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ORIGINAL PAPER

The influence of structural complexity and reef habitat types on flight initiation distance and escape behaviors in labrid fishes

José de Anchieta C. C. Nunes · Cláudio L. S. Sampaio · Francisco Barros

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Abstract Structural complexity is a key parameter for fish on reef habitats. Several studies have investigated the influence of this variable on aspects of reef fish population and community dynamics. However, there is a lack of knowledge on the influence of structural complexity on antipredator behavior. Here we studied the effect of habitat type and structural complexity on flight initiation distance (FID) and the escape behaviors of four labrid fishes (*Halichoeres brasiliensis*, *H. penrosei*, *H. poeyi* and *Sparisoma axillare*) on two different reef habitats (coral and rocky reefs). Habitat type influenced the FID of three of the studied species (*H. brasiliensis*, *H. penrosei* and *S. axillare*), and structural complexity negatively influenced the FID of two species (*H. brasiliensis* and *S. axillare*). The frequency of escape behaviors varied between species. All of them showed high frequency of the 'run away' behavior and low frequency of the 'leave the habitat' behavior. On coral reefs, structural complexity influenced the 'fled to the holes' for *S. axillare* only. Reef ecosystems worldwide are being modified by anthropogenic activities. Our results suggest that if such activities reduce structural complexity, then 'seascapes of fear' for labrid fishes will become more widespread, which could lead to negative consequences in the reef ecosystems.

Introduction

Habitat structural complexity can influence behavior and distribution of fish (Jones and Syms 1998; Floeter et al. 2007). Some experimental studies indicate that an increase in structural complexity can reduce mortality (Hixon and Beets 1993; Almany 2004). However, changes in prey behaviors due to shifts in complexity are not yet well understood. Krajewski et al. (2010) suggest that substrata with distinctive structure and associated fauna can offer different types of resources (e.g., prey and shelter) and may influence fish activity. Therefore, predator–prey interactions are influenced by the relationship between habitat characteristics and fish behavior.

The flight initiation distance (FID), which is the distance a predator can approach the prey before it flees (Blumstein 2003), is commonly used as a methodology to assess prey decision-making and wariness (Januchowski-Hartley et al. 2011). This metric has been widely used on birds (Blumstein 2003; Blumstein et al. 2003, 2005), lizards (Cooper et al. 2002; Cooper 2008, 2009), and mammals (Runyan and Blumstein 2004; Stankowich 2008). For reef fishes, most studies on FID have focused on the impacts of fishing through comparisons between protected and exploited areas (Feary et al. 2011; Januchowski-Hartley et al. 2011, 2012, 2013). No studies have yet evaluated potential differences in fish FID on habitats with different complexities. Rocky reefs have lower complexity when compared to coral reefs, but also support a rich fauna and flora (Ferreira et al. 2001). There is a need to test if fish can modify the

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J. A. C. C. Nunes (✉) · F. Barros
Programa de Pós-Graduacão em Ecologia e Biomonitoramento, Laboratório de Ecologia Bentônica, Universidade Federal da Bahia, Ondina, Salvador, BA 40170-115, Brazil
e-mail: anchietanunesba@gmail.com

J. A. C. C. Nunes
ECUS, Institute of Education, Science and Socio-Environmental Utility, Rio Vermelho, Salvador, BA 41940-250, Brazil

C. L. S. Sampaio
Departamento de Engenharia de Pesca, Unidade de Ensino Penedo, Universidade Federal de Alagoas, Maceió, AL, Brazil

antipredator behaviors according to structural complexity and if that happens in the same way on different habitats.

Caution behavior (preflight behavior) also influences the success of predation. Moreover, it is dependent on species' trophic groups and life history characteristics (Januchowski-Hartley et al. 2011). On the other hand, escape behaviors have not been evaluated for reef fishes in different types of habitats. These behaviors probably affect the distribution of reef fishes within and among reef habitats and may alter the structure of assemblages.

The fishes of the Labridae family exhibit a great variety of body shapes and several morphological adaptations for feeding. Consequently, they have trophic versatility (Fulton and Belwood 2002), which is important in structuring reef communities (Hobson 1975; Deloach and Humann 1999). Wrasse species of the *Halichoeres* genus are considered highly diverse and widely distributed in the Atlantic Ocean (Rocha et al. 2010). These species are diurnal, exhibiting opportunistic behavior and feeding on invertebrates (Sazima et al. 1998, 2005; Coni et al. 2007, 2010). According to Nunes et al. (2013), rocky reef complexity influences foraging activity of three *Halichoeres* species. Yet, there are no studies on the behavior of these species on other reef habitats. Parrotfishes of the *Sparisoma* genus are recorded only in the Atlantic Ocean, being the most speciose scarid genus in this ocean basin (Bernardi et al. 2000; Streelman et al. 2002). This genus is ecologically diverse, with a wide range of feeding modes and patterns of habitat use (Bernardi et al. 2000; Streelman et al. 2002; Bonaldo et al. 2006).

Here we studied the FID and escape behaviors of two species harvested by spearfishing (*Halichoeres brasiliensis* and *Sparisoma axillare*) and two non-harvested (*H. penrosei* and *H. poeyi*). The study was carried out on two different habitats: coral and rocky reefs. Specifically, we investigated (1) if labrid fishes on habitats with more structural complexity have shorter FID than on less complex habitats and (2) if escape behaviors are related to reef structural complexity and (3) if the frequencies of escape behaviors vary between reef habitats. Such variation was expected due to the higher availability of refuge resources (e.g., holes at short distances), especially on coral reefs.

Methods

Study area

This study was carried out on reefs in Todos os Santos Bay, Bahia state, Northeast Brazil. We studied FID and escape behaviors of four labrids in six areas, being three of them coral reefs (13°07′S–38°43′W) and three rocky reefs (13°00′S–38°32′W). All sites studied have high fishing pressure. Coral reefs studied were dominated by the corals: *Mussismilia* spp., *Siderastrea* sp., *Millepora* spp. and *Porites branneri* Rathbun 1887. The coralline algae, macroalgae and the articulated calcareous algae *Halimeda* sp. were also found within the area (for details see Miranda et al. 2013). Rocky reefs studied were predominantly colonized by filamentous algae, macroalgae and zoanthids [*Palythoa caribaeorum* (Duchassaing and Michelotti 1860) and *Zoanthus sociatus* (Ellis and Solander 1786)]. The black sea urchin *Echinometra lucunter* (Linnaeus 1758), ascidians and colonies of corals *Favia gravida* (Verrill 1868) and *Siderastrea* sp. (in lower abundance when compared to coral reefs) were also found within the area (for details see Maia-Nogueira et al. 2010).

Flight initiation distance and escape behaviors

We estimated fish FID through snorkeling. A snorkeler would reproduce spearfisher behavior (according to Januchowski-Hartley et al. 2011, 2012) by swimming directly toward the fish at a constant speed (~0.7 m/s^{-1}, measured using portable GPS at sea surface). When the fish fled, the distance between the end of the speargun and the place where the fish was, prior to fleeing, was measured with a tape measure and represented the estimated FID. The same precautions were taken from the authors cited above, whereby fishes were only targeted if they were feeding or swimming normally (see also Deloach and Humann 1999). We also considered flight to have occurred when the fish increased its swim speed to greater than the approach speed of the diver (Januchowski-Hartley et al. 2011, 2012). We estimated FID of 60 individuals of each of the four species: 30 on coral reefs and 30 on rocky reefs.

There is no consensus on the influences of body size on FID (Gotanda et al. 2009; Feary et al. 2011); therefore, only adults were selected based on size and color. There are considerable differences in color among these labrids, as well as between the life phases within each species (Martha and Jones 2002; Nunes et al. 2013), and only adults were selected based on size and color. Terminal phases (TP) were easily distinguished by their bolder color patterns (except *H. poeyi*), where changes in morphology and size were utilized.

Fish escape responses usually consist of a C-start maneuver, which involves the unilateral contraction of the body musculature into a 'C' shape (Bohorquez-Herrera et al. 2013). Escape behaviors were immediately observed after each FID sample and categorized in: 'Leave the habitat,' where fish swam in the direction of unconsolidated substratum (usually sand); 'Run away,' where fish fled swimming away; 'Fled to the hole,' where the fish sought a hole and went into hiding; 'Curiosity,' where the fish fled and curiously returned swimming near the diver; and

Table 1 Results of the analysis of covariance (ANCOVA) testing the influence of structural complexity (estimated by rugosity index) and habitat types (with two levels: coral reefs and rocky reefs) on FID) of the four labrid species

	d.f.	Sum Sq.	Mean Sq.	F	*P*
H. brasiliensis					
Habitat	1	0.241	0.241	56.68	<0.001*
Complexity	1	0.170	0.170	40	<0.001*
Habitat complexity	1	0	0	0	0.953
Error	56	0.238	0.004	–	–
H. penrosei					
Habitat	1	0.191	0.191	9.03	0.004*
Complexity	1	0.002	0.002	0.11	0.737
Habitat complexity	1	0.002	0.002	0.14	0.713
Error	56	1.190	0.021	–	–
H. poeyi					
Habitat	1	0.001	0.001	0.05	0.830
Complexity	1	0.002	0.002	0.05	0.816
Habitat complexity	1	0.009	0.009	0.26	0.611
Error	56	2.092	0.037	–	–
S. axillare					
Habitat	1	0.145	0.145	38	<0.001*
Complexity	1	0.779	0.779	203.97	<0.001*
Habitat complexity	1	0.003	0.003	0.79	0.377
Error	56	0.214	0.003	–	–

* Significant difference

'Fled into group,' where fish swam into a group. All escape behaviors were observed in the maximum limit of 2 meters from the diver.

Structural complexity

The structural complexity was studied using the Rugosity index (RI) (Graham and Nash 2013). In order to measure rugosity, a 1-m chain was draped over the substrate, conforming as closely as possible to all of its contours and crevices, and a measure of the actual surface distance relative to the linear distance was thus obtained (Luckhurst and Luckhurst 1978). For each FID observation, rugosity was measured where fish fled; thus, 240 samples were obtained. Rugosity index (RI) was calculated as: RI = linear/surface. Linear was the distance covered when the chain was pulled taut, and surface was the linear distance between the start and the end of the chain while over the bottom.

Data analysis

One-way ANOVA was used to test for significant differences in structural complexity (estimated by the Rugosity index) between reef habitats. Analysis of covariance (ANCOVA) was used to investigate if structural complexity (a continuous variable) and type of reef habitats (two categories: coral reefs and rocky reefs) influenced FID (dependent variable) of labrids. The normality and the homogeneity of the data were assessed with quantile–quantile (Q–Q) plots and the Levene's test, respectively. FID was log ($x + 1$) transformed. ANOSIM was performed to test if there was any difference in the frequencies of escape behaviors between reef habitats. Bray-Curtis similarity test was utilized for this analysis (Clarke et al. 2006). When escape behaviors varied significantly within species, we used nonlinear logistic regression to evaluate the influence

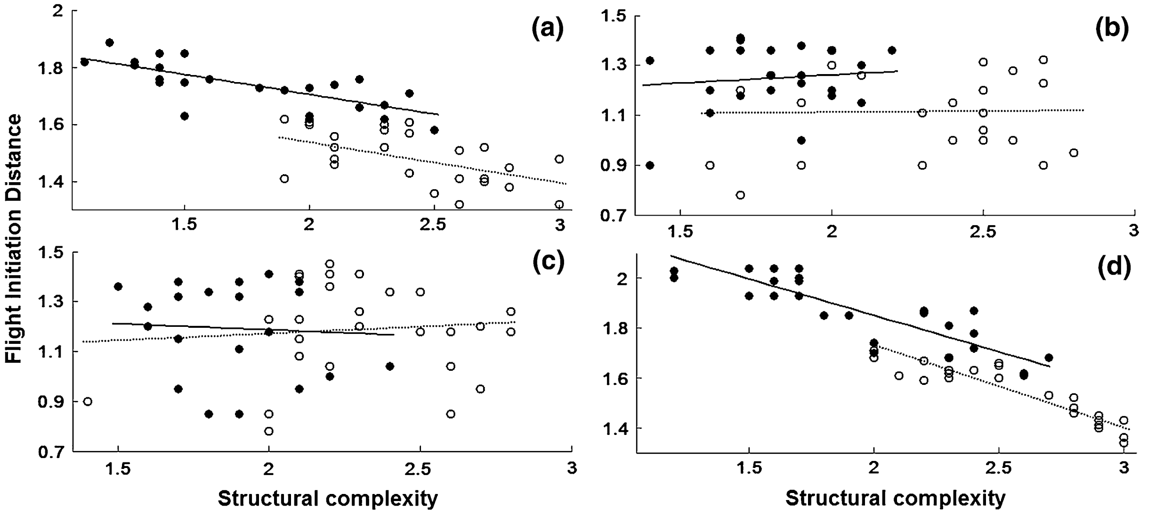

Fig. 1 Relationship between habitat types and structural complexity and FID. *Black dots* represent the measurements on rocky reefs; *white dots* represent the measurements performed on coral reefs. *Continuous line* represents best fit for rocky reefs and *dotted line* for coral reefs. **a** *H. brasiliensis*, **b** *H. penrosei*, **c** *H. poeyi* and **d** *S. axillare*. FID was log ($x + 1$) transformed

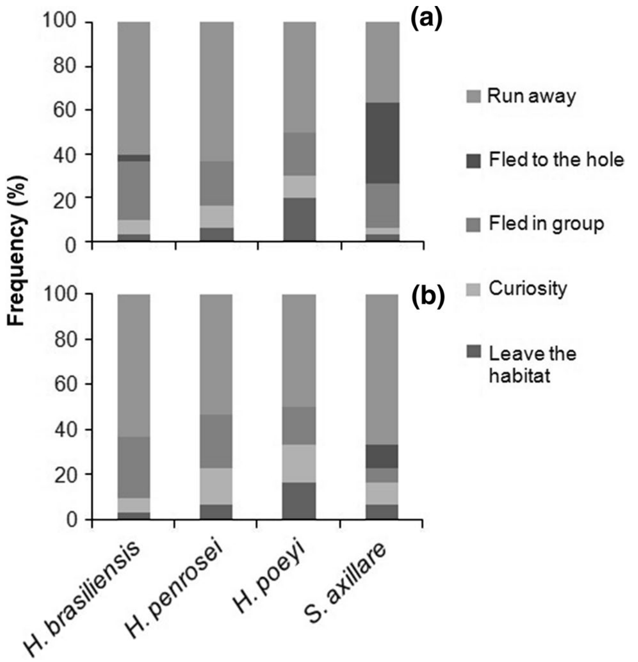

Fig. 2 Frequency of each escape behavior categories for the four studied species of Labrids. In (**a**), we show frequencies observed on coral reefs, and in (**b**), we show frequencies on rocky reefs. Note that 'fled to the hole' was not observed in *Halichoeres* species, except for *H. brasiliensis* on coral reefs

of structural complexity on two escape behaviors ('fled in group' and 'fled to the hole'). Those behaviors were chosen because structural complexity is positively correlated with fish densities and with number of shelters (Hixon and Beets 1993; Graham and Nash 2013). Logistic regression analyses were performed in StatSoft STATISTICA, version 8.0. ANOVA and ANCOVA were performed using Software R version 2.12.1 for Windows R 40 (R Development Core Team 2012). The Primer Software was used for ANOSIM analysis (Clarke and Warwick 2001). For all tests, the α-value adopted was 0.05.

Results

ANCOVA analysis showed significant differences on FID between the studied habitat types (Table 1). We found that the FID of *H. brasiliensis*, *H. penrosei* and *S. axillare* was higher on rocky reefs when compared to coral reefs (Fig. 1 a, b, d). There were significant differences in the structural complexity between the two studied habitats ($F = 159$; $P < 0.01$). Higher values of the RI were obtained on coral reefs (2.4 mean ± 0.33 SD) than on rocky reefs (1.8 ± 0.4). Structural complexity negatively influenced FID in *H. brasiliensis* and *S. axillare* (Fig. 1; Table 1).

Table 2 Logistic regression between structural complexity and the two escape behaviors ('fled to the hole' and 'fled in group') for *S. axillare*

Behavior	Habitat	χ^2	df	*P*
Fled to the hole	Coral reef	13.705	1	<0.001*
Fled in group	Coral reef	0.011	1	0.915
Fled to the hole	Rocky reef	2.407	1	0.120
Fled in group	Rocky reef	0.011	1	0.915

* Mean significant difference

The frequencies of escape behaviors varied between species and habitats (Fig. 2). Only *S. axillare* developed the behavior 'fled to the hole' in both habitats, with this behavior being more frequent on coral reefs. 'Leave the habitat' and 'curiosity' reached higher values for *H. poeyi* and *H. penrosei* on both habitat types (Fig. 2 a, b). 'Run away' was the most common escape behavior for all species. 'Fled in group' was more frequent for *H. brasiliensis* than for other species. There were significant differences in the frequency of escape behaviors for *S. axillare* (Global $R = 0.071$; $P = 0.009$); however, no differences were found for *H. brasiliensis* (Global $R = -0.017$; $P = 0.98$), *H. penrosei* (Global $R = -0.012$; $P = 0.79$) and *H. poeyi* (Global $R = -0.02$; $P = 0.95$).

Logistic regression showed that the escape behavior 'fled to the hole' of *S. axillare* on coral reefs was influenced by structural complexity, and adults of this species require complex habitats to use holes as a refuge from predators (Table 2). Conversely, this species was not significantly influenced by structural complexity when developed the 'fled in group' behavior on coral and rocky reefs and 'fled to the hole' on rocky reef habitats.

Discussion

The species of *Halichoeres* and *Sparisoma* studied can be found in several types of habitats (Rocha 2004; Rocha et al. 2005; Bonaldo et al. 2006; Nunes et al. 2013), and their FIDs vary according to different habitats. We believe that in complex habitats, the higher density of preys (see Hixon and Beets 1993) could be explained by antipredator behavior and flight capacity. Thus, the antipredator behavior and flight capacity could probably help to understand this pattern described by Hixon and Beets (1993), once the prey species would need to be able to reach the shelters within reef habitats or to keep a safe distance from the predators (when foraging). Habitat use is known to be correlated with swimming ability (Fulton et al. 2001), and it shapes coral reef fish assemblages (Fulton and Bellwood 2004; Fulton et al. 2005). We believe that the capacity to escape and strategies of antipredator behavior to be also correlated with the species' swimming ability.

The study showed that the FID was strongly associated with structural complexity for two studied species: *S. axillare* and *H. brasiliensis.* Results for those species showed the decrease in the FID inhabitats with higher structural complexity, probably because sites with higher structural complexity have more shelter and can provide more possibilities to short escapes than areas with lower structural complexity. On the other hand, *H. penrosei* and *H. poeyi* were not influenced by structural complexity. These species inhabit zones with less rugosity, especially *H. poeyi*, which can be easily found on the edges of coral and rocky reefs (Rocha et al. 2005; Nunes et al. 2013).

We argue that methodology used can provide good results for harvest species, however, to develop studies on FID of non-harvest species; artificial predators might bring better results than human stimulus, since predator recognition is often dependent upon experience (Griffin et al. 2001; Stankowich and Blumstein 2005), and variation in predator lethality influences the predator recognition abilities (Blumstein et al. 2006).

Generally, coral reefs are naturally more complex environments in comparison with rocky reefs. Corals and the other reef builder organisms (such as crustose coralline algae) through their hermatypic actions are constantly acting for the increase in tridimensional complexity, which is directly associated with the increase in biodiversity (Hoegh-Guldberg 2006; Hughes et al. 2007; Graham et al. 2014). In rocky reefs, Ferreira et al. (2001) suggested that complexity is determined mainly by the density of holes, caused by the superposition of boulders. There are different methods to assess structural complexity, from arbitrary visual ratings (Polunin and Roberts 1993) to the more recent digital rugosity (Dustan et al. 2013). We used a fairly common methodology on reef habitats studies, i.e., chain method (Graham and Nash 2013; Chaves and Monteiro-Neto 2009). However, when rugosity is measured using a chain, different surfaces can reach similar rugosity. For instance, one reef with several small crevices (i.e., shelters) may show the same rugosity of another reef with one single depression or one single boulder. Thus, FID and escape behaviors will be likely different in spite of the same estimates of rugosity. Future studies should properly investigate how number of shelters and obstacles can influence FID and escape behaviors.

The most frequent escape behavior of all four species of labrids was 'run away.' On coral reefs, several individuals of *S. axillare* exhibited 'fled to holes' as a significant antipredator behavior. Conversely, *H. penrosei* and *H. poeyi* never 'fled to holes.' *Halichoeres* species always searched for open areas without obstacles during the escape. The increase in complexity may increase the number of obstacles, making it more difficult to run away from predators. On the other hand, if obstacles are overcome, flight could be facilitated through confounding predators on which way they should follow to find the prey. 'Leave the habitat' presented low frequency for all species probably due to higher chances of predation in such areas. Thus, we believe that habitat configuration might be determinant in the choices of antipredator behaviors. The present study strongly suggest that further research involving flight ecology should include escape behaviors as an important way to better understand the indirect consequences of predation.

This paper highlights the importance of structural complexity on FID and escape behaviors. Reef ecosystems are in global decline because of growing pressures on biodiversity (Bellwood et al. 2004; Jackson 2008, 2010). In Brazil, reef ecosystems are following worldwide trends of degradation with impacts including coral diseases (Francini-Filho and Moura 2008), bycatch and overfishing (Floeter et al. 2007; Nunes et al. 2010), nutrient enrichment (Costa et al. 2000), sedimentation (Loiola et al. 2013), as well as the aquarium trade (Gasparini et al. 2005; Sampaio and Nottingham 2008). These human-mediated disturbs directly or indirectly endanger corals (the main reef builder) and favors non-builder and tolerant organisms (such as macroalgae), affecting reef growing and consequently structural complexity (Bryant et al. 2000; Bellwood et al. 2004; Hughes et al. 2007; Halpern et al. 2008). Many coral reefs are changing in composition species due to the different vulnerability and recovery potential of corals and other organisms, consequence of the various human impacts (Graham et al. 2014). These ecosystem modifications could affect the behavior (e.g., FID and escape behaviors) of reef fishes and its ecological relationship (e.g., predation, territorialism, competition for shelter).

'Landscapes of fear' are perceptual areas of fear defined topographically by differing levels of predation risk across space and time (Laundré et al. 2010). In the ocean, 'seascapes of fear' were recognized for marine mammals (Wirsing et al. 2008). For reef fishes, fear (measured by flight initiation distance) was higher outside marine-protected areas (Januchowski-Hartley et al. 2012). However, there are many gaps involving the ecology of fear for reef fishes. In general, our results suggest that 'seascapes of fear' will increase with the increase in habitat degradation (by reduction of structural complexity), and it could have many negative consequences in the reef ecosystems.

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