

Coral reef fish association with macroalgal beds on a tropical reef system in North-eastern Brazil

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Abstract. Macroalgal beds are recognised for their role as nursery and feeding grounds for several marine species. This study was conducted in the Tamandaré reef complex within the limits of the Costa dos Corais Marine Protected Area (MPA), North-eastern Brazil. The macroalgal bed studied is subjected to several disturbances, especially from tourism. The reef fish were assessed with free dives during the day and night using visual censuses within transects (20 × 2 m) and random swims. The percentage algal cover was estimated using quadrats (40 cm²). The behavioural traits of the fish also provided an understanding of their habitat use. In total, 68 fish species were recorded. The most abundant species were representatives of the families Labridae, Pomacentridae, Acanthuridae and Haemulidae. *Sargassum polyceratum*, *Dictyopteris delicatula* and *Canistrocarpus cervicornis* were the most abundant macroalgae. Because the most abundant fish trophic guild included primarily mobile invertebrate feeders (41.8%) and carnivores (28.4%), it is suggested that the high-canopy macroalgae harbour epiphytic invertebrates, which these fish use for food. Thereby, the study area would act as important nursery and feeding grounds. Tourism activity (e.g. laying chairs, trampling and anchoring) may disrupt fish behaviour and life-history traits and result in damage that would require mitigation through environmental awareness and law enforcement in the most affected areas.

Additional keywords: associated macrofauna, macroalgal beds, nursery areas, shelter.

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Introduction

Tropical shallow-water ecosystems encompass a large diversity of habitats with different structural complexity (e.g. coral reefs, sand banks, seagrass beds, mangroves and algal beds). These habitats are used as a refuge by a huge number of coral reef fish species within various trophic guilds, sizes and life stages (Parrish 1989; Beck *et al.* 2001; Cocheret de la Morinière *et al.* 2003; Pereira *et al.* 2010).

Macroalgal environments are recognised as important settlement and nursery sites for macroinvertebrates (Epifanio *et al.* 2003; Thomsen 2010) as well as for the ichthyofauna, especially when coral reefs are nearby (Win 2010). These areas provide habitat complexity, abundant food sources (Meekan and Choat 1997) and refuge from predators (Levin and Hay 1996). Additionally, macroalgal production is an important component of food webs (Epifanio *et al.* 2003).

These habitats can strongly influence the habitat choices of adult fishes on coral reefs and the composition and density of their fish assemblages (Jones 1988; Meekan and Choat 1997; Anderson and Millar 2004). These influences occur because the survival (Rooper *et al.* 1998) and density-dependent mortality processes (Hixon and Webster 2002) of the algal bed communities are related to the architecture and physical characteristics of

the predominant species (Levin and Hay 1996; Sano 2001; Galst and Anderson 2008).

In the last decade, the role of seagrass beds and mangroves as nursery habitats for particular fish species has received considerable attention as a link to adjacent coral reef and/or offshore habitats (Nagelkerken and Van der Velde 2002; Cocheret de la Morinière *et al.* 2004; Mumby *et al.* 2004). Nevertheless, despite their importance, only a few studies have investigated the community structure and ecological role of tropical marine fish in macroalgal beds (e.g. Anderson 1994; Ornellas and Coutinho 1998; Rossier and Kulbicki 2000).

Sargassum is the most abundant macroalga along the south-eastern Brazilian shore (Paula and Eston 1987) and may form dense and wide complex environments that provide substrate to epiphytes and food, spawning, and shelter habitat to a wide range of organisms (Ornellas and Coutinho 1998). In this context, the purpose of the present study was to assess the coral reef fish community associated with a macroalgal bed of a tropical ecosystem because most of the studies concerning similar associations have been conducted in subtropical or temperate reef areas (e.g. Ornellas and Coutinho 1998; Guidetti 2000; Ruitton *et al.* 2000). The studied algal bed is subjected to several stresses caused by tourism activity (e.g. laying chairs,

trampling and anchoring), and these stresses jeopardise not only the inhabitants of this habitat but also those of adjacent systems. The major issues addressed herein are whether this algal bed supports specific fish assemblages from adjacent reefs and the degree to which possible exchanges occur between these assemblages and those of the adjacent reefs. These issues were addressed by assessing the contribution of the life stages of the reef fish species of the algal bed and the habitat use of the reef fishes within the bed.

Materials and methods

Study area

The present study was conducted in the Tamandaré reef complex of Pernambuco State in North-eastern Brazil ($8^{\circ}44'26''\text{S}$ and $35^{\circ}05'11''\text{W}$). The tropical reefs of Tamandaré are located at the northern limit of the Costa dos Corais marine protected area (i.e. APA Costa dos Corais), which extends 135 km along the North-eastern coast of Brazil. The hydrographic conditions in the region are influenced by a tropical climate with an alternating regime of rainy (May to September) and dry (October to May) seasons reaching maximum temperatures of 26 and 30°C, respectively (Maida and Ferreira 1997) and by the fluvial inflow of rivers. The habitats surveyed in this study comprised algal beds and sandbanks adjacent to reef crests at depths ranging from 0.5 to 2.5 m (Fig. 1).

Field sampling

Reef fish community

Surveys were conducted between January and May 2010 every two weeks during low-tide periods. Rover-diver counts (Baron *et al.* 2004) were used to build a checklist of fish species

and obtain qualitative data *a priori* for the reef fish community during day and night periods. The divers swam randomly and recorded the maximum number of species encountered. In addition, any new records observed and/or photographed on different occasions until mid 2012 (casual observations) were included on the checklist. During daylight periods, strip-transect sampling (Brock 1954) was also conducted ($n = 120$, with 20 per month). The transects were laid haphazardly along the algal bed, where the mobile species were counted first, and then the cryptobenthic and sedentary species were assessed with intensive searching over the same transect. The fish were counted within 2 m (1 m to each side of the observer) (Ferreira *et al.* 2001) and categorised as juveniles or adults using visual estimates of the total length and coloration. Analyses of similarity (ANOSIM) were performed to verify the variability of species richness and abundance throughout the months of the study using PRIMER 5.0 software (Clarke and Gorley 2001).

The fish were then grouped into seven major trophic categories based on the main species in their diet using methods adapted from Ferreira *et al.* (2004) to search for general patterns of habitat use. The categories included: territorial herbivores (TERH), which are fishes that aggressively defend territories and feed primarily on algae but also on invertebrates associated with algae; roving herbivores (ROVH), which are large, mobile fishes with different behaviours such as browsing and roving; invertebrate feeders (INV), which feed mostly on sessile and mobile invertebrates; carnivores (CAR), which feed on invertebrates but also include fishes in their diet; piscivores (PIS), which feed exclusively on fishes; planktivores (PLK), which feed on plankton; and omnivores (OMN), which feed on algae, detritus and small invertebrates (see Table 1).

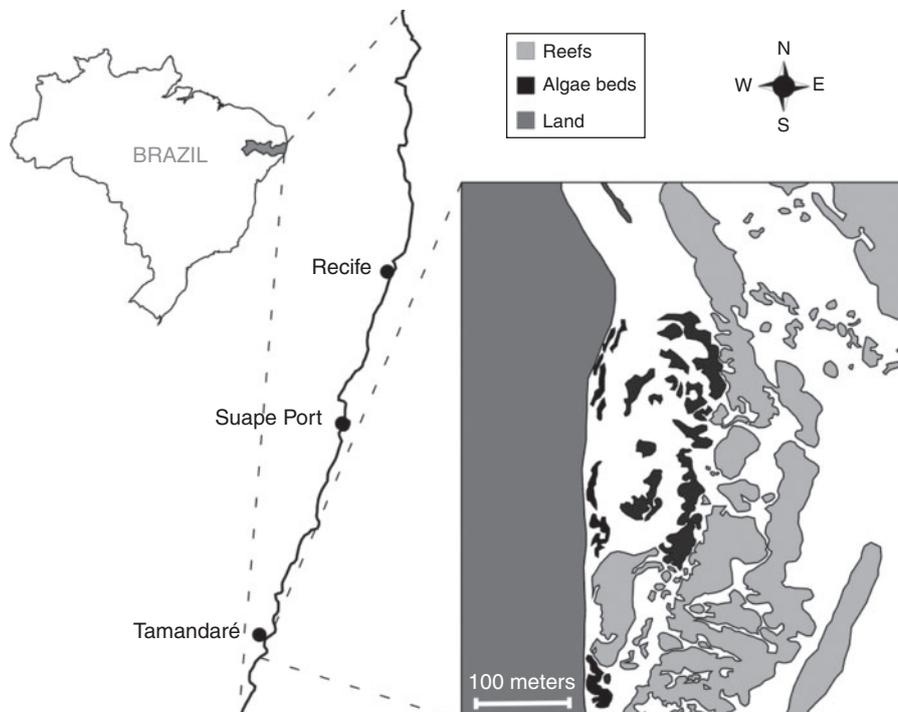


Fig. 1. Map of study area, showing the reefs and algal beds on Tamandaré reef complex – North-eastern Brazil.

Table 1. List of species observed in macroalgal beds within the Tamandaré reef complex with the relative abundance (%) and frequency of occurrence (%) of the most important species
 Including record type: T-transsects; Ph-photographic records; R-random swins; O-casual observations; day period: D-day; N-night; trophic category: TERH-Territorial Herbivores; ROVH-Roving Herbivores; INV-Invertebrate feeders; CAR-Carnivores; PIS-Piscivores; PLK-Planktivores; Omnivores; and habitat use: S-Shelter; F-Feeding; N-Nursery; R-Reproduction

Family	Scientific name	Juveniles Mean ± s.e.	Adults Mean ± s.e.	Relative abundance (%)	Frequency of occurrence (%)	Record type	Day period	Trophic group	Habitat use
Dasyatidae	<i>Dasyatis marianae</i> Gomes, Rosa & Gadig, 2000	0.01 ± 0.01	—	0.02	0.83	T	D	CAR	F
Muraenidae	<i>Gymnothorax funebris</i> Ranzani, 1839	—	—	—	—	Ph	D/N	CAR	F,S
	<i>Gymnothorax vicinus</i> (Castelnau 1855)	—	0.02 ± 0.01	0.04	1.67	T/R	D	CAR	F,S
Ophichthidae	<i>Muraena pavonina</i> Richardson 1845	0.01 ± 0.01	—	0.02	0.83	T	D	CAR	F
	<i>Myrichthys ocellatus</i> (LeSueur, 1825)	0.13 ± 0.04	0.12 ± 0.04	0.55	16.7	T/R	D	INV	N,F,S
	<i>Ahlia egmontis</i> (Jordan, 1884)	0.01 ± 0.01	—	0.02	0.83	T/Ph	D	INV	F,S
	<i>Ophichthus ophis</i> (Linnaeus, 1758)	—	—	—	—	Ph	D	CAR	F,S
Engraulidae	<i>Anchoa</i> sp.	—	—	—	—	R	N	PLK	F
Synodontidae	<i>Synodus intermedius</i> (Spix & Agassiz, 1829)	—	—	—	—	Ph	D	PIS	F,S
Ogcocephalidae	<i>Ogcocephalus vespertilio</i> (Linnaeus, 1758)	—	—	—	—	Ph	D	INV	F,S
Hemiramphidae	<i>Hemiramphus brasiliensis</i> (Linnaeus, 1758)	—	—	—	—	R	N	CAR	F
Holocentridae	<i>Holocentrus ascensionis</i> (Osbeck, 1771)	—	—	—	—	R	N	INV	F,S
	<i>Myrtristis jacobus</i> Cuvier, 1829	—	—	—	—	O	N	PLK	S
Aulostomidae	<i>Aulostomus maculatus</i> Valenciennes, 1841	—	—	—	—	R	N	CAR	F,S
Dactylopteridae	<i>Dactylopterus volitans</i> (Linnaeus, 1758)	—	0.01 ± 0.01	0.02	0.83	T	D	INV	F,S
Scorpaenidae	<i>Scorpaena plumieri</i> Bloch, 1789	—	0.02 ± 0.01	0.04	1.67	T/R	D/N	CAR	F,S
Epinephelinae	<i>Alphesstes afer</i> (Bloch, 1793)	0.03 ± 0.02	—	0.07	2.50	T/R	D/N	CAR	F,S
	<i>Cephalopholis fitha</i> (Linnaeus, 1758)	—	—	—	—	O	D	CAR	F,S
	<i>Epinephelus adscensionis</i> (Osbeck, 1771)	0.25 ± 0.05	—	0.55	18.33	T/R	D	CAR	F,S
	<i>Serranus flaviventris</i> (Cuvier, 1829)	—	—	—	—	O	D	CAR	F,S
Apogonidae	<i>Astrapogon punctulatus</i> (Poey, 1867)	—	—	—	—	Ph	N	PK	S
	<i>Phaeophthys pigmentaria</i> (Poey, 1860)	—	—	—	—	Ph/R	N	PK	S
Lutjanidae	<i>Lutjanus alexandrei</i> Moura & Lindeman, 2007	0.02 ± 0.01	—	0.04	1.67	T/R	D/N	INV	N,S,F
	<i>Lutjanus synagris</i> (Linnaeus, 1758)	—	—	—	—	O	D	CAR	N,F
	<i>Ocyurus chrysurus</i> (Bloch, 1791)	0.02 ± 0.02	—	0.04	0.83	T	D	INV	N,F
Carangidae	<i>Carangoides bartholomaei</i> (Cuvier & Valenciennes, 1833)	—	—	—	—	R	D	PIS	F
	<i>Selene vomer</i> (Linnaeus, 1758)	—	—	—	—	O	D	CAR	S,F
Gerreidae	<i>Eucinostomus lefrovi</i> (Goode, 1874)	0.34 ± 0.17	0.27 ± 0.13	1.34	14.17	T/R	D/N	INV	S,F
Haemulidae	<i>Haemulon aurolineatum</i> Cuvier, 1830	1.57 ± 0.67	0.04 ± 0.04	3.53	8.33	T/R	D	INV	N,S,F
	<i>Haemulon parra</i> (Dasmarest, 1823)	3.86 ± 0.76	0.05 ± 0.04	8.56	55.83	T/R	D/N	INV	N,S,F
	<i>Haemulon plumieri</i> (Lacépède, 1802)	1.22 ± 0.21	—	2.67	31.67	T/R	D/N	INV	N,S,F
	<i>Haemulon squamipinna</i> Rocha & Rosa, 1999	0.59 ± 0.12	0.09 ± 0.06	1.49	22.50	T/R	D/N	INV	N,S,F
Sparidae	<i>Archosargus rhomboidalis</i> (Linnaeus, 1758)	—	—	—	—	Ph	N	INV	F
Sciaenidae	<i>Pareques acuminatus</i> (Bloch & Schneider, 1801)	0.04 ± 0.02	—	0.09	3.33	T	D	INV	N,F
	<i>Odonotocion dentex</i> (Cuvier, 1830)	—	—	—	—	R	N	INV	S,F
Mullidae	<i>Pseudupeneus maculatus</i> (Bloch, 1793)	0.3 ± 0.16	0.03 ± 0.02	0.72	10.83	T/R	D/N	INV	N,S,F
	<i>Mulloidichthys martinicus</i> (Cuvier, 1829)	—	—	—	—	O	D	INV	F
Chaetodontidae	<i>Chaetodon striatus</i> Linnaeus, 1758	1.19 ± 0.17	0.2 ± 0.07	3.04	42.50	T/R	D/N	INV	N,S,F
Pomacanthidae	<i>Pomacanthus paru</i> (Bloch 1787)	0.04 ± 0.02	—	0.09	2.50	T/R	D	OMN	N,F

(Continued)

Table 1. (Continued)

Family	Scientific name	Juveniles Mean ± s.e.	Adults Mean ± s.e.	Relative abundance (%)	Frequency of occurrence (%)	Record type	Day period	Trophic group	Habitat use
Pomacentridae	<i>Abudefduf saxatilis</i> (Linnaeus, 1758)	0.68 ± 0.2	—	1.49	14.17	T	D	OMN	S,F
	<i>Stegastes fuscus</i> (Cuvier, 1830)	0.5 ± 0.12	0.04 ± 0.02	1.18	18.33	T	D	TERH	N,F
Labridae	<i>Stegastes variabilis</i> (Castelnau, 1855)	8.76 ± 0.59	0.56 ± 0.15	20.41	81.67	T/R	D	TERH	N,S,F
	<i>Halichoeres brasiliensis</i> (Bloch, 1791)	0.04 ± 0.02	—	0.09	3.33	T	D	INV	N,F
	<i>Halichoeres penrosei</i> Starks, 1913	0.01 ± 0.01	—	0.02	0.83	T	D	INV	F
	<i>Halichoeres poeyi</i> (Steindachner, 1867)	10.12 ± 0.58	0.14 ± 0.07	22.47	80	T/R	D	INV	N,S,F
	<i>Doratonotus megalepis</i> Günther, 1862	0.05 ± 0.02	—	0.11	4.17	T/R	D/N	INV	N,S,F
	<i>Scarus trispinosus</i> Valenciennes, 1840*	—	—	—	—	O	D	ROVH	N,F
	<i>Sparisoma amplum</i> (Ranzani, 1842)	0.08 ± 0.03	—	0.18	5.00	T/R	D	ROVH	N,F
Blenniidae	<i>Sparisoma axillare</i> (Steindachner, 1878)	3.77 ± 0.3	—	8.25	72.50	T/R	D	ROVH	N,F
	<i>Sparisoma frondosum</i> (Agassiz, 1831)	0.03 ± 0.02	—	0.07	1.67	T/R	D	ROVH	N,F
	<i>Sparisoma radians</i> (Valenciennes, 1840)	3.37 ± 0.4	—	7.38	54.17	T	D	ROVH	N,F
	<i>Scarus zelindae</i> Moura, Figueiredo & Sazima, 2001	—	—	—	—	Ph	D	ROVH	N,F
	<i>Ophioblennius trinitatis</i> Miranda Ribeiro, 1919	—	—	—	—	Ph	D	TERH	S,F
	<i>Labrisomus nuchipinnis</i> (Quoy & Gaimard, 1824)	0.04 ± 0.02	0.04 ± 0.02	0.18	5	T/R	D	CAR	S,F,R
	<i>Labrisomus cricota</i> Sazima, Gasparini & Moura, 2002	0.08 ± 0.03	—	0.18	6.67	T	D	CAR	S,F
Labrisomidae	<i>Malacocentrus delalandii</i> (Valenciennes, 1836)	0.09 ± 0.03	0.05 ± 0.02	0.31	10.83	T/R	D	INV	S,F
	<i>Malacocentrus</i> sp1	—	0.02 ± 0.01	0.04	1.67	T	D	INV	N,S,F
	<i>Coryphopterus glaucofraenum</i> Gill, 1863	—	0.01 ± 0.01	0.02	0.83	T	D	INV	S,F
	<i>Bathygobius soporator</i> (Valenciennes, 1837)	—	—	—	—	Ph	D	INV	S,F
	<i>Acanthurus bahianus</i> Castelnau, 1855	5.17 ± 0.63	0.01 ± 0.01	11.34	61.67	T/R	D/N	ROVH	N,S,F
	<i>Acanthurus chirurgus</i> (Bloch, 1787)	1.34 ± 0.24	0.06 ± 0.03	3.07	35	T/R	D	ROVH	N,S,F
	<i>Acanthurus coeruleus</i> Bloch and Schneider, 1801	0.03 ± 0.01	—	0.07	2.50	T	D	ROVH	F
Sphyraenidae	<i>Sphyraena barracuda</i> (Edwards, 1771)	—	—	—	—	O	D	CAR	F
	<i>Sphoeroides spengleri</i> (Bloch, 1785)	—	0.02 ± 0.01	0.04	1.67	T	D	INV	S,F
Tetraodontidae	<i>Sphoeroides testudineus</i> (Linnaeus 1758)	0.04 ± 0.02	0.04 ± 0.02	0.18	5	T/R	D	INV	S,F
	<i>Diodon holocanthus</i> Linnaeus 1758	—	—	—	—	R	N	INV	S,F
Diodontidae	<i>Bothus lunatus</i> (Linnaeus, 1758)	—	—	—	—	Ph	D	CAR	F
	<i>Paralichthys brasiliensis</i> (Ranzani 1842)	—	—	—	—	Ph	N	CAR	F

Table 2. Species composition of algal functional groups

Functional group	Species
Thick-leathery	<i>Sargassum polyceratium</i> , <i>Padina</i> sp
Sheet-like	<i>Dictyopteris delicatula</i>
Jointed-calcareous	<i>Jania capillacea</i> , <i>Jania adherens</i> , <i>Halimeda opuntia</i>
Filamentous	<i>Gelidium crinale</i> , non-identified filamentous algae
Coarsely branched	<i>Acanthophora spicifera</i> , <i>Gelidiella acerosa</i> , <i>Caulerpa sertularioides</i> , <i>Caulerpa racemosa</i>
Encrusting	<i>Lithothamnion</i> sp
Others	<i>Dictyosphaeria cavernosa</i>

The inclusion of species in these categories was based on the information available in the literature (e.g. Randall 1967, Ferreira *et al.* 2004). The species for which we could find no information were categorised with similar species of the same genus. The habitat use was also determined by species to account for the main ecological role of this environment. This categorisation considered the circumstance in which each species was observed as follows: sheltered (when hiding in crevices or vegetation); feeding (in the water column or nipping on algae, sand or other potential food sources); nursery (while in the recruit and juvenile life stages); and reproduction (during courtship behaviour). Additionally, the fish behaviour and associations were observed using the *ad libitum* method (Altmann 1974) while taking notes and photographs whenever possible.

Macroalgal community

The community inside the algal bed was characterised by estimating the total cover of algal species using point-intercept counts. Twelve 20-m strip transects were haphazardly laid on the algal substrate, and five quadrats (40 cm²) were placed at 5-m intervals on each transect ($n = 60$). Each quadrat contained 49 intercept points ($n = 2940$), where the organism underneath was identified in the field. The observed macroalgae were assigned for data analysis to the following ecologically meaningful groups described by Littler and Littler (1984) based on functional morphology: filamentous; sheet-like; coarsely branched; thick, leathery; and jointed and encrusting calcareous algae. The group 'other' was used for fragments of the alga *Dictyosphaeria*, which could not be classified in any of the functional groups proposed by these authors (Table 2).

Results

Fish community data

The transect counts yielded a total of 4567 individuals from 20 families and 42 species, of which 21 were recorded only as juveniles and another 21 as both juveniles and adults. Throughout the sampling period of five months, the richness and abundance remained extremely similar, with no significant differences and averages per transect of 8 species (ANOSIM, $R = 0.283$, $P = 0.0001$) and 43 fish (ANOSIM, $R = 0.302$, $P = 0.0001$). These results indicate high overlap and, consequently, stability within the fish community throughout the months of this study. The transect counts together with additional sightings, which included the day and night rover-diver counts and casual observations, resulted in new records for 26 species (see examples in Fig. 2) and a total of 68 species in 34 families (Table 1).

During the study, the most abundant species were *Halichoeres poeyi* (mean \pm s.e., 10.12 ± 0.58 fish 40 m^{-2}), *Stegastes variabilis* (8.76 ± 0.49), *Acanthurus bahianus* (5.17 ± 0.63), *Haemulon parra* (3.86 ± 0.75), *Sparisoma axillare* (3.77 ± 0.29) and *Sparisoma radians* (3.37 ± 0.39), all in the juvenile stage (Fig. 3a). Together, these species represented $\sim 80\%$ of the total number of fishes documented in the visual census and were recorded in more than 50% of the transects (Table 1). Certain species contributed to a lesser extent to the total composition at the adult life stage, but were observed at the juvenile phase in large abundances: *S. variabilis* (0.56 ± 0.15), *Eucinostomus lefroyi* (0.27 ± 0.13), *Chaetodon striatus* (0.2 ± 0.06), *H. poeyi* (0.14 ± 0.07) and *Myrichthys ocellatus* (0.12 ± 0.03) (Fig. 3b). Habitat use also showed that most of the recorded species exploited this habitat as a nursery (25 species, 36.7%), for shelter from predators (39 species, 59.3%) and as feeding grounds (65 species, 95.6%); the nursery role of this habitat is worth noting as the abundance, independent from composition, was higher for species found as juveniles, and these fish were also included in the other categories, once nursery sites provide them with shelter and feeding grounds as well (Table 1).

Fish trophic structure

The trophic groups found in the study area comprised mainly fish that feed on invertebrate fauna (invertebrate feeders and carnivores), which together accounted for nearly 70% of the fish and contributed appreciably to the species richness of the local ichthyofauna (Fig. 4). However, extremely few carnivores were detected in the fish counts. *Halichoeres poeyi*, an invertebrate feeder, was the major component and composed $\sim 22\%$ of the total abundance (see Table 1). Roving herbivores, such as surgeonfish and parrotfish, contributed with fewer species (Fig. 4) but were quite frequent (Table 1) and found in large numbers (Fig. 5), especially *A. bahianus* and *S. axillare*. Although territorial herbivores corresponded to only 4% of the species richness, the representative pomacentrid, *Stegastes variabilis*, was responsible for the appreciable abundance of this group ($\sim 20\%$ of the total abundance, see Table 1). Planktivores, as much as carnivores, were observed but infrequently.

Macroalgal community

The community within the algal beds was mostly composed (% cover \pm s.e.) of thick, leathery algae (26.42 ± 1.31), followed by sheet-like species (12.48 ± 0.99) (Fig. 6). The thick, leathery group basically contained *Sargassum polyceratium*, whereas the sheet-like algae consisted of *Dictyopteris delicatula* and *Dictyota cervicornis*.

Other macroalgal functional forms together represented less than 6% of the bottom cover, while reef-building organisms, such as encrusting algae and corals (e.g. *Lithothamnion* sp. and *Siderastrea stellata*, respectively), comprised a minor portion of the bottom cover ($\sim 0.25\%$). Sponges were also present but represented less than 2% of the organisms observed.

Reef fish behaviour

During underwater visual censuses and random observations, several reef fish behaviours were recorded in the macroalgal

beds (Fig. 7a–f). These behaviours included feeding associations (e.g. nuclear following, ephemeral feeding associations and aggregations), mixed-species schooling, and courtship behaviours.

The ‘nuclear-following’ behaviour is a feeding interaction recorded on several occasions and involving bottom-feeding species (e.g. *Pseudupeneus maculatus*, *Mulloidichthys martinicus* and *Haemulon* spp.). The recorded event (Fig. 7a) involving *Pseudupeneus maculatus* included the common mojarra, *Eucinostomus lefroyi*, as its follower. Other less complex foraging associations, namely, the ‘ephemeral foraging association’ (*sensu* Pereira *et al.* 2012), were recorded involving the eel, *Myrichthys ocellatus*, and several opportunistic reef fish species (e.g. *Halichoeres poeyi* and *Labrisomus nuchipinnis*) (Fig. 7b). Predation events were also recorded among reef fishes associated with the algal beds, as shown in Fig. 7c. During the

observation, a juvenile grouper, *Epinephelus adscensionis*, fed upon the redlip blenny, *Ophioblennius trinitatis*.

Mixed-species schooling behaviour was recorded for juvenile individuals of *Pseudupeneus maculatus* in schools primarily composed of species of the genus *Haemulon* (*H. aurolineatum* and *H. parra*) while the fish hovered over clumps of *Padina antillarum* (Fig. 7d). Additionally, *Eucinostomus lefroyi* and *Lutjanus alexandrei* were recorded schooling with other *Haemulon* spp.

The courtship behaviour of *Labrisomus nuchipinnis* was also observed in the studied macroalgal beds. The event lasted ~30 min, and during this period, the *L. nuchipinnis* male presented its characteristic colour, displaying a yellow body and red area on the head (Fig. 7e). Aggregations with up to twelve individuals of the butterfly fish, *Chaetodon striatus*, were also observed feeding in the water column (Fig. 7f).

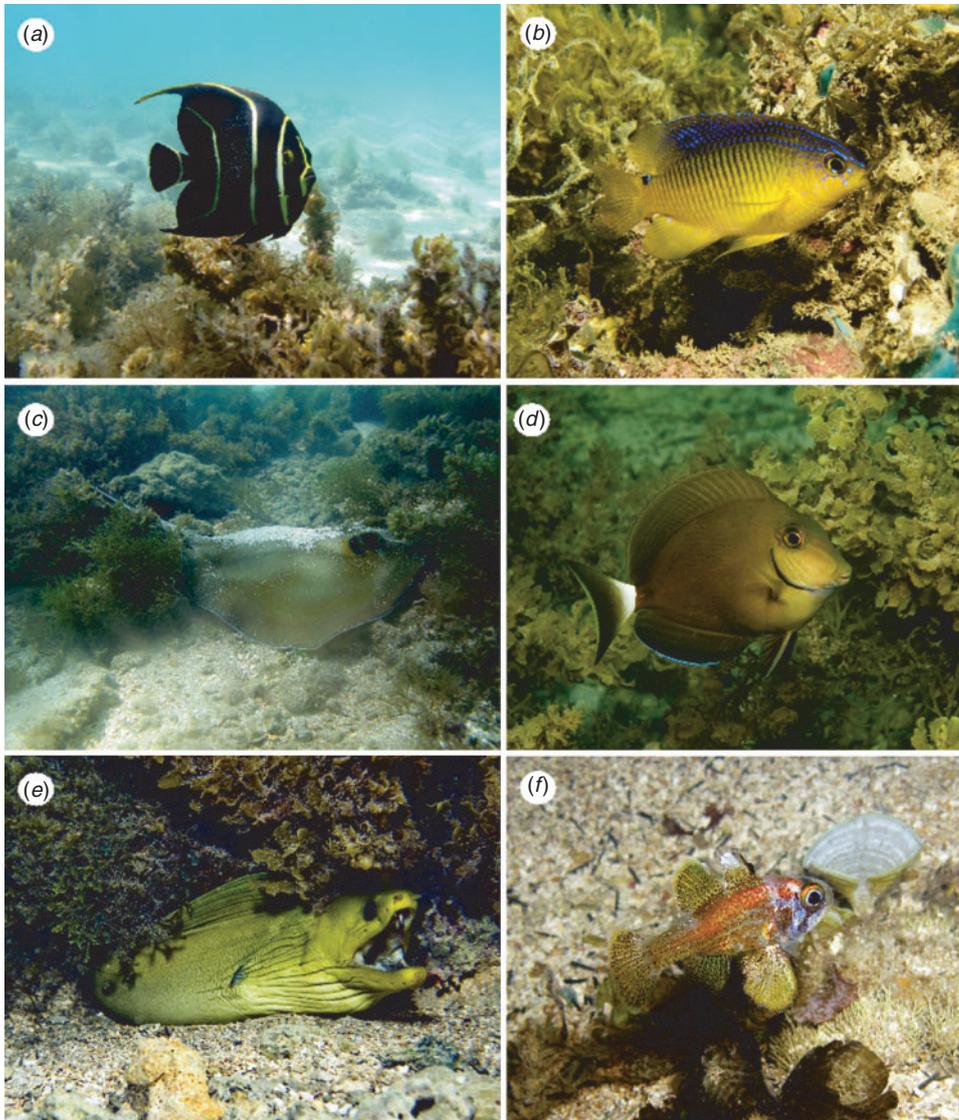


Fig. 2. Some species observed in the macroalgae bed of the Tamandaré reef complex during the day (D) and night (N) periods. (a) – *Pomacanthus paru* (D); (b) – *Stegastes variabilis* (D); (c) – *Dasyatis marianae* (D); (d) – *Acanthurus bahianus* (D); (e) – *Gymnothorax funebris* (N); (f) – *Astrapogon puncticulatus* (N).

Discussion

This study reveals important information regarding the poorly known ichthyofauna and algal communities on this tropical algal bed, expanding upon the results of earlier research (Ferreira *et al.* 1995). It was found that newly settled and early juveniles

were the dominant component of the fish community studied (80%), which consisted primarily of wrasses (Labridae) and damselfish (Pomacentridae). In addition to wrasses and damselfish, the surgeonfish (Acanthuridae), parrotfishes (Labridae) and grunts (Haemulidae) were also common as juveniles. Generally, the reef fish fauna recorded in the algal beds is using the area as a nursery, considering the greater abundance of juveniles of some species in comparison with adjacent reefs. From the algal beds, the fishes may migrate to nearby reefs when conditions become suitable for their establishment. Furthermore, some juvenile individuals were also observed in single- and multiple-species feeding schools, as recorded by Pereira *et al.* (2011) on adjacent coral reefs, indicating that this area is used not only as a nursery but also as feeding grounds for the juvenile stages. Ontogenetic changes in behaviour and habitat use, recorded in several coral reef species (Werner and Gilliam 1984; Nagelkerken *et al.* 2000; Kimirei *et al.* 2011), play an important role in habitat choice, especially because each life

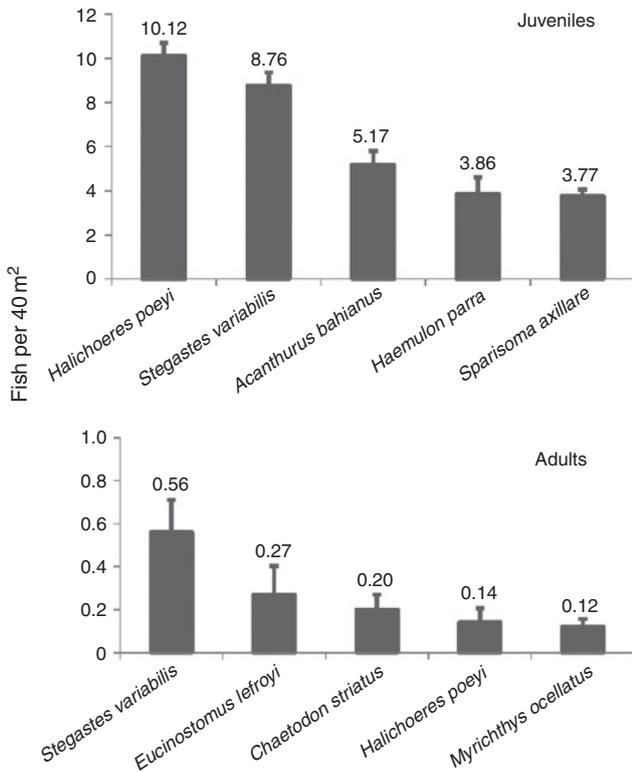


Fig. 3. Mean abundance (±s.e.) of juveniles and adults recorded on transect-counts.

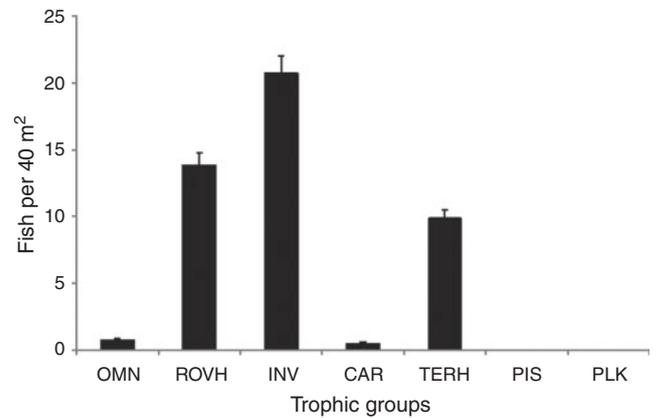


Fig. 5. Mean abundance (±s.e.) of individuals on each trophic group obtained from transect-counts.

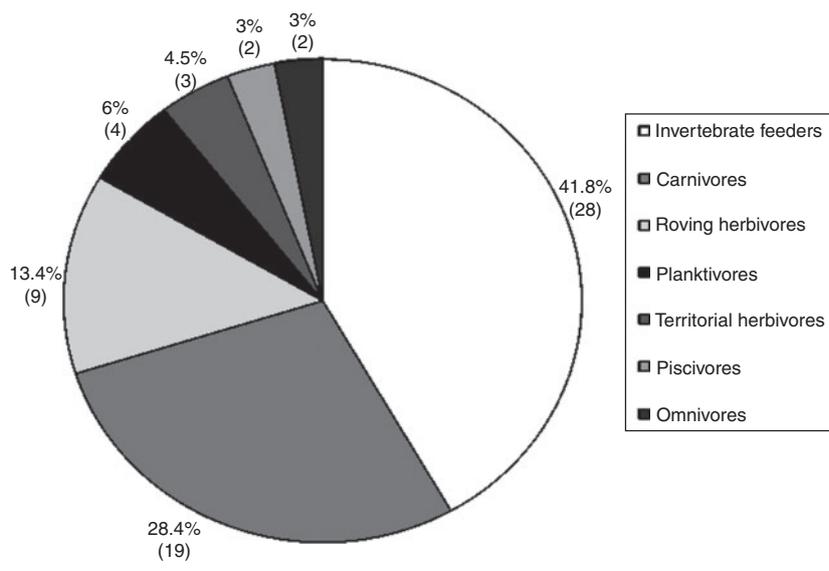


Fig. 4. Richness percentual contribution (%) of each trophic group in the study area, recorded on visual census and posterior sightings. Number os species in ().

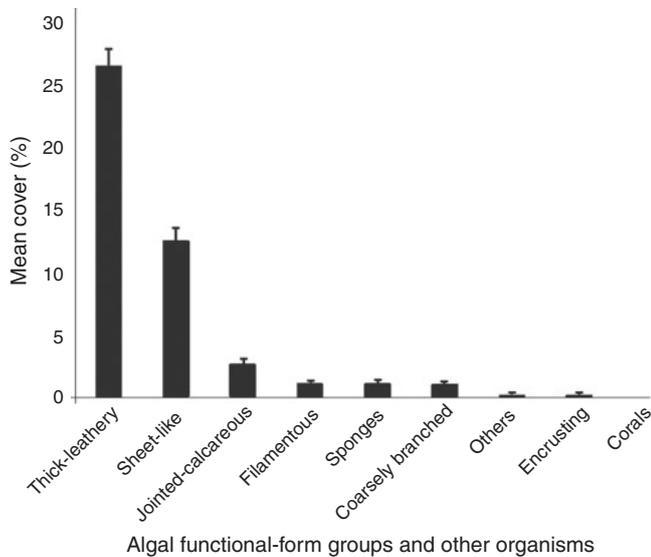


Fig. 6. Mean percentage of cover (\pm s.e.) of algae functional groups and other organisms in the studied algal beds.

stage has specific requirements for refuge and food. For instance, circumventing predators in the initial life stages can be as imperative as finding available space in the reef, and schooling confers protection while feeding.

However, the algal beds are not an exclusive habitat for most of the reef fish species, with some of them also observed on nearby coral reefs as adults (Ferreira *et al.* 1995). The study area could not be considered a nursery for all the observed species, as some of them were only observed as adults while feeding or sheltering during the day (nocturnal species) or night (diurnal species). Some schooling species, such as *Anchoa* sp. and *Hemirhamphus brasiliensis*, were also observed feeding in the water column. Some species, however, can be extremely attached to these environments during earlier stages, such as *Stegastes variabilis*. This attachment is likely to have a strong influence on nearby adult populations. Other species known to be common residents of this habitat, such as *Doratonotus megalepis* (Ferreira *et al.* 2010) and *Dactylopterus volitans* (Ferreira *et al.* 1995), are rarely observed off these algal beds or, in some cases, in adjacent reef patches with a high cover of macroalgae clumps, indicating a preference for these complex habitats.

The relationship of the fish abundance to the macroalgal beds exists because the beds provide not only space for settlement but also increased food availability (Ornellas and Coutinho 1998). Macroinvertebrate abundance and species diversity have already been linked to the macroalgal biomass in other habitats (Stoner 1980; Gore *et al.* 1981; Everett 1994). Further analysis of stomach contents and the use of stable isotope tracers would generate additional information to directly connect fish abundance with the availability and origin of their consumed prey. Nevertheless, there are several lines of strong evidence (e.g. high densities and richness of invertebrate-feeding species) to indicate that such a relationship occurs in the study area, especially considering the major trophic groups and *in situ* feeding interactions observed.

The great abundance in these algal beds of territorial herbivores, mainly *Stegastes variabilis*, provided an important example of nursery and feeding ground use by juveniles. This species does not feed mainly upon associated invertebrates but relies on epiphytic algae and diatoms (Feitosa *et al.* 2012), which are known to be of high nutritional value (Hoey and Bellwood 2010). This association is commonly observed for other algal-dominated environments; for example, damselfish utilise less palatable macroalgae, such *Sargassum* spp., which facilitates the growth of their preferred algae (Ceccarelli *et al.* 2005).

The structural complexity provided by the most abundant algal species observed in the studied area, *Sargassum polyceratum*, indicates that these environments provide important food resources. *Sargassum* spp. harbour a great number of epiphytic invertebrates within their branching structure in both tropical and subtropical habitats (Jacobucci *et al.* 2006; Venekey *et al.* 2008). Therefore, it is expected that the algal beds of the Tamandaré reef complex could also shelter a diverse associated fauna (e.g. Amphipoda, Copepoda, Isopoda and Tanaidacea) used as food resources by many invertebrate-feeding species (McCormick 1995; Pereira and Jacobucci 2008) and even by 'territorial herbivores' with a high trophic plasticity (see Feitosa *et al.* 2012 for a review). Factors other than the presence or absence of algae must also influence the temporal distribution of the ichthyofauna. The life cycles of the species constituting the community can be intricately linked to algal bed seasonality, as found by Godoy and Coutinho (2002) in South-eastern Brazil. However, it is extremely difficult to assess the fish community in the studied algal bed using a non-destructive approach with visual estimations because the visibility decreases considerably in these shallow environments during the rainy season.

The loss of coral reefs, mangroves and seagrass areas through natural processes, anthropogenic influences and bleaching events have already caused significant declines in the diversity and abundance of reef fish species (Wilson *et al.* 2006; Pratchett *et al.* 2008; McCormick *et al.* 2010). Changes in the composition and structure of fish habitats are expected to alter the outcome of ecological processes, such as habitat selection, competition and predation (Pratchett *et al.* 2008). Therefore, because of the high fragility of the coral reef environment and the adjacent habitats (Hughes *et al.* 2003), knowledge is required to access how these changes will affect the ecological processes that structure the reef fish communities.

The role of mangroves and seagrass meadows as nursery ecosystems is an established ecological concept that is usually considered adequate to justify the protection and conservation of these areas. Because of the ongoing worldwide decline of these habitats, macroalgal beds might be functioning as surrogates in locations where other nurseries are undermined. Given the close proximity of the algal bed to coral reefs, the natural bed potentially acts as a source of colonists for the reefs. A considerable number of species, including valuable species for local fisheries such as parrotfishes, were recorded using the algal beds at different life stages, mainly juvenile stages, and also interacting in a variety of ecological contexts. These facts stress the imperative of conserving the algal bed habitat and its associated species.

Pollution, overfishing and uncontrolled tourism are the major threats observed in the study area, which is located in the upper

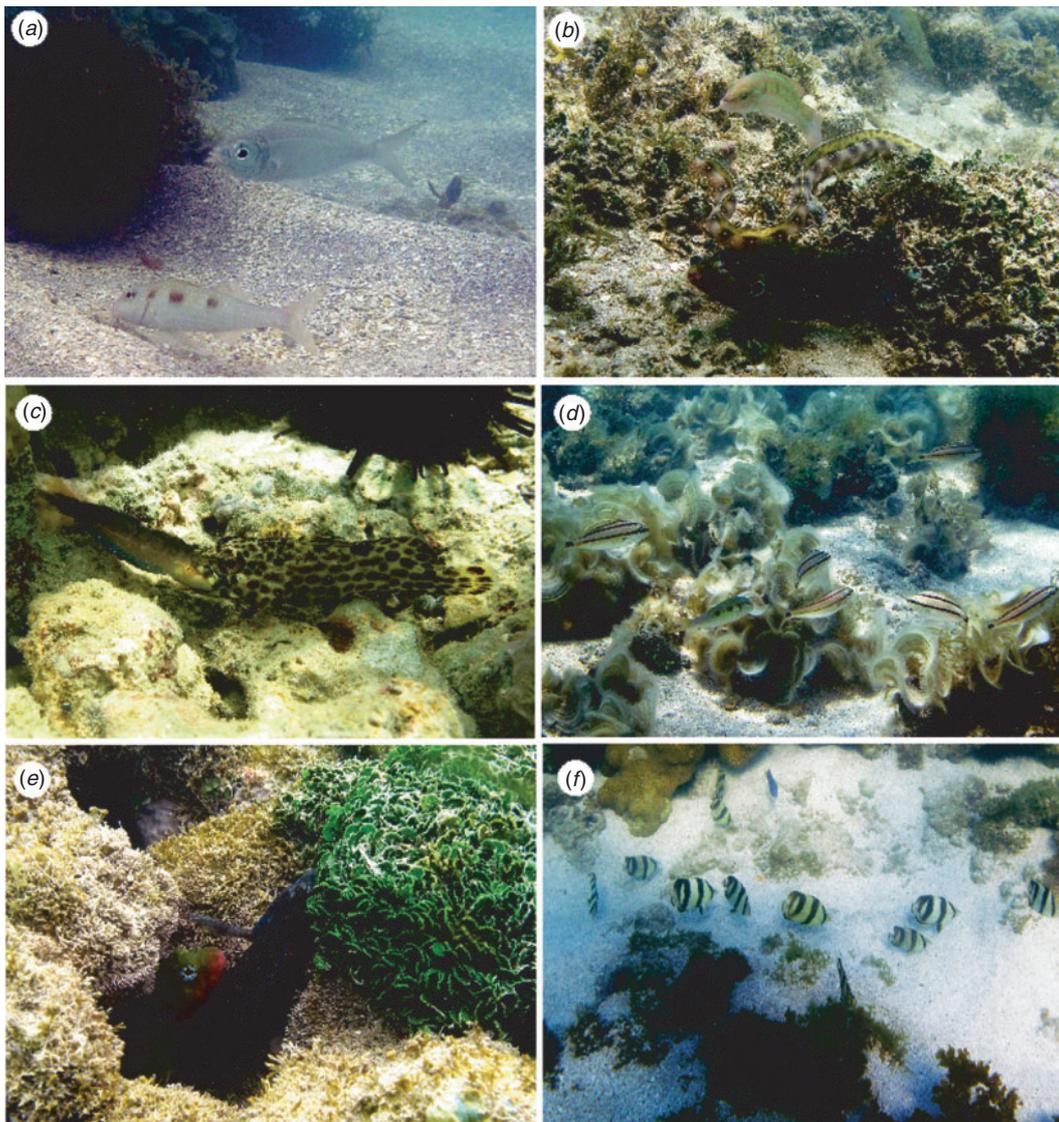


Fig. 7. Photographic records of reef fish behaviour observed on macroalgae beds of the Tamandaré Reef complex. (a) – ‘Nuclear-following’ behaviour; (b) – ‘Ephemeral foraging interaction’; (c) – Predation; (d) – Mixed schools; (e) – Courtship behaviour; (f) – Feeding aggregations.

limit of the marine protected area called APA Costa dos Corais (the largest marine protected area in Brazilian waters). Furthermore, the algal beds are formed at sites near the beach where the beds are likely the most vulnerable to human influences, especially from the summer tourist activities (Ferreira *et al.* 1995). We suggest that such influences should be mitigated through increased human awareness and law enforcement; in addition, a better understanding of these nursery habitats will allow more efficient use of the limited funds, time and labour available for their conservation and management.

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