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UTILIZAÇÃO DA ACÚSTICA SUBMARINA PARA IDENTIFICAR O PADRÃO NICTEMERAL DE PEIXES NA ZONA NERÍTICA E DE QUEBRA DE PLATAFORMA DO ARQUIPÉLAGO DE FERNANDO DE NORONHA

Recife
2022

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Dissertação apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco como requisito parcial para a obtenção do título de Mestra em Oceanografia.

Área de Concentração: Oceanografia Abiótica.

Orientador: Prof. Dr. Arnaud Pierre Alexis Bertrand.

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RESUMO

A acústica submarina é uma técnica interessante para o acompanhamento de processos que ocorrem durante o ciclo nictemeral, visto que ela permite amostragens simultâneas em várias escalas espaço-temporais. Utilizar esse tipo de metodologia dentro de recifes tropicais, onde apesar da biodiversidade elevada ainda se encontram subestudados, nos fornece melhor compreensão da dinâmica no sistema costeiro. Atualmente, o que se sabe sobre recifes de corais tropicais é que há uma mudança quase que completa na composição das espécies de peixes quando se compara dia e noite. Portanto, o objetivo deste trabalho foi caracterizar a distribuição tridimensional de peixes na zona nerítica e áreas adjacentes à quebra da plataforma da Ilha de Fernando de Noronha em função do ciclo nictemeral. Para isso, foram utilizadas filmagens subaquáticas durante o dia combinadas com observações acústicas de bifrequência diurnas e noturnas. O *Melichthys niger* foi a espécie mais abundante enquanto a família carangidae foi a mais representativa nas imagens de vídeo. A biomassa acústica de peixes se reduziu drasticamente à noite indicando que a maioria deles se abriga no fundo nesse período e que aqueles que apresentam um comportamento oposto representam provavelmente uma parte menor da biomassa total de peixes na região. Curiosamente, a biomassa de peixes e a biomassa de organismos não identificados como peixes (não-peixes), apresentaram um padrão oposto, com os peixes desaparecendo da coluna de água quando não-peixes, que são presas potenciais para muitas espécies de peixes, são mais abundantes. Decifrar este comportamento requer mais investigação. A metodologia utilizando acústica submarina se mostrou viável na observação da distribuição de peixes ao longo do ciclo nictemeral. Por fim, os resultados deste trabalho poderão contribuir para o desenvolvimento de políticas de conservação e manejo no arquipélago de Fernando de Noronha.

Palavras-chave: acústica de multifrequência; comportamento de peixes; recife tropical; Fernando de Noronha; migração vertical.

ABSTRACT

Underwater acoustics is an interesting technique for monitoring processes occurring during the diel cycle, as it allows simultaneous sampling at various spatio-temporal scales. Using this type of methodology within tropical reefs, where despite the high biodiversity they are still understudied, provides us with a better understanding of the dynamics in the coastal system. Currently, what is known about tropical coral reefs is that there is an almost complete change in fish species composition when comparing day and night. Therefore, the aim of this work was to characterize the three-dimensional distribution of fishes in the neritic zone and areas adjacent to the shelf break of Fernando de Noronha Island as a function of the diel cycle. For this, daytime video images were combined with daytime and nighttime bifrequency acoustic observations. The acoustic biomass of fish reduced drastically at night indicating that most of them shelter on the bottom during this period and that those showing an opposite behaviour probably represent a smaller part of the total fish biomass in the region. Interestingly, fish biomass and the biomass of organisms not identified as fish (no-fish), showed an opposite pattern, with fish disappearing from the water column when non-fish, which are potential prey for many fish species, are more abundant. Deciphering this behaviour requires further investigation. The methodology using underwater acoustics proved to be viable in the observation of fish distribution over the nictemeral cycle. Finally, the results of this work may contribute to the development of conservation and management policies in the Fernando de Noronha archipelago.

Keywords: multifrequency acoustics; fish behaviour; tropical reef; Fernando de Noronha; vertical migration.

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1 INTRODUÇÃO GERAL

Os ecossistemas marinhos são ambientes complexos em que inúmeros fatores, bióticos e abióticos, se interligam. Processos físicos, por exemplo, podem afetar parâmetros físicos, químicos e biológicos, assim como influenciar no comportamento da biota (BERTRAND *et al.*, 2008;). Essa complexidade se reflete nas mais diferentes escalas e estas, por sua vez, são de extrema importância para se compreender os fenômenos dos quais se quer estudar, pois cada processo, e a resposta dos organismos a esses processos, ocorrem em escalas diferentes (LEVIN, 1992). Diante disso, o ciclo nictemeral, representando uma escala temporal de 24 horas, apresenta grande relevância no ambiente marinho, visto que as interações ecológicas observadas ao se estudar um determinado local durante o dia são extremamente diferentes daquelas observadas no mesmo local durante a noite (e.g. BENOIT-BIRD *et al.*, 2001; CARDINALE, 2003; FREON, 1996; KALTENBERG; BENOIT-BIRD, 2009).

Inúmeros são os motivos para as diferenças existentes entre o ecossistema marinho diurno e o noturno, contudo um dos exemplos mais relevantes são as Migrações Verticais Diurnas (MVD). Essas migrações são estudadas há décadas e realizadas diariamente pelo zooplâncton e por organismos das comunidades de peixes mesopelágicos (BAYLY, 1986; LAMPERT, 1989; BENOIT-BIRD *et al.*, 2001; Hays, 2003; van Haren; Compton, 2013; John *et al*., 2016; Romero-Romero *et al.*, 2019; Eduardo *et al*., 2020), acabando por influenciar no comportamento de predadores de topo (eg. BENOIT-BIRD; AU, 2003; BERTRAND *et al.*, 2006). Nessas migrações os organismos de águas mais profundas sobem para próximo da superfície ao entardecer, para se alimentar durante a noite, onde permanecem até o amanhecer quando voltam para as camadas mais profundas (LAMPERT, 1989).

Para identificar esse tipo de padrão é necessário um acompanhamento espaço-temporal, o que não ocorre nos métodos tradicionais de amostragem. Diante disso, a utilização da acústica submarina permite amostragens simultâneas, em várias escalas espaço-temporais, fornecendo informações qualitativas e quantitativas dos organismos, desde o zooplâncton até os predadores de topo (BERTRAND, 2003; BERTRAND *et al.*, 2014), o que a torna um método chave para a abordagem ecossistêmica. Esse método envolve a produção e recepção de sinais sonoros que possibilitam a observação dos organismos com alta resolução espacial e temporal (BENOIT-BIRD; LAWSON, 2016). Métodos utilizando acústica submarina representam uma alternativa abrangente para se obter índices de abundância de espécies de peixes, sem a extração dos indivíduos (SIMMONDS; MACLENNAN, 2005).

No nordeste do Brasil, a acústica ativa foi pouco utilizada até o momento. A metodologia foi aplicada na região em 2004 no Programa de Avaliação do Potencial sustentável de Recursos Vivos na Zona Econômica Exclusiva (REVIZEE), visando principalmente a comunidade de peixes e organismos maiores (HAZIN, 2009). Mais recentemente, foi aplicada no intuito de elaborar um algoritmo para discriminar as comunidades acústicas em grupos de peixes, zooplâncton e algas (VARGAS *et al*., 2017) e para quantificar a resposta acústica individual de duas espécies de peixes, nesse caso foi aplicada juntamente com filmagens subaquáticas (SALVETAT *et al.*, 2020).

Os dois últimos trabalhos citados, foram realizados em ilhas oceânicas, habitats isolados que nunca tiveram contato com o continente (GILLESPIE, 2007; PAULAY, 1994). Isso torna estas regiões importantes, pois além de apresentarem um número considerável de espécies endêmicas (FLOETER; GASPARINI, 2000; PAULAY, 1994), ainda suportam populações de peixes que não são encontrados no oceano aberto, além de serem fontes pontuais de ovos e larvas que irão compor a comunidade ictioplanctônica das águas oceânicas ao redor (BOEHLERT; MUNDY, 1993). Nesse contexto, o Arquipélago de Fernando de Noronha (AFN) representa um oásis dentro das águas oligotróficas do Oceano Atlântico tropical.

Das ilhas oceânicas brasileiras, o AFN é o que apresenta maior riqueza de espécies de peixes recifais, além de uma diversidade de peixes demersais e pelágicos que têm um importante papel na vida socioeconômica local, fornecendo recursos para a pesca artesanal que é, juntamente com o turismo, a base para a sobrevivência das comunidades locais (SERAFINI *et al.*, 2010; DOMINGUEZ *et al.*, 2016). Dentro dos recifes tropicais, o entardecer e o amanhecer, representam momentos de transição em que, ao entardecer, espécies de peixes diurnas praticamente desaparecem da coluna d’água enquanto as noturnas emergem de seus esconderijos, o oposto ocorre ao amanhecer (Hobson, 1965; 1972; 1973). Portanto, o que se sabe sobre recifes de corais tropicais é que há uma mudança quase que completa na composição das espécies quando se compara dia e noite (Brewin et al., 2016; Hobson 1973; Rooker and Dennis, 1991). Apesar da importância da compreensão da dinâmica ictia sobre a plataforma, a maioria dos estudos se concentram em ecossistemas pelágicos oceânicos. A dinâmica no sistema costeiro, em particular os tropicais, onde a biodiversidade é mais elevada, permanece subestudada. Diante disso, neste trabalho utilizei a acústica ativa juntamente com filmagens subaquáticas para compreensão desses ecossistemas ao longo do ciclo nictemeral de forma a testar a seguinte hipótese: Em decorrência do ciclo nictemeral existe uma mudança na composição da comunidade de peixes sobre a plataforma e região adjacente a quebra da plataforma de Fernando de Noronha.

Este trabalho foi estruturado na forma de artigo científico. O capítulo um apresenta a utilização das imagens de vídeo para identificar as espécies de peixes presentes durante o dia e da acústica submarina para quantificar a biomassa acústica de peixes e dos demais organismos vivos não identificados como peixes (não-peixes), nas regiões de zona nerítica e área adjacente a quebra da plataforma do Arquipélago de Fernando de Noronha, ao longo do ciclo nictemeral. Este tipo de estudo contribui para a compreensão das variações espaço-temporais dos organismos, utilizando métodos não-letais e não-destrutivos ao ecossistema marinho, de forma a contribuir para aplicações de medidas de conservação tanto para o turismo quanto para a pesca na região.

2 OBJETIVOS

Este trabalho foi desenvolvido com os seguintes objetivos:

2.1 OBJETIVO GERAL

Caracterizar a distribuição tridimensional de peixes na zona nerítica e áreas adjacentes a quebra da plataforma da Ilha de Fernando de Noronha em função do ciclo nictemeral.

2.2 OBJETIVOS ESPECÍFICOS

a) Identificar os peixes observados nas imagens de vídeos à nível de espécie;
b) Caracterizar a distribuição horizontal dos peixes identificados nas imagens de vídeo ao longo da zona nerítica e áreas adjacentes a quebra da plataforma;
c) Aplicar o algoritmo desenvolvido por Salvetat *et al*. (under review) nos dados acústicos para separar os peixes dos não-peixes;
d) Quantificar e comparar a variabilidade da biomassa acústica de peixes e dos não-peixes em função da distribuição horizontal e do ciclo nictemeral.

3 DIEL PATTERN OF FISH BIOMASS IN NERITIC AND SHELF-BREAK AREAS IN A TROPICAL ATLANTIC ARCHIPELAGO

Manuscrito submetido à revista Marine Ecology

Diel pattern of fish biomass in neritic and shelf-break areas in a tropical Atlantic archipelago

ABSTRACT

Diel vertical migrations are the largest animal migrations on Earth in terms of biomass. While the diel cycle is widely studied in the open ocean, few studies have focused on the neritic part. Still, this pattern is particularly important in tropical coral reefs, where the composition of fish species changes almost completely between day and night. To provide further advances on the understanding of fish diel behaviour in a neritic tropical system and adjacent shelf-break area, we combined diurnal video footage with both diurnal and nocturnal bi-frequency acoustic observations. This experiment was performed in Fernando de Noronha off Northeast Brazil, a typical tropical oceanic archipelago. Fish biomass drastically reduced at night indicating that most fish shelter in the bottom during the night and that fish presenting an opposite behaviour likely represent a minor part of the total fish biomass of the region. Interestingly, fish biomass and no-fish biomass presented an opposite pattern with fish clearing the water column when no-fish, which are potential prey for many fish species, are more abundant. Deciphering this behaviour requires further investigation.

Keywords: vertical migration, underwater video, multifrequency acoustics, fish behaviour, tropical reef, Fernando de Noronha

1 Introduction

Diel Vertical Migrations (DVM), which occur in all oceans, are the largest animal migrations on Earth in terms of biomass (Hays, 2003; van Haren and Compton, 2013; John *et al.*, 2016). They are performed by zooplankton, crustaceans, gelatinous, fish, and cephalopods that make up the mesopelagic community (Bayly, 1986; Lampert, 1989; John *et al.*, 2016; Romero-Romero *et al.,* 2019). In these migrations, mesopelagics rise at dusk and obtain organic carbon by feeding near the surface during the night, where they remain until dawn (Bayly, 1986;

Lampert, 1989; Langbehn *et al*., 2019). During the day, they return to the deeper layers where they breathe, defecate and, in some cases, feed (Romero-Romero *et al.,* 2019; Boyd et al., 2019; Cavan *et al*., 2019; Davison *et al*., 2013; Eduardo *et al*., 2020a). This vertical movement serves as an energetic link between the epipelagic and mesopelagic environments, contributing significantly to the carbon transport between these regions (Hudson *et al.,* 2014; John *et al*., 2016; Langbehn *et al*., 2019; Longhurst *et al.*, 1990; Romero-Romero *et al.,* 2019; Eduardo *et al*., 2020b). In conjunction to the DVM, a horizontal migration between the oceanic and neritic zone can occur. This pattern was observed near two Hawaiian Islands where, at night, the mesopelagic community was not only migrating vertically but also entering the shallower waters over the shelf (Benoit-Bird *et al*., 2001), illustrating the fact that DVM can be more complex than usual, depending on the area.

Although photo-stimulus associated with predator-prey relationships is considered the main driver for DVM (Bayly, 1986), other factors such as latitude, topography, thermohaline structure, presence of deoxygenated waters or prey availability, are important forcing factors (Neilson and Perry, 1990; Bertrand *et al*., 2006; Bianchi *et al*., 2013; van Haren and Compton, 2013; Eduardo *et al*., 2020b). The fact that migrations occur in both neritic and pelagic zones does not mean that they are governed by the same elements. For example, in the coastal zone, organisms can perform DVM to avoid being dumped into the open ocean through tidal dynamics (Neilson and Perry, 1990) or to improve their foraging efficiency (Neilson and Perry, 1990; Rooker and Dennis, 1991). Over the shelf, many fish species, usually omnivores and herbivores, are active in the water column during the day and shelter or sleep on the bottom at night while other species are inactive during the day and active at night (Brewin et al., 2016; Hobson 1973; Rooker and Dennis, 1991). This pattern is particularly important in tropical coral reefs, where the composition of fish species changes almost completely between day and night (e.g., Hobson, 1965; 1973). While the diel cycle is widely studied in the open ocean, few studies have focused on the neritic part. Actually, the vast majority of studies on the species composition, distribution and abundance patterns of tropical fishes are carried out by visual or optical methods (visual observation and video footage) during the day (e.g. McIntyre *et al*, 2015; Schmid *et al*., 2020). Such methods provide precise information, but the coverage is limited spatially and temporally, especially at night (Fitzpatrick *et al*., 2012; Harvey *et al*., 2012; Lowry *et al*., 2012; Sheaves *et al*., 2020). The nocturnal world remains largely undiscovered. This means that only 50% of the dynamics taking place in an ecosystem are usually considered.

In this context, active acoustics represents a non-destructive method that helps to fill the gap of most methods (Bertrand *et al*., 2008; Godø *et al.*, 2012; 2014; Benoit-Bird and Lawson, 2016). Indeed, underwater acoustics allows the simultaneous observation of a variety of ecosystem components from zooplankton to top predators, providing qualitative and quantitative information at high spatial and temporal resolution (Bertrand *et al.*, 2014; Benoit-Bird and Lawson, 2016). However, here too, the application of acoustic methods to study diel cycles has mainly concerned oceanic pelagic ecosystems. Dynamics in coastal system, in particular tropical ones where biodiversity is higher, remains understudied.

To provide further advances on the understanding of fish diel behaviour in a neritic tropical system and adjacent shelf-break area, we combined diurnal video footage with both diurnal and nocturnal bi-frequency acoustic observations. To describe the spatiotemporal dynamics over a diel perspective we adapted the "magic square" approach from Bertrand *et al*. (2008). This methodology consists of repeating transects in the form of a closed polygon for a given number of hours. This allows obtaining data varying in time and space but are repeated in space over time. This experiment was performed in the tropical archipelago of Fernando de Noronha off Northeast Brazil. This typical tropical archipelago is protected by a series of legal instruments, besides being contained within two environmental protection areas, and classified as an UNESCO World Heritage Site (https://whc.unesco.org/en/list/1000/).

In this context, here we describe the diel pattern of demersal and pelagic fishes as well as the no-fish community along the diel cycle in a tropical reef ecosystem. First, we describe the fish community present during the day. Then, we quantify the diel variation of fish and no-fish acoustic biomass in both the neritic and adjacent shelf-break areas.

2 Material and Methods

2.1 Study area and survey design

The Fernando de Noronha Archipelago (FNA) is located about 345 km off the northeastern Brazilian coast (**Figure 1**). It is classically divided into the south-east windward side exposed to the prevailing south-easterly winds and subject to the greatest impact from waves and currents, and the north-west leeward side, the most protected place (Soto, 2001). Here we use acoustic measurements and underwater footages data collected in the windward side where the bottom habitat was dominated by a complex mixture of sand, stones, coral, rhodolith and algae (Salvetat *et al*., under review). Data were acquired using a 10 m long fishing boat that operated at an average speed of 3 knots. The survey design was an adaptation of the "magic square" approach of Bertrand *et al*. (2008). It consisted of 12 fixed rectangular transects (2.3 x 1 km each) positioned to obtain data from both the neritic and adjacent shelf-break zone (the shelf-break occurs at ~50 m depth). The 'magic rectangle' experiment was performed during 12 continuous hours (14:00-2:00 GMT) on April 18-19, 2019, a full moon period, as part of the campaign Fish Acoustics around Fernando de Noronha 3 (FAROFA 3) (Bertrand, 2019). See Bertrand *et al*. (2020) to access acoustic data and Salvetat *et al*. (2020a) for video data.

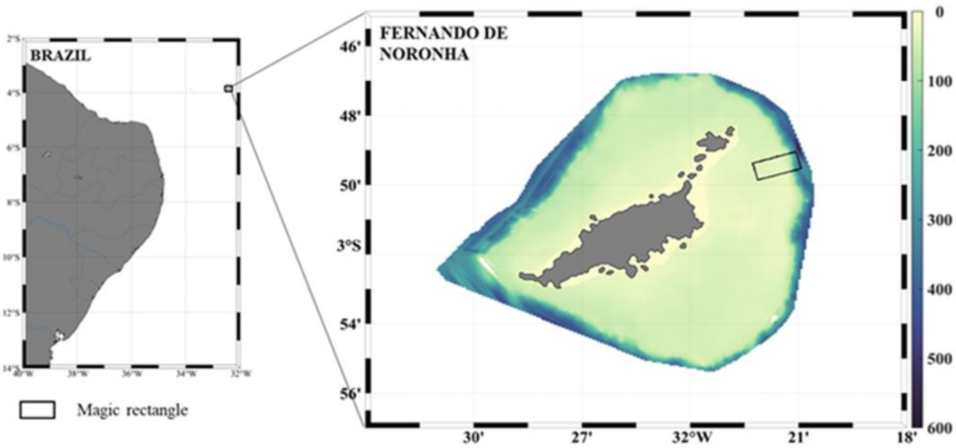

Figure 1. Study area. The black solid line indicates the position of the magic rectangle.

2.2 Underwater footage and fish identification

Video images were acquired continuously along the magic rectangle transect at daytime only (14:00-20:00 GMT). Six hours of footage were recorded with a GoPro Hero 3+ camera operating in HD at 1,080 p and 60 frames per second mounted on a paravane, towed to the back of the boat by a cable within length 30 m. Solomon Coder software (Péter, 2019) was used to perform a detailed analysis of the underwater footage. Fish species were identified to the lowest possible taxonomic level. To estimate relative abundance, we used an adaptation of the total viewing duration of a fish species during a filming sequence (Ellis and DeMartini, 1995). Here we considered the total time of filming sequences where a given taxa was observed that we call 'screen time'. In addition, for the census of fish of a given taxon, we used the maximum number of individuals (MaxN) present in a single video frame at any time of the video (Priede et al., 1994). As we performed video transects, the MaxN was cumulated each 3 seconds of record. To estimate the abundance of each taxon observed by video, we used the sum of the maximum values of the MaxN of each video (TMaxN).

2.3 Acoustic data acquisition and processing

Acoustic data were collected during the 12h of the magic rectangle experiment using two scientific SIMRAD EK80 split-beam echo sounders operating at frequencies of 70 and 200 kHz with power of 600W and 90W, respectively and a pulse duration fixed at 1.024 ms. Standard-target calibration of the echosounder was conducted prior to data acquisition (Demer *et al*., 2015). During the surveys, they were connected to two transducers attached by a stainless-steel pole on the port side of the boat and operated simultaneously in the narrowband mode.

The acoustic data were scrutinized, corrected and analysed with the software Matecho (Perrot *et al.,* 2008). During the cleaning, the bottom line was corrected. The first 3 m from the transducers were excluded because they refer to the near field, a chaotic region due to the proximity to the transducer and the numerous and successive sound waves that leave and arrive at the device. To study the horizontal distribution of fish-like and no-fish echoes, we used the Nautical Area Scattering Coefficient (NASC or s_A, in $m^2.nm^{-2}$), an index of acoustic biomass, for each ping integrated over the water column. Data were echo-integrated in 0.2 m high layers over 1 ping with a -90 dB threshold, from 3 m down to 100 m depth. To discriminate between scatters attributed to fish (fish-like) and those originated by other organisms (no-fish), e.g., gelatinous and crustaceans, we applied the methodology developed by Salvetat *et al*. (under review). This method is based on thresholds on (i) volume backscattering strength Sv (Sv, in dB re 1 m^{-1}; see Maclennan *et al*., 2002 for acoustic definitions), (ii) the bi-frequency sum of Sv, and (iii) the variance of Sv. See Salvetat *et al.* (under review) for a detailed description of the methodology.

Since data distribution was not normal, to test for difference in fish-like and no-fish acoustic biomass ($\log10(s_A+1)$) according to the diel periods (day vs. night) and domain (inshore vs shelf-break), we used the non-parametric Mann-Whitney test. Day and night periods were defined based on the solar elevation angle with day when the altitude is >18° and night with altitude ≤ 18° (Lehodey *et al*., 2014).

3 Results

3.1 Setting the scene: actors in play during the day

In total, we identified 11 species belonging to 9 families and 5 orders in the videos (**Table 1**). The family Carangidae was the most diverse with 4 identified and 1 unidentified species, followed by the Balistidae with 2 identified species. The families Ginglymostomatidae, Lutjanidae, Malacanthidae, Sphyraenidae and Monacanthidae each have 1 identified species, while Bothidae and Ostraciidae 1 unidentified species.

Although the Carangidae presented the greatest number of representative species, Balistidae dominated the footage. *Melichthys niger* was by far the dominant species in the 6 hours of filming with over 2 hours of screen time, followed by *Canthidermis sufflamen* with 8 minutes. The other species appeared for less than one minute each. The high abundance of *Melichthys niger* and *Canthidermis sufflamen* when compared to the other species can also be observed through TmaxN (**Table 1**).

Table 1. List of fish species, total screen time of observation for each species (in hours, minutes and seconds) for the whole footage and the sum of the maximum values of the MaxN of each video (TMaxN).

Order	**Family**	**Species**	**Popular name**	**Screen time (HH:MM:SS)**	**TmaxN**
Carangiformes	Carangidae	*Caranx crysos*	Blue Runner	00:00:22	61
		Caranx latus	Horse-eye jack	00:00:05	2
		Caranx lugubris	Black-jack	00:00:38	15
		Caranx spp.	-	00:00:04	2
		Elagatis bipinnulata	Rainbow runner	00:00:05	27
Orectolobiformes	Ginglymostomatidae	*Ginglymostoma cirratum*	Nurse shark	00:00:29	8
Perciformes	Lutjanidae	*Lutjanus jocu*	Dog snapper	00:00:16	5
	Malacanthidae	*Malacanthus plumieri*	Sand tilefish	00:00:02	1
	Sphyraenidae	*Sphyraena barracuda*	Great barracuda	00:00:05	2
Pleuronectiformes	Bothidae	Unidentified	-	00:00:06	1
Tetraodontiformes	Monacanthidae	*Cantherhines macrocerus*	American whitespotted filefish	00:00:08	1
	Balistidae	*Canthidermis sufflamen*	Ocean triggerfish	00:08:17	363
		Melichthys niger	Black triggerfish	02:14:25	8685
	Ostraciidae	Unidentified	-	00:00:02	1

Horizontally (**Figure 2**), the black triggerfish *Melichthys niger* was distributed throughout the inshore area of the magic rectangle. Its abundance decreased while approaching the shelf-break. On the opposite, the ocean triggerfish *Canthidermis sufflamen* peaked at the shelf-break, except for the observation of one shoal in the inshore part of the magic rectangle. Most other species were observed in the neritic area except for *Caranx crysos*, *C. lugubrism* and *Elagatis bipinnulata* that peaked at the shelf-break.

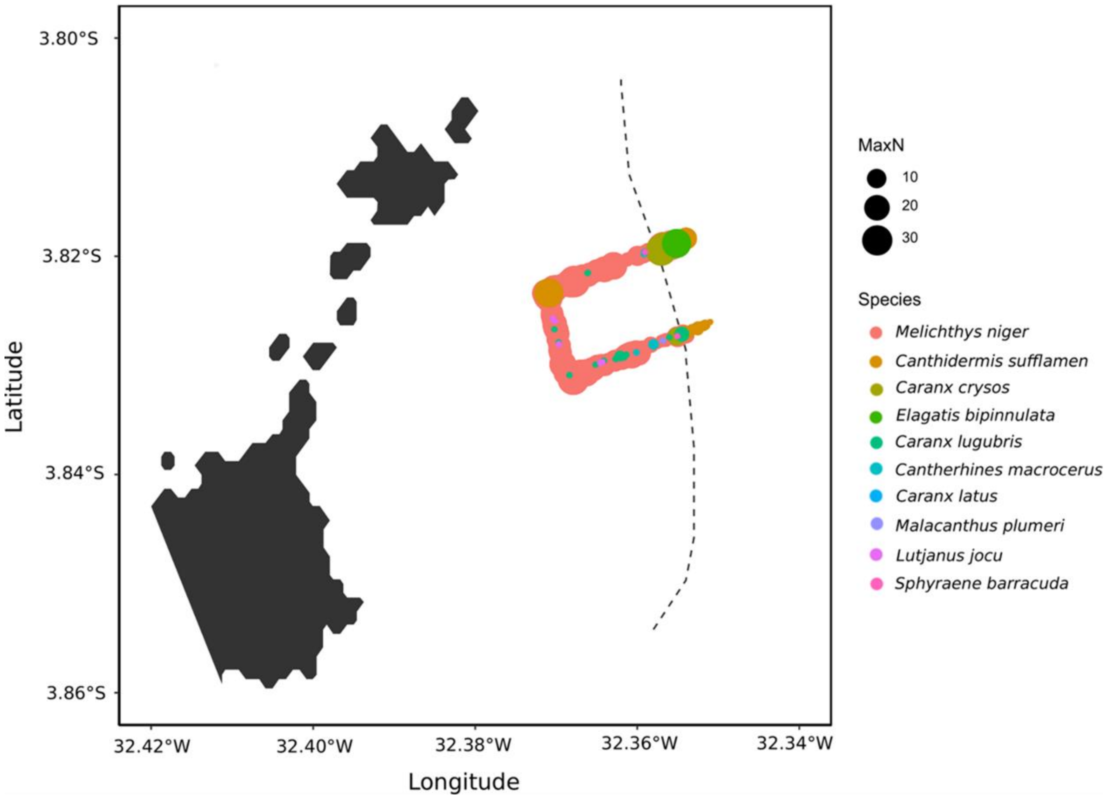

Figure 2. Horizontal distribution of fish species observed in video images along the magic rectangle, considering the maximum number of individuals observed for each video frame (MaxN). The black dotted line shows the 50 m isobath representative of the limit of the shelf break.

3.2 Diel variation of acoustic biomass

Overall, fish-like acoustic biomass (**Figure 3**) was significantly higher during the day than at night (mean log10(s_A+1) day/night: 2.64/1.78; p= <0.0001). This pattern was observed over the shelf (2.75/1.77; p= <0.0001) and at the shelf break, but at a lesser extent (2.07/1.80; p= <0.0001). During the day, fish-like acoustic biomass was significantly higher over the shelf than at the shelf-break (inshore/shelf-break: 2.75/2.07; p= <0.0001). However, no such significant differences were observed at night (1.77/1.80; p= 0.2). Note that at the sunset and during the night some very high fish-like s_A value were observed (**Figure 3**). They correspond to dense fish schools observed both on the shelf and at the shelf-break (**Supplementary Figure S1**).

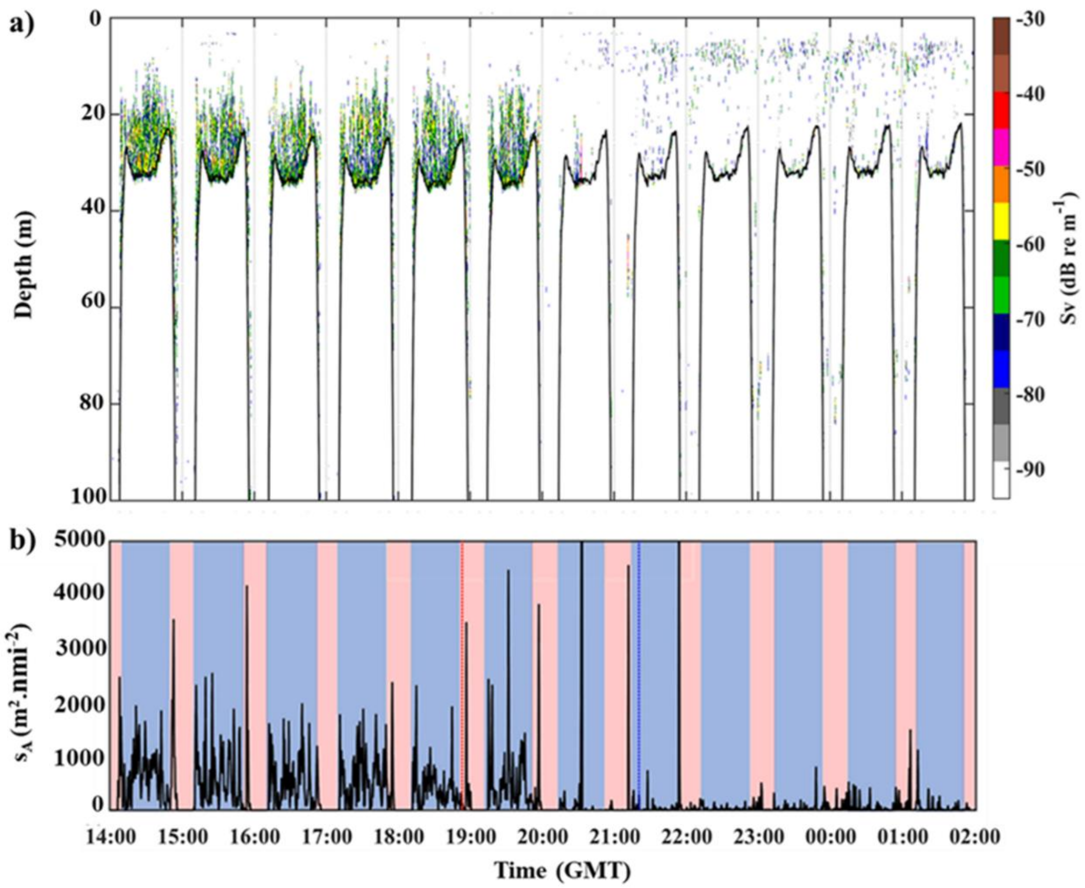

Figure 3. Echogram at 70 kHz of fish-like echoes (a) and (b) corresponding fish like acoustic biomass (s_A) during the magic rectangle transects as a function of time. In (a) the black line represents the sea bottom; in (b) the areas filled in blue and pink represent inshore and shelf-break areas, respectively; the red and blue vertical dotted lines depict the beginning and end of sunset, respectively.

The no-fish acoustic biomass (**Figure 4**) was significantly higher at night than during the day (mean log10(s_A+1) day/night: 2.07/2.26; $p= <0.0001$). This pattern can be observed both inshore (1.98/2.05; $p= <0.0001$) and at the shelf-break (2.25/2.55; $p= <0.0001$). During the day, the no-fish acoustic biomass was significantly higher at the shelf-break than over the shelf (mean log10(s_A+1) inshore/ shelf-break: 1.98/2.25; $p= <0.0001$). The same patterns was observed at night (2.05/2.55; $p= <0.0001$).

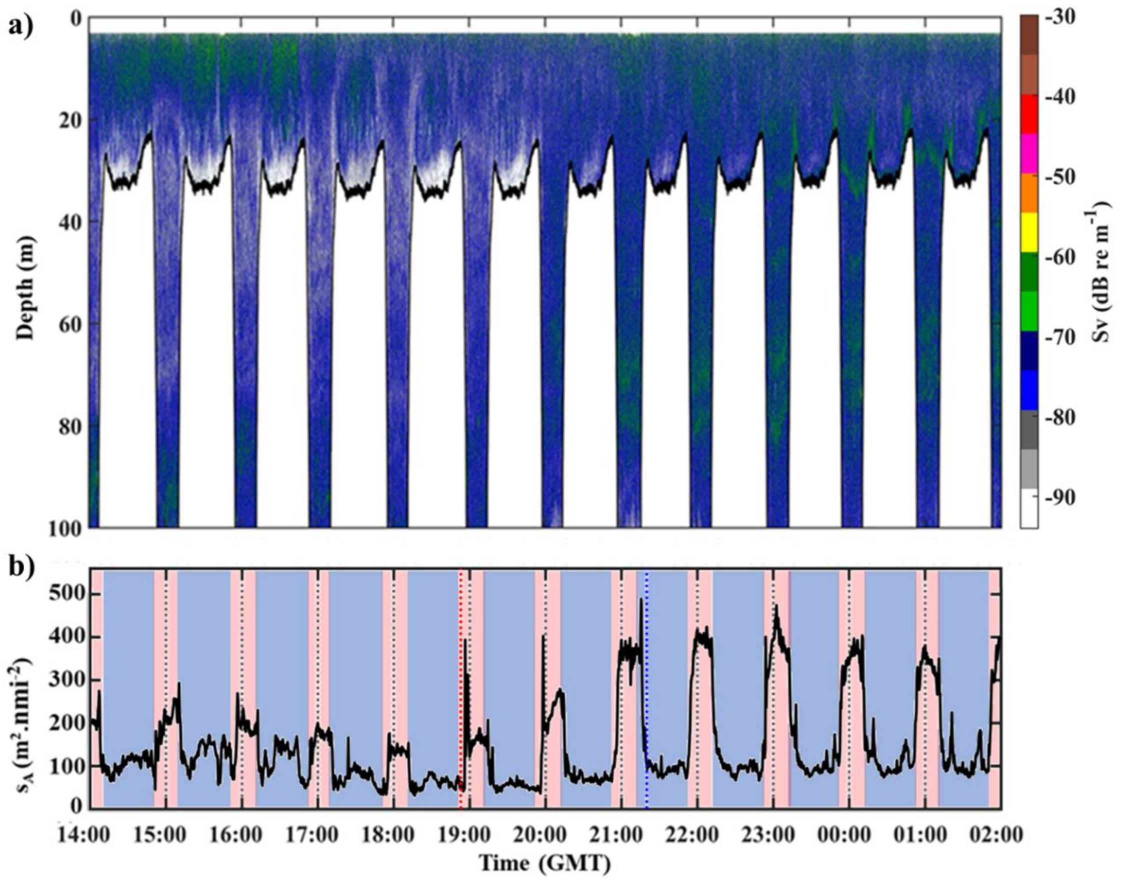

Figure 4. Echogram of no-fish echoes at 70 kHz (a) and (b) no-fish acoustic biomass (s_A) during the magic rectangle transects as a function of time. In (a) the black line represents the sea bottom; in (b) the areas filled in blue, and pink represent inshore and shelf-break areas, respectively; the red and blue vertical dotted lines depict the beginning and end of sunset, respectively.

4 Discussion

4.1 Setting the scene: actors in play

Oceanic islands, due to their isolation, usually show low taxonomic richness, but many endemic species (Paulay, 1994; Floeter and Gasparini, 2000; Gillespie, 2007; Mendes *et al*, 2018). FNA is no different. With up to 167 identified fish species it is marked by a considerable number of endemism and is dominated by a few abundant species in the reefs fish fauna (Floeter and Gasparini, 2000; Floeter *et al*., 2001; 2008; Ferreira *et al*., 2004; Krajewski and Floeter, 2011). All species identified through the video images had been previously observed in the region (Soto, 2001; Schmid *et al*., 2020).

Belonging to the family Balistidae, the black triggerfish *Melichthys niger* was by far the most abundant species in video footage (**Table 1**). This pattern was only reported by Salvetat et al (under review) that used the same methodology and by Schmid *et al.* (2020). This last study was based on baited remote underwater video observations likely attracting the voracious triggerfish. Usually observed in large shoals in the video images of this study, *M. niger* is known to be successful at colonizing oceanic islands (Kavanagh and Olney, 2006). Its plastic diet is an important factor in this regard, allowing it to occupy ecological niches where key species are absent (Mendes *et al*., 2019). In addition, their high abundance can also be associated with the high hydrodynamics present in the study area (windward side) (Gasparini and Floeter, 2001; Feitoza *et al.*, 2003; Kavanagh and Olney 2006; Salvetat *et al*., under review).

While *M. niger* is a demersal species, the ocean triggerfish *Canthidermis sufflamen*, the second more observed species in video footage can present an oceanic distribution (Salvetat, *et al*., 2020b; under review). Triggerfishes together with *Caranx crysos*, *Caranx latus*, *Caranx lugubris* and *Lutjanus jocu*, were observed in the FNA associated with spinner dolphins while foraging on their faeces or vomit (Sazima *et al.*, 2003; 2006). Carangidae is reported as the most representative family in FNA (Soto, 2001; Schmid *et al*., 2020), the same could be observed in this work even if the total of observations was low (**Table 1**). All species of carangids identified in this study, except *Caranx latus*, as well as *Lutjanus jocu* and *Sphyraena barracuda*, are part of the main species caught in the FNA by artisanal fisheries (Dominguez, *et al*., 2016). *Ginglymostoma cirratum* was the only species of elasmobranch observed in video images. According to Schmid *et al.* (2020) this species is recorded in large numbers in the archipelago, however in this study we only observed few individuals resting at the bottom.

Some fish could not be identified because of the distance to the camera. In addition, various individuals probably fled or hid in sponges, the sand or in the reefs themselves. This is corroborated by the acoustic data, where in some cases fish-like echo traces were observed near the bottom although they were not observed on the videos.

According to video footage, the no-fish echogram was dominated by gelatinous (salps, siphonophores and ctenophores), fish larvae (including leptocephalus) and fragments of pelagic algae (Salvetat *et al.,* under review). In addition, crustaceans, that could not be observed in videos, likely contributed to the no-fish acoustic data (Salvetat *et al*., under review).

4.2 Diel patterns

The algorithm developed to discriminate between fish-like and no-fish echoes was validated by Salvetat *et al.* (under review) using a large amount of video observations. We are therefore confident that the fish-like echograms actually correspond to fish.

In the neritic area, fish acoustic biomass was one order of magnitude higher during the day than at night with most fish echoes vanishing at dusk (**Figure 3**). The same pattern was observed at the shelf-break but to a lesser extent since the difference was only two-folds. In tropical reef ecosystems, there is an almost complete change in fish composition when comparing day and night (Hobson, 1972; 1975; Brewin *et al*. 2015). *M. niger*, by far the most abundant species, is very active during the day but rests at night, sleeping beyond rocks or coral (Brewin *et al*., 2015; Mendes *et al*., 2019). This behaviour pattern is clearly observed in our data. Other species observed during the day are also known to be active during the day and to rest during the night. This is the case for *Caranx latus*, *Cantherhines macrocerus*, *Canthidermis sufflamen* and *Malacanthus plumieri* of which the last species, *Malacanthus plumieri,* is known to hide in the bottom at night (Clark *et al*., 1988; Silvano, 2001; Auster and Lindholm, 2002; Sazima *et al.*, 2003; 2006; Weiss *et al.*, 2006; Vasconcellos *et al*., 2011). The barracuda is a transient predator that shows its peak activity during the day, but can also forage during the night, especially full moon nights (Hobson 1965; 1973; Randall, 1967; Rooker, *et* al., 2018; Campanella *et al*., 2019). In all cases, even when resting, the barracuda does not hide and should be observable by acoustics whatever the diel period. However, it only constitutes to a minor part of the fish abundance in our observations and other studies in FNA (Salvetat *et al*., under review). The nurse shark *Ginglymostoma cirratum* actively feeds during the night but since it is associated to the bottom, it may not be detected by acoustics and here again its biomass is low compared with other reef fish. On the contrary, five species we observed during the day, i.e., *Caranx crysos, C. lugubris, Elagatis bipinnulata* and *Lutjanus jocu* have both diurnal and nocturnal foraging habits (Brown *et al*., 2010; Keenan *et al*., 2007; Pavičić *et al*., 2014; Fischer *et al*., 1990; Sazima *et al*., 2006; Vaske *et al*., 2006; Randall, 1967). These species likely contribute to the echoes we observed at night. Besides, a variety of reef fish, mostly planktivorous, shelter in caves, holes and even sea urchins during the day and exhibit an active nocturnal behaviour (Lubbock and Edwards 1981; Greenfield and Johnson, 1990; Soto, 2001; Randall, 2005; Giglio *et al.*, 2018). In FNA it is the case for *Apogon americanos*, *Phaeoptyx pigmentaria*, *Heteropriacanthus cruentatus* or *Holocentrus adscensionis* that are reported in the literature (Soto, 2001; Schmid *et al*., 2020) but were not observed in video images. If present, these species were likely unabundant in the study area considering the drastic decrease in fish biomass we observed during the night.

The lesser difference in diel fish acoustic biomass at the shelf-break could be due to a specific specie composition with a higher proportion of pelagic species such as *Decapterus macarellus*, *Seriola* spp, *Elagatis bipinnulata* or *Thunnus* spp (Salvetat *et al*., under review) that stay in the water column all along the diel cycle. Actually, we observed small-pelagic fish school at the shelf-break during the full-moon night (**Supplementary Figure S1**). In addition, the vertical migration of mesopelagic fish may contribute to the fish biomass we observed at night at the shelf-break. Besides the classical diel vertical migration of mesopelagic organisms offshore, in Hawaiian Islands Benoit-Bird *et al*., (2001) reported a horizontal migration with mesopelagic entering neritic waters at night. Mesopelagic fish may thus concentrate at the shelf-break at night.

Interestingly, fish biomass and no-fish biomass presented an opposite pattern with fish clearing the water column when non-fish, potential prey for many fish species, are more abundant. Deciphering this behaviour requires further investigation.

In conclusion, by combining multifrequency acoustics and video footage over a tailored survey design we provide further knowledge on the fish diel behaviour in a neritic and adjacent shelf-break tropical ecosystem. Fish biomass drastically reduced at night indicating that most fish shelter in the bottom during the night and that fish presenting an opposite behaviour likely represent a minor part of the total fish biomass in the region.

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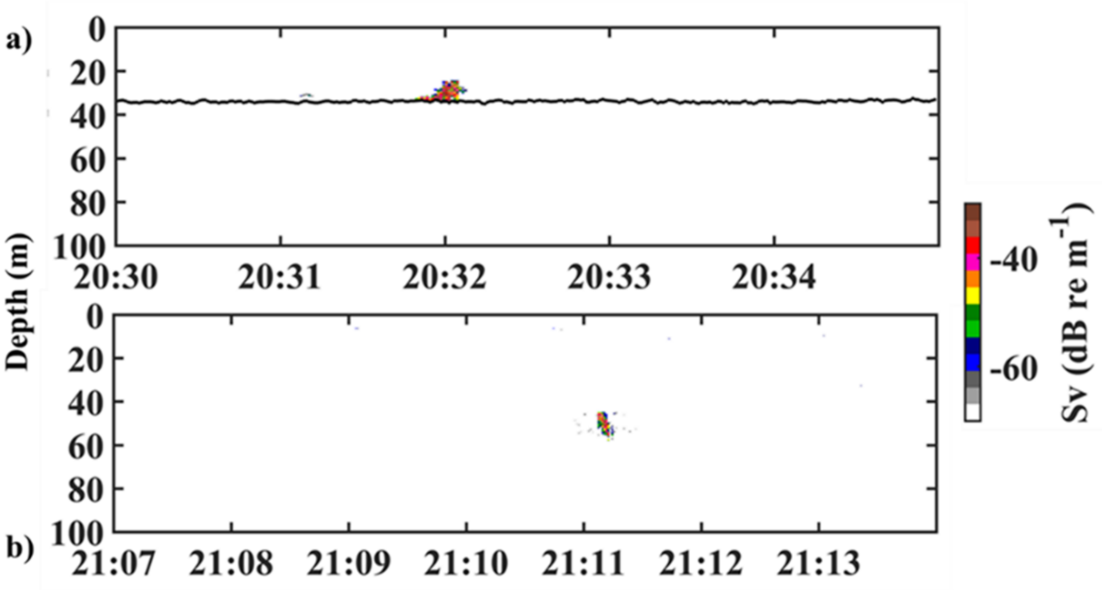
SUPPLEMENTARY MATERIAL

Contents:

- **Supplementary Figure S1**



Supplementary Figure S1. Example of echograms revealing the presence of dense fish schools observed over the shelf (a) and at the shelf-break (b). On the x-axis the time in GMT.

4 CONSIDERAÇÕES FINAIS

A utilização da acústica de bifrequência se mostrou uma boa alternativa para se observar a distribuição da ictiofauna ao longo do ciclo nictemeral, não só pela capacidade do método de acompanhar os acontecimentos na escala espaço-temporal em que ocorrem, mas também pelo fato de ser uma metodologia não destrutiva.

O principal objetivo deste trabalho, caracterizar a distribuição tridimensional de peixes na zona nerítica e áreas adjacentes a quebra da plataforma da Ilha de Fernando de Noronha em função do ciclo nictemeral, foi cumprida, assim como os objetivos específicos. A principal contribuição deste trabalho foi observar que a biomassa acústica de peixes se reduziu drasticamente durante a noite, corroborando com a hipótese proposta neste trabalho. Essa redução sugere que a maioria dos peixes se abriga no fundo nesse horário e que os peixes que apresentam um comportamento oposto provavelmente representam uma parte menor da biomassa total de peixes na região. Além disso, foi possível se obter informações, sobre determinadas espécies, que podem trazer benefícios para o turismo e pesca artesanal na região, como a alta abundância do *Melichthys niger* e maior representatividade da família Carangidae.

Por fim, os resultados deste trabalho podem contribuir para o desenvolvimento de políticas de conservação e manejo no arquipélago de Fernando de Noronha. Contudo, a redução drástica da biomassa acústica de peixes, quando a biomassa de possíveis presas aumenta na coluna d’água, deixam claro a necessidade de mais estudos para melhor compreensão do comportamento dos organismos marinhos na região.

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