b and c) indicate the Tukey HDS results from mixed-design ANOVAs between factors "Species" and "Daily phases". Asterisks highlights the significant diel variabilities within each species: $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).



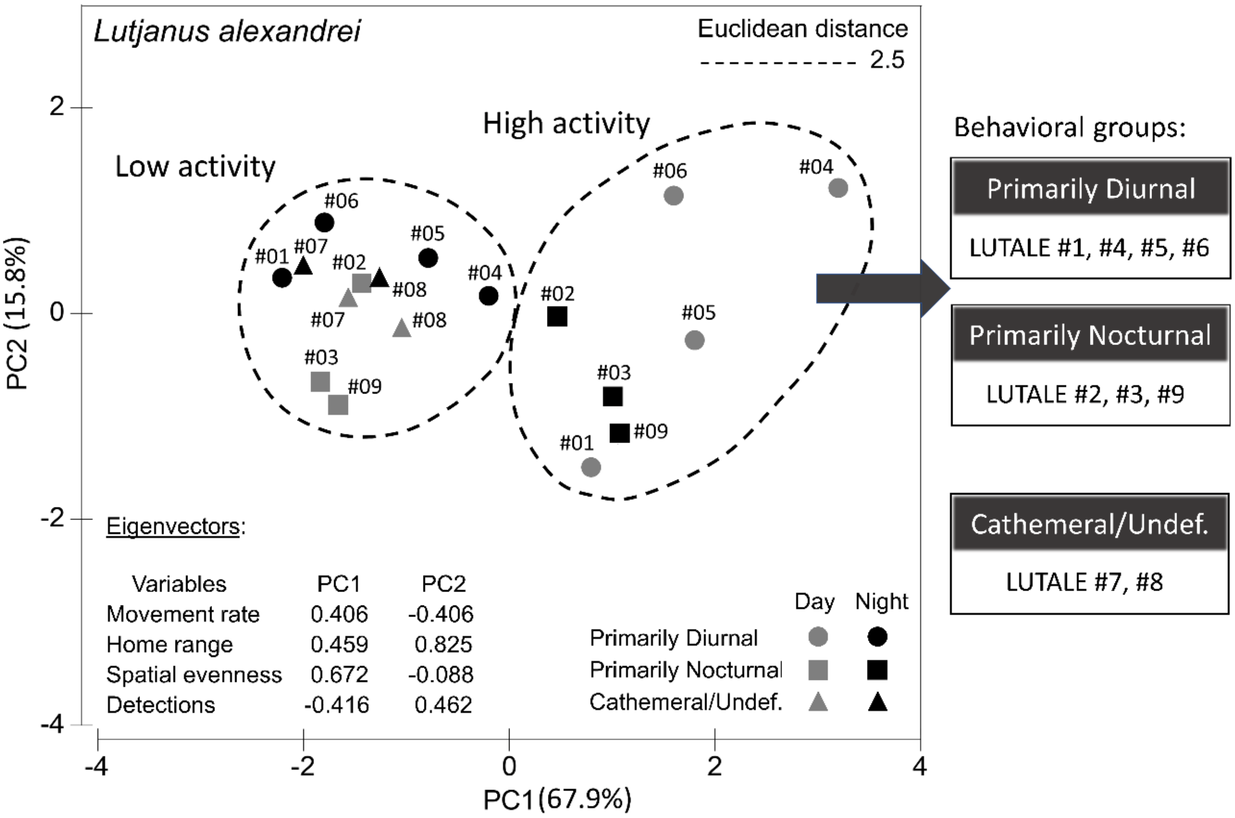
Fonte: Autor (2021)

Figure 3 – Principal Component Analysis (PCA) of the diurnal (grey circles) and nocturnal (black circles) activity patterns of *Sparisoma axillare* individuals, based on the number of detections (h^{-1}), movement rate (m.h^{-1}), home range (km^2) and spatial evenness values. The first two axes explained nearly 89% of the total variance. Overlaid contour lines from hierarchical cluster analysis indicates the formation of two clearly distinct groups: a Low Activity group including the nocturnal activity patterns of all fish and a High Activity group comprising all the diurnal activity patterns.



Fonte: Autor (2021)

Figure 4 – Principal Component Analysis (PCA) of the diurnal (grey shapes) and nocturnal (black shapes) activity patterns of *Lutjanus alexandrei* individuals, based on the number of detections (h^{-1}), movement rate ($m.h^{-1}$), home range (km^2) and spatial evenness values. The first two axes explained nearly 84% of the total variance. Overlaid contour lines from hierarchical cluster analysis indicates the formation of two clearly distinct groups: a Low Activity and a High Activity group. Three behavioral groups of fish could also be inferred: Primarily Diurnal (circles), Primarily Nocturnal (squares) and Cathemeral/Undefined (triangles).



Eigenvectors:

Variables	PC1	PC2
Movement rate	0.406	-0.406
Home range	0.459	0.825
Spatial evenness	0.672	-0.088
Detections	-0.416	0.462

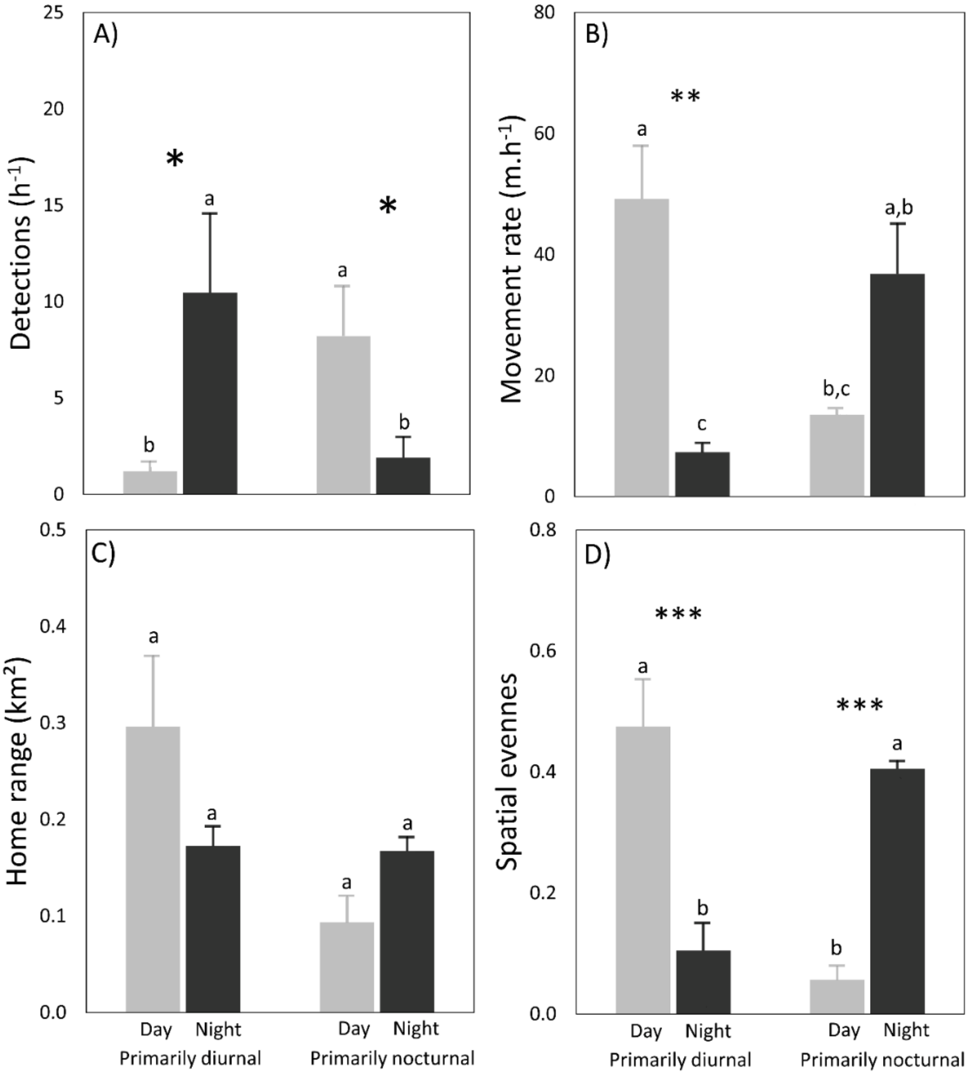
Fonte: Autor (2021)

Table 4 – Repeated measures PERMANOVA and Mixed-design ANOVAs results for the effects of “Behavioral groups” (between-subject factor, two levels: Primarily diurnal and Primarily nocturnal) and “Daily phase” (within-subjects factor, two levels: day and night) on the activity patterns indicators: detections (h^{-1}), movement rate ($m.h^{-1}$), home range (Km^2) and spatial evenness. Significant values are shown in bold text.

RM PERMANOVA	**Source**	**df**	**MS**	**Pseudo-F**	**P(MC)**	**Unique perms**
Main test	Behavioural groups	1	4.36	1.89	0.18	35
	Daily phases	1	0.71	0.91	0.45	9953
	Fish ID (Behavioral groups)	5	11.6	2.94	**0.03**	9931
	Behavioral groups x Daily phases	1	27.8	35.4	**<0.001**	9932
	Res	5	0.77			
	Total	13				
Pair-wise test	**Behavioral groups (P. diurnal x P. nocturnal)**			**t**	**P(MC)**	**Unique perms**
	Within day			3.23	**<0.01**	35
	Within night			3.13	**0.01**	35
	Daily phases (day x night)					
	Within Primaily Diurnal group			4.13	**<0.01**	425
	Within Primaily Nocturnal group			7.02	**0.01**	38
Mixed-design ANOVA	**Source**	**df**	**MS**	**F**	**P**	**Tukey HDS**
Detections (h^{-1})	Behavioral groups	1	0.004	0.03	0.86	
	Daily phases	1	0.01	0.35	0.58	
	Behavioral groups x Daily phases	1	1.14	33.7	**<0.01**	Fig. 05 (A)
	Error	5	0.03			
Movement rate ($m.h^{-1}$)	Behavioral groups	1	0.02	0.90	0.39	
	Daily phases	1	0.13	4.38	0.09	
	Behavioral groups x Daily phases	1	1.18	39.7	**0.001**	Fig 05 (B)
	Error	5	0.03			
Home range (km^2)	Behavioral groups	1	0.005	3.49	0.12	
	Daily phases	1	0.001	0.28	0.62	
	Behavioral groups x Daily phases	1	0.004	8.26	**0.03**	Fig 05 (C)
	Error	5	0.001			
Spatial evenness	Behavioral groups	1	0.001	0.65	0.46	
	Daily phases	1	0.000	0.003	0.96	
	Behavioral groups x Daily phases	1	0.05	432.2	**<0.001**	Fig 05 (D)
	Error	5	0.000			

Fonte: Autor (2021)

Figure 5 – Bar plots of the mean (± S.E.) values for the activity pattern indicators estimated for the Lutjanus alexandrei behavioral groups (Primarily diurnal (n = 4) and Primarily nocturnal (n = 3)) during day (light grey bars) and night (dark grey bars) phases: Detections (h^{-1}; A), movement rate ($m.h^{-1}$; B), home range (Km²; C) and spatial evenness (D). Letters (a, b and c) indicate the Tukey HDS results from mixed-design ANOVAs between factors "behavioral groups" and "daily phases". Asterisks highlights the significant diel variabilities within each behavioral group: $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).



Fonte: Autor (2021)

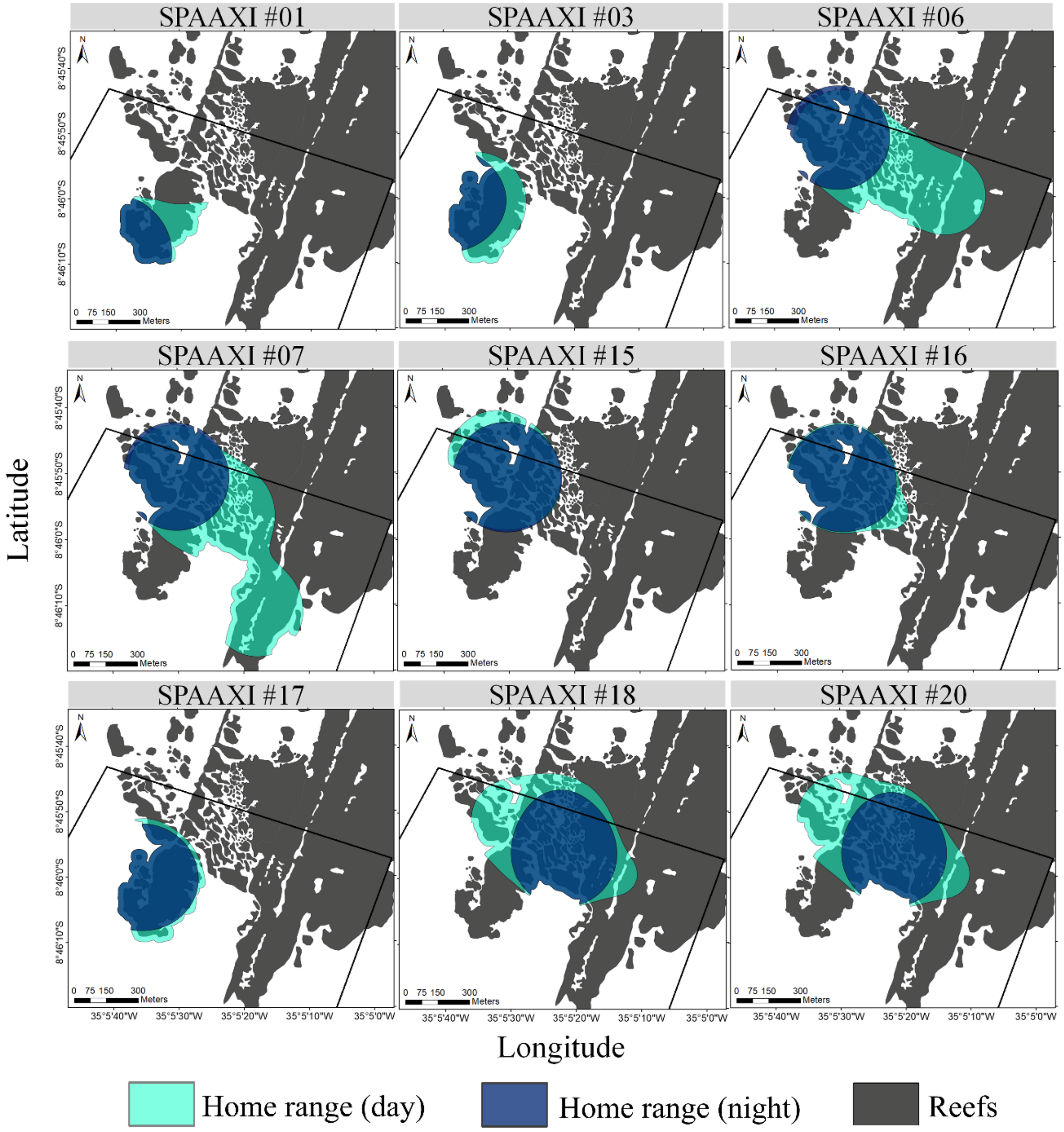
Overall, both species exhibited high Overlap Indexes (OI) and short Centroid Distances (CD) between their diurnal and nocturnal home ranges (Table 5). Student's t test showed no significant differences between species for OI (t = 0.37, p=0.72) and CD (t = 0.67, p = 0.51). Fish total length was not significantly correlated with OI for both species (*S. axillare*, r = -0.22, p = 0.57 and *L. alexandrei*, r = -0.50, p = 0.17). For *S. axillare*, mean HR overlapping area was 0.15 ± 0.02 km² (range 0.21 – 0.07 km²) (Figure 6). On average, 36 ± 6 % of the total HR was exclusively diurnal, while considerably smaller portions (0.8 ± 0.4 %) were used only during the night. For *L. alexandrei*, mean HR overlapping area was 0.14 ± 0.02 km² (range 0.21 – 0.07 km²) (Figure 7). Regarding the behavioural groups, highest OI and shortest CD were observed for the Cathemeral/Undefined individuals (Table 5) totaling up to 98% of the HR shared between diurnal and nocturnal phases. No significant differences on OI and CD were observed between Primarily Diurnal and Primarily Nocturnal groups (Student's t-test, t = 0.58, p = 0.59 and t = 0.14, p = 0.89, respectively). However, percentage of HR occupied exclusively during the day was, on average, 40 times greater for the Primarily Diurnal group (34 ± 13 %) in comparison to the Primarily Nocturnal group (0.9 ± 0.8 %) (Figure 8). On the contrary, exclusively nocturnal HR area was 15 times greater for the Primarily Nocturnal group (46 ± 11 %) than the observed for the Primarily Diurnal group (3.2 ± 0.9 %) (Figure 8).

Table 5 – Mean (±S.E.) Overlap Indexes and centroid distances between day and night home range areas for both species and *L. alexandrei* behavioral groups.

Species/ Behavioral groups	**Overlap Index Mean ± SE (Min-Max)**	**Centroid distance (m) Mean ± SE (Min-Max)**
Sparisoma axillare	0.63 ± 0.06 (0.40 - 0.88)	99 ± 36 (12 - 313)
Lutjanus alexandrei		
All individuals	0.67 ± 0.08 (0.39 - 0.98)	85 ± 29 (2.3 - 232)
Primarily Diurnal (#1, #4, #5, #6)	0.63 ± 0.12 (0.39 - 0.91)	132 ± 55 (19 - 232)
Primarily Nocturnal (#2, #3, #9)	0.53 ± 0.09 (0.40 - 0.72)	79 ± 14 (57 - 104)
Cathemeral/Undefined (#7, #8)	0.97 ± 0.01 (0.96 - 0.98)	3.1 ± 0.8 (2.3 – 3.8)

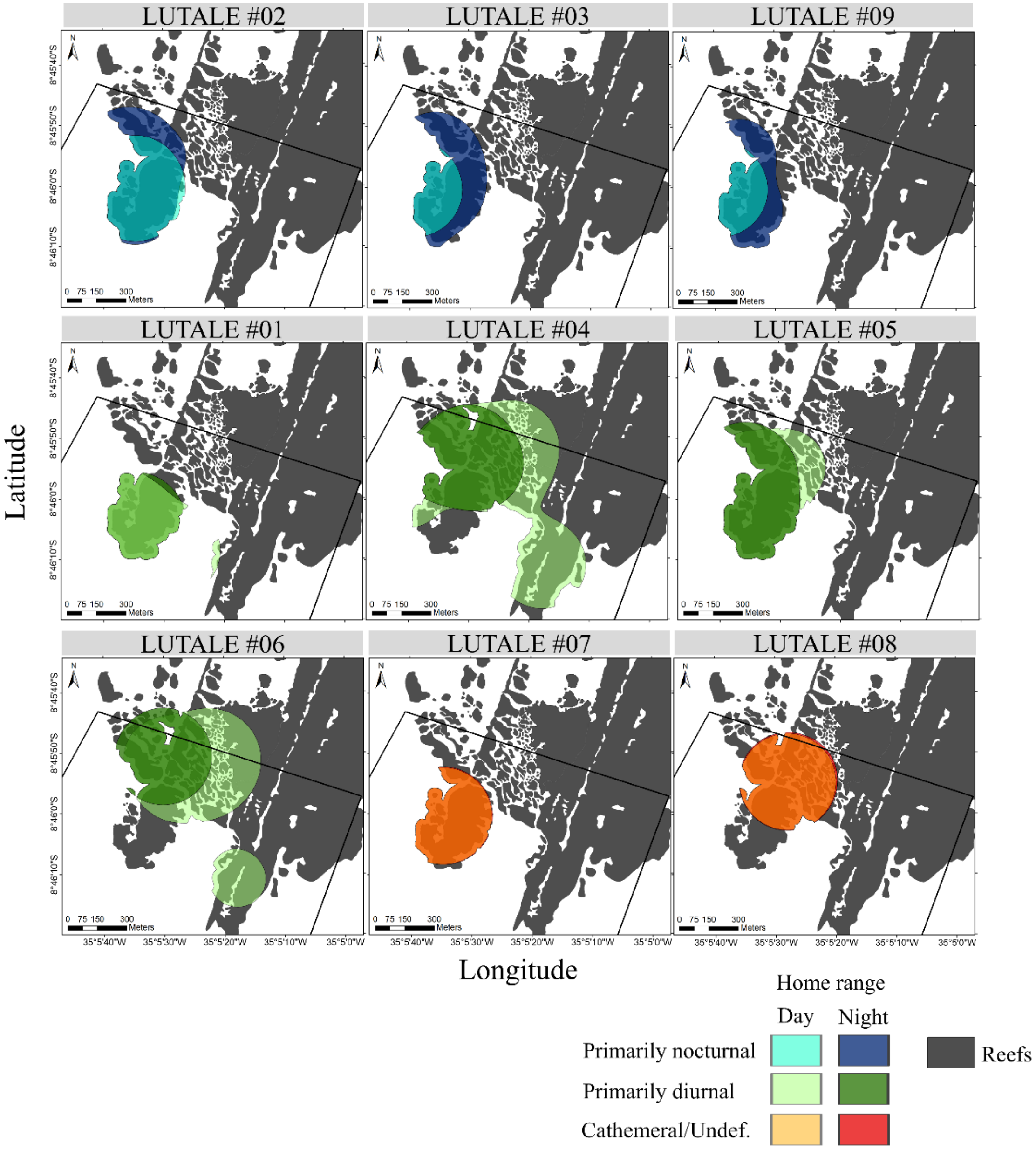
Fonte: O Autor (2021)

Figure 6 – Home range estimates for the selected *Sparisoma axillare* individuals during day and night in the coastal reefs of Tamandaré-PE. Black line represents the NTZ boundary.



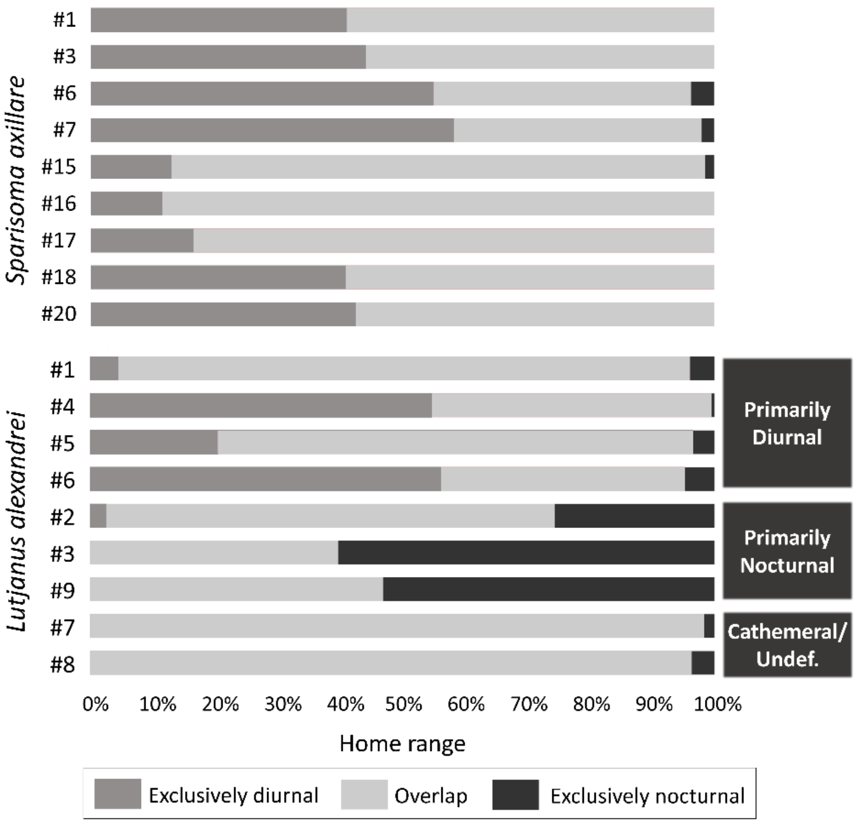
Fonte: O Autor (2021)

Figure 7 – Home range estimates for the *Lutjanus alexandrei* behavioral groups (Primarily Diurnal, Primarily Nocturnal and Cathemeral/Undefined) during day and night in the coastal reefs of Tamandaré-PE. Black line represents the NTZ boundary.



Fonte: O Autor (2021)

Figure 8 – Percentage of exclusively diurnal, overlapping and exclusively nocturnal home range areas for *Sparisoma axillare* and *Lutjanus alexandrei* individuals in the coastal reefs of Tamandaré-PE.



Fonte: O Autor (2021)

DISCUSSION

Diel variability on fish behavior is commonly observed on reef habitats (TRAVERS *et al*., 2006; AZZURRO *et al*., 2007; MYERS *et al*., 2016) and has been empirically reported through the use of acoustic telemetry for several species (JADOT *et al*., 2002; MARCH *et al*., 2010; VILLEGAS-RÍOS *et al*., 2013; DI LORENZO *et al*., 2016). In this study, we present the first investigation of diel variations in the activity patterns for reef fish species in Brazil. The observed data confirmed the expected pattern for *S. axillare* as a diurnally active species while *L. alexandrei* presented an intra-population mixed day/night activity pattern**.**

Most *S. axillare* and *L. alexandrei* individuals exhibited a 24-hour periodicity on their number of detections. Detection probability is likely to change accordingly to fish behavior, so temporal patterns are expected as fish alternate their behaviors over the diel cycle between a period of high activity (e.g., swimming/foraging behavior) and a period of low activity (e.g., resting/sheltering behavior). Besides fish behavior, detection probability can also be strongly influenced by environmental factors such as wave action, current speed, turbidity, and biological noise (HEUPEL *et al.*, 2006; CAGUA *et al.*, 2013), which cannot be ruled out without the use of sentinel tags (PAYNE *et al.*, 2010; KESSEL *et al.*, 2014). In the present study, however, the absence of diel differences on detection probability in the range tests (GIACALONE *et al.*, 2016) and the intraspecific variability on the mean number of hourly detections observed for both species, with some individuals being more detected during the day while others were more detected at night, suggest that detection probability is likely related to the individuals' diel activity patterns rather than background noise.

For demersal species, a positive relationship between number of detections and level of fish activity is often assumed on the assessment of behavioral diel patterns, as individuals would remain sheltered during low activity periods with reduced detection probability (MARCH *et al.*, 2010; ALÓS *et al.*, 2011; VILLEGAS-RÍOS *et al.*, 2013; AFONSO *et al.*, 2016). Such pattern is commonly observed for parrotfishes during nighttime (OGDEN; BUCKMAN, 1973; DUBIN; BAKER, 1982; SADOVY *et al.*, 2003) and seemed to be the case of the seven *S. axillare* individuals that had very few (or none) nocturnal detections (therefore, excluded from the activity pattern indicators analysis) and explains the overall reduced nocturnal RI for the species. Indeed, the complexity of the Tamandaré reef system, with interconnected caves running under the reefs and patch reefs acting as barriers may present a challenge to detection. The acoustic array design, however, was organized to maximize detection and indeed, some fish seemed to have rested at exposed sites with an unobstructed line-of-sight between the individual and nearby receivers, resulting in an even higher number of detections during their low activity periods. Notwithstanding, detection probability could have been negatively affected by fish mobility, due to the obstruction of the acoustic signal as fish actively displace among the reef structures (TOPPING *et al.*, 2006; GANDRA *et al.*, 2018). We observed that the mean number of hourly detections were negatively related to movement rate, home range, and spatial evenness for both species. Therefore, in complex coral reef areas, precaution should be taken when analyzing diel behavior considering only the number of detections as it can lead to erroneous conclusions. The estimate of others activity pattern indicators (i.e., movement rate, home range and spatial evenness) in the present study helped to elucidate the *S. axillare* and *L. alexandrei* diel behaviors.

Sparisoma axillare had a clear diurnal behavior at species level, characterized by significantly higher values for the activity pattern indicators during daytime, except for the number of hourly detections. On average, movement rate was 20 times greater during daytime, which is clearly related to longer diurnal displacements over the reef, resulting in larger home ranges (~1.6 times greater) and higher spatial evenness (~3.6 times greater) during this period. Moreover, PCA indicated that a diurnal activity was consistent for all individuals. Swimming and feeding behavior were commonly observed for *S. axillare* during diurnal fish surveys regularly performed in the area, while no active parrotfish were observed during the nocturnal dives conducted at the beginning of the study. Such markedly diurnal behavior is consistent with the observed for other parrotfish species (DUBIN; BAKER, 1982; LINDHOLM *et al.*, 2006; HOWARD *et al.*, 2013; DAVIS *et al.*, 2017). The reduced spatial evenness values registered at night also revealed a strong site fidelity to their sleeping areas (OGDEN; BUCKAMAN, 1973). Sleeping sites were located within individual's daytime activity areas as indicated by the overall high overlap and short centroid distances between diurnal and nocturnal home ranges, as well as by the near absence of home range areas used exclusively at night. The absence of conspicuous diel migrations was also observed for *Scarus rivulatus* (WELSH; BELLWOOD, 2012a) and *Chlorurus microrhinos* (WELSH; BELLWOOD, 2012b), however displacements of up to several hundred meters between spatially distinct daytime foraging areas and nighttime shelters have been shown for other parrotfish species (MEYER *et al.*, 2010; HOWARD *et al.*, 2013; GARCIA *et al.*, 2015; DAVIS *et al.*, 2017).

A diel behavior characterized by crepuscular shifts between preferred diurnal shelters and nocturnal foraging habitats, or by a nocturnal increase on fish movements within reef habitats have been demonstrated by acoustic telemetry studies for some *Lutjanus*, thus suggesting a primary nocturnal behavior for these species: *L. griseus* (LUO *et al.*, 2009), *L. synagris* (KENDALL *et al.*, 2017), *L. monostigma* (HONDA *et al.*, 2016) and *L. apodus* (HITT *et al.*, 2011a, 2011b; GARCIA *et al.*, 2015; HUIJBERS *et al.*, 2015; ROOKER *et al.*, 2018). However, snappers may also feed opportunistically during the day (HOBSON, 1965; ROOKER, 1995; STARCK, 1971), and some species are more active during daylight or crepuscular hours (HOBSON *et al.*, 1981; MUELLER *et al.*, 1994; TINHAN *et al.*, 2014), thus indicating that plasticity would be expected on the snappers' diel behavior. Such plasticity has been reported for *L. campechanus* in the Gulf of Mexico, with studies showing increased fish movement during the night (TOPPING; SZEDLMAYER, 2011a, 2011b; MCDONOUGH; COWAN, 2013), day (PIRAINO; SZEDLMAYER, 2014; WILLIAMS-

GROVE; SZEDLMAYER, 2017), twilight (FROEHLICH *et al*., 2019) or even mixed patterns (WILLIAMS-GROVE; SZEDLMAYER, 2016).

A mixed diel behavior was observed for the tagged *L. alexandrei*, with co-occurring groups of individuals displaying contrasting diel patterns. Three fish showed higher activity during the day (Primarily Diurnal group) while four fish had increased activity at night (Primarily Nocturnal group). Individuals showed higher values for movement rate, home range and spatial evenness during their respective periods of increased activity. Two fish had no diel variability (Cathemeral/Undefined group) with similar values for all the activity patterns indicators during day and night.

Few studies have demonstrated mixed diel activity patterns within reef fish species by means of acoustic telemetry (*e.g.*, FOX; BELLWOOD, 2011; KOECK *et al*., 2013; WILLIAMS-GROVE; SZEDLMAYER, 2016). In such studies, opposite diel patterns (*i.e.*, diurnal and nocturnal patterns) were observed between groups of individuals residing in distinct locations, whereas individuals sharing the same habitat displayed the same diel activity pattern. Inter-habitats differences in biological factors such as prey availability, inter- and intra-specific competition, and predation risk were suggested as the likely driving mechanisms for the observed contrasting patterns, as individuals would adapt their behaviors accordingly to the characteristic of the habitats in order to improve fitness and survivability (VAN VALEN, 1965; MACARTHUR; PIANKA, 1966).

The present study was performed within a marine no-take zone where the density of *L. alexandrei* is locally high (as shown in Chapter 3). Thus, increased intra-specific competition might also have promoted an individual-level diversification of the diel activity patterns in order to reduce the competition among conspecifics (BOLNICK *et al*., 2003; SVANBÄCK; BOLNICK, 2007; CACHERA *et al*., 2017). Contrasting diel patterns within fish populations have also been related to ontogeny (MAGNAN; FITZGERALD, 1984; Roussel; BARDONNET, 1999; REEBS, 2002; VERWEIJ *et al*., 2006). Although this species is known to perform ontogenetic migration between mangrove (where they spend their early years) and reef habitats (ASCHENBRENNER *et al*., 2016), only similar sized fish were tagged within reef sites. No significant differences were observed in fish size between Primarily Diurnal and Primarily Nocturnal groups), what might suggest that the observed opposite diel patterns represented individual variations not related to fish ontogeny. Moreover, the fact that individuals with opposite diel patterns co-occurred both spatially (i.e., overlapping home ranges) and temporally (i.e., overlapping detection periods) also suggest that these contrasting patterns are not related to environmental factors (FRASER *et al*., 1993; GREENWOOD;

METCALFE, 1998; FRASER *et al*., 2011) or to differences on detection probability among reefs areas (CAGUA *et al*., 2013; KESSEL *et al*., 2014).

Several fish from both species also showed 12 hours cyclic detection patterns compatible with the semidiurnal tidal regime present in the region. Tide can be a major influence in most areas, but particularly where the tidal range is high and in shallow reef areas where tidal variation interacts with topography. During visual surveys and remote monitoring by fixed cameras, snappers were repeatedly observed forming large resting schools in caves at low tide hours, exiting the caves as tide rose and turbulence increased. Displacements of few hundred meters following a tidal cycle were documented for the sparid *Chrysophrys auratus* in a New Zealand estuary (HARTILL *et al*., 2004), while the lutjanid *Aprion virescens* made tidal displacements of up to 24 km at Hawaiian atolls (MEYER *et al*., 2007b). Tidal rhythmicity on fish movement has also been documented by acoustic telemetry studies for other species (ARENDT *et al*., 2001; HUMSTON *et al*., 2005; MARTINS *et al*., 2020). Nevertheless, further analysis is required to completely disentangle *S. axillare* and *L. alexandrei* movement patterns from tidal effect on detection probability.

The Tamandaré coastal reef complex is located within an area of overlapping MPAs, created to protect the local rich biodiversity and the goods and services provided, such as an intense artisanal fishery and a growing tourism industry (FERREIRA *et al*., 2007). In spite of the existence of several MPAs in the region, and laws protecting endangered species, effective protection occurs mainly within the border of established NTZs. Use regulation of the coastal and marine environment is under discussion by local governments, including MPA managers, and community members. Insights on the diel variations in movement and home range of reef fish species can indicate feeding and resting grounds where vulnerability may be higher to human impacts, and thus help to guide conservation policies. Nighttime spear fishing for instance, has been banned in several regions due to severe depletion of herbivorous fish populations and consequent impacts on coral reefs. The bumphead parrotfish (*Bolbometopon muricatum*) is an emblematic example of a species extremely vulnerable to night spearfishing (PEARSE *et al*., 2018), but similar susceptibility may occur for other species, particularly in their adult stage (COLI; SADOVY DE MITCHESON, 2012).

The present study demonstrated a clear diurnal pattern for *S. axillare*, whereas an intra-population diel variability was observed for *L. alexandrei* activity patterns, indicating that biological factors may interact to determine individual fish behavior. Further studies such as fine-scale acoustic telemetry and diet analysis are necessary to fully understand the differences in resources used between *L. alexandrei* behavioral groups. It was also noted that the NTZ may function as a night and day refuge for reef species and individuals with contrasting diel habits. Present results may help to guide the management and conservation plans of MPAs within coral reef environments.

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5 CONSIDERAÇÕES FINAIS

O uso de telemetria acústica como ferramenta em estudos sobre ecologia de peixes marinhos tem se tornado cada vez mais recorrente nas últimas décadas. Isso tem sido possível graças à redução dos custos e desenvolvimento de novas tecnologias, que vem possibilitando também a realização de estudos de longo prazo para um número cada vez maior de espécies e indivíduos. Dentre as suas diversas aplicações, a telemetria acústica tem se revelado uma técnica eficaz no planejamento e avaliação de áreas marinhas protegidas, em especial das áreas *no-take*, em todo o mundo. Além disso, considerando-se os impactos nos habitats marinhos causados pelas ações humanas e alterações climáticas, a telemetria acústica surge como uma ferramenta importante para inferir e prever como os organismos e comunidades se reorganizam quando confrontados com as mudanças ambientais. No entanto, no Brasil o número de estudos em telemetria acústica marinha ainda é baixo. Assim, espera-se que os incentivos para estudos de eficácia de MPA e a participação brasileira em redes colaborativas internacionais e regionais possam ajudar a preencher esta lacuna.

No presente estudo, os padrões espaço-temporais na movimentação de duas espécies endêmicas no Brasil, o peixe-papagaio *Sparisoma axillare* e a baúna *Lutjanus alexandrei*, ambas de grande importância para a pesca local, porém com características distintas em seus ciclos de vida, foram investigados em uma área *no-take* (NTZ) nos recifes costeiros de Tamandaré. Através dos censos visuais, foi demonstrado efeito em termos de aumento da densidade e tamanho dos peixes para ambas as espécies em comparação a outras áreas do recife abertas à pesca e ao turismo. Enquanto monitoradas, ambas as espécies apresentaram uma alta residência e com a maior parte dos seus *home ranges* e *core ranges* inseridos na NTZ. O *home range* utilizado pelas espécies foi pequeno, revelando a existência de subgrupos de indivíduos dentro das populações ocupando áreas espacialmente distintas do recife. Este estudo demonstrou a eficiência da NTZ estabelecida nos recifes costeiros de Tamandaré. Contudo os resultados também indicam a existência de *spillover* de peixes adultos e realçam a importância da gestão dos recifes adjacentes a NTZ onde a pressão de pesca é elevada. Além disso, devido aos indícios observados de migração ontogenéticas das espécies, a proteção de áreas que abrigam peixes adultos e em fases maduras são necessárias para manter os estoques saudáveis e capazes de continuar a suprir uma pressão pesqueira elevada.

As variações nictemerais (*i.e.*, relacionadas aos ciclos diários de claro e escuro) na movimentação das espécies foram também investigadas. Um comportamento claramente diurno foi observado para *Sparisoma axillare*, relacionado a uma alta atividade alimentar durante o dia e um período de descanso noturno. Já para *L. alexandrei*, pode-se observar um comportamento misto com indivíduos com grupos de indivíduos apresentando maiores atividades em períodos do dia opostos. A existência de heterogeneidades nos comportamentos nictemerais entre os indivíduos de uma mesma população e faixa de tamanho corporal, são raramente reportadas. Fatores biológicos como uma elevada competição intraespecífica podem estar contribuindo para a diversificação dos comportamentos individuais dentro das populações. Foi também observado que a NTZ de Tamandaré pode funcionar com um refúgio diurno e noturno, protegendo áreas de alimentação e abrigo, para ambas as espécies. Este campo de estudo é bastante promissor e os resultados obtidos apontam para a necessidade de estudos mais detalhados para a compreensão de características locais e da variabilidade individual e suas possíveis causas. A telemetria acústica mostrou-se eficiente para fornecer informações sobre a ecologia espacial das espécies estudadas e sobre a eficiência e o funcionamento da NTZ estabelecidas nos recifes costeiros de Tamandaré. Os resultados do presente estudo são relevantes para a gestão local, constituída por várias unidades de conservação a nível municipal, estadual e federal. Além disto, o estabelecimento de outras NTZs ao longo da costa está previsto no plano de gestão da APA Costa dos Corais. Os resultados aqui obtidos demonstram que pequenas NTZs que protegem parte da paisagem marinha e assim abrigam algumas espécies durante parte de seu ciclo de vida, são uma medida importante e eficaz para a redução da mortalidade por pesca e conservação das populações de peixes de recifais, podendo assim guiar outras medidas de gestão semelhantes.

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