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Diel changes in fish assemblages of Southwest Atlantic rocky reefs

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Abstract The alternation of light and darkness drives species' activities, and identifying diel rhythms is critical for understanding the ecology and representing the biodiversity of a range of communities. This study aimed to investigate diel changes in rocky reef fish assemblage composition and structure and to identify the most underestimated nocturnal species. We performed visual counts of rocky reef fishes along six times of the day (dawn, morning, afternoon, dusk, early night, and night) within three consecutive days. Distinct fish assemblages were observed, with species from multiple trophic levels during the day, while planktivorous and invertebrate feeders dominated the nighttime. Dawn and dusk shared diurnal and nocturnal species with long active periods, with no records of exclusively crepuscular species. Fish richness and abundance increased from dawn to a peak in the morning or afternoon and decreased at dusk with the lowest values during the night. Nocturnal planktivorous and invertivorous species would be severely underestimated using only diurnal samples, suggesting a potential bias to the understanding of the trophic dynamics. We discussed the underlying processes driving short-term dynamics of reef fish assemblages (e.g., predation risk and prey availability) and highlighted the need for a better representation of twilight and night periods in reef fish ecological studies.

Keywords Circadian rhythms · Reef fishes · Shallow rocky reefs · Ilha Grande bay

Introduction

The diel cycle of light intensity is one of the most significant drives that develop the circadian rhythms of reef fishes. The alternation of light and darkness synchronizes daily rhythms of physiology and behavior that determines the organism's temporal niche, restricting their biological activities to specific times of day and night (Kronfeld-schor et al. 2013). Reef fish distributions may change markedly as diurnally and nocturnally active species exchange places (Willis et al. 2006). However, studies of reef fish rarely consider short-term effects on the assemblage composition, structure, and function. Considering that nocturnal species represent an important

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component of the community, our knowledge of reef fish dynamics may be limited if only daylight surveys are undertaken.

Diel activity changes in reef fishes are primarily related to trade-offs between predation risk and feeding influenced by the extreme changes in light intensity (Milinski 1993; Campanella et al. 2019). During twilight, the ability of diurnal fishes in detecting their prey is impaired, which reduces the capture efficiency (Helfman 1986). In contrast, nocturnal fishes usually undergo major evolutionary visual adaptations to detect prey (Partridge 1990; Holzman et al. 2007; Cortesi et al. 2020; de Busserolles et al. 2021). Also, low light levels increase the risk of predation because the ability to detect predators is reduced, whereas the visual acuity of piscivorous predators increases (Hobson 1979; Helfman 1986; Danilowicz and Sale 1999; Campanella et al. 2019). On the other hand, a major factor that contributed to the nocturnal disposition of multiple species was probably the capacity to avoid daytime active predators (McCauley et al. 2012). In that way, sheltering in cracks and refuges of the reef is a common feature for both diurnal and nocturnal species. Diurnal fishes emerge from nocturnal shelters at dawn, display an active feeding during the day, and retreat to shelter at dusk (Collette and Talbolt 1972; Hobson 1972; Mallet et al. 2016). Conversely, nocturnal fishes are not seen in the water column during the day, emerging from their shelters at dusk or after nightfall (Ebeling and Bray 1976; Annese and Kingsford 2005).

Despite studies on the diel activity of conspicuous reef-associated species are well represented in the literature (e.g., squirrelfishes, triggerfishes, and wrasses), small cryptic reef lineages (e.g., blennies and gobies) and nocturnal species (e.g., Pempherids and Apogonids) are underrepresented (Myers et al. 2015; Dornburg et al. 2017; Koeda et al. 2021). Moreover, most studies focused on diel movements between resting and feeding sites (e.g., seagrass to reefs), with short-term dynamics of shallow reef fish assemblages still scarce. The existing studies confirmed day-night shifts in fish assemblages, with the highest diversity, richness, biomass, diversity of trophic groups, and abundance associated with the daylight period (Santos et al. 2002; Azzurro et al. 2007, 2013; Harvey et al. 2012; Hinojosa et al. 2020; Collins et al. 2022). Conversely, the twilight period (dawn and dusk) shares many species, some of which are nocturnal and others diurnal (Myers et al. 2015). Most of these findings contrasted day-night assemblage data, and the evaluation along different times of the day may give a more holistic view of fish assemblage dynamics.

In the southwest Atlantic coast, reef fish assemblages are relatively well represented by studies from shallow tropical and subtropical reefs to mesophotic areas (Ferreira et al. 2004; Teixeira-Neves et al. 2015; Rosa et al. 2016; Pinheiro et al. 2018; de Araújo et al. 2020; Moura et al. 2021). However, diel changes in marine community structure have been neglected, probably due to a lack of tested methodologies and sufficient resources to perform replicates of samples at night (Aguzzi et al. 2013; Barker and Cowan 2018; Hinojosa et al. 2020). To our knowledge, the basic description of the structure of shallow reef fish assemblages along their daily rhythm is lacking for the southwest Atlantic reefs, with the existing studies focusing on vessel reefs, recently published by Cardoso et al. (2020). The aim of this study was to investigate diel changes in rocky reef fish assemblage composition and structure and identify the most underestimated nocturnal species.

Material and methods

Study area

This study was conducted in the rocky reefs of Ilha Grande Bay (23° 01′ 34″ S; 44° 30′ 05″ W) on the Brazilian southeastern coast (Fig. 1). The main physiographic structure of the study area consists of narrow rocky shores covered by granite boulders, ending in a sandy bottom substrate which starts at a 4–7 m depth (Kjerfve et al. 2021). The water surface temperature can range from 15 to 33 °C (Barboza and Skinner 2021), with salinity ranging from 29 to 36 (de Oliveira Dias and Bonecker 2008). Local water masses are influenced by winds and tides with an average amplitude of 1.6 m (Nogueira et al. 1991).

The two studied rocky reefs are located on the coastline of Ilha Grande bay and are separated by a sand beach of 400 m of extension. Sites have similar environmental characteristics (e.g., depth, exposure to waves, temperature, and salinity). Depth at the studied sites varies between 1.5 and 2 m in the mid part of the rocky reef and 4–6 m at the sand/rock interface.

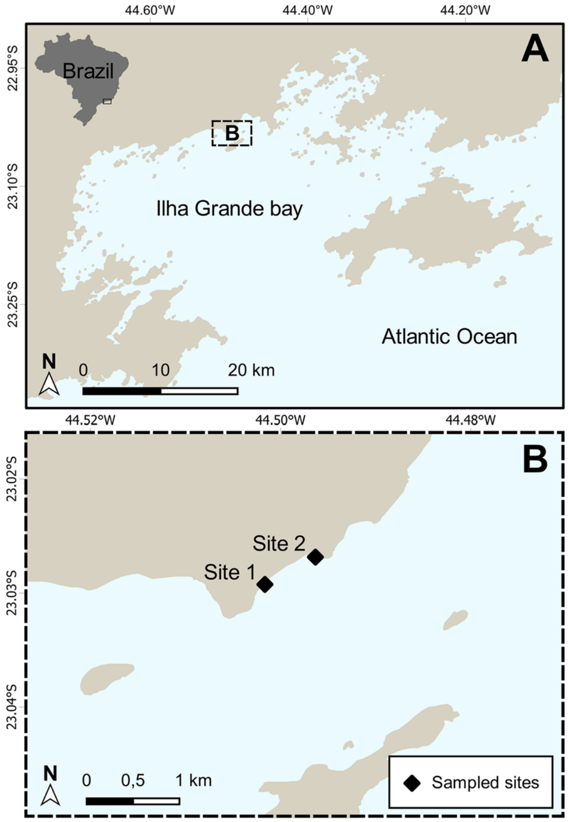

Fig. 1 Map of Ilha Grande Bay, southwestern Atlantic, Brazil (**A**), showing the sampling sites (**B**)

Fish surveys

Sampling was conducted during May 2010, within three consecutive days, to minimize temporal bias. Fish assemblage was assessed using underwater visual census (UVC) in shallow rocky bottoms (2-m depth) along transects 20-m long and 2-m wide (40 m^2), following Floeter et al. (2007). Transects were performed in an area of approximately 8.000 m^2 of each site. Two sites were sampled daily along the diel cycle of light intensity comprising the twilight, day, and night periods as follows: dawn – 05:50, morning – 08:30, afternoon – 14:00, dusk – 17:30, early night – 19:30, and night – 21:00. Three replicates were performed at each hour per site, totaling 108 samples (2 sites × 3 days × 6 sampling hours × 3 replicates). Sites were simultaneously sampled using surface snorkeling by two teams of two divers each. Additional UVCs were also carried out using the same methodology during June 2010 to assess the underestimation of nocturnal species. At each site, 12 transects were performed at 14:00 (afternoon) within two consecutive days, totaling 24 transects (2 sites × 2 days × 1 sampling hour × 6 replicates). Twilight and nocturnal dives were conducted using handheld torchlight to explore the transect and a headlamp to take notes (500–1200 lumens, white light). Samples were performed under good visibility conditions (>6 m visibility) during neap tide. The time of sunrise during the sampling period was 06:25, and the time of sunset was 17:25.

Fish species were categorized into trophic groups according to the available literature (Ferreira et al. 2001, 2004; Floeter et al. 2007; Pinheiro et al. 2018) and complementary data from FishBase (Froese and Pauly 2022). Seven categories of trophic groups were used: carnivores, mobile invertivores, omnivores, planktivores, roving herbivores, sessile invertivores, and territorial herbivores.

Data analysis

Species richness estimates were quantified with the Bootstrap algorithm using the software Estimate S 8.2 (Colwell, 2011). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to compare the structure, richness, and abundance of the fish assemblage between sampling hours (6 levels, fixed), sites (2 levels, random), and day (3 levels, random). When a factor (main effect or interaction) in the model was not significant, the *p*-value was higher than 0.25 and the proportion of variability explained by the factor was lower than 5%; we removed the factor from the analysis following Engqvist (2005). PERMANOVA pairwise tests were performed to assess differences in fish parameters between sampling hours for each site separately. A principal coordinates analysis (PCO) was used to explore the diel variation in assemblage structure for each site. The fish species vectors driving the ordination were determined through Pearson correlations (>0.4) and overlaid on the PCO plots.

A percentage similarity analysis (SIMPER) was used to assess the underestimation of nocturnal species if only diurnal sampling had been applied. The data were organized into a new matrix containing fish species abundances of transects performed in May 2010 (14:00 and 19:30, 6 samples each per site) and in June 2010 (14:00, 12 samples per site).

The percentage of contribution of nocturnal species to the similarity of diurnal/nocturnal assemblages was compared with that obtained from only diurnal sampling. PERMANOVA pairwise comparisons were performed to investigate the diel cycle variation of selected species (frequency of occurrence > 0.3 and PCO axis correlations > 0.4) for each site separately. The Monte Carlo procedure was used to calculate *p* values (pMC) when the number of unique permutations was very low. Prior to multivariate analysis, the fish assemblage data were square root transformed to reduce the influence of more abundant and rare species. Bray-Curtis similarity matrices were calculated for multivariate data, while Euclidean distance matrices were used for univariate measures. Multivariate and univariate analyses were conducted using PRIMER 6.0 + Permanova software (Anderson et al. 2008).

Results

Fish composition

A total of 2676 individuals were observed, belonging to 42 species and 28 families (Supplementary Table 1). The most abundant species during day hours (8:30 and 14:00) were chere-chere grunt (*Haemulon steindachneri*) (52.2%), sergeant-major (*Abudefduf saxatilis*) (15.9%), Brazilian blenny (*Malacoctenus delalandii*) (5.0%), tomtate grunt (*Haemulon aurolineatum*) (4.4%), South American silver porgy (*Diplodus argenteus*) (4.2%), comb grouper (*Mycteroperca acutirostris*) (3.3%), and banded butterflyfish (*Chaetodon striatus*) (3.2%). During the night (19:30 and 21:00), the most abundant species were high-hat (*Pareques acuminatus*) (40.1%), banded butterflyfish (*C. striatus*) (13.4%), and glassy sweeper (*Pempheris schomburgkii*) (12.4%). The twilight (05:50 and 17:30) were characterized by species observed during the day (*H. steindachneri*, *M. acutirostris*) (44.3% and 5.0%, respectively) and night hours (*P. acuminatus*) (12.4%). Those species had more than 50% of the frequency of occurrence.

The total number of species was higher during day hours (08:30 and 14:00, 31 species), had the lowest values during the night (19:30, 16 species; 21:00, 17 species), and intermediate values during dusk and dawn (05:50, 22 species; 17:30, 21 species) (Supplementary Table 1). These values corresponded between 75 and 92% of Bootstrap estimators for each time of the day. Nine species were observed during all sampling hours, 18 species were observed during the day and night, while twilight hours also had 18 species in common.

The most abundant trophic group was mobile invertivorous fishes (represented mainly by *H. steindachneri* during the day; *P. acuminatus* [*night*], *P. acuminatus* and *H. steindachneri* [*twilight*]) (Fig. 2). Omnivorous fishes (mainly represented by *A. saxatilis*) and roving herbivorous (mainly represented by *Sparisoma frondosum*) were more abundant during dawn and day hours, while territorial herbivorous (*Stegastes fuscus*) showed similar relative abundances throughout the day. Sessile invertivorous and carnivorous fishes were more abundant during twilight and night hours. Planktivorous fishes (represented by *P.*

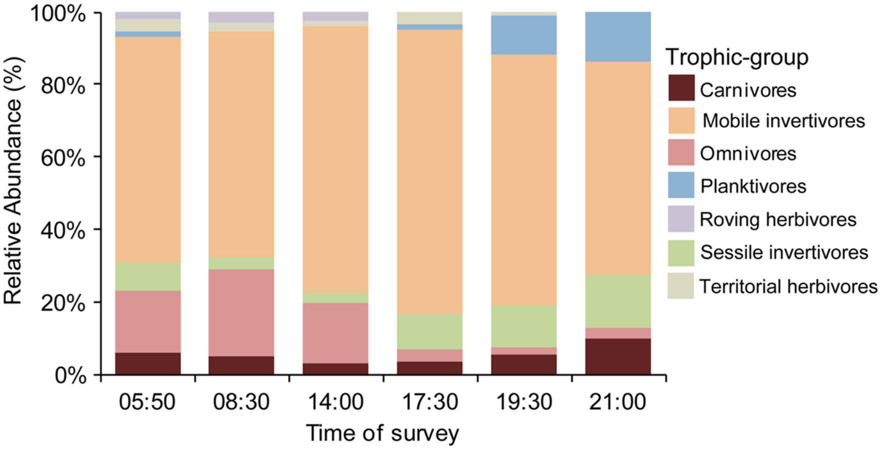

Fig. 2 Relative proportions in the number of individuals by trophic category (total proportion for both sites)

schomburgkii) were observed mainly during the night (Fig. 2).

Diel cycle variation

Fish assemblage structure varied between hours, sites, and the interaction term (hour × site), but not between days (excluded from the analysis [$p > 0.25$ and the proportion of variability explained $< 5\%$]) (Table 1). The assemblage structure differed between dawn (05:50), day (08:30), and night (19:30 and 21:00) hours for both sites (Table 2). Twilight hours (05:50 and 17:30) had similar assemblages, while differences between dusk (17:30) and night hours were observed only for site 1 (Table 2).

Table 1 Results of PERMANOVA testing for differences in fish assemblage structure in response to sampling hour, site, and interaction effects

Source	df	SS	MS	Pseudo-F	P (perm)
Hour	5	88,356	17,671	4.672	***
Site	1	8572.2	8572.2	4.925	***
Hour*site	5	18,908	3781.6	2.172	***
Res	96	167,090	1740.5		
Total	107	282,920			

df, degrees of freedom; *SS*, sum of squares; *MS*, mean sum of squares; *ns*, not significant

*$p < 0.05$

**$p < 0.01$

***$p < 0.001$

The first PCO axis contained 35.7% and 40% of the total variation for site 1 and site 2, respectively, and was associated with day-night variation in reef fish assemblage (Fig. 3). *Pareques acuminatus* and *P. schomburgkii* were associated with night hours, while a richer assemblage (*H. steindachneri*, *A. saxatilis*, *C. striatus*, *M. delalandii*, *M. acutirostris*, *S. frondosum*) represented daylight samples (Fig. 3, Supplementary Table 2). The second PCO axis contained 15.8% and 14.6% of the variation for sites 1 and 2, respectively, and was represented by species observed during twilight hours (*P. acuminatus*, *M. acutirostris*, *H. aurolineatum*, and *P. schomburgkii*) (Fig. 3, Supplementary Table 2).

The nocturnal species ranked among the most contributing to the similarity (SIMPER). *Pareques acuminatus* contribution increased to 16.2% (day/night samples grouped) in site 1 and from 8.5% to 20.11% in site 2, becoming the second most contributing species for both sites. *Pempheris schomburgkii* became the sixth most contributing species to the similarity of site 1 with 7.3%.

Fish richness and density

Fish richness and abundance differed between hours, while differences between sites occurred only for fish richness. Fish abundance also varied for the interaction term (hour × site; Table 3). The daylight hours had the highest fish richness and abundances, in contrast to night and twilight hours for both sites (Fig. 4). The diel variation in fish richness

Table 2 Pairwise results from PERMANOVA comparing the fish assemblage structure between sampling hours for each site separately

	Hour	05:50		08:30		14:00		17:30		19:30		21:00	
		S.1	S.2	S.1	S2	S.1	S.2	S.1	S.2	S.1	S.2	S.1	S.2
Dawn	05:50	-	-	-	-	-	-	-	-	-	-	-	-
Morning	08:30	***	***	-	-	-	-	-	-	-	-	-	-
Afternoon	14:00	***	***	*	ns	-	-	-	-	-	-	-	-
Dusk	17:30	ns	ns	***	***	***	***	-	-	-	-	-	-
Early night	19:30	*	***	***	***	***	***	***	ns	-	-	-	-
Night	21:00	*	***	***	***	***	***	***	ns	ns	ns	-	-

S.1, site 1; *S.2*, site 2; *ns*, not significant

*$p < 0.05$

**$p < 0.01$

***$p < 0.001$

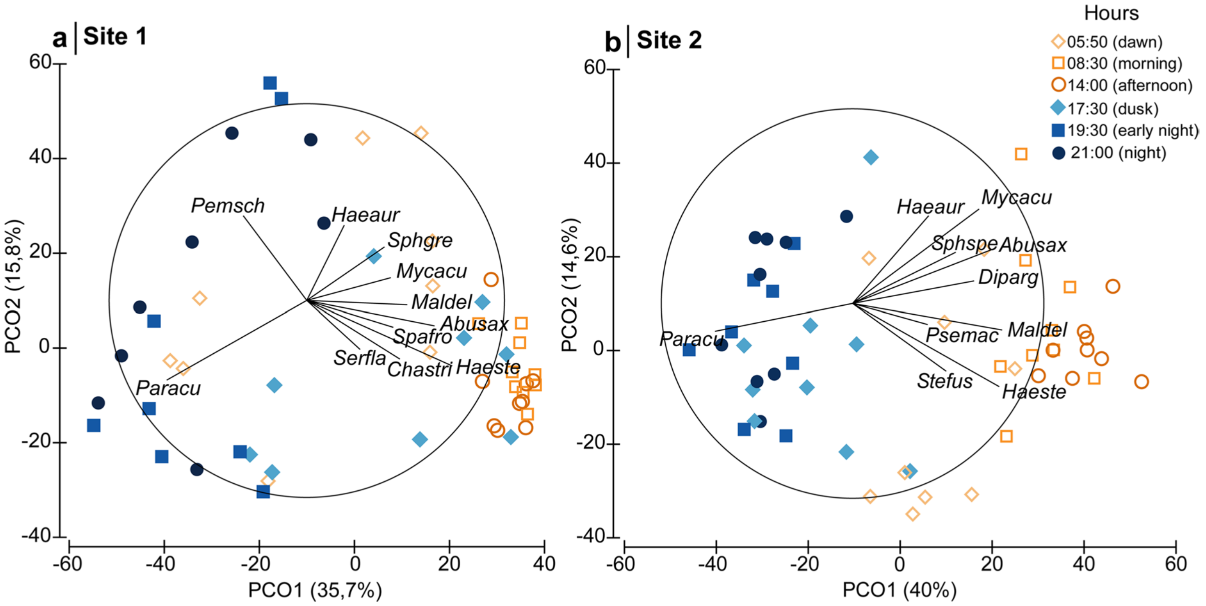

Fig. 3 Principal coordinate analysis (PCO) with reef fish abundance data at (**A**) site 1 and (**B**) site 2. Sampling hours are color-coded to evidence diel cycle variation in fish assemblage structure. Only the species with the greatest contribution to the ordination are shown. Species codes: Abusax – *Abudefduf saxatilis*; Chastri – *Chaetodon striatus*; Diparg – *Diplodus argenteus*; Haeaur – *Haemulon aurolineatum*; Haeste – *Haemulon steindachneri*; Maldel – *Malacoctenus delalandii*; Mycacu – *Mycteroperca acutirostris*; Paracu – *Pareques acuminatus*; Pemsch – *Pempheris schomburgkii*; Psemac – *Pseudupeneus maculatus*; Serfla – *Serranus flaviventris*; Spafro – *Sparisoma frondosum*; Sphgre – *Sphoeroides greeleyi*; Sphspe – *Sphoeroides spengleri*; Stefus – *Stegastes fuscus*

Table 3 PERMANOVA results based on Euclidian distance measures for fish richness and abundance

Source	df	SS	MS	Pseudo-F	P (perm)
Fish richness					
Hour	5	16.787	3.3574	24.804	***
Site	1	1.3443	1.3443	15.168	***
Hour*site	5	0.67679	0.135	1.5273	ns
Res	96	8.5079	0.088		
Total	107	27.316			
Abundance					
Hour	5	490.49	98.098	17.66	***
Site	-	-	-	-	-
Hour*site	5	27.775	5.5549	4.3097	***
Res	97	125.03	1.2889		
Total	107	643.29			

df, degrees of freedom; *SS*, sum of squares; *MS*, mean sum of squares; *ns*, not significant

A hyphen "-" means factor removed (not significant, *p* value > .25 and the proportion of variability explained < 5%)

*$p < 0.05$

**$p < 0.01$

***$p < 0.001$

was more pronounced in site 1 due to higher values in the morning (08:30, 9.2±0.54 species) compared to afternoon (14:00, 7.1±0.48), and twilight hours (05:50, 5.0±0.86; 17:30, 5.2±0.64) compared to night hours (19:30, 2.6±0.52; 21:00, 2.7±0.57). Fish abundance was also higher in the morning (08:30, 75.5±12.1 individuals) compared to the afternoon in site 1 (14:00, 45.8±5.8), and twilight hours (5:50, 13.8±4.9; 17:30, 16.5±3.5) compared to early night (19:30, 4.5±0.8).

Diel variations of selected species

The abundance of diurnal species increased from dawn to a maximum during morning or afternoon, with a decrease at dusk (Fig. 5). Depending on the site, some species were more abundant during morning (*A. saxatilis*, $t = 1.15$, $p = 0.008$, at site 1; and *M. acutirostris*, $t = 2.4$; $p = 0.02$, at site 1 and 2) compared to afternoon, while *H. steindachneri* ($t = 2.3$; $p = 0.03$, at site 2) had the opposite trend. *Chaetodon striatus* and, to a lesser extent, *M. acutirostris*

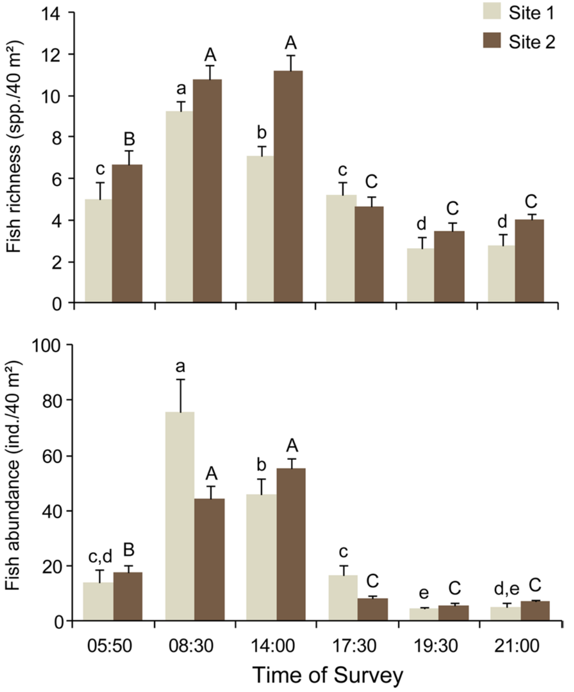

Fig. 4 Mean fish richness and density (ind./40 m^2) along the diel cycle. Subscript and capital letters show pairwise results from PERMANOVA for site 1 and site 2, respectively

were observed during the night hours, but at smaller densities. However, *C. striatus* remained inactive during the night resting on the substrate. *Stegastes fuscus* and *C. striatus* showed a long active period, being observed from dawn to dusk. The most common species during the night (*P. acuminatus*) exhibited a larger active period from dusk to dawn, while *P. schomburgkii* abundance was higher at night compared to dusk ($t = 7.2$; pMC = 0.005).

Discussion

This study showed that the sampling hour can strongly affect the reef-fish composition, fish richness, total abundance, and the abundance of selected species. A richer assemblage with fishes in multiple trophic levels characterized diurnal samples, while a smaller assemblage of invertebrate feeders and planktivorous fishes occurred during the night. Twilight hours were represented by both diurnal and nocturnal reef fish species, reflecting this transitional period. Nocturnal sciaenids and pempherids showed cryptic behavior during the day, sheltering in holes and crevices, while at night, they were much more visible. In contrast, diurnally active species (such as labrids, acanthurids, and pomacentrids) were not seen at night.

Day-night shifts in fish composition are primarily related to feeding behavior in response to the abundance and activity patterns of the prey (Harvey et al. 2012, Hinojosa et al. 2020). The nocturnal activity of *P. schomburgkii* is associated with the abundance of the meroplanktonic crustaceans (especially amphipods) that rise from the bottom into the water column after dark (Gladfelter 1979; Annese and Kingsford 2005; Koeda et al. 2021). Similarly, the sciaenid *P. acuminatus* is active during the night following the availability of mobile invertebrates, such as Brachyuran crabs, which remain buried in the substrate during the day to avoid predators (De La Rosa et al. 2020). Nocturnal reef fishes have evolved several adaptations to increase the light sensitivity of their eyes, providing better acuity to catch their prey (Cortesi et al. 2020; de Busserolles et al. 2021). Moreover, reef fishes can use sound as an orientation for nocturnal movements (Simpson et al. 2008; Spence 2017) and to detect prey activity (Tavolga and Wodinsky 1963), as observed by Ramcharitar et al. (2006a) for *P. acuminatus*.

In contrast, several diurnal fish species of this study feed on invertebrates that remain concealed in macroalgal beds or sand bottoms during the day to avoid predation (Wenger et al. 2018; Hinojosa et al. 2020; Vieira et al. 2021). Grunts (*Haemulon* spp.) feed on crustacean groups with low dispersal capacity (Thomas and Cahoon 1993) that are primarily associated with macroalgal beds (Jacobucci and Leite 2002; Tanaka and Leite 2003). Mullid fishes such as *Pseudupeneus maculatus* use barbels in the detection of small crustaceans that inhabit macroalgae or soft sediments (Mccormick 1995). The flying gurnard *Dactylopterus volitans* preys on benthic crustaceans and small fishes, scratching and probing the bottom with the inner rays of its pectoral fins (Sazima et al. 2005; Davenport and Wirtz 2019). These behaviors are in response to mechanisms used by prey to avoid predation that is higher during the day (Campanella et al. 2019).

Diurnal fishes also perform a visual detection of the prey, actively searching for them or adopting a sit-and-wait predation strategy (Gibran 2007; Vieira

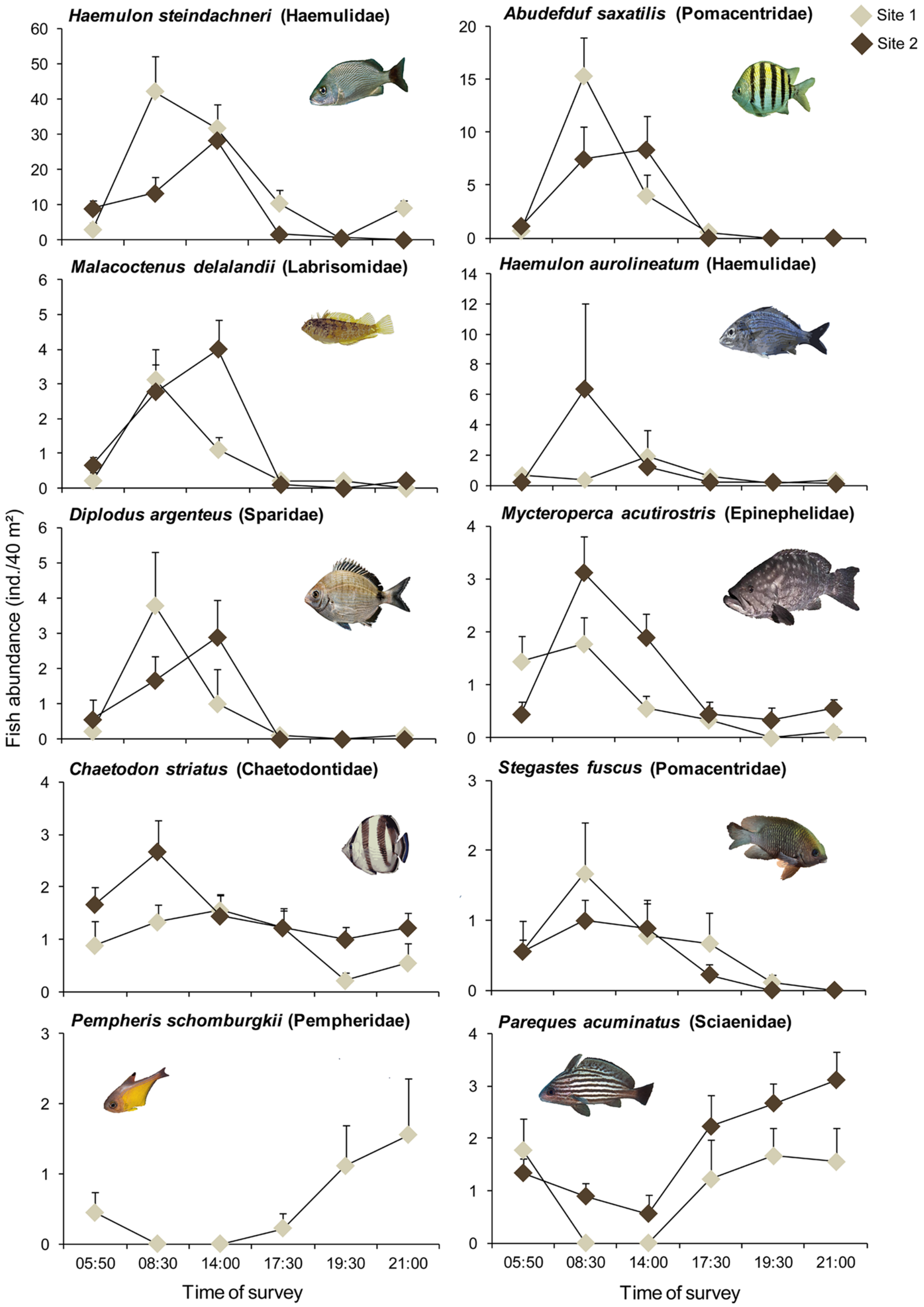

Fig. 5 Changes in mean density of selected fish species along the diel cycle

et al. 2021). In this study, the higher abundance of the carnivore *M. acutirostris* during dawn and morning hours compared to dusk (17:30) is probably associated with the predation of small fish (Gibran 2007) that can emerge from nocturnal shelters at a light intensity lower than the one they retreat at dusk (Rickel and Genin 2005). At low light levels, the distance between predator and prey decreases, which may influence the foraging success (Fiksen et al. 2002; Bosiger and McCormick 2014). In contrast, the butterflyfish *C. striatus* that feeds mainly on sessile invertebrates (Liedke et al. 2016) was observed actively swimming from dawn to dusk, while individuals observed at night were inactive. The feeding activity of *C. striatus* starts about 30 min after sunrise and ends shortly before nightfall, but the lowest feeding rates are recorded in the early morning and late afternoon (Bonaldo et al. 2005).

The territorial herbivore *S. fuscus* was also observed throughout the day, but its diel-feeding activity is affected by the time spent in territorial defense against surrounding individuals and the quality of the available food resources (Barneche et al. 2009; Silveira et al. 2020). Nevertheless, *S. fuscus* showed high feeding rates in the afternoon (Ferreira et al. 1998a), as observed for other territorial damselfishes (McDougall and Kramer 2007; Souza et al. 2011) and roving herbivorous (Bruggemann et al. 1994; Bonaldo et al. 2006; Welsh and Bellwood 2012; Afeworki et al. 2013). The highest feeding activity of herbivorous fish in the afternoon compared with the early morning correlates with the midday peak algal nutrient that remains relatively constant throughout the afternoon (Ferreira et al. 1998b; Zemke-White et al. 2002; Bonaldo et al. 2006; Luise Bach and Smith 2021).

The similarity between dawn and dusk assemblages is associated with fish movements among resting and foraging sites (Rickel and Genin 2005; Mallet et al. 2016), resulting in the highest community turnover (Luise Bach and Smith 2021). For example, at dawn, we observed *H. steindachneri* emerging from their nocturnal shelters simultaneously with *P. acuminatus* returning to resting. However, being active during twilight increases the fish's own risk of predation (Campanella et al. 2019). *Pareques acuminatus* that feeds on the benthos was relatively abundant during twilight, while Pempherids that feed exposed in the water column wait for nightfall to leave the shelter, avoiding predators (Koeda et al. 2021; LMN and TPTN personal observations). Pempherids form large schools inside caves and exhibit a high site fidelity returning to the same shelter or moving to nearby shelters (<20 m of distance) before dawn (Annese and Kingsford 2005; Koeda et al. 2021). Thus, the variability in *P. schomburgkii* abundance between our sites may be related to the availability of large shelters.

We identified that planktivorous trophic guild would be severely underestimated without nocturnal sampling, especially due to the sweeper *P. schomburgkii* absence during the day (8:30 and 14:00). Pempherid fishes have a rapid growth associated with their feeding behavior at that they can full up their stomach every night with zooplankton (Koeda et al. 2016). Furthermore, sweepers are a food resource for large carnivores (Koeda et al. 2017). Similarly, the mobile invertebrate feeder *P. acuminatus* became the second most contributing species to the similarity of the reef and may play an important role in controlling the density of benthic infauna. The underestimation of nocturnal fishes is likely to increase for areas that potentially harbor a richer nocturnal assemblage, as for insular reefs of Ilha Grande bay where cardinalfishes (Apogonidae) (*Apogon americanus*, *Phaeoptyx pigmentaria*, and *Astrapogon puncticulatus*) were registered (Creed et al. 2007). Apogonids form a major component of nocturnal reef fish assemblages, both in terms of species diversity, numerical abundance, and biomass production (Marnane and Bellwood 2002; Collins et al. 2022).

The light used in this study allowed us to easily recognize fish species and visually explore the transect, with no clear escape behavior observed when the torches were turned on, as also reported by other nocturnal studies (Azzurro et al. 2007; Hinojosa et al. 2020). Also, the use of 2-m wide transects and high visibility of the study sites enable fish counts. However, the color of the artificial light can affect fish behavior, with a decrease in the abundance and frequency of some species (e.g., *Haemulon aurolineatum* and *Phaeoptyx pigmentaria*) using white light (Fitzpatrick et al. 2013; Lucena et al. 2021). Nevertheless, a study testing the effects of different light colors (white, blue, and red) on nocturnal fish assemblages in a subtropical rocky reef did not detect any influence on total density, species richness, and fish assemblage structure (Lucena et al. 2021).

We found that mobile invertebrate feeders dominated all sampling hours, but their richness was higher during the day compared to night. Diurnal invertebrate feeders observed in this study are known to actively search for prey on different substrata (e.g., macroalgae, sand), while nocturnal sciaenids are considered hearing specialists (Myrberg and Fuiman 2002; Ramcharitar et al. 2006b). On the other hand, planktivorous fish that forage in the water column were mainly represented by pempherids that seem to wait for nightfall to leave caves. Twilight assemblages were represented by both diurnal and nocturnal species with long active periods (*C. striatus*, *S. fuscus*, *P. acuminatus*) with no records of exclusively crepuscular species. The increasing efforts on sampling reefs have considerably expanded our knowledge of reef fish dynamics, but wrong assumptions can be made when nighttime sampling is ignored. Several ecological problems well documented in the literature (e.g., the influence of environmental drives, the effectiveness of marine protected areas, and impact assessment) are based solely on diurnal sampling. Thus, extending sampling to twilight and night hours may improve our understanding of ecological processes that generate biodiversity patterns.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethical approval This is an observational study. The Research Ethics Committee has confirmed that no ethical approval is required.

Conflict of interest The authors declare no competing interests.

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