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Diver presence increases egg predation on a nesting damselfish

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A R T I C L E I N F O

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A B S T R A C T

Scuba diving is a form of ecotourism that has demonstrably negative impacts on benthic sessile organisms through diver-induced mechanical damage, but we know relatively less about the direct and indirect impacts of divers on fishes and the communities they live in. Damselfishes (Pomacentridae) are an ideal model to study to understand the effects of human presence on fish behavior because they are common, often territorial and exclusively demersal egg spawners. We experimentally studied the short-term effect of diver presence on egg-guarding behavior of a damselfish, the sergeant major, *Abudefduf saxatilis*. We found that the mere presence of a scuba diver changed the short-term behavior of sergeant majors during their reproductive phase, which resulted in a 92% increase in the frequency of opportunistic predation on their eggs. Identifying the consequences of this human-driven trophic interaction will allow us to evaluate its ecological importance and, if important, guide management efforts to mitigate human impacts.

1. Introduction

Recreational and ecotourism visits to natural areas is growing globally (Balmford et al., 2009; 2015) and is often assumed to be compatible with biodiversity conservation while providing income and employment to local people. However, human presence may have multiple effects on biodiversity, especially on animals (Geffroy et al., 2015). The capacity of individuals and communities to adapt to human presence is largely unknown. Non-lethal disturbances are often drivers of change for both individuals and the communities they live in (Larson et al., 2016). Such potential detrimental effects need to be better understood to guide management efforts on behavioral changes that translate into effects on ecosystem processes (Wilson et al., 2020).

In the marine realm, negative effects of wildlife tourism have mostly been seen in ecologically sensitive and highly visited sites with poor management (Trave et al., 2017). Globally, among marine wildlife tourism activities, scuba diving is one of the most popular, occurring in many tropical and temperate destinations (Garrod and Gössling, 2008). Detrimental ecological impacts of diving have largely focused on sessile reef organisms like corals and gorgonians due to their vulnerability to mechanical damage (Au et al., 2014; Giglio et al., 2020a). Less studied effects of diving are related to behavioral changes in mobile animals such as fishes and sea turtles (Hayes et al., 2016; Bessa et al., 2017; Nunes et al., 2018). Early studies of human impacts on fishes focused on the detrimental effects of fish feeding, which have been shown to modify natural patterns of fish assemblages (Milazzo et al., 2005; Ilarri et al., 2008). Based on these negative effects, fish feeding was banned in many diving destinations.

Human presence in the aquatic environment may change the dynamics of fish assemblages and their behavior (Albuquerque et al., 2014; Bessa and Gonçalves-de-Freitas, 2014). The mere presence of a diver may change the behavior of fish because of fear effects, especially in territorial and sedentary fish which are tied to a particular location (De Brauwer et al., 2018; Benevides et al., 2019). Such behavioral change may be enhanced during the breeding phase when individuals may guard nests and eggs (Milazzo et al., 2006; Netto and Krohling, 2012). Prior work has shown that divers may influence fishes' territory size, movement, foraging, nesting, and anti-predator behavior (Bessa et al., 2017; Emslie et al., 2018; Nunes et al., 2018). For instance, diver presence has been reported to increase the time damselfish hide in refuges while decreasing the time that they allocate to foraging and aggressive behavior (Benevides et al., 2019). Another study documented a 50% reduction in reef fish cleaning behavior at sites visited by divers compared to non-visited sites (Titus et al., 2015).

Damselfishes (Pomacentridae) have been models to study the effects of human presence on fish behavior because they are common, often

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territorial, are involved in multiple interactions (Cantor et al., 2018), and are exclusively demersal egg spawners. Studies have used nesting damselfishes to investigate the effects of human disturbance in their behavior, such as boat noise (McCloskey et al., 2020) and diving tourism (Milazzo et al., 2006). The sergeant major, *Abudefduf saxatilis*, is an abundant and widely distributed damselfish in the Atlantic. In Brazil, the spawning period occurs from November to January (Bessa et al., 2007). Females select mates and lay adhesive eggs within nests previously prepared (Foster, 1987; Francini-Filho et al., 2012). The male defends demersal eggs during embryonic development and hatching occurs between 3 and 6 days after spawning (Robertson et al., 1993). Egg-guarding males repel other fish from the nests' vicinity through agonistic behaviors and provide care by aerating the eggs (Itzkowitz, 1990). However, damselfish eggs may be preyed on by other species or, in some instances, cannibalized by the male if the expected benefits of defending them suddenly are reduced (Foster, 1987; Cheney, 2008). A high incidence of predation in the Pacific suggests that damselfish eggs can be an important seasonal food resource for juvenile and cryptobenthic fishes (Jan, 1995).

Tourism activities have been shown to modify sergeant major's behavior and interfere with breeding, resulting in fewer and smaller nests (Yosef et al., 2019). Diver presence was reported to disturb damselfishes' behavior during the spawning period, providing predators that aggregate and then follow divers around an opportunity to feed on damselfish eggs (Araújo et al., 2004). In this study, we experimentally investigated if diver presence alters sergeant major behavior during their reproductive season by changing agonistic behavior of egg-guarding males toward potential egg predators and whether this affected the frequency of egg predation. We hypothesized that: (1) fear effects from diver disturbance would reduce sergeant majors' patrolling and aggressive behavior toward egg predators; and (2) the presence of divers would increase opportunistic predation on sergeant major's eggs.

2. Material and methods

2.1. Study site

We studied the behavior of sergeant majors *A. saxatilis* in the waters off Alcatrazes island (24°06′55.55″ S, 45°41′34.51″ W), southeastern Brazil. The island is part of the Alcatrazes archipelago, located 30 km from the mainland. Alcatrazes island is surrounded by rocky reefs covered mainly by turf and macroalgae and harboring one of the greatest biomass of reef fish along the Brazilian coast (Morais et al., 2017). It is considered one of the most conserved coastal sites in Brazil due to the high effectiveness of the two no-take marine protected areas covering the archipelago and contains the Alcatrazes Wildlife Refuge and Tupinambás Ecological Station (Rolim et al., 2019). The Alcatrazes Wildlife Refuge allows recreational and educational activities. Since 2018, recreational scuba diving is practiced around reefs surrounding the island, attracting divers from different regions and profiles (Marconi et al., 2020). Diving tourism management is well implemented and limits the number of divers per day, requires mandatory pre-dive briefings, and requires guided dives by trained staff.

2.2. Data collection

Data were collected in Austral summer of 2019–2020 on shallow rocky reefs around Alcatrazes island at depths ranging from 4 to 10 m. Sergeant major nests were chosen haphazardly along the reef, totaling 37 nests with eggs. Nests were separated by at least 5 m from each other. Observations were conducted between 0900 and 1500 h so as to maximize both visibility and fish activity. Remote underwater weighted cameras (GoPro Hero 5) were deployed on the seafloor at a distance of ~1.5 m from each sergeant major nest. All sampled nests were in vertical rocks ~90° to avoid the influence of different nesting positions on the defensibility of egg-guarding (Itzkowitz, 1990). Videos were recorded immediately after the camera was positioned in front of the sergeant major nest. Each nest was filmed for six minutes for each control phase (diver absent) and treatment phase (diver present). The diver present sample was conducted immediately after the control. The treatment consisted of scuba diver swimming slowly to within 1.5 m of the sergeant major nest, and simulated a diver observing a subject. The duration of diver presence sampling was defined based on our observation of the average time that largest dive parties (10 divers) remained close to the reef, and a given damselfish nesting site, during the dive. Data collection was performed under responsible agencies' environmental and ethical permits (ICMBIO permit #62932–1).

2.3. Data analysis

We scored videos using the behavioral observation software BORIS v. 7.9.7 (Friard and Gamba, 2016). We verified that after a diver set up the camera, fish returned to normal behavior within 60 s and resumed nest surveillance (see SM1). To be conservative, we excluded the first three minutes of each video for the control phase considering this as a fish acclimation phase and then scored the remaining six min – 3 min control followed by 3 min diver presence.

In the videos, we quantified the frequency of agonistic behavior toward potential predators for each egg-guarding sergeant major, described as chasing when the egg-guarding male rapidly swam toward the intruder. We quantified the number of egg bites from each individual nest predator and species, the number of chases from the egg-guarding sergeant major, and we identified the predator species when possible. Focal individual observations were conducted during the entire video record. When an individual swimming out the footage we infer if it was the same individual based on body size, color pattern and the distance between exit and coming back position in the nest.

We tested for differences between the abundance of sergeant major egg predator species between the control and diver present groups using Wilcoxon matched pairs, signed rank test. Two repeated-measures permutational multivariate analysis of variance (PERMANOVA) (nests as repeated measurement, i.e., fixed factor) (Anderson, 2017) models were fitted to test for differences in the: 1) the total number of chases by egg-guarding sergeant majors; and 2) the total number of nesting predator bites between during control and diver presence groups (with two levels, control "C" and diver presence "T") along with the minute of recording (1, 2 and 3, treated as repeated measures). The PERMANOVAs were based on 999 permutations and models used a resemblance matrix with Euclidean distances. The PERMANOVAs were fitted using Primer 6+ (Anderson et al., 2008). All other analyses were performed in the R software v. 4.0.1 (R Core Development Team, 2018). We set our alpha to 0.05.

3. Results

A total of nine species foraged on sergeant major's eggs, but only three were observed during both the control and diver presence treatment, where the abundance was significantly different for all (Table 1). Almost all egg predators were juveniles, with the exception of ringneck blenny, *Parablenius pillicornis*, where the only individual recorded was an adult.

3.1. Does scuba diver presence change the behavior of egg-guarding sergeant majors?

Egg-guarding sergeant majors actively swam around "patrolling" during the control phase, chasing individuals who closely approached their nests (Fig. 1 a, b). However, when divers were present, formerly egg-guarding fishes moved into refuges. Opportunistic predators took advantage of the lack of patrolling from egg-guarding sergeant majors to forage on eggs (Fig. 1 c, d). While no differences were observed throughout time (Pseudo-$F = 1.68$, $p = 0.18$), agonistic behavior (i.e.,

Table 1
Mean (±SE) abundance of sergeant major nesting eggs predators in control and diver presence video recordings. The total number of individuals recorded for each treatment (i.e., Control and Diver presence) is represented by the letter N. Significant differences from Wilcoxon tests are in bold. Statistical tests were not performed on the last five species due to the small sample size (< 5 individuals).

Species	Control		Diver presence		*P*-value
	Abundance	N	Abundance	N	
Malacoctenus delalandii	0.39 ± 0.10	15	2.71 ± 0.43	103	**< 0.001**
Abudefduf saxatilis	0.13 ± 0.07	5	0.31 ± 0.14	12	0.2
Stegastes fuscus	0.03 ± 0.03	1	0.26 ± 0.07	10	**0.003**
Elacatinus figaro	0	0	0.24 ± 0.11	9	**0.05**
Parablennius marmoreus	0	0	0.05 ± 0.05	2	–
Parablennius pilicornis	0	0	0.03 ± 0.03	1	–
Labrisomus nuchipinnis	0	0	0.03 ± 0.03	1	–
Haemulon aurolineatum	0	0	0.03 ± 0.03	1	–
Paraclinus spectator	0	0	0.03 ± 0.03	1	–

total number of chases) against intruders was reduced significantly when a diver was present (Pseudo-$F = 59.14$, $p = 0.001$), decreasing from a mean (±SE) of 1.74 ± 0.18 to 0.18 ± 0.05 times per sample (Fig. 2a). Fish that received chase from a sergeant major egg-guarding trended to a lower number of successful bites, except for intraspecific predation from sergeant major in the diver presence phase (Fig. 2b).

3.2. *Does scuba diver presence increase the frequency of opportunistic predation on sergeant major eggs?*

No significant difference was observed among the number of egg predator bites over the minutes (Pseudo-$F = 1.44$, $p = 0.2$). Nevertheless, the total number of predator bites on sergeant major nests was significantly higher when a diver was present than when no diver was present (Pseudo-$F = 35.43$, $p = 0.001$) (Fig. 3a). Significantly more predator bites were seen when a diver was present in all analyzed species, *Malacoctenus delalandii* (Pseudo-$F = 50.39$, $p = 0.001$), *A. saxatilis* (Pseudo-$F = 5.57$, $p = 0.01$), *S. fuscus* (Pseudo-$F = 15.72$, $p = 0.001$) and *Elacatinus figaro* (Pseudo-$F = 4.56$, $p = 0.007$) (Fig. 3b).

Besides engaging in more bites, we also observed more individual fish predating eggs during the diver disturbance phase (Fig. 4). For the most abundant predator, *Malacoctenus delalandii*, the average number of bites per sample increased from 7.3 ± 2.06 ($n = 18$ individuals) on the control phase to 19.2 ± 1.41 ($n = 103$ individuals) during the diver disturbance. For *A. saxatillis*, the number of individuals and bites increased ~2-fold during the diver disturbance.

4. Discussion

Our results show the mere presence of a scuba diver changed the short-term behavior of sergeant majors during their reproductive phase, which resulted in an increased frequency of opportunistic predation on their eggs. In the control phase, egg-guarding sergeant majors actively swim around their eggs, and chase potential egg predators. However, their behavior changed dramatically when a scuba diver was present, where the most common behavior was seeking refuge in a crevice near the nest. This happens because many animals, including sergeant majors, react similarly to human presence as they react to predators (Frid and Dill, 2002). Other examples of humans changing the behavior of reef fishes include changed patterns of feeding (Benevides et al., 2019), courting (Heyman et al., 2010), resting (Barker et al., 2011; Giglio et al., 2019), and cleaning mutualisms (Titus et al., 2015; Giglio et al., 2020b). Importantly, we have shown that scuba diver disturbance increased by 92% the frequency of egg predation on sergeant major eggs.

Although the predators were natural, they have taken advantage of human disturbance to increase their hunting success. These predators usually are juvenile cryptobenthic species that were close to the nests as they are sheltered or camouflaged in sea urchins, crevices, and macroalgae. Predators thus opportunistically fed on sergeant major eggs, which are an abundant resource during the reproductive season (Araújo et al., 2004; Bessa et al., 2007). Egg predation usually occurs when the egg-guarding sergeant major was distracted by chasing other fish or when the predator was camouflaged in the benthos. While only a few species have been described as natural predators of sergeant major eggs [e.g., *Elacatinus figaro* (Araújo et al., 2004) and *S. fuscus* (Cervigón, 1993)], we expect more species to engage in this behavior since cryptobenthic fish have plastic feeding preferences (Brandl et al., 2018). For instance, our results suggest that sergeant major eggs may be an

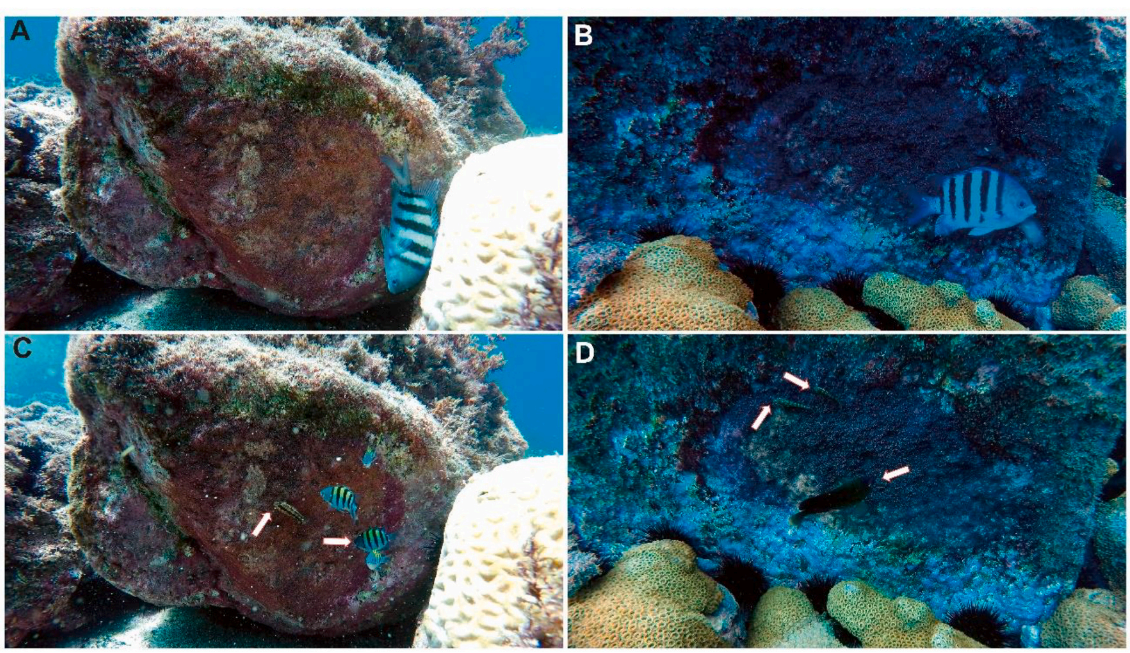

Fig. 1. Sergeant major behavior during the control (A and B) and scuba diver presence phase (C and D). Note that egg-guarding males are present when the diver was absent (control phase). However, the contrary occurs when the diver was present, providing an opportunity for predators (illustrated with white arrows) to forage on eggs that are attached to the rock.

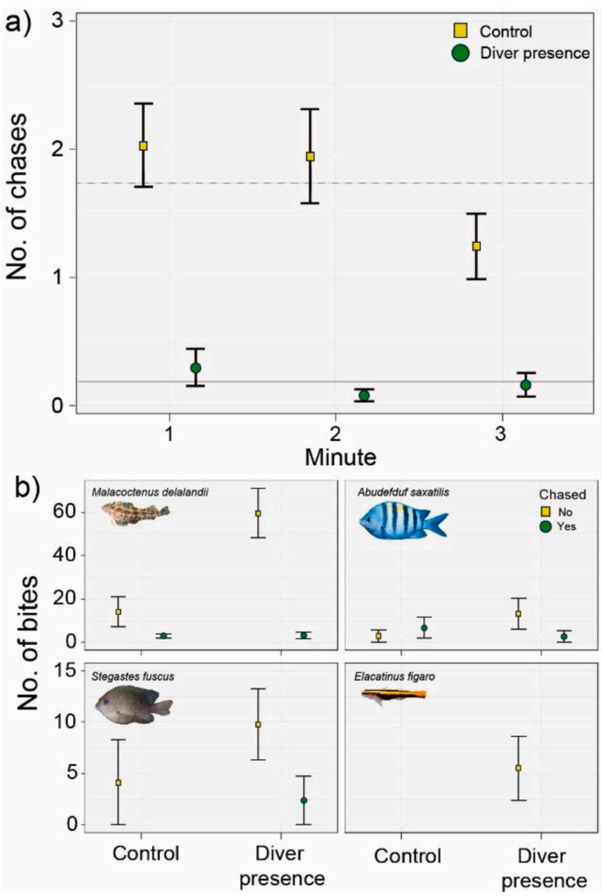

Fig. 2. a) Chases (Mean ± SE) by egg-guarding sergeant majors over the sampling time between control and scuba diver presence groups; and b) Bites (Mean ± SE) when the opportunistic predator received or not chase from egg-guarding sergeant major. In plot A, the mean number of chases per sampling is represented as dashed horizontal lines for control and continuous line for diver presence.

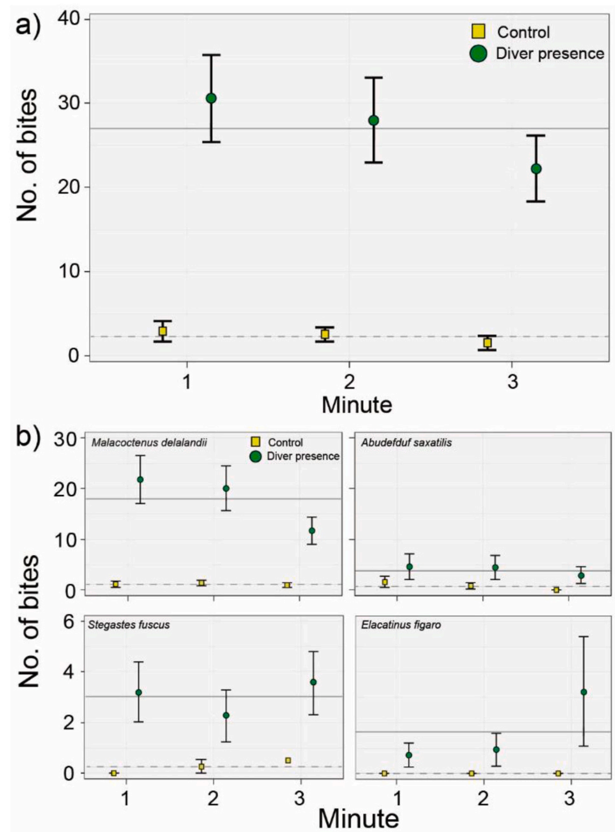

Fig. 3. a) Mean (±SE) number of predator bites over time in control and treatment groups; and b) mean (±SE) number of bites from the four most abundant predators. In all plots, the mean number of chases per sampling is represented as dashed horizontal lines for control and continuous line for diver presence.

important seasonal food resource for *Malacoctenus delalandii,* accounting for ~75% of fish predator recorded in our sampling. Interestingly, the main food items already reported to *M. delalandii* includes zoobenthonic crustaceans, mollusks and worms (Cervigón, 1993). Fish eggs predation by *M. delalandii* is firstly reported here and is highly influenced by the presence of diver distracting the egg-guarding sergeant major, revealing that behavior changes due to diver presence on only one species may trigger a chain of behavioral changes also in an assemblage or community levels.

Predation on the eggs of sergeant majors and other damselfish species has been reported to be facilitated by divers in other locations (Milazzo et al., 2006). Unnatural aggregations of fishes (10–60 individuals) are formed and follow divers and when egg-guarding damselfish seek refuge from divers, the fishes forage on their eggs (Cheney, 2008; Netto and Krohling, 2012). Thus, some predatory fishes that are able to habituate to human divers and follow them, directly benefit from the fear created by divers much in the same way cattle egrets benefit from cattle flushing up insects. Among damselfishes, a common scenario after such an attack is parents abandoning or cannibalizing their offspring, which may reflect the loss of expected benefits combined with the rather fixed costs of guarding their remaining clutch (Milazzo et al., 2006; Cheney, 2008). In areas with many divers, even in a well-regulated ecotourism site, these human-mediated changes in predation rates on eggs may have significant detrimental impacts on damselfish reproductive success (Milazzo et al., 2006). A potential limitation of this study is that effect of the diver presence might be enhanced since we did not use different fish for all treatments or randomize the order of application in our samples. However, we suggest that our sampling time simulates a diving tourism party and our results are a reliable proxy of short-term changes in egg-guarding damselfishes.

Interestingly, we did not see unnatural aggregations of predatory fishes following divers around off Alcatrazes island. This may be because the area had only been open for diving for two years and this may be insufficient time for predatory fish to habituate to humans, or perhaps there are too few humans to drive habituation. However, it also could be that the close supervision of divers by their guides prevents them from approaching within 1 m of the reef surface and this might not provide a sufficient stimulus to scare the sergeant majors into their refuges. Understanding how antipredator behavior can be changed by humans remains an important question to be answered (Geffroy et al., 2015; Bessa et al., 2017). On the other hand, identify key behavioral indicators to monitoring may represent a fast and low-cost tool to be taken in account to planning and manage tourism visit programs, especially within marine protected areas where most impacts of human presence may only be detectable by other tools after some years of cumulative impact (e.g., benthic cover changes).

A deeper understanding of how humans influence reef fish trophic relationships may help managers identify factors that drive ecosystem changes (Wilson et al., 2020). Not all human disturbances will change behavior in such a way that it affects ecosystem processes. Indeed, sergeant majors are common and abundant in Brazil, where they are adapted to reef environments and have a flexible diet (Ferreira et al., 2004). The species has been positively affected by fish feeding, increasing in abundance at sites where feeding occurs (Ilarri et al., 2008; Feitosa et al., 2012). However, with the banning of fish feeding in most

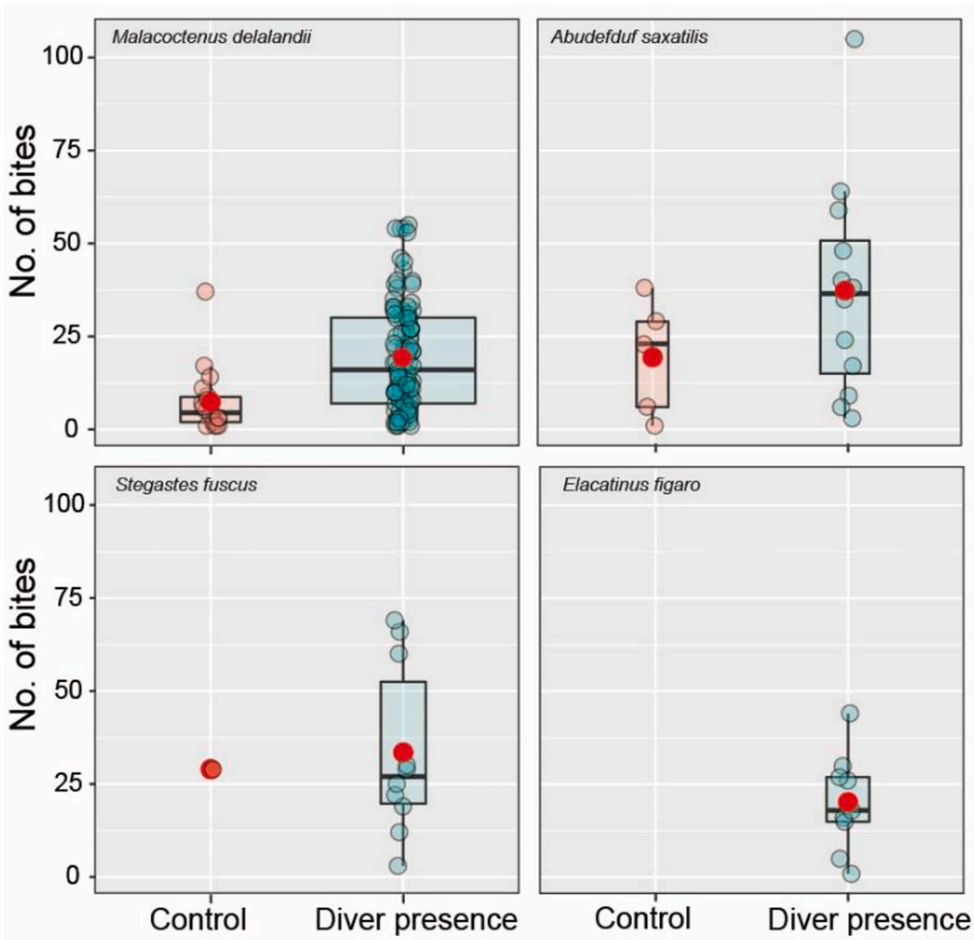

Fig. 4. Number of bites on seargent major eggs per individual from the four most representative species. The width of the boxplots is proportional to the number of fish individuals. Semitransparent points are the raw data and the red dot is the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sites, the new effect – diver disturbance – may be detrimental to sergeant majors, but positive for cryptobenthic predators. The effects on ecological processes driven by this human-induced behavioral change in fish behavior and increased egg predation require further study.

In conclusion, our study shows that diver presence cause short-term changes in the behavior of egg-guarding damselfishes and increases predation on eggs. Reducing the time that divers are engaged in stationary activities (e.g., taking photos) on sites with demersal eggs, may minimize disturbances in sergeant majors during this critical phase and decrease opportunistic egg predation. Predation on sergeant major eggs may represent a selective force in molding defense tactics that is adapted to areas with no human disturbance. Identifying the consequences of this trophic interaction will allow us to verify if it is ecologically important to ecosystem processes and if yes, guide management efforts to mitigate human impacts.

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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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