

Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns

S. R. FLOETER*†, C. E. L. FERREIRA‡,
A. DOMINICI-AROSEMENA§ AND I. R. ZALMON*

**Lab. de Ciências Ambientais, Universidade Estadual do Norte Fluminense,
Av. Alberto Lamego, 2000, Campos dos Goytacazes, RJ, 28 013-600, Brasil,*

‡*Depto. de Oceanografia, IEAPM, Rua Kioto 253, Arraial do Cabo, RJ, 28 930-000,
Brasil and §Center for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 6, 28 359,
Bremen, Germany*

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Trophic strategies and spatial use habits were investigated in reef fish communities. The results supported the hypothesis of differential use of food resources among tropical and higher latitude reef fishes, *i.e.* the number of species and relative abundance of fishes relying on relatively low-quality food significantly decreased from tropical to temperate latitudes. The species: genus ratio of low-quality food consumers increased toward the tropics, and was higher than the overall ratio considering all fishes in the assemblages. This supports the view that higher speciation rates occurred among this guild of fishes in warm waters. It was also demonstrated that density of herbivorous fishes (the dominant group relying on low-quality food resources) in the western Atlantic decreased from tropical to temperate latitudes. Spatial use and mobility varied with latitude and consequently reef type and complexity. Fishes with small-size home ranges predominated on tropical coral reefs.

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Key words: community structure; herbivory; latitudinal gradient; macroecology; reef fishes.

INTRODUCTION

Fish diversity characteristically decreases from tropical to temperate latitudes (Ebeling & Hixon, 1991; Hobson, 1994; Briggs, 1995). In the Atlantic Ocean, the Caribbean is the centre of diversity, both in terms of fishes and corals (Briggs, 1995; Veron, 1995; Floeter & Gasparini, 2000). The extent to which fish trophic structure is modified between tropical coral reefs of the Caribbean and marginal rocky reefs of the Atlantic, however, remains unknown.

A functional categorization approach could be a useful tool for gathering broad-scale data on community structure, transcending taxonomic boundaries (Bellwood *et al.*, 2002). Thus, it is possible to infer general evolutionary trends based on ecologically relevant attributes such as feeding performance

†Author to whom correspondence should be addressed at present address: National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, 735 State Street Suite 300, Santa Barbara, CA 93 101-5504, U.S.A. Tel.: +1 805 882 9218; fax: +1 805 892 2510; email: floeter@nceas.ucsb.edu

(*i.e.* functional morphology, physiology and biomechanics), mobility amplitude and resource-use patterns used by reef fishes. Trophic strategies, food availability and spatial use habits certainly play an important role in shaping patterns of abundance and habitat distribution in fishes (Harmelin-Vivien, 1989; Bellwood *et al.*, 2002; Wainwright & Bellwood, 2002).

Trophic strategies are an important functional attribute that could be distinct between tropical and temperate regions. For example, the relative diversity of herbivorous fishes is known to decrease drastically in colder waters (Horn, 1989; Choat, 1991; Ebeling & Hixon, 1991). In a recent review, Harmelin-Vivien (2002) hypothesized an evolutionary trend toward the better use of less energetic food resources among tropical reef fish communities (in contrast to temperate areas), based on qualitative comparisons between feeding behaviours and fish phylogeny and biogeography. She argued that the high diversity of fishes occurring on coral reefs is related to the sustained higher temperatures in the tropics over geological time, and to the more efficient use and transfer of energy permitted by long-term temperature stability. Planktivore, piscivore and motile invertebrate-feeding fishes that eat high protein and energy-rich food with high assimilation rates (Bowen *et al.*, 1995) form the most diverse trophic group worldwide (Randall, 1967; Harmelin-Vivien, 1989; Jones *et al.*, 1991; Ferreira *et al.*, 2004). Many reef fishes, however, exhibit morphological and physiological specialization to exploit comparatively low-quality resources like algae, seagrasses, detritus and sessile invertebrates (*e.g.* sponges, cnidarians and ascidians) and indeed sustain large populations in the tropics (Choat, 1991; Bruggemann, 1994; Dunlap & Pawlik, 1996; Hill, 1998). Although abundant and easy to locate, these resources are usually structural and chemically defended against grazing (Hay, 1991, 1997; Paul, 1992; Epifânio *et al.*, 1999; Burns & Ilan, 2003; Burns *et al.*, 2003) and their processing and assimilation present a major challenge to the digestive system (Horn, 1989; Choat, 1991; Meylan, 1991; Choat & Clements, 1998). Compared to carnivores, they have to ingest larger quantities of food to compensate for low nutritional value (Bruggemann *et al.*, 1994; Bowen *et al.*, 1995; Ferreira *et al.*, 1998*a, b*; Horn, 1998). For example, herbivorous fishes may eat many times their required energetic needs in order to gain enough nitrogen from seaweeds (Hay, 1991). Some parrotfishes (Scaridae) spend over 90% of the day foraging, taking thousands of bites per day (Carpenter, 1986; Hay, 1991; Bruggemann, 1994; Bruggemann *et al.*, 1994), and the same occurs with sponge-eating angelfishes (Pomacanthidae) (Dunlap & Pawlik, 1996). Corallivores, herbivores, detritivores and omnivores also tend to have longer intestines than do carnivores, whose diets are more nutritious (Goldschmid *et al.*, 1984; Horn, 1989, 1998; Elliott & Bellwood, 2003). An explanation for this pattern is that fishes relying on low-protein diets require longer guts, *i.e.* large surface area relative to volume, in order to process the large amount of poor-quality food needed (Horn, 1998).

Another functional aspect that could differentiate tropical fish assemblages from colder ones is the spatial use and mobility patterns of fishes. At tropical coral reefs, many species (mainly herbivores or sessile invertebrate feeders) have small-size home ranges or swim close to the coral matrix (Harmelin-Vivien, 1989). Some even defend their territory in a very aggressive way, like the herbivorous damselfishes (Pomacentridae) (Robertson, 1996; Ceccarelli *et al.*,

2001). Structural complexity has been correlated to reef fish space utilization (Luckhurst & Luckhurst, 1978) and abundance (Bell & Galzin, 1984; Friedlander & Parrish, 1998; S.R. Floeter, C.E.L. Ferreira & J.L. Gasparini unpubl. data) indicating that biogenic reefs could potentially sustain higher fish densities than non-reef-building peripheral areas, especially site-attached species. In true coral reefs, structural complexity is associated with coral growth form, especially those arborescent or branching forms in the shallower waters. On rocky shore systems, topographic complexity relies mostly on the presence or absence of holes (Ferreira *et al.*, 2001; S.R. Floeter, pers. obs.).

In contrast to previous publications (Harmelin-Vivien, 1989, 2002), the present work examined trophic strategies, spatial use and mobility patterns, based on quantitative (*i.e.* relative abundance and density) data collected along a broad latitudinal gradient in the Atlantic, as well as published data. Two specific questions were addressed: 1) is diversity and abundance of fishes that use relatively low-caloric food resources higher in the tropics than in subtropical or temperate regions? 2) Does fish spatial use (*i.e.* differential mobility and home-range patterns such as schooling behaviour and territoriality) vary according to latitude and reef type (*i.e.* coral *v.* rocky reefs)?

MATERIALS AND METHODS

DATASETS

Three datasets were used, the first one with relative abundance of reef fishes derived from replicated strip transects: underwater visual censuses (UVC) conducted in the Bocas del Toro, Panama (Caribbean), Guarapari Islands (south-east Brazil) and Arvoredo (south Brazil) (Table I). The sampling design included different habitats within each site, covering reefs of various depths, exposures and complexity profiles. Replicated point-count censuses from the Canaries (Bortone *et al.*, 1991; Falcon *et al.*, 1996; Hajagos & Van Tassell, 2001) were also included in the database. Assembling data from different sampling methods is always problematic for statistical purposes, however, in a recent method re-evaluation, Samoilys & Carlos (2000) did not find significant differences between transect and point-count visual censuses for many taxa.

In order to verify if the results obtained from the four sites could be generalized for their entire regions, a second database was compiled from the literature, with the addition of seven more sites: Florida Keys, 24°39' N (Bohnsack & Bannerot, 1986); Cayos Cochinos, Honduras, 15°56' N (Clifton & Clifton, 1998); Manuel Luiz Reefs, north-east Brazil, 0°52' S (Rocha & Rosa, 2001); Tamandaré, north-east Brazil, 8°45' S (B.P. Ferreira, unpubl. data); Abrolhos Reefs, north-east Brazil, 17°30' S (C.E.L. Ferreira, unpubl. data); Arraial do Cabo, south-east Brazil, 23°S (C.E.L. Ferreira, unpubl. data); south-east Mediterranean, Spain, 37°38' N (García-Charton & Pérez-Ruzafa, 2001); southern Italy, 35°35' N (Mazzoldi & Girolamo, 1997). Original densities were converted in relative abundances in order to standardize data collected through different methodologies.

A third database was assembled to examine if actual densities support conclusions obtained from relative abundance data. This approach was based on densities derived from 20 × 2 m (40 m²) standardized transects conducted in four localities in the western Atlantic (Panama, Abrolhos Reefs, Guarapari Islands and Arvoredo). Censuses were performed on all locations, and included juveniles of all species. Selected similar sheltered and shallow reefs (<10 m) were chosen on each location, because this is the preferred habitat for 'herbivorous' species. Herbivores (including detritivores, Wilson *et al.*, 2003) were analysed in detail due to their important role in the organization of shallow marine benthic communities, and to the knowledge accumulated about this guild in the last decades (Horn, 1989; Choat, 1991; Hixon, 1997; Choat & Clements, 2002; Wilson *et al.*, 2003).

TABLE I. Site characteristics and number of reef fish species richness (bold) with respective relative abundance (percentage of species number in parenthesis) in each diet category (food quality = nutritional value) and their mobility. Fish data were derived from visual census. Category definitions are the same as in Figs 1 and 5. Data from south-eastern Spain were added for comparison

	Bocas (Caribbean)	Guarapari Island (south-east Brazil)	Arvoredo (South Brazil)	Canaries ¹ (Macaronesia)	Spain ² (Mediterranean)	South-east
Latitude	9°N	20°S	27°30'S	28°N		37°N
SWT range (°C)	27–33	19–24	17–24	16–24		14–24
Coral richness (species)*	54 ³	14 ⁴	1 ⁴	0		0
Coral cover (%)	21–4 ³	4–6 ⁵	~0	0		0
Number of census	125	166	85	57		140
Fish diversity						
Number of fish species	97	81	62	61		45
Number of fish genera	52	53	44	48		30
Species : genera ratio	1.9	1.5	1.4	1.3		1.5
Trophic strategies						
High-quality	63 (64.9)	56 (69.1)	39 (61.5)	40 (65.6)		33 (73.3)
Intermediate	5 (5.2)	4 (4.9)	4 (7.7)	16 (26.2)		11 (24.4)
Low-quality	29 (29.9)	21 (25.9)	18 (30.8)	5 (8.2)		1 (2.2)
Species : genera ratio ⁶	2.4	1.9	1.6	1.0		1.0
Spatial use and mobility						
Category 1	29 (29.9)	24 (29.6)	22 (34.6)	29 (47.5)		22 (51.2)
Category 2	48 (49.5)	38 (46.9)	26 (42.3)	17 (27.9)		18 (41.9)
Category 3	20 (20.6)	19 (23.5)	14 (23.1)	15 (24.6)		3 (7.0)

* , Reef-building scleractinian + millepores; ¹ , Fálcon *et al.* (1996), Bortone *et al.* (1991); ² , García-Charton & Pérez-Ruzafa (2001); ³ , Guzmán & Guevara (1998); ⁴ , Floeter *et al.* (2001); ⁵ , W. Krohling & S.R. Floeter (unpubl. data); ⁶ , only fishes utilizing low-quality diets.; SWT, sea surface temperature.

TROPHIC STRATEGIES

In all databases every genus was classified according to its diet (*i.e.* trophic guild and associated food quality) and spatial use and mobility (Table II). They were divided in three classes based on food quality: (1) high-quality, fishes that feed on highly energetic (with high protein content) and easily digestible food, *e.g.* zooplankton (Norrbin & Bamstedt, 1984), mobile invertebrates and fishes (Brey *et al.*, 1988; Bowen *et al.*, 1995); (2) low-quality, fishes that eat relatively low-energy content resources, generally with lower assimilation rates and indigestible components, *e.g.* high ash content (Meylan, 1991; Montgomery & Targett, 1992; Bowen *et al.*, 1995). Among this food are algae, seagrasses and detritus (all relatively protein-poor), and sessile invertebrates (*e.g.* cnidarians, hydrozoans and sponges, usually with high percentage of inorganic components in tissues). These resources generally contain structural (*e.g.* calcium carbonate) and chemical defences against grazing such as secondary metabolites (Paul, 1992; Pawlik, 1993; Pawlik *et al.*, 1995; Hay, 1997; Burns & Ilan, 2003; Burns *et al.*, 2003). Although various authors have recently demonstrated that the nutritional value of sponges and gorgonians (Chanas & Pawlik, 1995; O'Neal & Pawlik, 2002), detritus (Wilson, 2002; Wilson *et al.*, 2003) and endolithic algae (Bruggeman, 1994) are higher than previously thought, these resources have to be consumed in large amounts and the costs of their processing and assimilation are high (Horn, 1989; Choat, 1991; Meylan, 1991; Bowen *et al.*, 1995; Choat & Clements, 1998); (3) intermediate-quality, fishes that forage both on algae and some protein-rich animal food, *i.e.* omnivores (Montgomery & Targett, 1992). The problem of grouping reef fishes in broad diet categories has been widely discussed in recent reviews (Jones *et al.*, 1991). Fish feeding plasticity makes categorization into independent trophic groups difficult. In this study, however, every genus was assigned to one of three food quality categories associated with eight major trophic guilds (Table II) in order to search for general patterns. Dominant food items were determined from direct behavioural observations, stomach content analysis as well as the available literature (Randall, 1967; Froese & Pauly, 2003; pers. obs.).

Fishes have evolved a wide variety of ways to obtain their food and meet their energy and nutritional requirements (Horn, 1998). Overall diet quality is a function of the relationship between food composition and digestive physiology. The three proposed categories based on 'food quality' do not imply that a better general nutrition is obtained by any of the categories. Feeding strategies maximizing ingestion rates or presenting specialized digestion (*e.g.* microbial fermentation) are also successful ones. Indeed, the highest growth rates reported for freshwater fishes occur in herbivorous and detritivorous species (Bowen *et al.*, 1995; Choat & Clements, 1998).

SPATIAL USE AND MOBILITY

Each species was also assigned to one of three categories based on mobility patterns and home-range sizes: category 1, species with high mobility, generally associated with schooling behaviour in the water column (*i.e.* mid-water carnivores and planktivores) or demersal species with wide horizontal displacements (*e.g.* roving herbivores, sparids and mullids); category 2, demersal relatively sedentary species that live in close association with the reef substratum, including serranids, haemulids, labrids and chaetodontids; category 3, site-attached species with very small home ranges, many of them presenting territorial behaviour (*e.g.* damselfishes, labrisomids and gobies).

STATISTICAL ANALYSES

MANOVA (repeated measures) were used to test for differences among locations concerning mean relative abundances of food quality groups and spatial use and mobility categories. One-way ANOVA were performed to analyse total fish densities and densities of herbivores (Zar, 1999). Appropriate transformations (\log_{10} , square root or arc-sin) were applied when necessary in order to stabilize the variances when necessary (Underwood, 1997). Additional Student–Newman–Keuls (SNK) multiple comparisons

TABLE II. Food quality, mobility and trophic classification of reef fish genera in the four studied sites. Families are arranged according to Nelson (1994)

Family	Genus	Trophic guild	Food quality	Mobility	Family	Genus	Trophic guild	Food quality	Mobility
Ogcocephalidae	<i>Ogcocephalus</i>	C	H	3	Sciaenidae	<i>Spondylitiosoma*</i>	O	I	1
Synodontidae	<i>Synodus</i>	P	H	3		<i>Odontoscion</i>	C	H	2
Holocentridae	<i>Holocentrus</i>	MI	H	2		<i>Pareques</i>	MI	H	2
	<i>Myripristis</i>	PL	H	2		<i>Sciaena*</i>	C	H	2
	<i>Sargocentrum</i>	MI	H	2		<i>Umbrina</i>	MI	H	2
Aulostomidae	<i>Aulostomus</i>	P	H	2	Mullidae	<i>Mulloidichthys</i>	MI	H	1
Scorpaenidae	<i>Scorpaena</i>	C	H	3		<i>Mullus</i>	MI	H	1
Centropomidae	<i>Centropomus</i>	C	H	1		<i>Pseudupeneus</i>	MI	H	1
Serranidae	<i>Alphestes</i>	C	H	2	Chaetodontidae	<i>Chaetodon</i>	SI	L	2
	<i>Cephalopholis</i>	C	H	2	Pomacanthidae	<i>Holacanthus</i>	SI	L	2
	<i>Dermatolepis</i>	C	H	2		<i>Pomacanthus</i>	O	L	2
	<i>Diplectrum</i>	C	H	2	Kyphosidae	<i>Kyphosus</i>	RH	L	1
	<i>Epinephelus</i>	C	H	2	Cirriiidae	<i>Amblycirrhitus</i>	MI	H	3
	<i>Hypoplectrus</i>	C	H	2	Pomacentridae	<i>Abudefduf</i>	O	I	1
	<i>Mycteroperca</i>	P	H	2		<i>Chromis</i>	PL	H	1
	<i>Paranthias</i>	PL	H	1		<i>Microspathodon</i>	TH/D	L	3
	<i>Rypticus</i>	C	H	2		<i>Stegastes</i>	TH/D	L	3
	<i>Serranus</i>	MI	H	3		<i>Bodianus</i>	MI	H	2
	<i>S. tortugarum</i>	PL	H	2	Labridae	<i>Centrolabrus*</i>	MI	H	2
Grammatidae	<i>Gramma</i>	MI/PL	H	3		<i>Clepticus</i>	PL	H	1
Priacanthidae	<i>Heteropriacanthus</i>	MI	H	2		<i>Coris*</i>	MI	H	2
	<i>Priacanthus</i>	C	H	2		<i>Doratonotus</i>	MI	H	2
Carangidae	<i>Carangoides</i>	P	H	1		<i>Halichoeres</i>	MI	H	2
	<i>Caranx</i>	P	H	1		<i>Thalassoma</i>	PL	H	1
	<i>Decapterus</i>	P	H	1		<i>Xyrichtys</i>	MI	H	3
	<i>Elagatis</i>	P	H	1	Scaridae	<i>Cryptotomus</i>	RH	L	1
	<i>Pseudocaranx</i>	PL	H	1		<i>Scarus</i>	RH/D	L	1

TABLE II. Continued

Family	Genus	Trophic guild	Food quality	Mobility	Family	Genus	Trophic guild	Food quality	Mobility
Lutjanidae	<i>Seriola</i>	P	H	1	Labrisomidae	<i>Sparisoma</i>	RHD	L	1
	<i>Trachinotus</i>	MI	H	1		<i>Labrisomus</i>	C	H	3
	<i>Lutjanus</i>	C	H	2		<i>Malacocentrus</i>	MI	H	3
	<i>Ocyurus</i>	C	H	1	Blenniidae	<i>Ophioblennius</i>	TH/D	L	3
Haemulidae	<i>Anisotremus</i>	MI	H	2		<i>Parablennius</i>	O	I	3
	<i>Haemulon</i>	MI	H	2	Chaenopsidae	<i>Emblemariopsis</i>	MI	H	3
	<i>Orthopristis</i>	MI	H	2	Tripterygiidae	<i>Emmeanectes</i>	MI	H	3
	<i>Parapristipoma*</i>	MI	H	2		<i>Tripterygion*</i>	MI	H	3
	<i>Pomadasys</i>	MI	H	2	Gobiidae	<i>Coryphopterus</i>	PL	H	3
	<i>Archosargus</i>	O	I	1		<i>Elacatinus</i>	MI	H	3
Sparidae	<i>Boops</i>	O	I	1		<i>Gobius*</i>	MI	H	3
	<i>Calamus</i>	MI	H	1		<i>Yanneaugobius*</i>	O	I	3
	<i>Dentex*</i>	C	H	1	Acanthuridae	<i>Acanthurus</i>	RH/D	L	1
	<i>Diplodus</i>	O	I	1	Bothidae	<i>Bothus</i>	C	H	3
	<i>Lithognathus*</i>	MI	H	1	Balistidae	<i>Balistes</i>	MI	I	1
	<i>Oblada*</i>	O	I	1	Monacanthidae	<i>Aluterus</i>	O	L	1
	<i>Pagellus*</i>	O	I	1		<i>Cantherhines</i>	O	I	1
	<i>Pagrus</i>	C	I	1		<i>Stephanolepis</i>	O	I	1
	<i>Sarpa*</i>	RH	L	1	Ostraciidae	<i>Acanthostracion</i>	O	I	1
	<i>Sparus*</i>	O	I	1	Tetraodontidae	<i>Canthigaster</i>	SI	L	2

C, carnivore; P, piscivore; MI, mobile invertebrate feeder; SI, sessile invertebrate feeder; PL, planktivore; O, omnivore; RH, roving herbivore; TH, territorial herbivore; D, detritivore; H, high-quality food; I, intermediate; L, low; 1, high mobility; 2, relatively sedentary; 3, site attached. *, not present in the western Atlantic.

of means test were performed as a *post hoc* test (Zar, 1999). When transformations did not produce homogeneous variances, ANOVA was used nevertheless because of its robustness, following Underwood's (1997) recommendation. A setting of $\alpha=0.01$ was used to compensate for the increased likelihood of Type I error (Underwood, 1997). A multivariate canonical correspondence analysis (CCA) was conducted to explore the generality of large-scale trends in food resource use among 11 sites in the Atlantic, *i.e.* the second database (ter Braak & Verdonschot, 1995). The *t*-test was employed for comparing the average feeding rate of the ocean surgeonfish *Acanthurus bahianus* Castelnau in Panama and south-eastern Brazil.

RESULTS

UTILIZATION OF FOOD RESOURCES

Fish species using food resources of high nutritional value were dominant in all sites, both in terms of diversity and relative abundance, ranging from 62 to 73% of the total number species and 52 to 65% of counted fishes (Table I and Fig. 1). The number of species and relative abundance of fishes relying on low-energy food significantly decreased towards higher latitudes (Fig. 1 and Table I). The species : genus ratio of this fish guild decreased toward colder waters (2.4 in Bocas, 1.9 in Guarapari, 1.6 in Arvoredo and 1.0 in the Canaries) and it was higher than the overall ratio considering all fishes in the western Atlantic assemblages (Table I). On the other hand, fishes that fed on intermediate-quality resources (*i.e.* algae, detritus and also animal protein) were highly abundant at colder peripheral sites (Arvoredo and Canaries) and their proportional importance diminished in warmer locations (Fig. 1). Their species richness also increased with latitude (Table I), and the omnivorous sparids were the main speciose family in this guild.

A sharp decrease in the importance of fishes depending on low-caloric food could be observed in relation to the minimum water temperature of locations. A ratio of mean relative abundance of fishes that feed on high-quality resources divided by mean relative abundance of fishes using intermediate or low-quality diets revealed a consistent trend (Fig. 2).

A CCA analysis performed with data from 11 sites along the Atlantic (Fig. 3) showed the same trends observed in the four detailed studied sites (Fig. 1), confirming that a consistent regional generalization could be drawn. Trophic strategies accounted for 45.6% of the variance in the weighted averages. Tropical sites were all clustered following the trend of better use of low-quality resources (intraset correlations between diet and site scores = 0.819). On the right side of the diagram, high-quality (-0.939) and intermediate diets (0.319) affected the marginal eastern Atlantic and the Mediterranean sites. A balance of intermediate (*i.e.* omnivore) and low-quality category influenced high latitude rocky reefs on the Brazilian coast.

DENSITY OF HERBIVORES AND DETRITIVORES

Standardized visual censuses in four sheltered and shallow localities in the western Atlantic provided comparable data on densities of reef fishes along an extensive latitudinal gradient. Total density of fishes was similar in all tropical

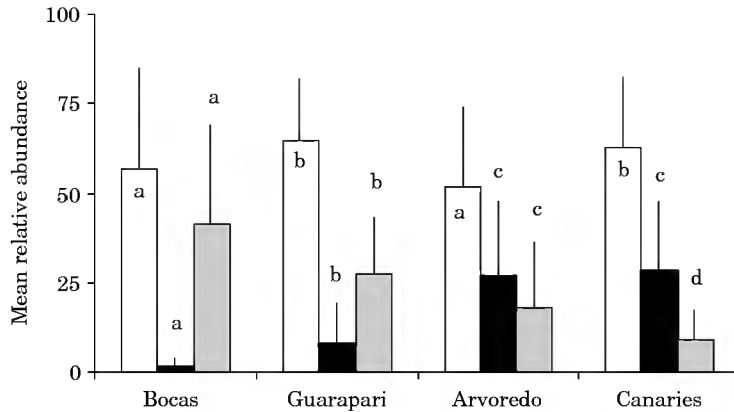


FIG. 1. Mean \pm s.d. relative abundance of food quality categories: high-quality (\square) (fishes that feed on high protein and energy content food, which are highly digestible, *e.g.* macro-plankton, mobile invertebrates and fishes), low-quality (\blacksquare) (fishes that eat relatively low-energy content resources, with indigestible components such as algae, seagrasses, detritus, sponges and cnidarians and intermediate-quality (\blacksquare) (fishes that forage both on algae and protein-rich animal food, *i.e.* omnivores). MANOVA showed that all categories varied significantly between locations ($P < 0.001$); different lower case letters indicate significantly different (Student–Newman–Keuls test, $P < 0.01$) values and those with the same lower case letter are not significantly different ($P > 0.01$).

sites: Bocas del Toro, Panama, Abrolhos, north-east Brazil and Guarapari, south-east Brazil ($175\text{--}200$ fishes 100 m^{-2}) and only half of it was found on Arvoredo (92 fishes 100 m^{-2}) in the southern Brazil (Fig. 4). Total density and relative proportion of herbivores follow a clear significant latitudinal trend (158 fishes 100 m^{-2} constituting 79% of fishes counted in Bocas del Toro, Panama,

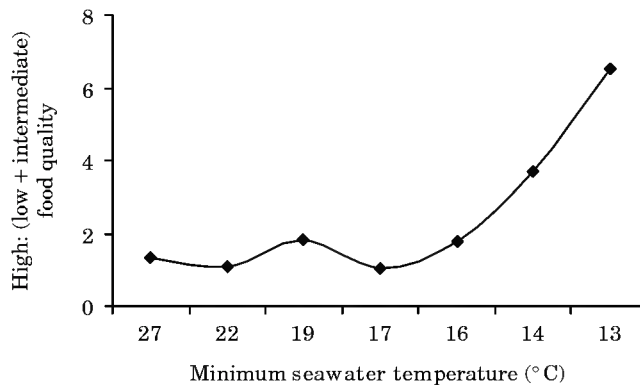


FIG. 2. High-quality: (intermediate + low) quality food ratio in relation to minimum water temperature. Data from relative abundances derived from visual censuses: Bocas del Toro, Panama, 9°N ; Abrolhos Reefs, north-east Brazil, $17^{\circ}30'\text{S}$ (C.E.L. Ferreira unpubl. data); Guarapari Islands, south-east Brazil 20°S ; Arvoredo, $27^{\circ}30'\text{S}$; Canaries, Macaronesia, 28°N (Fálcon *et al.*, 1996; Bortone *et al.*, 1991; Hajagos & Van Tassell, 2001); south-east Mediterranean, Spain, $37^{\circ}38'\text{N}$ (García-Charton & Pérez-Ruzafa, 2001); Santa Catalina Island, California, U.S.A. $33^{\circ}30'\text{N}$ (Hobson & Chess, 2001).

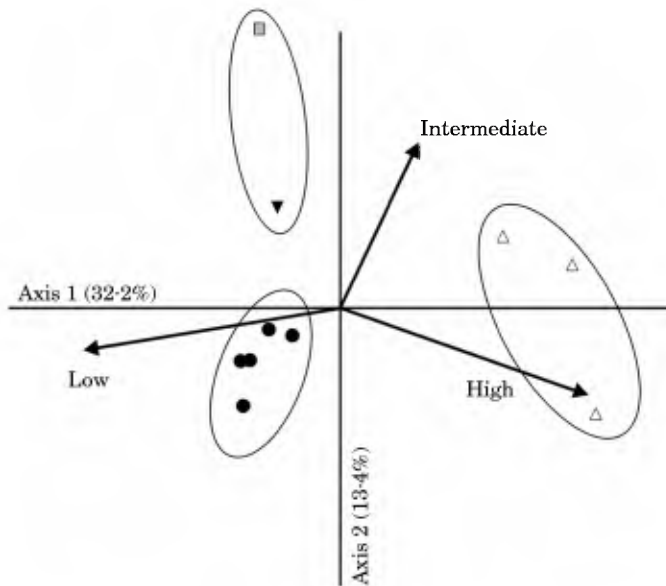


FIG. 3. Canonical correspondence analysis ordination diagram with reef sites and diet categories (→) (see Fig. 1). The sites were: tropical (●) [Florida Keys, 24°39' N (Bohnsack & Bannerot, 1986); Cayos Cochinos, Honduras, 15°56' N (Clifton & Clifton, 1998); Bocas del Toro, Panama, 9°N; Manuel Luiz Reefs, north-east Brazil, 0°52' S (Rocha & Rosa, 2001); Tamandaré, north-east Brazil, 8°45' S (B.P. Ferreira unpubl. data); Abrolhos Reefs, north-east Brazil, 17°30' S (C.E.L. Ferreira unpubl. data); Guarapari Islands, south-east Brazil 20°S], south-east (▼) and southern Brazil (■) [Arraial do Cabo, south-east Brazil, 23°S (C.E.L. Ferreira unpubl. data); Arvoredo, southern Brazil 27°30' S] and north-east Atlantic (△) [Canaries, Macaronesia, 28°N (Fálcón *et al.*, 1996; Bortone *et al.*, 1991; Hajagos & Van Tassell, 2001); south-east Mediterranean, Spain, 37°38' N (García-Charton & Pérez-Ruzafa, 2001); southern Italy, 35°35' N (Mazzoldi & Girolamo, 1997)].

99 and 57% on Abrolhos Reefs, north-east Brazil, 41 and 23% on Guarapari Island, south-east Brazil, and 19 and 21% on Arvoredo Archipelago in the south).

MOBILITY AND HOME-RANGE PATTERNS

Regarding the amplitude of fish spatial use and mobility, the category 1 (high mobility generally associated with schooling behaviour) is proportionally more diverse in the Canaries (Table 1) where it also achieves significantly higher relative abundance (Fig. 5). Schooling sparids and the omnivorous pomacentrid genus *Abudefduf* are abundant in the marginal sites. On the Canarian Archipelago, the planktivorous *Thalassoma* and *Chromis* are also very abundant. Relatively sedentary species (category 2) are a diverse group in tropical sites (Table 1), and are highly abundant in the Brazilian sites (Fig. 5). This is because of the high relative abundance of haemulids, holocentrids and the labrid genus *Halichoeres* on Guarapari Islands, and serranids (primarily *Mycteroperca*) and the puffers (*Sphoeroides*) on Arvoredo. Site-attached species (category 3) are the dominant group in the Caribbean in terms of abundance (66.5% of the counted fishes; Fig. 5). Gobiids and territorial damselfishes are mainly responsible for

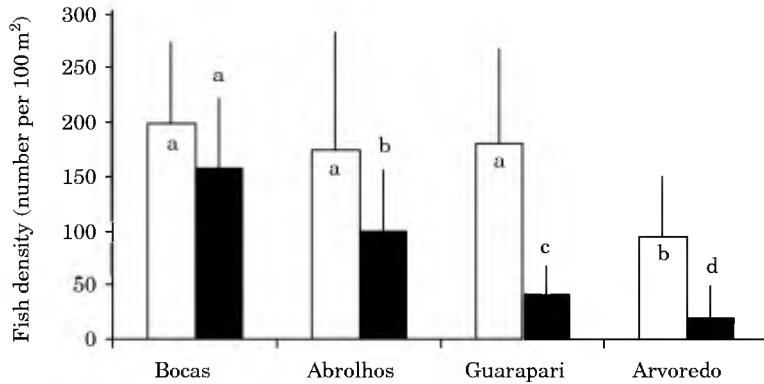


FIG. 4. Mean + s.e. total fish densities (\square) and herbivores only (\blacksquare) at four sites in a latitudinal gradient along the western Atlantic. Data were derived from 20×2 m transects (visual censuses) in selected shallow (<10 m deep) sheltered habitats at: Bocas del Toro, Punta Hospital, 9°N ($n=60$); Abrolhos, Timbebas reefs, $17^{\circ}30'\text{S}$ ($n=56$); Guarapari Island, 20°S ($n=84$); Arvoredo, $27^{\circ}30'\text{S}$ ($n=85$). ANOVA showed that all categories varied significantly between locations ($P < 0.001$); different lowercase letters indicate significantly different (Student–Newman–Keuls test, $P < 0.01$) values and those with the same lower case letter are not significantly different ($P > 0.01$).

these figures. On the Brazilian coast, site-attached species account for 15–30% decreasing to just 1.3% in the Canaries. Many fishes in category 3 are small and cryptic and are often underestimated by UVC (Willis, 2001). Their diversity and abundance are probably higher than indicated in Fig. 5, especially on tropical reefs.

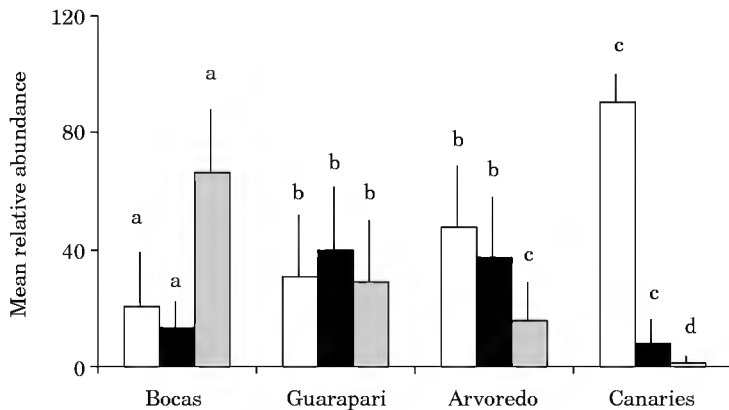


FIG. 5. Mean + s.d. relative abundances of categories of spatial use (mobility and home-range size): category 1, (\square) (species with high mobility, generally associated with schooling behaviour in the water column or demersal species with wide horizontal displacements); category 2 (\blacksquare) (demersal relatively sedentary species that live in close association with the reef substratum, including serranids, haemulids, labrids and chaetodontids); category 3 (\blacksquare) (site-attached species with very small home-ranges, many of them presenting territorial behaviour). MANOVA showed that all categories varied significantly between locations ($P < 0.001$); different lower case letters indicate significantly different (Student–Newman–Keuls test, $P < 0.01$) values and those with the same letter were not significantly different ($P > 0.01$).

DISCUSSION

Species richness declines from Bocas del Toro to the Canaries conforming to the general trend of decreasing fish diversity from tropical to temperate latitudes (Hobson, 1994; Briggs, 1995). These trends could be related to: (1) differential extinction rates suffered in peripheral areas due to sea-level and temperature changes over geological time (Briggs, 1966, 1995; Vermeij & Rosenberg, 1993), (2) differences in recent speciation rates, decreasing from tropical to temperate sites, as indicated by the species per genus ratios found (Table I), and (3) habitat availability (and heterogeneity) and resource diversity and temporal persistence (tropical *v.* temperate reefs; Holbrook *et al.*, 1990).

IS THERE A TREND TOWARD THE USE OF LOW-ENERGY FOOD RESOURCES AMONG TROPICAL REEF FISHES?

Harmelin-Vivien (2002) presented qualitative data of herbivorous fish species and their significant correlation with latitude (increasing richness towards the equator), and also showed that the percentage of algae in the diet of blenniid and gobiid fish species on coral reefs was higher than in warm-temperate waters. In the present study, it was unequivocally demonstrated that although planktivores, piscivores and carnivores preying on motile invertebrates dominated in all sites, the relative abundance of fishes that fed on algae, organic detritus and sessile invertebrates decreased from tropical to temperate latitudes. These differences are probably not related to differences in the abundance of food resources between latitudes, because algae, seagrasses and sessile invertebrates (except for reef-building corals) are also abundant and available (although seasonal for some algae species) for feeding in temperate zones (Holbrook *et al.*, 1990; Fasola *et al.*, 1997; Pawlik, 1998; Harmelin-Vivien, 2002; Pihl & Wennhage, 2002). Differences, however, could be driven by algae productivity (Russ, 2003) and rate of detritus decomposition (higher on tropical reefs; Cebrian, 2002).

The species: genus ratio of low-quality food consumers increased towards the tropics, and was higher than the overall ratio considering all fishes in the assemblages. This supports the view that higher speciation rates occurred among this guild of fishes in warm waters. Indeed, low-quality feeders contain the morphologically derived taxa, indicating a relationship between radiation and the energetic value of the food (Table II; Bruggemann, 1994; Harmelin-Vivien, 2002). The higher diversity and abundance of low-quality feeders (*i.e.* herbivores and sessile invertebrate feeders) in lower latitudes compared to marginal areas could be viewed as a reflection of a progressive adaptation to the use low-energy food sources (Harmelin-Vivien, 2002).

Although herbivory, spongivory and corallivory by fishes is known to affect distribution and abundance of benthic organisms (Lewis, 1985; Horn, 1989; Hixon, 1997; Hill, 1998; Pawlik, 1998), these feeding strategies are a relatively recent evolutionary phenomenon (Wood, 1999; Bellwood & Wainwright, 2002; Bellwood, 2003). Herbivores and sessile invertebrate browsers are found in the most derived families (Table II), and within these families extended adaptations to use poor-quality resources are found in the morphologically most derived genera (Motta, 1989; Bellwood, 1994; Harmelin-Vivien, 2002). Cooper & Vitt

(2002) found the same trend in lizards. The 'Cenozoic marine grazing revolution' appears to mark a major shift in the ecological structure of coral reefs due to changes in the nature of fish-based predation. During this transition, fish faunas went from primarily carnivorous in the Mesozoic to a large variety of grazers or browsers in the Cenozoic (Wood, 1999; Bellwood & Wainwright, 2002; Bellwood, 2003).

In colder peripheral sites, such as the southern Brazilian coast, the Canaries or the Mediterranean, fishes that feed on intermediate-quality food (*e.g.* omnivorous sparids) have higher abundance and diversity, compared to warmer sites. It seems that these fishes could exploit low-nutritional resources only if they are associated with substantial portions of highly digestible animal protein. So, they could fulfil their metabolic needs to live in harsh colder environments. Bowen *et al.* (1995) interpreted omnivory as a compromise strategy in which protein from scarce animal prey is complemented by energy from abundant primary foods. At Santa Catalina, California, U.S.A. two nominally herbivores, *Girella nigricans* (Ayres) and *Medialuna californiensis* (Steindachner), differ from most tropical herbivores in consuming a relatively large number of invertebrates on a seasonal basis (Holbrook *et al.*, 1990; Hobson & Chess, 2001). In winter, when preferred algae are scarce and when fermentative digestion processes could be less efficient, it seems necessary to increase feeding on animal protein. In North Carolina, U.S.A., a similar behaviour was observed (M. Hay, pers. comm.) with omnivorous fishes shifting diets with changes in temperature. When it was warm, they consumed more seaweed. As temperature dropped they consumed more animal material, and eventually refused to eat any seaweed once temperatures were $<17^{\circ}\text{C}$.

'HERBIVOROUS' FISHES: A TROPICAL PHENOMENON?

The density (and relative proportion) of herbivores and detritivores censused in similar habitats, with standardized procedures, significantly decreases toward higher latitudes. Meekan & Choat (1997) when comparing the Caribbean and the Great Barrier Reef to New Zealand reefs also found the same pattern. Within the herbivores, some differences were obvious. Fishes that have an important part of their diet constituted by detritus and calcified material (scarids and acanthurids) achieve higher densities in warmer sites (Bruggemann, 1994; Ferreira *et al.*, 2004). Conversely, kyphosids and some sparisomatines that feed on macroalgae increase their relative abundance at higher latitudes on the Brazilian coast (Ferreira *et al.*, 2004). On the Great Barrier Reef, scarids on the southern limit of their range consume more macroscopic algae compared to those on lower latitudes (J.H. Choat, pers. comm.). The domination of exclusive selective macroalgae feeders, which use a special digestion by hind gut fermentation and symbionts ('true herbivores'; Choat & Clements, 2002) such as kyphosids, odacids, aplodactylids and stichaeids) is also found in New Zealand temperate rocky reefs (Jones, 1988; Meekan & Choat, 1997; Choat & Clements, 1998; Mountfort *et al.*, 2002). Other counter-examples, however, complicate the situation (*e.g.* the browsing acanthurid *Acanthurus coeruleus* Bloch & Schneider are only found in the tropical Atlantic, and macroalgae eating siganids are more diverse and abundant at lower latitudes in the Pacific).

Herbivory pressure seems to be lower in higher latitudes not only due to lower density of herbivores, but because feeding rates (bites per unit time) are generally lower too (Choat & Clements, 1993), which is probably a reflection of lowered metabolism in colder water. For example, parrotfishes of the genus *Sparisoma* have average biting rates during the daytime (1100–1600 hours) of 30–35 bites per 5 min in south-east Brazil (Ferreira *et al.*, 1998b) and Azores (J.P. Barreiros, pers. comm.), and of 55–65 bites per 5 min in Panama (C.E.L. Ferreira & S.R. Floeter, unpubl. data). Also, the roving acanthurid *Acanthurus bahianus* Castelnau have an average grazing rate of 88 ± 30 bites per 5 min (mean \pm s.d.) in south-east Brazil, where water temperature usually falls to 18–19°C (Ferreira *et al.*, 1998b), and more than the double (196 ± 43 bites per 5 min) in the tropical Bocas del Toro, Panama (*t*-test, d.f. = 121, $P < 0.0001$). This pattern seems to indicate that below a critical temperature, nutrient assimilation may fall below metabolic requirements, thus physiological constraints associated with size and an ectothermic metabolism could be excluding many ‘herbivorous’ fishes from temperate and higher latitudes (Gaines & Lubchenco, 1982; Horn, 1989). Further studies should also consider if productivity and algae and detritus chemical composition are linked with the herbivorous fish abundance patterns found.

It is worth noting that the capacity to ‘make a living’ from plant material has been found for a long time in terrestrial vertebrate populations, probably since the Permian (Sues & Reisz, 1998). In fishes there is clearly a much later ‘time-horizon’ in the appearance of herbivory (Bellwood & Wainwright, 2002). Although some fishes occupying cold water habitats (down to 45°S) are herbivores, feeding exclusively on macroscopic algae and maintaining rates of fermentative digestion in a similar way to terrestrial endotherms (Mountfort *et al.*, 2002), the great majority of marine fish ‘herbivores’ have tropical affinities and are rare in temperate environments in the Atlantic. These fishes find their optimal environmental factors in the tropics (Choat, 1991; Bruggemann, 1994; Ferreira *et al.*, 2004). It is thus clear that the real trophic status of herbivorous fishes in the Atlantic requires further detailed studies (Choat & Clements, 2002).

DO FISH SPATIAL USE AND MOBILITY VARY WITH LATITUDE AND REEF TYPE?

Differential mobility and home range patterns (*e.g.* schooling behaviour and territoriality) are expected to occur if: 1) distinct foraging strategies are used to access unpredictable and spaced resources (*e.g.* plankton) and 2) there is variation in reef type and complexity (*e.g.* coral and rocky). Horizontal and vertical fish distribution in space is not uniform across the reef complex. Its heterogeneity operates at two scales, the geomorphological reef zones (macrohabitat), and the specific fish habitats (microhabitat). Bellwood *et al.* (2002) found highly congruent patterns of habitat use (sheltered *v.* exposed) of labrids, in terms of functional characteristics at global biogeographical scales.

On high-latitude reefs, fishes presenting high mobility or wide horizontal displacements (category 1) are proportionally more diverse and achieve significantly higher abundances. These fishes generally exhibit schooling behaviour, which is the privileged foraging tactic used by fishes that have to roam over

large areas to find patchy or randomly distributed food (e.g. plankton and small clupeids). High-latitude environments are generally affected by seasonal temperature changes and unpredictable upwelling processes (Ebeling & Hixon, 1991; Sala & Boudouresque, 1997; Pihl & Wennhage, 2002). High mobility fishes, usually in large schools, are less reliant on the reef substratum for protection, and seem to respond more readily to environmental fluctuations, i.e. they are better able to move among reefs and vertically in the water column in response to the availability of resources or to satisfy their environmental preferences, such as optimal temperature. Among fishes that thrive well in these marginal reefs are the omnivorous schooling sparids (*Diplodus*), the sargent major (*Abudefduf*), and the planktivorous *Chromis*.

In a highly complex substratum, species sheltering in reef crevices or holes or in near-reef sand or rubble are expected. Structural complexity or bottom relief has been positively correlated to reef fish abundance in coral reefs (Bell & Galzin, 1984; Friedlander & Parrish, 1998), tropical and subtropical rocky shores (Aburto-Oropeza & Balart, 2001; Ferreira *et al.*, 2001; S.R. Floeter, unpubl. data), and temperate reefs (García-Charton & Pérez-Ruzafa, 1998). On tropical reefs, relatively sedentary taxa (category 2) such as the labrid genus *Halichoeres*, haemulids, chaetodontids and serranids form the most diverse group detected by UVC. In terms of abundance, fishes with small-size home ranges (category 3) predominate on coral reefs (67% of the counted fishes in Bocas del Toro, Panama). Similar values are found on coral reefs worldwide (72% at Tulear, Madagascar; 61% at Moorea, French Polynesia; Harmelin-Vivien, 1989). Substratum complexity promoted by coral growth (especially branching forms) seems to provide adequate microhabitats for small territorial fishes such as pomacentrids and gobies. On many tropical reefs, territorial damselfishes are extremely abundant, and the areas they defend can occupy >70–80% of the surface of some reef habitats (Robertson & Lassig, 1980; Ferreira *et al.*, 1998a; Ceccarelli *et al.*, 2001). The higher diversity and abundance of type 3 species can also be linked to their diets. Most of them defend algae or feed on detritus which is more available in the tropics. In other words, home range size and 'food security' are probably linked and confounding factors.

In summary, the data support the situation proposed by Harmelin-Vivien (2002) that trophic structure of tropical fish communities contrast with those from temperate regions in terms of more efficient use of relatively low-quality food resources. In relation to the spatial use and mobility, relatively sedentary species form the most diverse group on tropical reefs, although fishes with small-size home ranges dominate in terms of abundance. Not all patterns found in the Atlantic, however, are likely to be general at the global-scale because of the different evolutionary histories and diversity profiles among ocean basins (Van Alstyne *et al.*, 2001; Bellwood & Wainwright, 2002). For example, a significant decrease in the proportion of species and densities of herbivorous fishes from tropical to temperate waters is observed worldwide (Horn, 1989; Meekan & Choat, 1997; S.R. Floeter and C.E.L. Ferreira, unpubl. data), but in terms of relative biomass, temperate New Zealand is an exception with herbivores presenting similar values as tropical locations (Jones, 1988). Thus, further comparative studies between the Atlantic and the Indo-Pacific

regions regarding functional characteristics of species (*e.g.* spatial use, mobility and resource-use patterns) are needed.

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