Patterns of variation in behaviour within and among reef fish species on an isolated tropical island: influence of exposure and substratum

JOÃO PAULO KRAJEWSKI[1,2], SERGIO R. FLOETER[3], GEOFFREY P. JONES[2] AND FOSCA P.P. LEITE[1]

[1]Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, SP, 13083-970, Brazil, [2]School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia, [3]Departamento de Ecologia e Zoologia, CCB, Universidade Federal de Santa Catarina, Florianópolis, SC, 88010-970, Brazil

Here we studied the activity budgets of nine common reef fish in the oceanic archipelago of Fernando de Noronha, off northeast Brazil. Species were variable in their behaviour between different sites and similarities in their activity budgets were not necessarily associated with their trophic group. For four species we investigated the relationship of their activity budgets to wave exposure and substratum composition. Staying close to the substratum was positively correlated to wave exposure for most species and foraging was negatively correlated to exposure for two species. By behaving this way, these fish may save energy by avoiding swimming in higher water flux. In contrast to relationships with wave exposure, the responses to substratum composition were species specific. Our results highlight that the activity budgets of fish living in oceanic rocky reefs can be variable and influenced by the local and temporal variation in environmental variables.

INTRODUCTION

Animals vary greatly in the way they allocate time to the different daily activities necessary for their growth, survival, and reproduction. Such variation in behaviour is also common among individuals of the same species and can have major influences on their fitness (Cuthill & Houston, 1997; Jones, 2002; Bonaldo & Krajewski, 2007). Typical time budgets have been related to phylogenetic status (Brooks & McLennan, 1991), stage of development (e.g. Jones 2002; Bonaldo & Krajewski, 2007), sex (Mathisen *et al.*, 2003; Stiver *et al.*, 2006) and a range of environmental factors including habitat structure (e.g. Cartar & Real, 1997; Dagosto & Yamashita, 1998; Valdés-Muñoz & Mocheck, 2001), presence of predators (e.g. Milinski & Heller, 1978; Forsgren & Magnhagen, 1993; Murphy & Pitcher, 1997), abundance and distribution of food resources (Massaro *et al.*, 2000; Rastogi *et al.*, 2006) and temperature (e.g. Russell, 1971; Gass *et al.*, 1999).

Tropical reef fish exhibit a wide range of activity patterns that vary among and within species at any one location (Collette & Talbot, 1972; Valdés-Muñoz & Mocheck, 2001). Water movement is one of the major environmental factors structuring fish communities (Jones & Syms, 1998), and especially the movement of planktivorous fish (Hobson, 1974; Bray *et al.*, 1981; Hobson & Chess, 1986; Hamner *et al.*, 1988; Hamner & Wolanski, 1988). Recently, field and laboratory studies investigated the specific effects of water flow on the behaviour and energetic processes of benthic coral reef fish (Bellwood & Wainwright, 2001; Fulton *et al.*, 2001; Fulton & Bellwood, 2002a; Johansen *et al.*, 2007a). Wave exposure was shown to be a major factor influencing the activity of some common wrasses and damselfish, and several generalizations were made about their behaviour. It was found that fish tend to avoid the water column, where flux is higher, and stay longer in refuges on the bottom when there is high water flow (Fulton *et al.* 2001; Fulton & Bellwood, 2002a; Johansen *et al.* 2007a). It was also found that species with different swimming capabilities respond in different degrees to hydrodynamics (Fulton & Bellwood, 2005; Johansen *et al.*, 2007a).

Substratum composition is another environmental variable capable of influencing fish distribution and behaviour (Jones & Syms 1998; Valdés-Muñoz & Mocheck, 2001; Floeter *et al.* 2007; Sabater & Tofaeono 2007). The distinct structure and associated fauna of different bottom types may offer different resources (e.g. prey and shelter) to reef fish and, thus, substratum composition of reefs may influence fish activity. Nevertheless, there is no study, to our knowledge, that aimed to verify whether substratum composition could influence the activity budgets of different species of reef fish.

Despite the advances in the understanding of the relationships between reef fish behaviour and environmental

Corresponding author:
J.P. Krajewski
Email: jpaulokra@yahoo.com.br

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variables, especially water movement, most research on this topic has been conducted in high diversity coral reefs. These habitats are structurally complex and offer a wide range of environmental conditions to their inhabitants (Levinton, 1995; Bellwood & Wainwright, 2002). As a consequence, fish in high diversity systems may specialize in living/using habitats with particular features (e.g. Bouchon-Navarro & Bouchon, 1989; Jennings *et al.*, 1996; Munday *et al.*, 1997; Gardiner & Jones, 2005). Oceanic rocky reefs, on the other hand, are less structurally complex and less biologically diverse (Floeter *et al.*, 2008). In these habitats, species have usually less refuges from water movement and are exposed to varying hydrodynamics (currents and wave exposure) coming from open seas. In order to survive in oceanic reefs, fish must be able to cope with the different conditions present there either by resisting to the varying conditions or by quickly changing and adapting their behaviour. Therefore, understanding the effects of environmental variables on fish behaviour in tropical oceanic reefs is fundamental to evaluate how the activity budgets of reef fish in general are influenced by these variables and whether the current predictions about coral reef fish may also be applied to other reef systems.

In this paper we take a multi-species comparative approach to better understand the relationships between reef fish behaviour, wave exposure and benthic composition in the field. The activity budgets of nine abundant and widely distributed reef fish species were studied in a tropical Western Atlantic oceanic island and our main goals were to examine whether behavioural similarities among species were related to taxonomic or trophic status, whether fish activity varies spatially and whether it may be correlated to wave exposure and substratum composition. Our main hypotheses were that: (1) fish species would stay mostly closer to the bottom, avoid the water column and forage less in places with high wave exposure, in an attempt to avoid extra energetic expenditure in high wave exposure; (2) fish responses to wave exposure would be less significant for good swimmers; and (3) activity budgets may vary with substratum composition, especially for fish that forage mainly on the bottom.

MATERIALS AND METHODS

Study sites

The study was conducted at the Fernando de Noronha Archipelago (03°50′S 32°25′W), an oceanic island 345 km off north-eastern Brazil, from 22 June to 17 July 2007. We studied eight volcanic rocky reefs: Cagarras, Canal, Porto, Buraco da Raquel, north shore of Praia da Conceição, Laje Dois Irmãos, south shore of Praia do Sancho and north shore of Baía do Sueste (Figure 1). Cagarras (CG) is a sheltered rocky reef down to 34 m depth. Canal (CN) is located between Rata and Meio islands, subject to high wave exposure, and up to 12 m deep. Porto (PO) is a shallow (< 5m deep) reef located in a sheltered sandy bay. Buraco da Raquel (RQ) is a reef lagoon with rocky and sandy bottom and a maximum depth of 3 m at low tide. Conceição (CO) is a reef adjacent to a sandy beach, up to 12 m deep. Laje Dois Irmãos (LJ) is a rocky reef lying about 15 – 26 m deep with a high per cent coral cover. Sancho (SS) is a steep reef adjacent to a sandy beach, up to 12 m deep. Sueste (SU) is a shallow sheltered

bay with rocky and sandy bottom, but it is frequently exposed to high surge typical on the east coast on the archipelago. Visibility ranged from 3 to 30 m and water temperature varied from 27 – 28°C at all sites.

Procedure

We studied the behaviour of nine reef fish species: the damselfish (Pomacentridae) *Abudefduf saxatilis*, the grouper (Serranidae) *Cephalopholis fulva*, the grunts (Haemulidae) *Haemulon chrysargyreum* and *H. parra*; the wrasses (Labridae) *Halichoeres radiatus*, *H. dimidiatus* and *Thalassoma noronhanum*; and the goatfish (Mullidae) *Mulloidichthys martinicus* and *Pseudupeneus maculatus*. These species were chosen because they are very abundant at Fernando de Noronha and widely distributed (Humann & Deloach, 2002; Floeter *et al.*, 2008). Thus, they are good targets to study the influence that varying environmental variables have in the behaviour of fish species able to cope with a wide range of conditions. The species above were also chosen because they represent major reef fish families (Bellwood & Wainwright, 2002).

We made a general comparison of broad behavioural categories among the studied species. Also, for *C. fulva*, *H. chrysargyreum*, *H. radiatus* and *T. noronhanum* we compared their behaviour among sites and investigated the correlation of behavioural categories to wave exposure and substratum cover. Observations were conducted from 0900h to 1600h and care was taken to equally distribute samples during morning and afternoon and at high and low tides at each study site. This approach was chosen to minimize time of day effect on behaviour, which is beyond the scope of this paper. Only the sites SU and RQ were sampled just during high and low tides respectively, as these sites are accessible to divers only under these conditions.

To record fish behaviour and the relative abundance of substratum types, we randomly positioned belt transects of 20 × 2 m in each study site. Fish survey is feasible in this transect width even in the lowest visibility of some study sites and this transect length fits in reef areas with similar habitat characteristics (Floeter *et al.*, 2007). We conducted a total of 91 transects around the archipelago, which were allocated proportionally to the reef areas of each study site (13 in CG, 13 in CN, 18 in SS, 10 in LJ, 4 in PO, 16 in CO, 7 in SU and 10 in RQ). To standardize our observations, data about fish behaviour were all collected by the first author using the scanning methodology (Lehner, 1998). During this procedure the diver swam over transects at a constant speed, recording all the individuals of the study species and their behaviour at the time they were seen. To avoid possible effects of ontogenetic variation, only individuals showing adult coloration (Humann & Deloach, 2002) were investigated. The behaviour of each individual fish was classified into one of the following eight categories: (1) swimming continually within 30 cm of the bottom (SB); (2) immobile within 30 cm of the bottom (IB); (3) swimming continually in the water volumn, at least 30 cm above the substratum (SC); (4) immobile in the water column, at least 30 cm above the substratum (IC); (5) foraging (e.g. pursuing prey, probing or digging in to the substratum) or biting prey (FO); (6) being cleaned by cleaner fish (BC); (7) cleaning other fish (C); and (8) defending nest, guarding egg mass (DN). Only one record was taken for each fish individual, to minimize the risk of non-independent data.
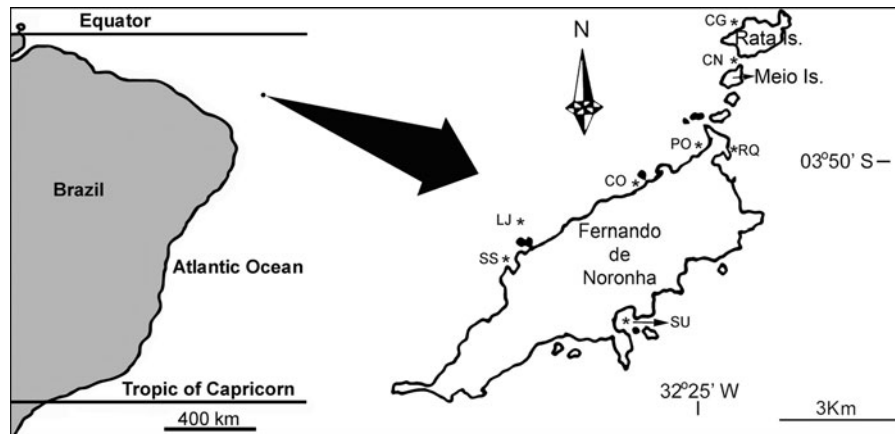
Fig. 1. The study sites at the Fernando de Noronha Archipelago: (CG) Cagarras, (CN) Canal, (PO) Porto, (RQ) Buraco da Raquel, (CO) Praia da Conceição, (LJ) Laje Dois Irmãos, (SS) Praia do Sancho and (SU) Baía do Sueste.

The relative abundance of each substratum type in each transect was estimated by the photoquadrats method (Preskitt *et al.*, 2004). In short, while the first diver collected data on fish behaviour, a second diver simultaneously swam behind him, keeping a distance of at least 5 m, and took five photographs of the bottom at haphazardly chosen points, each corresponding to an area of 40 × 60 cm. The substrata were classified into one of the seven following categories: (1) non-consolidated (NC), which includes sand and rubble; (2) epilithic algal matrix (EAM), turf algae with sediments; (3) green algae (GA), mostly *Caulerpa verticillata*; (4) brown algae (BA), mostly *Dictyota* spp., *Dictyopteris* spp., *Padina* spp. and *Sargassum* spp.; (5) sponge (S); (6) colonial cnidarians (CN), mainly stony corals, zoanthids and *Millepora* spp.; and (7) bare rock (BR). The relative coverage of each substratum was estimated by classifying 20 random points on each photograph according to the seven categories above. The photoquadrats were analysed in the coral point count with Excel Extension software (CPCe v3.4) (Kohler & Gill, 2006).

We also recorded the depth and estimated the wave exposure in each transect. Wave exposure was classified within an arbitrary scale from 0 to 8, where the score 8 is the highest exposure recorded among the sites. This classification was based on the previous dive experience of the first and second authors, who have been conducting research in the archipelago for ten consecutive years.

Analysis

We compared the behaviour of different species with a cluster analysis using the mean percentage of behaviours displayed at all sites for each species. In this analysis we also classified species in trophic groups, according to the literature (Randall, 1967; Sierra *et al.*, 2001, Floeter *et al.*, 2007) and data on their diet in Fernando de Noronha (Krajewski, unpublished data). Also, for the most abundant species (*C. fulva*, *H. chrysargyreum*, *H. radiatus* and *T. noronhanum*) we compared their behaviour among the four sites (CN, SS, CO and RQ), where at least 19 individuals of each species were found.

For *C. fulva*, *H. chrysargyreum*, *H. radiatus* and *T. noronhanum*, we compared the behavioural categories to wave exposure in each transect using simple linear regressions with a randomization test. Significance levels were estimated with N = 10000 re-samplings (Manly, 1997). For each

species, only transects with 10 or more individuals recorded were considered for the analysis. Also, for each species we only considered for the analysis behaviours in which the mean frequencies among all sites were higher than 20%, otherwise the analysis would not be feasible.

The general relationship among the environmental variables and most frequently displayed behaviours of the studied species was analysed in a redundancy analysis (RDA). We excluded from the analyses substrata with average relative abundance lower than 5%. We obtained the ordination diagram and both the marginal (independent effect of a variable) and conditional effects (the effect that the variable adds to the analysis with all variables together) of each variable in the general behavioural display of each species. These effects were expressed by their lambda value, which gives an estimate of the percentage of variation on species behaviour that could be explained by the independent factor (Leps & Smilauer, 2007).

To allow statistical analyses, all data on percentage of display and substratum cover were arcsine transformed (Zar, 1999; Leps & Smilauer, 2007). Data considering behaviours were transformed using the formula: $\arcsin\sqrt{(x + 3/8)/(n + 3/4)}$, where x is the number of individuals in the given behavioural category in a given transect and n is the total number of individuals in the transect (Zar, 1999).

RESULTS

Cluster analysis identified a number of behavioural groupings (Figure 2). The three wrasse species studied (*H. dimidiatus*, *H. radiatus* and *T. noronhanum*), along with *H. parra*, were grouped mainly because of the high displays of swimming on the bottom and foraging. The behaviour of *C. fulva* was also similar to these four species, but presented a higher proportion of immobility at the bottom (IB) (Figure 2). *Haemulon chrysargyreum* and *M. martinicus* were more similar to each other than to the other species of their respective families. *Pseudupeneus maculatus* behaved differently than any other species, since it presented an extremely high percentage of foraging (FO). The behavioural groupings recorded are not necessarily related to the evolutionary history or trophic group of the fish (Figure 2).

All studied species varied greatly in behaviour between different sites (Figure 3). *Halichoeres radiatus* showed the
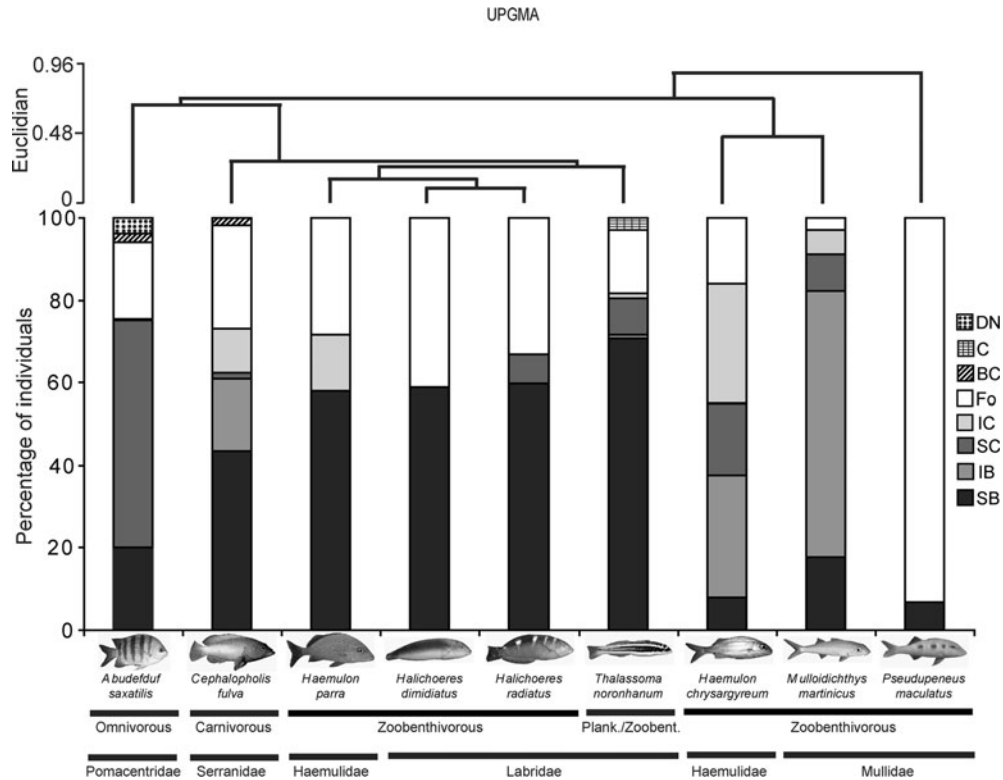
Fig. 2. The studied species grouped according to the percentage of individuals (average among all studied sites) displaying the eight behavioural categories considered in all study sites: SB, swimming on the bottom; IB, immobile on the bottom; SC, swimming on the water column; IC, immobile on the water column; FO, foraging; BC, being cleaned; C, cleaning; DN, defending nest.

Fig. 3. Behavioural variation (% of individuals displaying each behavioural category) of four studied species in four different study sites. Behavioural categories: SB, swimming on the bottom; IB, immobile on the bottom; SC, swimming on the water column; IC, immobile in the water column; FO, foraging; BC, being cleaned; C, cleaning; DN, defending nest. Numbers of observed individuals are in parentheses.
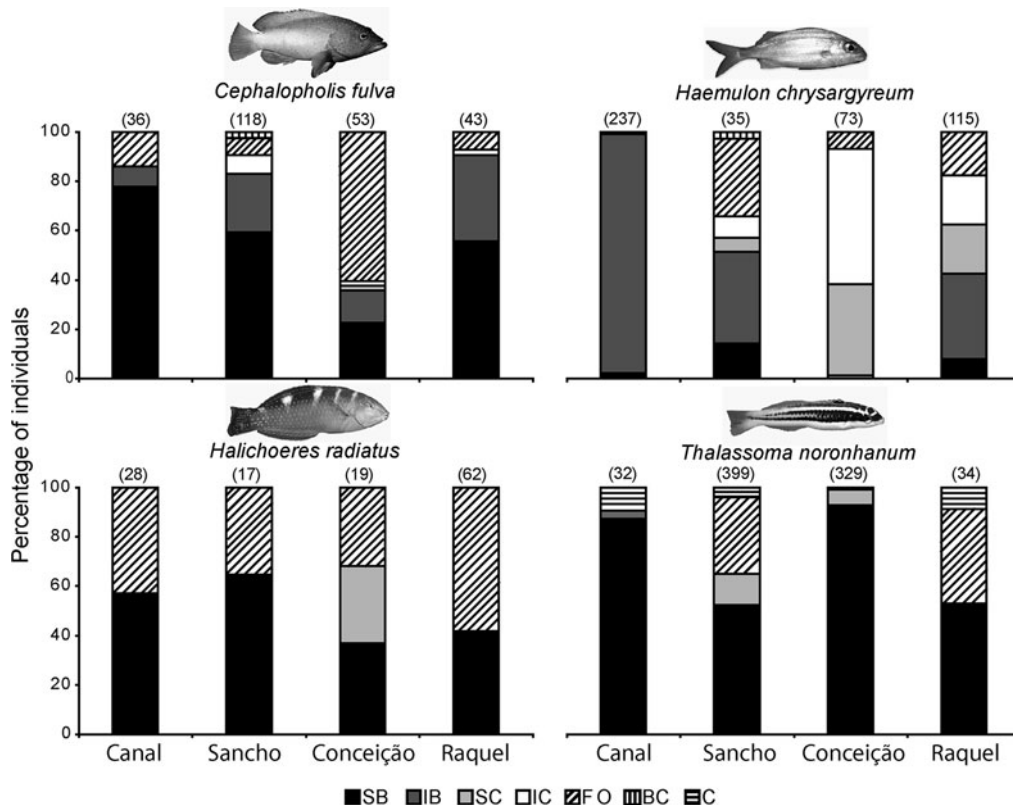
least variation between sites, but, even so, the display of FO varied from 31 to 58% and the frequency of SC from 0 to 31% among the studied sites.

For *C. fulva* and *H. radiatus* there was a significant positive correlation between wave exposure and proximity to the bottom (swimming or immobile), but for *H. chrysargyreum* this relationship was marginally significant (*P* = 0.06). Also, a negative correlation between wave exposure and foraging was found for *H. chrysargyreum* and *H. radiatus* (Figure 4). For all species, except *C. fulva*, there was no relationship between water column use and exposure. For *T. noronhanum* no relationship between any behaviour and wave exposure was found (Figure 4).

In contrast to the relationship between fish behaviour and wave exposure, which are more similar among species, the behavioural response to substratum composition was generally weaker and species-specific (Figure 5; Table 1). For example, the behaviour of *C. fulva* was mostly influenced by brown algae, *H. chrysargyreum* by EAM and *H. radiatus* by non-consolidated substratum (Table 1). However, the behaviour of *T. noronhanum* was not greatly influenced by any of the environmental variables measured.

DISCUSSION

Behavioural variation among and within species

In this study we found that similarities of the general behaviour of some species are not necessarily associated with their phylogenetic relationship or trophic group. This is clear for two species pairs studied, *Haemulon* species and the goatfish. Although each pair consists of species of the same trophic group, family, and even the same genus, they are very different in their behaviour. *Haemulon chrysargyreum* and *M. martinicus*, for example, are more similar to each other than to species of their own families, which is probably because they may also be nocturnal, and sometimes remain inactive in the water column during the day (Randall, 1967; Krajewski *et al.*, 2004, 2006). Thus, common evolutionary history and trophic ecology are not prerequisites nor necessarily imply that species behave similarly as neither have similar functional roles on the reefs (Sazima, 1986).

The behavioural variation within species or taxonomic groups is largely corroborated by studies on herbivorous
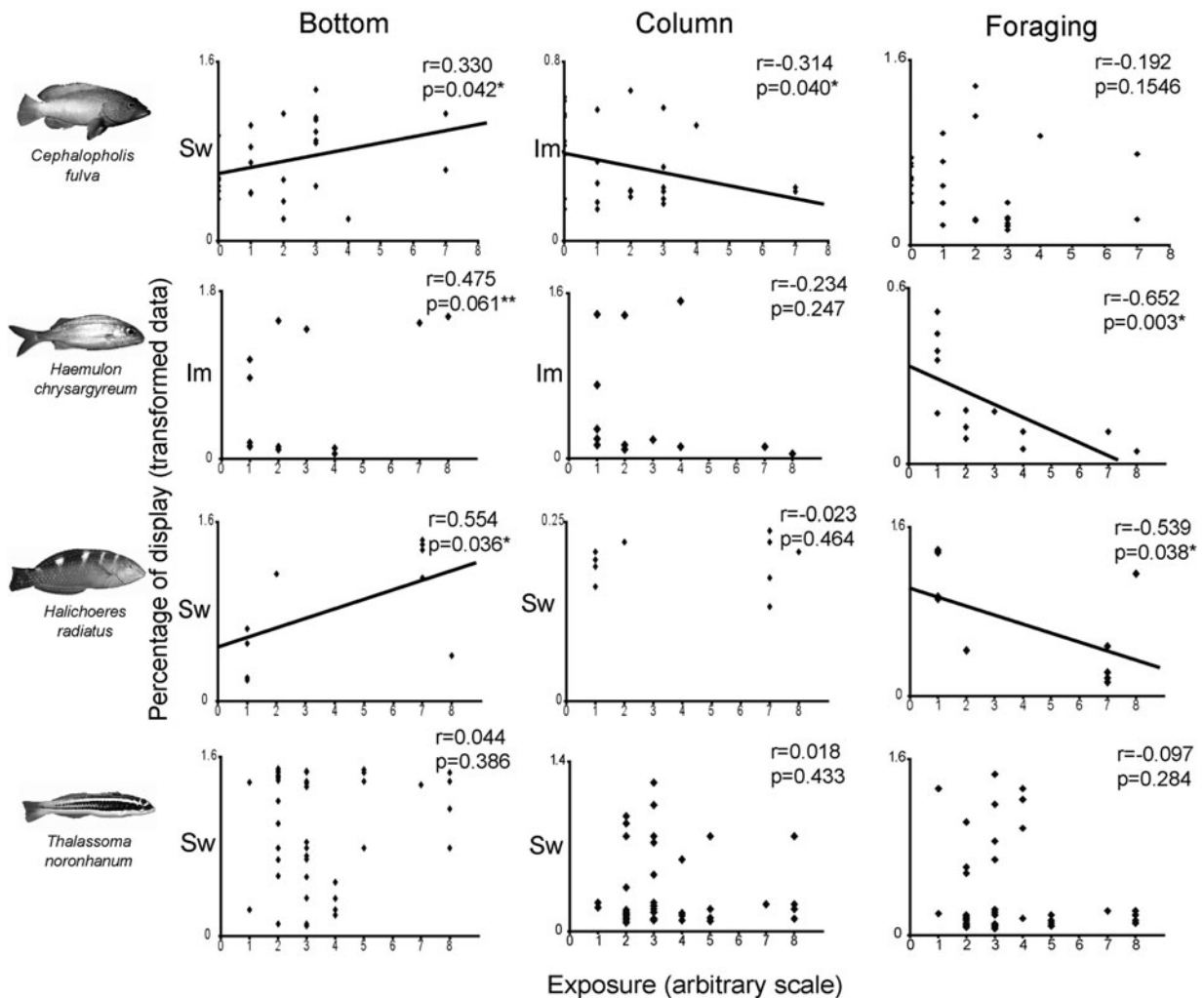

Fig. 4. Relationship between staying in the bottom or water column (swimming or immobile) and foraging with exposure for four studied species. Each point corresponds to a single transect. The displayed values are from arcsine transformed data. Legends are as follows: Sw, swimming; Im, immobile; *, significant values; **, marginally significant values.
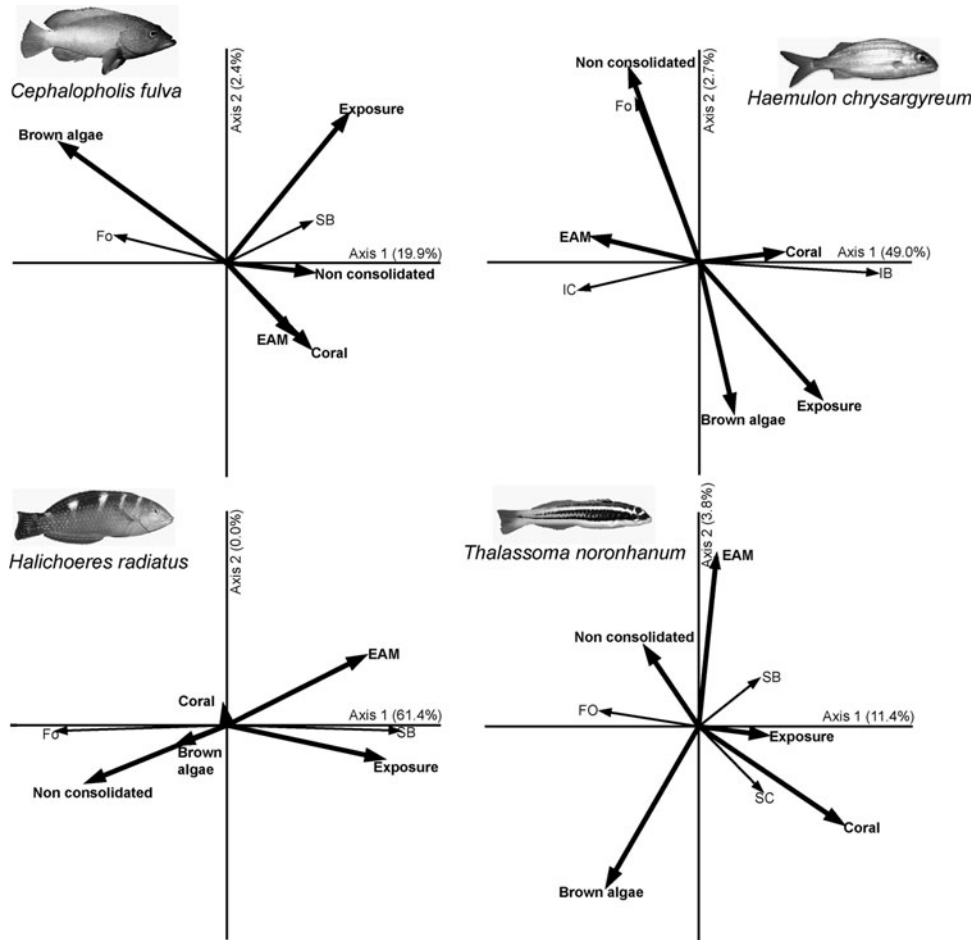
Fig. 5. Redundancy analysis (RDA) diagram showing the relationship among exposure and substratum composition (bold) and the main behaviours displayed by four reef fish in the Fernando de Noronha Archipelago. Legends are as follows: SB, swimming on the bottom; IB, immobile on the bottom; SC, swimming on the water column; IC, immobile on the water column; FO, foraging.

fish. Formerly considered as a uniform group, herbivorous fish species were shown to be very different in their behaviour and functional roles on reefs (Bellwood & Choat, 1990; Bellwood *et al.*, 2003). These differences in ecology and functional role were shown to vary among species of the same family (Bellwood & Choat, 1990) and, for single species, during development (Bonaldo *et al.*, 2006; Bonaldo & Krajewski,

2007; Bonaldo & Bellwood, 2008). Studies on the patterns of behavioural variation within and among carnivorous reef fish are scarce. However, the variation in behaviour and resource use recorded here and elsewhere (Randall, 1967; Valdés-Muñoz & Mocheck, 2001) strongly suggests that carnivorous fish may also be highly variable in their general behaviour both within families and species. As the functional

Table 1. Marginal (Marg.) and conditional (Cond.) effects of exposure and bottom composition on the behaviour of four reef fish species at the Fernando de Noronha Archipelago. Environmental variables: BA, brown algae; Cor., coral; EAM, epilithic algae matrix; Expos., exposure; NC, non-consolidated substratum.

	Cephalopholis fulva		*Haemulon chrysargyreum*		*Halichoeres radiatus*		*Thalassoma noronhanum*	
	Variable	Lambda	Variable	Lambda	Variable	Lambda	Variable	Lambda
Marg. effects	BA	0.12	Expos.	0.16	Expos.	0.30	Expos.	0.3
	Expos.	0.07	EAM	0.11	NC	0.24	EAM	0.09
	Cor.	0.03	NC	0.07	EAM	0.23	NC	0.10
	NC	0.03	Cor.	0.06	BA	0.03	BA	0.12
	EAM	0.02	BA	0.02	Cor.	0.00	Cor.	0.00
Cond. effects	BA	0.12	Expos.	0.16	Expos.	0.30	Cor.	0.05
	Expos.	0.08	Cor.	0.12	EAM	0.09	BA	0.04
	Cor.	0.01	EAM	0.03	NC	0.10	Expos.	0.02
	NC	0.01	BA	0.06	BA	0.12	EAM	0.00
	EAM	0.00	NC	0.15	Cor.	0.00	NC	0.04

role of fish on reefs is directly dependent on fish behaviour, the variation in the activity of fish and its relationship with environmental variables should be further considered in any study aiming to understand or modelling fish impact on reefs.

We also found that single species may greatly vary their activities between nearby sites with different environmental characteristics. Future research that investigates the variation in behaviour and its effects on fish condition (energetic processes) will be fundamental to elucidate to what extent fish are truly versatile in their behaviour without affecting their fitness (Jones & McCormick, 2002).

Wave exposure and fish behaviour

Our results support most findings and predictions that experimental work and field data from coral reef fish has found for fish behavioural responses to water flow (Fulton *et al.*, 2001; Fulton & Bellwood, 2005; Johansen *et al.*, 2007a, 2008). Most studied species tended to stay close to the bottom in sites with high water movement. By behaving this way, such species may save energy avoiding swimming in the higher water layers, which have higher water flux (Johansen *et al.*, 2007b), in exposed sites.

Foraging was also negatively correlated to exposure for two species (*H. chrysargyreum* and *H. radiatus*) and this is probably a mechanism to avoid the high energetic costs of searching for prey in sites with high wave exposure. Benthic invertebrate foragers, and especially searcher invertebrate feeders such as most wrasses and grunts, usually need to move long distances in search for prey (Choat, 1982). Under high wave exposure, swimming demands high energy expenditure and some invertebrate feeders seem to avoid extra energy expenditure by avoiding foraging under high wave exposure (Johansen *et al.*, 2007a). The non-significant relationship between exposure and foraging of *C. fulva* is more difficult to interpret. This result may have been caused by an underestimation of *C. fulva* foraging behaviour in the present study, as this species frequently acts as an ambush predator, remaining immobile close to the bottom (Nemtzov, 1993; Sazima *et al.*, 2005). Thus, we may have classified some instances of *C. fulva* foraging into the category 'immobile on the bottom'. However, as when ambushing this grouper does not face the dilemma of the high energetic cost of searching prey in long forays in exposed sites, as wrasses and grunts do, it is possible that high wave exposure does not inhibit its foraging.

The relationship between exposure and staying (swimming or immobile) in the water column is less clear. Only for *C. fulva* was there a significant negative correlation between staying immobile on the water column and wave exposure, which can be explained by the strong association of this species to the bottom. As with most grouper species, *C. fulva* is not a fast swimmer and stays mostly close to the bottom. Thus, it may venture in the water column only when there is low water movement and the costs of swimming and manoeuvring do not demand too much energy (Johansen *et al.*, 2007a).

As with several *Haemulon* spp., *H. chrysargyreum* gains protection against predators by gathering in large schools in mid-water during the day (Krajewski *et al.*, 2004). Getting very close to the bottom could prevent such school formation and increase the chance of predation. Also, as *H. chrysargyreum* is primarily nocturnal and stays mostly inactive during the day (Krajewski *et al.*, 2004), it does not face an energetic cost for staying in the water column as high as an active fish does. Thus, the absence of significant negative correlation between water column use and exposure for this species is probably due to the protective advantage of staying in schools in the water column and the fact that it does not face an excessive increase in the energetic costs to maintain this formation. For *H. radiatus* there was also no relationship between water column use and wave exposure but this can be explained by the fact that this species hardly ever swims in the water column.

The clearest exception among all studied species was *T. noronhanum*, since there was no relationship between any of its behaviour and wave exposure. The genus *Thalassoma* has one of the highest aspect–fin ratios among common reef fish families (e.g. Labridae, Pomacentridae and Acanthuridae) (Wainwright *et al.*, 2002), suggesting that *Thalassoma* spp. have high swimming performances. It is therefore possible that *T. noronhanum* is capable of swimming in highly exposed sites without expending proportionally much more energy and thus, its activity is not significantly affected by water movement. The species is, indeed, recorded to be extremely abundant in well exposed oceanic sites (Rosa & Moura, 1997; Gasparini & Floeter, 2001; Floeter *et al.*, 2008; Krajewski & Floeter, in preparation).

Our results, along with recently published data considering reef fish behaviour and distribution on different water flow conditions (Bellwood & Wainwright, 2001; Fulton *et al.*, 2001, 2005; Fulton & Bellwood, 2002a, 2004, 2005; Johansen *et al.*, 2007a, b, 2008) corroborate the idea that wave exposure is one of the major physical factors influencing the distribution and activity budget of a range of tropical reef fish.

Substratum composition and fish behaviour

The first pattern that we noticed was that behavioural responses to substratum composition were not universal. This was expected as several traits of the fish biology, such as living or foraging substratum selection, which could mediate the relationship with bottom cover, are species specific and not a universal physical response, as seen for water flow.

Because reef fish spend a large amount of time foraging (Fulton & Bellwood, 2002b), we could expect that their foraging substratum preferences mediate behavioural responses to substratum composition. For example, there was a negative relationship between foraging and brown algae (BA) abundance for *H. chrysargyreum*. As this species forages mostly on BA (Krajewski *et al.*, in preparation) it may have a higher feeding success in such a substratum and, thus, would spend less time searching for food in places with high BA cover. However, it seems that this response is mostly due to indirect effects of exposure, since BA occurs in places with moderate to high exposure, where *H. chrysargyreum* tends to forage less. The latter explanation is supported by the higher marginal and conditional effect of exposure than that of BA on the behaviour of *H. chrysargyreum*. Wave exposure could also explain why there was a positive relationship between foraging and non-consolidated substratum for *H. chrysargyreum* and *H. radiatus*, since such a substratum is more abundant in places with low exposure. In both cases it seems that exposure alone can account for the behavioural responses recorded.

For *C. fulva* there was a positive relationship of foraging with brown algae and this relationship is held even with BA occurring generally in places with generally high exposure, where due to the effect of exposure the fish would be supposed to forage less. Such a relationship strongly suggests that the abundance of BA is influencing the activity of *C. fulva*. However, there is no information about foraging substratum use for this species and it is difficult to understand what process is causing this behavioural response.

Benthic composition is a complex variable, which can occur in several different combinations and may influence fish in different ways and intensities. Species may not respond to the abundance of a single substratum, but rather to the different sets of combinations of substrata available on the reefs. This is probably why we did not find relationships between general behavioural responses and the relative abundances of some particular substrata. The effect of particular bottom types on the behaviour of species may be better assessed by experimental research, where it is possible to control environmental variables. Also, as species differ in their relationships with substrata, further knowledge on their natural history and substratum use is fundamental to develop specific hypotheses predicting their responses to varying benthic compositions.

CONCLUSION

We found that even species that cope with a wide range of environmental variables (i.e. are widely distributed) and live in oceanic habitats, where hydrodynamics are highly variable, display local variation in their activity budgets in response to wave exposure. For the most part, species tended to stay close to the bottom and forage less in sites with high wave exposure. This behavioural response to wave exposure was also recorded for coral reef fish species in previous studies and appears to be a strategy of fish in general to minimize energy expenditure in conditions where swimming may demand excessive energy (Bellwood & Wainwright, 2001; Fulton *et al.*, 2001; Johansen *et al.*, 2007a). The only exceptions to this pattern seem to be fish with good swimming performances, such as *Thalassoma* spp. (Wainwright *et al.*, 2002; Fulton & Bellwood, 2004). The behavioural responses of reef fish to substratum composition seem weaker and more species-specific. Rather than unique responses to each factor, it is possible that environmental factors act in synergy and that fish behaviour is dynamically influenced by the local and temporal variation in environmental factors. The ability of fish to quickly respond to the environment, and adapt their behaviour, can directly influence their fitness and functional role on reefs and our findings highlight the importance of future studies on the variation in activity and behaviour of reef fish.

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Correspondence should be addressed to:
J.P. Krajewski
Departamento de Biologia Animal
Universidade Estadual de Campinas
Campinas, SP, 13083-970, Brazil
email: jpaulokra@yahoo.com.br