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Follower fish of the goldspotted eel *Myrichthys ocellatus* with a review on anguilliform fish as nuclear species

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Abstract

In a nuclear-follower fish foraging association, the follower benefits from food uncovered or flushed out when the nuclear fish disturbs the bottom, while nuclear species generally do not seem to be benefiting. Among nuclear species, eels (anguilliform fish) are known to be one of the most represented groups. Here we investigated the frequency and time duration of foraging associations among the goldspotted eel *Myrichthys ocellatus* and reef fish in a subtropical marginal reef. In addition, we reviewed nuclear eel species and their followers described in the literature. From a total of 211 goldspotted eels observed, seven follower species were recorded in 19% of the samples. The average time of the following associations per species ranged from 40 to 190 s. Four species were reported for the first time as *M. ocellatus* followers (*Bodianus rufus*, *B. pulchellus*, *Stephanolepis hispidus*, and *Serranus baldwini*) and three of them have never been reported in the literature as eel followers (*B. pulchellus*, *S. hispidus,* and *S. baldwini*). The literature describes 13 eel species acting as nuclear for 66 fish species, represented mainly by groupers and sea basses. The size of the eel was not correlated with the size of its follower and neither with the number of described follower species. The nuclear role of eels is likely to be an important component of the trophic ecology of small and medium-sized macrocarnivore fish.

Keywords: Reef fish behavior, Southwestern Atlantic, Foraging associations, Nuclear and follower, Reef fish, Interspecific associations

Background

Interspecific associations are common in structurally and ecologically complex ecosystems such as coral reefs. Among reef fish, interspecific foraging associations are characterized by the opportunistic joining of individuals from two or more species during feeding [1, 2]. It comprises a "nuclear species" that disturbs the bottom while foraging and exposing potential preys to opportunist or generalist predator species known as "follower" [3]. The nuclear-follower association has been described for a diversity of species that varies from small mobile invertebrate feeders to large piscivores [4–8]. Considering that this association is relatively common, it is believed to play an important role in the trophic ecology of reef fish [9]. The nuclear-follower association is commensal by benefiting the follower with easier access to inaccessible prey, higher feeding success, lower energy expenditure on foraging, and lower susceptibility to predation [6]. On the other hand, it is hypothesized that nuclear species do not gain benefits from feeding and may even be impaired due to food competition with followers [2]. Nevertheless, nuclear species can benefit from social feeding such as vigilance against predators and avoid that some prey escape. Also, it has been suggested that the nuclear-follower associations can increase the foraging opportunities for both species [10].

Anguilliform fish (hereafter referred to as "eels" for simplicity) are among the most representative nuclear species in the nuclear-follower associations [6, 11]. Eels often forage on clumps of algae, sand banks, and between reef crevices, where they prey on crabs and small fish.

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Their body shape enables them to access crevices that are inaccessible to most fish [12] and, therefore, they represent potential nuclear species for opportunistic follower fish. However, feeding associations involving eels have only been descriptively investigated despite their potential importance. For instance, it remains unknown whether the body size of nuclear species influences the number of reported followers and whether a particular fish genus is more prone to associate with eels than to other genera.

We investigated the nuclear-follower associations using the goldspotted eel *Myrichthys ocellatus* as a nuclear species in a subtropical marginal reef. The species is mostly nocturnal, feeds primarily on crabs, although it may also forage during the daytime [13, 14]. Specifically, this study aims to examine the frequency and time of the nuclear-follower associations among reef fish. In addition, we conducted a review on the eel species that have been globally described as nuclear and the number of follower species and then investigated the relationship between the eel body size and the amount and type of follower species.

Methods

Study site

The study was conducted in Arraial do Cabo, southeastern Brazil (22°57′S, 42°01′W). The region consists of an isthmus and three islands dominated by rocky shores. The sites surveyed were mostly composed of coastal rocky reefs with depths of 4–12 m and water temperature of 17–26 °C. This region has major ecological and conservation relevance on the Brazilian coast, as it is the southern distributional limit of some tropical species, with local fauna encompassed by both tropical and temperate species [15, 16].

Data collection and analysis

We conducted underwater observations through scuba diving (ca. 44 h) and snorkeling (ca. 13 h) between April and August 2015. Divers swam along coastal rocky reefs (2–8 m depth) searching for *M. ocellatus*. When an individual was found, we visually estimated its total length (TL) based on the collector experience in underwater visual census surveys and checked for the presence of any following fish. When an eel was followed by any fish, the observer started to record the duration. The eel observations lasted for five min, in which the behavior was classified as being moving, foraging, or resting. When a follower was present, we estimated its TL and recorded the behavioral interactions, for instance, if it touched a nuclear eel or presented agonistic behavior toward conspecifics to defend an advantageous position next to the eel. Divers maintained a minimum distance of 3 m from the fish to avoid disrupting the behavior of the eel and its followers. The relationship between the size of nuclear and the follower species was assessed with the Spearman rank correlations since the data were nonparametric.

The literature review was conducted through the search tools *Scopus* and *Google Scholar* using the words "follower + fish + eel"; "nuclear + follower + reef fish" and "following + behavior". We included only peer-reviewed literature in the analysis. From the selected papers, we recorded those that mentioned nuclear-follower interaction among eels and fish. The follower species were categorized according to the trophic categories as macrocarnivore, mobile invertebrate feeder, and omnivore [17, 18]. The maximum size of nuclear eel species was described according to Froese & Pauly [19]. The relationships between the maximum body size of nuclear species and (1) the number of follower species, and (2) the maximum body size of nuclear and follower species were assessed by using the Spearman rank correlation.

Results

Followers of *Myrichthys ocellatus*

A total of 211 sightings of *M. ocellatus* were recorded. The body size ranged from 30 to 100 cm TL (average = 64 cm ± 6 SE). Most of the specimens recorded were foraging along the reef, disturbing the bottom (92%), and few were resting (8%). The followers were observed to be following 41 eels (i.e., 19% of the observed *M. ocellatus* had followers), and the overall average time of association was 98 ± 22 s (Table 1). Seven species were recorded as followers, of which four belonged to the family Labridae (*Halichoeres brasiliensis*, *H. poeyi*, *Bodianus pulchellus,* and *B. rufus*), one to Serranidae (*Serranus baldwini*), one to Epinephelidae (*Mycteroperca acutirostris*), and one to Monacanthidae (*Stephanolepis hispidus*). The most frequently recorded followers were *B. rufus* (n = 12), *S. hispidus* (n = 9), and *H. brasiliensis* (n = 5) (Table 1). Most follower species were mobile invertivores (n = 5 species), with only one species each of macrocarnivore and omnivore.

Overall, the size of *M. ocellatus* was significantly correlated to the size of its followers (r = 0.42; $p = 0.007$; Table 1). Among all observed interactions, *B. rufus* presented the highest number of agonistic interactions toward conspecifics (n = 12 events) and touched *M. ocellatus* more frequently (n = 6; Table 2). *H. brasiliensis* and *S. baldwini* were the only species that did not present agonistic interactions. No agonistic interactions were registered between the nuclear and follower species.

Anguilliform fish as nuclear species

We found 22 studies reported eels as nuclear species, all of which included reef-associated species from the

Table 1 Follower fish of *Myrichthys ocellatus* recorded in Arraial do Cabo, Brazil

Family	Species (no. of events)	Interaction duration (s)	Mean body size of the nuclear species	Mean body size of the follower species (cm) *M. ocellatus*	Spearman rank correlation result
Labridae	*Halichoeres brasiliensis* (7)	69.3 ± 6.1	69 ± 6	27 ± 2	r = 0.7; p = *0.04*
Labridae	*Halichoeres poeyi* (4)	40 ± 12	56 ± 11	16 ± 1	r = 0.25; p = 0.7
Labridae	*Bodianus pulchellus* (5)	122 ± 24	57 ± 8	19 ± 1	r = 0.36; p = 0.5
Labridae	*Bodianus rufus* (12)	145 ± 27	69.6 ± 4.1	28.3 ± 0.9	r = 0.07; p = 0.8
Monacanthidae	*Stephanolepis hispidus* (10)	65 ± 4.2	59 ± 6	24 ± 1	r = 0.54; p = 0.1
Epinephelidae	*Mycteroperca acutirostris* (1)	190	75	35	*
Serranidae	*Serranus baldwini* (2)	45 ± 12	68 ± 5	9 ± 2	*
	All events	96.6 ± 21.4	64 ± 3	25 ± 1	r = 0.42; p = *0.007*

* Statistical tests were not done due to the small sample size. *P*-values in italic are significant. The deviations are standard errors

Table 2 Frequency of interactions among follower fish of *Myrichthys ocellatus* in Arraial do Cabo, Brazil

Species	Behavior	
	Agonistic against conspecifics	Touch nuclear
Halichoeres brasiliensis	0	2
Halichoeres poeyi	0	0
Bodianus pulchellus	5	3
Bodianus rufus	8	4
Stephanolepis hispidus	3	2
Mycteroperca acutirostris	0	2
Serranus baldwini	5	0

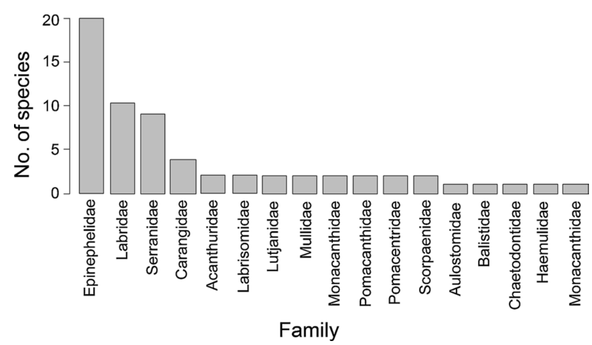

Fig. 1 Number of fish species described as followers of eels, according to the family, found in 22 peer-reviewed publications

tropical (n = 16) and subtropical (n = 6) shallow reefs. In these papers, 78 nuclear-follower associations were described, in which 13 eel species were recorded as being nuclear (11 species of Muraenidae and two of Ophichthidae), and 66 reef fish species from 17 families were recorded as followers. Most follower species belonged to Epinephelidae (n = 20), followed by Serranidae (n = 10), and Labridae (n = 10; Fig. 1). Considering the trophic category, followers were mostly macrocarnivores (MCAR, n = 33; 53%), followed by mobile invertivore feeders (MINV, n = 18; 29%); roving herbivores (ROVH) and sessile invertivore feeders (SINV) (each with 3 species); planktivores (PLK), and territorial herbivores (TERH) (each with 2 species); and omnivores (OMNI, n = 1; Table 3). Overall, the average number of follower species for each eel species was 5.2 ± 1.3 SE, and the highest number of follower species was reported for *M. ocellatus* (20 species) and *Gymnothorax griseus* (16 species; Fig. 2). The relationship between the maximum body size of the anguilliform nuclear species (overall mean: 131 ± 21 cm), and: (1) the number of follower species; and (2) the maximum body size of nuclear and follower species were not significant (r = − 0.02, $p = 0.9$ and r = 0.2, $p = 0.06$, respectively).

Discussion

Followers of *Myrichthys ocellatus*

This study describes four new species acting as followers of *M. ocellatus*: *Bodianus rufus*, *B. pulchellus*, *Serranus baldwini,* and *Stephanolepis hispidus*. The first three species have never been described as followers of anguilliform fish. *M. ocellatus* possess a suite of adaptations, such as round and elongated body that enables it to move through the reef and explore complex structures like narrow interstices (i.e., crevices, holes, cracks). These features promote *M. ocellatus* as a potential nuclear species even for small reef fish such as verified herein as also mentioned elsewhere [13, 20]. *M. ocellatus* is distributed throughout the Atlantic ocean [21] and it is common in Brazilian shallow waters [17, 18, 22]. Given its abundance and its role as nuclear, the species is suggested to have a relevant functional role in the trophic ecology of reef fish through the facilitation of food access and an increase in

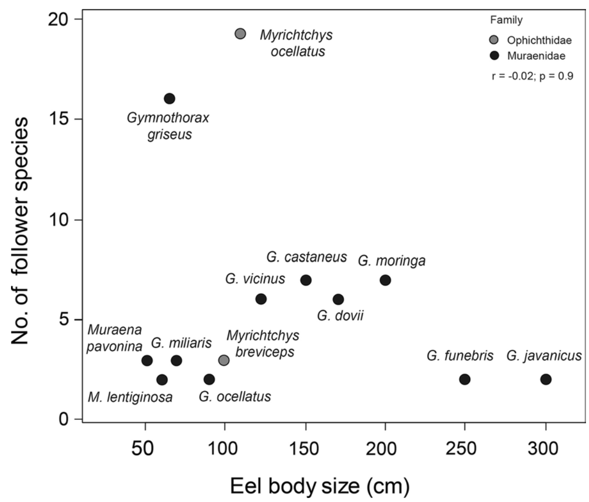

Fig. 2 Relationship between the maximum body size of the eel (total length) and the number of fish follower species described in the literature

the feeding success of follower fish [5, 23]. However, the frequency in which the interactions occur was unknown, and surveys only described opportunistic behavioral aspects of the event [13, 14, 20, 24]. To the best of our knowledge, this study presents the first data on duration and frequency (presence x absence) of following interactions with an eel species. Followers of *M. ocellatus* were relatively common (19% of the individuals observed) and performed short-time opportunistic associations with no more than 190 s. In fact, associations were observed when eels were actively disturbing the bottom to attract the attention of followers.

Comparisons of the size of both the nuclear and follower fish are also missing in the literature. Some studies have only speculated on the relationship between the size of nuclear and the follower fish species [25]. We found a relationship between the size of nuclear and follower to *H. brasiliensis* and for all species grouped. This can be explained because the amount of disturbance created by the foraging nuclear fish is suggested to influence the size and number of followers [9]. Species that cause a relatively high amount of disturbance such as *M. ocellatus* [13], are suggested to attract more followers [2].

During the present study, wrasses (Labridae) and filefish (Monacanthidae) were observed following *M. ocellatus* in pairs, occasionally displaying aggressive behavior toward conspecifics that attempted to join the foraging association. This aggressive behavior (*short chases* and *displacements*) aimed to maintain the fish dominance of the advantageous position next to the eel to avoid sharing the benefits of following the nuclear individual with conspecifics [14]. *B. rufus* was also aggressive toward the diver who was conducting the behavioral observations. Arraial do Cabo is considered as a popular diving site [26]; and this behavior is likely to benefit the nuclear species towards curious divers, especially photographers, who often approach such subjects to take photo [27]. A less frequent interaction observed was the touch by the follower on nuclear species. This type of contact by follower species is suggested to act as a stimulus to the nuclear fish to continue foraging [1, 28].

A previous literature review [13] reported 12 species of followers of *M. ocellatus*, of which five species were groupers. Nevertheless, in Arraial do Cabo, we recorded only one species of grouper (*Mycteroperca acutirostris*) in a single event. This low frequency of groupers in following associations may be related to the marked decrease in the abundance of groupers in the region during the last three decades as a consequence of overfishing [29, 30]. Therefore, changes in the fish community caused by anthropogenic activities can be affecting interspecific associations, thereby influencing the reef trophodynamics.

Anguilliform fish as nuclear species

Anguilliform fish are followed by a variety of species, mainly macrocarnivores from the families Epinephelidae and Serranidae (groupers and sea basses), which represent half of the species described so far. These fish are considered to be inquisitive, they display opportunistic feeding behavior, and are known for following a wide range of reef fish species [4, 31, 32], as well as sea stars [33] and octopuses [4]. The main follower species of eels, the coney grouper *Cephalopholis fulva* is highly opportunistic and has been reported in interspecific feeding associations as a follower [3, 9], mimic [34], or even a preying cleaner species [35]. Remarkably, the four species of roving herbivorous and two territorial herbivorous were described as followers of *M. ocellatus* and *Gymnothorax*. Herbivorous are likely to feed on items made available by the nuclear species, such as pieces of algae loosened or unearthed by the nuclear fish [9].

Findings from this survey suggest that size of nuclear species is not a predictor of the number of follower species. The number of follower species is more likely to be related to the active foraging behavior of nuclear species. For instance, *M. ocellatus* (species with the highest number of followers - Table 3) is a small-sized species (max. 110 cm) which behavior is described as "vigorous and agitated" [13]. This active behavior and the foraging activity increased the amount of disturbance produced by the nuclear species, thereby attracting more followers [5]. In addition, the diversity of habitats where *M. ocellatus* forage may also explain the high amount of followers verified. This species is known to forage in a diversity

Table 3 Summary of nuclear-follower associations between eels and reef fish found in the literature

Nuclear eel species	Follower species	Trophic category	Location	Source
Muraenidae				
Gymnothorax castaneus	*Balistes verres*	MINV	Gulf of California (TEP)	[5]
Gymnothorax castaneus	*Bodianus diplotaenia*	MINV	Gulf of California (TEP)	[5]
Gymnothorax castaneus	*Epinephelus labriformis*	MCAR	Gulf of California (TEP)	[5]
Gymnothorax castaneus	*Cephalopholis panamensis*	MCAR	Gulf of California (TEP)	[5]
Gymnothorax castaneus	*Holacanthus passer*	SINV	Gulf of California (TEP)	[5]
Gymnothorax castaneus	*Mycteroperca rosacea*	MCAR	Gulf of California (TEP)	[5, 36]
Gymnothorax castaneus	*Rypticus bicolor*	MCAR	Gulf of California (TEP)	[5]
Gymnothorax dovii	*Caranx melampygus*	MCAR	Malpelo island (TEP)	[7]
Gymnothorax dovii	*Dermatolepis dermatolepis*	MCAR	Malpelo island (TEP)	[7]
Gymnothorax dovii	*Aulostomus chinensis*	MINB	Malpelo island (TEP)	[7]
Gymnothorax dovii	*Mycteroperca olfax*	MCAR	Malpelo island (TEP)	[7]
Gymnothorax dovii	*Seriola rivoliana*	MCAR	Malpelo island (TEP)	[7]
Gymnothorax dovii	*Bodianus diplotaenia*	MINB	Malpelo island (TEP)	[7]
Gymnothorax funebris	*Carangoides bartholomaei*	MCAR	Brazil (SWA)	[4]
Gymnothorax funebris	*Cephalopholis fulva*	MCAR	Brazil (SWA)	[4, 37]
Gymnothorax griseus	*Aethaloperca rogaa*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Cephalopholis argus*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Cephalopholis hemistiktos*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Cephalopholis miniata*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Epinephelus fasciatus*	MCAR	Red Sea (WEI)	[6, 28]
Gymnothorax griseus	*Grammistes sexlineatus*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Parupeneus cyclostomus*	MINV	Red Sea (WEI)	[6]
Gymnothorax griseus	*Pterois volitans*	MCAR	Red Sea (WEI)	[6, 28]
Gymnothorax griseus	*Scorpaenopsis gibbosa*	MCAR	Red Sea (WEI)	[6]
Gymnothorax griseus	*Thalassoma rueppellii*	PLK	Red Sea (WEI)	[28]
Gymnothorax griseus	*Variola louti*	MCAR	Red Sea (WEI)	[6]
Gymnothorax javanicus	*Epinephelus fasciatus*	MCAR	Red Sea (WEI)	[6]
Gymnothorax javanicus	*Plectropomus pessuliferus*	MCAR	Red Sea (WEI)	[1]
Gymnothorax miliaris	*Cephalopholis cruentata*	MCAR	Caribbean (WEA)	[11]
Gymnothorax miliaris	*Cephalopholis fulva*	MCAR	Caribbean (WEA)	[11]
Gymnothorax miliaris	*Rypticus saponaceus*	MCAR	Caribbean (WEA)	[11]
Gymnothorax moringa	*Acanthurus bahianus*	ROVH	Caribbean (WEA)	[11]
Gymnothorax moringa	*Bodianus rufus*	MINV	Caribbean (WEA)	[11]
Gymnothorax moringa	*Cephalopholis cruentata*	MCAR	Caribbean (WEA)	[11, 38]
Gymnothorax moringa	*Cephalopholis fulva*	MCAR	Caribbean (WEA)	[11]
Gymnothorax moringa	*Chaetodon capistratus*	SINV	Caribbean (WEA)	[11]
Gymnothorax moringa	*Holacanthus tricolor*	SINV	Caribbean (WEA)	[11]
Gymnothorax moringa	*Scarus taeniopterus*	ROVH	Caribbean (WEA)	[11]
Gymnothorax ocellatus	*Diplectrum* spp.	MCAR	Brazil (SWA)	[39]
Gymnothorax ocellatus	*Lutjanus* spp.	MCAR	Brazil (SWA)	[39]
Gymnotorax vicinus	*Acanthurus coeruleus*	ROVH	Brazil (SWA)	[4]
Gymnotorax vicinus	*Carangoides bartholomaei*	MCAR	Brazil (SWA)	[4]
Gymnotorax vicinus	*Cephalopholis fulva*	MCAR	Brazil (SWA)	[4]
Gymnotorax vicinus	*Haemulon parra*	MINV	Brazil (SWA)	[4]
Gymnotorax vicinus	*Halichoeres radiatus*	MINV	Brazil (SWA)	[4]
Gymnotorax vicinus	*Pseudupeneus maculatus*	MINV	Brazil (SWA)	[4]
Gymnothorax sp.	*Bodianus diplotaenia*	MINV	Gulf of California (TEP)	[36]
Gymnothorax sp.	*Epinephelus labriformis*	MCAR	Gulf of California (TEP)	[36]

Table 3 continued

Nuclear eel species	Follower species	Trophic category	Location	Source
Muraena pavonina	*Caranx latus*	MCAR	Brazil (SWA)	[4]
Muraena pavonina	*Cephalopholis fulva*	MCAR	Brazil (SWA)	[4]
Muraena pavonina	*Labrisomus conditus*	MINV	Brazil (SWA)	[4]
Muraena lentiginosa	*Alphestes immaculatus*	MCAR	Mexico (TEP)	[40]
Muraena lentiginosa	*Serranus psittacinus*	MINV	Mexico (TEP)	[40]
Ophichthidae				
Myrichthys breviceps	*Cephalopholis fulva*	MCAR	Caribbean (WEA) and Brazil (SWA)	[4, 11, 13, 24]
Myrichthys breviceps	*Epinephelus adscensionis*	MCAR	Brazil (SWA)	[41]
Myrichthys breviceps	*Hypoplectrus puella*	MCAR	Caribbean (WEA)	[11]
Myrichthys ocellatus	*Acanthurus bahianus*	ROVH	Brazil (SWA)	[20]
Myrichthys ocellatus	*Bodianus pulchellus*	MINV	Brazil (SWA)	This study
Myrichthys ocellatus	*Bodianus rufus*	MINV	Brazil (SWA)	This study
Myrichthys ocellatus	*Epinephelus adscensionis*	MCAR	Brazil (SWA)	[13, 24, 41]
Myrichthys ocellatus	*Epinephelus marginatus*	MCAR	Brazil (SWA)	[14, 17, 33]
Myrichthys ocellatus	*Halichoeres brasiliensis*	MINV	Brazil (SWA)	[13] This study
Myrichthys ocellatus	*Halichoeres poeyi*	MINV	Brazil (SWA)	[20] This study
Myrichthys ocellatus	*Halichoeres radiatus*	MINV	Brazil (SWA)	[4]
Myrichthys ocellatus	*Labrisomus cricota*	MINV	Brazil (SWA)	[20]
Myrichthys ocellatus	*Labrisomus nuchipinnis*	MINV	Brazil (SWA)	[20]
Myrichthys ocellatus	*Lutjanus alexandrei*	MCAR	Brazil (SWA)	[13]
Myrichthys ocellatus	*Mycteroperca acutirostris*	MCAR	Brazil (SWA)	[13] This study
Myrichthys ocellatus	*Mycteroperca bonaci*	MCAR	Brazil (SWA)	[24]
Myrichthys ocellatus	*Rypticus bistrispinus*	MCAR	Brazil (SWA)	[24]
Myrichthys ocellatus	*Serranus baldwini*	MINV	Brazil (SWA)	This study
Myrichthys ocellatus	*Serranus flaviventris*	MINV	Brazil (SWA)	[24]
Myrichthys ocellatus	*Stegastes fuscus*	TERH	Brazil (SWA)	[20]
Myrichthys ocellatus	*Stegastes variabilis*	TERH	Brazil (SWA)	[20]
Myrichthys ocellatus	*Stephanolepis hispidus*	OMNI	Brazil (SWA)	This study
Myrichthys ocellatus	*Thalassoma noronhanum*	PLK	Brazil (SWA)	[4]
Myrichthys ocellatus	*Ulaema lefroyi*	MINV	Brazil (SWA)	[13]
Myrichthys sp.	*Epinephelus fasciatus*	MCAR	Red Sea (WEI)	[6]

Acronyms for trophic categories as follows: *MCAR* macrocarnivore, *SINV* sessile invertebrate feeder, *MINV* mobile invertebrate feeder, *OMNI* omnivore, *PLK* planktivore, *ROVH* roving herbivore, *TERH* territorial herbivore. Nuclear and follower species are listed in ascending alphabetical order. *WEA* western Atlantic, *SWA* southwestern Atlantic, *TEP* tropical eastern Pacific, *WEI* western Indian

of environments, such as rocky/coral reefs, algae-rodolith beds, and sand and mud bottoms; therefore, this is likely to increase the variety of followers [13].

Eels can be followed by groups of fish, as reported for other nuclear fish species [9, 13]. However, the data on the number of followers of eels in a group of fish are rarely available. The ecological implications of this foraging association and how changes in reef fish community structure (e.g., due to overfishing) can influence the frequency and complexity of such interactions remain unclear. Further studies should include quantitative data on foraging association such as duration, the number of followers at the same time, as well as the food intake rates.

Abbreviations

TL: total length; cm: centimeter.

Authors' contributions

MLFT and VJG collected, analysed the data and drafted the manuscript. TCM and PHCP wrote the manuscript. All authors read and approved the final manuscript.

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Competing interests
The authors declare that they have no competing interests.

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