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ATIVIDADE DE FORRAGEAMENTO DE TRÊS ESPÉCIES SINTÓPICAS DE *SPARISOMA* (PERCIFORMES: SCARIDAE) NO ARQUIPÉLAGO DE FERNANDO DE NORONHA, PERNAMBUCO

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“Não há muito que se possa fazer com um aluno que desconhece a análise da multivariância e a lógica da seleção natural; mas também não é possível formar um bom cientista – embora talvez se possa forjar um tecnocrata razoável – se o indivíduo em questão nunca lê nada além dos periódicos profissionais de sua área de atuação”.

Stephen Jay Gould

Para Ivan, João e Cris, meus queridos colegas e amigos,

que me conduziram com muito carinho e

atenção pelo mundo dos peixes recifais.

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Resumo - Os peixes-papagaio (Perciformes: Scaridae) são importantes componentes das guildas de herbívoros e detritívoros de recifes tropicais e subtropicais. Estes peixes são hermafroditas seqüenciais protogínicos e geralmente apresentam fases dicromáticas seqüenciais, denominadas inicial (fêmeas ou machos) e terminal (somente machos). Este estudo caracterizou o forrageamento de *Sparisoma amplum, S. axillare* e *S. frondosum*, espécies sintópicas de Scaridae no Arquipélago de Fernando de Noronha, Pernambuco. As três espécies diferiram na seleção e preferência de substrato usado para forrageio, mas indivíduos iniciais e terminais de mesma espécie apresentaram preferência e seleção de substrato semelhante, exceto *S. amplum*. O padrão de distribuição das taxas de forrageamento ao longo do dia foi semelhante entre indivíduos de mesma espécie, mas diferente entre indivíduos de espécies distintas. Indivíduos em fase inicial apresentam maior freqüência de forrageamento que indivíduos terminais e apenas indivíduos de fase inicial forragearam agrupados em locais rasos, nos quais os indivíduos terminais defendiam territórios. Indivíduos em fase terminal das três espécies de *Sparisoma* sp. forragearam em grupo em áreas de maior profundidade. As três espécies também se associaram a outras espécies recifais, como o budião-de-Noronha (*Thalassoma noronhanum*), que segue os peixes-papagaio durante o forrageamento e os limpa quando interrompem momentaneamente seu forrageamento. As três espécies também procuraram estações fixas de limpeza. Indivíduos em fase inicial foram seguidos mais freqüentemente pelo budião e procuraram menos as estações de limpeza, que os de fase terminal. Indivíduos em fase inicial possivelmente foram seguidos com maior freqüência, por *T. noronhanum*, porque forragearam com maior freqüência. Como os indivíduos em fase inicial são limpos durante o forrageamento, não precisam procurar as estações de limpeza com tanta freqüência como fazem os indivíduos em fase terminal.

Abstract - Parrotfishes are important components of the herbivore and detritivore guilds of tropical and subtropical reefs. These fishes are protogynous hermaphrodites which change colour and sex, from initial phase females or males (IP) to terminal phase males (TP). The foraging of *Sparisoma amplum*, *S. axillare* and *S. frondosum* was studied at Fernando de Noronha Archipelago, tropical West Atlantic, where these parrotfishes are syntopic. The three species differed in substrate selection and preference, but IP and TP individuals of the same species preferred the same substrate type, except for *S. amplum*. Feeding rates of IP individuals were higher than those of TP ones but the distribution of feeding frequencies throughout the day of IP and TP individuals of the same species was similar. Initial phase individuals of all three species foraged in groups at shallow sites, whereas terminal phase ones defended territories there. Terminal phase individuals of *S. amplum* and *S. frondosum* were recorded foraging in groups at deeper sites. The suggestion is made that for TP individuals, shallow sites are mostly reproductive areas and deeper sites are foraging areas. The three parrotfish species also associate with other reef species, such as the Noronha-wrasse (*Thalassoma noronhanum*), a fish that follows the scarids during the foraging and cleans them when they interrupt momentarily their feeding. At the study site, the parrotfishes are also cleaned at fixed cleaning stations of gobies, wrasses and shrimps. Initial individuals were followed more often by the Noronha wrasse and posed at fixed cleaning stations less frequently than the terminal ones. Initial phase fishes probably are followed more often by the Noronha wrasse because they forage more than the terminal ones. Since the IP individuals were cleaned by *T. noronhanum* while foraging, they have no need to stop this activity to pose at cleaning stations as the TP individuals have to do.

INTRODUÇÃO GERAL

Os peixes-papagaio (Perciformes: Scaridae) incluem cerca de 85 espécies de peixes de médio porte, distribuídas nas áreas tropicais e subtropicais dos Oceanos Índico, Pacífico e Atlântico (Helfman et al. 1997; Froese & Pauly 2005; Randall et al. 1997). Os scarídeos apresentam hábito diurno e são abundantes na maioria dos ambientes recifais (Starck & Davis 1966; Robblee & Zieman 1984; Lewis & Wainwright 1985; Ferreira et al. 2004).

Scarídeos são hermafroditas seqüenciais protogínicos e geralmente apresentam fases dicromáticas seqüenciais (Fig. 1.1), denominadas inicial (fêmeas ou machos) e terminal (somente machos) (Winn & Bardach 1957; Robertson 1972; Robertson & Warner 1978). De uma maneira geral, as fases adultas de mesma espécie de Scaridae são facilmente distinguíveis, já que indivíduos de fase terminal geralmente apresentam cores mais brilhantes e chamativas que os de fase inicial (e.g. Humann & DeLoach 2002, Randall et al. 1997).

Fig. 1.1. Indivíduos em fase inicial (**a**) e terminal (**b**) do peixe-papagaio *Scarus taeniopterus* do Caribe (Fotos: JP Krajewski).

O sistema social de Scaridae é complexo, havendo um grande número de espécies territoriais (e.g. Buckman & Ogden 1973; Ogden & Buckman 1973; Van Rooij et al. 1996a, b). A defesa de território por scarídeos é variável, mas fortemente intraespecífica (e.g. Buckman & Ogden 1973; Ogden & Buckman 1973; Van Rooij et al. 1996a, b). Territórios de *Scarus croicensis*, no Caribe, são defendidos por um indivíduo dominante de fase inicial, que pode ser auxiliado por um indivíduo de fase terminal (Buckman & Ogden 1973). Por outro lado, em espécies de *Sparisoma* sp., machos terminais defendem territórios, para locais de acasalamento, posse de fêmeas e alimentação (Barlow 1975, Van Rooij et al. 1996a, c). Conseqüentemente, indivíduos de *Sparisoma* spp. em fase terminal investem grande quantidade de tempo nadando na coluna d'água, aparentemente patrulhando seus territórios e perseguindo vigorosamente indivíduos terminais da mesma espécie (Van Rooij et al. 1996c).

Os scarídeos forrageiam no substrato (hábitos bentônicos) e se alimentam principalmente de substratos compostos por algas associadas a rochas ou corais mortos (Hiatt & Strasburg 1960; Bellwood & Choat 1990; Choat 1991; Bruggemann et al. 1994a, b, c). Embora anteriormente os scarídeos tenham sido classificados como peixes herbívoros, com dieta predominada por algas, estudos recentes com scarídeos verificaram que grande parte da dieta destes peixes inclui grande quantidade de detritos, um material considerado mais nutritivo que algas (Wilson et al. 2003; Ferreira et al. no prelo). Assim, muitos autores consideram, atualmente, algumas espécies de scarídeos como herbívoro-detritívoras ou detritívoras (Wilson et al. 2003).

Espécies de Scaridae são divididas em dois grupos distintos quanto ao modo de forragear: escavadoras e raspadoras (Bellwood & Choat 1990). As raspadoras apresentam mandíbulas relativamente frágeis, investem freqüentemente contra o substrato e exploram principalmente substratos de superfície côncava. As escavadoras apresentam mandíbulas fortes, investem contra o substrato esparsamente, exploram substratos de diferentes formatos superficiais e retiram porções do substrato ao se alimentarem (Bellwood & Choat 1990). Assim, durante a alimentação, os scarídeos, principalmente escavadores, retiram da matriz do substrato algas e outros organismos bentônicos, além de detritos e sedimentos, deixando cicatrizes no substrato e criando novas áreas para recolonização (Fig. 1.2a) (Hiatt & Strasburg 1960; Randall 1961,1965; Brock 1979; Bellwood & Choat 1990). Como conseqüência, os scarídeos estão entre os principais agentes bioerosivos dos recifes, modificando a topografia recifal (Bellwood & Choat 1990; Bellwood et al. 2003).

Os peixes-papagaio são também considerados como um dos principais produtores de sedimentos dos recifes, já que porções do substrato ingeridas juntamente com algas são trituradas durante a digestão e eliminadas nas fezes em forma particulada (Fig. 1.2b) (DeLoach 1999; Froese & Pauly 2005).

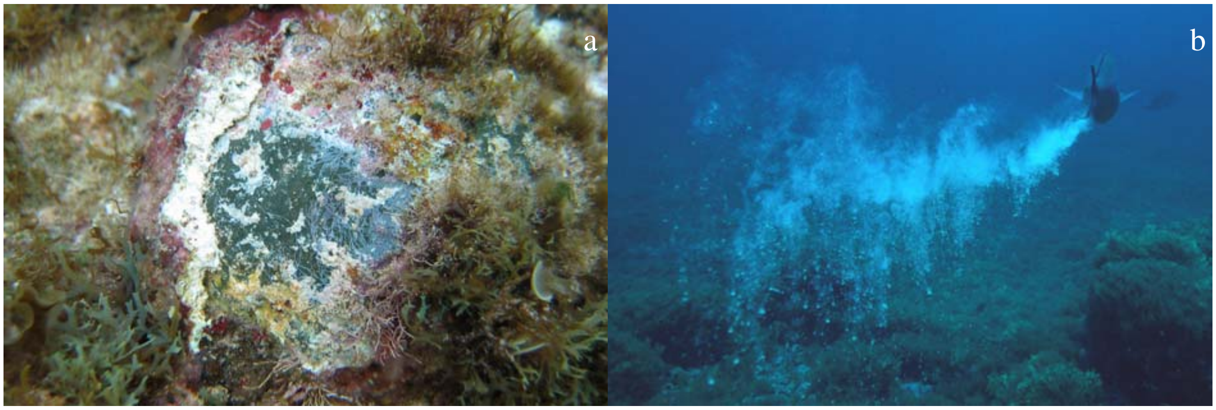

Fig. 1.2. Os peixes-papagaio retiram porções de substrato duro durante a alimentação, abrindo novas áreas para colonização do recife (**a**). Porções de rochas ou corais ingeridas juntamente com algas são eliminadas nas fezes em forma particulada (**b**), o que faz dos scarídeos um dos principais produtores de sedimentos dos recifes (Fotos: JP Krajewski).

Scarídeos simpátricos apresentam diferenças no uso de recursos alimentares (Bruggemann et al. 1994b; McAfee & Morgan 1996). No Caribe, espécies simpátricas que apresentam diferentes modos de forragear podem explorar substratos com morfologia de superfícies distintas (Bruggemann et al. 1994b). Por outro lado, espécies simpátricas de Scaridae que apresentam o mesmo modo de forragear podem diferir quanto à seleção de substrato para forrageio (McAfee & Morgan 1996). Espécies co-ocorrentes de Scaridae também podem diferir em outros aspectos durante o forrageamento, tais como microhábitat ocupado no recife e horário em que ocupam um determinado ambiente (McAfee & Morgan 1996).

Existe grande variação na organização social de espécies de Scaridae durante o forrageamento, uma vez que podem forragear solitários, em pequenos grupos ou em cardumes de centenas de indivíduos (Winn & Bardach 1960; Ogden & Buckman 1973; Koltes 1993). Geralmente, espécies de *Sparisoma* forrageiam individualmente ou em pequenos grupos (Winn & Bardach 1960; Barlow 1975; Koltes 1993). Entretanto, a organização social de scarídeos, durante o forrageamento, pode variar entre indivíduos de mesma espécie (e.g. Barlow 1975; Ogden & Buckman 1973; Koltes 1993; Van Rooij et al. 1996b, c), já que indivíduos em fase inicial geralmente formam grupos de forrageamento mais freqüentemente que os na fase terminal (Barlow 1975; Fig. 1.3). Ainda, indivíduos na mesma fase reprodutiva podem apresentar diferentes tipos de organização social e comportamento (territorial ou não), de acordo com as características da área do recife (Ogden & Buckman 1973; Koltes 1993; Van Rooij et al. 1996b, c).

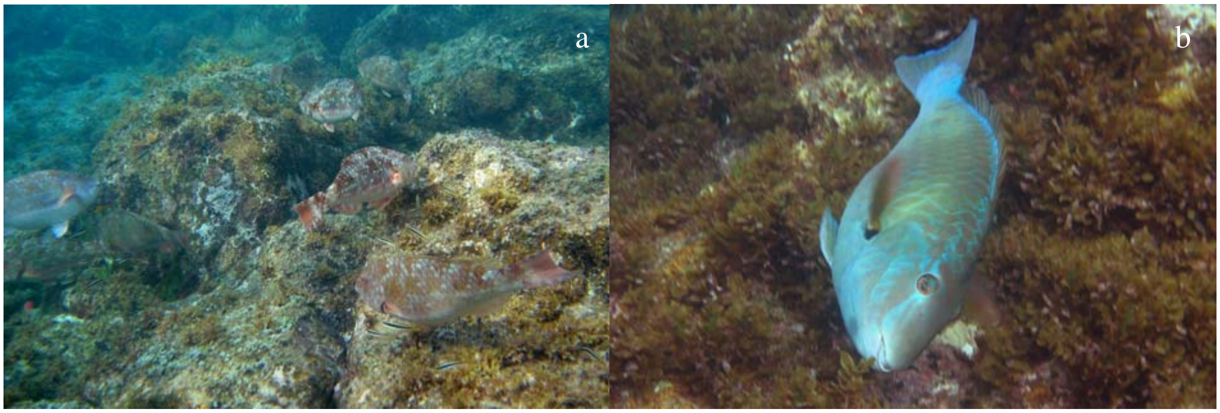

Fig. 1.3. *Sparisoma axillare* em fase inicial, forrageando em grupo (**a**); *S. frondosum* em fase terminal, forrageando solitário (**b**) (Fotos: JP Krajewski e RM Bonaldo).

No Atlântico Sul Ocidental ocorrem espécies de peixe-papagaio dos gêneros *Cryptotomus*, *Scarus* e *Sparisoma* (Froese & Pauly 2005). O gênero *Sparisoma*, endêmico do Atlântico, é bastante diversificado, apresentando espécies de diferentes hábitos alimentares (escavadores e raspadores) e ocupando diferentes ambientes, de bancos de angiospermas marinhas a recifes e corais (Bernardi et al. 2000; Streelman et al. 2002; Ferreira et al. 2004). Revisões taxonômicas recentes consideram cinco espécies de Scaridae, anteriormente consideradas espécies com distribuição ampla – do Caribe ao Brasil – como endêmicas do Atlântico Sul Ocidental: *Scarus trispinosus*, *Sparisoma amplum*, *S. axillare*, *S. frondosum* e *Sparisoma tuiupiranga* (Moura et al. 2001, Gasparini et al. 2003). No Brasil, as espécies anteriormente identificadas como *S. viride*, *S. rubripinne* e *S. chrysopterum* são atualmente denominadas, respectivamente, de *S. amplum*, *S. axillare* e *S. frondosum* (Fig. 1.4) (Moura et al. 2001). As três espécies ocorrem do Maranhão a Santa Catarina e são sintópicas no Arquipélago de Fernando de Noronha, Pernambuco (Moura et al. 2001). Entretanto, registros recentes comprovam a ocorrência de *S. frondosum* na parte sudeste do Caribe (Humann & DeLoach 2002; LA Rocha com. pess.).

Fig. 1.4. Indivíduos em fase inicial e terminal de *Sparisoma amplum* (**a,b**), *S. axillare* (**c,d**) e *S. frondosum* (**d,e**) (Fotos: JP Krajewski e RM Bonaldo).

Associações alimentares entre peixes-papagaio e outras espécies recifais

Os peixes papagaios são comumente observados em associações alimentares com outras espécies recifais (e.g. Strand 1988; Francini-Filho et al. 2000; Sazima et al. 2005). Uma dessas associações é a simbiose de limpeza, na qual um peixe se alimenta de parasitas, muco e tecidos danificados da superfície corporal de outros peixes, os clientes (Losey 1971, 1987; Grutter 1999). Scarídeos estão entre os clientes preferidos de diversas espécies de limpadores (Losey 1972, 1974; Grutter & Bshary 2003, 2004), uma vez que seu corpo é coberto por muco abundante, um material nutritivo (Lewis 1970; Gorlick 1980; Ebran et al. 1999; Arnal & Morand 2001; Arnal et al. 2001).

Os scarídeos também participam das associações compostas por peixes nucleares e seguidores (Strand 1988), nas quais espécies seguidoras, geralmente predadores oportunistas, alimentam-se de invertebrados e pequenos peixes expostos pelo distúrbio no substrato causado pelo forrageamento das espécies nucleares (Hobson 1974; Fricke 1975; Fishelson 1977; Ormond 1980; Gibran 2002). Espécies de Scaridae podem atuar tanto como nucleares quanto como seguidoras (Strand 1988, obs. pess.).

No Arquipélago de Fernando de Noronha, *S. amplum*, *S. axillare* e *S. frondosum* freqüentemente formam associações de limpeza e nucleares com o budião-de-Noronha, *Thalassoma noronhanum* (Labridae), peixe muito comum no arquipélago (Francini-Filho et al. 2000; Sazima et al. 2005). O budião-de-Noronha segue os scarídeos durante o forrageamento, alimentando-se de partículas e invertebrados expostos pelo distúrbio no substrato e limpando momentaneamente os peixes-papagaio quando estes interrompem seu forrageamento (Sazima et al. 2005). No arquipélago, os peixes-papagaio também podem ser limpos em estações de limpeza de diversas espécies de peixes, como *T. noronhanum,* *Elacatinus randali e Pomacanthus paru* e dos camarões *Lismata* sp. e *Stenopus hispidus* (obs. pess.).

Área de estudo

O Arquipélago de Fernando de Noronha está situado a cerca de 400km da costa nordeste do Brasil. O arquipélago é formado por 21 ilhas e ilhotas, sendo que a maior delas (Fernando de Noronha) tem 10km de comprimento e 27km^2 (Fig. 1.5) (Linsker 2003; www.noronha.pe.gov.br). O arquipélago tem origem vulcânica e está situado sobre o pico de uma montanha submersa cuja base está à cerca de 4.500m de profundidade. Assim, a costa do arquipélago apresenta declive acentuado e a poucos metros da costa a profundidade pode ultrapassar os 100m (Linsker 2003).

Os recifes de Fernando de Noronha são compostos principalmente por rochas cobertas por algas pardas e sedimento. A costa noroeste da ilha, denominada "Mar de Dentro" apresenta mar calmo durante os meses de maio a novembro (nesta área foi feita a maioria das observações do presente estudo). Na costa sudeste, conhecida como "Mar de Fora", o mar é batido durante a maior parte do ano, ficando relativamente calmo durante os meses de novembro a abril (Linsker 2003).

A principal área de estudo está localizada na Praia da Conceição, no "Mar de Dentro" (Fig. 1.5b, 1.6). A área é composta por recife rochoso e planície arenosa adjacente. Nas áreas de costão rochoso predominam cinco tipos de substrato: 1) algas epilíticas (matriz dominada por algas vermelhas coralináceas); 2) algas verdes epilíticas (matriz dominada por *Caulerpa racemosa* ou *Cladophoropsis* sp.); 3) macroalgas pardas (*Dictyota* sp., *Dictyopteris* sp. e *Sargassum* sp.); 4) cobertura mista de algas e areia (composta principalmente por areia, algas coralináceas, algas verdes calcificadas e *Dictyota* sp.) e 5) rochas (substrato coberto por algas coralináceas crostosas ou composto por rocha aparentemente nua) (Fig. 1.7). A profundidade varia de 1 a 10m, a temperatura é constante ao longo do ano, variando entre 27-28°C e a visibilidade subaquática pode variar entre 5-25m.

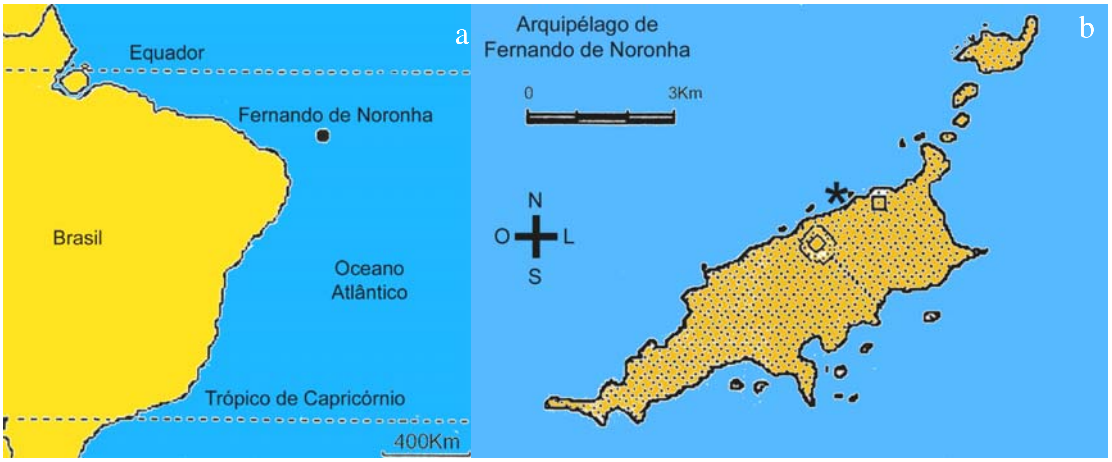

Fig. 1.5. Localização do Arquipélago de Fernando de Noronha no Atlântico Ocidental e mapa do arquipélago (**a**). A principal área de estudo, Praia da Conceição, está marcada com “*” no mapa do arquipélago(**b**).

Fig. 1.6. Costão rochoso da Praia da Conceição, Fernando de Noronha, principal área de estudo (Fotos: JP Krajewski).

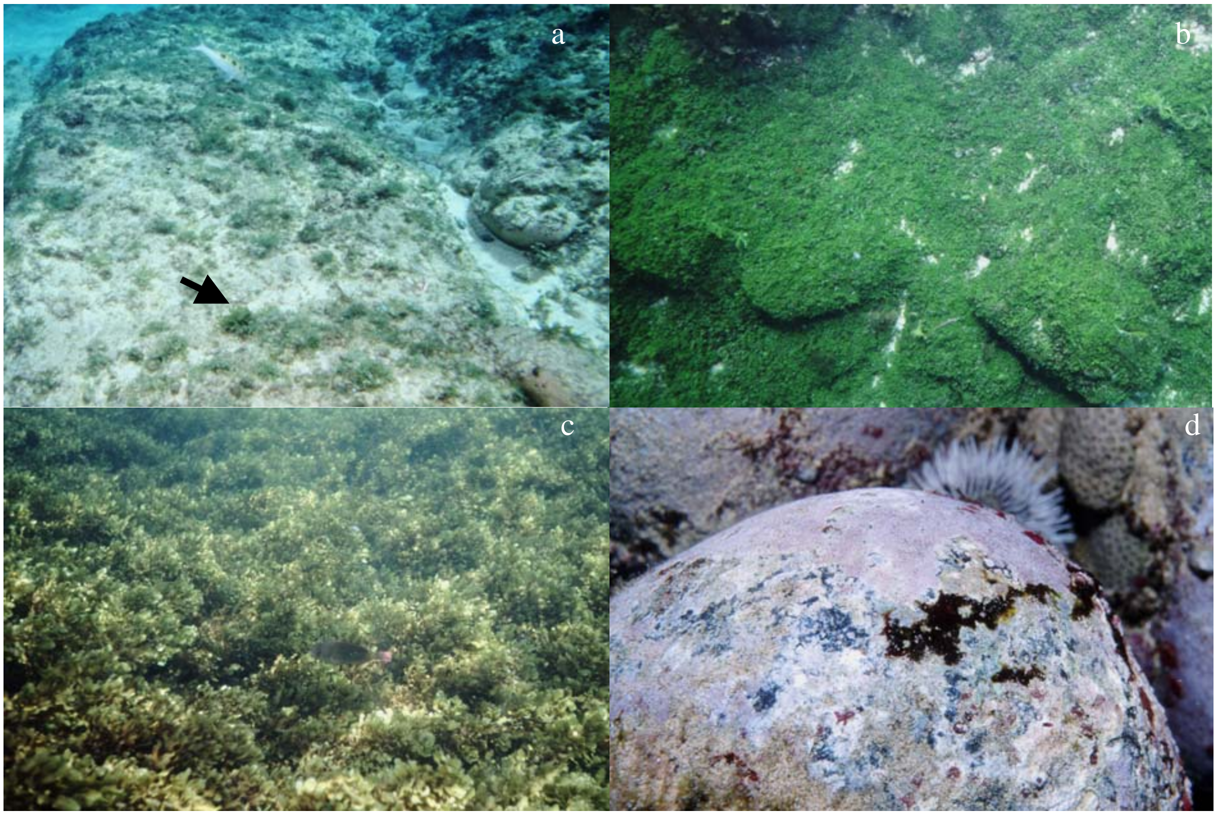

Fig. 1.7. Os cinco tipos principais de substrato encontrados na Paia da Conceição: cobertura mista de algas e areia (**a**); algas epilíticas (**a**, seta); algas verdes epilíticas (**b**); macroalgas pardas (**c**); rochas cobertas por algas calcáreas incrustantes (**d**) (Fotos: JP Krajewski).

Foram feitas observações e registros em vídeo e fotografia em outras regiões do arquipélago, como Canal da Ressurreta, Laje Dois Irmãos, Praia do Porto e Praia do Sancho, todas localizadas no "Mar de Dentro". O Canal da Ressurreta é uma planície de algas calcárias e pardas, cuja profundidade é de cerca de 12m. A Laje Dois Irmãos é um recife rochoso com predomínio de colônias de coral pétreo, principalmente por *Montastrea cavernosa* e de 14-25m de profundidade. A Praia do Porto é um recife rochoso raso (até 3m) com planície arenosa adjacente. A Praia do Sancho é semelhante à Praia da Conceição, mas apresenta profundidade de cerca de 10m e maior abundância de corais pétreos.

Objetivos

Considerando a análise da literatura na introdução, são examinadas, no presente estudo, as seguintes questões sobre a atividade de forrageamento de *S. amplum*, *S. axillare* e *S. frondosum* no Arquipélago de Fernando de Noronha:

1. Existe seleção de substrato, durante o forrageamento, entre as três espécies de *Sparisoma* e suas duas fases adultas, inicial e terminal?
2. Caso haja seleção de substrato, há diferença na seleção de substrato, durante o forrageamento, entre as três espécies e as respectivas fases inicial e terminal?
3. Existe diferença na freqüência alimentar (número de investidas contra o substrato por minuto) das três espécies ao longo do dia?
4. Existe diferença na freqüência alimentar de indivíduos em fase inicial e terminal da mesma espécie?
5. As três espécies diferem quanto ao período e microhábitat ocupados no recife?
6. As três espécies forrageiam solitárias ou em grupos?
7. Indivíduos em fase inicial e terminal das três espécies de *Sparisoma* diferem quanto à freqüência em que se associam ao budião-de-Noronha?
8. Indivíduos em fase inicial e terminal das três espécies de *Sparisoma* diferem quanto à freqüência com que visitam estações de limpeza?

Os dois manuscritos que compõem o corpo principal da tese respondem às questões acima propostas. O primeiro manuscrito responde às questões um a seis e o segundo manuscrito responde às questões sete e oito.

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CAPÍTULO 1

Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic

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Abstract Parrotfishes are important components of the herbivore and detritivore guilds of tropical and subtropical reefs. These fish are protogynous hermaphrodites which change color and sex, from initial phase females or males (IP) to terminal phase males (TP). We studied the foraging behaviour of *Sparisoma amplum*, *S. axillare* and *S. frondosum*, three syntopic scarids on the rocky reefs of Fernando de Noronha Archipelago, tropical West Atlantic. The three parrotfish species differed in substrate selection and preference, but IP and TP individuals of the same species preferred the same kind of substrates, except for *S. amplum*. Feeding rates of IP individuals were higher than those of TP individuals but the distribution of feeding frequencies throughout the day of initial and terminal phase individuals of the same species was similar. Initial phase individuals of all three species foraged in groups at shallow sites, whereas TP ones defended territories there. Terminal phase individuals of *S. amplum* and *S. frondosum* were recorded foraging in groups at deeper sites. We suggest that for TP individuals, shallow sites are mostly reproductive areas and deeper sites are foraging areas. The general foraging pattern we found for *S. amplum*, *S. axillare* and *S. frondosum* is similar to patterns found for other parrotfish species in the Caribbean and the Pacific.

Introduction

Parrotfishes (Perciformes: Scaridae) include about 85 tropical and subtropical reef fish species (Helfman et al. 1997; Froese & Pauly 2005; Randall et al. 1997). Scarids in the shallows are diurnal foragers and are important components of the herbivore and detritivore guilds on coral reefs (e.g., Bouchon-Navarro and Harmelin-Vivien 1981; Choat and Bellwood 1985; Lewis and Wainwright 1985; Wilson et al. 2003).

Scarids are protogynous hermaphrodites that change color and sex as adults, from initial phase (IP) females or males to terminal phase (TP) males (Winn and Bardach 1957; Robertson 1972; Robertson and Warner 1978). Territorial behaviour is well documented for some Caribbean species of Scaridae (e.g., Barlow 1975; Buckman and Ogden 1973; Ogden and Buckman 1973; Van Rooij et al. 1996 a, b). Territory defence is intraspecific, and the terminal phase males of *Sparisoma* spp. defend an area that appears to have a dual function: reproduction and feeding (Barlow 1975; Van Rooij et al. 1996 a, c). Thus, TP individuals spend a large amount of time in the water column, apparently patrolling their territories and chasing away conspecific males (Van Rooij et al. 1996c).

Parrotfishes are bottom foragers that feed on multispecific algal turfs, endolithic microalgae over dead corals, seagrass, macroalgae, and live coral (Hiatt and Strasburg 1960; Choat 1991; Bruggemann et al. 1994c; Ferreira and Gonçalves in press). Although scarids were once regarded as a single herbivorous group, presently they are divided in two main functional groups, excavators and scrappers, which differ in their feeding apparatus morphology and foraging behaviour (Bellwood and Choat 1990). Studies on resource use by sympatric parrotfish species in the Caribbean indicate that those species with similar feeding mode differ in substrate selection, although IP and TP individuals of the same species have similar substrate selection (e.g. Bruggemann et al. 1994c; McAfee and Morgan 1996).

Recent taxonomic revisions of parrotfishes of Southwest Atlantic recognize five endemic species, formerly misidentified as species ranging from the Caribbean to Brazil (Moura et al. 2001; Gasparini et al. 2003). The species formerly identified in Brazil as *S. viride*, *S. rubripinne* and *S. chrysopterum* are presently recognized as *S. amplum*, *S. axillare* and *S. frondosum* respectively (Moura et al. 2001). These last three species are syntopic at the Fernando de Noronha Archipelago, off Northeastern Brazil, tropical West Atlantic (pers. obs.). Recent records of *S. frondosum* extend its range to Southeast Caribbean (Humann & DeLoach 2002; LA Rocha pers. comm.).

We studied the foraging of *Sparisoma amplum*, *S. axillare* and *S. frondosum* at Fernando de Noronha Archipelago, and our study addressed the following questions: 1) Is there any substrate selection while foraging by the three *Sparisoma* species as well as their two adult phases? 2) If present, does the substrate selection differ between initial and terminal phase individuals of the same species and between the three species? 3) Do the feeding rates of the three species differ throughout the day? 4) Is there any difference in the feeding rates of the initial and terminal phases of the same species? 5) Do the three species differ in the period and microhabitat they occupy on the reef? 6) Do the three species and their initial and terminal phases forage solitary or on groups?

Material and methods

Study site

The field study was conducted at Fernando de Noronha Archipelago (3^o54'S, 32^o25'W), 345 km off the coast of NE Brazil (see Maida and Ferreira 1997 for map and description), from June to July 2002, May to July 2003 and October 2004. The main study site was located at the Praia da Conceição on the main island, a rocky shore with adjacent sand flat. The rocky substrate is covered mostly by brown, red and green algae, and scarcely by the hydrocoral *Millepora* sp., the stony corals *Siderastrea* sp. and *Montastrea cavernosa*, and by zoanthid colonies. At the sand flat there are sparse rocks covered by algal turfs and a mixed substrate composed by sand and algae. This site was selected for most observational sessions due to abundance of initial and terminal individuals of the three *Sparisoma* species, and depths adequate to observational sessions from close quarters even while on water surface. During our study, horizontal visibility ranged 8-25 m, and water temperature was 27^oC. Depth at the study site ranged 2-10 m. Observations were also conducted at four additional sites: Praia do Porto, a shallow rocky shore (up to 3m), but with adjacent sand flat; Praia do Sancho, a site similar to Praia da Conceição, but with hard coral colonies more abundant and depth about 10m; Laje Dois Irmãos, a rocky reef at about 14-25m depth, with abundant coral colonies of the stony coral *M. cavernosa*; and Canal da Ressurreta, a brown and calcareous algae flat, at about 12m depth. At the four additional sites we made qualitative observations on foraging behaviour of the three *Sparisoma* species.

Procedure

The foraging of the three *Sparisoma* species was recorded over 22 non-consecutive days mainly while snorkelling. During observational sessions of 60-150 min, "focal animal" and "all occurrences" samplings (Altmann 1974; Lehner 1979) were used in 1080 min of direct observation. Observations were conducted at daytime from morning (0900h) to afternoon (1800h).

Foraging substrate selection of the three species was assessed by following individuals for 3-5 min and counting the number of bites on several substrate types. The foraging substrate was categorized in five main types: 1) algal turfs (sets of algae composed mostly by corallinaceous algae); 2) brown macroalgae (*Dictyota* sp., *Dictyopteris* sp. and *Sargassum* sp.); 3) green algae (sets of algae composed mostly by *Caulerpa racemosa* or *Cladophoropsis* sp.); 4) mixed substrate (composed mostly by sand and a set of coralline and green calcified algae, and *Dictyota* sp.) and 5) rock either covered by crustose coralline algae, or apparently bare. Substrate types foraged on infrequently (*Millepora* sp. and sand) and substrates not foraged at all (anthozoan colonies) were combined into a sixth category called "others". We also recorded bites of *Sparisoma* on pieces of brown macroalgae (*Dictyota* sp., *Dictyopteris* sp. and *Sargassum* sp.) drifting on the water column. However, this latter substrate type was not included in the substrate selection analysis, since it was rarely taken by the three parrotfish species and because its availability changed throughout the day and daily. Individuals were not followed over successive periods to lessen the risk of biased samples (c.f. Birkeland and Neudecker 1981).

Of a total of 249 foraging bouts recorded, 60 were in the morning (0900h–1100 h), 76 in the "noon" (1101h-1400h), 47 in the afternoon (1401h–1600 h) and 66 in the late afternoon (1601h-1800h). Additionally, from these 249 bouts, 69 were of *S. amplum* (50 of IP individuals and 19 of TP ones), 83 were of *S. axillare* (47 of IP individuals and 36 of TP ones) and 97 of *S. frondosum* (46 of IP individuals and 51 of TP ones).

We estimated the availability of the five foraging substrate types with eight transects 25-35m length and 1.5m wide, which started on the rocky shore and ended on the sandy area where the three parrotfish species were still seen feeding. Transects were video recorded from a standardized distance, and still video frames were obtained from the whole transects to evaluate the availability of each substrate type.

We assessed the parrotfishes' distribution and social organization while foraging censusing them visually in two microhabitats, the rocky shore and the interface between the rocky shore and the sandy flat, in two periods of daytime: morning (0900h-1130h) and afternoon (1500h-1700h). We established 5m x 100m transect lines and recorded all *Sparisoma* adult individuals in view, characterising them by species, phase, social organization (solitary or groups), and number of individuals in the group (modified from Brock 1954; 1982; Sale 1980; Lewis and Wainwright 1985; McAfee and Morgan 1996). We made 49 transects: 25 in the morning and 24 in the afternoon (28 in the rocky shore and 21 in the sand flat).

Statistical analysis

We used the Ivlev's electivity index (Krebs 1989) to verify the preference or rejection of each substrate type by each phase and species. The electivity index was calculated as follows:

$E_i = (r_i - n_i) / (r_i + n_i)$,

in which E_i is the electivity measure for the i substrate type; r_i is the percentage of bites of each *Sparisoma* species on i substrate and n_i is the percentage of i substrate in the studied site. Electivity index varies from -1 to 1, in which values close to +1 indicate higher preferences and values close to -1 indicate lesser preference or avoidance (Krebs 1989). To generate a 95% confidence interval around the observed E_i, we used non-parametric bootstrapping procedures, in which individual fishes are used as sample units (10,000 randomisations). The confidence limits are determined using the percentile method (Manly 1998). Additionally, we calculated the differences between the recorded values of E_i for both initial and terminal phases of a given species. We tested the significance of this difference using a two-independent sample randomisation test (Manly 1998), in which individual fishes are used as sample units (10,000 randomisations).

Three-way ANOVA was used to compare the number of bites per min, i.e., feeding frequency among six categories (IP and TP individuals of the three species) for successive periods of daytime: morning (0900h-1100h), noon (1101h-1400h), afternoon (1401-1600) and late afternoon (1601h-1800h). Since the three-way ANOVA identified differences for most of the parameters analyzed, we used one two-way ANOVA for each species to compare more specifically the feeding frequency between two categories (IP and TP individuals of same species). In the two-way ANOVA for *S. axillare* and *S. frondosum* we considered the four above-mentioned periods. In the two-way ANOVA for *S. amplum* we considered three periods: morning, afternoon, and late afternoon, since we had fewer data on the feeding activity of terminal phase individuals in the noon period. For periods that the two-way ANOVA was significant, *a posteriori* tests were made comparing period pairs to identify which period(s) caused the differences. Data were examined for normality of residuals and homogeneity of variances, and we used the logarithmic transformation when the original data had no proprieties needed for the parametric tests (Zar 1999).

The G test for contingency table was again used to compare the number of individuals of each species in the two main areas of the reef (rocky shore and interface). This test was performed for two periods: morning and afternoon (Zar 1999).

The G test for the 2x2 contingency table was used to compare number of events in which the IP and TP individuals of each species foraged solitary or in groups (Zar 1999). The same test was used to compare the number of groups at two main areas of the reef (rocky shore and interface). This test was performed for two daytime periods: morning and afternoon (Zar 1999).

Results

Substrate selection and preference

The three *Sparisoma* species foraged over the same substrate types, but the proportional use of each type differed among the three species. We found general patterns on the foraging of the three *Sparisoma* species as well as their two adult phases, including the preference for foraging in algae turfs and rocky substrate and the avoidance of brown macroalgae and the "other" substrates (Fig. 2.1b and f). With respect the other two substrates (mixed substrate and green algae) the selection of substrates varies among species (Fig. 2.1). The phase of individuals also affects substrate selection in *S. amplum*. Initial phase individuals of *S. amplum* showed higher preference to algal turfs than TP individuals (Fig 2.1a). On the other hand, IP individuals avoided mixed substrate, which was preferred by TP individuals (Fig 2.1d). Also, green algae, which was not selected for foraging by *S. amplum* IP individuals, was strongly avoided by TP individuals of same specie (Fig 2.1c). The latter difference was also recorded to *S. axillare* IP and TP individuals (Fig 2.1c).

We recorded two IP individuals of *S. amplum* and one IP individual of *S. frondosum* taking bites of the hydrocoral *Millepora* sp. Additionally, all three species and their two phases took occasional bites on drifting pieces of brown algae, mostly *Dyctiota* sp., *Dyctiopteris* sp., and *Sargassum* sp.

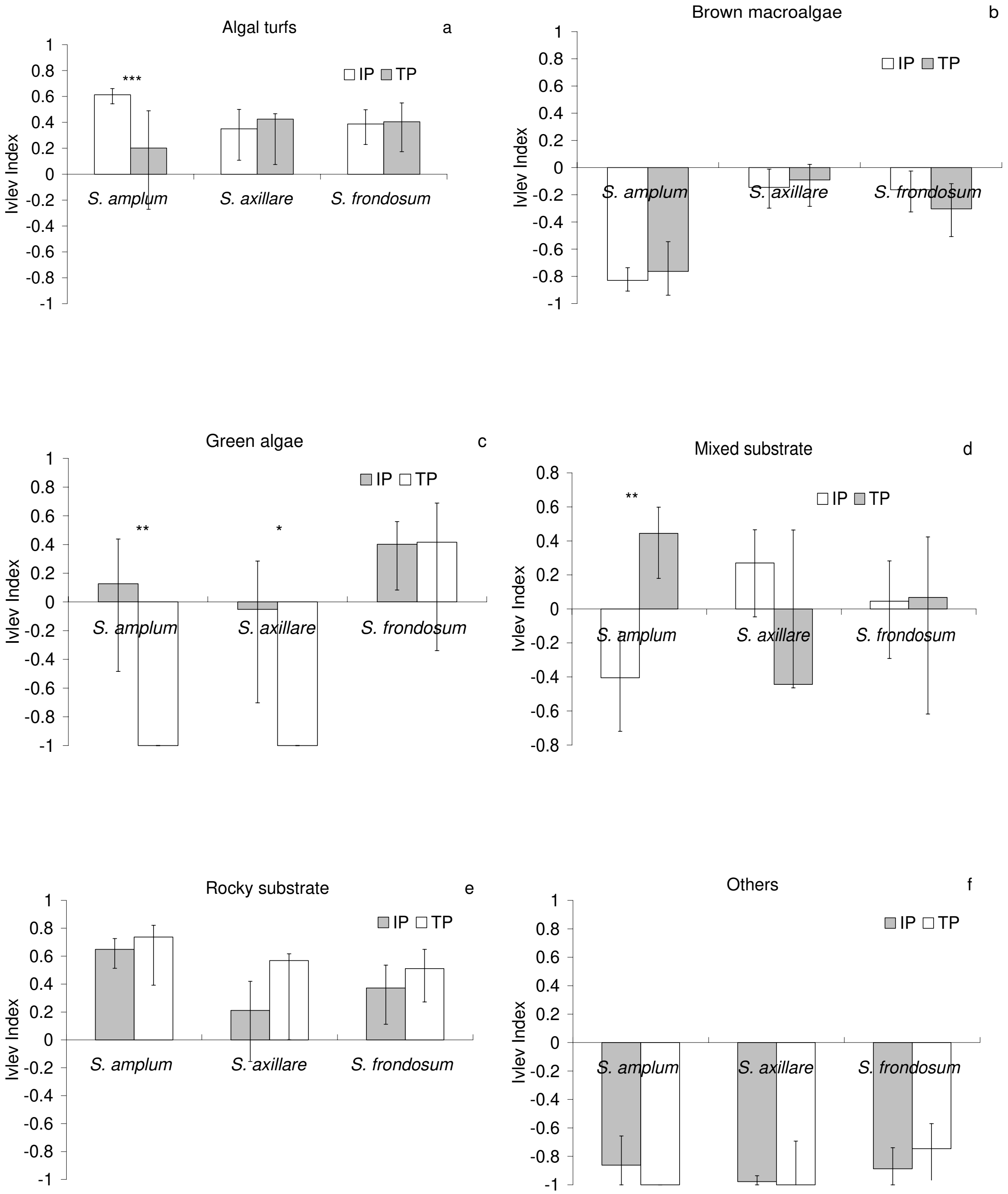

Fig. 2.1. Substrate selection (Ivlev's electivity index) for six substrate types by the adult phases of three species of *Sparisoma* at Fernando de Noronha Archipelago. Positive values indicate higher preference of the substrate while negative values indicate lower preference

or rejection (see text for further details): algal turfs (a), brown macroalgae (b), green algae (c), mixed substrate (d), rocky substrate (e) and others (f). Bars represent bootstrap-generated 95% confidence intervals. Significance in inter-phase comparisons is indicated by: * = $P<0.05$, ** $P< 0.01$, *** $P < 0.001$ and $P < 0.0001$.

Feeding frequencies

We found differences in the feeding frequencies of the three species (F=4.46, *df*=2, P=0.0013). *Sparisoma frondosum* showed the highest feeding frequencies, but *S. amplum* and *S. axillare* had similar ones (Fig. 2.2). The feeding frequencies of IP individuals of *S. amplum* (x = 4.97 ± sd = 1.99), *S. axillare* (x = 5.17 ± sd = 2.02) and *S. frondosum* (x = 4.94 ± sd = 2.30) were similar, but TP individuals of *S. frondosum* (x = 3.85 ± sd = 2.24) had higher feeding frequencies than *S. amplum* (x = 1.96 ± sd = 1.75) and *S. axillare* (x = 2.14 ± sd = 1.73) (Fig. 2.2). Initial phase individuals of the three species showed higher feeding frequencies than the TP ones (Fig. 2.2, Table 1).

The pattern of the diel feeding frequencies of IP and TP individuals of the same *Sparisoma* species was similar and we found that *S. amplum* and *S. axillare* differed on their feeding rates throughout the day, while *S. frondosum* did not (Table 1). *Sparisoma amplum* increased its feeding frequency throughout the day, while *S. axillare* showed its highest feeding frequencies between 1100h-1600h (Fig. 2.2).

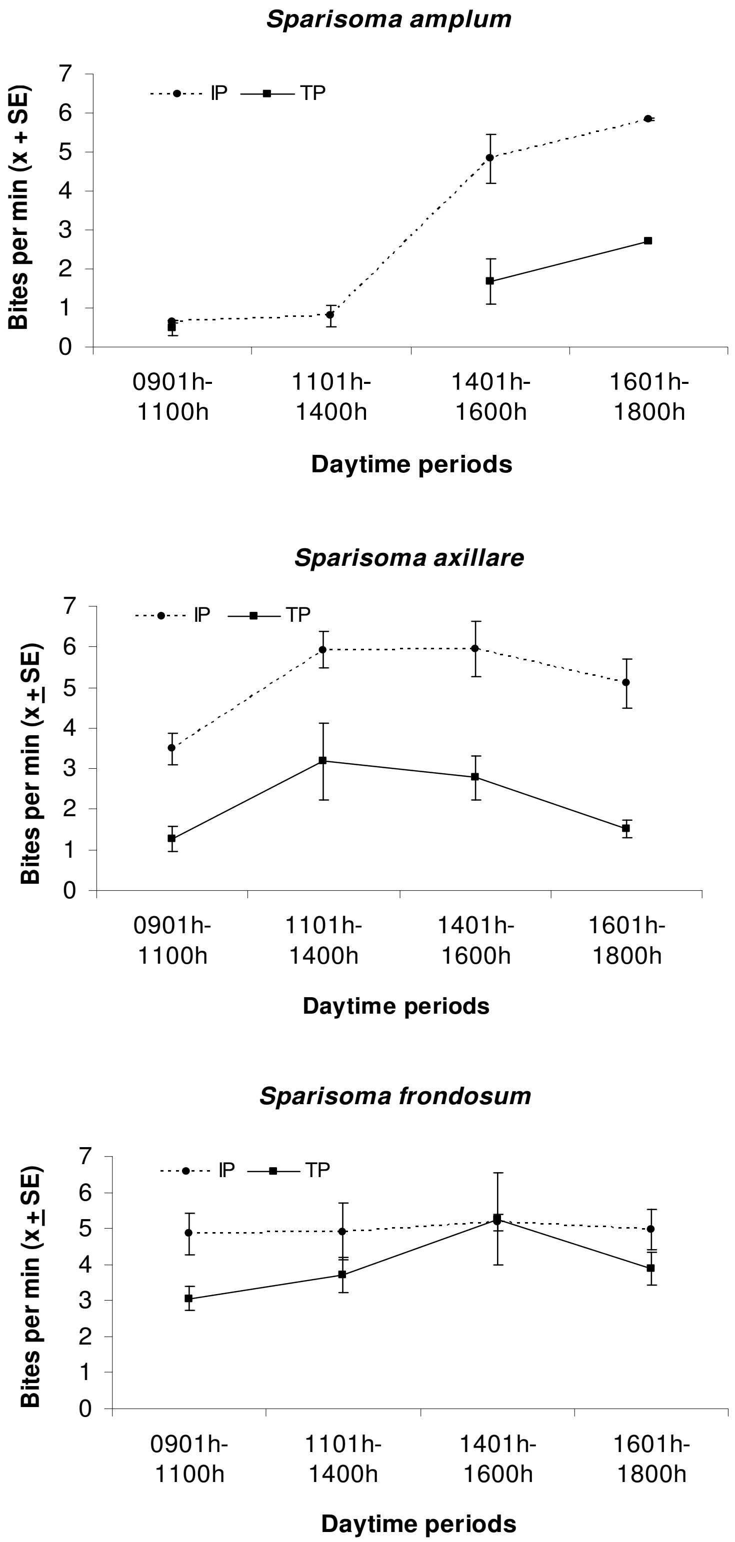

Fig. 2.2. Feeding frequencies of initial (IP) and terminal phase (TP) individuals of three *Sparisoma* species at Fernando de Noronha Archipelago.

Table 1. Two-way ANOVA for feeding frequencies (bites per minute) of three *Sparisoma* species at Fernando de Noronha Archipelago. The factors considered for analysis for each species were: reproductive phase (initial and terminal) and daytime period.

Source	*df*	SS	F	p
S. amplum				
Time	2	0.659	13.804	0.000
Phase	1	1.480	61.958	0.000
Interaction	2	0.092	1.934	ns
S. axillare				
Time	3	0.566	6.448	0.001
Phase	1	1.997	68.210	0.000
Interaction	3	0.041	0.470	ns
S. frondosum				
Time	3	9.780	0.612	ns
Phase	1	29.747	5.585	0.020
Interaction	3	9.709	0.608	ns

Distribution of the three *Sparisoma* species on the reef

We recorded a total of 403 *Sparisoma* individuals on the transects. From these, 38 were *S. amplum* (35 IP individuals and three TP ones); 219 *S. axillare* (210 IP individuals and nine TP ones); and 154 *S. frondosum* (75 IP individuals and 79 TP ones).

Sparisoma amplum abundance did not change throughout the day, but the abundance of *S. axillare* and *S. frondosum* differed between morning and afternoon (Table 2). *Sparisoma frondosum* was the most abundant species during the morning, whereas *S. axillare* was the most abundant species during the afternoon (Table 2). *Sparisoma amplum* and *S. frondosum* were more abundant in the rocky shore, while *S. axillare* was more abundant in the interface (Table 2).

Table 2. Number of individuals of three *Sparisoma* species in two daytime periods, morning (0900h-1130h) and afternoon (1500h-1700h), and on two microhabitats, interface and rocky shore, at Fernando de Noronha Archipelago.

Sparisoma species	Number of individuals			
	Morning		Afternoon	
	Interface	Rocky shore	Interface	Rocky shore
S. amplum	1	17	8	14
S. axillare	24	1	103	87
S. frondosum	46	78	14	16

Foraging groups

The three *Sparisoma* species foraged most frequently solitary than in groups at the Praia da Conceição (Table 3). Additionally, we recorded only IP individuals of the three *Sparisoma* species foraging in groups at the same site. *Sparisoma axillare* was the parrotfish most frequently found in groups and which formed the largest aggregations (Table 4).

Sparisoma axillare was found most frequently in groups during the afternoon and on the interface, while *S. frondosum* foraged most frequently in groups during the morning and on the rocky shore. We recorded only one homospecific group of *S. amplum*, which foraged on the rocky shore during the morning (Table 4). We recorded three heterospecific foraging groups at the Praia da Conceição, two of them composed by *S. axillare* and *S. frondosum* IP individuals, and one composed by *S. amplum* and *S. axillare* IP individuals.

Table 3. Number of individuals of three *Sparisoma* species foraging in two daytime periods, morning (0930h-1100h) and afternoon (1500h-1700h), and two social categories, solitary and grouped, at Praia da Conceição, Fernando de Noronha Archipelago.

Sparisoma species	Number of individuals			
	Morning		Afternoon	
	Solitary	On group	Solitary	On group
S. amplum	14	2	19	0
S. axillare	9	12	100	86
S. frondosum	90	28	31	0

Table 4. Homospecific foraging groups and individuals per group of three *Sparisoma* species in two daytime periods, morning (0930h-1100h) and afternoon (1500h-1700h), and two microhabitats, rocky shore and interface at the Praia da Conceição, Fernando de Noronha Archipelago.

Sparisoma species	Number of homospecific groups (average of individuals per group)			
	Morning		Afternoon	
	Rocky shore	Interface	Rocky shore	Interface
S. amplum	1 (2)	0	0	0
S. axillare	0	1 (12)	5 (6)	9 (6.22)
S. frondosum	3 (3)	1 (3)	0	0

At the Praia do Sancho and Praia do Porto the three *Sparisoma* species seem to behave in the same way as we recorded at the Praia da Conceição. However, we observed aggregations of about 50 *S. frondosum* TP individuals foraging at the Laje Dois Irmãos at about 15m depth. We also recorded two foraging aggregations of about 15 *S. amplum* TP individuals at the Canal da Ressurreta at about 12m. In both situations, the TP individuals foraged continuously and very close to each other, not displaying any territorial behaviour.

The foraging homo and heterospecific groups of IP and TP individuals of the three species at the Praia da Conceição, Canal da Ressurreta and Laje Dois Irmãos showed some similarities. All of them were static groups (aggregations), since the individuals did not move across the reef and they ate continuously moving very little along a small area.

Behavioural patterns during the foraging activity

Initial and terminal phase individuals of *S. amplum* and *S. axillare* had different behaviours while foraging at the Praia da Conceição. Initial phase individuals of these two species generally swam slowly taking bites of the substrate continuously. On the other hand, TP of *S. amplum* and *S. axillare* spent a large amount of time in the water column patrolling their territories using the same routes and chasing away conspecific individuals. *Sparisoma frondosum* IP and TP individuals behaved in a similar way as the two precedent species. Although *S. frondosum* TP individuals displayed no territorial patrolling behaviour, it was frequently observed chasing away conspecific individuals. All agonistic interactions were recorded between conspecific fishes, which could be either IP or TP individuals (i.e., no interspecific agonistic displays were recorded during the study).

We observed three courtship bouts during the study. Two of them were observed at the Praia do Sancho: one involved *S. amplum* and the other *S. axillare*. The third bout was observed at the Praia da Conceição and involved *S. frondosum*.

Discussion

Substrate selection and preference

The three *Sparisoma* species and their initial and terminal phases selected their foraging substrates and differed in this substrate selection, as already recorded in other studies on substrate use by parrotfishes (e.g. Bruggemann et al. 1994b, c; McAfee and Morgan 1996). One of this studies includes *Sparisoma viride*, *S. rubripinne* and *S. chrysopterum* (McAfee and Morgan 1996), the three Caribbean species most closely related to the Brazilian endemics *S. amplum*, *S. axillare* and *S. frondosum*, respectively (Moura et al. 2001).

All three *Sparisoma* species here studied rejected macroalgae for foraging as already recorded in other studies on parrotfish foraging (e.g. McAfee and Morgan 1996). Macroalgae, especially brown algae, have compounds that deter herbivory by reef fishes and invertebrates (Hay 1991; Vallim et al. 2005). Although macroalgae was not selected by any of the three *Sparisoma* species, it comprised a considerable portion of the diet of *S. axillare* and *S. frondosum*. Thus, secondary compounds of brown macroalgae may not strongly deter herbivory by these parrotfishes. Our suggestion is strengthened by the high amount of macroalgae ingested by other *Sparisoma* species, such as *S. rubripinne* and *S. aurofrenatum* in the Caribbean (McAfee and Morgan 1996). Also, *S. amplum*, *S. axillare*, *S. frondosum*, *Scarus trispinosus* and *Scarus zelindae* ingest large amounts of macroalgae (about 40% of their gut contents) at Abrolhos Archipelago, Brazil (Ferreira and Gonçalves in press).

The substrate types selected for foraging by the three scarids studied at Fernando de Noronha (algal turfs and mixed substrate) are apparently rich in sediment and detritus, components with high nutritional value in the reef environment (Wanders 1976; Adey and Steneck 1985; Wilson et al. 2003; Choat et al. 2004). This result is in accordance to recent studies on diet of herbivorous fishes, which found that the diet of parrotfish species in the Pacific and Atlantic have significant proportions of substrates rich in detritus (Wilson et al. 2003, Ferreira and Gonçalves in press).

In our study no *Sparisoma* species fed on dead or live hard coral colonies, which contrasts with studies on other species of the same genus in the Caribbean (e.g. Bruggemann et al. 1994c; McAfee and Morgan 1996; Bruckner and Bruckner 1998; Bruckner et al. 2000; Sánchez et al. 2004). Hard corals are very rare at the Praia da Conceição (our pers. obs.), which may explain why this substrate type remained unused in our records. Also, most of the few hard corals colonies found at this study site were alive, whereas *Sparisoma* species forage mostly on dead hard coral colonies (e.g. Bruggemann et al. 1994c; McAfee and Morgan 1996), except *S. viride*, which also forages on live coral colonies (Bruckner & Bruckner 1998; Bruckner et al. 2000; Sánchez et al. 2004). On the other hand, our three *Sparisoma* species select positively rocky substrate, which seems covered by similar algae types that grow over dead corals. As dead corals are scarce at the study site, the three parrotfishes may obtain these algae by feeding on rocks.

The fire coral *Millepora* sp., the most common colonial cnidarian at our study site, is a stinging species, which possibly explain the few records of *Millepora* being foraged by reef fishes (e.g. Randall 1967). Even so, we recorded *Sparisoma* individuals taking bites off this stinging coral, possibly to be used as territorial marks in a way similar to other *Sparisoma* species in the Caribbean (e.g. Bruggemann et al. 1994c; Van Rooij et al. 1995).

The similarities in substrate selection by IP and TP individuals of the same species (except for *S. amplum*) agree with a study on resource use by sympatric parrotfishes in the Caribbean (McAfee and Morgan 1996).

Feeding frequencies

The higher feeding frequencies we recorded for *S. frondosum* were due to the behaviour of TP individuals, which displayed higher feeding frequencies when compared with those from TP individuals of *S. amplum* and *S. axillare*. Additionally, the higher feeding frequency of *S. frondosum* TP males may be explained by its continuous foraging. *S. amplum* and *S. axillare* TP individuals patrolled their territories constantly and consequently foraged less than *S. frondosum* TP individuals.

The feeding frequency of IP individuals of all three *Sparisoma* species was higher than that of TP individuals of same species, which contrasts with studies in the Caribbean, in which IP and TP individuals of the same species showed similar feeding frequencies (e.g. Bruggemann et al. 1994c; McAfee and Morgan 1996). Our results may be explained by the behavioural differences of IP and TP parrotfishes at our study site. Terminal *S. amplum* and *S. axillare* individuals spent a large amount of time chasing away conspecific males and apparently patrolling their territories and consequently foraged less than IP individuals. Even *S. frondosum* TP males (which did not patrol territories but spent a large amount of time chasing away conspecific individuals) had lower feeding rates than initial individuals of the same species.

However, we suggest that TP *Sparisoma* individuals have higher feeding frequencies, form groups and do not establish territories in deeper sites, such as the Laje Dois Irmãos and Canal da Ressurreta, where we observed them feeding continuously on aggregations and not displaying any territorial behaviour. On the other hand, we observed spawning activities and territorial behaviour of TP individuals of all three *Sparisoma* species at the Praia da Conceição and Praia do Sancho, which may indicate that these shallower areas are used as reproductive sites, besides feeding grounds for IP individuals.

These suggestions agree with studies on *S. viride* in the Caribbean, where TP males change their behaviour according to the habitat characteristics (Koltes 1993; Van Rooij et al. 1996c). In shallow areas, *S. viride* is found on "multi-male groups" composed by up to 14 TP males and about twice as many initial individuals (Van Rooij et al. 1996c). In deeper areas, *S. viride* is found in "one-male groups", which consist of one TP male and 1-14 initial females, and where the males have higher degree of territoriality, since the time TP *S. viride* individuals spend on agonist interactions is significantly higher on deeper sites (Van Rooij et al. 1996c). In Fernando de Noronha, the pattern seems to be the opposite, since TP males of *S. amplum, S. axillare* and *S. frondosum* were found feeding aggregated in deeper areas and patrolled territories and chased away individuals of their own species in shallow areas. On the other hand, territories of *Scarus croicensis* in Panama are in shallow reefs (up to 3m) and appear to serve mostly as feeding and occasional spawning grounds (Buckman and Ogden 1973), in a way somewhat similar to what we found for three *Sparisoma* species in Fernando de Noronha. The main difference between *S. croicensis* territories and those of the three *Sparisoma* species studied here is that both IP and TP individuals of *S. croicensis* defend territories (Buckman and Ogden 1973), whereas only TP males were recorded defending territories.

Similarities between the diel feeding frequencies pattern of IP and TP individuals of the same *Sparisoma* species may indicate that some characteristics of the foraging behaviour are kept when the individuals change from the initial to the terminal phase. This suggestion is strengthened by the similarities in substrate selection for foraging by initial and terminal phase individuals of same species.

The higher feeding frequencies we found for *S. amplum* and *S. axillare* in afternoon and noon, respectively, agree with the diel feeding frequencies of other parrotfish species, and for other herbivorous fish species as well (e.g. Bruggemann et al. 1994a; McAfee and Morgan 1996; Ferreira et al. 1998; Zemke-White et al. 2002). These results may be explained by the higher nutritional quality of algae in the afternoon due to the increase of starch content in algae throughout the day (Taborsky and Limberger 1980; Zemke-White et al. 2002). Additionally, the main substrate types consumed by the three *Sparisoma* species (algal turfs, mixed substrate and crustose coralline algae) are mostly composed by red algae, which has an increasing potentially digestible organic fractions along the day (Bruggemann et al. 1994a).

Distribution of the three *Sparisoma* species on the reef

The higher abundance of *S. amplum* and *S. axillare* IP individuals when compared with TP individuals of same species may be explained by the fact that only TP individuals patrolled territories. When patrolling territories, TP males constantly chased away conspecific individuals, which likely reduce the occupancy of the area by other males, especially the TP ones. This suggestion lends support from our finding that IP and TP individuals of *S. frondosum* – whose TP individuals did not patrol territories – had similar abundances. Our findings of the abundance of *S. amplum* and *S. axillare* at the Praia da Conceição agree with the social system of *Sparisoma viride* in the Caribbean, since TP males of this species are less abundant in areas where their degree of territoriality is higher (Van Rooij et al. 1996c).

The differences in the reef occupation by the three *Sparisoma* species indicate that they have some partition of time and microhabitat. *Sparisoma axillare* and *S. frondosum*, the two most abundant parrotfishes at the Praia da Conceição, differed in their densities throughout the day. On the other hand, *S. amplum*, the rarest parrotfish at our study site, occurred in low densities on both the morning and the afternoon. Additionally, *S. axillare* and *S. frondosum* differed in microhabitat occupancy, since the latter was most frequent on the rocky shore and the former on the interface, which strengthen the suggestion of time and microhabitat partitioning between these *Sparisoma* species.

The differences in reef occupation by the three *Sparisoma* species here studied agree with studies on the distribution of herbivorous fishes in the reef environment (e.g. McAfee and Morgan 1996; Dias et al. 2001). A study on resource partitioning by five parrotfish species in the Caribbean shows that they differ in their habitat occurrence (McAfee and Morgan 1996). Moreover, a recent study on resource and habitat sharing by the surgeonfishes *Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus* in North-eastern Brazil reefs demonstrates that these also have some degree of microhabitat segregation (Dias et al. 2001).

Foraging groups

The social organization of all three parrotfish species during their foraging at the Praia da Conceição was similar to those recorded for other *Sparisoma* species in the Caribbean (e.g. Winn and Bardach 1960; Barlow 1975; Koltes 1993), since they mostly foraged solitarily. Moreover, IP individuals of the three *Sparisoma* species aggregated more frequently while foraging than the TP ones, as also recorded for other species in the Caribbean (e.g. Barlow 1975).

Our data indicate that the occurrence of foraging groups of the three *Sparisoma* species depends mostly on the abundance of a given species on the reef. *Sparisoma frondosum* was the commonest species found aggregated in the morning and at the rocky shore, the same period and microhabitat in which it was the most abundant *Sparisoma* species at the Praia da Conceição. On the other hand, *S. axillare* was the commonest species grouped during the afternoon and at the interface, the same period and microhabitat in which it was the most abundant *Sparisoma* species at the same study site. *Sparisoma amplum*, the rarest *Sparisoma* species in both periods, was rarely recorded in groups. The only *S. amplum* foraging group we recorded was found on the rocky shore in the morning, the microhabitat where this species was commonest during this period.

Our suggestion that the occurrence of groups and the number of aggregated individuals depends mostly on a given species density is strengthened by the composition of the heterospecific groups recorded at the Praia da Conceição. All heterospecific groups included *S. axillare*, the most abundant *Sparisoma* species at the study site.

Conclusion

The three *Sparisoma* species here studied differed in all analysed features and seem to partition the foraging substrate, time and microhabitat at the Praia da Conceição, a result which agree with other studies on parrotfishes (e.g. McAfee and Morgan 1996). The differences between the three species may lead to the coexistence of *S. amplum*, *S. axillare* and *S. frondosum* in the Fernando de Noronha reefs, since we have recorded no agonistic interactions among individuals of different species. Additionally, even the occurrence of foraging groups of the three *Sparisoma* species seems to have some degree of segregation, since the groups occurred in different period and microhabitat of the reef.

The differences between the three *Sparisoma* species and between their initial and terminal phases indicate that related species and adult individuals of the same species may have different effects in the system they occupy. Additionally, the differences in the foraging behaviour of TP parrotfish males in different areas of the reef (Koltes 1973; Van Rooij et al. 1996c; this study) indicate that even individuals of the same species and reproductive phase may differ on their impact on different areas of the reef. Actually, most studies on parrotfishes found differences in resource use and behaviour between species or reproductive phases (Bruggemann et al. 1994b; McAfee and Morgan 1996; this study) and even individuals of the same reproductive phase (Van Rooij et al. 1996c; this study). These results emphasize the need to consider the functional role of a given species and even individuals of the same species when formulating management strategies, especially due to the increasing condition of species and biodiversity loss in tropical reefs (e.g. Ferreira and Gonçalves 1999; Bellwood et al. 2003; Gasparini et al. 2005; Ferreira et al. 2005).

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CAPÍTULO 2

Cleaning associations do differ between initial and terminal phase individuals of three *Sparisoma* species (Perciformes: Scaridae) at Fernando de Noronha Archipelago, tropical West Atlantic

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Abstract Parrotfishes (Scaridae) are large, abundant and conspicuous members of coral reef fish communities that forage over reefs during daytime. These fishes are protogynous hermaphrodites, which change color and sex, from initial phase (IP) females or males to terminal phase (TP) males. At the Fernando de Noronha Archipelago, tropical West Atlantic, three parrotfish species are syntopic, *Sparisoma amplum*, *S. axillare* and *S. frondosum*. We compared cleaning episodes recorded for these scarids during their feeding activity. All three parrotfish species were cleaned "on the move" by the Noronha wrasse (*Thalassoma noronhanum*) and occasionally sought bottom-based cleaning stations tended by gobies, angelfishes, wrasses and shrimps. Initial individuals were followed more often by the Noronha wrasse than the TP ones and only terminal phase individuals were recorded posing at cleaning stations. Initial phase fishes forage more than the TP ones and thus are probably followed more often by the Noronha wrasse, which capitalizes upon food items exposed by the parrotfishes. Since the IP individuals were cleaned by *T. noronhanum* while foraging, they have reduced need to seek cleaning stations.

Introduction

Parrotfishes (Perciformes: Scaridae) are large, abundant and conspicuous members of herbivorous reef fish communities that forage over reefs during daytime (Robblee and Zieman 1984; Lewis and Wainwright 1985; McAfee and Morgan 1996). Most of the Scarids are protogynous hermaphrodite and have differentiated sexual stages, and change color and sex from initial phase (IP) females or males to terminal phase (TP) males (Robertson 1972; Robertson and Warner 1978). Many Scaridae species are territorial (e.g. Barlow 1975; Buckman & Ogden 1973; Van Rooij et al. 1996a, b) and TP males of *Sparisoma* sp. defend their breeding and feeding territories against conspecific males (Barlow 1975; Van Rooij et al. 1996c; RMB pers. obs). Thus, these males spend a large amount of time on the water column, apparently patrolling their territories and chasing away conspecific males (Van Rooij et al. 1996c; RMB pers. obs.).

Many feeding associations on reef environment involve parrotfish species (e.g., Strand 1988; Francini-Filho et al. 2000; Sazima et al. 2005a). A common kind of association between reef fishes is cleaning symbiosis, where a “cleaner” fish feed on ectoparasites, mucus and diseased tissues on the body of its “client” fish (Losey 1971; 1987; Grutter 1999). Scarids are among the preferred clients of many cleaner fishes (Losey 1972, 1974; Grutter and Bshary 2003, 2004), probably due to the quality of the nutritive mucus recovering their body (Lewis 1970; Gorlick 1980; Ebran et al. 1999; Arnal and Morand 2001; Arnal et al. 2001). Another kind of feeding association is recorded among “nuclear” foraging species followed mainly by opportunistic predators (Hobson 1974; Fricke 1975; Ormond 1980; Aronson and Sanderson 1987), where parrotfishes usually act as the nuclear species (Sazima et al. 2005a). Followers prey mostly on invertebrates and small fishes exposed by the substrate-disturbing activities of the nuclear fishes (Fishelson 1977; Ormond 1980; Gibran 2002).

Three syntopic scarid species are common at Fernando de Noronha Archipelago, tropical West Atlantic, *Sparisoma amplum*, *S. axillare* and *S. frondosum* (Moura et al. 2001). These three parrotfish species seek the Noronha wrasse (*Thalassoma noronhanum*) at mid-water cleaning stations and are also cleaned near the bottom, outside these stations (Francini-Filho et al. 2000). However, these three parrotfish species are frequently followed by the versatile Noronha wrasse, a very opportunistic forager (Sazima et al. 2005a). While following parrotfishes, the Noronha wrasse capitalizes upon food particles made available by the activity of the nuclear fish and when they momentarily interrupt feeding the wrasse also inspect and clean them (Sazima et al. 2005a).

We compared cleaning episodes recorded for the three syntopic scarids during their feeding activity, focusing on the following questions: 1) Do IP and TP individuals of each species of *Sparisoma* differ in the frequency that they are followed by the Noronha wrasse? 2) Do IP and TP individuals of each species of *Sparisoma* differ in the frequency that they visit cleaning stations of wrasses, gobies, angelfishes, and shrimps?

Material and methods

The field study was conducted at Fernando de Noronha Archipelago (3°54'S, 32°25'W), 345 km off the coast of NE Brazil (see Maida and Ferreira 1997 for map and description), from May to June 2003. Behavioral interactions between the scarids and the Noronha wrasse were recorded at the Praia da Conceição, on the main island, a rocky shore with adjacent sand flat. This site was selected for most observational sessions due to abundance of IP and TP individuals of the three *Sparisoma* species, and depths adequate to observational sessions from close quarters even while on water surface. During our study, depth ranged 2-10 m, horizontal visibility ranged 8-25 m, and water temperature was 27^{o}C.

We assessed the frequency of scarids being followed by the Noronha wrasse with 58 transects 5x100m, recording all the adult parrotfishes, their species and reproductive phase, and whether or not they were associated to the Noronha wrasse. We recorded a total of 226 *Sparisoma* individuals in the transects: 47 *S. amplum* (26 IP individuals and 21 TP ones); 136 *S. axillare* (117 IP individuals and 19 TP ones); and 66 *S. frondosum* (35 IP individuals and 31 TP ones).

The frequency a parrotfish sought cleaning stations was assessed by following focal individuals during 5min bouts, recording whether the individual posed at a cleaning station during its foraging or not. In a total of 95 bouts, 36 were of *S. amplum* (18 of IP individuals and 18 of TP ones); 30 of *S. axillare* (16 of IP individuals and 14 of TP ones); and 29 of *S. frondosum* (15 IP individuals and 14 TP ones).

The G test for goodness of fit was used to compare the frequency of IP and TP individuals of each *Sparisoma* species posing at fixed cleaning stations. The same test was also used to compare the number of IP and TP individuals of each *Sparisoma* species that were followed by *T. noronhanum* (Zar 1999).

Results

All three parrotfish species were cleaned "on the move" by the Noronha wrasse and occasionally sought the mid-water cleaning stations tended by this cleaner. When followed by *T. noronhanum*, foraging parrotfishes ceased momentarily their activity and adopted a typical inviting posture to be cleaned (see Wicksten 1998 for postures). Also, parrotfishes posed at bottom-based cleaning stations tended by the neon goby *Elacatinus* cf. *randalli*, the juvenile angelfish *Pomacanthus paru* and the shrimp *Stenopus hispidus*. These cleaning stations were tended on rocky outcrops located between the rocky shore and the sandy flat. Parrotfishes that sought bottom-based cleaning stations behaved in the same manner that parrotfishes which were cleaned "on the move", posing to the cleaner and keeping motionless while cleaned. However, parrotfishes that sought bottom-based cleaning stations had to leave their feeding sites to seek these stations, while parrotfishes cleaned "on the move" were cleaned at their foraging sites.

Initial phase individuals of the three *Sparisoma* species were followed more often by the Noronha wrasse than TP ones (*S. amplum* $G_1=5.88$, $p<0.005$, *S. axillare* $G_1=10.10$, $p<0.001$, *S. frondosum* $G_1=11.34$, $p<0.005$, Fig. 3.1 and 3.2). On the other hand, only TP individuals of the three *Sparisoma* posed at fixed cleaning stations (Fig. 3.3 and 3.4).

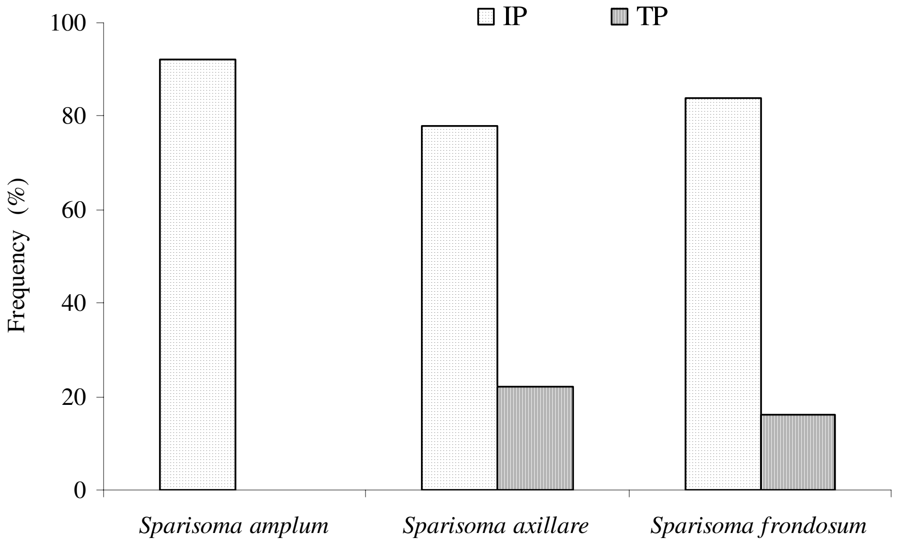

Fig. 3.1. Frequency (%) of initial (IP) and terminal phase (TP) individuals from three syntopic Scaridae species (*Sparisoma amplum*, *S. axillare* and *S. frondosum*) followed by the Noronha wrasse (*Thalassoma noronhanum*) at Fernando de Noronha Archipelago.

Fig. 3.2. An initial phase individual of the parrotfish *Sparisoma amplum* followed by five individuals of the Noronha wrasse (*Thalassoma noronhanum*).

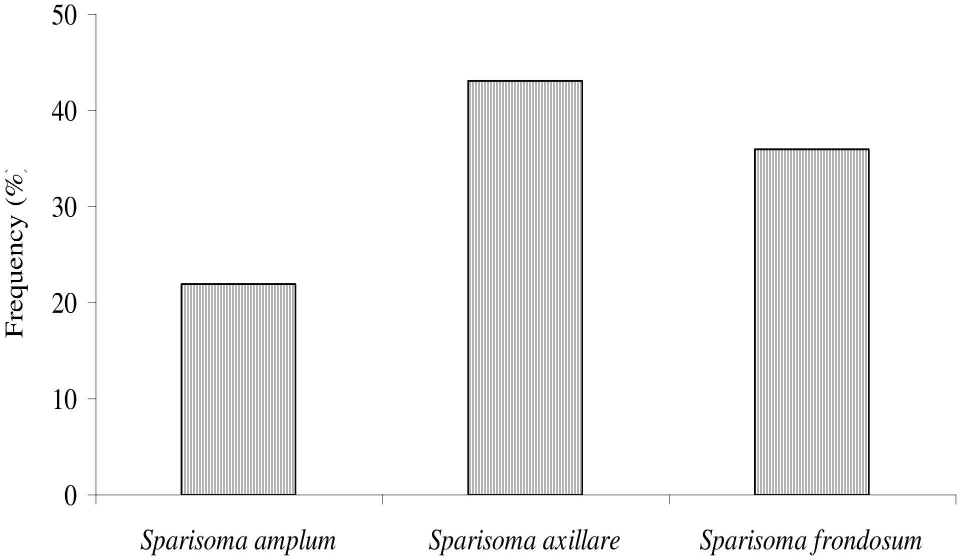

Fig. 3.3. Frequency (%) of TP individuals from three syntopic parrotfish species (*Sparisoma amplum*, *S. axillare* and *S. frondosum*) that posed at cleaning stations at Fernando de Noronha Archipelago.

Fig. 3.4. Four neon gobies (*Elacatinus* cf. *randalli*) inspecting and cleaning a terminal phase individual of parrotfish (*Sparisoma axillare*) at bottom-based cleaning station.

Discussion

The Noronha wrasse is the most abundant species at several sites around the Fernando de Noronha Archipelago and a very active cleaner of reef fishes (Francini-Filho et al. 2000). Additionally, it was recorded to clean the common octopus (*Octopus* cf. *vulgaris*) at the archipelago (Sazima et al. 2004). In a recent study *T. noronhanum* was recorded to frequently follow the three *Sparisoma* species to capitalize upon drifting particles released by the nuclear fishes and to clean these (Sazima et al. 2005a). The three *Sparisoma* species herein studied were recorded amongst the less preferred clients in mid-water stations, representing together only 1.49 % of the total cleaning events recorded in the most extensive study on the Noronha wrasse cleaning activity (Francini-Filho et al. 2000). On the other hand, in our study, the Noronha wrasse frequently followed and cleaned the three *Sparisoma* species. We believe that the type of cleaning activity the wrasse is engaged in a particular moment may explain these differences. At mid-water cleaning stations, the wrasses clean mostly planktivorous clients and rarely the three *Sparisoma* species (Francini-Filho et al. 2000). Preference towards planktivorous clients at these stations is possibly related to their habits of crowding at stations and their occurrence in mid-water close to the stations (Francini-Filho et al. 2000). On the other hand, when following nuclear fish, the wrasse commonly cleans parrotfish if the opportunity arises, i.e., the nuclear fish momentarily stop foraging and pose to the cleaner (Sazima et al. 2005a).

Additionally, the Noronha wrasse is able to tend temporary cleaning stations at several sites on the reef (Sazima et al. 2005a, b). The nocturnally active glassy sweeper (*Pempheris schomburgki*) was recorded as a client of the Noronha wrasse at temporary cleaning stations near the clients' daytime refuges (Sazima et al. 2005b).

The high frequency of following association between the Noronha wrasse and IP individuals of *Sparisoma* species rather than TP ones can be explained by the differences on the feeding frequencies and behavior of these two phases at our study site. At the Praia da Conceição, IP individuals of the three *Sparisoma* species have higher feeding rates than TP ones, since *Sparisoma* TP individuals spend much time patrolling their territories and expulsing conspecific males (RMB pers. obs.). Since *T. noronhanum* capitalizes upon food items originated by the parrotfishes feeding activities (Sazima et al 2005a), it might be more advantageous to the Noronha wrasse to follow the IP individuals, which forage more frequently and slowly than the TP ones.

The feeding behavior of terminal phase individuals of *S. amplum*, *S. axillare* and *S. frondosum* seems to change according to the habitat they occupy at Fernando de Noronha Archipelago (RMB pers. obs.). In shallow areas the TP individuals were found patrolling territories and chasing away conspecifics, while in deeper areas they were found feeding continuously on aggregations and not exhibiting any territorial behaviour (RMB pers. obs.). Thus, it is possible that the frequency of following associations between the Noronha wrasse and TP individuals of *Sparisoma* sp. also differs according to the habitat characteristics. In this case, we surmise that the Noronha wrasse will follow TP individuals of *Sparisoma* sp. more frequently in deeper areas, where they forage more slowly and continuously than in the shallows.

The fact of only TP individuals posed at fixed cleaning stations can be explained by the frequency that they are followed by the Noronha wrasse. As the IP individuals are constantly followed by the Noronha wrasses, which remove ectoparasites when the parrotfishes interrupt foraging and pose (Sazima et al 2005a), these individuals would only complement their parasite removal by seeking cleaning stations. On the other hand, *Sparisoma* TP individuals were rarely followed by the Noronha wrasse and, thus have to seek cleaning stations for most of parasite removal.

Cleaning, at some periods of the day, may have high energetic cost to the client in terms of reduced foraging opportunities (Grutter et al. 2002). Thus, cleaning by follower Noronha wrasse while foraging may be advantageous to the scarids, since they do not have to stop their foraging activity and seek for cleaning stations to get rid of parasites (Sazima et al. 2005a).

Clients with high parasitic load are regarded to seek more frequently and spend more time at cleaning stations (Grutter 2001). However, we did not record differences in the overall frequency of cleaning symbiosis between IP and TP individuals, but how the phases were cleaned. Thus, we believe that the lower frequency of IP individuals visiting cleaning stations recorded in this study is related to their distinct foraging behaviour rather than to presumed in parasitic load (e.g. Grutter 2001). The cleaning symbiosis is possibly important for both IP and TP individuals, but IP individuals are mainly cleaned outside cleaning stations and the TP individuals in fixed cleaning stations.

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CONCLUSÃO GERAL

No presente estudo, *S. amplum*, *S. axillare* e *S. frondosum* diferiram na seleção de todos os aspectos analisados durante o forrageamento (substrato, tempo e microhábitat), o que concorda com estudos sobre outras espécies de Scaridae, principalmente no Atlântico Ocidental (e.g. Bruggemann et al. 1994a, b; McAfee & Morgan 1996). As diferenças encontradas no forrageamento destas três espécies de *Sparisoma* poderiam minimizar a sobreposição no uso de recursos quando em simpatria ou sintopia. Entretanto, não pode ser concluído, a partir dos resultados obtidos, que as diferenças no forrageamento de *S. amplum*, *S. axillare* e *S. frondosum* sejam necessariamente um mecanismo para minimizar sobreposição no uso de recursos ou competição, já que tais diferenças podem ter sido causadas por uma competição passada ou simplesmente por diferenças geradas durante a especiação, não relacionadas necessariamente à competição (Pianka 1999).

Indivíduos em fase inicial e terminal de mesma espécie de *Sparisoma* também diferiram em vários aspectos de seu forrageamento no presente estudo. Algumas diferenças, como a organização social durante o forrageamento, já haviam sido registradas em estudos anteriores sobre Scaridae no Caribe (e.g. Barlow 1975; Van Rooij et al.a, b). Entretanto, o fato de indivíduos em fase inicial das três espécies aqui estudadas forragearem com maior freqüência que os indivíduos terminais difere de outros estudos, que não encontraram distinção na freqüência alimentar de indivíduos adultos de Scaridae em diferentes fases (e.g. Bruggemann et al. 1994b; McAfee & Morgan 1996). É possível que estudos anteriores sobre espécies de *Sparisoma* não tenham encontrado diferenças na freqüência alimentar devido às características das áreas onde os estudos foram feitos, uma vez que indivíduos em fase terminal diferem no forrageamento de acordo com as características locais (e.g. Barlow 1975; Koltes 1993; Bruggemann et al. 1994b; Van Rooij et al. 1996a, b). No presente estudo, em áreas rasas do arquipélago e situadas junto à ilha principal, indivíduos terminais das três espécies de *Sparisoma* forragearam pouco, ficando ocupados com comportamento territorial na maior parte do tempo. Por outro lado, em áreas do arquipélago com maior profundidade e localizadas fora da ilha principal, os indivíduos terminais forragearam continuamente e não exibiram comportamento territorial. Provavelmente, a freqüência de forrageamento de indivíduos terminais seja maior em locais mais profundos do arquipélago e, assim, mais semelhante à de indivíduos de fase inicial. Assim, é possível que os estudos em que indivíduos iniciais e terminais não diferiram na freqüência alimentar (e.g. Bruggemann et al. 1994b; McAfee & Morgan 1996) tenham sido feitos em locais nos quais os indivíduos terminais forrageiam mais continuamente e, assim, não exibem comportamento territorial com a freqüência observada no presente estudo.

As diferenças encontradas no comportamento alimentar e na freqüência de forrageamento de indivíduos de fase inicial e terminal das três espécies de *Sparisoma* aqui estudadas refletiram no seu tipo de organização social durante o forrageamento. Na Praia da Conceição, indivíduos iniciais forragearam continuamente, enquanto os terminais forragearam pouco e exibiram comportamento territorial. Como conseqüência, indivíduos de fase inicial foram freqüentemente observados forrageando em grupos, enquanto os terminais apenas forragearam solitários. Por outro lado, em locais do arquipélago em que indivíduos terminais de *Sparisoma* não apresentaram comportamento territorial, sua organização social foi semelhante à de indivíduos iniciais, já que forragearam mais continuamente e em grupos.

Além de influenciar o tipo de organização social, as diferenças no forrageamento de indivíduos iniciais e terminais influenciaram também as associações alimentares formadas entre as três espécies de *Sparisoma* e outras espécies recifais. Assim, na principal área de estudo (Praia da Conceição), indivíduos iniciais foram seguidos com maior freqüência pelo budião-de-Noronha (*Thalassoma noronhanum*) que os indivíduos terminais. A provável explicação para essa diferença é que indivíduos iniciais forrageiam mais continuamente e são, portanto, espécies nucleares mais vantajosas para o budião, que se beneficia da perturbação causada no substrato pelos peixes-papagaio (Sazima et al. 2005). As diferenças entre as três espécies de *Sparisoma* também refletiram na freqüência com que indivíduos iniciais e terminais requisitaram limpeza em estações de limpeza. No local de estudo, as principais espécies que estabelecem estações de limpeza são: o budião-de-Noronha, juvenis de paru-preto (*Pomacanthus paru*), néon (*Elacatinus randalli*) e camarões-limpadores (*Lismata* sp. e *Stenopus hispidus*). Indivíduos em fase inicial são limpos enquanto seguidos por *T. noronhanum* e, conseqüentemente, não precisam requisitar limpeza em estações de limpeza fixas com a mesma freqüência que os indivíduos em fase terminal. É possível, porém, que em locais nos quais forrageiem com maior freqüência, os indivíduos terminais sejam seguidos por *T. noronhanum* com freqüência semelhante à de indivíduos iniciais. Neste caso, é possível supor que a freqüência com que indivíduos terminais requisitariam limpeza em estações de limpeza com menor freqüência. Assim, as diferenças encontradas entre indivíduos iniciais e terminais podem refletir não apenas no forrageamento destas espécies, mas também no de outras espécies recifais, como *T. noronhanum* e outras espécies limpadoras de peixes e camarões.

As diferenças encontradas no forrageamento das três espécies de *Sparisoma* e entre indivíduos de fase inicial e terminal indicam que indivíduos adultos da mesma espécie podem ter diferentes efeitos nos sistemas em que ocorrem. Ainda, diferenças no comportamento de forrageamento de peixes-papagaio da mesma espécie e na mesma fase reprodutiva em diferentes áreas do recife (Ogden & Buckman 1973; Koltes 1993; Bruggemann et al. 1994b; Van Rooij et al. 199a, b; este estudo) indicam que esses indivíduos podem diferir no impacto que causam em diferentes áreas do recife. De fato, em grande parte dos estudos em Scaridae (Koltes 1993; Bruggemann et al. 1994b; McAfee & Morgan 1996; este estudo) foram encontradas diferenças no uso de recursos e comportamento de forrageamento entre espécies, fases reprodutivas, ou mesmo indivíduos na mesma fase reprodutiva (Koltes 1993; Bruggemann et al. 1994b; McAfee & Morgan 1996; este estudo). Esses resultados enfatizam a necessidade de considerar a função desempenhada por uma determinada espécie (e mesmo por adultos de mesma espécie) na formulação de estratégias de manejo ambiental, principalmente devido à crescente perda de espécies e biodiversidade em recifes tropicais (e.g. Ferreira & Gonçalves 1999; Bellwood et al. 2003; Gasparini et al. 2005; Ferreira et al. 2005).

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