aqua, Journal of Ichthyology and Aquatic Biology

The Noronha wrasse: a "jack-of-all-trades" follower

Cristina Sazima[1,2], Roberta Martini Bonaldo[1], João Paulo Krajewski[1] and Ivan Sazima[1]

1) Departamento de Zoologia e Museu de História Natural, Caixa Postal 6109, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, Brazil. Fax: +55 (19) 3289 3124. E-mail: csazima@gmail.com
2) Departamento de Zoologia, Caixa Postal 199, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brazil

Accepted: 07.03.2005

Keywords
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 reef 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 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 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 zooplanctívoro, 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.

Zusammenfassung
Bei der Vergesellschaft der Korallenfische während der Nahrungssuche gibt es immer eine oder mehrere Kern-Arten (hauptsächlich Bodenwühler), denen opportunistische Beutegreifer nachfolgen. Die Folger profitieren von der Nahrung, die bei den bodenwühlenden Aktivitäten der Kern-Arten aufgedeckt oder aufgescheucht wird. Im Fernando-de-Noronha-Archipel im Südwest-Atlantik stellten wir fest, dass der Plankton fressende, benthische Wirbellose aufsammelnde und putzende Lippfisch *Thalassoma noronhanum,* auch als Noronha-Lippfisch bezeichnet, sich als höchst vielseitiger Fresser, eine Art „Allerwelts-Fisch" betätigt, während er Korallenfischen folgt. Der Noronha-Lippfisch vergesellschaftet sich mit 15 verschiedenen Korallenfisch-Arten, um sich von den durch sie bei der Nahrungssuche aufgestöberten Partikeln zu ernähren. Folgende Typen des Nahrungserwerbs ließen sich an dem Lippfisch im Gefolge der Korallenfische feststellen: 1) Aufpicken der vom Bodengrund gelösten Partikel; 2) Aufnahme aus dem Maul wieder ausgestoßener Teile; 3) Aufnahme der mit dem Kot ausgeschiedenen Partikel; 4) Putztätigkeit bei dem Kern-Fischen. Häufig folgte der Lippfisch den Papageifischen *Sparisoma frondosum, S. axillare, S. amplum* oder dem Grunzer *Haemulon parra.* Das wählerische und variable Nahrungsverhalten, das hier bei *T. noronhanum* im

Gefolge der Korallenfische beobachtet wurde, scheint bei den Folger-Fischen selten zu sein. Doch zeigen einige Lippfisch-Arten einen ähnlich oppurtunistischen Nahrungserwerb, sodass sie wahrscheinlich Anwärter für ein entsprechend gezieltes Nahrungsverhalten sind.

Résumé

Le comportement associé de suiveurs, entre poissons récifaux, concerne une ou plusieurs espèces “nucléaires” fourrageantes (surtout des fouilleurs de fond), suivies par des prédateurs opportunistes. Les suiveurs profitent de la nourriture edégagée ou chassée par l’action des poissons qui fouillent le fond. A l’archipel Fernando de Noronha, sud-ouest de l’Atlantique, nous avons repéré le labre mangeur de plancton, cueilleur d’invertébrés benthiques et nettoyeur, *Thalassoma noronharum,* dont le nom commun est Labre de Noronha, agissant comme un fourrageur polyvalent, une espèce de “touche-à-tout”, sur la trace de poissons récifaux. Le Labre de Noronha s’associe avec 15 espèce de poissons récifaux pour fourrager parmi les particules soulevées par les activités alimentaires de ces poissons récifaux. Le Labre déploie quatre types de comportement de fouille quand il suit des poissons récifaux en train de fourrager: 1) la cueillette de parcelles perdues; 2) le ramassage de parties rejetées; 3) le ramassage de particules déféquées, 4) le nettoyage de poissons “nucléaires”. Le Labre était souvent reperé à la suite de poissons perroquets, *Sparisoma frondosum, S. axillare, S. amplum* et le Grondin *Haemulon parra.* La façon de fourrager, éclectique et variée, rapportée ici pour *T. noronharum,* quand il suit des poissons récifaux, semble rare parmi les espèces de poissons suiveurs. Néanmoins, certaines espèces de Labres montrent également des habitudes de fouille trés opportunistes, qui en font des candidats probables à la démonstration d’un répertoire d’un éclectisme similaire pour fourrager.

Sommario

Le associazioni tra pesci di barriera comprendono uno o più nuclei di specie foraggiere (principalmente scavatori di fondo) seguite da predatori opportunistici. Questi traggono profitto dal cibo messo allo scoperto o dissotterrato dalle attività di fondo dei pesci nucleari. Nell’Arcipelago Fernando de Noronha, Atlantico sudoccidentale, abbiamo registrato planctivori, predatori di invertebrati bentonici e il labride pulitore *Thalassoma noronhanum,* comunemente noto come il tordo di Noronha, un procacciatore molto versatile, una sorta di “factotum” al seguito di altri pesci di barriera. Il tordo di Noronha si trova in associazioni con altre 15 specie di pesci per raccogliere il nutrimento da particelle derivanti dall’attività alimentare di questi pesci. Il labride mostra quattro tipi di comportamento specifici per il procacciamento del cibo al seguito di altri pesci di barriera: 1) rastrellamento di particelle cadute sul fondale; 2) rastrellamento di particelle espulse; 3) rastrellamento di particelle defecate; 4) ripulitura dei pesci nucleari. Il labride è stato per lo più rinvenuto al seguito di pesci pappagallo delle specie *Sparisoma frondosum, S. axillare* e *S. amplum* e del pesce grugnitore *Haemulon parra.* Il repertorio alimentare eclettico e variabile qui registrato per *T. noronhanum* al seguito di altri pesci di barriera sembra raro tra altri pesci dalle abitudini simili. Ciò nonostante, alcune specie di labridi hanno abitudini alimentari molto opportunistiche che li rendono probabili candidati per mostrare repertori alimentari eclettici simili.

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;

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

Family	Nuclear species	Author's name and date
Haemulidae (grunts)	*Anisotremus surinamensis*	(Bloch, 1791)
	Haemulon parra	(Desmarest, 1823)
Mullidae (goatfishes)	*Mulloidichthys martinicus*	(Cuvier, 1829)
	Pseudupeneus maculatus	(Bloch, 1793)
Pomacentridae (damselfishes)	*Abudefduf saxatilis*	(Linnaeus, 1758)
Labridae (wrasse)	*Halichoeres dimidiatus*	(Agassiz, in Spix & Agassiz, 1831)
	Halichoeres radiatus	(Linnaeus, 1758)
Scaridae (parrotfishes)	*Sparisoma amplum*	(Ranzani, 1842)
	Sparisoma axillare	(Steindachner, 1878)
	Sparisoma frondosum	(Agassiz, 1831)
Acanthuridae (surgeonfishes)	*Acanthurus coeruleus*	(Bloch & Schneider, 1801)
Balistidae (triggerfishes)	*Melichthys niger*	(Bloch, 1786)
Monacanthidae (filefishes)	*Aluterus scriptus*	(Osbeck, 1765)
Ostraciidae (boxfishes/	*Acanthostracion polygonius*	Poey, 1876
trunkfishes)	*Lactophrys trigonus*	(Linnaeus, 1758)

Table II. 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/voided faeces). *Sparisoma* spp. expelled particles mostly through the mouth, whereas *H. parra* and *H. radiatus* sifted them mostly through the gill cover openings.

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

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.

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 (down to 3 m) suited observation at close quarters, even from the surface.

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

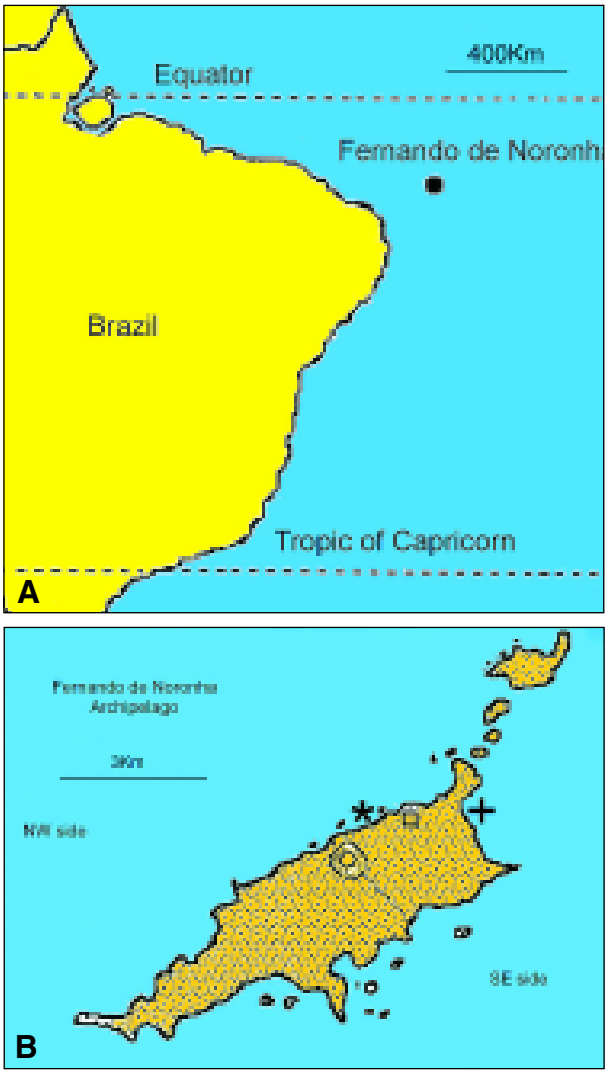

Fig. 1 A-B. A) Location of Fernando de Noronha Archipelago off the coast of Brazil (Western South Atlantic) and **B)** our two main study sites in the archipelago (*Praia da Conceição and +Buraco da Raquel). Modified from Maida & Ferreira (1997).

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). Swimming at constant 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 in the 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 total length (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 expelled particles from the mouth or gill openings of the nuclear fish; 3) eating faecal particles voided

Fig. 2. A retinue of initial phase Noronha wrasses *(Thalassoma noronhanum)* associated with an initial phase parrotfish *(Sparisoma frondosum).* Photo by J. P. Krajewski.

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

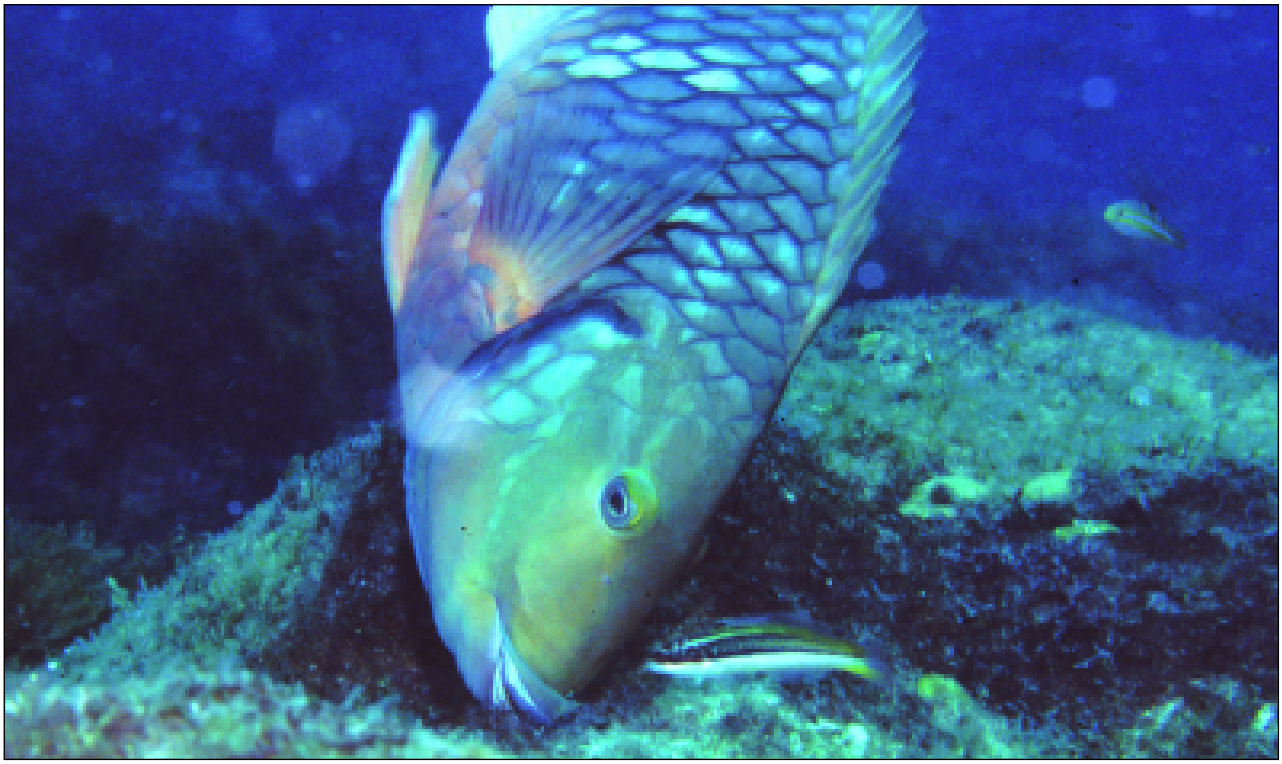

Fig. 4. An initial phase *Thalassoma noronhanum* positioned close to the mouth of an initial phase parrotfish, *Sparisoma amplum*. Photo by C. Sazima.

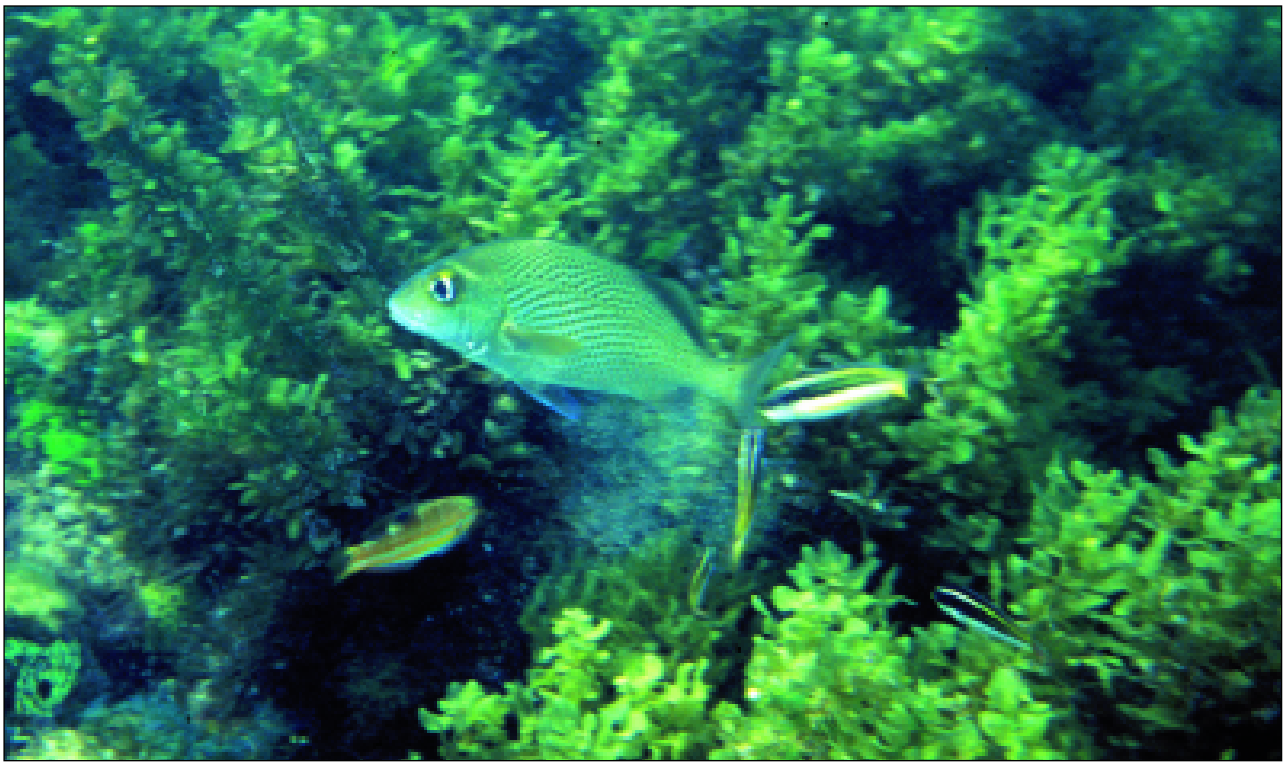

Fig. 5. Three initial phase *Thalassoma noronhanum* eating particles sifted and expelled by a foraging grunt, *Haemulon parra* (a *Halichoeres radiatus* is joining the group – on the left). Photo by C. Sazima.

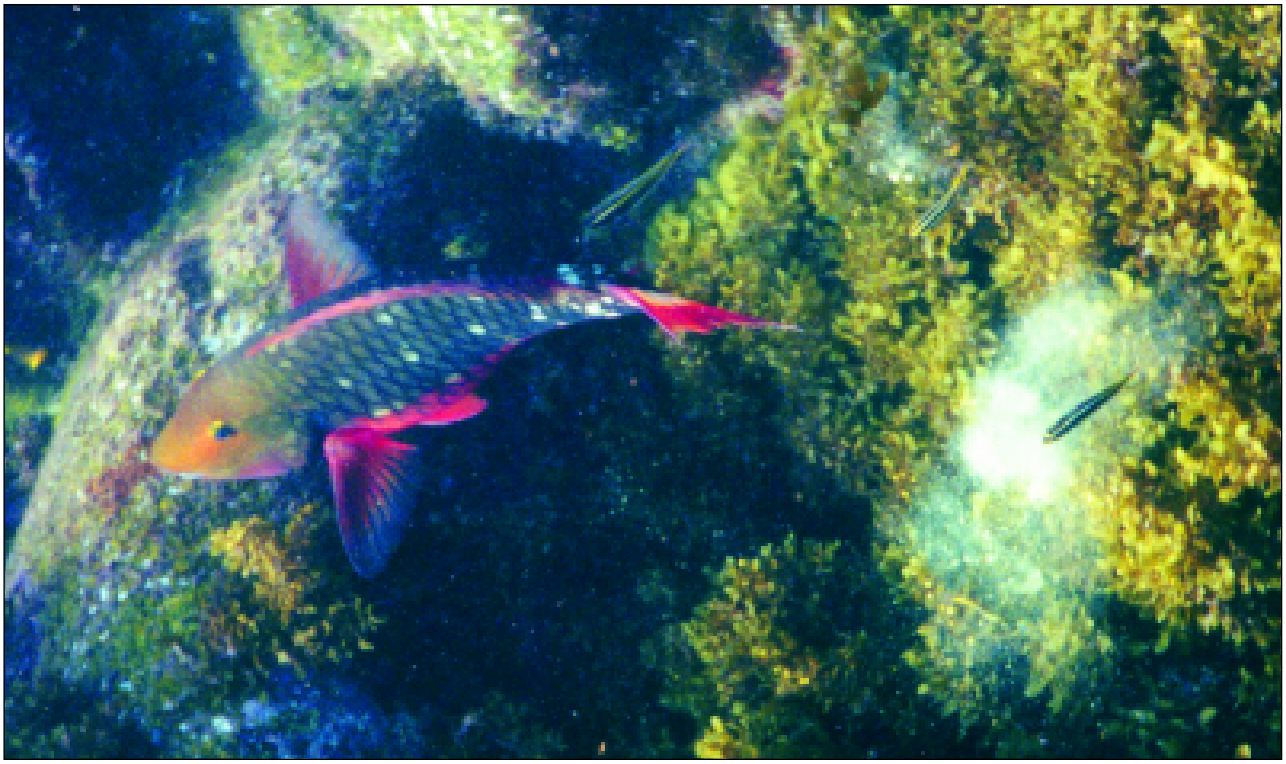

Fig. 6. Three initial phase *Thalassoma noronhanum* following a defaecating initial phase *Sparisoma amplum*. One wrasse is feeding on particles from the cloud of faeces voided by the parrotfish. Photo by R. M. Bonaldo.

Fig. 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.

by the nuclear fish; 4) cleaning the 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.

We recorded *T. noronhanum* following 15 reef fish species (Table I): 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).

In making quantitative records (Table II), 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 II). 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 II 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 defaecated particles voided by parrotfishes (Table II 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 the individual drifting particles of faeces. We recorded cleaning behaviour (see Losey, 1987 for cleaning symbiosis) in wrasse interacting with two

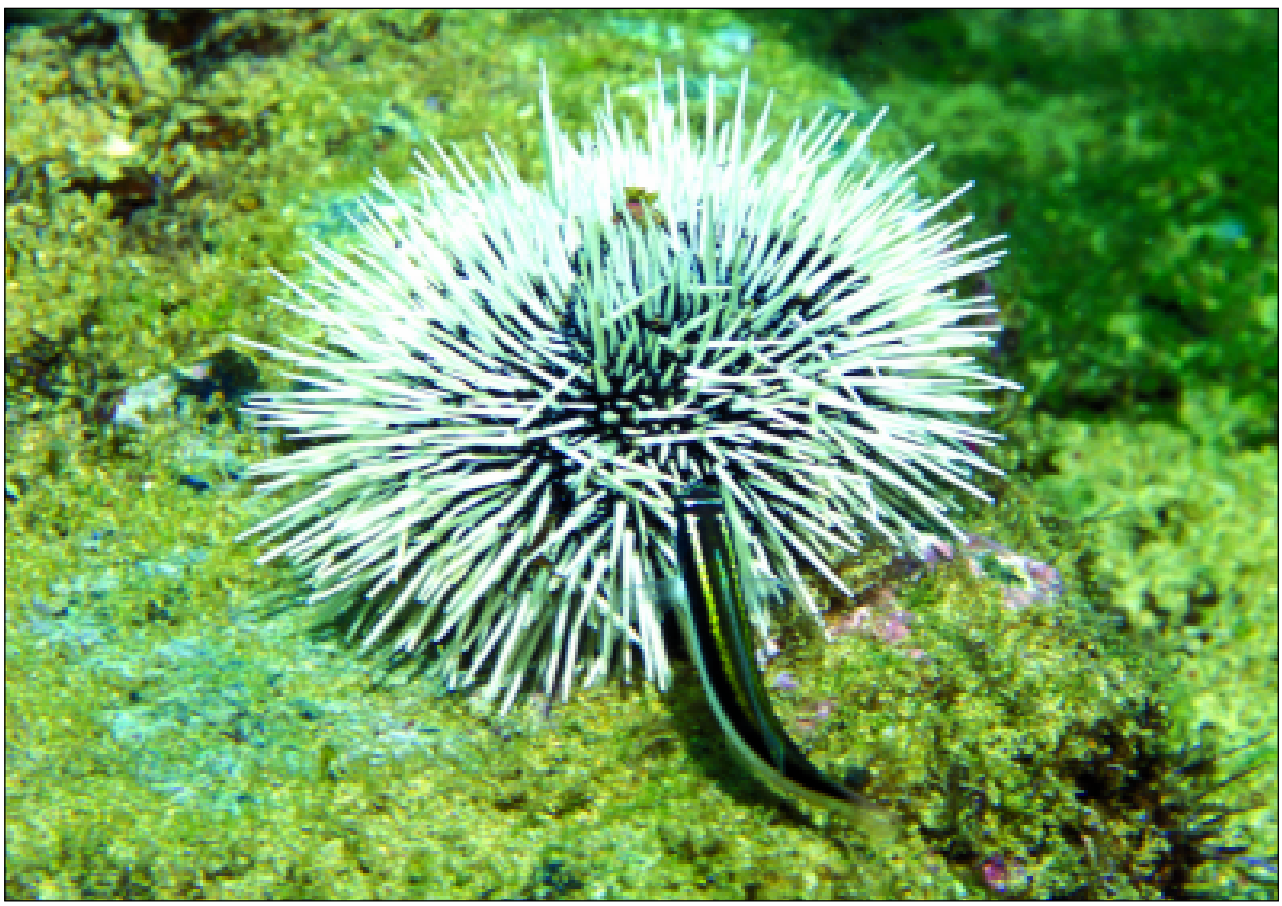

Fig. 8. An initial phase *Thalassoma noronhanum* tearing off parts of the tube feet of an exposed sea urchin (possibly *Tripneustes ventricosus)*. Photo by I. Sazima.

Sparisoma species (Table II). 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 their foraging activities and the wrasses either continued to follow or stopped following the nuclear fish. We also recorded the Noronha wrasse following and cleaning a triggerfish, *Melichthys niger* (Bloch, 1786) as well as a foraging group of surgeonfishes, *Acanthurus coeruleus* (Bloch & Schneider, 1801).

During both qualitative and quantitative recording, Noronha wrasses 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 fish species. The parrotfishes followed were mostly initial phase individuals. Wrasses 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, wrasses also followed couples and foraging groups of three or more individuals. On one occasion wrasses followed a group of 17 *S. amplum* and on another, 16 *A. coeruleus*.

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 – 67.3% of the total number of surveyed individuals. The nuclear species most commonly associated with the wrasse had the following relative abundances: *S. axillare* (4.5%), *S. frondosum* (1.5%), *S. amplum* (0.6 %), and *H. parra* (1.4%). The remaining 11 nuclear species accounted for 24.6%.

The very versatile nature of *T. noronhanum* feeding behaviour, even while simply behaving as a benthic feeder, is illustrated by its tearing out bits of sea urchins' tube feet whenever an opportunity arose, when a sea urchin was moves 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 S*parisoma*, as these defaecated 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 behaviour, 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 wrasses 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 midwater cleaning stations were visited by highly preferred clients. The Noronha wrasse is considered a specialized cleaner that cleans at midwater 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 midwater cleaning station, and thus can attend clients 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 similarly opportunistic nature of the cleaning system displayed 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 follows, 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 the 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 (Pomacentrida). 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 (Balistidae). 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 highly 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, the 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 logistic 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 making the necessary facilities readily available. 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 friend José Martins Silva-Jr., whose friendship and skills made our research at Fernando de Noronha both possible and pleasant.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49** (3,4): 227-265.

Aronson, R. B. & **S. L. Sanderson.** 1987. Benefits of heterospecific foraging by the Caribbean wrasse, *Halichoeres garnoti* (Pisces: Labridae). *Environmental Biology of Fishes*, **18**: 303-308.

Baird, T. A. 1993. A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: evaluation of the foraging consequences. *Environmental Biology of Fishes*, **38**: 393-397.

Booth, L. & **J. A. Peters.** 1972. Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour*, **20** (4): 808-812.

Carleton, M. D. & **S. L. Olson.** 1999. Amerigo Vespucci and the rat of Fernando de Noronha: a new genus and species of Rodentia (Muridae: Sigmodontinae) from a volcanic island off Brazil's continental shelf. *American Museum Novitates*, **3256**: 1-59.

Carvalho-Filho, A. 1999. *Peixes: costa brasileira*. Melro, São Paulo, 304 pp.

DeLoach, N. 1999. *Reef Fish Behavior: Florida, Caribbean, Bahamas*. New World Publications, Jacksonville, 359 pp.

Debelius, H. 1993. *Indian ocean, tropical fish guide*. Aquaprint, Neu Isenburg, 321 pp.

Diamant, A. & **M. Shpigel.** 1985. Interspecific feeding association of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Environmental Biology of Fishes*, **13**: 153-159.

Dubin, R. E. 1982. Behavioral interactions between Caribbean reef fish and eels (Muraenidae and Ophichthidae). *Copeia*, **1982** (1): 229-232.

Feitoza, B. M., Dias, T. L. P., Rocha, L. A. & **J. L. Gasparini.** 2002. First record of cleaning activity in the slippery dick, *Halichoeres bivittatus* (Perciformes: Labridae), off northeastern Brazil. *Aqua, Journal of Ichthyology and Aquatic Biology*, **5** (2): 73-76.

Fishelson, L. 1977. Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Elat (=Gulf of ‘Aqaba), Red Sea. *Israel Journal of Zoology*, **26**: 114-134.

Floeter, S. R. & **J. L. Gasparini.** 2000. The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology*, **56**: 1099-1114.

Francini-Filho, R. B., Moura, R. L. & **I. Sazima.** 2000. Cleaning by the wrasse *Thalassoma noronhanum*, with two records of predation by its grouper client *Cephalopholis fulva*. *Journal of Fish Biology*, **56**: 802-809.

Fricke, H. W. 1975. The role of behaviour in marine symbiotic animals. In: *Symbiosis, Symposia of the Society for Experimental Biology 29* (Eds. D. H. Jennings and D. L. Lee): 581-594. Cambridge University Press, Cambridge.

Froese, R. & **D. Pauly (Eds.)** 2004. *FishBase*. World Wide Web electronic publication. www.fishbase.org.

Gerking, S. D. 1994. *Feeding ecology of fish.* Academic Press, California, 416 pp.

Gibran, F. Z. 2002. The sea basses *Diplectrum formosum* and *D. radiale* (Serranidae) as followers of the sea star *Luidia senegalensis* (Asteroidea) in southeastern Brazil. *Brazilian Journal of Biology*, **62** (4A): 591-594.

Harmelin-Vivien, M. L. 2002. Energetics and fish diversity on coral reefs. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem* (Ed. P.F. Sale): 265-274. Academic Press, San Diego.

Helfman, G. S., Collette, B. B. & **D. E. Facey.** 1997. *The diversity of fishes*. Blackwell Science, Oxford, 528 pp.

Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *United States Fish and Wildlife Service Research Report*, **73**: 1-92.

Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin*, **72**: 915-1031.

Hobson, E. S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: *The ecology of fishes on coral reefs* (Ed. P.F. Sale): 69-95. Academic Press, San Diego.

Humann, P. 2002. *Reef fish identification: Florida, Caribbean, Bahamas*. New World Publications, Jacksonville, 481 pp.

Itzkowitz, M. 1979. The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum* (Pisces: Labridae). *Journal of Zoology*, *London*, **187**: 403-413.

Lehner, P. N. 1979. *Handbook of ethological methods*. Garland STPM Press, New York, 403 pp.

Losey, G. S. 1987. Cleaning symbiosis. *Symbiosis*, **4**: 229-258.

Losey, G. S., Balazs, G. H. & **L. A. Privitera.** 1994. Cleaning symbiosis between the wrasse *Thalassoma duperrey*, and the green turtle *Chelonia mydas*. *Copeia*, **1994**: 684-690.

Losey, G. S. 1971. Communication between fishes in cleaning symbiosis. In: *Aspects of the Biology of Symbiosis* (Ed T.C. Cheng): 45-76. University Park Press, Baltimore.

Lukoschek, V. & **M. I. McCormick.** 2000. A review of multi-species foraging associations in fishes and their ecological significance. *Proceedings of the 9th International Coral Reef Symposium*, **1**: 467-474.

Maida, M. & **B. P. Ferreira.** 1997. Coral reefs of Brazil: an overview. *Proceedings of the 8th International Coral Reef Symposium*, **1**: 263-274.

Nelson, J. S. 1994. *Fishes of the world*. John Wiley & Sons, New York, 600 pp.

Ogden, J. C. & **N. S. Buckman.** 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology*, **54** (3): 589-596.

Ormond, R. F. G. 1980. Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. *Journal of Zoology, London*, **191**: 247-262.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies on Tropical Oceanography*, **5**: 665-847.

Rocha, L. A., Guimarães, R. Z. P. & **J. L. Gasparini.** 2001. Redescription of the Brazilian wrasse *Thalassoma noronhanum* (Boulenger, 1890) (Teleostei: Labridae). *aqua, Journal of Ichthyology and Aquatic Biology*, **4** (3): 105-108.

Sazima, C., Grossman, A., Bellini, C. & **I. Sazima.** 2004. The moving gardens: reef fishes grazing, cleaning, and following green turtles in SW Atlantic. *Cybium*, **28** (1): 47-53.

Sazima, I. 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology*, **29**: 53-65.

Sazima, I., Sazima, C. & **J. M. Silva-Jr.** 2003. The cetacean offal connection: feces and vomits of spinner dolphins as a food source for reef fishes. *Bulletin of Marine Science*, **72** (1): 151-160.

Smith, C. L. 1997. *National Audubon Society Field Guide to Tropical Marine Fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermudas*. Alfred A. Knopf, New York, 718 pp.

Soares, M. S. C. & **J. P. Barreiros.** 2003. Following associations with the striped red mullet *Mullus surmuletus* Linnaeus, 1758 (Perciformes: Mullidae) from the Azores. *aqua, Journal of Ichthyology and Aquatic Biology*, **7** (4): 139-144.

Strand, S. 1988. Following behavior: interspecific foraging associations among Gulf of California reef fishes. *Copeia*, **1988** (2): 351-357.

Tresher, R. E. 1979. Social behavior and ecology of two sympatric wrasses (Labridae: *Halichoeres* spp.) off the coast of Florida. *Marine Biology*, **53**: 161-172.

Wainwright, P. C. & **D. R. Bellwood.** 2002. Ecomorphology of feeding in coral reef fishes. In: *Coral reef fishes, dynamics and diversity in a complex ecosystem* (Ed. P.F. Sale): 33-55. Academic Press, San Diego.