Hunting in a tough neighborhood: juvenile octopus interactions with territorial and follower fish

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Abstract: Octopuses are keystone species in shallow-water marine ecosystems. Although researchers mostly focus on predator-prey interactions, many non-lethal yet non-neutral interactions occur, particularly among fish. These range from possible cooperation through kleptoparasitism and scavenging to occasional octopus predation on an unwary fish. We evaluated some of these interactions using video recordings of juvenile *Octopus insularis* interacting with 10 fish species on Brazilian reefs, forming a repertoire of behaviors, examining when they were used, and tracking the consequences using Lag Sequence Analysis. We observed 101 interactions with seven non-territorial and three territorial fish species. Fish territoriality had a significant impact on fish behavior and octopus behavior. The duration of interactions was significantly longer in non-territorial fish. Interactions with territorial fish involved faster approaches and higher rates of behavioral change for both animals and were characterized by fish 'Jabs' and 'Swipes', and octopus Flinches and arm Slaps. Interactions with non-territorial fish were characterized by fish Follow and Circle, and the octopus continuing its hunt. Lag Sequence Analysis confirmed distinct and predictable behavioral sequences for each interaction type. These results demonstrate that during foraging octopuses need to navigate a complex set of relationships that are frequently conflictual.

Keywords: Follower-nuclear Behaviors; *Octopus insularis*; Sequence Analysis; Scavenging; Territory defense.

INTRODUCTION

Pressure from marine vertebrates, particularly fish (Packard 1972), has resulted in the selection of various cephalopod strategies to cope with both predators and competitors (Jaitly et al. 2022). Octopuses are often key species in marine ecosystems, with vital yet flexible roles in the integrity of marine food webs, predator-prey dynamics, and interspecific interactions (Taylor and Chen 1969; Karplus 2014; Dantas et al. 2021). The interactions involving octopuses and other animals in natural habitats are multiple, even though most studies focus on predator-prey dynamics (Jaitly et al. 2022; Fernández et al. 2025). When octopuses forage using chemo-tactile exploration with their arms, their disruptions of the substrate attract fish that feed on discards or steal food from other animals (Barnard 1984; Mather 1992; Karplus 2014). Such non-predatory interactions between foraging octopuses and different fish species can be intricate, including defense by territorial fish, which protect their eggs from all comers (Mather 1992). However, many generalist fish species take part in nuclear-follower interactions, in which one species explores the substrate and disturbs it, exposing potential prey for “follower” species (Strand 1988; Gibran 2002; Srinivasan et al. 2010; Karplus 2014).

Follower fishes are often opportunistic generalists (Karplus 2014), taking a variety of prey species in different situations. When attracted to foraging octopuses, they can be categorized as scavengers (Machado and Barreiros 2008), kleptoparasites (Mather 1992), cooperative partners (Sampaio et al. 2024), and occasional predators (Leite et al. 2009; Dantas et al. 2021). The relationship is often but only casually noted in field observations and depends on species, life stage, and relative size (Karplus 2014). Pereira et al. (2012), working with fishes and moray eels, found that nuclear-follower interactions are poorly identified since some of them are ephemeral and within a limited spatial range, and the same is true for interactions with octopuses as participants.

Descriptions of interactions with follower fishes have primarily relied on observational accounts that lack rigorous kinematic and behavioral analyses. Currently, such studies of the interactions between fish and octopuses have produced contrasting results, indicating that these associations can be detrimental for octopuses (Mather 1992), neutral for octopuses and beneficial for fish (Diamant and Shpigel 1985; Strand 1988; Forsythe and Hanlon 1997; Machado and Barreiros 2008; Somaweera and Somaweera 2021), or part of mutualistic associations and cooperation (Bayley and Rose 2020; Unsworth and Cullen-Unsworth 2012; Sampaio et al. 2024) (Table 1).

Table 1 Field research reports on interactions between fish and octopus species within the last 40 years (in chronological order; more information in supplementary material)

Octopus species	**Number of fish species**	**Number of fish genera**	**Number of fish families**	**Reference**
Callistoctopus macropus	6	5	4	Diamant and Shpigel (1985)
Octopus cyanea	6	4	3	
O. bimaculoides	5	4	3	Strand (1988)
O. insularis	3	3	3	Mather (1992)
O. cyanea	6	5	3	Forsythe and Hanlon (1997)
O. insularis	5	4	4	Sazima et al. (2007)
O. vulgaris	1	1	1	Machado and Barreiros (2008)

O. insularis	1	1	1	Krajewski et al. (2009)
O. insularis	1	1	1	Pereira et al. (2012)
O. cyanea	1	1	1	Unsworth and Cullen-Unsworth (2012)
O. cyanea	1	1	1	Vail et al. (2013)
O. cyanea	8	6	4	Zander (2016)
O. cyanea	3	3	2	Bayley and Rose (2020)
O. insularis	1	1	1	Felinto et al. (2020)
O. tetricus	1	1	1	Somaweera and Somaweera (2021)
O. cyanea	6	5	3	Sampaio et al. (2021)
O. cyanea	4	3	2	Sampaio et al. (2024)
O. tetricus	3	3	2	Pryor and Milton (2025)

Part of the difficulty in sorting out the interactions is that not all fish species have the same goal. In the Caribbean, Mather (1992) identified two groups of fish that interacted with *Octopus vulgaris* (later synonymized as *O. insularis*) as opportunistic followers and those that defended their eggs against potential invaders. Octopuses react to these fish in different ways, and previous studies indicate that octopuses adjust their behavior based on the type of stimulus they receive from the animals they interact with (Mather and Mather 2004; Meisel et al. 2013; Andrade et al. 2023).

For instance, *Octopus cyanea* mostly ignores fish during associations (see Forsythe and Hanlon 1997) although occasionally, octopuses slap their arms toward fish. While Mather (1992) saw this as self-protection, Sampaio et al. (2021) suggested that octopuses use physical retaliation as a strategy to coordinate the capture of prey or to drive away fish during the collaborative hunts (Sampaio et al. 2021).

Octopuses have many skin patterns, most for camouflage, but others, such as the dymantic/deimatic, appear in interspecies interactions, with some expressed unilaterally (Packard and Sanders 1971; Andrade et al. 2023). Details of these interactions, especially octopus reactions, must be examined more closely to determine the motivations. In humans (Liszkowski et al., 2012) and in some animals, such as chimpanzees (Veà and Sabater 1998) and crows (Emery and Clayton 2004), intentional signals are characterized by being directed at a receiver and having the primary purpose of influencing their behavior. Such collaboration involves communication across time and is very difficult to prove. Vail et al. (2014) demonstrated that octopuses (*O. cyanea*) can be attracted by fish (groupers) to areas with potential prey, but octopuses are well known for their curiosity and exploratory behavior (Mather 2022), and this is no indication of communicative planning. Bshary et al. (2006) showed such planning across time in associations between moray eels and groupers. When these two predators interact, this interspecific interaction also increases their hunting success rate, that is, they generate benefits for both parties involved. No such pattern has been found for octopuses and fish; clearly, octopus-fish relationships are based on complex interactions and with a range of influences, depending on how individuals interact. Sometimes, a potential scavenger may even end up as food for an octopus (Leite et al. 2009). This variation and the range of octopus species is all the more reason to investigate such interactions in detail.

The present study aims to identify and describe the interactions between several fish species and juvenile *Octopus insularis* in three different areas located in the Northeastern Brazilian coast. The paper traces sequences of behaviors during octopus-fish interactions, including durations of actions, and body patterns of octopuses, to characterize the flow of actions and reactions.

MATERIAL AND METHODS

Subjects and study area

Our target species, *Octopus insularis* Leite and Haimovici is a benthic octopus of medium size that inhabits shallow waters from Brazil to the Caribbean, including ocean islands (Leite et al. 2008; O'Brien et al. 2021). It is diurnally active (Mather 1988; O'Brien et al. 2023) and forages using visual localization and chemotactic exploration (Mather 1991), being a time-minimizing forager mainly of a wide variety of small crustaceans and bivalves. It also has a repertoire of body patterns for camouflage and communication (Mather and Mather 1994; Leite et al. 2009).

Field observations of juvenile *O. insularis* were made in Atol das Rocas Biological Reserve, Búzios Beach (Rio Grande do Norte), and Fernando de Noronha National Park, all located along the Northeastern Brazilian coast (Spalding et al. 2007). These sites are composed of rocks, coral reefs, and algae, particularly coralline species, and contain rich ecosystems that serve as natural nurseries, providing shelter and food for a wide variety of marine species (Bouth et al. 2011). This allows us to investigate the broader ecological dynamics and interspecies interactions of octopuses within Brazilian coastal environments.

Behavioral Assessment

Video recordings were taken using Focal Animal Sampling, observing one octopus at a time (Altman 1974). The first author filmed using Canon G16 and GoPro10 cameras while snorkeling during low tide periods between 7 and 12:00 am when we knew the octopuses might be foraging (Mather 1988; O'Brien et al. 2023). During snorkeling, the images were made with the diver positioned above or horizontally to the animals in the water column, since the environments were very shallow waters. The first author collected all data. Coding was performed using *Solomon coder* (Peter 2017) by the first author, and revised by the other two authors during the analysis of gathered information about the behaviors involved in octopus-fish interactions, and construction of an ethogram (Table 2). Behaviors were chosen based on proximity and limited to those seen when the fish was close enough for the octopus to reach it with any extensible arms in any direction (Mazzolai et al. 2013). We judged an interaction to begin when the fish or the octopus moved inside this distance and end when one moved beyond it. This criterion ensured specificity for potential responses while minimizing inaccuracies due to the limited camera coverage at greater distances. In addition, we recorded five octopus body patterns: Acute, Mottle, Uniform, All-body Blotch, and Half Blotch.

Fish species identification and classification as Territorial (T) and Non-territorial (NT) were based on Silveira et al. (2020), supplemented by our observations. Fish were easily divided into two species groups based on motivation (see Mather 1992): those that sought to defend territories and those that wanted feeding opportunities.

Statistical analyses

To investigate whether the type of fish (T vs NT) significantly influenced the octopuses' behavioral patterns during interactions, we applied the chi-square tests to assess the association between the type of fish and the behaviors, the body patterns observed in the octopuses, and if the frequencies of interactions change depending on the type of fish.

We used t-tests to find significantly different durations of interactions by T and NT fish. The Mann-Whitney U test was applied to (a) check the speed at which the fish approached during interaction with octopuses and (b) trace the rate of behavioral change in both octopuses and fish varied between the types of fish. We calculated each fish's 'speed proxy' by dividing the total duration of the "Approach" behavior by the number of occurrences of the behavior for each octopus. We used the interquartile range (IQR) method, which helps to identify extreme values in the data (Gupta et al. 2013). Any value below $Q1 - 1.5 \times IQR$ or above $Q3 + 1.5 \times IQR$ was considered an outlier and excluded. The Mann-Whitney test was used to compare the approach rate distributions between the two groups of fish (p-value < 0.05).

The selection of these statistical tests was based on the nature of the data and their distributions: the Chi-square test was used to analyze categorical data (frequencies of interactions/behaviors); the t-test was applied to compare means of continuous variables (duration) that met the assumptions of normality and homoscedasticity; and the Mann-Whitney U test, a non-parametric alternative, was chosen to compare variables (speed peoxy, rate of behavioral change) that did not follow a normal distribution or did not present homogeneous variances between groups. In all analyses, we considered a difference to be statistically significant when the p-value was less than 0.05.

Lag Sequence Analysis (LSA) was used to analyze possible influences on each participant's behavior during interactions. The analysis focused on two transitions, 'Octopus → Fish' and 'Fish → Octopus'. Due to the accelerated nature of interactions with T-fish, we used a 0.2-second lag, and, for NT-fish, where interactions last longer, a 2-second lag. We examined the probability of transitions in different Lags (1, 2, 3, 4, and 5) and removed duplicate consecutive behaviors to ensure that the analysis focused on actual transitions rather than repeated behaviors. A chi-square test of independence was performed to determine whether there was a statistically significant association among the transitions observed in the LSA. The test was applied to contingency tables created from the LSA results. Standardized residuals were calculated to identify specific transitions that contributed significantly to the overall chi-square statistic. A significance level of 0.05 was used, and transitions with standardized residuals greater than 1.96 were considered significant contributors to the observed associations. Statistical analyses were performed with R (RCore Team 2021).

RESULTS

We observed 101 interactions between 38 juvenile octopuses and fishes in 44 records, totaling 23'6" of interactions. There were 10 species of fish interacting with juvenile octopuses, seven NT-species (*Acanthurus coeruleu*s Bloch and Schneider, *Carangoides bartholomaei* G. Cuvier, *Cephalopholis fulva* Linnaeus, *Epinephelus adscensionis* Osbeck, *Haemulon parra* Desmarest, *Labrisomus nuchipinnis* Quoy and Gaimard, and *Lutjanus jocu* Bloch and J. G. Schneider), and three T-ones (*Coryphopterus glaucofraenum* T. N. Gill, *Stegastes sp.* Emery, and *Thalassoma sp.* Swainson).

Behaviors during interactions

During the interactions, we identified six actions in octopuses and seven in fishes (Table 2; Figure 1).

Table 2 A partial ethogram of actions seen during interactions between *Octopus insularis* and fish (several species)

Animals	Behaviors	Description
Octopus (usually on the substrate)	Crawl away	The octopus moves on the substrate away from the fish by push/pull of some arms, but other arms are not hunting.
	Crawl away hunting	The octopus moves on the substrate away from the fish by push/pull of some arms, but other arms are hunting.
	Crawl away with negative reactions	The octopus moves on the substrate away from the fish by push/pull of some arms, but other actions are producing reactions (Slap, Head retraction, and/or Jet) to the fish.
	Crawl to hunting	The octopus moves on the substrate towards the fish by push/pull of some arms, but other arms are hunting.
	Stopped	The octopus stays in one location on the substrate by contact with some arms without moving any part of its body (except the mantle/funnel for ventilation).
	Stopped hunting	The octopus stays in one location on the substrate by contact with some arms, but other arms are hunting.
	Stopped with negative reactions	The octopus stays in one location on the substrate by contact with some arms other actions are producing reactions (Slap, Head retraction and/or Jet) towards the fish.
	Swim away	The octopus jet propels itself through the water away from the fish.
Fish (always in the water)	Approach (Swim to)	The fish moves towards the octopus.
	Circle	The fish swims circularly around the octopus, keeping the same distance but changing angular orientation (> 45 degrees).
	Follow	The fish maintains the same distance to the octopus as both move in parallel, octopus first.
	Swipe	The fish moves quickly in an arc towards and away from the octopus, without contact.
	Move away (Swim away)	The fish moves away from the octopus.
	Jab	The fish swims quickly to and makes contact with the octopus, usually with the head.
	Stopped	The fish stays in one location.

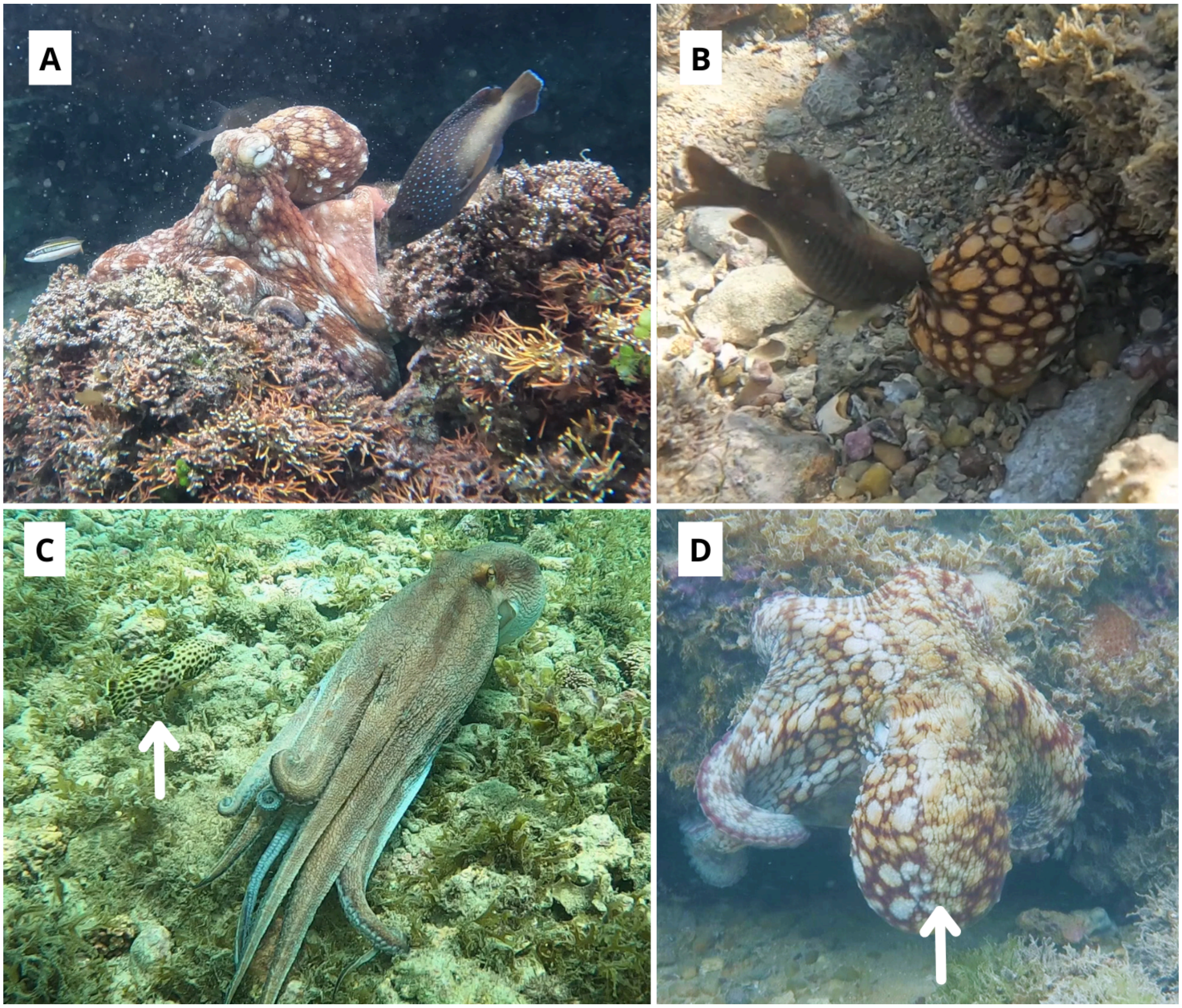

Fig. 1 Video frames of juvenile *O. insularis* interacting with different fish species during hunting. In (A) the NT-fish *Cephalopholis fulva* is performing Stop while the octopus is hunting in the substrate; (B) a T-fish *Stegastes sp.* is Jabbing, and the octopus, while foraging, responds to the fish's approach by performing the Blotch body pattern and retracting its head (Shrinks); (C) the octopus is swimming, and the NT-fish *Epinephelus adscensionis is* following; and (D) Half Blotch displayed in wild juveniles *O. insularis*, during interactions with T-fish. Photos: Michaella P. Andrade

Frequency, duration, and statistical analysis of behaviors

Fish territoriality significantly affects the octopuses' behaviors. 'Crawl to hunting' occurred significantly less frequently with T-fish, while 'Stop with negative reactions' happened more often in interactions with T-fish (Table 3). Moreover, fish territoriality significantly affected the patterns of fish behavior. NT-fish exhibited more 'Circle'; while T-fish exhibited more 'Approach', 'Swipe', and 'Swim away'. The 'Follow' actions were restricted to NT-fish and 'Jab' to T-ones (Table 4).

Table 3 Frequencies and percentages of juvenile octopus behaviors during interactions with T and NT-fishes. '*' indicates significant results in the chi-square test, and N/A is not applicable

Behaviors	**Frequencies (Percentages %)**	
	NT-fish	**T-fish**
Crawl away hunting	25 (24.03%)	13 (14.77%)
Crawl away with negative reactions	1 (0.96%)	6 (6.81%)
Crawl away	1 (0.96%)	6 (6.81%)
Crawl to hunting	12 (11.53%)	1 (1.13%)*
Stopped hunting	36 (34.61%)	27 (30.68%)
Stopped with negative reactions	9 (8.65%)	23 (26.13%)*
Stopped	15 (14.42%)	11 (12.5%)
Swim away	4 (3.84%)	1 (1.13%)

Table 4 Frequencies and percentages of fish behaviors during interactions with juvenile octopuses. '*' indicates significant results in the chi-square test

Fish behaviors	Frequencies (Percentages %)	
	NT-fish	T-fish
Stop	32 (28%)	31 (21%)
Approach (Swim to)	28 (24%)	38 (26%)*
Swipe	25 (22%)	34 (23%)*
Move away (Swim away)	23 (2%)	33 (23%)*
Circle	16 (14%)*	2 (1%)
Follow	13 (11%)*	0
Jab	0	7 (5%)

The frequency of interactions with octopuses between the T and NT-fishes was not significantly different. However, the average duration was longer for NT than T fishes. The speed of approach differed significantly between T and NT-fish, with T-fish approaching faster. The rate of change in octopus behavior was higher during interactions with T-fish. The same pattern was observed for the rate of change in fish behavior, which was higher in T-fish.

Octopus body patterns during interspecific interactions

Fish also impacted the octopuses' body patterns during the interaction, with the body pattern Half Blotch occurring only in interactions with T-fishes. When we analyze what happens before and after this body pattern in the behavior of T-fish, we find fish behavior changed significantly after the 'Half Blotch' pattern appeared in octopus. Specifically, the analysis of the standardized residuals revealed that the 'Move away' behavior was significantly more frequent after the appearance of the pattern, while the 'Approach' and 'Swipe' behaviors were less frequent.

Sequences of behaviors in interactions

Sequences of behavior between octopuses and fish differed between interactions with NT and T-fishes. However, as interaction durations were longer in interactions with NT-fish, we observed statistical significance in more sequences in a greater number of lags.

Significant departures from expected likelihood were as follows: during interactions with NT-fish, the octopus tended to crawl away when the fish approached or made a "swipe" movement. If the fish circled the octopus, the octopus continued to move, either crawling or hunting, within two steps. After the fish followed the octopus, it would probably stop or swim away (Figure 3A). When the octopus stopped, the fish approached or moved away. The fish was attentive to the octopus, which continued its hunt, stopping and starting again, without reacting in any significant way to the fish. The only exception was when the fish occasionally made a “swipe” movement near the octopus, which caused the octopus to crawl away (Figure 3B).

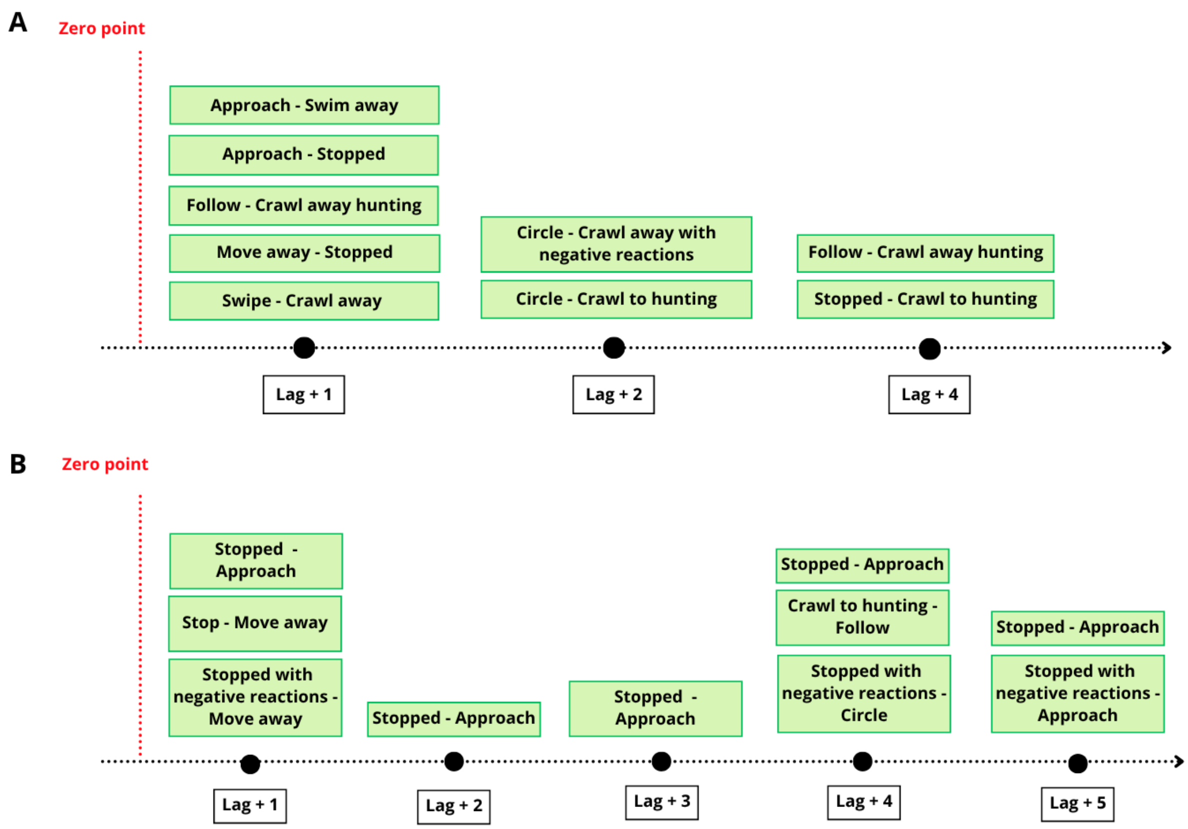

Fig. 3 Significant standardized residuals results of the chi-square test in the Lag Sequence Analysis of interactions between juvenile octopuses and NT-fish. (A) Sequence of fish → octopus behavior, (B) Sequence of octopus → fish behavior

During interactions with T-fish, as expected in territorial defense, the fish defended itself, interrupting the octopus' hunt and continuing to prevent it from hunting (Figure 4A). The octopus would also stop after the fish made a “swipe”. When the octopus moved away, the fish moved closer, either after one or two steps (Figure 4B).

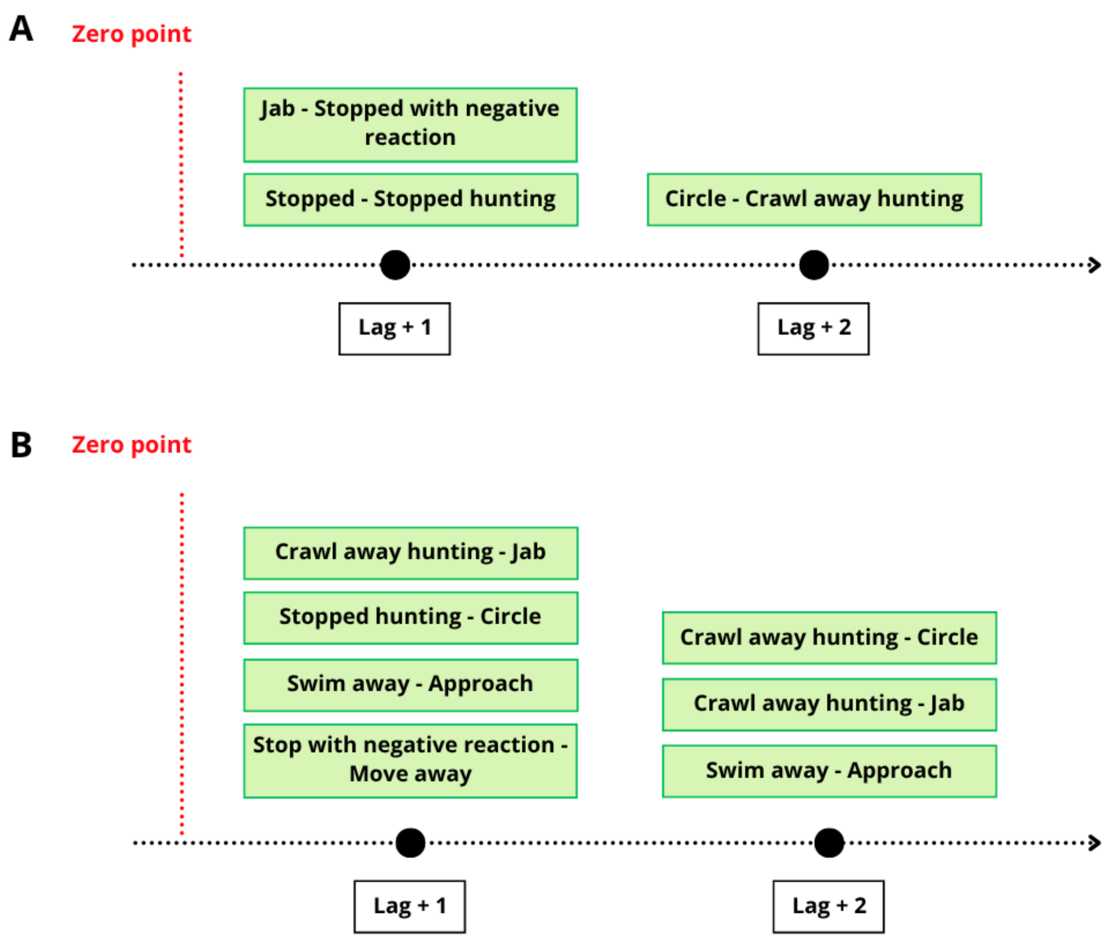

Fig. 4 Significant standardized residuals results of the chi-square test in the Lag Sequence Analysis of interactions between juvenile octopuses and T-fish. (A) fish → octopus behavior, (B) octopus → fish behavior.

DISCUSSION

Interactions between juvenile *O. insularis* and associated reef fish generate complex behavioral responses, significantly shaped by the functional role of the interacting fish. Our findings demonstrate that fish territoriality directly influences these encounters' nature, duration, intensity, and outcomes, reinforcing that such interspecific interactions are adaptive and highly context-dependent, going beyond simple categorizations.

Juvenile octopuses differentiate between T and NT-fish, adjusting their behavior accordingly. Encounters with T-species were characterized by fast fish approaches, significantly shorter durations, and higher rates of behavioral change for both participants, indicative of intense and escalating conflicts. Fish employed aggressive tactics such as 'Jab' and 'Swipe,' consistent with the defense of eggs or space (Mather 1992). In response, octopuses often ceased foraging and engaged in agonistic behaviors (Stop with negative reactions) or actively retreated (Crawl away), often interrupting their hunting activity. This corroborates previous indications that octopuses react defensively to non-predatory but threatening stimuli (Mather and Mather 2004; Meisel et al. 2013; Mather and Andrade 2023).

Interactions with NT-fish were significantly longer, characterized by the fish 'Follow' or 'Circle' the foraging octopus. These associations align with typical nuclear-follower dynamics, where followers capitalize on prey disturbed by the 'nuclear' forager (Strand 1988; Gibran 2002; Karplus 2014). Octopuses largely tolerated these followers, often continuing to hunt despite the proximity of the fish, similar to observations of *O. cyanea* (Forsythe and Hanlon 1997). Although followers benefit, our observations in *O. insularis* do not provide evidence for active cooperation or coordinated hunting as suggested for other octopus-fish dyads (Sampaio et al. 2021; 2024). The octopus's reactions to followers were generally neutral, suggesting that the interaction is primarily opportunistic for the fish with minimal demonstrated benefit and potentially little interference for the octopus in this context.

Our results build upon Mather (1992), who observed that octopuses exhibit distinct behavioral responses to different fish species. Additionally, our findings support the distinction proposed by Pereira et al. (2012) between "nuclear-following" and "ephemeral interactions". Although the authors focused on interactions between eels and fish, we observed a similar pattern in octopus-fish interactions. NT-fish fit into the nuclear-follower category, engaging in more prolonged interactions and covering a larger area to follow the octopus. In contrast, T-fish align with the ephemeral category, displaying shorter interactions and remaining within their territory rather than following the octopuses.

The present study is the first to analyze interactions between octopuses and fish using Lag Sequence Analysis, and it provided quantitative support for these distinct interaction pathways. For territorial encounters, the sequences revealed a reactive back-and-forth, with fish aggression triggering octopus defense, which could trigger further approach by the fish. For follower interactions, the sequences showed fish actions (Approach, Circle, Follow) often leading to continued octopus foraging unless a Swipe triggered avoidance, indicating a looser association primarily driven by octopus hunting activity.

An enigmatic finding is the specific use of the 'Half Blotch' body pattern during interactions with T-fish. The association between the display of this skin pattern and the subsequent 'Move away' of the territorial fish suggests a startle or deimatic display (Packard and Sanders 1971; Andrade et al. 2023). However, establishing direct causality remains a challenge, as body patterns are often exhibited in conjunction with other behaviors. It is therefore difficult to isolate whether the body pattern or the accompanying physical actions (e.g., arm movements or shrinking) are responsible for eliciting the fish's reaction. Future research should aim to disentangle these factors.

It is important to consider that our study focused on juvenile octopuses. This life stage is the longest in the development of octopuses, as they have a semelparous life history. But there is little information about behavioral shifts at maturity, or indeed exactly what indicators there are of this state (Mather 2006), nor the maturity state of octopuses that other authors were observing. Past the shift from a planktonic to a benthic lifestyle, there are no major changes in threat perception and survival strategies, although findings in *Octopus vulgaris* (Packard and Sanders 1971) demonstrated changes in body pattern responses to disturbance. The presumed increase in competence due to learning may alter foraging strategies, and increasing size might change tolerance of fish interference, but the fish in this study were also juveniles. Their smaller size and potentially higher vulnerability to harassment by T-fish may significantly influence the pronounced defensive strategies observed, such as the frequent display of the 'Half Blotch' pattern.

Despite the small sample size, the frequency analysis of fish behaviors (Table 4) revealed statistical significance. This suggests that, although the results represent only a first approximation, they are sufficiently robust to describe the behaviors in question. Therefore, these findings serve as a basis for future studies using larger samples to further investigate this issue.

These results reinforce the understanding that interactions between octopuses and fish are complex and exist from the early stages of life for both animals. Juvenile *O. insularis* navigates its 'difficult neighborhood' not with a fixed strategy but with a sophisticated repertoire of context-dependent behaviors. This adaptability is fundamental for survival and foraging efficiency within a dynamic reef ecosystem populated by diverse actors with competing interests. In addition to all other results, our study adds four new fish species in interspecific interactions with juvenile octopuses (*Acanthurus coeruleus*; *Carangoides bartholomaei*; *Epinephelus adscensionis*, and *Haemulon parra*). Ultimately, appreciating this intricate web of non-lethal interactions is crucial for understanding the full ecological significance of octopuses beyond their roles as predator and prey and recognizing their vital contribution to the structure and function of complex marine communities (Karplus 2014).

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