RESEARCH ARTICLE

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Geographical gradients of marine herbivorous fishes: patterns and processes

Abstract We present new data and the first rigorous analysis of latitudinal and thermal gradients of diversity, density and biomass of marine herbivorous fishes and review proposed explanatory mechanisms. Consistently, negative relationships between latitude, and positive relationships between sea surface temperature (SST), and relative richness and relative abundance of herbivorous fishes were found worldwide. Significant differences in the strength of gradients of richness and abundance with latitude and SST between tropical and extratropical zones were found consistently across ocean basins. Standardized sampling along the western Atlantic also showed negative relationships between latitude and total density and biomass. The trends, however, are driven by different components of the fish assemblages (i.e., scarids in the Caribbean and acanthurids in Brazil). Patterns of abundance along thermal gradients, generally associated with extensive latitudinal gradients, also were found at the local scale. Feeding rate of the ocean surgeonfish *Acanthurus bahianus* decreases with temperature more rapidly than the mean metabolic rate of teleost fishes. This relationship suggests a temperature-related physiological constraint. From the new standardized and comparative data presented and the review of the explanatory hypotheses, we conclude that temperature-related feeding and digestive processes are most likely involved in the distribution patterns of herbivorous fishes.

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Introduction

Herbivory is an important structuring force of communities (Cyr and Pace 1993; Polis 1999; Shurin et al. 2002). In shallow coral reefs worldwide, herbivory is ubiquitous and intense (Steneck 1988; Hay 1991). Herbivorous fishes have a profound impact on the distribution, abundance and evolution of tropical reef algae (Steneck 1983; Carpenter 1986; Lewis 1986; Hay 1991; Bellwood 2003) and are believed to mediate competition between fast-growing benthic algae and relatively slow-growing corals, allowing corals to flourish by limiting macroalgal standing crop (Hughes 1996; Miller 1998; Szmant 2001). On shallow reefs, fishes can take over 100,000 bites/m²/day (Hatcher 1981; Carpenter 1986; Bruggemann 1994), consuming almost all benthic algal production (Hatcher 1981; Carpenter 1986; Hay 1991; Ferreira et al. 1998). Fish are therefore the major link for energy transfer to higher trophic levels (Polunin and Klumpp 1992). In tropical freshwater streams, fish herbivory also can exert an important influence on plant communities (Wootton and Oemke 1992; Pringle and Hamazaki 1997; 1998).

Contrary to tropical systems, temperate reefs are typically algal-dominated communities characterized by low levels of herbivory (Mann 1973; Gaines and Lubchenco 1982). This contrasting pattern of herbivory between tropical and temperate marine systems may be related to a shift in the relative importance of herbivorous taxa; herbivorous fishes are dominant in the tropics, whereas urchins dominate temperate systems (Gaines and Lubchenco 1982; Lewis 1986; Andrew 1989; Jones and Andrew 1990).

Herbivory also changes qualitatively with latitude because of the different foraging characteristics of fishes and urchins. The high mobility, powerful and varied feeding apparatus, and visual acuity of many herbivorous fishes contrast sharply with the foraging tactics of urchins, which move about slowly, feed with limited and more uniform jaw action, and find food chemically rather than visually (Lubchenco and Gaines 1981; Gaines and Lubchenco 1982; Jones and Andrew 1990). Although urchins are often successful in controlling algal abundances, fishes on tropical reefs have higher biomass and per capita consumption rates relative to invertebrate herbivores (Carpenter 1986; Lewis 1986; Andrew 1989; Jones and Andrew 1990; Bellwood 2003).

The proportion of nominally herbivorous fish species in a fish community is known to decrease drastically from tropical to temperate and polar waters (Hiatt and Strasburg 1960; Horn 1989; Choat 1991; Ebeling and Hixon 1991). Nevertheless, clear latitudinal patterns of relative abundance, density and biomass remain unclear (cf. Horn 1989) because of the lack of studies covering wide latitudinal ranges with standardized sampling. Meekan and Choat (1997) compared herbivore density from New Zealand, Great Barrier Reef, and Panama, but their results, although interesting, should be interpreted with caution because of the limited number of locations included in the study. Ferreira et al. (2004) investigated trophic structure patterns of reef fishes along the extensive Brazilian coast and showed a clear decrease in relative abundance of roving herbivorous fishes toward colder waters, but they did not evaluate density or biomass patterns.

Proposed hypotheses explaining the latitudinal patterns in herbivorous fish abundance and diversity include: (1) insufficient time for evolution and range expansion into temperate waters (Mead 1970); (2) in temperate systems, seasonal food shortages of preferred algal taxa occur on time scales shorter than the generation time of fishes, which increases the selection pressure against herbivory by fishes (Barry and Ehret 1993); (3) latitudinal differences in algal toughness, nutritional quality, and chemical defenses that make temperate algae less usable by herbivorous fishes (Gaines and Lubchenco 1982; Cronin et al. 1997); (4) an evolutionary trend toward the more efficient use of less energetically rich food (e.g., algae, sponges) among tropical reef fish communities in contrast to temperate areas (Harmelin-Vivien 2002); (5) physiological constraints based on temperature conditions in which most herbivorous fishes cannot meet their energetic demands in temperate or polar waters (Gaines and Lubchenco 1982; Horn 1989; Horn and Ojeda 1999).

The goals of the present study were twofold: (1) to contribute new data on latitudinal gradients of diversity, abundance and biomass in marine herbivorous fishes and (2) to review proposed explanatory mechanisms, incorporating new evidence supporting or rejecting these processes. Specifically, we present a compilation of worldwide relative diversity and abundance data on herbivorous reef fishes and offer the first detailed data on the density and biomass of herbivorous fishes from an extensive latitudinal gradient in the western Atlantic Ocean. We also examine the possible role of temperature in limiting herbivorous reef fishes through the analysis of independent datasets at different spatial scales (i.e., thermal gradients associated with extensive latitudinal gradients and local geographical conditions within one degree of latitude). Finally, we compare feeding and metabolic rates of the ocean surgeonfish *Acanthurus bahianus* as functions of water temperature to determine whether the relationship of these two variables might indicate the possibility of a physiological constraint based on temperature limiting the majority of herbivorous fishes to warm-temperate and tropical waters. Although some of the relationships shown in this paper were known previously, they are reinforced here by new and independent data increasing the generality of diversity gradients in herbivorous fishes and allowing further investigations into regional scale differences and gradients in other variables, such as density and biomass. These new data presented together with additional information related to the proposed mechanisms driving this pattern extend previous work, and provide strong evidence that the effect of temperature on physiology partly drives latitudinal gradients in diversity, density, and biomass in herbivorous fishes.

Methods

Definition of herbivorous fishes

We use the general term "herbivorous fishes" throughout this paper to describe browsers on macroscopic algae, grazers on turfing algae, and consumers of detrital sedimentary material. Although species in the detritivore assemblage are not "true herbivores" (sensu Choat et al. 2002, 2004), they ingest around 30–40% of algae and seagrass material in Brazilian coral reefs (C.E.L.F. manuscript). These species historically have been classified as herbivores and are phylogenetically closely related to the other herbivorous species within their families, and their geographical patterns are consistent enough to allow analysis with the other herbivore groups. In addition, all fishes in this guild are known to cause disturbance on the algal assemblages.

Worldwide relative abundance and diversity

A database containing 55 localities ranging from the equator to 48°N and 55°S latitude and including both the Atlantic and the Indo-Pacific regions (see Appendix–Electronic Supplementary Material–for localities, latitudes and references) was used to derive the general worldwide pattern of relative diversity ($n = 46$ localities) and abundance ($n = 20$). Relative measures were calculated as the diversity or abundance of herbivores divided by the total fish diversity and abundance at each location. We used relative measures of diversity and abundance to control for declines in overall fish diversity and abundance with latitude.

Large-scale patterns in the atlantic

Underwater visual censuses (UVC) with standardized transect width (25 or 20×2 m) conducted by the authors in ten sheltered and shallow (< 10 m) localities in the western Atlantic provided standardized, comparable data on densities and biomass of herbivorous reef fishes along a tropical to warm-temperate latitudinal gradient. Data for species richness at four other locations and for relative abundance at three other locations were obtained from the literature (Appendix). Studies that sampled the entire fish community (either by the authors or from literature) were used for comparisons of species richness and relative abundance (Appendix). Short 2 m-wide transects were preferred because they allow sampling in a variety of visibility conditions and are more reliable for density counts given that they are in the focal range of the diver (S.R.F. and C.E.L.F, personal observation). A limitation of this method, however, is that narrow transects are biased against large or highly mobile fish, possibly underestimating the abundance of large scarids and vagile kyphosids. Quantitative data presented in this study are from the four conspicuous marine fish families (Acanthuridae, Kyphosidae, Pomacentridae, Scaridae) suitable for visual census techniques. These families make up the bulk of herbivore biomass in reef systems (Steneck 1988; Choat 1991; Williams and Polunin 2001). For species richness and relative proportion of species richness, all herbivorous species were included (i.e., the four families plus siganids and blenniids). Within the genus *Stegastes* (Pomacentridae), two mainly planktivorous species *Stegastes partitus* from the northwestern Atlantic and its Brazilian sister-species *S. pictus* were excluded from analyses of gradients in the western Atlantic.

Local-scale sampling at the channel islands, california

Abundance data from the three subtidal herbivores in southern California (i.e., the kyphosids: *Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) were collected by the Kelp Forest Monitoring program (KFM) of the Channel Islands National Park during 1996–2001 and related to the mean water temperature at a site over the same time period (see Davis et al. 1997 for sampling protocols). The KFM annually samples 13 rocky-reef sites from the north and south sides of Anacapa, Santa Cruz, Santa Rosa, and San Miguel islands (1–3 visits per summer). These sites lie within 0.16 degree of latitude (33.889°N–34.047°N) and present an east–west thermal gradient across the Southern California Bight. Fish densities were determined using timed roving-diver fish counts during each visit to a site. Mean relative abundance of herbivores was determined over the 6 years of sampling and regressed against mean water temperature at each site for the same time period.

Feeding rates

Estimates of feeding rates of the ocean surgeonfish *Acanthurus bahianus* were obtained by following individual fishes for a fixed time period (5 min) and are expressed as bites per minute. Counts were made during daytime hours (1100–1700) at three widely separated locations (Arraial do Cabo, SE Brazil, 23°S; Florida Keys, USA, 24°39′N; Bocas del Toro, Panama, 9°N). Feeding rates of this species also were compared with mean metabolic rate (resting oxygen consumption [mmol h^{-1}] for teleost fish [data from Clarke and Johnston 1999]) in relation to minimum water temperatures experienced at the three sites.

Sea surface temperatures

Data on sea surface temperatures (SST) used in the present study were obtained from Maida and Ferreira (1997), CARICOMP (2002), Channel Islands National Park's Kelp Forest Monitoring program, the NOAA website (http://www.noaa.gov/), references listed in the appendix, and unpublished data from the authors.

Statistical analyses

Regression analyses were conducted to determine the relationship among: (1) density, biomass, species richness, and relative abundance of herbivorous fishes with latitude and mean SST; and (2) abundance and relative abundance across the thermal gradient at the Channel Islands, California. A general linearized model (GLM) with interaction was used to test differences in regression slopes of relative richness and abundance against latitude and SST among regions and ocean basins. We classified as tropical of those locations where the minimum monthly mean temperature exceeded 20°C. We conducted the difference of slope tests (*t*-test) to determine differences between the slope of the regressions of relative abundance and relative richness against latitude and SST (Zar 1999). All relative richness and abundance

data were arcsine transformed to meet the assumptions of the statistical models. One-way analysis of variance (ANOVA) was conducted to test the hypothesis that feeding rate declines more rapidly than metabolic rate as temperature declines, i.e., the ratio between feeding rate and metabolic rate is different at different temperatures. A Student-Newman-Keuls (SNK) multiple comparisons test was used following the ANOVA to locate significant differences among means (Zar 1999).

Results

Highly significant negative relationships between latitude (and positive between mean SST) and relative abundance and relative richness (i.e., proportion of species in a given location) of herbivorous fishes were found worldwide (Fig. 1). Relative abundance decreases
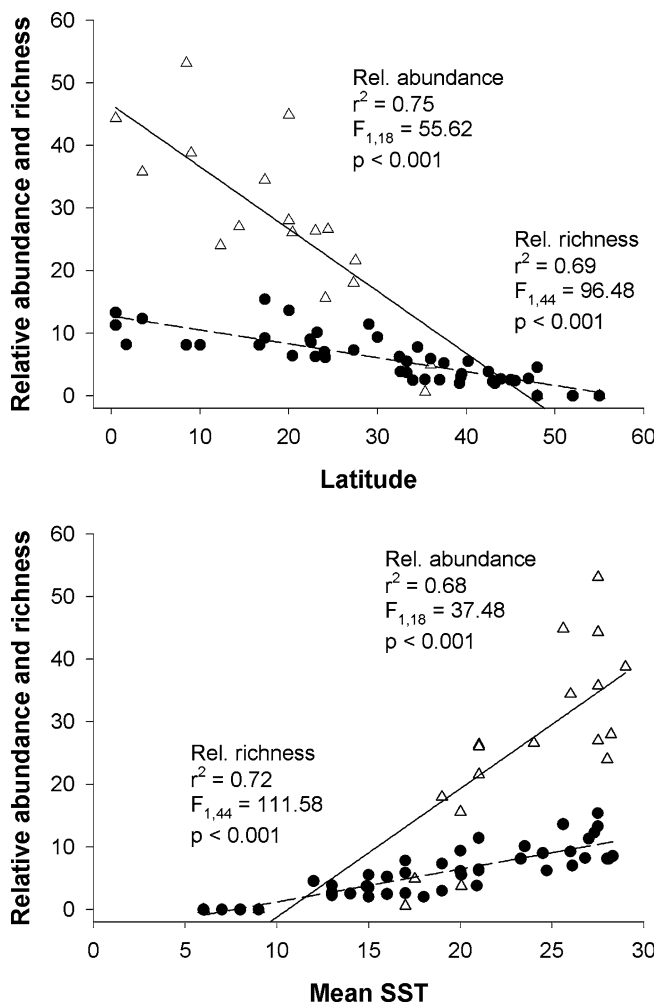

Fig. 1 Relationship between relative abundance (%–*triangles, solid line*) and relative richness (%–*black circles, dashed line*) of herbivorous fishes in shallow reef communities and latitude and mean sea surface temperature (SST). Both north and south latitudes were included. See Appendix (Electronic Supplementary Material) for localities, latitudes and references

faster with increasing latitude and increases faster with increasing temperature than relative richness (Fig. 1; Latitude: $t = 2.19$, df $= 64$, $P = 0.03$; SST: $t = 9.33$, df $= 64$, $P < 0.001$). Herbivorous fish species account for 6–15% (mean of 9.8 ± 2.7 SD) of total richness at tropical locations (i.e., minimum temperatures of 20°C) compared to 0–9% (mean of 3.6 ± 2.4 SD) on extratropical reefs.

Significant regional differences were found in the strength of richness gradients in herbivorous fishes (Fig. 2). The relationship between relative richness and latitude varied significantly between regions (GLM latitude×region interaction, $F_{3,39} = 3.99$, $P = 0.014$). A Tukey post-hoc test ($\alpha = 0.05$) revealed that the New Zealand region (sensu Francis 1996; see Appendix) exhibits a steeper regression slope than the other regions. In addition, the relationship between relative richness and SST varied significantly between regions ($F_{3,18} = 4.29$, $P = 0.018$). A Tukey post-hoc test ($\alpha = 0.05$) revealed that the New Zealand and northeastern Atlantic regions exhibit steeper regression slopes than the Brazilian region or worldwide pattern.

Additional significant differences were found in the strength of gradients of relative richness and abundance with latitude and SST between tropical and extratropical zones. Neither relative richness nor relative abundance was related to latitude or SST in tropical locations (Fig. 3). In contrast, both relative richness and abundance declined with latitude in the extratropical zone, and increased with SST in the extratropical zone (Fig. 3).

Although significant differences exist between the relationships of relative richness and abundance with latitude and SST in different regions and tropical versus extratropical locations, the patterns are consistent across ocean basins. Patterns of relative richness against latitude and SST are consistent between the Atlantic and Pacific oceans (GLM, Latitude×Ocean: $F_{1,41} = 2.07$, $P = 0.157$; SST×Ocean: $F_{1,14} = 0.92$, $P = 0.343$). Additionally, patterns of relative abundance against latitude and SST are consistent between the two ocean basins (GLM, Latitude×Ocean: $F_{1,16} = 0.27$, $P = 0.610$; SST×Ocean: $F_{1,16} = 0.192$, $P = 0.667$).

To determine whether gradients in herbivorous fish diversity and abundance are concomitant with changes in other community parameters, we calculated the relationship between latitude and total density, biomass, species richness and relative abundance of herbivores in the Atlantic Ocean (Fig. 4). Latitude showed significant negative associations with total density, biomass, species richness, and relative abundance of herbivores (Fig. 4). Because latitude was significantly correlated with minimum water temperature ($r^2 = 0.83$, $F_{1,12} = 50.97$, $P < 0.001$) across this region, it is not surprising that temperature was positively associated with total density ($r^2 = 0.71$, $F_{1,9} = 22.45$, $P = 0.001$), biomass ($r^2 = 0.60$, $F_{1,8} = 12.04$, $P = 0.008$), species richness ($r^2 = 0.84$, $F_{1,10} = 53.79$, $P < 0.001$), and relative abundance of herbivores ($r^2 = 0.63$, $F_{1,13} = 22.82$, $P < 0.001$).
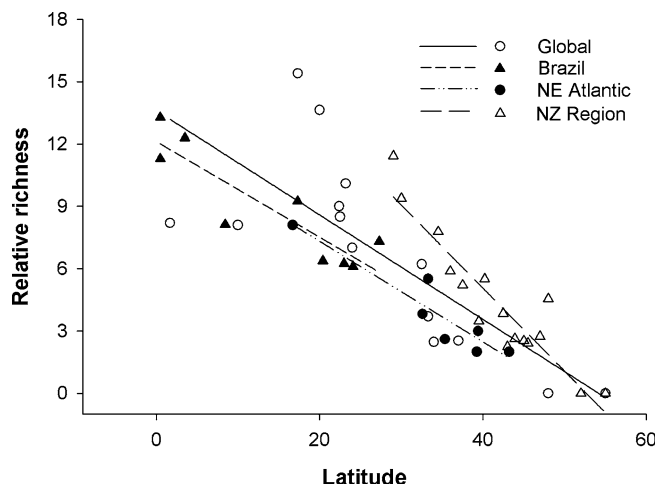
Fig. 2 Relationship between relative richness (%) of herbivorous fishes and latitude among different regions of the world ocean. Brazil: $r^2 = 0.80$, $F_{1,7} = 27.54$, $P = 0.001$; Northeastern Atlantic Region: $r^2 = 0.87$, $F_{1,5} = 33.77$, $P = 0.002$; New Zealand Region: $r^2 = 0.86$, $F_{1,12} = 82.79$, $P = 0.001$; Global (does not include sites previously used in the other regions): $r^2 = 0.58$, $F_{1,12} = 16.37$, $P = 0.002$

tions (Fig. 5). As expected by differences in size, the comparatively small pomacentrids contributed proportionally more to density than to biomass at all locations, with the opposite patterns occurring with relatively large scarids. Among the roving herbivores, scarids showed higher density and biomass than acanthurids in the Caribbean region, whereas the opposite pattern was observed in the Brazilian coast. Kyphosids exhibited higher density and biomass at higher latitudes (Fig. 5). Members of the genus *Scarus* were proportionally more abundant than those of *Sparisoma*, another parrotfish genus, in lower latitudes, and their abundance ratios were significantly and negatively related to latitude, in both hemispheres ($r^2 = 0.51$, $F_{1,7} = 6.158$, $P = 0.047$).

We investigated possible relationships between temperature and herbivory by fishes by examining the relationship between temperature and relative herbivore abundance in a region with temperature variation at the same latitude. A clear positive relationship was found between the relative abundance of the three subtidal herbivorous fish species in southern California and temperature (from 13°C to 17°C) within the same latitude (34°N—among the Channel Islands, Fig. 6).

In terms of thermal trends in algae consumption, the average feeding rate (bites/min) of the *Acanthurus bahianus* significantly increased with minimum water temperature from southeastern Brazil (17.5 ± 6.0 SD; 18°C) to Florida (26.1 ± 2.1 SD; 21°C) to Panama

Within-family relationships between latitude (and temperature) and density and biomass in the western Atlantic revealed a disproportional importance in density and biomass of different families at different loca-

Fig. 3 Relative richness (%) and relative abundance (%) plotted against latitude and mean SST for both tropical and extratropical regions. Those locations with a minimum monthly temperature below 20°C were classified as extratropical (*closed circles, solid line*), while all others were classified as tropical (*open circles, dashed line*)
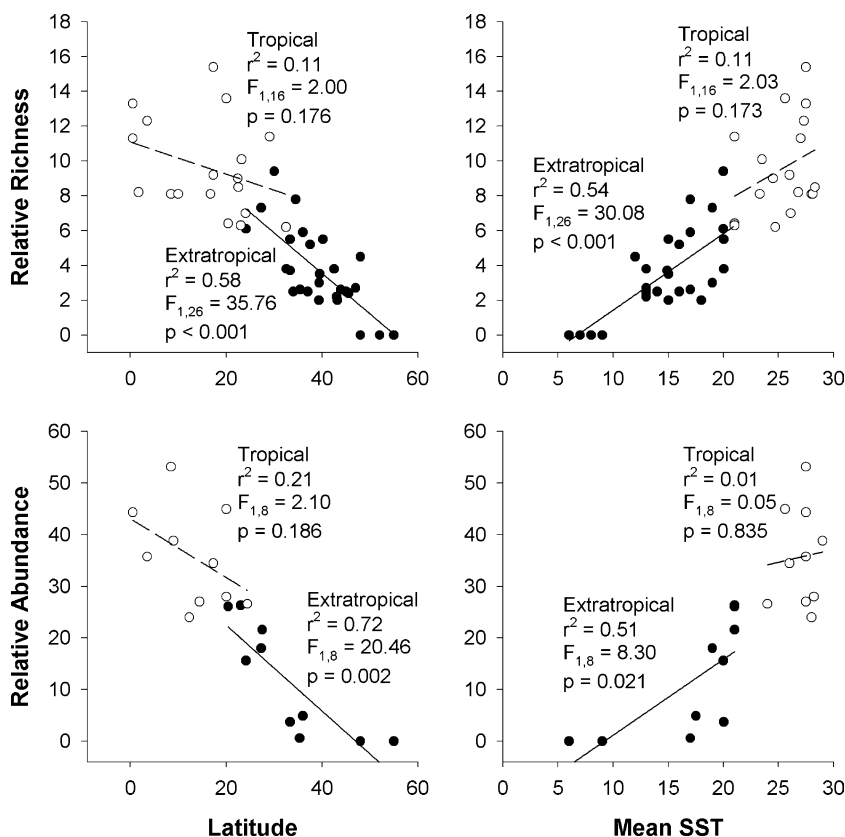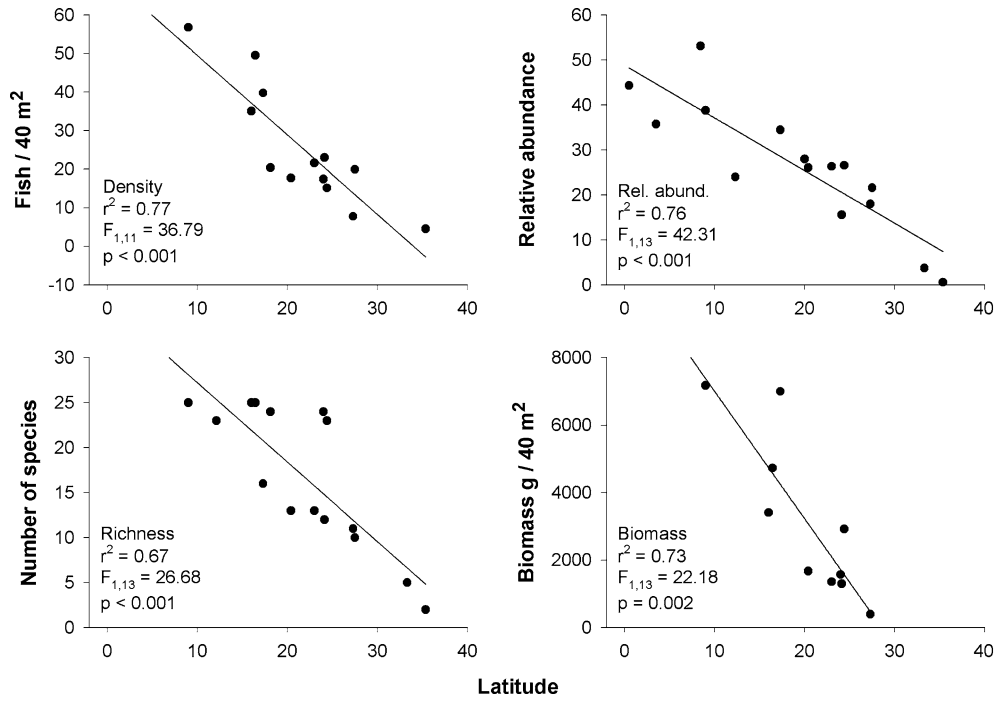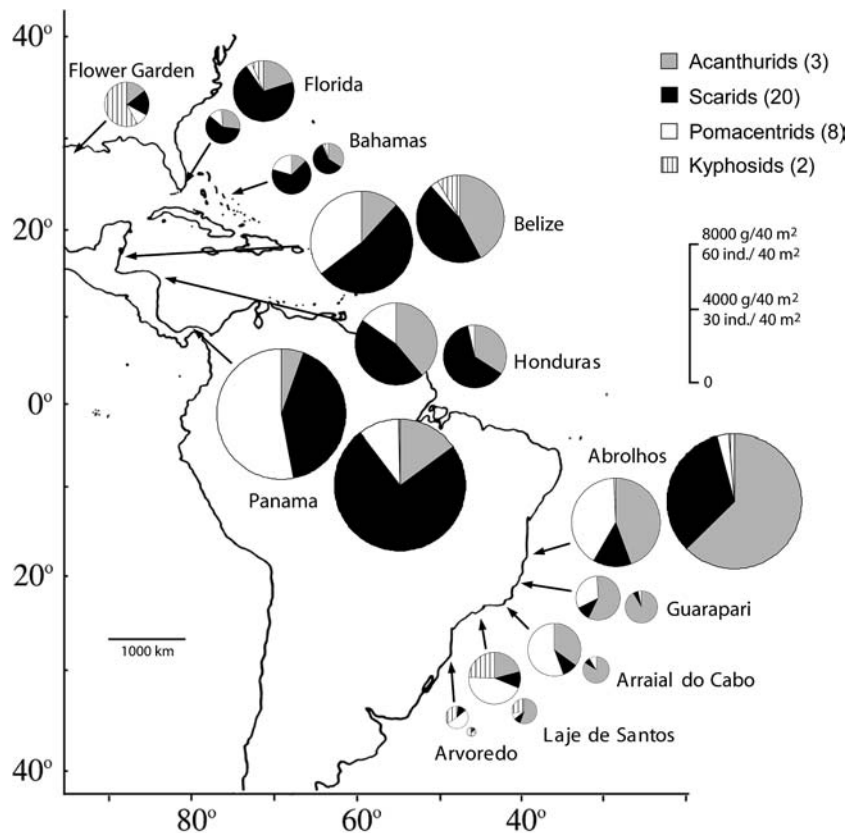
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Fig. 4 Density, relative abundance (%), richness and biomass of the four main herbivorous fish families combined (Acanthuridae, Kyphosidae, Pomacentridae, Scaridae) in relation to the latitudinal gradient in the Atlantic Ocean. Both north and south latitudes were included

$(39.2 \pm 8.9$ SD; 27.5°C) (ANOVA: $F = 60.062$, $P < 0.001$; SB $\neq$ FL $\neq$ PA), regardless of the fish size and diel period compared. The ratio between average feeding rate and metabolic rate in relation to minimum water temperature also showed significant differences between locations with minimum temperature below 20°C (southeastern Brazil) and above 20°C (Florida and Panama) (Fig. 7).

Fig. 5 Density and biomass of the four main herbivorous fish families (Acanthuridae, Kyphosidae, Pomacentridae, Scaridae) in the western Atlantic. *Pie diagrams* are sized relative to each other in terms of density (*left*) and biomass (*right*). Numbers in *parentheses* are the number of species in each family. *Horizontal bar* represents 1,000 km. *Vertical bar* scales the pies
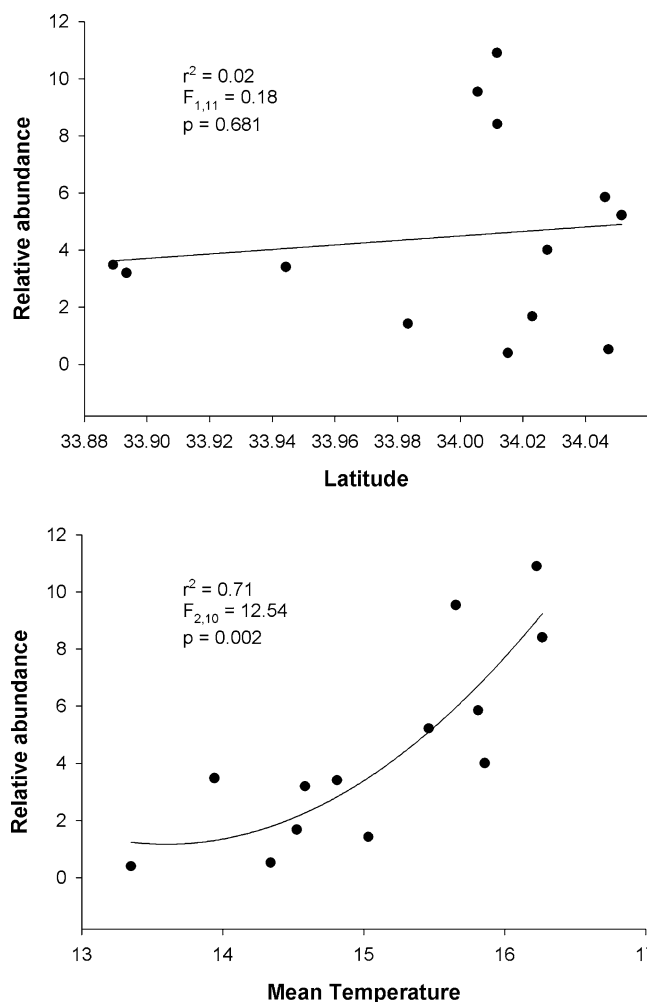
Fig. 7 Ratio between *Acanthurus bahianus* average feeding rate (bites/min) and metabolic rate (resting oxygen consumption [mmol h^{-1}] for teleost fish [data from Clarke and Johnston 1999]) in relation to minimum water temperature at the southeastern Brazil, Florida and Panama sites (from *left* to the *right*). ANOVA showed significant differences between temperatures ($F = 8.46$; $P < 0.001$). *Capital letters* above each mean indicate statistical groupings (SNK and Tukey's post-hoc tests), with different letters showing significantly different means

Fig. 6 Latitudinal and thermal gradient in the relative abundance (%) of the three most important herbivorous fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) at the Channel Islands, southern California (34°N). Mean relative abundance for each of the 13 sites over the period 1996–2001 is plotted against latitude and the mean SST during the same time period

Discussion

Patterns

The worldwide negative relationship we found between latitude and relative richness and relative abundance of herbivorous fishes allowed us to test persistent ideas with more comparable, quantitative datasets. Our analyses showed that the new data reinforced and clarified published trends (Horn 1989; Meekan and Choat 1997; Harmelin-Vivien 2002). Relative richness from independent datasets from different regions all showed significant relationships with latitude as well as SST, indicating that temperature cannot be discounted as a driving mechanism behind these latitudinal patterns. The fact that relative abundance decreases faster than relative r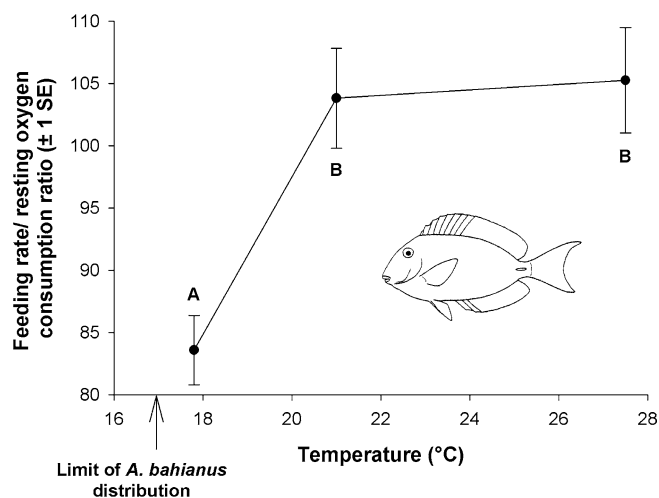ichness, however, suggests that community structure is even more sensitive to latitudinal changes than what would be detected from only examining occurrences of species. Differences in the strength of gradients between the New Zealand Region and other regions appear to reflect differences related to the tropical versus temperate character of this region compared to the others. When the strength of gradients were compared between all tropical versus extratropical sites, it became clear that above 20°C (tropical) differences in the relative richness and abundance of herbivorous fishes among localities are small and not significantly related to latitude or SST. On the other hand, the strength of the gradients among temperate and polar sites are greater and significantly declining with increasing latitude and increasing with decreasing temperature, regardless of the ocean basin considered. These patterns suggest a disproportional influence of temperature ranges below 20°C, affecting the distribution of herbivorous fishes. The tropics are thought to be relatively similar climatically (Terborgh 1973); therefore, if these patterns are climate driven, it is not surprising that there is little or no effect of latitude or temperature within this climatic zone.

Negative overall relationships between latitude and total density, biomass, species richness, and relative abundance of herbivores occur in Atlantic reef systems despite different histories and habitat characteristics (i.e., Brazil vs. Caribbean: Floeter et al. 2001; Ferreira et al. 2004). The trends, however, are driven by different components of the fish assemblages (i.e., scarids in the Caribbean and acanthurids in Brazil). This differing composition may reflect different evolutionary histories and habitat structure in the northern and southern

hemispheres. The dominance of scarids in the Caribbean, especially the higher abundance ratio of the genus *Scarus* relative to sparisomatines may reflect the greater degree of reef development and the pattern of colonization in this region. Bellwood (1994) suggests that the genus *Scarus* colonized the Caribbean through the Isthmus from Indo-Pacific ancestors, whereas the sparisomatines are of Tethyan origin. Fishes of the genus *Scarus* that reach the Brazilian coast appear to be recent relatives of Caribbean species (Moura et al. 2001). Distribution patterns of the genus *Scarus* worldwide seem to be related to the presence of coral reefs. The largest biomass of scarids as well as the highest ratio of *Scarus* to sparisomatines in Brazil is found in the major coral reef hotspot on the Brazilian coast (the Abrolhos reef complex; Leão and Kikuchi 2001).

Although anthropogenic forces have altered the density, biomass, and community structure of many nearshore fish communities, human impacts are not likely to have influenced our results. Human exploitation has not been limited now or historically by latitude, so it can be considered a constant across all systems. If anything, tropical fisheries tend to be less selective than temperate ones, so given the higher proportion of herbivorous species present, we may expect that they have received higher human impacts in the tropics. This differential impact would tend to lessen the differences in biomass/abundance, thus weaken our signal, yet the pattern is strong. Moreover, all of the sites we studied in the western Atlantic are protected areas or relatively lightly impacted sites. Finally, analyses dealing with species richness should not be influenced by fisheries because human-caused extinctions of marine herbivorous fishes have only been documented in a possible single case (Brazil; Ferreira et al. 2005). Analyses of biomass/abundance data, however, showed the same patterns with richness. If uneven fisheries impacts were biasing the results, one should expect differences between these patterns.

Processes

Five main explanatory mechanisms for latitudinal patterns in herbivorous fishes have been proposed in the literature. The first states that herbivorous fishes have had insufficient time to evolve and to expand their range into temperate waters (Mead 1970). Limited evidence exists to support this view. Most herbivorous species belong to the advanced Perciformes, and the radiation of this group is fairly recent, with limited time for these groups to spread into temperate waters (Horn 1989). Several advanced Perciformes such as Embiotocidae, Clinidae, and Flatfishes (Paralichthyidae, Pleuronectidae), however, are found in cold-temperate habitats, and they are entirely carnivorous and omnivorous; thus, the restriction to warmer waters appears to be limited to herbivorous and corallivorous species (Gaines and Lubchenco 1982; Harmelin-Vivien 2002). Westneat and

Alfaro (2005) showed that within the Labridae (scarids included), some relatively derived groups like *Oxyjulis*, *Notolabrus*, and some *Halichoeres* successfully invaded temperate waters and none of them is herbivorous. The cold higher latitude oceans are much younger than the tropical oceans (Brown and Lomolino 1998), and it may simply be that for herbivorous fishes, the adaptations are more difficult and take longer. If this is the case, then a further mechanism is needed to explain why the evolution of herbivory is so difficult in cold waters.

The second explanatory mechanism asserts that suitable food in temperate latitudes is seasonably unavailable at time scales greater than can be survived by herbivorous fishes (Barry and Ehret 1993; Arrington et al. 2002). Appropriate food, however, does not appear to limit the distributions of herbivorous fish species because many temperate habitats have larger standing stocks of algae, year-round, than tropical habitats (Mann 1973).

The third proposed mechanism states that latitudinal differences in algal toughness, nutritional quality, and chemical defenses make temperate algae less usable by herbivorous fishes (Gaines and Lubchenco 1982; Cronin et al. 1997). Although the toughness of the dominant algal groups in temperate waters may deter feeding of herbivorous fishes, many groups (e.g., girellids, kyphosids, and odacids) are able to feed successfully on these dominant brown algae in temperate waters (Russell 1983; M.D.B., unpublished data) or to digest brown algae even if they do not feed on them (Sturm and Horn 1998). Evidence is lacking for a latitudinal gradient in the nutritional quality of macroalgae (Irelan and Horn 1991). Algal assemblages in tropical waters, however, often are dominated by filamentous green and red algal species, whereas temperate algal assemblages frequently are dominated by brown algae, which may play some role in diet preference and digestibility. Chemical defenses, although important in deterring feeding by herbivores, do not always show clear latitudinal patterns in part as a result of the type of secondary compounds produced (Van Alstyne and Paul 1990). Bolser and Hay (1996), however, found some evidence that tropical seaweeds have stronger chemical defenses than temperate seaweeds. This pattern is opposite of what is required for latitudinal differences in algal quality to act as a mechanism driving the latitudinal diversity gradient in herbivorous fishes. These patterns are further compounded by the evolutionary arms race between algal defenses and herbivore resistance to algal defenses (Irelan and Horn 1991; Steinberg et al. 1995; Bolser and Hay 1996).

A fourth hypothesis, based on comparisons between feeding behavior and fish phylogeny and biogeography, states that an evolutionary trend toward the more efficient use of less energetic food resources (e.g., algae, sponges, coral polyps) has occurred primarily among tropical reef fish communities and that this trend has enhanced their species richness in warm waters in contrast to temperate areas (Harmelin-Vivien 2002). Floeter

et al. (2004) presented quantitative data corroborating this view. The relative abundance of fishes relying on relatively low-quality food (e.g., herbivores, corallivores, spongivores) decreases significantly from tropical to temperate latitudes. The species per genus ratio of low-quality food consumers also increases toward the tropics and more steeply than this ratio for all fishes in the assemblages. This relationship supports the view that higher speciation (or lower extinction) rates have occurred among this guild of fishes in warm waters.

The final mechanism involves the idea that most herbivorous fishes cannot meet their energetic demands in temperate or polar waters because of physiological constraints related to temperature (Gaines and Lubchenco 1982; Horn 1989; Horn and Ojeda 1999). A thermal constraint on the digestion of algae resulting from low temperatures is a relatively untested mechanism. We examined the role of temperature in limiting herbivorous reef fishes through an analysis of independent datasets at different scales and made a comparison of feeding and metabolic rates of the ocean surgeonfish *Acanthurus bahianus* as functions of water temperature.

Thermal gradients and physiological constraints

Thermal gradients in herbivorous fish diversity and abundance also could be noted at the local scale (in the same latitude–the Channel Islands; Fig. 6), regional scale (in the same latitude–Galapagos Archipelago; Edgar et al. 2004), as well as associated with extensive latitudinal gradients in different regions worldwide (Figs. 1, 2, 3, 4). Indeed, differences in feeding rates in relation to water temperature have been noted in the scale of hours at the same site (Ferreira et al. 1998). Thus, independent datasets revealed the important role that the temperature could play in the distribution of herbivorous fishes. The ultimate explanatory mechanisms, however, may have a physiological, ecological and evolutionary basis.

As in most ectotherms, metabolic rate in fishes increases with increasing temperature (Cossins and Bowler 1987; van Marken Lichtenbelt et al. 1997; Gillooly et al. 2001). Gut passage rate in ectotherms also increases with increasing temperature (Zimmerman and Tracy 1989; Horn and Gibson, 1990; Stevens and Hume, 1998). Assimilation efficiency, however, appears to be independent of temperature (Zimmerman and Tracy 1989; Horn and Gibson 1990; van Marken Lichtenbelt 1992; McKinnon and Alexander 1999). Because gut passage rate decreases more rapidly than metabolic rate as temperature declines, herbivorous ectothermic vertebrates may not be able to process enough food material to meet their metabolic demands at cooler temperatures. The higher diet quality and assimilation efficiency in carnivores and omnivores would require less food to be digested to meet the same metabolic demands. Because algae are relatively low-quality foods and harder to assimilate than animal material, the critical threshold

temperature required for a net positive energy balance should be higher for herbivores than for carnivores.

Cold-water herbivores often show behaviors and habitats that may be conducive to reducing metabolic demands, such as low mobility as seen in aplodactylids (M.D.B., personal observation) and stichaeids (Ralston and Horn 1986). Some species, however, such as *Odax pullus*, which occurs in 10°C water in New Zealand, show moderate activity levels indicating that these species may have additional adaptations to allow an herbivorous feeding mode in cold waters (Mountford et al. 2002; M.D.B., personal observation).

Feeding rate and metabolic rate increase with temperature, but likely with different scaling coefficients (Fänge and Grove 1979; Myrick and Cech 2000). Because the amount of food an animal can process is not counter-balanced by high assimilation efficiency at low temperature (Zimmerman and Tracy 1989; Horn and Gibson 1990; van Marken Lichtenbelt 1992; McKinnon and Alexander 1999), we would expect a temperature constraint on herbivore survival. We determined that the ratio of feeding rate to metabolic rate increases with temperature (Fig. 7), indicating that the scaling rates of these two processes with temperature are not equal and that feeding rate declines more rapidly with decreasing temperature than metabolic rate. If there is not a concomitant increase in digestive efficiency with the decline in the ratio of consumption to metabolism, then it is likely that the animal will be under greater nutritional stress at lower temperatures. Arguably, feeding rate differences among sites could be related to the type of algae consumed or differences in primary productivity. Both arguments seem not to be the case because *Acanthurus bahianus* eats a considerable amount of detritus and sediment and mostly the same algal species (or closely related species with the same general morphology and likely the same chemical composition) in the Caribbean and southeastern Brazil (Randall 1967; Ferreira 1998). Primary productivity is also similar between the Caribbean (1.9 g cm^{-2} day^{-1} at 2 m deep) and 0.3 at 8 m in Jamaica and St. Croix [Hackney et al. 1989]) and southeastern Brazil (0.9 to 4.8 g cm^{-2} day^{-1} at 2 m and 0.1 to 0.2 at 8 m [Ferreira 1998]).

We can now say that the stage may be set for such a temperature-mediated constraint, but we do not know the temperature threshold (i.e., at which temperature the herbivore could not survive). We still need to know whether the intercepts of the energy-in (consumption/assimilation) curve and energy-out (metabolism/reproduction) curve are such that the two lines cross within the thermal range of a given species. If they do and the pattern is consistent across many herbivorous species, then we have a real constraint. We need to know the exact temperature-consumption and temperature–metabolism relationships for many species. These data along with caloric information on the food and assimilation efficiencies will allow us to predict the threshold temperature for a series of herbivores occurring at different latitudes. Accumulation of such data might allow

1444

further generalization to be attained and also determination of whether the thresholds make ecological sense based on the geographic ranges of the target species.

Two temperature-mediated microbial processes are related to herbivorous fish nutrition: (1) Many herbivorous species depend on a diverse assemblage of intestinal microflora to aid in the digestion of plant and algal structural components (Horn 1989; Choat and Clements 1998), possibly digesting the microflora as a protein and nitrogen source. These microorganisms are thought to be thermally sensitive and may either not persist or be at too low a density at cold temperatures to degrade food items sufficiently (Kandel et al. 1994; Smith et al. 1996; Gatesoupe and Lesel 1998), and (2) Although traditionally viewed as "algae-eaters," many nominally herbivorous species have diets that include a large proportion of organic detritus and sediments (Crossman et al. 2001; Choat el al. 2002; Wilson et al. 2003). Decomposition rates (processing) and accumulation of bacteria-rich detritus seem to be higher in the tropics (Hatcher 1988; Cebrian 2002). These expected effects of temperature on the physiology and on protein-rich food sources (detritus) of herbivorous fishes suggest how temperature could largely restrict herbivorous-detritivorous fishes to tropical marine waters.

Marine herbivorous fishes present similar latitudinal patterns in diversity and abundance to terrestrial herbivorous reptiles (see Zimmerman and Tracy 1989) and subtidal invertebrates (Valentine et al. 2002). The fact that vertebrate ectotherms (fish and reptiles) are more successful in tropical or hot climates suggests that ectothermy could be linked to digestive physiology and implicated in the latitudinal or thermal patterns among these taxa. Although herbivorous mammals appear to be more diverse and abundant in temperate regions (Olff et al. 2002), grazing intensity is negatively correlated with latitude (Swihart and Bryant 2001). Herbivory intensity is also negatively correlated with latitude in insects (Coley and Aide 1991, Coley and Barone 1996). Thus, despite some inconsistencies in herbivore diversity patterns among different groups, the trend of increase in rates of herbivory at low latitudes appears to be consistent among several taxa.

In terms of evolutionary history, carnivory is often the ancestral condition from which herbivory evolved in several marine invertebrate groups (Vermeij and Lindberg 2000) and terrestrial lizards (Cooper and Vitt 2002). Harmelin-Vivien (2002) also argued that herbivory in marine fishes is characteristic of more derived families, and, within families, among the most derived genera (but see Clements et al. 2004). Among the Stichaeidae, a family of cool-temperate and polar fishes with only a few herbivores among its 60+ species, the herbivorous species attain the largest body sizes in the family (Horn 1989) and are members of a derived clade associated with relatively warm waters (Stoddard 1985). Furthermore, a strong phylogenetic effect is apparent in the herbivorous clade because a carnivore in the clade exhibits a digestive enzyme profile very similar to its closest relative, which is an herbivore (Chan et al. 2004; German et al. 2004). Examination of latitudinal patterns within a phylogenetic context may help explain the variation in latitudinal patterns found within the different herbivore functional groups (i.e., browsers, grazers, and detritivores).

Conclusions

Consistent negative relationships between latitude and relative richness and relative abundance of herbivorous fishes were found worldwide in our compilation and analysis of several new datasets. Negative relationships between latitude and total density and biomass were demonstrated for the western Atlantic. These patterns leave no doubt about the greater importance of fish herbivory in the tropics compared to temperate or polar zones. One can argue that the relative proportion of biomass at some temperate locations (New Zealand–Jones 1988; *Posidonia* seagrass in the Mediterranean–Francour 1997) are similar to tropical locations, but the actual biomass values are much smaller than those found in the tropics, as can be seen in Fig. 5 for the western Atlantic.

On the basis of the patterns presented and on our review of the explanatory hypotheses, temperature-related feeding and digestive processes are likely involved in the distribution patterns of herbivorous fishes. Clearly, more work is needed to establish the precise mechanisms underlying these temperature-related constraints and the thermal thresholds for herbivorous species.

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