

**ASSOCIAÇÕES ALIMENTARES EM PEIXES RECIFAIS,
COM DESTAQUE EM ESPÉCIES NUCLEARES E
SEGUIDORAS**

CRISTINA SAZIMA

**Tese apresentada ao Instituto de Biociências
da Universidade Estadual Paulista “Julio de
Mesquita Filho”, Campus de Rio Claro, para
obtenção do título de Doutor em Ciências
Biológicas (Área de Concentração: Zoologia).**

**Rio Claro
Estado de São Paulo-Brasil
Julho de 2006**

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CRISTINA SAZIMA

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Scientists are responsible for their research not only intellectually
but also morally

F. C.

Não é preciso ter uma idéia pronta do que você estará fazendo nas próximas
semanas, ou no ano que vem, porque se você já sabe o que vai acontecer e se
apega a esta idéia, abre mão de toda a gama de possibilidades

D. C.

Right Now God is killing
Moms and Dogs Because He Has to
Right Now your Memory is getting longer,
While your life is getting shorter

V. H.

Om Dhiyo Yonaha Prachodayat

When you get to where you wanna go
And you know the things you wanna know
You're smiling
When you said what you wanna say
And you know the way you wanna play
You'll be so high you'll be flying

R. B.

AGRADECIMENTOS

Prof. Dr. Ivan Sazima, pela orientação, confiança, amizade, pelas críticas e sugestões. Agradeço também pela sua dedicação, apoio, companhia e carinho, que me acompanham desde que nasci, mas que se intensificaram nos últimos dez anos, quando decidimos trabalhar junto.

Prof. Dr. Augusto Shinya Abe, pelas muitas oportunidades que me proporcionou, pela orientação, confiança, amizade e carinho de tantos anos.

Ao **Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)**, pela bolsa de doutorado concedida e à **Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP)**, pelo financiamento concedido ao projeto “História natural, ecologia e evolução de vertebrados brasileiros”, ao qual o presente estudo esteve vinculado.

Ao **Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA)**, através de Marcos Aurélio Silva, pela permissão de estudar peixes recifais em Fernando de Noronha. A todos os funcionários do IBAMA de Fernando de Noronha que, de diversas formas e em tantos momentos nos ajudaram em nossa pesquisa no arquipélago, e também pelo carinho e boa vontade com que sempre nos recebem.

À dupla **João Paulo Krajewski e Roberta Martini Bonaldo**, amigos queridos, por toda ajuda, boa vontade, co-autoria, idéias, companhia, carinho, risadas e diversão nestes anos de trabalho de campo e de computador. Vocês foram indispensáveis, além de muito agradável companhia, na realização deste trabalho.

A **José Martins da Silva Jr.**, em primeiro lugar, pela amizade, pelo carinho e por cuidar tão bem de toda a equipe quando nos recebe em Noronha. Agradeço, também, por toda ajuda, que veio de diversas formas, ao longo dos anos que nos conhece.

A todos os funcionários do **Centro Golfinho Rotador**, mas especialmente Lizete Pandolfo Jardim, Adriana Figueiredo e Ivan Santana, pela amizade, carinho, apoio e “galhos quebrados”.

Ao **Projeto TAMAR/IBAMA** de Fernando de Noronha, através de Cláudio Bellini e Alice Grossman, pelo apoio recebido e pela amizade e carinho.

Às operadoras de mergulho de Fernando de Noronha, **Águas Claras, Atlantis e Noronha Divers**, pelo apoio logístico, e generosidade nas saídas de mergulho e uso de equipamentos.

A todos os **funcionários da Universidade Estadual Paulista** (campus de Rio Claro), mas principalmente à Rute M. R. Camargo, Heloisa A. S. Nicoletti e Sandra M. G. Fuzaro, pelo auxílio e paciência.

A **Prof. Dra. Sulene N Shima**, pelo empenho e auxílio.

A **Marlies Sazima**, minha querida mãe, que em tudo vê flores, literalmente...

A **Ivan Sazima**, meu pai, pela paixão e pelo encanto que tem por todos os animais, inclusive eu!!

A **Ricardo Sazima**, meu irmão, pelo amor, carinho, companhia, incentivo, pelas lições que me ensina e pela vida compartilhada...

M. Cristina F. da Rosa, minha segunda mãe, pelo carinho que nos dá desde que eu tinha três anos de idade, e também pela amizade e paciência.

A todos os meus amigos queridos, de longa data ou não, **Juliana Attié Figueira Brandão Silva, Thiago P. Figueiredo, Cristiana Madjarof, Joana Cunha, Luciana Jankowski, Camila S. L. Guzzo, M. Beatriz C. P. Tilkian, Flavia B. J. Lino, Fernanda C. Silva, Flavia S. A. Teixeira, Paula A. N. dos Reis**, pela amizade, companhia, incentivo e carinho.

Ao **Museu de História Natural da Universidade Estadual de Campinas**, através de **Fátima e Beth**, pelo auxílio e paciência.

Aos amigos do Museu de História Natural, **André V. Lucci Freitas (“Baku”), Artur N. Furegatti, Cristiane Matavelli, Danilo B. Ribeiro, Prof. Keith Brown, Marcio Uehara-Prado e Mariana J. Magrini**, pela amizade, ajuda, risadas, almoços, cafezinhos e ótima convivência.

Ao **A. Marcelo Campos**, amigo muito querido, por seu carinho, cuidado, serenidade, apoio, conselhos e por tudo que me ensina.

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RESUMO

Acompanhar animais em atividade alimentar constitui um modo comum de forragear para peixes recifais que formam associações alimentares interespecíficas. Os peixes “seguidores” acompanham animais “nucleares” para aproveitar itens alimentares expostos ou produzidos através da atividade do nuclear. Tais associações alimentares são comuns para diversos tipos de peixes e outros animais, ocorrendo em variadas áreas geográficas. Este tipo de associação alimentar foi estudado no arquipélago oceânico de Fernando de Noronha, Atlântico Sul Ocidental tropical. O presente trabalho é composto de cinco artigos científicos, dispostos em quatro capítulos. O primeiro capítulo descreve associações alimentares entre peixes recifais e tartarugas marinhas. O segundo capítulo caracteriza o comportamento alimentar versátil de uma espécie de peixe recifal ao seguir outras espécies de peixes. O terceiro capítulo é composto de dois artigos; o primeiro trata da espécie de peixe nuclear mais comum e importante no arquipélago, ao passo que o segundo artigo descreve a associação entre seguidores e uma espécie de peixe cuja família não constava como nuclear. O quarto capítulo constitui uma revisão geral sobre o tema, com informações sobre o grupo de animais, na maioria peixes recifais, que forma associações alimentares interespecíficas como nucleares e/ou seguidores. A série de artigos científicos, apresentada no presente trabalho, amplia o conhecimento sobre agrupamentos alimentares e história natural da ictiofauna recifal no Atlântico Sul Ocidental tropical, além de modificar a situação deste tipo de associação alimentar na literatura científica mundial.

Palavras-chave: associações alimentares interespecíficas; espécies nucleares e seguidoras; peixes recifais; Atlântico Sul Ocidental tropical

ABSTRACT

Following behaviour is a foraging mode commonly recorded for reef fishes during heterospecific feeding associations. The followers escort so called nuclear foraging fishes and other animals to capitalise on food items exposed or produced by the activity of the nuclear ones. Such foraging associations are widespread and recorded for several fish and other marine animal taxa and geographic areas. This foraging mode was studied at the oceanic archipelago of Fernando de Noronha, tropical Southwest Atlantic. The present work is composed of five scientific papers, organized in four chapters. The first chapter describes foraging associations between reef fishes and marine turtles. The second chapter characterizes the variable foraging modes of a reef fish species while following other fishes. The third chapter is composed by two studies, the first dealing with the commonest and most important nuclear fish in the archipelago, while the second one describes the association between followers and a fish species in a family not previously recorded as a nuclear. The fourth chapter is an overview about this topic, with information about the assemblage of animals, mostly reef fishes, which engage in interspecific foraging associations as nuclears and/or followers. This series of articles broadens our understanding about feeding assemblages and natural history of reef fishes in the tropical Southwest Atlantic, besides modifying the knowledge on this type of foraging association.

Key-words: interspecific foraging associations; nuclear and follower species; reef fishes; tropical Southwest Atlantic

INTRODUÇÃO GERAL

Peixes recifais podem formar associações alimentares interespecíficas temporárias ao seguirem outros animais em atividade de forrageamento (Hobson, 1968; Strand, 1988; Lukoschek & McCormick, 2000). Neste tipo de associação, os peixes “seguidores” acompanham espécies “nucleares” para aproveitar itens alimentares expostos ou espantados pela atividade do nuclear, como pequenos invertebrados e peixes (e.g., Fricke, 1975; Ormond, 1980; Silvano, 2001). Em geral, a função de nuclear é exercida por peixes, mas espécies de polvos e estrelas-do-mar também estão registradas como nucleares (Ormond, 1980; Diamant & Shpigel, 1985; Gibran, 2002).

Em geral, a maioria das espécies nucleares somente é acompanhada por seguidores quando está se alimentando ativamente (Hobson, 1968; Ormond, 1980; Strand, 1988). A presença de perturbação no substrato parece ser o principal estímulo de atração e um componente necessário para a formação de uma associação entre seguidores e nucleares (Fricke, 1975; Fishelson, 1977; Strand, 1988). Sinais visuais induzem ao comportamento de seguir em peixes recifais (Fricke, 1975; Fishelson, 1977; Diamant & Shpigel, 1985) sendo que, tanto as nuvens de areia formadas pela perturbação do substrato, como as características dos nucleares (coloração, tamanho, formato) influenciam o comportamento dos seguidores (Fricke, 1975; Fishelson, 1977).

Entre os peixes recifais, as espécies nucleares geralmente são predadores carnívoros de diversas famílias e, eventualmente, herbívoros das famílias Acanthuridae e Scaridae (Ormond, 1980; Lukoschek & McCormick, 2000). Os seguidores são, em geral, espécies carnívoras ou generalistas, ao passo que espécies herbívoras são raramente registradas acompanhando peixes nucleares e não estão claramente definidas como seguidores (Strand, 1988; Lukoschek & McCormick, 2000; Dias et al., 2001). Hábitos oportunistas parecem ser uma característica comum às espécies registradas como seguidoras. Uma vez que a maioria das espécies de peixes apresenta uma tendência a hábitos alimentares oportunistas (Gerking, 1994; Bellwood et al., 2006), uma grande quantidade de espécies poderia atuar como seguidor em associações alimentares interespecíficas.

Diversas táticas de forrageamento podem ser empregadas por peixes carnívoros oportunistas, incluindo tocaia, aproximação sorrateira, disfarce e mimetismo (q.v.

Sazima, 1986; Keenleyside, 1979; Gerking, 1994). Algumas espécies utilizam, habitualmente, uma ou duas táticas para apanharem suas presas, ao passo que outras podem utilizar diversas táticas, de acordo com as circunstâncias (Hobson, 1968; Sazima, 1986; Gerking, 1994). Em associações alimentares interespecíficas, a plasticidade no comportamento alimentar está, aparentemente, relacionada a uma maior tendência de algumas espécies em se associar a nucleares (Strand, 1988). Portanto, predadores carnívoros que apresentam táticas de forrageamento variáveis provavelmente se associam a espécies nucleares.

Nas associações alimentares interespecíficas entre peixes recifais, algumas espécies carnívoras que atuam como nucleares podem, eventualmente, também agir como seguidoras, assim como alguns seguidores podem atuar como nucleares em determinadas situações (Fricke, 1975; Ormond, 1980; Strand, 1988). De fato, espécies de Mullidae, Labridae, Balistidae e Serranidae estão registradas atuando tanto como nucleares quanto como seguidores, numa mesma localidade (Fricke, 1975; Ormond, 1980; Strand, 1988; Aronson & Sanderson, 1987).

Numerosas espécies recifais carnívoras e oportunistas que apresentam, ao menos parcialmente, atividade de forrageamento diurna, formam associações alimentares interespecíficas (Ormond, 1980; Strand, 1988). Entretanto, não há informações sobre o número de espécies que se associa em torno deste “recurso”, para uma dada localidade ou comunidade. A maior parte dos estudos sobre associações alimentares interespecíficas do tipo nuclear-seguidor em peixes recifais enfatiza uma ou algumas poucas espécies de nuclear e/ou seguidor, ou algum tipo específico de associação (e.g., Diamant & Shpigel, 1985; Baird, 1993). Assim, um dos principais objetivos do presente trabalho é caracterizar este tipo de associação em um arquipélago oceânico, através do registro da composição, da riqueza e do número relativo de espécies envolvidas.

A associação entre nucleares e seguidores pode ser considerada comum no ambiente recifal, estando registrada para diversas espécies e em diferentes oceanos (Ormond, 1980; Diamant & Shpigel, 1985; Lukoschek & McCormick, 2000). No Brasil, o registro deste tipo de associação está restrito a seis estudos, em geral com observações esporádicas sobre associações entre nucleares e seguidores (Sazima, 1986; Dias et al., 2001; Feitoza et al., 2002; Silvano, 2001; Gibran, 2002; Gerhardinger et al., 2006). Entretanto, Silvano (2001) enfoca os hábitos alimentares de uma espécie de Carangidae

e descreve as associações alimentares interespecíficas para esta espécie. Também, dois destes estudos podem ser considerados específicos sobre este tipo de associação, um deles descrevendo a associação entre duas espécies de Serranidae e uma espécie de estrela-do-mar (Gibran, 2002) e o outro entre uma espécie de Serranidae e uma de Ophichtidae (Gerhardinger et al., 2006). O presente trabalho, composto de cinco artigos científicos distribuídos em quatro capítulos, amplia o conhecimento sobre agrupamentos alimentares e história natural da ictiofauna recifal no Atlântico sul ocidental, além de modificar a situação deste tipo de associação alimentar na literatura científica mundial.

No primeiro capítulo são apresentadas associações alimentares entre peixes recifais e tartarugas marinhas. Assim, três tipos de interações são registrados entre uma espécie de tartaruga e três espécies de peixes com hábitos alimentares onívoros e herbívoros: pastejo sobre o casco da tartaruga; limpeza de partes moles da tartaruga e comportamento de seguir a tartaruga. Os dois primeiros tipos de interações são conhecidos da literatura (embora sejam estudos feitos no Oceano Pacífico), ao passo que a associação alimentar do tipo nuclear-seguidor envolvendo peixes e tartarugas é inédita. Até o momento, apenas espécies de peixes e algumas espécies de invertebrados eram conhecidas como nucleares. Deste modo, um grupo adicional de animais vertebrados (quelônios) pode ser considerado como nuclear para espécies de peixes oportunistas em associações alimentares interespecíficas no ambiente recifal.

No segundo capítulo é apresentada uma espécie de peixe seguidor que exibe um comportamento alimentar muito versátil ao seguir outros peixes. Assim, são registrados quatro tipos de comportamento alimentar para este seguidor, ao acompanhar espécies nucleares em atividade de forrageamento: catação de partículas desprendidas do substrato pela atividade do nuclear; catação de partículas expelidas pelo nuclear; catação de partículas defecadas pelo nuclear e limpeza corporal do nuclear. Até o momento, apenas a ingestão de partículas ou organismos expostos ou espantados pela atividade do nuclear era conhecida para peixes seguidores. Deste modo, três formas adicionais de aproveitamento de itens alimentares podem ser consideradas para peixes recifais ao acompanhar espécies nucleares.

No terceiro capítulo são apresentados dois artigos, um deles extenso, sobre a espécie de peixe nuclear mais representativa de Fernando de Noronha, e um outro breve, sobre uma espécie de família inédita na função nuclear até então. Os dois artigos são, aqui,

incluídos num mesmo capítulo pois as duas espécies nucleares em questão apresentam características contrastantes em sua atividade, fornecendo uma comparação interessante. Assim, o primeiro consiste em um estudo quantitativo sobre a espécie nuclear mais comum no arquipélago e também a mais procurada pelos seguidores. Esta espécie nuclear apresenta hábitos fossadores, podendo forragear sozinha ou em grupos pequenos a grandes e em diversos tipos de substrato. Foram observadas diferenças em número de espécies, número de indivíduos e tamanho de indivíduos seguidores quando associados a indivíduos solitários ou agrupados desta espécie de nuclear. O segundo artigo apresenta observações sobre uma espécie de peixe que não apresenta hábitos fossadores, mas que por sua mera passagem pelo ambiente, ou ao examinar o substrato e revirar pedrisco com uso de suas nadadeiras, atrai espécies seguidoras. Foram registradas duas espécies, uma de Carangidae e uma de Serranidae, associadas a esta espécie de nuclear. Ambas as espécies de seguidores são carnívoros oportunistas.

No quarto e último capítulo é apresentada uma visão geral sobre as associações alimentares interespecíficas do tipo nuclear-seguidor em Fernando de Noronha, assim como uma revisão geral sobre o tema. Neste capítulo são registradas as principais espécies de nucleares e seguidores, assim como a associação mais comum para o arquipélago. Foram registradas diversas espécies agindo como nucleares, de invertebrados a tartarugas, assim como diversas espécies de peixes como seguidores. A associação mais comum no arquipélago é formada por uma espécie de Mullidae seguida por uma espécie de Labridae. Também, são apresentados padrões e tendências para este tipo de associação.

De modo geral, a série de estudos apresentada no presente trabalho altera o panorama existente sobre associações alimentares do tipo nuclear-seguidor em peixes recifais, além de contribuir para melhor compreensão do papel ecológico das espécies envolvidas neste tipo de interação.

Adicionalmente, é apresentado um artigo científico diretamente relacionado ao tema de estudo, publicado durante o desenvolvimento do presente trabalho (Apêndice 1). É descrito o forrageamento de uma espécie de moréia nas partes expostas de recifes durante a maré baixa. Moréias, em geral, estão entre os nucleares preferidos de muitas espécies de seguidores (Strand, 1988). Entretanto, a espécie estudada de moréia usa um repertório variado de caça e sua procura por presas é guiada principalmente pela visão,

sendo seu forrageamento discreto, assim atraindo pouca ou nenhuma atenção de outros peixes nas poças de maré.

CAPÍTULO 1

THE MOVING GARDENS: REEF FISHES GRAZING, CLEANING AND FOLLOWING GREEN TURTLES IN SW ATLANTIC

ARTIGO PUBLICADO:

Sazima C., Grossman A., Bellini C. & Sazima I. 2004. *Cybium*, 28: 47-53.

THE MOVING GARDENS: REEF FISHES GRAZING, CLEANING, AND
FOLLOWING GREEN TURTLES IN SW ATLANTIC

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Key words: symbiosis, fish foraging, *Chelonia mydas*, Southwest Atlantic,
Acanthuridae, Pomacentridae, Labridae

ABSTRACT. Reef fishes may associate with marine turtles and graze on their shells, or clean their head, neck and flippers. On a reef flat at Fernando de Noronha Archipelago, SW Atlantic, we recorded green turtles (*Chelonia mydas*) grazed, cleaned and followed by reef fishes. The green turtle seeks specific sites on the reef and pose there for the grazers and/or cleaners. Fishes recorded associated to green turtles included omnivorous and herbivorous reef species such as the damselfish *Abudefduf saxatilis* and the surgeonfishes *Acanthurus chirurgus* and *A. coeruleus*. The turtle is followed by the wrasse *Thalassoma noronhanum* only while engaged in foraging bouts on benthic algae. Following behaviour is a previously unrecorded feeding association between turtles and fishes.

RÉSUMÉ. Des jardins mobiles: des poissons de récif broutent, nettoient et suivent les tortues vertes dans l'Atlantique occidentale.

Des poissons de récif peuvent être associés à des tortues marines; ils broutent de algues poussant sur leurs carapaces cornées ou nettoient leur tête, cou et pattes. Sur un platier récifal de l'Archipel de Fernando de Noronha, Atlantique occidentale, on a observé des tortues vertes (*Chelonia mydas*) broutées, nettoyées et suivies par des poissons de récif. La tortue verte cherche des sites spécifiques dans les récifs, où elle pose pour que les poissons viennent brouter sur leur carapace et/ou les nettoyer. Les poissons associés à la tortue verte sont des espèces récifales omnivores, comme le poisson demoiselle *Abudefduf saxatilis*, ou herbivores comme les poissons chirurgiens *Acanthurus chirurgus* et *A. coeruleus*. La tortue est suivie par le labre *Thalassoma noronhanum* seulement pendant qu'il se nourrit d'algues benthiques. L'association entre tortues et poissons suiveurs est observée pour la première fois dans l'Atlantique occidentale.

INTRODUCTION

Marine herbivorous fishes may graze upon algal growth on turtles' shell, getting food and thus reducing drag for the turtle (Losey et al., 1994). Three species of surgeonfishes, *Acanthurus nigrifuscus*, *Ctenochaetus strigosus* and *Zebrasoma flavescens* are reported to graze on the green turtle, *Chelonia mydas*, in Hawaii (Losey et al., 1994). They graze largely on the shell, but occasionally may feed on skin areas,

and in both instances the surgeonfishes scrape the algae in their typical feeding pattern of tightly clustered bites (Losey et al., 1994). Herbivorous fishes that graze on turtles' shells and other body areas may consume molting skin from the head and neck, and apparently may remove ectoparasites as well, thus occasionally acting as cleaners (Losey et al., 1994).

Cleaning symbiosis is another kind of feeding association recorded between fishes and turtles (Booth & Peters, 1972; Losey et al., 1994). In this association the cleaners feed on ectoparasites, diseased or injured tissues, and mucus from the body surface of their "clients" (generally other fishes), which in their turn get rid of unwanted material (review in Losey, 1987). Several cleaner species hold cleaning stations, specific sites on the reef visited by clients seeking for cleaning services (Losey, 1978). Cleaning symbiosis in coral reefs involves fishes and shrimps as cleaners, and fishes as well as reptiles as clients (Feder, 1966; Hobson, 1969; Booth & Peters, 1972). Cleaning association with the turtle *Chelonia mydas* is reported for four reef fish species, the damselfish *Abudefduf sexfasciatus* and the wrasse *Thalassoma lunare* in Australia (Booth & Peters, 1972), as well as the wrasse *Thalassoma duperrey* and the puffer *Canthigaster jactator* in Hawaii (Losey et al., 1994). For marine turtles other than *C. mydas*, cleaning association is reported for the hawksbill *Eretmochelys imbricata* and the angelfish *Pomacanthus paru* in the Caribbean (Smith, 1988).

Following behaviour is an unrecorded feeding association between fishes and turtles, although a common habit among several reef fishes (e.g., Hobson, 1968; Diamant & Shpigel, 1985; Strand, 1988). Such feeding association implies in a "nuclear" species which disturbs the substrate during its foraging and thus displaces or uncovers hidden prey, and "follower" species which capitalize on this otherwise unavailable food supply (Hobson, 1968, 1974; Diamant & Shpigel, 1985; Strand, 1988). Several reef fish species have been recorded associated with octopuses, moray eels, rays, and other substrate-disturbing fishes (Karplus, 1978; Ormond, 1980; Diamant & Shpigel, 1985; Strand, 1988).

Herein we report on reef fishes grazing on, and cleaning, the green turtle (*Chelonia mydas*) on a reef flat at Fernando de Noronha Archipelago, SW Atlantic. Additionally, we record a wrasse species following the turtle while the latter is engaged in foraging bouts on benthic algae. Besides general observations on the cleaning association

between green turtles and their cleaners and followers, our study addressed the following questions: Does the grazing/cleaning association take place at any site of the reef flat or do the green turtles seek the cleaners at their stations? During inspecting and/or cleaning the turtle, do the cleaners concentrate on any specific body part? How do green turtles behave while being grazed/cleaned? What a planktivorous and cleaning wrasse (Francini-Filho et al., 2000) seeks while following a turtle?

MATERIAL AND METHODS

Our field observations were conducted at a reef flat of the Baía do Sueste, Fernando de Noronha National Marine Park, Fernando de Noronha Archipelago (03°50'S, 32°15'W), off NE Brazil (see Maida & Ferreira, 1997; Carleton & Olson, 1999 for maps and description). The interactions between turtles and fishes were first documented in February 1999 and then sporadically recorded from October 2001 to October 2002.

The study site is within an inlet and is composed by an inner, protected reef flat and shallow area near shore and an outer reef slope leading to deeper parts of the Baía do Sueste (Fig. 1). The flat and the slope are build by sandy bottom and irregular rocky patches sparsely to thickly covered by brown foliose algae, red coralline algae, and stony corals (Maida et al., 1995; Sanches & Bellini, 1999; pers. obs.).

The behavioural events involving reef fishes and green turtles were recorded over 56 days while snorkelling. During the observational sessions of 1-12 min we used 'focal animal' sampling, in which all occurrences of specified actions were recorded (Altmann, 1974). Beside records pencilled on plastic slates, behavioural events were photographed and video-recorded, the tape being on file at the Museu de História Natural, Universidade Estadual de Campinas (ZUEC tape # 14) and at the Tamar/Ibama quarters in the National Marine Park of Fernando de Noronha Archipelago.

The analysed video-recorded sequence, with the turtle posing and the fishes inspecting and feeding, lasted for about 11 min. We considered fishes facing the turtle and positioned less than 15 cm away from its body as inspecting it, and scored a feeding nip only when it was unmistakably recognized as such. For precision sake we used only the video-taped sequence in which feeding nips could be unmistakably counted (about 4

min). Hence, our inspection/feed counts presumably underestimate the number of feeding nips, especially those on the turtle's shell due to its disruptive pattern and the thus sometimes blurred effect.

Due to the protected status of the study site we refrained from sampling grazer/cleaner individuals for gut contents, as this would imply spear-fishing and use of this gear would raise strong opposition from both the islanders and the tourists (pers. obs.). However, we scraped off material from the shell and soft parts of the turtles (N=2) to gain insight into what may be available as food to the grazers and cleaners. The material sampled from the turtles, collected exclusively from cleaned individuals, was examined and identified under a stereomicroscope and a microscope. Additionally, we inspected three turtles visually for the presence of larger attached organisms (e.g., barnacles, leeches).

RESULTS

We recorded green turtles foraging on benthic algal banks at high tide in a relatively large area of the reef flat of the Baía do Sueste (Fig. 1) at sites 1-2 m deep. Fishes following the foraging turtles were recorded at these feeding grounds only. On the other hand, grazing/cleaning associations were restricted to the deeper (2.5-4.5 m) parts of the slope (Fig. 1), where we recorded two cleaning stations at the high tide.

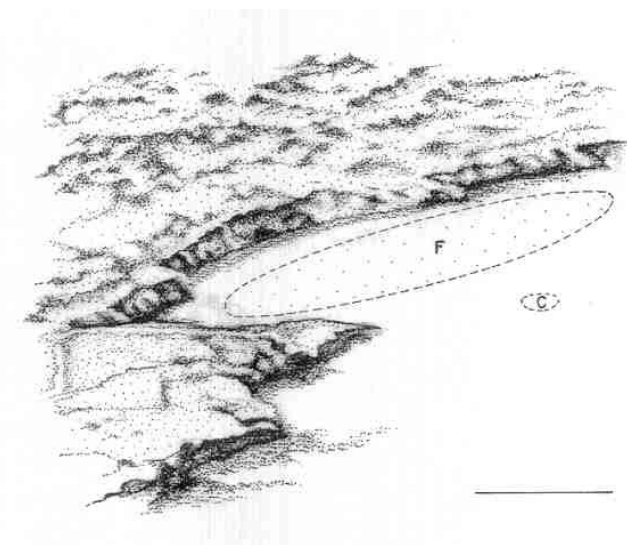


Figure 1. Green turtle's feeding (F) and cleaning (C) grounds at the Baía do Sueste, Fernando de Noronha Archipelago, SW Atlantic. Scale bar = 50 m.

The two cleaning stations were held by the ubiquitous damselfish *Abudefduf saxatilis* and the surgeonfishes *Acanthurus chirurgus* and *A. coeruleus*. The cleaning stations were located at calcareous concretions and rocky outcrops where the cleaners (12-25 individuals about 7-12 cm TL) concentrated and hovered about 0.5-1.5 m above the station and/or the bottom.

The three above-mentioned reef fish species were recorded inspecting the green turtle's shell, but only the doctorfish (*A. chirurgus*) was actually feeding on this body part (Table 1). The grazing behaviour by surgeonfishes on turtles was recorded only at the cleaning stations, simultaneously to inspection and cleaning of its soft parts by other individuals of the same or other species (Table 1). The grazing by surgeonfishes on the green turtle's shell followed their usual bite pattern while grazing on bottom algae at the study site (pers. obs.).

Table 1. Reef fish species, inspection and feeding nips at body parts of the green turtle (*Chelonia mydas*), as scored from 4 min video-recording at the Baía do Sueste, Fernando de Noronha Archipelago, SW Atlantic.

Fish species	Inspections/feeding nips (n = fishes close to the body part)		
	Shell	Flippers	Head/neck
Pomacentridae			
<i>Abudefduf saxatilis</i>	3/0 (n = 1)	16/3 (n = 1-2)	13/13 (n = 1-2)
Acanthuridae			
<i>Acanthurus chirurgus</i>	16/6 (n = 1-8)	35/14 (n = 1-6)	10/9 (n = 1-3)
<i>Acanthurus coeruleus</i>	2/0 (n = 1)	8/2 (n = 1-2)	1/0 (n = 1)

Cleaning/grazing on the green turtles' soft parts was recorded for the damselfish and both the two surgeonfish species (Table 1). This was preceded by a characteristic inspection usually followed by feeding nips on the turtles' skin surface. Some of the bites were forcible and clearly directed to particular, visible items on the turtle's skin. On occasions the turtle moved its forelimbs to chase away fishes that were feeding in

this way. The most inspected and cleaned body parts were the flippers (Table 1). Neck and head areas were also inspected and cleaned, whereas the anal region went untouched by the fishes.

Tufts of small filamentous algae dominated the samples scrapped off the turtles. The brown *Ectocarpus* cf. *breviarticulatus* (Ectocarpaceae) and the red *Herposiphonia secunda* (Rhodomelaceae) were present in similar amount in the soft parts (neck, limbs) samples. Other algae were rare on these samples, including the green *Cladophora* sp. (Cladophoraceae) and the red *Jania* cf. *adhaerens* (Corallinaceae). The brown *E.* cf. *breviarticulatus* dominated the shell samples as well, whereas *H. secunda* was scarce there. In the shell samples we also found a plantule of the brown *Dictyota* sp. (Dictyotaceae). We found no parasites or other epizoic animals in our samples. On the visually inspected turtles, besides the aforementioned algae, we found very few turtle barnacles on the shell (see Bugoni et al., 2001 for brazilian commensal barnacles of sea turtles).

At the cleaning stations the turtles displayed characteristic soliciting postures (cf. Losey et al., 1994). While being grazed and/or cleaned a turtle remained almost motionless with its flippers extended and drooped downward, in a posture more exaggerated than that illustrated by Booth & Peters (1972). Its neck was extended and bent downward throughout most of the cleaning session. While engaged in a cleaning association, the turtle hovered above or by the cleaning station, about 0.5-1.5 m away from the bottom.

We recorded no inspecting by cleaner fishes or cleaning associations while the green turtle was foraging, and recorded no feeding activities by the turtle while it was attended at the cleaning stations. The turtle seemed rather to concentrate on the cleaning, and held its position close to the station using discrete limb movements. We recorded the turtle raising to the surface for breathing, and thereafter actively seeking the same site where it was being cleaned before the surfacing.

At the green turtles' feeding areas (Fig. 1) we recorded another kind of association with reef fishes. While on a foraging bout the turtle selected and picked up benthic algae on the reef flat and was occasionally followed by the wrasse *Thalassoma noronhanum*. One to four fish (6-8 cm TL) were recorded closely following the turtle, and feeding on drifting particles turned loose from the bottom by the turtle's feeding activity. The fish

approached the turtle's fore-body mostly when the latter picked up the algae stirring the substrate a little (Fig. 2).



Figure 2. A green turtle foraging on benthic algae, followed by four individuals of the wrasse *Thalassoma noronhanum* (close to left side of carapace) on a reef flat at Fernando de Noronha Archipelago, SW Atlantic. Curved carapace length about 54 cm. From a video-record frame by A. Grossman.

DISCUSSION

Several reef fish species that act as cleaners occupy cleaning stations or areas, either permanent or temporary, mostly located on conspicuous portions of the reefs (Feder, 1966; Losey, 1987; Sazima et al., 1999). The cleaning stations at the Baía do Sueste follow the general pattern found for other reef species that act as cleaners in mid-water aggregations, e.g., the labrid *Thalassoma noronhanum* and the chaetodontid *Chaetodon striatus* (Francini-Filho et al., 2000; Sazima & Sazima, 2001). The stations held by the damselfish and surgeonfishes were conspicuous within the relatively bare reef flat

environment, which rendered the hovering cleaners easy to find by humans (and presumably by the turtles as well).

Surgeonfishes are regarded as an almost entirely herbivorous group and dependent on algae as their primary food (Randall, 1967; Böhlke & Chaplin, 1968; Earle, 1972). The algal-eating acanthurids are able to exploit diverse micro-habitats during their foraging (e.g., Earle, 1972; Hobson, 1974; Losey et al., 1994), and the three species of *Acanthurus* recorded on the Brazil's coast feeds on algae growing on sand surface, attached to rocks, and drifting in the water column (Dias et al., 2001). Even if foraging mostly on algae, *Acanthurus bahianus* and *A. chirurgus* may be regarded as omnivores that supplement their herbivorous diet with detritus, benthic micro-fauna, and plankton as well (Randall, 1967; Duarte & Acero, 1988). Furthermore, searching for other food sources and/or situations may be a common trait for some *Acanthurus* species (Duarte & Acero, 1988; Dias et al., 2001). Thus, algae attached to the shell of marine turtles represent another grazing opportunity for those species able to notice and exploit this food source. Moreover, besides the algae on the shell the opportunistic acanthurids may take molting skin and perhaps ectoparasites as well, both items found on the turtles' soft parts (Booth & Peters, 1972; Losey et al., 1994). Thus, the feeding association of acanthurids with marine turtles is likely related to their ability to exploit diverse micro-habitats while foraging plus their flexible diets, even if mostly based on algae (Randall, 1967; Duarte & Acero, 1988; Dias et al., 2001; Losey et al., 1994).

Brown and red algae dominated the samples scrapped off the turtles. These two major taxa of marine macroalgae present lower value than green algae as food for fishes, based on their nutrient and energy contents (Montgomery & Gerking, 1980). However, brown and red algae compose the bulk of food in stomach contents of the western Atlantic *Acanthurus* species (Randall, 1967; Duarte & Acero, 1988; Dias et al., 2001), and we submit that these algae are consumed by those individuals grazing on the turtle. Based on their inspection prior to the nips we suppose the grazers visually select the algae they will pick on the turtle's body. Visual selection seems habitual for some algae grazers, including the green turtle (Montgomery & Gerking, 1980; Sazima & Sazima, 1983; Dias et al., 2001).

So far the Atlantic damselfish *Abudefduf saxatilis* is recorded as an occasional cleaner of reef fishes only (Colin, 1975; Sazima, 1986; Carvalho-Filho, 1999). In this study,

however, it was recorded cleaning green turtles, picking at algae, molting skin, and perhaps small ectoparasites as well. Similarly, the Pacific *Abudefduf troschelii*, besides cleaning reef fishes (Hobson, 1968; McCourt & Thomson, 1984), picks off molting skin of submersed marine iguanas, *Amblyrhynchus cristatus* (Hobson, 1969). The also Pacific *Abudefduf sexfasciatus* occasionally plucks algal growth from green turtles positioned in mid-water (Booth & Peters, 1972). Species of *Abudefduf* are omnivorous benthic-feeders which may also forage for plankton in the water column (Hobson, 1968; Randall, 1967; Fishelson, 1970; Carvalho-Filho, 1999; Sazima & Sazima, 2001). Nevertheless, Hobson (1971) suggests that substrate-picking predators which also feed on drifting plankton have traits well-suited to perform cleaning. Thus, we predict that cleaning by species of *Abudefduf* on turtles will eventually be found in other areas.

Marine turtles bear ectoparasites such as coronulid and platylepadid barnacles (Bugoni et al., 2001), as well as occasional leeches (pers. obs.), whereas reef fishes are infested mostly by copepods and isopods (Grutter, 1994, 1999). We suggest that turtle cleaners do not specialise in this kind of symbiosis, as the habitual and more specialized cleaner species feed mostly if not exclusively on ectoparasitic crustaceans of fishes (Feder, 1966; Losey, 1971; Hobson, 1971; Grutter, 1999). Only particular individuals of the wrasse *Thalassoma duperrey*, an opportunistic and versatile forager, are reported to specialise on parasitic turtle barnacles in Hawaii (Losey et al., 1994). Thus, we suggest that in most instances marine turtles are cleaned by reef fishes which are opportunistic feeders, and/or by those which have a broad diet (even if only occasionally, such as the acanthurids). Indeed, records on reef fishes cleaning reptiles are restricted to substrate-pickers, omnivores, and non-obligate cleaner species (Hobson, 1969; Booth & Peters, 1972; Smith, 1988; Losey et al., 1994; Moll, 1995; this study).

The behaviour of *Chelonia mydas* we recorded at the cleaning stations is undoubtedly an instance of grazing and cleaning symbiosis between reef fishes and marine reptiles (Losey, 1971; Losey et al., 1994). The turtle did not simply passed by or loitered at the cleaning stations, but concentrated on cleaning activities. Additionally, no foraging was ever recorded at the cleaning stations. As the green turtle feeding grounds at the Baía do Sueste do not overlap with the cleaning area, we surmise that the turtles seek for specific sites on the reef to be grazed and/or cleaned. This assumption is strengthened by our observation on a turtle raising to the surface to breathe during a cleaning

interaction, and thereafter returning to the same site to resume the cleaning session. Moreover, at cleaning stations the turtles displayed typical soliciting postures, such as hovering in a motionless posture and relaxing the flippers/neck to an extended downward position (see Booth & Peters, 1972; Smith, 1988; Losey et al., 1994 for illustration and description). Additionally, the turtles' forelimb movements to repel an occasional "hasty" cleaner probably are an aversive response to a plausibly painful stimulus due to the removal of a parasite embedded in the skin and/or a sensitive (wounded?) skin portion. These aversive responses are reminiscent of the jerking or shuddering movements performed by fish and turtle clients after an aching bite from their cleaners (Losey, 1971; Losey et al., 1994; Sazima et al., 1999).

Several species of follower fishes are recorded associated with animals as diverse as octopuses, moray eels, rays and other fishes disturbing the substrate during their feeding activity (Karplus, 1978; Ormond, 1980; Diamant & Shpigel, 1985; Strand, 1988). Fish followers are previously unrecorded associated with marine turtles, even though these reptiles are common in the reef environment, particularly during their foraging (e.g., Sazima & Sazima, 1983; Sanches & Bellini, 1999). *Chelonia mydas* grazes primarily on benthic algae and ingests apical portions of larger algae, whereas the smaller ones may be torn away entirely (Sazima & Sazima, 1983). Thus, the feeding behaviour of the green turtle disturbs the substrate, raising drifting particles and uncovering small crustaceans associated to the algae and has the potential to attract fishes which feed on these food types, as is the case of the wrasse *Thalassoma noronhanum* recorded herein. The Noronha wrasse is reported as a benthic invertebrates-picker, plankton-eater, and a cleaner holding mid-water cleaning stations (Francini-Filho et al., 2000; Rocha et al., 2001). However, we noticed that this wrasse is a very versatile forager, that besides picking off plankters and small benthic organisms, acts as follower and part-time cleaner of parrotfishes, grunts and other substrate-disturbing fishes, and often feeds on their faeces (coprophagy, see Sazima et al., in press). It likely perceives diverse foraging situations and use several kinds of food supplies, acting as a sort of "jack-of-all-trades" forager (see Losey et al., 1994 for comments on *T. duperrey*). Being a cleaner, *T. noronhanum* may perhaps clean the green turtle along with its following behaviour, making shifts between these two roles, a suggestion that remains to be verified. At our study site we recorded such shifts in cleaning and following roles for this wrasse when

associated with larger fishes like species of the parrotfish *Sparisoma* and the grunt *Haemulon parra*.

Grazing and substrate-disturbing marine vertebrates other than turtles most probably attract fish followers as well. While foraging on algae, marine iguanas (*Amblyrhynchus cristatus*) are likely candidates to play a nuclear role for opportunistic micro-carnivores as well as planktivores and foragers on particulate matter such as labrids (Hobson, 1991). Marine grazing mammals such as dugongs (*Dugong dugon*) and manatees (*Trichechus manatus*) would play a similar nuclear role for fish followers over the sea grass flats and algae beds they forage on.

Taken together, data from the literature and our observations indicate that feeding associations between reef fishes and marine turtles (and other marine vertebrates as well) may be widespread, albeit little studied. Even if widespread, the possibility remains that these are events very localised in space and/or time, or that this is an uncommon behaviour restricted to a few communities and/or populations of reef fishes, which would explain the scarcity of reports about this kind of marine symbiosis (see these views in Losey et al., 1994; Sazima et al., in press).

ACKNOWLEDGEMENTS

We thank the Projeto Tamar and the Centro Golfinho Rotador (through J.M. Silva-Jr.) for logistical support at Fernando de Noronha Archipelago; J.P. Krajewski and R.M. Bonaldo for help with field work; M. Sazima for help with algae identification; A.S. Abe and J. Zuanon for suggestions on the manuscript; the Ibama for permission to study reef fishes at the Marine National Park of Fernando de Noronha; the CNPq, FAEP-Unicamp, FAPESP and Fundação Pró-Tamar for essential financial support (Projeto TAMAR is affiliated with IBAMA, comanaged by the Fundação Pró-TAMAR, and officially sponsored by Petrobras).

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CAPÍTULO 2

THE NORONHA WRASSE: A “JACK-OF-ALL-TRADES” FOLLOWER

ARTIGO PUBLICADO:

Sazima C., Bonaldo R.M., Krajewski J.P. & Sazima I. 2004. Aqua, Journal of Ichthyology and Aquatic Biology, 9: 97-108.

THE NORONHA WRASSE: A JACK-OF-ALL-TRADES FOLLOWER

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Key words: *Thalassoma noronhanum*; Labridae; variable foraging; feeding associations; reef fishes; SW Atlantic

ABSTRACT. Following association between reef fishes involves opportunistic predators following one or more foraging nuclear species (mainly bottom-diggers). The followers benefit from food uncovered or flushed out when the nuclear fishes disturb the bottom. At the Fernando de Noronha Archipelago, south-west Atlantic, we recorded the plankton eater, benthic invertebrate picker, and cleaner wrasse *Thalassoma noronhanum*, commonly known as the Noronha wrasse, acting as a very flexible feeder - a kind of “jack-of-all-trades” - while following reef fishes. The Noronha wrasse associated with 15 reef fish species, feeding on drifting particles made available as the latter foraged on the bottom. The wrasse displayed four types of feeding behaviour while following foraging reef fishes: 1) eating particles stirred up; 2) eating particles expelled by the foraging fish; 3) eating faecal particles; 4) cleaning the nuclear fish. The wrasse was commonly recorded following the parrotfishes *Sparisoma frondosum*, *S. axillare*, *S. amplum*, and the grunt *Haemulon parra*. The variable feeding behaviour here recorded for *T. noronhanum* while following reef fishes seems rare among follower fish species. Nevertheless, some wrasse species have very opportunistic foraging habits as well, which render them likely candidates to display a flexible feeding behaviour.

RESUMO. Entre os peixes recifais, uma ou mais espécies nucleares (em geral fossadoras no substrato) atraem espécies seguidoras oportunistas durante sua atividade alimentar. Os seguidores aproveitam itens alimentares expostos pela atividade escavadora dos nucleares. No Arquipélago de Fernando de Noronha, Atlântico Ocidental, registramos o labrídeo *Thalassoma noronhanum*, conhecido como budião-de-Noronha, de hábito zooplactívoro, zoobentívoro e limpador, atuando como um forrageador muito versátil ao seguir peixes recifais. Registramos este labrídeo associado a 15 espécies de peixes recifais, aproveitando as partículas em suspensão originadas pela atividade alimentar dos nucleares. *Thalassoma noronhanum* exibiu quatro tipos de comportamento alimentar ao seguir os nucleares: 1) cata de partículas desprendidas do substrato; 2) cata de partículas expelidas; 3) cata de partículas defecadas; 4) limpeza do peixe nuclear. O labrídeo foi comumente registrado associando-se aos budiões *Sparisoma frondosum*, *S. axillare*, *S. amplum* e à corcoroca *Haemulon parra*. O comportamento alimentar variável, aqui registrado para *T. noronhanum* ao seguir outras espécies de peixes recifais, aparenta ser raro entre os peixes seguidores. Entretanto,

algumas espécies de labrídeos apresentam hábitos muito oportunistas, sendo, também, prováveis candidatas a apresentar comportamento alimentar flexível.

INTRODUCTION

Coral reefs harbour a great variety of fish species that associate with several organisms, but mainly with other fishes that are foraging (Hobson, 1974; Gibran, 2002; Harmelin-Vivien, 2002; Sazima et al., 2003). Many species of reef fish, called “cleaners”, feed on ectoparasites, mucus and diseased tissues on a wide range of cooperative fishes known as “clients” (Losey, 1971, 1987). Another common feeding association between reef fishes involves opportunistic predators following “nuclear” foraging species (Hobson, 1974; Fricke, 1975; Ormond, 1980). These “followers” consume invertebrates and small fishes that are flushed out when the nuclear fishes disturb the substrate (e.g., Fishelson, 1977; Ormond, 1980; Gibran, 2002).

The Noronha wrasse, *Thalassoma noronhanum* (Boulenger, 1890) is a labrid endemic to the coast of Brazil (Western South Atlantic), and is especially abundant around the oceanic islands of the Atol das Rocas and the Fernando de Noronha Archipelago (Rocha et al., 2001; Humann, 2002; Froese & Pauly, 2004). The Noronha wrasse is a reef-associated species regarded as a plankton eater and a benthic invertebrate picker (Francini-Filho et al., 2000; Rocha et al., 2001). Additionally, at the oceanic islands of Trindade (off the south-east coast of Brazil), Atol das Rocas and Fernando de Noronha (off the north-east coast) initial phase individuals of this wrasse act as cleaners to several species of reef fishes (Carvalho-Filho, 1999; Francini-Filho et al., 2000; Rocha et al., 2001).

The Noronha wrasse was recently recorded at the Fernando de Noronha Archipelago while following green turtles and picking up drifting particles stirred up by their foraging activity (Sazima et al., 2004). The wrasse was also recorded cleaning a few species of substrate-disturbing fish as well as feeding on their faeces (Sazima et al., 2004). Wrasses are well-known followers of many fish species, from single nuclear individuals to large foraging groups (e.g., Aronson & Sanderson, 1987; Baird, 1993; Lukoschek & McCormick, 2000; Feitoza et al., 2002), and several species of *Thalassoma* act as followers (e.g., Fishelson, 1977; Ormond, 1980; Ogden & Buckman,

1973; Soares & Barreiros, 2003). However, until Sazima et al. (2004) recorded the Noronha wrasse cleaning and eating faeces while following, no opportunistic associate was known to do more than take food items exposed by nuclear fishes (e.g., Fishelson, 1977; Ormond, 1980; Gibran, 2002). The flexibility of feeding behaviour recorded for the Noronha wrasse stands out as a novelty for the nuclear-follower interaction and also for any other foraging association among reef fishes.

We report here on the flexible feeding behaviour displayed by the Noronha wrasse while associated with larger species of reef fish at the Fernando de Noronha Archipelago. Besides generally observing the feeding behaviour of this wrasse, we considered the following: 1) The number and types of feeding behaviour shown by the Noronha wrasse while following reef fishes. 2) The possible relation between the two colour phases (initial and terminal) and following behaviour. 3) The species of reef fishes followed by the wrasse. 4) The relation between feeding behaviour and the nuclear species being followed. 5) Features common to the different nuclear species. We use the name “jack-of-all-trades” for a fish with such flexible feeding behaviour, and suggest that some other wrasse species may behave similarly.

MATERIAL AND METHODS

The flexible feeding behaviour of *Thalassoma noronhanum* was recorded at the Fernando de Noronha Archipelago (03°50'S, 32°25'W), about 345 km off north-east Brazil (Fig. 1). See Carleton & Olson (1999) for description of the archipelago. Behavioural interactions between the Noronha wrasse and its nuclear species were recorded at several sites around the archipelago, but most quantitative record sessions took place at two sites: the Praia da Conceição and Buraco da Raquel. The first site was a rocky shore with adjacent sand flat, and the second a lagoon reef with a sand and rubble substrate. Both featured boulders and ledges covered mostly by green, brown and red algae, stony corals and fine sand sediment. Both sites were chosen because large numbers of Noronha wrasse were present, as were substrate-disturbing fishes. The substrate consisted of mixed sand, gravel and rock, and the depth (up to 3 m) suited observation at close quarters, even from the surface.

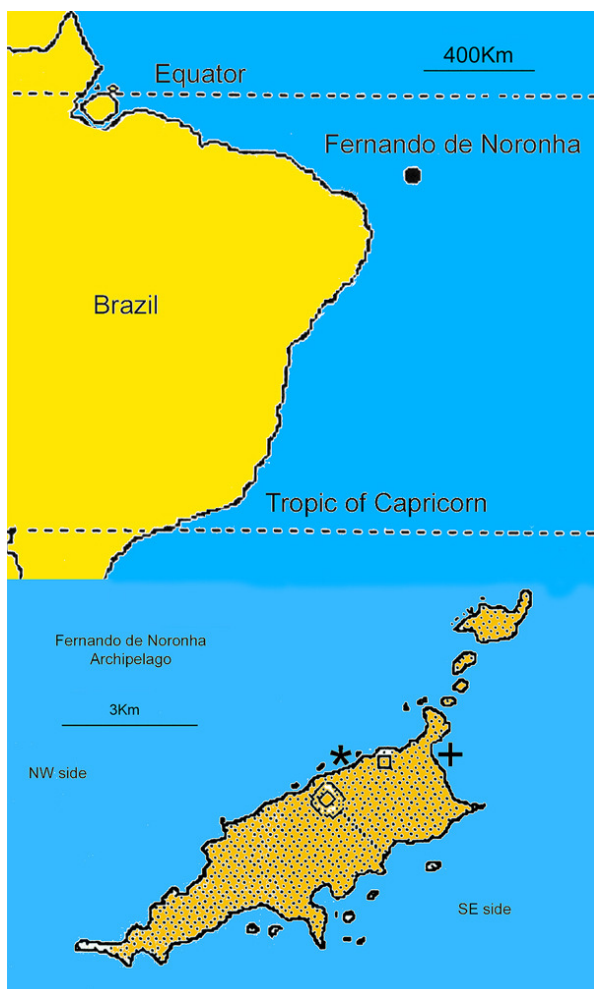


Figure 1. Location of Fernando de Noronha Archipelago off the coast of Brazil (Western South Atlantic) and our two main study sites in the archipelago (*Praia da Conceição and +Buraco da Raquel). Modified from Maida & Ferreira (1997).

At our study sites, we recorded *T. noronhanum* in both initial and terminal phases. The initial phase comprises juveniles and females with colour in life composed by brown, white and yellow background and a black spot on dorsal fin. The terminal phase comprises males with bluish or purple body with yellow-green head and dark blue bands on head (Rocha et al., 2001). Besides differences in life coloration the initial and terminal phases are also distinct in many features, such as abundance in the reef, spawning, and general behaviour (Rocha et al., 2001; our pers. obs.).

We recorded associations between the followers and the nuclear fishes while snorkelling and scuba diving. Observation sessions lasted between 30 and 90 minutes and totalled 736 minutes. Focal animal sampling was used: all occurrences of specified

actions were recorded (Altmann, 1974; Lehner, 1979). We completed 12 observation sessions on 12 non-consecutive days, in June and July 2002, and in May, June and November 2003. Behavioural events were written on plastic slates, photographed and video recorded. The tapes were placed on file at the Museu de História Natural, Universidade Estadual de Campinas (ZUEC tapes # 18 and 19).

We quantified the records of the types of feeding behaviour displayed by the Noronha wrasse (see Results section). While recording we followed a particular nuclear individual (or group) - which was already being followed by the Noronha wrasses – for up to 120 seconds and noted the feeding behaviour of both follower and nuclear fishes. Each instance of a particular feeding behaviour by *T. noronhanum* was counted as one feeding event, irrespective of the number of wrasse individuals that exploited the food source. The wrasse might exhibit one or more types of feeding behaviour (and a particular type of feeding behaviour might be displayed one or more times) while following a particular nuclear individual or group.

We also estimated the abundance of the Noronha wrasse and its nuclear species at one study site (Praia da Conceição). Using a constant swimming speed, we carried out underwater visual counts on strip transects 60 m long and 10 m wide (N=12 for rocky bottom, and N=12 for the interface between rocky and sandy bottoms). The censuses were carried out morning and afternoon in June 2003 on three non-consecutive days. To standardise data collection and minimise errors, all the counts were made by the same observer. The minimum size of the fishes counted was 5 cm (TL) for *T. noronhanum* and 15 cm TL for the nuclear species.

RESULTS

Four types of feeding behaviour were displayed by *T. noronhanum* while following reef fishes: 1) eating particles stirred up from the bottom by the nuclear fish; 2) eating particles expelled from the mouth or gill openings of the nuclear fish; 3) eating faecal particles voided by the nuclear fish; 4) cleaning nuclear fish that had momentarily stopped foraging.

We recorded 1-15 *T. noronhanum* individuals following nuclear reef fishes (N=188 records), and feeding on drifting particles derived from their foraging activities, as well

as cleaning them. The individuals observed following the nuclear species were mostly initial phase (3-12 cm TL) (Fig. 2). We recorded just two terminal phase wrasse followers: one of about 12 cm TL associated with a terminal phase parrotfish, *Sparisoma amplum* (Ranzani, 1842), and another of about 14 cm TL associated with a terminal phase *Sparisoma frondosum* (Agassiz, 1831), both feeding on drifting particles freed from the substrate by the parrotfishes (Fig. 3). Whatever activities they were engaged in, initial phase individuals were far more commonly observed than terminal phase fishes in the surveyed areas.



Figure 2. A retinue of initial phase Noronha wrasses (*Thalassoma noronhanum*) associated with a terminal phase parrotfish (*Sparisoma amplum*). Photo by J.P. Krajewski.

We recorded *T. noronhanum* following 15 reef fish species (Table 1): two species of grunt (Haemulidae), two goatfishes (Mullidae), one damselfish (Pomacentridae), two wrasses (Labridae), three parrotfishes (Scaridae), one surgeonfish (Acanthuridae), one triggerfish (Balistidae), one filefish (Monacanthidae), one boxfish and one trunkfish (both Ostraciidae).



Figure 3. A terminal phase *Thalassoma noronhanum* associated with a foraging terminal phase parrotfish, *Sparisoma frondosum*. Photo by C. Sazima.

Table 1. Fifteen reef fish species followed by the Noronha wrasse (*Thalassoma noronhanum*) at Fernando de Noronha Archipelago. Taxonomic arrangement follows Nelson (1994).

Families	Nuclear species	Authors' name and date
Haemulidae (grunts)	<i>Anisotremus surinamensis</i>	(Bloch, 1791)
	<i>Haemulon parra</i>	(Desmarest, 1823)
Mullidae (goatfishes)	<i>Mulloidichthys martinicus</i>	(Cuvier, 1829)
	<i>Pseudupeneus maculatus</i>	(Bloch, 1793)
Pomacentridae (damselfishes)	<i>Abudefduf saxatilis</i>	(Linnaeus, 1758)
Labridae (wrasse)	<i>Halichoeres dimidiatus</i>	(Agassiz, in Spix & Agassiz, 1831)
	<i>Halichoeres radiatus</i>	(Linnaeus, 1758)
Scaridae (parrotfishes)	<i>Sparisoma amplum</i>	(Ranzani, 1842)

	<i>Sparisoma axillare</i>	(Steindachner, 1878)
	<i>Sparisoma frondosum</i>	(Agassiz, 1831)
Acanthuridae (surgeonfishes)	<i>Acanthurus coeruleus</i>	(Bloch & Schneider, 1801)
Balistidae (triggerfishes)	<i>Melichthys niger</i>	(Bloch, 1786)
Monacanthidae (filefishes)	<i>Aluterus scriptus</i>	(Osbeck, 1765)
Ostraciidae (boxfishes/trunkfishes)	<i>Acanthostracion polygonius</i>	Poey, 1876
	<i>Lactophrys trigonus</i>	(Linnaeus, 1758)

In making quantitative records (Table 2), we assessed the feeding behaviour types used by the Noronha wrasse while following six nuclear species (each of them was recorded at least twice). Thus, we recorded 463 feeding events in 128 records (68 % of the total number of records) involving *T. noronhanum* and the nuclear fishes (Table 2). Grazing parrotfishes (Fig. 4) were responsible for most of the particles loosened from the bottom and eaten by the wrasse, whereas expelled particles mostly came from the foraging activities of the grunt, *Haemulon parra* (Desmarest, 1823) (Table 2 and Fig. 5). We noted that the drifting particles resulting from foraging by parrotfishes and grunts were taken by the Noronha wrasse in the same way as they take individual food particles from the plankton, i.e. with visually oriented strikes. *Thalassoma noronhanum* was commonly recorded feeding on sinking clouds of defecated particles voided by parrotfishes (Table 2 and Fig. 6), although the wrasses were occasionally recorded ingesting particles from *H. parra* faeces as well. When close to a cloud of faeces, the wrasse promptly picked out individual drifting particles from it. We recorded cleaning behaviour (see Losey, 1987 for cleaning symbiosis) in wrasse interacting with two *Sparisoma* species (Table 2). The cleaning interactions took place when the nuclear species momentarily stopped foraging and posed for the follower wrasses, which stopped following and engaged in cleaning. The parrotfishes hovered near the bottom, adopting a typical head-up posture, inviting the wrasses to approach and clean them (Fig. 7). The wrasses inspected and cleaned the nuclear fish for up to 20 sec. After cleaning, the parrotfishes resumed its foraging activities and the wrasses would continue or not to follow the nuclear fish. We also recorded the wrasse following and cleaning a

triggerfish, *Melichthys niger* (Bloch, 1786) as well as a foraging group of surgeonfishes, *Acanthurus coeruleus* (Bloch & Schneider, 1801).



Figure 4. An initial phase *Thalassoma noronhanum* positioned close to the mouth of an initial phase parrotfish, *Sparisoma amplum*. Photo by C. Sazima.

During both qualitative and quantitative recording, the Noronha wrasse were mostly observed following parrotfishes (N= 122 records): *Sparisoma frondosum* (N= 45), *Sparisoma axillare* (Steindachner, 1878) (N= 42), and *S. amplum* (N= 35). There were 39 records for the grunt *H. parra*, and 27 records for the other 11 reef species. The parrotfishes followed were mostly initial phase individuals. Wrasse were recorded following terminal phase parrotfishes on only seven occasions for *S. frondosum* and once for *S. amplum*. The nuclear species followed by the wrasses were mostly solitary (182 records, 97 % of the total). However, the wrasses also followed couples and foraging groups of three or more individuals. On one occasion the wrasses followed a group of 17 *S. amplum* and on another, 16 *A. coeruleus*.

Table 2. Quantitative records of the four foraging behaviour types displayed by the Noronha wrasse (*Thalassoma noronhanum*) while following six reef fish species at Fernando de Noronha Archipelago. Within the boxes, the first number refers to feeding bouts displayed by the wrasse, whereas the second number refers to the moments a particular resource was available (e.g., picking up/faeces voided). *Sparisoma* spp. expelled particles mostly through the mouth, whereas *H. parra* and *H. radiatus* sifted them mostly through the gill cover openings.

Fish species	Foraging behaviour (N) / Resource availability (N)			
	eating particles stirred up	eating expelled particles	eating faecal particles	cleaning nuclear fish
<i>Sparisoma axillare</i> (N=40)	136/204	5/5	14/22	3/3
<i>Sparisoma amplum</i> (N=32)	166/216	7/7	9/21	0/0
<i>Sparisoma frondosum</i> (N=31)	38/54	6/6	7/9	10/11
<i>Haemulon parra</i> (N=20)	11/13	38/40	0/0	0/0
<i>Halichoeres radiatus</i> (N=3)	3/3	6/6	0/0	0/0
<i>Mulloidichthys martinicus</i> (N=2)	4/4	0/0	0/0	0/0

We estimated the abundance of the Noronha wrasse and the 15 nuclear species visually, and included in our estimate both the nuclear fish being followed by the wrasse, as well as those that foraged on the bottom disturbing it but were not associated with the wrasse at the moment of the census. The Noronha wrasse was the most abundant fish – 67.34 % of the total number of surveyed individuals. The nuclear species most commonly associated with the wrasse had the following relative abundances: *S. axillare* (4.47 %), *S. frondosum* (1.53 %), *S. amplum* (0.59 %), and *H. parra* (1.44 %). The remaining 11 nuclear species accounted for 24.63 %.



Figure 5. Three initial phase *Thalassoma noronhanum* eating particles sifted and expelled by a foraging grunt, *Haemulon parra* (a *Halichoeres radiatus* is joining the group – on the left). Photo by C. Sazima.



Figure 6. Three initial phase *Thalassoma noronhanum* following a defecating initial phase *Sparisoma amplum*. One wrasse is feeding on particles from the cloud of faeces voided by the parrotfish. Photo by R.M. Bonaldo.

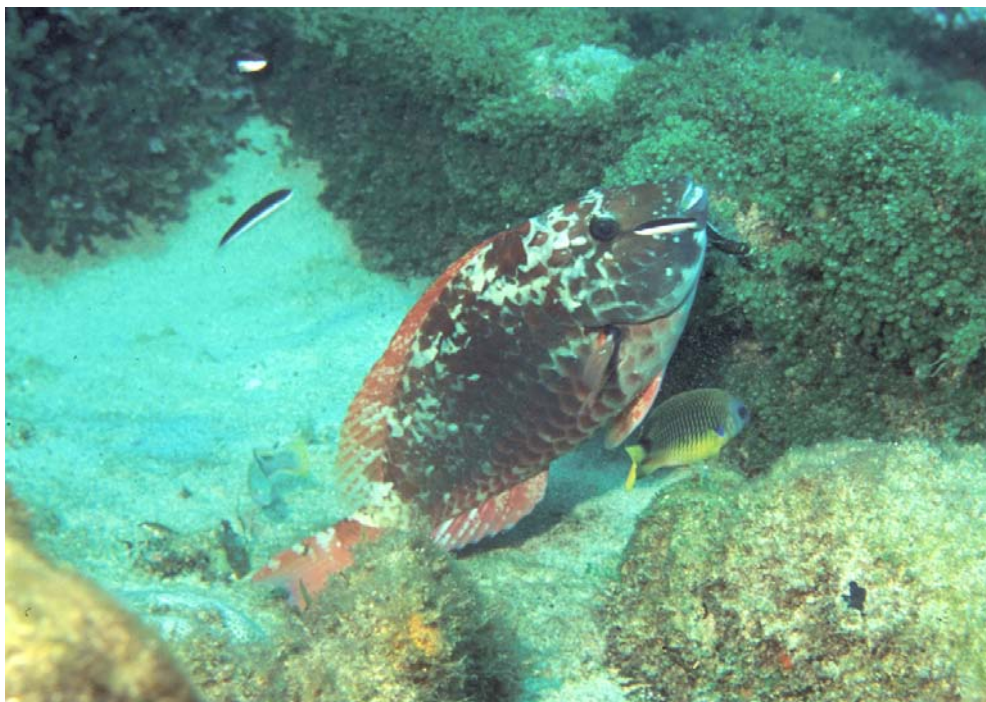


Figure 7. An initial phase *Sparisoma frondosum* momentarily ceasing its foraging and posing head-up, about to be cleaned by its initial phase *Thalassoma noronhanum* followers. Photo by J.P. Krajewski.

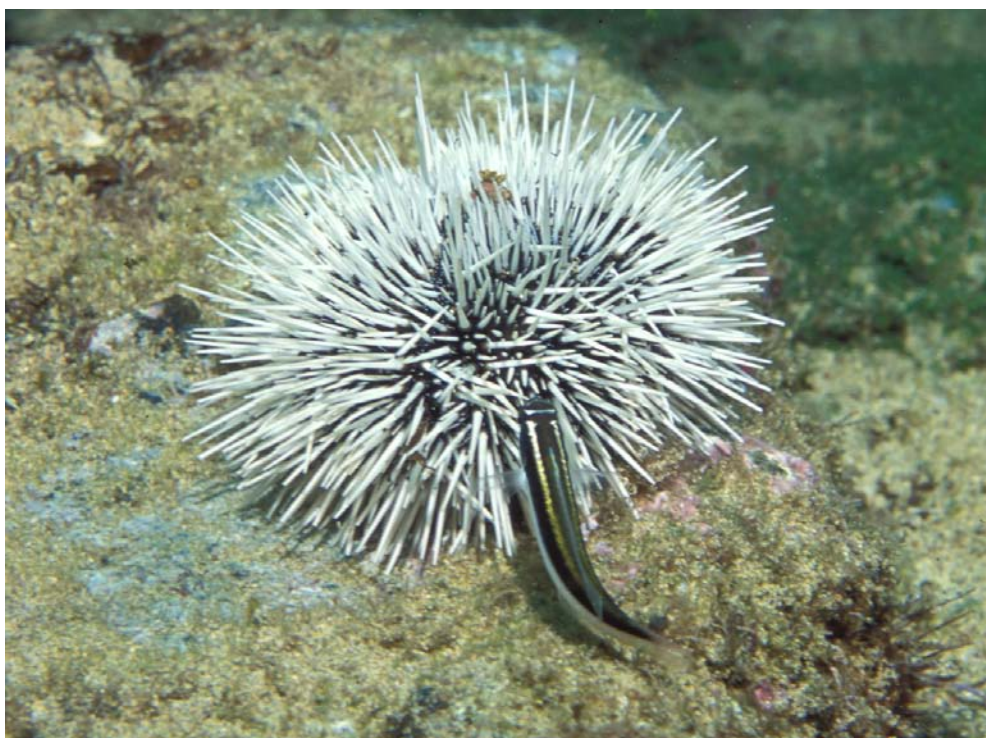


Figure 8. An initial phase *Thalassoma noronhanum* tearing off parts of the tube feet of an exposed sea urchin (possibly *Tripneustes ventricosus*). Photo by I. Sazima.

The very versatile nature of *T. noronhanum* feeding behaviour, even while simply behaving as a zoobenthivore is conveniently illustrated by its tearing out portions of sea urchins' tube feet whenever an opportunity arose, e.g., a sea urchin moving in the open (Fig. 8).

DISCUSSION

The Noronha wrasse was frequently recorded feeding on particles stirred up from the bottom. This trait is likely to be related to the relative abundance of parrotfishes and to their continuous foraging on algae and the mixed sand-algae substrate in the surveyed areas (our pers. obs.). The three *Sparisoma* species followed by the wrasse display behaviour common to many grazers, i.e. scraping algae and other encrusting organisms from the bottom (Gerking, 1994; Smith, 1997), often stirring up potential food particles in the process. The grunt *H. parra* is a carnivorous, sand-probing species that commonly forages on sand-flats and sea grass beds (Randall, 1967; Smith, 1997). Its gut contents apparently consist of much more sand, algae, and bottom detritus than do those of the other Atlantic grunt species (Randall, 1967). *Haemulon parra* usually sifted particles through its gill openings while feeding (pers. obs.), a behaviour similar to that of several detritivorous species that separate edible organic matter from inedible ingested sediment (Sazima, 1986; Helfman et al., 1997). Because of this, *H. parra* provided the bulk of expelled particles taken by the wrasse, and although it did not forage as continuously as the parrotfishes, it is here regarded as an important nuclear species and food provider. Parrotfishes usually void on the move, spreading their faeces over the reef (DeLoach, 1999). Thus, faecal particles eaten by follower wrasse were mostly provided by the three species of *Sparisoma*, as these defecated while foraging, producing clouds of slowly-sinking particles.

Most planktivorous fishes feed by visually-guided strikes at individual prey (Hobson, 1991; Wainwright & Bellwood, 2002). Although not considered to be a strictly planktivorous species (cf. Hobson, 1991), *T. noronhanum* is often seen ingesting individual plankters in the water column (Rocha et al., 2001; our pers. obs.). Thus, the ingestion of stirred-up, expelled, or voided particles is most probably related to this wrasse's plankton-eating habits, as these particles form temporary clouds of suspended

organic matter in the water column. The ability to capitalize on these food supplies may be regarded as a simple behavioural step from “standard” plankton-eating; the wrasse picks off drifting particles and individual plankters in a similar way. We believe that when picking ectoparasites off a client’s body the wrasse also aims and strikes at individual prey.

The cleaning of nuclear fish by following wrasses, though not seen as often as the other types of feeding behaviours, took place whenever a parrotfish stopped feeding and began to hover. *Sparisoma* species are on record as being among the less preferred clients of station-based *T. noronhanum* at Fernando de Noronha (Francini-Filho et al., 2000). The apparently unusual attraction to and cleaning of parrotfishes we recorded for following Noronha wrasse may be partly explained by the fact that cleaning interaction occurred under very different circumstances from those recorded by Francini-Filho et al. (2000) – where mid-water cleaning stations were visited by highly-preferred clients. The Noronha wrasse is considered a specialized cleaner that cleans at mid-water stations above conspicuous coral heads or rocks, and occasionally outside these stations (Francini-Filho et al., 2000). Furthermore, a single Noronha wrasse may establish and tend a temporary mid-water cleaning station, and thus can attend clients virtually anywhere (our pers. obs.). Cleaning interactions between followers and nuclear fishes are therefore mostly related to the Noronha wrasse’s ability to tend these temporary stations, a feature that suits both partners in this type of interaction. Establishing and tending temporary cleaning stations in the water column may be considered opportunistic behaviour, as the cleaning interactions may take place anywhere on the reef. Itzkowitz (1979) records a similarly opportunistic nature of the cleaning system used by another cleaner wrasse, *Thalassoma bifasciatum* (Bloch, 1791). The activities of this cleaner wrasse involve cleaning groups, wandering individuals, and stationary individuals, either hovering or actively swimming. The clients respond to them opportunistically, apparently not learning the location of the cleaners themselves, but reacting to any small group of wrasses (Itzkowitz, 1979). Thus, one may say that the wrasse does not develop a constant relationship with the client it momentarily follow, and cleaning may be rightly regarded as another feeding mode in the variable feeding repertoire of this wrasse.

Another noteworthy feature of the Noronha wrasse's opportunistic feeding behaviour is the number and diversity of fish species with which this wrasse associates: 15 species in nine families with diverse feeding habits (see Randall, 1967; Froese & Pauly, 2004 for diets). Nevertheless, all reef fish species followed by the Noronha wrasse displayed a common trait, giving rise to drifting particles by foraging, and/or being cleaned at places other than mid-water cleaning stations. *Thalassoma noronhanum* associates with three main "food-providing groups" of nuclear fishes that make food available by 1) disturbing the substrate, 2) expelling particles and 3) voiding faeces over the reef. Examples in the first group are zoobenthivores and roving herbivores such as goatfishes (Mullidae), wrasses (Labridae), grunts (Haemulidae), rays (Dasyatidae), parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and even boxfishes (Ostraciidae), and filefishes (Monacanthidae). Into the second group fall grunts, parrotfishes, and other particle-sorting species such as mojarras (Gerreidae) and bonefish (Albulidae) when feeding near the reef. The third group includes parrotfishes, which habitually spread their faeces over the reef. We predict that the Noronha wrasse would also associate with a few additional faeces-spreading herbivores and planktivores, such as chubs (Kyphosidae) and damselfishes. Although not a fish, the spinner dolphin *Stenella longirostris* (Gray, 1828) occasionally voids its faeces near reef pinnacles, where they may be fed on by the Noronha wrasse (Sazima et al., 2003).

Cleaning symbiotic clients could constitute a fourth group providing food for the Noronha wrasse. This group would include the greatest diversity of nuclear species, since any fish followed by the wrasse is a potential client. However, the cleaning association depends on the nuclear fish stopping foraging, and posing for the wrasse. Potential clients the Noronha wrasse may follow include surgeonfishes, angelfishes (Pomacanthidae), grunts, parrotfishes, rays, boxfishes, and triggerfishes. Francini-Filho et al. (2001) mention predation of *T. noronhanum* by a grouper client, *Cephalopholis fulva* (Linnaeus, 1758) near the bottom and outside the cleaning stations, a situation it may face while acting as a client's follower. We therefore suppose that *T. noronhanum* would not follow highly piscivorous species such as groupers (Serranidae) and snappers (Lutjanidae) to engage in one or more of its four types of feeding behaviour. Additionally, groupers usually hunt as stalking predators and snappers are partly diurnal

feeders with increased foraging activity at night (Hobson, 1968, 1974; Sazima, 1986), and thus would not act as nuclear fishes for *T. noronhanum*.

The abundance, distribution and behaviour of different colour phase individuals of several wrasse species are distinct and varied. (e.g., Itzkowitz, 1979; Thresher, 1979; DeLoach, 1999). Cleaning has been recorded for *T. noronhanum* initial phase individuals only (Francini-Filho et al., 2001). However we recorded terminal phase wrasses following reef fish and ingesting food particles on two occasions, indicating that they retain at least a little of the opportunistic feeding behaviour so evident in initial phase individuals. As initial colour phase individuals were more commonly observed than terminal ones, we suppose the scarcity of records for terminal phase individuals following reef fishes is related to their low abundance on the reef (Floeter & Gasparini, 2000; Rocha et al., 2001). In addition, colourful terminal phase males of some wrasse species spend most of their time in the water column patrolling their territories (Itzkowitz, 1979; Thresher, 1979), a type of behaviour we also recorded for the Noronha wrasse, which feeds little while patrolling (our pers. obs.).

The variable feeding behaviour here recorded for the Noronha wrasse may be considered a “local” feature in the biology of this species. Brazil’s oceanic islands seem to provide some specific conditions apparently not found, or rarely found, elsewhere on the coast (e.g. Sazima et al., 2003, 2004). We suggest that the varied feeding repertoire recorded for *T. noronhanum* at Fernando de Noronha is related to its oceanic habitat. Even the cleaning habits of the Noronha wrasse, common at oceanic sites such as Fernando de Noronha Archipelago, Atol das Rocas, and Trindade Island (Floeter & Gasparini, 2000; Rocha et al., 2001) have still to be verified for coastal sites in Brazil. We predict that Noronha wrasse from the oceanic Trindade Island and Atol das Rocas will show variable feeding behaviour similar to that recorded at Fernando de Noronha. Besides reef fishes, the Noronha wrasse followed a turtle as it grazed on benthic algae, disturbing the bottom and stirring up particles or uncovering small invertebrates (Sazima et al., 2004). Although following association is common to several reef fishes and even a few invertebrates (e.g. Hobson, 1968; Strand, 1988; Gibran, 2002), this kind of symbiosis between wrasses and turtles has only been recorded at Fernando de Noronha (Sazima et al., 2004).

Apparently, most *Thalassoma* species mostly feed on a wide variety of benthic invertebrates, except for *T. amblycephalum* (Bleeker, 1856) which, besides cleaning reef fishes, mostly feeds on zooplankton (Debelius, 1993; Froese & Pauly, 2004). Nevertheless, five species, namely *T. bifasciatum*, *T. duperrey* (Quoy & Gaimard, 1824), *T. hardwicke* (Bennett, 1830), *T. lucasanum* (Gill, 1862) and *T. noronhanum* consume a wide range of food items including zooplankton, and to some extent, four of these species act as cleaners (Randall, 1967; Hobson, 1974, 1968; Losey et al., 1994; Francini-Filho et al., 2000; Froese & Pauly, 2004). *Thalassoma duperrey* is a highly opportunistic species, standing close to the jaws of parrotfishes to feed on prey uncovered by their substrate-disturbing activities (Hobson, 1974). Additionally, *T. lunare* (Linnaeus, 1758), *T. duperrey*, and *T. noronhanum* even associate with marine turtles (Booth & Peters, 1972; Losey et al., 1994; Sazima et al., 2004), which further attests to their opportunistic foraging. We predict that, when following reef fishes, other *Thalassoma* species would display variable, highly opportunistic foraging behaviour, similar to that described here for *T. noronhanum*. Four species, *T. bifasciatum*, *T. duperrey*, *T. hardwicke* and *T. lucasanum*, all of which have a broad diet and are able to feed on planktonic organisms, are likely candidates.

Although the Noronha wrasse does not diverge greatly from its usual feeding tactic of singling out individual prey or particles of food (from the bottom, the water column or even from a clients' body), it displays a very variable repertoire of feeding modes, exploiting the abundant food made available by nuclear reef fishes. We believe that the variable feeding repertoire of the Noronha wrasse while following reef fishes is related to its ability to notice new feeding opportunities. Apparently, Noronha wrasse learn to spot nuclear foraging fishes, recognize them as potential food providers, and regularly follow them, thus turning this otherwise opportunistic feeding into usual feeding behaviour.

The ingestion of particles and/or organisms exposed or flushed out as nuclear reef fishes disturb the bottom is the only feeding behaviour presently described for follower species (e.g., Fricke, 1975; Strand, 1988; Soares & Barreiros, 2003), except for a brief mention (Sazima et al., 2004) of the Noronha wrasse as a follower, part-time cleaner and faeces-eater. Thus, eating particles stirred up from the bottom seems to be the only type of feeding behaviour that corresponds to the usual meaning of 'following

associations' (e.g., Fricke, 1975; Dubin, 1982; Diamant & Shpigel, 1985; Strand, 1988). The variable and highly opportunistic types of feeding behaviour recorded here for a follower seem restricted at the present to the Noronha wrasse. We therefore find it very proper to regard this fish as a "jacks-of-all-trades" follower.

ACKNOWLEDGEMENTS

We thank the Centro Golfinho Rotador (J. M. Silva-Jr.) and the Projeto Tamar (C. Bellini and A. Grossman) for logistical support at Fernando de Noronha Archipelago; the Ibama (M.A. Silva) for the issue of study permits at Fernando de Noronha Archipelago, for logistic support and a warm reception. We thank the aqua copy editor for kindly and patiently improving our English. We also thank Águas Claras and the Atlantis diving centres for allowing the free use of their facilities; the CAPES, CNPq, FAEP-Unicamp, and FAPESP for essential financial support. CS and IS are recipients of scholarships from the CNPq – Brasil. We dedicate this paper to our dear friend José Martins Silva-Jr., whose friendship and skills made our research at Fernando de Noronha both possible and pleasant.

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CAPÍTULO 3

**THE GOATFISH *PSEUDUPENEUS MACULATUS* AND ITS FOLLOWER
FISHES AT AN OCEANIC ISLAND IN THE TROPICAL WEST ATLANTIC**

ARTIGO NO PRELO:

**Sazima C., Krajewski J.P., Bonaldo R.M. & Guimarães Jr P.R. 2006. Journal of
Fish Biology**

**A NON-DIGGING ZOOBENTHIVOROUS FISH ATTRACTS TWO
OPPORTUNISTIC PREDATORY FISH ASSOCIATES**

ARTIGO PUBLICADO:

Sazima C. & Grossman A. 2005. Neotropical Ichthyology, 3(3): 441-445

THE GOATFISH *PSEUDUPENEUS MACULATUS* AND ITS FOLLOWER FISHES
AT AN OCEANIC ISLAND IN THE TROPICAL WEST ATLANTIC

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Key words: *Pseudupeneus maculatus*; Mullidae; nuclear and follower fishes; foraging
associations; reef fishes; Equatorial West Atlantic

ABSTRACT. This study examines the influence of a substrate-disturbing forager, the spotted goatfish (*Pseudupeneus maculatus*) on the assemblage of its escorting, opportunistic-feeding fishes. At Fernando de Noronha Archipelago (tropical West Atlantic) the spotted goatfish *P. maculatus* is a ubiquitous, so-called nuclear fish that forages singly or in groups, and attracts a varied assemblage of follower fishes including herbivorous species. Followers attracted to goatfish foraging singly differed from followers of goatfish foraging in groups in several characteristics. The larger the nuclear fish group, the greater the species richness and number of individuals of followers. Moreover, groups of foraging goatfish attracted herbivores, not recorded for goatfish foraging singly. The size of follower individuals increased with the size and the number of foraging goatfish. The zoobenthivorous habits of the spotted goatfish and its ability to disturb a variety of soft substrata render it an important nuclear fish for several follower species of the reef fish assemblage at Fernando de Noronha.

INTRODUCTION

Following behaviour is a foraging mode commonly recorded for reef fishes during heterospecific feeding associations (e.g., Ormond, 1980; Strand, 1988; Lukoschek & McCormick, 2000; Sazima et al., 2005). The followers escort foraging so called nuclear fishes and other animals to capitalise on food items exposed or produced by the activity of the nuclears, including stirred organic particles and algae, uncovered or flushed small invertebrates and fishes, and even faeces (e.g., Fricke, 1975; Ormond, 1980; Silvano, 2001; Sazima et al., 2005). Such foraging associations are widespread and recorded for several fish and other marine animal taxa and geographic sites (Diamant & Shpigel, 1985; Lukoschek & McCormick, 2000; Gibran, 2002; Sazima et al., 2005).

Following behaviour, as other types of social foraging habits, may enhance the fitness of individuals within the group and provide increased protection from predators (Aronson & Sanderson, 1987; Baird, 1993; Lukoschek & McCormick, 2000; Auster & Lindholm, 2002). However, relationships of costs and benefits for both nuclear and follower species are not clearly defined and following behaviour is sometimes regarded as a type of commensalism (Lukoschek & McCormick, 2000; but see Baird, 1993). Nevertheless, several fish species of many families and trophic levels engage in

following behaviour and spend up to 25% of their time in this association type (Strand, 1988; Lukoschek & McCormick, 2000).

Goatfish species (Mullidae) are noted as either nuclear or follower fishes (e.g., Aronson & Sanderson, 1987; Sikkel & Hardison, 1992; Lukoschek & McCormick, 2000). The spotted goatfish, *Pseudupeneus maculatus* (Bloch), dwells on sandy and rocky bottoms in reef areas in the West Atlantic (Starck & Davis, 1966). This goatfish is a zoobenthivore (benthic carnivore) and uses its chin barbels to search for food over substrata types as diverse as sand, rubble, and rocks covered with sand and algae (Randall, 1967; Carvalho-Filho, 1999). The spotted goatfish is diurnally active and may be very abundant locally, foraging either solitary or in groups, small to large (Starck & Davis, 1966; Munro, 1976; Carvalho-Filho, 1999). Thus, the overall habits of the ubiquitous *P. maculatus* would render it a nuclear fish attractive for a variety of opportunistic follower fishes.

At Fernando de Noronha Archipelago, tropical West Atlantic, the spotted goatfish is a common species, which uses variable feeding modes over several habitat types (pers. obs.). To assess how the foraging nuclear goatfish influence the behaviour of potential follower fishes, four main questions were addressed in the present study: 1) How many and which species follow the spotted goatfish? 2) Is the followers' species richness or number of individuals related to the number of foraging goatfish? 3) Are there differences in the trophic categories of followers associated with goatfish foraging singly or in groups? 4) Does the size or the number of foraging goatfish influence the size of associated follower individuals? The answers to these questions bring new insights about the organization of heterospecific associations (see Lukoschek & McCormick, 2000). Additionally, the present study is the first attempt to relate the characteristics and habits of the nuclear fish to the followers' species richness and their distribution in heterospecific associations.

MATERIAL AND METHODS

The foraging activity and associations between *P. maculatus* and its follower fishes were recorded at Fernando de Noronha Archipelago (03°50'S, 32°25'W), about 345 km off the coast of north-east Brazil, tropical West Atlantic (see map in Sazima et al.,

2005). Preliminary data were gathered in June 2001, the core of the study being carried out in June 2002, May-July 2003, November 2003, and October 2004. Records on the foraging associations were made at seven sites around the archipelago, all of these with similar features: bottom composed with rocky reefs covered mostly with green, brown and red algae, stony corals and fine sand sediment, with adjacent sand flats. The substrata over which the goatfish foraged consisted of mixed sand, gravel, and rock.

Foraging activities and associations of goatfish with followers were recorded while snorkelling and scuba diving in observation sessions of 30-120 minutes, totalling 2534 minutes over 34 non-consecutive days. Behavioural data were recorded directly on slates, photographed, and video-recorded. A voucher DVD with selected video-recordings is on file at the Museu de História Natural of the Universidade Estadual de Campinas (ZUEC # 01). Associations between foraging goatfishes and their followers were assessed with the use of instantaneous samplings (Altmann, 1974), in which the fish species, number of individuals and their estimated sizes were recorded on plastic slates with standardised sketches, for each studied association. Total length (TL, cm) was visually estimated both for the nuclear and follower fishes. For a better assessment, followers were grouped in four size classes: “very small” (about 4-11 cm), “small” (about 12-22 cm), “medium” (about 23-35 cm) and “large” (about 36-50 cm).

The following pairwise relationships were analysed by least squares regression with randomization test, and significance levels were estimated with $N = 10000$ resamplings (Manly, 1997): A) species richness of followers and the number of foraging goatfish; B) number of follower individuals and the number of foraging goatfish; C) size of the largest follower individual and the size of the largest nuclear goatfish individual; D) size of the largest follower individual and the number of foraging goatfish. The relationship between gregarious behaviour (coded as “singly” or “groups”) and the size ratio between nuclear and follower individuals (coded as “the nuclear is larger than the follower” and “the follower is larger than the nuclear”) was tested using the χ^2 test (Zar, 1999).

RESULTS

A total of 223 foraging associations were recorded for *P. maculatus* (10-30 cm TL, mean \pm SE = 19.29 ± 0.13 ; N = 495). Of these, 120 associations (about 54%) contained a goatfish foraging singly and 103 (about 46%) contained groups of 2-36 goatfish (mean \pm SE = 10.87 ± 0.66). Seventeen reef fish species were recorded associated with the goatfish (Table 1). Zoobenthivore fish species dominated among the followers, with exception of five mainly herbivorous species and one omnivorous wrasse (Table 1).

Table 1. Reef fish species recorded as followers of the spotted goatfish (*Pseudupeneus maculatus*) at Fernando de Noronha Archipelago. Trophic category and minimum and maximum sizes (TL, cm) of the followers, the condition of the foraging goatfish (single or grouped) and number of observations. Taxonomic arrangement of families follows Nelson (1994), genera and species in alphabetical order.

Families and specific names of followers	Trophic category	Size	Goatfish condition (N)
Aulostomidae (trumpetfishes)			
<i>Aulostomus strigosus</i> Wheeler	Zoobenthivore/Piscivore	35-48	Grouped (3)
Serranidae (groupers and sea basses)			
<i>Cephalopholis fulva</i> (Linnaeus)	Zoobenthivore	10-25	Grouped (42)/Single (22)
Malacanthidae (tilefishes)			
<i>Malacanthus plumieri</i> (Bloch)	Zoobenthivore/Piscivore	17	Grouped (2)
Carangidae (jacks)			
<i>Caranx bartholomaei</i> (Cuvier)	Zoobenthivore/Piscivore	25-40	Grouped (30)/Single (1)
<i>Caranx latus</i> (Agassiz)	Zoobenth./Pisc./Plankt..	15-20	Grouped (10)/Single (6)
Haemulidae (grunts)			
<i>Anisotremus surinamensis</i> (Bloch)	Zoobenthivore	23-38	Grouped (3)

<i>Haemulon chrysargyreum</i> (Günther)	Zoobenthivore	15	Single (1)
<i>Haemulon parra</i> (Desmarest)	Zoobenthivore	12-20	Grouped (5)
Mullidae (goatfishes)			
<i>Mulloidichthys martinicus</i> (Cuvier)	Zoobenthivore	19	Single (1)
Labridae (wrasses)			
<i>Halichoeres dimidiatus</i> (Agassiz, in Spix and Agassiz)	Zoobenthivore	11-20	Single (5)/Grouped (3)
<i>Halichoeres radiatus</i> (Linnaeus)	Zoobenthivore	06-28	Single (89)/Grouped (64)
<i>Thalassoma noronhanum</i> (Boulenger)	Zoobenth./Plankt./Cleaner	04-12	Single (10)/Grouped (3)
Scaridae (parrotfishes)			
<i>Sparisoma amplum</i> (Ranzani)	Herbivore	23	Grouped (1)
<i>Sparisoma axillare</i> (Steindachner)	Herbivore	16-38	Grouped (12)
<i>Sparisoma frondosum</i> (Agassiz)	Herbivore	20-32	Grouped (2)
Acanthuridae (surgeonfishes)			
<i>Acanthurus chirurgus</i> (Bloch)	Herbivore	18-22	Grouped (3)
<i>Acanthurus coeruleus</i> (Bloch & Schneider)	Herbivore	17-25	Grouped (2)

Species richness of followers increased ($R^2 = 0.35$; $P < 0.0001$; $N = 223$) with the number of foraging goatfish (Fig. 1). Goatfish foraging singly attracted one to three follower species (1.12 ± 0.03 ; $N = 120$) at a time, but one species was the commonest situation (88%). On the other hand, goatfish foraging in groups attracted one to six follower species at a time (1.79 ± 0.10 ; $N = 103$), two or more species being a common situation (51%). The number of follower individuals increased ($R^2 = 0.37$; $P < 0.0001$; $N = 223$) with the number of foraging goatfish (Fig. 1). Goatfish foraging singly attracted one to five follower individuals at a time (1.33 ± 0.07 ; $N = 120$), whereas goatfish foraging in groups attracted one to 13 follower individuals at a time (2.94 ± 0.25 ; $N = 103$).

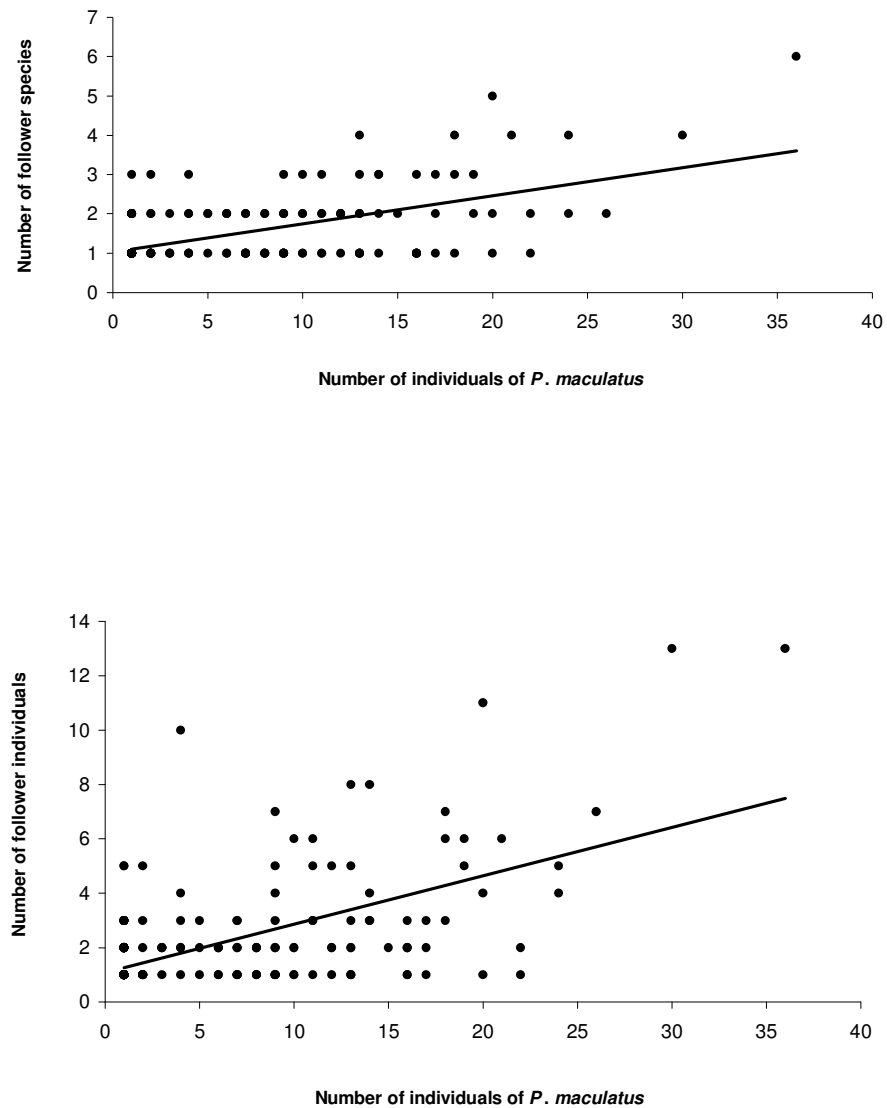


Figure 1. Quantitative relationships between follower fishes and the goatfish *Pseudupeneus maculatus* at Fernando de Noronha Archipelago. Follower fish species richness increased with the number of foraging goatfish (above). Number of follower individuals increased with the number of foraging goatfish (below).

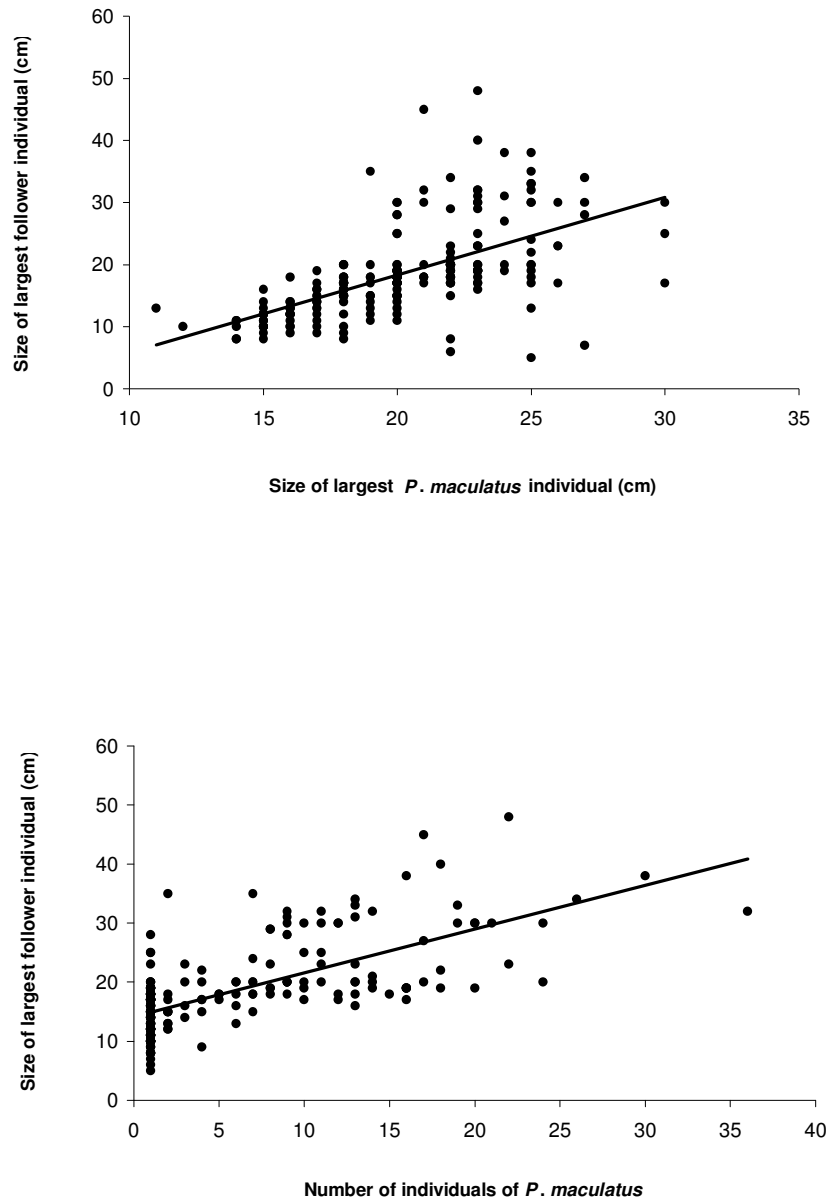


Figure 2. Quantitative relationships between follower fishes and the goatfish *Pseudupeneus maculatus* at Fernando de Noronha Archipelago. Size of the largest follower individual increased with size of the largest foraging goatfish individuals (above). Size of the largest follower individual increased with the number of foraging goatfish (below).

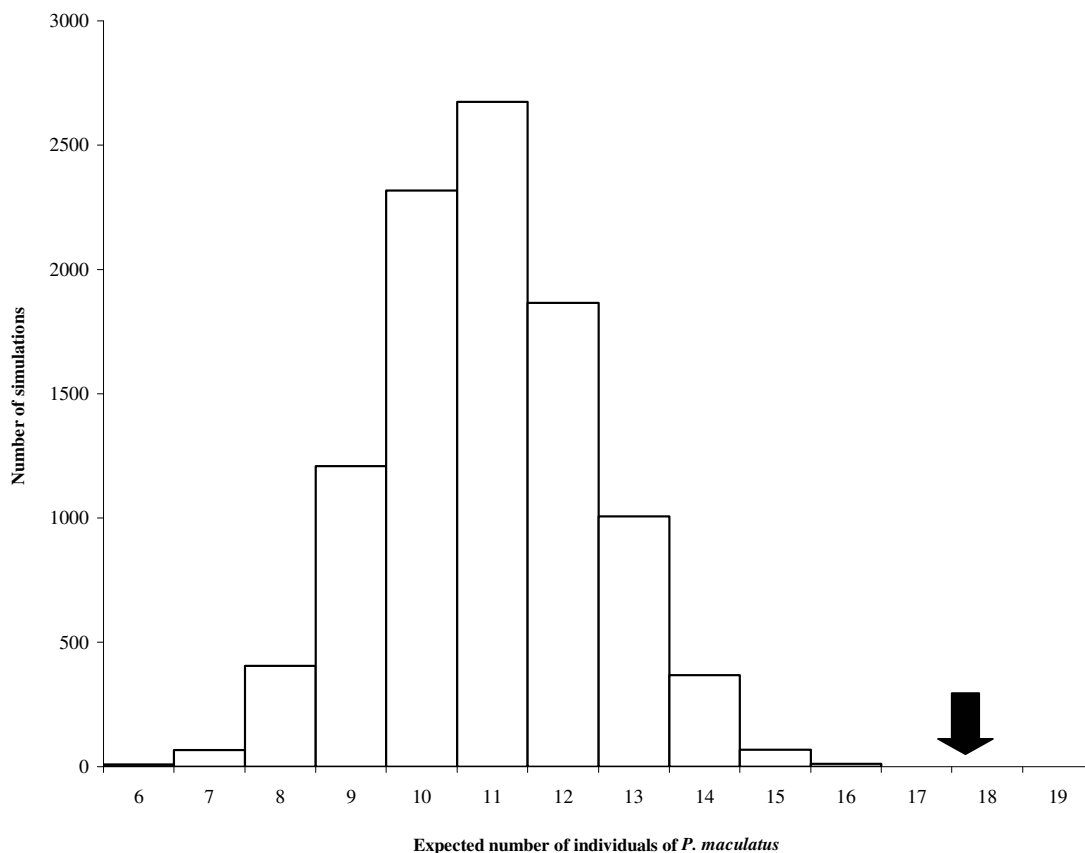


Figure 3. The distribution of the average number of *Pseudupeneus maculatus* individuals expected for follower assemblages containing herbivores under the assumption of randomness (10000 resamplings). The black arrow indicates the observed value for real data.

Besides zoobenthivores and/or piscivores, goatfish groups attracted five herbivores: *Sparisoma axillare* (Steindachner), *Sparisoma amplum* (Ranzani), *Sparisoma frondosum* (Agassiz), *Acanthurus chirurgus* (Bloch) and *Acanthurus coeruleus* Bloch & Schneider, none of which was recorded following goatfish foraging singly (Table 1). Whereas zoobenthivores were recorded in 100% of the associations, herbivores were recorded in only 7.6% of these, always following large goatfish groups (8-36 individuals; 18.18 ± 1.70 ; $N = 17$). To investigate if followers' assemblages with herbivores were non-randomly associated to large groups, an *a posteriori* randomization test (Manly, 1997) was performed. The group sizes of the goatfish were randomized among records of associations and the average number of goatfishes was computed for

followers' assemblages containing herbivores (10000 resamplings). No randomization achieved a group size equal or higher than that observed for herbivores, which indicates that the herbivores follow only larger groups of goatfish (Fig. 3).

The size of the largest follower increased with the size of the largest nuclear goatfish ($R^2 = 0.37$; $P < 0.0001$; $N = 223$) (Fig. 2). The size of the largest follower individual also increased with the number of foraging goatfish ($R^2 = 0.46$; $P < 0.0001$; $N = 223$) (Fig. 2). Goatfish foraging singly (12-30 cm TL) were mostly (92.5%, 111 records) larger than their followers (4-28 cm TL). On the other hand, for goatfish foraging in groups (10-30 cm TL), in about a half of the associations (57 records, 55.3%) the largest goatfish within the group was larger than the largest follower (6-48 cm TL, $\chi^2 = 41.2$, $P < 0.0001$). Disregarding the species, in a total of 463 follower fishes 69 individuals were very small (8.42 ± 0.26 cm), 308 were small (16.95 ± 0.15 cm), 78 individuals were medium (28.68 ± 0.40 cm) and only eight were large (40.00 ± 1.50 cm).

DISCUSSION

In heterospecific associations, the nuclear species attract mostly opportunistic carnivore predators (e.g., Fricke, 1975; Ormond, 1980; Lukoschek & McCormick, 2000). At Fernando de Noronha, the spotted goatfish seems to exert a pervasive influence on the assemblage of opportunistically foraging reef fishes that feed near the bottom. Zoobenthivorous and piscivorous species dominated among the followers of *P. maculatus* in the present study. However, an entirely different follower type, the herbivorous parrotfishes and surgeonfishes, was recorded here associated with the spotted goatfish. Most records on feeding associations involving these herbivores characterize them as nuclear fishes or do not describe their role at all (e.g., Ormond, 1980; Strand, 1988; Sazima et al., 2005, but see Lukoschek & McCormick, 2000; Dias et al., 2001). The suggestion is made that the herbivores join foraging groups to feed upon suspended items and pieces of algae loosened or unearthed by the nuclear and/or follower fishes. At Fernando de Noronha, parrotfishes and surgeonfishes have been reported to feed on floating particles including dolphin faeces (Sazima et al., 2003; pers. obs.).

As herbivores were only recorded following groups of eight or more goatfish, it is probable that their presence in the associations is related to larger numbers of nuclear fish. A group of goatfishes is likely to produce a considerable bottom disturbance and would thus provide herbivorous fishes with drifting bits of food (algae). Thus, herbivorous species would associate with nuclear species that form larger aggregations while foraging, an idea to be tested with additional records of heterospecific associations.

The number of nuclear foraging individuals influenced the followers' species richness and the number of follower individuals in the present study, the main reason probably being the amount of disturbance produced. Strand (1988) noted that the mean number of followers and their preferences for a particular nuclear species are related to the amount of disturbance created. Visual signals elicit following behaviour by opportunistic fish species (Fricke, 1975; Fishelson, 1977; Diamant & Shpigel, 1985), and both the sand clouds produced by the disturbance and specific features of the nuclear fish (shape, behaviour, coloration) influence the followers' behaviour (Fricke, 1975; Fishelson, 1977). Thus, a goatfish foraging singly may go unnoticed or be uninteresting to some fish species, whereas a foraging group would attract more attention. Notwithstanding the conspicuous and diverse consequences produced by variable numbers of foraging nuclear fish (both to the habitat and the follower fishes), we found no published comparative approach such as that presented here, which prevents additional considerations.

Several fish species may join foraging groups both for feeding and anti-predatory advantages that may occur simultaneously (Morse, 1977; Diamant & Shpigel, 1985; Strand, 1988; Auster & Lindholm, 2002). Feeding advantages would include minimizing effort duplication, food-finding facilitation, and catching uncovered and otherwise unavailable food (Morse, 1977). Anti-predatory advantages include vigilance, confusion effect, discouraging predators, cover-seeking, and dilution effect (Morse, 1977). Evidence of feeding advantages for nuclear and follower association is supported by several studies (e.g., Diamant & Shpigel, 1985; Aronson & Sanderson, 1987; Strand, 1988; Baird, 1993). However, anti-predatory advantages of this association still need to be verified (see Auster & Lindholm, 2000; Lukoschek & McCormick, 2000). It is here suggested that feeding and other advantages may be found even when a follower

associates with a single nuclear fish, but most likely a larger number of foraging nuclear fish increases some of these advantages.

The number and diversity of species engaged in following the spotted goatfish, recorded in the present study, indicate that the benefits are higher than the costs to the followers. The nuclear fish may also benefit from the association, since social stimuli from the follower fishes may increase foraging opportunities for the nuclear ones (Baird, 1993; Lukoschek & McCormick, 2000). However, food pilfering by followers may represent a high cost to the nuclear fish (Strand, 1988; Baird, 1993; Lukoschek & McCormick, 2000). Despite the dietary overlap between most followers and the spotted goatfish, no food pilfering or aggressive behaviour between them was here recorded, which indicates little if any cost to *P. maculatus*.

In the present study minimum and maximum sizes of goatfish foraging singly or in groups were similar. However, goatfish foraging singly were mostly larger than their followers, whereas grouped goatfish commonly attracted followers larger than themselves. The analysis of several pictures available in the literature (e.g., Diamant & Shpigel, 1985; Aronson & Sanderson, 1987; Auster & Lindholm, 2002) indicates a trend: followers are mostly smaller than the nuclear fish, especially when the latter is foraging singly. Although data on sizes of both nuclear and follower fishes are rarely available, some studies comment on the size relationships between associated foraging fishes (e.g., Sikkil & Hardison, 1992; Silvano, 2001; Gibran, 2002) and a few of them relate size classes of the followers to ontogenetic factors (Strand, 1988; Lukoschek & McCormick, 2000). However, another factor that may influence size classes of followers would again be the amount of disturbance created by the foraging nuclear fish. If this is the case, larger followers would be more prone to join large foraging groups due to the greater amount of disturbance they cause, which may dislodge greater amount of prey, as well as possibly more types and even larger sizes of prey. Thus, the maximum size of follower fishes in a foraging association seems to be mostly related to the number of nuclear individuals within the group rather than only to the size of the latter.

Sixteen follower species correspond to the largest list of fishes reported as associated with a nuclear species at a given locality, namely the goatfish *Parupeneus barberinus* at Lizard Island in the Southwest Pacific (Lukoschek & McCormick, 2000), a region with

greater reef fish species richness than the West Atlantic (e.g., Carvalho-Filho, 1999; Allen & Adrim, 2003). The richness notwithstanding, the number of follower species recorded for *Pseudupeneus maculatus* at Fernando de Noronha (present study) exceeds the above-mentioned record, and thus renders it the largest list of followers recorded to date. It is here suggested that the spotted goatfish has a pervasive influence on several opportunistically-feeding species in the reef fish community of Fernando de Noronha, and that the number of follower species is an indication of the importance of its role. Other goatfish species, especially those that form aggregations while foraging, are worth study in other areas to examine the view that nuclear fishes that produce substantial bottom disturbance are targeted by a varied assemblage of followers, as seems to be the case of *P. barberinus* at Lizard Island (Lukoschek & McCormick, 2000) and *P. maculatus* at Noronha (present study).

ACKNOWLEDGEMENTS

We thank 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 (C. Bellini and A. Grossman) for logistic support; Keith S. Brown Jr. for improving our English; the Águas Claras and the Atlantis diving centres for allowing free use of their facilities; and CAPES, CNPq, and FAPESP for essential financial support. CS is recipient of scholarships from the CNPq – Brasil. We dedicate this paper to I. Sazima, whose charming, skilful, and open mind showed us the windows for the study of reef fishes and their ways.

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A NON-DIGGING ZOOBENTHIVOROUS FISH ATTRACTS TWO
OPPORTUNISTIC PREDATORY FISH ASSOCIATES

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Key words: nuclear forager, following behaviour, foraging association, reef fishes,
Equatorial West Atlantic

ABSTRACT. Following behaviour among reef fishes involves mostly a digging nuclear species while foraging, which attracts opportunistic followers preying on the exposed organisms. The flying gurnard *Dactylopterus volitans* preys on benthic animals, mostly crustaceans and small fishes, scratching and probing the bottom with the inner rays of its pectoral fins. We recorded the flying gurnard being followed by two opportunistic predators, the yellow jack *Caranx bartholomaei* and the coney *Cephalopholis fulva* at Fernando de Noronha, off northeast Brazil. Albeit not actually digging the substrate, the flying gurnard acts as a nuclear species by exploring algae tufts and by its wandering near the boulders and ledges, disturbing and flushing out hidden animals which thus become available to predation.

RESUMO. Entre os peixes recifais, uma espécie fossadora nuclear em atividade de forrageamento pode atrair seguidores oportunistas que se alimentam de organismos expostos pela atividade do nuclear. O coió-voador *Dactylopterus volitans* alimenta-se de animais bentônicos, principalmente crustáceos e pequenos peixes, explorando o substrato com os primeiros raios externos de suas nadadeiras peitorais. Registramos o coió sendo seguido por dois predadores oportunistas, a guarajuba *Caranx bartholomaei* e a piraúna *Cephalopholis fulva*, em Fernando de Noronha, ao largo da costa Nordeste do Brasil. Apesar de não agir como uma espécie fossadora do substrato, o coió atua como uma espécie nuclear por explorar os tufos de algas e também pela sua passagem próxima às rochas e lajes, espantando e desentocando animais escondidos que, assim, tornam-se vulneráveis aos predadores.

Reef fishes may form temporary feeding associations with other vertebrates as diverse as dolphins and turtles (Sazima et al., 2003; Sazima et al., 2004), but mostly associate with other fishes (Hobson, 1974; Fricke, 1975; Fishelson, 1977). Foraging associations are widespread among reef fishes and include examples as diverse as cleaning symbiosis, foraging groups of browsers, aggressive mimicry and following (Fishelson, 1977; Losey, 1978; Ormond, 1980; Lukoschek & McCormick, 2000).

Following behaviour comprises mostly a ‘nuclear’ predator stirring the bottom during its foraging, and opportunistic ‘follower’ fishes that are attracted by this activity (Fricke, 1975; Strand, 1988; Soares & Barreiros, 2003; Sazima et al., 2005a). The

digging movements of a nuclear species usually attract these opportunistic fishes that feed on the exposed items (Fishelson, 1977; Ormond, 1980). The “clouds” of stirred sediment and the specific features of the nuclear fish are visual signals that seem to influence the followers’ behaviour (Fricke, 1975; Fishelson, 1977; Diamant & Shpigel, 1985).

Albeit not actually digging in the substrate, the flying gurnard *Dactylopterus volitans* (Dactylopteridae) scratches and probes the bottom with the inner rays of its pectoral fins (Randall, 1968; Nelson, 1994). Herein we report on the association of the flying gurnard, and its opportunistic followers, the yellow jack, *Caranx bartholomaei* (Carangidae) and the coney, *Cephalopholis fulva* (Serranidae) at the Fernando de Noronha Archipelago, off North-eastern Brazil.

The associations were recorded at the Fernando de Noronha Archipelago (03°50’S, 32°25’W), about 345 km off NE Brazil (see Maida & Ferreira, 1997 for map and description). Behavioural interactions between *D. volitans* and its followers were recorded at the Baía do Sueste (for *C. bartholomaei*) and Praia da Conceição (for *C. fulva*), in August 2002 and June 2003 respectively. The first site has a sandy and gravel bottom interspersed with rocky ledges that are sparsely to thickly covered by brown foliose algae, red coralline algae and stony corals (see description and illustrations in Maida et al., 1995; Maida & Ferreira, 1997; Sanches & Bellini, 1999). The second site is a rocky shore with an adjacent sand flat, boulders and ledges covered mostly by green, brown and red algae, stony corals and fine sediment (I. Sazima, pers. comm.).

We recorded the associations while snorkelling, in two observation sessions, totalling 50 min of direct observation. We used focal animal samplings, in which all occurrences of specified actions were recorded (Altmann, 1974; Lehner, 1979). Besides records pencilled on plastic slates, behavioural events were photographed. During our observations we followed the wandering *D. volitans* individuals (N=2) and recorded the fish species that were associated with this nuclear. We tried not to disturb the foraging *D. volitans* or its followers, keeping a distance of 1.5 to 2.5 m from the observed individuals (see also Soares & Barreiros, 2003). Observation sessions were concentrated in the daytime.

We recorded two instances of following behaviour involving foraging individuals of *D. volitans*. In one record a *Caranx bartholomaei* (25 cm total length, TL) escorted the

flying gurnard (20 cm TL) for about 20 seconds as it moved over a gravel substrate (Fig. 1). The second and more complete record on the flying gurnard foraging behaviour lasted about 20 minutes. Three individuals of *Cephalopholis fulva* (about 20 cm TL) followed the foraging *D. volitans* (30 cm TL) as it swam close to the bottom, inspecting algae tufts attached to the rocks. One *C. fulva* individual followed the flying gurnard for about 40 seconds, whereas the others left it after about 10 seconds.



Figure 1. The flying gurnard (*Dactylopterus volitans*; 20 cm TL) wandering close to the gravel substrate with its characteristic dotted coloration, escorted by a yellow jack (*Caranx bartholomaei*; 25 cm TL).

On both records the flying gurnard wandered on the edge of the rocky reef inspecting mostly the rocky substrate as well as the sandy bottom. It displayed its characteristic dotted pattern of coloration while swimming or walking over rocky or gravel substrate (Fig. 1) but turned whitish while over sandy areas.

Some serranids are considered territorialist at some extent, or even aggressive (Froese & Pauly, 2005). However, the *C. fulva* individuals which simultaneously followed the flying gurnard displayed none aggressive interactions. Although *C. bartholomaei* could also be expected to display agonistic behaviour towards conspecifics, no other

individual attempted to approach the flying gurnard during our record. The foraging nuclear could be considered as a ‘moving feeding territory’ and encourage aggressive behaviour among followers, as recorded for *C. bartholomaei* while following the stingray *Dasyatis americana* (Dasyatidae) at Fernando de Noronha (CS, pers. obs.).

Dactylopterus volitans is regarded as a bottom dweller inhabiting coral reefs and able to “walk” over the substrate using its thoracic-placed pelvic fins (Randall, 1968; Nelson, 1994). With the specialised inner rays of its huge fan-like pectoral fins, the flying gurnard scratches and probes in the sand and/or turn over small rock pieces or rubble while foraging (Randall, 1967, 1968; Smith, 1997). Albeit not actually digging in the substrate while foraging, the flying gurnard plays the role of a nuclear predator and attracts attendant associates (see Lukoschek & McCormick, 2000 for a classification of following associations). The flying gurnard’s role as a nuclear species resembles that of some large parrotfishes (Scaridae) and triggerfishes (Balistidae) which break up coral, lift and turn over stones and rubble, and thus attract mainly small wrasses (Labridae) that prey on the disturbed small benthic organisms, stirred particles and even faeces (Ormond, 1980; Sazima et al., 2005a).

The flying gurnard feeds primarily on benthic crustaceans and small fishes (Randall, 1967; Froese & Pauly, 2005), and we observed benthic animals disturbed by the wandering *D. volitans*, especially juvenile and/or small fishes, that withdrew upon its approach. Therefore, several prey become potentially available to opportunistic followers by the mere wandering of a flying gurnard. Therefore, *D. volitans* plays the role of a nuclear species not only while exploring algae tufts, pieces of rocks and rubble, but also while simply wandering on the reef, as in both situations it may disturb potential prey for its followers.

Species of *Caranx* may be considered as highly piscivorous predators (Randall, 1967), but some of these also display opportunistic feeding, with variable foraging tactics (Potts, 1980; Baird, 1993; Silvano, 2001). Moreover, *Caranx latus*, *C. melampygus* and *C. ruber*, were recorded acting as followers of nuclear predators (e.g., Potts, 1980; Baird, 1993; Silvano, 2001). Thus, *C. bartholomaei*, which additionally forages mostly near the bottom (Randall, 1967; CS, pers. obs.), would be expected to behave as a follower of nuclear species, in accordance with the opportunistic foraging known for several Carangidae species (Potts, 1980; Sazima, 1998).

Jacks are rovers, whereas groupers (Serranidae) are mostly sedentary and sit-and-wait predators (Randall, 1967). However, groupers are also versatile followers, which associate with diverse species of reef fishes including eels, and also octopuses and sea stars (Karplus, 1978; Diamant & Shpigel, 1985; Gibran, 2002). *Cephalopholis fulva*, already recorded as a follower (Francini-Filho et al., 2000; Gibran, 2002; Froese & Pauly, 2005), inhabits reef areas where it hides under ledges or inside caves, feeding on small fishes and crustaceans (Randall, 1967; Francini-Filho et al., 2000; Froese & Pauly, 2005). Being an inquisitive, alert and opportunistic predator, as other epinepheline groupers (Karplus, 1978; Diamant & Shpigel, 1985; Sazima et al., 2005b), the coney would be expected to inspect almost every moving animal, the more so a foraging flying gurnard.

Foraging associations in fishes can be highly diverse and complex, involving interactions between members of different trophic groups (Lukoschek & McCormick, 2000; Sazima et al., 2004, 2005a). The searobin *Prionotus punctatus* (Triglidae) is also a carnivorous species, with foraging behaviour similar to that displayed by *D. volitans* (Carvalho-Filho, 1999; Froese & Pauly, 2005), thus herein suggested as a potential nuclear species. Also, we suggest that additional reef fish species might associate with foraging *D. volitans*. Wrasses (Labridae), such as *Halichoeres dimidiatus*, *H. poeyi* and *H. radiatus*, highly versatile species and opportunistic foragers (Sazima et al., 1998; Jones, 2002; CS, pers. obs.), are likely such candidates.

ACKNOWLEDGEMENTS

We thank the Projeto Tamar and the Centro Golfinho Rotador (through J.M. Silva-Jr.) for logistical support at Fernando de Noronha Archipelago; the Ibama for issuing study permits at the Fernando de Noronha Archipelago; FAPESP and Fundação Pró-Tamar for financial support. CS is recipients of scholarship from the CNPq – Brasil.

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CAPÍTULO 4

INTERSPECIFIC FORAGING ASSOCIATIONS OF REEF FISHES AND OTHER ANIMALS AT AN OCEANIC ARCHIPELAGO, WITH AN OVERVIEW OF NUCLEAR-FOLLOWER ASSOCIATIONS

ARTIGO SUBMETIDO:

**Sazima C., Krajewski, J.P., Bonaldo, R.M. & Sazima, I. Environmental Biology
of Fishes.**

INTERSPECIFIC FORAGING ASSOCIATIONS OF REEF FISHES AND OTHER
ANIMALS AT AN OCEANIC ARCHIPELAGO, WITH AN OVERVIEW OF
NUCLEAR-FOLLOWER ASSOCIATIONS

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Key words: feeding assemblages, following behaviour, Mullidae, Labridae, Serranidae,
tropical West Atlantic

ABSTRACT. Several fish species in many families and different trophic levels forage by following diverse fish species and other animals. This interspecific foraging association was examined at an oceanic archipelago in the tropical West Atlantic. We recorded 28 reef fish species, two invertebrate species, and one turtle species playing the nuclear role, and 27 reef fish species acting as followers. The puddingwife wrasse following the spotted goatfish was the commonest foraging association recorded. The spotted goatfish was the nuclear fish that attracted the largest number of follower species (68% of the total number of follower species), whereas the coney and the Noronha wrasse were the follower species that associated with the largest number of nuclear species (63% and 55% of the total number). About 20% of the reef fish species recorded in the archipelago engage in interspecific foraging associations. Substratum disturbance is a strong predictor for a fish displaying the nuclear role in the association, whereas the follower role may be predicted by carnivory. Additionally, we reviewed published examples of interspecific foraging associations in reef fishes and indicate here some trends for this foraging mode. Two speciose families (Serranidae and Labridae) contain most of the examples of follower fishes, whereas the nuclear ones are mostly represented by four families (Muraenidae, Mullidae, Labridae and Scaridae). Several families (~40%) that contain follower fishes also contain nuclear fishes, 43 species (~20%) acting in both roles.

INTRODUCTION

Reef fishes form temporary feeding associations by following other animals (Hobson, 1968; Strand, 1988; Lukoschek & McCormick, 2000). So called following association comprises a nuclear species disturbing the bottom while foraging, and opportunistic follower species that feed on the exposed items (Fricke, 1975; Lukoschek & McCormick, 2000; Sazima et al., in press). The nuclear role is mostly displayed by fishes, but octopuses, sea-stars, and turtles are recorded in such activity as well (Diamant & Shpigel, 1985; Gibran, 2002; Sazima et al., 2004). Following behaviour is widespread and recorded for many reef fish species of most trophic groups (e.g., Lukoschek & McCormick, 2000; Auster & Lindholm, 2002; Sazima et al., in press).

Among reef fishes, nuclear species are mainly predatory carnivores and occasionally herbivores from the Acanthuridae and Scaridae (Ormond, 1980; Lukoschek & McCormick, 2000; Sazima et al., 2005). Followers are usually carnivores or opportunistic feeding species, but this role includes some herbivores (Strand, 1988; Lukoschek & McCormick, 2000; Sazima et al., in press). Opportunistic feeding seems to be a common trait for species recorded in the follower role. Since most fishes tend to be opportunistic and generalists in their feeding habits (Gerking, 1994; Bellwood et al., 2006) the follower assemblages likely are composed of greater number of species than the nuclear ones.

Varied foraging tactics are employed by carnivorous fishes, including disguise, ambush, stalking, and roving (e.g., Sazima, 1986; Gerking, 1994; Krajewski et al., in press). Some species habitually use one or two tactics, whereas others may employ several tactics that vary considerably according to the circumstances (Hobson, 1968; Sazima, 1986; Gerking, 1994). In heterospecific foraging associations, feeding behaviour plasticity seems related to a high tendency of some species joining the nuclear species (Strand, 1988). Thus, carnivore predators with variable foraging tactics likely associate with large number of nuclear species.

Most studies on interspecific foraging associations and following behaviour in reef fishes focus on one or a few nuclear/follower species or a particular kind of association (e.g., Diamant & Shpigel, 1985; Baird, 1993; Sazima et al., in press, but see Ormond, 1980; Strand, 1988; Auster & Lindholm, 2002). The number of species within a local assemblage that engage in such type of association has been largely ignored (but see Auster & Lindholm, 2002). One aim of the present study is to assess the composition, richness, and relative number of species that engage in nuclear and follower feeding roles within a reef fish assemblage in an oceanic archipelago. This kind of information broadens our understanding of the ecological role of foraging associations, as both nuclear and follower species potentially affect the structure and composition of benthic invertebrate assemblages of the reef habitat.

We examine here interspecific foraging associations of reef fishes following nuclear species, especially other fishes at the oceanic archipelago of Fernando de Noronha in the tropical West Atlantic. We sought answers for the following main questions: 1) How many and which species act in the nuclear role? 2) How many and which species

act in the follower role? 3) Which species act most frequently as nuclear or follower in the associations? 4) Which is the commonest interspecific foraging association? 5) Do follower species with variable foraging tactics associate with large numbers of nuclear species? 6) What is the proportion of species in the studied reef fish assemblage that engage in interspecific foraging associations? Besides answering these questions, which contribute towards a more comprehensive framework of interspecific foraging associations in reef fishes, we examined published examples worldwide seeking patterns and trends in such a type of association.

MATERIAL AND METHODS

We recorded interspecific nuclear-follower associations at the oceanic archipelago of Fernando de Noronha (03°50'S, 32°25'W), about 345 km off the coast of north-east Brazil, tropical West Atlantic (see map in Sazima et al., 2005). Study sites were mostly composed of irregular rocky reefs sparsely to thickly covered with green, brown and red algae, hydrocorals, stony corals, colonial zoanthids and fine sand sediment, and adjacent sand flats. The substrata over which most nuclear species foraged consisted of mixed sand, gravel and rocks covered with algae and sessile invertebrates. Our field observations were conducted in June 2001 and 2002, May-July and November 2003, October 2004 and October-November 2005.

The foraging associations were recorded while snorkelling and scuba diving in observation sessions of 30-120 min, totalling 4308 min over 56 non-consecutive days. During the diving sessions we searched haphazardly for interspecific foraging associations and recorded every association observed with use of instantaneous sampling (Altmann, 1974). Records on plastic slates or photographs were used throughout the observation sessions. Foraging associations were recorded in the daytime from morning (0900 h) to afternoon (1800 h). We also conducted a few observations (300 min) from 1830 h to 2030 h searching for night time foraging associations.

Most of our results and discussion are based on our field observations. However, we also gathered data from literature to present some trends of interspecific associations worldwide. We analyzed the most important and complete studies on foraging associations (e.g., Ormond, 1980; Strand, 1988; Lukoschek & McCormick, 2000)

besides general observations on reef fish feeding behaviour (e.g., Hobson, 1968; Fishelson, 1977). We considered only those studies (Appendix 1) that mention clearly that a follower fish species exploits food items exposed or somehow made available by a nuclear species.

A nuclear species is habitually meant as a predator that disturbs or explores the bottom while foraging (e.g., Diamant & Shpigel, 1985; Strand, 1988; Sazima & Grossman, 2005). However, for the purpose of this overview we regard as a nuclear species any fish or other animal that by its foraging or moving on the substratum (or simply voiding in the water column) creates an otherwise unavailable feeding situation to opportunistic fish species. In this sense, a parrotfish is a nuclear species when its faeces are fed upon by other fishes (Sazima et al., 2005). The same applies to a brittle star or a sea star that moves under cover and flushes small invertebrates and fishes from their retreats (Gibran, 2002, present study). Additionally, an herbivore that disturbs the substratum (and stirs particles while foraging) falls within our nuclear category (Sazima et al., 2005). Moreover, in the present overview we regard as a follower species any fish that perceives the feeding conditions created by a nuclear species and forages in its close proximity. Thus, a follower is usually treated as an opportunistic species (e.g., Strand, 1988; Lukoschek & McCormick, 2000; Sazima & Grossman, 2005).

For the reef fish assemblage of Fernando de Noronha two logistic regression analyses (Tabachnick & Fidell, 2001) were performed on the role of the fish species in the feeding association. We considered the nuclear (coded as “nuclear” or “non-nuclear”) and follower (coded as “follower” or “non-follower”) roles as outcomes and five behavioural “predictors”: (1) substratum disturbance, (2) group foraging, (3) bottom foraging, (4) carnivory and (5) herbivory. Substratum disturbance was categorized in increasing levels ranging from 0 (species that forage in the water column) to 3 (species that cause great substratum disturbance while foraging). The other behavioural predictors were classified as “0” for absence and “1” for presence. In the analyses we considered all fish species recorded in heterospecific associations and also fish species that we assumed not to engage in heterospecific associations, haphazardly chosen from the community. Data from 56 species were used in each analysis: 26 nuclear species and 28 non-nuclear ones, and 26 follower species and 28 non-follower ones.

RESULTS

We recorded 28 reef fish species in 16 families, two invertebrate species in two families and one turtle species (totalling 31 species) in the nuclear role, and 26 reef fish species in 14 families in the follower role (Tables 1 and 3) at Fernando de Noronha. Among the foraging associations recorded between fishes, bottom-disturbing carnivores accounted for 74% of the species in the nuclear role, whereas roving or sedentary carnivores accounted for 72% of the species in the follower role (Table 1). Followers of species other than fishes also were mostly (75%) roving or sedentary carnivores (Table 3).

A total of 531 interspecific foraging associations of reef fishes following nuclear species were recorded in the archipelago. From these, 508 associations (95%) had fishes as the nuclear species, the spotted goatfish *Pseudupeneus maculatus* being the most frequent nuclear species (50%, N=258) (Table 2). In 23 associations (5%) octopuses, turtles, or brittle stars were the nuclear species, the octopus *Octopus* sp. being the most frequent nuclear species (82%, N=19) (Table 3). The puddingwife wrasse *Halichoeres radiatus* was the most frequent species following fishes (37%, N=187) (Table 2), whereas the coney *Cephalopholis fulva* was the most frequent species following invertebrates (65%, N=15) (Table 3).

Table 1. Family, species, role in feeding associations, and size range recorded for 36 reef fish species at Fernando de Noronha Archipelago, tropical West Atlantic. In case of double roles, the predominant one is placed first. Taxonomic arrangement of families follows Nelson (1994), genera and species in alphabetical order.

Family	Species	Role	Size range (cm)
Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	Nuclear	100-150
Dasyatidae	<i>Dasyatis americana</i>	Nuclear	37-120
Albulidae	<i>Albula</i> cf. <i>vulpes</i>	Nuclear	25-30
Muraenidae	<i>Gymnothorax funebris</i>	Nuclear	120-150

	<i>Gymnothorax vicinus</i>	Nuclear	35-85
	<i>Muraena pavonina</i>	Nuclear	28-70
Ophichthidae	<i>Myrichthys ocellatus</i>	Nuclear	37-70
Aulostomidae	<i>Aulostomus strigosus</i>	Follower	30-60
Dactylopteridae	<i>Dactylopterus volitans</i>	Nuclear/Follower	28-30
Serranidae	<i>Cephalopholis fulva</i>	Follower/Nuclear	10-30
	<i>Rypticus saponaceus</i>	Nuclear	27
Malacanthidae	<i>Malacanthus plumieri</i>	Nuclear/Follower	10-30
Carangidae	<i>Caranx bartholomaei</i>	Follower/Nuclear	25-45
	<i>Caranx crysos</i>	Follower/Nuclear	20-35
	<i>Caranx latus</i>	Follower	10-100
Lutjanidae	<i>Lutjanus jocu</i>	Follower	40
Haemulidae	<i>Anisotremus surinamensis</i>	Nuclear/Follower	11-70
	<i>Haemulon chrysargyreum</i>	Follower/Nuclear	8-18
	<i>Haemulon parra</i>	Nuclear/Follower	8-38
Mullidae	<i>Mulloidichthys martinicus</i>	Nuclear/Follower	16-26
	<i>Pseudupeneus maculatus</i>	Nuclear/Follower	10-30
Pomacentridae	<i>Abudefduf saxatilis</i>	Follower	7-10
Labridae	<i>Halichoeres dimidiatus</i>	Follower/Nuclear	5-20
	<i>Halichoeres radiatus</i>	Follower/Nuclear	6-30
	<i>Thalassoma noronhanum</i>	Follower	4-14
Scaridae	<i>Sparisoma amplum</i>	Nuclear/Follower	23-55
	<i>Sparisoma axillare</i>	Nuclear/Follower	14-50
	<i>Sparisoma frondosum</i>	Nuclear/Follower	20-50
Labrisomidae	<i>Labrisomus cf. nuchipinnis</i>	Follower	10-14
	<i>Malacoctenus sp.</i>	Follower	5-7

Acanthuridae	<i>Acanthurus chirurgus</i>	Nuclear/Follower	8-35
	<i>Acanthurus coeruleus</i>	Follower/Nuclear	8-35
Monacanthidae	<i>Aluterus scriptus</i>	Nuclear	50
Ostraciidae	<i>Lactophrys trigonus</i>	Nuclear/Follower	26-40
	<i>Acanthostracion polygonius</i>	Nuclear	20-30

Table 2. Nuclear fish species, their social behaviour while followed, and their follower fish species at Fernando de Noronha Archipelago, tropical West Atlantic. Numbers are absolute and relative frequencies (%) of associated fish species, where N= 508 recorded associations. Each nuclear species and its follower species in decreasing order of relative frequency of occurrence in the associations. Where social behaviour is double, the prevalent one is placed first. For family of each fish species, see Table 1.

Nuclear species	N (%)	Social behaviour	Follower species	N (%)
<i>Pseudupeneus maculatus</i>	258 (50.78)	Single, grouped	<i>Halichoeres radiatus</i>	149 (29.33)
			<i>Cephalopholis fulva</i>	88 (17.32)
			<i>Caranx bartholomaei</i>	44 (8.66)
			<i>Caranx latus</i>	35 (6.88)
			<i>Sparisoma axillare</i>	15 (2.95)
			<i>Thalassoma noronhanum</i>	9 (1.77)
			<i>Halichoeres dimidiatus</i>	7 (1.38)
			<i>Acanthurus coeruleus</i>	7 (1.38)
			<i>Acanthurus chirurgus</i>	6 (1.18)
			<i>Haemulon parra</i>	5 (0.98)
			<i>Aulostomus strigosus</i>	5 (0.98)
			<i>Anisotremus surinamensis</i>	4 (0.78)
<i>Sparisoma frondosum</i>	4 (0.78)			

			<i>Haemulon chrysargyreum</i>	2 (0.39)
			<i>Malacanthus plumieri</i>	2 (0.39)
			<i>Mulloidichthys martinicus</i>	1 (0.19)
			<i>Sparisoma amplum</i>	1 (0.19)
<i>Sparisoma frondosum</i>	52 (10.23)	Single	<i>Thalassoma noronhanum</i>	50 (9.84)
			<i>Anisotremus surinamensis</i>	1 (0.19)
			<i>Halichoeres dimidiatus</i>	1 (0.19)
<i>Dasyatis americana</i>	26 (5.11)	Single	<i>Caranx bartholomaei</i>	20 (3.93)
			<i>Caranx latus</i>	2 (0.39)
			<i>Cephalopholis fulva</i>	2 (0.39)
			<i>Halichoeres radiatus</i>	2 (0.39)
			<i>Halichoeres dimidiatus</i>	1 (0.19)
			<i>Dactylopterus volitans</i>	1 (0.19)
			<i>Lactophrys trigonus</i>	1 (0.19)
<i>Sparisoma axillare</i>	25 (4.92)	Single	<i>Thalassoma noronhanum</i>	25 (4.92)
<i>Haemulon parra</i>	24 (4.72)	Single, grouped	<i>Thalassoma noronhanum</i>	20 (3.93)
			<i>Halichoeres radiatus</i>	7 (1.38)
			<i>Halichoeres dimidiatus</i>	2 (0.39)
			<i>Caranx latus</i>	1 (0.19)
			<i>Cephalopholis fulva</i>	1 (0.19)
<i>Mulloidichthys martinicus</i>	23 (4.52)	Single, grouped	<i>Halichoeres radiatus</i>	20 (3.93)
			<i>Cephalopholis fulva</i>	3 (0.59)
			<i>Halichoeres dimidiatus</i>	2 (0.39)
			<i>Thalassoma noronhanum</i>	2 (0.39)
<i>Sparisoma amplum</i>	15 (2.95)	Single	<i>Thalassoma noronhanum</i>	15 (2.95)
<i>Anisotremus surinamensis</i>	11 (2.16)	Single, grouped	<i>Thalassoma noronhanum</i>	5 (0.98)

			<i>Caranx latus</i>	4 (0.78)
			<i>Caranx bartholomaei</i>	1 (0.19)
			<i>Halichoeres radiatus</i>	1 (0.19)
<i>Acanthurus chirurgus</i>	10 (1.97)	Grouped	<i>Pseudupeneus maculatus</i>	5 (0.98)
			<i>Caranx bartholomaei</i>	3 (0.59)
			<i>Haemulon parra</i>	3 (0.59)
			<i>Haemulon chrysargyreum</i>	2 (0.39)
			<i>Aulostomus strigosus</i>	2 (0.39)
			<i>Cephalopholis fulva</i>	1 (0.19)
			<i>Anisotremus surinamensis</i>	1 (0.19)
			<i>Sparisoma amplum</i>	1 (0.19)
<i>Gymnothorax vicinus</i>	9 (1.77)	Single	<i>Caranx bartholomaei</i>	7 (1.38)
			<i>Cephalopholis fulva</i>	6 (1.18)
			<i>Pseudupeneus maculatus</i>	1 (0.19)
			<i>Haemulon parra</i>	1 (0.19)
			<i>Halichoeres radiatus</i>	1 (0.19)
			<i>Acanthurus coeruleus</i>	1 (0.19)
<i>Lactophrys trigonus</i>	9 (1.77)	Single	<i>Thalassoma noronhanum</i>	8 (1.57)
			<i>Halichoeres radiatus</i>	3 (0.59)
			<i>Malacoctenus sp.</i>	1 (0.19)
<i>Acanthurus coeruleus</i>	6 (1.18)	Grouped	<i>Caranx bartholomaei</i>	2 (0.39)
			<i>Thalassoma noronhanum</i>	2 (0.39)
			<i>Aulostomus strigosus</i>	1 (0.19)
			<i>Cephalopholis fulva</i>	1 (0.19)
			<i>Pseudupeneus maculatus</i>	1 (0.19)
			<i>Abudefduf saxatilis</i>	1 (0.19)

			<i>Anisotremus surinamensis</i>	1 (0.19)
			<i>Haemulon parra</i>	1 (0.19)
			<i>Sparisoma amplum</i>	1 (0.19)
<i>Acanthostracion polygonius</i>	6 (1.18)	Single	<i>Thalassoma noronhanum</i>	6 (1.18)
<i>Muraena pavonina</i>	5 (0.98)	Single	<i>Cephalopholis fulva</i>	3 (0.59)
			<i>Labrisomus cf. nuchipinnis</i>	2 (0.39)
			<i>Caranx latus</i>	1 (0.19)
<i>Halichoeres radiatus</i>	5 (0.98)	Single	<i>Cephalopholis fulva</i>	2 (0.39)
			<i>Pseudupeneus maculatus</i>	2 (0.39)
			<i>Thalassoma noronhanum</i>	2 (0.39)
<i>Malacanthus plumieri</i>	4 (0.78)	Single	<i>Halichoeres radiatus</i>	2 (0.39)
			<i>Halichoeres dimidiatus</i>	1 (0.19)
			<i>Thalassoma noronhanum</i>	1 (0.19)
<i>Caranx bartholomaei</i>	3 (0.59)	Single, grouped	<i>Cephalopholis fulva</i>	3 (0.59)
<i>Haemulon chrysargyreum</i>	3 (0.59)	Grouped, single	<i>Caranx latus</i>	1 (0.19)
			<i>Mulloidichthys martinicus</i>	1 (0.19)
			<i>Halichoeres radiatus</i>	1 (0.19)
			<i>Thalassoma noronhanum</i>	1 (0.19)
<i>Ginglymostoma cirratum</i>	2 (0.39)	Single	<i>Caranx bartholomaei</i>	2 (0.39)
			<i>Cephalopholis fulva</i>	1 (0.19)
			<i>Lutjanus jocu</i>	1 (0.19)
<i>Albula cf. vulpes</i>	2 (0.39)	Grouped	<i>Caranx crysos</i>	1 (0.19)
			<i>Abudefduf saxatilis</i>	1 (0.19)
<i>Gymnothorax funebris</i>	2 (0.39)	Single	<i>Cephalopholis fulva</i>	1 (0.19)
			<i>Caranx bartholomaei</i>	1 (0.19)
<i>Myrichthys ocellatus</i>	2 (0.39)	Single	<i>Cephalopholis fulva</i>	1 (0.19)

<i>Halichoeres dimidiatus</i>	2 (0.39)	Single	<i>Halichoeres radiatus</i>	1 (0.19)
			<i>Thalassoma noronhanum</i>	1 (0.19)
<i>Dactylopterus volitans</i>	1 (0.19)	Single	<i>Cephalopholis fulva</i>	1 (0.19)
<i>Cephalopholis fulva</i>	1 (0.19)	Single	<i>Thalassoma noronhanum</i>	1 (0.19)
<i>Rypticus saponaceus</i>	1 (0.19)	Single	<i>Cephalopholis fulva</i>	1 (0.19)
<i>Aluterus scriptus</i>	1 (0.19)	Single	<i>Aulostomus strigosus</i>	1 (0.19)
			<i>Cephalopholis fulva</i>	1 (0.19)

Table 3. Nuclear species other than reef fishes and their follower fish species at Fernando de Noronha Archipelago, tropical West Atlantic. Numbers are absolute and relative frequencies (%) of associated fish species, where N= 23 recorded associations. Each nuclear species and its follower species in decreasing order of relative frequency of occurrence in the associations.

Nuclear species	N (%)	Follower species	N (%)
Octopodidae (octopuses)	19 (82.6)	<i>Cephalopholis fulva</i>	14 (60.87)
<i>Octopus</i> sp.n.		<i>Halichoeres radiatus</i>	4 (17.39)
		<i>Pseudupeneus maculatus</i>	3 (13.04)
		<i>Caranx bartholomaei</i>	2 (8.7)
		<i>Caranx latus</i>	1 (4.34)
Cheloniidae (sea turtles)	2 (8.7)	<i>Pomacanthus paru</i>	1 (4.34)
<i>Eretmochelys imbricata</i>		<i>Halichoeres radiatus</i>	1 (4.34)
		<i>Thalassoma noronhanum</i>	1 (4.34)
Ophiidermatidae (brittle stars)	2 (8.7)	<i>Cephalopholis fulva</i>	1 (4.34)
<i>Ophioderma appressum</i>		<i>Malacoctenus</i> sp.	1 (4.34)

Pseudupeneus maculatus followed by *H. radiatus* was the most frequently recorded association, accounting for about 29% of all associations between fishes (Table 2). The same goatfish species followed by the coney *Cephalopholis fulva* was another common association (about 17%) (Table 2). The Noronha wrasse *Thalassoma noronhanum* as a follower of an herbivore, the parrotfish *Sparisoma frondosum*, ranked third in frequency (about 10%) (Table 2). Other associations had an occurrence of less than 10% each (Table 2).

Pseudupeneus maculatus was the nuclear fish that attracted the largest number of follower species, a total of 17 (about 68% of the total number of followers of fishes only) (Table 2). The coney *C. fulva* was the follower fish that associated with the largest number of nuclear species (17, about 63% of the total number of nuclear fish species). Two wrasse species, *T. noronhanum* and *H. radiatus*, also associated with a large number of nuclear fish species (15, about 55% and 10, about 37% respectively). The remainder follower species were recorded associated with less than 30% of the total number of nuclear fish species.

From the about 170 reef fish species recorded in the archipelago (Soto, 2001; A. Carvalho-Filho, pers. comm.), nearly 20% of these engage in interspecific foraging associations, playing the nuclear or the follower roles. About 50% of the bottom-disturbing carnivores and/or herbivores play the role of nuclear fishes in the interspecific foraging associations. On the other hand, about 25% of the roving or sedentary carnivores play the role of followers.

For the nuclear role logistic regression analyses, a test of the full model with all five predictors against a constant-only model was statistically reliable ($X^2 = 53.75$; $df = 5$; $p < 0.001$), which indicates that the predictors, as a set, distinguish between nuclear and non-nuclear species. The variance accounted by the model is high ($\rho^2 = 0.72$) and overall prediction success was also high (87%). However, only substratum disturbance (t-ratio = 38.46, $p < 0.001$; odds ratio = 8604055.68; regression coefficient = $B = 15.96$) and carnivory (t-ratio = 14.41, $p < 0.001$; odds ratio = 3387.4; $B = 8.12$) reliably predicted the nuclear role in the association. This indicates that the substratum disturbance is the strongest reliable predictor of the nuclear role in a foraging association.

For the follower role logistic regression analyses, a test of the full model with all five predictors against a constant-only model was statistically reliable ($X^2 = 15.82$, $df = 5$; $p < 0.01$), which indicates that the predictors, as a set, distinguish between follower and non-follower species. The variance accounted by the model is small ($\rho^2 = 0.21$) and overall prediction success was 62%. Only carnivory (t-ratio = 18.18, $p < 0.001$; odds ratio = 2239.93, $B = 7.71$) predicted the follower role in the association. Thus, although carnivory apparently predicts the follower role in the association, no behavioural predictors here examined can compose a model that strongly predicts the follower role in a foraging association.

During our night dives we observed the stingray *Dasyatis americana* in foraging activity ($N=5$). This ray is an important nuclear species for many followers at daytime (Table 2), and its night time foraging behaviour is similar to the observed during the day, excavating portions of the sand flat while searching for small invertebrates and fishes. This stingray was the only nuclear species we recorded foraging at night, but we observed no followers at night time.

Considering interspecific associations between fishes only, half of the species was recorded in both roles, i.e., as nuclear and follower ones. However, this switch was mostly recorded in different foraging bouts (i.e., rarely a nuclear species switched to the follower role in the same occasion). The most important nuclear species, *P. maculatus*, was recorded as follower of four nuclear species, including herbivores (Table 2). Highly opportunistic carnivores such as the coney *C. fulva* and the yellow jack *Caranx bartholomaei*, mainly recorded as followers, were also recorded in the nuclear role. Species of Haemulidae and Labridae commonly switched between the two roles.

In our study, four families (Carangidae, Haemulidae, Labridae, and Scaridae) accounted for 48% of the follower species (Fig. 1a). The remaining 52% were spread over 10 families (Fig. 1a). The proportion of species in each family that played the follower role was mostly high, 25% or more (Fig. 1a). The situation worldwide is somewhat different, as follower species are mostly represented by two families, Labridae and Serranidae (about 26% and 13% respectively) (Fig. 1b). The remaining 60% is spread over 25 families (Fig. 1b). The proportion of species in each family that play the follower role worldwide is usually low, including the two most speciose families, Labridae and Serranidae (Fig. 1b).

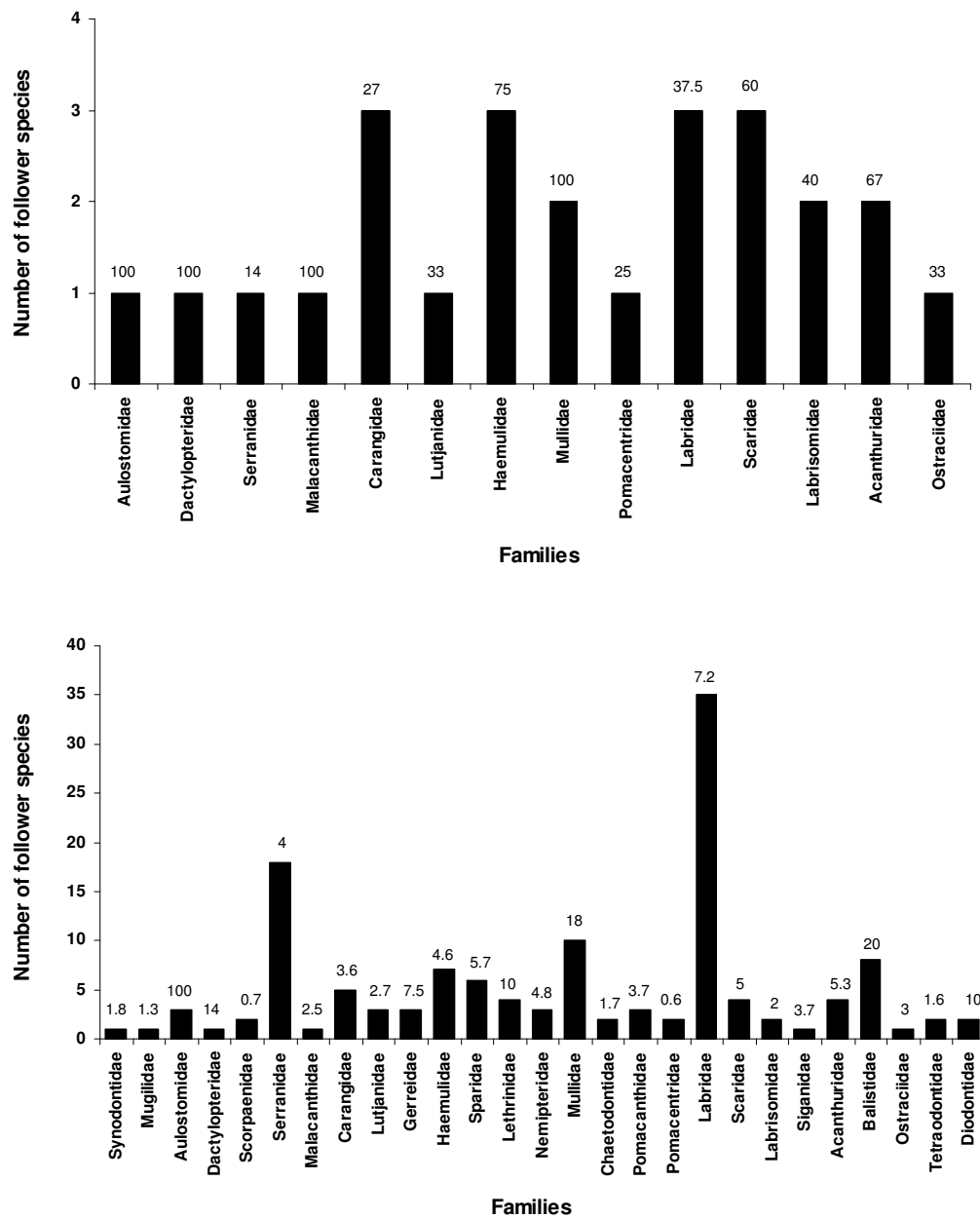


Figure 1. Above: Number of reef fish species recorded as followers of nuclear fishes at Fernando de Noronha. Numbers above each column is the proportion (%) of follower species recorded for each fish family in the archipelago. Number of follower species based on present study. Proportions calculated from data on fish species richness from the archipelago (Soto, 2001; A. Carvalho-Filho, pers. comm.). Below: Number of reef fish species recorded as followers of nuclear fishes worldwide. Numbers above each column is the proportion (%) of follower species recorded for each fish family. Number of follower species drawn from literature (Appendix 1) and present study. Proportions

calculated from data on fish species richness in Nelson (1994), Froese & Pauly (2006), and Munday & Jones (1998).

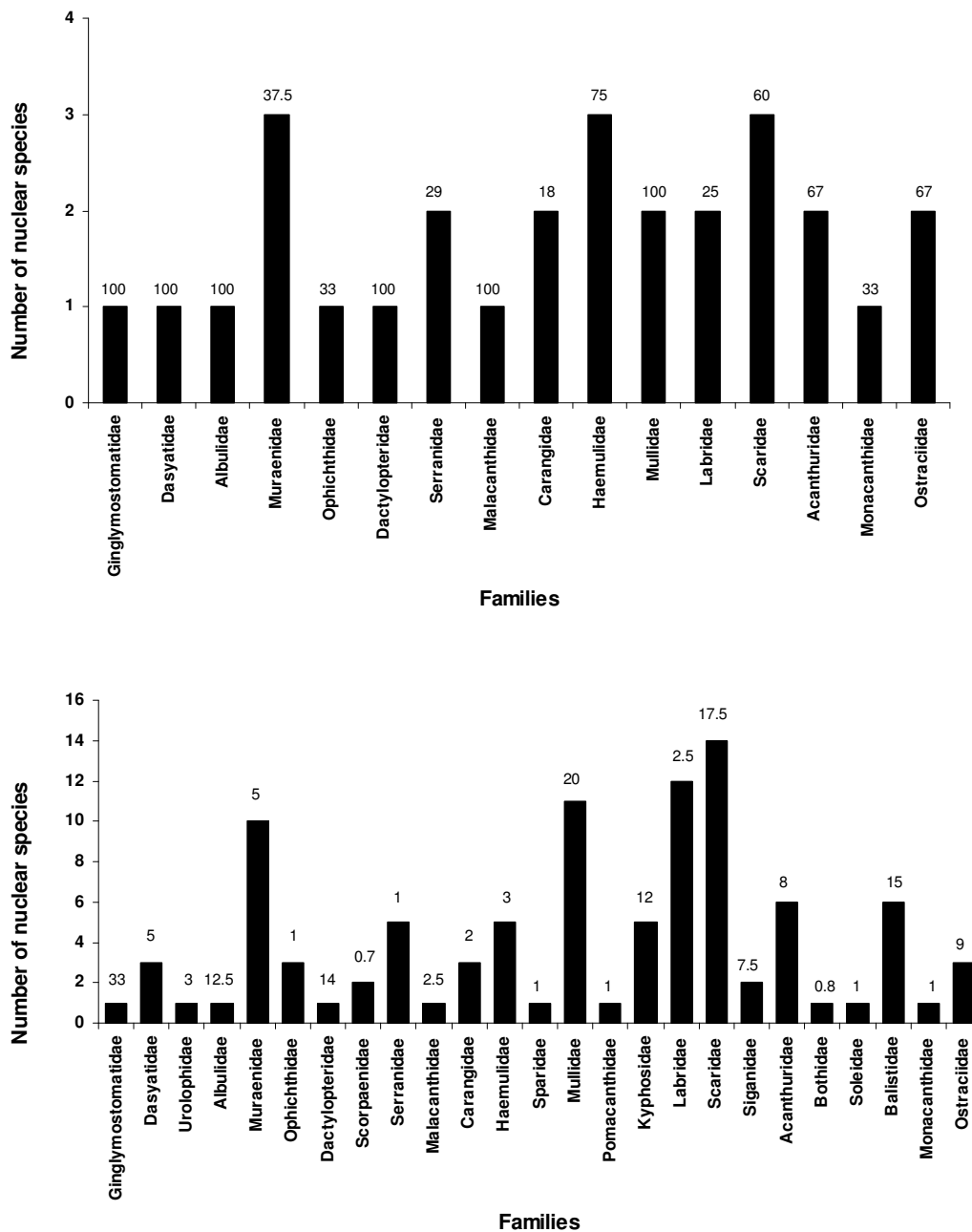


Figure 2. Above: Number of reef fish species recorded in the nuclear role in foraging associations at Fernando de Noronha. Numbers above each column is the proportion (%) of nuclear species recorded for each fish family in the archipelago. Number of

nuclear fish species based on present study. Proportions calculated from data on fish species richness from the archipelago (Soto, 2001; A. Carvalho-Filho, pers. comm.). Below: Number of reef fish species recorded in the nuclear role in foraging associations worldwide. Numbers above each column is the proportion (%) of follower species recorded for each fish family. Number of follower species is drawn from literature (Appendix 1) and present study. Proportions calculated from data on fish species richness in Nelson (1994), Froese & Pauly (2006), and Munday & Jones (1998).

At Fernando de Noronha three families (Muraenidae, Haemulidae and Scaridae) accounted for about 30% of the species recorded in the nuclear role, but several families also were well represented as the remaining 70% was spread over only 13 ones (Fig. 2a). The proportion of species that played the nuclear role in each family was usually high, 25% or more (Fig. 2a). On the other hand, about a half (47%) of nuclear species worldwide is represented by four families (Muraenidae, Mullidae, Labridae and Scaridae) (Fig. 2b). The remaining 53% is spread over 21 families (Fig. 2b). Mullidae and Scaridae, two of the four most represented families among nuclear fishes worldwide, have high proportion of species acting in this role (Fig. 2b).

We chose four types of nuclear fishes as representative of our study (Fig. 3). The spotted goatfish *P. maculatus* (Fig. 3a) represents the commonest nuclear species in foraging associations (Table 2). This goatfish may forage single or in small to large groups of up to 36 individuals and is a very active substratum-disturbing ubiquitous fish, which attracts a large and diverse array of follower species (Table 2). Moray eels (Fig. 3b) and snake eels played the nuclear role infrequently (Table 2), and were recorded mostly wandering on the reef unescorted. However, as these fishes habitually explore crevices and poke in holes, their hunting behaviour expose prey that other carnivores would not reach otherwise. Grazers, mainly *Sparisoma* species (Fig. 3c), were conspicuous in the reef fish assemblage and foraged throughout the day, scraping algae and other encrusting organisms from the bottom, and acted as important nuclear fishes for some followers (Table 2). Additionally, their faeces were used as food by one follower, the wrasse *T. noronhanum*. The stingray *D. americana* was recorded to forage single in our study, but nevertheless it disturbed large portions of the sandy bottom while foraging and thus raised large and well visible clouds of stirred sediment, thus

attracting several follower species (Fig. 3d). Among the nuclear species other than fishes, the octopus *Octopus* sp. was regularly followed by opportunistic carnivores (Table 3). The octopus foraged by entering holes and crevices in the rocks or poking its arms into interstices of the reef. Additionally, it frequently wrapped a rock with its mantle and thus prevented potential prey to evade.

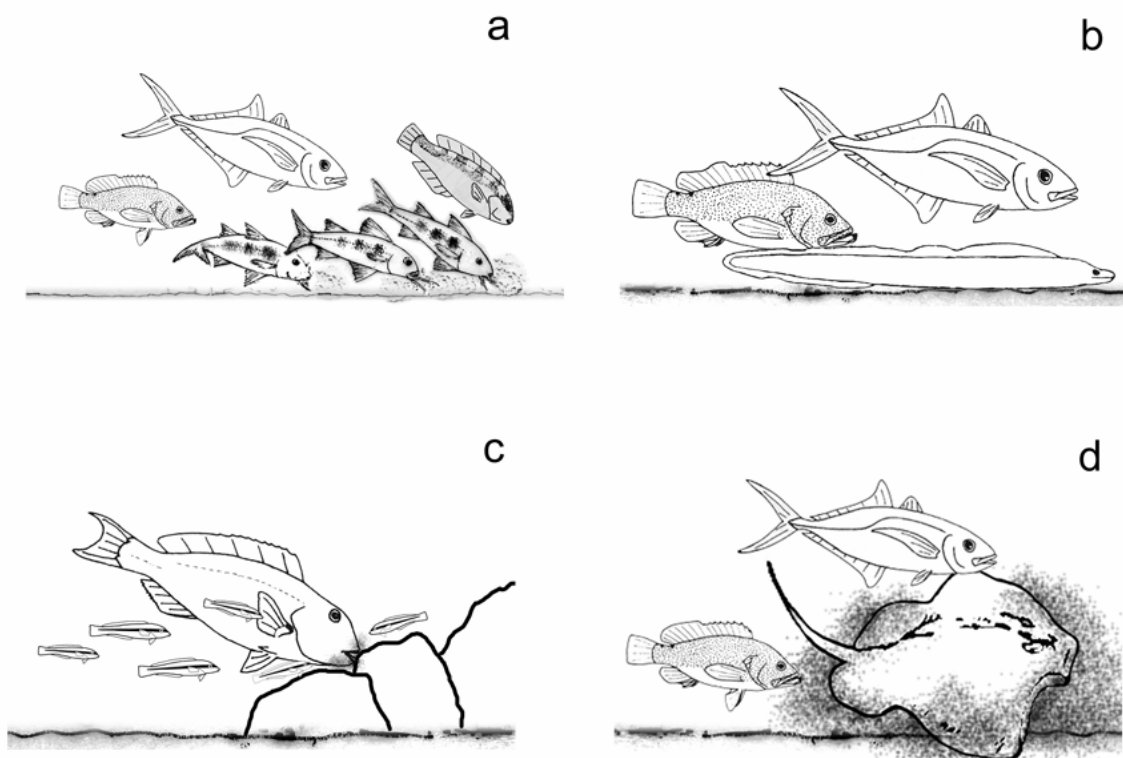


Figure 3. Nuclear fishes representative of the present study at Fernando de Noronha Archipelago, tropical West Atlantic. (a). The spotted goatfish *Pseudupeneus maculatus* foraging as a small group followed by the puddingwife wrasse *Halichoeres radiatus*, the yellow jack *Caranx bartholomaei*, and the coney *Cephalopholis fulva*. (b). The purplemouth moray *Gymnothorax vicinus* closely followed by the yellow jack *Caranx bartholomaei* and the coney *Cephalopholis fulva*. (c). A foraging Agassiz's parrotfish *Sparisoma frondosum* surrounded by a small group of the Noronha wrasse *Thalassoma noronhanum*. (d) A foraging southern stingray *Dasyatis americana* escorted by a yellow jack *Caranx bartholomaei* and a coney *Cephalopholis fulva* while stirring sand and other particles.

DISCUSSION

Our study has the broadest coverage of nuclear-follower foraging associations at a tropical reef assemblage to date. This coverage accounts for the variety (brittle-stars to turtles) and the number of species involved in such interspecific foraging association. A study on interspecific foraging associations in a temperate rocky reef in the Gulf of California, with a similarly broad coverage (Strand, 1988), records 21 nuclear species and 17 followers. The ratio between follower and nuclear species is 0.80 in the Gulf of California and 0.84 in Fernando de Noronha (present study). Additional studies on interspecific foraging associations in both tropical and temperate sites would clarify whether this similar ratio may be a trend for this association type.

The goatfish *Pseudupeneus maculatus* was the most prominent nuclear species at Fernando de Noronha, both in frequency of associations and number of follower species. Goatfishes are habitual as nuclear or follower species in heterospecific foraging associations (Fricke, 1975; Fishelson, 1977; Lukoschek & McCormick, 2000), and *P. maculatus* is already regarded as a ubiquitous nuclear species at our study site (Sazima et al., in press). Moray eels generally are prominent nuclear species that are followed regardless of their foraging or not, being even regarded as more rewarding to the followers than any other nuclear species (Diamant & Shpigel, 1985; Strand, 1988). However, at Fernando de Noronha moray eels are not favoured nuclear species. Aside the chained moray (*Echidna catenata*), which has few or no followers due to its peculiar hunting behaviour (Sazima & Sazima, 2004), nine additional moray and snake eel species at our study site could act as nuclear fishes and nonetheless only four of them were recorded in this role. We believe that this apparent lack of interest of followers in eels may be related to the ubiquity of *P. maculatus*, a very active and versatile forager (Sazima et al., in press).

The puddingwife *H. radiatus* (Labridae) and the coney *C. fulva* (Serranidae) stand out among the followers due both to their high frequency in the associations and by following a large number of nuclear species. Wrasses are a fish group well-known for its foraging versatility, which range from planktivory to durophagy and includes cleaning other fishes and anvil use to break large preys into smaller pieces (Itzkowitz, 1979; Coyer, 1995; Sazima et al., 2005). Several serranids, particularly epinepheline

groupers, are inquisitive fishes and display variable foraging behaviour, illness-feigning being one of the most notable tactics (Hobson, 1968; Diamant & Shpigel, 1985; Shpigel & Fishelson, 1989; Gibran, 2004). Both *Halichoeres radiatus* and *C. fulva* are highly opportunistic hunters and their ubiquity in interspecific foraging associations is likely related to their versatile behaviour. Not surprisingly, *H. radiatus* following *P. maculatus* was the commonest heterospecific foraging association recorded at Fernando de Noronha.

We found that a high proportion (~20%) of species in the reef fish assemblage of Fernando de Noronha engage in heterospecific foraging associations. No other study is available with such an estimative, and it would be rewarding to count with additional studies to clarify whether this proportion holds true for other tropical or temperate reef fish assemblages. Half of the bottom-disturbing carnivores and/or herbivores within the studied assemblage play the role of nuclear fishes, in agreement with our finding that substratum disturbance is a strong predictor of the nuclear role in the association. Thus, it seems acceptable to suggest that any fish that causes such disturbance has a high potential to act as a nuclear species. However, a few species that causes no substrate disturbance may occasionally play the nuclear role (e.g. a defecating one). Moreover, the proportion of roving or sedentary carnivores that act as followers agrees with our finding that carnivory may predict the follower role in an interspecific foraging association. Therefore, carnivorous species have a higher potential to act as followers than species in other trophic categories.

The zoobenthivore guild, especially the species that forage over soft bottoms, seems to be the only trophic group that may be consistently characterized as playing the nuclear role. Thus, we believe that most, if not all, species that have zoobenthivorous habits will eventually be recorded in the nuclear role. Moreover, the diverse array of escorts of each nuclear species may be related to some characteristics of this latter, such as degree of substratum disturbance, foraging versatility, and relative abundance (see a similar view in Sazima et al. in press). Accordingly, Mullidae seems to be the only taxonomic group that may be consistently characterized as composed entirely by actual or potential nuclear species. Several mullid species are already recorded as nuclear fishes worldwide (e.g., Fishelson, 1977; Strand, 1988; Lukoschek & McCormick, 2000; Sazima et al., in press) and this probably is a trend within the family.

Serranidae and Labridae are composed by a great number of species (Nelson, 1994; Froese & Pauly, 2006), which may largely account for these families containing most of the examples of follower fishes worldwide. Despite this species richness, relatively few species are present in heterospecific foraging associations (Itzkowitz, 1979; Ormond, 1980; Lukoschek & McCormick, 2000). Their presence in the associations is likely related to the inquisitive and opportunistic nature of several species within both families (e.g., Fishelson, 1977; Shpigel & Fishelson, 1989; Coyer, 1995; Gibran, 2004; Sazima et al., 2005). Nuclear species, on the other hand, are scattered among a greater number of families. However, the bottom-disturbing activity of Mullidae and Scaridae (Fishelson, 1977; Sazima et al., 2005; Sazima et al., in press) likely accounts for both their great number and high proportion of species acting as nuclear fishes.

In conclusion, the nuclear-follower interspecific association is likely an important, even if understudied component of the reef assemblages, both tropical and temperate. Nuclear species are diverse both in morphology and behaviour, foraging with the use of a wide array of bottom-disturbing tactics. Moreover, the nuclear role may be played either by fishes or other marine animals from invertebrates to turtles. Followers, on the other hand, comprise fishes only, which tend to display a more uniform feeding behaviour by exploiting food disclosed or made available by the variable foraging of the nuclear species.

ACKNOWLEDGEMENTS

We thank 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 (C. Bellini and A. Grossman) for logistic support; the Águas Claras, Atlantis and Noronha Divers diving centres for allowing free use of their facilities; the CAPES, CNPq, and FAPESP for essential financial support. CS and IS are recipients of scholarships from the CNPq – Brasil.

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DISCUSSÃO E CONSIDERAÇÕES FINAIS

O presente trabalho representa o mais completo estudo sobre associações alimentares do tipo nuclear-seguidor para uma comunidade recifal até o momento, o que explicaria, em parte, a variedade (de estrelas-do-mar até tartarugas) e o número de espécies, aqui registrados, para este tipo de associação. Um estudo comparável, em termos de variedade e número de espécies, feito em recifes temperados do Golfo da Califórnia, apresenta 21 espécies de nucleares e 17 de seguidores (Strand, 1988). Com base nestes dois estudos, foi possível calcular uma razão entre o número de espécies seguidoras e nucleares, que é 0.80 no Golfo da Califórnia e 0.84 em Fernando de Noronha. Estudos adicionais, sobre associações alimentares interespecíficas do tipo nuclear-seguidor, tanto em regiões tropicais como temperadas, poderiam indicar se esta razão representa uma tendência para este tipo de associação.

Uma alta proporção (~20%) de espécies da comunidade de peixes recifais em Fernando de Noronha forma associações alimentares interespecíficas. Embora não haja outro estudo disponível com este tipo de estimativa, seria muito interessante fazer comparações deste tipo para verificar se esta proporção seria semelhante para outras comunidades de peixes, tanto tropicais como temperadas.

Uma espécie de Mullidae, o saramunete *Pseudupeneus maculatus*, é a espécie de peixe nuclear mais importante em Fernando de Noronha, tanto em frequência de associações, como em número de espécies de seguidores. Espécies desta família são habituais em associações alimentares interespecíficas, agindo principalmente como nucleares, porém também como seguidores (Fricke, 1975; Fishelson, 1977; Lukoschek & McCormick, 2000). Por outro lado, moréias são importantes espécies nucleares em geral sendo seguidas independentemente de sua atividade alimentar (Diamant & Shpigel, 1985; Strand, 1988). Entretanto, em Fernando de Noronha, as espécies de moréias não parecem ser nucleares importantes. À parte da moréia-listada, *Echidna catenata*, que apresenta poucos seguidores, ou nenhum, devido ao seu tipo de forrageamento (q.v. Apêndice 1), nove espécies de moréias em Noronha poderiam atuar como nucleares, mas apenas quatro foram registradas como tal. A aparente falta de interesse dos seguidores por moréias pode estar relacionada à presença de *P. maculatus*, um peixe nuclear comum, muito ativo e versátil.

Halichoeres radiatus (Labridae) e *Cephalopholis fulva* (Serranidae) destacam-se entre as espécies de seguidores registradas no presente estudo, tanto por sua alta frequência nas associações, como pelo número de espécies nucleares a que se associaram. Muitas espécies de Labridae são bem conhecidas por sua versatilidade alimentar, que varia da planctofagia a durofagia (ingestão de presas com proteção resistente e dura), incluindo também a limpeza de outros peixes e o uso de rochas (“bigornas”) para quebrar presas grandes em porções menores (Itzkowitz, 1979; Coyer, 1995; Sazima et al., 2005). Diversas espécies de Serranidae, especialmente garoupas Epinephelinae, são peixes atentos e curiosos, que apresentam táticas alimentares variáveis, sendo que se fingir de doente ou morto é uma das mais notáveis (Hobson, 1968; Diamant & Shpigel, 1985; Shpigel & Fishelson, 1989; Gibran, 2004). Tanto *H. radiatus* como *C. fulva* são predadores muito oportunistas e a sua frequência nas associações alimentares interespecíficas provavelmente está relacionada a seu comportamento versátil. Desta forma, não é de surpreender que a associação alimentar interespecífica mais comum em Fernando de Noronha seja formada por *H. radiatus* seguindo *P. maculatus*.

Para a comunidade estudada, metade das espécies carnívoras e/ou herbívoras que perturbam o substrato foi registrada na função de nuclear. Esta proporção está de acordo com os resultados aqui apresentados de que perturbação do substrato possa ser considerada como um indicador da função nuclear nas associações. Assim, parece aceitável sugerir que qualquer peixe que provoque perturbação no substrato possui grande potencial de agir como nuclear para espécies seguidoras. Entretanto, mesmo espécies que provocam pouca ou nenhuma perturbação podem ocasionalmente agir como nucleares, como as que defecam na coluna d’água. De forma semelhante, a proporção de carnívoros sedentários ou errantes registrados como seguidores está de acordo com os resultados de que hábitos carnívoros sejam indicadores da função de seguidor nas associações. Assim, espécies de peixes com hábitos carnívoros apresentam um grande potencial para agirem como seguidores, em relação a espécies de outros grupos tróficos.

A guilda formada por zoobentívoros, principalmente as espécies que forrageiam em substratos não-consolidados, parece ser o único grupo trófico que poderia ser caracterizado consistentemente como nuclear. Assim, pode ser sugerido que a maioria,

se não todas as espécies que apresentem hábitos zoobentívoros, será registrada agindo como nuclear. Também, a diversa gama de acompanhantes de cada espécie nuclear pode estar relacionada a determinadas características da espécie nuclear, como grau de perturbação do substrato, versatilidade de forrageamento e abundância relativa. Desta forma, Mullidae parece ser o único grupo taxonômico que pode ser consistentemente caracterizado como inteiramente composto por espécies nucleares potenciais, ou de fato registradas. Diversas espécies de Mullidae constam como nucleares em diversas latitudes e regiões (e.g., Fishelson, 1977; Strand, 1988; Lukoschek & McCormick, 2000), indicando que esta seja uma tendência bem estabelecida nesta família.

De modo geral, duas famílias (Serranidae e Labridae) contribuem com a maior parte dos exemplos de peixes seguidores, provavelmente devido ao grande número de espécies que compõem estas famílias (Nelson, 1994; Froese & Pauly, 2006). Apesar desta riqueza de espécies, relativamente poucas espécies estão presentes em associações alimentares interespecíficas (e.g., Itzkowitz, 1979; Ormond, 1980; Lukoschek & McCormick, 2000). Sua presença nas associações provavelmente está relacionada à natureza inquisitiva e oportunista de diversas espécies nestas duas famílias (e.g., Fishelson, 1977; Shpigel & Fishelson, 1989; Coyer, 1995; Gibran, 2004). Por outro lado, as espécies nucleares estão distribuídas entre um número maior de famílias. Entretanto, duas famílias, Mullidae e Scaridae, contribuem com um grande número de espécies e também com uma alta proporção de espécies na família, agindo como nucleares, o que provavelmente está relacionado à sua atividade alimentar, que provoca perturbação no substrato (Fishelson, 1977).

Em síntese, as associações alimentares interespecíficas entre nucleares e seguidores são um componente importante, ainda que pouco estudado, das comunidades recifais, tanto tropicais como temperadas. Alguns padrões e tendências podem ser estabelecidos para este tipo de associação, levando em consideração os resultados apresentados na presente série de estudos e na literatura sobre o tema:

- 1) Peixes e outros animais marinhos, de invertebrados a tartarugas, podem agir como organismos nucleares. Por outro lado, apenas peixes agem como seguidores.

2) Espécies nucleares são diversas tanto na morfologia, como no comportamento, forrageando com o uso de uma ampla gama de táticas que, em geral, provocam perturbação no substrato.

3) Os seguidores apresentam um comportamento alimentar mais uniforme ao explorar alimento exposto ou produzido pela variável atividade alimentar das espécies nucleares.

4) Diversos grupos tróficos podem estar representados tanto entre os nucleares como entre os seguidores.

5) Perturbação do substrato por espécies nucleares pode ocorrer de diversas formas, desde a simples passagem de uma espécie predadora próxima ao fundo, ou a exploração de tufo de algas, até a escavação de substratos não-consolidados (o mais comum).

6) Espécies que provocam perturbação no substrato apresentam grande probabilidade de atuarem como nucleares.

7) Espécies de peixes com hábitos alimentares carnívoros apresentam grande probabilidade de atuarem como seguidores.

8) Espécies herbívoras em associações alimentares interespecíficas aproveitam itens alimentares em suspensão (algas e detritos) devido à perturbação do substrato, e também, para contornar ou sobrepujar a defesa de espécies herbívoras territoriais.

9) A presença de espécies herbívoras em associações alimentares interespecíficas está, aparentemente, relacionada a números altos de indivíduos nucleares, devido a um suposto maior grau de perturbação que agrupamentos provocam no substrato.

10) A riqueza de espécies de seguidores nas associações alimentares interespecíficas está, aparentemente, relacionada ao número de indivíduos nucleares, devido a um suposto maior grau de perturbação que agrupamentos provocam no substrato.

11) O número de indivíduos seguidores nas associações alimentares interespecíficas parece estar relacionado ao número de indivíduos nucleares, devido a um suposto maior grau de perturbação que agrupamentos provocam no substrato.

12) Os indivíduos seguidores são, em geral, de tamanho inferior ao do nuclear, principalmente quando apenas um indivíduo nuclear está ativo, forrageando.

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APÊNDICE 1

**DAYTIME HUNTING BEHAVIOUR OF *ECHIDNA CATENATA*
(MURAENIDAE): WHY CHAIN MORAYS FORAGING AT EBB TIDE HAVE
NO FOLLOWERS**

ARTIGO PUBLICADO:

**Sazima I. & Sazima, C. 2004. Aqua, Journal of Ichthyology and Aquatic Biology,
8: 1-8.**

DAYTIME HUNTING BEHAVIOUR OF *ECHIDNA CATENATA*
(MURAENIDAE): WHY CHAIN MORAYS FORAGING AT EBB TIDE HAVE NO
FOLLOWERS

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Key words: reef fishes, foraging behaviour, feeding specialization, prey handling,
Muraenidae, heterospecific associations, SW Atlantic

ABSTRACT. The diurnal foraging of the chain moray (*Echidna catenata*) for grapsid crabs on exposed reefs at ebb tide and in tide-pools was studied at Fernando de Noronha Archipelago, SW Atlantic. Four hunting tactics were recorded both under and out of the water: (1) active search at pool rims and rock bases with poking in crevices and holes; (2) stealthy approach to previously sighted prey; (3) chasing of prey; (4) ambush from under rocks and crevices. As the chain moray uses a variable hunting repertoire and its crab hunting is mostly visually guided, its generally unobtrusive foraging attracts little or no attention of tide-pool fishes. Additionally, part of its foraging is done out of the water on the exposed part of the reef, and thus no fish is able to follow the chain moray and gain advantage of its hunting activity.

RESUMO. O forrageamento diurno da moréia-listada (*Echidna catenata*) sobre caranguejos grapsídeos, na parte exposta de recifes e nas poças durante a maré baixa, foi estudado no Arquipélago de Fernando de Noronha, Atlântico Ocidental. Quatro táticas de caça foram registradas, tanto sob como fora da água: (1) procura ativa em bordas de poças e bases de rochas, incluindo esquadrihar em frestas e tocas; (2) aproximação sorrateira à presa previamente avistada; (3) perseguição da presa; (4) tocaia sob rochas e em frestas. Como a moréia-listada usa repertório variado de caça e sua procura por caranguejos é guiada principalmente pela visão, seu forrageamento discreto atrai pouca ou nenhuma atenção dos peixes nas poças de maré. Além disso, parte do seu forrageamento é feita fora da água e, assim, nenhum peixe é capaz de seguir a moréia e tirar proveito da sua atividade de caça.

INTRODUCTION

Moray eels (Muraenidae) and snake eels (Ophichthidae) forage mostly by poking in holes and crevices, feeding on invertebrates and fishes (Dubin, 1982; Abrams et al., 1983; Diamant & Shpigel, 1985). Foraging morays usually disturb the substrate and flush fishes and crustaceans from their retreats, an activity that attracts several species of opportunistic carnivorous fishes which follow the morays to feed on the uncovered prey (Dubin, 1982; Diamant & Shpigel, 1985; Strand, 1988), this following behaviour being recorded at night as well (Borges & Castro, 2003). Some of these opportunistic

predators are even attracted to a stationary moray and make contact with it to induce the moray to move on (Dubin, 1982; DeLoach 1999; IS and CS, pers. obs.).

The chain moray (*Echidna catenata*) dwells at shallow reef sites in the tropical Atlantic and specializes on crab prey (Randall, 1967, 1999; DeLoach, 1999). We report herein on the daytime foraging behaviour of the chain moray at Fernando de Noronha Archipelago, off northeast Brazil. As Böhlke & Chaplin (1968) report on a chain moray chasing a *Grapsus* crab out of the water, we hypothesised that this moray would search for crab prey visually guided (see Chave & Randall, 1979 for similar behaviour in the Pacific moray *Gymnothorax pictus*). If our assumption proves true, this kind of foraging would cause lesser substrate disturbance than most morays usually do while foraging (and which cause opportunistic followers to approach them). Thus, we additionally hypothesised that the foraging by the chain moray would preclude following behaviour by most if not all fishes, especially since the chain moray hunts in tide pools and on the exposed reef at ebb tide. Hence, we addressed three main questions in our study: (1) what are the hunting tactics of the chain moray? (2) is vision important in its foraging? (3) is the moray followed by other fishes, as are other eel species during their daytime foraging activity? As we found several crab remains on the reef, we additionally addressed the question of how a prey too large to be swallowed whole is handled under field conditions (see Miller, 1989 for handling behaviours in captive chain morays feeding on large prey).

MATERIAL AND METHODS

Fernando de Noronha Archipelago is situated at 03°50'S, 32°25'W, about 345 km east off north-eastern Brazil (see Maida & Ferreira, 1997 and Carleton & Olson, 1999, for map and description). Field observations were made on tide-pools and areas of the reef exposed at ebb tide, at the places called Enseada das Caieiras, Buraco da Raquel, and Praia do Boldró, in June and October 2001, June 2002, and May and June 2003.

Foraging chain morays were observed and followed during daylight hours at ebb tide, in session totalling 1105 min over 17 non-consecutive days. In the observational sessions of 10-55 min we used focal animal samplings, in which all occurrences of specified actions were recorded (Altmann, 1974). During observations, we focused on

the foraging behaviour of the moray and the reaction of fishes towards it, as well as on the hunting tactics and handling of prey employed by this crab predator. We also recorded feeding behaviour of other fishes while a moray was handling its prey. Live and dead sally lightfoot crabs (*Grapsus grapsus*) 2-7 cm across greatest carapace width were released nearby foraging morays to examine hunting and handling behaviour during staged encounters in the field. Dead crabs were slightly squeezed to release chemical cues to the morays. To assess the importance of visual role in the foraging behaviour of the chain moray, we dragged toy marine turtles tied to a nylon thread in front of ambushing or actively searching morays both underwater and out of water. The miniature turtles were made of acrylic painted orange or rubber painted green and black, and measured 4-5 cm in greatest length. In some of the tests the toy turtles were smeared on a squeezed dead crab to record the moray's reaction to crab-smelling toys versus ones with no crab smell.

We estimated the morays' total length (TL), the initial estimates being checked against measured live individuals. Nine morays were recognized by conspicuous individual markings (white patches or black blotches and spots on particular body parts), and thus our estimates of the total number of observed morays tend to be conservative. Moray vouchers are at the Museu de Zoologia da Universidade de São Paulo MZUSP (#47479) and Museu de História Natural da Universidade Estadual de Campinas ZUEC (#5804). Colour photos of foraging and prey handling morays were scanned and filed at ZUEC, three of them being available at FishBase (Froese & Pauly, 2003).

RESULTS

Thirty seven records of daytime foraging chain morays, involving at least 22 individuals (30-70 cm TL) were made at Fernando de Noronha. The morays moved over tide-pools and reef areas exposed at ebb tide (Fig. 1). While actively foraging on the shallows or out of water they were extremely wary and quickly hid under rocks or fled to deeper water upon approach (even a movement 2-3 m away from an alert moray caused its fleeing). While on move, a moray was often found with its body partly or

totally exposed, searching for its prospective prey. The time out of water while foraging ranged 3-24 min.



Figure 1. Rocky reef exposed at ebb tide in Fernando de Noronha Archipelago, and a large (65 cm TL) chain moray, *Echidna catenata*, searching for a crab (keeping still on rocks above and at moray's left) missed short while chased out of the water. Photos by I. Sazima.

We recorded four main hunting tactics for the chain moray both within the pools and out of water: (1) active search at pool rims and rock bases (visual inspection), including poking in crevices and holes (mostly tactile and/or chemical inspection?); (2) stealthy approach to previously sighted prey; (3) chase of prey both under and out of water; (4)

ambush from under rocks or from crevices, its head sometimes barely visible (this latter tactic was mostly employed within pools). One conspicuous trace of the first tactic (searching) is that while poking the moray moved slowly and unobtrusively, which caused little stirring of substrate. This characteristic probably is one cause for chain morays having few or no followers while hunting (see below).

Table 1. Hunting tactics and relative hunting success of chain morays (*Echidna catenata*) while foraging during daytime on sally lightfoot crabs (*Grapsus grapsus*) at ebb tide on reefs in Fernando de Noronha Archipelago, off northeast Brazil (n=31). Grasp refers to holding a crab after a strike even if the prey releases its appendages and free itself afterwards; ingest a crab mostly whole is here regarded as the actual success of each tactic after initial striking.

Hunting tactics	Strike= n (%)	Miss= n (%)	Grasp= n (%)	Ingest= n (%)
Ambush	11 (35.5)	3 (27.2)	8 (72.7)	5 (45.4)
Search	7 (22.6)	4 (57.1)	3 (42.8)	2 (28.5)
Stealth	7 (22.6)	1 (14.3)	6 (85.7)	5 (71.4)
Chase	6 (19.3)	1 (16.6)	5 (83.3)	4 (66.6)
Total	31 (100)	9 (29.0)	22 (70.9)	16 (51.6)

We perceived no regularity or a predictable sequence in these tactics except for chasing, which was mostly employed after missing a strike (Fig. 1) in any of the three other hunting tactics. A given moray may be in ambush from under a rock in a pool and strike at an intended prey with or without success (Fig. 2, Table 1), then either it chases the prey or leaves the pool and begins to move over the exposed part of the reef, visually searching for moving crabs. If a crab is spotted, the moray stealthily approaches and strikes (Fig. 3), again with or without success. On missing a strike the moray chases the crab if the prey is in view and moving, or it searches around the spot where the crab was missed. During this searching the moray frequently follows over and again its

exploratory path (in one instance up to eight times). After some time out of the water, the moray enters a pool and seeks a retreat, but it is not always clear whether it is again in ambush or simply resting for a while. Six individual morays (35-45 cm TL) followed for 12-55 min moved 2.5-6 m while foraging. One of these (35 cm TL) explored three pools consecutively within 55 min and stroke at crabs seven times during this period. Another moray (similar size) moved about 4 m inspecting the base of a cliff on the exposed reef and stroke only once during this period. Recorded success for the four hunting tactics of the chain moray varied but the overall foraging success was about 50% (Table 1).

The chain moray appears to rely heavily on vision when foraging, as moving crabs caused prompt orientation of the moray towards them and still crabs went undetected even at very close quarters (2-5 cm). While stealthily approaching a grazing crab one moray was misled by a darting goby and stroke at it (thus failing to grasp the crab), and soon after it stroke at a snail, *Nerita ascensionis* (Neritidae), that was moving near the now still crab. Another moray was following a queue of crabs moving at the rim of a pool, clearly guided by their movements on the rock cliff above; the moray suddenly stroke out of the water at the nearest crab but missed the intended prey and caused all the others to flee upwards the cliff. Additionally, the simple field tests we devised strengthen the concept of visually oriented hunting. The morays visually followed the moving (dragged) toy turtles with no crab smell and approached them in all staged encounters (n=11). The toys were grabbed (Fig. 4) while in motion (n=10; 90.9%) or were briefly inspected with no grabbing attempt (n= 1; 9.1%). After grabbing the toy the morays tried to retreat with their mouthed “prey” as they did with grabbed crabs. Motionless toys with no crab odour (n= 8) elicited no visible reaction from the morays. On the other hand, motionless toys with crab smell (n= 7) attracted the morays in all instances after a period of up to 70 sec, after which the morays grabbed the toy and hid.

When ready to strike, the moray’s fore-body forms a sigmoid curve, and the moray is able to strike at the prey with its body entirely exposed out of water, or its fore-body exposed and hind-body submersed (Fig. 2), or totally underwater. The morays usually strikes at the crabs from close quarters (about 5-10 cm). The crabs are either grabbed by their legs, when the moray strikes at the prey from below or sideways, or by their rear or in the middle of the carapace, when the moray strikes from above (Fig. 3). Crabs

grabbed by their legs often escape from the moray's grip detaching the seized appendages, in which case the moray would chase them for up to 5 m even if totally out of the water on the exposed part of the reef.

The sally lightfoot crabs cross tide-pools using two main ways, and in both of them they are liable to attacks by chain morays. One way is simply by walking on the bottom, in which case they may be struck either by an ambushing or a searching moray. The second way is astonishing at a first sight, as the crabs are able to run on the water surface for enough time to traverse a tide-pool about 3 m across. This ability, however, provides easily perceived signs for ambushing morays, which strike at the crabs under these circumstances (Fig. 2). Indeed, an easy way to locate an ambushing moray would be to induce the crabs to run over the water surface, and if in a given pool there is an ambushing moray, it will show up and try to grab a crab.

Live crabs released in staged encounters (n=8) were quickly perceived while moving, and either stealthily approached (if far from the moray) or almost immediately struck (if close to the moray). Dead crabs (n=5) required 10-50 sec to be located, but were grabbed and handled in the same way as live prey. Both in natural and in staged encounters small crabs were swallowed whole, whereas larger ones were dismantled with a combination of tugging, rotating, knotting (see Miller, 1989 for figures), and thrashing movements of the moray over the reef. Handling time was related to prey size, the largest crabs (carapace width 2.3-3.2 times larger than moray's head width) being dismantled and swallowed within 90-240 sec.

We recorded small tide-pool fishes to dispute the leftovers, such as the goby *Bathygobius soporator*, the most ubiquitous species in these pools, as well as juvenile damselfish, *Abudefduf saxatilis*. Small chain morays (6-15 cm TL) also were attracted and often grabbed at a leftover several times larger and heavier than themselves and tried to drag it to a retreat, probably to dismantle the piece in a place safe from larger fishes. In 33 out of the total of 37 observed foraging events (89.1%) we recorded no fishes following the chain moray, even if it inspected crevices in tide-pools during this activity. Only when the moray stirred the sandy bottom a little, one to a few small or juvenile fishes (mostly gobies and/or damselfishes) approached but moved away shortly thereafter.



Figure 2. An ambush by a chain moray (60 cm TL) from under a rock in a pool: above, sally lightfoot crabs running on the water surface to cross a tide-pool towards a large rock; below, the moray striking out of the water at a crab which climbed the rock near the ambush place (additional crabs visible on nearby rocks). Photos by J. P. Krajewski.

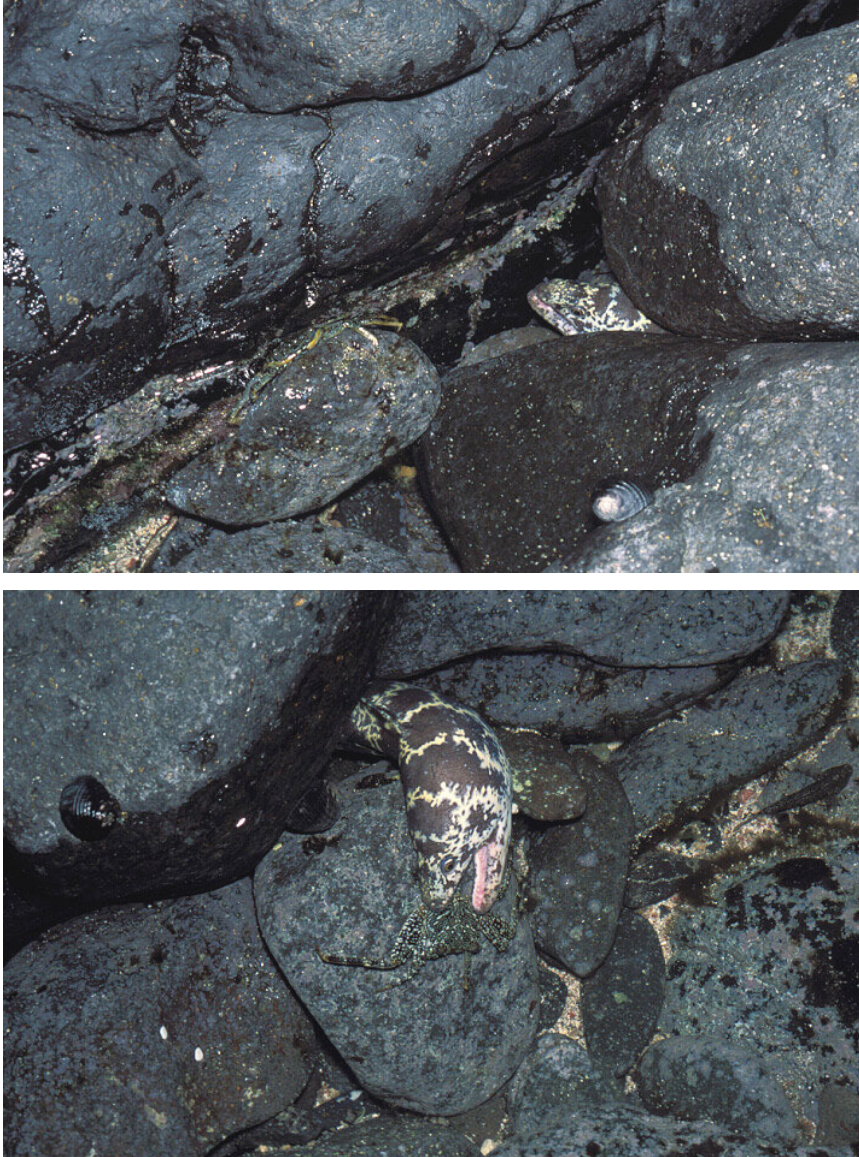


Figure 3. Chain morays (35-45 cm TL) foraging in tide pools: above, stealthily approaching a sally lightfoot crab, *Grapsus grapsus*, within a crevice (at the moray's left); below, grasping a crab from above and behind after a stealthy approach. Photos by I. Sazima.



Figure 4. Foraging chain morays (35 and 50 cm TL) attracted to toy turtles dragged nearby: above, emerging from under a rock to inspect a green and white rubber toy; below, striking at an acrylic turtle painted orange. Photos by I. Sazima.

DISCUSSION

Diurnally active morays forage mostly by poking within crevices and holes, and presumably are guided by olfactory, tactile, and visual cues (e.g., Bardach et al., 1959; Bardach & Loewenthal, 1959; Chave & Randall, 1971), but to what extent each of them is used under which circumstances remain to be examined. Our observations leave little doubt that stealthy approach and chase by chain morays while hunting for crabs on the reef parts exposed at ebb tide are two visually guided tactics (see comments on turtle toys below). The Pacific moray *Gymnothorax pictus* is another species that forages for crabs on exposed parts of the reef and relies mostly on vision to locate its prey (Chave & Randall, 1971). Also when lying in ambush in a tide-pool, the chain morays are clearly visually guided towards any moving object, and even a properly cast shadow may cause a moray to strike. However, olfactory and/or tactile cues probably prevail while the morays search within crevices and holes in pools. Moreover, crab pieces torn away during tugging, rotating or knotting, are presumably located afterwards by these two latter cues (nevertheless, even visual cues cannot be ruled out under these circumstances). The simple field tests we performed with turtle toys leave no doubt that the chain moray hunts visually guided, especially while out of the water but probably underwater as well. On the other hand, scent clearly plays an important role, as demonstrated by attraction of morays to motionless, crab-smelling toys, as well as to squeezed dead crabs. The role of scent orientation in the foraging behaviour of moray eels is already documented for several species (e.g., Bardach et al., 1959; Chaves & Randall, 1971; Borges & Castro, 2003).

The overall hunting success we recorded for the chain moray is surprisingly high, particularly in view of the keen eyesight, speed and agility of sally lightfoot crabs (Meinkoth, 1981; IS & CS, pers. obs.), the only recorded prey during our study. Our records indicate that active searching (visual and/or tactile and chemical inspection) may be the least successful hunting tactic. On the other hand, stealthy approach and chase seem to be the most successful, although chase is apparently used mainly (if not only) when a moray misses the strike at its intended prey while hunting by any of the other three tactics. Ambush hunting predators seldom chase their prey if the first strike

misses (Keenleyside, 1979) and this behaviour of the chain moray is surprising, especially when performed out of the water. We suggest that the apparently lesser success while searching by poking may be related to the moray grasping the crab mostly sideways and thus by the legs, whereas when chasing and stealthily approaching the moray grasps the crab mostly from behind or above, and thus the prey is unable to free itself by detaching its appendages. Ambush hunting is undoubtedly the least expensive tactic and also the least dangerous, as the moray attracts little or no attention of both potential prey and predators. We suggest that the choice of a particular hunting tactic from the variable repertoire of the chain moray may be the result of combined factors which include hunger level, energy expense, tide extent, as well as prey and cover availability.

Although foraging morays and other bottom feeding eels are among the predators most sought by several opportunistic following fishes (Diamant & Shpigel, 1985; Strand, 1988; Borges & Castro, 2003; CS & IS, pers. obs.), we recorded no “true” followers for the diurnally foraging chain morays at Fernando de Noronha Archipelago. The juvenile and small tide-pool fishes that capitalise on the leftovers can hardly be called followers in the sense habitually employed for this behaviour (e.g., Fricke, 1975; Dubin, 1982; Diamant & Shpigel, 1985; Strand, 1988). The dietary specialization of the chain moray on crabs probably is not related to the absence of followers, as other tropical Atlantic eels that specialise on crabs such as the snake eels *Myrichthys breviceps* and *M. ocellatus* (Ophichthidae) are regularly followed by several species of opportunistic carnivorous fishes (Dubin, 1982; DeLoach, 1999; IS & CS, pers. obs.). However, judging by their well developed, downwards directed nostrils and hunting behaviour, ophichthid crab-eating eels seem oriented towards their prey mostly by scent and/or touch, and habitually poke in holes and crevices during its foraging and cause substrate stirring (Dubin, 1982; IS, pers. obs.), thus producing the kind of stimuli needed to attract opportunistic followers (Fricke, 1975; Strand, 1988).

The virtual absence of followers may be partly explained by the unobtrusive foraging and almost no stirring of the bottom during the poking activity in holes and crevices by the chain moray. Substrate stirring releases approach and following by opportunistic carnivorous fishes (Fricke, 1975; Dubin, 1982; Strand, 1988). Moreover, most of the crab hunting by the chain moray seems visually guided, a foraging technique that

attracts little attention, if at all, of other fishes. Finally, part of the moray's foraging is done on the exposed part of the reef, and thus no other fish is able to follow the chain moray and gain advantage of its hunting activity. We suggest that the Indo-Pacific muraenid *Gymnothorax pictus*, which also forages on crustaceans and fishes on reef areas exposed at ebb tide (Chave & Randall, 1971), has few or no followers as well. However, chain morays foraging on deeper parts of the reef may have some followers even if its unobtrusive and slow searching would attract less fishes than other species of morays would do (Dubin, 1982; Diamant & Shpigel, 1985; Strand, 1988; CS & IS, pers. obs.). Relying on a single or predominant feeding tactic would render the foraging activity of the chain moray a predictable event both for the prey and other species as well, such as those following the moray. On the other hand, diversification and alternation of several hunting tactic may be regarded as an unpredictable event (thus, an element of surprise for the prey and perhaps a discouragement for the followers).

ACKNOWLEDGEMENTS

We thank the Centro Golfinho Rotador (J.M. Silva-Jr.) and Projeto Tamar (C. Bellini) for logistical support; R.M. Bonaldo and J.P. Krajewski for help with field work (the latter also for photographing morays); J. Zuanon for suggestions on the manuscript; the IBAMA (C. Bellini and M.A. Silva) for permission to study reef fishes at the Parque Nacional Marinho de Fernando de Noronha; the CNPq and FAPESP for essential financial support. This paper is dedicated to Ricardo Sazima for his continuous support, especially with our troubles related to PC working.

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