Fear-induced behavioural modifications in damselfishes can be diver-triggered

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ABSTRACT

Fear is a short-term response arisen from the way an animal perceives its environment when some threat makes it insecure. Thus, the risk perception of predation shapes the cost-benefit decisions associated with food and safety in animal communities. Even non-consumptive human-related activities such as ecotourism may influence species behavioural traits. Marine wildlife tourism might produce different impacts on organisms, stressing and modifying (directly or indirectly) species behaviour, physiology and habitat use. Understand the effects of human presence on site-attached fish' behaviour is crucial to elucidate how dive-tourism could shape their limited-range seascape. Given the importance of the territorial damselfishes as reef farmers and 'ecosystems engineers', here we investigated if the presence of SCUBA divers and snorkelers can disrupt the foraging and territorial defence of the Dusky damselfish, *Stegastes fuscus*. Experimental approaches (diver presence and absence) were applied in 30 territories of *S. fuscus* using underwater remote video cameras. Behavioural responses were analysed by considering the frequency of refuge, foraging and chase behaviours. Both recreational dive activities had an analogous role in frighten and disturb the Dusky damselfish activities. Considering the frequency of behaviours displayed in diver's absence vs presence, *S. fuscus* increased its refuge times from approximately 2% to 50% on SCUBA diver presence and from 9% to 43% in snorkeler presence. It is directly linked to the missed feeding opportunities, which reduced by half during both diver's presence. Damselfish's aggressiveness proportionally dropped (0.3%) during SCUBA diver presence but increased (2.4%) while snorkeler was present. However, the average frequency of chase behaviour reduced with both divers' approach. Interruptions in damselfish behaviour may modify the resource monopolization and productivity inside their territories, affecting its relationships with other species beyond the boundaries of their territoriality, and leading a possible change on its functional role in the reef community. Territorial reef fish behaviour and their relationship with divers' presence can provide a more holistic comprehension regarding the seascape of fear concept and could be useful as an indicator of human disturbances.

1. Introduction

The "landscape of fear" (LOF) is a well-grounded concept modelled to explain the fear-driven spatial pattern of habitat use and the behavioural outcome of predator-prey interactions in terrestrial and marine ecosystems (Gallagher et al., 2017; Laundré et al., 2010). In marine systems, the "seascape of fear" has been applied to mammals and sea turtles, which tend to decrease their use of high-quality foraging habitats in predators' presence (Heithaus et al., 2007; Wirsing et al., 2008). Likewise, the non-consumptive effect of predators (i.e. *risk-effect*, or the behavioural outcome of prey to predators' presence) has been demonstrated to alter herbivory and the small-scale distribution

patterns of prey in higher risk areas (Catano et al., 2016; Matassa and Trussell, 2011). Nevertheless, while the LOF concept has emerged having in mind the natural predator effect, it is essential to consider the fear-induced by human presence on prey' landscape/seascape, once humans have a competitive dominance over predators' population and predatory behaviour during hunting or fishing activities (Darimont et al., 2015; Madin et al., 2016).

The fear generated by exploratory activities may lead wild animals to perceive humans as a predator (Frid and Dill, 2002) or even more threatening than a natural predator (Ciuti et al., 2012; Clinchy et al., 2016). The human threat to marine ecosystems has been historically reported as a result of the direct *lethal effect* of predators harvesting (e.g. reducing predator abundance and biomass) (Heithaus et al., 2008; Jackson et al., 2001). However, the *risk effect* of human activity can also alter the seascape by modifying the perception of predation risk, influencing prey behavioural traits (Madin et al., 2016). For instance, even in ecotourism activities (commonly known as a low impact), humans can influence species activities dictating when, where or what the prey eats, affecting metabolic rates and communities' structure (Albuquerque et al., 2015; Barnett et al., 2016; Burgin and Hardiman, 2015).

Marine wildlife tourism (MWT), defined as tourism of observing and/or interacting with marine species in their natural environment, is a common activity often centred in providing viable economic opportunities for local communities (Burgin and Hardiman, 2015; Trave et al., 2017). Accordingly, it offers support for conservation and unique marine experiences, such as shark and whale encounter or shipwreck SCUBA diving (Trave et al., 2017). On the other hand, MWT is widely recognized to stress and modify directly or indirectly species behaviour/physiology as well as habitat use (Burgin and Hardiman, 2015; Lusseau, 2004; Rizzari et al., 2017). Therefore, the MWT impacts include physical damages on benthic organisms (Giglio et al., 2017; Giglio et al., 2016), behavioural disturbances in focal and non-focal species (Giglio et al., 2018; Rizzari et al., 2017), increase on stress and metabolic rates, and reduction on antipredator responses' learning due to boat noise traffic (Ferrari et al., 2018; Nedelec et al., 2017; Simpson et al., 2016) and food provisioning (Barnett et al., 2016). On highly mobile fishes, such as herbivorous, the threat of human presence in touristic areas has demonstrated to affect wariness (Benevides et al., 2018), abundance and assemblage structure (Albuquerque et al., 2015; Gil et al., 2015). Yet, the fear effect of MWT has been poorly tested in site-attached fishes and its importance could be currently underestimated.

Site-attached individuals may be unable to move away from stressed environments and since they have a limited range of movement, human-related activities could have a stronger pressure on those species. For example, reef dweller fishes must constantly make trade-off decisions to avoid potential fitness impairment (e.g. decrease in foraging, growth and reproduction rates) due to the risk perception of human approach, as observed for fishes associated with coral colonies (Pereira et al., 2016). In consequence, they spend more time closer or hiding within the coral branches, and decreases the swimming activity with diver's approach (Pereira et al., 2016). Despite the relevant evidence of diver influence on fish behaviour (Emslie et al., 2018; Titus et al., 2015; Watson and Harvey, 2007), we still have a poor comprehension regarding the fear induced by diver presence and its consequences on territorial fish's habitat use. This would increase the insights into the cumulative effect of repeated diver exposure on marine ecosystem function, moving beyond the understanding of the predator-prey relationship and expanding, even more, the seascape of fear models, since this concept has not yet been applied for a fish species spatially dependent. In addition, it would help conservation managers to make more appropriated interventions in diving destinations.

Between territorial fishes, damselfishes (Pomacentridae) are one of the most abundant and ecologically important on coral reefs (Ceccarelli et al., 2001, 2005). By defending their territories, these fishes display

evident aggressiveness towards potential intruders and/or competitors (Leal et al., 2015; Osório et al., 2006; Souza et al., 2011). Herbivory and weeding behaviour by damselfishes can modify diversity and biomass of algae and associated cryptofauna inside their territories, beyond increasing the productivity of the whole coral reef system (Ferreira et al., 1998; Hixon and Brostoff, 1983). Thus, these fishes represent an important ecological model to detect impacts on marine systems modulated by natural or anthropogenic stressors.

The present study aimed to investigate whether the presence of SCUBA divers and snorkelers can scare and disrupt the territoriality of the Dusky damselfish, *Stegastes fuscus* (Cuvier, 1830). *S. fuscus* is among the most common and aggressive species of the Pomacentridae family in the Brazilian coast. This species is abundant on coral colonies, algal, and rocky reefs (Leal et al., 2013; Medeiros et al., 2010; Osório et al., 2006) and display major influence over the benthic and fish assemblages (Ferreira et al., 1998; Osório et al., 2006). Here we tested the hypothesis that the diver's presence can modify *S. fuscus* individuals' behaviour, reducing their foraging and chase activities and increasing the frequency of refuge use.

2. Material and methods

2.1. Study area

Popularly known as the "Brazilian diving capital", the region of Arraial do Cabo, in the state of Rio de Janeiro, represent one of the most visited dive sites in Brazil, especially along the south-eastern coast (Giglio et al., 2017). Among the motivations for diving tourism, Arraial do Cabo highlights as a marine biodiversity hotspot in the South-western Atlantic, having one of the richest reef fish fauna of Brazilian coastal reefs (Ferreira et al., 2004; Floeter et al., 2001). This is favoured by the combining subtropical and warm-temperature habitats, with more exposed rocky shores seasonally bathed by upwelling events, and sheltered ones with tropical/subtropical conditions (Cordeiro et al., 2016). At least 13 SCUBA diving companies operate in the Arraial do Cabo Marine Extractive Reserve (ACMER), performing approximately 25.000 dives per year (Giglio et al., 2017). Beyond that, there are numerous nautical tourism boats serving snorkelers or visitors that only want sail between the small inlets. The ACMER was established as a sustainable use marine protected area in 1997 and despite the existence of commercial, recreational fishing and tourism zones and specific management rules, there is poor enforcement of environmental regulations and lack of no-take zones.

The study sites were selected based on intensity and type of recreational diving activities. Therefore, fish behaviour was assessed in two popular dive sites namely Forno (22°58′6.13"S, 42° 0′56.53"W), and Anequim (22°58′52.34"S, 41°59′3.43"W), which has as main activities snorkeling and SCUBA diving, respectively. At Forno, the benthos coverage is mainly composed by cnidarians (i.e. scleractinians, hydrocorals, zoanthids and octocorals), especially the zoanthid *Palythoa caribeaorum,* and branching hydrocorals *Millepora alcicornis* (Rogers et al., 2014). Epilithic algal matrix (EAM) is the most predominant benthic group at Anequim, followed by *M. alcicornis* in shallow and *P. caribeaorum* in deeper areas (> 9 m) (Giglio et al., 2017). These rock reef's cover in ACMER suggest this area as having less structural complexity and coral cover than at many coral reef dive destinations (Giglio et al., 2017). The former area is a mainland inlet, having access by land, diving or nautical tourism boats, whereas the latter one is located on a coastal island being the access only possible through diving or nautical tourism boats.

2.2. Data collection

Data were obtained in March 2017 at sheltered inshore rocky reefs, at depths between 1 m and 5 m. We randomly selected 15 territories of *S. fuscus* adults in each study site/dive activity (Snorkel at Forno beach

and SCUBA at Anequim), totalling 30 territories separated from each other by at least 4 m. All observations were gathered between 10 am and 3 pm due to the visibility conditions. Fish size was visually estimated and ranged between 11 cm and 13 cm total length and individuals with nests in their territories were excluded from analysis. In each territory, we applied two distinct experimental approaches: Control (C) – without diver presence, and Treatment (T) – with a stimulus of a diver.

In order to record *S. fuscus* behaviour in both experimental approaches, remote underwater video cameras were attached to dive weights and deployed on the seafloor at a distance of 1.0 m – 1.5 m from the Dusky damselfish territories. The territories were defined after a prior observation of the *S. fuscus* swimming, foraging and/or aggressive activity. One video camera was used in each territory to avoid further interference. After deployed, the camera was left recording for 20 min without interruption of any diver. Tourists that tried getting closer were warned to stay far to not interfere with the research. After this time, the research diver returned and then started the T, swimming around the damselfish territory (i.e. swimming above, or at same depth; swimming a little bit far and then close again) and simulating diver tourist behaviour (e.g. sometimes looking closer and/or trying to touch the fish) during 15 min.

In preliminary trials, it was observed that shifts in fish individual's behaviour could be caused by diver disturbance while deploying the camera. Consequently, it was assumed an acclimation period of fish between 3 and 5 min. Hence, the initial 5 min of each video from the control analysis were excluded.

2.3. Data analysis

All recorded videos were analysed in the Behavioural Observation Research Interactive Software – BORIS (Friard and Gamba, 2016), where were computed the frequency (number of times/recording minutes) of the following behaviours by individual focus: aggressiveness against other fishes (chasing behaviour), refuge (hiding in a shelter structure) and foraging (bites on the substrate).

In order to compare the behavioural responses of *S. fuscus* between C vs T, a repeated measures permutational multivariate analysis of variance (PERMANOVA) was calculated for each dive activity (snorkel and SCUBA), separately. It was based on 999 permutations, a binomial deviance resemblance matrix and on the design: 'experimental approach' as a fixed factor with two levels (C vs T). A repeated-measure was used because the samples are not independent (Anderson et al., 2008). Both experimental approaches (control and treatment) of the field experiment was conducted at the same individual and replicated in 30 individuals. In addition, a principal component analysis (PCA) was performed using 'FactorMineR' package (Lê et al., 2008) to summarize the datasets and investigate which behaviour could have more influence in describing the experimental approaches applied in each dive activity. Ellipses (CI = 95%) were drawn for each category (C and T) in each dive activity around the mean distance of each sample to the centroid over the PCA points.

Repeated measures PERMANOVA were performed in Primer 6+ (Anderson et al., 2008). PCA and all plots were conducted in R software (R Core Team, 2017). A significance level of $\alpha < 0.05$ was considered in all analysis.

3. Results

The effect of snorkel and SCUBA diver disturbance on *Stegastes fuscus* behaviour.

The influence of snorkeler was analogous to the SCUBA diver in affecting the *S. fuscus* behaviour. For both dive activities, when in the diver presence (T), *S. fuscus* chased the intruders away and foraged on substrate less frequently, and spent more time seeking refuge (Mean ± S.D.; SCUBA diver presence: chase = 0.53 ± 1.13;
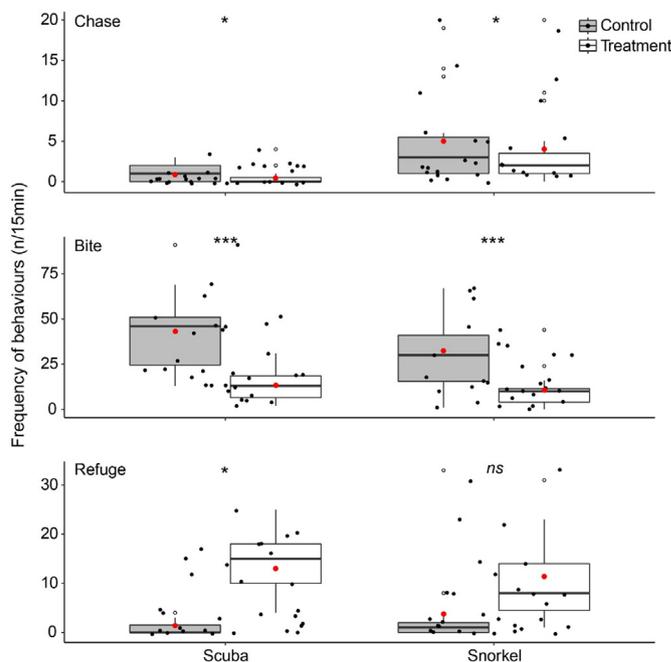

Fig. 1. Comparative behaviour performed by replicated *S. fuscus* individuals between the experimental approaches (Control vs Treatment – grey and white boxes, respectively) in each dive activity (SCUBA and snorkel). Values are the frequency of behavioural displays counts during 15 min. Boxes indicate 25th and 75th quantiles, the central line in the box is the median, whiskers are the Standard Error (the minimum and maximum distribution values) of the behaviour's frequency. Red dots represent mean values. ° = outliers. * indicate significance level: * < 0.05; ** < 0.01; *** < 0.001. *ns*: non-significant result from PERMANOVA for the comparisons between C and T. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bites = 13.20 ± 7.92; refuge = 13.87 ± 6.3/Snorkeler presence: chase = 3.87 ± 5.62; bites = 10.87 ± 11.03; refuge = 10.93 ± 8.66) than in diver absence (C) (Mean ± S.D.; SCUBA diver absence: chase = 1 ± 1.07; bites = 43.53 ± 20.97; refuge = 0.93 ± 1.39/ Snorkeler absence: chase = 5.13 ± 5.68; bites = 31.80 ± 20.49; refuge = 3.47 ± 8.46) (Fig. 1).

When the snorkeler stimulus was tested, significant differences between C and T were found for the frequencies of chase (PERMANOVA: Pseudo-*F* = 7.590, *p* = 0.02) and bites (Pseudo-*F* = 18.562, *p* = 0.001). However, there were no differences in the frequency of refuge rates (Pseudo-*F* = 1.564, *p* = 0.236) (Fig. 1). For SCUBA diver stimulus, differences were found in the three behavioural displays tested between C and T: chase (Pseudo-*F* = 171.41, *p* = 0.013), bites (Pseudo-F = 444.45, *p* = 0.001) and refuge (Pseudo-*F* = 46.308, *p* = 0.011) (Fig. 1).

Behavioural changes to snorkeler stimulus explain 78.72% of the total variability on data in the first two axes of PCA results (Fig. 2). An evident separation can be observed between C and T, where biting and refuge behaviours were the main responsible for data distribution in opposite directions on Dim. 1 (PCA eigenvalues: chase = 0.676, bites = −0.735, refuge = 0.771). Chasing behaviour was the main responsible for data distribution on Dim. 2 (PCA eigenvalues: chase = 0.718, bites = 0.472, refuge = −0.179) (Fig. 2).

Regarding the SCUBA diver stimulus, behavioural changes explain 82.57% of the total variability on data distribution in the first two axes of PCA. A separation between C and T was also observed. Biting behaviour influenced most of data distribution on Dim. 1 (PCA eigenvalues: chase = 0.524, bites = 0.833, refuge = −0.787), while chasing behaviour was the main responsible on Dim. 2 (PCA eigenvalues: chase = 0.844, bites = −0.164, refuge = 0.388) (Fig. 3).
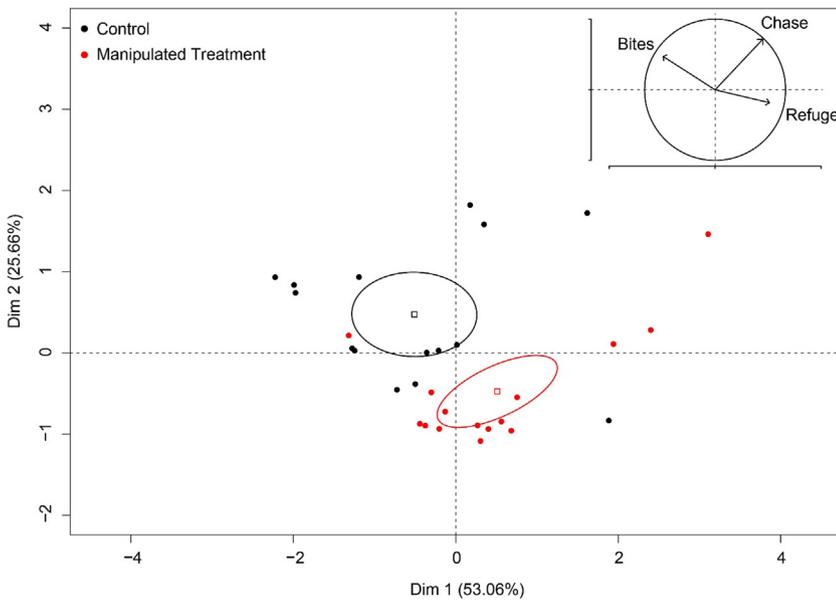
Fig. 2. Principal Components Analysis (PCA) results of *Stegastes fuscus* behaviours comparative between Control and Treatment to the snorkeler stimulus. Vectors represent the trends (direction and importance) of each behaviour. Ellipses are 95% confidence intervals around the mean of the sample's distribution for each category of experimental approaches.

4. Discussion

Behavioural changes of *S. fuscus* individuals indicated that this species has set some level of apprehension from the closest approach of a diver, refuging in holes or crevices and reducing but not ceasing its aggressiveness and foraging. Feeding opportunities were missed by the direct influence of divers' presence, either by snorkeling or by SCUBA diving. Thereby, our findings demonstrated that both dive activities play an analogous role, disrupting the Dusky damselfish behaviours and influencing its territory defence.

Reduction in *S. fuscus* foraging activity and an increase on refuge use express an antipredator (or vigilant) response to the diver stimulus. Economic models of refuge use predict that hiding in a refuge increase safety but often incur fitness costs for an individual or overall survival of a population (e.g. due the loss of time to foraging or loss of mating opportunities) (Cooper and Blumstein, 2015). Given that damselfishes are important ecosystem engineers (Jones et al., 2012), a suboptimal

hiding decision of *S. fuscus* could either lead them to starvation or drive negative consequences towards its community.

For example, the most evident impact of damselfishes' behaviour is over benthic algal assemblages within their territories, which is distinct regarding algal biomass, productivity (Ferreira et al., 1998), nitrogen fixation (Russ, 1987), species composition, diversity and successional patterns (Hixon and Brostoff, 1996). These differences between territories and surrounding areas may affect the density of cryptofaunal communities (small invertebrates) by creating refuges or enhancing food supplies, and local distribution of herbivorous fishes and invertebrates (e.g. sea urchins) (Ceccarelli et al., 2001; Ferreira et al., 1998; Hixon and Brostoff, 1996). As a result, the short-term behavioural changes caused by the 'fear effect' of a diver may lead to overall disturbances beyond the boundaries of their territories. Thus, this trend could have a strong influence on the species habitat use, competition and fitness, affecting the damselfish functional role on coral reefs.

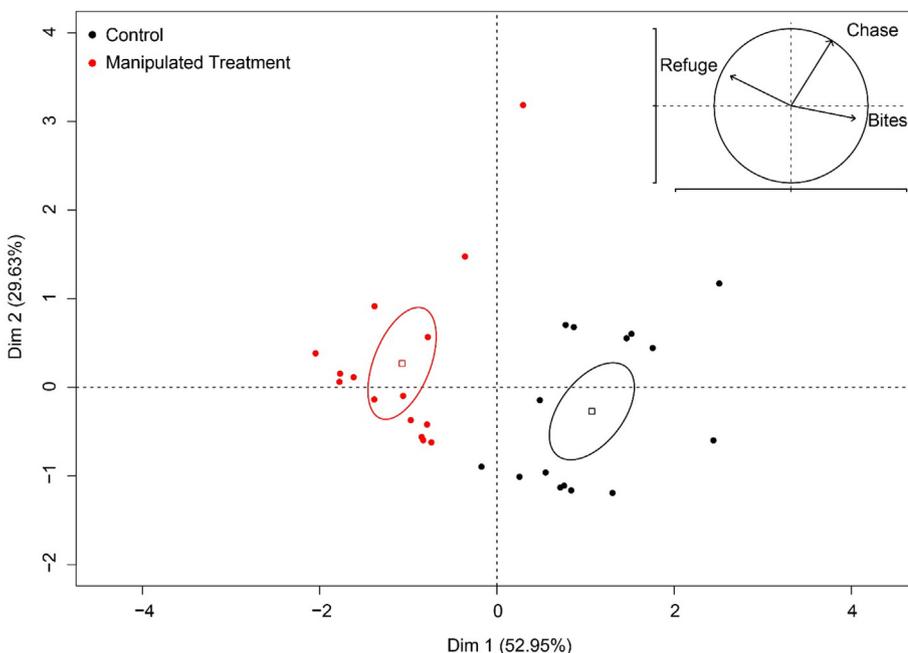In general, fish that live strongly associated with the habitat

Fig. 3. Principal Components Analysis (PCA) results of *Stegastes fuscus* behaviour comparative between Control and Treatment to the SCUBA diver stimulus. Vectors represent the trends (direction and importance) of each behaviour. Ellipses are 95% confidence intervals around the mean of the sample's distribution for each category of experimental approaches.

structure for settle, shelter or food may benefit of reducing encounter rates with predators and change its safety perception according to the coral complexity (e.g. the branch spacing and size) (Almany, 2004; Noonan et al., 2012; Pereira and Munday, 2016). For instance, the to-pographic complexity can alter how damselfish individuals assess the risk from an approaching threat, shifting from visual assessments to olfactory cues and balancing between fitness related activities, like foraging, in behalf of increasing the vigilance (McCormick and Löönnstedt, 2013). Here, we did not estimate the habitat complexity of the surveyed territories. Notwithstanding, take into account the territory complexity of damselfish could enlighten how the cost-benefit decisions to hiding from a diver are correlated to the habitat hetero-geneity, and whether it could shape the fish's antipredator behaviour in a higher coral cover area, where the diving industry is commonly at-tracted.

Changes in animal behaviour related to human impacts can improve individuals' likelihood to cope in altered environmental conditions and survive (Wong and Candolin, 2015). Nonetheless, human-related ac-tivities, especially in coastal zones, have been exposing many reef-as-sociated species to more than one stressor simultaneously (Hughes and Connell, 1999). This process contributes to a decrease in species adaptation success rates and increases severe fitness consequences (Tuomainen and Candolin, 2011; Wong and Candolin, 2015). As an example, coral reefs have been affected by global (climate change) and local (pollution and fishing) stressors (Johansen and Jones, 2011; Rummer and Munday, 2017; Sih et al., 2011; Zaneveld et al., 2016), which have been driving a reduction on reef resilience and decreasing ecosystem functioning (Bellwood et al., 2004; Ruppert et al., 2018). Considering that any reef exposed to human activity is vulnerable to at least one of those stressors, in touristic areas the diver's presence adds another stressful source for disrupt reef fish behaviour and reduce their ability to recover from a prior synergism of impacts.

Contrary to our results, Geffroy et al. (2015) have suggested that human presence in a nature-based tourism area can temporary lighten the antipredator behaviour of an individual (e.g. during summer tourism seasons), creating a 'human shield' syndrome as a result of habituation. Both habituation and sensitization to human presence occur over time and is related to different degrees of tolerance to a stimulus exposure (Bejder et al., 2009). Although we have measured the behavioural changes at a single point in time, not over a repeated or continuous exposure, the damselfish tolerance level did not tend to increase during the entire observation time with diver presence. Therefore, our behavioural observations provided one piece of evidence that habituation to diver presence may not occur in territorial fishes that inhabit high tourist visiting areas. Still, experimental designs testing an ongoing diver stimulus on the same individual through time will better able to detect fish responsiveness to a diving tourism routine of disturbance.

To assess how anthropogenic stressors have been affecting coral reefs, many reefs monitoring programs remain focused to include in-formation about abundance and length of key indicators species (Hodgson, 2000; Lang et al., 2010). However, a different database in-cluding species behaviour could be much more useful in providing in-formation related to human impact on reef ecosystems. Understand the behavioural responses of site-attached species to frequent human dis-turbance can play a pivotal role in precede management interventions before demographic response become evident (Greggor et al., 2016). Despite the lack of efficient communication between research and management actions, evidence for the effectiveness of animal beha-viour as a conservation tool has been growing and stimulating by de-monstrating how behaviour is a powerful indicator of the anthro-pogenic impact on marine ecosystems (Berger-Tal et al., 2016; Blackwell et al., 2016; Greggor et al., 2016).

Our findings demonstrated that diver presence might disrupt dam-selfish' functions and its influence on other species that are likely to alter territorial reef fishes ecological role. Future research questions

could be focused on testing a chronic effect (i.e. a persistent alteration) of how fear-induced behavioural changes driven by divers over site-attached fishes could influence the ecological role of this species on a coral reef, including long-term measurements of territorial fish ecology (e.g., the quantity and quality of food algae inside the territory, or the success in nest defence).

Considering management initiatives, a rigorous monitoring plan to dive-tourism activities should include the time of diving trips and the number of divers per trip. We demonstrated herein that the time of diver stimulus had effects on fish behaviour. Consequently, amplifying this disturbance to a 30 min or 1-h diving trip with more than one diver, could have a huge impact in territorial fish's behaviours. In addition, we suggest for a further study the evaluation of a minimum distance in which the diver could approach the marine animals without disrupting their behaviour (e.g. 1, 2 or 3 m), especially to site-attached organisms such as territorial fishes. It was observed during our fieldwork as a potential variable to reduce the effects of the fish vulnerability to human disturbances. In turn, it will improve the tourist's perceptions about having a responsible behaviour and conservation awareness while enjoying the contact with the marine environment.

In summary, our study shows that interruptions in damselfish be-haviour due to the diver's effect may modify its frequency in foraging and territory defence. Since individuals living in a reef dominated by human activities weigh diver's presence in their cost-benefit decisions, behavioural modifications can be used as an indicator of disturbances. Besides, these behavioural responses provide a more holistic compre-hension of the seascape of fear concept, including the effect of 'human as a predator' on the manner in which territorial fish use their reef-scape.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.03.009.

Acknowledgements

References

Albuquerque, T., Loiola, M., Nunes, J. de A.C.C., Reis-Filho, J.A., Sampaio, C.L.S., Leduc, A.O.H.C., 2015. In situ effects of human disturbances on coral reef-fish assemblage structure: temporary and persisting changes are reflected as a result of intensive tourism. Mar. Freshw. Res. 66, 23. https://doi.org/10.1071/MF13185.

Almany, G.R., 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141, 105–113. https://doi.org/10.1007/s00442-004-1617-0.

Anderson, M., Gorley, R.N., Clarke, R.K., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods, in Plymouth: Plymouth Marine Laboratory. pp. 214.

Barnett, A., Payne, N.L., Semmens, J.M., Fitzpatrick, R., 2016. Ecotourism increases the field metabolic rate of whitetip reef sharks. Biol. Conserv. 199, 132–136. https://doi.org/10.1016/j.biocon.2016.05.009.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment re-search: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar. Ecol. Prog. Ser. 395, 177–185. https://doi.org/10.3354/meps07979.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833. https://doi.org/10.1038/nature02691.

Benevides, L.J., Pinto, T.K., Nunes, J. de A.C.C., Sampaio, C.L.S., 2018. Fish escape be-havior as a monitoring tool in the largest Brazilian multiple-use marine protected area. Ocean Coast. Manag. 152, 154–162. https://doi.org/10.1016/j.ocecoaman.2017.11.029.

Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St. Claire, C.C., Swaisgood, R.R., 2016. A systematic survey of the integration of animal behavior into conservation. Conserv. Biol. 30, 744–753. https://doi.org/10.1111/cobi.12654.

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human-wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013.

Burgin, S., Hardiman, N., 2015. Effects of non-consumptive wildlife-oriented tourism on marine species and prospects for their sustainable management. J. Environ. Manag. 151, 210–220. https://doi.org/10.1016/j.jenvman.2014.12.018.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. https://doi.org/10.1111/1365-2656.12440.

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 39, 355–389. https://doi.org/10.1016/j.chemphys.2005.03.003.

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2005. Effects of territorial damselfish on an algal-dominated coastal coral reef. Coral Reefs 24, 606–620. https://doi.org/10.1007/s00338-005-0035-z.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0050611.

Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., Macdonald, D.W., 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behav. Ecol. 00, arw117. https://doi.org/10.1093/beheco/arw117.

Cooper, W.E., Blumstein, D.T., 2015. Escaping from Predators: An Integrative View of Escape Decisions. United Kingdom, Cambridge.

Cordeiro, C.A.M.M., Mendes, T.C., Harborne, A.R., Ferreira, C.E.L., 2016. Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. J. Fish Biol. 89, 939–958. https://doi.org/10.1111/jfb.12849.

Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. Science 349, 858–860. https://doi.org/10.1126/science.aac4249.

Emslie, M.J., Cheal, A.J., MacNeil, M.A., Miller, I.R., Sweatman, H.P.A., 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. PeerJ 6, e4886. https://doi.org/10.7717/peerj.4886.

Ferrari, M.C.O., McCormick, M.I., Meekan, M.G., Simpson, S.D., Nedelec, S.L., Chivers, D.P., 2018. School is out on noisy reefs: the effect of boat noise on predator learning and survival of juvenile coral reef fishes. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2018.0033.

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R., Peret, A.C., 1998. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. J. Exp. Mar. Biol. Ecol. 229, 241–264. https://doi.org/10.1016/S0022-0981(98)00056-2.

Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P., Joyeux, J.C., 2004. Trophic structure patterns of Brazilian reef shes: a latitudinal comparison. J. Biogeogr. 1093–1106. https://doi.org/10.1111/j.1365-2699.2004.01044.x.

Floeter, S.R., Guimaraes, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A., Gasparini, J.L., 2001. Geographic variation in reef-fish assemblages along the Brazilian coast. Glob. Ecol. Biogeogr. 10, 423–431. https://doi.org/10.1046/j.1466-822X.2001.00245.x.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 1–12.

Gallagher, A.J., Creel, S., Wilson, R.P., Cooke, S.J., 2017. Energy landscapes and the landscape of fear. Trends Ecol. Evol. 32, 88–96. https://doi.org/10.1016/j.tree.2016.10.010.

Geffroy, B., Samia, D.S.M., Bessa, E., Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. Trends Ecol. Evol. 30, 755–765. https://doi.org/10.1016/j.tree.2015.09.010.

Giglio, V.J., Luiz, O.J., Schiavetti, A., 2016. Recreational diver behavior and contacts with benthic organisms in the Abrolhos National Marine Park, Brazil. Environ. Manag. 57, 637–648. https://doi.org/10.1007/s00267-015-0628-4.

Giglio, V.J., Ternes, M.L.F., Mendes, T.C., Cordeiro, C.A.M.M., Ferreira, C.E.L., 2017. Anchoring damages to benthic organisms in a subtropical scuba dive hotspot. J. Coast. Conserv. 21, 311–316. https://doi.org/10.1007/s11852-017-0507-7.

Giglio, V.J., Ternes, M.L.F., Kassuga, A.D., Carlos, E.L., 2018. Scuba diving and sedentary fish watching: effects of photographer approach on seahorse behavior. J. Ecotourism 0, 1–10. https://doi.org/10.1080/14724049.2018.1490302.

Gil, M.A., Renfro, B., Figueroa-Zavala, B., Penié, I., Dunton, K.H., 2015. Rapid tourism growth and declining coral reefs in Akumal, Mexico. Mar. Biol. 162, 2225–2233. https://doi.org/10.1007/s00227-015-2748-z.

Greggor, A.L., Berger-Tal, O., Blumstein, D.T., Angeloni, L., Bessa-Gomes, C., Blackwell, B.F., St Clair, C.C., Crooks, K., de Silva, S., Fernández-Juricic, E., Goldenberg, S.Z., Mesnick, S.L., Owen, M., Price, C.J., Saltz, D., Schell, C.J., Suarez, A.V., Swaisgood, R.R., Winchell, C.S., Sutherland, W.J., 2016. Research priorities from animal behaviour for maximising conservation progress. Trends Ecol. Evol. 31, 953–964. https://doi.org/10.1016/j.tree.2016.09.001.

Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thomson, J., Bejder, L., 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J. Anim. Ecol. 76, 837–844. https://doi.org/10.1111/j.1365-2656.2007.01260.x.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Hixon, M.A., Brostoff, W.N., 1983. Damselfish as a keystone in reverse: intermediate disturbance and diversity of reef algae. Science 220, 511–513.

Hixon, M.A., Brostoff, W.N., 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol. Monogr. 66, 67–90. https://doi.org/10.2307/2963481.

Hodgson, G., 2000. Coral Reef Monitoring and Management Using Reef Check. Reef Check Glob Surv Program. http://www.reefcheck.org/PDFs/ICZM.pdf.

Hughes, T.P., Connell, J.H., 1999. Multiple stressors on coral reefs: a long-term perspective. Limnol. Oceanogr. 44, 932–940. https://doi.org/10.4319/lo.1999.44.3_part_2.0932.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, Bruce J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Stenec, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 80 (293), 629–637. https://doi.org/10.1126/science.1059199.

Johansen, J.L., Jones, G.P., 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. Glob. Chang. Biol. 17, 2971–2979. https://doi.org/10.1111/j.1365-2486.2011.02436.x.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386. https://doi.org/10.2307/3545850.

Lang, J.C., Marks, K.W., Kramer, P.R., Ginsburg, R.N., 2010. AGRRA Protocols Version 5.4. http://www.agrra.org/coral-reef-monitoring/fish-indicator/.

Laundré, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3 (1–7). https://doi.org/10.2174/1874213001003030001.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Leal, I.C.S., Pereira, P.H.C., De Araújo, M.E., 2013. Coral reef fish association and behaviour on the fire coral *Millepora* spp. in north-east Brazil. J. Mar. Biol. Assoc. UK. 93, 1703–1711. https://doi.org/10.1017/S0025315413000234.

Leal, I.C.S., de Araújo, M.E., da Cunha, S.R., Pereira, P.H.C., 2015. The influence of fire-coral colony size and agonistic behaviour of territorial damselfish on associated coral reef fish communities. Mar. Environ. Res. 108, 45–54. https://doi.org/10.1016/j.marenvres.2015.04.009.

Lusseau, D., 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecol. Soc. 9, 1–15.

Madin, E.M.P., Dill, L.M., Ridlon, A.D., Heithaus, M.R., Warner, R.R., 2016. Human activities change marine ecosystems by altering predation risk. Glob. Chang. Biol. 22, 44–60. https://doi.org/10.1111/gcb.13083.

Matassa, C.M., Trussell, G.C., 2011. Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. Ecology 92, 2258–2266. https://doi.org/10.1890/11-0424.1.

McCormick, M.I., Lönnstedt, O.M., 2013. Degrading habitats and the effect of topographic complexity on risk assessment. Ecol. Evol. 3, 4221–4229. https://doi.org/10.1002/ece3.793.

Medeiros, P.R., Souza, A.T., Ilarri, M.I., 2010. Habitat use and behavioural ecology of the juveniles of two sympatric damselfishes (Actinopterygii: Pomacentridae) in the South-Western Atlantic Ocean. J. Fish Biol. 77, 1599–1615. https://doi.org/10.1111/j.1095-8649.2010.02795.x.

Nedelec, S.L., Radford, A.N., Pearl, L., Nedelec, B., McCormick, M.I., Meekan, M.G., Simpson, S.D., 2017. Motorboat noise impacts parental behaviour and offspring survival in a reef fish. Proc. R. Soc. B Biol. Sci. 284, 20170143. https://doi.org/10.1098/rspb.2017.0143.

Noonan, S.H.C., Jones, G.P., Pratchett, M.S., 2012. Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish. Mar. Ecol. Prog. Ser. 456, 127–137. https://doi.org/10.3354/meps09687.

Osório, R., Rosa, I.L., Cabral, H., 2006. Territorial defence by the Brazilian damsel *Stegastes fuscus* (Teleostei: Pomacentridae). J. Fish Biol. 69, 233–242. https://doi.org/10.1111/j.1095-8649.2006.01095.x.

Pereira, P., Munday, P., 2016. Coral colony size and structure as determinants of habitat use and fitness of coral-dwelling fishes. Mar. Ecol. Prog. Ser. 553, 163–172. https://doi.org/10.3354/meps11745.

Pereira, P.H.C., Leal, I.C.S., de Araújo, M.E., 2016. Observer presence may alter the behaviour of reef fishes associated with coral colonies. Mar. Ecol. 37, 760–769. https://doi.org/10.1111/maec.12345.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. http://www.R-project.org/R Found Stat Comput Vienna, Austria.

Rizzari, J.R., Semmens, J.M., Fox, A., Huveneers, C., 2017. Observations of marine wildlife tourism effects on a non-focal species. J. Fish Biol. 91, 981–988. https://doi.org/10.1111/jfb.13389.

Rogers, R., de Oliveira Correal, G., de Oliveira, T.C., de Carvalho, L.L., Mazurek, P., Barbosa, J.E.F., Chequer, L., Domingos, T.F.S., de Andrade Jandre, K., Leão, L.S.D., de Andrade Moura, L., Occhioni, G.E., de Oliveira, V.M., Silva, E.S., Cardoso, A.M., de Castro e Costa, A., Ferreira, C.E.L., 2014. Coral health rapid assessment in marginal reef sites. Mar. Biol. Res. 10, 612–624. https://doi.org/10.1080/17451000.2013.841944.

Rummer, J.L., Munday, P.L., 2017. Climate change and the evolution of reef fishes: past and future. Fish Fish. 18, 22–39. https://doi.org/10.1111/faf.12164.

Ruppert, J.L.W., Vigliola, L., Kulbicki, M., Labrosse, P., Fortin, M.-J., Meekan, M.G., 2018. Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs. Glob. Chang. Biol. 24, e67–e79. https://doi.org/10.1111/gcb.13882.

Russ, G.R., 1987. Is rate of removal of algae by grazers reduced inside territories of

tropical damselfishes? J. Exp. Mar. Biol. Ecol. 110, 1–17. https://doi.org/10.1016/0022-0981(87)90062-1.

Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C.O., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nat. Commun. 7, 10544. https://doi.org/10.1038/ncomms10544.

Souza, A.T., Ilarri, M.I., Rosa, I.L., 2011. Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish *Stegastes rocasensis* (Actinopterygii: Pomacentridae). Environ. Biol. Fish 91, 133–144. https://doi.org/10.1007/s10641-010-9765-z.

Titus, B.M., Daly, M., Exton, D.A., 2015. Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the Bay Islands, Honduras. PLoS ONE 10, e0119645. https://doi.org/10.1371/journal.pone.0119645.

Trave, C., Brunnschweiler, J., Sheaves, M., Diedrich, A., Barnett, A., 2017. Are we killing them with kindness? Evaluation of sustainable marine wildlife tourism. Biol. Conserv.

209, 211–222. https://doi.org/10.1016/j.biocon.2017.02.020.

Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x.

Watson, D.L., Harvey, E.S., 2007. Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. Mar. Freshw. Behav. Physiol. 40, 85–103. https://doi.org/10.1080/10236240701393263.

Wirsing, A.J., Heithaus, M.R., Frid, A., Dill, L.M., 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Mar. Mammal. Sci. 24, 1–15. https://doi.org/10.1111/j.1748-7692.2007.00167.x.

Wong, B.B.M., Candolin, U., 2015. Behavioral responses to changing environments. Behav. Ecol. 26, 665–673. https://doi.org/10.1093/beheco/aru183.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. 7, 11833. https://doi.org/10.1038/ncomms11833.