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Does the colors of light matter? Testing different light color in nocturnal underwater visual censuses

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ABSTRACT

Most methods for assessing reef fish assemblages at night require artificial light, but the use of different colors of light may influence the results. We used data from 135 underwater visual censuses (UVCs) performed with different colors of light (red, blue and white) to evaluate the structure of fish assemblages on subtropical rocky reefs along three depth intervals. We did not detect any effect of the color of light on total density or fish species richness per transect, nor on the structure of the entire assemblage. However, the density of some of the most abundant species varied according to the color used. Red light showed the highest values of frequency of occurrence for most species, while the white light resulted in decreased abundance of some fish species. Our results emphasize the importance of choosing the color of light depending on the type of studies to be conducted. This will depend on the objectives of the research (e.g. inventory, behavior or community dynamics) and the target fish fauna (e.g. mobile or sedentary).

1. Introduction

Circadian rhythms influence fish movements among habitats, as well as their diel feeding and reproductive behavior (Nagelkerken et al., 2000). These rhythms can be modulated by internal mechanisms but also by external factors such as predation and other trophic interactions (Hammerschlag et al., 2010). Most tropical and temperate reef fish are diurnal (Helfman, 1986; Hobson, 1965), whereas only about 30% exhibit primarily nocturnal activity (Helfman, 1978). At least 13 families of reef fish are mainly composed of nocturnal species (Schmitz and Wainwright, 2011), with Apogonidae (cardinalfishes), Holocentridae (soldierfishes and squirrelfishes), Haemulidae (grunts) and Pempheridae (sweepers) the most widespread and well-known.

Assessing fish at night is not trivial, because it require extra ability from researchers and appropriate equipment, such as artificial lights. Thus, there is a large knowledge gap about 'what happens at night' on reefs (Myers et al., 2016). The use of artificial light can affect the behavior of animals (Rich and Longcore, 2006), but there is little information about the characteristics of light suitable for underwater behavioral studies (Fitzpatrick et al., 2013).

Life at night is not easy for species with poor eyesight under low or no light conditions (Warrant, 1999). Nocturnal fish species have relatively larger eyes than diurnal species (Schmitz and Wainwright, 2011). Fish eyes have two main types of light-sensitive cells that can be classified according to their structure and function. Rods capture light mainly at low levels, and cones mediate color vision in bright light (Harvey et al., 2012a), being capable to absorb light from short and long wavelengths of the light spectrum (Von der Emde et al., 2004). However, most coastal fish species investigated to date do not possess cones with sensitivity beyond ca. 550 nm (Von der Emde et al., 2004), which implies low or no sensitivity to red light.

With the increasing number of studies on dynamics and behavior of reef fish, the same techniques commonly used in daytime studies have been applied at night (Azzurro et al., 2007). However, these techniques require extensive testing and constant adjustments to eliminate or lessen the limitations related to the shortage of light. Underwater visual census (UVC) is the most widespread technique for assessing patterns of abundance and distribution of reef fish, as it is non-destructive, easily reproducible and cost-effective (see Harvey et al., 2004), although there are some limitations related to the presence and experience of the diver and type of gear used, that may

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influence the estimates (Harvey et al., 2002; Lopes et al., 2019). Complementary to UVCs, baited remote underwater videos (BRUVs) are increasingly being used to evaluate fish assemblages, especially in places that are difficult for divers to access, such as non-reef environments or deeper reefs (Mallet and Pelletier, 2014), and also to detect shy or elusive species (Pimentel et al., 2019). BRUVs are comparatively more expensive, time-consuming and selective than traditional UVCs because they require long shooting time and bait to attract fish (Fitzpatrick et al., 2013). Furthermore, while UVCs provide absolute estimates of density and biomass per unit area, BRUVs provide only relative estimates (Whitmarsh et al., 2017). These two methods are the most common for nocturnal fish assessments (Azzurro et al., 2007; Fitzpatrick et al., 2013). Nevertheless, differences in richness and abundance of fish species observed using different colors of light with BRUVs at night highlight the need to understand the influence of the color of light also during UVC surveys (Fitzpatrick et al., 2013). In addition, in a scenario of increasing anthropogenic pressure in which nighttime ecology has been particularly affected (Gaston, 2019), it is necessary to develop non-destructive and cost-effective methods to improve our understanding about the ecology of reef environments at night.

We aimed to evaluate the effects of different light 'colors' (white, blue and red) on the structure of nocturnal fish assemblages in a subtropical rocky reef using UVCs. Ultimately, this will allow for a more precise evaluation of nocturnal assemblages and provide a more complete understanding of fish assemblages in an integrated manner.

2. Methods

2.1. Study site

The study was conducted in the Arraial do Cabo Marine Extractive Reserve, a sustainable use marine protected area located in a subtropical rocky reef region in southeastern Brazil (22°57′57″ S, 42°1′40″ W). Local reefs present a high diversity of fish and benthic sessile organisms such as corals, gorgonians, zoanthids and sponges (Ferreira et al., 2001; Rogers et al., 2014), with clear waters (average horizontal visibility ~ 8 m) almost all year round and average water temperatures around 22 °C (Valentin, 1984). Three study sites with similar assemblages and topographic features (Cordeiro et al., 2016) were chosen for testing the influence of light color on the nocturnal fish assemblage.

2.2. Survey technique

Fish assemblage was assessed using underwater visual census (UVC) along replicated strip transects (20 × 2m). This method was chosen because it has been used to adequately sample reef fish throughout the Brazilian province (e.g. Floeter et al., 2007; Longo et al., 2015; Luiz et al., 2015). A trained scuba diver unwinds a 20-m long tape while counting and estimating the size of conspicuous swimming fish species >10 cm. On the way back, smaller (<10 cm), site-attached and cryptic species were counted (Fig. 1). In all UVCs each diver used a pair of flashlights (LED lamp, 1200 lumens, 6500K): one handheld to illuminate the field of view and a second as a headlamp. Three different light spectra were applied during the survey using color filters: red, blue, and no filter. Hereafter, the light without filter will be referred to as 'white'. The filters applied were standard filters provided by the flashlight manufactory (BigBlue®).

2.3. Experimental design

The survey design consisted of three factors: light colors (three levels, fixed: red, white, blue), site (random, three levels), and depth

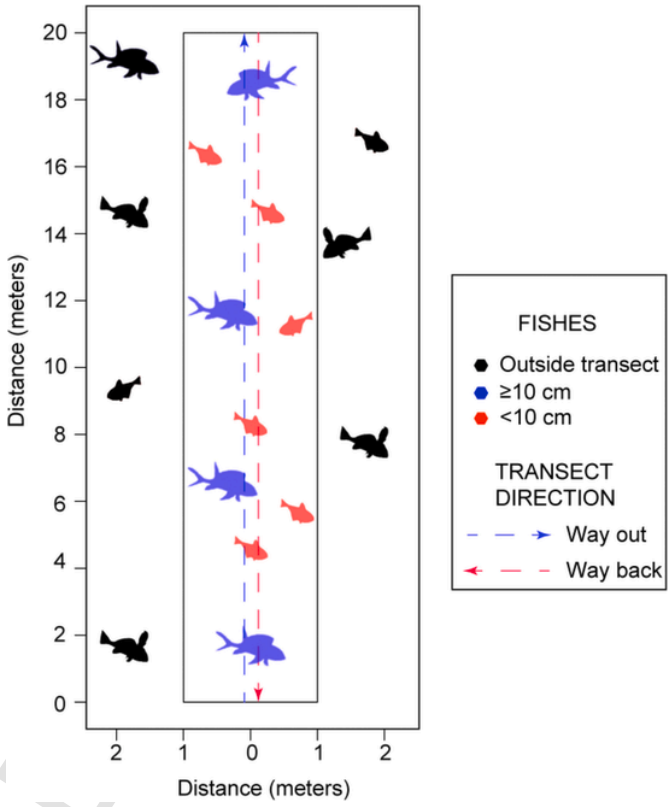

Fig. 1. Configuration of the nocturnal underwater visual census (UVC) using strip transect technique.

(three strata). In each site, each diver (three divers per night) conducted between one and three randomly distributed transects in each depth strata: shallow (<5 m), slope (6–10 m) and interface (11–15 m), registering the species that exhibited some nocturnal activity at the time of sampling. During each night survey, all divers used the same light color. All dives started 1 h after sunset (approx. 18:00) and ended between 19:00 and 22:00. Red, blue and white (no filter) lights were randomly used on different occasions, and no site was surveyed twice during the same night. This protocol was repeated changing the color of light at random, resulting in 135 strip transects (three light colors × three sites × three depth strata × five replicates). Sampling was performed in seven days within a four-month period, always during new moon, in the Austral winter of 2018. Sampling was conducted only in new moon to minimize possible differences in natural nocturnal light levels (e.g. more light reaching the reef during full moon compared to new moon phases).

We focused on those species that are active at night, especially those that feed predominantly at night (Helfman, 1986) (Table 1). However, a few species classified as diurnal on fish databases (Fishbase) (e.g. *Anisotremus virginicus, Myrichthys ocellatus, Ocyurus chrysurus* and *Synodus synodus*) were included in samples because were active during the sampling. Crepuscular predators such as *Epinephelus marginatus, Mycteroperca acutirostris* and *Mycteroperca interstitialis* were observed swimming and were also counted. We could not quantify in which type of activity all species were engaged with; thus, we could not precisely indicate if such behavior was triggered by divers or if it consisted in a nocturnal activity, except for feeding activities, as observed for *H. aurolineatum*.

Table 1
Results of SIMPER procedure showing the most important species contributing to the difference between each pair of depth strata. S = Shallow; M = Mid; I = Interface.

Comparison	Species	Cumulative contribution
S x M	*Haemulon aurolineatum*	0.54
	Phaeoptyx pigmentaria	0.64
	Holocentrus adscensionis	0.74
	Pareques acuminatus	0.83
S x I	*Haemulon aurolineatum*	0.58
	Holocentrus adscensionis	0.66
	Pareques acuminatus	0.74
	Phaeoptyx pigmentaria	0.77
	Sargocentron bullisi	0.80
M x I	*Haemulon aurolineatum*	0.57
	Phaeoptyx pigmentaria	0.66
	Holocentrus adscensionis	0.73
	Pareques acuminatus	0.78
	Astrapogon puncticulatus	0.80

2.4. Data analysis

The effects of light color on species richness, total density and density of those species that were recorded in at least two different light colors were investigated with generalized linear models (GLMs) with a Poisson distribution. When there were significant differences, a post-hoc test was performed (Tukey test) to verify the source of variation. The frequency of occurrence of species observed in at least two different light colors was tested using a Chi-square test.

To test if the light color, depth and site (random factor) influenced the composition of the nocturnal reef fish assemblage, a permutational multivariate analysis of variance (PERMANOVA) was performed using a Bray-Curtis dissimilarity matrix and 999 permutations followed by a SIMPER analysis to discriminate species contribution to the dissimilarities between pairs of groups (Clarke, 1993). Although all dives were conducted in depth strata, in the analysis, depth was used as a continuous variable as it was measured directly at each dive. All analyses were performed with the software R (R Core Team, 2017). The GLMs and Chi-square test were conducted with the "stats" package, PERMANOVA with the "adonis" function in the "vegan" package and SIMPER with the "vegan" package (version 3.3.4) (Oksanen et al., 2018).

3. Results

We recorded 4337 individual fish of 41 species representing 17 different families (Table 1). Almost 90% of all individuals registered belonged to only four species: *Haemulon aurolineatum* – Haemulidae (70%), *Holocentrus adscensionis* – Holocentridae (9%), *Pareques acuminatus* – Scianidae (5%) and *Phaeoptyx pigmentaria* – Apogonidae (4%).

3.1. Species density and richness

The maximum fish density recorded in transects was 163 individuals per 40 m^2 while using the blue light, compared to the maximum density recorded using the white light of 81 individuals per 40 m^2. The blue light showed the highest average density per transect (37.13 ± 4.83 SE) and the white the lowest (26.29 ± 2.96 SE) (Fig. 2a), although no significant differences were detected (LR $Chisq^2 = 3.76$; $Pr > 0.15$).

Although the surveys with the red light had the highest average species richness per transect/40 m^2 (5.70 ± 0.30 SE) (Fig. 2b), no statistically significant effect of light color was observed on species richness (LR $Chisq^2 = 2.80$; $Pr > 0.25$).

3.2. Nocturnal reef fish assemblage

The light color did not influence nocturnal fish assemblage composition (*pseudo-*$F_{2, 137} = 1.09$; $R^2 = 0.01$; $p = 0.30$), but differences were found among depth strata (*pseudo-*$F_{1, 137} = 6.61$; $R^2 = 0.05$; $P < 0.01$). The species that contributed the most to the dissimilarities between all three depth strata was *Haemulon aurolineatum* (in all cases with more than 50%), followed by *Phaeoptyx pigmentaria* and *Holocentrus adscensionis* in the comparisons between shallow and mid, mid and interface, whereas between shallow and interface, *H. adscensionis* and *Pareques acuminatus* were the second and third most important species (Table 1).

Density of the most abundant species varied according to the light color, where *H. aurolineatum* (LR $Chisq^2 = 92.19$; $Pr < 0.01$) showed lower densities with white light in comparison to the other two colors (Fig. 3). Density of *P. pigmentaria* was significantly lower under white light compared to blue (LR $Chisq^2 = 12.61$; $Pr < 0.01$); while density of both *H. adscensionis* and *P. acuminatus* were similar in all three light colors. (Table 2; Fig. 3). The frequency of occurrence of the species included in the analyses was similar for all light colors (Table 3).

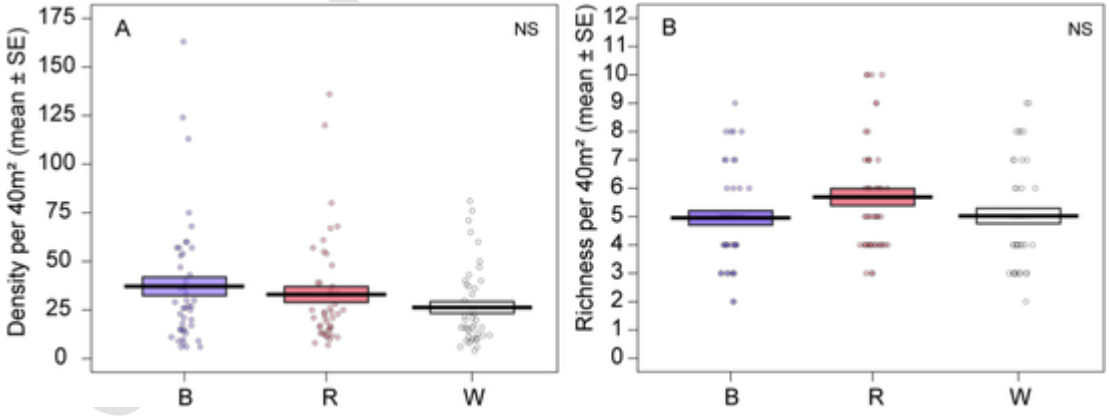

Fig. 2. Nocturnal reef fish density (A) and species richness (B) recorded with three different light colors: blue (B), red (R), and white (W). Dots represent individual transect values, horizontal bars represent mean values and error bars correspond to standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

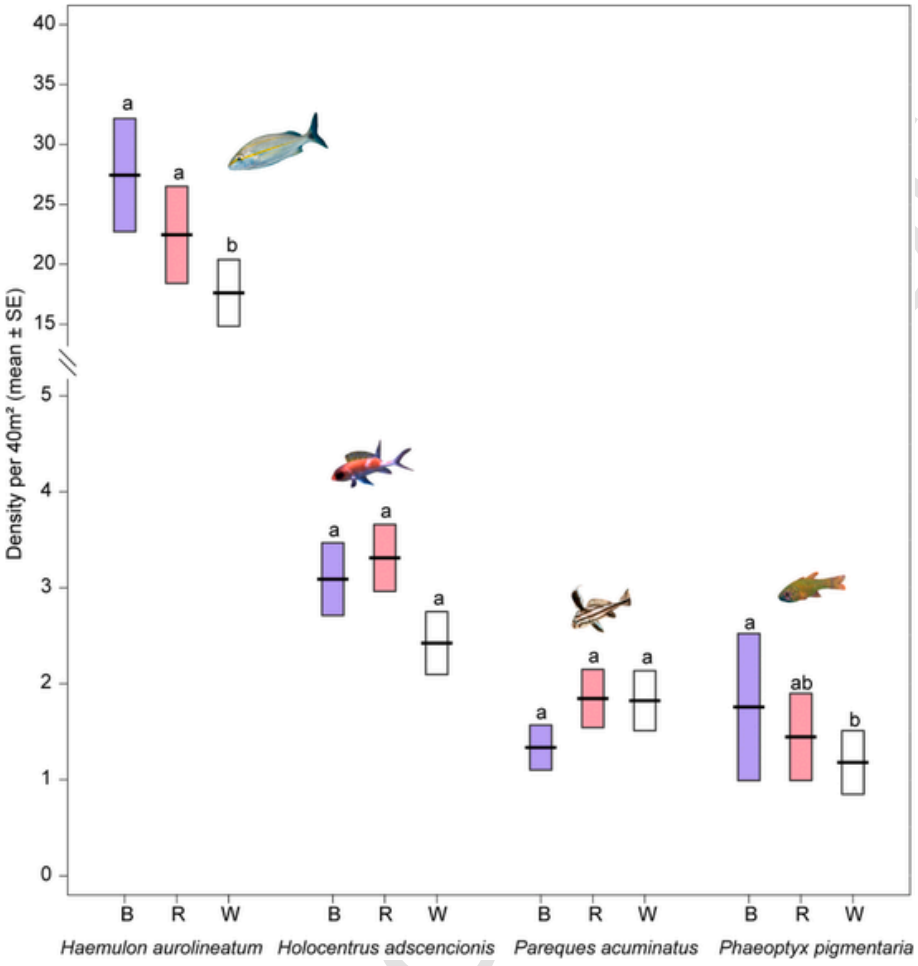

Fig. 3. Comparative density of the four most abundant nocturnal reef fish species using blue (B), red (R), and white (W) light colors. Different letters indicate significant differences (Tukey HSD), and error bars correspond to standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Six species were recorded exclusively using white light, and four using the red light but no species was recorded exclusively using blue light. The red light showed the highest frequency of occurrence for 12 of the 18 most abundant species (Table 2). The highest proportion of *Pempheris schomburgkii* and *Odontoscion dentex* were recorded with blue light. Apogonidae were mainly recorded using red light (Fig. 4).

4. Discussion

Our results did not evidence statistically significant differences in species richness, total fish density, composition or frequency of occurrence of the nocturnal reef fish assemblage using different light colors during underwater visual census. This indicates that, at least in our study area (i.e. a subtropical rocky reef in southwestern Atlantic), any of these light colors could be used to evaluate the structure of the nocturnal reef fish assemblage. However, we noticed changes in the behavior of some species during sampling depending on the light color used (beyond the scope of this paper), which suggests that for studies with a different focus (i.e. behavioral studies) the choice of light color matters. Studies using BRUVs in shallow coral reefs have identified differences in fish assemblage composition due to different colors of light (Fitzpatrick et al., 2013; Harvey et al., 2012b), while no differences were detected for mesophotic fish assemblages comparing different colors during daylight sampling using BRUVs (Birt et al., 2019). The reef fish assemblage surveyed seems to be more sensitive to light color using BRUVs because the footages are usually long, static and towards an unique direction (recommended duration of 50–60 min), thus the light properties may attract or repel fish species (Harvey et al., 2012a; Mallet and Pelletier, 2014; Whitmarsh et al., 2017). On the other hand, UVCs using strip transects are performed in shorter time intervals and are not fixed, which may have less influence on fish. However, we did find significant differences in the assemblage composition with depth, with *H. aurolineatum* being more abundant in the deep stratum which agrees with the fact that grunt species (Haemulidae) feed on invertebrate species over non-consolidate substrate (Helfman, 1986; Pereira et al., 2014).

Here, similar total abundance and species richness were recorded for all colors of light, but the red light presented the highest frequency of occurrence for most species. For instance, all species of Apogonidae were more frequent using red light, and this result also agrees with Fitzpatrick et al. (2013), who showed that *Apogon doederleini* was more abundant when red light was used during sampling with BRUVs in Western Australia. Apogonidae species inhabit caves and holes during the day and emerge during the crepuscular period or at night to feed on zooplankton and benthic invertebrates (Froese and Pauly, 2019). *Phaeoptyx pigmentaria* is a water column plankton feeder, while most other apogonids are benthopelagic invertebrate/plankton feeders (Bussotti et al., 2018). Apogonids are well adapted to nocturnal life and have a peak of wavelength absorption at 484–494 nm (*i.e.*, near blue) as adults (Munz and Mc-

Table 2
Fish species recorded during nocturnal visual census using blue, red and white colors. Values are average ± standard errors per 40 m^2, and numbers between parentheses indicate frequency of occurrence in replicates (%).

Family	Species	Light color		
		Blue	Red	White
Apogonidae	*Apogon americanus*	0.09 ± 0.05 (0.07)	0.09 ± 0.04 (0.09)	0.07 ± 0.04 (0.07)
	Apogon planifrons	0.13 ± 0.05 (0.13)	0.40 ± 0.14 (0.20)	0.09 ± 0.04 (0.09)
	Apogon pseudomaculatus	0.15 ± 0.09 (0.09)	0.29 ± 0.08 (0.24)	0.30 ± 0.19 (0.16)
	Apogon quadrisquamatus	–	0.16 ± 0.10 (0.07)	–
	Astrapogon puncticulatus	0.36 ± 0.19 (0.13)	0.29 ± 0.11 (0.16)	0.17 ± 0.08 (0.11)
	Phaeoptyx pigmentaria	1.68 ± 0.74 (0.29)	1.44 ± 0.45 (0.38)	1.15 ± 0.33 (0.31)
Diodontidae	*Chilomycterus spinosus*	0.17 ± 0.07 (0.13)	0.40 ± 0.10 (0.33)	0.22 ± 0.06 (0.22)
	Diodon holocanthus	–	–	0.02 ± 0.02 (0.02)
	Diodon hystrix	0.13 ± 0.05 (0.13)	–	0.07 ± 0.04 (0.07)
Gymnuridae	*Gymnura altavela*	–	–	0.02 ± 0.02 (0.02)
Haemulidae	*Anisotremus virginicus*	0.11 ± 0.07 (0.07)	0.22 ± 0.08 (0.16)	0.09 ± 0.04 (0.09)
	Haemulon aurolineatum	26.27 ± 4.58 (1.00)	22.47 ± 4.05 (0.96)	17.24 ± 2.70 (0.98)
	Haemulon parra	–	0.04 ± 0.04 (0.02)	0.02 ± 0.02 (0.02)
	Haemulon plumierii	0.26 ± 0.10 (0.16)	0.31 ± 0.10 (0.22)	0.17 ± 0.07 (0.16)
	Haemulon steindachneri	0.02 ± 0.02 (0.02)	0.07 ± 0.05 (0.04)	0.04 ± 0.04 (0.02)
Holocentridae	*Holocentrus adscensionis*	2.96 ± 0.37 (0.89)	3.31 ± 0.35 (0.82)	2.37 ± 0.33 (0.82)
	Myripristis jacobus	0.04 ± 0.03 (0.04)	0.04 ± 0.03 (0.04)	–
	Plectrypops retrospinis	–	–	0.02 ± 0.02 (0.02)
	Sargocentron bullisi	0.34 ± 0.16 (0.18)	0.29 ± 0.11 (0.20)	0.28 ± 0.10 (0.18)
Lutjanidae	*Ocyurus chrysurus*	0.04 ± 0.03 (0.04)	–	0.02 ± 0.02 (0.02)
Muraenidae	*Enchelycore nigricans*	–	–	0.02 ± 0.02 (0.02)
	Gymnothorax miliaris	–	0.02 ± 0.02 (0.02)	–
	Gymnothorax moringa	0.34 ± 0.09 (0.29)	0.49 ± 0.10 (0.42)	0.26 ± 0.07 (0.24)
	Gymnothorax vicinus	0.02 ± 0.02 (0.02)	0.07 ± 0.05 (0.04)	–
Narcinidae	*Narcine brasiliensis*	0.02 ± 0.02 (0.02)	–	0.02 ± 0.02 (0.02)
Ogcocephalidae	*Ogcocephalus vespertilio*	0.06 ± 0.04 (0.07)	0.04 ± 0.03 (0.04)	0.13 ± 0.07 (0.09)
Ophichthidae	*Myrichthys ocellatus*	–	0.02 ± 0.02 (0.02)	–
Pempheridae	*Pempheris schomburgkii*	0.38 ± 0.34 (0.07)	–	0.26 ± 0.22 (0.07)
Rhinobatidae	*Zapteryx brevirostris*	0.15 ± 0.06 (0.13)	0.13 ± 0.08 (0.09)	0.15 ± 0.11 (0.07)
Sciaenidae	*Equetus lanceolatus*	0.02 ± 0.02 (0.02)	0.02 ± 0.02 (0.02)	0.02 ± 0.02 (0.02)
	Pareques acuminatus	1.27 ± 0.23 (0.64)	1.84 ± 0.30 (0.73)	1.78 ± 0.31 (0.69)
	Odontoscion dentex	0.19 ± 0.12 (0.07)	0.09 ± 0.05 (0.07)	0.04 ± 0.04 (0.02)
Scorpaenidae	*Scorpaena brasiliensis*	–	0.02 ± 0.02 (0.02)	–
	Scorpaena isthmensis	0.19 ± 0.08 (0.13)	0.27 ± 0.09 (0.18)	0.44 ± 0.19 (0.22)
	Scorpaena plumieri	–	–	0.04 ± 0.03 (0.04)
	Scorpaenodes tredecimspinosus	–	–	0.04 ± 0.04 (0.02)
Serranidae	*Epinephelus marginatus*	0.02 ± 0.02 (0.02)	–	0.02 ± 0.02 (0.02)
	Mycteroperca acutirostris	0.04 ± 0.03 (0.04)	–	0.02 ± 0.02 (0.02)
	Mycteroperca interstitialis	0.02 ± 0.02 (0.02)	–	0.02 ± 0.02 (0.02)
	Rypticus bistrispinus	–	0.02 ± 0.02 (0.02)	0.07 ± 0.04 (0.07)
Synodontidae	*Synodus synodus*	0.06 ± 0.05 (0.04)	0.09 ± 0.05 (0.07)	–

Table 3
Chi-square test of frequency of occurrence values to the ten most abundant species among the colors blue, red and white colors.

Species	X^2	df	p-value
Haemulon aurolineatum	1.61	2	0.45
Holocentrus adscensionis	0.79	2	0.68
Pareques acuminatus	0.5	2	0.79
Phaeoptyx pigmentaria	0.35	2	0.84
Gymnothorax moringa	2.23	2	0.33
Chilomycterus spinosus	3.94	2	0.14
Sargocentron bullisi	0.22	2	0.90
Haemulon plumierii	0.75	2	0.69
Scorpaena isthmensis	1.52	2	0.47
Apogon pseudomaculatus	3.22	2	0.20

Farland, 1973). Thus, even during daytime, these species would be less affected by the red spectrum because of low absorption capacity, due to the natural low availability of this light spectrum underwater (Marshall, 2017).

Although fish density, frequency of occurrence and species composition were similar under different colors, we noticed that there were differences in the detectability and behavior of some species associated with the light color. Disturbances on fish behavior were more evident when using white light. *Haemulon aurolineatum,* the most abundant species, was less frequently recorded with white light, suggesting that this spectra is comparatively more aversive (Widder et al., 2005). Only one out of the three *Gymnothorax* species (moray eels), was observed with white light, while all moray eel species that were recorded in our study were recorded using red light. *Gymnothorax* species have a wavelength absorption ranging from 486 to 501 nm (Wang et al., 2011), and BRUV surveys have previously observed that red light does not disturb their behavior at

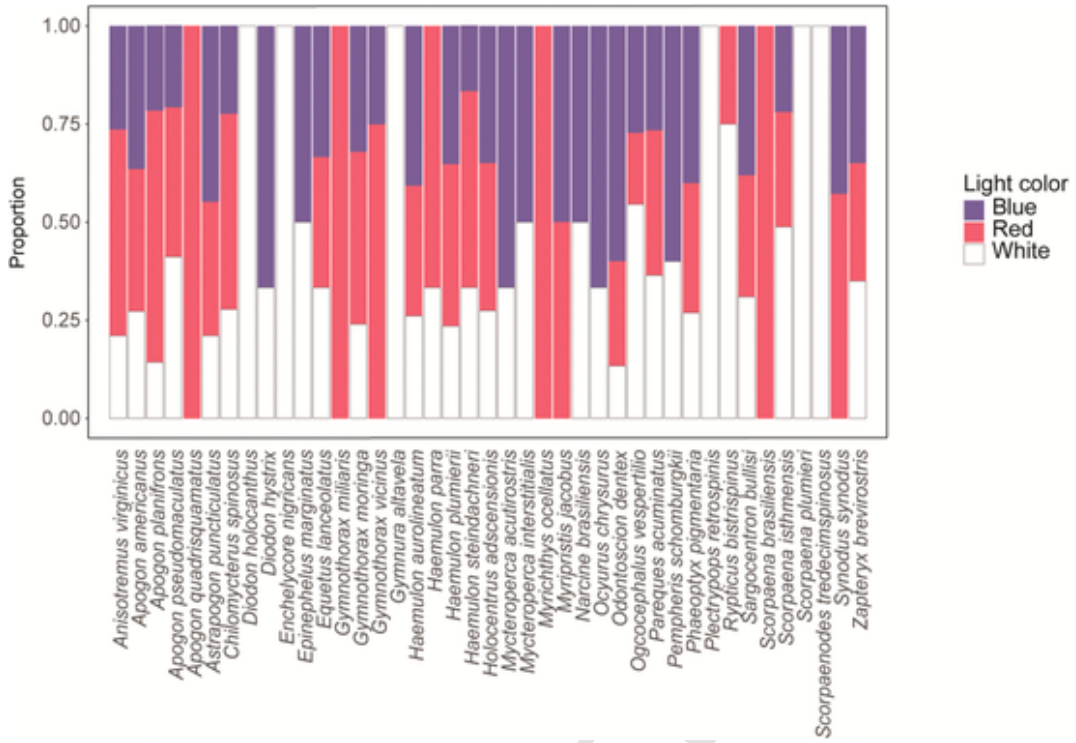

Fig. 4. Comparative relative occurrence of species surveyed at night using blue, red, and white light. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

night (Fitzpatrick et al., 2013). Mobile species were observed swimming away or changing their behavior when a flashlight was directed towards them, while sedentary and cryptobenthic species remained static. Thus, the use of flashlights is likely to affect more mobile fish species than sedentary ones. Although we did not evaluate behavioral responses to light colors, we noticed that several species showed aversion towards the white light. Thus, we strongly recommend that future research evaluates behavioral changes of fish species in the face of different light colors, by measuring the flight initiation distance or using distance sampling methods (Kulbicki and Sarramégna, 1999).

Ecological studies conducted at night are very scarce, and nocturnal fish are an important component in many reef systems (Helfman, 1986; Nagelkerken et al., 2000; Pereira et al., 2014). Understanding patterns of abundance and distribution of the nocturnal fauna is crucial for ecological and conservation purposes (Gaston, 2019). Thus, studies aiming to evaluate the structure of nocturnal fish assemblages should avoid using white light due to possible influence on fishes' behavior, although no statistical difference could be found on the metrics used to characterize the present reef fish assemblages. On the other hand, the red light did not substantially affect the behavior of any species from our observations, suggesting that red color is more appropriate when studying behavior of nocturnal species, as reported for freshwater (Jury et al., 2001; Vanderpham et al., 2012) and terrestrial studies (Finley, 1959). Our results emphasize the importance of choosing the most appropriate light color to be used with UVC for nocturnal surveys depending on the focus of the study. This will depend on the specific objectives of the research (e.g. inventory, behavior and community dynamics) or the fish fauna in focus (eg. mobile or sedentary). The advantages and limitations of using UVCs for diurnal fish surveys have been widely debated in literature and should be applicable to nocturnal sampling as well.

5. Conclusions

None of the metrics used to evaluate the composition of the nocturnal reef fish assemblage were significantly influenced by the light color (white, blue and red) during UVCs. However, highly mobile and some non-mobile nocturnal fish species were observed to be disturbed by the white light but not by the red light, which makes it advisable to use the latter for behavioral studies. In conclusion, the choice of light color for night UVCs depends on the objective of the study. Whereas both white, red and blue colors work well to evaluate the nocturnal fish assemblage structure in subtropical rocky reefs in Brazil, red light should be preferred to assess behavioral aspects of nocturnal fish. The detailed effects of light color on the behavior of fish species deserve future research, but we suggest that measuring flight initiation distance of mobile species using different light colors will help clarify this topic.

Author contributions

MBL, TCM and CELF conceived the research, MBL, TCM, MCB, LE, CAMMC and CELF conducted the fieldwork and MBL, TCM and CAMMC analysed the data. MB wrote the draft. Remaining authors provided edits and feedback. We confirm that the manuscript has been read and approved by all named authors, and that the order of authors listed in the manuscript has been approved by all of us and that we have followed the regulations of our institutions concerning intellectual property.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105261.

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