CSIRO PUBLISHING

Marine and Freshwater Research, 2017, **68**, 381–387
http://dx.doi.org/10.1071/MF15294

Short Communication

Following fish feeding associations in marine and freshwater habitats

José Sabino[A], *Luciana P. Andrade*[A], *Ivan Sazima*[B], *Fabrício B. Teresa*[C], *Sergio R. Floeter*[D], *Cristina Sazima*[B] and *Roberta M. Bonaldo*[E,F]

[A]Universidade Anhanguera-Uniderp, 79003-010, Campo Grande, MS, Brazil.
[B]Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brazil.
[C]Universidade Estadual de Goiás, 15054-000, Anápolis, GO, Brazil.
[D]Universidade Federal de Santa Catarina, 88010-970 Florianópolis, SC, Brazil.
[E]Universidade de São Paulo, 05508-900, São Paulo, SP, Brazil.
[F]Corresponding author. Email: robertabonaldo@gmail.com

Abstract. Following fish feeding associations are composed of nuclear species that disturb the substratum when foraging, and followers that capitalise on food resources. In marine and freshwater ecosystems, bottom disturbance is the main predictor of follower composition; hence, other features, such as fish behaviour, may also converge between these habitats. Comparisons of the following associations in marine and freshwater habitats could provide a better comprehension of this interaction, which is known to increase the feeding of participating species. We compared following associations between a marine reef and a freshwater stream. Associations in the freshwater resembled the following three iconic reef interactions: (1) a carnivorous follower moving in front of a nuclear species; (2) a shoal of omnivores feeding on particles loosened by the nuclear fish; and (3) a shoal of omnivores feeding on particles expelled by the nuclear fish. The major differences between the marine and freshwater associations were (1) the greater morphological variety of nuclear species in the reef and (2) the main nuclear species often foraged in groups in the reef, whereas the freshwater counterparts foraged solitarily. These similarities between the systems outnumbered the differences, probably because of the shared water environment and the relatively simple requirements for fishes in these associations.

Additional keywords: behavioural and ecological convergences, Brazil, multi-species interactions, nuclear–follower associations, reef fishes, stream fishes.

Received 3 August 2015, accepted 11 February 2016, published online 14 April 2016

Introduction

Marine and freshwater ecosystems may resemble each other in the behaviour and ecology of their fish communities, because these systems and their ichthyofauna share some structural and functional features (e.g. Emery 1978; Sazima 1986). These similarities are remarkable, given that fish fauna in marine and freshwater habitats have separate evolutionary histories, with little or no overlap in species and genera, because these fauna have gone through contrasting evolutionary and environmental pressures (Nelson 1994; Carrete Vega and Wiens 2012). However, a comparative study in a marine reef and a freshwater pond reported several common characteristics of the fish assemblages, such as feeding tactics, social feeding patterns, and interspecific associations, between these systems (Sazima 1986).

Interspecific fish feeding associations occur when individuals of two or more fish species forage together (Lukoschek and McCormick 2000). A variety of interspecific interactions among fishes occurs in both marine and freshwater habitats, such as cleaning (e.g. Carvalho *et al.* 2003; Grutter 2005), mimicry (Sazima 2002*a*, 2002*b*; Bessa *et al.* 2011) and social foraging associations (e.g. Lukoschek and McCormick 2000; Leitão *et al.* 2007; Sazima *et al.* 2007). However, the extent of similarities of these interactions between marine and freshwater habitats is a question rarely addressed (e.g. Emery 1978; Sazima 1986), and it could provide relevant information on the potential convergences in fish behaviour and ecology between these systems.

The following association (also termed nuclear–follower interaction in the literature) is a commensalistic, interspecific relationship in which one or more nuclear species disturb the substratum while foraging, thus attracting a variety of opportunistic, carnivorous and omnivorous species (the followers) that capitalise on food resources that are otherwise unavailable (e.g. Sazima *et al.* 2007; Krajewski 2009; Teresa *et al.* 2011). Following associations between fishes occur in marine (e.g. Lukoschek and McCormick 2000; Sazima *et al.* 2007) and freshwater ecosystems (e.g. Leitão *et al.* 2007; Teresa *et al.* 2014); however, most studies on this interaction have been conducted in the former habitat. These studies have shown that following associations are one of the most common interspecific feeding interactions in tropical reefs globally (Lukoschek and McCormick 2000). Additionally, species of a variety of fish families and trophic groups have been recorded, and usually spend a considerable amount of their feeding time in following interactions (Strand 1988; Lukoschek and McCormick 2000; Sazima *et al.* 2007). Therefore, there is a reasonable amount of information on fish behaviour, size and trophic groups of species in these interactions, especially for tropical reefs (e.g. Lukoschek and McCormick 2000; Sazima *et al.* 2007).

In freshwater habitats, the occurrence of following associations, as well as the diversity, behaviour and characteristics of the participating species, is underestimated, because few studies have examined this interaction in these systems (but see Leitão *et al.* 2007; Teresa and Carvalho 2008; Garrone-Neto and Sazima 2009; Teresa *et al.* 2011). However, previous studies have suggested that following associations in marine and freshwater ecosystems share some features, because bottom disturbance caused by the nuclear species is the main predictor of the composition of followers in both habitats (Krajewski 2009; Teresa *et al.* 2014). Therefore, follower fishes promptly react to the sediment suspension caused by the nuclear species, irrespective of the identity of the nuclear fish, in both ecosystems (Krajewski 2009; Teresa *et al.* 2014). This similarity of drivers of the nuclear–follower associations between these habitats, along with the overall resemblances in the structure and ichthyofauna of marine and freshwater systems (e.g. Emery 1978; Sazima 1986), indicates that other features of the nuclear–follower interaction, such as fish behaviour, may also converge between these habitats.

The assessments of fish behaviour in the nuclear–follower associations in marine and freshwater systems could advance our knowledge of fish feeding ecology, because this interaction can increase the feeding rates and foraging time of participating species, with potential effects on fish fitness and community dynamics (Diamant and Shpigel 1985; Aronson and Sanderson 1987; Baird 1993). Therefore, comparisons of following associations in marine and freshwater habitats could provide a better comprehension of this ubiquitous interaction in marine systems and possibly in freshwater habitats as well, by verifying whether fish behaviour in the nuclear–follower associations conforms to general characteristics in aquatic ecosystems. In this sense, we compared following fish feeding associations between a marine reef and a freshwater stream by assessing these interactions qualitatively and by commenting on their overall similarities and differences (see Sazima 1986 for this approach). Our initial assumption was that following associations conform to general characteristics, irrespective of habitat type.

Materials and methods

Surveys of following fish feeding associations

Observational sessions of heterospecific interactions between followers and nuclear fishes were conducted in two sites, namely, a marine reef, with an adjacent sandy flat, and a freshwater stream. The reef (Praia da Conceição) is located in the oceanic Fernando de Noronha Archipelago, off north-eastern Brazil, tropical West Atlantic (Sazima *et al.* 2007). The stream (Rio Olho d'Água) is located in the upper Rio Paraguay basin, Mato Grosso do Sul State, south-western Brazil (Teresa *et al.* 2011). These two sites were chosen because of a similar depth (~0.5–3 m), sandy bottom (mixed sand, gravel, rock and algae in the marine habitat; sand with trunks, branches, and rooted submerged macrophytes in freshwater) and underwater visibility (frequently >10 m). Data collection was conducted on four consecutive days in June 2003 for the reef habitat and on four consecutive days in May 2011 for the stream habitat. Foraging associations were recorded in the daytime from morning until the afternoon.

Following associations in the two studied systems were recorded during observational sessions while snorkelling. Each session lasted 40–125 min, for a total of 1075 min (515 min in the reef and 560 min in the stream). During the observational sessions, we randomly searched for interspecific following associations and recorded every association observed (hereafter referred as an 'event') with instantaneous sampling (Altmann 1974). For each event, we recorded the number of individuals and the species of each follower and nuclear fish. The events were recorded directly on plastic slates and photographed in both habitats. We estimated the total length of each fish against a ruler, placed on the bottom, or by measuring an object (pebble, plant piece) near the assessed fish. All of the fish individuals in the recorded events were classified into 'fish-like' or 'odd' body-morphology categories. A given foraging group was not followed over successive periods of time to reduce the risk of non-independent data collection; thus, all of the individual data are likely to have come from different events.

Fish surveys

Fish surveys were conducted to assess whether the observed disparities in the morphology of nuclear fishes and the size of the followers between systems (see Results) were an artefact of the greater diversity (morphological and taxonomic) in the reef. For this assessment, visual fish counts along belt transects (20 m long × 2 m wide) were conducted in the stream ($n = 25$) and in the reef ($n = 16$). This transect size was chosen because it was possible even in sites of low visibility, it fit in reef and stream areas with similar habitat structure and it was applied in previous studies in Brazilian aquatic systems (e.g. Krajewski and Floeter 2011; Teresa *et al.* 2011). Transects were randomly positioned within each habitat, with no overlap between them. During the surveys, a snorkeler swam under a standardised speed (~3 m min^{-1}), while deploying the transect tape. All of the fish individuals found along the surveys were classified into species, size class (10-cm intervals of total length) and body-morphology categories ('fish-like' and 'odd'). All of the surveys were conducted from 0900 to 1600 hours, and care was taken to equally distribute samples during the day.

Analyses

The *G*-test for goodness-of-fit was used to compare the observed frequencies of nuclear species with 'fish-like' (e.g. Labridae, Mullidae) and 'odd' (e.g. Dasyatidae, Muraenidae) body morphologies in the follower associations with their expected frequencies in the two studied habitats. The expected frequencies of each body-morphology category were considered as the mean proportion of individuals from each category in the fish

Table 1. Nuclear fishes and their follower fishes recorded at the Praia da Conceição, Fernando de Noronha Archipelago, Pernambuco, north-eastern Brazil

Nuclear species are listed in a decreasing order of the number of follower species. For each species, the family name is mentioned once (within the parentheses)

Nuclear species	Follower species
Pseudupeneus maculatus (Mullidae)	*Acanthurus chirurgus* (Acanthuridae)
	Anisotremus surinamensis (Haemulidae)
	Caranx bartholomaei (Carangidae)
	Caranx latus (Carangidae)
	Cephalopholis fulva (Serranidae)
	Halichoeres dimidiatus (Labridae)
	Halichoeres radiatus (Labridae)
	Sparisoma axillare (Labridae)
	Sparisoma frondosum (Labridae)
	Thalassoma noronhanum (Labridae)
Halichoeres radiatus	*Pseudupeneus maculatus*
	Thalassoma noronhanum
Haemulon parra (Haemulidae)	*Halichoeres radiatus*
	Thalassoma noronhanum
Mulloidichthys martinicus (Mullidae)	*Halichoeres radiatus*
Acanthostracion polygonius (Ostraciidae)	*Thalassoma noronhanum*
Dactylopterus volitans (Dactylopteridae)	*Cephalopholis fulva*
Gymnothorax funebris (Muraenidae)	*Cephalopholis fulva*

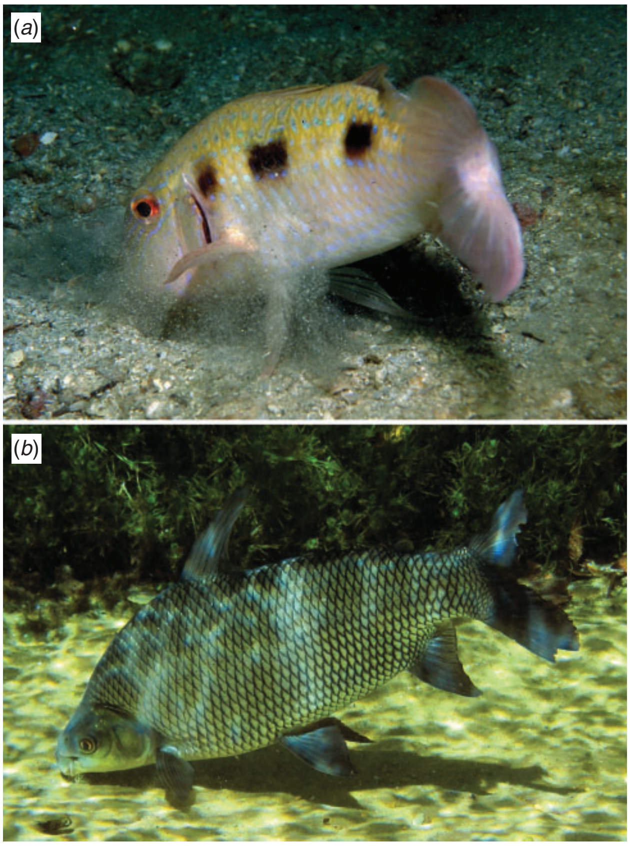

Fig. 1. Two bottom-disturbing fishes, (*a*) the goatfish (*Pseudupeneus maculatus*) in the reef of the Praia da Conceição, and (*b*) its counterpart, the prochilod (*Prochilodus lineatus*) in the clear-water stream Rio Olho D'Água.

surveys in each habitat. The observed frequencies were considered as the mean proportion of individuals from each category in the follower-association surveys. The *G*-test for Goodness-of-fit was also used to compare the observed frequencies of follower individuals of different body-size categories with their expected frequencies in the two studied systems. For both systems, the following two body-size categories were considered: small (size <20 cm) and medium (size ≥20 cm).

Results

We recorded seven nuclear and 11 follower species in the reef, and six nuclear and 11 follower species in the stream (Tables 1, 2). In the reef, one nuclear species, the goatfish, *Pseudupeneus maculatus* (Fig. 1), attracted a greater number of follower species than did the other nuclear species (Table 1). On the contrary, in the stream, the follower-species richness was more evenly distributed among the nuclear species (Table 2).

We observed marked similarities between the two studied systems. In both habitats, we recorded the following three main types of nuclear–follower associations: (1) a carnivorous follower moving in front of the digging nuclear fish; (2) a shoal of small omnivorous fishes feeding on particles loosened from the bottom by a single large nuclear fish; and (3) a shoal of small omnivorous fishes feeding on particles expelled by the nuclear fish.

Furthermore, two nuclear fish species also acted as followers in both studied habitats, namely, *P. maculatus* and *Halichoeres radiatus* in the reef and *Leporellus vittatus* and *Leporinus striatus* in the stream (Tables 1, 2).

The first main type of following association was observed, for instance, when the goatfish (*P. maculatus*) was followed by the wrasse (*H. radiatus*) in the reef, and when the leporinus (*L. macrocephalus*) was followed by the pike cichlid (*Crenicichla vittata*) in the stream (Fig. 2*a*, *b*). In both situations, the follower fish positioned itself very close to the mouth of the nuclear individual and commonly moved slightly ahead of the digging nuclear fish. The second type of association was the case of shoals of the small wrasse (*Thalassoma noronhanum*) capitalising on food particles loosened from the reef bottom by the parrotfish (*Sparisoma frondosum*). In the stream, this association was mirrored by numerous small tetras (*Odontostilbe pequira*) feeding on particles suspended by bites of the large prochilod (*Prochilodus lineatus*) at the bottom (Fig. 2*c*, *d*). Finally, the third type of following association was observed in the reef when the wrasse (*T. noronhanum*) consumed particles expelled (either leftovers from a mouthful or faeces) by the nuclear fish, such as the grunt (*Anisotremus surinamensis*). In the stream, this association occurred between the tetra (*O. pequira*) and the leporinus (Fig. 2*e*, *f*).

Table 2. Nuclear fish species and their follower fish species recorded at the Rio Olho D'Água, Mato Grosso do Sul, south-western Brazil
Nuclear species are listed in a decreasing order of the number of follower species. For each species, the family name is mentioned once (within the parentheses)

Nuclear species	Follower species
Leporinus macrocephalus (Anostomidae)	*Astyanax asuncionensis* (Characidae)
	Astyanax lineatus (Characidae)
	Astyanax marionae (Characidae)
	Characidium zebra (Crenuchidae)
	Crenicichla lepidota (Cichlidae)
	Crenicichla vittata (Cichlidae)
	Hyphessobrycon eques (Characidae)
	Jupiaba acanthogaster (Characidae)
	Leporinus striatus (Anostomidae)
	Odontostilbe pequira (Characidae)
Prochilodus lineatus (Prochilodontidae)	*Astyanax marionae*
	Characidium zebra
	Crenicichla lepidota
	Crenicichla vittata
	Hyphessobrycon eques
	Jupiaba acanthogaster
	Odontostilbe pequira
Leporellus vittatus (Anostomidae)	*Astyanax lineatus*
	Crenicichla lepidota
	Jupiaba acanthogaster
	Leporellus vittatus
	Leporinus striatus
	Odontostilbe pequira
Leporinus striatus (Anostomidae)	*Astyanax asuncionensis*
	Astyanax marionae
	Jupiaba acanthogaster
	Odontostilbe pequira
Parodon nasus (Parodontidae)	*Astyanax marionae*
	Jupiaba acanthogaster
	Odontostilbe pequira
Leporinus friderici (Anostomidae)	*Crenicichla lepidota*

The differences observed between the two studied habitats referred mostly to the shape and size of the fishes involved in the association, as well as the social behaviour of the most prominent nuclear fish. In both studied systems, one nuclear individual followed by one to several individuals usually formed the association. However, in the reef, the nuclear species that attracted the largest number of follower species (*P. maculatus*) often foraged in groups, whereas its freshwater counterpart (*L. macrocephalus*) was only observed alone.

Moreover, whereas in the stream, all of the nuclear species sported a 'fish-like' appearance, in the marine habitat, the nuclear species were both 'fish-like' and 'odd' body shapes. Examples of the latter were the moray eel (*Gymnothorax funebris*), the boxfish (*Acanthostracion polygonius*), and the flying gurnard (*Dactylopterus volitans*). The proportion of fish individuals with 'fish-like' and 'odd' body morphologies occurred as expected by the relative abundances of fish individuals with these morphologies in the marine system ($G_1 = 0.34$, $P = 0.56$) and in the freshwater system (no *G*-test required, as 100% of fish individuals recorded during both fish censuses and following association surveys were fish-like). One additional difference between the reef and the stream associations was the size of the followers. In the marine habitat, followers attained a larger size (4–48-cm total length, TL), whereas in the freshwater, the follower size was smaller (4–15 cm TL). The size distribution of followers differed from the expected by the abundance of fish individuals in both studied systems. In the marine system, follower individuals of the larger size were more frequent (78.40% of followers) than expected by their abundance (47.01%) in the environment ($G_1 = 20.50$, $P < 0.0001$). On the contrary, in the freshwater system, individuals in the small size classes occurred more frequently (96.05%) in fish-following associations than expected (70.31%) by their frequency of occurrence in the environment ($G_1 = 23.96$, $P < 0.0001$).

Discussion

The present study found marked similarities in the nuclear–follower associations between a marine and a freshwater system at a fine scale, i.e. in the foraging behaviour of interacting species. The studied association not only occurred in both systems, but was characterised by the same three main types of fish-following behaviour. These similarities were remarkable, especially considering the different origins and evolutionary histories of fishes in these habitats (Carrete Vega and Wiens 2012), with no species, genus or family being shared between the studied habitats. The observed striking convergence of fish behaviour in the studied association was likely to be a result of the similarities in the structure and function shared by both habitats (e.g. Emery 1978), the similar behaviour of their ichthyofauna (Sazima 1986), and the relatively simple requirements for this association (Krajewski 2009; Teresa *et al.* 2014).

The observed similarities between the marine and freshwater systems in the present study may provide some general insights for following associations in aquatic environments. Because the fish behaviour between two markedly different habitats highly resembled each other, it is probable that following associations in other freshwater and marine ecosystems conform to the general patterns of fish behaviour and feeding tactics herein recorded. Additionally, following associations are known to provide feeding benefits to follower and nuclear fishes in coral reefs (e.g. Aronson and Sanderson 1987; Baird 1993); therefore, species in freshwater habitats are likely to have similar advantages when taking part in these interactions. For example, in the Caribbean, a wrasse had higher bite rates when following goatfish than when foraging alone. This association is very similar to that of *Crenicichla vittata* following *Leporinus macrocephalus* in the stream in our study, and we expect that this follower also has increased feeding rates when following than when feeding alone. However, further studies of following associations between paired marine and freshwater systems are necessary to verify whether convergences in fish behaviour observed in our study are translated into feeding benefits to the follower and nuclear fishes in these habitats.

The three types of following associations recorded in both the reef and stream systems in the present study are well known for

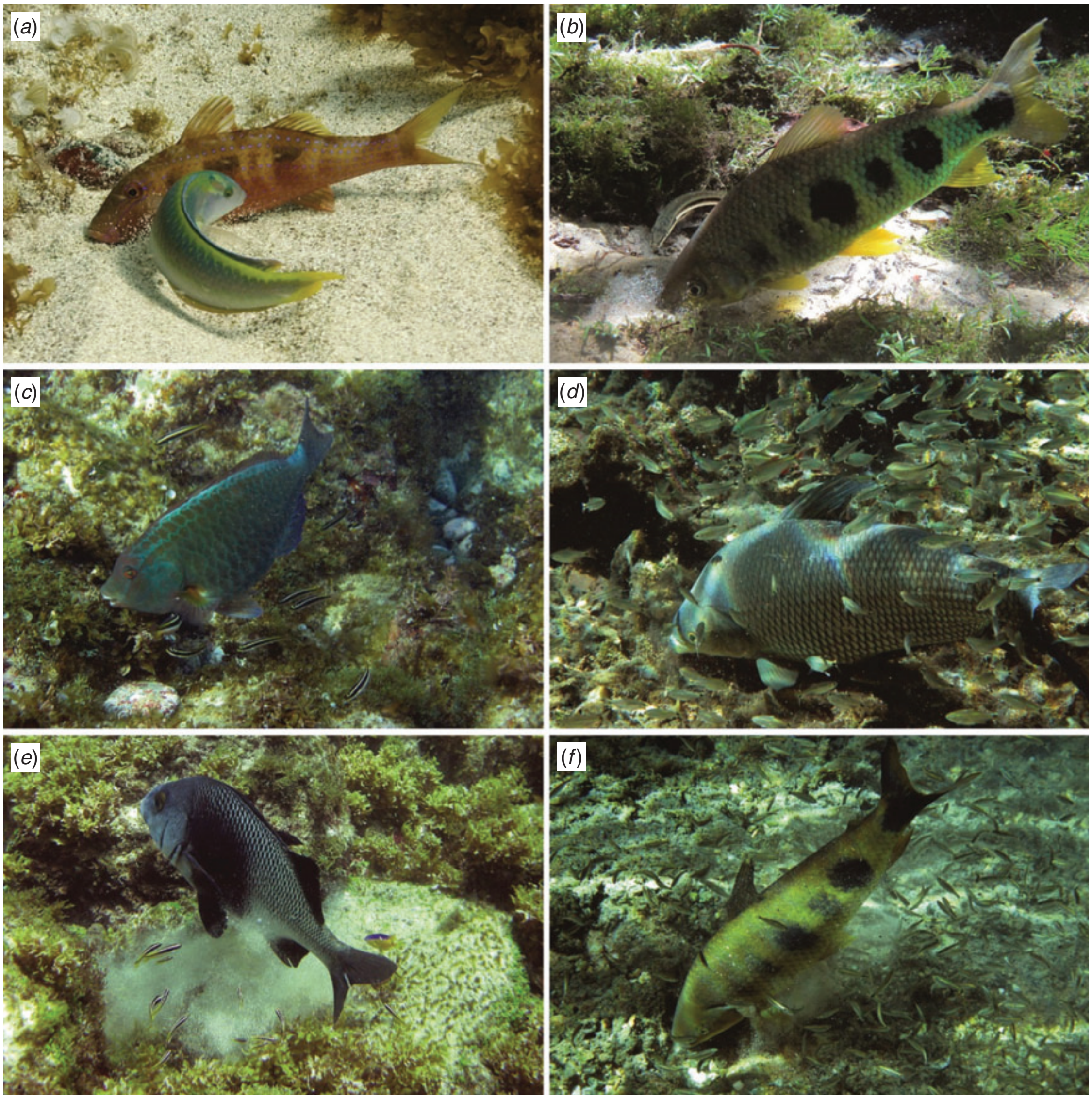

Fig. 2. Reef (left) and freshwater (right) following fish associations. (*a*) One of the most common nuclear fishes in the reef, the goatfish (*Pseudupeneus maculatus*), is followed by the wrasse (*Halichoeres radiatus*), and in the freshwater, (*b*) the leporinus (*Leporinus macrocephalus*) is followed by the pike cichlid (*Crenicichla vittata*). (*c*) Shoals of the small wrasse (*Thalassoma noronhanum*) feed on particles loosened from the reef bottom by the parrotfish (*Sparisoma frondosum*) and (*d*) numerous small tetras (*Odontostilbe pequira*) (besides a few *Astyanax* spp.) feed on particles suspended in the water due to bites of the large prochilod (*Prochilodus lineatus*) at the bottom. Particles expelled by nuclear fishes are fed on by smaller omnivorous follower fishes (*e*) such as the wrasse (*T. noronhanum*) with the grunt (*Anisotremus surinamensis*) in the reef, and (*f*) the tetra (*O. pequira*) with the leporinus in the stream.

reef fishes (e.g. Sazima *et al.* 2005, 2007). Convergences in species behaviour in following associations between systems have been previously recorded, especially considering feeding morphology and behaviour. For example, in freshwater systems, several piscivorous birds follow otters and cormorants to successfully feed on fish flushed to the shallows. The mammal and the bird may be considered as functionally equivalent, because both chase prey under water, surface periodically and cause fish to flee (D'Angelo and Sazima 2014). In terrestrial systems, large herbivores are followed by diverse assemblages of birds, which occasionally follow humans with lawn mowers, thus increasing their feeding rate and success (Smith 1971; Sazima 2008). However, the results of our study stand out because of the high degree of similarity we found between two different systems at a very fine scale, i.e. the foraging tactics and the behaviour of pairs of interacting species in reef and stream habitats.

Despite the marked similarities in the fish follower associations between the two studied systems, we still found clear differences in the social organisation of nuclear fishes and body morphology. The exclusive presence of nuclear fishes foraging in groups in the reef system was due to one species only, *P. maculatus*, which frequently forages in groups (Sazima *et al.* 2006; Krajewski 2009). Indeed, other goatish species (Mullidae) are also known to feed in groups, including following associations (e.g. Lukoschek and McCormick 2000; Randall 2014). However, although the social feeding by a nuclear species in the associations was dominated by only one species in the reef habitat, this association was very representative within the studied system, because *P. maculatus* attracted the largest number of follower species at the study site (Sazima *et al.* 2006).

The contrasts in the fish morphology of nuclear species between the two studied systems were likely to be a consequence of the natural differences in the ichthyofauna of the reef and stream habitats, as indicated by the similar abundance of 'fish-like' and 'odd' shaped fishes between following-association surveys and fish censuses in the two studied systems. Indeed, greater morphological diversity and size variety were observed in the reef, because this system included species such as eels, puffers and flying gurnards (Sazima *et al.* 2006, 2007), whereas the fish assemblage in the stream was entirely composed of fish-like species. However, in contrast to the nuclear-fish morphology, differences in the size of followers between the marine and the freshwater habitats were higher than expected given the abundances of different fish-size classes in each environment. A possible explanation for this difference may be the lower abundance of larger predatory fishes in the stream than in the reef during our sampling. As a consequence, smaller fishes could feel more comfortable exposing themselves when taking part in the following associations in the stream than in the reef. However, further studies would be necessary to verify the explanations for the observed differences in the size of follower fishes between the two studied habitats.

The similarities in the following associations in the two study systems were even more remarkable when considering the observed differences in the body size and shape of fish between the habitats. The following four particulars may explain the recorded similarities: (1) the water environment in both systems, which would provide some similar behavioural and evolutionary pressures on fish species in both systems; (2) the relatively simple requirements of the species in the studied association (i.e. a nuclear species causing disturbance on the benthos and a versatile follower, able to perceive the nuclear species' activity and exposed food items); (3) the trophic plasticity and opportunistic foraging characteristic of tropical freshwater (Abelha *et al.* 2001) and reef fishes (Bellwood *et al.* 2006); and (4) the relatively long exposure of potential food items, revealed by nuclear fishes, owing to flotation in the water column. Hence, despite the marked morphological differences in the ichthyofauna of the studied habitats, common environmental features between the marine and freshwater systems, along with the characteristics of the species acting as either follower or nuclear fishes, allowed for the observed convergences.

In summary, our main purpose was to explore the behavioural similarities and differences in fish-following associations in two ecosystem types, a marine reef and a freshwater stream. We found that fish behaviour in the nuclear–follower interactions had some universal features, irrespective of the habitat, despite marked differences in the body size and morphology of fish between the two studied systems. These marked resemblances provided some insights on the general patterns of fish behaviour in following associations and on the potential ecological benefits of this interaction to nuclear and follower fishes in aquatic systems in general. Therefore, the similarities of the fish-following associations between the marine and the freshwater habitats outnumbered the differences, and this scenario will likely occur in additional studies in freshwater systems.

Acknowledgements

We thank the Marine and Freshwater Research Associate Editor, Lee Baumgartner, and two anonymous reviewers for their helpful suggestions to improve the manuscript; the Ibama (M. A. Silva) for the study permits at Fernando de Noronha Archipelago and for logistic support; the Centro Golfinho Rotador (J. M. Silva Jr) and the Projeto Tamar for logistic support at Fernando de Noronha Archipelago; C. E. L. Ferreira and R. Morais for help with data collection; S. Duleba and E. Coelho from the Recanto Ecológico Rio da Prata for study permits and logistic support at Bodoquena Plateau; the CAPES, CNPq (grants #571295/2008-8 S.R. Floeter; #306169/2008-8 J. Sabino), FAPESP (grants #00/12339-2 I. Sazima and C. Sazima; #2008/03583-9 F.B. Teresa; #2012/24432-4 R. M. Bonaldo), and FUNDECT and Programa Biota-MS for essential financial support.

References

Abelha, C. F., Agostinho, A. A., and Goulart, E. (2001). Plasticidade trófica em peixes de água doce. *Acta Scientiarum* **23**, 425–434.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. doi:10.1163/156853974X00534

Aronson, R. B., and Sanderson, S. L. (1987). Benefits of heterospecific foraging by the Caribbean wrasse, *Halichoeres garnoti* (Pisces: Labridae). *Environmental Biology of Fishes* **18**, 303–308. doi:10.1007/BF00004883

Baird, T. A. (1993). A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiates*, and the bar jack, *Caranx ruber*: evaluation of the foraging consequences. *Environmental Biology of Fishes* **38**, 393–397. doi:10.1007/BF00007535

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., and Hoey, A. S. (2006). Functional versatility supports coral reef biodiversity. *Proceedings. Biological Sciences* **273**, 101–107. doi:10.1098/RSPB.2005.3276

Bessa, E., Carvalho, L. N., Sabino, J., and Tomazzelli, P. (2011). Juveniles of the piscivorous dourado *Salminus brasiliensis* mimic the piraputanga *Brycon hilarii* as an alternative predation tactic. *Neotropical Ichthyology* **9**, 351–354. doi:10.1590/S1679-62252011005000016

Carrete Vega, G., and Wiens, J. J. (2012). Why are there so few fishes in the sea? *Proceedings of the Royal Society of London – B. Biological Sciences* **279**, 2323–2329. doi:10.1098/RSPB.2012.0075

Carvalho, L. N., Arruda, R., and Zuanon, J. (2003). Record of cleaning behavior by *Platydoras costatus* (Siluriformes: Doradidae) in the Amazon Basin, Brazil. *Neotropical Ichthyology* **1**, 137–139. doi:10.1590/S1679-62252003000200009

D'Angelo, G. B., and Sazima, I. (2014). Commensal association of piscivorous birds with foraging otters in south-eastern Brazil, and a comparison of such relationship of piscivorous birds with cormorants. *Journal of Natural History* **48**, 241–249. doi:10.1080/00222933.2013.808714

Diamant, A., and Shpigel, M. (1985). Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Environmental Biology of Fishes* **13**, 153–159. doi:10.1007/BF00002584

Emery, A. R. (1978). The basis of fish community structure: marine and freshwater comparisons. *Environmental Biology of Fishes* **3**, 33–47. doi:10.1007/BF00006307

Garrone-Neto, D., and Sazima, I. (2009). The more stirring the better: cichlid fishes associate with foraging potamotrygonid rays. *Neotropical Ichthyology* **7**, 499–501. doi:10.1590/S1679-62252009000100015

Grutter, A. S. (2005). Cleaning mutualism in the sea. In 'Marine Parasitology'. (Ed. K. Rohde.) pp. 264–278. (CSIRO Publishing: Melbourne.)

Krajewski, J. P. (2009). How do follower reef fishes find nuclear fishes? *Environmental Biology of Fishes* **86**, 379–387. doi:10.1007/S10641-009-9533-0

Krajewski, J. P., and Floeter, S. R. (2011). Reef fish community structure of the Fernando de Noronha Archipelago (equatorial western Atlantic): the influence of exposure and benthic composition. *Environmental Biology of Fishes* **92**, 25–40. doi:10.1007/S10641-011-9813-3

Leitão, R. P., Caramaschi, E. P., and Zuanon, J. (2007). Following food clouds: feeding association between a minute loricariid and a characidiin species in an Atlantic Forest stream, southeastern Brazil. *Neotropical Ichthyology* **5**, 307–310. doi:10.1590/S1679-62252007000300011

Lukoschek, V., and McCormick, M. I. (2000). A review of multispecies foraging associations in fishes and their ecological significance. In 'Proceedings of the 9th International Coral Reef Symposium', 23–27 October 2000, Bali, Indonesia (Eds M. K. Moosa, S. Soemodihardjo, A. Soegiarto, K. Romimotarto, A. Nontji, Soekarno and Suharsono.) pp. 467–474. (Ministry of Environment of the Republic of Indonesia, Indonesian Institute of Sciences and International Society for Reef Studies: Jakarta.)

Nelson, J. S. (1994). 'Fishes of the World.' (Wiley: New York.)

Randall, J. E. (2014). The goatfishes *Parupeneus cyclostomus, P. macronemus* and freeloaders. *Aqua International Journal of Ichthyology* **20**, 61–66.

Sazima, C., Bonaldo, R. M., Krajewski, J. P., and Sazima, I. (2005). The Noronha wrasse: a jack-of-all-trades follower. *Aqua International Journal of Ichthyology* **9**, 97–108.

Sazima, C., Krajewski, J. P., Bonaldo, R. M., and Sazima, I. (2006). The goatfish *Pseudupeneus maculatus* and its follower fishes at an oceanic island in the tropical West Atlantic. *Journal of Fish Biology* **69**, 883–891. doi:10.1111/J.1095-8649.2006.01166.X

Sazima, C., Krajewski, J. P., Bonaldo, R. M., and Sazima, I. (2007). Nuclear–follower foraging associations of reef fishes and other animals at an oceanic archipelago. *Environmental Biology of Fishes* **80**, 351–361. doi:10.1007/S10641-006-9123-3

Sazima, I. (1986). Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology* **29**, 53–65. doi:10.1111/J.1095-8649.1986.TB04926.X

Sazima, I. (2002*a*). Juvenile snooks (Centropomidae) as mimics of mojarras (Gerreidae), with a review of aggressive mimicry in fishes. *Environmental Biology of Fishes* **65**, 37–45. doi:10.1023/A:1019654721236

Sazima, I. (2002*b*). Juvenile grunt (Haemulidae) mimicking a venomous leatherjacket (Carangidae), with a summary of Batesian mimicry in marine fishes. *Aqua International Journal of Ichthyology* **6**, 61–68.

Sazima, I. (2008). Mechanical cattle: lawn mowers attract the amooth-billed ani (*Crotophaga ani*) and a small assemblage of bird opportunists in southeastern Brazil. *Revista Brasileira de Ornitologia* **16**, 387–390.

Smith, S. M. (1971). The relationship of grazing cattle to foraging rates in anis. *Auk* **88**, 876–880. doi:10.2307/4083844

Strand, S. (1988). Following behavior: interspecific foraging associations among Gulf of California reef fishes. *Copeia* **1988**, 351–357. doi:10.2307/1445875

Teresa, F. B., and Carvalho, F. R. (2008). Feeding association between benthic and nektonic Neotropical stream fishes. *Neotropical Ichthyology* **6**, 109–111. doi:10.1590/S1679-62252008000100013

Teresa, F. B., Romero, R. M., Casatti, L., and Sabino, J. (2011). Habitat simplification affects nuclear–follower foraging association among stream fishes. *Neotropical Ichthyology* **9**, 121–126. doi:10.1590/S1679-62252011005000009

Teresa, F. B., Sazima, C., Sazima, I., and Floeter, S. R. (2014). Predictive factors of species composition of follower fishes in nuclear–follower feeding associations: a snapshot study. *Neotropical Ichthyology* **12**, 913–919. doi:10.1590/1982-0224-20140041