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# Large-scale species-richness gradients in the Atlantic Ocean

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The increase in species richness from the poles to the Equator has been observed in numerous terrestrial and aquatic taxa. A number of different hypotheses have been put forward as explanations for this trend, e.g. area and energy availability. However, whether these hypotheses apply to large spatial scales in marine environments remains unclear. The present study shows a clear latitudinal gradient from high to low latitude (from 80° N to 70° S) in marine species richness for 6643 species (fishes and invertebrates) in 10 different taxa dwelling in benthic and pelagic habitats on both sides of the Atlantic. The patterns in benthic taxa are strongly influenced by coastal hydrographic processes, with marked peaks and troughs, and consequently the gradients are not symmetric along both Atlantic sides. Pelagic taxa show a plateau-shaped distribution and the influence from coastal events on gradients could not be demonstrated. The relationships between species richness and different environmental factors indicate that area size does not explain the latitudinal pattern in benthic species richness on a large spatial scale. Sea-surface temperature (positive relationship) is the best predictor of this pattern for benthic species, and nitrate concentration (negative relationship) is the best predictor for pelagic species. The results call into question the existence of a single primary cause that would explain the pattern in marine species richness on a large spatial scale.

**Keywords:** latitudinal species richness; marine diversity; Atlantic Ocean; diversity gradients

## 1. INTRODUCTION

An apparently general feature in many taxa is the tendency for species richness to increase from the poles to the Equator (e.g. Rohde 1992; Gaston 1996, 2000; Brown & Lomolino 1998; Chown & Gaston 1999; Gaston & Blackburn 2000). This trend has been studied in numerous terrestrial (e.g. Wright *et al.* 1993) and marine taxa (Rex *et al.* 1993; Macpherson & Duarte 1994; Roy *et al.* 1998; Gray 2001a), although some exceptions have been detected, usually associated with depth or habitat characteristics (Clarke 1992; Rohde 1999; Gray 2001b). These exceptions have already been emphasized by Thorson (1957), who indicated an independent latitude–diversity relationship in the infauna, whereas the diversity was dependent on latitude in the epifauna. Other authors have questioned the existence of this gradient in the Southern Hemisphere, as a consequence of the high diversity of some taxa in Antarctic waters (Clarke 1992; Brey *et al.* 1994; Arntz & Gili 2001).

The primary causes that determine this pattern are still an important subject of discussion in ecology (Rohde 1992, 1999; Rosenzweig 1995). Among the different hypotheses that have been proposed to explain gradients in species richness, the species richness–energy hypothesis has received the greatest support, mostly from studies of terrestrial organisms (Wright 1983; Kerr & Packer 1997), being scarce in marine taxa (Roy *et al.* 1998, 2000). This hypothesis indicates that the number of species that can coexist in a zone is limited by the energy supply. Energy availability is usually represented by the mean annual temperature or factors that are strongly related to it (Roy *et al.* 1998). Other predictors of the species richness, such as area size (Rosenzweig 1995) or productivity (Margalef 1968, 1997), are usually not considered on a large scale

and their role in the general latitudinal gradient is not well investigated (Fraser & Currie 1996).

In the present study, the existence of the latitudinal gradient in marine species richness along both sides of the Atlantic Ocean, from 80° N to 70° S, is analysed for 6643 species (fishes and invertebrates) belonging to 10 different taxa dwelling in benthic and pelagic habitats. Furthermore, the relationship of this pattern to temperature, nitrates (NTRs), chlorophyll (CHL) and area size is studied as a test for species–energy, species–productivity and species–area hypotheses.

## 2. MATERIAL AND METHODS

### (a) *Data source*

The database on the latitudinal distribution of 6643 species in 10 different taxa dwelling in the Atlantic Ocean, from 80° N to 70° S was compiled by means of a comprehensive search of the primary literature. The following taxonomic groups were considered: Hydromedusae (294 species), Siphonophorae (107), Cephalopoda (243), Euphausiacea (41), Stomatopoda (98), Crustacea Decapoda (1979), Chaetognatha (41), Appendicularia (60), Salpida (31) and Pisces (3749). The main data source for each taxa was the following (see also the references cited in each work for a more complete list): Hydromedusae (Pages *et al.* 1992; Bouillon 1999), Siphonophorae (Pages & Gili 1992; Pugh 1999), Cephalopoda (Voss *et al.* 1998; Nesis 1999), Euphausiacea (Gibbons *et al.* 1999), Stomatopoda (Manning 1969, 1977), Crustacea Decapoda (Macpherson 1991; Udekem-d'Acoz 1999; Boschi 2000), Chaetognatha (Casanova 1999), Appendicularia (Esnal 1999), Salpida (Esnal & Daponte 1999) and Pisces (Randall 1983; Menezes & Figueiredo 1985; Whitehead *et al.* 1986; Böhlke 1989; Quero *et al.* 1990; Gon & Heemstra 1990). Furthermore, an additional and exhaustive search was carried out in the following journals that usually pub-

Table 1. Correlations between species richness and environmental variables in pelagic taxa.

(The partial and total correlations are obtained using stepwise multiple-regression analyses for the annual mean sea surface temperature (SST) (°C), annual mean surface CHL concentration ( $\mu\text{g l}^{-1}$ ), and annual mean surface NTR concentration ( $\mu\text{M}$ ). Only significant correlations and those included in the model have been listed (n.s., non-significant).)

|                | N species | partial R |      |          | total R |
|----------------|-----------|-----------|------|----------|---------|
|                |           | SST       | CHL  | NTR      |         |
| Hydromedusae   | 294       | n.s.      | n.s. | -0.63*** | 0.63*** |
| Siphonophorae  | 107       | n.s.      | n.s. | -0.44*   | 0.44*   |
| Chaetognatha   | 41        | n.s.      | n.s. | -0.42*   | 0.42*   |
| Appendicularia | 60        | n.s.      | n.s. | n.s.     | n.s.    |
| Salpida        | 31        | 0.31      | 0.11 | -0.25    | 0.46*   |
| Cephalopoda    | 132       | n.s.      | n.s. | -0.40*   | 0.40*   |
| Euphausiacea   | 41        | n.s.      | 0.20 | -0.48**  | 0.56**  |
| Decapoda       | 105       | n.s.      | n.s. | -0.64**  | 0.64**  |
| Pisces         | 465       | n.s.      | n.s. | -0.45**  | 0.45**  |

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

lish papers on the taxonomy and biogeography of Atlantic species: *Bulletin of Marine Science*, *Copeia*, *Crustaceana*, *FAO Fisheries Synopsis*, *Journal of Crustacean Biology*, *Journal of the Marine Biological Association of the United Kingdom*, *Polar Biology*, *Proceedings of the Academy of Natural Sciences of Philadelphia*, *Proceedings of the Biological Society of Washington*, *Revista de Biologia Tropical*, *Revista Brasileira de Zoologia*, *Scientia Marina* and *Smithsonian Contributions to Zoology*.

Most groups are exclusively pelagic, although Cephalopoda, Crustacea Decapoda and Pisces also have numerous benthic representatives, or only have benthic species (Stomatopoda) (see tables 1 and 2). The range of latitude covered by each species was recorded. The data on the occurrence of benthic species in the eastern Atlantic south of 35° S (southernmost boundary of the African continent) were not included in the analysis. For benthic species, the average depth of occurrence was also noted. Species with fewer than five records and species introduced by anthropogenic effects were excluded from the analysis. The resulting dataset comprises ca. 80% of the described species for each taxon in the Atlantic Ocean.

The latitudinal pattern of species richness was examined using all the species in each taxon present within 5° latitudinal bands (Stevens 1989; Macpherson & Duarte 1994; Roy *et al.* 1998). Species recorded in the water column, usually offshore of the continental shelf, were considered to be pelagic species. Neritic species were included in the benthic group. Most pelagic species are found offshore of the shelf break on both sides of the Atlantic and in oceanic waters; hence, all the pelagic species were considered together, comprising the number of species per 5° band between each coast. Large bathymetric ranges were considered for the most numerous benthic taxa (Crustacea Decapoda and Pisces): coastal (0–100 m), continental shelf and slope (100–1000 m) and continental rise–abyssal plain (more than 1000 m). The datasets for the benthic species were compiled separately for the two sides of the Atlantic and for the three bathymetric provinces and each species was included in only one province according to its average depth.

The geographical area along the two Atlantic coasts was calculated between 0 and 2000 m by 5° latitudinal increments

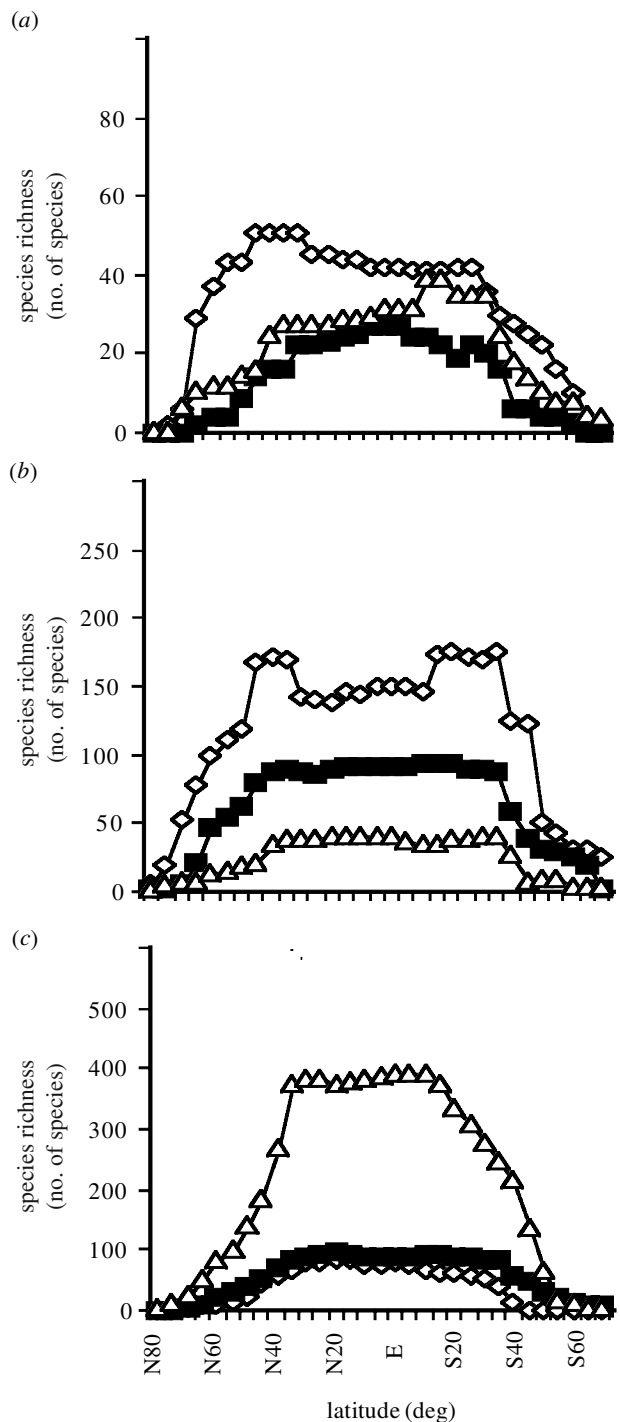


Figure 1. Latitudinal species-richness gradients for pelagic taxa. (a) Diamonds, Appendicularia; squares, Salpida; triangles, Chaetognatha. (b) Diamonds, Hydromedusae; squares, Siphonophorae; triangles, Euphausiacea. (c) Diamonds, Decapoda; squares, Cephalopoda; triangles, Pisces.

between the two poles. Data from GEBCO maps (e.g. Jones 1997) were digitized using an equidistant cylindrical projection. The mean annual sea-surface temperature (SST, °C) values for each 5° segment were used as a proxy for energy availability. Annual mean surface CHL ( $\mu\text{g l}^{-1}$ ) and NTR concentrations ( $\mu\text{M}$ ) were used as different proxies for ocean productivity. These three environmental datasets were taken from the *NOAA World Ocean Atlas* (Antonov *et al.* 1998; Conkright *et al.* 1998). A total of

Table 2. Correlations between species richness and environmental variables in benthic taxa along the eastern and western Atlantic. (The partial and total correlations are obtained using stepwise multiple-regression analyses for area size (area), annual mean sea surface temperature (SST) ( $^{\circ}\text{C}$ ), annual mean surface CHL concentration ( $\mu\text{g l}^{-1}$ ) and annual mean surface NTR concentration ( $\mu\text{M}$ ). Only significant correlations and those included in the model have been listed. (n.s., non-significant.))

|             | N species | partial R |         |          |         | total R |
|-------------|-----------|-----------|---------|----------|---------|---------|
|             |           | area      | SST     | CHL      | NTR     |         |
| Cephalopoda |           |           |         |          |         |         |
| eastern     | 56        | n.s.      | 0.50*   | n.s.     | n.s.    | 0.50*   |
| western     | 55        | n.s.      | 0.40*   | n.s.     | -0.40*  | 0.58**  |
| Stomatopoda |           |           |         |          |         |         |
| eastern     | 29        | n.s.      | 0.48*   | n.s.     | -0.37   | 0.66*   |
| western     | 69        | n.s.      | 0.53**  | -0.64*** | -0.45*  | 0.83*** |
| Decapoda    |           |           |         |          |         |         |
| eastern     |           |           |         |          |         |         |
| coastal     | 432       | n.s.      | 0.76*** | n.s.     | -0.28   | 0.77*** |
| shelf-slope | 292       | n.s.      | 0.91*** | n.s.     | -0.25   | 0.91*** |
| abyssal     | 78        | n.s.      | n.s.    | n.s.     | n.s.    | n.s.    |
| western     |           |           |         |          |         |         |
| coastal     | 713       | n.s.      | 0.61*** | -0.42*   | -0.31   | 0.74*** |
| shelf-slope | 320       | n.s.      | 0.40*   | -0.54**  | -0.22   | 0.63**  |
| abyssal     | 39        | n.s.      | n.s.    | n.s.     | n.s.    | n.s.    |
| Pisces      |           |           |         |          |         |         |
| eastern     |           |           |         |          |         |         |
| coastal     | 728       | n.s.      | 0.54**  | n.s.     | -0.26   | 0.59**  |
| shelf-slope | 424       | n.s.      | 0.55**  | n.s.     | n.s.    | 0.55**  |
| abyssal     | 167       | n.s.      | n.s.    | n.s.     | n.s.    | n.s.    |
| western     |           |           |         |          |         |         |
| coastal     | 1220      | n.s.      | 0.42*   | -0.36    | -0.56** | 0.73*** |
| shelf-slope | 586       | n.s.      | 0.43*   | -0.22    | 0.39*   | 0.64**  |
| abyssal     | 159       | n.s.      | n.s.    | n.s.     | n.s.    | n.s.    |

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

three environmental datasets was compiled: both of the Atlantic coasts and the oceanic province.

### (b) Statistical analysis

Due to the fact that species richness and the environmental variables were spatially autocorrelated, the data were transformed using first-order differencing prior to the analysis (Chatfield 1997; Roy *et al.* 2000). The resulting datasets were not sensitive to spatial autocorrelation and were not correlated with the latitude. Bivariate plots of the first difference of species richness and the predictor variables were analysed and tested using forward stepwise multiple-regression analysis. Area was only considered for the benthic taxon interrelationships. Three hypotheses for species richness were tested: area, energy availability and ocean productivity (Rohde 1992; Fraser & Currie 1996; Roy *et al.* 1998). The two measures considering indicators of ocean productivity (CHL and NTR concentrations) were not correlated ( $R$  ranges between 0.17 and 0.30,  $p > 0.10$  in all cases).

## 3. RESULTS

Figure 1 shows that the species richness for nine pelagic taxa (Hydromedusae, Siphonophorae, Cephalopoda, Euphausiacea, Crustacea Decapoda, Chaetognatha, Appendicularia, Salpida and Pisces) increases from the poles to *ca.*  $50^{\circ}\text{N}$  (Northern Hemisphere) and *ca.*  $40^{\circ}\text{S}$  (Southern Hemisphere); between these two parallels the increase is very small or non-existent. The four benthic groups (Cephalopoda, Stomatopoda, Crustacea Deca-

poda and Pisces) display a different pattern, that moreover also differs on either side of the Atlantic Ocean (figure 2). The eastern Atlantic organisms exhibit an increase from higher latitudes to the Equator, although species richness decreases in the vicinity of the two West African upwelling areas (Sahara, *ca.*  $20\text{--}15^{\circ}\text{N}$  and Benguela, *ca.*  $20\text{--}25^{\circ}\text{S}$ ). More taxa show similar species richness in the Mediterranean area ( $30\text{--}45^{\circ}\text{N}$ ) than the tropics (figure 2*a,c,e*). The number of Western Atlantic organisms increases considerably in the Caribbean Sea (*ca.*  $30\text{--}10^{\circ}\text{N}$ ), but species richness then clearly decreases around the Equator, reflecting the environmental effects of discharges from the Amazon River.

Stepwise multiple-regression analysis showed that the annual mean SST (positive relationship) and the mean annual surface NTR concentration (negative relationship) are the primary predictors of benthic and pelagic species richness, respectively (tables 1 and 2). NTR and CHL concentrations also explain part of the latitudinal variance exhibited by the benthic taxa. Area size does not explain the latitude-species-richness pattern on this scale for benthic taxa (this factor is not included in pelagic species analysis) and abyssal species patterns are not explained by any predictor (table 2).

## 4. DISCUSSION

The results show a clear latitudinal gradient in species richness of all the taxa examined, in agreement with the

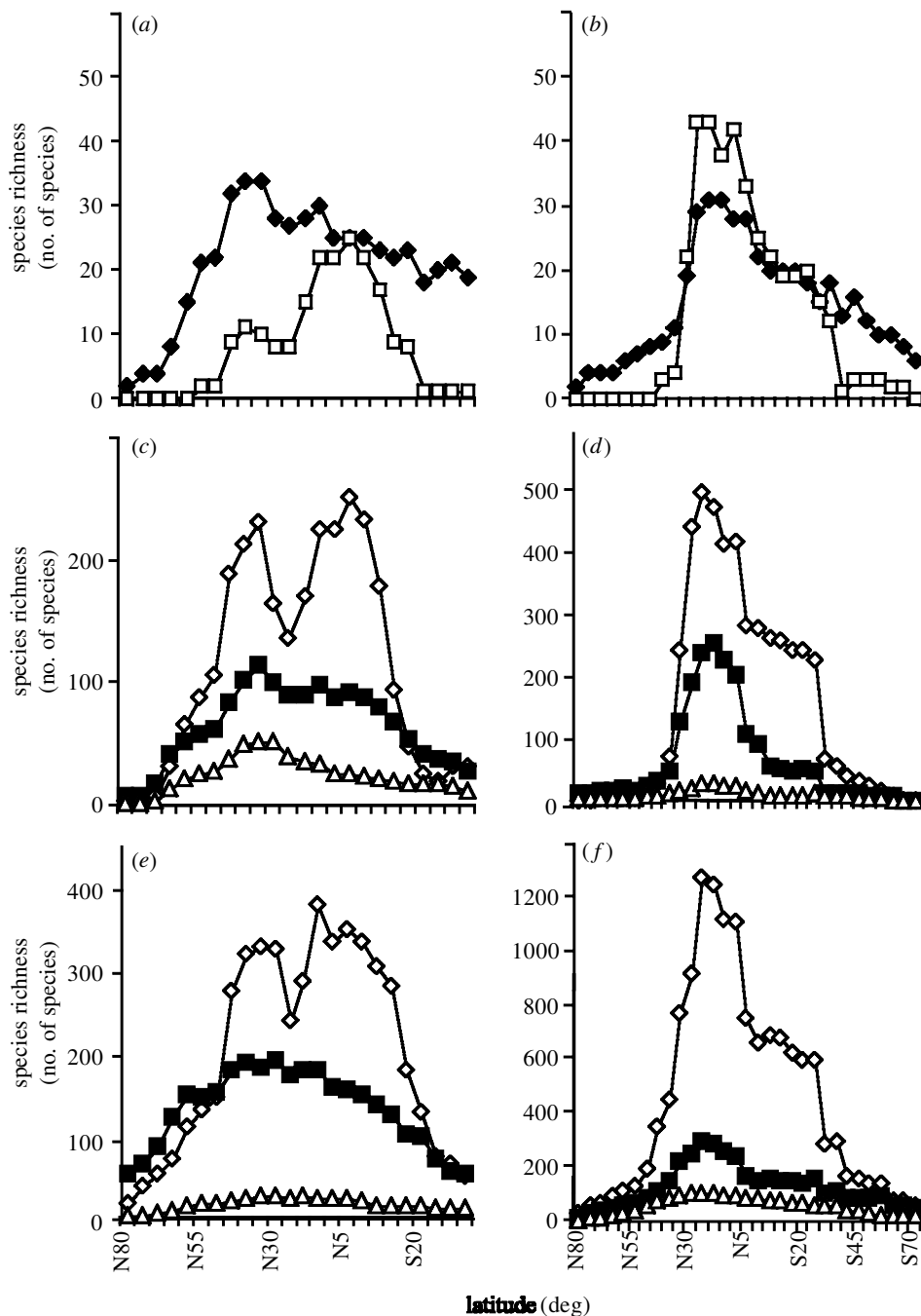


Figure 2. Latitudinal species-richness gradients for benthic taxa along the eastern (*a,c,e*) and western (*b,d,f*) Atlantic Ocean. (*a,b*) Cephalopoda and Stomatopoda; (*c,d*) Crustacea Decapoda; (*e,f*) Pisces. (*a,b*) Diamonds, Cephalopoda; squares, Stomatopoda. (*c-f*) Diamonds, coastal; squares, shelf; triangles, abyssal.

patterns observed in other marine taxa, including pelagic (Angel 1997; Boltovskoy *et al.* 1999) and benthic organisms (Macpherson & Duarte 1994; Rex *et al.* 1993, 2000; Roy *et al.* 1998, 2000). The results also stress the role of the Caribbean (30–10° N) and Mediterranean (30–45° N) areas as hot spots of marine biodiversity (Myers *et al.* 2000). However, the gradients do not show a bell-shaped distribution in species richness from the poles to the Equator. The patterns in benthic taxa are strongly influenced by hydrographic events (especially upwelling processes and river discharges), with marked peaks and troughs associated to these events and, consequently, the gradients are not symmetric along both Atlantic sides. Nevertheless, those groups that are less sensitive to these

events show a more homogeneous species-richness distribution (e.g. abyssal species). The pelagic taxa show a plateau-shaped distribution with the gradients not being influenced by these coastal events, although the strong decrease in species richness around 50° N and 40° S coincides with clear transitional oceanic domains, according to the biogeochemical provinces defined by Longhurst *et al.* (1995).

The patterns observed in the Southern Hemisphere indicate a decrease in species richness from the Equator to the Antarctic waters of all the taxa examined. These results are, in principle, not in agreement with the data observed in other benthic taxa around the Antarctic waters, e.g. sponges, bryozoans, polychaetes and echinoderms



(Brey *et al.* 1994; Arntz & Gili 2001; Gray 2001*b*). However, these Antarctic communities probably show the influence of historical processes (Brey *et al.* 1994) that have not seriously affected the taxa considered in this study.

As some authors have pointed out (Arntz & Gili 2001; Gray 2001*b*), the paradigm of the latitudinal distribution of species richness is still a subject of discussion in marine ecology (see also Lawton 1999). Area size does not explain the latitudinal pattern in benthic species richness on a large spatial scale, in agreement with Rohde (1992) and Roy *et al.* (1998). The existence of significant correlations between some environmental factors (SST, NTRs and CHL) and species richness in an analysis of a large number of taxa on both sides of the ocean, in both the Northern and Southern Hemispheres, in two different habitats (pelagic and benthic) and in the coastal and abyssal regions, supports the importance of these factors as determinants of species distribution on this large spatial scale. Although other variables may also exert a major influence on the latitudinal pattern of species richness (Rohde 1992; Fraser & Currie 1996; Gaston 2000; Gaston & Blackburn 2000; Levin *et al.* 2001), the energy availability hypothesis would appear to gain strength in benthic taxa. The results also indicate that the energy supply in marine ecosystems through coastal upwelling, river inputs or water-column mixing has an important role in determining the latitudinal distribution of species richness. However, the latitudinal patterns and species-richness–environmental-factor relationships observed in pelagic taxa question the existence of a unique predictor of these gradients. The species-richness–energy hypothesis indicates that the total number of species that can be found in an area is limited by the energy supply available (Wright 1983), although the processes that link energy and diversity may be indirect (Roy *et al.* 2000). The latitudinal gradients in species richness probably have a non-equilibrium explanation, including environmental mechanisms that are not mutually exclusive and other factors that are probably related to high-speciation rates and evolutionary time and are free of any disturbances sustained in the tropics through geological time (Jablonsky 1993; Rohde 1999; Crame 2000; Gaston 2000).

The results presented here indicate the importance of the supply of energy in the latitudinal diversity gradients, and also the importance of how this energy (from solar energy or oceanographic events) is used by the organisms (Margalef 1974). Productive areas, usually with pulse-like dynamics, have smaller numbers of species than oligotrophic ecosystems (Margalef 1974, 1997; see also Rex *et al.* 2000). As a consequence, the turnover rates, the number of trophic levels and the size spectra of the communities vary (Ahrens & Peters 1991; Macpherson & Gordoia 1996). The existence of these differences in the use of energy on a large scale should be considered in future studies that could improve current knowledge on the primary causes of the latitudinal gradients in species richness.

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